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A new small-bodied ankylosaurian dinosaur from the Upper Cretaceous of North Patagonia (Río Negro Province, Argentina)

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The most representative ankylosaurian remains from Argentina have been found in sediments of the Allen Formation (Campanian–Maastrichtian) in Salitral Moreno, Río Negro Province. Several authors have discussed the identity and history of these remains. In this study, we review all published material along with some new remains in order to summarize all the knowledge about these ankylosaurs. Previously published material includes a tooth, dorsal and anterior caudal vertebrae, a femur and several osteoderms. The new remains include synsacral and caudal elements, a partial femur and osteoderms. The anatomy of the tooth, the synsacrum, the mid-caudal vertebra, the femur and the osteoderms, and the histology of the post-cervical osteoderms, support a nodosaurid identification, as proposed in previous descriptions of the Salitral Moreno material. *Patagopelta cristata* gen. et sp. nov. is a new nodosaurid ankylosaur characterized by the presence of unique cervical half-ring and femoral anatomies, including high-crested lateral osteoderms in the half rings and a strongly developed muscular crest in the anterior surface of the femur. The ~2 m body length estimated for *Patagopelta* is very small for an ankylosaur, comparable with the dwarf nodosaurid *Struthiosaurus*. We recovered *Patagopelta* within Nodosaurinae, related to nodosaurids from the ‘mid’-Cretaceous of North America, contrasting the previous topologies that related this material with Panoplosaurini (Late Cretaceous North American nodosaurids). These results support a palaeobiogeographical context in which the nodosaurids from Salitral Moreno, Argentina, are part of the allochthonous fauna that migrated into South America during the late Campanian as part of the First American Biotic Interchange.

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Keywords: Patagopelta; Nodosauridae; Late Cretaceous; Salitral Moreno; Patagonia; Gondwana

Introduction

Ankylosauria is a clade of armoured ornithischian dinosaurs with a fossil record ranging from the Middle Jurassic to the Upper Cretaceous (Arbour & Currie 2016). The study of ankylosaurian diversity and interrelationships has undergone a strong reorganization over several decades, since the landmark taxonomic revisions by Coombs (1971, 1978), the more recent phylogenetic revisions of Coombs & Maryńska (1990), Carpenter (2001, 2012), Vickaryous *et al.* (2004), Thompson *et al.* (2012), and the subsequent contributions of Arbour & Currie (2016) and Arbour *et al.* (2016). Ankylosauria is

traditionally defined as the clade that comprises the taxa more closely related to *Ankylosaurus* than to *Stegosaurus* (Serenó 1998), and is subdivided into the families Ankylosauridae and Nodosauridae (Coombs 1978; Vickaryous *et al.* 2004). In addition, a recent redescription of several specimens of the thyreophoran *Scelidosaurus*, including its holotype (Norman 2020a), suggests that the Lower Jurassic ‘basal thyreophorans’ (non-eurypodan thyreophorans; see Sereno 1998) are more closely related to ankylosaurs than to stegosaurs.

Although ankylosaur diversity is quite well known, this is mostly true for materials from Laurasian landmasses, whereas ankylosaur remains from Gondwana

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are still elusive (Novas 2009; Pereda-Suberbiola *et al.* 2015; Maidment *et al.* 2021; Rozadilla *et al.* 2021; Soto-Acuña *et al.* 2021; and references therein). Currently, the few species known from Gondwana are ‘*Antarctopelta oliveroi*’ (Late Cretaceous of Antarctica; Salgado & Gasparini 2006; discussed by Arbour & Currie 2016, and considered by them a *nomen dubium*), ‘*Minmi paravertebra*’ (Early Cretaceous of Australia; Molnar 1980; also considered a *nomen dubium* by Arbour & Currie 2016), *Kunbarrasaurus ieveri* (Early Cretaceous of Australia; Leahey *et al.* 2015; previously identified as *Minmi* sp. by Molnar 1996), *Spicomellus afer* (Middle Jurassic of Morocco; Maidment *et al.* 2021) and *Stegouros elegassen* (Upper Cretaceous of Chile; Soto-Acuña *et al.* 2021).

In South America, the few known ankylosaurian remains have been found in rocks belonging to several Upper Cretaceous units of Argentina and Chile. The Argentinian record includes mainly isolated osteoderms from the Neuquén Group in the Neuquén Province (Huene 1929; Novas 2009), the Puerto Yeruá Formation in the Entre Ríos Province (de Valais *et al.* 2003), the La Colonia Formation in the Chubut Province (Gasparini *et al.* 2015), the Allen Formation in the Río Negro Province (Murray *et al.* 2019), and fragmentary remains from the Chorrillo Formation in the Chubut Province (Rozadilla *et al.* 2021), and the Cerro Fortaleza Formation in the Santa Cruz Province (Paulina-Carabajal *et al.* 2021).

The first ankylosaurian partial skeleton known from Argentina was found in sediments of the Allen Formation at Salitral Moreno, Río Negro Province, Argentina. It comprises a tooth and an incomplete post-cranial skeleton with many osteoderms (Salgado & Coria 1996; Coria & Salgado 2001; Arbour & Currie 2016; Ponce & Cerda 2017; Rigueti 2018). This specimen was initially identified as a nodosaurid ankylosaur based on the asymmetrical cingulum of the tooth crown and the proximal placement of the fourth trochanter in the femur (Salgado & Coria 1996; Coria & Salgado 2001). However, no phylogenetic analysis was made to test this proposal. Recently, Arbour & Currie (2016) made an updated phylogenetic analysis for Ankylosauridae and included the Argentinian material. These authors recovered the Argentinian specimen as a nodosaurid, corroborating the original proposal. Moreover, they recognized a novel morphology for the cervical osteoderms. However, the whole Nodosauridae is not fully resolved in the phylogeny of Arbour & Currie (2016). Later studies based on the same data matrix improved the topology and recovered the Argentinian ankylosaur as part of the Panoplosaurini (*sensu* Madzia *et al.* 2021; see also Arbour *et al.* 2016;

Rivera-Sylva *et al.* 2018; Zheng *et al.* 2018), thus related to the North American uppermost Cretaceous nodosaurids, such as *Edmontonia* and *Panoplosaurus*.

Coria & Salgado (2001) proposed that the presence of ankylosaurs in the Argentinian North Patagonia was due to a faunal interchange between the Americas that occurred during the Campanian–Maastrichtian age (see also Bonaparte 1986; Leanza *et al.* 2004; Goin *et al.* 2012). The results of Arbour & Currie (2016) and Arbour *et al.* (2016) support this biogeographical scenario. An alternative hypothesis suggested by Gasparini *et al.* (1996) and Agnolín *et al.* (2010) proposes a lineage of ankylosaurs that evolved in Gondwana since the Late Jurassic. Doubts regarding the allochthony of South American ankylosaurs were mainly based on the mixture of basal and specialized features of *Kunbarrasaurus* (Leahey *et al.* 2015), and its isolation from the Laurasian ankylosaurs during Early Cretaceous times (Gasparini *et al.* 1996). The recent finding of *Stegouros* and the establishment of the Parankylosauria partially solved this issue (Soto-Acuña *et al.* 2021), but did not explain the presence of nodosaurids in South America.

With the aim of summarizing all information about the South American ankylosaurs from the Argentinian North Patagonia, we re-evaluate here the previously described material and present new remains from the Salitral Moreno locality. The new remains were recovered both from the Museo Provincial Carlos Ameghino collection (MPCA) and from old loans to palaeontological collections other than the originally housing MPCA. We reanalyse the phylogenetic relationships in the light of this new material and discuss their implications for Late Cretaceous ankylosaurian palaeobiogeography.

Institutional abbreviations

MACN-Pv, Colección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; **MPCA**, Museo Provincial Carlos Ameghino, Cipolletti, Río Negro, Argentina; **NHMUK**, National History Museum, London, United Kingdom.

Geological context

All ankylosaurian remains described here were collected from the Lower Member of the Allen Formation (upper Campanian–lower Maastrichtian; Hugo & Leanza 2001a) at Salitral Moreno, almost 30 km south of General Roca (Río Negro Province, Argentina; Fig. 1). These were found in a few quarries from the same stratigraphical level within an area of approximately 50

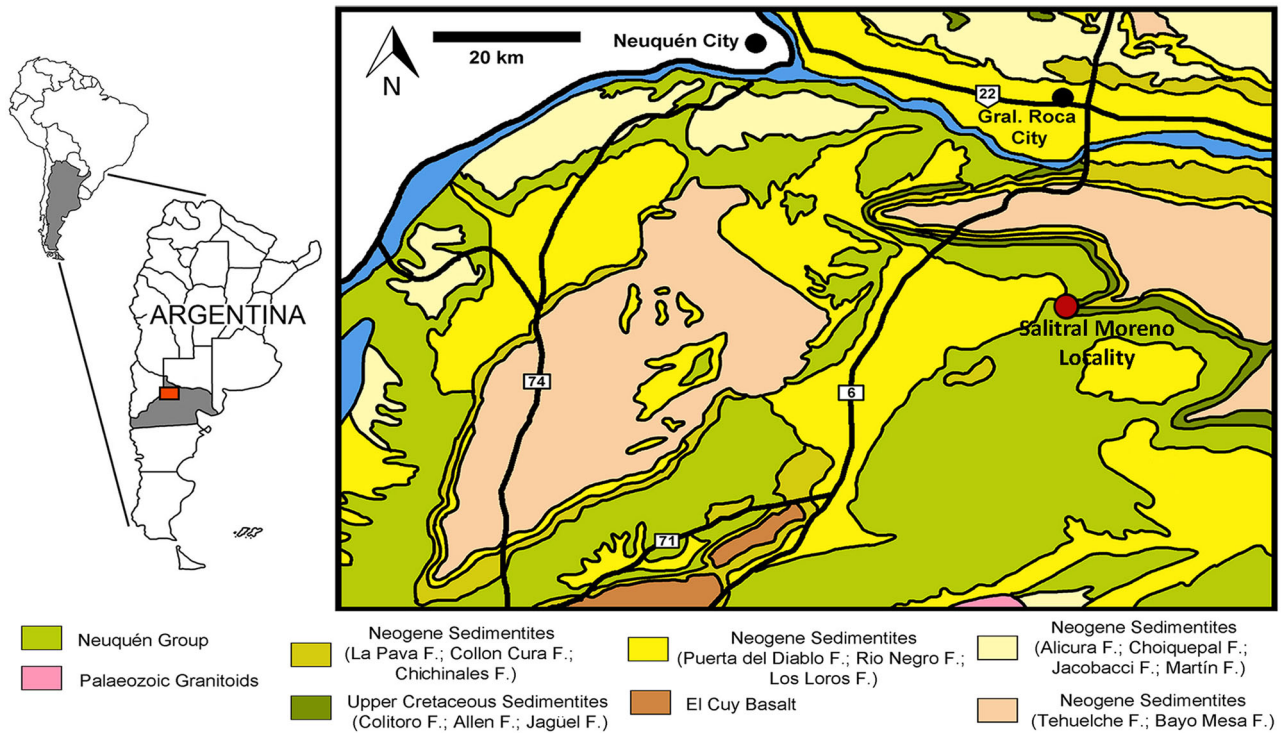


Figure 1. Locality and stratigraphy. South America and Argentinian maps (left). The red box indicates the detailed map locality (expanded at right). The coloured scale (bottom) represents the ages of sediments in the region, detailing the respective geological formations. The red circle indicates the site from which the Salitral Moreno nodosaurid remains were collected.

m² (Coria & Salgado 2001), along with several other materials, including titanosaurine and saltosaurine titanosaur remains (both bones and eggs; Powell 1987; Salgado & Coria 1993; Salgado & Azpilicueta 2000; Simón 2006; Garcia & Salgado 2013), hadrosaurids (Juárez Valieri *et al.* 2010; Cruzado-Caballero & Coria 2016; Cruzado-Caballero & Powell 2017), theropods (including birds), turtles, gastropods and plant remains (Powell 1987; Simón 2006).

