

First ornithopod remains from the Bajo de la Carpa Formation (Santonian, Upper Cretaceous), northern Patagonia, Argentina

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Abstract

In the last decades, the Argentinian ornithopod record has been increased with new and diverse bone remains found along all the Upper Cretaceous. Most of them are very incomplete and represent taxa of different size. As result, the studies about the palaeobiodiversity of the Ornithopoda clade in South America are complex. In this paper, new postcranial remains of an indeterminate medium-sized ornithopod from the Santonian Bajo de la Carpa Formation (Rincón de los Sauces, Neuquén province) are presented. They present diagnostic features of the Ornithopoda clade, and several characters that relate them with other Argentinian ornithopods, especially with the medium-sized members of the Elasmaria clade *sensu* Calvo et al. (2007) (*Macrogyphosaurus* and *Talenkauen*). The postcranial material allows to identify at least three different ontogenetic stages: adult, subadult more immature and subadult. These bones are the first record of Ornithopoda for the Bajo de la Carpa Formation and one of the very scarce Santonian records of this clade in South America. The diversity of the Late Cretaceous South American ornithopods presents two clear distributions: the Cenomanian-Santonian was characterized by small and medium [si4](#) euiguanodonts and elasmarians; and the Campanian–Maastrichtian by the medium sized elasmarian and large sized hadrosaurids.

Keywords: Ornithischia; Santonian; Patagonian; Biodiversity

1 Introduction

The ornithopods are the herbivorous dinosaurs with the greatest taxonomical diversity and time duration from the Mesozoic. Although, their remains are more abundant in the Northern Hemisphere ([Horner et al., 2004](#); [Norman et al., 2004](#); [Díaz-Martínez et al., 2015](#)), in the last decades new and important discoveries have been done in the Southern Hemisphere, mainly in Argentina (i.e., [Coria and Cambiaso, 2007](#); [Coria et al., 2007](#); [Ibircu et al., 2010, 2014](#); [Cruzado-Caballero, 2016](#); [Cruzado-Caballero and Coria, 2016](#); [Cruzado-Caballero et al., 2016a](#); [Cruzado-Caballero and Powell, 2017](#)). Up to date, eight species of ornithopods have been described: three basal ornithopods (*Gasparinisaura cincosaltensis* [Coria and Salgado 1996a](#); *Notohypsilophodon comodorensis* [Martínez 1998](#); *Anabisetia saldiviai* [Coria and Calvo 2002](#)), two elasmarians (*Talenkauen santacrucensis* [Novas, Cambiaso and Ambrosio 2004](#); *Macrogyphosaurus gondwanicus* [Calvo, Porfiri and Novas 2007](#)) and three hadrosaurid (*Secernosaurus koernerii* [Brett-Surman 1979](#); *Lapampasaurus cholinoi* [Coria, González Riga, and Casadio 2012](#); *Bonapartesaurus rionegrensis* [Cruzado-Caballero and Powell, 2017](#)). In addition, abundant fragmentary remains assigned to high taxonomic levels, such as indeterminate ornithopods, iguanodonts and hadrosaurids have been identified ([Cruzado-Caballero, 2015](#); [Cruzado-Caballero et al., 2016a, 2016b](#)).

In this work, we present new postcranial bones of indeterminate ornithopods found in the area of Cerro Overo by the Museo Argentino Urquiza team (Rincón de los Sauces, Neuquén province) during the prospection campaign of 2015–2016 ([Fig. 1](#)). Initially, the geological outcrops exposed in this area were assigned to the Anacleto Formation (Campanian) but recent studies in the same stratigraphical levels reassigned them to the Bajo de la Carpa Formation (Santonian, [Garrido, 2010](#)) of the Río Colorado Subgroup, Neuquén Group (Neuquén Basin). The Neuquén Group is

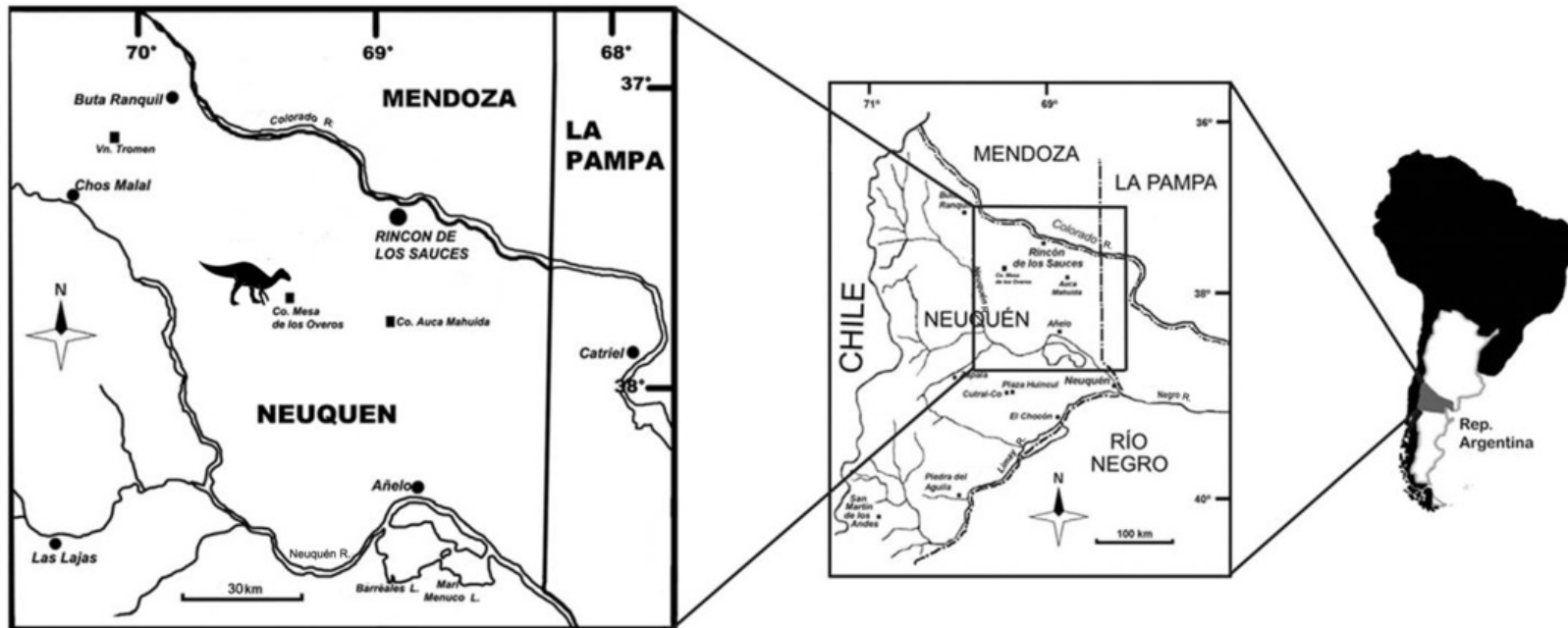


Fig. 1 Map showing the location of the Cerro Overo site (Rincón de los Sauces, Neuquén, Argentina). **Abbreviations:** Co, cerro; L, Lake; R, river; Vn, volcano.
alt-text: Fig. 1

The main goals of the present paper are: to describe the new ornithopod remains; to compare them with other Argentinian ornithopods; and to provide new insights into the palaeobiodiversity and paleobiogeography of the ornithopods in South America.

Institutional Abbreviations—MAU, Museo Argentino Urquiza (Rincón de los Sauces, Neuquén, Argentina).

