

## Paleontological discoveries in the Chorrillo Formation (upper Campanian-lower Maastrichtian, Upper Cretaceous), Santa Cruz Province, Patagonia, Argentina

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**Abstract:** The first fossil remains of vertebrates, invertebrates, plants and palynomorphs of the Chorrillo Formation (Austral Basin), about 30km to the SW of the town of El Calafate (Province of Santa Cruz), are described. Fossils include the elasmarian (basal Iguanodontia) *Isasicursor santacrucensis* gen. et sp. nov., the large titanosaur *Nullotitan glaciaris* gen. et sp. nov., both large and small Megaraptoridae indet., and fragments of sauropod and theropod eggshells. The list of vertebrates is also composed by the Neognathae *Kookne yeutensis* gen. et sp. nov., two isolated caudal vertebrae of Mammalia indet., and isolated teeth of a large mosasaur. Remains of fishes, anurans, turtles, and snakes are represented by fragmentary material of low taxonomical value, with the exception of remains belonging to Calyptocephalellidae. On the other hand, a remarkable diversity of terrestrial and freshwater gastropods has been documented, as well as fossil woods and palinological assemblages. The Chorrillo Formation continues south, in the Las Chinas River valley, southern Chile, where it is called Dorotea Formation. Both units share in their lower two thirds abundant materials of titanosaurs, whose remains cease to appear in the upper third, registering only elasmarians (Chorrillo Formation) and hadrosaurs (Dorotea Formation). Above both units there are levels with remains of invertebrates and marine reptiles. It is striking that the dinosaurs of the lower two thirds of the Chorrillo and Dorotea formations are represented by large basal titanosaurs and Megaraptoridae coelurosaurs, being the Saltasaurinae and Aeolosaurinae sauropods and Abelisauridae theropods totally absent. In contrast, these taxa are dominant components in sedimentary units of central and northern Patagonia (e.g., Allen, Los Alamitos, La Colonia formations). Such differences could reflect, in part, a greater antiquity (i.e., late Campanian-early Maastrichtian) for the Chorrillo fossils, or, more probably, different environmental conditions. Thus, knowledge of the biota of the southern tip of Patagonia is expanded, particularly those temporarily close to the K-Pg boundary.

**Key words:** Chorrillo Formation, Southern Patagonia, Late Cretaceous, fossils

**Resumen:** Hallazgos Paleontológicos en la Formación Chorrillo (Campaniano-Maastrichtiano, Cretácico Superior), Provincia de Santa Cruz, Patagonia, Argentina. Se describen los primeros restos fósiles de vertebrados, invertebrados, plantas y palinómorfos de la Formación Chorrillo (Cuenca Austral), aflorante unos 30km al SW de la localidad de El Calafate (Provincia de Santa Cruz). Los fósiles de dinosaurios no avianos incluyen el elasmario (Iguanodontia basal) *Isasicursor santacrucensis* gen. et sp. nov., el titanosaurio

gigante *Nullotitan glaciensis* gen. et sp. nov., Megaraptoridae indet. de tamaños pequeño y grande, y fragmentos de cáscaras de huevo pertenecientes a saurópodos y terópodos. La lista de vertebrados se compone también del Neognathae *Kookne yeutensis* gen. et sp. nov., dos vértebras caudales aisladas de Mammalia indet., y dientes aislados de un mosasaurio de gran tamaño. Han sido colectados también restos de peces, anuros, tortugas y serpientes los cuales están representados por material fragmentario de escaso valor taxonómico, con la excepción de restos pertenecientes a Calyptocephalellidae. Por otra parte, ha sido documentada una notable diversidad de gasterópodos terrestres y dulceacuícolas, así como leños fósiles y asociaciones palinológicas. La Formación Chorrillo se continúa hacia el sur, en el valle del río Las Chinas, Chile, en donde es denominada Formación Dorotea. Ambas unidades comparten en sus dos tercios inferiores abundante material de titanosaurios, cuyos restos dejan de aparecer en el tercio superior, registrándose solo elasmarios (Fm Chorrillo) y hadrosaurios (Fm Dorotea). Por encima de ambas unidades existen niveles con restos de invertebrados y reptiles marinos. Llama la atención que los dinosaurios de los dos tercios inferiores de las formaciones Chorrillo y Dorotea estén representados por titanosaurios basales de gran tamaño y celurosaurios Megaraptoridae, estando ausentes los Saltosaurinae, Aeolosaurinae y Abelisauridae, los cuales son componentes dominantes en las unidades sedimentarias del Maastrichtiano de la provincia de Chubut y del norte patagónico (p.ej., formaciones Allen, Los Alamitos y La Colonia, por ejemplo). Estas diferencias podrían reflejar, en parte, una mayor antigüedad (i.e., Campaniano tardío -Maastrichtiano temprano) para los fósiles de Chorrillo. Se amplía así el conocimiento de las biotas del extremo sur de Patagonia, en particular de aquellas temporalmente cercanas al límite K-Pg.

**Palabras clave:** Formación Chorrillo, Patagonia austral, Cretácico Tardío, fósiles.

## INTRODUCTION

The Chorrillo Formation (Upper Cretaceous, Campanian-Maastrichtian; Arbe, 2002; Nullo *et al.*, 2006) extensively crops out to the south of Centinela River, Santa Cruz Province, southern Patagonia, Argentina (Figure 1). The Chorrillo Formation extends NE to SW as a narrow band with a maximum E-W width of 2 kms. The Chorrillo Formation continues southward on the Chilean side, being partially equivalent to the Dorotea Formation (Upper Cretaceous, Campanian-Maastrichtian; Macellari *et al.*, 1989; Vogt *et al.*, 2014; González Abarca, 2015; Manriquez *et al.*, 2019).

Feruglio (in Fossa Mancini *et al.*, 1938) was the first to call “Estratos de Chorrillo” (i.e., “Chorrillo Beds”) to these rocks cropping out to the south of the Argentino Lake, indicating the presence of fossil logs and dinosaur bones (Feruglio, 1944-45). Aside from these citations concerning the presence of unspecified dinosaur remains, the first to discover a partial sauropod skeleton was Francisco Nullo in 1980, then geologist of Argentine Geological Survey, while exploring the top of the hills of the Alta Vista farm (“estancia”). Nullo informed on the discovery to the renowned paleontologist José Bonaparte, who collected a partial cervical vertebra of such titanosaur specimen (see description below). Bonaparte illustrated the titanosaur bones -still yielding on the ground- in a popular book about South American dinosaurs (Bonaparte, 1996). From the same locality, Bonaparte also collected (but did not describe) some isolated theropod re-

mains, including a partial ulna and a shed tooth, forming part of the Paleontological Collection of the Museo Argentino de Ciencias Naturales, in Buenos Aires.

Recent explorations carried out in La Anita and Alta Vista farms, approximately 30 km SW from El Calafate city, allowed relocation of the titanosaur specimen discovered by Nullo, but also resulted in the discovery of novel vertebrate remains, which are described below. The explorations were carried out on from January 13<sup>th</sup>-17<sup>th</sup> and March 14<sup>th</sup>-19<sup>th</sup>, 2019.

The complex topography of the region made the access somewhat difficult, even for 4x4 vehicles, thus long and exhausting walks were required to reach the fossil sites. Notwithstanding such circumstantial inconveniences, a rich collection of fossils made up by large titanosaur bone fragments, theropod remains, medium-sized ornithopods, tiny vertebrate bones, gastropods, and plant remains, starts to be amassed from this southern region of the Argentine Patagonia.

The fossil remains studied below, the first to be formally described from the Chorrillo Formation, shed valuable information on a wide variety of Late Cretaceous organisms in the southern cone, complementing the fossil record that has been obtained from equivalent stratigraphic levels in the geographically close Las Chinas River Valley, in southern Chile (Leppe *et al.*, 2014; González Abarca, 2015; Manriquez *et al.*, 2019).

## GEOLOGICAL SETTING

We follow the stratigraphic interpretations

expressed by Nullo *et al.* (2006) in recognizing in the study area the following stratigraphic succession (from bottom to top): Alta Vista, La Anita, La Irene, Chorrillo, and Calafate formations. Both Alta Vista and La Anita bedrocks form the high cliffs of the homonymous farms. The dinosaur-bearing beds of the Chorrillo Formation form continuous outcrops on the high plateaus on the top of these hills (Figure 1). In Argentina these beds extend to the international border with Chile, close to the “Hito Bagueales 2” (Figure 1; Nullo *et al.*, 2006). The top of the Chorrillo Formation laterally inter-fingers and is overlaid by the marine Calafate Formation (Marensi *et al.* 2004; Odino Barreto *et al.*, 2018). The rock succession comprehended by La Anita, La Irene and Chorrillo formations conforms an upper Campanian-early Maastrichtian regressive episode, started with the deltaic deposits of the La Anita Formation, and followed upwards by braided and meandering fluvial deposits of the La Irene and Chorrillo formations (Arbe & Hechem, 1984; Macellari *et al.*, 1989; Nullo *et al.*, 2006; Moyano Paz *et al.*, 2018; Tettamanti *et al.*, 2018).

Tettamanti *et al.*, (2018) synonymized Cerro Fortaleza, La Anita, La Irene, and Chorrillo formations under the name of “Upper Cretaceous Continental Deposits”. We concur with these authors in interpreting these lithologically similar beds as part of a same diachronic episode of Campanian through Maastrichtian continental sedimentation. However, we prefer to keep the original lithostratigraphic names for these units, waiting for more paleovertebradological information from both Chorrillo and Cerro Fortaleza beds, eventually offering more confident age determinations for these beds.

Regarding the age of the Chorrillo Formation, it has to be no older than the underlying Early Campanian Alta Vista beds (the age of which is based on abundant marine invertebrates; Blasco *et al.*, 1980; Nullo *et al.*, 2006) and the Maastrichtian La Irene Formation (the age of which is based on palynological assemblages; Povilauskas *et al.*, 2008). Moreover, the Chorrillo Formation inter-fingers to the SE with the shallow marine deposits of the Cerro Cazador Formation (Macellari, 1988), which yielded the associated presence of *Eubaculites* and *Maorites*, interpreted as early Maastrichtian in age (Nullo *et al.*, 2006). The Chorrillo Formation is overlaid by the marine Calafate Formation, considered to be late Maastrichtian based on dinoflagellate cysts association (Marensi *et al.*, 2004; Guler *et al.*,

2005; Nullo *et al.*, 2006). In sum, the dinosaur-bearing, continental deposits of the Chorrillo Formation exposed at the top of the high plateaus of the La Anita and Alta Vista ranges, may be early Maastrichtian in age. Evidence from the equivalent Dorotea beds supports, however, that the lower thirds of the Chorrillo Formation be late Campanian, at least (see below).

The Argentine sequence formed by both the continental Chorrillo and the marine Calafate formations resembles the sedimentary unit that in southern Chile is named as Dorotea Formation (F. Nullo, pers. comm.). As Cecioni (1957) and Katz (1963) have noted, rock units cropping out on both sides of the international border are inseparable from a formational point of view. This observation also applies for Chorrillo plus Calafate (on the Argentine side) and Dorotea (in Chile), which exhibit almost the same lithological characteristics and fossil content. The Dorotea Formation includes basal and middle sections equivalent to Chorrillo, and an upper section resembling, both lithologically and in fossil content, to the Calafate Formation.

The stratigraphic succession of the Chorrillo Formation is made up by intercalated levels of greenish and reddish sandstones, intercalated by some conglomeratic banks. Important is to say that the following description is tentative, requiring for more detailed stratigraphic and sedimentological surveys. Immediately above the La Anita beds, the base of the Chorrillo Formation is characterized by green mudstones with fragmentary plant remains. Following upwards there is a bank of conglomerates and coarse sandstones containing abundant fossil wood and badly preserved leaves. These stratigraphic levels with abundant plant remains are replaced upwards by the already mentioned greenish and reddish sandstone levels, with an approximate thickness of 250m (Nullo *et al.*, 2006), containing dinosaur and other vertebrate remains. Such succession is capped by a meter thick sandstone bank, green in color, bearing abundant specimens of tiny bivalves (approximately 2-3 cm long), including ostreids, mytilids and pectinids (see below for taxonomic identification). The sequence of greenish and reddish sandstones is cyclic and monotonous, thus being difficult to recognize discrete members.

We informally separate the Chorrillo beds into three “levels”, but this arbitrary subdivision depends on future sedimentological studies. The titanosaur bones originally discovered by F. Nullo come from the lower third of the formation, but

remains of titanosaurs of similar size also come from the middle portion of the unit. A thick bank of conglomerates exposes on the base of the upper third of the Chorrillo Formation, and above it repeats again the alternate sequence of greenish and reddish sandstones bearing dinosaur remains. The upper levels of the Chorrillo Formation yielded abundant remains of different individuals of a single species of a basal iguanodontian, mixed with several shed teeth of a large, indeterminate mosasaur. The sequence ends with a conglomeratic level (approximately one-meter-thick), overlaid by a bank (roughly one meter thick) made up by slender and elongate bivalves (*Gryphaeostrea* cf. *G. callophyla* Ihering, 1903 and *Cubitostrea* cf. *C. ameghinoi* Ihering, 1902, indeterminate Mytilidae and Pectinidae; D. Pérez, B.Santelli, and M.Álvarez, pers. comm.). This couple of banks (conglomerate plus bivalves) represents the base of the Calafate Formation.

For southern Chile, Manriquez *et al.*, (2019) described the stratigraphic sequence of the Dorotea Formation and its fossil content. At the base of the formation, they identified leaf impressions of a variety of taxa; from the middle section (exposed in a fossil spot they name “Saurópodo”) they described (in addition to plants) titanosaur, ornithischian, and bird bones, turtle and frog fragments, and mammal and theropod teeth. The paper by Manriquez *et al.* (2019) does not specify the taxonomic referral of the fossils collected, and no reference of the completeness of the collected materials is offered. However, such fossil assemblage from the “Saurópodo Member” looks similar to the lower and mid-sections of the Chorrillo Formation. Interesting is to say that the levels of “Saurópodo Member” are comprehended by radiometric datings below (74.9my) and above (71.7my), thus strongly suggesting these deposits correspond to the Campanian-Maastrichtian boundary (Manriquez *et al.*, 2019).

In sum, general aspect of Chorrillo plus Calafate beds resembles the sequence of Dorotea beds, suggesting these units represent a same sedimentary sequence. However, precise correlation between these beds requires further stratigraphy survey of the entire region. Besides, future exploration and study also need to be done to elucidate if the Chorrillo Formation is equivalent or not with the dinosaur-bearing, continental deposits of the Cerro Fortaleza Formation (radiometrically dated as Campanian; Sickman *et al.*, 2018), exposed north of Argentino Lake, on both margins of the La Leona River.

## MATERIALS AND METHODS

### Study area

The fossil remains come from different spots and stratigraphic levels, within an area of approximately 2000 m<sup>2</sup> (Figure 1). The fossil spots are the following:

-Nullo site (locality 1): Yielded six titanosaur bone accumulations, which do not necessarily correspond with discrete individuals. Stratigraphically it corresponds to the lower third of the Chorrillo Formation.

-Titanosaur tibia site (locality 2): This place provided a single, well preserved titanosaur tibia, titanosaur eggshells, sauropod teeth, theropod eggshells, avian coracoid, snake vertebra, and fish teeth. This site yielded the woods described above. Stratigraphically it corresponds to the lower third of the Chorrillo Formation.

-Megaraptorid site (locality 3): This place provided fragments of a single large, indeterminate Megaraptoridae, represented by 2 vertebrae, proximal pubis and rib fragments. Invertebrate bioturbations were found in close proximity. Stratigraphically this locality corresponds with the middle portion of the Chorrillo Formation.

-Puma cave site (locality 4): 50 specimens of terrestrial molluscs have been collected from mid-levels of the Chorrillo beds, in close proximity to mammalian, turtle, snake, ornithopod and theropod bone remains, and sauropod teeth. Six articulated caudal vertebrae of a large titanosaur come from 10 m far from this fossil spot. All these specimens were produced by the same stratigraphic level, corresponding to the middle portion of the Chorrillo Formation.

-Ornithopod site (locality 5): Association of different sized specimens corresponding to a single, new species of an elasmarian ornithopod, represented by vertebrae, phalanges, a, and metatarsals. Found in close association with seven mosasaur teeth. Stratigraphically it corresponds to the upper third of the Chorrillo Formation, roughly 20 meters below the beds with marine molluscs (interpreted as the base of the Calafate Formation).

### Collected material

The collected materials belong to the collection of the Museo Padre Molina, Río Gallegos, Santa Cruz province. Some specimens, coming from the same site and stratigraphic levels, were collected in 1981 by J.F. Bonaparte and are housed at the Vertebrate Paleontology Collection, Museo Argentino de Ciencias Naturales “Bernardino

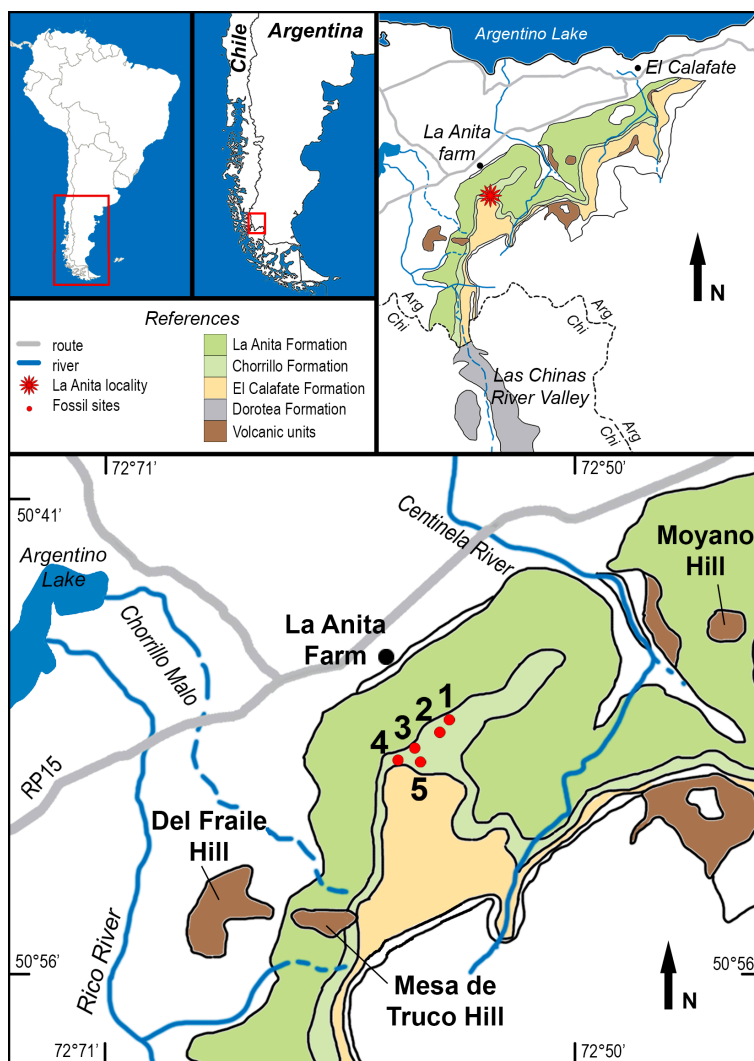


Figure 1. Map showing studied area. Numbers 1 through 5 indicate the localities from which fossil specimens were collected.

Rivadavia” (MACN), Buenos Aires.

### Specimen preparation

Vertebrates were extracted and prepared as is the usual technique in vertebrate paleontology. Most bones here described do not need mechanical preparation because they were found free of sediment in most cases. The bones that were embedded in sedimentary matrix were prepared with mechanical hammers at the Laboratorio de Anatomía Comparada y Evolución de los Vertebrados preparation lab.

The fossil woods were thin-sectioned in transverse (TS), longitudinal tangential (TLS) and longitudinal radial (RLS) sections, and stu-

died using light Microscopy (Olympus BX51). At least 25 measures were taken, and data is given as the mean and standard deviation, and range (in parenthesis). For the generic classification of the studied woods we followed the key for fossil genera proposed by Philippe & Bamford (2008). Descriptive terminology used here follows the IAWA list of microscopic features for softwood identification (Baas *et al.*, 2004), with the addition of terms defined in Philippe and Bamford (2008), seriation and contiguity indices proposed by Pujana *et al.* (2016). Pit counting method follows suggestions made by Philippe *et al.* (2013). The palynological samples were treated following standard techniques for extraction and

concentration of palynomorphs (Volkheimer & Melendi, 1976). Observations were made with an Olympus BX-51 microscope while photographs were taken with an Olympus DP25 digital camera. Coordinates of the illustrated specimens are given as England Finder coordinates.

#### Institutional abbreviations

**MPM**, Paleontological Collection, Museo Regional Provincial “Padre Molina”, Río Gallegos, Santa Cruz province, Argentina; **MACN-Pv**, Paleontological Vertebrate Collection, RN, Río Negro Collection, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina.

#### SYSTEMATIC PALEONTOLOGY

Vertebrata Cuvier, 1812

Teleostei Müller, 1844

Genus and species indeterminate

**Referred material:** MPM 21516, three crushing tooth crowns (locality 4) (Figure 2E-G).

**Description:** Three isolated crushing teeth crowns have been collected. The largest one is 13mm in diameter. They are subcircular in contour in occlusal view, with a gently convex occlusal surface, and a concave ventral surface. The tooth bases show concentric growth lines on the ventral side.

**Comments:** Crushing teeth similar to those described here resemble pharyngeal teeth of semionotiforms, sparids, sciaenoids, and basal percoids, among others (e.g., Cione, 1987). Similar teeth were previously reported from the Maastrichtian Loncoche (González Riga, 1999; Previtera & González-Riga, 2008), Los Alamitos (Cione, 1987), and Allen (Martinelli & Forasiepi, 2004) formations. The semionotiform genus *Lepidotes*, was repeatedly reported from Argentina, and South America (Arratia & Cione, 1996). These semionotiforms bear crushing vomerine teeth, with short roots and exceptionally broad and rounded crowns, thus differing from the low crowns with concave roots here described (see Jain, 1985). Information at hand forbids referral of crushing teeth from the Chorrillo beds to any particular teleostean clade.

Amiiformes Hay, 1929

Amiidae Bonaparte, 1838

cf. Vidalamiinae Grande & Bemis, 1998

Genus and species indeterminate

**Referred material:** MPM 21517, isolated tooth (locality 2) (Figure 2 H).

**Description:** This is a lanceolate and acute tooth, with vitreous enamel surface. Under the enamel layer there is a relatively thick layer of dentine constituted by vascular canals. At its base, the tooth is not crenulated, indicating the absence of plicidentine. Tooth crown possesses elongated, narrow peduncles which are constricted below the apex. The apex is formed by a short, translucent, and flattened acrodin cap with both acute mesial and distal carinae.

**Comments:** The combination of lanceolate teeth lacking plicidentine at its base (presence of plicidentine is typical of lepisosteiforms; Cione, 1987; Grande, 2010) and a translucent cap with mesial and distal carinae is diagnostic of vidalamiine amiiform fishes (Grande & Bemis, 1998; Martinelli *et al.*, 2013). In spite of such similarities, the isolated nature of MPM 21517 precludes a more accurate determination.

The fossil record of Mesozoic amiiforms in the southern Hemisphere is strongly biased (Grande & Bemis, 1998; Martinelli *et al.*, 2013; Brito *et al.*, 2017). From the southern cone, only three localities have yielded amiid remains (Bogan *et al.*, 2010, 2013), of which only two (i.e., El Anfiteatro and Cerro Tortuga localities, Río Negro province, Argentina; Bogan *et al.*, 2010) belong to the Late Cretaceous. Because of their fragmentary nature, these remains from Río Negro have indeterminate affinities below family level. Present report, if correctly identified, constitutes an important addition to the meager record of the clade for the continent, and may represent the southernmost record for Amiiformes.

Anura Fischer von Waldheim, 1813

Genus and species indeterminate

**Referred material:** MPM 21518, isolated tibiofibula (locality 4) (Figure 2D).

**Description:** The distal halves of a tibia and a fibula have been collected. These bones are separated by a narrow and relatively shallow longitudinal groove. The distal end of each bone is subcircular in cross-section. Based on preserved fragments, the tibiofibula may have been measured 25 mm when complete.

**Comments:** The presence of an elongate and fused tibiofibula is a feature diagnostic of anurans (Jenkins & Shubin, 1998). However, the morphology of the distal half of tibiofibula lacks diagnostic features to offer a more precise allocation within the clade. Present specimen, to-

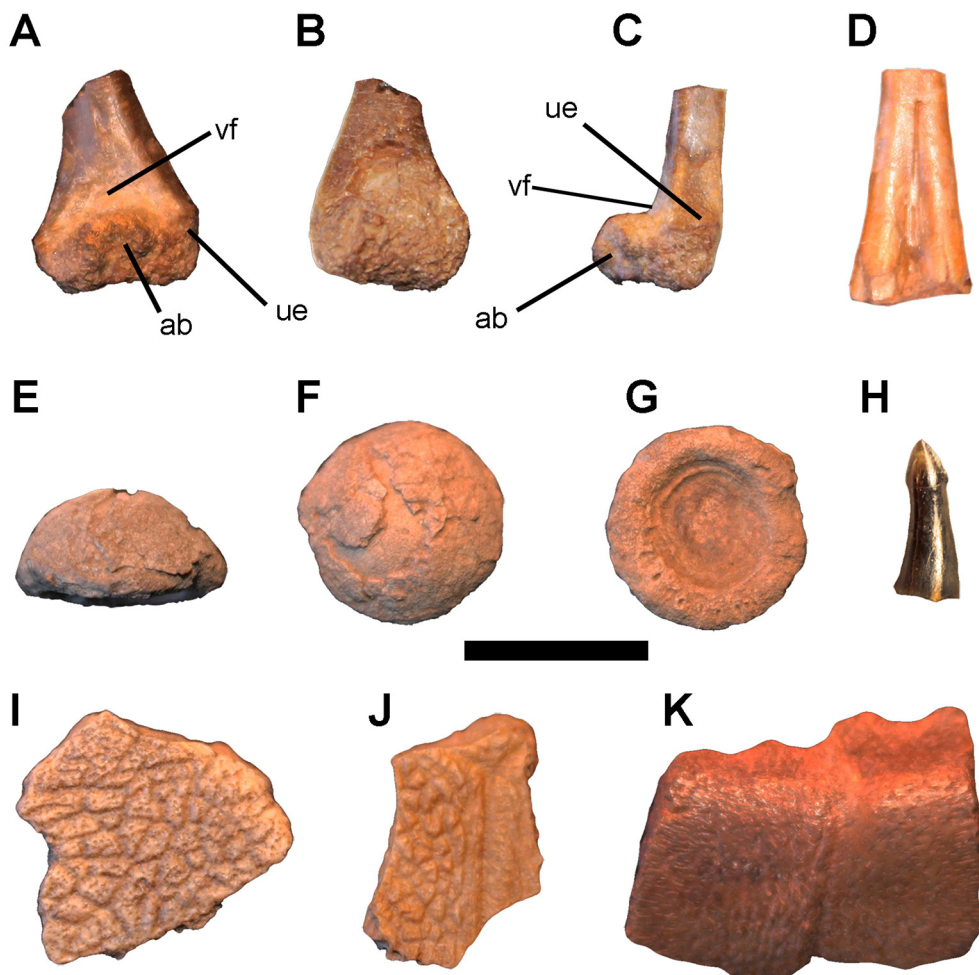


Figure 2. Fishes, anurans, and turtles. (A-C), Indeterminate Calyptocephalellidae, MPM 21519, distal end of right humerus with eroded distal margin in anterior (A), posterior (B), and medial (C) views. (D) Indeterminate anuran, MPM 21518, incomplete tibiofibula. (E-G) Indeterminate Teleostei, MPM 21516, tooth crown in lateral (E), occlusal (F), ventral (G) views. (H) cf. Vidalamiinae indet., MPM 21517, isolated tooth in side view. (I-K) Indeterminate Chelidae, carapace fragments. (I) Plastral fragment. (J) Incomplete costal plate. (K) Middle peripheral plate. **Abbreviations:** ab, articular ball; ue, ulnar epicondyle; vf, ventral fossa. Scale bar: 5 mm.

gether with remains described below, represents the southernmost records for a fossil frog from the Late Mesozoic.

Calyptocephalellidae Reig, 1960  
Genus and species indeterminate

**Referred material:** MPM 21519, distal end of right humerus with eroded distal margin (locality 4) (Figure 2A-C).

**Description:** The distal end of the humerus (1.5 mm in maximum transverse width), probably belongs to an adult individual, as suggested by degree ossification and well-finished structures.

The distal articular ball, as well as both epicondyles, are distally eroded. The humeral shaft is subtriangular in cross-section, with a relatively sharp crest running along its medial margin, which probably ended in a well-developed deltoid crest as it occurs in living anurans. The distal end of humerus bears a ball-shaped and ventrally projected articular condyle, bordered by similar-sized, flange-like, and transversely expanded ulnar and radial epicondyles. The ulnar epicondyle shows a flattened anterior surface that is separated from the articular ball by a shallow groove. The radial epicondyle is broader than the ulnar epicondyle and its anterior surface is concave

and crescent-shaped in anterior view. The ventral fossa is not clearly outlined.

**Comments:** MPM 21519 exhibits the following unique combination of features, only observed in the extant genus *Calyptocephalella* (Báez, 1987; Otero *et al.*, 2014): 1) distal articular ball large and placed at the center of the distal end; 2) prominent, subequal-sized and flange-like radial and ulnar epicondyles, resulting in a roughly symmetrical distal end; 3) humeral shaft distally unexpanded; 4) poorly defined ventral fossa. The incomplete nature of MPM 21519 does not allow referral the specimen beyond the family level.

The Mesozoic record of anurans in South America is patchy. Basal anurans of the clade Pipoidae have been recorded from the Early Cretaceous of Brazil (Carvalho *et al.*, 2019) and from mid-to Late Cretaceous localities of Brazil and Argentina (see Báez, 2000). The record of neobatrachians is also restrictive, being currently represented by nearly complete specimens from the Early and Late Cretaceous of Brazil (e.g., Báez & Perí, 1989; Báez *et al.*, 2009, 2012), and disarticulated specimens from Campanian-Maastrichtian localities in Chubut and Río Negro provinces of Argentina (i.e., Báez, 1987; Martinelli & Forasiepi, 2004; Muzzopappa & Baez, 2009; Agnolin, 2012).

Most neobatrachians are represented by highly fragmentary remains assigned to the non-monophyletic clade “Leptodactylidae”, and most of them have been assigned (or related with) the living Helmeted toad *Calyptocephalella* (Báez, 1987; de la Fuente *et al.*, 2007; Agnolin, 2012), the only extant member of Calyptocephalellidae. This genus is currently restricted to a single species, *Calyptocephalella gayi*, being endemic from the temperate region of south-central Chile (Otero *et al.*, 2014). However, during the Mesozoic and Cenozoic, calyptocephalellids were geographically widespread, with possible reports from Late Cretaceous of India, Africa and Madagascar (see Agnolin, 2012). In South America, Calyptocephalellids are recorded from Late Cretaceous to Miocene beds, in several localities along the Patagonia of Argentina and Chile (Agnolin, 2012; Otero *et al.*, 2014). Because of its great antiquity, calyptocephalellids were considered as being part of the “ancient assemblage” or “Andean-Antarctic” batrachofaunas that inhabited the southern end of South America during the Mesozoic, up to Miocene times (Vuilleumier, 1968; Cei, 1980; see Agnolin, 2012).

Testudines Linnaeus, 1758

Chelidae Gray, 1825

Genus and species indeterminate

**Referred material:** Chelid materials include MPM 21520 (consisting in two peripheral and one costal plates; locality 2), MPM 21521 (consisting of an anterior peripheral, one mid-peripheral, three posterior peripherals, fragment of plastral bridge, three incomplete costal plates, and distal end of radius; locality 4) (Figure 2 I-K). Based on locality and size differences, specimens belong to at least two different individuals.

**Description:** In both localities, available specimens were found in an area of few square meters. However, the different degree of preservation and different size of the specimens indicate the presence of different individuals. The plates resemble each other in being relatively thin and in having a similar ornamentation, suggesting that all belong to the same taxon. Largest available plates suggest a maximum carapace length of 40cm, approximately. Peripheral plates are relatively small and dorsoventrally thin. Mid-peripherals show relatively small and shallow costal fossae. There is no suture for the contact with costal plates. Plate decoration consists of small and well-defined polygonal figures, separated by anastomosed sulci. In some sections the polygons became smaller, conferring the plate a rugose texture. Preserved costal plates are incompletely preserved. They show ornamentation similar to that of peripheral plates, but polygons are more elongate.

**Comments:** In spite of the incomplete nature, available specimens can be referred with confidence to Chelidae, based on the combined presence of free peripheral plates lacking firm contact with the costal ones, and external surface decoration consisting of dichotomizing sulci and polygons (Broin & De la Fuente, 1993; Lapparent de Broin & De la Fuente, 2001; Lapparent de Broin, 2003). Plates here described are indistinguishable from those reported by Broin (1987) under the name of “Chelidae indet. N° 3”, and by Gasparini & de la Fuente (2000) as “Chelidae indet. N°5”, from the Maastrichtian Los Alamitos and La Colonia formations (Río Negro and Chubut provinces, respectively).

Squamata Opper, 1811

Serpentes Linnaeus, 1758

Genus and species indeterminate

**Referred material:** MPM 21522, partial mid-



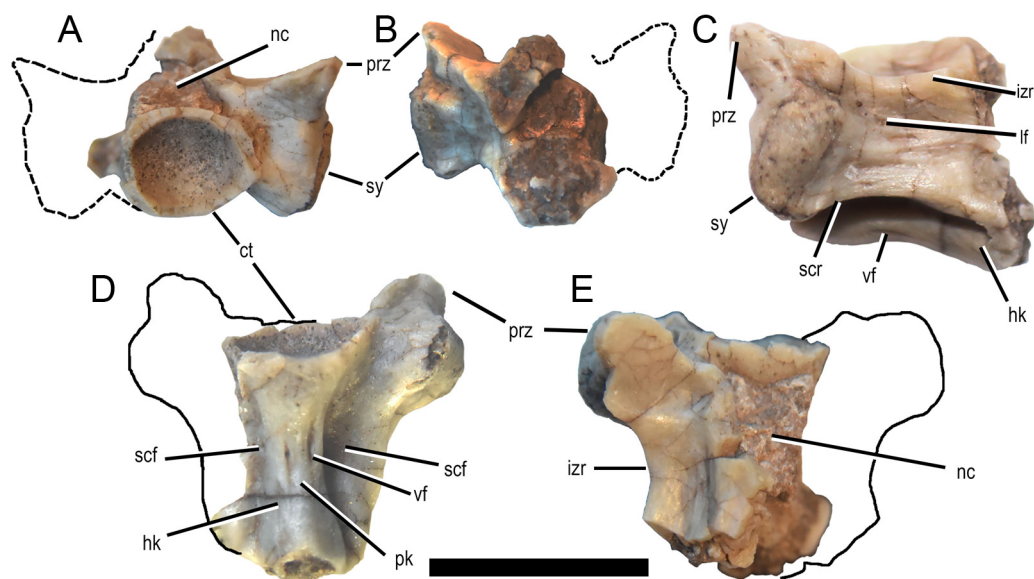


Figure 3. *Serpentes* indet. (MPM 21522) partial mid-posterior vertebra in anterior (A), posterior (B), lateral (C), ventral (D) and dorsal (E) views. **Abbreviations:** *ct*, cotyle; *izr*, interzygapophyseal ridge; *hk*, haemal keel; *lf*, lateral foramen; *prz*, prezygapophysis; *pk*, pseudo keel; *scf*, subcentral foramen; *scr*, subcentral ridge; *sy*, synapophysis; *vf*, ventral foramen. Scale bar: 5 mm.

posterior vertebra (locality 4) (Figure 3).

**Description:** MPM 21522 is a small vertebra, 7mm long, consisting of centrum, left prezygapophysis, and ventral region of the neural canal. As in most snakes, it shows an anteroventrally facing articular cotyle, subcentral ridges, grooves and foramina and synapophyses. This element is identified as a preloacal vertebra because of the absence of pleurapophyses, lymphapophyses, and hemapophyses (LaDuke, 1991). It shares a combination of characters present in middle and posterior preloacals (wide and shallow haemal keel, elongated vertebral centrum, and synapophyses with a strong lateral component ventrally located).

In anterior view the articular cotyle is sub-circular in contour. The neural canal was dorso-ventrally low and with a subtriangular contour in anterior view. There are two well-defined paracotylar foramina, located close and at mid height of the cotyle. The foramina are situated within shallow paracotylar fossae, adjacent to the left side of the cotyle. The prezygapophysis has the articular facet inclined about 20° above the horizontal plane, and barely surpass the lateral margin of the paradiapophysis (=synapophysis). The ventral margin of the synapophysis is lower than the ventral margin of the articular cotyle.

In dorsal view, the prezygapophyseal facet is oval-shaped, with its main axis obliquely orien-

ted, about 40-50° from the sagittal plane. At the base of the facet there is a well-defined and small fossa. The prezygapophyseal accessory process is absent and the interzygapophyseal rim is shallow.

The posterior articular condyle is below the level of paradiapophysis. The neural canal seems taller than in anterior view, and is sub-triangular in contour. A small portion of the posterodorsal surface of the vertebral centrum is preserved, and bears no medial keel.

