

## New fossiliferous locality from the Anacleto Formation (Late Cretaceous, Campanian) from northern Patagonia, with the description of a new titanosaur

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**Abstract:** Here we describe a new fossil invertebrate and vertebrate assemblage from a previously unknown locality of the Anacleto Formation (Campanian, Upper Cretaceous), near General Roca city, Río Negro Province, Argentina. The specimens were found in a single fossiliferous layer, which yielded bivalves and gastropods, including the first fossil record of the terrestrial clade Megalomastomatidae and the first undoubted record for the terrestrial subulinid *Leptinaria*. Vertebrates are represented by fishes (lepisosteids, percomorphs, and the dipnoan *Metaceratodus kaopen*), chelid turtles, a single crocodyliform scute, an indeterminate pterosaur, an incomplete meridiolestidan mammalian jaw, and abelisaurid and rinconsaurian titanosaur dinosaurs. The latter is represented by several individuals of a small and gracile-limbed form. The phylogenetic analysis recovers a monophyletic Rinconsauria including the new taxon, plus *Rinconsaurus*, *Pitekunsaurus*, *Overosaurus*, and *Muyelensaurus*. The new titanosaur indicates that rinconsaurians were characterized by a body shape that was different from other titanosaurs, with brachiosaur-like posture, gracile limbs, and protonic tail. The faunistic assemblage is characterized by the abundance, but low diversity, of chelid turtles and a very low number of crocodyliforms. This taxonomic composition is reminiscent of other faunal assemblages of the latest Cretaceous of northern Patagonia, but differs markedly from Campanian assemblages known from North America and Europe.

**Key words:** Campanian, Argentina, Titanosauria, Rinconsauria, Chelidae, Gastropoda

**Resumen:** Nueva localidad fosilífera de la Formación Anacleto (Cretácico Tardío, Campaniano) en Patagonia norte, con la descripción de un nuevo titanosaurio. En la presente contribución se describe una nueva asociación de invertebrados y vertebrados fósiles provenientes de una localidad previamente desconocida de la Formación Anacleto (Campaniano, Cretácico Superior), cerca de la ciudad de General Roca, provincia de Río Negro, Argentina. Los especímenes fueron recolectados en un mismo nivel estratigráfico incluyendo bivalvos y gasterópodos terrestres, entre estos últimos el primer registro fósil de la familia Megalomastomatidae y el primer registro indudable del subulinido *Leptinaria*. Los vertebrados están representados por peces (lepisostéidos y el dipnoo *Metaceratodus kaopen*), tortugas quelíidas, un pterosaurio indeterminado, una mandíbula de mamífero meridiolestido, una placa de un crocodyliformes y dinosaurios, incluyendo abelisáuridos indeterminados y un nuevo titanosaurio rinconsáurido. Este último está representado por varios individuos pertenecientes a una forma de tamaño pequeño y miembros relativamente gráciles. El análisis filogenético recupera un Rinconsauria

monofilético que incluye al nuevo taxón, así como *Rinconsaurus*, *Pitekunsaurus*, *Overosaurus* y *Muyelensaurus*. El nuevo titanosaurio indica que los rinconsáuridos formaban un clado caracterizado por una morfología corporal diferente a la de otros titanosaurios, con una postura del tipo braquiosaurio, miembros gráciles y cola con curvatura protónica. El conjunto faunístico se caracteriza por la abundancia, pero baja diversidad, de tortugas quelidas y un número muy reducido de crocodyliformes. Esta composición taxonómica recuerda a otras asociaciones faunísticas del Cretácico tardío del norte de la Patagonia, pero difiere notablemente de los conjuntos conocidos para el Campaniano de América del Norte y Europa.

**Palabras clave:** Campaniano, Argentina, Titanosauria, Rinconsauria, Chelidae, Gastropoda

## INTRODUCTION

The Neuquén Basin, situated along the southwestern margin of Gondwana (30–40° S), developed as a significant depocenter from the Late Triassic to the Paleogene. The foreland basin sedimentation of the Neuquén Group, is dated between 100–107 Ma (Gómez *et al.*, 2022), a process that resulted in the orientation of drainage systems, predominantly sourcing from the west (see Cobbold & Rosello, 2003; Howell *et al.*, 2005; Tunik *et al.*, 2010). Over a span of approximately 30 million years, sedimentation included materials eroded from the fold-and-thrust belt and contributions from a contemporaneous volcanic arc (Tunik *et al.*, 2010; Di Giulio *et al.*, 2012; Balford & Carrapa, 2016; Fennell *et al.*, 2017; Borghi *et al.*, 2019; Gómez *et al.*, 2019, 2022), all of which are included in the Neuquén Group. Notably, the upper part of the Neuquén Group is well exposed in the northern part of Río Negro Province, with the Bajo de la Carpa and Anacleto formations being identified as the primary units within this interval (Hugo & Leanza, 2001). Paleomagnetic analyses by Dingus *et al.* (2000) suggested an early to middle Campanian (78.3 Ma) maximum depositional age for the Anacleto Formation. Recently, Gómez *et al.* (2022) determined the first U-Pb ages in detrital zircons from this formation at Paso Córdoba (Río Negro Province), situated 25 km north of the study area, indicating a maximum depositional age of  $78.6 \pm 1.7$  Ma (middle Campanian) for the Anacleto Formation, based on a sample of younger Cretaceous zircons.

Fossil vertebrates from the Anacleto Formation are less well-known than those from other stratigraphic units (*e.g.*, Allen, Los Alamitos formations). Among non-dinosaurian vertebrates, dipnoans, lepidosaurs, chelid turtles, peirosaurid crocodyliforms, and dryolestoid mammals were reported (Goin *et al.*, 1986; Turner & Calvo, 2005; Scanferla & Canale, 2007; Apesteguía *et al.*, 2007; Brizuela & Albino, 2011; Martinelli *et al.*, 2012; Forasiepi *et al.*, 2012; Maniel *et al.*, 2023). Among dinosaurs, the record

includes ornithopods (Coria & Salgado, 1996), abelisaurid and megaraptorid theropods (Coria *et al.*, 2002a; Sereno *et al.*, 2008; Gianechini *et al.*, 2015; Baiano *et al.*, 2021), and titanosaurs (Chiappe *et al.*, 1998, 2001, 2004; Chiappe & Coria, 2004). The latter encompasses the gracile-limbed lithostrotians *Laplatasaurus araukanikus* (von Huene, 1929) and *Narambuenatitan palomoi* Filippi, García & Coria, 2011, the saltasaurine *Neuquensaurus australis* (Lydekker, 1893; Powell, 1986; Salgado *et al.*, 2005), and the gigantic *Barrosasaurus casamiquelai* (Salgado & Coria, 2009). Several derived titanosaurs coming from Anacleto beds, also include *Pitekunsaurus macayai* (Filippi & Garrido, 2008; see below), *Rinconsaurus caudamirus* (Calvo & González Riga, 2003; Pérez-Moreno *et al.*, 2022, 2023), and *Overosaurus paradasorum* (Coria *et al.*, 2013; see below), but their stratigraphic position was questioned (Filippi, 2015). The titanosaurs *Pellegrinosaurus powelli* Salgado, 1996 and *Antarctosaurus wichmannianus* von Huene, 1929 were assigned to the Anacleto Formation, but their exact stratigraphic position is uncertain (Leanza *et al.*, 2004; Cerda *et al.*, 2021). Vertebrate tracks have also been reported (Coria *et al.*, 2002b; Díaz-Martínez *et al.*, 2018, 2022; De Valais *et al.*, 2020; Tomaselli *et al.*, 2022).

The new fossiliferous locality here reported is located within the Marín family Farm (39° 22' 43.8" S; 67° 41' 24.1" W), which is located close to Paso Córdoba locality, at 10 km at the southwest of General Roca city (Fig. 1). The Marín locality consists of few scattered badlands and low hills that delimit the eastern margin of the "Salitral Moreno" lowlands. In spite of the relatively small size of the outcrops, they yielded a large number of fossil specimens.

## MATERIALS AND METHODS

### Sedimentological settings

A detailed metric-scale survey was conducted using Jacob's staff and Brunton-type structural compass for measurements. Field observations

facilitated the characterization of sedimentary facies based on lithology, sedimentary structures, geometry, and lateral variability. The facies nomenclature was based on the system proposed by Miall (1996, 2014). Sedimentary facies were grouped into facies associations (AF) to delineate the depositional environment.

### Paleontological settings

Fossil collecting methodology (for both vertebrates and invertebrates) includes mostly surface-collected elements, applying in some places typical sieving techniques. It was shown by several authors that surface-collected and sieving collecting methods are comparable, suggesting very minor biases related to collection method (Cullen *et al.*, 2016).

There is no standard practice for reporting relative abundance of taxa from a fossiliferous locality. Some authors provide data including number of specimens belonging to each taxon, minimum number of individuals, and different percentages. However, as remarked by Dodson (1987) and Lehman (1997), experience suggests that whatever method is employed, the relative abundance of taxa is relatively similar in different calculations. In any case, in this contribution we opt to determine the taxonomic diversity and composition calculating the Number of Individual Specimens (NISP) (skeletal elements identified by bone type and taxon), which has proven to be an effective means for determining faunal abundance at a site (Badgley, 1986; Dodson, 1987; Fiorillo, 1989). Among the elements recovered in the assemblage, turtles are particularly problematic for determining relative abundance at a fossil site because they can add a lot of fragmented specimens that can inflate their number and importance. We follow Hutchinson & Archibald (1986) and Fiorillo (1989) in a conservative method, which includes the final number of repeated elements, obvious size differences, complete or easily identified plates, and a large amount of material.

Processing sedimentary samples for microfossils and palynomorphs was unsuccessful as all analyzed samples were sterile (P. Santamarina and E. Vera, pers. comm.).

The photographs of gastropods were taken with a camera Nikon, with the exception of Figure 3C–D, which were taken by scanning electron microscope (SEM).

In the case of sauropods, we follow the definition of Rinconsauria published by Calvo *et al.* (2007). Appendicular anatomical nomenclature

of titanosaurs follows that employed by González Riga *et al.* (2019) and vertebral anatomy follows Wilson (1999).

### Phylogenetic analysis

The new titanosaur was scored in a modified version of Pérez-Moreno *et al.* (2024), which is based on Carballido *et al.* (2017)'s dataset (Supplementary Data 1). This matrix consists of 103 taxa and 432 characters, to which we add here the new titanosaur and 3 new characters based on published data sources (Calvo & González Riga, 2003; González Riga *et al.*, 2009; Coria *et al.*, 2013). Further, we modified character 108, with the addition of a new character state 4 [ch 108: tooth crowns, cross-sectional shape at mid-crown: 0, elliptical; 1, D-shaped; 2, sub-cylindrical; 3, cylindrical; 4, cylindrical, with labial and lingual surfaces separated by longitudinal crests or carinae (see Calvo *et al.*, 2007)] and character 431 with the addition of a new character state 2 [ch 431: posterior caudal vertebrae, central, height difference between the anterior and posterior articular face: null (0); present but little developed (1); strongly developed (2)]. The first round of analyses resulted in a poorly resolved tree topology (see below; Supplementary Data 1). In this way, we exclude the wildcard taxa *Daxiatitan binglingi* You, Li, Zhou & Ji, 2008, *Ninjatitan zapatai* Gallina, Canale & Carballido, 2021, *Titanomachya gimenezi* Pérez-Moreno, Salgado, Carballido, Otero & Pol, 2024 and *Narambuenatitan palomoi*. This resulted in a data matrix of 100 taxa and 435 characters (Supplementary Data 1).

The data matrix was analyzed with TNT v.1.5 (Goloboff & Catalano 2016). We conducted the analysis using equally implied weights, under the “New Technology Search” in which “Sectorial Search”, “Ratchet”, “Drift”, and “Tree Fusing” are applied together with the traditional search procedures, such as Wagner Trees, Tree Branch Reconnection (TBR), and Subtree-Pruning- Regrafting (SPR) algorithms, to find the Minimum Length Trees (MLTs). From the 100 hits replicates, a total of 250,000 most parsimonious trees (MPTs) of 1539 steps length were obtained, which are summarized using a strict consensus.

As a branch support measure, Bremer support was calculated, and as a measure of branch stability, a bootstrap resampling analysis (Felsenstein, 1985) was conducted, performing 10,000 pseudoreplicates. Bremer support was calculated after searching for suboptimal trees

and not with the script that accompanies the program (Ezcurra, 2016). Both absolute and GC (Goloboff *et al.*, 2003) bootstrap frequencies are also reported (Supplementary Data 1).

**Institutional abbreviations.** MACN-In, Invertebrate Collection, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Ciudad Autónoma de Buenos Aires, Argentina; MPCN-Pi, Colección Paleontología de Invertebrados, Museo Patagónico de Ciencias Naturales “Juan Carlos Salgado”, General Roca, Río Negro, Argentina; MPCN-Pv, Colección Paleontología de Vertebrados, Museo Patagónico de Ciencias Naturales “Juan Carlos Salgado”, General Roca, Río Negro, Argentina.

## RESULTS

### Facies Analysis

**Pelitic Facies.** The finest-grained facies are represented by massive (Fm) and laminated (Fl) pelites, ranging in color from grayish to reddish. They are weakly consolidated, laterally extensive tabular beds, reaching lengths of several tens of meters. Vertebrate remains and mollusks were identified in these facies (Fig. 1).

**Heterolithic Facies.** These facies alternate between sandy and muddy compositions, tabular geometry, and thicknesses of 15–20 cm. The muddy heteroliths exhibit mottling, indicative of pedogenic processes (Fig. 1).

**Sandy Facies.** These facies are composed of medium to fine-grained sandstones; massive (Sm), with undulitic lamination (Sr), parallel stratification (Sp), and tangential cross-stratification of low and high angles (St). They are arranged in tabular to lenticular beds, extending laterally for tens of meters. The lenticular beds show erosive bases, while the tabular ones have sharp bases. The massive sandstone facies, towards the top of the section, are affected by load deformation structures. At the top of the section and in the sandstone facies with tangential cross-stratification and undulitic lamination, traces assigned to *Skolithos* isp. were identified (Fig. 1).

### Sedimentary Paleoenvironments

The facies analysis allows for the recognition and definition of three facies associations: (I) lacustrine facies association, (II) wet interdune facies association, and (III) dry interdune and dune facies association. The lacustrine facies association (I) is represented by massive (Fm) and laminated (Fl) pelites. The origin of these facies is associated with decantation processes in low-

energy zones occurring during the final stage of flow velocity decay (Bridge, 2003). Additionally, the presence of mollusks indicates relatively stable water bodies associated with a low-energy environment (Paz *et al.*, 2014). The wet interdune facies association (II), located in the middle and upper part of the section, is represented by sandy and muddy heterolithic facies, as well as sandy facies. The heterolithic facies generally present pedogenetic features such as mottling and undifferentiated bioturbation. Regarding the sandy facies, they exhibit load deformation structures. This facies association consists of sandstones with tangential cross-stratification of low angles and undulitic lamination. The intercalation of pelitic levels between the cross-stratified sets is common. Each traction event allows for the identification, by the presence of *Skolithos* isp., of colonization windows in the massive sandstone facies. In layers equivalent with those studied here and outcropping 25 km to the north, Paz *et al.* (2014) interpreted that the sets with tangential cross-stratification of low angles represent the migration stages of the frontal faces of the dunes within the wet interdunes, while the thin levels of pelites alternating between the dune sets mark the re-establishment of normal sedimentation processes (dominant decantation) within the water bodies. Load deformation structures (*e.g.*, convolute stratification) were also identified. These structures were also documented by Ponce *et al.* (2018) in localities to the north of the study area, and their genesis is related to concurrent sediment sliding processes associated with partial material liquefaction. Most fossil vertebrates and invertebrates here reported come from these facies.

Finally, medium to fine-grained sandstones with high-angle tangential cross-stratification (St) were identified at the top of the surveyed section. These facies correspond to the dry interdune and dune facies association (III). The facies analysis done in this work corroborates the proposal previously made by Paz *et al.* (2014), Díaz-Martínez *et al.* (2018), and Gómez *et al.* (2022), which indicated an increase in the aridity of the depositional system towards the top of the studied succession.

## SYSTEMATIC PALEONTOLOGY

MOLLUSCA Linnaeus, 1758

BIVALVIA Linnaeus, 1758

UNIONOIDA Stoliczka, 1871

HYRIIDAE Swainson & Berry, 1840

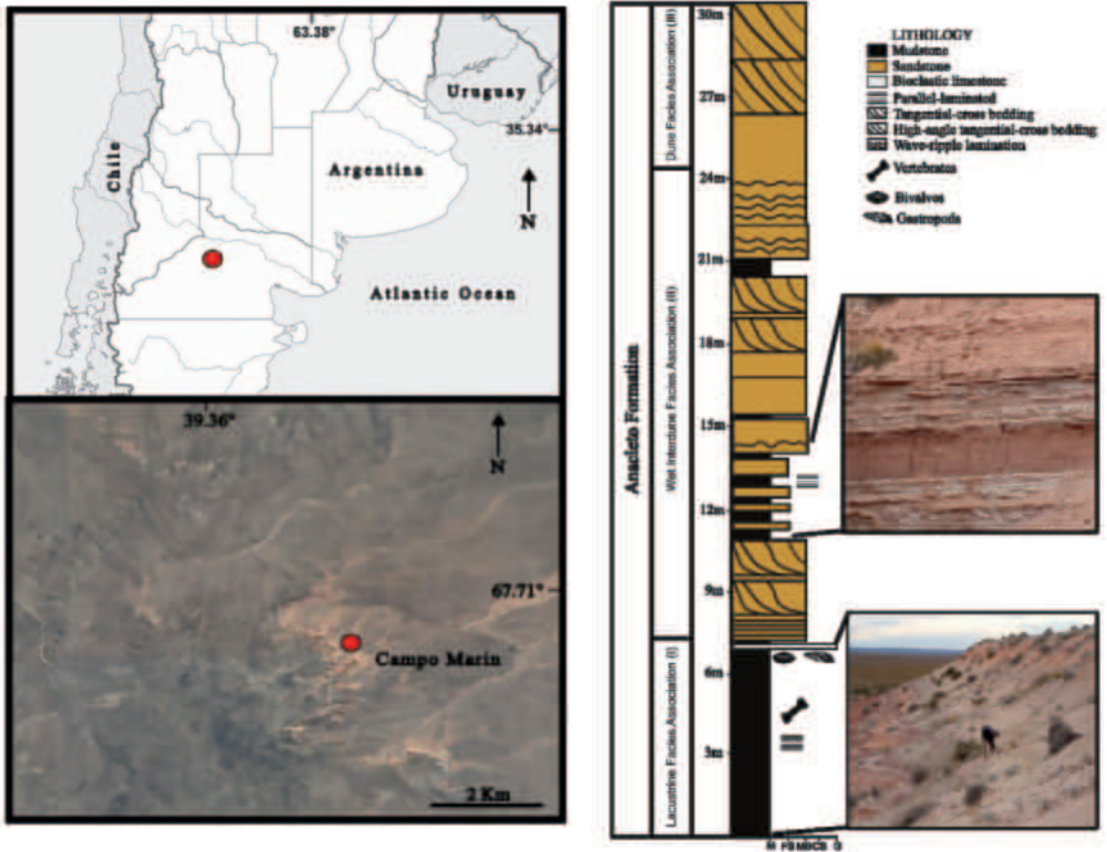


Fig. 1. Geographic map showing the location of Marín family Farm and associated stratigraphic profile, showing main sedimentary facies and levels that yielded fossil specimens here described.