2 Geological setting

During the Late Cretaceous the Neuquén Basin (northern Patagonia and part of Cuyo regions, Argentina) started a foreland stage, give place to a thick succession of continental red beds that includes extensive fluvial deposits and associated aeolian sedimentites. This succession is known lithostratigraphically as Neuquén Group (Cenomanian–lower Campanian), reaching an estimated maximum thickness of 1200 m (Cazau and Uliana, 1973). From the first geological descriptions of these deposits at the end of the nineteenth century, it was noticed the frequent presence of dinosaur remains, for which reason it was called for a long time as “areniscas con dinosaurios”, “formación de dinosaurios”, “capas con dinosaurios” or “estratos con dinosaurios” (Valentin, 1897; Roth, 1898; Wichmann, 1916; Windhausen, 1922; Keidel, 1925; among others).

The Bajo de la Carpa Formation integrate the upper part of the Neuquén Group (Río Colorado Subgroup), and offers a wide variety of lithofacies that include a domain of aeolian deposits in the eastern part of the basin, and low-sinuosity to braided fluvial deposits in the center and northern area de the basin (Heredia and Calvo, 1997, 2002; Caldwell and Albino, 2001; Sánchez et al., 2006; Garrido, 2010). According different authors, a Santonian age is inferred for these deposits (Legarreta and Gulisano, 1989; Bonaparte, 1991; Hugo and Leanza, 2001; Garrido, 2010).

Up until five years ago, the paleontological record of the Bajo de la Carpa Formation was mainly restricted to the findings realized in aeolian deposits of the eastern part of the basin, represented by abelisaurids and alvarezsaurids (Bonaparte, 1991; Martinelli and Vera, 2007), fossil birds (Alvarenga and Bonaparte, 1992; Chiappe and Calvo, 1994), abundant remains of the snake *Dinilysia patagonica* (Smith-Woodward, 1901), and a broad variety of terrestrial crocodiles (Smith-Woodward, 1896; Bonaparte, 1991; Fiorelli and Calvo, 2007; Martinelli and Pais, 2008). In the fluvial facies of this unit, only isolated remains of crocodiles and turtles were reported (Gasparini et al., 1991; Lapparent de Broin and de la Fuente, 2001; Garrido, 2010; Martinelli et al., 2012), as well as sauropod eggshells (Garrido and Calvo, 2004) and remains of the titanosaur *Bonitasauria salgadoi* Apesteguía, 2008.

Recent field works developed at the north central area of the basin, close to Rincón de los Sauces city, have allowed stratigraphically relocating to the titanosaurs *Rinconsaurus caudamirus* Calvo and Riga, 2003, and *Overosaurus paradasorum* Coria et al., 2013, within the fluvial deposits of the Bajo de la Carpa Formation (Filippi, 2015). Likewise, a new broad fossil vertebrate palaeodiversity for the same deposits was recently cited by Filippi et al. (2015) and Cruzado-Caballero et al. (2016), integrated by fish (Dipnoi) remains, theropod eggs, and a numerous bones of a broad variety of sauropod, theropod and ornithopods dinosaurs.

In the study area, the Bajo de la Carpa Formation exhibit a thickness of 108 m, composed by thick beds of medium to fine-grained size sandstones and interbedded red massive mudstones, interpreted as anastomosed fluvial system deposits (Méndez et al., 2015). Ornithopod fossil remains were found disarticulated in two different levels situated in the last 30 m of this unit, associated to crevasse splay and muddy floodplain deposits. At both levels, the bones were found scattered in a reduced area (less than 36 m²).

3 Systematic palaeontology

Ornithischia [Seeley, 1887](#)

Ornithopoda [Marsh, 1881](#)

Ornithopoda indet. ([Figs. 3–5](#))

Horizon and locality. Santonian, Bajo de la Carpa Formation, Cerro Overo fossil locality, near Rincón de los Sauces.

Material. MAU-Pv-CO-564 to 565, two fragments of cervical vertebrae; MAU-Pv-CO-569 to 572 and MAU-Pv-CO-574 to 575, five caudal vertebrae centra; MAU-Pv-CO-576, a fragmentary left coracoid; MAU-Pv-CO-577, a fragmentary right ischium; MAU-Pv-CO-578, a fragmentary left pubis; MAU-Pv-CO-579, a right phalanx II.

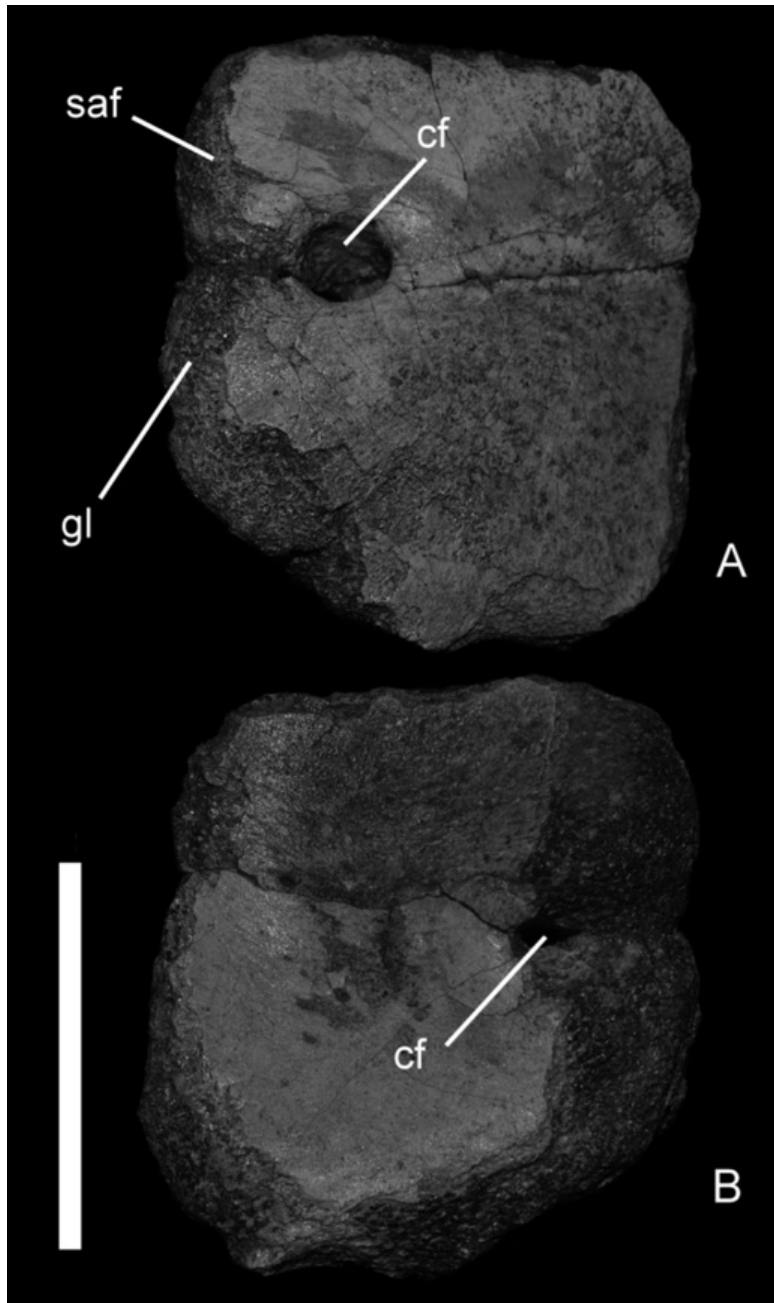


Fig. 3 Coracoid MAU-Pv-CO-576 in: A, lateral; B, medial views. **Abbreviations:** cf, coracoid foramen; gl, glenoid; s, suture; saf, scapular articular face. Scale bar equals 5 cm.

