

Osteology of Ornithopod *Macrogyphosaurus gondwanicus* (Dinosauria, Ornithischia) from the Upper Cretaceous of Patagonia, Argentina

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ABSTRACT

Macrogyphosaurus gondwanicus is the largest Elasmaria (Dinosauria, Ornithischia) known up to the date, from the Upper Cretaceous of Patagonia. The present contribution provides a detailed description of *Macrogyphosaurus* anatomy based on the holotype and only known specimen. This dinosaur presents several unique features along its vertebral column that distinguishes it from other ornithopods: the neck is notably elongated by the acquisition of an additional cervical vertebra, having 10 cervical plus 14 dorsal vertebrae, being the number of dorsals minor than in other taxa, which usually have 16. This implies that *Macrogyphosaurus* represents a new ornithopod morphotype, with long neck and short thorax. Moreover, three autapomorphies are here added to the original diagnosis of *Macrogyphosaurus*: presence of poorly developed diapophyses in the cervical vertebrae, anterior and posterior processes on the boat-shaped haemal arches, and a pubic foot in the postpubic process. The dorsoventral length of haemal arches indicate the ventral limit of the *M. caudofemoralis longus* and their posterior tapering so as the dorsal limit of the *M. ilio-ischiocaudalis* and its posterior ascension and dominance in the posterior-most portion of tail, resembling to the tail of some coelurosaur dinosaurs.

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1. Introduction

Traditionally considered as infrequent and eclipsed by saurischian taxa, the record of ornithischian dinosaurs in South America has been considerably increased in the last years (i.e., Coria and Salgado, 1996; Salgado and Coria, 1996; Salgado et al., 1997; Coria and Calvo, 2002; Porfiri and Calvo, 2002, 2006; Novas et al., 2004; Calvo et al., 2007; Cambiaso, 2007; Coria et al., 2007; Ibiricu et al., 2010; Juárez Valieri et al., 2010; Coria et al., 2012; Canudo et al., 2013; Apesteguía et al., 2015; Cruzado-Caballero and Powell, 2017; Cruzado-Caballero et al., 2016, 2018, 2019; Ibiricu et al., 2019). Among non-hadrosaurian euiguanodontians, there is *Macrogyphosaurus gondwanicus* Calvo, Porfiri and Novas (2007), recovered from the Upper Cretaceous of

Neuquén Basin, Patagonia, Argentina (Fig. 1). The remains of this dinosaur consist of an almost complete vertebral column, ribcage and pelvic girdle, representing the largest and stouter member of Elasmaria (Coria and Salgado, 1996; Coria and Calvo, 2002; Rozadilla et al., 2019).

Macrogyphosaurus was first described by Calvo et al. (2007) as a basal member of Euiguanodontia, and together with *Talenkauen santacruensis* Novas, Cambiaso and Ambrosio (2004), were used to propose the clade Elasmaria for the first time (Calvo et al., 2007). The composition of Elasmaria was changing (Calvo et al., 2007; Boyd, 2015; Rozadilla et al., 2016; Rozadilla et al., 2019) and within this clade were included medium to large sized basal iguanodontians from South America (i.e. *Gasparinisaura* Coria and Salgado, 1996; *Notohypsilophodon* Martínez, 1998; *Macrogyphosaurus* Calvo et al., 2007, *Talenkauen* Novas et al., 2004; *Anabisetia* Coria and Calvo, 2002), Antarctica (i.e. *Trinisaura* Coria et al., 2013; *Morrosaurus* Rozadilla et al., 2016), Australia (i.e. *Fulgurotherium* Huene, 1932; *Qantassaurus* Rich and Vickers-Rich, 1999, “*Atlascopcosaurus*” Rich and Vickers-Rich, 1989) and Africa (i.e. *Kangnasaurus* Houghton, 1915),

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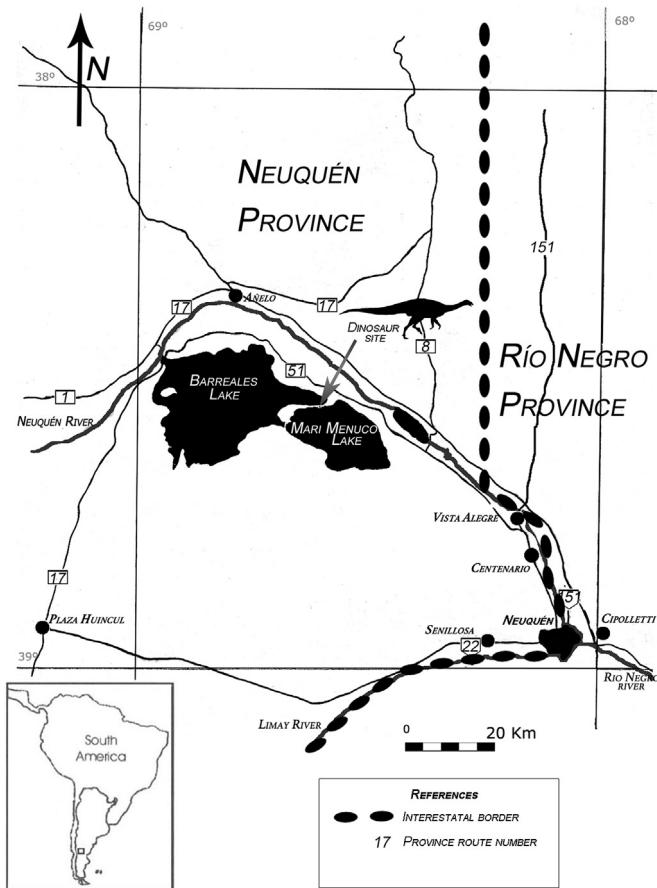


Fig. 1. Map showing the location of the Mari Menuco lake (Neuquén, Argentina).

highlighting that this clade was more widely distributed than previously thought (Rozadilla et al., 2019).

The anatomy of *Macrogyphosaurus gondwanicus* was preliminary provided by Calvo et al. (2007). In this regard, the aim of the present work is to provide a detailed description of holotype and only known material of this species, as well as to compare with other ornithopods, and discuss implications for elasmarian diversity.

2. Material and methods

2.1. Osteological nomenclature

We employ traditional, or 'Romerian' orientation terms (Wilson, 2006). 'Anterior' and 'posterior', for example, are used rather than the veterinarian alternatives 'rostral' or 'cranial' and 'caudal'. We follow Wilson (1999) and Wilson et al. (2011) regarding the terminology for vertebral laminae and fossae, respectively.

Institutional abbreviations: MLP, Museo de La Plata, La Plata, Argentina; MPM, Museo Padre Molina, Río Gallegos, Santa Cruz; MUCPv, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina; NMV P, Museum of Victoria, Melbourne, Victoria, Australia, Paleontological collections.

3. Systematic palaeontology

DINOSAURIA Owen (1842)

ORNITHISCHIA Seeley (1887)

ORNITHOPODA Marsh (1881)

EUIGUANODONTIA Coria and Salgado (1996)

ELASMARIA Calvo, Porfiri and Novas (2007)

Macrogyphosaurus Calvo, Porfiri and Novas (2007)

Type species. *Macrogyphosaurus gondwanicus* Calvo, Porfiri and Novas (2007)

Diagnosis: As for genus, for monotype.

Macrogyphosaurus gondwanicus Calvo, Porfiri and Novas (2007)
 Figures 2-12

Emended diagnosis: *Macrogyphosaurus gondwanicus* is a medium to large sized elasmarian ornithopod diagnosed by the presence of ten cervical vertebrae; fourteen dorsal vertebrae; transversely short diapophyses in the cervical series; last dorsal with well-developed hyposphene; sternal ribs flattened, twisted and distally expanded; distal haemal arches being boat-shaped and showing anterior and posterior processes; postpubic process with a small distal foot.

Holotype: MUCPv-321, incomplete skeleton of an adult individual that it includes an almost complete vertebral column, eight cervical vertebrae (from C3 to C10; C8 is currently lost, atlas and axis is missed), 14 dorsal vertebrae (complete series), six sacral vertebrae, thirteen caudal vertebrae, a cervical rib, eleven dorsal ribs; nine haemal arches, sternum, right and left pelvic girdles, and three thoracic mineralized plates.

Remarks: The holotype of *Macrogyphosaurus gondwanicus* is the only hitherto known specimen.

Locality and horizon: In the original publication, the authors commented that the specimen was found 60 km NW from Neuquén city, on the west coast of the Mari Menuco lake (Neuquén, Argentina; Fig. 1) in the Portezuelo Formation, Neuquén Group; Upper Cretaceous (Coniacian). Nonetheless, Garrido (2010) analysed the entire Neuquén Basin and reinterpreted the rocks where *Macrogyphosaurus* holotype as a unit distinguished from the Portezuelo Formation, and consequently it was named as Sierra Barrosa Formation. This unit shows a succession of fine to limy sandstones to mudstones, corresponding to overflow and flood plains deposits, with well-developed palaeosols (Garrido, 2010). Sierra Barrosa Formation represents a palaeoenvironment of sinuous river systems with a dominant sandy load. The age of this formation, based on its stratigraphical relation, ranges from middle to upper Coniacian. Palaeontological remains are scarce, counting with turtle plates, crocodile teeth and the megaraptorid theropod *Murusraptor barrosaensis* Coria and Currie (2016). Nonetheless, the stratigraphy of the site where *Macrogyphosaurus* was unearthed is under revision, and future works will provide a clearer perspective of the site.

3. Description

3.1. Cervical vertebrae series

Macrogyphosaurus possess, together with *Talenkauen*, one of the most complete necks among southern ornithopods. *Macrogyphosaurus* preserves eight post-axis cervical vertebrae. In this regard, counting the lost atlas and axis elements, its neck counts with ten vertebrae, representing the longest neck among Elasmaria. In related taxa that the neck is preserved (e.g. *Talenkauen*; Novas et al., 2004; Rozadilla et al., 2019), the neck has nine cervical vertebrae, the plesiomorphic condition for Ornithopoda (Norman et al., 2004; Rozadilla et al., 2019). Hence, *Macrogyphosaurus* resembles more derived iguanodontians, such as *Tenontosaurus* Ostrom, 1970, *Iguanodon bernissartensis* (Boulenger, 1881) and

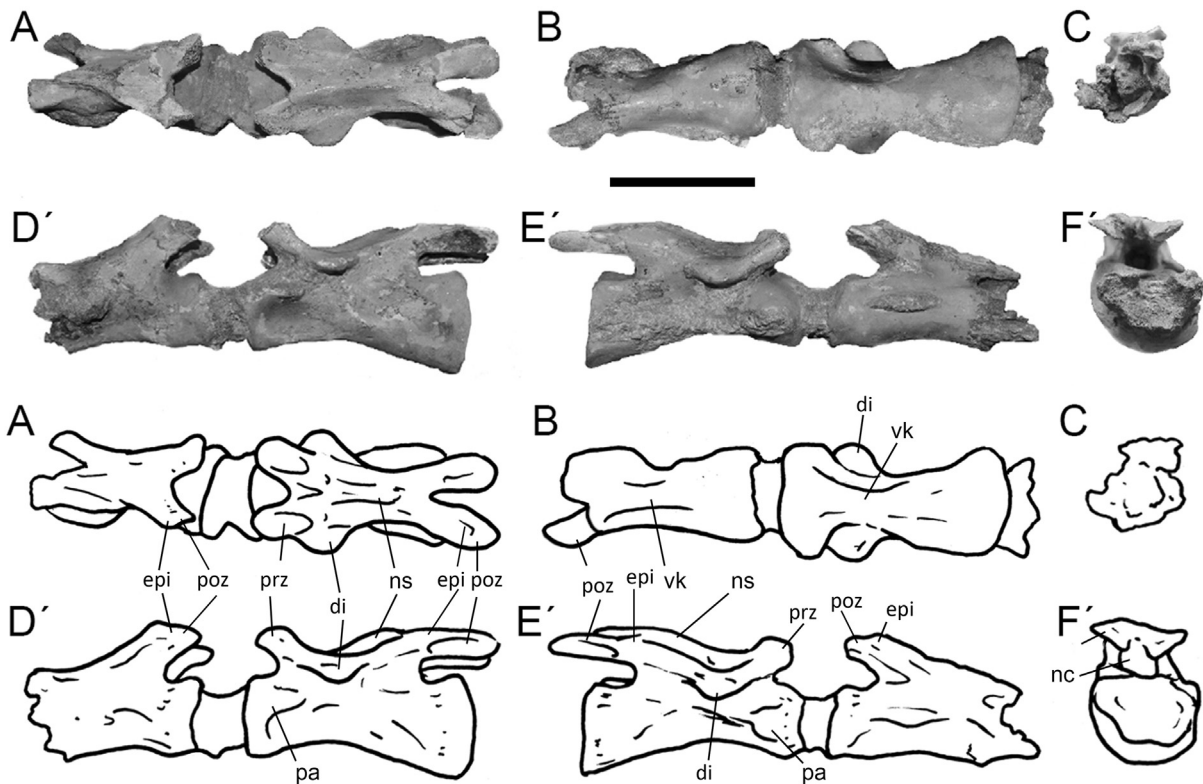


Fig. 2. *Macrogrypusaurus gondwanicus* 3–4 cervical vertebrae in A, dorsal; B, ventral; C, anterior; D–E, lateral; F, posterior views. Abbreviations: di, diapophysis; epi, epipophysis; nc, neural canal; ns, neural spine; pa, parapophyses; poz, postzygapophysis; prz, prezygapophysis; vk, ventral keel. Scale bar equals 5 cm.

Ouranosaurus Taquet, 1976, in which the neck has between ten and eleven vertebrae (Taquet, 1976; Norman, 1980, 1986, 2004).

In *Macrogrypusaurus*, as in others elasmarians (e.g. *Talenkauen*; *Notohyphilophodon*, *Anabisetia*, *Mahuidacursor*; Coria and Calvo, 2002; Ibiricu et al., 2014; Cruzado-Caballero et al., 2019; Rozadilla et al., 2019) cervical vertebrae has a proportionally low neural arch and anteroposteriorly longer centra than in non-elasmarian taxa (i.e. *Hypsilophodon* Huxley, 1869; *Thescelosaurus* Gilmore, 1913; *Dryosaurus* Marsh, 1894; *Tenontosaurus*, *Iguanodon*; Galton, 1974a, b, 1981, 2009; Norman, 1980, 1986, 2004; Norman et al., 2004; Tennant, 2013). The ventral surface of the centra bears a sharp ventral ridge and show deep lateral depressions.

Among Elasmaria, *Macrogrypusaurus* cervical vertebrae are strongly reminiscent to that seen in *Talenkauen* on its gross anatomy. Nonetheless, in *Macrogrypusaurus* those elements are bigger, stouter, and do not show the same degree of lateral compression seen in the vertebral centra of *Talenkauen* (Rozadilla et al., 2019). Further, the anteroposterior length of cervical centra increases along the series, resulting in conspicuously elongate posterior elements, as occurs in *Talenkauen*, *Mahuidacursor* and *Gasparinisaura*, resulting in notably elongate posterior elements (Cruzado-Caballero et al., 2019; Rozadilla et al., 2019). This, together with the presence of an additional cervical vertebra shows that the neck of *Macrogrypusaurus* was the largest among elasmarians.

The neural spine is very low when compared with other basal ornithopods (e.g. Galton, 1974a; b Norman et al., 2004), even respecting other elasmarians (e.g. *Talenkauen*, *Mahuidacursor*, *Anabisetia*; Coria and Calvo, 2002; Cruzado-Caballero et al., 2019; Rozadilla et al., 2019). This is barely protruding in the most anterior elements, but increases its high backwards the series, being sub-triangular in outline with a gently convex dorsal edge in lateral

view. Nonetheless, the neural spine is always proportionally lower when compared with other related taxa. Two low spinoprezygapophyseal laminae connect the neural spine to the posterior margin of prezygapophyses. There is a spinoprezygapophyseal fossa between these laminae.