*Diplodon* Spix, 1827  
*Diplodon* sp.

**Referred material.** MPCN-Pi 1240, six internal shell molds (Fig. 2A–D).

**Description.** All specimens are represented by internal molds, with occasional and mostly poorly preserved shell remains. Fragmentation and abrasion are low, and encrustation and bioerosion are absent. Anyway, some nacreated areas can be observed in the inner layer of some specimens. All the molds indicate that the bivalves were buried with the valves articulated, but some specimens retain a small aperture between the valves, and others show a vertical displacement between the valves, probably a post-burial event.

**Measurements.** Specimen 1: maximum height, 20.4 mm; maximum length, 37.5 mm; maximum width (including the two valves), 15.3 mm. Specimen 2: maximum height, 22.1 mm; maximum length, 44.2 mm; maximum width (including the two valves), 21.1 mm. Specimen 3: max-

imum height, 24.5 mm; maximum length, 45.9 mm; maximum width (including the two valves), 18.8 mm.

**Remarks.** According to the shape of the molds, and especially to the presence of striation in the umbonal zone of one specimen (Fig. 2A), the specimens are identified as *Diplodon* sp. When compared with other Mesozoic Southern species of the genus, specimens here described resemble in the radial striation of the umbonal area and the overall shape the species *Diplodon bodenbenderi* Doello-Jurado 1927, from the Late Cretaceous of the Neuquina Basin (Allen and Loncoche formations; see Manceñido & Damborenea, 1984; Parras & Griffin, 2013, and references therein), and *Antediplodon esperanzaensis* Camacho, 1957 from the Jurassic Mount Flora Formation from Antarctic Peninsula (see Martínez *et al.*, 2020). General shape also resembles *D. batoviensis* Martínez & Figueiras, 1991 from the Late Jurassic Tacuarembó Formation of Uruguay. The poor preservation of the specimens

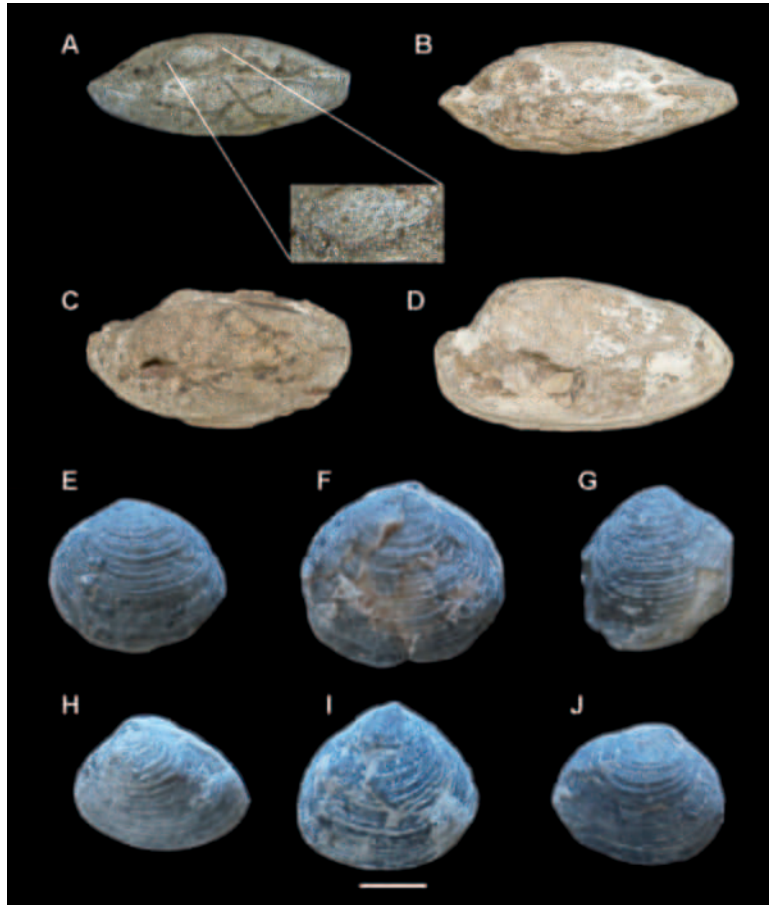


Fig. 2. (A–D) *Diplodon* sp., MPCN-Pi 1240, two internal shell molds, (A–B) dorsal and (C–D) lateral views. (E–J) *Cyanocyclus dinosauriorum* MPCN-Pi 1241, six shells, in lateral view. Scale bars = 5 mm (E–J), 1 cm (A–D).

here reported precludes a clear referral beyond the generic level.

Gigli *et al.* (2019) reported the presence of *Diplodon* from transitional units between Anacleto and Allen formations, but without figures or description of the specimens. Thus, present report constitutes the first unambiguous record of the genus from the Anacleto Formation.

VENEROIDA Adams & Adams, 1856

CORBICULIDAE Gray, 1847

*Cyanocyclus* Blainville, 1818

*Cyanocyclus dinosauriorum* (Doello-Jurado,  
1927)

**Referred material.** MPCN-Pi 1241, 57 articulated shells (Fig. 2E–J).

**Remarks.** The specimens are referred to *C. dinosauriorum* and differ from the closely related *C. pehuenchensis* by having a subrectangu-

lar oval contour, with the length exceeding the height, a posterior position of the umbones, and a tendency to develop more lamellous comarginal ornamentation (Manceñido & Damborenea, 1984). The species was previously reported from Anacleto Formation by several authors (see Manceñido & Damborenea, 1984).

GASTROPODA Cuvier, 1797

CAENOGASTROPODA Cox, 1960

ARCHITAENIOGLOSSA Haller, 1890

CYCLOPHOROIDEA Gray, 1847

MEGALOMASTOMATIDAE Blanford, 1864

*Aperostoma* Troschel, 1847

*Aperostoma* sp.

**Referred specimen.** MPCN-Pi 1242, four incomplete shells (Fig. 3A).

**Description.** Known by flattened and incomplete helicoid molds, having 1.5 whorls; umbil-

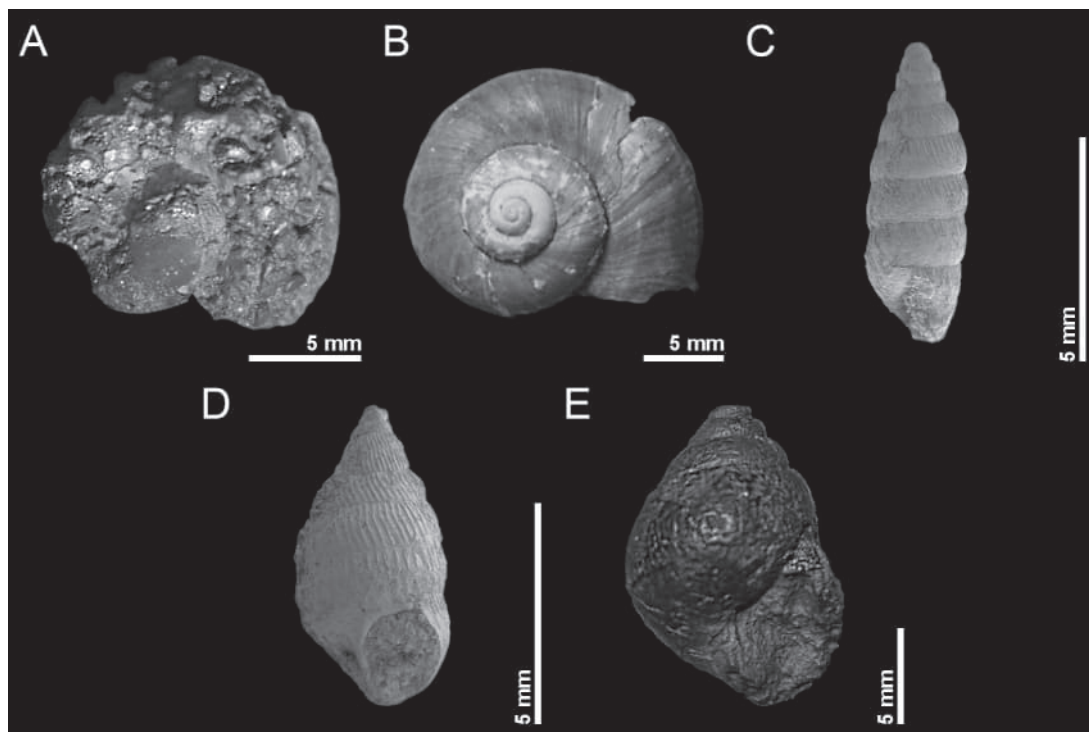


Fig. 3. (A) *Aperostoma* sp., MPCN-Pi 1242, incomplete shell, in dorsal view. (B) *Aperostoma inca*, MACN-IN 40.844, shell of extant specimen found at the margins of Lipeo river, just opposite to Baritú National Park, Santa Victoria department, North Salta, NW Argentina, in dorsal view. (C) *Allopeas* sp., MPCN-Pi 1243, shell, in dorsal view. (D) *Leptinaria* sp., MPCN-Pi 1244, shell, in dorsal view. (E) *Bulimulus* sp., MPCN-Pi 1245, shell, in dorsal view. Scale bar = 5 mm.

icate; subcircular aperture, descendent; matrix constituted by cemented coarse granules.

**Measurements.** Main diameter, 16.0 mm; height, 8.8 mm.

**Remarks.** Numerous species of the family inhabit tropical South America, including Brazil (Simone, 2006) and Perú (Ramírez *et al.*, 2003). The only species of the genus present in northern Argentina is *Aperostoma inca* (d'Orbigny, 1835). This is characterized by a depressed shell, last whorl descendent; large umbilicus, sutures marked, low spire, 6 to 7 whorls, aperture circular and corneous operculum, spiral striae on the last whorls (Fig. 3B; Fernández & Morris, 1984). *Aperostoma inca* currently lives in Maldonado hill at El Rey and Baritú National Parks, in Salta Province, northern Argentina. These areas belong to the Sierras Subandinas region, characterized by a warm climate and abundant rainfalls, especially in summer (Fernández & Morris, 1984).

STYLOMMATOPHORA (Schmidt, 1855)  
SUBULINIDAE Fischer & Crosse, 1877

*Allopeas* Baker, 1935

*Allopeas* sp.

**Referred specimen.** MPCN-Pi 1243, single shell (Fig. 3C).

**Description.** Medium-sized fusiform shell, having at least 8 whorls with regular growth; axial ribs curved, retractives, 30 in the last whorls, no intercostular axial striae; aperture small, slightly oblique; protoconch smooth.

**Measurements.** Main diameter, 8.05 mm; height, 2.9 mm.

**Remarks.** A fossil belonging to the extinct species *Allopeas agnolini* was described from lower levels of the Late Cretaceous (Maastrichtian) Chorrillo Formation at La Anita farm, Santa Cruz Province, Argentina (Miquel, 2024). This species differs in that it has 6 slightly convex whorls, the last whorl very expanded, with axial ribs oblique and irregular, and sutures marked rather inclined (Miquel, 2024; Fig. 2G, Tab. 5).

*Leptinaria* Beck, 1837  
*Leptinaria* sp.

**Referred specimen.** MPCN-Pi 1244, single shell (Fig. 3D).

**Description.** Shell small, almost pyramidal; with, approximately, 8 adult whorls, the first two plano-convex, the last two whorls very broad; spire low with rapid growth; teleoconch with retractile axial ribs, approximately 40 in the last whorls, no intercostal axial striae; aperture almost circular; protoconch with 2 whorls, smooth.

**Measurements.** Main diameter, 8.2 mm; height, 4.3 mm.

**Remarks.** *?Leptinaria* sp. was described from La Anita farm, Santa Cruz Province, Argentina, in lower levels of the late Cretaceous (Maastrichtian), Chorrillo Formation. This species differs in having high spire, 6 whorls slightly convex with regular growth, last whorl large, suture marked, rather inclined, and aperture wide and rounded (Miquel, 2024; Fig. 2I, Tab. 6). Present record confirms the presence of the genus *Leptinaria* in Cretaceous sediments.

ORTHALICOIDEA Albers & Martens, 1860

BULIMULIDAE Tryon, 1867

*Bulimulus* Leach, 1814

*Bulimulus* sp.

**Referred specimen.** MPCN-Pi 1245, single shell (Fig. 3E).

**Description.** Medium-sized shell, short spire and last whorl large and wide, first whorls convex and with regular growth, sutures marked, spire broken; aperture long, not wide, narrowing towards its extreme, umbilical region obscured by matrix.

**Measurements.** Total length, 18.8 mm; main diameter, 12.3 mm; whorls, 4 (broken).

**Remarks.** The cast here described is somewhat similar to that of the extant species *Bulimulus rushii* Pilsbry, 1897, from Uruguay and Argentina (Scarabino, 2003). Recently, a Cretaceous *Bulimulus* sp. was described from La Anita farm, Santa Cruz Province, Argentina, in lower levels of the late Cretaceous (Maastrichtian), Chorrillo Formation. These specimens differ in having plano-convex whorls, except the last whorl rather convex with sutures inclined, somewhat deep, and a larger aperture (Miquel, 2024; Fig. 2L, Tab. 8).

VERTEBRATA Cuvier, 1812

ACTINOPTERYGII Cope, 1867

HOLOSTEI Müller, 1844

GINGLYMODI Cope, 1872

LEPISOSTEIFORMES Hay, 1929

LEPISOSTEIDAE Cuvier, 1825

Lepisosteidae indet.

**Referred material.** MPCN-Pv 1011, a basioccipital and 5 isolated vertebrae (Fig. 4A–K).

**Description.** The basioccipital (Fig. 4A–C) exhibits a bilobed concave articular surface for articulation with the first vertebra (Fig. 4A). Dorsally to the concave surface, the bases of the neural arches can be observed. Ventral to the concavity, it is a bone with numerous antero-posterior striations, indicating an extensive articular surface for the parasphenoid (Fig. 4B). Laterally, there is a foramen for the passage of the intermetameric artery (Fig. 4C).

Available vertebrae are opisthocoealous and identified as belonging to the abdominal region (Fig. 4D–K). One of them has a more anteroposteriorly compressed body (3.7 mm), suggesting its more anterior position within the series (Fig. 4D–G). All these vertebrae exhibit parapophyses for articulation with the ribs, which, although fractured, are clearly defined (Fig. 4F). The neural arches are fused to the respective vertebral body, but are also fragmentary (Fig. 4E, J). In ventral view, folds and grooves are observed, as well as a longitudinal keel. The longest vertebra measures 3.7 mm in total length.

**Remarks.** The specimens here described exhibit a combination of traits that is unique to Lepisosteidae: opisthocoealous vertebrae with deep lateral fossae and deep ventral keel with a deep longitudinal excavation (Cione, 1987; Grande, 2010; Szabó *et al.*, 2016). Some authors argued that vertebral morphology may be taxonomically useful (*e.g.*, Gayet & Meunier, 1986, 2001; Gayet *et al.*, 2002). However, the isolated and poorly informative nature of the specimens here described, allow us to consider them as Lepisosteidae indet.

Lepisosteids are frequent in the Late Cretaceous of South America and Argentina (*e.g.*, Cione, 1987; Gayet & Brito, 1989; González Riga, 1999; Gayet *et al.*, 2001; Martinelli & Forasiepi, 2004; Martinelli & Teixeira, 2015; Agnolín *et al.*, 2024). However, these remains are mostly fragmentary, encompassing elements such as scales, vertebrae, and teeth that were regarded as indeterminate Lepisosteidae (González Riga, 1999; Martinelli & Forasiepi, 2004; Agnolín *et al.*, 2024) or cf. *Atractosteus* (Cione, 1987).

ACANTHOPTERYGII Rosen & Patterson, 1969

PERCOMORPHA Cope, 1871

Percomorpha indet.