The Allen Formation belongs to the Malargüe Group, and represents depositional events related to the earliest Atlantic transgressive event that occurred during the latest Cretaceous in North Patagonia (Casamiquela 1978; Hugo & Leanza 2001a; and references therein). Several recent studies consider the Allen Formation to have been deposited in a continental environment, evolving from a fluvial to deltaic Lower Member of moderate energy with local presence of coastal dunes (in the Paso Córdoba locality, Armas & Sánchez 2013), to lagoon and fine-grained, low-energy marine deposits in the Middle Member, and finally to restricted conditions represented by evaporites in the Upper Member (Hugo & Leanza 2001a, b; Rodríguez 2011). Others have proposed a transitional environment with variable degrees of marine influence (e.g. Bertels 1969; Andreis *et al.* 1974; Uliana 1979; Barrio 1990; Casadío 1994; Armas

& Sánchez 2011, 2013). Rodríguez (2011) summarized most previous interpretations (mostly of both the Lower and Middle members) to conclude that the Allen Formation represents a marginal marine environment deposited in a transgressive context, where extensive lowlands (including fluvial systems) were flooded without reaching a fully marine contact. The presence of bentonite layers also shows some connection to the active volcanic arc. The Upper Member is interpreted by most authors as a restriction of the basin resulting in evaporitic deposition (Rodríguez 2011, and references therein). Its abundant fossil content also shows a mixture of continental and fresh- to brackish-water taxa (see Wichmann 1927, in ‘the Lacustrine Senonian’, equivalent to the Allen Formation; Hugo & Leanza 2001a, b; Leanza *et al.* 2004; Martinelli & Forasiepi 2004; O’Gorman *et al.* 2011; Garcia & Salgado 2013; and references therein).

Bone preservation seems consistent with the fluvial to deltaic interpretations proposed for the Lower Member of the Allen Formation. Unfortunately, field data for these specimens is somewhat imprecise, and therefore taphonomic comments must be taken with caution. Most ankylosaurian elements have pristine surface texture, or have breakages with minimal abrasion, suggesting a high energy but short-distance transporting flow (Martin

1999; Rogers & Kidwell 2007; and references therein). The well-preserved external surface of bones that evidence low biostratigraphic effects also suggests a high sedimentation rate, compatible with marginal regions of a fluvial to deltaic environment. On the other hand, some elements, such as the distal end of a femur (MPCA-SM-709) and a mid-caudal vertebra (MPCA-SM-708), are broken and strongly abraded, suggesting a probable lag-deposit origin (Martin 1999; Rogers & Kidwell 2007; and references therein). In addition, these elements have the same colour and their exposed cancellous bone is filled with the same fine greyish pelitic-sized sediment, very different from the yellowish sandy infilling of most of the other ankylosaur bones. This reflects the heterogeneity of the sediments in these layers. The higher erosion is not necessarily due to fluvial transport from its original deposition (Aslan & Behrensmeyer 1996), but may have been caused by the higher energetic conditions in some regions of the channel profile (e.g. river bed), suggesting a similar origin. Also, some of the well-preserved elements (e.g. some osteoderms, such as MPCA-SM-73 and MPCA-SM-715, the dorsal vertebra MPCA-SM-68 and the complete femur MPCA-SM-1) and the eroded femora (MPCA-SM-709) show bore traces and furrows probably due to bioerosion (see Britt *et al.* 2008), also suggesting long exposure prior to final burial (Martin 1999; McHugh *et al.* 2020).

Material

Several previous works have studied samples of the ankylosaurian material collected from the Salitral Moreno site (see [Supplemental material Table 1](#)). All the known remains were reviewed and are considered in this study. Several specimens of different dinosaur species were collected from a few nearby quarries from the same stratigraphical level (Garcia & Salgado 2013). However, the exact quarry and association of most of the ankylosaurian remains is currently unknown (LS, pers. obs.). Some anatomical variation in the ankylosaurian remains attests to the presence of more than one individual. Small differences in the size of dorsal and caudal vertebrae suggest the presence of at least two individuals. Also, variation in both size and degree of fusion between vertebral elements in the two available synsacral pieces (MPCA-SM-703 and MPCA-SM-704) suggests at least a third, immature specimen. Additional variation among caudal vertebrae, such as the presence of ventral ridges or a smooth surface, could be explained by intraspecific variation. A few elements do appear to preserve original anatomical associations, such as a cervical neural arch and a cervical osteoderm (MPCA-SM-700a, b) in almost natural

position. The right and left femora (MPCA-SM-1 and MPCA-SM-709) are the same size, and may belong to the same individual. Although most remains are either dispersed or belong to several specimens as expected by the geological context, anatomical features and the few associated materials allows us to consider these to represent the same new taxon.

New material described here includes a quadratojugal horn (MPCA-SM-710), a partial cervical neural arch with an associated osteoderm (MPCA-SM-700a, b), dorsal vertebrae (MPCA-SM-701, 702), two synsacral elements (MPCA-SM-703, 704), anterior and mid-caudal vertebrae (MPCA-SM-705, 706, 707, 708), a femoral distal end (MPCA-SM-709), and several cervical (MPCA-SM-711, 712, 713, 714) and post-cervical (MPCA-SM-715, 716, 717, 718, 719, 720, 721, 722, 723, 724 and 725) osteoderms. For osteoderm terminology we follow Ford (2000), with the exception of the transverse placement of osteoderms (the terms primary and secondary are replaced here by lateral and distal, respectively, as in Burns & Currie 2014).

Three osteoderms were thin sectioned following the standard protocol for palaeohistological samples (Cerdeña *et al.* 2020). The thin sections were studied with a Leica DM750 P petrographic microscope using transmitted normal and polarized light with a lambda filter. For osteoderm histology we follow the terminology of Scheyer & Sander (2004).

To test phyletic dwarfism in ankylosaurs, we used the femoral length as a proxy for body length, and mapped this into our topology (see ‘Phylogenetic analysis’ below). We generated a script including each terminal node, one character (femoral length, coded using both literature and first-hand measurements) and our strict consensus. The mapping was made in Mesquite (version 3.2, see Maddison & Maddison 2019) under the parsimony criterion. The results and the data set are included in the [Supplemental material](#). A reduced version of the mapped consensus is figured below.

Systematic palaeontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Thyreophora Nopcsa, 1915

Ankylosauria Osborn, 1923

Nodosauridae Marsh, 1890

Patagopelta cristata gen. et sp. nov.

(Figs 2–12)

Type species. Holotype: MPCA-SM-78 (cervical half-ring element).

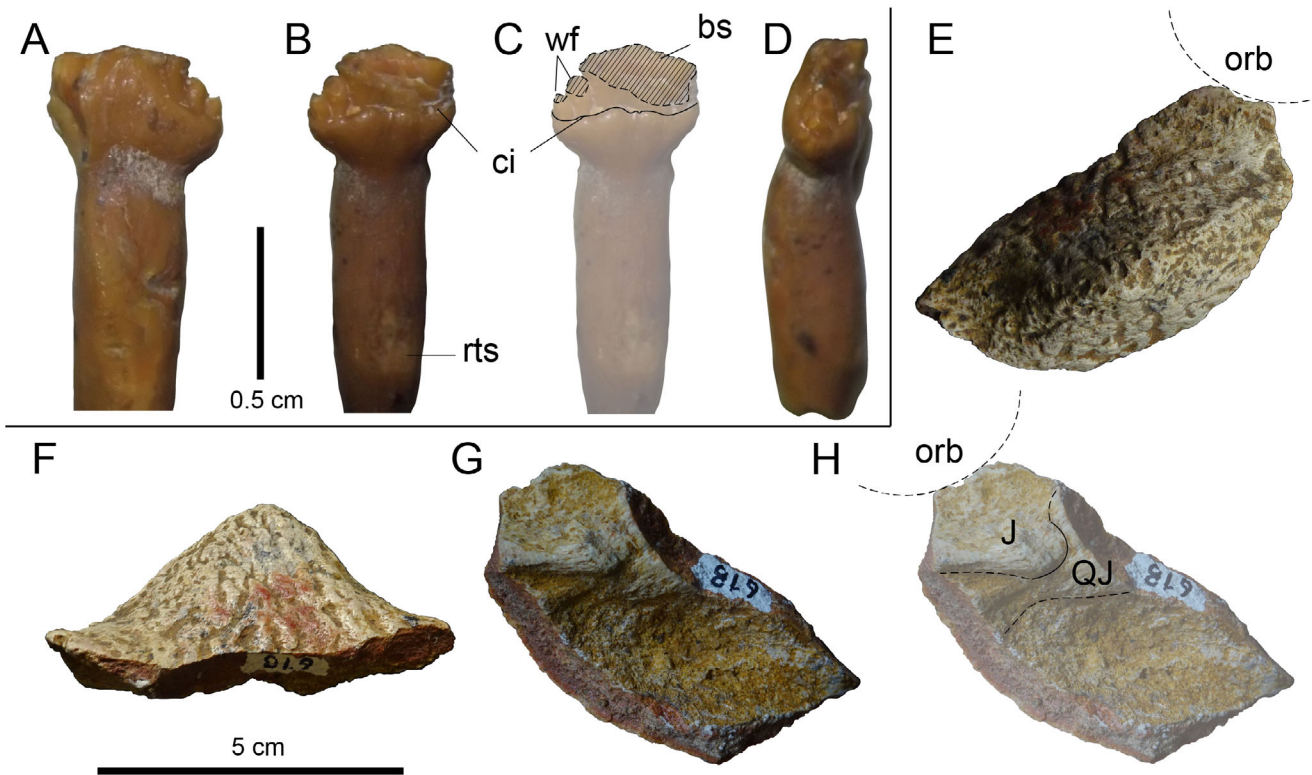


Figure 2. Cranial remains. **A–D**, MPCA-SM-77, isolated tooth in **A**, labial, **B**, **C**, lingual and **D**, edge (?distal) views. MPCA-SM-710 (quadratojugal horn) in **E**, right lateral, **F**, dorsal, and **G**, **H**, medial views. **Abbreviations:** **bs**, broken surface; **ci**, cingulum; **J**, jugal; **orb**, orbit; **QJ**, quadratojugal; **rts**, replacement tooth surface; **wf**, wear facets.

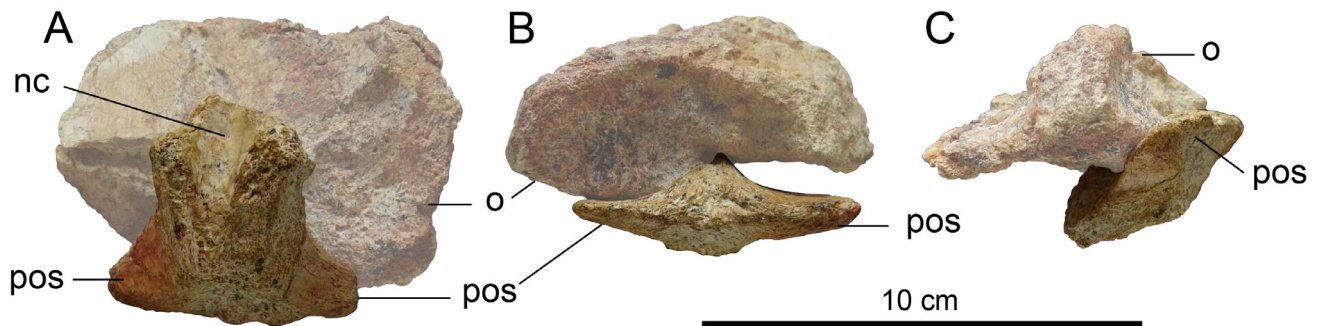


Figure 3. Cervical vertebra. **A–C**, MPCA-SM-700a and MPCA-SM-700b (MPCA-SM-700b attenuated), in **A**, ventral, **B**, posterior and **C**, left lateral views. **Abbreviations:** **nc**, roof of the neural canal; **o**, osteoderm; **pos**, postzygapophysis.