The prezygapophyses are anterodorsally projected. In the anterior vertebrae these are transversely narrower and more anteriorly projected than in posterior elements. Their articular surface is wide, ovoidal in contour and dorsomedially facing. Moreover, the prezygapophyses fuse with the diapophyses backwards the series. Between the prezygapophysis and the diapophysis there is a sub-oval supraprezygodiapophyseal fossa.

The postzygapophyses are posterolaterally projected, showing a gentle dorsal curvature, as is common among basal ornithopods (Sereno, 1986; Norman, 2004; Norman et al., 2004). The articular surfaces are long and ovoidal in contour, being lateroventrally facing. The size of the postzygapophyses increases though posterior elements of the series, being thicker and more posteriorly projected. The epipophyses are present at the dorsal surface of the postzygapophyses as occurs in *Talenkauen* and *Anabisetia* (Novas et al., 2004; Cambiaso, 2007; Novas, 2009; Rozadilla et al., 2016, 2019). The lateral surface of the epipophysis is concave, the medial one is nearly flat, and its dorsal edge is a sharp longitudinal ridge.

The Cervical 3 and Cervical 4 (Fig. 2) bear sub-triangular epipophyses in the dorsal surface of the postzygapophyses, as occurs in *Talenkauen* and *Anabisetia* (Novas et al., 2004; Cambiaso, 2007; Novas, 2009; Rozadilla et al., 2016, 2019). In the Cervical 3 vertebra, the lateral surface of the epipophysis is concave, the medial one is nearly flat, and its dorsal edge is a sharp longitudinal ridge. On the other hand, the Cervical 4 epipophyses are smaller than in the Cervical 3, being represented by a small tubercle that

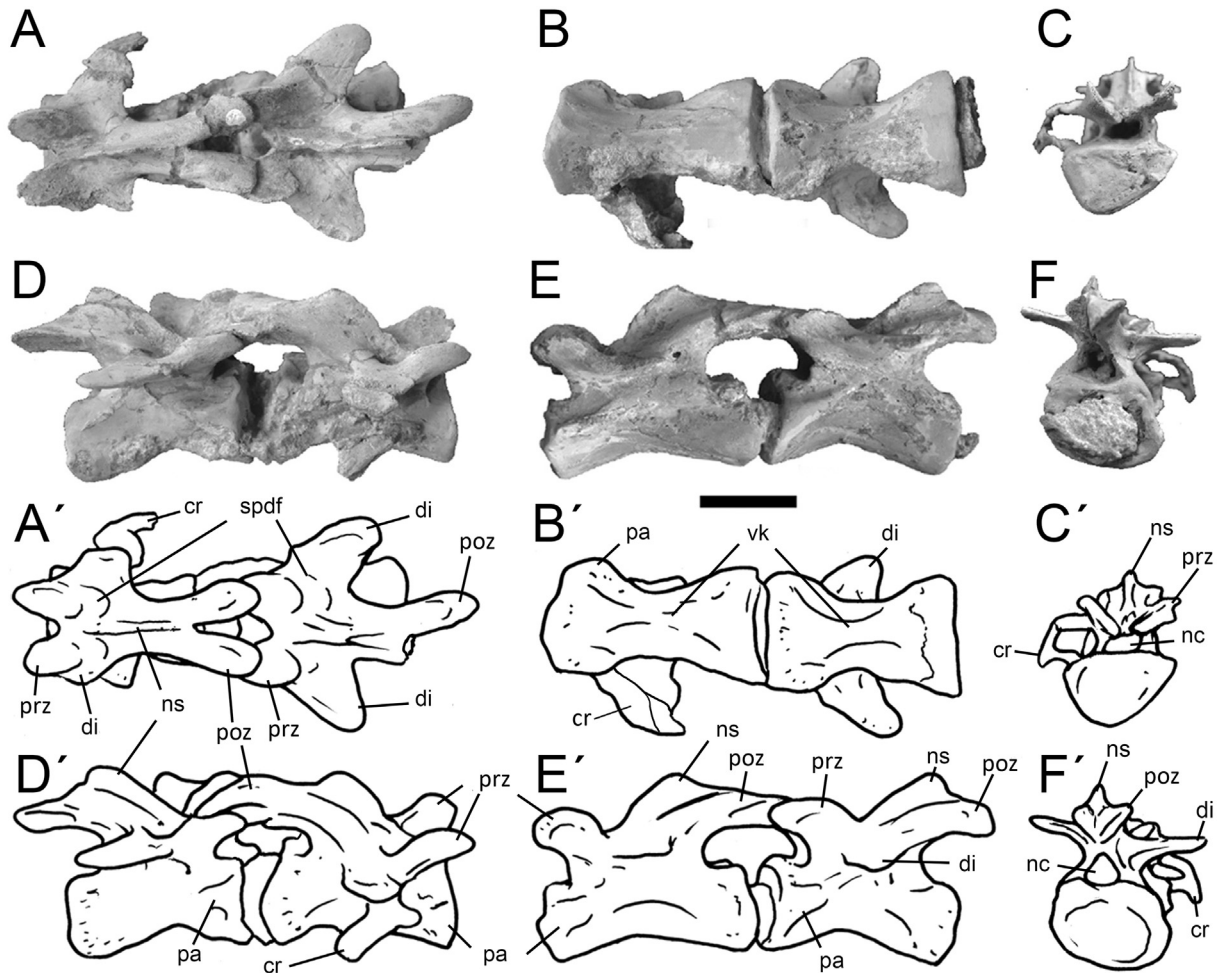


Fig. 3. *Macrogryposaurus gondwanicus* 9–10 cervical vertebrae in A, dorsal; B, ventral; C, anterior; D–E, lateral; F, posterior views. Abbreviations: di, diapophysis; nc, neural canal; ns, neural spine; pa, parapophyses; poz, postzygapophysis; prz, prezygapophysis; vk, ventral keel. Scale bar equals 5 cm.

anteriorly extends as a dorsolateral ridge along the proximal portion of the postzygapophysis, as occurs in *Talenkauen* (Rozadilla et al., 2019).

The diapophyses of *Macrogryposaurus* are laterally short when compared with that of other ornithomorphs (e.g. *Talenkauen*, *Mahuidacursor*, *Anabisetia*, *Dryosaurus*, *Hypsilophodon*; Galton, 1974a, 1981; Norman, 2004; Norman et al., 2004; Cambiaso, 2007; Cruzado-Caballero et al., 2019; Rozadilla et al., 2019). Nonetheless, backwards the neck, the diapophyses are more laterally projected. In the C10 vertebra (Fig. 3), the transversal width of the diapophyses is greater than the anteroposterior length of its centrum. The ventral surface of the diapophysis lacks well-defined centrodiaepiphyseal laminae, unlike *Talenkauen* (Rozadilla et al., 2019). Along the series, the diapophyses get more fused to the prezygapophyses than its respective previous element, with a stout prezygodiaepiphyseal lamina that connects the diapophysis with its respective prezygapophysis. Dorsally, there is the supraprezygodiaepiphyseal fossa which is small, subcircular and strongly attached to the articular surface of the prezygapophysis. In the most posterior cervical vertebrae, the supraprezygodiaepiphyseal fossa is practically confluent with the articular surface of the prezygapophysis. The neural canal is subcircular in contour, anteriorly and posteriorly. It is continued by a wide dorsal groove on the cervical centrum which are present in all the posterior half of the neck vertebrae.

The parapophyses are sub triangular in contour, bulky and anteroposteriorly extended. It shows a concave ventral surface, and lateral depressions to articulate the capitulum of its corresponding rib. The parapophyses become bigger, thicker and more dorsally located through posterior cervical vertebrae.

The cervical centra are anteroposteriorly long and dorsoventrally low. This length increases along the consecutive elements of the neck, being cervical nine and ten more stouter vertebrae. The centra are laterally compressed which gives an hour-glass outline in ventral view. The anterior articular is ovoidal in contour, being more transversely wider than dorsoventrally tall. On the other hand, the posterior articular surface is sub-circular. The centra are slightly amphicoelous. In ventral view, the anterior half of the neck vertebrae lacks a well-defined ventral keel, differing from *Talenkauen* (Rozadilla et al., 2019) but in the posterior vertebrae the ventral keel is well developed, being stouter in the C10. The anterior ventral surface of cervical 10 shows a smooth and rounded ventral keel, which disappears posteriorly.

3.2. Dorsal vertebrae series

Macrogryposaurus holotype shows a complete dorsal series composed by 14 vertebrae (Fig. 4–6). This number is lower than in most ornithomorphs, which have between 15 and 16 vertebrae (Norman et al., 2004; Calvo et al., 2007). This may be related with

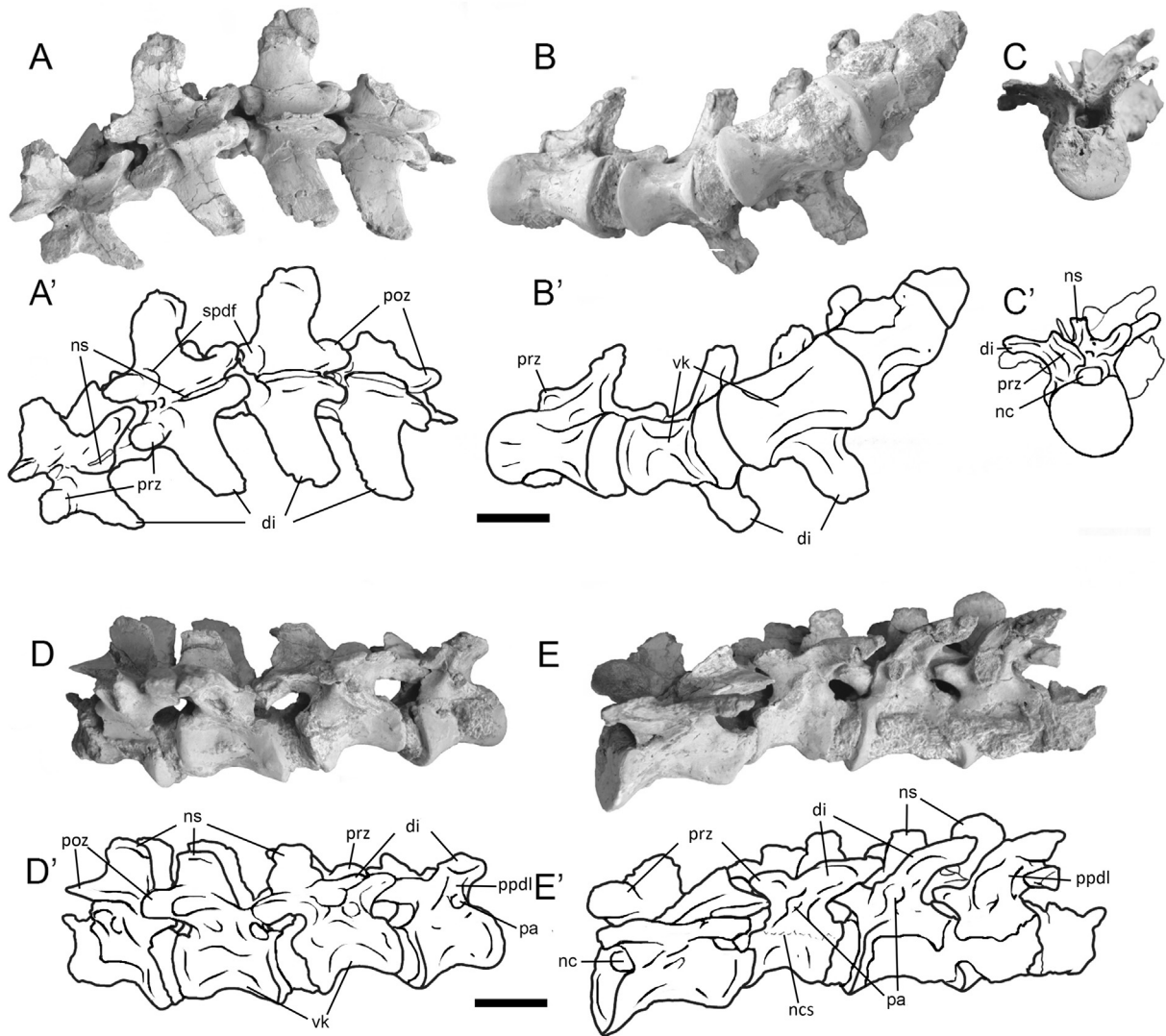


Fig. 4. *Macrogyphosaurus gondwanicus* 1–4 dorsal vertebrae in A, dorsal; B, ventral; C, anterior; D–E, lateral views. Abbreviations: cdl, centrodiaepophyseal lamina; di, diapophysis; nc, neural canal; ncs, neurocentral suture; ns, neural spine; pa, parapophyses; poz, postzygapophysis; prz, prezygapophysis; ppdl, paradiapophyseal fossa; vk, ventral keel. Scale bar equals 5 cm.

the cervicalization of the first dorsal that distinguish this dinosaur from other elasmarians (see Rozadilla et al., 2019).

The first four dorsal vertebrae (D1–D4) are articulated among them and with their ribs (Fig. 8). Most of the anatomy of the middle and posterior dorsal vertebrae are obscured by the sediment and other bones.

Dorsal vertebra 1 is strongly reminiscent in anatomy to the last cervical (C10; Fig. 3). Its neural spine is dorsoventrally low and subtriangular contour in lateral view. The neural arch is slightly higher than in cervical vertebrae and slightly anteroposteriorly shorter. The centrum is strongly elongated as in last cervical vertebra. The prezygapophyses are posteriorly located and emplaced in the dorsomedial portion of the diapophyses. Its articular surface is ventromedially directed, subcircular in shape and proportionally wider than in the posterior cervical vertebrae. The postzygapophyses are anteroposteriorly shorter than in last cervical vertebrae and the articular surfaces are ovoidal in contour. The diapophyses are anteroposteriorly wider than in the cervical vertebrae, being subtriangular in dorsal view and having a rounded distal end. The diapophyses are wider transversely than the

anteroposterior length of the centrum. Ventrally a paradiapophyseal lamina is present. The paradiapophyseal lamina is semilunar in cross-section and is relatively thicker than in C10. This lamina is anteriorly and posteriorly delimited by shallow fossae. The parapophyses are subcircular in shape and located at the medioventral surface of these buttresses. A small anterior centroparapophyseal lamina is present. The neural canal is sub-circular in this and all dorsal vertebrae. The vertebral centrum is anteroposteriorly longer than in more posterior dorsal vertebrae. Its ventral surface is concave when viewed from the side. In ventral view, it shows an hour-glass contour. It is stouter than cervical centra, and the ventral longitudinal keel is thicker than in preceding vertebrae.