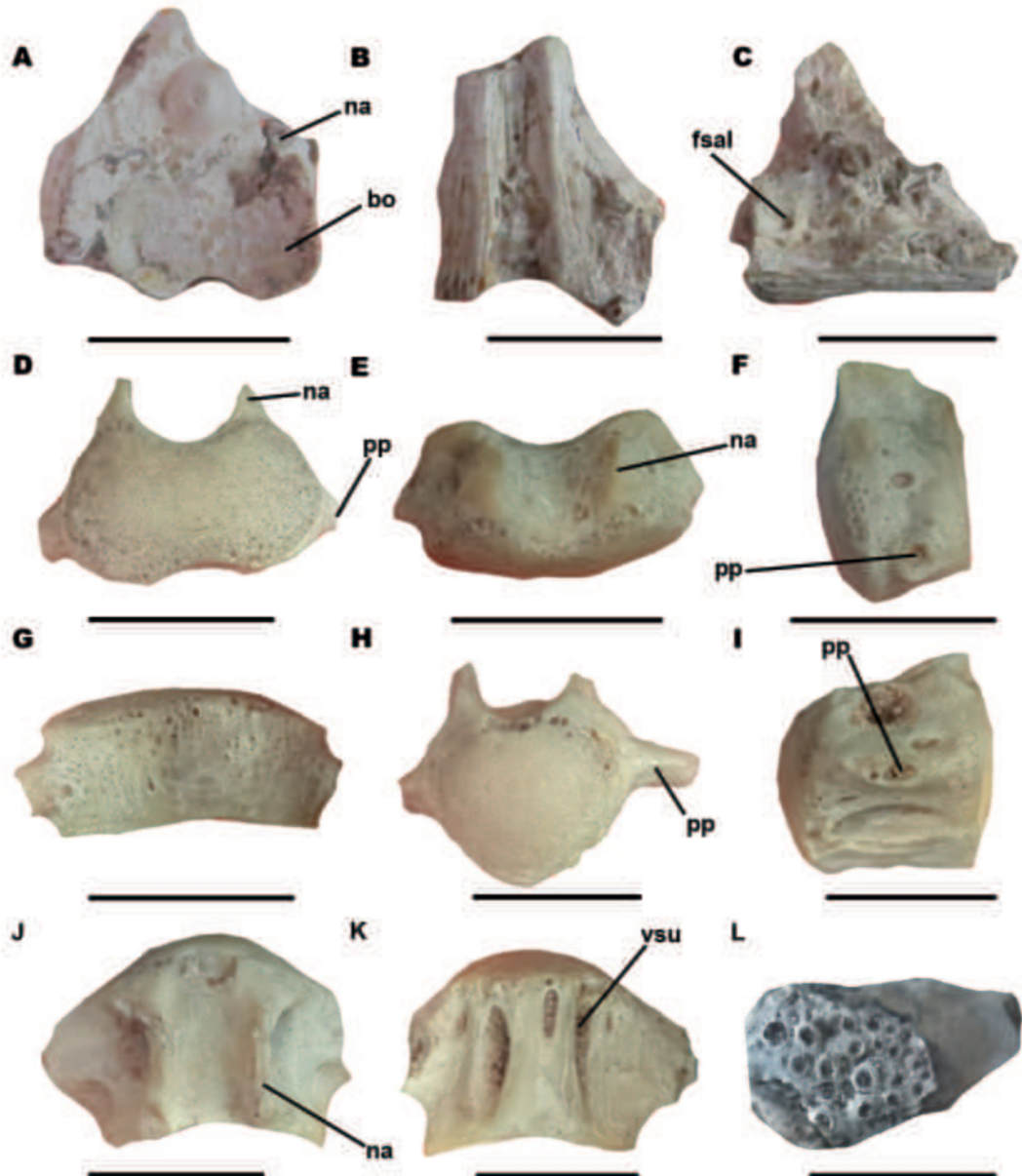


Fig. 4. (A–K) *Lepisosteiformes* indet., MPCN-Pv 1011, cranial and postcranial elements, basioccipital in (A) posterior, (B) ventral, and (C) lateral views; anterior abdominal vertebra in (D) anterior, (E) dorsal, (F) lateral, and (G) ventral views; posterior abdominal vertebra in (H) anterior, (I) lateral, (J) dorsal, and (K) ventral views. (L) *Percomorpha* indet. MPCN-Pv 1035, pharyngeal plate in occlusal view. Abbreviations: bo, basioccipital; fsal, lateral foramen for intermetameric artery; na, neural arch; pp, parapophysis; vsu, ventral sulcus. Scale bar = 0.5 mm.

**Referred material.** MPCN-Pv 1035, incomplete pharyngeal plate (Fig. 4L).

**Description.** The fragment corresponds to a small section of a pharyngeal plate referred to *Percomorpha*. It measures just over half a centimeter. The occlusal surface contains multiple

semicircular alveoli, which likely served as anchors for teeth. The medial surface of the bone has a straight edge, along which the alveoli are arranged in an orderly pattern. The teeth are not preserved.

**Discussion.** Many bony fishes exhibit modifications of their branchial arches to enhance food

processing (Liem, 1973). In some cases, the pharyngeal arches have evolved into a functional set of jaws, referred to as the pharyngeal jaw apparatus. Among many Percomorpha, this apparatus consists of two independent upper and two lower bones, which are sutured, forming a single structure (Casciotta & Arratia, 1993; Burrell, 2016). The incomplete nature of the specimen does not allow referring to it beyond the Percomorpha level.

Similar structures have been described at other paleontological sites in Patagonia Argentina, such as Los Alamitos and Loncoche (Cione, 1987; González Riga, 1999).

SARCOPTERYGII Romer, 1955

DIPNOI Müller, 1845

CERATODONTIDAE Gill, 1872

*Metaceratodus* Chapman, 1914

*Metaceratodus* cf. *M. kaopen* (Apesteuguía,  
Agnolín & Claesson, 2007)

**Referred material.** MPCN-Pv 1012, 5 prearticular tooth plates and 3 pterygopalatine tooth plates (Fig. 5A–N).

**Description.** The pterygopalatine tooth plates are fused to the pterygopalatine bone (Fig. 5A). On the dorsal surface of this bone, the circular base of the ascending process is located at the level of the second denticulation (Fig. 5B). Medially, the anterior portion of the symphysis with dorsoventrally grooves is visible (Fig. 5C–D). The pterygopalatine tooth plates have five denticulations, with the first being the longest and narrowest (Fig. 5E). The inner angle is positioned at the level of the second cleft.

Wear on the pterygopalatine tooth plates is evident on the posterior side of the denticulations and on the occlusal surface. In the first case, wear facets form on the posterior side of the denticulations, indicated by enamel loss (Fig. 5E). Additionally, a pronounced wear facet is present in the anterior portion of the first denticulation, near the inner angle. On the occlusal surface, wear is noticeable due to wear patterns caused by jaw movement. Furthermore, wear causes the last two denticulations to merge and form a step.

The prearticular tooth plates are fused to the prearticular bone (Fig. 5H). In all recovered specimens, the symphysis area of this bone is not preserved (Fig. 5I). In ventral and labial view, there is the Ruge's canal divided by a ridge (Fig. 5J).

The prearticular tooth plates have four denticulations. The first denticulation is the longest and has a slightly widened base (Fig. 5K–L). The

medial edge of the prearticular tooth plates tends to be curved (Fig. 5H, K), while the lingual edge is straighter (Fig. 5H). The inner angle is positioned slightly ahead of the second denticulation (Fig. 5H, L)

Wear on the prearticular tooth plates is mainly evidenced by wear facets on the anterior side of the denticulations (Fig. 5M). The wear of the last denticulation forms the spur that is elevated in labial view (Fig. 5N).

**Remarks.** The tooth plates are referred as to *Metaceratodus* cf. *M. kaopen* due to the presence of distinctive features in the pterygopalatine tooth plates, such as an obtuse inner angle (R1 and RN) located at the level of the second cleft, a step formed by the wear of the last two denticulations, and a wear facet anterior to the first denticulation (Panzeri, 2023). Additionally, the prearticular tooth plates exhibit an inner angle at the level of the first cleft. However, some specimens do not preserve all the diagnostic features of the species due to taphonomic damage (transported and fractured specimens; Fig. 5K–M). On the other hand, some exceptionally well-preserved materials might represent early ontogenetic stages (Fig. 5H–J), which may distort the morphology of certain characters, such as the widening of the first denticulation in prearticular tooth plates (Fig. 5Q–R).

Excepting some anomalous specimens (Panzeri & Muñoz, 2022), up to now, all Mesozoic dipnoans from Argentina have presented five denticulations in the pterygopalatine tooth plates and four in the prearticular tooth plates (Panzeri *et al.*, 2020, 2022). *Metaceratodus kaopen*, is a species previously restricted to the Anacleto Formation (Fig. 5O–R; Apesteuguía *et al.*, 2007; Cione & Gouiric Cavalli, 2012).

TESTUDINATA Klein, 1760 [*sensu* Joyce *et al.*,  
2020a]

PLEURODIRA Cope, 1865 [*sensu* Joyce *et al.*,  
2020b]

CHELIDAE Lindholm, 1929 [*sensu* Joyce *et al.*,  
2021]

Indeterminate genus and species

**Referred materials.** MPCN-Pv 1014, odd neural; MPCN-Pv 1015, free peripheral; MPCN-Pv 1016, two neurals, left costal 1, 3 free peripherals, 1 bridge peripheral, 10 costals, and indeterminate fragments; MPCN-Pv 1017, even neural; MPCN-Pv 1018, costal 1, 1 free peripheral, and undetermined fragments; MPCN-Pv 1019, free peripheral and left costal 1; MPCN-Pv 1020,



Fig. 5. Tooth plates of *Metaceratodus kaopen*, (A–N) MPCN-Pv 1012, pterygopalatine tooth plates, (A) tooth plate illustrating the wear pattern (arrows) and position of the inner angle (dashed line), (B) dorsal view with the base of the ascending process, (C) medial wear facet, (D) surface of the pterygopalatine bone symphysis, (E) wear facets posterior to the denticulations, (F–G) step formation due to wear of the last denticulations (arrow); prearticular tooth plates, (H) prearticular tooth plate illustrating the position of the inner angle and (I–J) the bone, (K) base of the widened first denticulation, (L–M) tooth plate with anterior wear of the denticulations, (N) spur formation (arrow); pterygopalatine tooth plates, (O) MPCN-PV-SN 7, pterygopalatine tooth plate, (P) MPCN-PV-SN 5, pterygopalatine tooth plate, (Q) MPCN-PV-1-004 prearticular tooth plate, and (R) MPCN-PV-SN 4 prearticular tooth plate referred to *Metaceratodus kaopen* from the Anacleto Formation (Panzeri, 2023). Abbreviations: af, anterior wear facet; pf, posterior wear facet; sy, symphysis. Scale bar = 1 cm.

neural ?1, left costal 1, and 2 free peripherals articulated; MPCN-Pv 1021, two peripherals articulated; MPCN-Pv 1022, neural, costal, pygal, peripheral, ?right hypoplastron, and indeterminate fragments; MPCN-Pv 1023, peripheral (Fig. 6).

**Description.** Specimens assigned to Chelidae gen. et sp. indet. from Marín farm share a subtle ornamentation formed by shallow anastomosed sulci belonging to a small to mid-sized turtle (20–25 cm of carapace length). Neural 1 is rectangular in contour, being longer than wide (Fig. 6A). It is crossed by the sulcus separating vertebrae 1 and 2. This sulcus has an anterior inflexion in the midline (Fig. 6A). In the preserved specimens, marginal scutes are restricted to peripheral plates. Besides, the body wall seems to have been large, because marginal scutes covered a narrow area in visceral view of peripheral plates (Fig. 6B, F). Costal 1 is a large element whose potential contacts were the nuchal antero-medially, peripherals 1–3 antero-laterally, neural 1 medially and costal 2 posteriorly. In visceral view, costal 1 bears thoracic ribs 1 and 2 and the scar for the axillar buttress (Fig. 6C–D). There is a costal plate, probably number 5 or 6, that bears an unusual pattern of scutes. This costal bears the sulcus separating two vertebral scutes (probably vertebrae 3 and 4) and the sulcus separating two pleural scutes (probably pleurals 3 and 4) (Fig. 6A). This scute pattern could have been caused by a malformation or it could represent an autapomorphy of this taxon. As there is no other costal showing this feature, we prefer to leave it as an anomaly for the moment. A putative right hypoplastron is identified; however due to the nature of the specimen only the base of the inguinal buttress is identified (Fig. 6G–H).

**Remarks.** These small and poorly decorated chelids from Marín could be similar to the Chelidae 4 recognized by de Broin (1987) for Los Alamitos Formation and to the Chelidae gen. et sp. indet 3 recognized by Martinelli & Forasiepi (2004) for Allen Formation.

Specimens MPCN-Pv 1014, MPCN-Pv 1017, and probably MPCN-Pv 1023 belong to bigger specimens than the mid-sized species recognized above. These bigger specimens could represent more mature specimens or they could belong to another, bigger, taxon. Due to their fragmentary nature, we prefer to identify all these specimens as belonging to a single taxon.

HYDROMEDUSINAE Georges, Birrell, Staint, McCord & Donnellan 1998 [*sensu* Joyce *et al.*, 2021]

cf. *Yaminuechelys* sp.

**Referred materials.** MPCN-Pv 1024, neural and left peripheral 3, 1 bridge peripheral, 3 free peripherals, costal fragment, fragment of right xiphoplastron; MPCN-Pv 1025, ?right xiphoplastron tip, and fragment of ?costal; MPCN-Pv 1026, fragments of peripherals and a cervical neural arch with both postzygophyses; MPCN-Pv 1013, proximal end of humerus (Fig. 7).

**Description.** The specimens assigned here as to cf. *Yaminuechelys* sp. comprise large plates with evident ornamentation formed by polygons and dichotomized furrows (Fig. 7A–D). These plates correspond to turtles with carapace lengths more than 60 cm. Among the specimens, there is a portion of a neural arch of a cervical vertebra (MPCN-Pv 1026) which bears the paired postzygophyses contacting each other in the midline posteriorly. This is a feature present in *Yaminuechelys* and in other long-necked chelids (*e.g.*, *Hydromedusa*, *Chelodina*). The proximal end of the humerus MPCN-Pv 1013 is expanded as is common in turtles. The humeral head is ovoid, being elongated along the proximo-distal axis. The medial process is well-developed being larger than the lateral process as is common in turtles. The medial process is rounded as in other chelids (*e.g.*, The lateral process is curved toward the intertubercular side. In the intertubercular view, a small secondary intertubercular fossa is present (Hermanson *et al.*, 2024).

**Remarks.** *Yaminuechelys* is a clade of turtles well-represented in the fossil record of the Cretaceous–Paleocene of Patagonia. They have been recorded in the Loncoche (Previtera & González Riga, 2008), Anacleto (de la Fuente *et al.*, 2010, 2015), Allen (Chelidae gen. et sp. indet. 1 of Martinelli & Forasiepi, 2004), Los Alamitos (Chelidae 1 of de Broin, 1987), La Colonia (Orizabala *et al.*, 2020), Salamanca (Bona & de la Fuente, 2005), Roca (Bona *et al.*, 2009), and probably Dorotea (Alarcón-Muñoz *et al.*, 2020; Moyano-Paz *et al.*, 2022) formations. There are three named species in the genus (*Y. gasparinii*, *Y. sulcipeculiaris*, and *Y. maior*), however, the specimens from Marín Farm are very fragmentary and do not allow a more precise taxonomic assignment.

Indeterminate genus and species

**Referred materials.** MPCN-Pv 1027, 1 free peripheral; MPCN-Pv 1028, 3 free peripherals, fragment of costal, left xiphoplastron, fragment

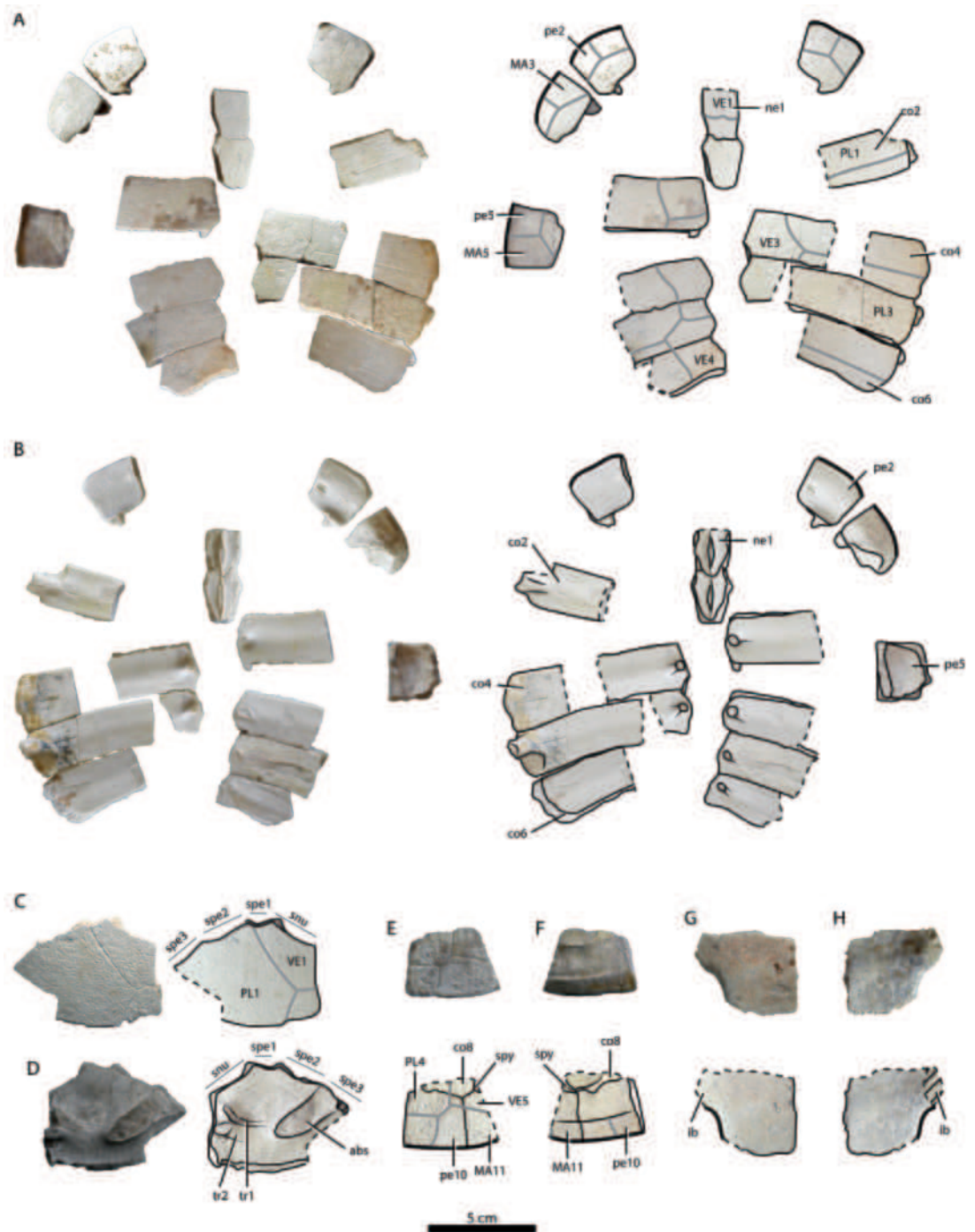


Fig. 6. Chelidae genus and species indeterminate, (A–B) MPCN-Pv 1016, carapacial remains in (A) dorsal and (B) visceral views; (C–D) MPCN-Pv 1020, left costal 1 in (C) dorsal and (D) visceral views; (E–F) MPCN-Pv 1021, left peripherals 10 and 11 in (E) dorsal and (F) visceral views. (G–H) MPCN-Pv 1022, ?right hypoplastron, in (G) dorsal and (H) visceral views. Abbreviations: abs, axillar buttress; co, costal plate; ib, inguinal buttress; MA, marginal scute; ne, neural plate; pe, peripheral plate; PL, pleural scute; snu, suture with nuchal plate; spe, suture with peripheral plate; spy, suprapygial; tr, thoracic rib; VE, vertebral scute. Scale bar = 5 cm.