The centrum has a parallelogram-shaped profile in lateral view, with the posterior region in a lower level than the anterior region. The paradiapophysis is massively built, with no clear differentiation from the both dia- and parapophyses. The paradiapophysis is sub-rectangular in contour and is postero-ventrolaterally faced, with a strong lateral component. Posterior to it, at mid-length of the vertebral length, there is a lateral foramen. The diapophyseal region is wider and more posteriorly placed than the parapophyseal region. Posterior to the paradiapophysis there is a moderately developed subcentral ridge that laterally surrounds the subcentral fossa. The haemal keel is low and ventrally concave, and the subcentral foramina are not visible due the great depth of the subcentral fossa.

In ventral view, the vertebral centrum is sub-triangular shaped, its lateral margins converging

posteriorly. The haemal keel is transversely wide and is hourglass shaped, with the anterior region transversely wider than the posterior half. The subcentral fossae are well developed and laterally delimit the haemal keel. On the ventral surface of the haemal keel there are present two foramina. Between them there is a pseudo-keel that extends all the length of the haemal keel. This pseudo-keel is poorly-developed, but distinctive.

**Comments:** Albino (Albino, 1986, 1987, 1994; see also Martinelli & Forasiepi, 2004) described several serpent taxa based on isolated vertebrae from the Latest Cretaceous (Maastrichtian) Los Alamos Formation, Rio Negro province. These specimens belong to basal snakes of the “madtsoiid” grade. More recently, Gómez *et al.* (2008) described from coeval beds the “anilioid” *Australophis anilioides* from northern Patagonia. In spite of this relative rich record, they restrict to the NW corner of Patagonia. Thus, present report extends paleogeographic distribution of these reptiles up to the southern region of South America.

In spite of being incomplete, the specimen MPM 21522 shows a combination of characters unique among snakes. Presence of a paracotylar foramen is shared with madtsoiids, *Dinilyisia*, several specimens of *Colombophis* (Simpson, 1933; Albino, 1986, 1994, 2000; Rage & Wagner, 1999; Scanlon, 2006), boiids (Albino, 2010), and it is variably present among anilioids (Hsiou *et al.*, 2019). Paracotylar foramina are absent in *Najash*, *Menarana*, and most anilioids (Rage, 1984, 1998; Gómez *et al.*, 2008; Zaher *et al.*, 2009; La Duke *et al.*, 2010). As occurs in the madtsoiids *Madtsoia*, *Adinophis*, and *Alamitophis*, MPM 21522 presents two paracotylar foramina (Simpson, 1933; Albino, 1994; La Duke *et al.*, 2010; Pritchard *et al.*, 2014).

Resembling *Dinilyisia*, and the madtsoiids *Alamitophis* (Albino, 1986; MACN-RN 27,38), *Nidophis*, *Menarana* and *Madtsoia pisdurensis* (La Duke *et al.*, 2010; Mohabey *et al.*, 2011; Vasile *et al.*, 2013), the prezygapophysis of MPM 21522 extends slightly beyond the lateral margin of the synapophysis. In *Colombophis* and anilioids (Rage, 1984, 1998; Hsiou *et al.*, 2010) the prezygapophyses extend much further than the synapophyses, whereas the reverse condition applies for *Najash*, *Adinophis*, *Gigantophis*, *Nanowana*, *Patagoniophis* and several *Madtsoia* species (Scanlon, 1997; Rage, 1998; Zaher *et al.*, 2009; La Duke *et al.*, 2010; Pritchard *et al.*, 2014). The absence of a prezygapophyseal accessory process is a plesiomorphic feature shared by

MPM 21522, madtsoiids, and *Najash* (Rage & Wagner, 1999; Albino, 2000; Scanlon, 2006; La Duke *et al.*, 2010; Mohabey *et al.*, 2011; Zaher *et al.*, 2009).

The haemal keel present in MPM 21522 is low and wide, similar to the condition of posterior preloacal vertebrae in most madtsoiids and anilioids. It is flanked by two small subcentral foramina, as occurs in posterior preloacal vertebrae of *Dinilyisia* (MACN-RN 116). Furthermore, MPM 21522 differs from all known madtsoiids and other fossil snakes because of the presence of a pseudo-keel, flanked by two foramina located on slits, on the ventral surface of the haemal keel. A somewhat similar condition is found in *Colombophis* and in the supposed tropidophiid *Dunnophis* (Rage, 1984), where the haemal keel is wide and flat and two subcentral foramina are present on the ventral surface of the keel; however, there is no presence of a pseudo-keel (Rage, 1984; Hsiou *et al.*, 2010). Rage (2013) reported for *Paraungaliophis* a ventral longitudinal keel producing a shallow sagittal ridge, but this keel differs from MPM 21522 in being sharp and restricted to the posterior end of the keel. Another distinguishable feature of MPM 21522 is that the foramina present on the ventral surface are placed in a slit, similar to the anilioid *Hoffstetterella*, where the subcentral fossa of the anterior and mid preloacal vertebra are located within slits (Rage, 1998).

The synapophyses of MPM 21522 is well developed and the diapophyseal and parapophyseal regions are plesiomorphically poorly differentiated. This condition is also present in *Alamitophis*, *Colombophis*, *Anilius* and *Coniophis* (Rage, 1984; Albino, 1994; Hsiou *et al.*, 2010). On the contrary, the synapophyses in most of the madtsoiids and the anilioid *Hoffstetterella* are well-defined into para- and diapophyseal regions (Simpson, 1933; Rage, 1998; Zaher *et al.*, 2009; La Duke *et al.*, 2010; Mohabey *et al.*, 2011; Vasile *et al.*, 2013; Pritchard *et al.*, 2014; Rio & Mannion, 2017), a derived condition found in all alethinophidian snakes (Rieppel *et al.*, 2002; Apesteguía & Zaher, 2006).

As in *Dinilyisia*, *Najash*, and the madtsoiids *Madtsoia madagascarensis*, *Nidophis* and *Menarana* (Zaher *et al.*, 2009; La Duke *et al.*, 2010; Vasile, 2013), the subcentral ridges and fossae in MPM 21522 are well developed. This contrast with some madtsoiids (e.g., *Madtsoia*, *Gigantophis*, *Adinophis*) and most anilioids (Simpson, 1933; Rage, 1998; Gómez *et al.*, 2008; Mohabey *et al.*, 2011; Pritchard *et al.*, 2014; Rio

& Mannion, 2017; Hsiou et al., 2010) which have poorly defined subcentral ridges and fossae.

In lateral view, a lateral foramen can be observed in most madtsoiids and anilioiids (Simpson, 1933; Rage, 1998; Albino, 2000; Zaher et al., 2009; La Duke et al., 2010; Vasile et al., 2013; Pritchard et al., 2014).

The interzygapophyseal constriction in MPM 21522 is shallow as in *Dinilysia*, *Madtsoia pisidurensis* and most anilioiids (Rage, 1998; Gómez et al., 2008; Mohabet et al., 2011), which differ from *Najash*, *Colombophis* and most madtsoiids, where it is notably deep (Simpson, 1933; Rage, 1998; Zaher et al., 2009; La Duke et al., 2010; Vasile et al., 2013; Rio & Mannion, 2017; Hsiou et al., 2010).

In spite of its distinctiveness, MPM 21522 is here regarded as an indeterminate Serpentes because of its fragmentary condition.

cf. *Rionegrophis madtsoioides* Albino,  
1986

**Referred materials:** MPM 21523, partial vertebra (locality 2) (Figure 4).

**Description:** MPM 21523 is an incomplete vertebra, approximately 14 mm long as preserved. As in most snakes, the cotyle faces anteroventrally, the subcentral ridges and grooves are well-defined, and synapophysis are present. The vertebra corresponds to the precloacal region because of the absence of pleurapophyses, lymphapophyses, and hemapophyses (LaDuke, 1991). Due to the tall and narrow haemal keel, and the absence of a hypoapophysis, this element corresponds to the mid-precloacal region.

The cotyle is notably deep and dorsolaterally flanked by a deep paracotylar foramen. The distal end of the prezygapophysis is missing, thus the presence of a prezygapophyseal process remains unknown. In dorsal view, the prezygapophysis shows a subtriangular contour, its major axis forming an angle about 45° with the sagittal plane. The paradiapophysis is widely exposed; the diapophysis region of the synapophysis is more developed and more posteriorly located than the parapophyseal region of the synapophysis.

The condyle is prominent, sub-circular shaped in posterior view, and slightly dorsally pointed. The ventral surface of centrum exhibits on its posteriormost region an haemal keel, flanked by two small depressions, probably representing the posterior portion of the subcentral grooves. Subcentral ridges are present.

**Comments.** Due to the fragmentary na-

ture of MPM 21523, comparisons are limited. However, its size and general morphology closely resembles *Rionegrophis madtsoioides* (Albino, 1986). MPM 21523 shows a well-developed and narrow haemal keel, similar to some madtsoiids and the anilioiid *Hoffstetterella brasiliensis* (Scanlon, 1997; Rage, 1998; Vasile et al. 2013), whereas *Dinilysia* and *Najash* show a notably wider haemal keel (Zaher et al. 2009; MACN-RN 2019). Further, the synapophysis of MPM 21523 resembles most madtsoiids synapophyses because the diapophysis is wider than the parapophysis.

Presence of a well-developed keel present on the dorsal surface of the centrum is shared with *Alamitophis* and *Rionegrophis madtsoioides* (Albino, 1986; MACN-RN 27, 32). However, MPM 21523 differs from *Alamitophis* and resembles *Rionegrophis* in the presence of a subtriangular-shaped centrum when viewed dorsally or ventrally.

In gross-morphology and main features MPM 21523 resembles *Rionegrophis madtsoioides*. However, its fragmentary nature precludes a clear determination, and thus is identified here as cf. *Rionegrophis madtsoioides*.

Squamata Oppel, 1811  
Mosasauridae Gervais, 1852  
Genus and species indeterminate

**Referred material.** MPM 21524, seven isolated teeth (locality 5) (Figure 5).

**Description.** Seven mosasaur teeth have been collected from the upper levels of the Chorrillo Formation, all of them coming from a single fossil spot which also yielded ornithopod remains (described below). We assume these teeth, found in close association, belong to a single mosasaur individual. Available teeth share the following combination of characters supporting their referral as to Mosasauridae (Hornung & Reich, 2015): 1) crowns bearing distal and mesial carinae, 2) different level of enamel striation, 3) crown polygonal-shaped in cross-section, and 4) crown tip posteriorly curved.

Available teeth can be sorted into two different types, in accordance with size, enamel ornamentation and morphology. One type is represented by fragments of three large teeth, the best preserved of which has an almost complete crown (Figure 5A-C), being 44 mm in total height and 20 mm in diameter at its base. The basal quarter of these teeth is devoid of enamel, striations, and carinae, indicating proximity to bone

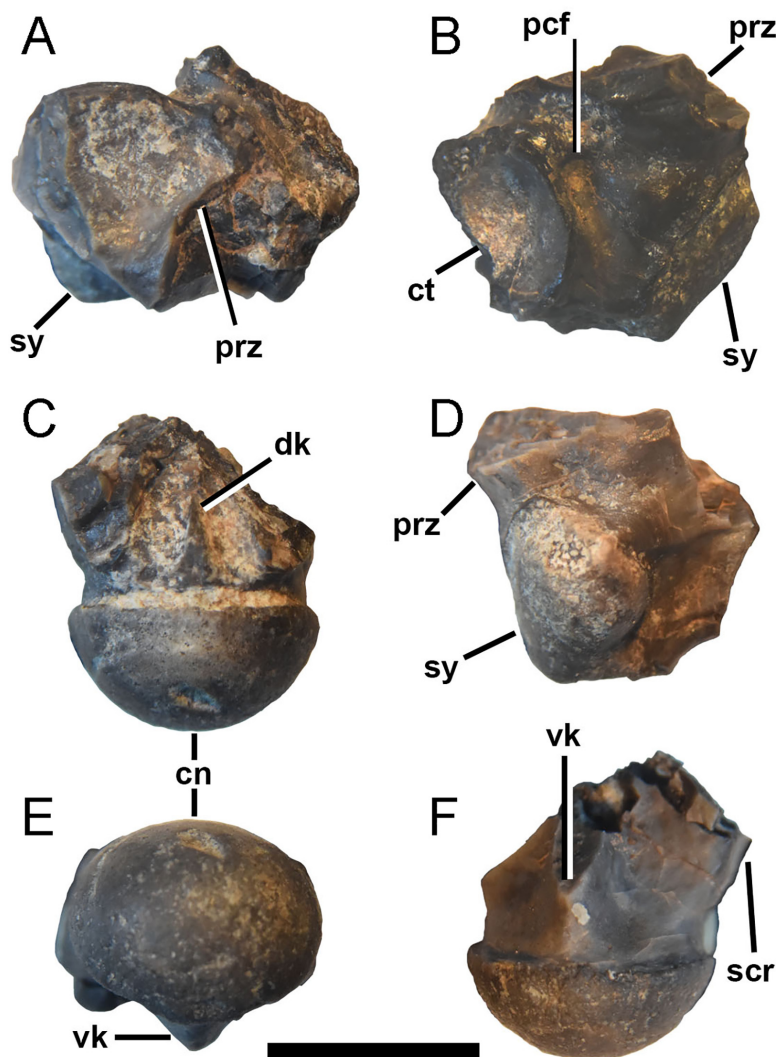


Figure 4. cf. *Rionegrophis madtsoiids* (MPM 21523), one partial vertebrae in dorsal (A, C), anterior (B), lateral (D), posterior (E) and ventral (F) views. **Abbreviations:** ct, cotyle; cn, condyle; dk, dorsal keel; pcf, paracotylar foramina; prz, prezygapophysis; scr, subcentral ridge; sy, synapophysis; vk, ventral keel. Scale bar: 5 mm.

attachment (Figure 5). The crowns are conical-shaped, being only slightly distally curved in side view. Tooth crowns lack striations on their apical quarter, but show a gently convex wear facet. Crown bases are elliptical in cross-section, with the labial side strongly convex and lingual side slightly more flattened than the opposite side. Mesial and distal carinae are sharp and devoid of serrations, being the distal carina stronger than the mesial one. Applying the terminology for enamel ornamentation used by Hornung & Reich (2015) these crowns have primary and secondary striae with no ramifications, with some of the primary striae converging apically with

secondary striae. Labially, the crowns exhibit three main convex prism faces (sensu Hornung & Reich, 2015), which are absent on the lingual surface.

The second tooth type is represented by an almost complete tooth crown (Figure 5D,E). It is small sized (total height 15mm, basal diameter 10mm), subtriangular-shaped in side view, and elliptical in cross-section. Both mesial and distal margins are slightly convex. The labial side of the crown is smooth and devoid of ornamentation, whereas the lingual side bears fine basal striae. The base of this tooth is devoid of enamel.

**Comments.** The Campanian-Maastrichtian fos-

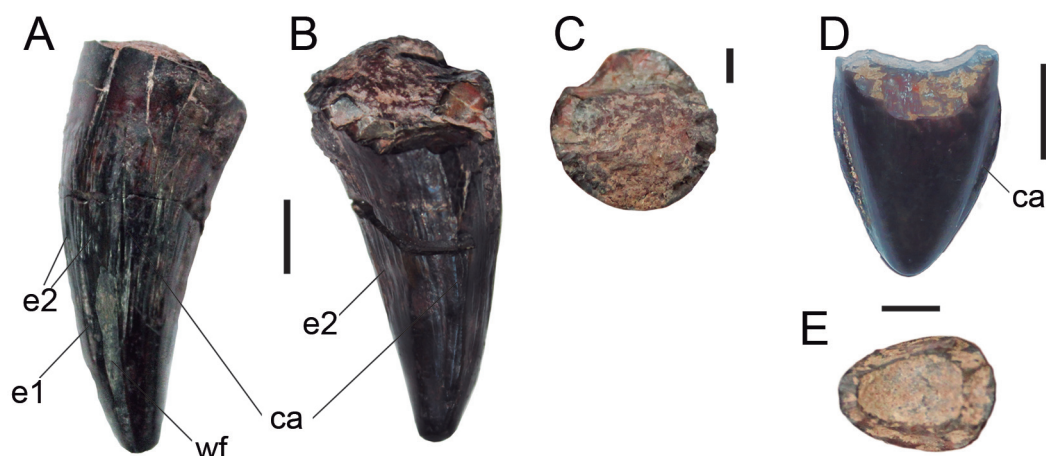


Figure 5. Mosasauridae indet. (MPM 21524). Tooth types 1 (A-C) and 2 (D-E) in mesial (A), distal (B), basal (C, E), and lingual views. **Abbreviations:** e1, primary striation; e2, secondary striation; ca, carina; wf, wear facet. Scale bars: 10 mm.

sil record of mosasaurs described for southern Patagonia and Antarctic Peninsula includes remains referred as to mosasaurines, halisaurines, tylosaurines, and plioplatecarpines (Ameghino, 1893; Gasparini & Del Valle, 1981; Martin *et al.*, 2002; Otero *et al.*, 2017). Most of them are based upon shed teeth and isolated vertebrae, and have been considered of dubious affinities by Novas *et al.* (2002). Currently, only two taxa have been confidently identified on the basis of cranial, dental and postcranial remains: *Taniwhasaurus antarcticus* (Novas *et al.*, 2002; Fernandez & Martin, 2007) and *Kaikaifile hervei* (Otero *et al.*, 2017), both of them belonging to Tylosaurinae. Teeth of *Taniwhasaurus antarcticus* (Novas *et al.*, 2002) differ from those reported here in having slenderer and posterolingually curved crowns, narrower striae, and feebly developed unserrated carinae. Besides, teeth here described resemble the large Antarctic mosasaur *Kaikaifile* on their large size, overall shape and cross section of the crown. However, teeth of *Kaikaifile* bear only a mesial carina and are more finely striated.

Several tooth remains from the Late Cretaceous of Antarctica have been reported as belonging to indeterminate mosasaurines (e.g., Martin, 2006; Martin and Crame, 2006). These teeth differ from those here described in being more labiolingually compressed, with enamel surface smooth, and prism faces greater and flatter. Besides, isolated teeth from Antarctica referred as to tylosaurines and platecarpines (e.g., Martin, 2006; Martin & Crame, 2006) consist on poorly preserved materials, precluding detailed comparisons with present specimens.

Teeth of *Mosasaurus* aff. *M. hoffmani* from the Late Cretaceous of Río Negro province (Fernández *et al.*, 2008) differ from those reported here in having lingual surface wider, and enamel surface smooth. Teeth of “*Liodon argentinus*” (Ameghino, 1893), from the Cenomanian Mata Amarilla Formation, Pari Aike, Santa Cruz province, share with those collected in Chorrillo beds in bearing both anterior and posterior carinae, but differ in being more laterally compressed, with stronger carinae and serration in the anterior carina.

In sum, MPM 21523 could not be referred to any of the previously listed Patagonian and Antarctic mosasaur taxa, and thus they are considered as Mosasauridae indet.

Some authors (e.g., Lindgren, 2005; Fernández, 2008; Lindgren & Siverson, 2002, 2004) have conferred a great taxonomic value to mosasaur shed teeth, taking them as enough evidence for the presence of a particular mosasaur family, or even mosasaur genera. However, we agree with Caldwell and Diedrich (2005) in that the taxonomic importance of dentition has been overestimated. For example, the presence of strong facets has been considered diagnostic for mosasaurines, instead the presence of deep striations was interpreted distinctive for plioplatecarpines (e.g., Martin & Crame, 2006). However, as indicated by specimens from the Chorrillo beds, these characters are vague and are present in many non-related taxa. It has been shown that tooth morphology varies along dental series of a single individual (see for example Konishi *et al.*, 2012), and some taxa display up

to four distinct tooth types along the jaws (e.g., Schulp *et al.*, 2004; Thevenin, 1896; Otero *et al.*, 2017). Further, ontogenetic changes have been also recognized in mosasaur literature (Lindgren & Siverson, 2004). In sum, we consider that the taxonomic value of isolated mosasaur teeth have to be taken with caution.

Regarding the possible paleoenvironmental significance of mosasaur teeth, it is outstanding their close taphonomic association with ornithopod bones. The presence of mosasaur remains is suggestive of marine influence during the entombing of basal iguanodontians. This resembles the El Puesto “member” of the upper third of the Dorotea Formation, which yielded hadrosaurs remains (Jujihara *et al.*, 2014; Soto Acuña *et al.*, 2014), immediately below marine levels with aquatic fossils (including mosasaurs; Soto Acuña *et al.*, 2016).

Dinosauria Owen, 1842  
Ornithischia Seeley, 1887  
Ornithopoda Marsh, 1881  
Euiguanodontia Coria & Salgado, 1996  
Elasmaria Calvo, Porfiri & Novas, 2007

*Isasicursor santacruzensis* gen. et sp. nov.

Figure 6

**Holotype.** MPM 21525, proximal end of left tibia (Figure 7). The specimen comes from locality 5.

**Paratypes:** MPM 21526, incomplete cervical centrum; MPM 21527, two dorsal vertebrae; MPM 21528, sacrum lacking sacral 3rd; MPM 21529, 30 caudal vertebrae; MPM 21530, proximal end of right scapula ; MPM 21531, distal half of left humerus; MPM 21532, iliac process of left pubis; MPM 21533, set of juvenile specimens represented by proximal end of right femur , three proximal end of left femora, three distal end of left femora, and two fragments of femur mid-shaft; MPM 21534, distal end of tibia; MPM 21535, proximal and distal end of metatarsal II; MPM 21536, distal end of left metatarsal III; MPM 21537, proximal and distal ends of metatarsal IV of a juvenile individual; MPM 21539, pedal phalanges I-1, II-1, IV-2/IV-3; MPM 21540, six pedal ungual phalanges; MPM 21541, pedal phalanges II-2 and III-2 of juvenile individuals. As for the holotype, all the referred specimens come from locality 5.

**Diagnosis.** Medium-sized elasmarian ornithopod having the following autapomorphies: 1) ventrally arched sacrum; 2) peg-and-socket ar-

ticulation between the first and second sacral vertebrae in ventral view; 3) tibia with strongly proximally projected and thickened cnemial crest, 4) lateral condyle of tibia with an additional anterolateral process; and 5) metatarsal II with a proximally displaced collateral ligament pit on its lateral surface.

The preserved elements of the hindlimb, especially metatarsals are more robust than other elasmarians of comparable size, such as *Morrosaurus* and *Talenkauen*.

**Horizon and Locality.** Collected specimens come from locality 5.

**Etymology.** *Isasicursor* honors the skilled technician Marcelo P. Isasi (Conicet - MACN), who discovered the remains of this new iguanodontian, and *cursor*, meaning runner in Latin; *santacruzensis*, in regards to Santa Cruz, the Argentine province where fossils were found.

## Description

**Cervical vertebra** (Figure 8). The only recovered cervical vertebra of *Isasicursor* is represented by the anterior third of a centrum. In anterior view the articular surface is concave and roughly hexagonal in contour. The parapophyses are represented by poorly developed processes, subtriangular in contour when viewed from the side. Ventral to the parapophyses the lateral surfaces of centrum are transversely concave. In ventral view, there is a sharp ventral longitudinal keel, a condition considered synapomorphic for Elasmaria (Rozadilla *et al.*, 2019).

**Dorsal vertebrae** (Figure 8). Two incomplete dorsal vertebrae are preserved. The centra are laterally compressed, conferring an hourglass contour in ventral view. In lateral view, the ventral margin of the centra possesses ventral buttresses near the anterior and posterior articular surfaces, with a concave margin between them. The anterior and posterior articular surfaces are slightly concave and oval in contour. They are dorsoventrally taller than transversely wide, indicating these centra correspond to the mid-dorsal series. The ventral surface bears a stout ventral keel, as occurs in most basal ornithopods including elasmarians (*i.e.*, Coria & Salgado, 1996; Martínez, 1998; Coria & Calvo, 2002; Novas *et al.*, 2004; Calvo *et al.*, 2007; Coria *et al.*, 2013; Ibiricu *et al.*, 2014; 2019; Cruzado-Caballero *et al.*, 2019; Rozadilla *et al.*, 2019). Some vascular foramina are present on the lateral and ventral surfaces of the centra.

**Sacral vertebrae** (Figure 9). The sacrum is represented by six disarticulated

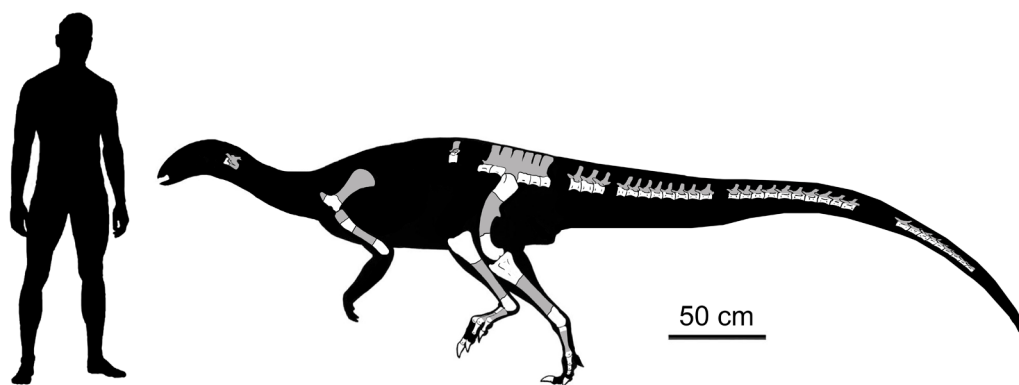


Figure 6. *Isasicursor santacruzensis* gen. et sp. nov. Skeletal reconstruction and body shape, indicating the discovered bones in white.

centra, corresponding to sacrals 1, 2 and 4, 5 and 6. They lack signs of fusion and pneumatization, and the intervertebral attachment surfaces are ornamented by radiating grooves.

The sacrum is relatively stout, with ventral margin is strongly arched in side view, a condition absent in other known elasmarians. The first sacral is box-shaped and is the transversely wider element of the series. In ventral view, its anterior margin is notably transversely wide and presents large, fan-like transverse processes that bear articulation facets for the sacral ribs. This strong lateral projection is shared with *Jeholosaurus* and *Anabisetia* (Cambiaso, 2007; Han et al., 2012), whereas in *Macrogyphosaurus* these projections are feebly developed and in *Sektensaurus* are totally absent (Ibiricu et al., 2019; Rozadilla et al., 2019). The articular surface for ribs is oval in contour and bears a rugose surface, being dorso-laterally facing. The anterior articular surface of the centrum is kidney-shaped, dorsoventrally low and transversely wide. The posterior surface has a dorsoventrally oriented groove that ends in a socket-like pit on its ventral margin. This pit articulates with a process located on the anteroventral surface of the second sacral, resulting in a peg-and socket articulation. In other elasmarians, such as *Gasparinisaura* and *Sektensaurus* the contact between both elements is nearly flat (Ibiricu et al., 2019; Rozadilla et al., 2019). On the ventral surface, this sacral has a shallow ventral keel located at the bottom of a wide and shallow longitudinal groove. Some nutritious foramina occur on the ventral and lateral surfaces of the centrum.

The second sacral centrum is box-shaped and transversely compressed, which results in an hourglass outline in ventral view. The posterior

end of the centrum bears sacral rib facets, which expand laterally resulting in the transversely widest portion of the bone. The sacral rib facet is anteroposteriorly short, with a rugose attachment surface. The ventral surface of centrum has a smooth longitudinal keel, which projects anteriorly into a peg-like process that fits into the socket present in the posterior surface of the first sacral. On the sides of this ventral keel there are subparallel and shallow longitudinal grooves. The anterior articular surface of the centrum is suboval in contour, with the main axis transversely oriented. The posterior articular surface is suboval in contour, being slightly transversely wider than the anterior half of centrum.

The third sacral is not preserved. The fourth sacral is box-shaped and its lateral surface bears laterally projected processes for the attachment with the sacral ribs on its anterior and posterior ends. The anterior attachment for the sacral rib is more dorsally located and anteroposteriorly elongated than the posterior one. These surfaces are concave and rugose. The ventral surface of centrum shows a shallow median longitudinal groove. A low median ridge exists near its anterior end. The anterior articular surface of centrum is rugose and sub-quadrangular in contour, instead the posterior articular surface is hexagonal-shaped and transversely wider than the anterior one.

The fifth sacral vertebra is box-shaped, with a trapezoidal outline in ventral view, its anterior end transversely wider than its posterior one. The floor of the neural canal is narrow and bears an oval pit at mid-length. Sacral rib facets are anteroposteriorly elongate and located at the anterior half of the bone. These articulation surfaces are suboval in contour and show strong rugosi-

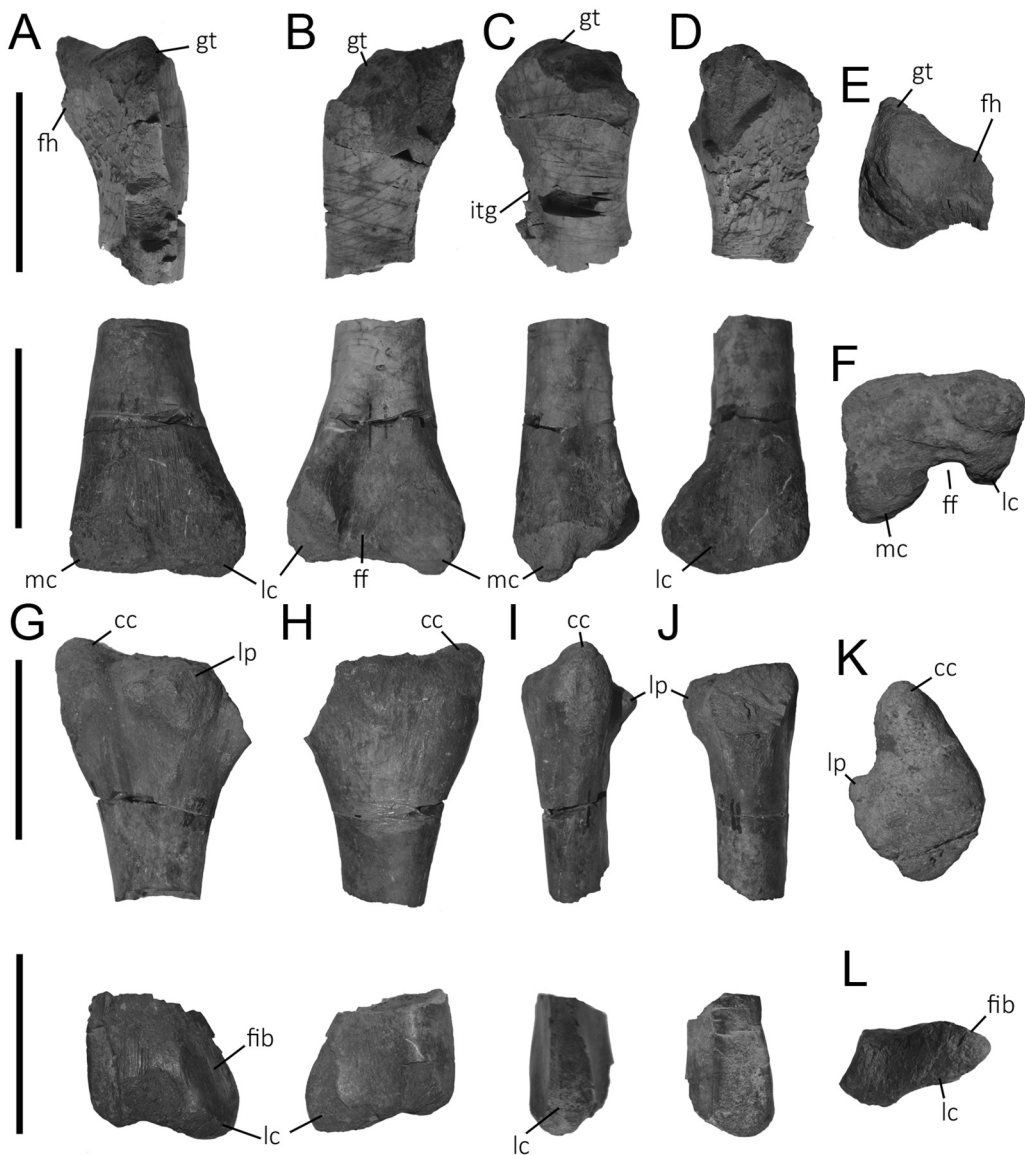


Figure 7. *Isasicursor santacruensis* gen. et sp. nov. Femur (MPM 21533a) in (A) anterior, (B) posterior, (C) lateral, (D) medial, (E) proximal and (F) distal views. Tibia (MPM 21525a) in (G) lateral, (H) medial, (I) anterior, (J) posterior, (K) proximal and (L) distal views. **Abbreviations:** cc, cnemial crest; fib, fibular facet; ff, flexor fossa; fh, femoral head; gt, greater trochanter; itg, intertrochanteric groove; lc, lateral condyle; lp, lateral process; mc, medial condyle. Scale bar: 10 cm.

ties on its attachment surface. Posterior and dorsal to the sacral rib facets, the centrum becomes transversely narrower. The ventral surface of centrum bears a shallow and wide longitudinal groove, with a low and smooth ridge restricted to its anterior margin. The anterior articular surface is suboval in contour, dorsoventrally low and transversely wide. Its dorsal edge has an anterior process that fits into the concavity of the

posterior surface of the preceding vertebra. The posterior articular surface is sub-quadrangular in contour, dorsoventrally high and transversely narrower than the anterior articular surface.

The sixth sacral vertebra is represented by a weathered centrum. The centrum is box-shaped, with a wide and shallow longitudinal ventral groove. Few nutritious foramina exist on its lateral and ventral surfaces. The anterior articular sur-



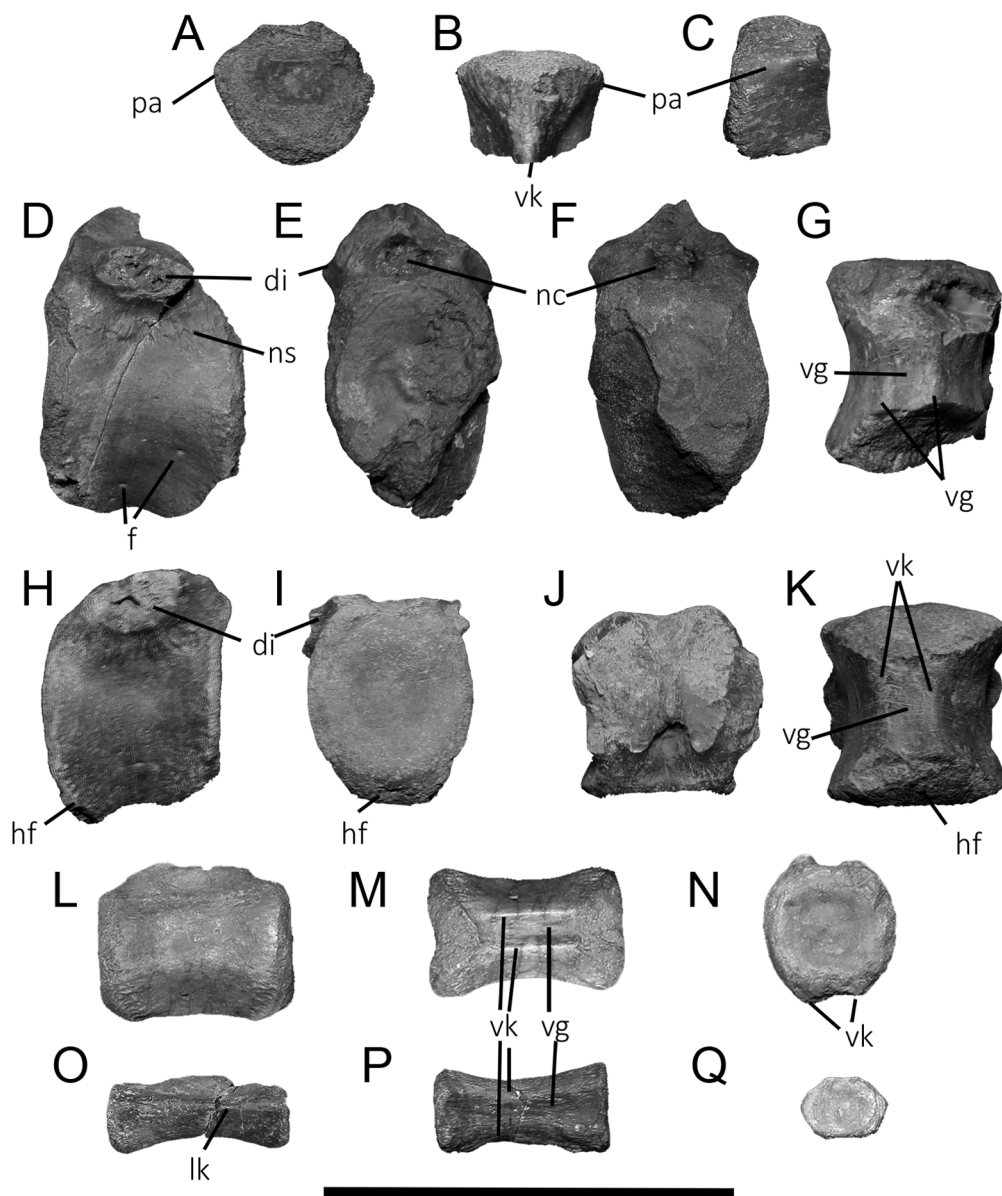


Figure 8. *Isasicursor santacruensis* gen. et sp. nov. Selected vertebral elements. Cervical vertebra (MPM 21526) in (A) anterior, (B) ventral and (C) lateral. Dorsal Vertebra (MPM 21527) in (D) lateral, (E) anterior, (F) posterior and (G) ventral views. Proximal caudal vertebra (MPM 21529) in (H) lateral, (I) anterior, (J) dorsal and (K) ventral views. Middle caudal vertebra (MPM 21529) in (L) lateral, (M) ventral and (N) anterior views. Posterior caudal vertebra (MPM 21529) in (O) lateral, (P) ventral and (Q) anterior views. **Abbreviations:** di, diapophysis; hf, haemal facet; lk, lateral keel; nc, neural canal; ns, neural suture; vg, ventral groove; vk, ventral keel. Scale bar: 5 cm.

face is sub-rectangular in contour. There is a small prominence at the lateral margin that contacts a shallow concavity present at the posterior articular surface of the preceding vertebra, resulting in a shallow peg and socket articulation. The posterior articular surface is subcircular in contour.