Dorsal vertebra 2 shows a subrectangular neural spine in lateral view (Fig. 4). The prezygapophyses are shorter than in the first dorsal, and its posterior margin contacts the supra-prezygodiapophyseal fossa. Between the prezygapophyses there is a prespinal fossa which tapers dorsally to reach the point where the prezygapophyses start. The diapophyses and subrectangular shaped and larger than in preceding vertebrae. The

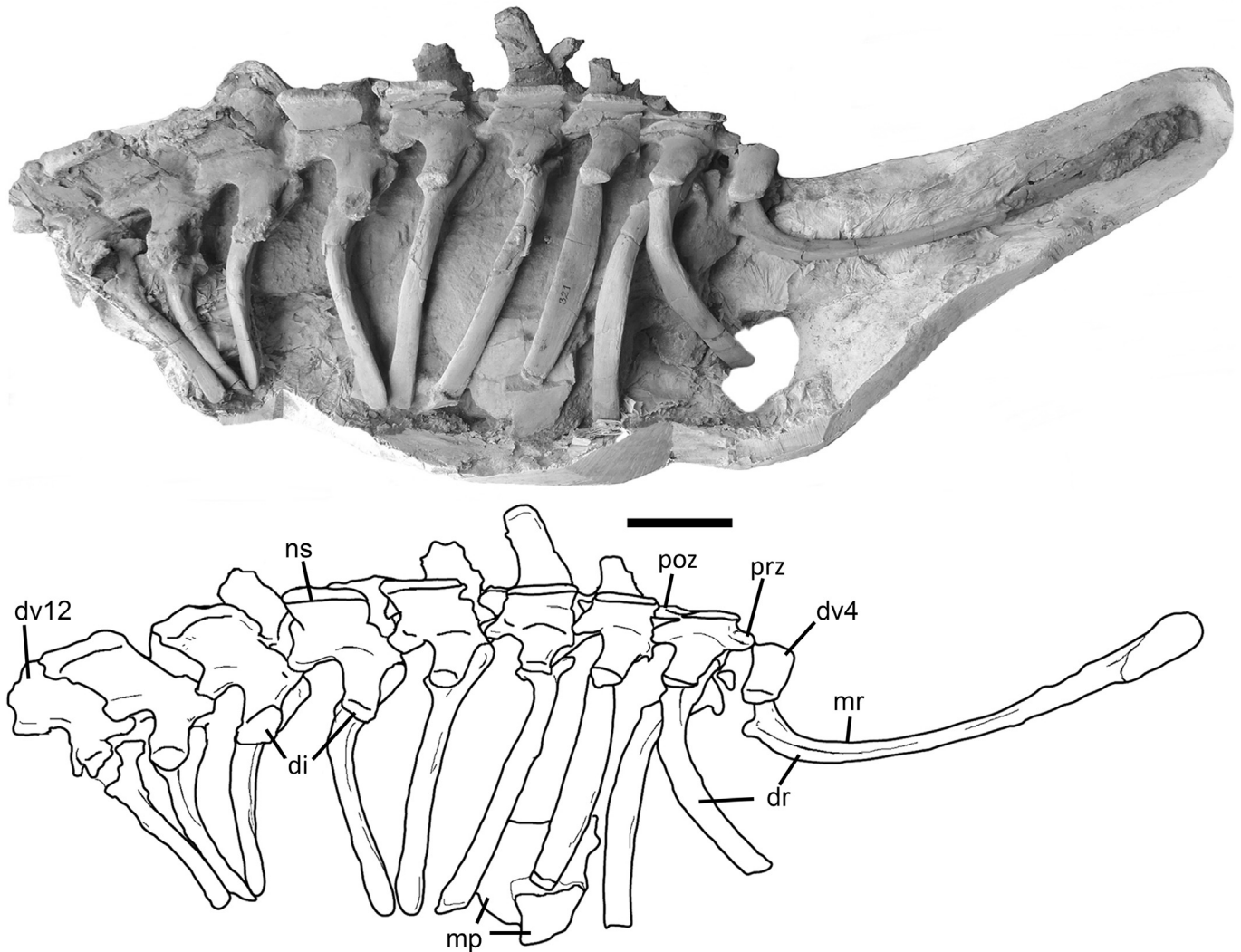


Fig. 5. *Macrogrypusaurus gondwanicus* dorsal vertebrae and ribs in articulation in dorsal view. Abbreviations: di, diapophysis; dr, dorsal rib; dv4, dorsal vertebra 4; dv12, dorsal vertebra 12; mr, medial ridge; mp, mineralized plates; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis. Scale bar equals 5 cm.

centrodiapophyseal laminae are subtriangular in cross-section. The parapophyses are similar to that in the first dorsal vertebra, being slightly larger and more posteriorly and dorsally located. The centrum is shorter and stouter than in previous elements.

Dorsal vertebra 3 is similar to more posterior elements of the dorsal series (Fig. 4). The neural arch is higher than the preceding vertebrae, with a neural spine that is subrectangular in contour, with a straight dorsal in lateral view. The prezygapophyses and postzygapophyses are sub-equal in size, due to the shortening of the latter when compared with anterior elements. The diapophyses show quadrangular distal ends and are anteroposteriorly longer and transversely greater than preceding vertebrae. The ventral surface of the diapophyses shows a well-developed centrodiapophyseal lamina, delimited by the parapophyses on its anterior edge. The parapophyses are larger than in preceding vertebrae, showing a posteroventrally faced articular surface. Laterally projected parapophyses are present from third to the last dorsal vertebra. The centrum is parallelogram-shaped in lateral view, with the ventral portion of the anterior margin being anteriorly projected, and the dorsal portion of the posterior one, posteriorly projected. The size of the centrum is larger than in the

second dorsal, but similar to more distal dorsal vertebrae, so as the morphology of its ventral keel.

Dorsal vertebra 4 is similar in morphology to the D3 (Fig. 4). The neural spine is higher and anteroposteriorly longer. The diapophyses are wider, so as their centrodiapophyseal lamina, which are proportionally thicker. The parapophyses are wider, and more dorsally and anteriorly located, approaching the anterior margin of the parapophyses. The centrum is also parallelogram shaped, resembling to preceding vertebra. The ventral surface of the centrum shows a small longitudinal keel.

All dorsal vertebrae posterior to the fourth vertebra remain articulated among them and to their corresponding dorsal ribs (Fig. 9). Through the most posterior dorsal vertebrae, the neural arches become dorsoventrally higher, especially its neural spine, which becomes taller, anteroposteriorly longer, and transversely thicker. In this regard, more distal dorsal vertebrae show a large-sized and sub-quadrangular neural spine. The three anterior neural spines are sub-quadrangular in shape, have a straight and more posterior are trapezoidal when viewed from the side. The prezygapophyses and postzygapophyses are similar to more anterior dorsal vertebrae, only differing in a slight increment in

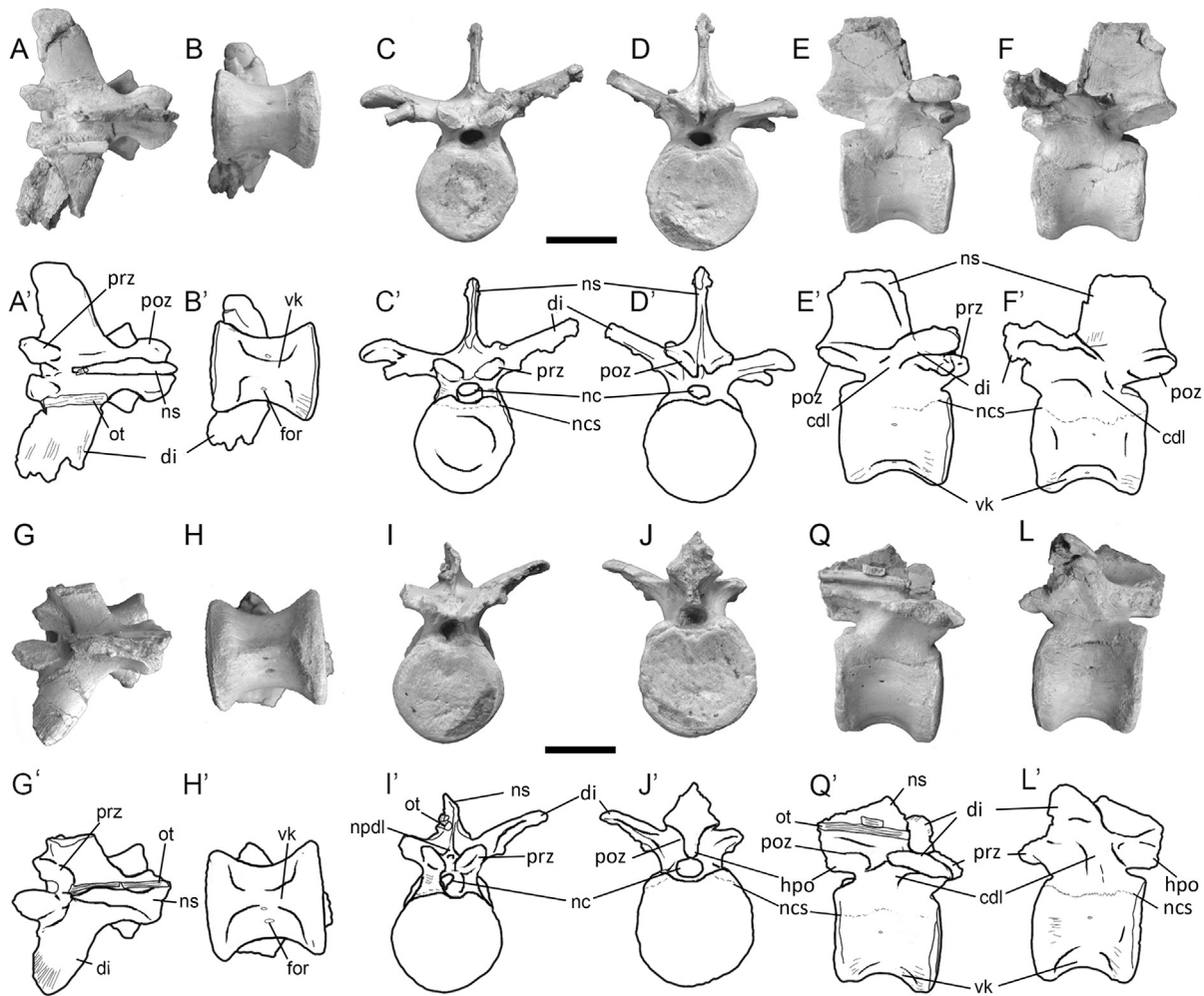


Fig. 6. *Macrogryposaurus gondwanicus* 13–14 dorsal vertebrae in A, G, dorsal; B, H, ventral; C, I, anterior; D, J, posterior; E–F, Q–L, lateral views. Abbreviations: cdl, centrodiapophyseal lamina; di, diapophysis; for, foramen; hpo, hyposphene; nc, neural canal; ncs, neurocentral suture; npdl, neuroprezygapophyseal lamina; ns, neural spine; ot, ossified tendons; poz, postzygapophysis; prz, prezygapophysis, vk, ventral keel. Scale bar equals 5 cm.

the anteroposterior extension of the postzygapophyses. The diapophyses and parapophyses form the transverse processes, being the parapophyses located on the anteromedial margin of the diapophyses. Diapophyses are poorly dorsally projected in anterior vertebrae, but posterior elements show a well-developed dorso-lateral projection. The centrodiapophyseal laminae are well-developed, subrectangular in cross section. Dorsal vertebrae from ninth to fourteenth show proportionally larger transverse processes, being more laterally projected than in preceding vertebrae. More posterior elements show a subcircular neural canal. The neurocentral suture is more visible through most posterior elements of the dorsal series, showing an incomplete fusion between the centrum and the neural arch, indicating that the animal was not skeletally mature. The centra has anterior and posterior articular surfaces subcircular in contour, being slightly amphicoelous as in *Thescelosaurus*, *Talenkauen*, *Notohypsilophodon* and *Mahuidacursor* (Galton, 1974a,b; Novas et al., 2004; Ibiricu et al., 2014; Cruzado-Caballero et al., 2019). The ventral surface of the centrum shows a shallow longitudinal keel as in *Talenkauen*, *Mahuidacursor*, *Notohypsilophodon* and *Trinisaura* (Novas et al., 2004; Coria et al., 2013; Ibiricu et al., 2014; Cruzado-Caballero et al., 2019; Rozadilla et al., 2019).

Dorsal vertebra 13 is similar in shape to remaining dorsal vertebrae. The diapophyses have a less developed centrodiapophyseal lamina than in previous elements (Fig. 6 A–F). The parapophyses are strongly anteroventrally oriented. The centrum is subrectangular in contour when laterally viewed, being slightly longer than high, it is subcircular in shape in anterior and posterior views. A stout longitudinal keel is present along the ventral surface of the centrum. Some vascular foramina are present at the lateral and ventral part of this centrum.

Dorsal vertebrae 14 is very similar to its precedent vertebra although, it is a little bit larger (Fig. 6 G–L). The prezygapophysis is ovoidal in shape and ventromedially directed. The posterior surface of the neural arch shows an hyposphene; this structure was recognized as an autapomorphic feature for *Macrogryposaurus* (Calvo et al., 2007). The two slightly inclined ventromedially postzygapophyses reach the dorsoventral wall of the hyposphene on the mid-line. The transversal section of the hyposphene is trapezoidal in shape. The base of the hyposphene is supported by the medial centropostzygapophyseal lamina (Apesteguía, 2005). It arises dorsally from the centrum and surround the neural canal.

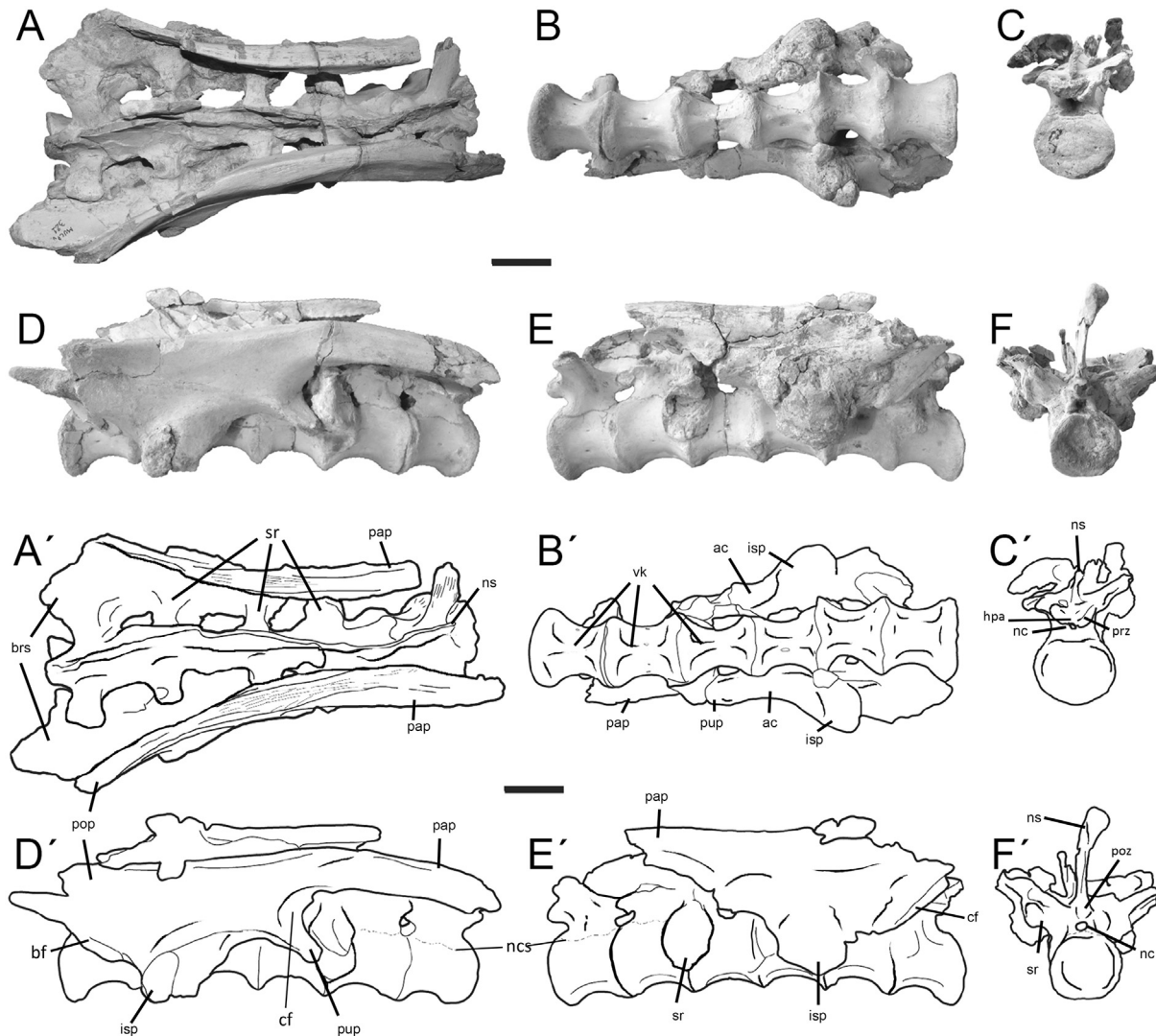


Fig. 7. *Macrogryposaurus gondwanicus* sacral vertebrae and ilia in A, dorsal; B, ventral; C, anterior; D–E, lateral; F, posterior views. Abbreviations: ac, acetabulum; cf, cupedicus fossa; hpa, hypantrum; isp, Ischiadic process; nc, neural canal; ncs, neurocentral suture; ns, neural spine; pap, preacetabular process; pop, postacetabular process; poz, postzigapophysis; pup, pubic process; prz, prezigapophysis, sr, sacral rib; vk, ventral keel. Scale bar equals 5 cm.