Fig. 7. cf. *Yaminuechelys* sp., MPCN-Pv 1024 and MPCN-Pv 1025, (A) peripheral plate; (B) peripheral plate; right xiphiplastron in (C) ventral and (D) visceral views; neural arch of a cervical vertebra, MPCN-Pv 1026, in (E) left lateral, (F) ventral, and (G) posterior views; proximal end of left humerus, MPCN-Pv 1013, in (H) capitular, (I) ulnar, (J) intertubercular, (K) radial, and (L) proximal views. Abbreviations: hh, humeral head; is, ischiadic scar; lp, lateral process; MA, marginal scute; mp, medial process; na, neural arch; PL, pleural scute; poz, postzygapophysis; sif, secondary intertubercular fossa. Scale bar = 5 cm.

of plastron, and indet. fragment; MPCN-Pv 1029, 3 free peripherals; MPCN-Pv 1030, free peripheral; MPCN-Pv 1031, pygal, 5 free peripherals, 2 costals, and indeterminate fragments (Fig. 8).

**Description.** Small to mid-sized turtles (20–25 cm of carapace length). The plates assigned to this taxon are highly ornamented with polygons and dichotomized sulci, similar to *Yaminuechelys*

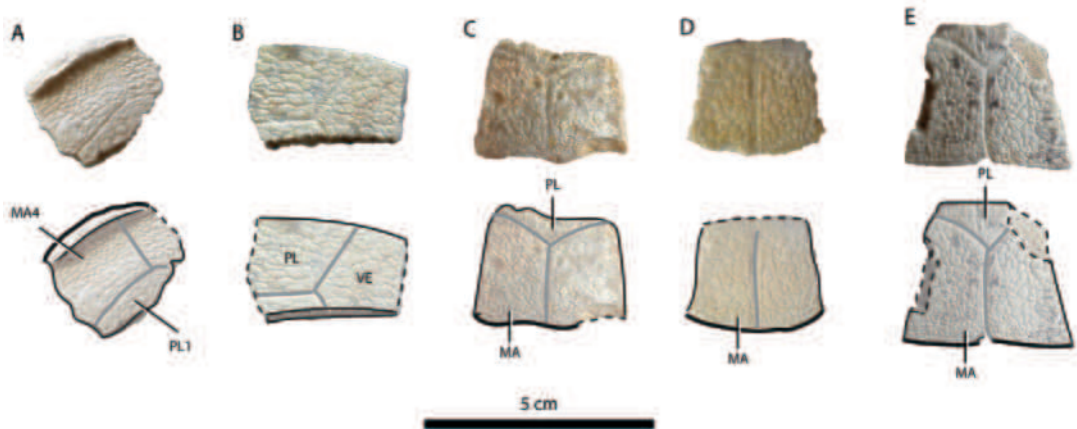


Fig. 8. Hydromedusinae gen. et sp. indet., (A) MPCN-Pv 1027, left peripheral 3; (B) MPCN-Pv 1031, costal plate; (C–D) MPCN-Pv 1029, peripheral plates; (E) MPCN-Pv 1031, peripheral plate. Abbreviations: MA, marginal scute; PL, pleural scute; VE, vertebral scute. Scale bar = 5 cm.

but with denser and smaller polygons, showing a more granuloid pattern. It is interesting to note that one preserved peripheral 3 (Fig. 8A) has an upturned border.

**Remarks.** This Hydromedusinae might be similar to the taxon identified as number 3 by de Broin (1987) for Los Alamos Formation and Chelidae gen. et sp. indet. 5 identified by Gasparini & de la Fuente (2000) for La Colonia Formation.

MAMMALIA Linnaeus, 1758

MERIDIOLESTIDA Rougier, Apesteeguía & Gaetano, 2011

?MESUNGULATOIDEA Rougier, Apesteeguía & Gaetano, 2011

Indeterminate genus and species

**Referred material.** MPCN-Pv 1036, fragment of right dentary (Fig. 9).

**Description and comparisons.** MPCN-Pv 1036 is assigned to Meridiolestida by the following combination of features: 1) labial alveolar margin lower than the lingual at the level of molars (Forasiepi et al., 2012; Martinelli et al., 2021; Rougier et al., 2021b); and 2) mesiodistally compressed root in the last molars (Rougier et al., 2011). MPCN-Pv 1036 is reminiscent to mesungulatoids and differs from most non-mesungulatoid meridiolestidans due to the presence of subcircular posterior molar roots and labial/buccal dentary margins that are strongly unequal in height (Harper et al., 2018; Rougier et al., 2021b). Thus, MPCN-Pv 1036 is tentatively assigned to Mesungulatoidea.

MPCN-Pv 1036 is a relatively large-sized

meridiolestidan, comparable in size to an indeterminate meridiolestidan (Forasiepi et al., 2012; Rougier et al., 2021a), smaller than *Mesungulatum* Bonaparte & Soria, 1985, *Orretherium* Martinelli et al., 2021, and *Coloniatherium* Rougier et al., 2009, but larger than *Groebertherium* Bonaparte, 1986b, *Cronopio* Rougier, Apesteeguía & Gaetano, 2011, *Necrolestes* Ameghino, 1891, *Leonardus* Bonaparte, 1990, *Reigitherium* Bonaparte, 1990, and *Solanotherium* Connelly, Cardozo, Montgomery & Rougier, 2024 (Chornogubsky, 2011; Rougier et al., 2011, 2012, 2021b; Chimento et al., 2012; Harper et al., 2018). The preserved fragment measures 7.1 mm anteroposteriorly, and the mandibular height at the labial border, at the level of anterior edge of the last alveolus, is 4.9 mm.

The preserved fragment is a posterior portion of the right dentary, with part of one alveolus and a complete posteriormost alveolus, including remnants of a molar root. The anterior alveolus is slightly wider than the posterior one. These posterior alveoli, including the root, are subcircular (or slightly kidney-shaped) in occlusal view, being wider than they are long. In the preserved root, a radicular canal of subcircular contour is present. There is no marked interalveolar process, and the separation between the alveoli is very narrow, indicating that the roots of each molar were close together, similar to *Peligrotherium*, *Coloniatherium*, and unlike *Reigitherium* and *Orretherium* (Forasiepi et al., 2012; Harper et al., 2018; Martinelli et al., 2021; Rougier et al., 2021b). Posterior to the preserved alveoli, there is a small hole, located near the lingual edge. The base of coronoid process is pre-

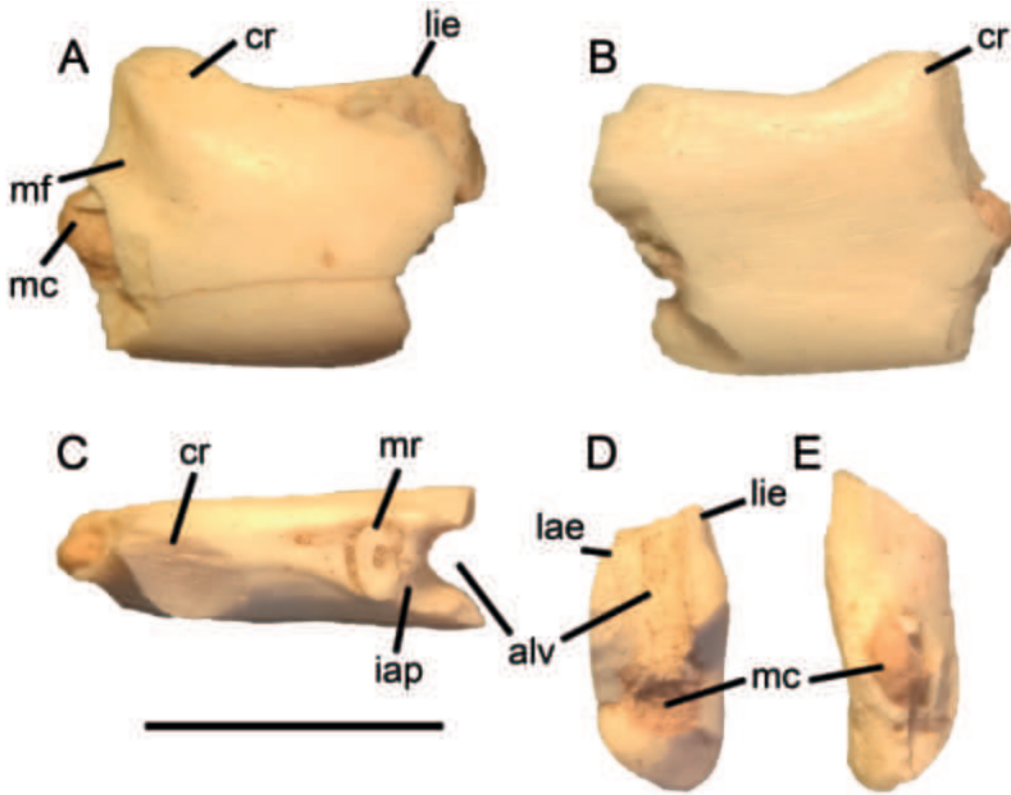


Fig. 9. Right lower jaw of a meridiolestidan mammal, MPCN-Pv 1036, in (A) labial, (B) lingual, (C) occlusal, (D) mesial, and (E) distal views. Abbreviations: alv, alveolus; cr, coronoid process; iap, interalveolar process; lae, labial edge; lie, lingual edge; mc, mandibular canal; mf, masseteric fossa; mr, molar root. Scale bar = 5 mm.

served, which is subcircular in cross-section (as in *Coloniatherium*, and unlike *Necrolestes*, the Coniacian specimen, *Reigitherium*, *Orretherium*, and *Peligrotherium*; Páez Arango, 2008; Rougier *et al.*, 2009, 2021a, 2021b; Chimento *et al.*, 2012; Forasiepi *et al.*, 2012; Harper *et al.*, 2018; Martinelli *et al.*, 2021) and is positioned well behind the last alveolus, showing a pronounced retro-molar space. The base and alveolar level form an obtuse angle (as in *Reigitherium*, Harper *et al.*, 2018; Rougier *et al.*, 2021b), unlike most meridiolestidans, in which this angle is almost straight (e.g., *Peligrotherium*, *Coloniatherium*, the Coniacian specimen, *Necrolestes*, *Cronopio*, *Orretherium*; Páez Arango, 2008; Rougier *et al.*, 2009, 2011, 2012; Chimento *et al.*, 2012; Forasiepi *et al.*, 2012; Wible & Rougier, 2017; Martinelli *et al.*, 2021). The labial and lingual margins are sharp, forming pronounced ridges. Both margins are highly unequal, with the lingual margin much higher than the labial margin. Posterior to the coronoid process, there is a slight concavity corresponding to part of the masseteric fossa. In

mesial and distal views, a large mandibular canal filled with sediments can be seen.

**Remarks.** This specimen together with a partial jaw of an indeterminate meridiolestidan (Goin *et al.*, 1986; Forasiepi *et al.*, 2012) represent the only findings of mammals in the Anacleto Formation beds (see Rougier *et al.*, 2021a).

CROCODYLIFORMES Hay, 1929  
Indeterminate genus and species

**Referred material.** MPCN-Pv 1032, incomplete osteoderm (Fig. 10A)

**Remarks.** The specimen shows an ornamentation composed of subcircular pits separated by ridges (Ortega *et al.*, 2000; De Andrade *et al.*, 2011; Lio *et al.*, 2019). This pattern of ornamentation is present in osteoderms of all crocodyliforms except for some specific clades that either lack ornamentation (metriorhynchids) or have a vermiculate ornamentation composed by shallow grooves and sinuous crests (Pol *et al.*, 2013), such as sphagesaurians and sebe-



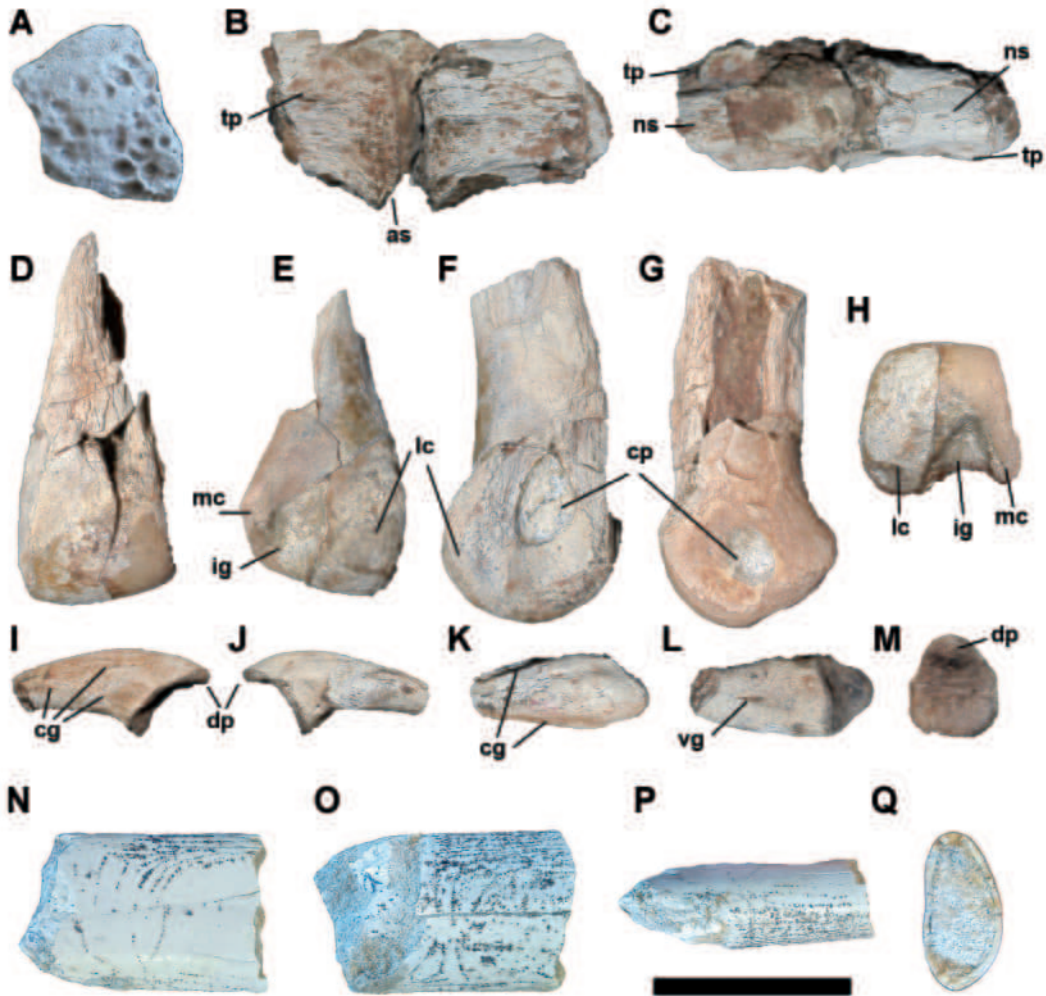


Fig. 10. Crocodyliformes, Pterosauria, and Theropoda specimens from Marín farm. (A) Crocodyliformes cf. Neosuchia, genus and species indeterminate, MPCN-Pv 1032, partial scute in dorsal view. (B–M) Abelisauridae, indeterminate genus and species, MPCN-Pv 1033, two incomplete caudal vertebrae in (B) lateral and (C) dorsal views; distal metatarsal II from the right side in (D) dorsal, (E) ventral, (F) lateral, (G) medial, and (H) distal views; left ungual pedal phalanx IV-5 in (I) lateral, (J) medial, (K) dorsal, (L) ventral, and (M) proximal views. (N–Q) Pterosauria indet., MPCN-Pv 1037, wing metacarpal in (N) ventral, (O) dorsal, (P) side, and (Q) cross-section. Scale bar = 3 cm.

cosuchians (Gasparini, 1981, 1984; Pol *et al.*, 2014). Among the crocodyliforms recorded in the Late Cretaceous of Gondwana, the two groups that bear the plesiomorphic pitted ornamentation pattern in osteoderms are uruguaysuchids (including the diverse genus *Araripesuchus*) and peirosaurids (Ortega *et al.*, 2000; da Silva Marinho *et al.*, 2006; Pol & Gasparini, 2007).

PTEROSAUMORPHA Kuhn-Schnyder & Rieber, 1986

PTEROSAURIA Kaup, 1834  
Indeterminate genus and species

**Referred material.** MPCN-Pv 1037, possible wing metacarpal (Fig. 10N–Q).

**Description.** The specimen consists of a shaft fragment of about 3.5 cm in length and 2.4 in maximum width. It is elliptical D-shaped in the cross-section and is flattened dorsoventrally. The dorsal surface shows a subtle longitudinal groove, whereas the ventral surface is gently convex. The external bone surface is smooth, and shows a very thin cortex (~1.2 mm), tending to be thicker at the edges.

**Remarks.** Despite the lack of articulations, identification as a pterosaur is based on its

very thin bone cortex, which is an uncontroversial pterosaurian feature (Kellner *et al.*, 2019). Its large size indicates that it is referable to non-Archaeopterodactyloidea Pterodactyloidea (Kellner, 2003). Wing metacarpals of pterosaurs are elongated and usually D-shaped in cross-section (Wellnhofer, 1985; Kellner *et al.*, 2019), quite similar to MPCN-Pv 1037. In contrast, phalanges from the wing finger tend to show subtriangular or t-shaped cross-section (Kellner *et al.*, 2019).

Present record constitutes the first finding of a pterosaur from Anacleto Formation beds in Patagonia.