Paratypes. MPCA-SM-710 (quadratojugal boss), MPCA-SM-77 (tooth), MPCA-SM-700a (partial cervical neural arch; associated with the osteoderm 700b), MPCA-SM-68, 69, 70, 701, 702 (dorsal vertebrae), MPCA-SM-703, 704 (synsacral compound elements), MPCA-SM-71, 72, 73, 705, 706, 707, 708 (caudal vertebrae), MPCA-SM-1, MPCA-SM-709 (complete and partial femora), MPCA-SM-700b (osteoderm associated with the vertebra 700a), 711, 712, 713, 714 (cervical

half-ring osteoderms), MPCA-SM-41a, 41b, 42a, 42b, 43, 74, 75, 76, 715, 716, 717, 718, 719, 720, 721, 722, 723, 724 and 725 (postcervical osteoderms); and four thin sections of postcervical osteoderms.

Referred material. MACN-PV-RN 1149 (five osteoderms; see Murray *et al.* 2019).

Diagnosis. Small ankylosaur (body length ~2.2 m) that differs from all other Nodosauridae in having the

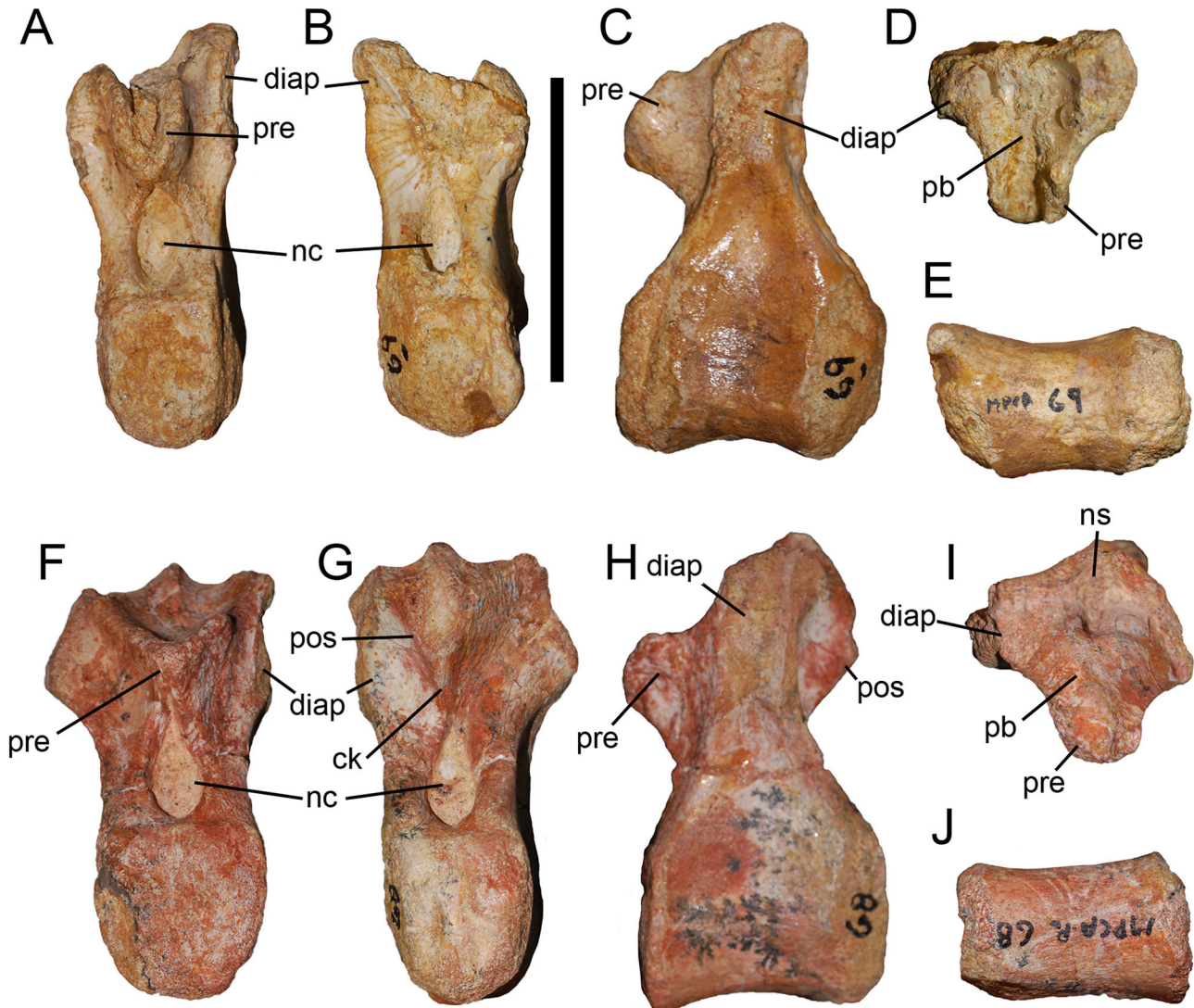


Figure 4. Dorsal vertebrae. **A–E**, MPCA-SM-69, in **A**, anterior, **B**, posterior, **C**, left lateral, **D**, dorsal and **E**, ventral views. **F–J**, MPCA-SM-68, in **F**, anterior, **G**, posterior, **H**, left lateral, **I**, dorsal and **J**, ventral views. **Abbreviations:** **ck**, central keel; **diap**, diapophysis; **nc**, neural canal; **ns**, neural spine; **pb**, prespinal basin; **pos**, postzygapophysis; **pre**, prezygapophysis.

following combination of characters: strongly developed muscular crests (muscularis caudalis, muscularis cranialis and the anterior trochanter) on the anterior surface of the femur; cervical half rings of unique morphology, bearing both high-keeled lateral osteoderms with a central inflection and distal spine-like osteoderms with anteriorly compressed edges, all fused across their basal edges forming a thick band with strongly sutured contacts.

Derivation of name. The generic name *Patagopelta* is derived from ‘*Patago*’ (referring to the Argentinian Patagonia) and ‘*pelta*’ (shield in Greek), in reference to the region of the fossil site and the presence of a large number of osteoderms covering the dorsal surface of the body, respectively. The specific epithet *cristata* (crest in

Latin) refers to the presence of the diagnostic crests on both the anterior surface of the femur and the lateral osteoderm of the cervical rings.

Occurrence. Salitral Moreno locality, almost 30 km South of General Roca, Río Negro Province, Argentina; Allen Formation (upper Campanian–lower Maastrichtian; Hugo & Leanza 2001a).

Description

Measurements of all elements are given in the [Supplemental material Table 2](#) (non-dermal bones) and [Supplemental material Table 3](#) (osteoderms).

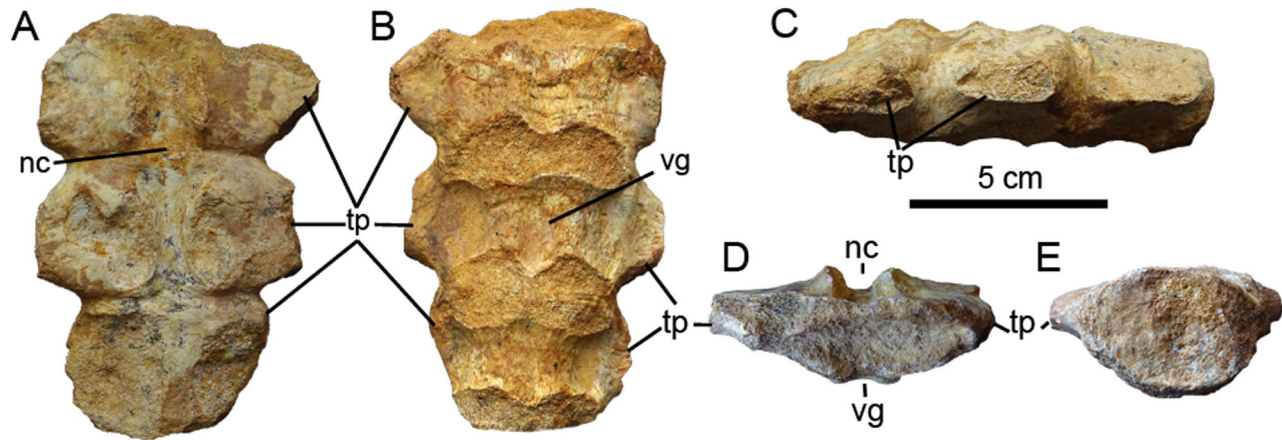


Figure 5. Synsacral vertebrae. A–E, MPCA-SM-703, in A, dorsal, B, ventral, C, left lateral, D, anterior and E, posterior views. **Abbreviations:** nc, neural canal; tp, transverse processes, vg, ventral groove.

Cranial skeleton

Cranial material is represented by a single isolated tooth (MPCA-SM-77, Fig. 2A–D) that is redescribed after Coria & Salgado (2001), and an element that probably belong to the quadratojugal and jugal bones with associated armour (MPCA-SM-710, Fig. 2E–H).

Cranial fragment. MPCA-SM-710 (Fig. 2E–H) is a low, subconical, laterally compressed and ornamented element, resembling the quadratojugal horn of ankylosaurs (see Carpenter *et al.* 1995; Ford 2000; Parsons & Parsons 2009). In both lateral and anterior views, the piece is symmetrical. The anterior edge of the boss is subtly constricted laterally from the base to the apex. Ventrally, the piece is concave. The external texture is strongly ornamented with pits or small foramina and furrows, the latter being larger towards the basal edges. The ventral texture is obscured by sediment. Almost all basal edges of the boss are broken. The only preserved part of the basal edges comprises accessory bones that converge and fuse under the boss. The texture of these accessory bones is smooth, as in non-dermal bones. One of the bones seems to be the jugal, bearing a thin and smooth edge, probably the ventral orbital margin. Across the broken bone it is not possible to see with the naked eye the sutural contact of these accessory bones with an external osteoderm (suggesting co-growing remodeled elements, as was proposed by Vickaryous *et al.* 2001 and Ósi *et al.* 2021 based on histology). In this context, the associated non-dermal bones could be the quadratojugal and the jugal. The overall shape resembles the symmetrical quadratojugal horn of *Hungarosaurus*, *Sauropelta*, *Silvisaurus* and *Edmontonia* (Carpenter & Kirkland 1998; Burns 2015; Ósi *et al.* 2021), contrasting with the asymmetrical boss of other

nodosaurids (e.g. *Europelta*, *Niobrarasaurus* and *Polacanthus*; Carpenter & Everhart 2007; Kirkland *et al.* 2013; Blows 2015), the more asymmetrical and anteroposteriorly longer horn of ankylosaurids (Tumanova 2000; Arbour & Currie 2013a; Arbour *et al.* 2014), and the strongly reduced element in the parankylosaur *Kunbarrasaurus* (Leahey *et al.* 2015).