3.3. Sacral vertebrae series

The sacrum of *Macrogryposaurus* is composed by six fused vertebrae (Fig. 7). These vertebrae are proportionally larger and transversely wider than in any other basal ornithopods, including elasmarians (i.e. *Hypsilophodon*; *Thescelosaurus*; *Gasparinisaura*; *Talenkauen*; *Notohypsilophodon*; *Anabisetia*; *Sektensaurus*; Galton, 1974a, b; Coria and Salgado, 1996; Salgado et al., 1997; Coria and Calvo, 2002; Cambiaso, 2007; Ibiricu et al., 2014; 2019; Rozadilla et al., 2019).

The neural arch of the first sacral is partially preserved, anteroposteriorly width and transversely narrow. It is crossed by numerous ossified tendons, as occurs in posterior dorsal vertebrae. The transverse processes are slender, and project dorsally and anterolaterally, and their distal ends expand dorsoventrally and anteroposteriorly. The surface for capitulum and tuberculum of the rib are present. The prezigapophysis shows a hypantrum that articulates with the hyposphene of the last dorsal, resembling the morphology of the last dorsal.

The second sacral vertebra shows a smaller transverse process. The sacral ribs are fused with the vertebra to form a structure that

extends along the posterior end of its neural arch and the centrum. This structure is bulky and expands ventrally, showing a lateral notch that medially embraces the pubic peduncle of the ilium and the iliac processes of the pubis.

The third and fourth sacral vertebrae show transverse processes fused ventrally with the sacral ribs. The transverse processes are short and sub-quadrangular in shape, and laterally contact the iliac blade. In the fifth sacral vertebra, the transverse processes are slightly larger and contact the brevis shelf. On the other hand, the sixth sacra vertebra shows a larger transverse process, with fan shaped expansions on its distal end and fused to the respective sacral rib. The neural spine is almost completely fused with the fifth vertebra. It is backwardly oriented and the anterodorsal end surpasses the posterior margin of the centra. These lateral expansions contact iliac brevis shelf.

In general, the sacral centra anatomy resembles that found in other ornithopods (i.e. *Hypsilophodon*, *Thescelosaurus*, *Dryosaurus*, *Notohypsilophodon*, *Talenkauen*; Galton, 1974a, b; Norman et al., 2004; Cambiaso, 2007; Ibiricu et al., 2014; Rozadilla et al., 2019). These are thick bones. The anteroposterior length differs slightly between the elements, being the first two sacral vertebrae and the

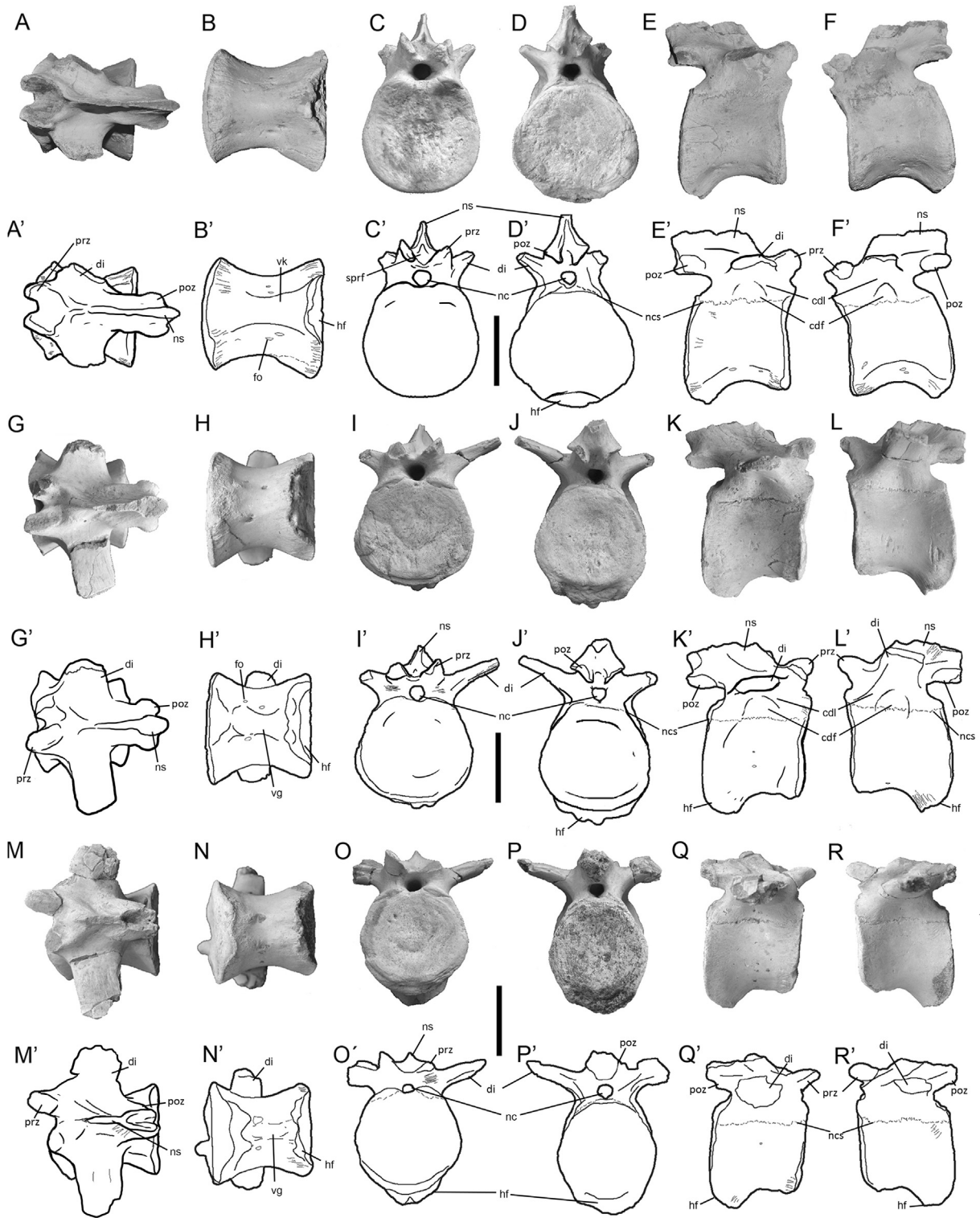


Fig. 8. *Macrogryposaurus gondwanicus* 1–3 caudal vertebrae and ilia in A, G, M, dorsal; B, H, N, ventral; C, I, O, anterior; D, J, P, posterior; E–F, K–L, Q–R, lateral views. Abbreviations: cdl, centrodiapophyseal lamina; di, diapophysis; fo, foramen; hf, haemal facet; nc, neural canal; ncs, neurocentral suture; ns, neural spine; poz, postzigapophysis; prz, prezigapophysis; vg, ventral groove; vk, ventral keel. Scale bar equals 5 cm.

last one is the longest of the series. In ventral view, these elements are pulley shaped. The first four sacral vertebrae bear a ventral keel, while the ventral surface of the last two sacral vertebrae are flat and smooth, unlike *Sektensaurus* who only have a ventral keel in the first and second vertebrae (Ibárricu et al., 2019). Some of the centra show several small and crescent-shaped vascular foramina.

3.4. Caudal vertebrae series

On the original paper Calvo et al. (2007) indicates that there are sixteen caudal vertebrae. We were able to identify thirteen caudal vertebrae represented by the three more-anterior caudal centra (Fig. 8) and 6 posterior ones (Fig. 9). The tail anatomy of elasmarian

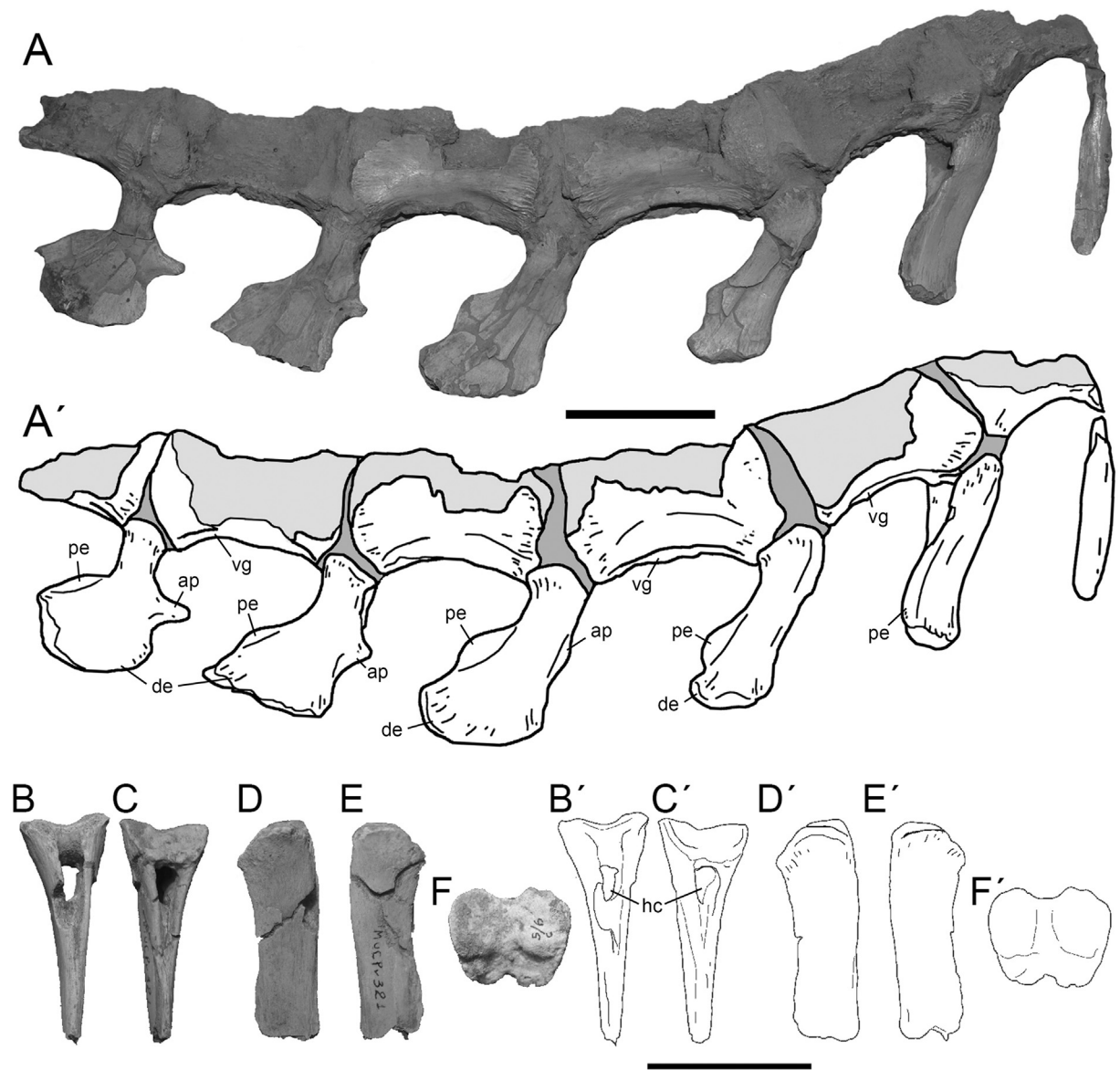


Fig. 9. *Macrogryphosaurus gondwanicus* caudal vertebrae and haemal arches in A, D–E, lateral; B, anterior; C, posterior; F, dorsal views. Abbreviations: ap, anterior process; de, distal expansion; hc, haemal canal; pe, posterior expansion; vg, ventral groove. Scale bar equals 5 cm.

ornithopods is poorly known, its knowledge restricted to *Gasparinisaura* (Coria and Salgado, 1996; Salgado et al., 1997) and isolated elements of some taxa (*Talenkauen*, *Notohypsilophodon*, *Kangnasaurus*; Cooper, 1985; Novas et al., 2004; Ibricu et al., 2014; Rozadilla et al., 2019).

Most proximal caudal vertebrae are strong and thick bones (Fig. 8). The neural arches are fragmentary, lacking distal ends of neural spines and distal end of transverse processes. The neural spines are posteriorly located on the neural arch and almost dorsally projected in the most proximal vertebra, whereas the neural spines are strongly posterodorsally projected in the dorsal anterior vertebra. Both laterals of the neural spine base there are shallow cavities, which extend posterodorsally, following the neural spine axis.

The transverse processes proximal anterior vertebrae are anterolaterally projected and subrectangular in shape, showing a slight constriction on its base (Fig. 8 A–F). The ventral surface of these processes is excavated by a median crescent-shaped

centrodiapophyseal fossa. More distal caudal vertebrae show the transverse processes that are laterally projected. These processes are subrectangular shape and transversely shorter in dorsal view, while its ventral fossa is less developed than in preceding caudal vertebrae.

The third caudal vertebra presents its transverse processes slightly posterolaterally projected, suggesting it belongs to a more distal portion of the proximal tail (Fig. 8 M–R). These transverse processes seem to be subrectangular shaped, and its centrodiapophyseal fossae are smaller than in the previous vertebra. The prezygapophyses, are wider than in the last dorsal vertebra. In proximal anterior caudal vertebrae, these are separated from the transverse processes by a well-marked ridge. Its articular surfaces are dorsomedially facing and sub-ovoidal in contour. Between prezygapophyses there is a spinoprezygapophyseal fossa, which shows two lateral small laminae. On the last proximal caudal, the ridge between the prezygapophyses and transverse processes is rounded high and stout.