**Caudal vertebrae** (Figure 8). Thirty caudal vertebrae, corresponding to different individuals, have been recovered. These vertebrae belong to the anterior, median and posterior portions of the tail. Anterior caudal vertebrae are robust and slightly amphicoelous. The neural arches preserve the base of the diapophyses, which is

suboval in cross-section. The centra are dorsoventrally taller than anteroposteriorly long; they are laterally concave, resulting in a spool-shaped profile in ventral view. In lateral view, the ventral margin of the centra shows an extensive haemal facet, which is sub-triangular in contour and strongly anteroventrally oriented. The ventral surface of the centra bears a deep longitudinal groove. Shallow longitudinal striations are present near both anterior and posterior articular surfaces.

Mid-caudals are represented by isolated centra. These are slightly amphicoelous, and dorsoventrally lower and anteroposteriorly longer than in anterior caudals. The lateral surface shows lateral longitudinal ridges, which become sharper towards the distal end of the tail. In ventral view, the centra are hourglass-shaped and show a ventral longitudinal groove, which becomes deeper towards the distal end of the tail. The haemal facet is relatively smaller than in anterior caudals. The anterior and posterior articular surfaces are subcircular in contour and sub-equal in size and shape.

Vertebrae of the distal section of the tail resemble those of the middle section, excepting for being anteroposteriorly longer and with more prominent lateral longitudinal ridges, resulting hexagonal-shaped in cross-section. The ventral longitudinal groove is well developed and bounded by two subparallel longitudinal ridges. Distal caudals are indistinguishable from other basal ornithopods (e.g. *Gasparinisaura*, *Anabisetia*, *Talenkauen*, *Macrogryphosaurus*, *Diluvicursor*, *Sektensaurus*, *Trinisaura*, *Jeholosaurus*; Coria & Salgado, 1996; Cambiaso, 2007; Calvo *et al.*, 2007; Barrett *et al.*, 2011; Han *et al.*, 2012; Barrett, 2016; Herne *et al.*, 2018; Ibiricu *et al.*, 2019; Rozadilla *et al.*, 2019).

**Scapula** (Figure 10). The right scapula is represented by its proximal end. It is anteroposteriorly extensive, with thick acromial process. It narrows anteriorly, showing a wide and flat dorsal surface. The acromial process is laterally expanded, forming the deltoid rim, which delimits the dorsal margin of a shallow deltoid fossa. The glenoid cavity is severely damaged. It is ventrolaterally oriented and its anterior margin is delimited by a shallow supraglenoid fossa. This fossa is subcircular in contour and is ornamented by small striations, being relatively shallow, as occurs in *Gasparinisaura* and *Trinisaura* (Coria & Calvo, 2002; Coria *et al.*, 2013), whereas in *Anabisetia*, *Talenkauen* and *Mahuidacursor* it shows a deep supraglenoid fossa (Coria & Calvo,

2002; Cruzado-Caballero *et al.*, 2019; Rozadilla *et al.*, 2019). Near the coracoidal suture the medial surface of the scapula is covered by numerous ligament scars. The coracoidal articular facet is sub-rhomboidal in outline and strongly rugose.

**Humerus** (Figure 10). The left humerus is represented by isolated and incomplete shaft and distal end. The shaft is laterally bowed, as synapomorphic for Elasmaria (e.g., *Anabisetia*, *Notohypsilophodon*, *Talenkauen*, *Trinisaura*, *Sektensaurus*, *Mahuidacursor*; Martínez, 1998; Coria & Calvo, 2002; Novas *et al.*, 2004; Coria *et al.*, 2013; Ibiricu *et al.*, 2014; 2019; Cruzado-Caballero, 2019; Rozadilla *et al.*, 2019). The deltopectoral crest is reduced and represented by a low ridge, its lateral surface crossed by longitudinal muscle scars, as diagnostic for Elasmaria (e.g., *Anabisetia*, *Notohypsilophodon*, *Talenkauen*, *Trinisaura*, *Sektensaurus*, *Mahuidacursor*; Martínez, 1998; Coria & Calvo, 2002; Novas *et al.*, 2004; Coria *et al.*, 2013; Ibiricu *et al.*, 2014; 2019; Cruzado-Caballero, 2019; Rozadilla *et al.*, 2019), in contrast with the well-developed deltopectoral crest present in most ornithopods, including *Gasparinisaura* (Coria & Salgado, 1996; Rozadilla *et al.*, 2019). The anterior surface of the humeral shaft is concave, while the posterior one is convex. The medial surface bears an oval nutritious foramen. The shaft is reniform in cross-section. The distal end of the bone is slightly transversely expanded. The anterior surface of the bone is deeply concave proximal to the distal condyles. In distal view, the lateral condyle is more extensive than the medial one. The flexor fossa is transversely wider than the extensor one.

**Pubis**. The pubis is only represented by the iliac process. This process is oval in cross-section. The articular margin is almost flat and slightly projected ventrally in a short process, being not fused with the obturator process, indicating a posteriorly opened obturator foramen, resembling the condition of basal ornithopods (e.g., *Hypsilophodon*, *Gasparinisaura*, *Anabisetia*, *Trinisaura*; Galton, 1974a; Coria & Calvo, 2002; Cambiaso, 2007; Barrett *et al.*, 2011; Coria *et al.*, 2013).

**Femur** (Figures 7, 11). The femora are represented by several specimens, including a proximal end belonging to a juvenile individual. The femoral head is not preserved, but the neck is well-defined. The greater trochanter is completely preserved only in the juvenile specimen. In proximal view, the lateral margin of the greater trochanter is sigmoidal in outline. In lateral

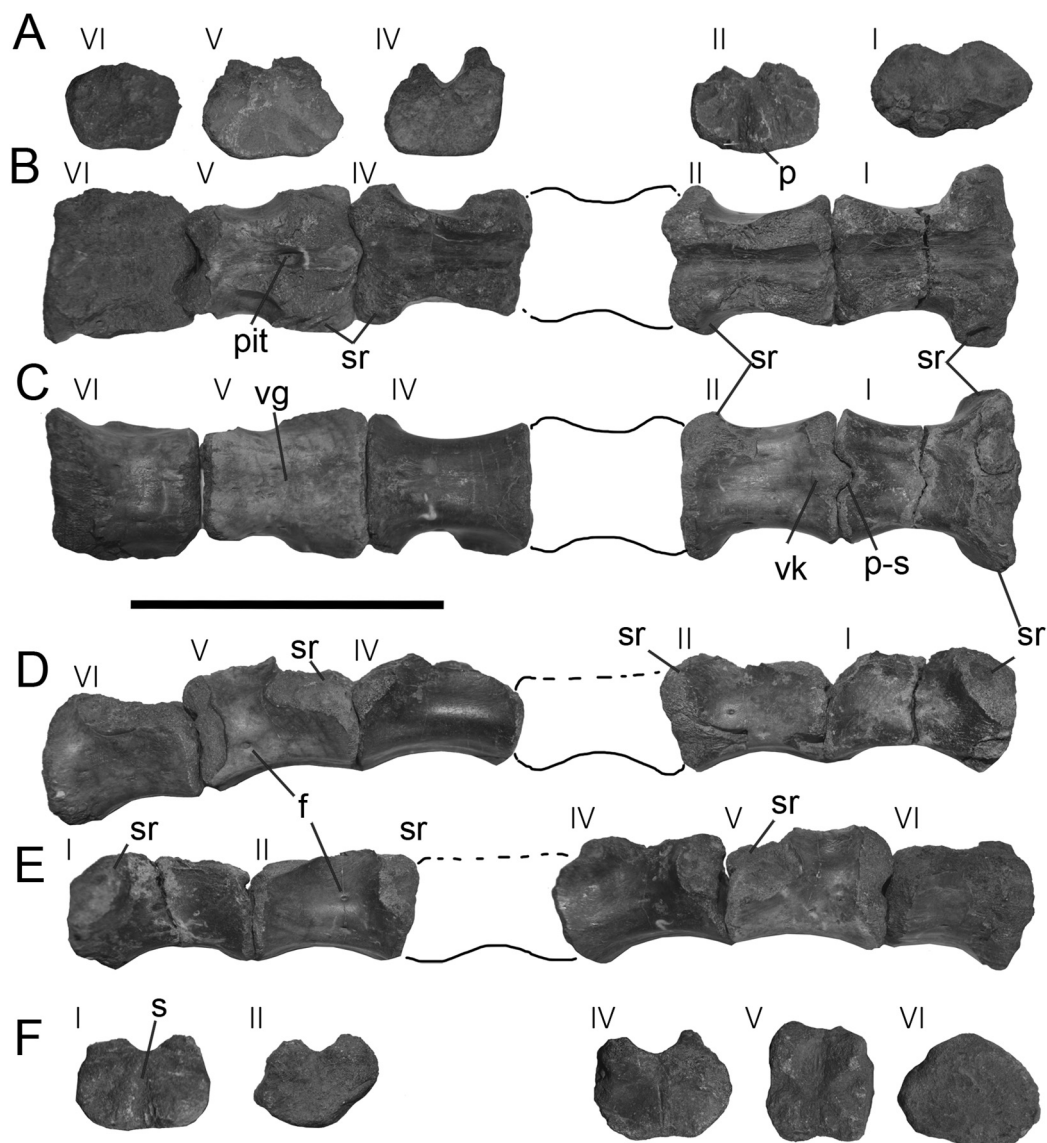


Figure 9. Sacrum of *Isasicursor santacruzensis* gen. et sp. nov. (MPM 21528) in (A) anterior, (B) dorsal, (C) ventral, (D) right, (E), left and (F) posterior views. I-VI indicates anteroposterior position in vertebral series. **Abbreviations:** f, vascular foramen; p, peg; **pit**, pit; **p-s**, peg and socket articulation; s, scar; **sr**, sacral rib; **vg**, ventral groove; **vk**, ventral keel. Scale bar: 3 cm.

view, this trochanter is proximally convex, and is medially delimited by the groove that separates it from the lesser trochanter. This indicates that the lesser trochanter was not fused to the major one, a condition different from *Gasparinisaura* (Coria & Salgado, 1996). The lesser trochanter is represented by its base, indicating that towards its anterior end it was notably narrow, a condition shared with *Morrosaurus*, *Anabisetia*, *Trinisaura* and *Gasparinisaura* (Coria &

Salgado, 1996; Coria & Calvo, 2002; Coria et al., 2013; Rozadilla et al., 2016).

The lateral surface near the proximal end shows a bump ornamented with longitudinal scars, which likely represents the anchoring of the for the *M. iliofemoralis externus*. The anterior surface between the greater trochanter and the femoral head is concave. The femoral shaft is subtriangular in cross-section, being posteriorly flat and anteriorly narrow.

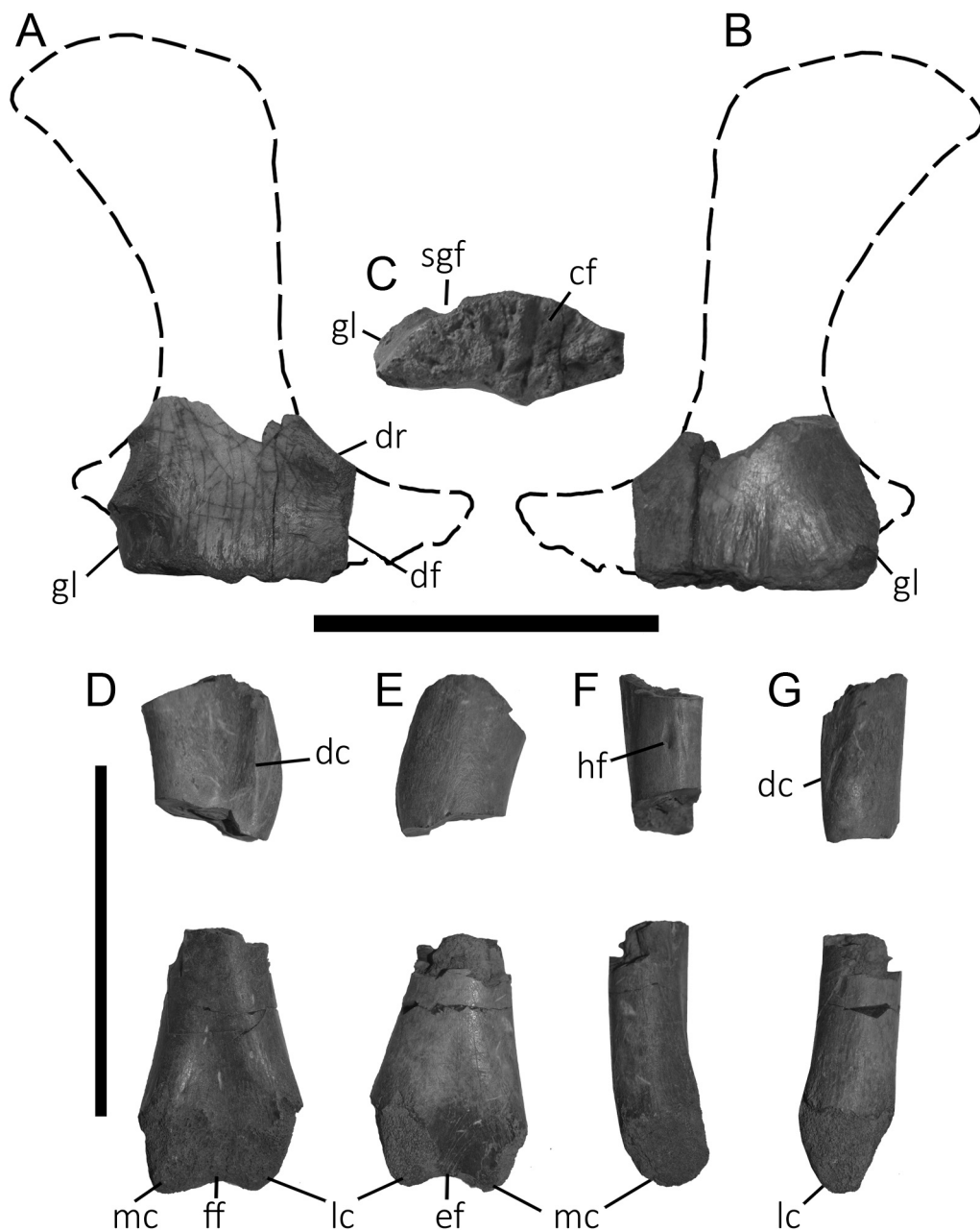


Figure 10. *Isasicursor santacrucensis* gen. et sp. nov. Scapula (MPM 21530) in (A) lateral (B), medial and (C) coracoidal views. Humerus (MPM 21531) in (D) anterior, (E) posterior, (F) medial and (G) lateral views. **Abbreviations:** dc, deltopectoral crest; df, deltopectoral fossa; dr, deltopectoral rim; ef, extensor fossa; ff, flexor fossa; gl, glenoid fossa; hf, humeral foramen; lc, lateral condyle; mc, medial condyle; sgf, supraglenoid fossa. Scale bar: 10 cm.

The distal end of the femur is transversely expanded. In distal view, the medial condyle is transversely wider than the lateral one. This asymmetry is present in many elasmarians, such as *Anabisetia*, *Morrosaurus* and *Kangnasaurus*,

as well as in more derived Iguanodontia (Cooper, 1985; Coria & Calvo, 2002; Norman 2004; Norman *et al.*, 2004; Rozadilla *et al.*, 2016). The medial condyle has a sub-rectangular outline, and slightly tapers posteriorly. In medial view,

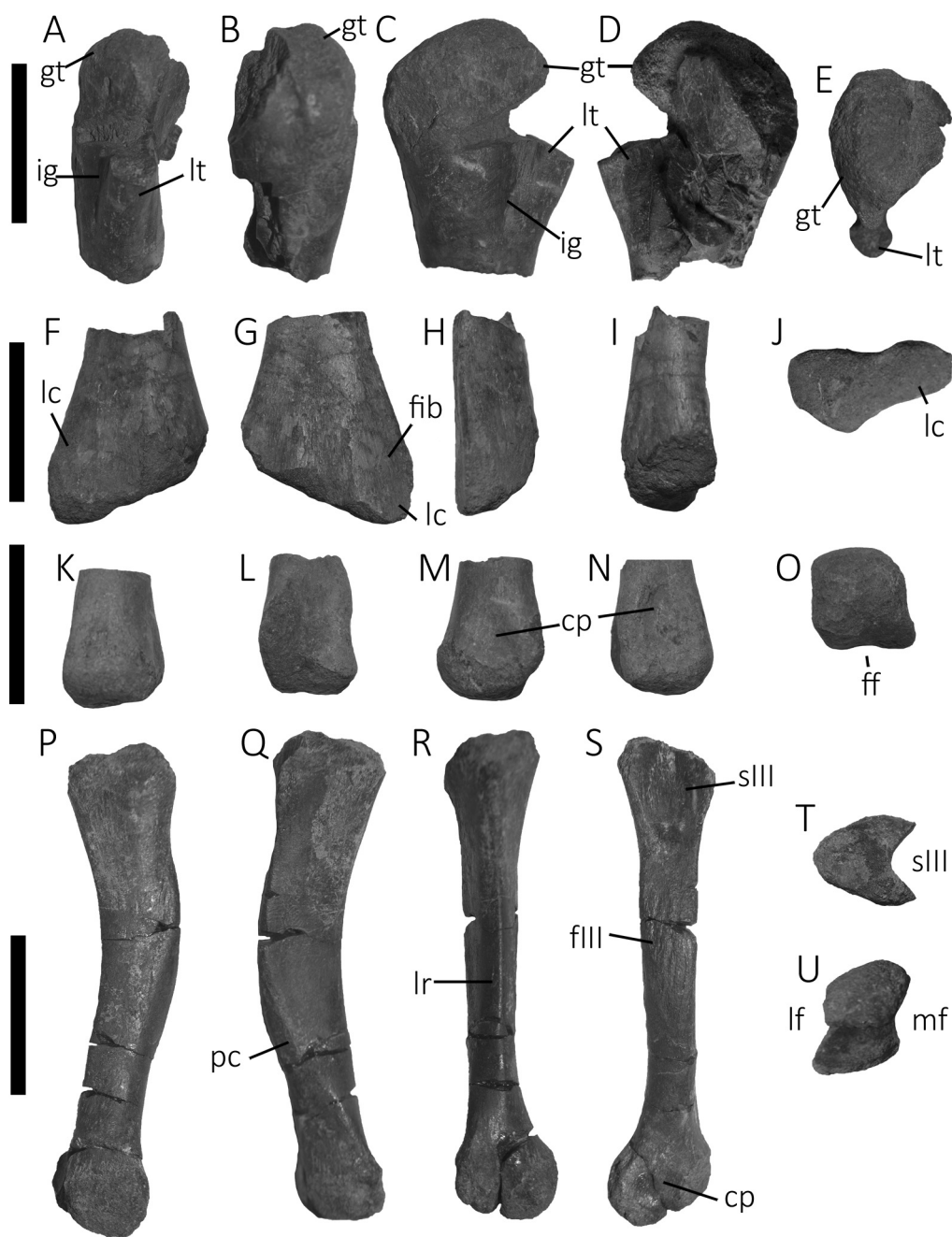


Figure 11. *Isasicursor santacruensis* gen. et sp. nov. Selected juvenile materials. Right femur (MPM 21533b) in (A) anterior, (B) posterior, (C) lateral (D) medial and (E) proximal views. Left tibia (MPM 21534b) in (F) anterior, (G) posterior, (H) lateral (I) medial and (J) distal views. Metatarsal II in (K) anterior, (L) posterior, (M) lateral (N) medial and (O) distal views. Metatarsal IV (MPM 21538b) in (P) anterior, (Q) posterior, (R) lateral (S) medial (T) proximal and (U) distal views. **Abbreviations:** cp, collateral pit; fib, fibular facet; gt, greater trochanter; ig, intertrochanteric groove; lc, lateral condyle; lf, lateral fossa; lr, lateral ridge; lt, lesser trochanter; mf, medial fossa; pc, plantar crest; sIII, surface for mtt III. Scale bar: 3 cm.

the medial condyle is posteriorly expanded and its medial surface is smoothly concave. The lateral condyle is gently laterally projected, resulting in a well-defined longitudinal groove on its lateral surface. This groove separates the lateral condyle from the tibiofibular crest. The medial condyle is not laterally expanded as in *Morrosaurus* and *Kangnasaurus* (Cooper, 1985; Rozadilla *et al.*, 2016). The anterior surface of the bone lacks a well-developed extensor fossa, a condition shared with many basal ornithopods, such as *Thescelosaurus*, *Hypsilophodon*, *Jeholosaurus*, *Gasparinisaura*, *Trinisaura*, *Notohypsilophodon* and “*Fulgurotherium*” (Galton, 1974a,b; Molnar & Galton, 1986; Coria & Salgado, 1996; Coria *et al.*, 2013; Martínez, 1998; Han *et al.*, 2012; Ibiricu *et al.*, 2014), while *Anabisetia*, *Morrosaurus*, *Kangnasaurus*, *Tenontosaurus*, Rhabdodontidae, Dryosauridae and Ankylopollexia show a well-developed extensor groove (Cooper, 1985; Sereno, 1986; Coria & Calvo, 2002; Norman, 2004; Norman *et al.*, 2004; Godefroit *et al.*, 2009; Rozadilla *et al.*, 2016). In posterior view, the flexor fossa is deep and limited laterally and medially by stout ridges that end in the distal condyles.

**Tibia** (Figure 7, 11). The proximal end of the tibia is anteroposteriorly expanded, its proximal surface is medially inclined and exhibits a rugose surface. The cnemial crest is anteriorly extended and is strongly proximally projected, resulting in a subtriangular profile in lateral view. This trait is unique for *Isasicursor*, different from the remaining ornithopods in which the cnemial crest does not project further proximally than the articular surface of the tibia (e.g. *Gasparinisaura*, *Notohypsilophodon*, *Tenontosaurus*, *Ouranosaurus*; Coria & Calvo, 1996; Tennant, 2013; Ibiricu *et al.*, 2014; Bertozzo *et al.*, 2017), or has a distally deflected anterior margin (e.g. *Anabisetia*, *Talenkauen*, *Morrosaurus*, *Zalmoxes*; Coria & Calvo, 2002; Godefroit *et al.*, 2009; Rozadilla *et al.*, 2016, 2019). The cnemial crest of *Isasicursor* is transversely thickened and shows a proximally rounded apex. In lateral view, the lateral crest shows a straight anterior margin. In *Isasicursor* it is more extensive than in *Kangnasaurus*, *Talenkauen* and *Morrosaurus* (Cooper, 1985; Novas *et al.*, 2004; Rozadilla *et al.*, 2016, 2019). The lateral condyle is subtriangular in proximal view. It shows a well-developed process at the anterolateral corner, being absent in other basal ornithopods such as *Gasparinisaura*, *Anabisetia*, *Talenkauen*, *Jeholosaurus*, *Kangnasaurus*,

*Notohypsilophodon*, *Hypsilophodon*, *Zalmoxes*, *Trinisaura*, and the iguanodontian *Ouranosaurus* (Galton, 1974a; Cooper, 1985; Coria & Salgado, 1996; Cambiaso, 2007; Godefroit *et al.*, 2009; Barrett *et al.*, 2011; Han *et al.*, 2012; Ibiricu *et al.*, 2014; Bertozzo *et al.*, 2017; Rozadilla *et al.*, 2019). The lateral surface of the lateral condyle is convex and rugose. The posterior margin of the lateral condyle is defined by a dorsoventrally oriented groove. There is a notch between the lateral and the posteromedial processes. The medial surface of the cnemial crest is posteriorly delimited by a low prominence. The tibial shaft is oval in cross-section on its proximal third.

The distal end of tibia of *Isasicursor* is transversely expanded and anteroposteriorly compressed. The distal malleoli are weathered. Both have a subtriangular outline in anterior view and are distally rounded, as occurs in related taxa with the exception of *Morrosaurus*, in which the medial condyle has a sharp trapezoidal outline (Cooper, 1985; Coria & Salgado, 2002; Cambiaso 2007; Ibiricu *et al.*, 2014; Rozadilla *et al.*, 2016). The lateral malleolus is transversely wider and more distally projected than the medial one. The anterior surface of the lateral malleolus bears a mound-like longitudinal crest, as occurs in *Talenkauen* and *Anabisetia* (Cambiaso, 2007; Rozadilla *et al.*, 2019). Lateral to this crest there is a smoothly concave surface for contact with the fibula. This crest and concave surfaces are shallower in the juvenile specimen. The posterior surface of the lateral malleolus is concave. In the juvenile specimen of *Isasicursor*, the lateral malleolus is anteroposteriorly narrower. The medial malleolus is subtriangular in distal view, concave anteriorly and convex posteriorly, lacking the anterior curvature present in *Morrosaurus* and *Trinisaura* (Barrett *et al.*, 2011; Rozadilla *et al.*, 2016). The distal malleoli are separated anteriorly by a shallow anterior intermalleolar fossa and posteriorly by a thick intermalleolar crest. The anterior intermalleolar fossa is shallower in the juvenile specimen.

**Metatarsals** (Figures 11, 12). Metatarsal II of *Isasicursor* is represented by isolated proximal and distal ends. The proximal end is anteroposteriorly expanded and transversely compressed a condition that was previously considered synapomorphic for *Elasmaria* by Rozadilla *et al.* (2016, 2019). However, metatarsal II of *Isasicursor* is not as expanded anteroposteriorly as in *Anabisetia* and *Diluvicursor* (Coria & Calvo, 2002; Herne *et al.*, 2018). The lateral surface of metatarsal II shows a flattened surface for artic-

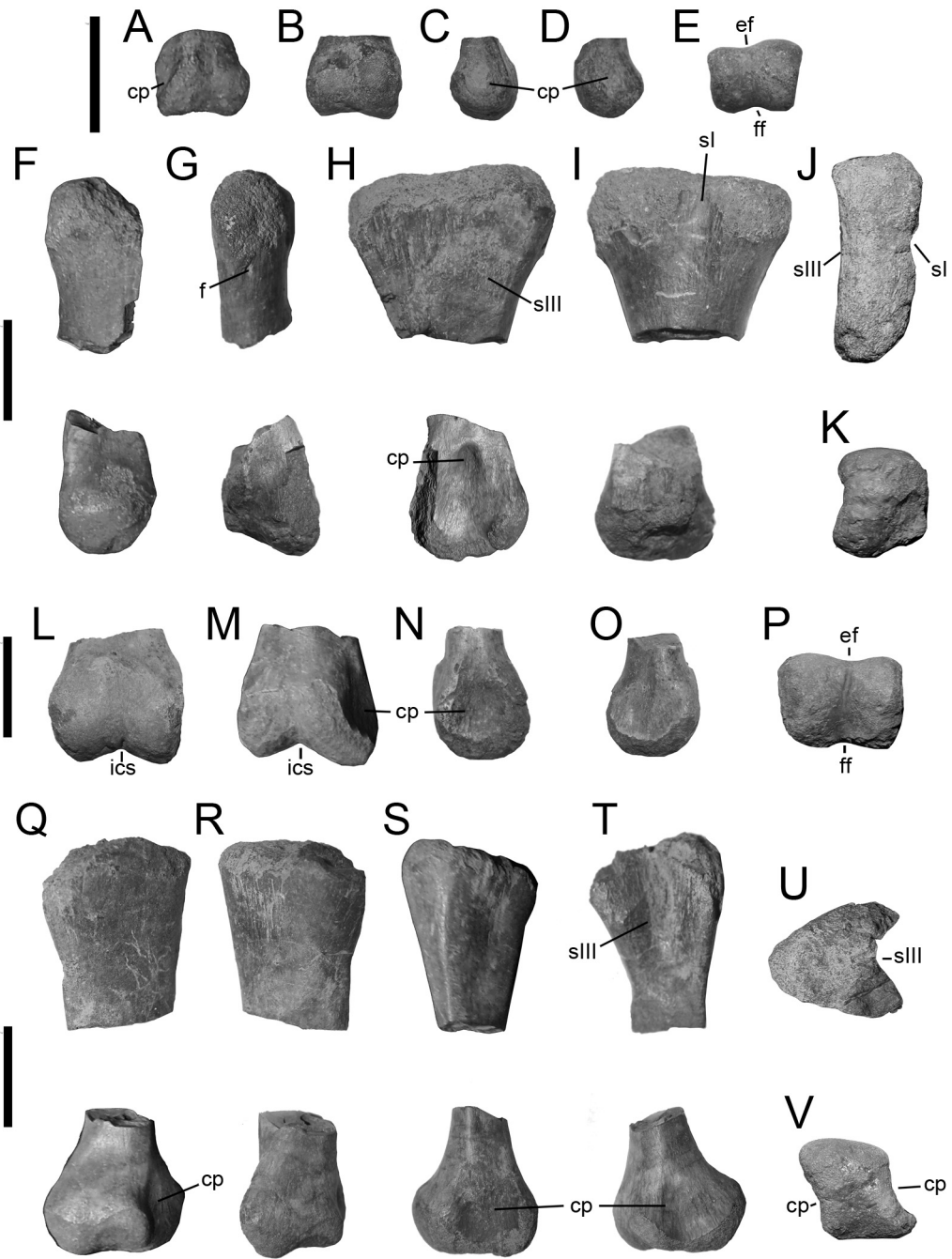


Figure 12. *Isasicursor santacruzensis* gen. et sp. nov. Metatarsal I in (A) anterior, (B) posterior, (C) lateral, (D) medial and (E) distal views. Proximal (above) and distal end (below) of metatarsal II (MPM 21535a) in (F) anterior, (G) posterior, (H) lateral, (I) medial (J) proximal and (K) distal views. Metatarsal III (MPM 21536) in (L) anterior, (M) posterior, (N) lateral, (O) medial and (P) distal views. Proximal (above) and distal end (below) of metatarsal IV (MPM 21537) in (Q) anterior, (R) posterior, (S) lateral, (T) medial (U) proximal and (V) distal views. **Abbreviations:** cp, collateral pit; ef, extensor fossa; f, foramen; ff, flexor fossa; ics, intercondylar sulcus; sI, surface for the mtt I; sIII, surface for the mtt III. Scale bar: 3 cm.

ulation with the medial surface of metatarsal III. The anterior surface of the bone is transversely thicker than the posterior one and is more laterally expanded. The distal end of metatarsal II has a sub-rectangular outline in distal view. The anterior surface is smooth and bears a rounded distal articular surface that is distally convex. The posterior surface has a deep flexor groove. The lateral surface is deeply concave and bears a distinct and deep collateral ligamental pit that is proximally located. This condition is absent in other elasmarians and may constitute an autapomorphy of *Isasicursor*. The lateral condylid is transversely thicker than the medial one. In an available juvenile metatarsal II (MPM 21535) both extensor and flexor grooves and collateral ligamental pits are shallower.

Metatarsal III is only represented by its distal end. The articular surface is asymmetrical in shape, being proximally expanded at its medial surface. The distal condylids are separated by a well-developed intercondylar groove. In distal view, the condyles are asymmetrical, the medial one being larger than the lateral one, resembling the condition of *Anabisetia* (Coria & Calvo, 2002; Cambiaso, 2007), but differing from that of *Morrosaurus*, which shows a notably larger lateral condylid (Rozadilla *et al.*, 2016). The lateral surface of the bone has a deep and sub-circular collateral pit, while the medial one is shallower.

Metatarsal IV is represented by several elements of different specimens. The most complete metatarsal IV belongs to a juvenile specimen, while larger specimens are represented by isolated proximal and distal ends. The proximal end is transversely expanded and is subtriangular in proximal view, with a tapering lateral surface, as occurs in *Gasparinisaura*, *Anabisetia*, *Thescelosaurus* and *Trinisaura* (Galton, 1974b; Coria & Salgado, 1996; Coria & Calvo, 2002; Barrett *et al.*, 2011), whereas in *Talenkauen*, *Morrosaurus* and *Styracosterna* the lateral surface is rounded (Norman, 2004; Rozadilla *et al.*, 2016; 2019). The proximal surface is gently concave and its posterior margin is more proximally extended than the anterior one. The medial surface is deeply concave with a narrow proximal groove that receives the lateral process of metatarsal III. Distal to this groove, the medial surface of the bone shows a flat contact for the lateral surface of metatarsal III. The anterior and posterior surfaces of the proximal end of the bone are flattened and smooth. In cross section, the bone is subtriangular proximally and oval distally. The lateral margin of the shaft shows a

sharp longitudinal keel. The anterior surface of the shaft is smooth, while the posterior one possesses an oblique ridge that runs from the medial margin to the lateral distal condyle. The distal end is strongly anteroposteriorly expanded. In anterior view, the articular surface lacks a well-defined extensor groove. In lateral view, there is a shallow collateral pit that is suboval in contour and with a strongly anteriorly projected anterior articular surface. In distal view, the articular surface has sub-parallelogram outline, with its anterior margin more laterally projected than the posterior one. The posterior margin is medially projected, forming a lip-like process that projects laterally, a condition shared with *Anabisetia* and *Trinisaura* (Cambiaso, 2007; Barrett *et al.*, 2011). This projection posteriorly bounds the outer collateral pit. In posterior view a shallow flexor groove separates both condylids.

MPM 21538 is proximodistally short and transversely stout. In related taxa, such as *Gasparinisaura*, *Anabisetia* and *Morrosaurus*, the adult specimens possess a more slender metatarsal IV than in different-sized *Isasicursor* specimens (see Coria & Salgado, 1996; Cambiaso, 2007; Rozadilla *et al.*, 2016).

**Phalanges** (Figure 13). Pedal toes of *Isasicursor* are represented by several damaged phalanges belonging to several individuals. Available phalanges are relatively stout and short, with a flattened ventral surface and wide and deep collateral ligamental pits.

Phalanx I-1 is represented by its distal end. The distal trochlea is well developed, with low condyles divided by a deep intercondylar groove. The preserved portion of the shaft is slender and the distal trochlea is strongly transversely expanded. Deep and sub-circular collateral pits are present. Phalanx II-1 shows a concave and subtriangular-shaped proximal articular surface. The proximal end narrows distally. The medial surface has several muscular scars near its proximal surface, which are continuous ventrally with a ventral ridge. In ventral view, the proximal portion of this phalanx possesses two collateral ridges, in which the medial one is more robust and ventrally extended. The lateral ridge is shallower and more laterally projected. These ridges are separated by a proximal concavity. The shaft is sub-rectangular in cross-section. Three notably anteroposteriorly short phalanges from digit IV were recovered. We identify these elements as IV-2/IV-3? The proximal surface is weathered, but shows a well-developed dorsoventral ridge separating it symmetrically, as occurs in phalanges of



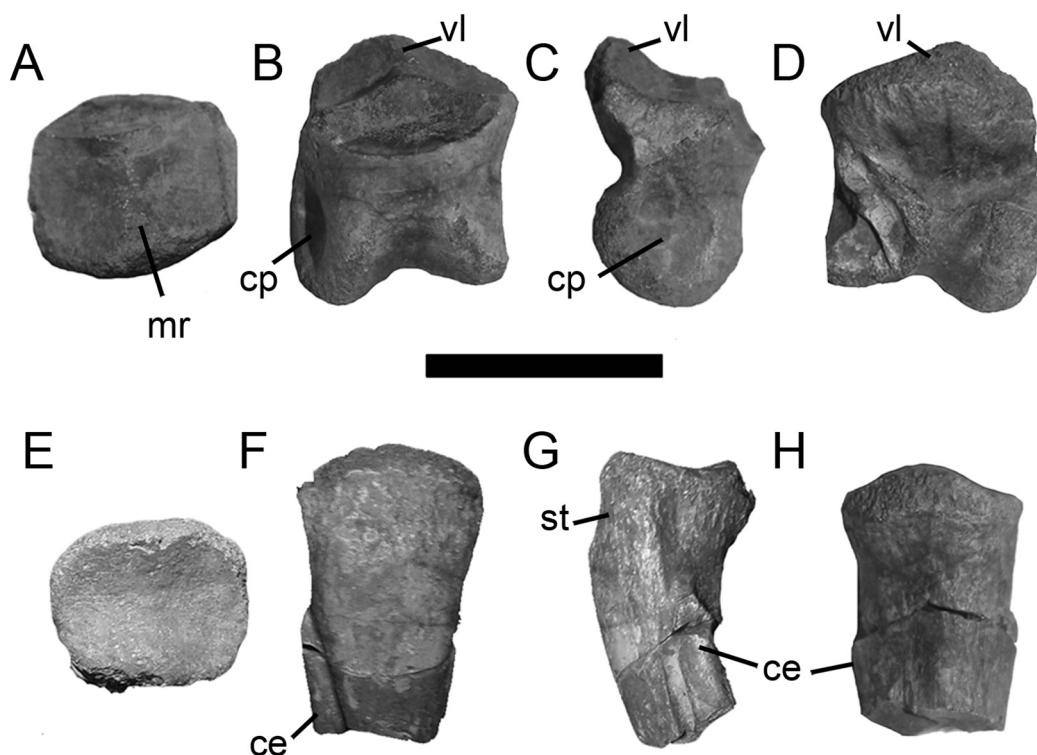


Figure 13. *Isasicursor santacruzensis* gen. et sp. nov. Pedal phalanx IV-2/IV-3? (MPM 21539) in (A) proximal, (B) dorsal, (C) lateral and (D) ventral views. Ungual phalanx (MPM 21540) in (E) proximal, (F) dorsal, (G) lateral and (H) ventral views. **Abbreviations:** ce, collateral expansions; cp, collateral pit; mr, median ridge; st, striations; vl, ventral lip. Scale bar: 3 cm.

the fourth digit in other elasmarians (Rozadilla *et al.*, 2019). The ventral margin of the proximal surface is proximally projected, forming a well-developed posteroventral process. The distal trochlea is well-defined and is proximally delimited by a transversely oriented groove. In the dorsal surface of the bone there is a small extensor pit proximal to the distal articular surface. Distal condyles are well developed and separated by a deep intercondylar groove. Deep collateral pits occur at the sides of each distal condyle. These phalanges are anteroposteriorly short, as occurs in *Talenkauen* and derived iguanodontians (Norman *et al.*, 2004; Norman 2004; Rozadilla *et al.*, 2019), whereas more basal ornithopods and smaller elasmarians show proportionally longer pedal phalanges (Coria & Calvo, 2002; Cambiaso, 2007; Coria *et al.*, 2013).