Tooth. The tooth (MPCA-Pv-77) has a laterally compressed leaf-shaped crown with distal denticles, although most are eroded. The base of the crown is slightly swollen and crossed mid-height by a well-developed asymmetrical cingulum, as occurs in nodosaurids and parankylosaurs (e.g. *Antarctopelta*, *Edmontonia*, *Sauropelta*, *Stegouros* and *Struthiosaurus*; Pereda-Suberbiola & Galton 2001; Ósi *et al.* 2016; Soto-Acuña *et al.* 2021). Lingually, the cingulum has a sigmoidal to irregular profile. On the labial side, it is elevated centrally, confluent with the apical denticle. The base of the apical denticle and four associated denticles, the first mesial and the last three distals, are preserved. These denticles are separated by shallow grooves that extend to the cingulum, although this extension cannot be determined for more apical broken denticles. The lingual surface of the crown is quite eroded. Wear facets on the denticles are present on the lingual side (suggesting a maxillary origin). A strong constriction delimits and separates the crown from the root proximally. The root is sub-cylindrical, large and elongated. The lingual side of the root bears a proximal sub-rectangular facet for the replacement tooth. Tooth comparison with other ankylosaurs is difficult due to the large eroded surface. However, the denticles are quite large, as is more typical for nodosaurids (e.g. *Edmontonia*, *Europelta*, *Hungarosaurus* and *Sauropelta*; Ósi *et al.* 2016) than

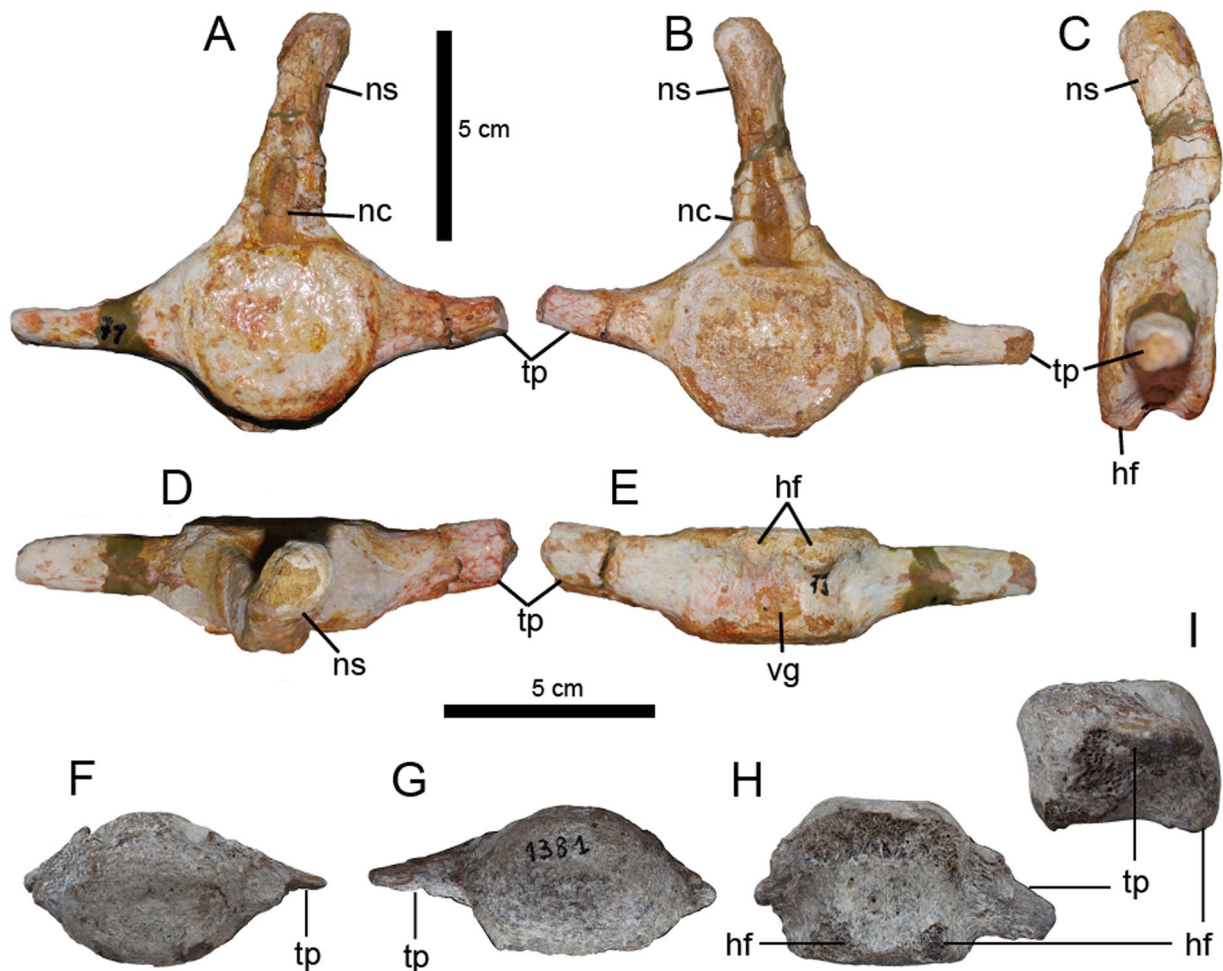


Figure 6. Caudal vertebrae. A–E, MPCA-SM-71, in A, anterior, B, posterior, C, right lateral, D, dorsal and E, ventral views. F–I, MPCA-SM-708, in F, anterior, G, posterior, H, ventral and I, left lateral views. **Abbreviations:** hf, haemal arch facets, nc, neural canal; ns, neural spine; tp, transverse process, vg, ventral groove.

for ankylosaurids or parankylosaurs (Mallon & Anderson 2014; Soto-Acuña *et al.* 2021).

Axial skeleton

The axial elements include a partial cervical neural arch, four dorsal vertebrae, two synsacral fragments and seven caudal vertebrae. Dorsal and caudal elements are re-described after Coria & Salgado (2001). New cervical (MPCA-SM-700a), dorsal (MPCA-SM-701 and 702) and some caudal (MPCA-SM-705, 706 and 707) elements do not provide significant taxonomic information, thus contrasting the novelties of the new synsacral (MPCA-SM-703, 704) and caudal (MPCA-SM-708) material. Axial elements are similar to those of ankylosaurs in general (see Ostrom 1970; Arbour & Currie

2013a; Burns 2015; Zheng *et al.* 2018; Raven *et al.* 2020; Soto-Acuña *et al.* 2021).

Cervical vertebra. MPCA-SM-700a (Fig. 3A–C) is the partial neural arch of a cervical vertebra associated with a cervical osteoderm (see description below; Fig. 3, o). The neural arch ventrally shows the roof of the neural canal (Fig. 3A, nc), bearing a small foramen on its mid-line. The postzygapophyses are elevated above the base of the diapophyses, and are laterally expanded posteriorly as in the cervical vertebrae of several ankylosaurs (e.g. *Edmontonia*, *Europelta*, *Polacanthus*, *Saichania*, *Silvisaurus*, etc.; see Gilmore 1930; Eaton 1960; Coombs 1971; Carpenter *et al.* 2011; Kirkland *et al.* 2013; Blows 2015). Most of the postzygapophyses and the neural spine and neural arch pedicels are eroded. The whole neural arch is rotated about 30° on its

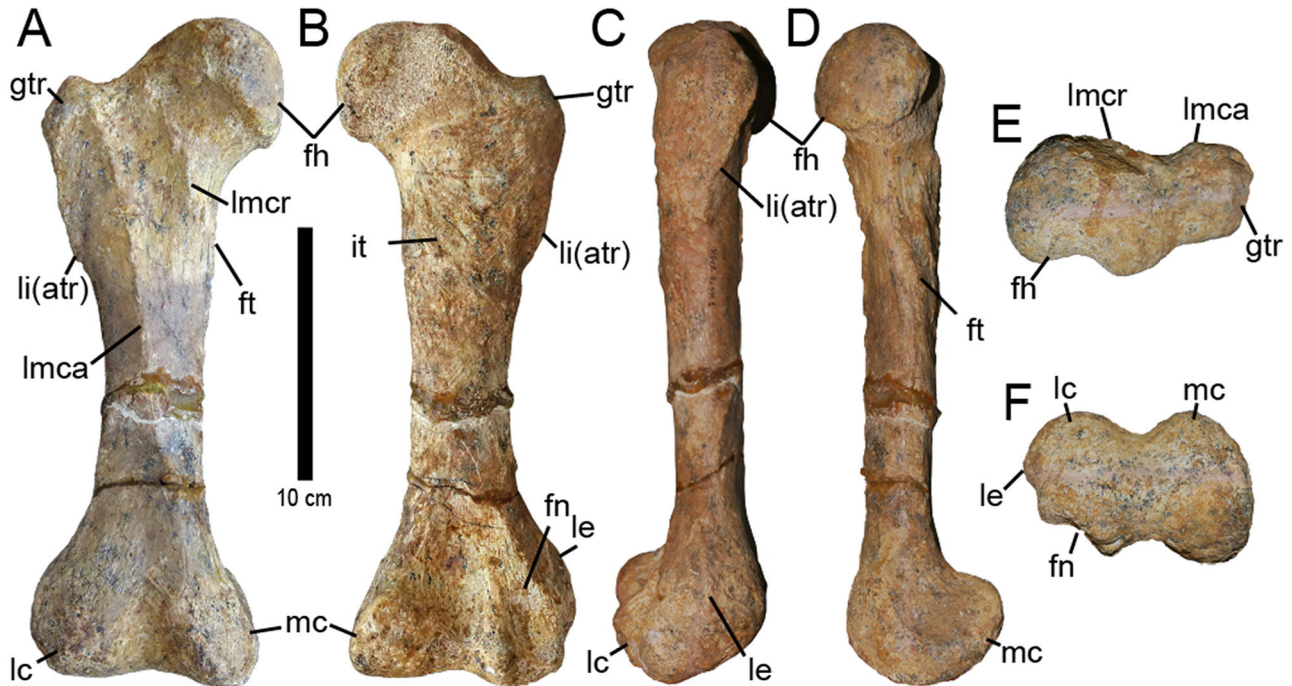


Figure 7. Femur. A–F, MPCA-SM-1, in A, anterior, B, posterior, C, lateral, D, medial, E, proximal and F, distal views. **Abbreviations:** fh, femoral head; fn, fibular notch; ft, fourth trochanter; gtr, greater trochanter; it, interwoven texture; lc, lateral condyle; le, lateral epicondyle; li (atr), linea intermuscular (associated to the anterior trochanter); lmca, linea muscularis caudalis; lmcr, linea muscularis cranialis; mc, medial condyle.

vertical axis with respect to the osteoderm due to post-mortem deformation.

Dorsal vertebrae. The material includes five mid to posterior dorsal vertebrae and one cast (MPCA-SM-70 is a cast of MPCA-SM-701). Although all elements share the same general morphology (Fig. 4A–E), MPCA-SM-68 is larger and slightly more robust than the others (Fig. 4F–J). Dorsal centra are longer antero-posteriorly than high dorsoventrally and higher dorsoventrally than wide transversely, although they are not elongated as in *Jinyunpelta* (Zheng *et al.* 2018) and *Polacanthus* (Blows 2015). Articular surfaces are flat, with expanded borders relative to the middle part of the vertebral centrum. These surfaces are sub-rounded with a straight dorsal edge. The neural arch is high, with dorsally elongate and transversely wide pedicels surrounding a vertically oval to teardrop-shaped neural canal. The neural arch across the pedicels is as wide as the centrum, a morphology also seen in *Crichtonpelta* (Lü *et al.* 2007), *Gastonia* (Kinneer *et al.* 2016), *Polacanthus* (Blows 2015) and *Struthiosaurus* (Pereda-Suberbiola & Galton 2001). The lateral surfaces of the neural arch are sub-triangular in lateral view, with anterior and posterior centrodiaepophyseal laminae defining a sub-triangular fossa on the ventral surface of the diapophyses like those described in *Hylaeosaurus*,

Polacanthus and *Struthiosaurus* (Seeley 1881; see also Bunzel 1871; Raven *et al.* 2020). The parapophyses are not preserved, although their bases are placed high in the neural arch, similar to the condition in *Gastonia*, *Hylaeosaurus* and *Polacanthus* (Kinneer *et al.* 2016; Raven *et al.* 2020). A large sub-triangular concave vestibule (‘prespinal basin’ *sensu* Coria & Salgado 2001) is placed centrally between the neural spine and the prezygapophyses. The prezygapophyses are ventrally fused at the midline and ‘U’-shaped in anterior view, as commonly occurs in ankylosaurs (e.g. *Ankylosaurus*, *Edmontonia*, *Euoplocephalus*, *Sauropelta*, *Stegouros*), except in *Hungarosaurus* (Ostrom 1970; Carpenter 2004; Ösi 2005; Arbour & Currie 2013a; Burns 2015; Soto-Acuña *et al.* 2021). Neural spines, diapophyses and postzygapophyses are broken in all specimens. The bases of the diapophyses are steeply inclined (55–60° from the horizontal) and are dorsally expanded antero-posteriorly (‘T’-shaped in cross-section, as in all ankylosaurs except *Mymoorapelta*; Arbour & Currie 2016). The bases of the postzygapophyses form a central rounded keel or buttress that contacts the dorsal edge of the neural canal, as occurs in other ankylosaurs (e.g. *Crichtonpelta*, *Euoplocephalus*, *Gastonia*, *Hylaeosaurus*, *Polacanthus* and *Sauropelta*; Ostrom 1970; Arbour & Currie 2013a; Blows 2015; Kinneer *et al.* 2016; Raven *et al.* 2020). There are no visible sutures between the