alt-text: Fig. 3

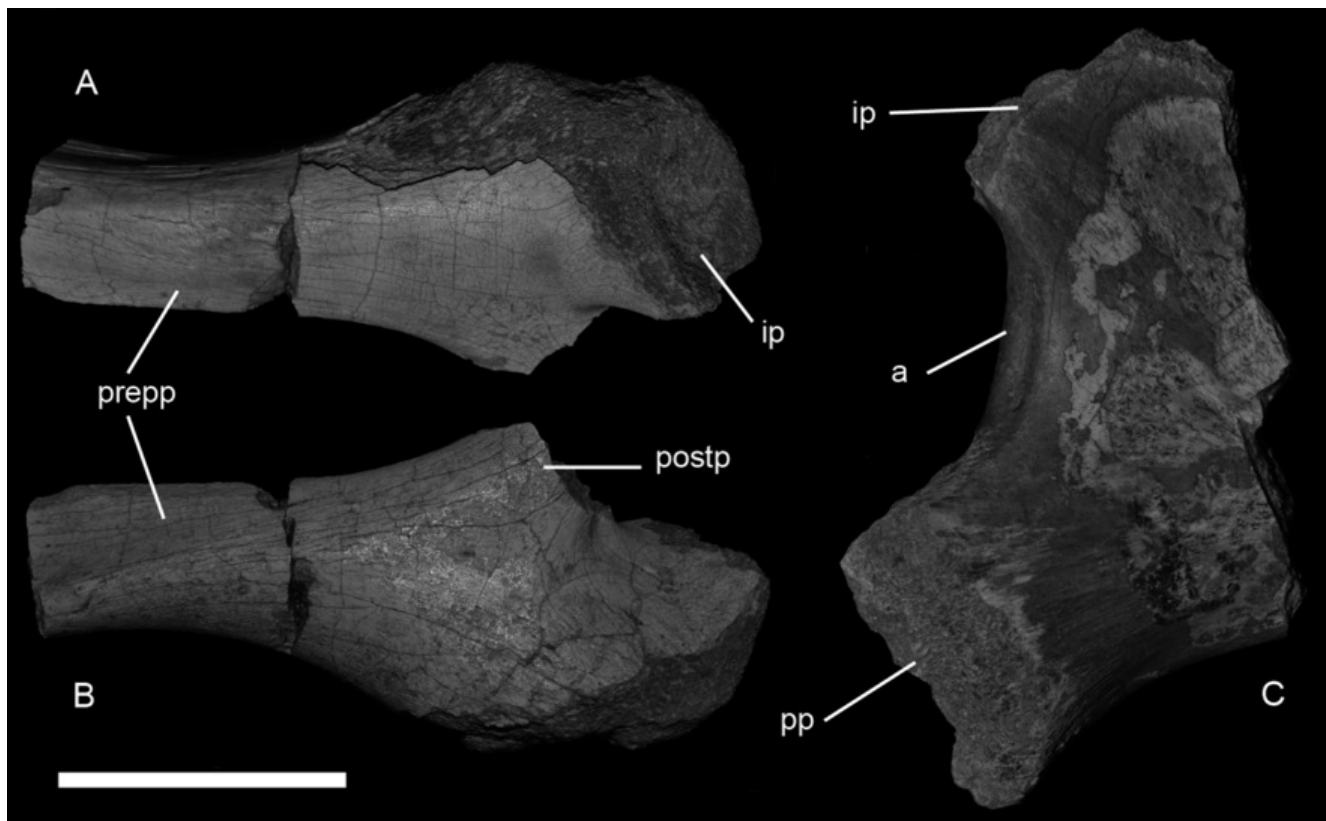


Fig. 4 Indeterminate ornithopod remains from Bajo la Carpa Fm, northern Patagonia. A–B, pubis MAU-Pv-CO-578 in: A, medial; and B, lateral views. C, ischium MAU-Pv-CO-577 in: C, medial view. **Abbreviations:** **a**, acetabulum; **ip**, iliac peduncle; **pp**, pubis peduncle; **prepp**, prepubic process; **postp**, postpubic process. Scale bar equals 5 cm.

alt-text: Fig. 4

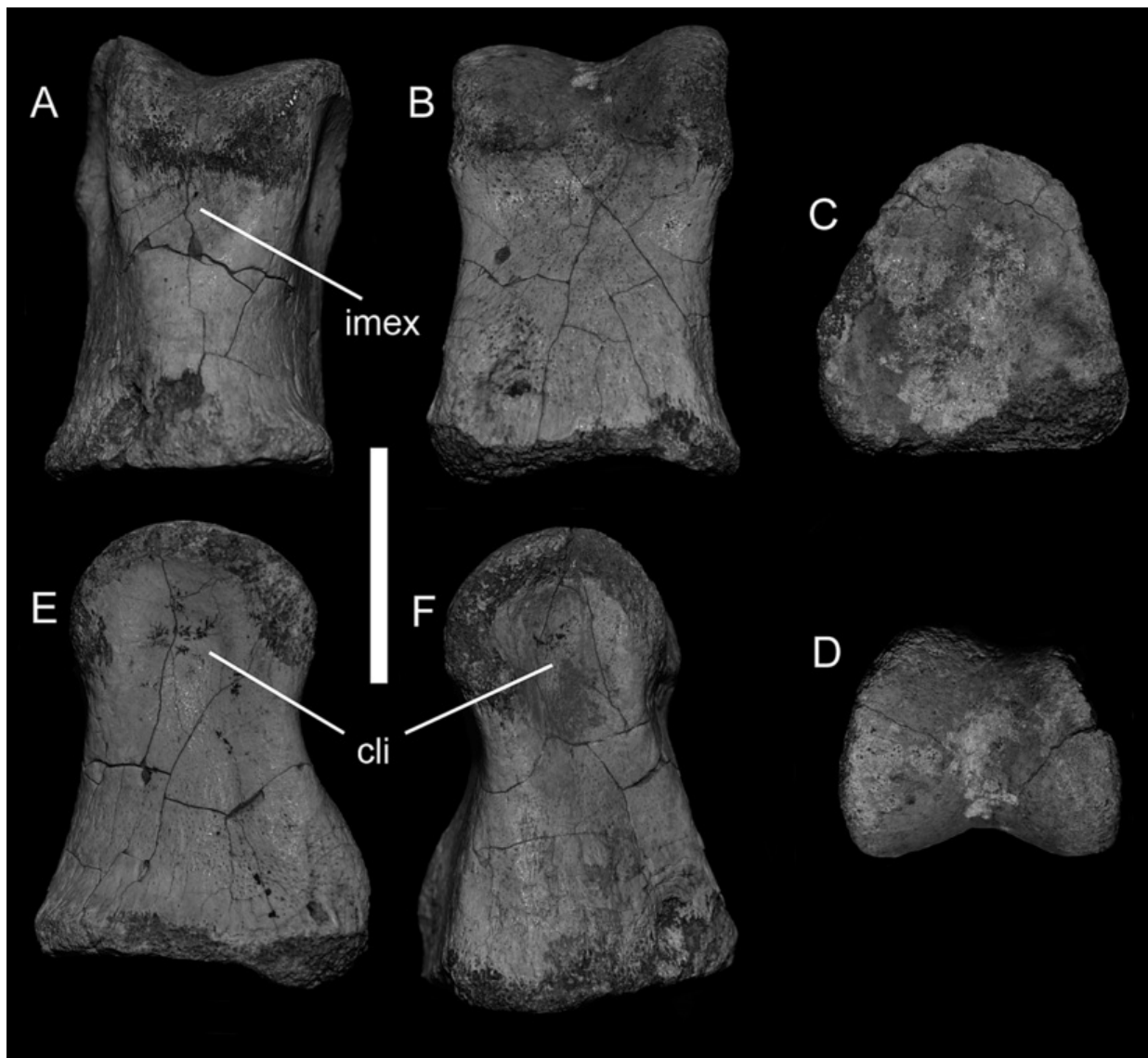


Fig. 5 Indeterminate ornithopod remains from Bajo la Carpa Fm, northern Patagonia. A–D, phalanx MAU-Pv-CO-579 in: A, dorsal; B, ventral; C, posterior; and D, anterior views. **Abbreviations:** cli, collateral ligament insertion; imex, insertion *M. extensor*; vg, vascular groove. Scale bar equals 2 cm