At least six pedal unguals were recovered. We tentatively identify the most complete elements as unguals of the third digit. The proximal surface is suboval in proximal view, being transversely wider than dorsoventrally deep. This surface is asymmetrically divided by a dorsoventral ridge,

with the lateral articular surface larger than the medial one. The dorsal margin of the articular surface projects proximally into a proximal lip. The blade is dorsoventrally flattened, and slightly medially curved. The dorsal surface is smooth and convex, while the ventral one is flat. The unguual possesses two flattened longitudinal step-like expansions that are dorsally delimited by a longitudinal collateral groove. The distal end of the unguual is notably acute. The unguual is decorated with striations near its proximal and distal ends and on the ventral surface. The flexor tubercle is represented by a poorly developed and transversely expanded bump, decorated with muscle-scar striations. The overall morphology of these phalanges resembles that of other basal ornithopods (e.g., Norman *et al.*, 2004; Canudo *et al.*, 2013), but contrasting with the blunt hoof-like unguals of styracosternan ornithopods (e.g., Norman 2004; Horner *et al.*, 2004).

**Comments.** The morphology of the proximal end of femur and humerus shows synapomorphic features supporting *Isasicursor* belongs to the Elasmaria (e.g., cervical vertebrae laterally

compressed and with a sharp ventral keel; laterally bowed humerus with a rudimentary deltopectoral crest; femur with greater trochanter showing a sigmoidal lateral margin in proximal view; and metatarsal II laterally compressed in proximal view; Rozadilla *et al.*, 2016; 2019). Among elasmarians, *Isasicursor* shows unique features in several elements, especially the proximal end of tibia and sacrum, indicating that it is a clearly distinctive and diagnosable taxon. Its size is similar to that of larger taxa, such as *Sektensaurus*, *Morrosaurus*, *Talenkauen* and *Macrogryphosaurus*. However, the incomplete nature and dissociated preservation of available material precludes the recognition of the relationships of *Isasicursor* within Elasmaria.

The Upper Cretaceous record of basal iguanodontians from Argentina and Antarctica includes the Cenomanian-Turonian *Talenkauen* and *Anabisetia*, and the Campanian *Trinisaura* and *Morrosaurus* from Antarctica (Coria *et al.*, 2013), whereas *Sektensaurus* has a poorly constrained age that ranges from Coniacian to Maastrichtian (Ibircu *et al.*, 2018). Previous reports of Campanian-Maastrichtian basal ornithopods from Northern Patagonia were dismissed (Agnolin *et al.*, 2010). In this way, *Isasicursor* constitutes the first Maastrichtian basal iguanodontian from the southern cone.

Ornithopods are frequently recorded as taphonomic associations composed by several individuals (e.g. Horner & Makela, 1979; Salgado *et al.*, 1997; Andrzejewski *et al.*, 2019). *Isasicursor* is known from several specimens corresponding to different sizes that likely represent different ontogenetic stages, found together in a reduced fossiliferous spot (i.e., a bed roughly 5 m long and 0.50 m thick). This leads to the interpretation that this taxon had a gregarious behavior, at least at the time of their death. In South America the finding of different individuals in close association is common, as demonstrated by *Talenkauen santacruensis*, in which the holotype specimen was found associated with a neonatal tooth (Egerton *et al.*, 2013), and *Anabisetia* and *Gasparinisaura* which are known from several individuals (Salgado *et al.*, 1997; Coria & Calvo, 2002). This may indicate that *Isasicursor* and other elasmarians were gregarious, a condition well-known among their Laurasian counterparts (Andrzejewski *et al.*, 2019).

Hadrosaurs appear in the South American fossil record at the Campanian-Maastrichtian time span, being represented by abundant remains corresponding to different species (Brett-

Surman, 1979; Bonaparte *et al.*, 1984; Juarez-Valieri *et al.*, 2010; Coria *et al.*, 2012; Cruzado-Caballero & Powell, 2017). These dinosaurs were outstanding components of the South American “Allenian vertebrate assemblage” (see Leanza *et al.*, 2004), which includes other herbivorous dinosaurs such as titanosaurs and ankylosaurs (Bonaparte, 1986). In a global context, the record of Campanian-Maastrichtian basal ornithopods suggests a decline in diversity with respect to previous times, whereas hadrosaurs exhibit a notorious “evolutionary explosion” during the end of the Late Cretaceous (Horner *et al.*, 2004). In that time span, basal ornithopods are nearly exclusively represented by the European Rhabdodontidae and the North American Thescelosauridae (Weishampel *et al.*, 2003; Boyd *et al.*, 2009; Ösi *et al.*, 2012; Boyd, 2015). The same seems to be true for South America, where ornithopods are only represented by small to medium sized elasmarians.

The discovery of diverse elasmarian in Campanian-Maastrichtian beds of Patagonia and Antarctica (e.g. *Trinisaura*, *Morrosaurus*, *Sektensaurus*, *Isasicursor*; Ibircu *et al.*, 2010; 2019; Coria *et al.*, 2013; Rozadilla *et al.*, 2016) suggest that some of these basal ornithopods coexisted with hadrosaurs. This, together with the much smaller size of elasmarians, suggests that some kind of niche partitioning occurred among Gondwanan ornithopods (see Brett-Surman, 1979; Case *et al.*, 2000).

Sauropoda Marsh, 1878  
Titanosauriformes Salgado, Calvo & Coria, 1993  
Titanosauria Bonaparte & Coria, 1993  
Genus and species indeterminate

**Referred material:** MPM 21542, three isolated teeth (locality 4).

**Description.** Available teeth lack the tip of the crown and most of the enamel. They are pencil-like as typical for titanosaurs (e.g. García & Cerda, 2010). The enamel is smooth and the teeth are subcircular in cross-section. There is no clear difference in thickness between crown and root.

**Comments.** The general crown outline is similar in the three collected teeth, including a pencil-like general aspect with poor labiolingual compression and lacking mesial and distal carinae. These are features typical of titanosaur dentition (García & Cerda, 2010). Further, the absence of needle-like teeth and lack of strong enamel ornamentation, argue against rebbachisaurid af-

finities for the collected specimens (Salgado *et al.*, 2004). In sum, MPM 21542 is regarded as Titanosauria indet.

?Colossosauria González Riga, Lamanna, Otero, Ortíz, Kellner and Ibiricu, 2019

*Nullotitan glaciaris* gen. et sp. nov.

Figure 14

**Holotype.** MACN-PV 18644 and MPM 21542, the specimen consists of isolated cervical centrum (presumably Cv3; MACN-PV 18644), fragmentary cervical rib shaft, dorsal rib shaft fragments, several caudal vertebrae, fragmentary left scapula, proximal and distal ends of right femur, almost complete right tibia, fibula, and astragalus. The holotype specimen comes from locality 1. It also includes an isolated cervical catalogued with collection number MACN-PV 18644 by J. F. Bonaparte in 1981, and then catalogued as cf. *Antarctosaurus*. Later, Bonaparte *et al.* (2002) interpreted this titanosaur as related with *Aeolosaurus*; Powell (2003), instead, referred the material as to Titanosauridae indet.

**Referred specimens.** The following specimens were collected from other nearby localities, from levels above and below the holotype: 1) MPM 21545, complete humerus, lacking cortex of mid-shaft, partial rib, and vertebra, which were found preserved *ex situ*, about 100 meters far from the place of the holotype specimen. These elements were found relatively high on the slope, indicating they correspond to a different individual than the holotype. Further, the humerus belongs to an individual smaller than the holotype. 2) MPM 21546 (locality 1), isolated and partially preserved distal caudal centra. 3) MPM 21547 (locality 5), sequence of five mid-caudal vertebrae with their respective haemal arches, found articulated *in situ*. This specimen still remains in the field. 4) MPM 21548 (locality 2), isolated complete left tibia. 5) MPM 21549 (locality 2), proximal to mid-caudal centrum, found *ex situ* some meters far from the isolated tibia.

**Stratigraphic provenance.** All aforementioned specimens come from the lower and middle sections of the Chorrillo Formation, being absent from the upper third of this unit. The upper-most record is from locality 4, which was found from beds lying above a thick conglomerate bank. This later specimen is not yet numbered, still remaining in the field. This later specimen still remains unnumbered, waiting to be excavated from the field.

**Diagnosis.** Large titanosaurian sauropod diagnosable on the basis of the following combination of characters (autapomorphies marked with an asterisk\*): 1) anterior caudal centra notably anteroposteriorly short, its transverse diameter duplicating its anteroposterior length; 2) proximal and mid-caudal centra with lateral and ventral surfaces profusely excavated by large blind depressions\*; 3) mid-caudal vertebrae with lateral surface with a tabicate large fossa below the transverse process; 4) centra of all available caudal vertebrae lacking signs of pneumatization; 5) mid-caudals with a deep ventral longitudinal furrow surrounded by two longitudinal thick ridges; 6) fibula with a pronounced sigmoid curvature when viewed anteriorly or posteriorly\*; and 7) distal end of tibia strongly anteroposteriorly compressed and more transversely expanded than in other titanosaurs.

**Etymology.** *Nullotitan*, in honor of geologist Francisco E. Nullo, discoverer of the holotype specimen, and *titan*, powerful giant; the specific name *glaciaris* refers to the majestic Perito Moreno Glacier, observable from the excavation site.

**Remarks.** Fossil remains of sauropods from Chorrillo beds, albeit fragmentary, consist of bones, teeth and egg-shell fragments. Bones that are here referred as to *Nullotitan glaciaris* were found broken and forming different bone accumulations, spread over 100 square meters on a slope surface. All collected elements belong to large titanosaur sauropods, and no overlapping bones exist among these five discrete bone accumulations. The available bones that were found *in situ*, come from a reduced spot of hard green sandstone exposed at the top of the slope; in contrast, the remaining sets of bones were collected down on the slope, and were exposed *ex situ*, but some of them still preserving bits of the green sandstone exposed on the top of the slope. No dermal ossifications have been discovered in Chorrillo beds, either isolated or in association with bone remains.

**Description.** Almost all the collected titanosaur bones belong to large sized individuals. Estimated length of the holotype specimen almost probably surpassed 20 meters long, based on extrapolations of available elements with the fairly complete titanosaurs *Dreadnoughtus* and *Patagotitan* (Lacovara *et al.*, 2014; Carballido *et al.*, 2017).

**Cervical vertebra** (Figure 15). Neck vertebrae are represented just by a single, incomplete centrum, collected by J. F. Bonaparte in 1981

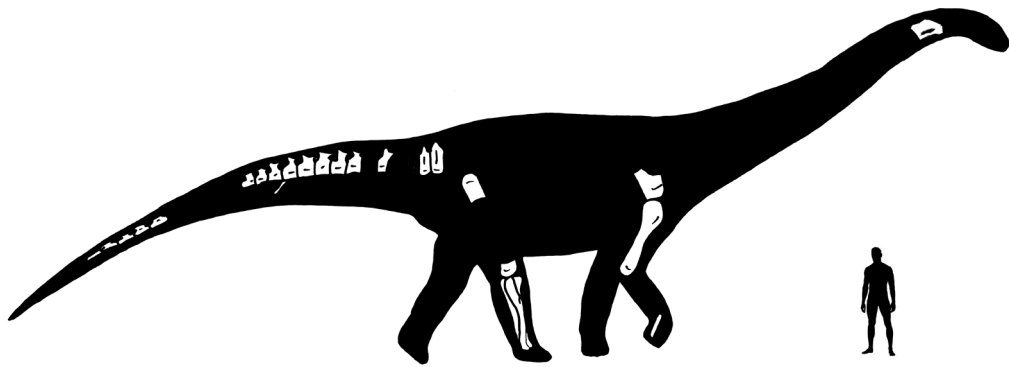


Figure 14. *Nullotitan glaciaris* gen. et sp. nov. Silhouette showing the recovered elements.

(MACN-PV 18644). It is elongate (45cm long) and dorsoventrally low (22cm). The centrum is opisthocoelous. The parapophyses are tabular shaped, dorsoventrally depressed, and anteroposteriorly extended. The sides of the centrum are deeply excavated between parapophysis and diapophysis, bearing a large and elliptical pleurocoel at the bottom of the excavation. In anterior view the vertebra is cross-shaped, due to the development of para- and diapophyses bounding the centrum. There are subhorizontally oriented longitudinal ridges that run from diapophyses to parapophyses. The ventral surface of centrum is flattened and smooth, as is usual in basal sauropods (*Tazoudasaurus*, *Shunosaurus*, *Patagosaurus*), basal macronarians (*Camarasaurus*), and titanosaurs (*Malawisaurus*, *Rapetosaurus*, *Isisaurus*, *Trigonosaurus*, *Neuquensaurus* and *Saltasaurus*), and unlike some basal Titanosauriformes (*Giraffatitan*, *Paluxysaurus* and *Tendaguria*) and diplodocoids (*Apatosaurus*, *Diplodocus* and *Limaysaurus*) where it is transversely concave. This combination of features suggests it may correspond to Cv3. The internal structure is camelate, as occurs in some basal Titanosauriformes (*Giraffatitan*), basal somphospondylians (*Erketu*, *Ligabuesaurus*, *Phuwiangosaurus*), titanosaurs (*Mendozasaurus*, *Malawisaurus*, *Rapetosaurus*, *Isisaurus*, *Trigonosaurus*, *Alamosaurus*, *Neuquensaurus*, *Saltasaurus*) and some diplodocoids (*Apatosaurus* and *Diplodocus*), and unlike other sauropods where inner pneumaticity of the cervical centrum is absent (e.g., *Patagosaurus*) or present but with several small and complex internal cavities (*Camarasaurus*, *Limaysaurus*). **Caudal vertebrae** (Figures 16-18). The holotype of *Nullotitan glaciaris* includes different caudal elements, corresponding to proximal and middle section of the tails. Most of them are only

represented by incomplete centra, with limited information regarding transverse processes and neural arches. Location of each of these isolated elements along the caudal series is tentative and based on the ratio between anteroposterior length vs. transverse width of centra, contour of centra (i.e., proportional development of primary and secondary lateral surfaces), presence and relative development of articular surfaces for haemal arches, degree of convexity of the posterior articulation of centrum, and profusion and size of blind perforations on lateral and ventral surfaces. In contrast with cervical elements, all available caudals are apneumatic, and the internal tissue is compact.

Proximal caudals characterize for the following combination of features: 1) anteroposteriorly short centra; 2) centrum transversely wide and elliptical-shaped in anterior view; 3) lateral and ventral surfaces profusely excavated by large, blind perforations; 4) centrum lateral surface (below transverse process) steeply inclined ventrally and medially; 5) transverse processes dorsoventrally deep and anteroposteriorly compressed. Mid-caudals exhibit: 1) squared-shaped centra in side view; 2) ball-shaped distal articular surface; 3) centra with a deep ventral longitudinal furrow; 4) blind excavations reduced in size, but still abundant in number; 5) transverse processes reduced in size, cone-shaped, and located at centrum mid-height. Finally, distal caudals exhibit: 1) relatively elongate centra; and 2) posterior articular surface cone-shaped and transversely wide in posterior view.

Regarding the distribution among Titanosauria of the blind, apneumatic excavations which do not enter inside the centrum, there are some cases in which similar depressions exist (see Martinelli *et al.*, 2011). For ex-

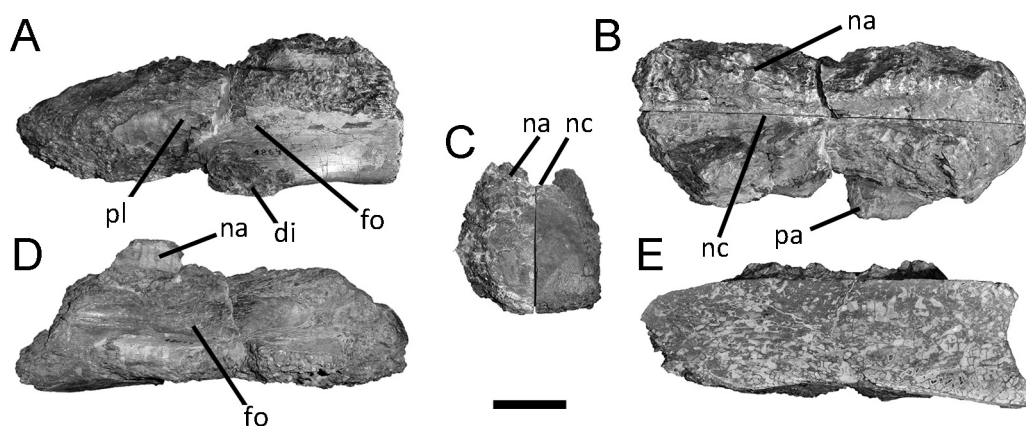


Figure 15. *Nullotitan glaciarius* gen. et sp. nov. Cervical vertebra (MACN Pv 18644) in left lateral (A), dorsal (B), posterior (C), right lateral (D), and longitudinal section (E) views. **Abbreviations:** di, diapophysis; fo, fossa; na, neural arch; nc, neural canal; pa, parapophysis; pl, pleurocoele. Scale bar: 10 cm.

ample, in *Drusilasaura* the ventral surface of Cd4? exhibits a pair of large elliptical openings which were considered autapomorphic for this species (Navarrete *et al.*, 2011). Similarly, Salgado (1996) reported on caudals 2 through 4 of *Pellegrinisaurus* the presence of small holes on each side of the centrum. However; in *Nullotitan* the excavations are larger than in other titanosaurs, and much more abundant.

The following description of caudal elements positions the ventral surface of centrum on the horizontal plane. The dorsoventral axis of centrum (especially in proximal caudals) is vertically positioned, and forming a right angle with the ventral surface of centrum. Thus, the floor of the neural canal results inclined ventrodistally (in side view) with respect to ventral surface of centrum. This means that the caudal series, when reconstructed articulated in line with the sacrum, show the neural canal inclined, accompanying the dorsoventral lowering of vertebrae.

**Caudal 1<sup>st</sup>?** (Figure 16). It is represented by most of its centrum and the base of the neural arch. The later one occupies a central to cranial position in lateral view, similar to other titanosaurs (e.g., *Patagotitan*; Carballido *et al.*, 2017). The centrum is 40 cm in transverse width, 34 cm in dorsoventral depth, and 22 cm in anteroposterior length (but probably 25 cm when complete). Transverse processes are broken at their bases but revealing a prominent vertical structure. They are dorsoventrally deep, extending over the dorsal half of the lateral centrum surface. In side view it is seen that the transverse process occupies a central position on the lateral surface of the vertebra. The anterior articular surface is

surrounded by a well-developed rim. The dorsal part of transverse processes extends dorsally, well above level of neural arch. Transverse processes are cranially concave and caudally convex. On its cranial surface, the transverse process bears a pair of large, eye-shaped, blind excavations. On the surface behind the transverse process, there is only one of these excavations. Below the transverse processes, the centrum becomes strongly constricted due to the ventromedial slope of the lateral surface. Notably, this lateroventral surface of the centrum exhibits large and blind, randomly distributed perforations, consisting in fossae separated by ridges. The lateroventral surface of centrum forms an inflexion with the flattened ventral surface. The ventral surface of the centrum is perforated by isolated longitudinally oriented, blind depressions, which develop on the posterior half of the bone.

The cranial articular surface is deeply concave. The distal articular cone is eroded, so its caudal projection is difficult to discern; however, it seems to have been hemispheric, as usual among titanosaurs.

The neural canal is oval-shaped, with its floor concave that widens posteriorly (in dorsal view). The later region is highly vascularized, as suggested by abundant foramina. On the posterior surface of the base of neural arch, there is a median fossa immediately above the neural canal. No facets for haemal arches are present.

**Caudal 2<sup>nd</sup>?** (Figure 17). It is represented by the dorsal half of centrum and the badly preserved bases of the neural arch, including the base of the right transverse process. As in Cd1st, the centrum is anteroposteriorly very short, but

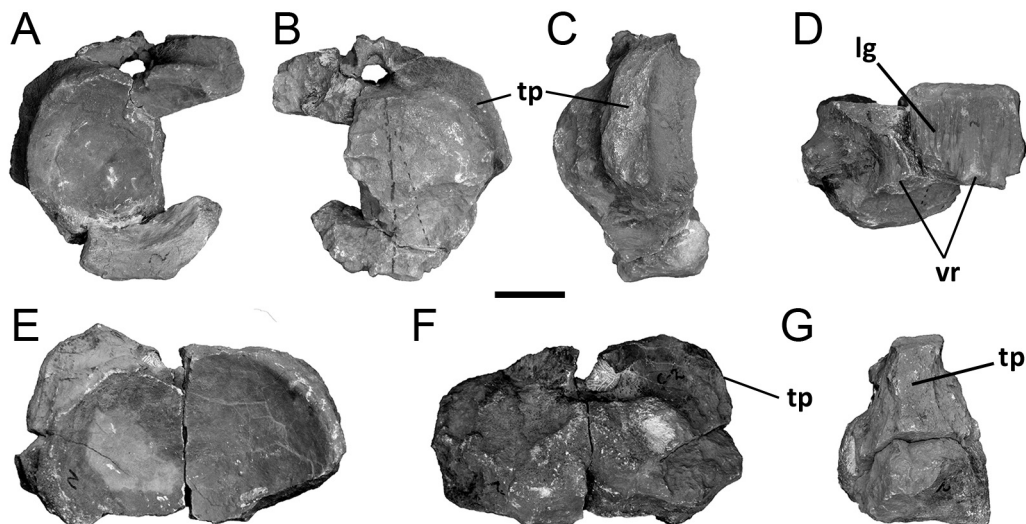


Figure 16. *Nullotitan glaciaris* gen. et sp. nov. Caudal vertebrae ?1st (A-D) and ?2nd (E-G) (MPM 21542) in anterior (A, E), posterior (B, F), right lateral (C, G), and ventral (D) views. **Abbreviations:** **lg**, longitudinal groove; **tp**, transverse process. Scale bar: 10 cm.

transversely wide. The transverse processes are eroded, but the preserved portions indicate they were dorsoventrally deep. However, they are shallower than in Cd1st, due to the lower margin in a higher position on the lateral surface. The cranial and caudal surfaces of the transverse process are concave-convex, as in Cd1st. Regarding the blind depressions, they are similar to those of Cd1st. The cranial articular surface seems more concave than in Cd1st. The floor of the neural canal is fan-shaped in dorsal view, being transversely expanded towards the rear.

**Caudal 4<sup>th</sup> or 5<sup>th</sup>?** (Figure 18). It is represented by most of the centrum and base of neural arch and base of left prezygapophysis. The centrum is dorsoventrally and transversely smaller than the caudals previously described, but it is anteroposteriorly as long as these centra. The lateral surface of centrum orientates lateroventrally. The base of right transverse process is sub-conical, and it locates immediately below level of neural canal. Due to the higher position of transverse process, the lateral surface of centrum is more developed than in more proximal caudals. In sharp difference from more proximal caudals, the base of the transverse process reaches the anterior margin of centrum, thus the later results devoid of a lateral surface in front the transverse process. Regarding the blind depressions, they are similar to those of more proximal caudals, being more developed towards the posterior margin of centrum. Blind depressions on the ventral sur-

face are more elongate and deeper than those of the lateral surface. The ventral surface of centrum is almost flat.

The base of prezygapophysis indicates that it was anterodorsally projected. The base of the spinoprezygapophyseal lamina, the only portion preserved, is nearly horizontal and sharp. On the internal surface of neural arch, behind the base of prezygapophysis, and above the intraprezygapophyseal lamina (TPRL), there is an elongate fossa. The floor of neural canal is flat; it widens posteriorly as in the remaining proximal caudals. Due to poor preservation, there is no evidence of facets for articulation with the haemal arches.

**Mid-caudals** (Figure 18). Possible caudals 11 and 12 are preserved. Because it is not easy to elucidate the respective position of these vertebrae, we describe them together. They are approximately half the size of the available proximal caudals. The base of the neural arch occupies most of the anteroposterior length of centrum (discounting the hemispherical posterior articular surface). The floor of the neural canal exhibits foramina and longitudinal grooves on its posterior half. The centrum is damaged along the anterior articular rim. The caudal surface is hemispherical, but slightly eccentric in side view, with the maximum convexity on the dorsal half. In distal view, the contour of the articular surface is sub-quadrangular, with the major axis vertically oriented. The lateral surface has a large fossa below the transverse process, as well

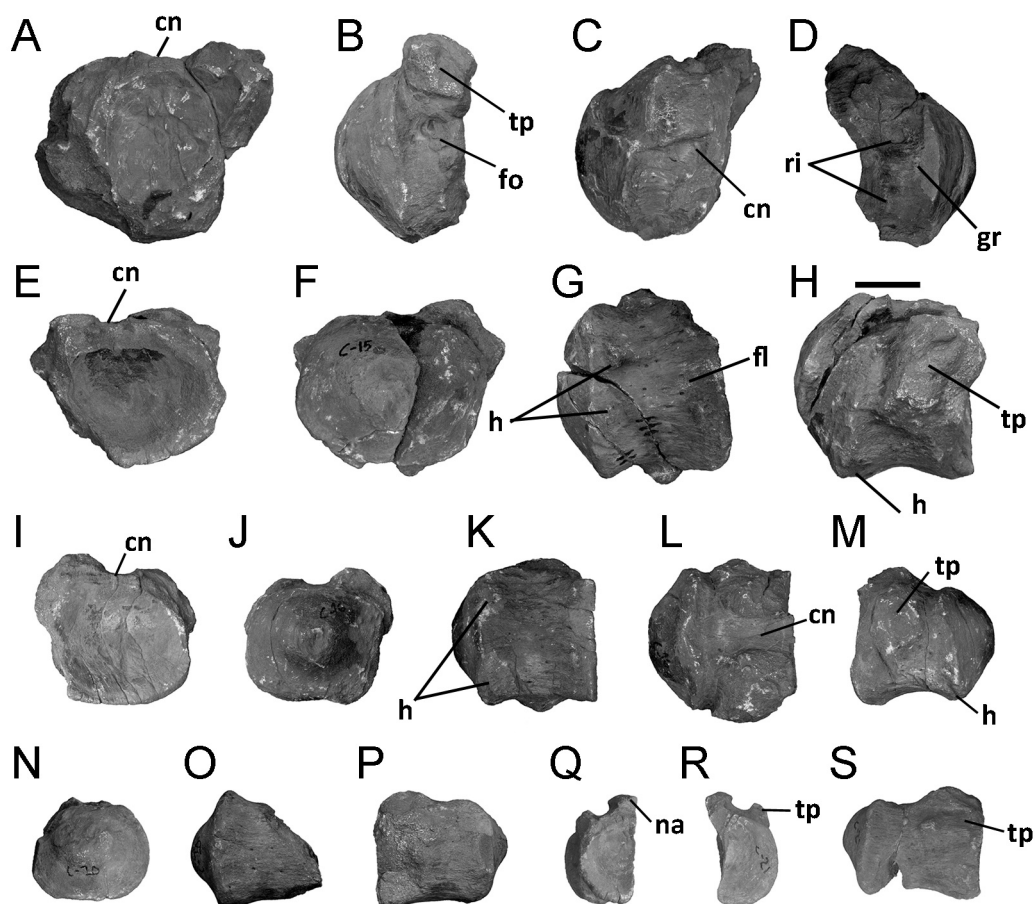


Figure 17. *Nullotitan glaciaris* gen. et sp. nov. Caudal vertebrae ?11th (A-D), ?15th (E-H), ?16th (I-M), ?20th (N-Q), and ?21th (R, S) (MPM 21542). The elements are figured in anterior (A, E, I, Q, R), lateral (B, H, M, P, S), dorsal (C, L), ventral (D, G, K, O), posterior (F, J, N) views. **Abbreviations:** cn, neural canal; tp, transverse process; fo, fossa; h, haemal facet; gr, groove; na, neural arch. Scale bar: 10 cm.

as deep blind depressions, which are located on the central region of the centra.

The ventral surface exhibits a deeply excavated central depression, flanked by strong longitudinal ridges. The inner side of these ridges exhibits randomly distributed, and longitudinally elongate foramina, which are much smaller than the blind fossae described for the proximal caudals. Facets for articulation with the haemal arches are present. Transverse processes are located at level of neural canal, and the preserved bases suggest they were robust.

**Caudals 15<sup>th</sup> and 16<sup>th</sup>** (Figure 18). They are quadrangular in caudal view, being wider than tall, different from the mid-caudals described above. The posterior surface is less spherical than in previous caudals, and the spherical articulation is placed on the center of the surface

and with a flat surface surrounding it.

In caudal 15, the articulation for the haemal arches, placed on the posteroventral border of centrum, are closer to each other (5 cm) than in caudal 16th (6-7 cm); the primary lateral surfaces (Salgado & García, 2002) are dorsoventrally oriented and dorsoventrally deeper (7cm) than in caudal 16th (4cm), where they are ventrally oriented. According to the interpretation of Salgado and García (2002), this would indicate that the *M. caudofemoralis* extended distally as much as caudal 16th.

**Distal caudal centra** (Figure 18). No complete distal centra are available. The centra are procoelous, and notably dorsoventrally compressed. The anterior articular surface is subcircular in contour. The posterior articular surface is kidney-shaped and shows an eccentric distal cone,

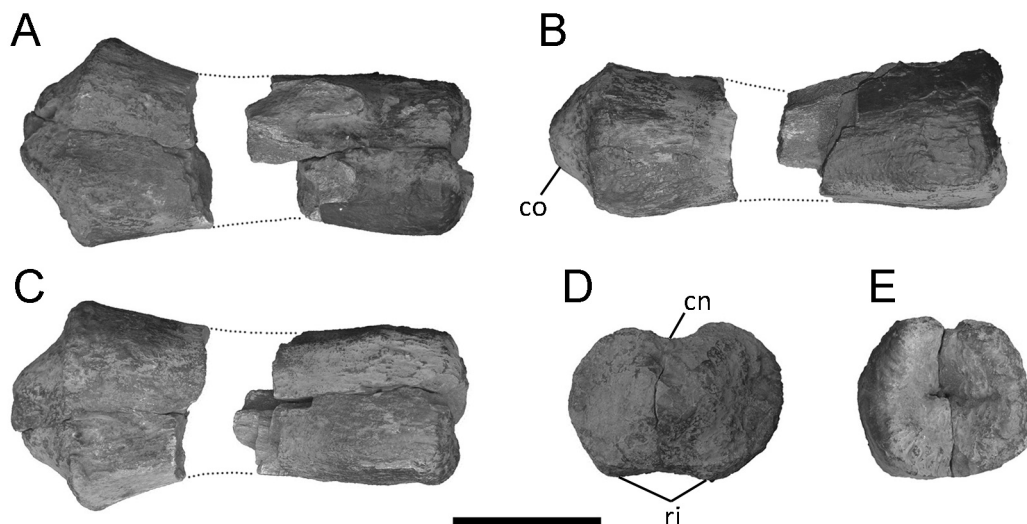


Figure 18. *Nullotitan glaciaris* gen. et sp. nov. Distal caudal vertebrae (MPM 21542) in dorsal (A), lateral (B), ventral (C), posterior (D), anterior (E) views. **Abbreviations:** cn, neural canal; co, articular cone; ri, ridge. Scale bar: 10 cm.

dorsally displaced. At least in caudal 19th, the primary lateral surfaces are constrained to the ventral face of centrum.

**Haemal arches.** Haemal arches are represented by two single elements. They are rod-shaped and proximally opened. In lateral view they show a gentle sigmoid curvature.

**Scapula** (Figure 19). The central portion of a left scapula is preserved (the following description assumes the long axis of scapula as vertically oriented). This portion of the scapula lacks both glenoidal and acromial regions. It is a plate-like bone, medially concave and laterally convex. The most notable feature preserved on this fragmentary scapula is a medial tubercle with a muscle scar located dorsal to the level of the acromial process and close to the anterior margin of the bone. The tubercle is triangular-shaped, with the apex oriented ventrally. Such prominence has been also reported in other titanosauriforms (e.g., *Wintonotitan*, *Alamosaurus*; D'Emic, 2012; Poropat *et al.*, 2015). A ventromedial process is observed on the ventral margin of the scapula, as reported in *Ligabuesaurus* (Bonaparte *et al.*, 2006).

**Humerus** (Figure 20). A fairly complete right humerus (MPM 21545) is available. It measures 114 cm in total length, 44 cm in maximum proximal width, and 40 cm of maximum distal width (mid-shaft is damaged, and its reconstructed maximum width is estimated in 25 cm). The robust index (RI; maximum distal width/total length) of *Nullotitan*

is estimated in 0.28, being comparable to that of *Epachthosaurus* (RI=0.27), *Mendozasaurus*, (R=0.24; Martínez *et al.*, 2004; Mannion & Otero, 2012), *Patagotitan* (RI estimated=0.28; Carballido *et al.*, 2017), and *Notocolossus* (RI =0.28; González Riga *et al.*, 2016). These humeral proportions differ from the robust humeri (RI more than 0.28) of *Dreadnoughtus* (RI=0.33), *Neuquensaurus* (RI=0.35, Salgado *et al.*, 2005; Otero, 2010), *Saltasaurus* (RI=0.36; Powell, 2003), and *Opisthocoelicaudia* (RI=0.41; Borsuk-Bialynicka, 1977). Bonaparte *et al.* (2002) considered the humerus of *Nullotitan* similar to *Aeolosaurus rionegrinus* (Powell, 2003) in their slender proportions, but the RI of the latter one can not calculated because the humerus is incomplete.

The humeral deltopectoral crest of *Nullotitan* is markedly expanded distally as it occurs in practically all sauropods. In *Nullotitan*, the greater anterior expansion of the lower portion of the deltopectoral crest is placed at nearly 25% of the total length of the bone beginning from the top. This means a shorter deltopectoral crest, with values more similar to those of basal titanosaurs such as *Paralititan* and *Epachthosaurus* the ratio is nearly 31% (Smith *et al.*, 2001; Martínez *et al.*, 2004). In other forms, in turn, the deltopectoral crest is more distally extended, such as in *Elaltitan* (36%; Mannion & Otero, 2012), *Dreadnoughtus* (37%), *Patagotitan* (33.6%; Carballido *et al.*, 2017), *Narambuenatitan* and *Mendozasaurus*



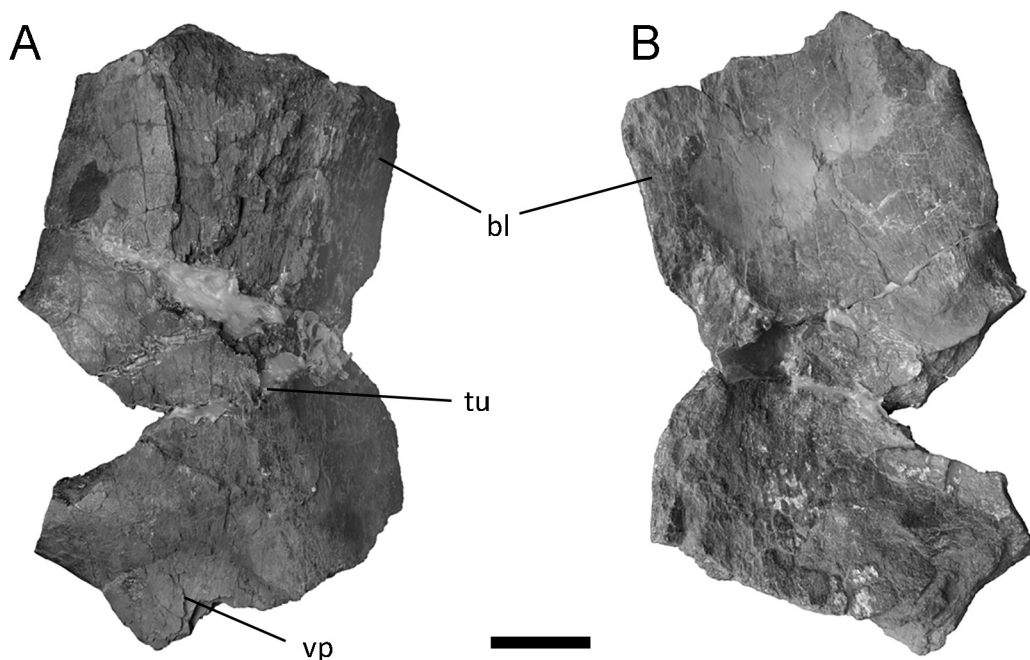


Figure 19. *Nullotitan glaciaris* gen. et sp. nov. Left scapula (MPM 21542) in lateral (A), and medial (B) views. **Abbreviations:** **bl**, blade; **tu**, tubercle; **vp**, ventral process. Scale bar: 10 cm.