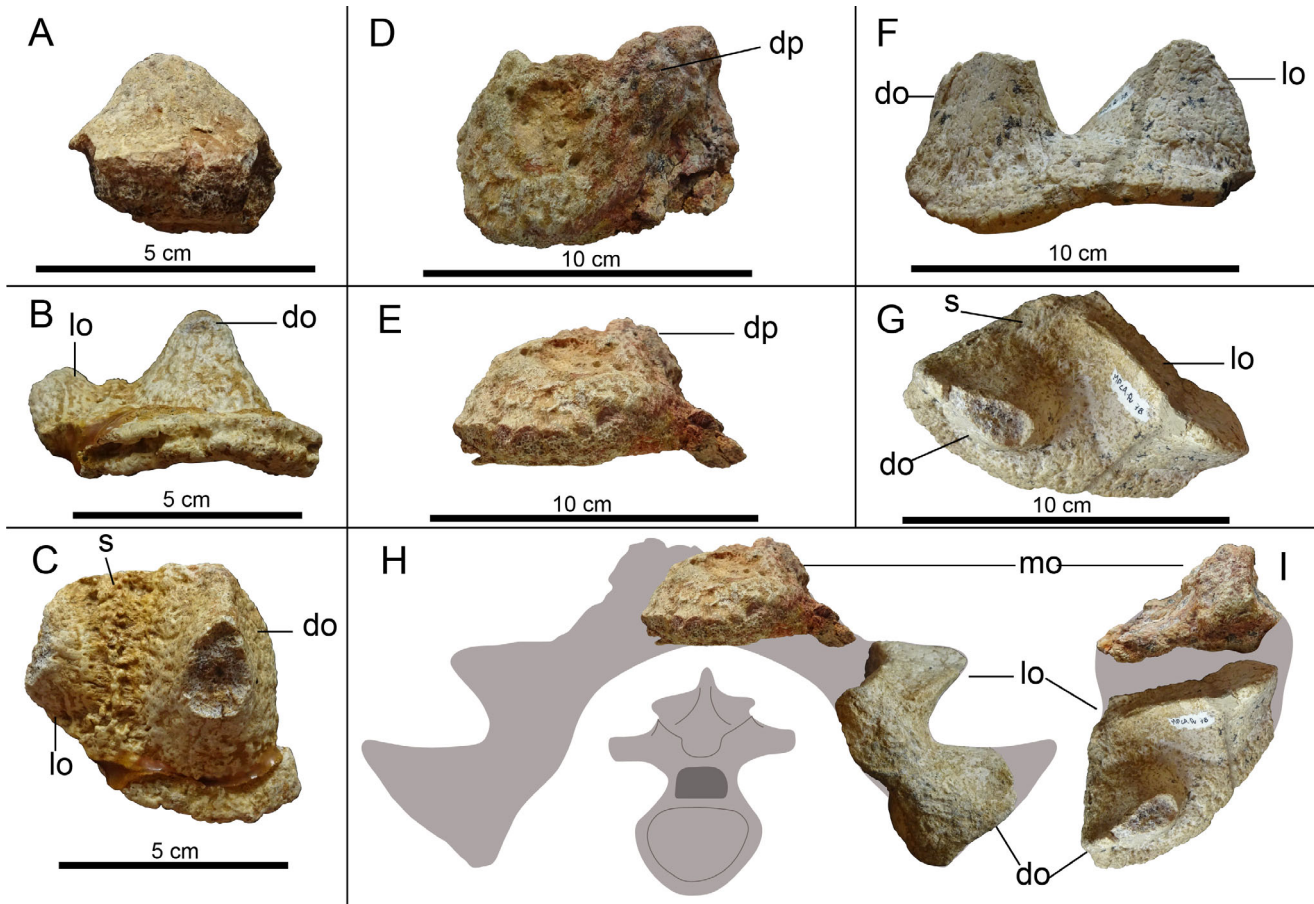


Figure 8. Cervical osteoderms. **A**, medial osteoderm MPCA-SM-711 in right lateral view; **B**, **C**, fused lateral and distal osteoderms MPCA-SM-712 in posterior (**B**) and dorsal (**C**) views; **D**, **E**, medial osteoderm MPCA-SM-700b in dorsal (**D**) and anterior (**E**) views; **F**, **G**, fused lateral and distal osteoderms MPCA-SM-78 (holotype of *Patagopelta cristata*) in posterior (**F**) and dorsal (**G**) views; **H**, **I**, reconstruction of a cervical half ring using MPCA-SM-700b and MPCA-SM-78 in anterior (**H**) and left lateral (**I**) views (the illustrated cervical vertebra is based on that of *Sauropelta*, modified from Ostrom 1970). **Abbreviations:** **do**, distal osteoderm; **dp**, dorsal prominence; **lo**, lateral osteoderm; **mo**, medial osteoderm; **s**, suture.

vertebral centrum and the neural arch in all vertebrae, therefore showing fully fused neurocentral sutures. Laterally, the centrum of MPCA-Pv-68 bears barely visible longitudinal striations. It also bears a sub-central pit with a ventral furrow in the posterior articular surface, probably due to bioerosion.

Synsacrum. Two synsacral fragments are here described for the first time. The larger piece (MPCA-SM-703, Fig. 5) is composed of three fused vertebral centra that preserve the base of the transverse processes, and the base of the pedicels of the neural arch only in the posterior-most vertebra. Vertebral centra are equal in length, although these gradually widen transversely and descend dorsoventrally towards the anterior end of the piece. The articular surface of the anterior centrum is strongly compressed dorsoventrally. It is slightly concave transversely but strongly concave dorsoventrally; thus, its dorsal and ventral borders project anteriorly. The

articular surface of the posterior centrum is mainly flat and slightly sub-ovate horizontally, bearing a small central concavity (notochordal pit). The three vertebral centra are fused. Ventrally, the centra bear two paramedian, longitudinal, rounded ridges surrounding a median longitudinal shallow groove, as is present in several nodosaurids (e.g. *Edmontonia*, *Hungarosaurus*, *Niobrariasaurus*, *Nodosaurus*, *Peloroplites*, *Polacanthus*, *Sauropelta* and *Struthiosaurus*; Lull 1921; Gilmore 1930; Pereda-Suberbiola 1994; Carpenter *et al.* 1995; Garcia & Pereda-Suberbiola 2003; Ósi 2005; Carpenter *et al.* 2008; Raven *et al.* 2020) but absent in parankylosaurians (e.g. *Stegouros*, Soto-Acuña *et al.* 2021; *Antarctopelta*, FR, pers. obs.). Transverse processes are low dorsoventrally and sub-rectangular in cross-section, extending from the anterior to the posterior edges of the vertebral centra. A dorsoventrally low section of the transverse processes (relative to more anterior sacral ribs) is also present in

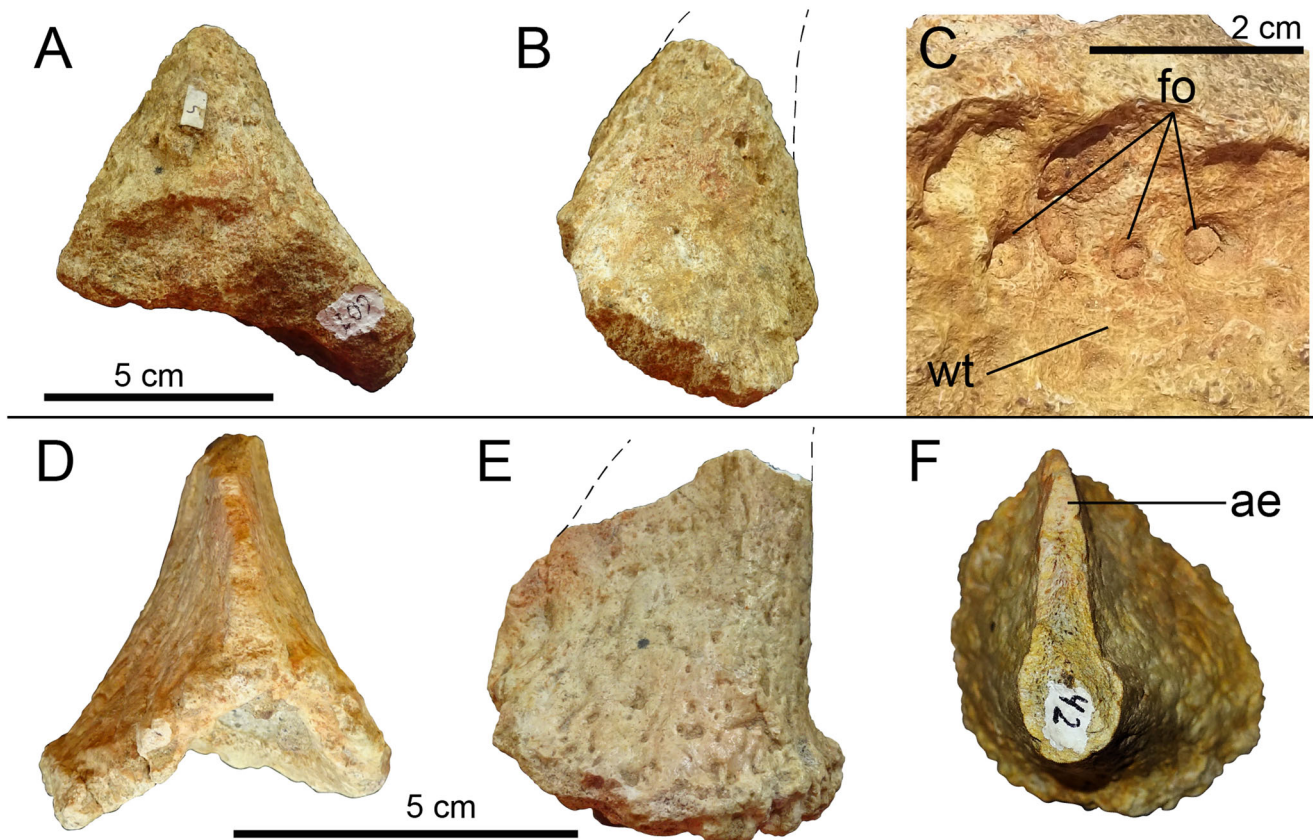


Figure 9. Cervicopectoral osteoderms. A–C, large osteoderm (?presacral spine) MPCA-SM-715 in (A) anterior and (B) left lateral views, and (C) detail of the base texture (see the woven texture and the large foramina); D–F, transitional osteoderm MPCA-SM-42a in (D) anterior, (E) right lateral and (F) dorsal views. Dashed lines are speculative and represent the absent apexes of both elements. **Abbreviations:** ae, anterior compressed edge; fo, foramina; wt, woven texture.

the last sacral and caudosacral vertebrae of other ankylosaurs (e.g. the Mongolian ankylosaurine specimen MPC 100/1305, *Gargoyleosaurus*, *Panoplosaurus*, *Polacanthus*; Sternberg 1921; Carpenter *et al.* 2011; Arbour & Currie 2013b; Carpenter *et al.* 2013; Burns 2015; Raven *et al.* 2020; and in the third sacral vertebra of *Antarctopelta*, FR, pers. obs., *contra* Salgado & Gasparini 2006). These are fully fused to each respective vertebral centrum. The base of the neural canal is narrow transversely, elongated and hourglass-shaped in dorsal view, as in dorsal and caudal vertebrae. The neural canal is not strongly enlarged. Based on the shape and size of the centra and transverse processes, comparisons with other ankylosaurs allow us to recognize in this piece the last sacral and two caudosacral vertebrae. Two caudosacral vertebrae are common among euankylosaurs, although some ankylosaurids may have three (see Pereda-Suberbiola 1994; Carpenter *et al.* 2008; Arbour & Currie 2013a). Caudosacrals are absent in parankylosaurs (Soto-Acuña *et al.* 2021).