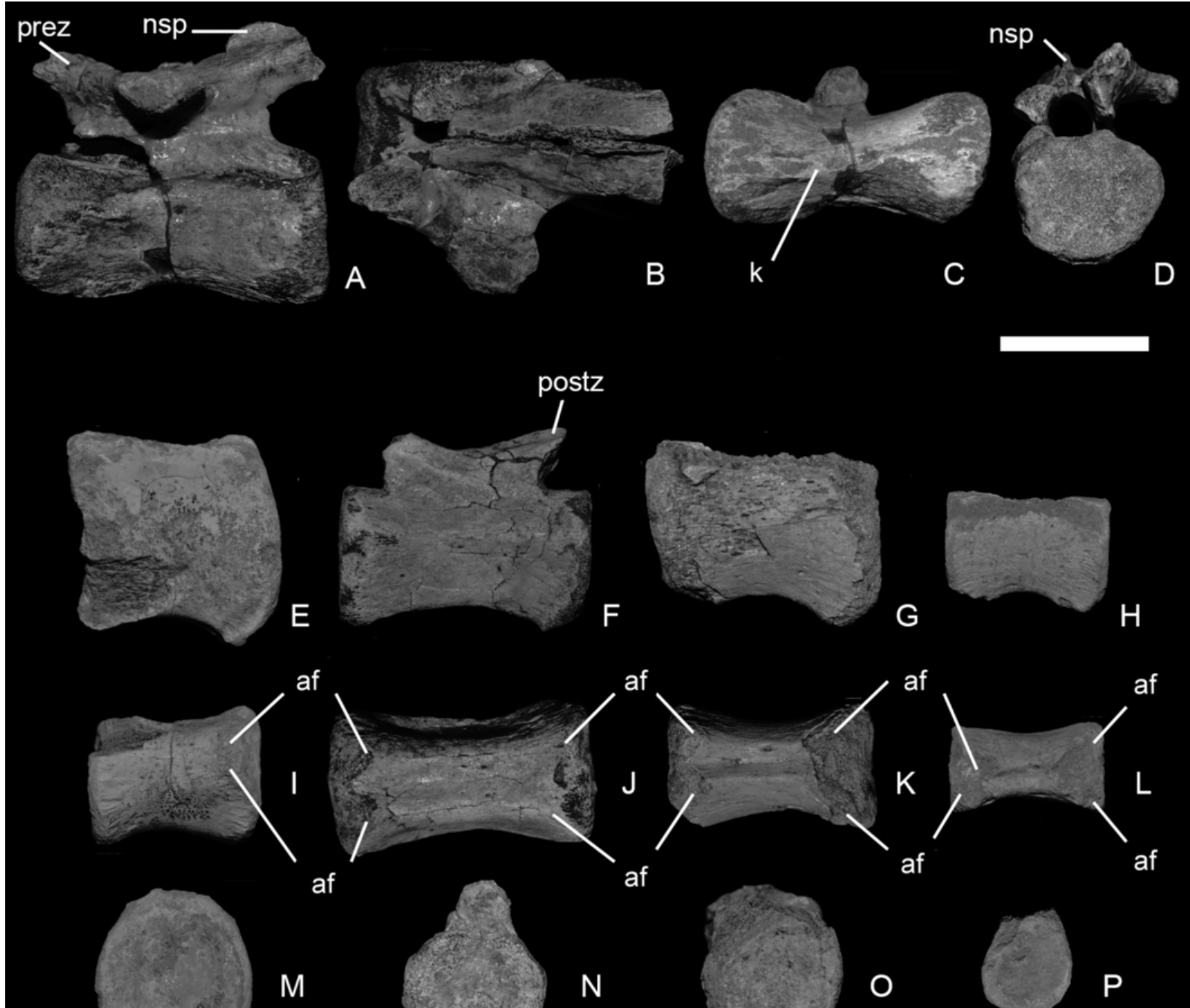
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3.1 Description and comparison

3.1.1 Cervical vertebrae

A partial neural arch of a cervical vertebra (MAU-Pv-CO-565) and an almost complete cervical vertebra slightly eroded (MAU-Pv-CO-564, Fig. 2A–C) have been found. MAU-Pv-CO-565 preserves only the left side of the neural arch including part of the transversal process. MAU-Pv-CO-564 exhibits a spool-shaped centrum with a broad ventral keel as in other basal ornithopods (Norman et al., 2004). It has an anteroposterior length/dorsoventral height ratio slightly greater than 2, as in other Patagonian ornithopods as *Gasparinisaura*, *Anabisetia* and *Talenkauen* (Cambiaso, 2007). MAU-Pv-CO-564 has an anteroposterior length similar to the seventh and eighth cervical vertebrae of *Macrogyphosaurus*, this can indicate a similar position in the cervical series to MAU-Pv-CO-564. The articular surfaces are heart-shaped and amphiplatyan as in *Macrogyphosaurus* and the eighth and ninth cervical vertebrae of other basal ornithopods and differs to the moderate opisthocoelic vertebrae of *Talenkauen* (Norman et al., 2004; Calvo et al., 2007; Cambiaso, 2007). The hour-glass shaped of the centrum and the presence of a sharp ventral ridge in ventral view are sharing with *Macrogyphosaurus* and *Talenkauen* (Calvo et al., 2007; Cambiaso, 2007). The articular surfaces are sloping anterior and posteriorly,

respectively, but not that much as in *Macrogryphosaurus* (Calvo et al., 2007). The neural arch shows the suture with the centrum indicated an immature stage (Fig. 2A). The neural spine is partially preserved. It is lateromedially narrow and its dorsal border edge is convex in lateral view. The transverse processes are located dorsally to neural arch as in the most posterior cervical vertebra of *Talenkauen* (Cambiaso, 2007). The right prezygapophysis is broken and the left is almost complete. Both are located anteriorly to the base of the neural spine, the articular surface of the left prezygapophyses has oval-shaped, is flat and is directed upwards and inwards. The postzygapophyses are not preserved.