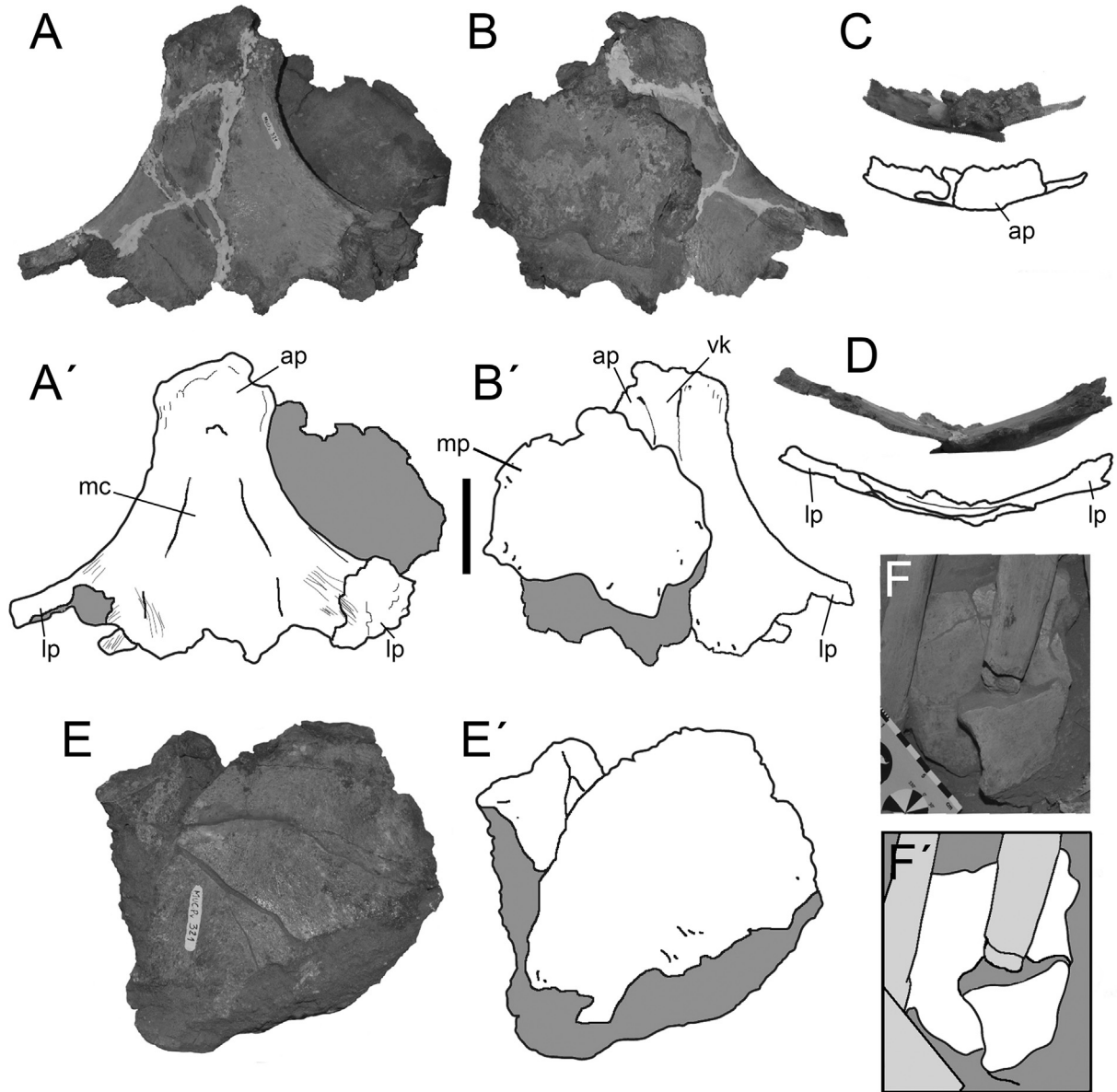


Fig. 10. *Macrogyphosaurus gondwanicus* sternum and mineralized thoracic plates in A, dorsal; B, ventral, C, anterior, D, posterior, F, lateral views. Abbreviations: ap, anterior process; lp, lateral process; mc, median concavity; vk, ventral keel Scale bar equals 5 cm.

The postzygapophyses show a relatively uniform morphology in this part of the tail. These processes are more dorsally arched and posteriorly projected than in posterior dorsal vertebrae. The articular surfaces of the postzygapophysis are subcircular in shape and lateroventrally facing. They are located posterior to the posterior margin of the centrum. Between the neural arches and centra, the neurocentral suture is visible as occurs in dorsal vertebrae. The centra are amphicoelous with both articular surfaces being subcircular in contour. In lateral view, the centra are anteroposteriorly shorter than transversely wider, with a deeply concave ventral surface. In ventral view, these are hour-glass in shape, and the ventral surface shows a longitudinal thick keel. This keel resembles that of the sacral vertebrae, being transversely stout, with straight parallel sides and a smooth surface. The posterior edge

of the ventral surface shows a well-developed articular surface for the haemal arches. These are mound structures that project anteroventrally from the ventral margin of the posterior articular surface of the centra. The articular surface for haemal arches is posterodorsally facing and crescent-shaped, with its posterior side being convex and the dorsal one nearly straight. These get less developed backwards the caudal series. Over the medial dorsal surface of some elements transverse processes there are fragments of ossified epiaxial tendons.

Six elements of the posterior portion of the mid-section of the tail were recovered (Fig. 9). These strongly weathered, and all of them lack neural arches, being only preserved by incomplete centra. These centra are anteroposteriorly longer and dorsoventrally lower than in most proximal elements of the series. In lateral view, these bones show straight anterior and posterior articular

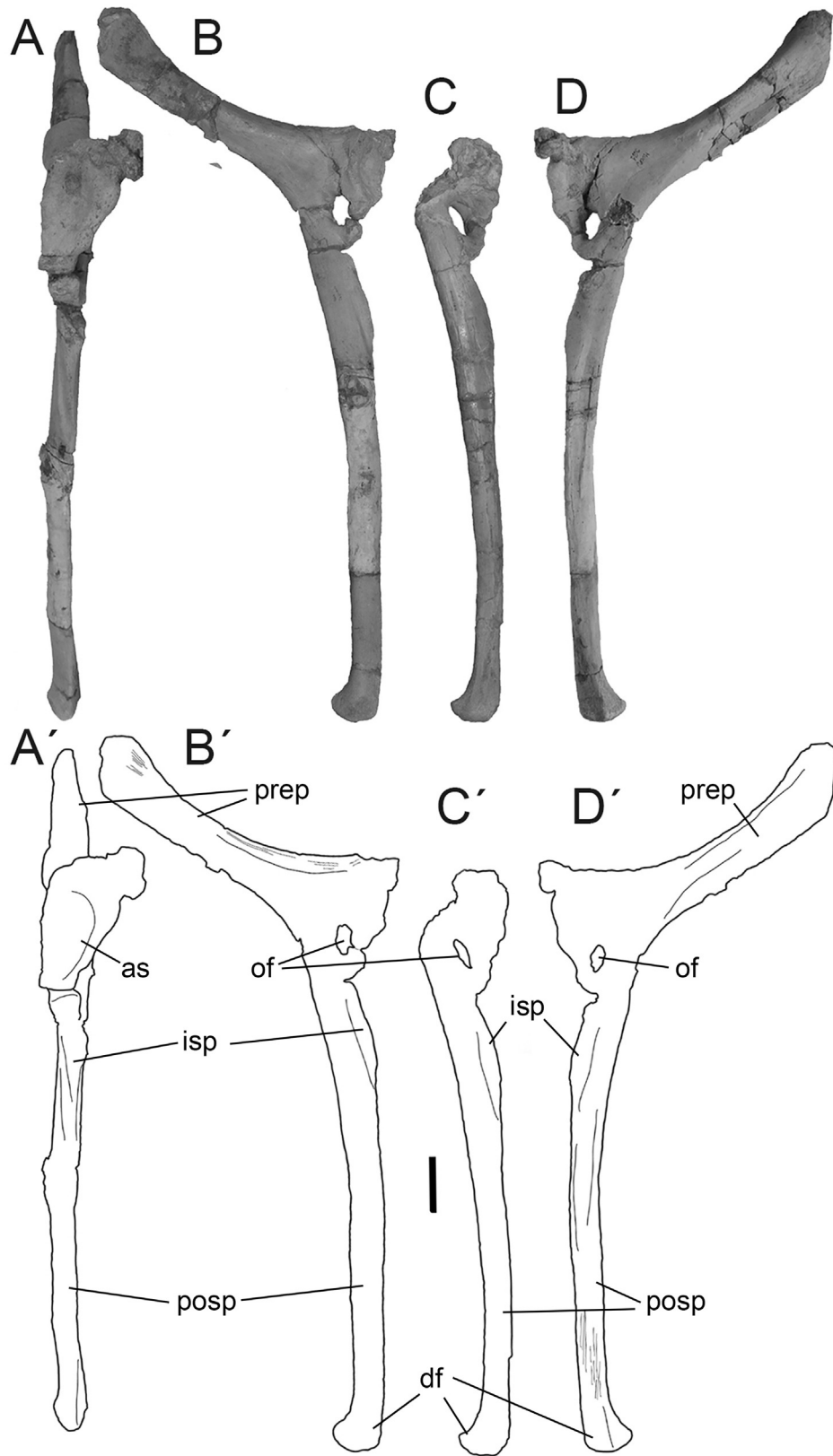


Fig. 11. *Macrogyphosaurus gondwanicus* pubis in A, dorsal; B–D, lateral views. Abbreviations: as, Acetabular surface; df, distal foot; isp, ischiadic process; of, obturator foramen; posp, postpubic process; prep: prepubic process. Scale bar equals 5 cm.

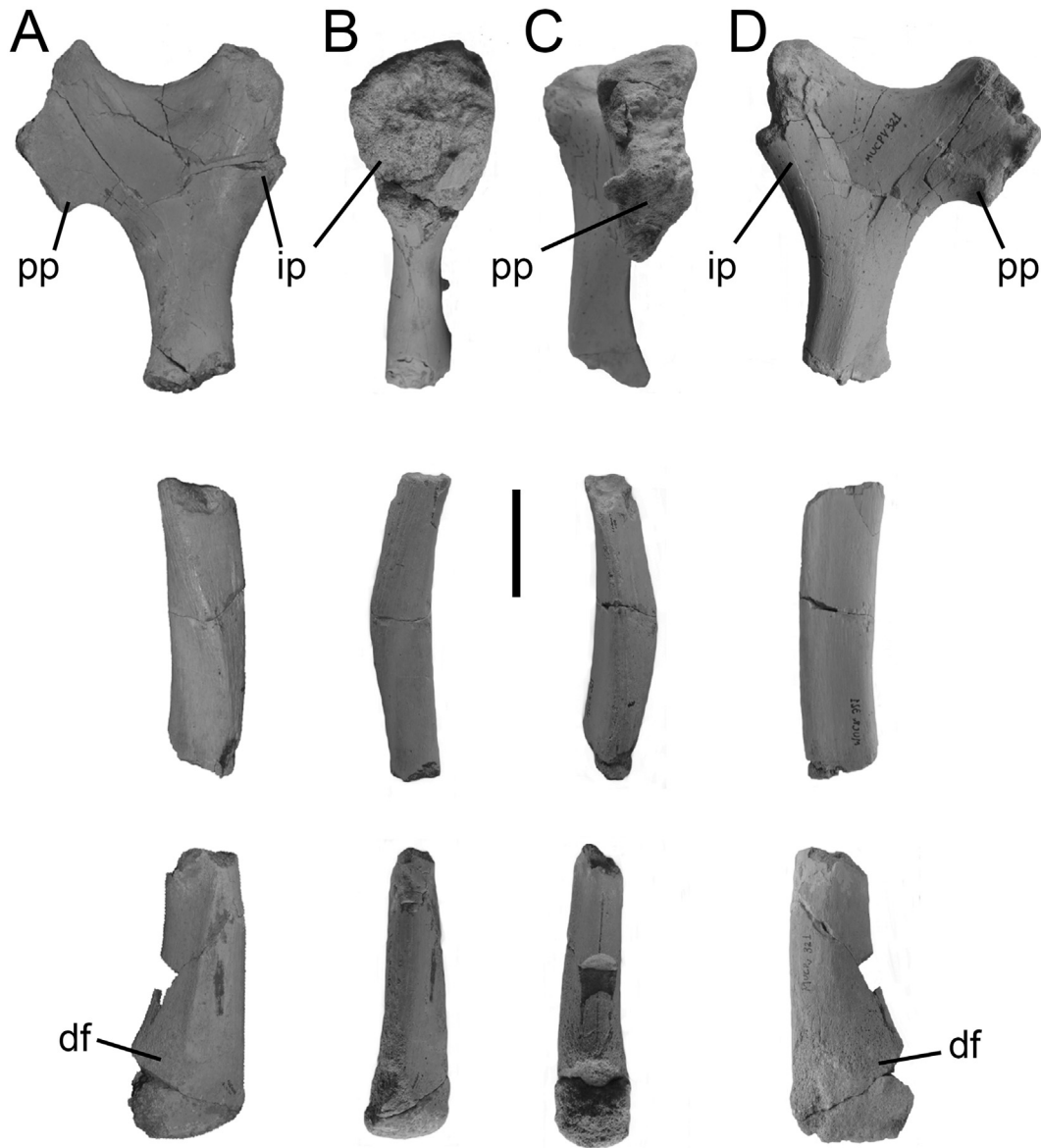


Fig. 12. *Macrogyphosaurus gondwanicus* ischium in A, D, lateral; B, dorsal; C, ventral views. Abbreviations: df, distal foot; ip, iliac process; pp, pubic process. Scale bar equals 5 cm.

surfaces, except on its ventral quarter where the haemal arches articular surfaces develop. Near the articular surfaces, the lateral surface of the centra exhibit well marked longitudinal muscle scars. Lateral surfaces of centra show a longitudinal concavity on their ventral half. Dorsal to it, the centrum is thicker, whereas it gets ventrally narrower to from a sort of ridge, as in the most proximal caudal vertebrae. Nonetheless, the ventral surface of these keel, shows a median longitudinal groove. On most proximal caudal vertebra of this portion of the series, this groove is deeper, but becomes shallower to most posterior elements.

3.5. Cervical ribs

The only cervical rib preserved in *Macrogyphosaurus* is fragmentary, being represented only by its proximal end. The tuberculum is dorsoventrally expanded and it is relatively shorter than the capitulum. The capitulum is transversely expanded and

dorsoventrally low. The articulated rib to the vertebra forms a lateral canal that is 4 cm width and 1, 5 cm in height.

3.6. Dorsal ribs

Eleven dorsal ribs have been recovered (Fig. 5). These are articulated with their corresponding dorsal vertebra. Ribs are stout and slender bones, and show a strong lateral bowing, following the body trunk curvature. These are bicapital ribs, showing well-developed and differentiated capitulum and tuberculum. The former is larger than the latter, being anteromedially projected. Its shaft is rod-shaped and its proximal articular surface is rounded. The tuberculum is poorly projected from the shaft, conforming flat and dorsolaterally faced articular surface, that contact the ventral surface of the vertebral transverse process.

In lateral view, the shaft slightly widens towards its distal end. The fourth preserved rib widens at mid-shaft. The distal end is sub-quadrangular in contour in anterior ribs, with its anterior edge

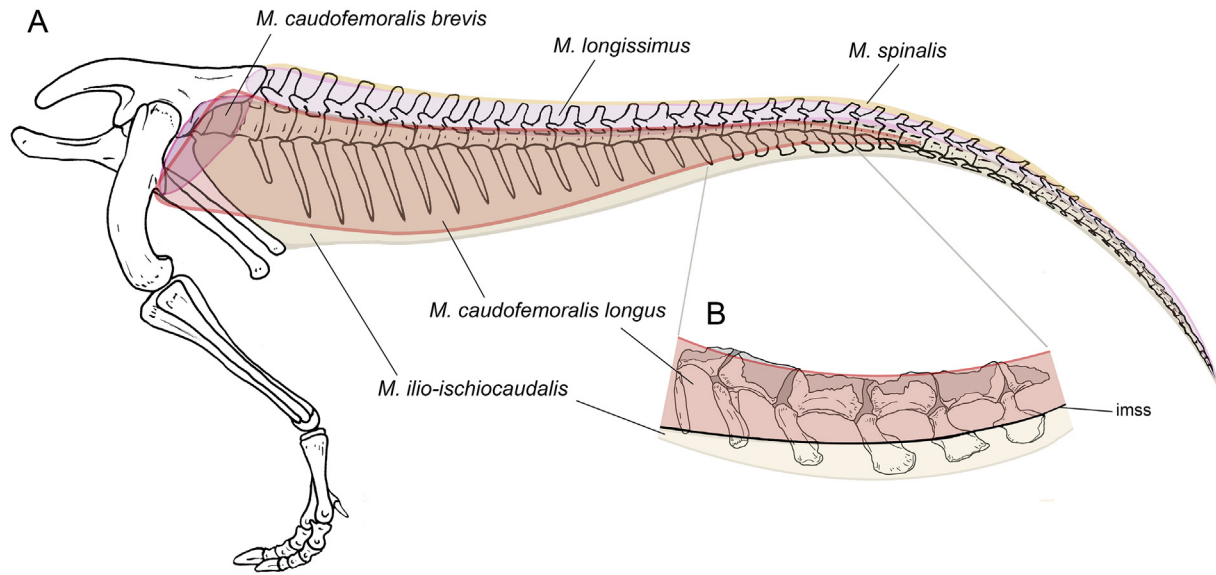


Fig. 13. A, Schematic hindlimb and tail of *Macrogyphosaurus gondwanicus* in lateral view with full caudal musculature reconstructed. B, Detail of the preserved portion of the tail associated with haemal arches, and where the *M. ilio-ischiocaudalis*/*M. caudofemoralis* septum (imss) would have been.

more distally projected than the posterior one. On the other hand, posterior ribs show a rounded distal end in lateral view. In cross-section, the bone is subtriangular in contour, tapering medially and presenting a prominent medial ridge that extends along the length of the rib. The length of the dorsal ribs is greater on its anterior elements, but from the seventh or eighth dorsal vertebrae, these become proximodistally shorter.