MPCA-SM-704 is composed of two very low dorso-ventrally and sub-ovate fused vertebral centra. It is

smaller than MPCA-SM-703 and the sutures between the centra are both visible and partially fused (a groove is present between them). In addition, although partially eroded, the articular surfaces with the neural arches do not seem broken but disarticulated. This may suggest that this piece belongs to a non-adult individual, unlike that of MPCA-SM-703.

Caudal vertebrae. The material includes five anterior caudal vertebrae, one anterior to middle centrum, and one mid-caudal centrum. The anterior caudal vertebrae (MPCA-SM-71, 72, 705, 706 and 707; Fig. 6A–E) have short centra with gently concave to flat articular surfaces (the posterior is always slightly more concave; MPCA-SM-72 also bears notochordal pits). Although the articular surfaces are sub-parallel, the anterior articular surfaces of the centra are slightly displaced dorsally with respect to the posterior, so the vertebrae incline anteriorly when standing on a horizontal surface, as occurs in other ankylosaurs (e.g. *Edmontonia*, *Mymoorapelta*, *Niobrarasaurus* and *Texasetes*; Mehl 1936; Kirkland & Carpenter 1994; Carpenter *et al.* 1995; Coombs 1995a).

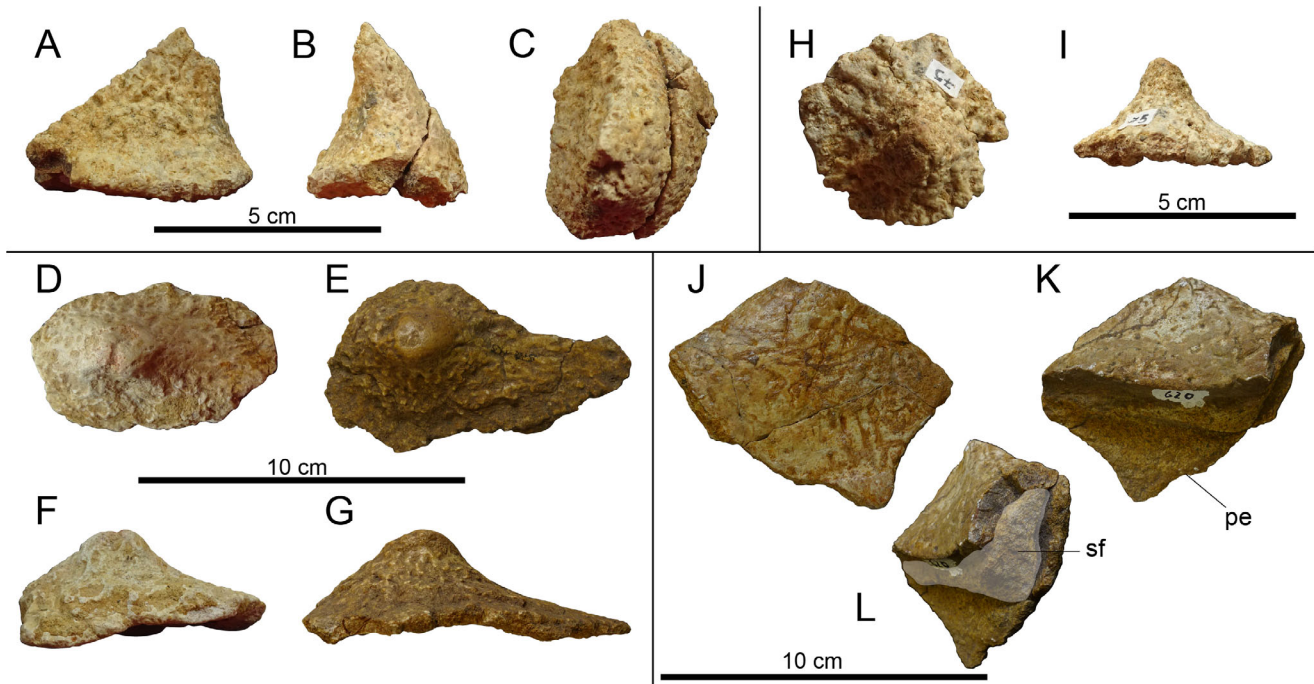


Figure 10. Postpectoral osteoderms. **A–C**, thoracic osteoderm MPCA-SM-41a in **(A)** left lateral, **(B)** posterior and **(C)** dorsal views; **D–G**, thoracic to sacral osteoderms **(D, F)** MPCA-SM-41b and **(E, G)** MPCA-SM-721 in **(D, E)** dorsal and **(F, G)** right lateral views; **H–I**, caudal osteoderm MPCA-SM-75 in **(H)** dorsal and **(I)** right lateral views; **J–L**, caudal plate MPCA-SM-720 in **(J)** dorsal, **(K)** ventral and **(L)** posteroventral views. **Abbreviations:** **pe**, projected basal edge; **sf**, sedimentary filling.

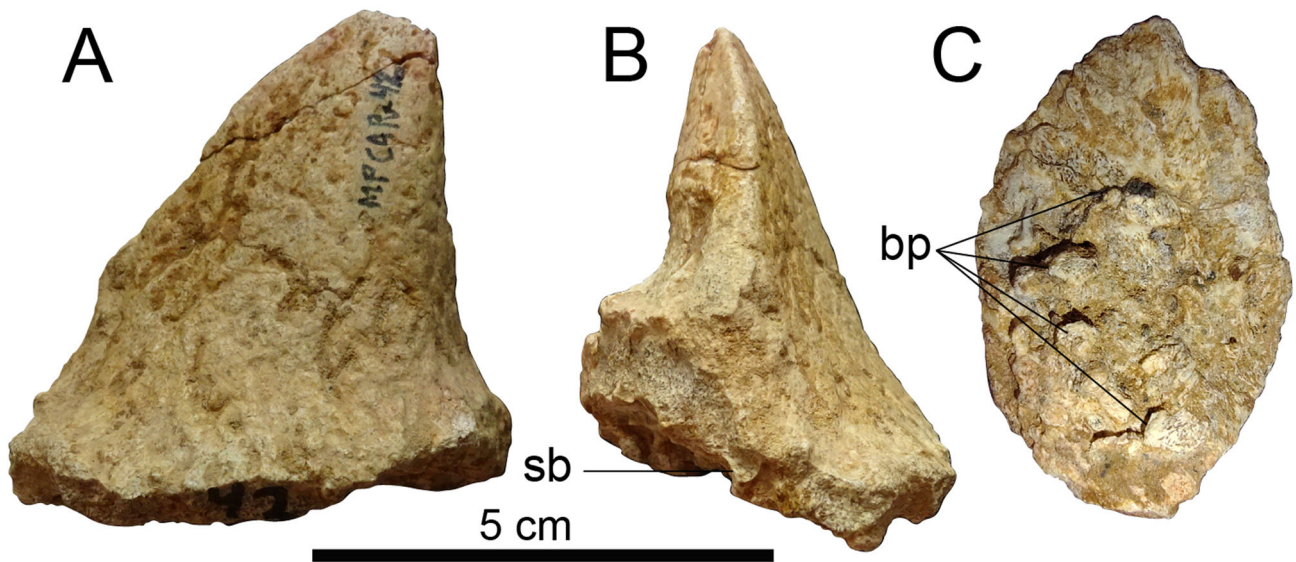


Figure 11. Indeterminate osteoderms. **A–C**, MPCA-SM-42b in **(A)** left lateral, **(B)** anterior and **(C)** ventral views. **Abbreviations:** **bp**, basal projections; **sb**, stepped base.

The articular surfaces of the centra are rounded in MPCA-SM-71, and slightly wider transversely than dorsoventrally high (mainly the posterior one) in MPCA-SM-72, 706 and 707. Ventrally, the centrum of

MPCA-SM-71 bears a median shallow groove surrounded by rounded paramedian ridges. Posteriorly, these ridges develop into the articular facets for haemal arches (chevrons). Ventral surfaces of the centra in

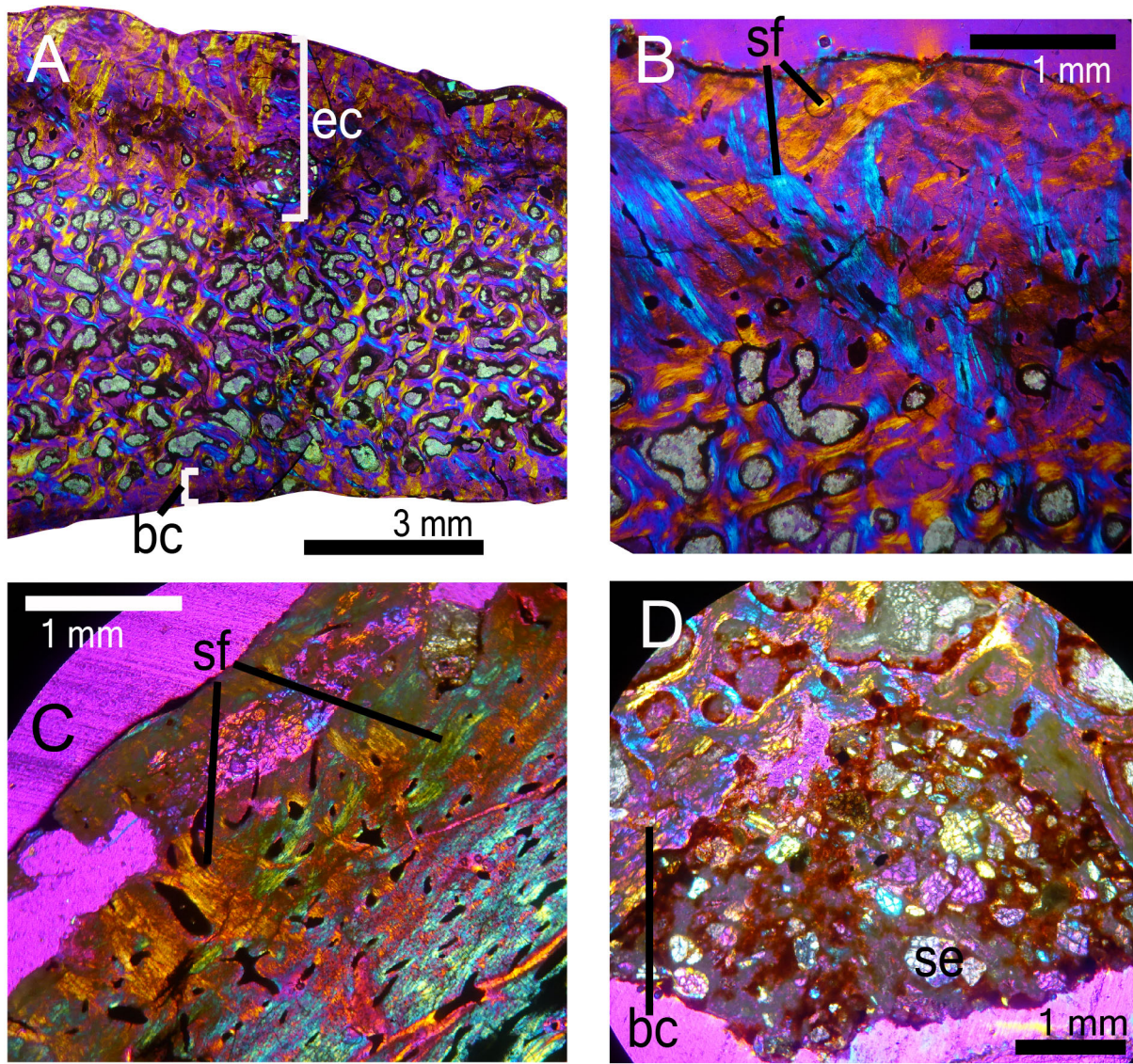


Figure 12. Osteoderm histology (under polarized light plus lambda filter). **A**, thin section of a postpectoral osteoderm showing the general microstructure of the bone (stacking of several images); **B**, detail of the external cortex of a postpectoral osteoderm showing the Interwoven Structural Fiber Bundles (ISFB); **C**, detail of the external cortex of a solid-based osteoderm (?presacral spine) showing the ISFB (large spaces in the external-most cortex are broken bone); **D**, detail of the basal cortex of a deep-based osteoderm (?caudal plate) with sediment filling. **Abbreviations:** bc, basal cortex; ec, external cortex; se, sediment filling; sf, structural fibres.