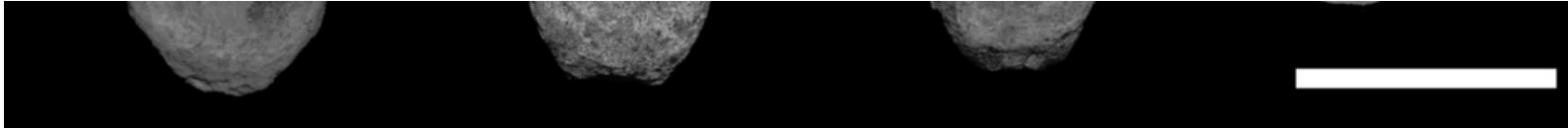


Fig. 2 Indeterminate ornithopod remains from Bajo la Carpa Fm., northern Patagonia. A–D, cervical vertebrae MAU-Pv-CO-564 in: A, lateral; B, dorsal; C, anterior; and D, ventral views. E, I, M, caudal vertebra MAU-Pv-CO-574; F, J, N, caudal vertebra MAU-Pv-CO-569; G, K, O, caudal vertebra MAU-Pv-CO-570; H, L, P, caudal vertebra MAU-Pv-CO-571 in: E to H, lateral; I to L, ventral; and M to P, posterior views. **Abbreviations:** af, articular facet; k, keel; nsp, neural spine; prez, prezygapophysis; postz, postzygapophysis; trvp, transverse process. Scale bar equals 5 cm.

alt-text: Fig. 2

3.1.2 Caudal vertebrae

Five caudal vertebrae centra have been recovered (MAU-Pv-CO-569 to 571 and 574 to 575; Fig. 2D–O). These centra do not present taphonomic modifications. Only MAU-Pv-CO-569 preserves the base of the neural arch (Fig. 2F–N). The centra show characters of the basal ornithopods: amphicoelous and hexagonal articular surfaces and bodies progressively lower and slenderer toward the distal end of the tail (Norman et al., 2004). These centra exhibit different ontogenetic stages. MAU-Pv-CO-570, 571 and 575 show the neurocentral suture unfused, as in immature individuals (Fig. 2G–H, K–L, O–P). MAU-Pv-CO-574 perhaps had the neural arch fused but this zone is broken and eroded (Fig. 2E–M). MAU-Pv-CO-569 has part of the neural arch fused. The centra of all vertebrae are anteroposteriorly longer than dorsoventrally tall. These have a double rounded border with a furrow between them. MAU-Pv-CO-574 and 575 only have haemal facets in the posterior border, this indicate a possible anterior position in the caudal series. The rest of the centra have haemal facets in both borders indicate more posterior positions in the series. The ventral margin of the centra is concave in lateral view.

3.1.3 Coracoid

MAU-Pv-CO-576 corresponds to a left fragment of coracoid with the sternal process broken (Fig. 3A–B). Its proportions are similar to the fragmentary coracoid of *Talenkauen* (Novas et al., 2004). It is anteroposteriorly wide and lateromedially narrow. The lateral side is flat and the medial side is slightly concave. The coracoid foramen is circular-shaped in lateral view and ellipsoidal-shaped in medial view as in *Talenkauen* (Novas et al., 2004). The foramen does not contact directly with the scapulocoracoid suture but there is an almost close sulcus in lateral (Fig. 3A) and medial side that connects the foramen with the scapulocoracoid suture (Fig. 3B), unlike *Talenkauen* where the sulcus only observes in the medial side (Cambiaso, 2007). The angle between the articular surfaces is of 135°.

3.1.4 Pubis

MAU-Pv-CO-578 is a right pubis fragmentary with the prepubic process and the iliac peduncle preserved (Fig. 4A–B). It has a similar size than the same bone corresponding to *Macrogrypusaurus* (Calvo et al., 2007). The prepubic process is slender, anteroposteriorly elongate, thickness lateromedially and very narrow dorsoventrally like *Macrogrypusaurus* unlike *Talenkauen*, which has a narrow lateroventrally prepubic process (Calvo et al., 2007; Cambiaso, 2007). An elongate prepubic process is the general condition for most basal ornithischians, except in basal forms such as *Heterodontosaurus* (Crompton and Charig, 1962) and *Eocursor* (Butler, Smith and Norman 2007), where it is short and robust (Norman et al., 2004; Makovicky et al., 2011). This process is anteriorly projected; the dorsal edge is concave and the ventral edge is apparently straight, as in the fragment corresponding of *Macrogrypusaurus* and unlike *Talenkauen* which has a convex ventral edge, in lateral view (Calvo et al., 2007; Cambiaso, 2007). Its transversal section in the base of the prepubic process is triangular like *Macrogrypusaurus* and unlike *Talenkauen* with an ellipsoidal transversal section (Calvo et al., 2007; Cambiaso, 2007). The iliac peduncle is big, robust and posteriorly directed. Its articular surface is concave, quadrangular and is posteriorly directed as in *Anabisetia* and *Macrogrypusaurus* (Calvo et al., 2007; Cambiaso, 2007).

3.1.5 Ischium

MAU-Pv-CO-577 is a proximal fragment of a right ischium (Fig. 4C). This fragment preserves the iliac and pubic peduncles. The iliac peduncle has a quadrangular articular surface and is slightly longer than the pubic peduncle, as in other basal ornithopod (Norman et al., 2004). The pubic peduncle is not complete; the preserved part of the articular surface is rectangular. The acetabulum is large, concave and shows a sulcus between both peduncles in medial view.

3.1.6 Phalanges

Two pedal phalanges have been found: a proximal phalanx of a left digit IV (MAU-Pv-CO-579) and an ungual phalanx likely belong to digit II or IV (MAU-Pv-CO-580). MAU-Pv-CO-579 has been considered as a proximal phalanx due to its proximal articular facet is concave (see Dieudonné et al., 2016; Fig. 5A–D). It is asymmetric dorsoventrally; typical of digit II and IV phalanges (see Dieudonné et al., 2016). In addition, the proximal articular surface is triangular and projected ventrally as occur in the proximal phalanges of digit IV. The medial condyle is dorsoventrally developed, whereas the lateral condyle is rather distally projected. These features support the identification of this bone as a phalanx of a left digit (*sensu* Dieudonné et al., 2016). The proximal articular surface is triangular and the distal articular surface is rectangular. It is robust and has a subtriangular mid-shaft cross-section. The distal articular facet presents a midline groove that separates the joint surface in two approximately equal-sized condyles. These features are present in non-hadrosaurid ornithopods and in some theropods (L. D-M. *pers. obs.*). The insertions of the collateral ligament are marked as a depression in lateral and medial views like the mark of *M. extensor* in dorsal view. In basal ornithopods (see Zheng et al., 2012) like *Talenkauen*, *Gaspardinisaura* and *Anabisetia* the insertions show deep pits and the hadrosaurids lack this type of insertion (see Díaz-Martínez et al., 2012).

4 Discussion

The cervical vertebra (MAU-Pv-CO-564) shows a spool-shaped centrum and a broad median ventral keel. Both features are typical of the basal ornithopods (Norman et al., 2004). In the vertebral body, the ratio between anteroposterior length/dorsoventral height is similar to other Argentinian ornithopods (*Gaspardinisaura*, *Anabisetia* and *Talenkauen*; Cambiaso, 2007). The anteroposterior length of the vertebral body is similar to the seventh and eighth cervical vertebrae of *Macrogrypusaurus* (Calvo et al., 2007). The articular surfaces are amphiplatyan as in *Macrogrypusaurus* and the eighth and ninth cervical vertebrae of basal ornithopods (Norman et al., 2004; Calvo et al., 2007). The ventral ridge is sharp like in *Macrogrypusaurus* and *Talenkauen* (Novas et al., 2004; Calvo et al., 2007). The transversal processes are located dorsally to neural arch as in *Talenkauen* (Novas et al., 2004). Based on all these features, the cervical vertebra is assigned to an indeterminate ornithopod similar to *Macrogrypusaurus* and *Talenkauen*.

The Caudal vertebrae (MAU-Pv-CO-569 to 570 and 573 to 575) show typical features of the Ornithopoda clade (spool-shaped centra, amphicoelous and hexagonal articular surfaces; Norman et al., 2004). Due to these remains not sharing specific features, except the size with *Macrogrypusaurus* and *Talenkauen* (Novas et al., 2004; Calvo et al., 2007), that permit to refer the specimens to a taxon higher than the Ornithopoda, these remains are assigned to an indeterminate ornithopod.