DINOSAURIA Owen, 1842

THEROPODA Marsh, 1881

ABELISAUROIDEA Bonaparte, 1991

ABELISAUROIDEA Bonaparte & Novas, 1985

Indeterminate genus and species

**Referred material.** MPCN-Pv 1033, disarticulated two middle caudal vertebra, right metatarsal II, left unguis pedal phalanx IV-5 possibly from the same individual (Fig. 10D–M).

**Description.** The two middle caudal centra are incomplete and were found in articulation. The preserved base of the transverse process is anteroposteriorly short and originates at the posterolateral area of the neurocentral suture (Fig. 10B–C). Both caudal centra are sub-elliptical in cross-section and lack pleurocoels resembling the middle caudal vertebrae of other abelisaurids (O'Connor, 2007; Méndez, 2012). The anterior-most vertebra has a wide articular surface for the haemal arch.

The right metatarsal II is represented only by its distal end. The preserved part of the shaft is laterally compressed, and the bone is transversely expanded towards the distal end. In distal view, the medial condyle is globose and robust whereas the lateral one is narrow and smaller, both are separated by a deep intercondylar groove. This groove is obliquely oriented when viewed posteriorly. The medial collateral pit is smaller and deeper than the lateral one, which in turn is large and shallow.

Unguis phalanx of digit IV is almost complete, only lacking its distal end. The lateral and medial surfaces have Y-shaped vascular grooves, surrounding a sub-triangular bump close to the proximal articular surface, a feature widespread in Abelisauroida (Novas *et al.*, 2004a). In proximal view, the claw is asymmetrical in contour and bears a low median ridge separating the articular surface into two facets. The overall mor-

phology resembles the pedal unguis of digit IV of *Aucasaurus* (Coria *et al.*, 2002a; Baiano, 2021). In lateral view, the unguis is dorsoventrally depressed through its body, is poorly recurved and bears a well-developed proximodorsal lip which projects farther posteriorly than the proximoventral one. The ventral surface is nearly flat and has a deep median longitudinal groove. Numerous minute pits are scattered over the lateral, medial and ventral surfaces of the phalanx, close to the proximal articular area.

**Remarks.** The metatarsal II of MPCN-Pv 1033 is notably similar in size and morphology to the metatarsal II of *Aucasaurus*. In distal view, both show a similar contour in which the lateral condyle is much wider than the medial one. Further, both MPCN-Pv 1033 and *Aucasaurus* have wide and deep dorsal extensor fossa. The unguis phalanx IV is notably similar to the phalanx IV of *Aucasaurus* in the development of the dorso-proximal lip, and the presence of grooves on the ventral flat surface (Coria *et al.*, 2002a; Baiano *et al.*, 2021).

The incomplete nature of MPCN-Pv 1033 precludes a referral beyond Abelisauridae level. Abelisaurid remains from Anacleto Formation include *Aucasaurus garridoi* (Coria *et al.*, 2002a) and an indeterminate species MPCN-PV 69 (Gianechini *et al.*, 2015; Baiano *et al.*, 2021). *Abelisaurus comahuensis*, once thought to belong to this unit, has been recently regarded as coming from Allen Formation (Maastrichtian) (Bonaparte & Novas, 1985; Delaloye & Garrido 2017). The abelisaurid remains presented here are similar in size when compared to MPCN-PV 69 and *Aucasaurus*.

SAUROPODA Marsh, 1878

TITANOSAURIA Bonaparte & Coria, 1993

RINCONSAURIA Calvo, González Riga &

Porfiri, 2007

*Chadititan calvoi* nov. gen. et sp.

**Derivation of the name.** Chadi, from the Mapundungum, meaning salt; the specific epithet honors the late Jorge O. Calvo (1962–2023) a great colleague that recently passed away, who described several titanosaurs and coined the name Rinconsauria.

**Holotype.** MPCN-Pv 1034, 5 proximal caudal vertebrae, 4 distal caudal vertebrae, proximal end of left and right humeri, proximal end of right and left ulnae, distal end of left ulna, distal end of right radius, proximal end of left pubis, proximal and distal end of right femur, proximal

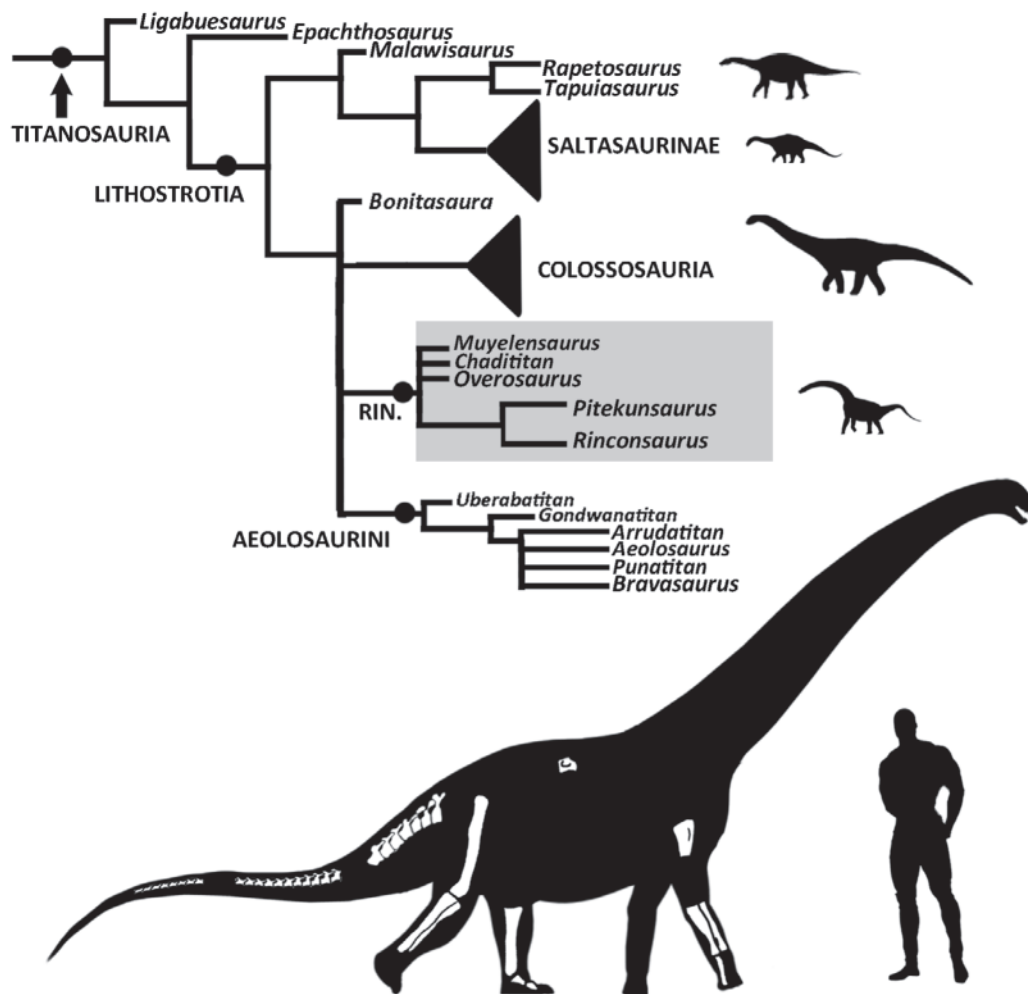


Fig. 11. (A) simplified cladogram showing the phylogenetic position of *Chadititan calvoi* nov. gen. et sp. among titanosaurs (see Supplementary Data 2); (B) silhouette of *Chadititan calvoi* nov. gen. et sp., showing the available bones belonging to different individuals.

end of left tibia, proximal and distal end of right tibia, proximal and distal end of right fibula, indeterminate metapodials (Fig. 11).

**Paratypes.** MPCN-Pv 1035, 1 incomplete caudal vertebra, proximal end of right humerus, incomplete right coracoid, proximal end of right femur, proximal end distal end of right tibia; MPCN-Pv 1036, distal end of right tibia; MPCN-Pv 1037, proximal end of right humerus, proximal end of right ulna, incomplete left tibia preserving proximal and distal ends, incomplete proximal end of right tibia, indeterminate metapodials; MPCN-Pv 1038, nearly complete right femur; MPCN-Pv 1039, very small specimen, probably representing a juvenile individual, composed by 1 dorsal vertebral centrum, 3 incomplete caudal verte-

bral centra, proximal end of left ulna, proximal end of right tibia, incomplete and indeterminate metacarpals and metatarsals; MPCN-Pv 1040, 2 incomplete caudal vertebrae, fragmentary metatarsals, left distal end of metatarsal IV and articulated phalanx IV-1, right metatarsal IV with articulated phalanx IV-1, right phalanges III-1 and III-2 (ungual); MPCN-Pv 1041, 3 incomplete caudal vertebrae.

All available specimens of *Chadititan calvoi* are represented by poorly preserved and incomplete skeletons belonging to small individuals, coming from different sites, but from the same stratigraphic level. The well-ossified distal end of long bones, together with the entirely fused neural arch and centrum of caudal vertebrae are

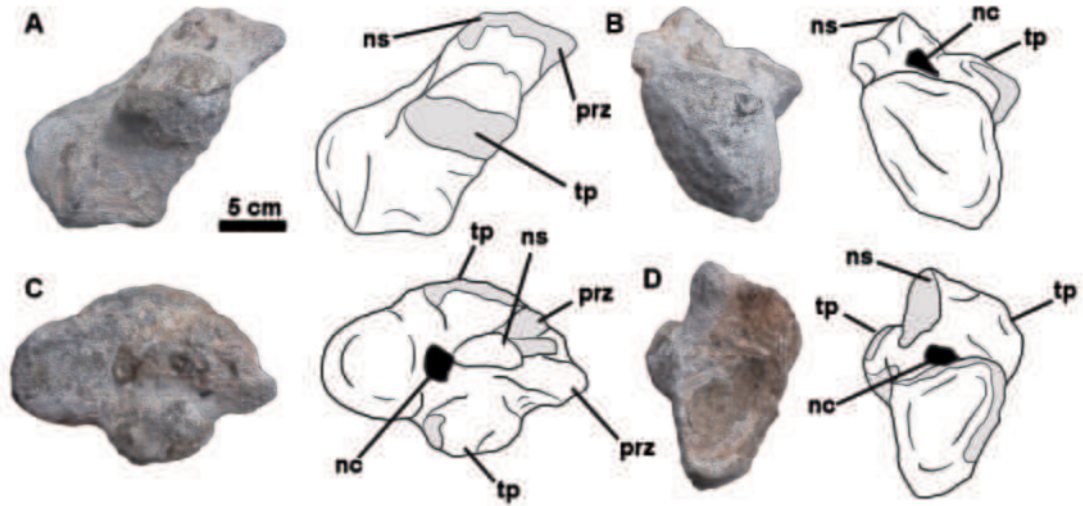


Fig. 12. *Chadititan calvoi* nov. gen. et sp., anterior caudal vertebra of holotype MPCN-Pv 1034 in (A) left lateral, (B) posterior, (C) dorsal, and (D) anterior views. Abbreviations: nc, neural canal; ns, neural spine; prz, prezygapophyses; tp, transverse process. Scale bar = 5 cm.

congruent with the somatic maturity of the individuals.

**Diagnosis.** Very small and gracile rinconsaur titanosaur (preserved femoral length of 73.5 cm) diagnosed on the basis of the following combination of characters: straight-shafted femur lacking a lateral protuberance (shared with *Muyelensaurus*; poorly developed in *Rinconsaurus* and present and forming a shelf-like prominence in *Pitekunsaurus*; Calvo & González Riga, 2003; Filippi & Garrido, 2008), femoral head dorsomedially projected, far from the level of the greater trochanter (shared with *Rinconsaurus* and *Muyelensaurus*; not dorsally oriented in *Pitekunsaurus*; Filippi & Garrido, 2008), gracile humerus (robust, with expanded proximal end in *Rinconsaurus* and *Narambuenatitan*; Calvo & González Riga, 2003; Filippi *et al.*, 2011) with very deep anterior excavation having well-defined dorsal and lateral margins, low olecranon on ulna (as in *Narambuenatitan* and *Muyelensaurus*; prominent and bump-like in *Pitekunsaurus*; Filippi & Garrido, 2008), procoelous caudals (amphicoelous-biconvex or amphicoelous-opisthocelous-biconvex caudal centra in *Rinconsaurus* and *Pitekunsaurus*; Calvo & González Riga, 2003; Filippi & Garrido, 2008), and anterior caudals with neural arch continuous with the anterior margin of the vertebral centrum (shared with *Muyelensaurus*; separated by a notch and posterior to the anterior margin of the vertebral centrum in *Pitekunsaurus*, *Rinconsaurus*,

and *Overosaurus*; Calvo & González Riga, 2003; Calvo *et al.*, 2007; Filippi & Garrido, 2008). In spite that *Chadititan calvoi* shows few overlapping materials with *Overosaurus*, the anterior and posterior caudals of *Overosaurus* are notably box-like, shorter and transversely as wide or wider than long, whereas in *Chadititan* vertebrae are elongate and transversely compressed (width/length index is between 0.5 to 0.4 in anterior caudals of *Chadititan*; 0.7 to 0.78 in anterior caudals of *Overosaurus*; see Coria *et al.*, 2013).

**Description.** All known specimen are congruent in that *Chadititan calvoi* was a very small and gracile-built titanosaur. When compared with the femoral length of *Bonatitan*, the estimated body length of *Chadititan* may be estimated at about 7 meters long. It is worthy to mention that no single osteoderm was found in the area. Since no osteoderms were found in association with other rinconsaurians, it is possible to speculate that they were absent in these titanosaurs (the mention of a possible rinconsaur having osteoderms was made by Filippi *et al.* (2023), but this remains unpublished).

**Caudal vertebrae.** All caudal vertebrae are strongly procoelous and relatively long and narrow (Figs. 12–14). Anterior caudal vertebrae of *Chadititan* are somewhat distorted, being transversely compressed and with the neural arch incompletely preserved. All vertebrae lack neural spines, which are represented by their bases. These indicate that the neural spine was relatively thick and anteroposteriorly narrow. The

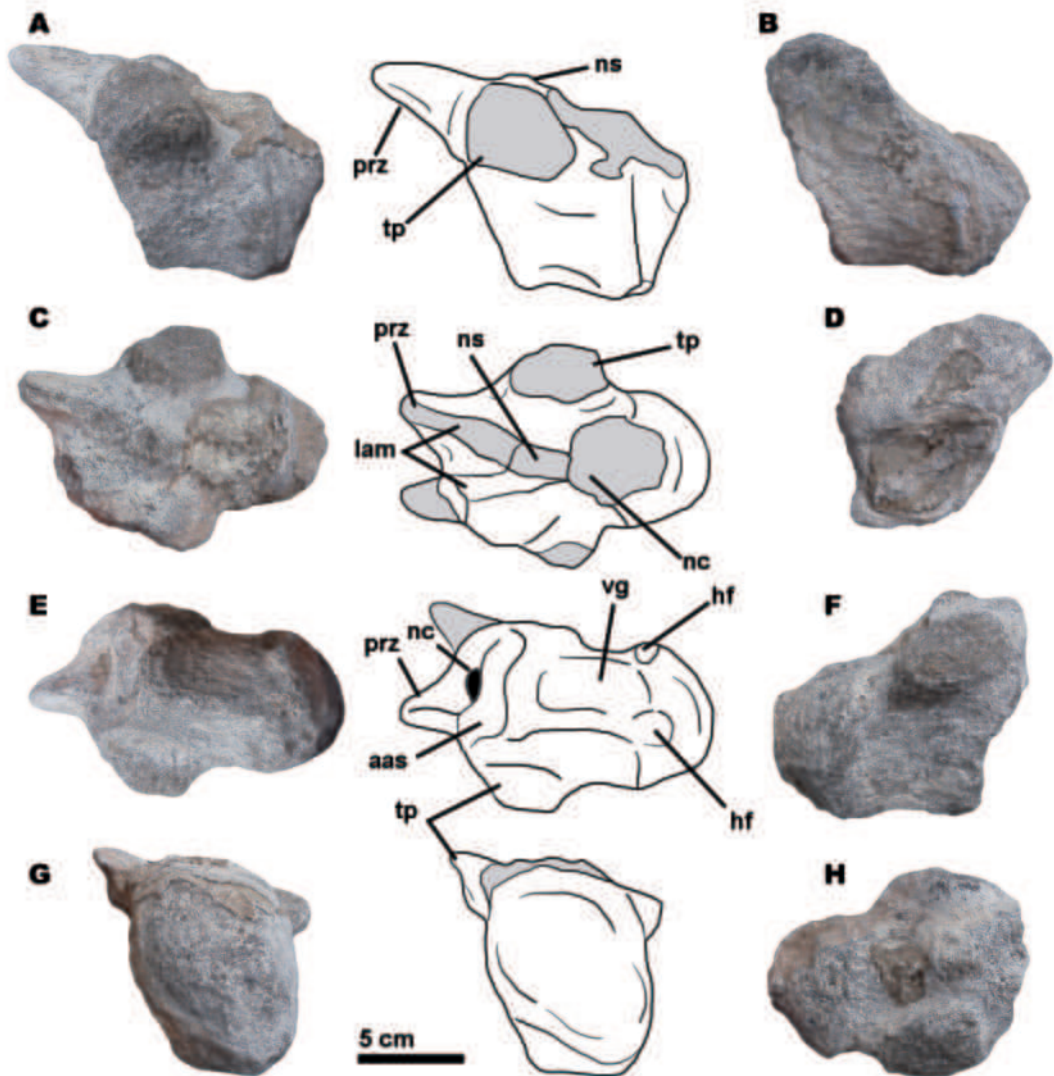


Fig. 13. *Chadititan calvoi* nov. gen. et sp., two anterior caudal vertebrae of holotype MPCN-Pv 1034 in (A–B) left lateral, (C, H) dorsal, (D) anterior, (E) ventral, (F) right lateral, and (G) posterior views. Abbreviations: aaf, anterior articular surface of centrum; hf, haemal facet; lam, spinoprezygapophyseal lamina; nc, neural canal; ns, neural spine; prz, prezygapophyses; tp, transverse process. Scale bar = 5 cm.

neural spine is located close to the anterior margin of the vertebral centrum.

The vertebral centra are notably elongate, much narrower than long (the width/length index is between 0.5 to 0.4). The lateral walls of the centra are tall and gently concave, and delimit a relatively narrow ventral surface. This gives to the centrum a smooth hourglass outline in ventral view. On its ventral surface there is a longitudinal groove delimited by two longitudinal ridges.