MPCA-SM-72 and 706 are transversely rounded and the chevron facets are smaller than those in the other vertebrae. However, MPCA-SM-707 bears a longitudinal ridge ventrally. Laterally projected bar-like transverse processes are positioned at mid-height on the lateral surfaces of the centra in the anterior caudals, as in some nodosaurids (e.g. *Niobrariasaurus*, *Polacanthus*, *Sauropelta*; Coombs 1971; Carpenter *et al.* 1995; Blows 2015) and probably *Antarctopelta* (Salgado & Gasparini 2006), and in contrast with the higher placement of transverse processes in most ankylosaurs (e.g. *Akainacephalus*,

Euoplocephalus, *Hungarosaurus*, *Peloroplites*, *Stegouros*; Ósi 2005; Carpenter *et al.* 2008; Arbour & Currie 2013; Wiersma & Irmis 2018; Soto-Acuña *et al.* 2021). The neural arch (preserved in MPCA-SM-71 and 707) is slightly anteriorly inclined and bears slender pedicels. The neural canal is sub-triangular, high and narrow. The neural spine is short, posteriorly directed, gently expanded transversely and rounded distally, similar to that of the anterior caudals of *Gastonia* (Kinneer *et al.* 2016), *Edmontonia* (Burns 2015) and *Ankylosaurus* (Carpenter 2004). Zygapophyses are not preserved.

MPCA-Pv-73 has a centrum that is higher dorsoventrally than long anteroposteriorly and wider transversely than dorsoventrally high, and slightly longer anteroposteriorly than the anterior caudals. The articular surfaces are sub-ovate and not decoupled, as they are in the anterior caudals. The anterior surface is flat and the posterior surface is slightly concave. Ventrally, the surface is flatter than in the anterior caudals and the facets for chevrons are broken. Transverse processes share the same morphology and robustness as those of the anterior caudals. Relative centrum dimensions and articular surface orientations suggest that this centrum is placed between the anterior and middle caudals.

The mid-caudal vertebra MPCA-SM-708 (Fig. 6F–I) is a newly identified element. It has a dorsoventrally compressed centrum slightly wider transversely than long anteroposteriorly, resembling those of *Europelta* (Kirkland *et al.* 2013) and *Gargoyleosaurus* (Kilbourne & Carpenter 2005). The articular surfaces seem oval, although their broken edges preclude an accurate contour identification. The articular surfaces are subtly anteriorly inclined, although less than in the anterior caudals. Ventrally, two subtle paramedian low rounded ridges project anteriorly from the articular facets for the chevrons. The surface between these ridges is flat to gently concave and bears several foramina. Well-developed transverse processes are directed slightly posterolaterally, and extend distally more than half the centrum width. Although the transverse processes are highly eroded, the section in lateral view seems more dorsoventrally compressed than that seen in the anterior caudals. The bases of the transverse processes are large and extend almost the entire length of the centrum. Large transverse processes persisting beyond the middle of the caudal series are also present in *Europelta* (Kirkland *et al.* 2013), *Gargoyleosaurus* (Kilbourne & Carpenter 2005), NHMUK PV OR3789 (*Hylaeosaurus oweni*; Pereda-Suberbiola 1993a; Raven *et al.* 2020), *Nodosaurus* (Lull 1921), *Polacanthus* (Blows 2015; Raven *et al.* 2020) and parankylosaurs (Salgado & Gasparini 2006; Soto-Acuña *et al.* 2021). Other nodosaurids bear only small button-like transverse processes, like those in *Hungarosaurus* (Ösi 2005; Ösi *et al.* 2019) and *Niobrariasaurus* (Mehl 1936; Carpenter *et al.* 1995; see also Everhart 2014), or lateral ridges, as occurs in *Sauropelta* (Ostrom 1970) and *Struthiosaurus* (Pereda-Suberbiola & Galton 2001). In ankylosaurids, transverse processes are absent in the handle of the distal half of the tail (or present only in the first handle vertebra; see Coombs 1995b; Arbour 2009; Carpenter *et al.* 2011; Arbour & Currie 2016). The neural arch is completely eroded.

Appendicular skeleton

The appendicular elements include a complete right femur (MPCA-SM-1) and the distal end of a left femur (MPCA-SM-709). The complete femur is redescribed after Salgado & Coria (1996), Coria & Salgado (2001) and Arbour & Currie (2016).

Femora. MPCA-SM-1 (Fig. 7) is a complete right femur. It bears a straight shaft with strongly expanded ends as is common in euankylosaurs (Coombs 1971), and more expanded than in the parankylosaur *Stegouros* (Soto-Acuña *et al.* 2021). The femoral head is well developed and hemispherical, and it is separated from the shaft by a strong neck and medially displaced. This condition is common in nodosaurids (e.g. *Europelta*, *Hungarosaurus*, *Niobrariasaurus*, *Nodosaurus*, *Polacanthus*, *Sauropelta*, *Struthiosaurus*; Lull 1921; Ostrom 1970; Carpenter *et al.* 1995; Pereda-Suberbiola & Galton 2001; Ösi 2005; Kirkland *et al.* 2013; Raven *et al.* 2020), contrasting with the less developed neck and sub-quadrangular femoral head of the parankylosaur *Stegouros* (Soto-Acuña *et al.* 2021) and the neckless, rounded proximal femoral head of ankylosaurids (e.g. *Pinacosaurus*, *Euoplocephalus*; Currie *et al.* 2011; Arbour & Currie 2013a). The femoral head projects farther proximally than the lateral trochanteric region, as occurs in *Dongyangopelta*, *Edmontonia*, *Hoplitosaurus* and *Polacanthus* (Chen *et al.* 2013; Burns 2015; Arbour & Currie 2016; Raven *et al.* 2020). The greater trochanter and the crista trochanteris (*sensu* Carpenter & Kirkland 1998) are pronounced. The greater and anterior trochanters are fully fused with no visible groove between. Both trochanters are separated from the femoral head by a pronounced trochanteric fossa. Both the pronounced trochanteric fossa and greater trochanter are strongly similar to those of *Sauropelta* (Ostrom 1970) and *Niobrariasaurus* (Carpenter *et al.* 1995), unlike the more continuous proximal edge of the femur of *Stegouros* (Soto-Acuña *et al.* 2021) and ankylosaurids (e.g. Lü *et al.* 2007; Currie *et al.* 2011; Arbour & Currie 2013a). The proximally placed greater trochanter in *Patagopelta* and most nodosaurids (Ostrom 1970; Coombs 1971; Carpenter *et al.* 1995; Carpenter & Kirkland 1998; Pereda-Suberbiola & Galton 2001; Kirkland *et al.* 2013) strongly contrasts with the laterally placed trochanter in *Edmontonia longiceps* (Burns 2015).

The anterior surface of the femur is crossed by three strong rugose ridges. The lateral-most ridge (linea intermuscularis *sensu* Arbour & Currie 2016) is associated with the anterior trochanter and extends laterodistally to one-third of the femoral length. The second and central ridge (linea muscularis caudalis *sensu* Arbour & Currie 2016) extends from the proximolateral corner anterior to the trochanters to the proximal region of the medial condyle (as stated by Coria & Salgado 2001; *contra* Arbour

& Currie 2016, who said that it extends towards the lateral condyle). Its proximal half is rugose and its distal half is smooth. Crossing the base of the neck of the femoral head, the third ridge (*linea muscularis cranealis sensu* Arbour & Currie 2016) extends mediolaterally to one-third of the femoral length, where it contacts the fourth trochanter. Arbour & Currie (2016) mentioned that these muscular ridges are faintly visible in *Nodosaurus* and *Hoplitosaurus*. *Niobrariasaurus* (Carpenter *et al.* 1995), *Peloroplites* (Carpenter *et al.* 2008), and *Texasetes* (Carpenter & Kirkland 1998) also bear subtle muscular ridges in the anterior surface of the femur. However, the femoral ridges in all these taxa are not as strong as those in *Patagopelta*.

The fourth trochanter is a low rugose ridge placed proximally on the medial side of the shaft, as usually occurs in nodosaurids (Lull 1921; Ostrom 1970; Carpenter *et al.* 1995; Pereda-Suberbiola & Galton 2001; Ósi 2005; Raven *et al.* 2020) and contrasting with the mid- to distally placed fourth trochanter in ankylosaurids (Arbour & Currie 2013a). It extends from the base of the neck to the proximal third of the femoral length. Another ridge is present on the lateral surface of the distal half of the femur. This ridge is proximodistally orientated, from the mid-length of the femoral shaft to the lateral surface of the lateral condyle. It seems that this ridge rises from the *linea muscularis caudalis*, although the broken bone in this region precludes identification of its correct location. Muscular ridges in the anterior surface of the femur were described in *Nodosaurus*, *Hoplitosaurus* (Arbour & Currie 2016), *Niobrariasaurus* (Carpenter *et al.* 1995), *Peloroplites* (Carpenter *et al.* 2008) and *Texasetes* (Carpenter & Kirkland 1998). However, those of *Patagopelta* are much more strongly developed.

The distal condyles are well developed, with the medial condyle larger than the lateral one in distal and posterior views. The lateral condyle bears a large lateral fossa, and in posterior view, there is a well-defined fibular notch. In this regard, the articular surface of the lateral condyle is posteriorly developed as a small prominence (tibiofibular crest; the condylid of Salgado & Coria 1996). A similar structure of the lateral condyle lying along a lateral fossa was described in *Hoplitosaurus* (Gilmore 1914), *Nodosaurus* (Lull 1921; Fig. 6B, C, n, notch) and *Texasetes* (Coombs 1995a), and is also seen in several other nodosaurids, such as *Edmontonia* (Burns 2015), *Gargoyleosaurus* (Kilbourne & Carpenter 2005), *Niobrariasaurus* (Carpenter *et al.* 1995), *Polacanthus* (Pereda-Suberbiola 1991), *Sauropelta* (Coombs 1971) and *Silvisaurus* (Eaton 1960). *Peloroplites* (Carpenter *et al.* 2008), *Stegouros* (Soto-Acuña *et al.* 2021), and most Ankylosauridae (Carpenter 2004; Lü

et al. 2007; Carpenter *et al.* 2008; Carpenter *et al.* 2011; Currie *et al.* 2011; Arbour & Currie 2013a) seem to lack such a compressed lateral condyle. The intercondylar fossa is well developed in the anterior and posterior surfaces, although it is very faint distally. The lateral epicondyle (lateral projection of the distal end of the femur) is a subtle crest. The medial condyle bears a slight central depression on its medial surface. Proximal to the condyles, most of the posterior surface of the femur is flatter than the transversely convex anterior surface. Distal to the femoral head, the proximal half of the posterior surface has a strongly rugose, interwoven texture (coarser than those present in the basal surface of osteoderms; see ‘Dermal armour’ description below). A ‘textile’ texture in the proximal, posterior surface of the femur was also described for *Nodosaurus textilis* (Marsh 1889; Lull 1921), although it has never been clearly figured. Carpenter & Kirkland (1988) revised the diagnosis of the species and did not mention such a feature. Moreover, the available photographic material of the holotype of *Nodosaurus textilis* (YPM VP 001815.A) from the Yale Peabody Museum webpage does not show a similar textural pattern to that in *Patagopelta* (striae in the former seem to be more proximo-distally orientated, not interwoven as they are in the latter).