The coracoid (MAU-Pv-CO-576) apparently has the typical oval shape that presents the majority of ornithopods (Cambiaso, 2007). The foramen is close to the sulcus in medial and lateral side connecting it with the scapulocoracoid suture. In *Talenkauen* the sulcus is only present in the medial side (Cambiaso, 2007). Therefore, it is assigned to an indeterminate ornithopod.

The pubis (MAU-Pv-CO-578) is similar to the basal ornithopods (slender prepubic process; Norman et al., 2004). The articular face of iliac peduncle is posteriorly directed (Coria and Calvo, 2002; Calvo et al., 2007). MAU-Pv-CO-578 share with *Macrogrypusaurus* a triangular transversal section (wide dorsal side and a narrow ventral side); different from *Talenkauen* that has an ellipsoidal transversal section (Calvo et al., 2007; Cambiaso, 2007). The size is approximately equal to the

Macrogyphosaurus pubis (Calvo et al., 2007). Thus, this bone is assigned to an indeterminate ornithopod similar to *Macrogyphosaurus*.

The ischium (MAU-Pv-CO-577) present some features common with other ornithopods, such as the iliac peduncle has a quadrangular articular face and is slightly longer than the pubic peduncle (Norman et al., 2004). Due to this is assigned to an indeterminate ornithopod.

The proximal phalanx IV-1 MAU-Pv-CO-579 presents a depression in the collateral ligament insertion and *M. extensor insertions*. Basal ornithischians and basal ornithopods present both insertions very deep marked (Zheng et al., 2012), as occur in theropod dinosaurs, while hadrosaurid ornithopods have very shallow insertions (Moreno et al., 2007; Díaz-Martínez et al., 2012). Ornithopods of South American as *Anabisetia*, *Gasparinisaura*, *Notohypsilophodon* and *Talenkauen* present more marked and deeper insertions than MAU-Pv-CO-579. We consider it as indeterminate ornithopod phalanx.

Three different ontogenetic stages have been identified with the described above material allow to discuss the ontogenetic stages (adult, subadult more immature and subadult) of some bones. The caudal vertebra MAU-Pv-CO-569 shows the remains of the neural arch fused to the centrum (adult ontogenetic stage). This is a typical feature of the adult dinosaurs. The cervical vertebra MAU-Pv-CO-564 has a visible suture between the neural arch and the centrum (subadults ontogenetic stage). This feature is present in subadult individuals, and is similar in size with those of *Macrogyphosaurus* and *Talenkauen* that are considered subadults as well. The neural arches and the centra are completely unfused (a more immature subadult ontogenetic stage) in three caudal vertebrae (MAU-Pv-CO-570, 571 and 575). They represent three more immature subadults.

Taking into account the above descriptions and comparisons, the new material is classified as Ornithopoda indet. Moreover, it presents affinities with the elasmarian *Macrogyphosaurus* and *Talenkauen*.

4.1 Late Cretaceous biodiversity of South American ornithopods

The Late Cretaceous South American ornithopod record is scarce and its biodiversity is poorly known (see references in Díaz-Martínez et al., 2015, 2016; Cruzado-Caballero, 2016) when compared with coeval sauropod and theropod dinosaurs. Almost all this record is located in Argentina, with the exception is of an indeterminate ornithopod from Turonian-Santonian of Uruguay (Huene, 1934; M. Soto, *pers. comm.* in Novas, 2009).

The ichnological record is scarcer than the skeletal one (see Díaz-Martínez et al., 2015, 2016). Few track sites with ornithopod tracks of Cenomanian age are cited from Brazil and Argentina (Calvo, 1991; Carvalho, 2001). In addition, large ornithopod tracks have been cited in the uppermost Cretaceous of Argentina and Peru (Alonso, 1980; Alonso and Marquillas, 1986; Jaillard et al., 1993; Díaz-Martínez et al., 2016). All the putative trackmakers of these tracks are related with large-sized iguanodontian ornithopods (see Díaz-Martínez et al., 2015, 2016). There are no data of Late Cretaceous small ornithopod tracks in South America. The similarities between theropod and basal ornithopod tracks (see Wright, 2004) can cause that ornithopod tracks have been misidentified as theropod ones.

In Argentina, several lithostratigraphic units from Cenomanian to Maastrichtian have yielded ornithopod remains (Fig. 6, Tables 1–3). Although there were found ornithopod bones in all the Upper Cretaceous stages, almost all this record is composed by fragmentary remains without diagnostic characters that allow assigning them to a more specific taxon or studying their phylogenetic relationships (Tables 1–3). Thus, representative biodiversity studies of South American ornithopods are difficult to performance.



Fig. 6 Distribution map of the ornithopod record in Argentina during Late Cretaceous. Black triangle: ornithopod record during Cenomania–Turonian; white triangle: ornithopod record during Coniacian–Santonian; circle: ornithopod record during Santonian–Maastrichtian. Scale 500 km.
alt-text: Fig. 6

Table 1 South American ornithopod record during Cenomania-Turonian (Late Cretaceous).

alt-text: Table 1

Number	Locality	Taxon	Current status	Age	Stratigraphic unit	References
1	Plaza Huincul (Neuquén)	Iguanodontia indet.	Iguanodontia indet.	Cenomanian	Huincul Fm. (ACG pers. obs.),	Coria et al. (2004) Coria et al. (2007)

	province)				Río Limay Subgroup, Neuquén Group	
2	Southeastern of the Colhué Huapi lake (Chubut province)	Ornithopoda indet.	Ornithopoda indet.	Turonian—middle Cenomanian	Bajo Barreal Fm., Upper Member	Ibiricu et al. (2010)
3	Neighboring of Buen Pasto (Chubut province)	<i>Notohypsilophodon comodorensis</i>	<i>Notohypsilophodon comodorensis</i>	Turonian—middle Cenomanian	Bajo Barreal Fm., Chubut Group	Martínez (1998) Ibiricu et al. (2014)
4	Agrio del Medio (Neuquén province)	Ornithopoda indet.	Ornithopoda indet.	Turonian—late Cenomanian	Huincul Fm., Río Limay subgroup, Neuquén Group	Canudo et al. (2013)
5	Cerro Bayo Mesa (Neuquén province)	<i>Anabisetia saldiviai</i>	<i>Anabisetia saldivia</i>	Turonian	Cerro Lisandro Fm., Río Neuquén subgroup, Neuquén Group	Coria and Calvo (2002)

Table 2 South American ornithopod record during Coniacian—Santonian (Late Cretaceous).

alt-text: Table 2

Number	Locality	Taxon	Current status	Age	Stratigraphic unit	References
6	Southwestern coast of Mari Menuco lake (Neuquén province)	<i>Macrogyphosaurus gondwanicus</i>	<i>Macrogyphosaurus gondwanicus</i>	middle/late Coniacian	Sierra Barrosa Fm., Río Neuquén subgroup, Neuquén Group	Calvo et al. (2007)
7	Northern coast of Los Barreales lake (Neuquén province)	Iguanodontia indet.	Iguanodontia indet.	Coniacian	Portezuelo Fm., Río Neuquén subgroup, Neuquén Group	Porfiri and Calvo (2002) Calvo and Porfiri (2003)
8	Bandera Hill (Neuquén province)	Iguanodontia indet.	Iguanodontia indet.	Coniacian	Portezuelo Fm., Río Neuquén	Coria and Cambiaso (2007)

Table 3 South American ornithopod record during Santonian–Maastrichtian (Late Cretaceous).