(35%; Filippi et al., 2011; González Riga et al., 2018).

**Femur** (Figure 21). The femoral head and neck are poorly preserved. They seem to be proximomedially elongate, describing an obtuse angle with the longitudinal axis of femur, a condition typical for titanosauriforms (González Riga et al., 2019).

The femur shaft shows a minimum width of about 44 cm, and the distal end of the right femur is 53 cm in maximum transverse diameter, with globe-shaped, sub-equal articular condyles, 28 cm in anteroposterior diameter. They are separated through a marked anteroposterior constriction, visible in distal aspect. This separation is also evident on the cranial surface, which exhibits a shallow distal concavity. In correlation, the cranial surface of distal femur forms a wide, shallow but deeply grooved, extensor sulcus. Articular condyles are not extended on the cranial surface of the distal end. Subequal distal condyles may indicate that *Nullotitan* is close to the lithostrotian clade (Upchurch et al., 2004), but the lack of dorsomedial beveling of the distal condyles onto the cranial side of the shaft excludes it from Saltasaurinae (Wilson, 2002). The medial surface of distal femur is flat but strongly decorated by proximodistally oriented ridges almost probably corresponding with the

insertion of adductor muscles. The tibial condyle is more conical-shaped (in cranial view) than the more rounded lateral condyle. Also, the later one is carved by deep sulci, giving a brain-like aspect, different from the tibial condyle with a less marked decoration. Both the tibiofibular crest and the posterior projection of the medial condyle are broken at their bases. The distal end of femur described above resembles that of *Mendozasaurus*. Notably, the femur shaft (immediately proximal to the distal condyles) is highly compressed anteroposteriorly (10cm).

**Tibia** (Figure 22). The tibia of the holotype (MPM 21542) consists of a right element, broken and slightly distorted. It measures 105 cm in total length, and 44 cm in maximum distal width. It exhibits remarkable features interpreted as diagnostic for the species (see below). A second tibia (MPM 21548), discovered in isolation, is tentatively referred as to the same genus and species, although its features do not completely agree with those of the holotype.

The tibia of *Nullotitan* is robust. As in other titanosaurs, the distal end of tibia of *Nullotitan* is transversely expanded to twice midshaft breadth (Ullman & Lacovara, 2016) and the proximal end is anteroposteriorly expanded. However, the distal end of tibia of *Nullotitan* is strongly anteroposterior compressed and more trans-

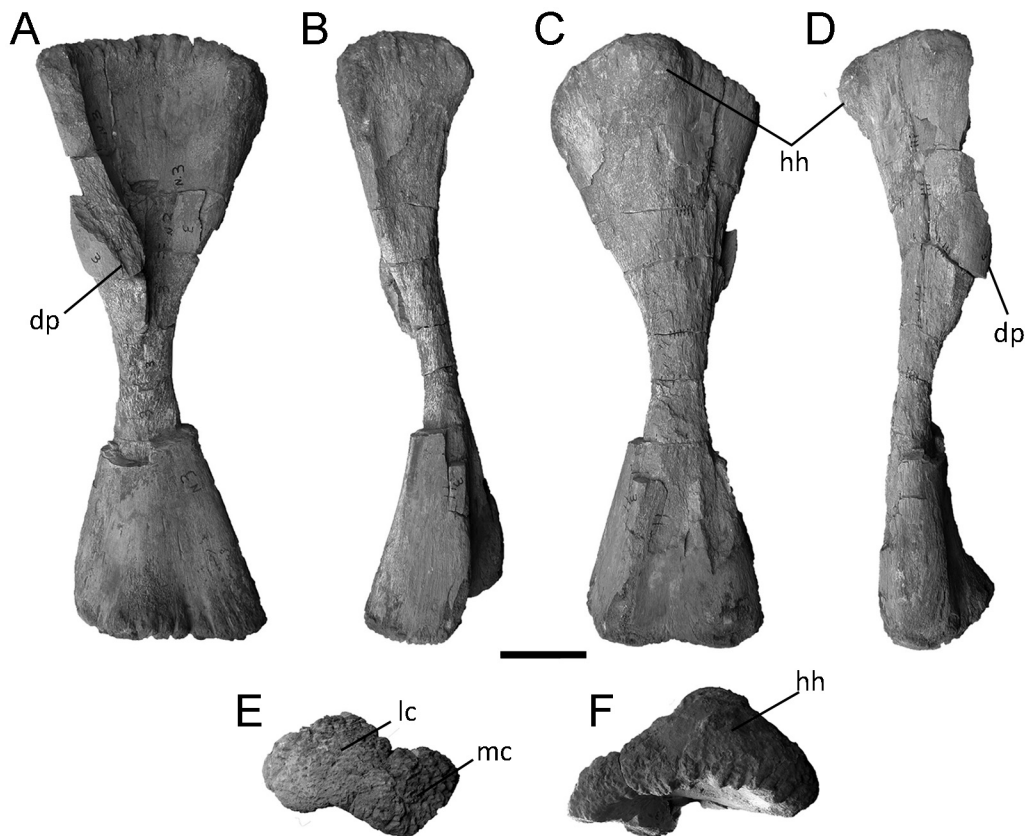


Figure 20. *Nullotitan glaciensis* gen. et sp. nov. Right humerus (MPM 21546) in anterior (A), lateral (B), posterior (C), medial (D), distal (E), and proximal (F) views. **Abbreviations:** **dp**, deltopectoral crest; **hh**, humeral head; **lc**, lateral condyle; **mc**, medial condyle. Scale bar: 10 cm.

versely expanded than in other titanosaurs (e.g., *Mendozasaurus*; González Riga *et al.*, 2019), suggesting that may constitute an autapomorphic trait of *Nullotitan*.

**Fibula** (Figure 23). A nearly complete right fibula is available. The fibula of *Nullotitan* measures 109 cm long, being a bit longer than the fibula of *Dreadnoughtus* (103 cm; Lacovara *et al.*, 2014). The fibula of *Nullotitan* is robust (RI=0.4), more than *Neuquensaurus* (RI=0.172-0.232; Otero, 2010), but less than in *Uberabatitan* (0.6).

The anterior margin of the bone is straight, whereas the posterior one is strongly sigmoid, much more than in other titanosaurs (for instance, *Uberabatitan*, *Mendozasaurus*, *Elaltitan*; Salgado & Carvalho, 2008; Silva Junior *et al.*, 2019; González Riga *et al.*, 2018; Mannion & Otero, 2012). The fibular shaft is also strongly sigmoidal in posterior view, with the lateral surface markedly convex at level of the biceps tubercle (Figure 23C). In general terms, the fibula is similar to that of *Dreadnoughtus* (Ullman &

Lacovara, 2016). The sigmoid curve present in both *Nullotitan* and *Dreadnoughtus* is exaggerated in lateral view, for the notable anteroposterior expansion of both proximal and distal ends of the bone. In lateral view, the proximal margin of the fibula is nearly horizontally oriented, as occurs in *Dreadnoughtus* (Ullman & Lacovara, 2016), *Mendozasaurus* (González Riga *et al.*, 2018), *Saltasaurus* (Powell, 2003), and *Neuquensaurus* (Otero, 2010), and unlike other titanosaurs such as *Uberabatitan* (Salgado & Carvalho, 2008; Silva Junior *et al.*, 2019) in which it is posteriorly inclined. On the lateral surface, there is the tubercle for the *M. iliofibularis*.

**Astragalus** (Figure 24). As usual among sauropods, the astragalus is conical-shaped, with an excavated lateral surface for articulation with the calcaneum and the fibula, and a pointed end oriented medially, which is partially broken and coincident with the medial expansion of the distal end of tibia. Apparently, the medial expansion of astragalus was more developed in *Nullotitan*

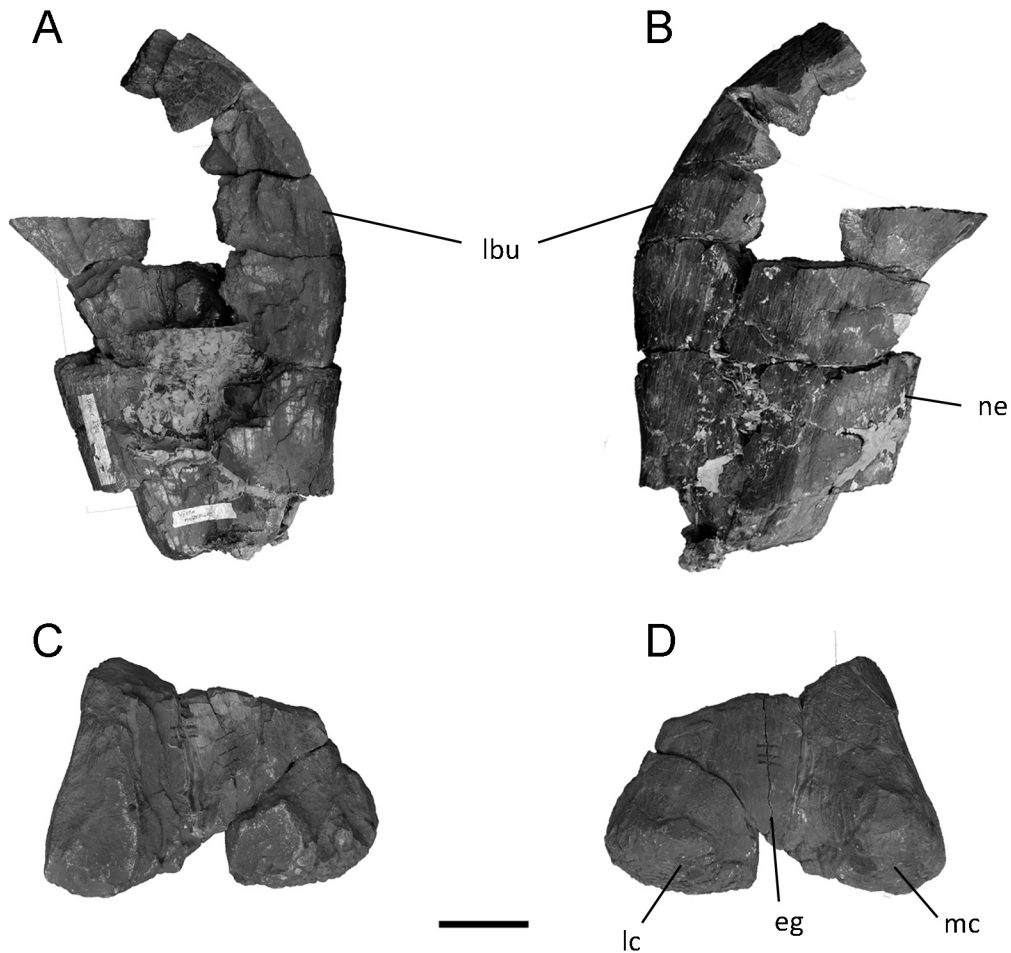


Figure 21. *Nullotitan glaciaris* gen. et sp. nov. Proximal (A-B) and distal (C-D) ends of right femur (MPM 21542) in anterior (A, C), and posterior (B, D) views. **Abbreviations:** eg, extensor groove; lc, lateral condyle; lbu, lateral bump; mc, medial condyle; ne, neck. Scale bar: 10 cm.

than in *Uberabatitan* (Salgado & Carvalho, 2008; Silva Junior *et al.*, 2019). The ascending process of the astragalus is low.

**Comparisons.** Because of the paucity of the available materials, the phylogenetic position of *Nullotitan* among titanosaurs is difficult to discern. This taxon exhibits features diagnosing Titanosauria, as well as characteristics of less inclusive clades such as Lithostrotia, Colossosauria, and Lognkosauria (González Riga *et al.*, 2019). In addition, *Nullotitan* lacks features diagnosing the derived titanosaur clades Saltosauridae and Aeolosaurini.

*Nullotitan* exhibits the following titanosaurian features: caudal vertebrae procoelous, with neural arches located on the anterior half of centrum; femur medially bowed on its proximal end; presence of a prominent lateral bulge distal

to the greater trochanter; and femoral shaft anteroposteriorly compressed (Salgado *et al.*, 1997; Mannion *et al.*, 2013; González Riga *et al.*, 2019). Furthermore, presence of subequal-sized condyles on distal femur may suggest lithostrotian affinities for *Nullotitan* (Upchurch *et al.*, 2004). Characters of Colossosauria present in *Nullotitan* are: deltopectoral mediolateral thickness of anterior attachment surface with distal half mediolaterally expanded relative to proximal half and a value near 0.15 of minimum mediolateral width vs. proximodistal length (González Riga *et al.*, 2019).

Proximal caudals of *Nullotitan* are notably anteroposteriorly short, showing awl-like transverse processes and a slightly convex posterior articular surface. This combination of traits is also shared with most lognkosaurians (González

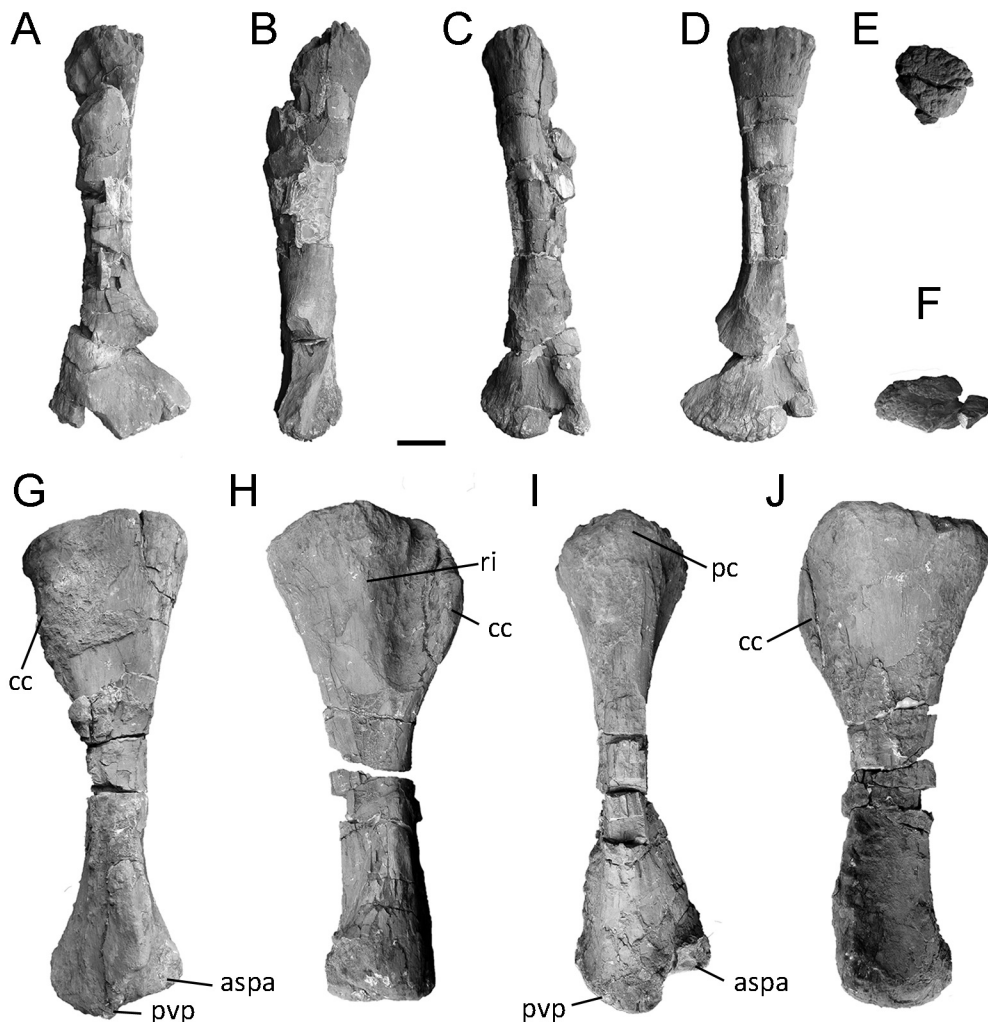


Figure 22. *Nullotitan glaciensis* gen. et sp. nov. Tibia (A-F) right tibia of MPM 21542 specimen and (G-J) left tibia of MPM 21548 specimen. The elements are figured in anterior (A, G), medial (B, H), posterior (C, I), lateral (D, J), proximal (E) and distal (F) views. **Abbreviations:** aspa, ascending process for astragalus; cc, cnemial crest; pc, proximal condyle; pvp, posteroventral process; ri, ridge. Scale bar: 10 cm.

Riga et al., 2019).

As follows, we compare *Nullotitan* with other gigantic members of the colossosaurian clade Lognkosauria (sensu Carballido et al., 2017; González Riga et al., 2019). This clade is actually composed by the genera *Argentinosaurus*, *Futalognkosaurus*, *Mendozasaurus*, *Notocolossus*, *Patagotitan*, *Puertasaurus*, *Dreadnoughtus* and *Drusilasaura* (Carballido et al., 2017; González Riga et al., 2018, 2019). *Patagotitan*, *Futalognkosaurus*, and *Notocolossus* show the first caudal transverse processes with a notably dorsoventrally narrow base, a condition not observed in *Nullotitan* (Carballido et al.,

2017). In addition, *Patagotitan* shows a ventral pocket at the base of centrum, which is absent in *Nullotitan*. *Notocolossus*, *Futalognkosaurus*, *Dreadnoughtus* and *Puertasaurus* show vertebrae that are proportionally anteroposteriorly longer than *Nullotitan*, with a distal articular surface more spherical. Also, in *Notocolossus* and *Futalognkosaurus* the transverse processes are more dorsally located on the sides of centra (Lacovara et al., 2014). As occurs in *Patagotitan*, the mid-caudals show a large fossa below transverse process (Carballido et al., 2017). However, in *Nullotitan* this fossa is tabicated by an obliquely oriented ridge of bone.

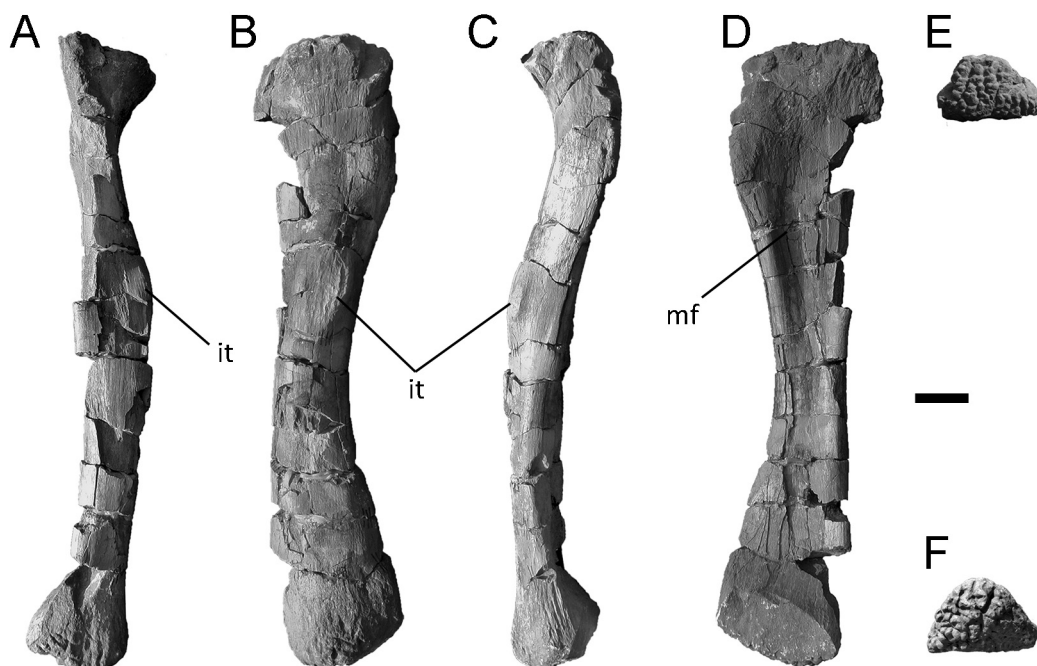


Figure 23. *Nullotitan glaciaris* gen. et sp. nov. Right fibula (MPM 21542) in anterior (A), lateral (B), posterior (C), medial (D), proximal (E), and distal (F) views. **Abbreviations:** *it*, iliofibularistubercle; *mf*, medial fossa. Scale bar 10 cm.

As already said, proximal caudal centra distinguish for the presence of profuse blind excavations. These are considered autapomorphic for the new species. Small vascular foramina were reported in caudal vertebrae of some titanosaurs (Mannion & Calvo, 2011; Mannion et al., 2013), but are much smaller than in *Nullotitan*. The excavations in caudals of *Nullotitan* are elongate and subparallel to the main axis of the tail. On proximal caudals, the excavations are relatively large (i.e., 5 cm long in a centrum 22 cm long), but are reduced or absent in more distal caudals. Such excavations are randomly distributed over centrum surface, being different from the symmetrical ventral perforations present in some titanosaurs, such as *Pellegrinisaurus* and *Drusilasaura* (Salgado, 1996; Navarrete et al., 2011). Clearly, the perforations do not invade the vertebral centrum. Such pattern of blind randomly distributed excavations, resemble the excavations observed on the nuchal crest of felids (Duckler, 1997), which are produced by muscular activity, particularly overstretched muscles that create depressions (due to bone necrosis) at attachment sites. In humans, this pattern is evidenced in athletic individuals who place high strain on selected active muscles and have skeletal responses at attachment sites in consequence (Duckler, 1997). Our best guess is that such large

and elliptical-shaped blind excavations on the proximal caudals of *Nullotitan* (as well as other titanosaurs) may have anchored thick tendons of hypaxial and epaxial muscles. If this interpretation proves to be correct, then it represents a different anatomical adaptation for tail support and movement control than that known in other dinosaurs.

Humeral proportions of *Nullotitan* (RI=0.28) are more gracile in comparison with the robust humerus exhibited by *Dreadnoughtus* (RI=0.33), *Elaltitan* and *Argyrosaurus* (Huene, 1929; Powell, 2003; Mannion & Otero, 2012; Lacovara et al., 2014; González Riga et al., 2019). Although *Nullotitan* exhibits a RI similar to that of *Notocolossus*, this genus exhibits a humerus with markedly asymmetrical proximal margin in anterior view (nearly straight laterally but strongly expanded and rounded proximomedially) (González Riga et al., 2019), features absent in *Nullotitan*.

The proximal end of the femur is strongly medially bent in *Nullotitan*, forming a large convex surface that is not present in *Dreadnoughtus*, *Mendozasaurus*, and *Patagotitan*. In respect to robustness of femur, *Nullotitan* resembles more *Dreadnoughtus* than *Patagotitan* and *Mendozasaurus*, which show a more elongate and narrow femur. The fibula of *Nullotitan* is

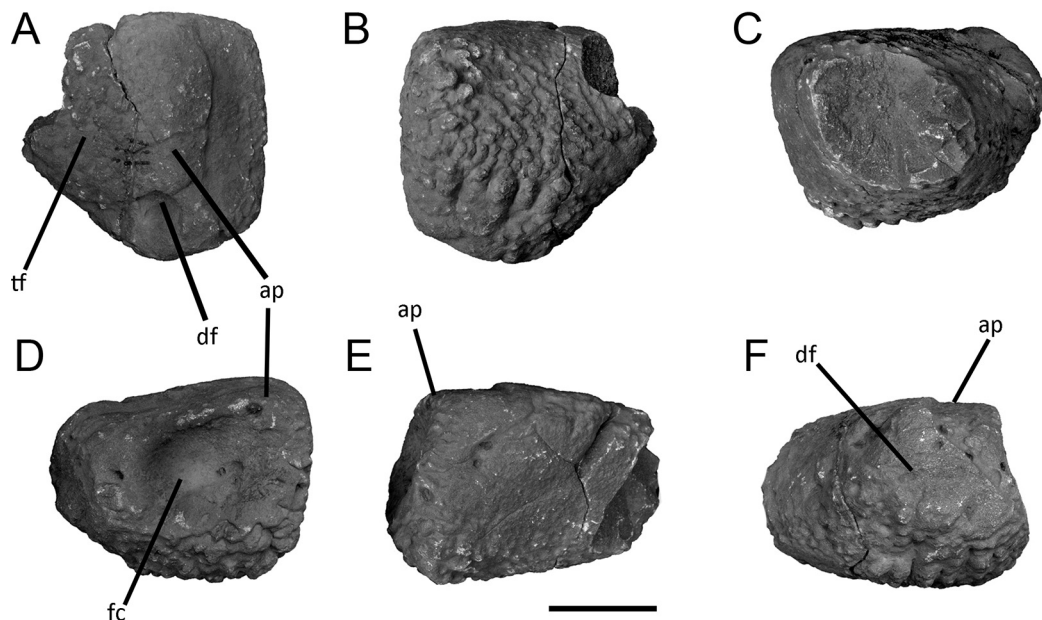


Figure 24. *Nullotitan glaciaris* gen. et sp. nov. Right astragalus (MPM 21542) in dorsal (A), ventral (B), anterior (C), lateral (D), posterior (E), and medial (F) views. **Abbreviations:** ap, ascending process; df, dorsal fossa; fc, calcaneum facet; tf, tibial facet. Scale bar: 10 cm.

different from that of other large titanosaurs, including *Dreadnoughtus* and *Argentinosaurus* (Bonaparte & Coria, 1993), in being strongly sigmoidal in both anterior and lateral views.

In the case of *Drusilasaura*, the few overlapping elements preclude proper comparisons with *Nullotitan*. Both taxa share proximal caudals strongly anteroposteriorly compressed with awl-like transverse processes that extend towards the vertebral centrum, a longitudinal ventral groove delimited by thick ridges, and distal caudals dorsoventrally compressed (Navarrete *et al.*, 2011). However, *Drusilasaura* apomorphically shows two large ventral foramina that are absent in *Nullotitan*. Further, *Drusilasaura* lacks the blind fossa present along the lateral surface of caudal vertebrae of *Nullotitan*.

*Nullotitan* differs from saltasaurids (*sensu* González-Riga *et al.*, 2019) in having proximal caudals anteroposteriorly short, with posterior articular surfaces slightly convex, and apneumatic centra. These are plesiomorphic traits indicating that *Nullotitan* is not related with saltasaurids, which usually have caudal vertebrae with dorsoventrally depressed and strongly procoelous centra, and highly pneumatic centra and neural arches (e.g., Powell, 1993; Salgado *et al.*, 1997; Bonaparte *et al.*, 2000; Salgado & Azpelicueta, 2000; Rose, 2007; Taylor, 2009; González Riga

*et al.*, 2019). In this regard, the ventral aspect of the caudal vertebrae of *Nullotitan* is unique in that the proximal and distal caudals show a relatively flat ventral surface of centrum, whereas mid-caudals exhibit a deep longitudinal furrow surrounded by two thickened ridges. Presence of deep ventral furrow in *Nullotitan* should not be confused with the deep pneumatic excavations present in derived titanosaurs such as *Saltasaurus* and *Rocasaurus* (Powell, 2003; Salgado & Azpelicueta, 2000).

Besides, caudal vertebrae of *Nullotitan* differs from the caudal type reported for aeolosaurines (*i.e.*, *Aeolosaurus patagonicus* and *A. colhuehuapensis*; Powell, 2003; Casal *et al.*, 2007; Martinelli *et al.*, 2011) because in the latter ones the neural arches are strongly inclined anteriorly and have a more developed procoelous condition. Thus, the sum of features of the caudal vertebrae of *Nullotitan* clearly distinguishes it from other Late Cretaceous derived titanosaurs from South America.

In sum, although the scarcity of currently available materials of *Nullotitan* precludes a clear taxonomic referral, its anatomical details (mainly from the caudal vertebrae), support it as a valid gen. et sp.. Also, the large size of *Nullotitan*, in joint with the lack of saltasaurid and aeolosaurine features, plus all the character-

istics listed above suggest its placement among colossosaurian titanosaurs.

### Theropod dinosaurs

Remains of theropod dinosaurs (including birds) collected in the Chorrillo beds include several isolated bones and a single tooth identified as Megaraptoridae indet., as well as some pedal phalanges referred with doubts to Noasauridae and Unenlagiidae. Besides, eggshell fragments are described as belonging to Theropoda indet. Available evidence, albeit fragmentary, clearly shows that the dinosaur fauna from the Chorrillo Formation was taxonomically diverse, formed by clades also documented in other regions of Patagonia and Gondwana, but with an apparent dominance of megaraptorids over other theropod groups. From the equivalent Dorotea Formation in Chile, Manriquez et al. (2019) mention the discovery of theropod teeth, but no details on their phylogenetic affinities was given.

Coelurosauria Huene, 1914  
 Megaraptora Benson, Carrano and Brusatte,  
 2010  
 Megaraptoridae Novas et al., 2013  
 Megaraptoridae gen. et sp. indet. 1

**Referred material.** MPM 21545, fragmentary specimen composed of a posterior dorsal centrum, transverse process of a dorsal vertebra, partial neural arch of a caudal vertebra, fragments of two indeterminate vertebrae, rib fragments and proximal end of pubis (locality 3) (Figure 25). The specimen was found in a 5x3 m surface area.

**Horizon.** Base of the upper third of the Chorrillo Formation, lying above a thick bank of conglomerates.

**Description.** Available elements belong to a megaraptorid similar in size to *Aerosteon* (Sereno et al., 2008), approximately 8-9 meters in whole length.

**Dorsal vertebrae.** The isolated centrum is incomplete, lacking most of its dorsal portion. It probably corresponds to a posterior dorsal vertebra, with transverse width vs maximum length ratio of 1.16, almost the same as dorsal 10th of *Aerosteon*. The anterior articular surface of centrum is concave, but the posterior one is flat. The lateral surfaces are remarkably concave, as occurs with other big-sized theropods (Brochu, 2003; Sereno & Brusatte, 2008). Ventrally, the centrum is smooth and transversely convex. This condition is observed in other big-sized megarap-

torids as *Aerosteon* and *Murusraptor*, in which these surfaces become progressively deeper posteriorly. Large paired pleurocoels are present on both sides of the centrum; they are separated by a wide and oblique septum, a diagnostic feature of Megaraptoridae (Novas et al., 2013). The pleurocoels penetrate the centrum medially and slightly ventrally. The internal structure of the centrum is camellate, as occurs in other megaraptorids (e.g. *Orkoraptor*, *Megaraptor*; Calvo et al., 2004; Novas et al., 2008; Benson et al., 2010, 2012; Porfiri et al., 2014).

An isolated transverse process is interpreted as belonging to a dorsal vertebra. It is oval in cross section, and with camellate internal structure. Distally the process bears a concave and oval surface for articulation with the rib tuberculum. The articular surface of the process is proportionally much bigger than in the cervical vertebrae of other theropods.

**Caudal vertebra.** This element is represented by the right side of a neural arch, including the base of the transverse process and the base of the postzygapophysis. The presence of a tall neural arch suggests it corresponds to the proximal third of the tail. As in other vertebral elements, this neural arch possesses a camellate internal structure. The preserved part of the neural arch appears to be dorsoventrally more depressed than in *Aoniraptor* and *Murusraptor* (Coria & Currie, 2016; Motta et al., 2016), but similar to *Megaraptor* and *Orkoraptor* (Novas, 1998; Novas et al., 2008). The transverse process is robust, dorsoventrally tall and posterolaterally directed. Below it there is the anterior centrodiapophyseal lamina, which is robust and anteroventrally directed, delimiting anteriorly the prezygadiapophyseal-centrodiapophyseal fossa, and posteriorly the centrodiapophyseal fossa. The presence of two laminae delimiting three fossae is observed in other megaraptorids such as *Aoniraptor*, *Orkoraptor*, *Murusraptor*, and *Megaraptor* (Calvo et al., 2004; Novas et al., 2008; Coria & Currie, 2016; Motta et al., 2016). In contrast, in other theropod groups (e.g., abelisaurids, carcharodontosaurids, tyrannosaurids) the neural arch lacks these laminae below the transverse process. Interestingly, the anteroventral limit of the prezygadiapophyseal-centrodiapophyseal fossa is made up by an anteroposteriorly wide and anteriorly inclined lamina. This robust lamina is observed in *Aoniraptor*, *Murusraptor* and *Megaraptor*, but not in *Aerosteon* and *Orkoraptor*. The postzygapophysis is small and slightly longer than wide. Above it, the postspinal laminae

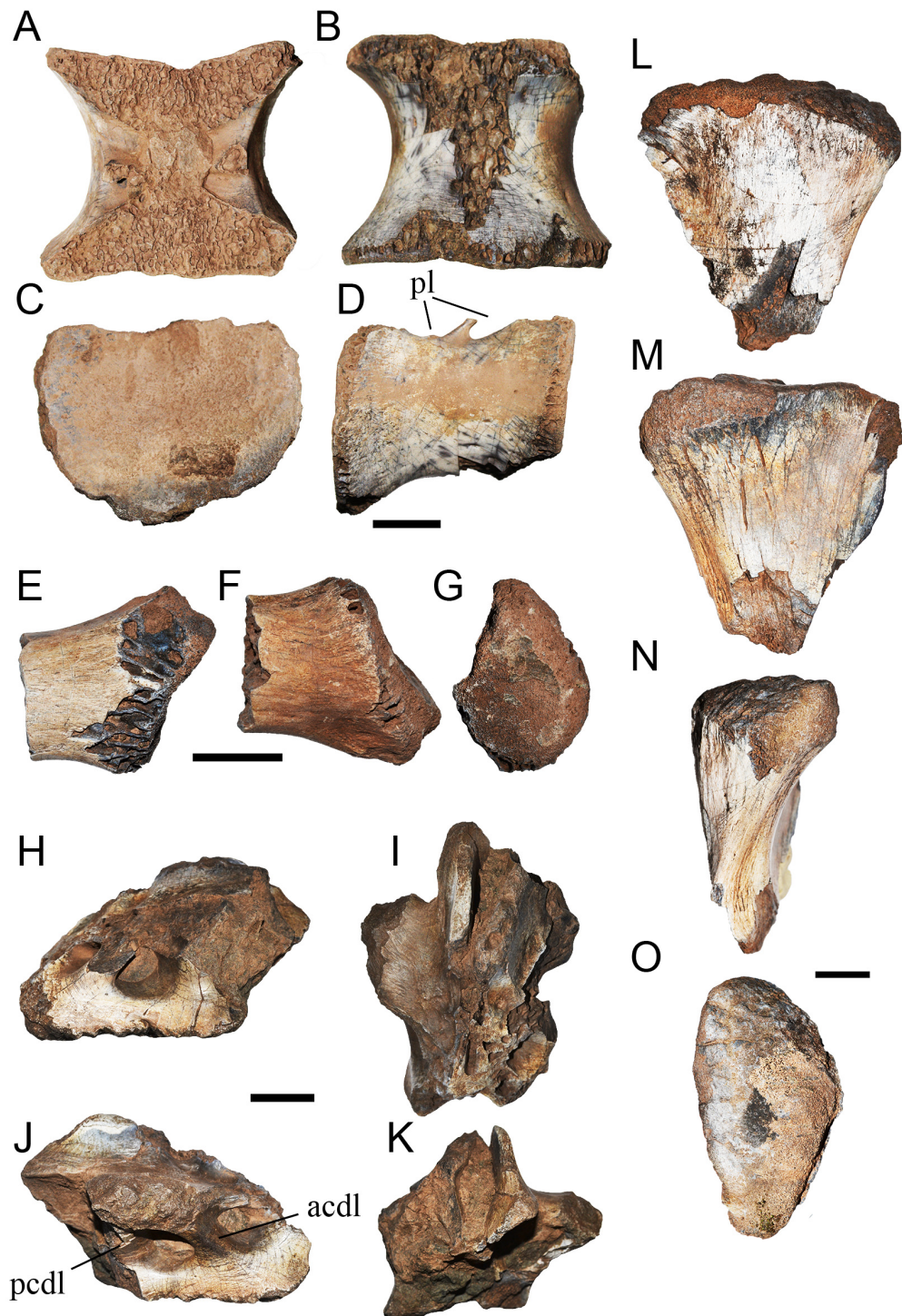


Figure 25. Megaraptoridae indet. (MPM 21545). (A-D) Partial dorsal centrum in dorsal (A), ventral (B), posterior (C) and right lateral (D) views. (E-G) Isolated dorsal transverse process in anterior (E), posterior (F) and distal (G) views. (H-K) Partial caudal neural arch in left lateral (H), dorsal (I), right lateral (J) and anterior (K) views. (L-O) Proximal end of right pubis in lateral (L), medial (M), anterior (N) and proximal (O) views. **Abbreviations:** **acdl**, anterior centrodiapophyseal lamina; **pcdl**, posterior centrodiapophyseal lamina; **pl**, pleurocoel. Scale bars 3 cm



ascends vertically and delimits the postspinal fossa. This fossa is narrow and does not show interspinous ligament tuberosity.

**Pubis.** The pubis is represented by the proximal end of the right bone. Its lateral surface is convex, while the medial one is both anteroposteriorly and dorsoventrally concave. The medial surface shows vertical striations probably for ligament attachment. The anterior margin is transversely thick and convex in cross-section, whereas the posterior margin is thin and sharp. The pubis is oval in proximal view, with a rugose articular surface for the iliac pedicle, and seems morphologically less complex than in other megaraptorans, such as *Aerosteon* or *Murusraptor* (Serenó et al., 2008; Coria & Currie, 2016). The proximal margin of pubis seems simple, lacking differentiation into acetabular, ischiadic and iliac articular surfaces present in another megaraptorids.