3.7. Haemal arches

The proximal end of an anterior haemal arch was preserved (Fig. 9 B-F). This bone is B-shaped in proximal view. The haemal canal is ovoidal in contour, dorsoventrally tall and transversely narrow. The haemal canal of mid-haemal arches is subcircular in contour as occurs in *Talenkauen* (Rozadilla et al., 2019). Its shaft is slightly curved, with its posterior margin concave. Most posterior haemal arches are subtriangular in contour when viewed laterally, as occurs in *Gasparinisaura* (Coria and Salgado, 1996) *Diluvicursor* Herne, Tait, Weisbecker, Hall, Nair, Cleeland and Salisbury (2018) and some indeterminate ornithomorphs from Australia (Rich and Vickers-Rich, 1999; Herne et al., 2016).

Six haemal arches are found in articulation with its corresponding middle-distal caudal vertebrae (Fig. 9 A). The most anterior element of this series is badly damaged and the shaft is sigmoidal in outline when laterally viewed, with its distal half more posteriorly projected. Its posterior margin bears a short keel-like process which is laterally concave. The distal end of the bone is rounded in lateral view and is transversely wider than the rest of the shaft.

Next haemal arch maintains this sigmoidal shape, with its distal end more posteriorly oriented than in previous elements. The anterior margin of the bone presents the same sigmoidal outline than in preceding haemal arch. Nonetheless, it shows a small anterior projection on its distal end. On the other hand, the posterior edge shows these posterior expansions more developed than in preceding element. This expansion is strongly posteriorly extended, but proximodistally shorter than in previous haemal and does not reach the distal end of the bone. It constitutes a crescent-shaped posterior process. This posterior process is separated by a distal concave surface, from the strongly expanded distal

end. In this regard, anterior and posterior expansions result in a distal end that is anteroposteriorly wider than in preceding elements.

Posterior haemal arch presents a wide anteroposteriorly expanded distal end with respect to previous haemal arches. Its anterior edge is not sigmoidal and presents a small and crescent-shaped anterior process on its mid-height. The posterior surface of the haemal shaft shows an expanded posterior process, which is more proximally located on the shaft and more posteriorly projected than in anterior elements. Dorsal to this process the posterior edge of the shaft is deeply concave, whereas on its distal end, the bone is strongly posteriorly expanded, resulting in a fan-shaped haemal arch. Its distal margin is gently convex.

Next haemal arch shows a small subtriangular anterior process that separates the concave dorsal and ventral halves of the anterior margin of the bone. Distally, the anterior edge of the distal end of the bone shows a more developed anterior projection. On the other hand, the posterior margin shows a distal process which is longer proximodistally than in preceding haemal arches, and the concavity that separates it from distal expansion of the haemal arch is shallower. The distal end of the bone is lost, but its posterior expansion is more extended than in preceding elements.

Last preserved haemal arch is the anteroposteriorly longer and the proximodistally shorter element of the preserved haemal series. Its anterior margin bears a finger-like anterior process, wider and more anteriorly projected than in other haemal arches. The anterior edge of the distal end of the bone is anteriorly expanded and rounded in lateral view, separated from the anterior projection by a narrow and deep concavity. On the other hand, the posterior edge shows a posterior process that is proximodistally longer than in other haemal arches, but is poorly posteriorly projected. Posterior and distal edges of the distal end are lost. In anterior view, the haemal canal is transversely narrow, being proximally wider and a groove distally.

3.8. Mineralized thoracic plates

Four intercostal plates have been recovered on *Macrogyphosaurus* holotype (Fig. 10 B, D-E). Plates of this kind have been found in the closely related taxa *Talenkauen* and *Mahuidacursor*

(Novas et al., 2004; Rozadilla et al., 2019; Rozadilla et al., 2019) and the Laurasian taxa *Hypsilophodon*, *Thescelosaurus*, and *Othnielosaurus* Galton, 2007 (Butler and Galton, 2008; Boyd et al., 2009, 2011). In *Macrogyphosaurus* these plates are wide and subtriangular to subcircular in contour, being transversely narrow. In the most posterior elements recovered, there is a posterior subrectangular expansion as occurs in *Thescelosaurus* (Boyd et al., 2009, 2011). These elements are larger and wider than in *Talenkauen* (Rozadilla et al., 2019), where the plates are sub-rhomboidal in contour, anteroposteriorly short and dorsoventrally long, and from *Mahuidacursor*, where the plates are sub-rectangular (Cruzado-Caballero et al., 2019). *Macrogyphosaurus* holotype exhibits two mineralized plates on the ventral surface of the sternum (Fig. 10 B, D; Calvo et al., 2007). Calvo and collaborators (2007) claim this condition as autapomorphic for this dinosaur, but it is probable that this anomalous position is due to taphonomic transport of these elements. In this regard, we do not consider this as an autapomorphic feature for *Macrogyphosaurus*.

3.9. Sternum

Macrogyphosaurus presents an unusual sternum among ornithopods, only shared with the closely related *Mahuidacursor* (Cruzado-Caballero et al., 2019) (Fig. 10 A-B). The sternal plates, that in most ornithopod taxa are separate elements, here are fused on a single large sternal plate. This element is almost complete, only lacking most of its distal process and their posterior margin. This plate is triradiate (Calvo et al., 2007) with a main body formed by the parred sternal plates that fuse each other across the midline. The distal processes are broken so that it is not possible to know if these was rod-shaped as in derived iguanodontians (Norman, 2004).

The sternal plate is transversely wide and subtriangular in outline both in ventral or dorsal view. Its anterior process is transversely wide, with concave lateral margins and a rounded anterior margin. Both in anterior as in posterior view, the sternum is V-shaped, in a wide angle. Its ventral surface, is obscured by a mineralized plate.

At the lateral sides of the anterior process, there are small and irregular marks that could represent intercostal notches for the attachment of the sternal ribs (Galton, 1974a; Godfrey and Currie, 2004). In anterior view, this process is stout and dorsally concave. In cross section, this portion of the bone is transversely thicker than the posterior one. Its posterior edge is highly weathered, but presents two wide crescent-shaped projections near the mid-line of the bone. Two posterolateral processes projects at the sides of the sternum. These processes are dorsoventrally thin. The right posterolateral process is well preserved, being subrectangular in contour when dorsally viewed, with concave anterior and posterior margins. The distal end of these processes is lost.

Ossified sternal plates are uncommon among saurischian dinosaurs, being ambiguously present in paravians (Holtz et al., 2004; Norell and Makovicky, 2004; Godfrey and Currie, 2004). Otherwise, most ornithischians show an ossified sternum. Among Ornithopoda, basal taxa (e.g. *Hypsilophodon*, *Thescelosaurus*, etc), these are reniform and show a sagittal ridge where each element contacts its pair (Galton, 1974a; Norman et al., 2004). In more derived ornithopods (*Iguanodon*, *Lurdursaurus*, hadrosaurids; Norman, 1980, 1986, 2004; Horner et al., 2004), sternal plates are axe-shaped, with an anterior aliform portion, were both sterna meet, and posterior rod-like processes. These sternal plates are more distant between them than in more basal ornithopods. An ossified and fused sternum could provide, together with the mineralized intercostal plates, stiffness to the ribcage of *Macrogyphosaurus* (Butler and Galton, 2008; Boyd et al., 2011).

Among elasmarians, *Macrogyphosaurus* sternum is the only one recovered to the date. Calvo and collaborators (2007) considered sternal anatomy as an autapomorphic feature for this dinosaur. Nonetheless, because none other Gondwanan basal ornithopod has preserved sternal plates, this morphology is more widely distributed than we thought.

3.10. Ilium

Both ilia are preserved and articulated with the sacrum, being the left one highly weathered (Fig. 7). The ilium is anteroposteriorly elongate and stout, lacking the posterior end of the postacetabular process. The dorsal margin of the ilium is slightly sigmoidal in lateral view, as occurs in many iguanodontians (e.g. *Talenkauen*, *Anabisetia*, *Gasparinisaura*, *Dryosaurus*, *Tenontosaurus*, *Iguanodon*; Galton, 1975, 1981, 2009; Norman, 1980, 1986; Norman et al., 2004; Sereno, 1986; Coria and Salgado, 1996; Coria and Calvo, 2002; Novas et al., 2004; Novas, 2009; Tennant, 2013; Calvo et al., 2007; Rozadilla et al., 2019), differing from *Trinisaura* Coria, Moly, Reguero, Santillana and Marensi (2013), *Hypsilophodon*, *Thescelosaurus* and *Orodromeus* Horner and Weishampel, 1988, where this margin is straight (Galton, 1974a, b; Scheetz, 1999; Norman et al., 2004; Boyd et al., 2009; Coria et al., 2013). In dorsal view, the ilia are medially convex and laterally concave, being more laterally offset on its posterior end, at the level of brevis shelf.

The preacetabular process is anteriorly projected with a ventrally curved anterior end as occurs in most iguanodontians (Sereno, 1986; Norman et al., 2004). The dorsal margin of the preacetabular process is convex while its ventral margin is deeply concave. Its medial wall is in wide contact with the second sacral rib. The preacetabular process is thicker and anteroposteriorly shorter than in *Anabisetia* and *Talenkauen* (Coria and Calvo, 2002; Rozadilla et al., 2019) but resembling *Gasparinisaura* (Coria and Salgado, 1996). As in most ornithopod, with the exception of *Anabisetia* (Coria and Calvo, 2002), this process does not reach the anterior end of the prepubic process. the ventral surface of the preacetabular process bears the cuppedicus fossa, which is anteroposteriorly long and shallow.

The pubic peduncle is gracile, being proximodistally short and subtriangular in shape in lateral view as occurs in *Gasparinisaura*, *Anabisetia*, and *Talenkauen* (Coria and Salgado, 1996; Coria and Calvo, 2002; Rozadilla et al., 2019), but different from the condition *Trinisaura*, where it is dorsoventrally longer and acute (Coria et al., 2013). In lateral view, its acetabular surface is flat, while the anterior one is oblique, its medial surface is very wide. The lateral surface shows a crest that posteriorly forms the supracetabular rim. The pubic peduncle is subtriangular in lateral view and in cross-section. This process has a rounded distal end.

The ischial peduncle is posteroventrally projected and larger than the pubic one. The posterodorsal acetabular edge is oblique in lateral view. This surface is transversely thicker distally, dorsally narrow transversely, while its medial edge expands anteriorly to form a posteromedial acetabular wall. Its posterior margin is transversely thick and slightly concave in lateral view, as occurs in most ornithopods (i.e. *Gasparinisaura*, *Anabisetia*, *Trinisaura*, *Dryosaurus*, *Iguanodon*; Norman, 1980, 1986; Norman et al., 2004; Galton, 1981; Coria and Salgado, 1996; Coria and Calvo, 2002; Coria et al., 2013). The anterior surface of the ischial process forms part of the acetabulum presents a rugose acetabular flange and a smooth lateral wall anteromedially directed; both surfaces are separated by a smooth acetabular rim. In spite of presenting a triangular and horizontal flat ischial articulation, there is a small vertical medial articulation too. This surface is in contact with the ventral part of fourth sacral vertebra.

The postacetabular lacks its posterior end, but presents a similar anatomy than in some related taxa (i.e. *Talenkauen*, *Gasparinisaura*, *Anabisetia*; Coria and Salgado, 1996; Coria and Calvo, 2002; Rozadilla et al., 2019). In dorsal view, the brevis shelves posteromedially extend in sub-rhomboidal structures. This shape is probably that due to the broken distal end of the postacetabular process. The brevis shelf is dorsoventrally flat, showing a smoothly concave dorsal surface that attaches the sacral ribs of fifth and sixth sacral. In ventral view, its ventral surface shows a deep and longitudinal brevis fossa.

3.11. Pubis

Both pubes have been recovered. The left pubis is almost complete, only lacking the middle part of the postpubic process, while the right one is only represented by the postpubic process (Fig. 11). The prepubic process is anteriorly projected with a slightly dorsally projected anterior end. In lateral view, this process is dorsally concave and a shallowly convex ventrally. On its anterior portion this process is transversely compressed, as occurs in *Anabisetia*, *Talenkauen*, *Tenontosaurus*, *Dryosaurus* and *Ankylopolexia* (Galton, 1981; 2009; Coria and Calvo, 2002; Norman et al., 2004; Novas et al., 2004; Novas, 2009; Tennant, 2013; Rozadilla et al., 2019). It becomes thicker posteriorly, and shows a flat dorsal surface and a strongly curved ventral one just posterior to the iliac process. By contrast, in *Gasparinisaura*, *Hypsilophodon*, *Thescelosaurus* and other basal taxa, the prepubis has a rounded shape in cross section (Galton, 1974a, b, 2009; Coria and Salgado, 1996; Norman et al., 2004; Boyd et al., 2009). The length of the prepubic process subequal to 80% of the length of the “postpubic” process (see the measure tables in Appendix B). Its acetabular surface is stout, rugose and concave, being its medial margin more slightly posteriorly projected to form the anteromedial portion of the inner acetabular wall.

Ventral to the posterior margin of the acetabulum there is a transversely compressed and rugose surface that received the pubic peduncle of the ischium. More distally, there is a subcircular shaped obturator foramen. The obturator foramen is posteriorly enclosed by a thin rod of bone (Maidment and Barret, 2011).

The postpubic process is posteroventrally projected, forming an angle greater than 150° with the prepubic process, as occurs in basal ornithopods (Norman et al., 2004; Calvo et al., 2007). The postpubic process is stout, slightly curved and sub-oval to subtriangular shaped in cross-section. This process is very long, it has almost the same length as the shaft preserved of the posterior process of the ischium. A long postpubic process is shared with *Anabisetia*, *Gasparinisaura*, *Trinisaura*, *Hypsilophodon*, *Orodromeus*, *Tenontosaurus*, *Yandurosaurus*, *Haya*, *Lesothosaurus* (Galton, 1974a; He and Cai, 1984; Coria and Salgado, 1996; Scheetz, 1999; Coria and Calvo, 2002; Norman, 2004; Makovicky et al., 2011; Coria et al., 2013; Baron et al., 2017). It is posteriorly bowed on its most proximal portion, but it is mainly straight distally. Distal to the obturator foramen the pubis is stout, showing a posterior flange. This flange is gently convex and proximodistally long, occupying the proximal quarter of the postpubic process. The distal end of the pubis shows a small pubic foot. This structure is rare within ornithischians, with *Lesothosaurus* only having a slightly expanded distal end of the postacetabular process but without having to have foot shape (Baron et al., 2016). In this regard, this might be an autapomorphic feature for *Macrogyphosaurus*. This foot presents a sub-triangular anterior edge anteriorly projected. The articular surface between pubes is sub triangular in contour, and proximodistally elongated, extending along the distal quarter of the bone.