alt-text: Table 3

Number	Locality	Taxon	Current status	Age	Stratigraphic unit	References
9	Pair-Aike (Santa Cruz province)	" <i>Loncosaurus argentinus</i> "	Ornithopoda indet.	Cenomanian–Santonian	Mata Amarilla Fm.	Molnar (1980a) Coria and Salgado (1996a) Coria and Cambiaso (2007)
10	Cerro Overo fossil locality, Rincón de los Sauces (Neuquén province)	Ornithopoda indet.	Ornithopoda indet.	Santonian	Bajo de la Carpa Formation, Río Colorado subgroup, Neuquén Group	This paper
10	Puesto Hernández quarry (Neuquén province)	Ornithopoda indet.	Ornithopoda indet.	Late Coniacian–late Santonian	Plottier Fm., Río Neuquén subgroup, Neuquén Group	Cruzado-Caballero et al. (2016)
11	El Anfiteatro (Río Negro province)	Ornithopoda indet.	Ornithopoda indet.	late Coniacian–late Santonian	Plottier Fm., Río Neuquén subgroup, Neuquén Group	Salgado et al. (2009a)
	Guichón (Paysandú Department)	Ornithopoda indet.	Ornithopoda indet.	Turonian–Santonian	Mercedes Fm.	Huene, 1934 ; M. Soto, <i>pers. comm.</i> in Novas (2009)
12	Cinco saltos (Río Negro province)	<i>Gasparinisaura cincosaltensis</i>	<i>Gasparinisaura cincosaltensis</i>	Santonian early–Campanian	Anacleto Fm., Río Colorado subgroup, Neuquén Group	Coria and Salgado (1996b) Salgado et al. (1997) Coria (1999) Dingus et al. (2000) Coria and Cambiaso (2007)
13	Triñailao, Valcheta (Río Negro province)	Hadrosauridae indet.	Hadrosauridae indet.	Santonian?–Campanian?	Río Colorado subgroup?	
14	Cerro Mesa, South of Villa Regina (Río Negro province)	Hadrosauridae indet.	Hadrosauridae indet.	Late Campanian	Allen Fm., Malargüe Group	Corsolini (2014) Coria (2016)
15	South-east of	Hadrosauridae	Hadrosauridae	Campanian–Maastrichtian?	Bajo Barreal	Luna et al. (2003)

	Lake Colhué Huapi (Chubut province)	indet.	indet.		Fm., Upper Member	
16	La colonia (Chubut province)	Hadrosauridae indet.	Hadrosauridae indet.	Campanian–Maastrichtian	La Colonia Fm.	Hill et al. (2002) Gasparini et al. (2015)
17	Between Paso del Sapo and Cerro Cóndor (Chubut province)	Hadrosauridae indet.	Hadrosauridae indet.	Campanian–Maastrichtian	Paso del Sapo Fm.	Apesteguía and Cambiaso (1999) Apesteguía et al. (2012)
18	Cona Niyeu, 9 de Julio Departament (Río Negro province)	Hadrosauridae indet.	Hadrosauridae indet.	Late Campanian–early Maastrichtian	Los Alamos Fm.	Cruzado-Caballero (2015)
18	Bajo Colorado, Ingeniero Jacobacci, 5 de Mayo Departament (Río Negro province)	Hadrosauridae indet.	Hadrosauridae indet.	Campanian–middle Maastrichtian	Angostura Colorada/Coli Toro Fm.	Cruzado-Caballero (2015)
18	Cerro Mesa, Ingeniero Jacobacci, 5 de Mayo Departament (Río Negro province)	Hadrosauridae indet.	Hadrosauridae indet.	Campanian–early/middle Maastrichtian	Angostura Colorada/Coli Toro Fm.	Casamiquela (1964)
13	Bajo Santa Rosa, Valcheta (Río Negro province)	Hadrosauridae indet.	Hadrosauridae indet.	Late Campanian?–early Maastrichtian?	Los Alamos Fm.?	
19	Lamarque (Río Negro province)	Hadrosauridae indet.	Hadrosauridae indet.	Late Campanian–early Maastrichtian	Los Alamos Fm.	Martinelli and Forasiepi (2004)
20	Salitral Moreno site, General Roca (Río Negro province)	<i>Willinakaqe salitranensis</i>	Hadrosauridae indet.	Late Campanian–early Maastrichtian	Allen Fm., Malargüe Group	Juárez Valieri et al. (2010) Cruzado-Caballero and Coria (2016)
20	Salitral Moreno site,	<i>Willinakaqe salitranensis</i>	<i>Bonapartesaurus rionegrensis</i>	Late Campanian–early Maastrichtian	Allen Fm., Malargüe	Juárez Valieri et al. (2010) Cruzado-Caballero and Powell (2017)

	General Roca (Río Negro province)				Group	
21	Arroyo Verde región Puelén Departament (Río Negro province)	<i>Kritosaurus australis</i>	<i>Secernosaurus koernerii</i>	Late Campanian—early Maastrichtian	Los Alamitos Fm.	Bonaparte et al. (1984) Wagner (2001) Prieto-Marquez and Salinas (2010)
22	Islas Malvinas site (La Pampa province)	<i>Willinakaqe salitranensis</i>	<i>Lapampasaurus cholinoi</i>	Late Campanian—early Maastrichtian	Allen Fm., Malargüe Group	González Riga and Casadío (2000) Juárez Valieri et al. (2010) Coria et al. (2012)
23	Los Hornos Hill, Argentino lake (Santa Cruz province)	<i>Talenkauen santacruensis</i>	<i>Talenkauen santacruensis</i>	Maastrichtian	Pari Aike Fm.	Novas et al. (2004)
24	Chico River, east of Lake Colhué Huapi (Chubut province)	<i>Secernosaurus koernerii</i>	<i>Secernosaurus koernerii</i>	Maastrichtian	Bajo Barreal Fm., Chubut Group	Brett-Surman (1979) Bonaparte and Powell (1980)

In the Cenomanian–Turonian, apart from indetermined ornithopods and iguanodonts ([Coria and Salgado, 1996a,b](#); [Coria et al., 2004, 2007](#); [Ibircu et al., 2007](#); [Canudo et al., 2013](#); [Table 3](#)), members of small-sized Euiguanodontia and medium-sized Elasmaria have been identified. *Notohypsilophodon comodorensis* [Martínez, 1998](#) (an elasmarian *sensu* [Boyd, 2015](#)) was found in the Bajo Barreal Formation (middle Cenomanian–Turonian) in Chubut province, Argentina. Finally, in the Turonian Cerro Lisandro Formation (Neuquén province, Argentina), the euiguanodont *Anabisetia saldiviai* [Coria and Calvo, 2002](#) was described. The taxon “*Loncosaurus argentinus*” [Molnar, 1980](#) (Mata Amarilla Formation, Cenomanian–Santonian) is considered as *nomen vanum* (see [Coria and Cambiaso, 2007](#)). Out of Argentina there is an indeterminate ornithopod from Turonian–Santonian of Uruguay.

In the Coniacian–Santonian, some fragmentary remains were classified as Ornithopoda indet. ([Salgado et al., 2009](#); [Cruzado-Caballero et al., 2016](#); in this work) and Iguanodontia indet. ([Porfiri and Calvo, 2002](#); [Calvo and Porfiri, 2003](#); [Coria and Cambiaso, 2007](#)). In the middle-upper Coniacian of Sierra Barrosa Formation (Neuquén province, Argentina) the bones of *Macrogyphosaurus gondwanicus* [Calvo et al., 2007](#), a medium-sized elasmarian ornithopod, were identified. In addition, as it is suggested above, the herein studied remains that belong to medium sized indeterminate ornithopods present affinities with the Elasmaria clade, being the first ornithopod record of the Santonian Bajo de la Carpa Formation. On the other hand, in the Santonian–lower Campanian rocks of Anacleto Formation (Río Negro province, Argentina) some almost complete skeletons of a small sized iguanodont, *Gasparinisaura cincosaltensis* [Coria and Salgado, 1996](#), were found ([Coria and Salgado, 1996b](#); [Salgado et al., 1997](#); [Coria, 1999](#); [Dingus et al., 2000](#); [Coria and Cambiaso, 2007](#); [Salgado et al., 2009a](#)).