**Discussion.** MPM 21545 exhibits the following megaraptorid synapomorphies: 1) dorsal centra with two pleurocoels separated by a septum (Novas et al., 2013); and 2) two centrodiapophyseal laminae separating three fossae below the transverse process of the anterior-middle caudal vertebrae (Calvo et al., 2004). This morphology is absent in other theropods such as ceratosaurs, spinosaurids, allosauroids, tyrannosauroids, and ornithomimosaurs.

#### Megaraptoridae gen. et sp. indet. 2

**Referred material.** MPM 21546, isolated dorsal centrum (locality 4) (Figure 26).

**Description.** This small vertebra measures 2.72 cm long, 2.43 cm tall, and 2.79 cm wide. It is internally pneumatized through a complex pattern of lateral pleurocoels, similar to those of megaraptoran theropods (e.g., Sereno et al., 2008). Based on extrapolations with complete theropods (e.g., *Allosaurus*; Madsen, 1976), we estimate this specimen being approximately three meters long. The maturity of the specimen is uncertain, but the small size of the element together with the lack of fusion with the neural arch suggests it corresponds to a juvenile. This vertebra is even smaller than those of the juvenile specimen of *Megaraptor namunhuaquii* described by Porfiri et al. (2014).

The centrum has a slightly concave anterior articular surface and a flat posterior one, as occurs in posterior dorsal vertebrae of megaraptorids (e.g., *Murusraptor*, *Aerosteon*; Sereno et al., 2008; Coria & Currie, 2016). The lateral and ven-

tral surfaces are concave. Laterally, the centrum shows a rounded fossa with an anterior pleurocoel and a posterior pleurofossa separated by an oblique septum, as it occurs in other megaraptorans (e.g., *Fukuiraptor*, *Aerosteon*, *Megaraptor*, *Murusraptor*, *Tratayenia*). The centrum is quadrangular in side view, devoid of articular surfaces for both ribs and haemal arches, thus indicating it may correspond to the posterior dorsals. Also, the ventral surface is smooth and transversely convex, contrasting with the caudal vertebrae of megaraptorans, which possess strong ventral keels (Méndez et al., 2012; Motta et al., 2016). Furthermore, in this element the posterior articular surface is flat but the anterior one shows a moderate concavity. In dorsal view, the floor of the neural canal is shallow and has a constant transverse width. This condition is observed in isolated dorsal centra of the megaraptorids *Aerosteon* and *Murusraptor* (Serenó et al., 2008; Coria & Currie, 2016), while the caudal centra of these theropods have a neural canal constricted around mid-length. In lateral view, the centrum is squared-shaped in outline, contrasting with other megaraptorids, in which the centrum is shorter and taller (e.g., *Megaraptor Aerosteon*, *Murusraptor*, *Tratayenia*; Sereno et al., 2008; Coria & Currie, 2016; Porfiri et al., 2014, 2018). However, Wilson et al. (2016) noted that this feature seems size-dependant, and may be related with the fact that all of the above mentioned megaraptorids are 8-10 meters long.

**Comments.** Up to now, the Patagonian record of Megaraptoridae corresponds to large-sized animals, approximately 8-9 m long. For their size and relative abundance, these theropods may have constituted the main predators during the Early Maastrichtian in southern Patagonia. Even juveniles may have played an important ecological role in these southern dinosaur faunas, considering that the specimen here reported attained a whole length of, at least, 2 m. This means that megaraptorids probably preyed upon different sized herbivore dinosaurs (small to medium sized elasmarians, and bigger titanosaurs) in the course of their ontogeny.

#### Megaraptoridae gen. et sp. indet. 3

**Referred material.** MACN-Pv 19066, isolated shed tooth crown, presumably coming from the lower levels of the Chorrillo Formation (Figure 27). Collected by J. F. Bonaparte in 1981 on the same large area were the holotype of *Nullotitan glaciensis* was found.

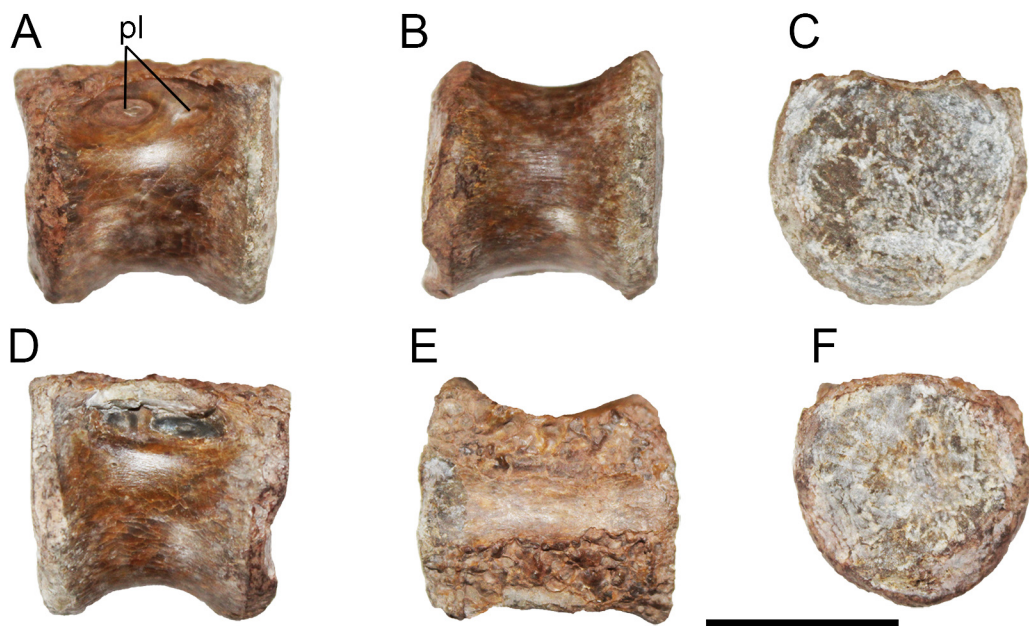


Figure 26. Megaraptoridae indet. (MPM 21546). (A-F) Posterior dorsal centrum in left lateral (A), ventral (B), posterior (C), right lateral (D), dorsal (E) and anterior (F) views. **Abbreviations:** pl, pleurocoel. Scale bar: 3 cm.

**Description.** MACN-PV 19066 is represented by a shed tooth crown that lacks its apex, a portion of the mesial margin, and some denticles in the distal margin. The crown is slightly curved to the right in distal view and the mesial carina is displaced to the right of the distal one, thus indicating that the tooth represents a left anterior maxillary or dentary dental piece. The crown has an apicobasal height of 19.0 mm, a basal labiolingual width of 6.8 mm, and a basal mesiodistal length of 10.7 mm.

The crown is distinctly recurved in labial and lingual views, with the apex being located distally to the base, as occurs in other megaraptorans (e.g. *Fukuiraptor*: Azuma & Currie, 2000; *Australovenator*, Hocknull *et al.*, 2009; *Megaraptor*, Porfiri *et al.*, 2014; *Orkoraptor*, Novas *et al.*, 2008; *Murusraptor*, Coria & Currie, 2016). The entire labial surface of the crown is apicobasally and mesiodistally convex, whereas the distal one-third of the lingual surface is apicobasally concave. This concavity produces the slight curvature of the crown in distal view. The rest of the lingual surface is homogeneously convex. The distal margin of the crown possesses a sharp carina that begins 1 mm from the base and reaches the apicalmost preserved portion of the crown. This carina is serrated along its entire length, with a rather constant density of five denticles per mm. Thus, the density of den-

ticals of MACN-PV 19066 is higher than that in *Fukuiraptor kitadaniensis* (3–4 denticles per mm; Azuma & Currie, 2000), *Orkoraptor burkei* (3–4 denticles per mm; Novas *et al.*, 2008) and *Megaraptor namunhuaiquii* (3–4 denticles per mm; MUCPv 595). The denticles are mesiodistally deeper and apicobasally tall and their main axis is orthogonal to the distal edge of the crown, resembling the condition in the above mentioned megaraptorans. The distal denticles of MACN-Pv 19066 have a rounded edge and are separated from each other by short interdenticular sulci that do not extend as blood grooves, as occurs in megaraptorids (e.g., *Australovenator*, *Megaraptor*, *Orkoraptor*, *Murusraptor*; Hocknull *et al.*, 2009; Porfiri *et al.*, 2014; Novas *et al.*, 2008; Coria & Currie, 2016). In contrast, at least some check tooth crowns of the non-megaraptorid *Fukuiraptor* have well-defined, oblique-basally oriented blood grooves (Azuma & Currie, 2000). The mesial surface is considerably labiolingually broader than the distal one and has a carina which extends along the total length of the crown. The carina reaches the apicalmost preserved portion of the crown and lacks denticles, as occurs in *Megaraptor* (Porfiri *et al.*, 2014), *Orkoraptor* (Novas *et al.*, 2008) and *Murusraptor* (with exception of the premaxillary teeth of this species; Coria & Currie, 2016). In contrast, *Fukuiraptor* (Azuma & Currie, 2000) and *Australovenator*

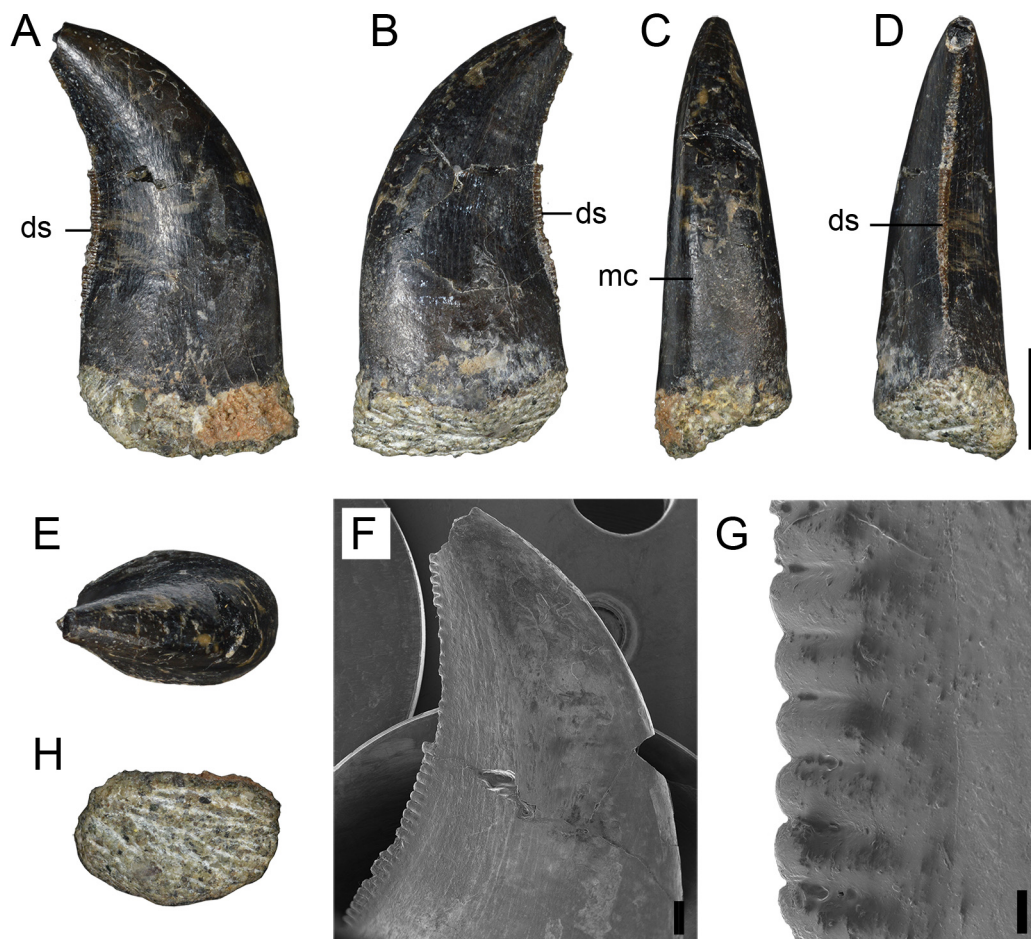


Figure 27. Megaraptoridae indet. (MACN-Pv 19066), isolated shed tooth crown in (A), labial; (B), lingual; (C), mesial; (D), distal; (E), apical; and (H), basal views. F, G, selected anatomical details. **Abbreviations:** **ds**, distal serrations; **mc**, mesial carina. Scale bar: 1 cm.

(Hocknull *et al.*, 2009) possess denticles on both mesial and distal carina. As far as it is preserved, the enamel of MACN-Pv 19066 is smooth, without wrinkles or wear facets. In contrast, extensive wear facets, but not wrinkles, are usually present in other megaraptorids (e.g. Novas *et al.*, 2008; Hocknull *et al.*, 2009). The base of the crown is sub-oval in cross-section, with a labial margin distinctly more convex than the lingual one. There is no labiolingual constriction of the base of the crown, contrasting with the eight-shaped cross-section of the base of the crowns of the megaraptorids *Orkoraptor* (Novas *et al.*, 2008), *Murusraptor* (Coria & Currie, 2016) and *Megaraptor* (Porfiri *et al.*, 2014).

**Comments.** MACN-PV 19066 can be referred to Megaraptoridae because of the presence of the following combination of characters: strongly

distally recurved crown, with apex located distal to the base, and absence of mesial serrations. The Chorrillo Formation megaraptorid tooth differs from those of other megaraptorids in its higher density of distal denticles and the absence of an 8-shaped cross-section at the base of the crown (Novas *et al.*, 2013). Although MACN-PV 19066 suggests the presence of a previously unknown megaraptorid taxon we refrain of erecting a new species because of the fragmentary condition of the megaraptorid specimens currently known from the Chorrillo Formation.

Abelisauroidea Bonaparte and Novas, 1985  
Noosauridae Bonaparte and Powell, 1980  
Gen. et sp. indet.

**Referred material.** MPM 21547, isolated right

pedal phalanx IV-2? (locality 4) (Figure 28).

**Description.** The non-ungual pedal phalanx is almost complete, lacking the ventral portion of the distal condyles. The bone is 15 mm long and 8 mm high proximally. The element is proximodistally short, dorsoventrally deep, and transversely narrow. The proximal articular surface of the phalanx has a dorsoventral keel separating two concavities, the medial one being slightly wider than the lateral one. Proximally, the phalanx has a well-developed ventral projection, sub-triangular in contour as viewed from above. The phalanx is ventrally flat and smooth. Dorsally is transversely narrower with respect to the ventral surface, a condition resembling other abelisauroids (e.g., Novas & Bandyopadhyay, 2001; Novas *et al.* 2004; Brissón Egli *et al.*, 2016). Distally, the medial condyle is more developed than the lateral one. The lateral collateral ligament pit is wider and deeper than the medial one.

**Comments.** The pedal phalanx MPM 21547 resembles Noasauridae in being transversely narrow and dorsoventrally deep, a condition shared with *Velocisaurus* and *Vespersaurus* (Brissón Egli *et al.*, 2016; Langer *et al.*, 2019). Further, a well-developed, transversely thick, and posteriorly extended posterodorsal process is also shared with noasaurids, including *Noasaurus*, *Ligabueino*, *Velocisaurus* and *Vespersaurus* (Langer *et al.*, 2019), constituting a synapomorphic feature of Noasauridae (Agnolin & Chiarelli, 2010). However, in the case for the phalanx here described the ventral projection proximally surpasses the level of the dorsal lip, contrasting with known noasaurids in which the projections are sub-equal in proximal extension (e.g., *Laevisuichus*, *Noasaurus*; Novas & Bandyopadhyay, 2001, Sampson *et al.*, 2001, Novas *et al.*, 2004; Agnolin & Chiarelli, 2010; Brissón Egli *et al.*, 2016).

Noasaurids have been recorded in different Late Cretaceous localities of Gondwana, including India (Novas & Bandyopadhyay, 2001; Novas *et al.*, 2004), Africa (Sampson *et al.*, 2001) and South America (Bonaparte & Powell, 1980; Bonaparte, 1991; Brissón Egli *et al.*, 2016; Langer *et al.*, 2019; Martinelli *et al.*, 2019). Present specimen constitutes the southernmost record for this theropod family, and forms part of a small-sized theropod fauna also integrated by megaraptorids and unenlagiids (see below).

Paraves Sereno, 1997

Unenlagiidae Bonaparte, 1999

Gen. et sp. indet.

**Referred material.** MPM 21548, pedal unguual of digit II; MPM 21549, phalanx III-2. (locality 4) (Figure 28).

**Description.** MPM 21548 consist on the proximal portion of the unguual phalanx of right pedal digit II, lacking its proximodorsal lip. The unguual is laterally compressed, being 9.9 mm in transverse width, comparable in size with the correspondent unguual of *Neuquenraptor argentinus* (MCF PVPH 77; Novas & Pol, 2005; Brisson *et al.*, 2017). It is elliptical-shaped in cross-section, with collateral grooves asymmetrically placed, as typical of paravians (Rauhut & Werner, 1995). The lateral surface is flat, while the medial one is dorsoventrally convex. The proximoventral flexor tubercle is well-developed and shows rugosities on its ventral surface, as typically occurs among paravian theropods (e.g., Ostrom, 1969). The proximal articular surface presents a well-defined dorsoventral keel separating two sub-equals concavities. The ventral margin of unguual forms a cutting edge that is continuous with the lateral surface of the unguual blade. The cutting edge is medially displaced, as it also occurs in other paravians (e.g., *Neuquenraptor*, *Deinonychus*, *Velociraptor*, *Buitreraptor*; Ostrom, 1969; Norell & Makovicky, 1999; Makovicky *et al.*, 2005; Brisson Egli *et al.*, 2017). The longitudinal collateral grooves are proximally forked, depicting the characteristic horizontal oriented “Y”-shaped groove.

Besides, specimen MPM 21549 is a complete pedal non-ungual phalanx, probably corresponding to pedal phalanx III-2. It was found nearby MPM 21548 and their sizes are congruent to refer them to a single individual. Phalanx MPM 21549 measures 45 mm long and 19 mm high, being larger than that of *Neuquenraptor* (Brisson Egli *et al.*, 2017).

The proximal articular surface lacks the medial keel and shows a sub-triangular contour, with a straight ventral margin. The proximodorsal lip has a sub-triangular profile in dorsal view, proximally surpassing the level of the articular surface. The proximal articular surface is gently concave. The proximal portion of the ventral surface has a rugose and flat shelf. Distally, the extensor fossa is wide. The distal condyles are circular-shaped in lateral view and have wide collateral ligament pits. In lateral view, the distal condyles slightly surpass the dorsal margin of the body of the phalanx.

**Comments.** Unenlagiids were recorded in NW Patagonia and NW Argentina (Agnolin and Novas, 2013). MPM 21548 and MPM 21549 con-

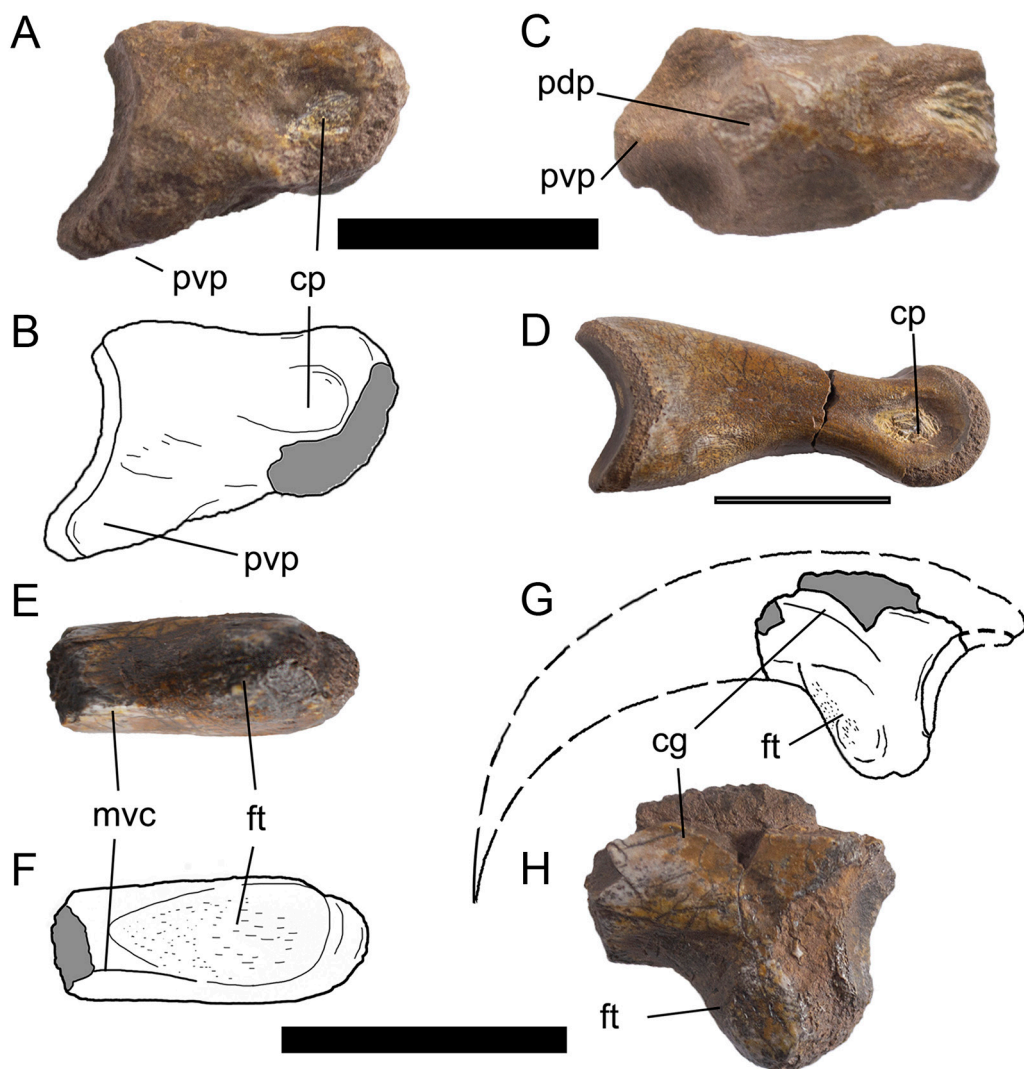


Figure 28. Theropod pedal elements. (A-C), isolated noasaurid right pedal phalanx IV-2? (MPM 21547) in medial (A-B) and dorsal (C) views; (D-H), Unenlagiid pedal elements. Right pedal phalanx III-2 (MPM 21549, D) and right pedal ungual of digit II (MPM 21548, E-G) in lateral (D), ventral (E, F), and medial (G-H) views. **Abbreviations:** cp, colateral pit; ft, flexor tubercle; mvc, medioventral crest; pdp, posterodorsal process; pvp, posteroventral process. Scale bar: 10 cm

stitute the southernmost unenlagiid record for South America. This unenlagiid, similar in size and shape to *Neuquenraptor*, expands the meagre record of Maastrichtian unenlagiids from Argentina, up to the date represented by the large bodied *Austroraptor* (Novas et al., 2009).

Aves Linnaeus, 1758  
Ornithurae Haeckel, 1866

*Kookne yeutensis* nov. gen. et sp.

**Holotype.** MPM 21550, incomplete right coracoid lacking sternal end and proximal end damaged (locality 2) (Figure 29).

**Diagnosis.** Medium-sized derived ornithurine diagnosable on the basis of the following unique combination of characters (autapomorphies marked by an asterisk\*): 1) robust coracoidal shaft with well-defined and proximodistally extended procoracoid process; 2) *ligamentum coracoscapulare ventralis* forming a well-defined scar, resulting in a notch that separates the scapular cotyla from the *facies articularis humeralis*; 3)

*facies articularis humeralis* ovoidal in shape, with its distal half more transversely expanded than the proximal half; 4) cup-shaped impression for the acrocoracohumeral ligament, with thickened and well-defined margins\*.

**Etymology.** “*Kookne*”, mythological swan companion of the Aonikenk hero Elal; and *yeutensis*, from “yeut”, “mountain” in Aonikenk language.

**Description.** *Kookne yeutensis* is represented by an isolated coracoid lacking the sternal end and showing badly damaged acrocoracoidal process. The coracoid is robust, and belongs to a medium-sized bird, the size of a tern (maximum preserved proximodistal length of coracoid is 23.4 mm, minor coracoidal transverse width is 4.8 mm, and the preserved transverse width at level of scapular cotyla is 6.3 mm). The distal end of the bone exhibits a transverse linear ridge for the impression of the *M. sternocoracoidei*. This ridge is obliquely oriented and runs from the laterodistal to the medioproximal edges of the bone.

The procoracoid process is present, but lacks its distal tip. It is represented by an acute lamina. This process is relatively dorsoventrally short, distally extending as a narrow but well-defined ridge, constituting the medial edge of the distal half of the coracoid. Distal to the procoracoid process there is a strap-like impression for the *M. subscapularis*, as is observed in modern anseriforms (e.g., *Anas*) and *Maaqwi* (McLachlan *et al.*, 2017). At the base of the procoracoidal process there is a small, ellipsoidal-shaped foramen for the *N. supracoracoidei*. This foramen penetrates the bone dorsally and leaves the bone medially, within the *supracoracoidei* groove. This foramen is distal to the medial margin of the scapular cotyla, and is slightly recessed.

The scapular cotyla is roughly subtriangular in contour. The margins of the cotyle are notably thick, especially the lateral and distal ones. Laterally, the distal margin of the cotyle is delimited by a notch formed by the scar of the *ligamentum coracoscapulare ventralis*. This scar separates the scapular cotyle from the articular surface for the humerus. The humeral articular surface is relatively large, roughly ovoidal in contour and its surface is slightly concave. Its distal half is transversely wider than its proximal half. The lateral margin is slightly thickened. Its distal end is more proximally located than the distal level of the scapular cotyla and is delimited by the scar of the *ligamentum coracoscapulare ventralis*. The humeral articular surface is laterodorsally oriented and slightly proximally tilted. The proximal edge of the humeral articular surface

is narrow and bifurcates in two main ridges that delimit a well-defined and cup-shaped impression for the acrocoracohumeral ligament. The dorsal crest becomes proximally prominent and medially wraps the triosseous canal.

The lateral surface of the coracoid shows a subtriangular flattened surface with its tip pointing distally. This surface is ventrally delimited by a very narrow but conspicuous ridge corresponding with the *M. supracoracoidei*. Distal to this ridge, there is preserved the proximalmost portion of the intermuscular ridge between the *M. coracobrachialis caudalis* and *M. supracoracoideus* (see Jasinoski *et al.*, 2006).

In medial view the coracoid shows a very deep and wide triosseal canal. This is represented by the excavation for the *M. supracoracoidei* which forms a deep groove that is distally extended as a narrow sulcus reaching the distal end of the procoracoidal process. Proximally, this groove shows a dorsal depression that is subcircular in contour.

**Comments.** The coracoid is one of the most diagnostic elements of the avian skeleton (Hope, 2002). Because of its taphonomical attributes, the coracoid is the most commonly preserved element among Mesozoic birds (see Higgins, 1999; Longrich *et al.*, 2011). In spite of being represented by a single, isolated coracoid, *Kookne* is referred to derived Ornithurae by having an acrocoracoid process that curves medially to embrace a wide and deep triosseal canal, and a broad furcular articulation (Agnolin, 2010; McLachlan *et al.*, 2017). Within Ornithurae, the coracoid is similar to *Palintropus*, *Ichthyornis*, and more derived forms in having a ligament scar on the dorsal surface of the acrocoracoid (Longrich, 2009). As occurs in *Ichthyornis* and crown Aves it exhibits a triosseal canal passing ventral to the scapular articular facet (McLachlan *et al.*, 2017). Further, *Kookne* is more derived than *Ichthyornis*, and resembling crown Aves, in having the following features: humeral articular facet anteriorly displaced relative to the scapular articular facet, scapular and humeral facets well-separated each other, and acrocoracoid that medially wraps the triosseal canal (Hope, 2002; Agnolin, 2010; McLachlan *et al.*, 2017). In sum, all features exhibited by *Kookne* are shared with derived Ornithurae, mostly Neornithes. In this way, we refer *Kookne* to crown birds.

Mesozoic Neornithines or stem-Neornithines are scarce in the fossil record. Most taxa are grouped within Cimolopterygidae (Longrich, 2009; Agnolin, 2010; Longrich *et al.*, 2011; McLachlan *et al.*, 2017), Palintropidae (Brodtkorb,

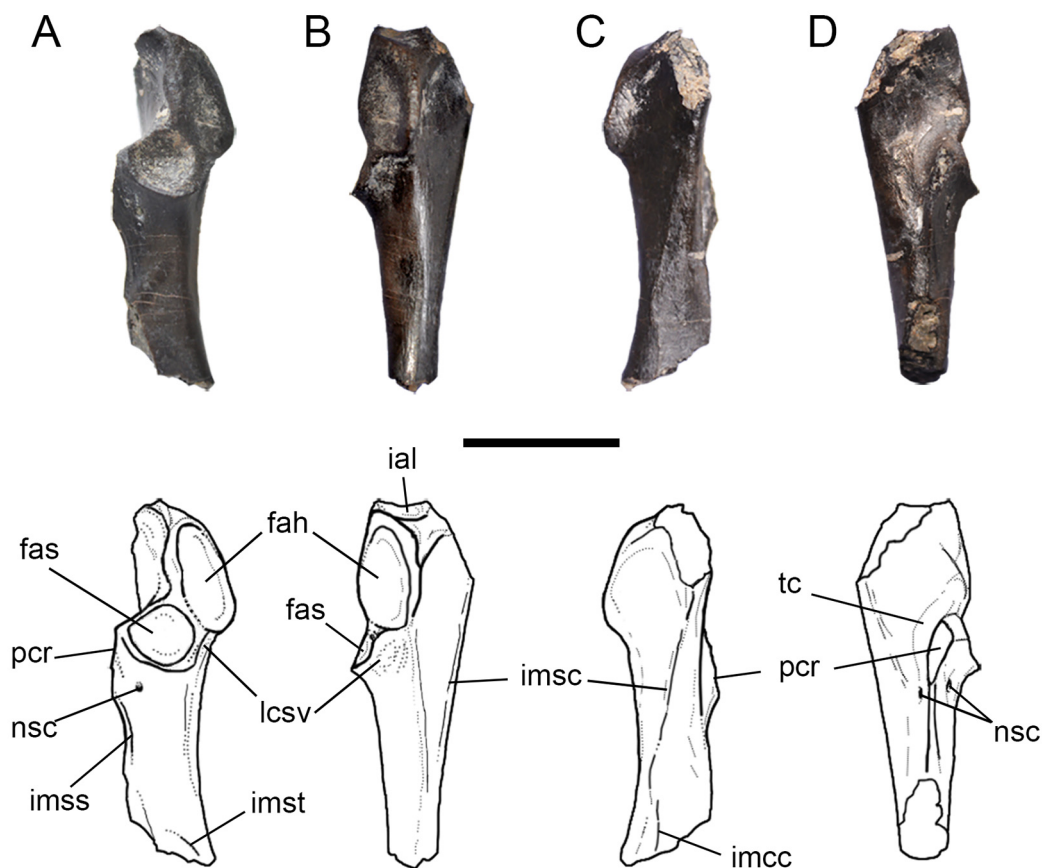


Figure 29. *Kookne yeutensis* gen. et sp. nov. Right coracoid (MPM 21550; holotype) in dorsal (A), lateral (B), ventral (C) and medial (D) views. **Abbreviations:** **fah**, facies articularis humeralis; **fas**, facies articularis scapularis; **ial**, impression for the acrocoracohumeral ligament; **imcc**, impressio for the m. *coracobrachialis caudalis*; **imsc**, impressio for the m. *supracoracoideus*; **imss**, impressio of the m. *subscapularis*; **imst**, impressio for the m. *sternocoracoidei*; **lcsv**, ligamentum *coracoscapularis ventralis*; **nsc**, foramen for *n. supracoracoidei*; **pcr**, procoracoidal process; **tc**, triosseal canal. Scale bar: 1 cm

1970; Hope, 2002), and Vegaviidae (Agnolin *et al.*, 2017). *Kookne* does not fit with any previously named derived ornithurine from the Mesozoic. It differs from *Palintropus* and kin by a large number of features, including retention of a well-developed procoracoidal process, foramen for *N. supracoracoidei* proximally located at the base of the procoracoid process, scapular facet not laterodistally positioned, and ventral margin with a straight anterior edge (Hope, 2002).

Further, *Kookne* differs from Vegaviidae in lacking thickened bone cortex on the coracoid and in having more gracile proportions (McLachlan *et al.*, 2017). Detailed comparisons with *Vegavis* resulted in the following differential features: in *Kookne* the procoracoid is more ventrally extended, the humeral facet is dorsolaterally faced (instead of being laterally faced as in *Vegavis*), the

ventral margin is straight (instead of strongly concave as in *Vegavis* and *Maaqwi*) resulting in a subvertically oriented acrocoracoid process.

Cimolopterygids are a widespread clade of Cretaceous and possibly Paleogene birds that include a large variety and diversity of morphotypes (Longrich, 2009). Most cimolopterygids are based on isolated and often fragmented coracoids, with a wide morphological divergence. However, cimolopterygids share some common traits that are absent in *Kookne*. For example, *Cimolopteryx* and *Lamarqueavis* show a very large and distally located foramen for the *N. supracoracoidei*, procoracoid process laminar and dorsoventrally extended, and humeral articular surface dorsoventrally oriented (Brodtkorb, 1963; Hope, 2002; Agnolin, 2010). This combination of characters is absent in *Kookne*.

*Iaceornis* is a purported neornithine coming from the Late Cretaceous of USA, and described by Hope (2002) under the name of *Apatornis* (see also Clarke, 2004). It was previously referred to Galloanseres (Hope, 2002; Clarke, 2004). It sharply differs from *Kookne* in having a notably elongate omal end, with proportionately smaller acroracoid and humeral facet, and a narrow scapular cotyla and shallower triosseal canal (Hope, 2002; Clarke, 2004).

Among neornithines, *Kookne* shows a combination of characters (e.g., well-developed acroracoid and procoracoid processes, well-developed foramen for *N. supracoracoidei*, coracoidal shaft relatively short and stout) clearly distinguishing it from ratites, tinamids, galliforms, gruiforms and podicipediforms (Hope, 2002). Further, the coracoid of *Kookne* differs from that of Charadriiformes in that the humeral facet is not large and ovate, the foramen for the *N. supracoracoidei* is not caudally recessed from the scapular cotyla, and the scapular cotyla is not particularly large and subcircular in contour (Hope, 2002). Further, in charadriiforms the humeral facet and coracoidal shaft are usually medially tilted (Hope, 2002).

*Kookne* is reminiscent of Anseriformes in sharing several derived features, including: transverse linear ridges within the *impressio sternocoracoidei* (Ericson, 1997; Mayr & Smith, 2001); expanded articular surface for the furcula (a feature recovered diagnostic for Anseriformes in recent analyses; Clarke *et al.*, 2016); ventral border of sulcus for the *M. supracoracoidei* columnar-shaped, and increasing in diameter towards the clavicular facet; and well-defined fossa within the supracoracoideus groove (Hope, 2002), and well-excavated *acroracohumeralis* impression (Mayr & Smith, 2001). In *Kookne* the *ligamentum coracoscapulare ventralis* forms a well-defined scar, a feature shared with Anseriformes (Hope, 2002). A similar condition is observed in *Ceramornis* (figured as “lateral fossa” by Longrich *et al.*, 2011), but in this case the fossa is notably wider and crescent-shaped. In sum, this combination of characters strongly suggests anseriform affinities for *Kookne*. However, its fragmentary nature makes this referral tentative.

Most frequently cited Latest Cretaceous anseriforms belong to Presbyornithidae. Presbyornithid coracoid, as exemplified by *Presbyornis* and *Telmatornis*, is characterized by a notably elongate neck and narrow humeral facet which is proximodistally expanded and notably flattened, scapular facet large and subcircular

in contour, and foramen for *N. supracoracoidei* more distally located (Hope, 2002; De Pietri *et al.*, 2016). This combination of traits is absent in *Kookne*. In addition, *Kookne* differs from the early Paleocene anseriform *Conflictio* in retaining a foramen for the *N. supracoracoidei*, humeral shaft more robust, and scapular facet ovoidal, among other minor details (see Tambussi *et al.*, 2019).

In spite of its fragmentary nature, *Kookne* represents an important addition to the fossil record of Late Cretaceous birds from the in South America and Antarctica. Most relevant evidence comes from NW Argentina, NW Patagonia, and Antarctic Peninsula (e.g., Agnolin, 2010; Agnolin *et al.*, 2017). Bird remains have been also recorded from the Dorotea Formation (Manriquez *et al.*, 2019). *Kookne* expands avian diversity for the southern extreme of Patagonia, and demonstrates, in join with *Lamarqueavis* and *Vegavis*, that an important morphological divergence existed in the southern cone during Maastrichtian times (Agnolin *et al.*, 2006; Agnolin, 2010; Clarke *et al.*, 2016). This also supports the idea (firstly expressed by Chatterjee, 2002) that the Southern Hemisphere played a key role in the origin and early evolution of modern birds.

### Dinosaur eggshells

Abundant dinosaur eggshells have been recorded from the lower and middle sections of the Chorrillo Formation. Dinosaur egg-shell fragments of two types have been collected from Titanosaur tibia (locality 2) and Puma Cave (locality 4) sites. The microstructural patterns observed in the eggshells agrees with that previously described for sauropods (i.e., Fusioolithidae) and theropods (i.e., Prismatoolithidae).

Oofamily Fusioolithidae Fernández & Khosla, 2015

*Fusioolithus* Fernández & Khosla, 2015

*Fusioolithus* ichnosp.

**Referred material.** MPM 21543, thirty four eggshells collected from locality 4; MPM 21544, twenty two eggshells collected from locality 2 (Figure 30).