3.12. Ischium

Both ischia have been recovered, being both represented by proximal, middle and distal fragments (Fig. 12). These fragments show that *Macrogyphosaurus* ischium was a slender and rod-like bone. On the proximal end of the bone there are two well-developed processes: the iliac and the pubic one. These are separated by a deep concavity, which forms the posteroventral wall of the acetabulum, in lateral view. Iliac and pubic processes are subequal in size, as occurs in some nearly related taxa (i.e. *Gasparinisaura*, *Anabisetia*; Coria and Salgado, 1996; Coria and Calvo, 2002).

The iliac process is roughly subtriangular shaped in lateral view, with a rounded and rugose proximal margin. The articulation surface to receive the ilium is subtriangular in outline and located on the medial side of the iliac process. The pubic process is subquadrangular in lateral view and is anteriorly projected to contact with the pubis. The anterior margin of this process is subtriangular in contour, with an anteriorly oriented apex and a dorsal and a ventral surface. In anterior view, the dorsal half of the pubic process is subquadrate, while the ventral half is subtriangular. These halves are separated by a lateromedial constriction. This process is more anteriorly offset from the ischium main body than the iliac one, showing a wide neck between these.

Fragments of the ischium show that it exhibited a long, slender and posteriorly curved shaft, being anteriorly arched and posteriorly concave. Near its mid-length, the ischial shaft is laterally twisted and forms the inter-ischial articular surface, which seems to be proximodistally long. At this point, the shaft presents a sub-oval contour in cross-section. The distal end of the bone is slightly expanded, but do not form a distinct foot-like structure. Its medial side presents some scars, indicating that left and right ischia contact each other distally (Calvo et al., 2007). Its distal end is sub-oval in shape when viewed distally.

4. Discussion

4.1. *Macrogyphosaurus* neck

Cervical series in most elasmarians remain poorly known, with the exception of *Talenkauen*, which holotype preserves an almost complete neck, only lacking the atlas. *Talenkauen* neck is constructed by nine cervical vertebrae (Novas et al., 2004; Novas, 2009; Rozadilla et al., 2019) which is the plesiomorphic count for Ornithopoda (Sereno, 1986; Norman et al., 2004). Cervical vertebrae in elasmarians present some unique features with regard to other ornithopods (Norman, 2004; Norman et al., 2004): are gracile, anteroposteriorly elongate and dorsoventrally low, bearing low neural arches (Rozadilla et al., 2016, 2019). Thus, elasmarians have a proportionally longer neck than most Laurasian ornithopods (i.e. *Hypsilophodon*, *Dryosaurus*, *Thescelosaurus*; Galton, 1974a; b, 1981, 2009).

Therefore, *Talenkauen* and probably related taxa (i.e. *Anabisetia*, *Notohypsilophodon*, *Mahuidacursor*) have an elongated neck related with the anteroposteriorly elongation of each cervical centrum fitting with the third model for neck enlargement proposed by Mateus et al. (2009), in which the neck enlarges by individual elongation of the vertebrae (Rozadilla et al., 2019).

Nonetheless, *Macrogyphosaurus* shows, counting the lost atlas and axis, ten cervical vertebrae, resembling in this aspect to more derived iguanodontians (Sereno, 1986; Norman, 2004) and implying the addition of a vertebra on the cervical series. Furthermore, this dinosaur counts with fourteen dorsal vertebrae, which represent a lower number than most ornithopods, where the usual count is fifteen to sixteen, as occurs in the closely related

Talenkauen (Novas et al., 2004). Therefore, it is probable that *Macrogyphosaurus* long neck was formed by the elongation of cervical elements as well as by the cervicalization of the first dorsal vertebra, following the first model for neck enlargement proposed by Mateus et al. (2009).

Regarding cervical vertebrae of *Macrogyphosaurus*, these are slenderer than in other elasmarians. Moreover, morphology of C9 of *Talenkauen* is similar to the C10 of *Macrogyphosaurus*, whereas the morphology of the C9 is intermediate between the ninth and the eighth cervical vertebrae of *Talenkauen*. *Macrogyphosaurus* cervical vertebrae show diapophyses proportionally short when compared with other ornithopod taxa. These are rounded and strongly fused to their correspondent prezygapophysis, forming short and stout aliform lateral expansions. In this regard, this diapophyseal anatomy supports the idea of a neck narrower and more gracile than other ornithopods and could be considered an autapomorphic feature for *Macrogyphosaurus*.

4.2. *Macrogyphosaurus thorax*

Macrogyphosaurus dorsal vertebral series is shorter when compared with other ornithopods (i.e. *Talenkauen*, *Mahuidacursor*, *Hypsilophodon*, *Thescelosaurus*, *Dryosaurus*, *Iguanodon*; Galton, 1974a, b, 1981, 2009; Sereno, 1986; Norman, 1980, 1986, 2004; Norman et al., 2004; Novas et al., 2004; Cruzado-Caballero, 2019; Rozadilla et al., 2019), showing only fourteen elements. If we assume that the anterior-most dorsal vertebra joined the cervical series to form the tenth cervical, there is another dorsal vertebra that is still wanting (the ornithopod have between 15 and 16 vertebrae). Sacral vertebrae in *Macrogyphosaurus* are six, a count that is primitive for ornithopods and thus, no dorsal appears to be added to the sacrum. In this regard, it could be assumed that the wanting element was lost from *Macrogyphosaurus* vertebral column. Therefore, *Macrogyphosaurus* presents a shortening of the thorax.

Nonetheless, the fact of *Macrogyphosaurus* being the only elasmarian that added a vertebra on its cervical series and shortened its body trunk, could imply that this dinosaur represents a new ornithopod morphotype with proportionally long neck and short thorax in Gondwana.

One of the most remarkable features of *Macrogyphosaurus*, that share with *Mahuidacursor* is an ossified and fused triradiate sternum (Cruzado-Caballero et al., 2019). As aforementioned in the description, most ornithopods present independent sternal plates, that in derived taxa, becomes elongate and slender structures. *Macrogyphosaurus* and *Mahuidacursor* show a sternum that recalls to the stouter sternal plates of basal ornithopods, but totally fused between them on its mid-line. This sternum recalls on its main structure to the stiff sternum found in some paravians. Nonetheless, the structures and processes of *Macrogyphosaurus* and *Mahuidacursor* sternum can hardly been homologized to those of paravian taxa. It is worth to mention that in paravian sterna, the posterior margin of these bones is subtriangular and acute, whereas in *Macrogyphosaurus* and *Mahuidacursor* this margin is concave. On the other hand, is the anterior margin of *Macrogyphosaurus* sternum which is subtriangular and strongly projected anteriorly. The presence of ossified and fused sternal elements in a unique sternum could provide, together with the mineralized intercostal plates, stiffness to the ribcage of *Macrogyphosaurus* (Butler and Galton, 2008; Boyd et al., 2011).

4.3. *On Macrogyphosaurus tail*

With the exception of *Gasparinisaura*, *Macrogyphosaurus* presents the best-preserved tail within Elasmaria, with many

vertebrae and haemal arches. Regarding haemal arches, these have been found in several taxa (i.e. *Gasparinisaura*, *Anabisetia*, *Talenkauen*, *Trinisaura*, *Macrogyphosaurus*; Coria and Salgado, 1996; Cambiaso, 2007; Coria et al., 2013; Rozadilla et al., 2019), showing, in some cases, an anteroposterior expansion on its distal end, which is an uncommon anatomy for ornithopod haemal arches. This was considered an autapomorphy for *Gasparinisaura* (Coria and Salgado, 1996), and then a synapomorphy for Elasmaria (Ibircu et al., 2010; Rozadilla et al., 2016).

As indicated in the descriptive section, the complex transition between proximal and distal elements, and the differential development of anterior and posterior processes and expansions (Fig. 9) may imply a more complex musculature on the distal tail of Gondwanan ornithopods (Fig. 13; Novas, 2009; Rozadilla et al., 2016), than other taxa with a conservative haemal morphology (i.e. *Hypsilophodon*, *Thescelosaurus*, *Orodromeus*, *Dryosaurus*, *Tenontosaurus*, *Iguanodon*; Galton, 1974a, b, 1981; Norman, 1980, 1986, 2004; Norman et al., 2004; Forster, 1990; Scheetz, 1999; Boyd et al., 2011; Tennant, 2013).

The haemal arches of *Macrogyphosaurus* show a progressive change from simple, rod-shaped proximal haemal arches, to elements that are wider on its distal end and strongly expanded backwards. Moreover, there are anterior and posterior processes, whose development varies throughout the series, especially on the anterior process, which gets anteriorly longer and digitiform in posterior haemal arches. Furthermore, these processes become closer to vertebral centra in posterior elements, the same as the distal margins, defining dorsoventrally shorter haemal arches through posterior tail. Because anterior and posterior processes of the haemal arches are absent in other taxa, are here interpreted as a possible autapomorphic feature for *Macrogyphosaurus*. Nonetheless, due the scarce recovered haemal arches in other elasmarians, we do not dismiss that this morphology was more widely distributed.

The anterior and posterior processes of the haemal arches remind the scars present on several coelurosaur theropods (i.e. *Ornithomimus* Marsh, 1890; *Gorgosaurus* Lambe, 1917; *Tyrannosaurus* Osborn, 1905; Brochu, 2003; Persons and Currie, 2011; Rauhut, 2003). Persons and Currie (2011) interpreted these scars as the insertion point for the skeletogenous septum that divided the *M. caudofemoralis longis* from the *M. ilio-ischiocaudalis*. Furthermore, the anteroposterior ascension and eventual posterior disappearance of this scar along the series is, therefore, taken to mark the *M. ilio-ischiocaudalis* gradual dorsal intrusion, so as the distal tapering of the *M. caudofemoralis longis*.

In anterior haemal arches, this skeletal septum is limited to the distal margin of the haemal arches, being the *M. caudofemoralis longus* strongly developed and covering the entire lateral surface of the bones. On the other hand, the *M. ilio-ischiocaudalis* is externally recovering the *M. caudofemoralis longus*. Therefore, when the *M. caudofemoralis longus* tapers posteriorly and disappears, the *M. ilio-ischiocaudalis* becomes the main muscle of the lateral and ventral tail. Thus, the ventral expansion of the haemal arches of *Macrogyphosaurus* and related ornithopods, is related to larger areas for the attachment of *M. ilio-ischiocaudalis*. This muscle controls the lateral and ventral movements of the tail, and therefore, larger haemal attachment areas imply that this muscle was strongly developed at mid to posterior portions of tail, than in other ornithopods with primitive shaped haemal arches (Persons et al., 2013; Rozadilla et al., 2016).

Anterior and posterior processes in *Macrogyphosaurus* haemal arches that mark the limit between the *M. caudofemoralis* and the *M. ischiocaudalis* are here considered as an autapomorphic character for this dinosaur (Fig. 13). This is the first time that these structures are observed in Ornithischia. In this aspect,

Macrogyphosaurus haemal arches resembles more to the coelurosaur-like haemals than to other ornithischians.

5. Conclusions

Present contribution provides a detailed description of osteological materials of the ornithopods dinosaur *Macrogyphosaurus*. This constitutes the largest Elasmaria known hitherto and provides important information about the vertebral column and pelvic girdle of these ornithopods.

The analysis of its anatomy shows that *Macrogyphosaurus* was the largest Elasmaria, approaching the size of more derived iguanodontians, but being more graceful than these taxa. Furthermore, *Macrogyphosaurus* presents an elongate neck with an additional vertebra and a dorsal series with a lower number than in related ornithopods (Calvo et al., 2007). In this regard, *Macrogyphosaurus* represents a unique morphotype indicating that the diversity of forms was far diverse among Gondwanan ornithopods.

Three autapomorphic character are here added to *Macrogyphosaurus*, which implies the presence of poorly developed diapophyses in the cervical vertebrae; anterior and posterior processes on the boat-shaped haemal arches; and the distal end of the postpubic process expanded in a foot. The former, indicate that *Macrogyphosaurus* shows a proportionally longer and slender neck than related ornithopods. On the other hand, haemal arch anatomy shows the ventral limit of the *M. caudofemoralis longus* and its posterior tapering so as the dorsal limit of the *M. ilioischio-caudalis* and its posterior ascension and dominance on the most posterior tail resembling to a coelurosaur-like tail (Persons and Currie, 2011; Persons et al., 2013).

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References

Apesteguía, S., 2005. The evolution of the hyposphene-hypantrum complex within Sauropoda. In: Tidwell, V., Carpenter, K. (Eds.), *Thunder-Lizards: the Sauropodomorph Dinosaurs*, vols. 248–267, p. 495.

Apesteguía, S., Gallina, P.A., Canale, J.L., Rigueti, F., Garderes, J.P., 2015. Nuevos registros de Stegosauria (Ornithischia, Thyreophora) del Cretácico Inferior temprano de Neuquén: el registro más antiguo de Sudamérica. XXIX Jornadas Argentinas de Paleontología de Vertebrados, p. 15.

Baron, M.G., Norman, D.B., Barrett, P.M., 2017. Postcranial anatomy of *Lesothosaurus diagnosticus* (Dinosauria: Ornithischia) from the Lower Jurassic of southern Africa: implications for basal ornithischian taxonomy and systematics. *Zoological Journal of the Linnean Society* 179 (1), 125–168.

Boulenger, G.A., 1881. Sur l'arc pelvien chez les dinosaures de Bernissart. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique: Sciences de la Terre* 3 (1), 600–608.

Boyd, C.A., 2015. The systematic relationships and biogeographic history of ornithischian dinosaurs. *PeerJ* 3, e1523.

Boyd, C.A., Cleland, T.P., Novas, F.E., 2011. Osteogenesis, homology, and function of the intercostal plates in ornithischian dinosaurs (Tetrapoda, Sauropsida). *Zoology* 130, 305–313.

Boyd, C.A., Brown, C.M., Scheetz, R.D., Clarke, J.A., 2009. Taxonomic revision of the basal neornithischian taxa *Thescelosaurus* and *Bugenasaura*. *Journal of Vertebrate Paleontology* 29 (3), 758–770.

Brochu, C.A., 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computer tomographic analysis of the skull. *Journal of Vertebrate Paleontology* 22 (4), 1–138.

Butler, R.J., Galton, P.M., 2008. The 'dermal armour' of the ornithopod dinosaur *Hypsilophodon* from the Wealden (Early Cretaceous: Barremian) of the Isle of Wight: a reappraisal. *Cretaceous Research* 29 (4), 636–642.

Calvo, J.O., Porfiri, J.D., Novas, F.E., 2007. Discovery of a new ornithopod dinosaur from the Portezuelo Formation (Upper Cretaceous), Neuquén, Patagonia, Argentina. *Arquivos Do Museu Nacional Rio De Janeiro* 65, 471–483.

Cambiaso, A.V., 2007. Los ornitópodos e iguanodontes basales (Dinosauria, Ornithischia) del Cretácico de Argentina y Antártida. Unpublished PhD thesis. Universidad Nacional de Buenos Aires, Argentina, 412 pp.

Canudo, J.I., Salgado, L., Garrido, A., Carballido, J., 2013. Primera evidencia de dinosaurios ornitópodos en la base de la Formación Huincul (Cenomaniense Superior-Turonense, Cuenca Neuquina, Argentina). *Geogaceta* 53, 9e12.

Cooper, M.R., 1985. A revision of the ornithischian dinosaur *Kangnasaurus coetzeei* Houghton, with a classification of the Ornithischia. *Annals of the South African Museum* 95 (8), 281–317.

Coria, R.A., Calvo, J.O., 2002. A new iguanodontian ornithopod from the Neuquén Basin, Patagonia, Argentina. *Journal of Vertebrate Paleontology* 22, 503–509.