Finally, the Santonian–Maastrichtian ornithopod record is composed mainly by large sized hadrosaurids ([Coria and Cambiaso, 2007](#)). Almost all this record is fragmentary and it is considered as Hadrosauridae indet. ([Casamiquela, 1964](#); [Coria and Cambiaso, 2007](#); [Cruzado-Caballero, 2015](#); [Coria, 2016](#); [Cruzado-Caballero and Coria, 2016](#)), but three hadrosaurids were described: *Secernosaurus koernerii* [Brett-Surman 1979](#) in the Maastrichtian Bajo Barreal Formation (Chubut province) and upper Campanian–lower Maastrichtian Los Alamitos Formation (Río Negro Formation); *Lapampasaurus cholinoi* [Coria, González Riga, and Casadío 2012](#) in the upper Campanian–lower Maastrichtian Allen Formation (La Pampa province); and *Bonapartesaurus rionegrensis* [Cruzado-Caballero and Powell, 2017](#) in the upper Campanian–lower Maastrichtian Allen Formation (Río Negro province). The unique non-hadrosaurid ornithopod record found in Maastrichtian rocks is the medium sized elasmarian *Talenkauen santacruensis* [Novas et al., 2004](#) (Pari Aike Formation, Santa Cruz province).

Based on the above data, it would be presumed that: a) during the Cenomanian–Santonian the ornithopod diversity was characterized by small and medium sized euiguanodonts and elasmarian; b) in the Campanian–Maastrichtian there were medium sized elasmarian and large sized hadrosaurids, being the later the most abundant taking into account the number of findings. The Campanian–Maastrichtian of the Antarctica presents the same ornithopod diversity (see [Rozadilla et al., 2016](#)).

As well as the Elasmaria clade is present in South America (at least in Argentina) in all the Upper Cretaceous, the Euiguanodontia and Hadrosauridae have a particular temporal distribution. Euiguanodontids are located between Cenomanian and Santonian. The lack of this record in the Campanian–Maastrichtian could be due to a taphonomical bias or an ecologic replacement. Towards this second option, in the Campanian–Maastrichtian the establishment of land connections between Gondwana and Laurasia produced the presence of immigrant taxa like the hadrosaurids (see [Leanza et al., 2004](#)) that could compete for the ecologic niches. However, taking into account the difference of size between euiguanodontids and hadrosaurids is improbable an ecologic replacement, unless a global or regional change could modify the ecosystems (e.g., the late Campanian Atlantic flooding episode over Patagonia, see [Legarreta et al., 1989](#); [Malumian and Carames, 1995](#); [Parras et al., 1998](#)).

5 Conclusions

The material studied herein present diagnostic features of the Ornithopoda clade, and several characters that suggest affinities with other Argentinian ornithopods, especially with the medium-sized members of the Elasmaria clade (*Macrogyphosaurus* and *Talenkauen*). The material belongs to at least three different ontogenetic stages (an adult, a more immature subadult and a subadult). The bones found in the Cerro Overo site are the first ornithopod remains of this clade from Bajo de la Carpa of Santonian in age (Neuquén Group, Neuquén province, Argentina). Based on the Late Cretaceous ornithopod record in South America (almost all found in Argentina), the diversity presents a temporal distribution. The medium sized elasmarian are present in all the Upper Cretaceous, from Cenomanian to Maastrichtian. On the other hand, the small sized euiguanodonts were identified in Cenomanian–Santonian rocks, and disappear just when the large hadrosaurids arrived from the Northern hemispheres during the Campanian–Maastrichtian.

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Queries and Answers

Query: Please check affiliation ‘4’.

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Query: Please check the spelling of the term ‘euiguanodonts’ throughout the article, and correct if necessary.

Answer: Line 375, in the sentence "Euiguanodontids are located between Cenomanian and Santonian." change by: "Euiguanodonts are located between Cenomanian and Santonian. " Line 381. In the sentence "However, taking into account the difference of size between euiguanodontids and hadrosaurids..." change by "However, taking into account the difference of size between euiguanodonts and hadrosaurids..."

Query: The sentence "The Neuquén Group is" seems to be incomplete. Please check for missing words/phrases and complete the sentence.

Answer: Delete the sentence: "The Neuquén Group is"

Query: Please note that the text "andand" given below the paragraph "In the study area, the Bajo de la Carpa Formation..." has not been retained. Kindly check and amend if necessary.

Answer: Delete one "and"

Query: Please check the spelling of the term ‘opisthocoelic’ in sentence ‘The articular surfaces are heart-shaped and...’, and correct if necessary.

Answer: Correct by: opisthocoelous

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Answer: Change the citation please. The correct list is: Canudo et al., 2013; Coria and Salgado, 1996a; Coria et al., 2004, 2007; Ibiricu et al., 2010 Moreover, in the sentence "In the Cenomania-Turonian, apart... " the Table 3 is incorrect, changing it by Table 1. In the sentence "In the Coniacian–Santonian, some fragmentary..." add after "in this work" ;Table 2. In the sentence "Finally, the Santonian–Maastrichtian ornithopod...." add after "(Coria and Cambiaso, 2007)" ; Table 3.

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Answer: Delete: Ibiricu et al (2007) Add: Coria, R. A. 1999. Ornithopod dinosaurs from the Neuquen Group, Patagonia, Argentina; phylogeny and biostratigraphy. Proceedings of the Second Gondwanan Dinosaur Symposium. National Science Museum Monographs, Eds. Y. Tomida, T. H. Rich & P. Vickers-Rich, Eds. Y. Tomida, T.H. Rich & P. Vickers-Rich, 15, 47-60. Molnar, R. 1980. Australian Late Mesozoic terrestrial tetrapods: some implications. Mémoire Société géologique de France, N.S. 139, 131-143. Salgado, L., Canudo, J.I., Garrido, A.C., Ruiz-Omeñaca, J.I., García, R.A., de la Fuente, M.S. Barco, J.L., Bollati, R. 2009. Upper Cretaceous vertebrates from “El Anfiteatro” (Río Negro, Patagonia, Argentina). *Cretaceous Research*, 30, 767-784. Caldwell, M.W. y Albino, A.M. 2001. Palaeoenvironment and palaeocology of three Cretaceous snakes: *Pachyophis*, *Pachyrhachis*, and *Dinilysia*. In: S.F. Vizcaino, R.A. Farifla y C. Janis (Eds.), *Biomechanics and Palaeobiology of Vertebrates. Acta Palaeontologica Polonica* 46: 203–218. Rozadilla, S., Agnolin, F.L., Novas, F.E., Aranciaga Rolanda, A.M., Motta, M.J., Lirio, J.M., Isasi, M.P. 2016. A new ornithopod (Dinosauria, Ornithischia) from the Upper Cretaceous of Antarctica and its palaeobiogeographical implications. *Cretaceous Research*, 57, 311-324. Leanza, H.A., Apesteguía, S., Novas, F.E., de la Fuente, M. 2004. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. *Cretaceous Research*, 25, 61-87.

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