**Description.** The outer eggshell surface displays a compactitubercular ornamentation with coalescent nodes, showing partial fusion of shell units into more nodes (Figure 30A,B,E), with pore apertures located in the depressions among them. The eggshell is 0.97 mm thick and each node is about 0.7 mm in diameter. The pore system is



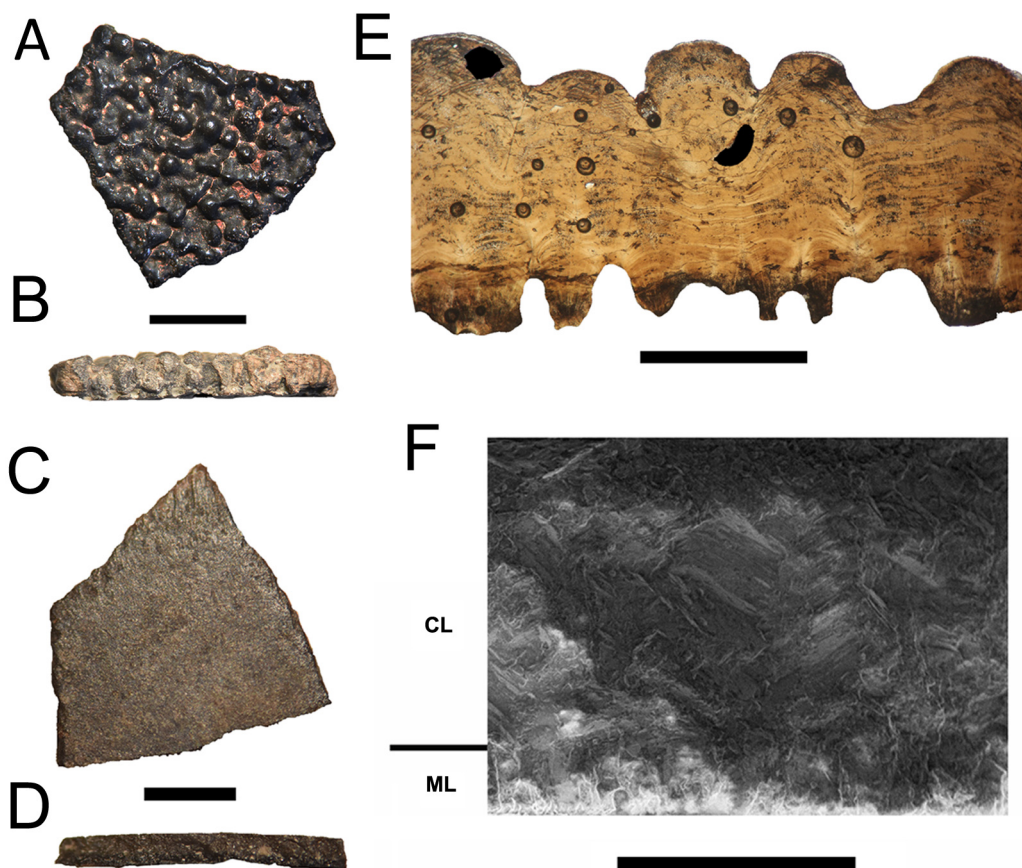


Figure 30. Dinosaur eggshells. (A-B, E) *Fusioolithus* sp. eggshell fragment (MPM 21543). A, external view; B, radial section; E, radial section showing the microstructure of the sample. (C-D, F) Prismaticoolithidae eggshell fragment (MPM 21551) (C) external view; (D) radial section; (F) radial section under MEB showing three main structural layers: mammillary, prismatic and external. **Abbreviations:** CL, continuous layer; ML, mammillary layer. Scale bar 1 mm in A-E, 200  $\mu\text{m}$  in F.

tubocanaliculate. This set of features allows referral of specimens MPM 21543 and MPM 21544 as to the *Fusioolithidae* oogenus *Fisuoolithus* (see Fernández & Khosla, 2016).

**Comments.** Late Cretaceous eggs and eggshells from Patagonia, usually interpreted as corresponding to Titanosauria, have been sorted into three different oofamilies: *Fusioolithidae*, *Faveoolithidae*, and *Megalolithidae*. The *Fusioolithidae*, including *Fusioolithus baghensis* Fernández & Khosla 2016, documented in the Campanian Anacleto Formation, Auca Mahuevo, Neuquen, and Maastrichtian Allen Formation from Santa Rosa and Trapalcó (Rio Negro). *Fusioolithidae* characterize by a dinosauroid-spherulitic basic type, tubospherulitic morphotype, tubocanaliculate pore system. Its ornamentation is compactituberculate. Thins sections shows that the accretion lines cross the bound-

ary between shell units starting on the one-third of the inner of the eggshell thickness and sometimes continue to the external surface. Eggshell is composed of circular cones without clearly demarcated boundary lines; the shell units are partially fused. The shell units are fan shaped similar to the eggs of oofamily *Megaloolithidae* but it differ in the nature of the eggshell units in which they are partially fused. (Fernández and Khosla, 2014).

Besides, *Faveoolithidae* is abundantly represented in Patagonia in Allen and Los Alamitos formations, Salitral Moreno, Rio Negro), and distinguish for being coarse-shell eggs, with compactituberculated ornamentation, filiesferulitic structural morphotype, and multicaniculated pore system. *Paquilloolithus rionegrinus* (Simón, 2006) has been referred to this oofamily.

Finally, *Megaloolithidae* is represented

*Megaloolithus jabalpurensis* (Fernández & Khosla, 2014; 2016), documented in Bajo de la Carpa Formation, Neuquén City, and the Campanian-Maastrichtian Allen Formation at Santa Rosa, Trapalcó, and Salitral Moreno (Rio Negro Province). These eggshells have a discrete-spherulitic morphotype, eggs are spherical to sub-spherical in shape with diameter variable from 140 to 160  $\mu\text{m}$ . The eggshell thickness ranges from 1.0 to 2.38 mm and shows compact-tuberculate ornamentation. The average node diameter is about 0.67 mm with diameter ranging from 0.35 to 1 mm. The shell units are fan shaped and of variable width and shape. The lateral margins of shell units are non-parallel. The average height/width ratio is 2.45:1. The growth lines are moderately arched upwards, and have tubocanalicate pore system (pore canals are straight).

Features enumerated above for MPM 21543 and MPM 21544 are consistent with Fusioolithidae, and sharply differ from both Faveoolithidae and Megaloolithidae. Faveoolithidae have 5 mm thick eggshells, while MPM 21543 and MPM 21544 are thinner, faveoolithid nodes from external surface are smaller than fusioolithid nodes, then faveoolithid eggshells have different pore canal system (multicanalicate) and shell units are multi-spherulitic (Mikhailov, 1997). On the other hand Megaloolithidae eggs have compact-tuberculate ornamentation, but each node at the external surface appears isolated. Shell units are sharply separated from each other, constituting an important difference with fusioolithid eggshells (Mikhailov, 1997).

Oofamily PRISMATOLITHIDAE Hirsch, 1994  
Ichnogenus and Ichnospecies indet.

**Referred material.** MPM 21551, five eggshells collected in locality 4 (Figure 30).

**Description.** The sculpture of the outer surface is nearly smooth, with some areas finely sculptured (Figure 30C,D and F). The eggshell is 0.2 through 0.3 mm thick. Observed under SEM it shows a prismatic structure separated into two different layers: a mammillary layer (ML), 0.06 mm thick, and a continuous layer (CL) 0.23 mm thick. The CL:ML ratio is 1:0.2. The boundary between layers is not abrupt. The mammillary layer exhibits a tabular structure, showing radial sections with slender mammillae with straight limits between each mammilla. The mammillae are built up by spherulites rising from the base

of the mammillae, with no evidence of nucleation center. These spherulites grow distally, up to the limit with the continuous layer, changing their orientation to form compact aggregates of vertical rhombohedral crystals. These crystals gradually change into the continuous layer. For this reason, and because of indistinct boundary, these eggshells belong to the “dinosauroid-prismatic basic type” (Mikhailov, 1997). The continuous layer reveals more homogeneous and compact tabular ultrastructure. The organic core is not preserved. Within the continuous layer, the prismatic and external zones can be distinguished, the last one showing a more compact material. This set of features allows referral of specimen MPM 21551as to the Prismatoolithidae oofamily.

**Comments.** Late Cretaceous eggs and eggshells from Patagonia interpreted as belonging to Theropoda are restricted to the single oospecies *Arriagadoolithus patagoniensis*, from the Maastrichtian Allen Formation, Río Negro (Agnolin *et al.*, 2012). MPM 21551 differs from *Arriagadoolithus patagoniensis* in that in the later one the shell is much thicker (about 1 mm), and the outer ornamentation is much more complex (it composes of low irregular nodes, isolated node-like ridges, low elongate ridges interconnected each other to form a net; Agnolin *et al.*, 2012).

Mammalia Linnaeus, 1758  
Genus and species indeterminate

**Referred material.** MPM 21552, anterior caudal vertebra (Figure 31 A-E), and MPM 21553, mid-to-posterior caudal vertebra (Figure 31 F-K). Both caudals were collected from locality 4.

**Description.** MPM 21552 and MPM 21553 are identified as caudal vertebrae of Mammalia on the basis of following combination of features: 1) platycoelous centra; 2) presence of two longitudinal keels on the ventral surface of centrum; 3) neural spine anteroposteriorly long and very low; 4) postspinal fossa present; 5) transverse processes aliform; 6) transverse processes divided into anterior and posterior portions, separated through a medial constriction; 7) transverse process with a blunt lip on both anterior and posterior ends; 8) prezygapophyseal process more extensive than the postzygapophyseal one; and 9) absence of neural canal. This set of characters is not observed in caudal vertebrae of other vertebrate groups, including turtles, lizards, crocodiles and dinosaurs.

The MPM 21552 is an incomplete posterior half of centrum of a relatively large vertebra, being robust and transversely wide (8.99 mm). The vertebral centrum is subcircular in transverse section, slightly dorsoventrally depressed, and becomes notably narrower at mid-length. The posterior articular surface is platycoelous. The base of the transverse processes is located at centrum mid-height, it is anteroposteriorly extended and reaching the posterior margin of centrum. The neural arch is poorly preserved. The bases of the postzygapophysial processes are located on the dorsolateral corner of centrum. The base of the neural spine is located on the middle portion of the dorsal surface of neural arch. The neural spine is posteriorly forked, bounding a narrow postespinal fossa, "V"-shaped in contour. On ventral surface the centrum has two shallow longitudinal keels. The combined presence of these keels in join with the position of transverse processes, indicate that this element is an anterior caudal vertebra.

MPM 21553 is a complete caudal vertebra, smaller (7.7 mm long and 4.3 mm of maximum transverse width) but proportionally more slender than MPM 21552. This vertebra is notably elongate and dorsoventrally depressed, being cylindrical in gross-shape. The centrum is transversely wide at both anterior and posterior ends, being more constricted at mid-length. Both articular surfaces are subcircular and with a shallow notochordal notch. Several nutrient foramina are present on the ventral surface of centrum. Both anterior and posterior transverse processes are separated by a constriction at mid-length; they are wing-shaped, sharp and slightly laterally projected. Transverse processes ends in blunt lips, probably representing the insertion of *M.ischiocaudalis* and *M.abductor caudae dorsalis* (Argot, 2003). The anterior lips are ventrally projected and are longer and more robust than the posterior lips. There is a small concave depression at the dorsal surface of the transverse processes for probable attachment of *M. sacrocaudalis dorsalis* (Kielan-Jaworowska & Gambaryan, 1994). On the ventral surface, the transverse processes exhibit a depression, deeper than the dorsal one, probably corresponding to the insertion of the *M. sacrocaudalis ventralis* (Kielan-Jaworowska & Gambaryan, 1994). The ventral surface of centrum has two, well-developed longitudinal keels, which extend along the anterior half of the vertebra. On the contrary, these keels are reduced on the posterior half of the centrum. These crests probably contacted

with the haemal arches.

The neural spine is low and feebly developed. Near the anterior and posterior ends, the neural spine is subdivided into two crests that delimit the preespinal and postespinal fossae, respectively. Prezygapophyseal processes are well developed, dorsolaterally projected and located laterally with respect to the preespinal fossa. Postzygapophyseal processes are absent. There are several nutrient foramina on both sides of the neural spine; one foramen is located between the anterior and posterior transverse processes. The position and shape of transverse processes and neural spine indicate that this element belongs to a mid-caudal or posterior portion of the tail.

**Comments.** Excepting for domestic species, comparative studies on caudal vertebrae in extant and extinct mammals are scarce (e.g., Horovitz & Sánchez-Villagra, 2003). Specimens here reported show transverse processes slightly laterally projected, low neural spines, and poorly developed ventral keels. This combination of characters is shared with mammals having long and gracile tails, as reported for *Jeholodens*, *Yanoconodon*, *Agilodocodon*, *Henkelotherium*, *Akidolestes*, *Eomaia*, *Pucadelphys*, and *Mayulestes*, for example (Nessov et al., 1998; Ji et al., 1999; Vázquez-Molinero et al., 2001; Ji et al., 2002; Argot, 2003; Luo et al., 2007; Chen & Luo, 2013; Meng et al., 2015). The morphology described above for MPM 21552 and MPM 21553 are also present in some living mammals with elongate tails, such as felids (e.g., *Panthera leo* MACN 21.621), platyrrhins (e.g., *Alouatta caraya* MACN 33.170), and metatherians (e.g., *Macropus giganteus* MACN 48.214).

As far as for Mesozoic mammals from South America, caudal vertebrae have been described only for *Vincelestes* (Rougier, 1993). Unlike MPM 21552 and MPM 21553, in *Vincelestes* the caudal vertebrae show different proportions, being notably short and stout, with enlarged transverse processes, higher neural spines, and very large neural canals (Rougier, 1993).

Some traits described above for *Vincelestes* have been also reported for other Mesozoic mammals, such as *Castorocauda*, *Fruitafossor*, and *Repenomamus* (Hu et al., 2005; Luo & Wible, 2005; Ji et al., 2006), as well as many Cenozoic and Recent mammals with robust tails (e.g., Paleonodonta, Pantodonta, Xenarthra, Pholidota, *Talpa*, and some rodents; Krause & Jenkins, 1983; Rose et al., 1992; Muizon et al., 2015). These taxa possess robust caudal vertebrae,

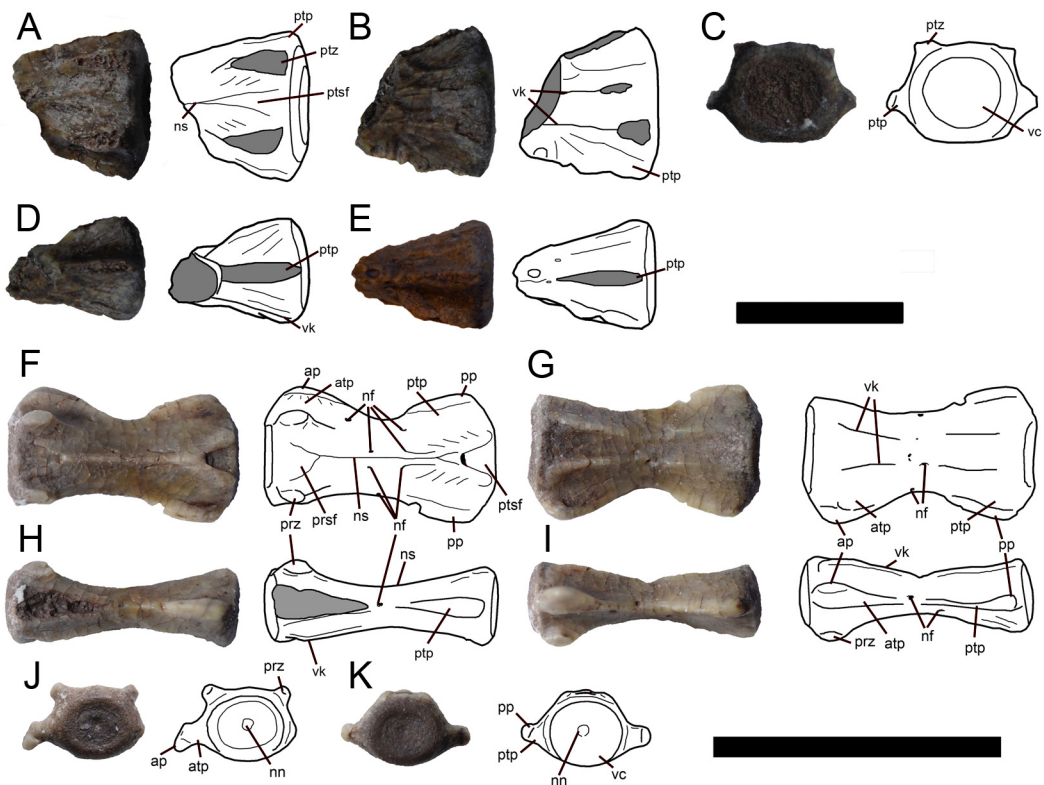


Figure 31. Mammalia indet, caudal vertebrae in **A, F**, dorsal; **B, G**, ventral; **C, K**, posterior; **D, H**, left lateral; **E, I**, right lateral; and **J**, anterior views. (**A-E**) MPM 21552 and (**F-K**) MPM 21553. **Abbreviations:** ap, anterior pit; atp, anterior transverse process; nf, nutrient foramina; nn, notochordal notch; ns, neural spine; pp, posterior pit; ptp, posterior transverse process; prsf, prespinal fossa; prz, prezygapophyseal process; ptsf, postspinal fossa; vc, vertebral centrum; vk, ventral keel. Scale bars: 10 mm.

with laterally extended transverse processes, high neural spines, postzygapophyseal processes present along the tail, and robust haemal arches. This robust tail has been related with either swimming or digging behaviors (Ji *et al.*, 2006).

MPM 21553 is a mid- to posterior caudal, perforated by several nutrient foramina and presence of transverse processes with marked muscle attachments. These two features suggest that the mammal from Chorrillo had a tail with marked neurovascular innervation and a strong muscular development, possibly related with a semi-arboreal lifestyle.

Upper Cretaceous beds from Patagonia (mainly Los Alamitos and Candeleros formations, Río Negro province) yielded a variety of gondwanatherians and meridiolestidans (Bonaparte, 1986; 1990; 1992; 1994; 2002; Rougier *et al.*, 2009a, 2009b, 2011), including forms the size of a squirrel, such as the meridiolestidans *Cronopio* and *Leonardus* (Rougier *et al.*, 2011; Chornogubsky, 2011). Whether the small-sized mammalian ver-

tebrae from the Chorrillo Formation belong to a meridiolestidan, need to be corroborated with more anatomical evidence.

#### Invertebrates: Freshwater and Land Mollusks

Abundant gastropod material (mainly fossil casts) has been collected at locality 4, corresponding to the base of the upper third of Chorrillo beds. Available material consists of 56 specimens, found in close association with isolated vertebrate remains. Mollusk specimens belong to the freshwater families Ampullariidae, Pleuroceridae, Tateidae and Physidae, as well as to the terrestrial families Holospiridae, Bulimulidae and Achatinidae. Aquatic forms predominate at level of families (60%), as well as number of collected specimens (80%).

Classification here followed corresponds to the WoRMS Editorial Board (2019). For some families, new genera and species will be described elsewhere (Miquel & Brito, in press).

Subclass Caenogastropoda Cox, 1959  
 Order Architaenioglossa Haller, 1892  
 Superfamily Ampullaroidea Gray 1824  
 Ampullariidae Gray, 1824  
*Pomacea* sp.

**Referred material.** MPM 21554, four fragmentary casts (Figure 32 A).

**Description.** Casts globose, with short spires, and last whorl very convex and with rapid growth. Larger specimen measures 18.1 mm of maximum size and 15.1 mm of maximum width, and 2.25 whorls.

**Comments.** Ampullariidae has a Gondwanan distribution, with fossil taxa from the Eocene of Africa, Asia and America (<http://www.bagniligia.it/WMSD/WMSDhome.htm>, 2017). Extant representatives are widely distributed in the Neotropical Region, with no living representatives in Patagonia (Castellanos & Landoni, 1995). *Pomacea*, in particular, has been recorded from the Eocene of La Pampa province (Argentina; Melchor *et al.*, 2002). Specimens here described represent the first Cretaceous worldwide record for Ampullariidae, and the southern-most record for the genus *Pomacea*.

Superfamily Cerithioidea Flemming, 1822  
 Pleuroceridae P. Fischer, 1885  
 Genus and species indeterminate

**Referred material.** MPM 21555, MPM 21556, two fragmentary casts (Figure 31, B-C).

**Description.** Casts with whorls of uniform growth, with last whorl well-developed; sutures delineated by an angular rim; one specimen with maximum size of 31.5 x 17.3 mm and 6 whorls. In another specimen, whorls are slightly convex, of regular growth, and suture marked with a quite strong shoulder; one specimen with maximum size of 20.1 x 11.6 mm and 5 whorls.

**Comments.** Pleuroceridae is known from the Lower Cretaceous (*Goniobasis multicarinata* Russell, 1932) from Alberta, Canada (Henderson, 1935). The genus *Paleanuclosa* Parodiz, 1969 has been recorded from Paleocene beds of South America, including *P. bullia* Ihering, 1907, *P. macrochilinoidea* Doello Jurado, 1927, *P. rionegrina* Parodiz, 1969, and *Paleanuclosa* sp. (Parodiz, 1969). Some taxa related with Pleuroceridae were also described from the Cenomanian Mata Amarilla Formation (*Pyrgulifera* Meek, 1872; Santa Cruz Province; Griffin & Varela, 2012). Extant representatives of Pleuroceridae inhabit aquatic systems in warm regions of South

America (Simone, 2006), being absent from Patagonia.

Superfamily Truncatelloidea Gray, 1840  
 Tateidae Thiele, 1925  
*Potamolithus* sp.

**Referred material.** MPM 21557, thirty-six fragmentary casts (Figure 31 D).

**Description.** Casts globose, with low spire and last whorl large and barely convex; one specimen with maximum size of 11.4 x 9.2 mm and 4.50 whorls.

**Comments.** Cretaceous record of Tateidae Forasiepi & López Armengol (1999) mentioned the presence of *Potamolithus windhausenii* (Parodiz, 1961) for the Los Alamitos Formation (Campanian – Maastrichtian) from Río Negro Province, Argentina. The genus has a restricted areal distribution in South America, comprehending the Río de la Plata basin and relict populations in southern Argentina and Chile (Miquel, 1998; de Lucía & Gutiérrez Gregoric, 2017). The specimens here described constitute the southern-most record of *Potamolithus*.

Superfamily Planorboidea Rafinesque, 1815  
 Physidae Fitzinger, 1833

**Referred material.** MPM 21558, *Physa* sp., one incomplete cast (Figure 32 E); MPM 215599, *Stenophysa* sp., two incomplete casts (Figure 32 F).

**Description.** Sinistral gastropods, ovoid to fusoid, with little to well-developed spire, and with last whorl prominent. One of the specimens referred as to *Physa* sp. has a maximum size of 8.9 x 5.5 mm and 1.5 whorls. Specimen referred as to *Stenophysa* sp. attains a maximum size of 13.7 x 7.5 mm and 4 whorls.

**Comments.** Physidae are pulmonate gastropods, historically classified in a confused way (Taylor, 2003). This family has an almost worldwide distribution, with no living representatives Patagonia.

Genus *Physa* has been reported from different Upper Cretaceous localities of North America (White, 1877; Taylor, 2003; Russell, 1935) and South America (Cabrera *et al.*, 2018; Mezzalira, 1974; Ghilardi *et al.*, 2011). For Patagonia, the species *Physa doeringi* Doello Jurado, 1927, and *Physa wichmanni* Parodiz, 1961, have been described for the Maastrichtian-Danian Jagüel Formation (Río Negro province; Salvador *et al.*, 2018). Thus, discovery of specimens of *Physa* in

the Campanian - Maastrichtian Chorrillo beds expands to the south the paleobiogeographic distribution of the genus. Regarding *Stenophysa* Martens, 1898, the specimens collected from the Chorrillo Formation represent the first world-wide Cretaceous records for this genus.

Superfamily Achatinoidea Swainson, 1840  
 ?Achatinidae Swainson, 1840  
 ?Subulininae P. Fischer & Crosse, 1877

**Referred material.** MPM 21560, MPM 21561, two fragmentary casts and shells (Figure 32 G-H).

**Description.** Fragments with general appearance of "Subulinidae", one of them large, with axial sculpture, and another specimen medium and smooth. The former with maximum size of 14.4 x 8.9 mm and 2 whorls; the latter with maximum size of 16.2 x 11.0 mm and 2 whorls.

**Comments.** Subulininae is recorded from the upper Paleocene of the Americas (Zilch, 1959) and the Eocene of China (Pan, 1977). In South America, the subulinine genus *Neobeliscus* Pilsbry, 1896 is recorded from the Miocene Pebas Formation (Brazil). Extant subulinines inhabit South America (Simone & Mezzalana, 1994; Salvador *et al.*, 2018), being absent from Patagonia. The specimens collected from the Chorrillo Formation may represent the first records for the subfamily for the Cretaceous world-wide.

Urocoptoidea Pilsbry, 1898  
 Holospiridae Pilsbry, 1946  
*Holospira* sp.

**Referred material.** MPM 21562, one fragmentary cast (Figure 32 I).

**Description.** Columnar shape, with numerous whorls, which rapidly reaches a large size and then progresses more slowly; available specimen attains a maximum size of 18.5 x 8.5 mm and 10 whorls.

**Comments.** This record constitutes the first one of *Holospira* for South America, also constituting the oldest known record for the entire family worldwide.

Superfamily Orthalicoidea Martens, 1860  
 Bulimulidae Tryon, 1867  
 Genus and species indeterminate

**Referred material.** MPM 21563, MPM 21564, five fragmentary casts (Figure 32 J-K).

**Description.** General aspect "bulimoid", similar to the extant genus *Bulimulus* Leach, 1814, *Bostryx* Troschel, 1847, and *Naesiotus* Albers, 1850, of medium size, with several whorls that increase its size gradually; one specimen with maximum size of 23.3 x 16.0 mm and other ones with maximum size of 13.9 x 7.6 mm, with 6 and 8.5 whorls, respectively.

**Comments.** This is a family with extant relict populations in Patagonia (Breure, 1979). Some Cretaceous Bulimulidae recorded from South America include: *Bulimulus klappenbachi* (Parodiz, 1969) from the Queguay Formation (Uruguay, Late Cretaceous) (Cabrera *et al.*, 2018; Veroslavsky *et al.*, 2019); others, more modern, are *Thaumasthus patagonicus* Parodiz, 1946 (Eocene), *Paleobulimulus eocenicus* Parodiz, 1949 from the Eocene-Miocene of Chubut (Argentina), and *Bostryx* sp. and *Bulimulus* sp. from the Eocene of La Pampa (Argentina) (Melchor *et al.*, 2002; Salvador *et al.*, 2018). *Bostryx* sp. aff. *Bostryx jujuyensis* (Holmberg, 1900) as *Bulimulus* aff. *jujuyensis* was mentioned from early Late Miocene of Catamarca (Miquel, 1995; Salvador *et al.*, 2018). The specimens here reported constitute the first record for the family for the Cretaceous of Patagonia.

#### Marine invertebrates

Fossil marine invertebrates are represented by a few taxa that were collected from locality 5. Rock samples (MPM 21565; MPM 21566) contain different bivalve species. Preliminary determinations encompass bivalves of diverse clades, including ostreids of the genera *Gryphaeostrea* (species similar to *G. callophyla* Ihering, 1903) and *Cubitostrea* (species similar to *C. ameghinoi* Ihering, 1902), pectinids related with the Danian species "*Chlamys*" *salamanca* Ihering, 1902, and an indeterminate Mytilidae (D. Pérez, B. Santelli, and M. Álvarez, pers. comm.).

#### Plants - Fossil woods

Pinidae Cronquist, Takht & Zimmerm. 1966  
 ?Podocarpaceae Endlicher 1847  
 Fossil genus *Podocarpoxyylon* Gothan 1904  
 Type species *Podocarpoxyylon juniperoides*  
 Gothan, in Gagel (1904)  
*Podocarpoxyylon dusenii* Krausel 1924

**Referred material.** MPM 21568, fragmentary wood from locality 1 (Figure 33).

**Description.** Growth ring boundaries distinct. Latewood consisting of c.6 tracheids with re-

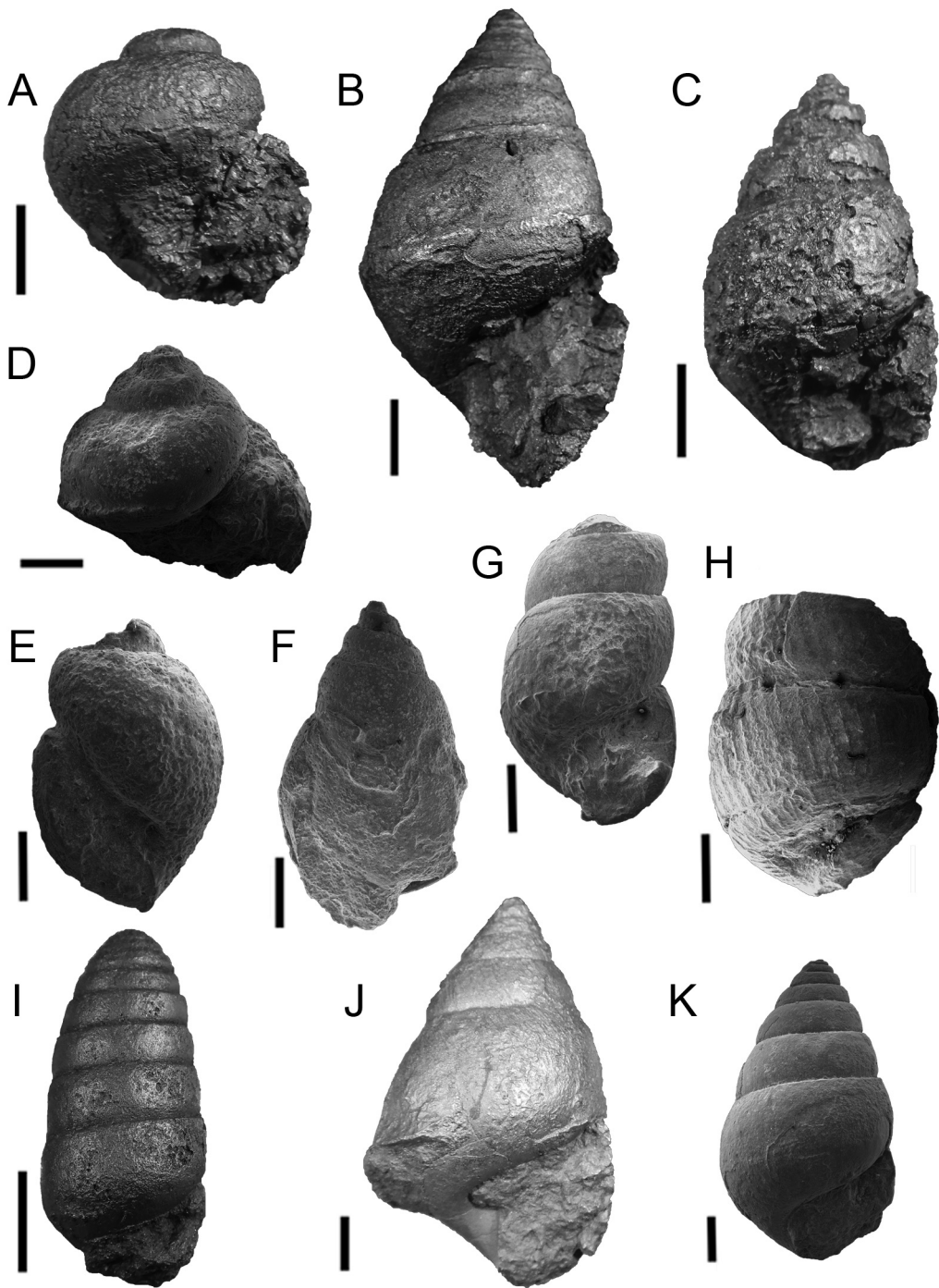


Figure 32. Gastropoda. **A**, Ampullariidae. *Pomacea* sp. MPM 21554. **B**, Pleuroceridae. Genus et species indet. MPM 21555. **C**, Pleuroceridae. Genus et species indet. MPM 21556. **D**, Tateidae. *Potamolithus* sp. MPM 21557. **E**, Physidae. *Physa* sp. MPM 21558. **F**, *Stenophysa* sp. MPM 21559. **G**, Achatinidae. Genus et species indet. MPM 21560. **H**, Achatinidae. Genus et species indet. MPM 21561. **I**, Holospiridae. *Holospira* sp. MPM 21562. **J**, Bulimulidae. Genus et species indet. MPM 21563. **K**, Bulimulidae. Genus et species indet. MPM 21564. Scale bars 0.5 cm in **A-C**, **I** and **J**. Scale bars 2 mm in **D-H** and **K**.

duced radial diameter. Transition from earlywood to latewood gradual. Earlywood tracheid tangential diameter  $24.8 \pm 7$  ( $16.9\text{--}46.5$ )  $\mu\text{m}$ . Latewood tracheids thin walled. Intercellular spaces rare to absent. Tangential pits and axial parenchyma not observed.

Rays homogeneous, parenchymatous, with cells  $20 \pm 4$  ( $11.7\text{--}28.5$ )  $\mu\text{m}$  in vertical diameter. Horizontal and end walls of ray parenchyma cells smooth. Rays very low to medium,  $3 \pm 2$  ( $1\text{--}9$ ) cells high, uniseriate and with a frequency of  $4 \pm 1$  ( $2\text{--}6$ ) rays per mm.

Tracheid radial pitting uniseriate ( $S_i = 1$ ), abietinean, with  $C_p = 7\%$ . Radial pits circular to oval  $12.5 \pm 1.1$  ( $9.6\text{--}14.1$ )  $\mu\text{m}$  in vertical diameter. Cross-field pitting podocarpoid, 1 (rarely 2) pits per cross field. When 2 pits are present, they are arranged vertically. Cross-field pits  $8.3 \pm 1.3$  ( $6.8\text{--}11.1$ )  $\mu\text{m}$  in vertical diameter. Pits oval, oblique, with narrow areola.

**Comments.** Krausel (1924) erected this species for specimens recovered at Santa Cruz Province, Argentina. Following his description, this taxon is characterized by: lack of axial parenchyma, cross-fields with one (or rarely 2) pits, uniseriate pitting of the radial walls of the tracheids, and uniseriate (rarely biseriate) rays 1–20 cells tall. The material here studied falls within the described features by Krausel for this taxon. Rays described by Krausel (1924) seem to be taller than our materials, but this feature may show intraspecific variation (Carlquist, 1988; Poole *et al.*, 2001). Provenance data of the original specimen of this taxon is unclear, and Krausel (1924) states that it was found near the La Leona River. Coordinates provided by this author suggest that it was found at the northern margin of the Lago Argentino, near La Leona river mouth. The age of this taxon is currently regarded as Cenozoic, as originally pointed by Krausel (“Tertiär”), given its unclear stratigraphic provenance.

*Podocarpoxylon aparenchymatosum* Gothan from the Eocene (and probably the Paleocene) of Antarctica (Pujana *et al.*, 2014; Pujana & Ruiz, 2017) shares with the material here studied the absence of axial parenchyma, but rays are taller ( $9(1\text{--}17)$ ). Furthermore, cross-fields typically have 2 pits, reaching up to 5, whereas the specimens here studied have only one (or rarely 2 pits). *Podocarpoxylon fildesense* Zhang & Wang from the Paleocene of Antarctica has slightly taller rays, and cross-fields typically have 1–2 pits, but up to 4 pits per cross fields were reported (Zhang & Wang, 1994; Poole *et al.*, 2001; Pujana & Ruiz, 2017), and may be synonym of *P. aparenchy-*

*matosum* (Pujana *et al.*, 2014). *Podocarpoxylon garciae* Del Fueyo (1998) from the Campanian–Maastrichtian Allen Formation has axial parenchyma, a feature not recorded in the specimens here studied. *Podocarpoxylon mazzoni* (Petriella) Müller-Stoll & Schultze-Motel, an ubiquitous taxon found in Campanian–Maastrichtian to Paleocene units of northern Patagonia differs from this species by having uniseriate to triseriate pits in radial walls, partially biseriate (and locally triseriate) very tall rays, and septa-like structures (see Vera *et al.*, 2019, and references therein).

**Affinities.** Many species of *Podocarpoxylon* have been recognized from regions where no conclusive Podocarpaceae remains were identified, supporting the fact that this type of wood cannot be conclusively referred to Podocarpaceae (see discussion in Pujana & Ruiz, 2017). Nevertheless, given that gymnosperm pollen grains recorded in this unit, are essentially represented by Podocarpaceae (see below), the fossil woods are tentatively referred to this family.