Coria, R.A., Currie, P.J., 2016. A New Megaraptorian Dinosaur (Dinosauria, Theropoda, Megaraptoridae) from the Late Cretaceous of Patagonia. *PLoS One* 11 (7), e0157973.

Coria, R.A., Salgado, L., 1996. A basal Iguanodontia (Ornithopoda – Ornithischia) from the Late Cretaceous of South America. *Journal of Vertebrate Paleontology* 16 (3), 445–457.

Coria, R.A., Cambiaso, A.V., Salgado, L., 2007. New records of basal ornithopod dinosaurs in the Cretaceous of North Patagonia. *Ameghiniana* 44 (2), 473–477.

Coria, R.A., Riga, B.G., Casadio, S., 2012. Un nuevo hadrosáurido (Dinosauria, Ornithopoda) de la Formación Allen, Provincia de La Pampa, Argentina. *Ameghiniana* 49 (4), 552–572.

Coria, R.A., Moly, J.J., Reguero, M., Santillana, S., Marensi, S., 2013. A new ornithopod (Dinosauria; Ornithischia) from Antarctica. *Cretaceous Research* 41, 186–193.

Cruzado-Caballero, P., Powell, J., 2017. *Bonapartesaurus rionegrensis*, a new hadrosaurine dinosaur from South America: implications for phylogenetic and biogeographic relations with North America. *Journal of Vertebrate Paleontology* 37 (2), e1289381.

Cruzado-Caballero, P., Filippi, L.S., Méndez, A.H., Garrido, A.C., Díaz-Martínez, I., 2018. First ornithopod remains from the Bajo de la Carpa Formation (Santonian, Upper Cretaceous), northern Patagonia, Argentina. *Cretaceous Research* 83, 182–193.

Cruzado-Caballero, P., Filippi, L.S., Méndez, A.H., Garrido, A.C., Valieri, R.D.J., 2016. New record of ornithopod dinosaur from the Plottier Formation (Upper Cretaceous), Patagonia, Argentina. *Annales de Paléontologie* 102 (2), 145–160.

Cruzado-Caballero, P., Gasca, J.M., Filippi, L.S., Cerda, I.A., Garrido, A.C., 2019. A new ornithopod dinosaur from the Santonian of Northern Patagonia (Rincón de los Sauces, Argentina). *Cretaceous Research* 98, 211–229.

Forster, C.A., 1990. The postcranial skeleton of the ornithopod dinosaur *Tenontosaurus tilletti*. *Journal of Vertebrate Paleontology* 10, 273–294.

Galton, P.M., 1974a. The ornithischian dinosaur *Hypsilophodon* (Huxley, 1869) from the Wealden of the Isle of Wight. *Bulletin of the British Museum (Natural History) Series Geology* 25, 1–152.

Galton, P.M., 1974b. Notes on *Thescelosaurus*, a conservative ornithopod from the Upper Cretaceous of North America, with comments on ornithopod classification. *Journal of Paleontology* 48, 148–167.

Galton, P.M., 1975. English hypsilophodontid dinosaurs (Reptilia: Ornithischia). *Palaeontology* 18, 741–752.

Galton, P.M., 1981. *Dryosaurus*, a hypsilophodontid dinosaur from the Upper Jurassic of North America and Africa. *Postcranial skeleton*. *Paläontologische Zeitschrift* 55, 271–312.

Galton, P.M., 2007. Teeth of ornithischian dinosaurs (mostly Ornithopoda) from the Morrison Formation (Upper Jurassic) of the Western United States. K. Carpenter (ed.), *Horns and Beaks: Ceratopsian and Ornithopod Dinosaurs*. Indiana University Press, Bloomington. In: Carpenter, K. (Ed.), *Horns and Beaks: Ceratopsian and Ornithopod Dinosaurs*. Indiana University Press, Bloomington, pp. 17–47.

Galton, P.M., 2009. Notes on Neocomian (Lower Cretaceous) ornithopod dinosaurs from England—*Hypsilophodon*, *Valdosaurus*, "*Camptosaurus*", "*Iguanodon*"—and referred specimens from Romania and elsewhere. *Revue de Paléobiologie* 28 (1), 211–273.

Garrido, A.C., 2010. Estratigrafía del Grupo Neuquén, Cretácico Superior de la Cuenca Neuquina (Argentina): nueva propuesta de ordenamiento litoestratigráfico. *Revista Del Museo Argentino De Ciencias Naturales* 12 (2), 121–177.

Gilmore, C.W., 1913. A new dinosaur from the Lance Formation of Wyoming. *Smithsonian Miscelanea Collection* 61, 1–5.

Godfrey, S.J., Currie, P.J., 2004. A theropod (Dromeosauidae, Dinosauria) sternal plate from the Dinosaur Park Formation (Campanian, Upper Cretaceous) of Alberta Canada. In: Currie, P.J. (Ed.), *Feathered dragons: studies on the transition from dinosaurs to birds*, vols. 144–149. Indiana University Press, p. 343.

Houghton, S.H., 1915. On some dinosaur remains from Bushmanland. *Transactions of the Royal Society of South Africa* 5, 259–264.

- He, X., Cai, K., 1984. The Middle Jurassic dinosaurian fauna from Dashampu, Zigong, Sichuan. In: *The ornithomimid dinosaurs*, vol. 1. Sichuan Scientific and Technological Publishing House, Chengdu, Sichuan, pp. 1–71.
- Herne, M.C., Tait, A.M., Salisbury, S.W., 2016. Sedimentological reappraisal of the *Leaellynasaura amicagraphica* (Dinosauria, Ornithomimidae) holotype locality in the lower Cretaceous of Victoria, Australia, with taphonomic implications for the taxon. In: KHOSLA, A., LUCAS, S.G. (Eds.), *Cretaceous Period: Biotic Diversity and Biogeography*. New Mexico Museum of Natural History and Science Bulletin, vol. 71, pp. 121–135.
- Herne, M.C., Tait, A.M., Weisbecker, V., Hall, M., Nair, J.P., Cleeland, M., Salisbury, S.W., 2018. A new small-bodied ornithomimid (Dinosauria, Ornithomimidae) from a deep, high-energy Early Cretaceous river of the Australian–Antarctic rift system. *PeerJ* 5, e4113.
- Holtz Jr., T.R., Molnar, R.E., Currie, P.J., 2004. Basal tetanurae. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*, second ed., vols. 71–110. University of California Press, Berkeley, p. 880.
- Horner, J.R., Weishampel, D.B., 1988. A comparative embryological study of two ornithomimid dinosaurs. *Nature* 332, 256–257.
- Horner, J.R., Weishampel, D.B., Forster, C.A., 2004. Hadrosauridae. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*, second ed., vols. 438–463. University of California Press, Berkeley, p. 880.
- Huxley, T.H., 1869. On *Hypsilophodon*, a new genus of Dinosauria. *Proceedings of the Geological Society of London* 204, 3–4.
- Ibárcicu, L.M., Martínez, R.D., Lamanna, M.C., Casal, G.A., Luna, M., Harris, J.D., Lacovara, K.J., 2010. A medium-sized ornithomimid (Dinosauria: Ornithomimidae) from the Upper Cretaceous Bajo Barreal Formation of Lago Colhue Huapi, southern Chubut Province. *Annals of Carnegie Museum* 79 (1), 39–50.
- Ibárcicu, L.M., Martínez, R.D., Luna, M., Casal, G.A., 2014. Reappraisal of *Notohypsilophodon comodorensis* (Ornithomimidae: Ornithomimidae) from the Late Cretaceous of Patagonia, Argentina. *Zootaxa* 3786 (4), 401–422.
- Ibárcicu, L.M., Casal, G.A., Martínez, R.D., Luna, M., Canale, J.L., Álvarez, B.N., Riga, B.G., 2019. A new ornithomimid dinosaur (Dinosauria: Ornithomimidae) from the Late Cretaceous of central Patagonia. *Cretaceous Research* 98, 276–291.
- Juárez Valieri, R.D., Haro, J.A., Fiorelli, L.E., Calvo, J.O., 2010. A new hadrosauroid (Dinosauria: Ornithomimidae) from the Allen Formation (Late Cretaceous) of Patagonia, Argentina. *Revista Del Museo Argentino De Ciencias Naturales* 12 (2), 217–231.
- Lambe, L.M., 1917. The Cretaceous theropod dinosaur *Gorgosaurus*. Canada Department of Mines. *Geological Survey* 100, 84.
- Maidment, S.C.R., Barrett, P.M., 2011. The locomotor musculature of basal ornithomimid dinosaurs. *Journal of Vertebrate Paleontology* 31 (6), 1265–1291.
- Makovicky, P.J., Kilbourne, B.M., Sadelir, R.W., Norell, M.A., 2011. A new basal ornithomimid (Dinosauria, Ornithomimidae) from the Late Cretaceous of Mongolia. *Journal of Vertebrate Paleontology* 31 (3), 626–640.
- Marsh, O.C., 1881. Principal characters of American Jurassic dinosaurs. Part V. *American Journal of Science Series* 3 (21), 417–423.
- Marsh, O.C., 1890. Description of new dinosaurian reptiles. *American Journal of Science* 39, 81–86.
- Marsh, O.C., 1894. The typical Ornithomimidae of the American Jurassic. *American Journal of Science Serie* 3 (48), 85–90.
- Martínez, R., 1998. *Notohypsilophodon comodorensis* gen. et sp. nov. Un Hypsilophodontidae (Ornithomimidae, Ornithomimidae) del Cretácico Superior de Chubut, Patagonia Central. *Acta Geologica Leopoldensia* 21 (46/47), 119–135.
- Mateus, O., Maidment, S.C., Christiansen, N.A., 2009. A new long-necked ‘sauropod-mimic’ stegosaur and the evolution of the plated dinosaurs. *Proceedings of the Royal Society of London B Biological Sciences* 276 (1663), 1815–1821.
- Norell, M.A., Makovicky, P.J., 2004. Dromaeosauridae. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*, second ed., vols. 196–209. University of California Press, Berkeley, p. 880.
- Norman, D.B., 1980. On the ornithomimid dinosaur *Iguanodon bernissartensis* from Belgium, vol. 178. *Memoir De l'Institut Royal Des Sciences Naturelles De Belgique*, pp. 1–105.
- Norman, D.B., 1986. On the anatomy of *Iguanodon atherfieldensis* (Ornithomimidae: Ornithomimidae), vol. 56. *Bulletin de l'Institut Royal Des Sciences Naturelles De Belgique*, pp. 281–372.
- Norman, D.B., 2004. Basal Iguanodontia. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*, second ed. University of California Press, Berkeley, pp. 413–437.
- Norman, D.B., Sues, H.D., Witmer, L.M., Coria, R.A., 2004. Basal Ornithomimidae. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*, second ed., vols. 393–412. University of California Press, Berkeley, p. 880.
- Novas, F.E., 2009. *The Age of Dinosaurs in South America*. Indiana University Press, Bloomington, p. 269.
- Novas, F.E., Cambiaso, A., Ambrosio, A., 2004. A new basal iguanodontian (Dinosauria, Ornithomimidae) from the Upper Cretaceous of Patagonia. *Ameghiniana* 41, 75–82.
- Osborn, H.F., 1905. *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Bulletin of the American Museum of Natural History* XXI, 259–265.
- Ostrom, J.H., 1970. *Stratigraphy and Paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin Area, Wyoming and Montana*. Peabody Museum of Natural History, Yale University 35, 234.
- Owen, R., 1842. Report on British fossil reptiles. Part II. In: *Report of Eleventh Meeting of the British Association for the Advancement of Science, held at Plymouth in July, 1841*. J. Murray, London, pp. 60–204.
- Persons, W.S., Currie, P.J., 2011. The Tail of *Tyrannosaurus*: Reassessing the Size and Locomotive Importance of the *M. caudofemoralis* in Non-Avian Theropods. *Anatomical Record* 294 (1), 119–131.
- Persons, W.S., Currie, P.J., Norell, M.A., 2013. Oviraptorosaur tail forms and functions. *Acta Palaeontologica Polonica* 59 (3), 553–567.
- Porfiri, J., Calvo, J.O., 2002. A new record of an ornithomimid dinosaur from the Upper Cretaceous of Neuquén, Patagonia, Argentina. *Primer Congreso latinoamericano de Paleontología de Vertebrados*. Santiago de Chile, Octubre del 2002, 45.
- Porfiri, J., Calvo, J.O., 2006. New cranial evidence of a small basal Ornithomimidae from the Late Cretaceous of Patagonia, Argentina. In: *IX Congreso Argentino de Paleontología y Bioestratigrafía*, vol. 2006. Academia Nacional de Ciencias, Córdoba Septiembre del, p. 88.
- Rauhut, O.W.M., 2003. *Special Papers in Palaeontology, The Interrelationships and Evolution of Basal Theropod Dinosaurs (No. 69)*. Blackwell Publishing.
- Rich, T.H., Vickers-Rich, P., 1989. Polar dinosaurs and biotas of the Early Cretaceous of southeastern Australia. *National Geographic Research* 5 (1), 15–53.
- Rich, T.H., Vickers-Rich, P., 1999. The Hypsilophodontidae from southeastern Australia. In: Tomida, Y., Rich, T.H., Vickers-Rich, P. (Eds.), *Proceedings of the Second Gondwana Dinosaur Symposium*. Natural Science Museum of Tokyo Monographs, pp. 167–180.
- Rozadilla, S., Agnolín, F.L., Novas, F.E., Aranciaga Rolando, A.M., Motta, M.J., Muñoz, G.L., Lirio, J.M., Isasi, M.P., 2016. A new ornithomimid (Dinosauria, Ornithomimidae) from the Upper Cretaceous of Antarctica and its palaeobiogeographical implications. *Cretaceous Research* 57, 311–324.
- Rozadilla, S., Agnolín, F.L., Novas, F.E., 2019. The Osteology of the Patagonian Ornithomimid *Talenkauen santacrucensis*.
- Salgado, L., Coria, R.A., 1996. First evidence of an ankylosaur (Dinosauria, Ornithomimidae) in South America. *Ameghiniana* 33 (4), 367–371.
- Salgado, L., Coria, R.A., Horedia, S.E., 1997. New materials of *Gasparrinisaura cincosaltensis* (Coria and Salgado, 1996) (Ornithomimidae, Ornithomimidae) from the Upper Cretaceous of Argentina. *Journal of Paleontology* 7, 933–940.
- Scheetz, R.D., 1999. *Osteology of Orodromeus makelai and the phylogeny of basal ornithomimid dinosaurs*. PhD thesis. Montana State University, Bozeman, p. 186.
- Seeley, H.G., 1887. On the classification of the fossil animals commonly called Dinosauria. *Proceedings of the Royal Society of London* 43, 165–171.
- Sereni, P., 1986. Phylogeny of the bird-hipped dinosaurs. *National Geographic Research* 2, 234–256.
- Taquet, P.H., 1976. Géologie et Paléontologie du gisement de Gadoufaoua (Aptien du Niger). *Cahiers de Paléontologie*. In: du C.N.R.S., p. 191.
- Tennant, J., 2013. Osteology of a Near-Complete Skeleton of *Tenontosaurus tilletti* (Dinosauria: Ornithomimidae) from the Cloverly Formation. Montana, USA. *ArXiv preprint arXiv:1304.2616*.
- Wilson, J.A., 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology* 19, 639–653.
- Wilson, J.A., 2006. Anatomical nomenclature of fossil vertebrates: standardized terms or ‘lingua franca’? *Journal of Vertebrate Paleontology* 26, 511–518.
- Wilson, J.A., D’Emic, M.D., Ikejiri, T., Moacdieh, E.M., Whitlock, J.A., 2011. A nomenclature for vertebral fossae in sauropods and other saurischian dinosaurs. *PLoS One* 6 e17114.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2019.104311>.