The neural arch of anterior caudals is continuous with the anterior margin of the centrum

(Figs. 12–13). The base of the arch indicates that it was strongly anteriorly slanted, and that partially overlapped the preceding vertebra. The prezygapophyses are elongate and narrow, with reduced prezygapophyseal facets. The spinoprezygapophyseal laminae are thick and well defined.

The neural canal is very small and subtriangular in contour. The interprezygapophyseal and diaprezygapophyseal laminae are thick and well-defined.

Posterior caudals are notably elongated, much narrower than long (the width/length in-

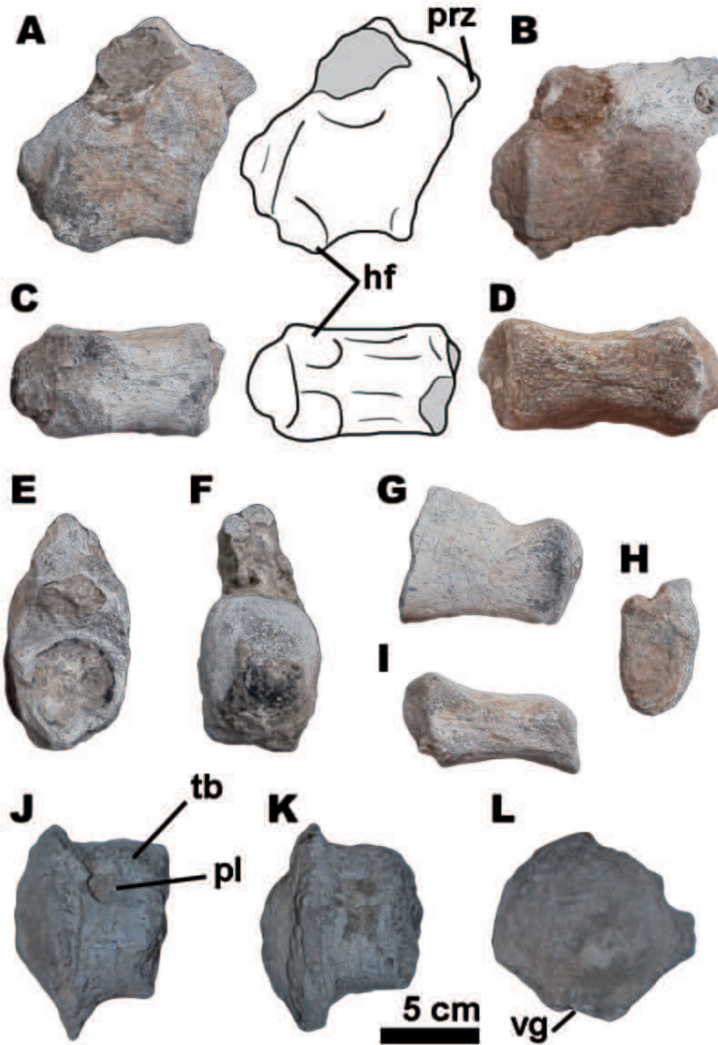


Fig. 14. Vertebrae of *Chadititan calvoi* nov. gen. et sp., posterior caudal vertebrae of holotype MPCN-Pv 1034 in (A–B) right lateral, (C–D, I) ventral, (E, H) anterior, (F) posterior, and (G) left lateral views; dorsal or sacral vertebra of MPCN-Pv 1039 in (J) left lateral, (K) ventral, and (L) anterior views. Abbreviations: hf, haemal facets; pl, pleurocoel; prz, prezygapophyses; tb, tabicate pleurocoel; vg, ventral groove. Scale bar = 5 cm.

dex is about 0.40 to 0.45) (Fig. 14G–I). The posterior half of the centrum is much dorsoventrally lower than the anterior one. The lateral walls of the centra are tall and nearly straight, and delimit a relatively narrow ventral surface. On its ventral surface there is a longitudinal groove delimited by two longitudinal ridges that end on prominent haemal facets.

In these vertebrae the neural spine is not located at the level of the anterior margin of the centrum. The prezygapophyses are strongly anterodorsally oriented and the postzygapophyses are nearly horizontally oriented.

**Possible sacral or dorsal vertebra.** A single

and incompletely preserved centrum is available. The centrum has an eye-shaped pleurocoel, as occurs in most titanosaurs. It shows well-defined margins and shows an obliquely oriented crest at its inner surface that partially divides it (Fig. 14J–L). The expanded margins of the articular surface are strongly expanded, forming a prominent rim, a condition exhibited by posterior dorsals and posterior or anterior sacrals.

**Forelimb.** The proximal half of the humerus is very gracile and straight-shafted, with a poorly transversely expanded proximal end (Fig. 15). The medial margin of the bone is obliquely oriented and nearly straight, a condition reminis-

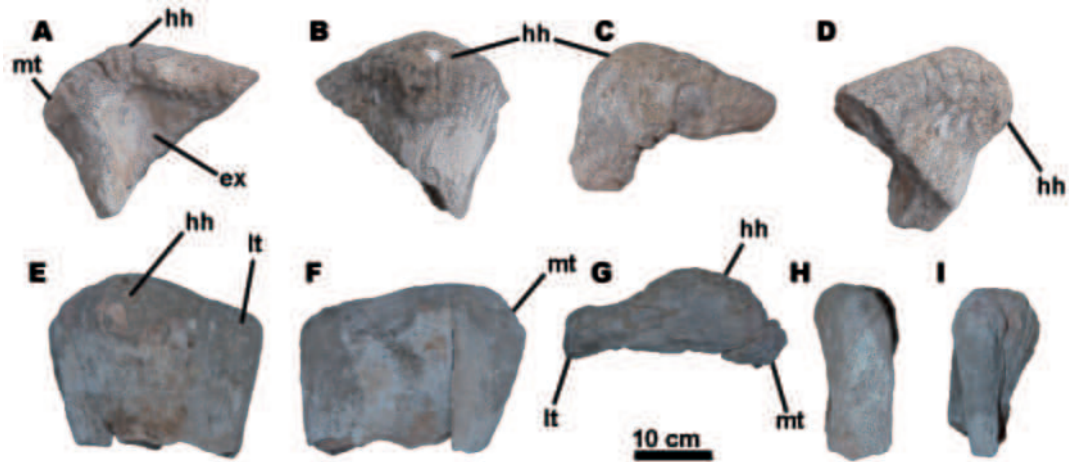


Fig. 15. *Chadititan calvoi* nov. gen. et sp., proximal end of left humerus of holotype MPCN-Pv 1034 in (A) anterior, (B) posterior, (C) proximal, and (D) lateral views; proximal end of right humerus of MPCN-Pv 1037 in (E) posterior, (F) anterior, (G) proximal, (H) lateral, and (I) medial views. Abbreviations: ex, anterior excavation; hh, humeral head; lt, lateral tubercle; mt, medial tubercle. Scale bar = 10 cm.

cent of that of *Rinconosaurus* (Pérez-Moreno et al., 2023). The humeral head is well-developed, prominent and bulbous, strongly medially placed. The medial tubercle is prominent. The proximal end of the humerus is strongly excavated anteriorly. The proximal and medial margins of this excavation are strongly delimited by thickened bone margins. In proximal view the humerus is kidney-shaped, with a strongly concave anterior margin and a deeply convex posterior one.

The ulna shows a relatively stout and triradate proximal end (Fig. 16). The proximal end is rugose, it shows a rounded, convex and strongly proximally projected olecranon process. The deep and well-excavated radial fossa separates prominent anteromedial and anterolateral processes. The anteromedial process is subtriangular in contour and relatively narrow and is slightly laterally curved towards its anterior end. The anterolateral process is relatively thick and poorly anteriorly extended, and is posteriorly delimited by a proximodistally extended longitudinal concavity. The proximal end of the ulna in the holotype specimen (MPCN-Pv 1034) is taphonomically compressed, resulting in a strongly transversely compressed subtriangular contour.

The distal end of a right radius shows a poorly defined anterior fossa, which is not observed in distal view (Fig. 16G–H, O). The posteromedial and posterolateral condyles are well-defined and separated by a shallow concavity. The medial condyle is more distally projected than the lateral one.

**Pelvic girdle.** The only element representing

the pelvic girdle is the proximal and distal end of pubis. The proximal end is represented by a relatively thick and expanded and dorsally oriented iliac peduncle. Pubic acetabular rim and iliac articular surface meet at an angle of about 10° and are nearly continuous, being separated by a low crest. The iliac articular surface is very deep and wide, ovoidal in contour and is strongly laterally exposed, suggesting that the pubic blade was notably laterally tilted. The anteroproximal corner of the pubis is strongly anteriorly extended and is subtriangular in contour. In medial view the pubic surface is nearly flat. The area of the pubic foramen has not been preserved. The distal end is poorly preserved, but indicates that the pubis was anteroposteriorly and transversely expanded, forming a boot as in other titanosaurs.

**Hindlimb.** The femur is notably elongate and gracile; its shaft is strongly anteroposteriorly compressed (Fig. 17). It shows poorly transversely expanded proximal and distal ends. The femoral head is globose and strongly proximomedially oriented, with a strong medial projection. It is much more proximally extended than the major trochanter.

The lateral margin of the shaft is nearly straight, it lacks a lateral bump and is gently medially curved. The medial margin of the shaft is slightly concave. The preserved part of the shaft indicates that the fourth trochanter was located distal to the proximal third of the bone, probably at shaft mid-length.

The distal end of the bone is much more expanded than the proximal one. Distal condyles

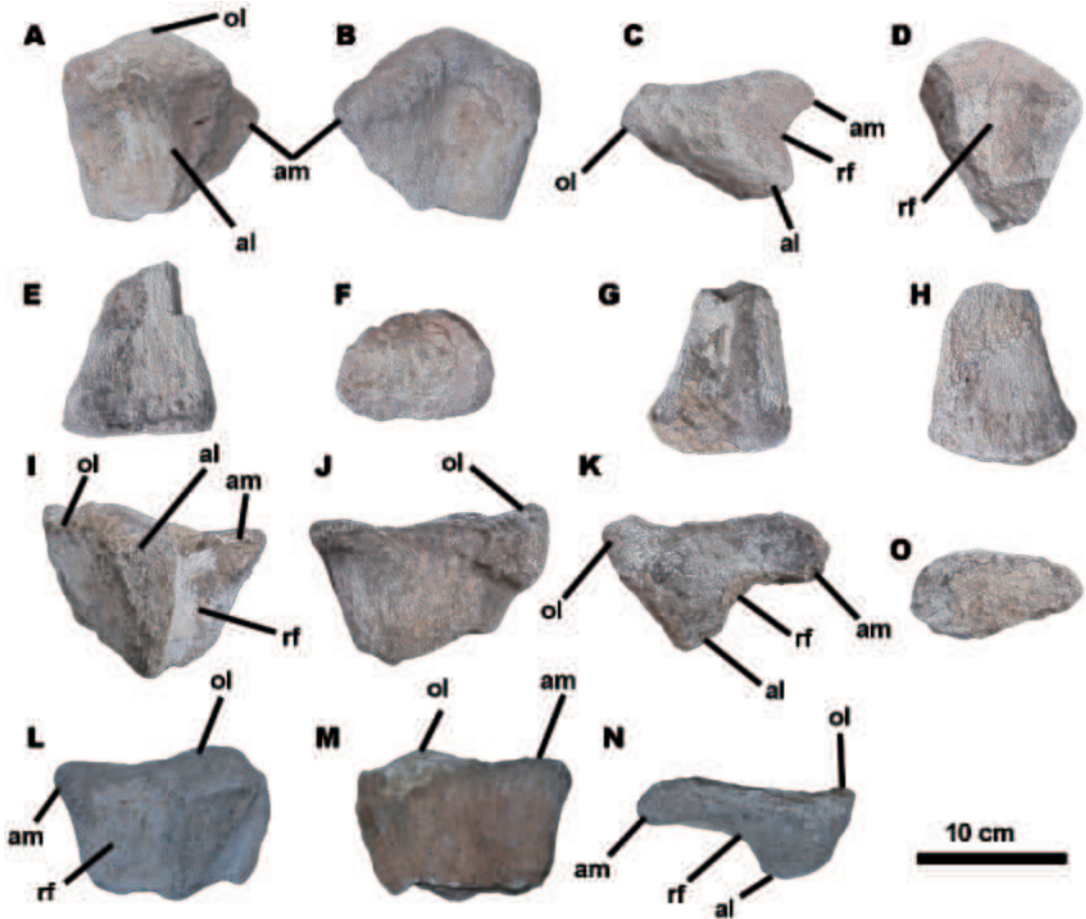


Fig. 16. Ulna and radius of *Chadititan calvoi* nov. gen. et sp., proximal end of right ulna of MPCN-Pv 1037 in (A) lateral, (B) medial, (C) proximal, and (D) anterior views; distal end of left ulna of holotype MPCN-Pv 1034 in (E) posterior and (F) distal views; distal end of right radius of MPCN-Pv 1034 in (G) lateral, (H) medial, and (O) distal views; proximal end of right ulna of MPCN-Pv 1034 in (I) lateral, (J) medial, and (K) proximal views; proximal end of left ulna of MPCN-Pv 1034 in (L) lateral, (M) medial, and (N) proximal views. Abbreviations: al, anterolateral process; am, anteromedial process; ol, olecranon; rf, radial fossa. Scale bar = 10 cm.

are sub-equally extended distally and are separated by a deep intercondylar groove. The lateral condyle and tibiofibular crest are separated by a gently concave to nearly straight surface. The medial condyle is notably narrow and strongly posteriorly oriented, being much more prominent than the tibiofibular crest. The anterior intercondylar groove is well excavated and proximally extended.

The tibia is relatively gracile and with poorly expanded proximal and distal ends (Fig. 18). Because there is no single completely preserved tibia, its length, when compared with the femur, cannot be estimated. The proximal end of tibia is roughly subcircular in contour, with its anteroposterior axis being subequal with the trans-

verse one. The cnemial crest is notably thin and poorly anteriorly extended; it is slightly laterally tilted. It is separated from the rest of the bone by a very deep and well defined, proximodistally extended excavation.

The distal end of the tibia is ovoidal in contour, being poorly transversely expanded (Fig. 18E–I). The distal condyles are subequal in distal extension, the posterior one being narrower than the anterior one and with its lateral margin being proximally extended. Both are separated by a shallow and poorly defined notch.

Metatarsal IV is gracile and transversely narrow (Fig. 19A–D). The articular surface for the metatarsal V is represented by a shallow and poorly defined groove. Medially, exists a deeply



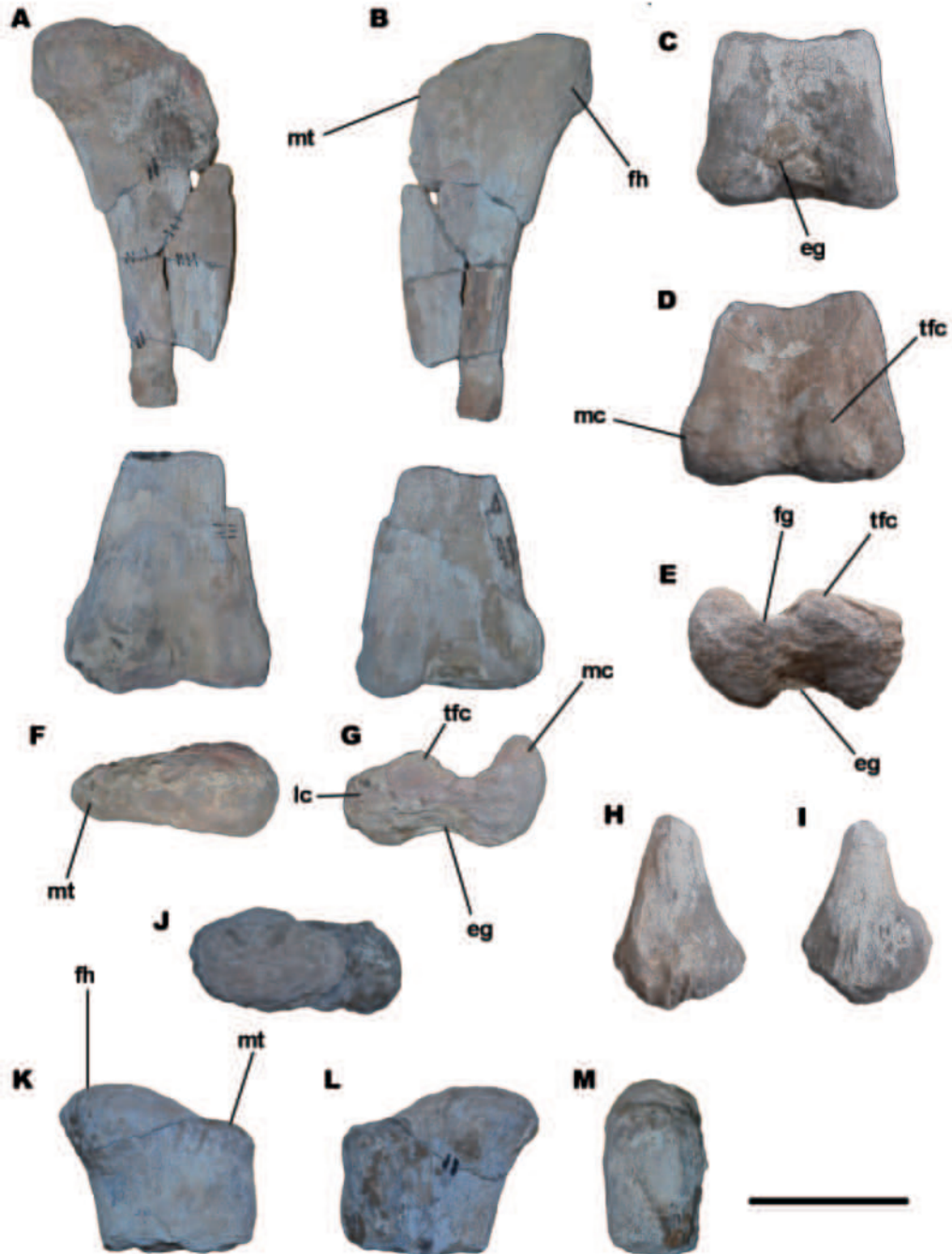


Fig. 17. *Chadititan calvoi* nov. gen. et sp., nearly complete right femur of MPCN-Pv 1038 in (A) anterior, (B) posterior, (F) proximal, and (G) distal views; distal end of right femur of holotype MPCN-Pv 1034 in (C) anterior, (D) posterior, (E) distal, (H) lateral, and (I) medial views; proximal end of right femur of MPCN-Pv 1035, in (J) proximal, (K), posterior, (L) anterior, and (M) lateral views. Abbreviations: eg, extensor groove; tfc, tibiofibular crest condyle; fg, femoral groove; fh, femoral head; lc, lateral condyle; mc, medial condyle; mt, major trochanter. Scale bar = A-I, 20 cm; J-L, 10 cm.