### Palynology

Well-preserved palynological assemblages were obtained for the first time from the Chorrillo Formation. Two palynological samples (MPM 21570, 21571; Figure 34) were recovered from locality 3 and yielded palynofloras with a moderate specific diversity. Eighteen spore species, 7 gymnosperm pollen grains and 4 angiosperm pollen grains were identified. The assemblage is characterized by the presence of spores related with different ferns (Polypodiopsida), such as Gleicheniaceae (*Clavifera triplex* (Bolkhovitina) Bolkhovitina 1966 and *Gleicheniidites senonicus* Ross 1949), Osmundaceae (*Baculatisporites comaumensis* (Cookson) Potonie 1956, *Baculatisporites kachaikensis* Archangelsky & Llorens 2005) and Polypodiaceae (*Tuberculatosporites parvus* Archangelsky 1972). It is also recorded the family Dicksoniaceae (*Trilites fasolae* Archangelsky 1972, *Trilites* sp. cf. *T. parvullatus* Krutzsch 1959 and *Trilites* sp. cf. *T. tuberculiformis* Cookson 1947), and particularly *Cyatheacidites annulatus* Cookson ex Potonie 1956, with affinities with extant genus *Lophosoria* C. Presl. Other fern spores cannot be related to any particular family, such as *Concavissimisporites* sp., *Laevigatosporites ovatus* Wilson & Webster 1946 and *Leptolepidites* sp. cf. *L. major* Couper 1953, and representatives of the genus *Cyathidites* Couper. Within the latter, three species are identified, namely:



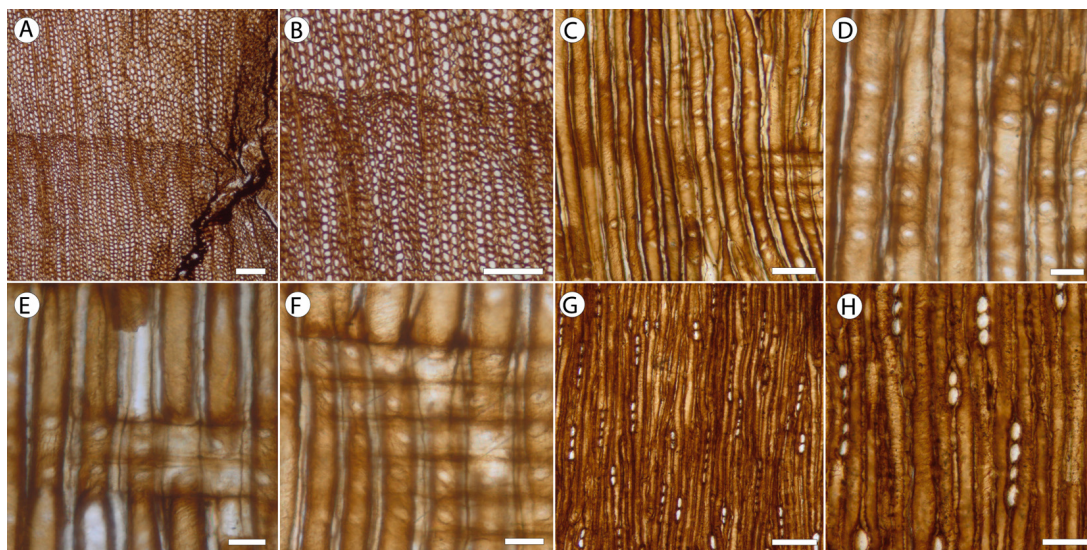


Figure 33. *Podocarpoxylon dusenii* Kraüsel 1924. **A**, (MPM 21568) Growth ring in a transverse section (TS). Bar: 20  $\mu$ m. **B**, (MPM 21568) Detail of growth ring (TS). Bar: 20  $\mu$ m. **C**, (MPM 21567) Spaced uniseriate radial pitting and cross fields (LRS). Bar: 50  $\mu$ m. **D**, (MPM 21567) Spaced uniseriate radial pitting and cross fields (LRS). Bar: 20  $\mu$ m. **E**, **F**, (MPM 21567) Cross fields with 1 or 2 podocarpoid pits (LRS). Bar: 20  $\mu$ m. **G**, (MPM 21567) Uniseriate rays (LTS). Bar: 20  $\mu$ m. **H**, (MPM 21567) Detail of uniseriate rays (LTS). Scale bar: 50  $\mu$ m

*Cyathidites australis* Couper 1953, *C. minor* Couper 1953 and *C. rafaeli* Burger 1980, all psilate triangular spores related to Cyatheaceae, Dicksoniaceae, Dipteridaceae, or Matoniaceae. Lycopodiopsida are recorded with spores referable to Selaginellales (*Ceratosporites equalis* Cookson & Dettmann 1958 and *Foveosporites canalis* Balme 1957) and Lycopodiales *Retitriletes austroclavatidites* (Cookson) Doring *et al.*, in Krutzsch 1963).

Gymnosperm pollen grains are less diverse than spores, and are represented by taxa related to Podocarpaceae (*Microcachryidites antarcticus* Cookson 1947, *Phyllocladidites mawsonii* Cookson 1947 ex Couper 1953, *Podocarpidites ellipticus* Cookson 1947, *P. sp. cf. P. herbstii* Burger 1966, *P. sp.*, and *Trichotomosulcites subgranulatus* Couper 1953) and pteridosperms (*Vitreisporites signatus* Leschik 1955).

Similarly, the angiosperm pollen grains show a low diversity, being *Peninsulapollis gilli* (Cookson) Dettmann and Jarzen 1988 the only angiosperm abundant in the studied palynoflora (at least representing 90% from the total angiosperm pollen grains). This species is related to Proteaceae, probably with *Beauprea*-like forms (Dettman & Jarzen, 1988). Other taxa include *Clavatipollenites* sp. (related to the Chloranthaceae), *Tricolpites reticulatus* Cookson 1947 ex Couper 1953 (related to *Gunnera*), along

with *Tricolpites* sp. (of unknown affinities), being all these species scarce in the assemblages recovered from Chorrillo Formation.

## DISCUSSION

### 1. Dinosaur assemblages

#### 1.1. Vertebrate assemblage yielded by Chorrillo and Dorotea Formations

Marcelo Leppe (e.g., Leppe *et al.*, 2014; Vogt *et al.*, 2014; Manriquez *et al.*, 2019) has conducted successful explorations in the Las Chinas River Valley (NE from the Torres del Paine National Park, Magallanes Region, Ultima Esperanza Province, Chile). This locality is approximately 4.2 km southeast from the border to Argentina (Figure 1). Leppe and crew reported semi-articulated skeletons of dinosaurs at levels of the Dorotea Formation. Dinosaur remains include indeterminate titanosaurs, ornithischians, and also abundant hadrosaur remains (e.g., Leppe *et al.* 2014, Jujihara *et al.*, 2014; Soto Acuña *et al.*, 2014; Vogt *et al.*, 2014; Manriquez *et al.*, 2019). In Las Chinas River Valley, Leppe *et al.* (2014) distinguished three stratigraphic sections for the Dorotea Formation: the lower Casa Las Chinas, the middle Saurópodo, and the upper El Puesto section. The Saurópodo stratigraphic section shows abundance of titanosaur remains, and may be partially equivalent to the lower and mid-

de levels that shed the many titanosaur remains of the Chorrillo beds. In Las Chinas site the El Puesto section sheds at its base *Nothofagus* leaf imprints, followed upward by levels with abundant hadrosaur remains, and plesiosaur and mosasaur bones at the top of the section. The El Puesto is considered here equivalent with the upper portion of the Chorrillo Formation, on the Argentine side, which shed the basal iguanodontian *Isasicursor* associated with the mosasaur teeth.

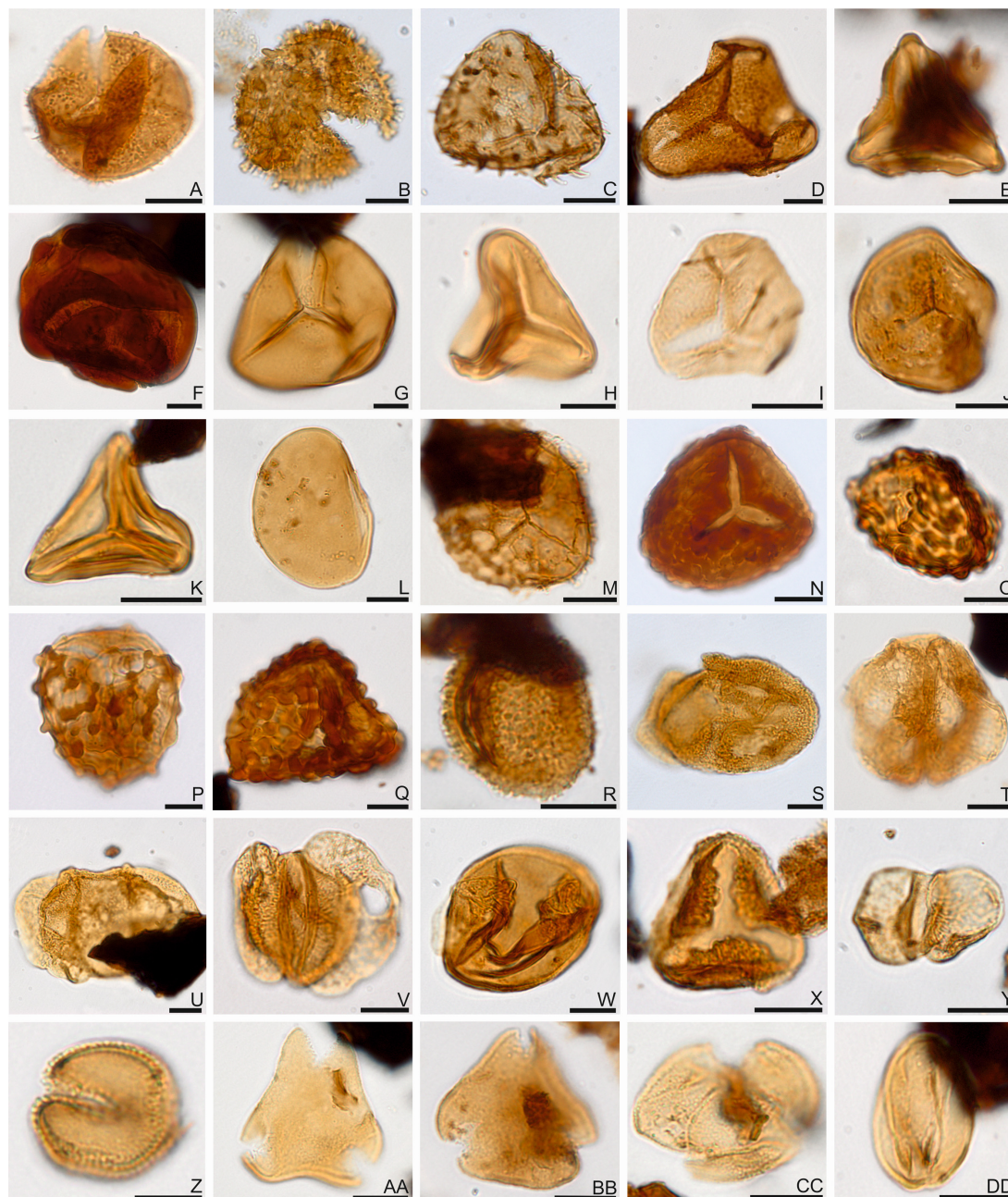
Current information about tetrapod taxonomic diversity in both Chorrillo and Dorotea includes turtles, ophidians, colossosaurian titanosaurs, basal iguanodontians, hadrosaurids, megaraptorids, abelisauroids, basal paravians, basal neornithes, and mammals. Integrative studies on both sides of the Argentina-Chile border will eventually result in considerable increase in knowledge of this Maastrichtian ecosystem from the southern tip of South America.

## 1.2. Dinosaur-bearing beds from southern Patagonia

Dinosaur-bearing beds of Upper Cretaceous age crop out in the SW corner of Santa Cruz province, comprising the vicinities of Viedma Lake (to the north) up to Argentino Lake (to the south), as well as along La Leona River, the water course connecting both lakes. These dinosaur-bearing beds extend south, crossing the international border with Chile, including (from north to south) Mata Amarilla, Cerro Fortaleza, Chorrillo and Dorotea. The stratigraphic correlations among these continental beds have been, and still are, a theme of intense debate among geologists (see, Varela *et al.*, 2012; Sickman *et al.*, 2018). Available

radiometric dating shows that the Mata Amarilla Formation is Cenomanian in age (approximately 97my; Varela *et al.*, 2012), Cerro Fortaleza Formation is Campanian (around 76.2Ma, based on studies by Sickman *et al.*, 2018), and upper terms of the Dorotea is Maastrichtian (as supported by radiometric dating and paleontological evidence; Manriquez *et al.*, 2019). Explorations carried on in SW Santa Cruz province by the senior author since 1998, have produced different dinosaur species from these beds: Mata Amarilla, in proximities of the Sheuen River, afforded carcharodontosaurid remains (Novas *et al.*, 1999) which are congruent with a Cenomanian age obtained by radiometric studies (Varela *et al.*, 2012). The Cerro Fortaleza beds, at Cerro de Los Hornos fossil site, shed different dinosaur taxa (i.e., *Talenkauen*, *Orkoraptor*, *Puertasaurus*, *Dreadnoughtus*; Novas *et al.*, 2004, 2005, 2008; Lacovara *et al.*, 2014) which resemble forms from the Neuquina Basin (i.e., *Macrogryphosaurus*, *Megaraptor*, *Futalognkosaurus*) recorded in the Turonian Portezuelo Formation (Calvo *et al.*, 2007). The age based on paleovertebradological fossil content does not fit with the radiometric ages obtained by Sickman *et al.* (2018) which support a Campanian age for the Cerro Fortaleza Formation. Besides, the upper third of the Dorotea Formation yielded abundant hadrosaurid material (Jujihara *et al.*, 2014; Soto Acuña *et al.*, 2014), as it also occurs in Maastrichtian localities from NW and Central Patagonia (e.g., Bonaparte *et al.*, 1984; Gasparini *et al.*, 2015; Brett-Surman, 1979; Becerra *et al.*, 2018). The Chorrillo beds apparently corresponds to an age (i.e., late Campanian-early Maastrichtian), intermediate between the Campanian Cerro

Figure 34 (next page). Palynology. **A**, *Baculatisporites comaumensis* (Cookson) Potonie 1956, MPM 21571-2:M62/1; **B**, *Baculatisporites kachaikensis* Archangelsky & Llorens 2005, MPM 21571-2:R48/1; **C**, *Ceratosporites equalis* Cookson & Dettmann 1958, MPM 21571-3:S40/0; **D**, *Concavissimisporites* sp., MPM 21571-3:H27/0; **E** *Clavifera triplex* (Bolkhovitina) Bolkhovitina 1966, MPM 21571-5:R42/3; **F**, *Cyatheacidites annulatus* Cookson ex Potonie 1956, MPM 21571-4:Z48/2; **G**, *Cyathidites australis* Couper 1953, MPM 21571-3:X55/4; **H**, *Cyathidites minor* Couper 1953, MPM 21570-6:T24/4; **I**, *Cyathidites rafaeli* Burger 1980, MPM 21570-6:D55/4; **J**, *Foveosporites canalis* Balme 1957, MPM 21571-6:C42/3; **K**, *Gleicheniidites senonicus* Ross 1949, MPM 21571-6:Y24/0; **L**, *Laevigatosporites ovatus* Wilson & Webster 1946, MPM 21571-6:C32/3; **M**, *Retitriteles austroclavatidites* (Cookson) Doring *et al.* in Krutzsch 1963, MPM 21571-4:Q41/0; **N**, *Trilites fasolae* Archangelsky 1972, MPM 21571-1:D36/1; **O**, *Leptolepidites* sp. cf. *L. major* Couper 1953, MPM 21571-2:O24/1; **P**, *Trilites* sp. cf. *T. tuberculiformis* Cookson 1947, MPM 21571-5:R57/0; **Q**, *Trilites* sp. cf. *T. parvullatus* Krutzsch 1959, MPM 21571-2:X58/2; **R**, *Tuberculosporites parvus* Archangelsky 1972, MPM 21571-6:O48/0; **S**, *Microcachryidites antarcticus* Cookson 1947, MPM 21571-3:Y36/0; **T**, *Podocarpidites* sp. cf. *Pellipticus* Cookson 1947, MPM 21571-3:S19/4; **U**, *Podocarpidites* sp. cf. *P. herbstii* Burger 1966, MPM 21571-2:B55/1; **V**, *Podocarpidites* sp., MPM 21571-2:H55/4; **W**, *Phyllocladidites mawsonii* Cookson 1947 ex Couper 1953, MPM 21571-1:Q63/4; **X**, *Trichotomosulcites subgranulatus* Couper 1953, MPM 21571-8:V31/0; **Y**, *Vitreisporites signatus* Leschik 1955, MPM 21571-8:J39/2; **Z**, *Clavatipollenites* sp., MPM 21571-7:V47/0; **AA**, *Peninsulapollis gilli* (Cookson) Dettmann & Jarzen 1988, MPM 21571-3:P31/6; **BB**, *Peninsulapollis gilli* (Cookson) Dettmann & Jarzen 1988, MPM 21571-7:L27/4; **CC**, *Tricolpites reticulatus* Cookson 1947 ex Couper 1953, MPM 21571-7:L48/3; **DD**, *Tricolpites* sp., MPM 21571-7:J28/3. Scale bar: 10  $\mu$ m.



Fortaleza and the upper Maastrichtian Calafate formations.

Summing up, we identify a succession of at least four different dinosaur assemblages from beds exposed in the SW corner of Santa Cruz: the oldest ones corresponding to the Cenomanian Mata Amarilla Formation, the Campanian Cerro Fortaleza Formation, the upper Campanian – lower Maastrichtian Chorrillo Formation, and

the upper Maastrichtian hadrosaurid-bearing levels of the Dorotea Formation. The sequence is capped by marine beds (i.e., Calafate, Monte Chico, and upper terms of Dorotea formations) which yielded remains of plesiosaurs and mosasaurs (Bonaparte *et al.*, 2002; Leppe *et al.*, 2014; Vogt *et al.*, 2014; Novas *et al.*, 2016; Soto Acuña *et al.*, 2016).

Such biostratigraphic succession has to be

taken as a tentative one, and new paleontological discoveries (dinosaurs in particular) are needed to confirm or correct these interpretations. An important topic requiring consideration concerns with the taxonomic distinctions that may exist between vertebrate faunas documented in the Chorrillo Formation with respect to the underlying Cerro Fortaleza beds. Both units share the same inclusive clades (i.e., Titanosauridae, Elasmaria, Megaraptoridae), although some generic distinctions exist among titanosaurians and elasmarians: the Chorrillo beds yielded *Nullotitan* and *Isasicursor*, while Cerro Fortaleza Formation yielded the titanosaurids *Puertasaurus* and *Dreadnoughtus*, and the elasmarian *Talenkauen*.

### 1.3. Paleobiogeographic comments on dinosaur faunas

The following preliminary paleobiogeographic interpretations emerge from comparing Maastrichtian dinosaur faunas from the Austral Basin with those from other regions of Gondwana:

**1.3.a.** Theropod records here reported include the southernmost records for unenlagiid paravians and noasaurid abelisauroids. In addition, at least three different megaraptorid specimens were found, indicating that this theropod clade was relatively abundant during the deposition of the Chorrillo Formation. The set of megaraptorid specimens described in the present paper constitutes evidence for their survival into the Maastrichtian. This information counters previous interpretations (Novas *et al.*, 2013) proposing megaraptorids went extinct before the Campanian, and that abelisauroids were dominant in Campanian-Maastrichtian theropod faunas (Novas, 2009). Recurrent discovery of megaraptorid remains in the Chorrillo beds, alongside with the paucity in abelisauroid remains, sharply contrast with the Campanian-Maastrichtian theropod assemblages from northern Patagonia, Madagascar and India, in which abelisauroids are common and megaraptorids virtually absent. Interestingly, theropod assemblages from the southern end of the continent resembles the early Late Cretaceous record from Australia, where carnivorous dinosaur assemblages were dominated by megaraptorids, whereas abelisauroids seem absent (Benson *et al.*, 2012; Novas *et al.*, 2013; Poropat *et al.*, 2019).

**1.3.b.** Regarding the presence of possible neornithine birds in the Chorrillo Formation, this clade has been recorded in northern Patagonia and

Antarctica, in contrast with the Late Cretaceous from Brazil and northwestern Argentina, where enantiornithines are the only known birds so far (see discussion in Agnolin, 2017). In spite that the fossil record of Mesozoic birds in the Southern Hemisphere is still relatively poor, the discovery of a variety of neornithine-related birds indicates that southern Gondwana constituted a cradle for the early evolution of extant bird clades (Ericson *et al.*, 2001; Cracraft, 2001; Agnolin *et al.*, 2016). **1.3.c.** Concerning sauropod dinosaurs, the Maastrichtian record of the clade in the Austral basin is still meagre. Together with the Chilean records (Manriquez *et al.*, 2019), *Nullotitan* represents one of southernmost records of Titanosauria for South America. The presence of large-sized forms in both Chorrillo and Dorotea coincides with that of the underlying Cerro Fortaleza beds, from which very large titanosaurs have been collected (*Puertasaurus*, *Dreadnoughtus*; Novas *et al.*, 2005; Lacovara *et al.*, 2014). This faunal component contrasts with the smaller-sized saltasaurines and mid-to large-sized aeolosaurines documented in lower latitudes of Gondwana (e.g., northern of Santa Cruz, Neuquén, Río Negro, and Salta provinces of Argentina, and São Paulo and Minas Gerais states of Brazil; Powell, 2003; Casal *et al.*, 2007; Santucci & Arruda-Campos, 2011).

Besides, the abundance of titanosaur specimens in southern Patagonia contrasts with the infrequent records of these herbivores in the Antarctic Peninsula (Novas, 2009; Cerda *et al.*, 2011). However, such distinction may be related with the marine-influenced paleoenvironments that dominated the Antarctic Peninsula during the Late Cretaceous. In agreement with this, titanosaurid bones are abundant in the continental deposits of the lower and middle thirds of the Chorrillo Formation, contrasting with the virtual absence of sauropods from the marine-influenced upper third of the unit, where ornithopod remains are recorded in association with mosasaur remains.

Sauropod bones have been reported from Las Chinas River Valley (Manriquez *et al.*, 2019). Although such discovery still awaits formal description, available information shows the common presence of large titanosaurs in both Dorotea and Chorrillo formations. Whether the remains of these animals from Chile and Argentina belong to a same titanosaur species needs to be confirmed. Previous contributions considered that gigantic titanosaurs were restricted to mid-Cretaceous times (pre-Campanian-Maastrich-

tian; Salgado and Bonaparte, 2007; Carballido et al., 2017), but recent research indicates that giant forms, such as *Antarctosaurus*, survived up to the Campanian-Maastrichtian time interval (Garcia and Salgado, 2013). *Nullotitan* confirms the survival of gigantic colossosaurian sauropods up to the latest Cretaceous.

Although knowledge on Maastrichtian dinosaur faunas from the southern tip of South America is just at the beginning, available information indicates that no small-sized sauropods (e.g., saltasaurines) have been found so far neither in Chorrillo nor in Dorotea beds, in contrast with their abundant record in northwestern Argentina and northern Patagonia. Such distinction, in join with the taxonomic differences noted above for Theropoda, suggest the influence of environmental controls in paleobiogeographic distribution of Patagonian dinosaurs.

**1.3.d.** In respect to ornithischians, documentation of the basal iguanodontian *Isasicursor*, constitutes a novelty of the present report, because it conforms the first Maastrichtian elasmarian for southern Patagonia. Basal iguanodontian diversity during Campanian-Maastrichtian time span in Southern Patagonia and Antarctic Peninsula (see Rozadilla et al., 2016) agrees with the idea expressed by Brown et al. (2011) indicating that basal ornithopods increased in diversity from the Campanian through the late Maastrichtian. Alongside basal iguanodontians, hadrosaurids are commonly found in Maastrichtian localities in NW and central Patagonia, as well as in the upper section of the Dorotea Formation, where they have been commonly recorded (Jujihara et al., 2014; Soto Acuña et al., 2014).

The Chorrillo Formation vertebrate assemblage has some similarities with those from the Late Cretaceous of Australia and Antarctica, including the common presence of Chelidae, Calyptocephalellidae, Elasmaria, and Megaraptoridae, together with the absence or scarcity of saltasaurine and aeolosaurine titanosaurs and abelisaurid theropods, dinosaur clades which are frequently documented in NW and central Patagonia. Such differences in faunal composition need to be investigated in depth to elucidate if they mirror different paleoenvironmental conditions in southern Patagonia.

## 2. Terrestrial and freshwater mollusks

Until relatively recently, the records of Mesozoic land snails were almost restricted to North America and Europe (Solem, 1979). In contrast, the Cretaceous records of conti-

ental gastropods from South America were barely represented by some specimens of the families Pleuroceridae (Early Cretaceous), Physidae (Early Cretaceous), Bulimulidae (Late Cretaceous) and “Endodontidae” (Late Cretaceous) (Salvador et al., 2018) (see Table 1). Pleuroceridae and Bulimulidae were unknown from Mesozoic beds, and their respective fossil records were restricted to the Cenozoic of Patagonia (Parodiz, 1969). Discoveries here reported from the Chorrillo Formation allow modifying this situation with the documentation of the first Mesozoic remains of Ampullariidae and Holospiridae for South America, and confirming the presence of Tateidae, Physidae and Bulimulidae in the South American Mesozoic. Further, such discoveries constitute the southernmost records for these families. Holospiridae is recorded for the first time in South America. Notably, almost all families exhibit features corresponding to new genera and species, which will be studied elsewhere (Miquel and Brito, in press).

Holospiridae is a group that currently lives in Central and North America, with numerous genera and species, with fossil records from the Paleocene of USA (Zilch, 1960). Excepting this group, the remaining families have been recorded in South America, some with numerous taxa, as Bulimulidae and Subulininae (Breure, 1979; Schileyko, 1999). Bulimulidae has a distribution restricted to Australasian and Neotropical realms (Solem, 1981). In Argentina, specimens of Bulimulidae are currently dispersed mainly in the north and center of the country, even in high altitudes in the Andes mountains (Breure, 1979). The Achatinidae Subulininae is recorded in wet tropical climates (Fernández, 1973; Schileyko, 1999).

Besides, Ampullariidae, Pleuroceridae, Tateidae and Physidae are abundant in rivers and lakes and can live in estuary environments of low salinity (e.g., Rio de la Plata, Argentina; Castellanos & Landoni, 1995). Holospiridae, Achatinidae and Bulimulidae would show the existence of areas with different tree formations, as well as habitats and microhabitats favorable for the development of gastropods, and some dry-humid climate seasonality.

## 3. Paleobotany and palynology

### 3.1. Comparisons with other Maastrichtian palynological assemblages from Patagonia.

In spite that present palynological report is preliminary, and the collected samples are meagre,

Table 1. Records of mollusks according to time and geographical area. ?Achatinidae is excluded because of the doubtful taxonomic location of the described fragments.

	CRETACEOUS South America	PALEOGENE South America	RECENT South America	RECENT Patagonia
Ampullariidae	X	X	X	---
Pleuroceridae	X	X	X	---
Tateidae	X	X	X	X
Physidae	X	X	X	---
Holospiridae	X	---	---	---
Bulimulidae	X	X	X	X

some interesting comparisons and conclusions are exposed as follows.

Povilauskas *et al.* (2008) reported palynofloras from the La Irene Formation (at Calafate hill, southwestern Santa Cruz Province), which underlies the Chorrillo Formation. The palynological assemblages from La Irene Formation share many species with those here studied, among them the presence of *Peninsulapollis gillii*. Furthermore, both Chorrillo and Irene Formations lack *Nothofagidites*. Angiosperms in the La Irene Formation show higher diversity than the one recorded in the assemblages here studied, including *Arecipites minutiscabratus* Mc. Intyre 1968, *Liliacidites cf. variegatus* Couper 1960, *Longapertites* sp., *Proteacidites* sp. and *Spinozonocolpites hialinus* Archangelsky & Zamaloea 1986 (Povilauskas *et al.*, 2008), currently absent from samples got in Chorrillo Formation.

Povilauskas (2016) reported diverse palynological assemblages obtained from the Cerro Cazador Formation (upper Campanian-lower Maastrichtian) from outcrops near Rio Turbio (southwest Santa Cruz Province) and from the Monte Grande Hill near the limit with Chile. These palynofloras share some species with those here studied, such as *Trilites fasolae*, *Cyatheacidites annulatus* and *Peninsulapollis gillii*. The angiosperm pollen grains are more diverse than the palynofloras here studied, and the genus *Nothofagidites* is recorded in low proportions in the Cerro Cazador Formation. Noteworthy, palynofloras from Cerro Cazador Formation lack subtropical to tropical families. The overlying Monte Chico Formation (upper Maastrichtian–Danian) studied by Povilauskas (2011, 2012, 2013, 2017) at the same localities, share several taxa with the Chorrillo Formation assemblages, including the marker taxon *Peninsulapollis gillii*. A floristic replacement seems apparent in the assemblages of Monte Chico

Formation, when compared with the ones present in the underlying Cerro Cazador Formation. Although *Nothofagidites* is still present in Monte Chico Formation, an increase in diversity of angiosperm families with tropical or subtropical distribution is recorded (Povilauskas, 2013).

The Danian Cerro Dorotea Formation (Povilauskas, 2017) contains a less diverse palynoflora, sharing with the assemblages of Chorrillo beds the presence of *Peninsulapollis gillii*, *Cyatheacidites annulatus*, and few other taxa. Noteworthy, this unit contains pollen referable to Bombacaceae, of tropical or subtropical distribution, along with *Nothofagidites* and Proteaceae.

Assemblages from the Dorotea Formation reported from Cerro Guido and other localities (Leppe *et al.*, 2012) contain no stratigraphically significant taxa. Some taxa, as *Baculatisporites kachaikensis*, *Gleichenites senonicus* and *Cyathidites minor* are shared with the Chorrillo Formation. Noteworthy, although five angiosperm pollen grains are reported from the Dorotea Formation, none of those is shared with the palynoflora here studied.

In summary, the palynofloras recovered from Chorrillo Formation share many taxa with units from southern Argentine Patagonia, including many species of spores and gymnosperm pollen grains, including *Peninsulapollis gillii*. Furthermore, the absence of *Nothofagidites* in the Chorrillo beds is shared with La Irene Formation. One remarkable difference with most of these palynofloras is the absence of pollen grains related with subtropical to tropical taxa, a feature shared with the Cerro Cazador Formation. However, the poor representation of angiosperm pollen grains on the palynofloras of Chorrillo Formation may be a preservation issue making comparisons less reliable. Future detailed studies based on a larger sample number would allow more detailed comparisons.

**3.2. Paleoclimatological implications.** The palynoflora recovered from Chorrillo Formation contains some taxa that, using modern analogs, may provide information regarding the paleoclimate where these plants grew. *Peninsulapollis* is allied to Proteaceae related with *Beauprea*, a genus that nowadays grow in temperate to cold environments (Quattrochio & Ruiz, 1999). The abundant and diverse ferns, along with subordinate Chloranthaceae, may have grown in the understory, associated with ponds, small streams or rivers just landward of the shoreline. *Cyatheacidites annulatus* is an indicative of ferns similar to the large fern *Lophosoria quadripinnata*, that lives in cloud forest in the tropics and in cool, wet regions further south (Hill et al., 2001). It grows in a variety of habitats and readily colonizes disturbed areas (Tryon & Tryon, 1982). Cantrill (1998) compiled and analyzed the distribution of this species, suggesting this fern grows in temperate to tropical climates. Finally, the arboreal stratum was essentially composed by Podocarpaceae, a conifer family almost entirely restricted to rainforest or wet montane environments (Hill & Brodribb, 1999).

In summary, presence of these taxa suggests cool and humid climatic conditions during the deposition of the Chorrillo Formation. The presence of well-developed growth rings in the fossil woods (see above) suggests periods of arrested growth.

**3.3. Palaeobiogeographical implications.** From a paleophytogeographical point of view, the region under study (i.e., southern Patagonia) constituted part of an intermixed/transitional floral province that extended in between two main provinces (Herngreen & Chlonova, 1981; Herngreen et al., 1996; Vajda & Bercovici, 2014): the Palmae province, ranging from the paleoequator up to northern Argentina and Chile, and characterized by the presence of palm pollen grains representing 10-50% of the palynological assemblages; and the *Proteacidites/Nothofagidites* province, well recorded in Antarctica. The Maastrichtian palynological assemblage recorded in La Irene, Chorrillo, Cerro Cazador and Monte Chico formations belongs to a transitional floral province, having neither *Proteacidites/Nothofagidites* nor palms as dominant elements (Herngreen & Chlonova, 1981; Herngreen et al., 1996; Vajda & Bercovici, 2014).

The late Campanian to Maastrichtian fossil plant record (both palynological and megafloristic) recovered from Patagonia (including those from southern Lago Argentino) reveals a mix-

ture of tropical (e.g., Arecales, Bombacaceae, Casuarinaceae, Aquillafoliaceae, Olacaceae) and austral (e.g., Nothofagaceae, Proteaceae) elements, suggesting cool-temperate to warm climatic conditions. However, assemblages from northern Patagonia (e.g., Allen, Lefipán, Paso del Sapo, Puntudo Chico, and Lago Colhué Huapí Formations) show a tendency towards a warmer climate respect to the southern ones, having yielded abundant palms (e.g., *Spinizonocolpites* Muller 1868, *Longapertites* Van Hoeken Klinkenberg 1964, *Palmoxylon* Schenk 1882), ecephalartoid cycads (e.g., *Wintucycas* Martínez et al., 2012, *Brunoa* Artabe et al., 2004, *Wordsellia* Artabe et al., 2004; see Martínez et al., 2018), and pollen grains of tropical-subtropical families (e.g. *Bombacidites* sp., *Ilexpollenites* sp., *Haloragacidites harrisii* (Couper) Harris in Mildenhall & Harris, *Anacolosidites diffusa* Archangelsky 1973). Proteaceae (e.g., *Peninsulapollis* gilli, *Proteacidites* sp., *Triatripollenites* spp.) and Podocarpaceae (*Podocarpidites* sp., *Phyllocladidites mawsonii* Cookson 1947 ex Couper 1953) are recorded in variable proportions in these assemblages. Nothofagaceae, on the other hand, are almost absent from these assemblages, being recorded in very small proportions in the Lefipán Formation (Barreda et al., 2012). Available information indicates that Maastrichtian floras from Patagonia were influenced by climatic conditions depending on latitude, a fact that should be extrapolated to vertebrate associations, as indicated above.

The palynological assemblages here studied may be, a priori, comparable with the ones at Cerro Cazador Formation, mostly by the absence of tropical or subtropical elements. However, for the time being, it is difficult to establish if the absence of these elements is reflecting a characteristic of the flora or a preservation artifact, since only two samples have been studied. Future works on the megafloristic and palynological assemblages of the Chorrillo Formation may shed light on the relationships between this ecosystem and others recorded in coeval units.

#### CONCLUDING REMARKS

Present contribution includes the first detailed description of fossil vertebrates, invertebrates, plants and pollen from the Chorrillo Formation. Previous reports of its fossil content consisted on brief mentions confirming the presence of dinosaur bones and fragmentary plant remains. Now, the taxonomic diversity is con-

siderably expanded with the description of different members of a Maastrichtian continental biota, including gastropods of a variety of aquatic and terrestrial families, and different groups of vertebrates including fishes, anurans, turtles, snakes, mosasaurs, titanosaurids, elasmarians, megaraptorids, neognathans, and mammals. Palynological assemblage from Chorrillo beds includes fern spores and both gymnosperm and angiosperm pollen. Although less diverse than other Maastrichtian units, the palynological content may increase with better sampled rock levels. Main novelties afforded by Chorrillo Formation include the remains of small vertebrates (especially birds and mammals), the survival of large titanosaurs and elasmarian into the Maastrichtian, and the documentation of a wide diversity of continental gastropods, the Cretaceous record of which remained virtually unknown from this region of Patagonia.

Maastrichtian vertebrate faunas associated with littoral environments have been extensively documented in northern and central Patagonia (e.g., Casamiquela, 1978; Gasparini *et al.*, 2015), and evidence gained in recent years from both Chorrillo and Dorotea formations, demonstrate that such faunal assemblage extended, with some distinctions, up to the southern extreme of South America. This conforms a sharp distinction with respect to North America, where marine flooding occurred at its maximum stage during Campanian times, being followed by a regressive phase during the late Maastrichtian (see Roberts & Kirschbaum, 1995). This is different from Patagonia, in which the maximum transgression occurred during the late Maastrichtian and persisted into the early Tertiary (see Malumián & Náñez, 2011). The paleoecological effects of such paleoenvironmental distinctions between South and North America need to be investigated in more detail.

A better knowledge of floristic and faunistic Maastrichtian record from southern South America will eventually contribute in future discussions about mass extinction occurred at K-Pg boundary, which are mostly based on Maastrichtian fossil record from the northern hemisphere.

Discussions about dinosaur mass extinction are mostly based on Maastrichtian fossil record from North America. South America, and other Gondwanan regions, are overlooked from these discussions, due to unavailability of dinosaur remains corresponding to latest Maastrichtian age. Aside from sharp distinctions in dinosaur taxo-

nomic composition, paleogeographic evolution of North America shows marine flooding during Campanian times, being in regressive phase during the Maastrichtian. This is different from Patagonia, in which the latter stage coincides with the maximum transgression persisting onto the early Cenozoic. Maastrichtian vertebrate faunas associated with littoral environments have been extensively documented in northern and central Patagonia (Casamiquela, 1978; Gasparini *et al.*, 2015), and evidence gained in recent years in Chorrillo and Dorotea Formations demonstrates that such faunal assemblage, but with some distinctions, extended up to the southern extreme of South America. Present contribution includes the first detailed description of fossil vertebrates, invertebrates, plants and palynomorphs from the Chorrillo Formation. Vertebrate and plant assemblages are similar to those of other southern Gondwana landmasses, including other Santa Cruz localities, Antarctica, and Australia. Further, in contrast with northern Patagonia and Chubut province, abelisaurid theropods and relatively small sauropods of the aeolosaurine and saltasaurine clades, are totally absent in latest Cretaceous Santa Cruz provinces. Further, in contrast to northern Patagonia, basal ornithopods are abundant in the Austral basin.

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