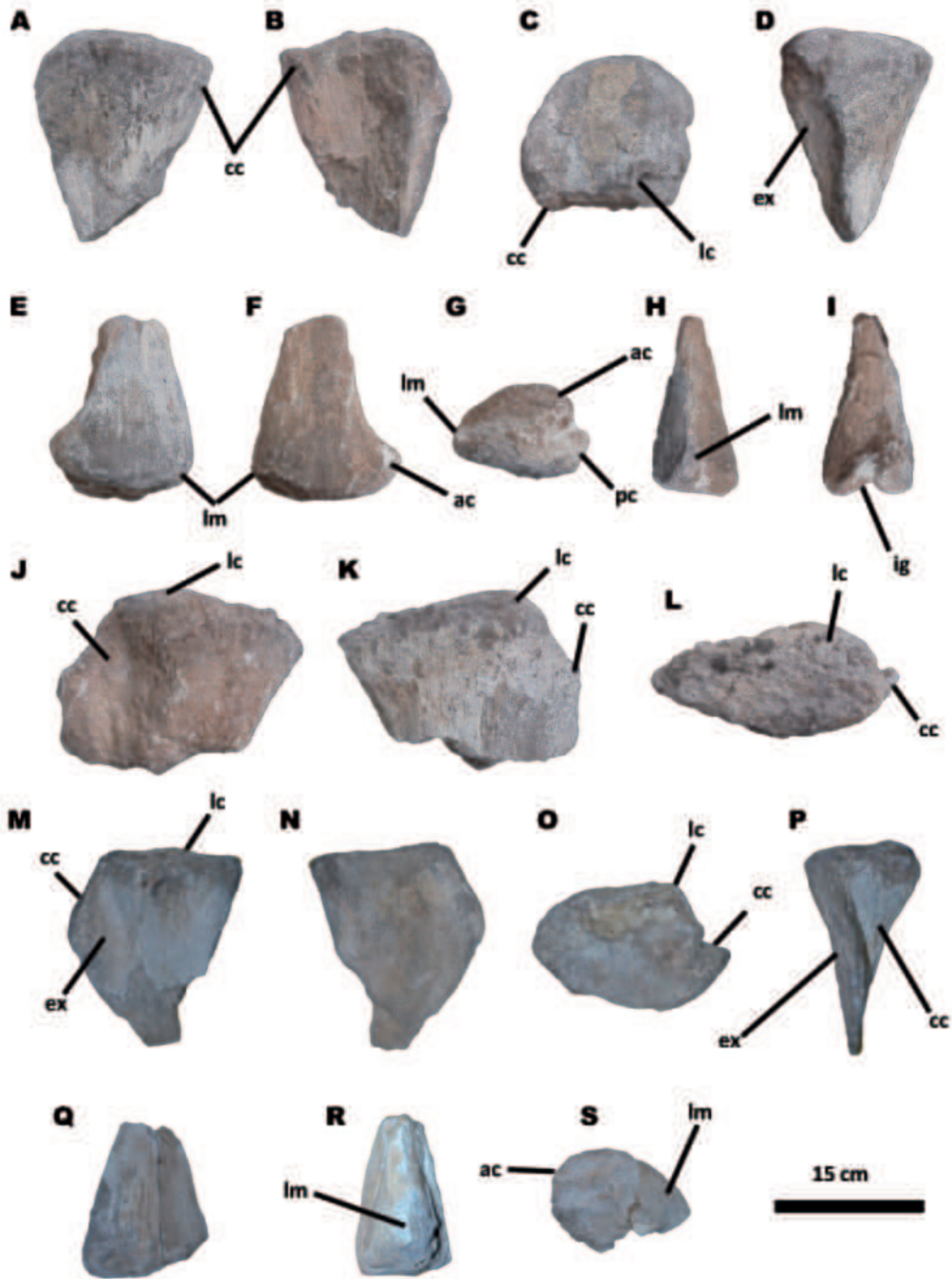


Fig. 18. Tibiae of *Chadititan calvoi* nov. gen. et sp., proximal end of left tibia of holotype MPCN-Pv 1034 in (A) medial, (B) lateral, (C) proximal, and (D) anterior views; distal end of right tibia of holotype MPCN-Pv 1034 in (E) posterior, (F) anterior, (G) distal, (H) lateral, and (I) medial views; proximal end of right tibia in (J) medial, (K) lateral, and (L) proximal views; right tibia of MPCN-Pv 1037 in (M) medial, (N) lateral, (O) proximal, (P) posterior, (Q) anterior, (R) posterior, and (S) distal views. Abbreviations: ac, anterior condyle; cc, cnemial crest; ex, medial excavation; ig, intercondylar groove; lc, lateral condyle; lm, lateral margin; pc, posterior condyle. Scale bar = 15 cm.

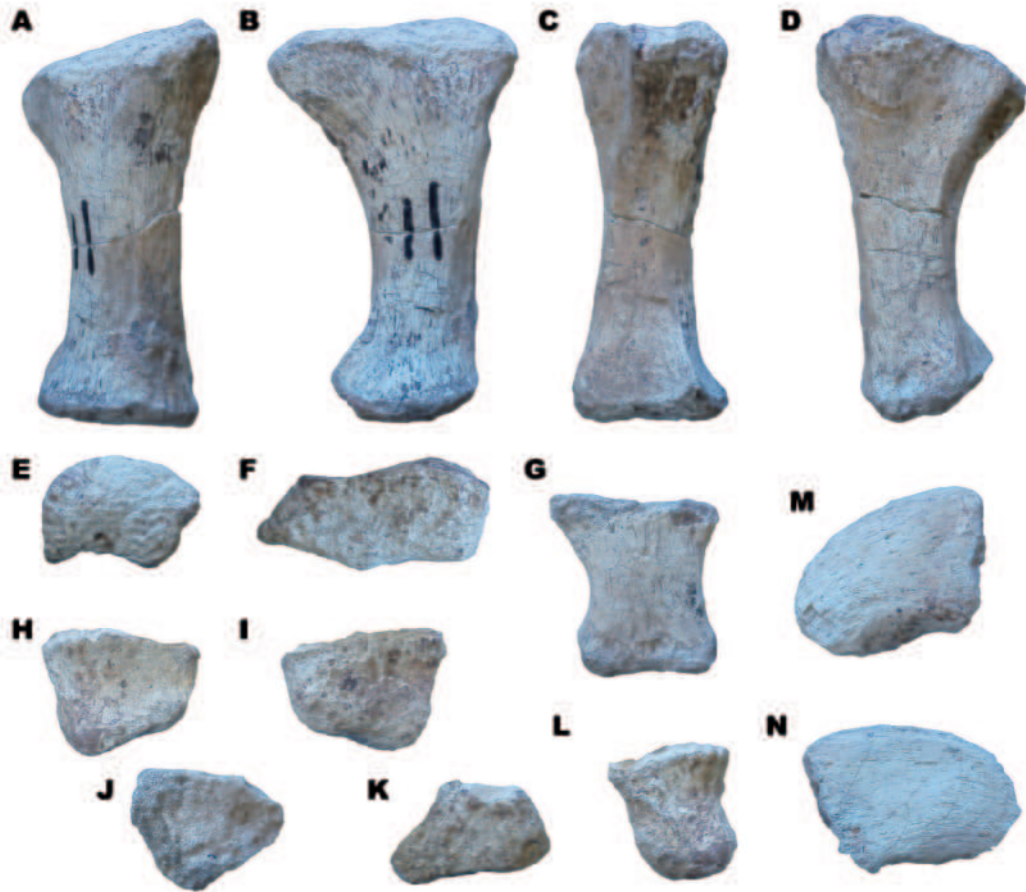


Fig. 19. *Chadititan calvoi* nov. gen. et sp., selected foot elements of MPCN-Pv 1040, right metatarsal IV in (A) anterior, (B) lateral, (C) posterior, (D) medial, (E) distal, and (F) proximal views; right phalanx IV-1 in (H) anterior, (I) posterior, (J) proximal, and (K) distal views; (G) right phalanx III-1 in dorsal view; right unguet phalanx III-2 in (M), medial and (N) lateral views. Scale bar = 4 cm.

excavated articular surface for metatarsal III, which is posteriorly delimited by a proximodistal ridge that separates it from a posteromedially oriented surface. In proximal view, this metatarsal is anteroposteriorly long and transversely narrow, with a roughly trapezoidal outline. The distal articular surface is nearly flat, and retains a small and poorly defined medial collateral pit. In distal view it is subrectangular in contour, with a poorly defined notch at its medial surface and with a gently convex lateral margin. As in other titanosaurs, phalanges IV-1 and III-1 are block-shaped, and with poorly defined proximal and distal articular surfaces (Fig. 19G–L). Ungual phalanx III-2 is transversely narrow and with a distally displaced flexor tubercle (Fig. 19M).

**Measurements of holotype.** Antermost preserved vertebra, maximum anteroposterior length of centrum, 18 cm; maximum dorsoven-

tral height of centrum, 7 cm; maximum dorsoventral height of centrum, including the preserved part of the neural arch, 11 cm. Humerus, proximal end, maximum transverse width 23.5 cm; proximal end, maximum transverse width of head, 13.5 cm. Ulna, proximal end, maximum anteroposterior length, 17 cm; proximal end, maximum transverse width at level of the anterolateral process, 12.5 cm. Tibia, proximal end, maximum anteroposterior length, 14 cm; maximum transverse width, 12 cm; distal end, maximum anteroposterior length, 8.5 cm; distal end, maximum transverse width, 14 cm. Femur, proximal head, maximum transverse (mediolateral) width, 16 cm; proximal head, maximum anteroposterior length, 11 cm; transverse width of the shaft, 17.5 cm; distal end, maximum transverse width, 23 cm; distal end maximum anteroposterior length at level of medial condyle, 14 cm.

**Measurements of paratype MPCN-Pv 1035.**

Humerus, maximum width of proximal end, 6.85 cm. Femur, maximum width of proximal end, 14.74 cm; proximal head, maximum transverse (mediolateral) width, 6.98 cm. Tibia, maximum anteroposterior length of proximal end, 12.8 cm; maximum transverse width of proximal end, 6 cm; maximum anteroposterior length of distal end, 4.95 cm; maximum transverse width of distal end, 6.2 cm.

**Measurements of paratype MPCN-Pv 1037.**

Humerus, proximal end maximum transverse width, 27.2 cm; maximum transverse width of humeral head, 8.5 cm. Ulna, proximal end maximum anteroposterior length, 20.7 cm; maximum transverse width at level of the anterolateral process, 8.5 cm. Tibia, maximum anteroposterior length of proximal end, 22.2 cm; maximum transverse width of proximal end, 12.48 cm; anterior projection of cnemial crest, 6.43 cm.

**Measurements of paratype MPCN-Pv 1038.**

Femur, maximum anteroposterior width, 6.19 cm; maximum anteroposterior width of head, 8.22 cm; maximum anteroposterior length of medial condyle, 12.12 cm; maximum transverse width of distal end, 22.5 cm.

**Measurements of paratype MPCN-Pv 1039.**

Tibia, proximal end, maximum anteroposterior length, 12.27 cm; maximum transverse width, 8.11 cm; anterior extension of cnemial crest, 3.17 cm. Ulna, proximal end, maximum anteroposterior length, 10.59; maximum transverse width at level of the anterolateral process, 8.69 cm.

**Remarks.** *Chadititan calvoi* was included within a phylogenetic analysis of titanosaurs, and it resulted well-nested within the clade Rinconsauria (Fig. 11; Supplementary Data 2). This clade also includes the genera *Pitekunsaurus*, *Muyelensaurus*, *Overosaurus*, and *Rinconsaurus*, and supported by six unambiguous synapomorphies [ch. 175(1), neural spine of anterior dorsal vertebrae slightly higher than the centrum; ch. 262(1), posterior caudal centra dorsoventrally flattened; ch. 352(0), fourth trochanter of femur located almost at the half of the shaft; ch. 431(2), strong height difference between the anterior and posterior articular faces of posterior caudal vertebrae; ch. 434 (1), ilium with notably dorsoventrally expanded iliac blade above the pubic peduncle; ch. 435 (1), ilium, preacetabular blade, with a ventrolaterally tapered end] (see Calvo & González Riga, 2003; Calvo *et al.*, 2007; Filippi & Garrido, 2008; Pérez-Moreno *et al.*, 2022, 2023). In spite of being relatively incomplete known, *Chadititan* shares with other rincosaurians

two unambiguous synapomorphies: distally positioned fourth trochanter on femur [ch. 352(0)] and posterior caudal vertebrae centra with a depressed posterior face [ch. 431(2)]. Further, *Chadititan* shares with other rincosaurians several additional features, including caudal vertebrae with elongate and anteriorly projected prezygapophyses, and a straight-shafted and gracile femur lacking a strong medial curvature on its proximal end (Calvo & González Riga, 2003; Calvo *et al.*, 2007; Filippi & Garrido, 2008; Pérez-Moreno *et al.*, 2021, 2023; Fig. 11).

In addition to the characters and comparisons carried out on the Diagnosis, there are additional features that distinguish *Chadititan* from closely related taxa. The presence of homogeneously procoelous caudal vertebrae of *Chadititan* separates it from the clade including the genera *Pitekunsaurus* and *Rinconsaurus*, which are characterized by a caudal sequence including biconvex, procoelous, opisthocelous, amphicoelous and amphiplatyan vertebrae [ch. 433(1)], and centra of anterior caudal vertebrae with strong height difference between the anterior and posterior articular faces [ch. 429(2)] (Calvo & González Riga, 2003; Filippi & Garrido, 2008; González Riga *et al.*, 2009; Pérez-Moreno *et al.*, 2021). On the other side, transversely narrow and elongate caudals distinguish *Chadititan* from *Overosaurus* and *Muyelensaurus*, in which the caudals are box-shaped, with flat and broad ventral surfaces (Coria *et al.*, 2013; Pérez-Moreno, 2023). This combination of characters, together with the differences noted in the diagnosis, indicate that *Chadititan* is a valid rincosaurian genus.

The clade Rinconsauria was first established by Calvo *et al.* (2007) with the aim to encompass the genera *Rinconsaurus* and *Muyelensaurus*. They defined the clade under the following words: “*Muyelensaurus*, *Rinconsaurus*, their most recent common ancestor and all of its descendants”. Later, Hechenleitner *et al.* (2020) and Pérez-Moreno *et al.* (2023), following the phylogenetic definition made by Calvo *et al.* (2007), recognized Rinconsauria as a more comprehensive group that included also members of Aeolosaurini because *Rinconsaurus* was depicted in their analysis as more closely related to aeolosaurines than to *Muyelensaurus*. The present phylogenetic analysis resulted in a closer relationship between *Rinconsaurus* and *Muyelensaurus* than either of these with Aeolosaurinae, leading to the recognition of Rinconsauria as a small clade of titanosaurs that includes not only *Rinconsaurus* and

*Muyelensaurus* (as originally proposed by Calvo *et al.*, 2007), but also *Chaditian*, *Pitekunsaurus*, and *Overosaurus*. Under this scenario the small clade Rinconsauria constitutes the sister group of *Aeolosaurini* (Fig. 11).

Rinconsauria includes slender, lightly built and small-sized titanosaurs (all being less than 11 m long) with straight limbs and a strongly modified pelvic girdle. *Rinconsaurus*, *Overosaurus*, and *Muyelensaurus* exhibit a proportionally short and extremely dorsoventrally tall ilium with its preacetabular process strongly laterally deflected and with a ventrolaterally tapering end (see Coria *et al.*, 2013), which is somewhat reminiscent of the basal titanosauriform *Brachiosaurus* (see Coria *et al.*, 2013), to which rinconsaurians are also similar in having a relatively straight femur and gracile and straight limbs. Tail anatomy of rinconsaurians is very similar to that of *Aeolosaurus* and *Arrudaitan* (Calvo & González Riga, 2003; Calvo *et al.*, 2007; Pérez-Moreno *et al.*, 2021), which were recently considered as having a protonic tail (Vidal *et al.*, 2021). A relatively straight femur and very gracile limbs, with a modified anterior tail vertebrae are features that among rinconsaurians are present also in *Chaditian*, suggesting that it shared with other members of the group a similar body shape.

## DISCUSSION AND CONCLUSIONS

Fossil vertebrates and invertebrates here described do not yield conclusive evidence about the environmental and climatic conditions under which the Marín Farm fossiliferous horizon was deposited. Many of the aquatic vertebrates (*e.g.*, dipnoans, lepisosteids, and percomorphs) are interpreted both as being restricted to freshwater environments, or to have some tolerance to brackish water. On the other hand, data provided by invertebrates appears to be more informative. Nowadays, unionoid bivalves live in a relatively broad spectrum of freshwater environments (Martínez & Rojas, 2004), but most frequently in lotic ones, around 1 m deep; they prefer moderate to somewhat fast currents and firm to moderately soft substrates, with ample range of grain sizes (Huehner, 1987; Dillon, 2004; Cummings & Graf, 2015). It is relevant to note that species with large and heavy shells can be found in water courses with relatively fast currents, a hard substrate, and coarse-grained sediment (Stanley, 1970; Bailey & Green, 1988; Cummings & Graf, 2015), which is not the case of the *Diplodon* sp.

recovered in present assemblage.

Knowledge of Cretaceous continental gastropods from Patagonia is very scarce (Salvador *et al.*, 2018), although it has increased in recent years (Novas *et al.*, 2019; Miquel, 2024). Gastropods from Marín Farm include strictly terrestrial Megalomastomatidae, Subulinidae, and Bulimulidae. This set of terrestrial gastropods point out environmental features that typically represent temperate-warm and humid conditions, such as occurring in northern Argentina forests.

In sum, the aquatic, semi-aquatic, and terrestrial organisms provide evidence for an inland freshwater community, of temperate-warm climate. This is congruent with sedimentological analysis that regards these beds as wet interdune facies association.

## Marín Farm locality and its implications on vertebrate and tetrapod assemblages from Patagonia

Lehman (1987) indicates that Campanian faunistic associations in North America are less explored when compared to Maastrichtian ones (but see Gates *et al.*, 2010; Mitchell *et al.*, 2012). The same may be applied to Patagonia, where late Campanian–Maastrichtian associations are studied in greater detail (*e.g.*, Allen, La Colonia, and Chorrillo formations; Martinelli & Forasiepi, 2004; Gasparini *et al.*, 2015; Novas *et al.*, 2019), than those belonging to the early to mid-Campanian, such as those of the Anacleto Formation. The only roughly coeval assemblage that was studied as a whole belongs to the Cerro Fortaleza Formation (Agnolín *et al.*, 2024), located in southern Santa Cruz Province (see below). In this way, the assemblage here described constitutes one of the first vertebrate and invertebrate terrestrial associations reported from Campanian age in northern Patagonia.

The Marín Farm assemblage described here may be included within Bonaparte (1991) “Neuquenian Vertebrate Age” or within the “Coloradoan Tetrapod Assemblage” of Leanza *et al.* (2004). Leanza *et al.* (2004) characterized the assemblage by a high diversity of abelisaurid and titanosaur sauropods. The latter include the co-existence of large and gracile limbed forms, together with the first occurrence of small and robust saltasaurines (Leanza *et al.*, 2004). The latter were regarded as a migratory wave completing the faunal mixture with northern Gondwanan forms (Leanza *et al.*, 2004). Leanza *et al.* (2004) also indicated the abundance of croc-

odyliforms, particularly notosuchians, that may represent 60% of the vertebrate record in some sites.

This characterization does not entirely fit with the assemblage here described (Fig. 20). Marín Farm association shows the occurrence of gracile limbed derived rincosaurians together with a larger titanosaur (not collected) and abelisaurids. Otherwise, saltasaurines and colossosaurs are absent. Furthermore, crocodyliforms are very scarce, with the occurrence of a single osteoderm.

Otherwise, this assemblage shares with coeval beds the abundance of rincosaur titanosaurs and the occurrence of the dipnoan *Metaceratodus kaopen* (Apesteguía *et al.*, 2007; Filippi & Garrido, 2008) (Fig. 20). One remarkable aspect that Marín Farm assemblage shares with late Campanian-Maastrichtian (Allenian *sensu* Leanza *et al.*, 2004) is the low diversity, but numerical abundance, of chelid turtles, and particularly the occurrence of the genus *Yaminuechelys* (Leanza *et al.*, 2004; de la Fuente *et al.*, 2015; Maniel & de la Fuente, 2016, 2017; Fig. 20).

The strong differences noted among different assemblages suggest that the concepts of “Neuquenian Vertebrate Age” (Bonaparte, 1991) or “Coloradoan Tetrapod Assemblage” (Leanza *et al.*, 2004) may need to be revised because at least some associations, such as that of the Anacleto Formation reported here, seem to contain a mixture of faunal elements belonging to the Coloradoan and the Allenian assemblages.

### Comparisons between Marín Farm and Cerro Fortaleza faunal assemblages

In Patagonia, aside from Marín Farm, the only locality that yielded a diverse faunal association of comparable chronostratigraphical context is that of Cerro Fortaleza, southwestern Santa Cruz Province (Novas *et al.*, 2002; Agnolín *et al.*, 2024). This makes comparisons between both assemblages particularly informative.

In spite that in Cerro Fortaleza a census of the relative number of specimens is still pending, published sources indicate that chelid turtles are by far the most common element in the association, being represented by three different species (Agnolín *et al.*, 2024), a diversity that is reminiscent of the Marín Farm assemblage. Further, in Cerro Fortaleza, crocodiles are very scarce and represented by a single form. Besides, in both assemblages lepisosteiform and dipnoan fishes are present, the latter represented by a single taxon. In the case of Marín Farm assem-

blage, dipnoans are represented by the species *Metaceratodus kaopen* which belongs to lineages typical of north and central Patagonia basins, whereas in the Austral basin, dipnoans belong to the *Atlantoceratodus* lineage (Cione *et al.*, 2007; Agnolín, 2010; Panzeri, 2024).

Dinosaurs are particularly abundant in Anacleto beds (Lydekker, 1893; von Huene, 1929; Powell, 1986; Coria & Salgado, 1996; Chiappe *et al.*, 1998, 2001, 2004; Dingus *et al.*, 2000; Coria *et al.*, 2002a; Calvo & González Riga, 2003; Chiappe & Coria, 2004; Salgado *et al.*, 2005; Filippi & Garrido, 2008; Sereno *et al.*, 2008; Salgado & Coria, 2009; Filippi *et al.*, 2011; Coria *et al.*, 2013; Gianechini *et al.*, 2015; Baiano *et al.*, 2021; Pérez-Moreno *et al.*, 2022, 2023), and constitute a valuable source for comparisons with coeval beds of Cerro Fortaleza Formation (Novas *et al.*, 2002, 2004b, 2005, 2008; Ezcurra *et al.*, 2010; Lacovara *et al.*, 2014; Paulina-Carabajal *et al.*, 2021; Agnolín *et al.*, 2024).

Top predatory niches during Campanian times in Northern Patagonia were mainly dominated by abelisaurids, with the single exception of the megaraptorid *Aerosteon*, found in the Anacleto Formation beds from southern Mendoza Province (Sereno *et al.*, 2008). Otherwise, in the Austral basin, including Cerro Fortaleza, the top predatory niche is dominated by megaraptorids, with much fewer abelisaurids (Novas *et al.*, 2013; Agnolín *et al.*, 2024). The Marín Farm assemblage shares with other northern Patagonia localities the presence of abelisaurid theropods, and so far megaraptorids are entirely absent at this site.

Regarding sauropods, some contributions indicate differences in composition between northern and southern Patagonia. For example, gigantic colossosaurians are absent from the record since the Campanian in the Neuquén Basin, whereas they appear to be abundant and diversified throughout the Campanian and Maastrichtian at Austral and Golfo San Jorge basins (see Novas *et al.*, 2019; Aranciaga-Rolando *et al.*, 2022; Pérez-Moreno *et al.*, 2024). In congruence, the gigantic colossosaurians are absent from the Marín Farm assemblage, but they are present and diverse in Cerro Fortaleza (Novas *et al.*, 2019; Aranciaga-Rolando *et al.*, 2022). On the other hand, rincosaurians and related taxa are abundant and diverse in the Neuquén Basin (including Marín Farm), whereas they are entirely absent in the Austral Basin (including Cerro Fortaleza; see Aranciaga-Rolando *et al.*, 2022).

The differences in faunistic composition be-

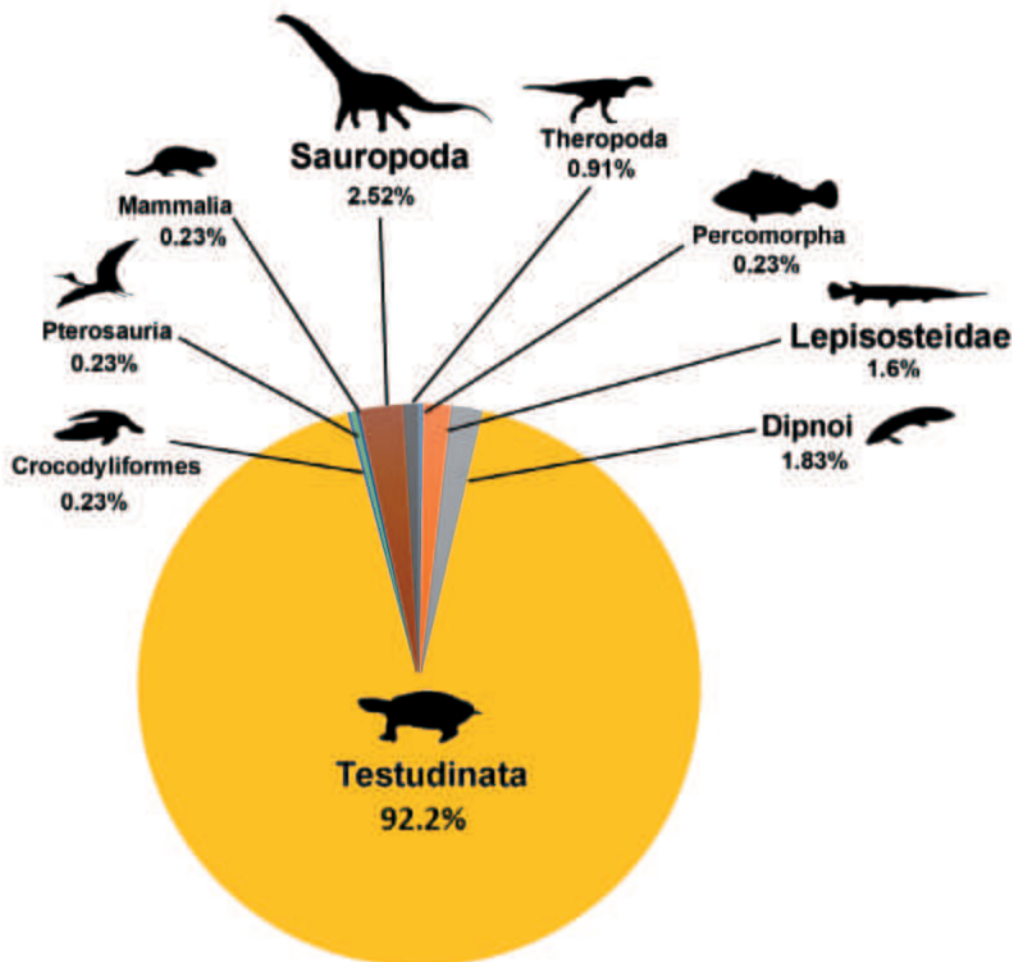


Fig. 20. Percentage of the total number of vertebrate specimens collected in Marín family Farm locality. Specimens MNI on each category: Percomorpha [1]; Lepisosteiformes [7]; Dipnoi [8]; Chelonia [403]; Mammalia [1]; Crocodyliformes [1]; Pterosauria [1]; Sauropoda [1]; Theropoda [4].

tween northern and southern Patagonia have been pointed out before by several authors (Novas *et al.*, 2013; Moyano-Paz *et al.*, 2022; Agnolín *et al.*, 2024). Here, based on the differences noted above, we suggest that such differentiation, at least for the case of vertebrates, may be traced up to Campanian times. A similar latitudinal provincialism has been reported in North America for the Campanian–Maastrichtian interval (Lehman, 1987, 1997; Sankey, 2008). Sankey (2008) supports that this provincialism is the exclusive result of climatic differences, particularly the degree of environmental aridity, and the same may possibly be applied to Patagonia (southern localities were more temperate and humid than the northern Patagonian locations, warmer and eventually less humid).

Although the sample size remains small, the preliminary account of the vertebrate diversity demonstrates that the Marín Farm assemblage constitutes a valuable source of information to understand faunistic evolution during the Campanian–Maastrichtian time lapse in Patagonia.

#### Comparisons with coeval faunistic assemblages of North America and Eurasia

One remarkable aspect that Marín Farm assemblage shares with other Campanian and Maastrichtian localities in Patagonia is the low diversity (here represented by three species), but numerical abundance, of chelid turtles, which here constitute more than the 90% of the entire vertebrate association (Fig. 20).

The abundance of turtles in Marín Farm assemblage, which outnumber other reptiles, contrasts with which is known in most Campanian localities from North America. In most of these sites, the turtles do not represent more than the 50% of the reptile assemblage (e.g., Hutchinson & Archibald, 1986; Fiorillo, 1989, 1991; Lehman, 1997; DeMar & Breithaup, 2006; Fanti & Miyashita, 2009; Cullen *et al.*, 2016), and are usually surpassed by dinosaur occurrences. Further, in these assemblages the turtles are taxonomically diverse, usually represented by more than six taxa (frequently 13), belonging to different lineages (Rowe *et al.*, 1992; Sullivan & Lucas, 2003, 2006; DeMar & Breithaup, 2006; Sankey, 2006; Cullen *et al.*, 2016). In this regard, Hutchinson & Archibald (1986) reported for the Hell Creek Formation the occurrence of at least 19 turtle taxa collected from penecontemporaneous deposits. In a similar way, in roughly coetaneous fossiliferous localities from Asia (e.g., Bostobe Formation, Western Kazakhstan; Nessov, 1984, 1995, 1997; Averianov *et al.*, 2016) turtles are diverse, resembling North American fossil sites. Nessov (1984) remarked that in some associations from eastern Asia, the turtles represented more than 50% of the entire vertebrate biomass. However, he does not indicate the number of specimens nor how the calculations were made, and thus, comparisons with the associations of Patagonia are difficult.

Otherwise, several European Campanian sites (e.g., eastern Austria, Romania, southern France, Spain, and Portugal) show a low taxonomic diversity, comparable to that of Patagonia, but in most cases turtles are not very abundant and do not reach the 50% of the reptile occurrences (e.g., Buffetaut *et al.*, 1996, 1997; de Broin & Murelaga, 1996; de Broin *et al.*, 1999; Pérez-García, 2009, 2012; Rabi *et al.*, 2013; Pereda-Suberbiola *et al.*, 2015; García *et al.*, 2015; Csiki-Sava *et al.*, 2015; Ortega *et al.*, 2015).

In different faunas from Campanian assemblages of the “Judithan age” of Alberta, Montana, and Texas from North America, Lehman (1997; see also Rogers *et al.*, 2024) indicated that among medium-sized reptiles, the turtles dominate each assemblage, followed by crocodylians which represent about one quarter. In the same line, Sankey & Baszio (2008) reported in several coeval sites from Texas that crocodiles constitute about 25% of the fauna. In some North American formations, such as the Cedar Formation in Utah, taxonomic diversity is high, up to 7 different taxa (Cifelli *et al.*, 1999). The

same seems to apply for the Western Kazakhstan and European reptiles associations of Campanian age (e.g., Rozhdstvensky & Khozatsky, 1967; Buffetaut, 1979; Nesov 1995, 1997; Buffetaut *et al.*, 1996, 1997; Buscalioni *et al.*, 1997, 1999, 2001; Rabi, 2008; Puértolas-Pascual *et al.*, 2011, 2014; Averianov *et al.*, 2016). This relative abundance strongly contrasts with the occurrence of a single crocodylian scute recovered in the Marín Farm, which represents less than 0.3% of the association. In this regard, the Marín Farm assemblage resembles Maastrichtian assemblages from Patagonia, which up to the date failed to yield relevant fossil crocodylians, which are notably scarce in highly prospected sites (e.g., Los Alamitos, Bajo de Santa Rosa, La Colonia; Bonaparte, 1987; Martinelli & Forasiepi, 2004; Gasparini *et al.*, 2015).

Another peculiarity of the Marín Farm assemblage is that dinosaurs do not outnumber other vertebrates, and shed teeth are absent in the area. Shed teeth were produced that animals that were alive at the time of deposition of the sediments, and not by carcass destruction (Bakker & Bir, 2004; Carrano & Vélez-Juarbe, 2006). Occurrence of high number of worn and shed predator teeth and herbivorous teeth indicate that the recorded dinosaurs were actively feeding in the environment. The lack of theropod or sauropod teeth distinguish the Marín Farm assemblage from other fossiliferous sites. It is possible to infer that the entire absence of teeth in the assemblage, together with the occurrence of several partially articulated and associated individuals of both titanosaur and abelisaurids, indicates that the burial site did not necessarily correspond to the place where they had their life activities. This is congruent with sedimentological analysis that regards these beds as wet interdune facies association, which was unlikely the habitat of these dinosaurs.

Titanosaurs are very common animals in most vertebrate associations from Gondwana (Bonaparte, 1986a; Bonaparte & Kielan Jaworowska, 1987). In the present case, the new rincosaur *Chadititan calvoi*, are represented by several individuals, being the most common dinosaur of the assemblage. In the phylogenetic analysis carried out above, rincosaurians are represented by five genera occurring in the Santonian–Campanian time lapse. As indicated by other authors, the limit between the Cenomanian and Turonian included an important extinction event and a faunistic turnover in Patagonia (Apesteguía, 2002; Coria & Salgado,



2005; Novas, 2009; Santamarina *et al.*, 2022). Posterior to this extinction, titanosaurian sauropods underwent an extensive radiation (Coria & Salgado, 2005; Salgado *et al.*, 2005; Gallina & Apesteguía, 2015; Apesteguía, 2007; Aranciaga-Rolando *et al.*, 2022; Pérez-Moreno *et al.*, 2024). The occurrence and abundance of *Chadititan* in the Marín Farm assemblage, together with the Turonian–Campanian rincosaur radiation here depicted, indicates that it is possible that they were part of such turnover, and of the “evolutionary explosion” that occurred after the Cenomanian together with the appearance of aeolosaurines, saltasaurines, and diverse basal eutitanosaurs (Pérez-Moreno *et al.*, 2024). This diversification peaked during the Campanian–Maastrichtian, where many localities of this period in northern Patagonia yielded more than one, and up to 6, coeval sauropod species (García & Salgado, 2012; Aranciaga-Rolando *et al.*, 2022; Pérez-Moreno *et al.*, 2024). It must be noted, however, that in the Campanian Marín assemblage, only a single titanosaur species (probably a second one represented by fragmented remains) was recovered. The absence of osteoderms (which also represent an indirect indication of sauropod diversity; Aranciaga-Rolando *et al.*, 2022) also supports a low sauropod diversity on the Marín Farm assemblage.

The differences noted between the Campanian–Maastrichtian faunal associations from Patagonia (with dominance of chelid turtles, very low diversity and abundance of crocodyliforms, and abundance of titanosaurs) and those from coeval units in North America likely reflect not only a different climatic and paleolatitudinal position, but also very different continental and evolutionary histories (Bonaparte, 1986a).

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#### Supplementary material

<http://revista.macn.gob.ar/ojs/index.php/RevMus/rt/suppFiles/885/0>

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