MPCA-SM-709 is the distal third of a left femur. This new element has the same dimensions as the right femur, and is quite similar, possibly belonging to the same individual. However, it is mostly eroded, in contrast to the excellent preservation of the complete femur. It also bears large shallow bores (see Britt *et al.* 2008), mainly in the anterior intercondylar region.

Dermal armour

The dermal elements include cervical and post-cervical armour. Cervical and post-cervical osteoderms are re-described after Coria & Salgado (2001) and Arbour & Currie (2016). The new cervical (MPCA-SM-700b, 711, 712, 713 and 714) and post-cervical (MPCA-SM-715, 716, 717, 718, 719, 720, 721, 722, 723, 724 and 725) osteoderms contribute significant taxonomic information. Although not described, MPCA-SM-712 was figured by Arbour & Currie (2016, fig. 2E).

Cervical armour. There are six elements of cervical armour: MPCA-SM-700b, 78, 711, 712, 713, 714 (Fig. 8A–G). All osteoderms are solid-based and larger pieces show a gentle curvature across the basal length. Osteoderms are strongly fused across the thick basal edges as they are in several nodosaurids (e.g. *Edmontonia*, *Gargoyleosaurus*, *Silvisaurus* and *Struthiosaurus*; Gilmore 1930; Carpenter & Kirkland 1998; Pereda-Suberbiola &

Galton 2001; Kilbourne & Carpenter 2005; see also Ford 2000), although sutures are only visible on the external surfaces. Striated boundaries delimit the base of the dorsal prominences (ridge or spine) of each osteoderm, and therefore flank the sutures between these. The distinct underlying bony band joining the osteoderms as in some ankylosaurids (see Ford 2000; Arbour & Currie 2013) is absent. Ventral to each osteoderm there is a subtle concavity. The ventral surface is mainly smooth and shows some large foramina (smaller and increasing in number towards the basal edges). Dorsally, the texture is rugose and bears a large number of pits and furrows. Although most ankylosaurs bear two to three half rings of cervical osteoderms (Carpenter 1990; Carpenter & Kirkland 1998; Ford 2000; Carpenter *et al.* 2011, 2013; Arbour & Currie 2013; Penkalski & Blows 2013; Ősi *et al.* 2019), none of the preserved elements can be assigned with confidence to a particular half ring.

The elements MPCA-SM-700a and 700b, an osteoderm and a cervical neural arch, respectively, were found associated. The shape and position of the osteoderm suggest a medial osteoderm. It is low-crested and strongly asymmetrical. The dorsal prominence seems diagonally displaced, so the element may be fused at the midline with the other half ring, as occurs in *Borealopelta* (Brown 2017; Brown *et al.* 2017), *Edmontonia rugosidens* (Burns 2015) and *Sauropelta* (Carpenter 1984), and contrasting with both the central peak/dome or anteroposteriorly directed keel in the medial osteoderm of other ankylosaurs (e.g. *Euoplocephalus*, *Gargoyleosaurus*, *Kunbarrasaurus*, *Saichania*, *Stegopelta*; Maryńska 1977; Ford 2000; Molnar 2001; Arbour & Currie 2013a; Carpenter *et al.* 2013). Although very broken, the osteoderm bears an extensive solid base. In addition to the association with a cervical vertebra, the low crest supports a medial cervical osteoderm, as usually occurs in nodosaurids (e.g. *Borealopelta*, *Edmontonia*, *Gargoyleosaurus*, *Sauropelta*, *Silvisaurus*; Carpenter & Kirkland 1998; Ford 2000; Carpenter *et al.* 2013; Brown *et al.* 2017). Another low, blunt dome-shaped and probably cervical osteoderm is MPCA-SM-711. It bears a subtle anterior edge from the base to the apex. It is slightly asymmetrical in lateral view, and mainly symmetrical anteriorly. The base is thick under the dorsal domed prominence, but its edges are fully eroded. Most of the external cortex on its right side is eroded. Visible internal vascular canals are mostly apically orientated. Several other canals are circularly or circumferentially orientated, and few transversely sectioned canals suggest a radial orientation. Based on the articulated *in situ* armour of *Borealopelta* (Brown *et al.* 2017), we identify MPCA-SM-711 as the medial osteoderm of the first cervical half

ring, and MPCA-SM-700b as the medial osteoderm of the second or third left cervical half ring (Fig. 8H, I).

MPCA-SM-712 is composed of both the distal osteoderm and the base of the lateral osteoderm. The distal osteoderm is sub-conical and low, and lacks its apex. It bears a marked anterior edge from the base towards the apex, and its dorsal prominence is rounded posteriorly. On the external surface, the suture between the osteoderms is visible and formed by a high, rugose central crest bordered by the above-mentioned striated boundaries. The preserved posterior basal edge of the whole fused piece is rugose and ventrally concave. It bears a deep furrow placed proximodistally and across the edge. The dorsal border of the furrow is subtly more extended, roofing the internal one. This piece probably belongs to a right anterior cervical half ring.

MPCA-SM-78 is the largest cervical piece in the studied material, and comprises the distal and the lateral osteoderms. Both osteoderms are larger than the corresponding elements in MPCA-SM-712. The osteoderms are strongly fused across their basal edges forming a thick band, thicker than in other nodosaurids (e.g. *Sauropelta*, *Edmontonia*; Carpenter & Kirkland 1998; Burns 2015) and resembling the thicker rings with basal osseous band of ankylosaurids (e.g. *Euoplocephalus*, *Shamosaurus*; Arbour & Currie 2013a, 2016). Sutured contacts are only visible in the dorsal surface and lack the marked crest visible in MPCA-SM-712. The distal osteoderm is sub-conical and its anterior half is laterally compressed, giving an acute anterior edge, from the base towards the apex. Posteriorly, it is transversely rounded. High spine-like distal osteoderms are also present in the cervical half rings of *Borealopelta*, *Edmontonia*, *Panoplosaurus*, *Sauropelta* and *Silvisaurus*, although these are much larger than those of *Patagopelta* (Carpenter 1990; Carpenter & Kirkland 1998; Brown *et al.* 2017). The lateral osteoderm bears a large, thick ridge with a central inflection that generates a faintly concave lateral side and a subtly convex medial one (somewhat 'D'-shaped in dorsal view). The anterior edge of the crest rises gradually and the thicker posterior edge descends more abruptly. The expanded basal edges of the whole piece are bordered by a line of small foramina. In some parts, these foramina are united by a shallow continuous groove, whereas the external border of the groove is subtly more expanded than the internal one. These grooves resemble the above described for MPCA-SM-712, although they are less pronounced. The lateral cervical osteoderm of *Patagopelta* roughly resembles those of some ankylosaurids (although lacking the central inflection) in being keeled or crested osteoderms (see CMN 0210, the holotype specimen of *Euoplocephalus*; Arbour & Currie 2013a). However, lateral osteoderms in

nodosaurids with three osteoderms per half ring are quite different. While some taxa bear high spine-like osteoderms (e.g. *Borealopelta*, *Silvisaurus*, *Sauropelta*; Carpenter & Kirkland 1998; Brown *et al.* 2017), others bear flat-keeled osteoderms with no inflection (e.g. *Edmontonia* and *Panoplosaurus*; Carpenter 1990). Anterior to both osteoderms the texture is roughened in *Patagopelta*. Based on the *in situ* armour of *Borealopelta* (Brown 2017; Brown *et al.* 2017), MPCA-SM-78 belongs to the second or third cervical half ring (Fig. 8H, I). The remaining two isolated osteoderms, MPCA-SM-713 and 714, are broken through their bases, and strongly resemble the lateral osteoderm and the distal spine of MPCA-SM-78, respectively.

Nodosaurids are characterized by the presence of low medial osteoderms along with high spine-like distal osteoderms on their cervical half rings. *Patagopelta* bears low domed to crested medial osteoderms, crested lateral osteoderms, and tall somewhat compressed spine-like distal osteoderms (Fig. 8H, I). This morphology differs from the arrangement in ‘mid’-Cretaceous North American nodosaurids, such as *Sauropelta*, *Silvisaurus* or *Borealopelta*, as these taxa bear low medial osteoderms but high lateral and distal spine-like osteoderms (Carpenter & Kirkland 1998; Brown *et al.* 2017). It also contrasts with the low-keeled cervical osteoderms observed in *Panoplosaurus* and *Edmontonia*, the latter also showing high distal spines (Carpenter 1990). Moreover, the cervical rings of *Patagopelta* seem to be an intermediate stage between these two groups. Therefore, the nature of the lateral osteoderm of the cervical half rings gives to *Patagopelta* a unique arrangement of the cervical armour among nodosaurids with three osteoderms per half ring.

Cervicopectoral armour. MPCA-SM-715 (Fig. 9A–C) is the larger osteoderm. This is a massive conical spine that lacks its apex and part of its basal edges. Anteriorly, the osteoderm bears a poorly developed edge from the base towards the apex (therefore the broken apical section is sub-triangular). Ventrally, the osteoderm is strongly concave, although the spine core is solid. In spite of the incompleteness of the basal edges, the base seems to be wider transversely than long anteroposteriorly (in contrast to the longer anteroposteriorly than wide transversely spines of ‘polacanthids’; Blows 2015). Externally, the texture is highly rugose and it is ornamented with foramina and apico-basally orientated furrows. Ventrally, it bears an interwoven texture bordering large foramina (larger than those of the external surface) which decreases in size towards the edges of the base. Several foramina are very large in diameter, probably altered by bioerosion (Fig. 9C). This element resembles the presacral and pectoral spines of

Europelta, *Gastonia* and *Polacanthus* (Gasulla *et al.* 2011; Kirkland *et al.* 2013, fig. 26A–D; Blows 2015, figs 7.21, 8.21; Raven *et al.* 2020). These spines bear a massive base and a projecting spine distally, after a clear inflection in the basal borders. A probable presacral spine was thin sectioned to study its histology (see below).

MPCA-SM-42a (Fig. 9D–F) is a large subconical spine, strongly compressed transversely in its anterior half. In lateral view, the anterior edge is convex and the posterior is straight. The base is expanded and bears a convex profile. The apex is absent, and the visible transverse section shows the anterior plate-like compression (anterior edge) and the posterior rounded expansion (spine body). In anterior view, it is triangular and mostly symmetrical, although the right border of the base is slightly more expanded than the left. The anterior edge of the base rises and is strongly concave. Ventrally, the contour of the base is sub-ovate. The basal surface is strongly concave. The edges of the base are strongly rugose with large foramina on the internal side. The basal surface is smooth with some small pits, and the rock matrix obscures it under the spine core. The external texture is ornamented with pits and furrows (mostly apico-basally orientated). As a whole, this element resembles the cervical to pectoral or transitional osteoderms of *Borealopelta* (Brown 2017; Brown *et al.* 2017) and *Sauropelta* (Carpenter & Kirkland 1998), and is similar to a spine-like osteoderm described for ‘*Rhodanosaurus*’ (Nopcsa 1929, taf. V, fig. 1, 2; Pereda-Suberbiola 1993b, fig. 3C, D).

Postpectoral armour. There are at least three distinct morphologies of postpectoral osteoderms and ossicles from the dorsal part of the armour (either thoracic or caudal), plus a caudal plate. These elements resemble those usually present in nodosaurids (e.g. *Edmontonia*, *Europelta*, *Polacanthus* and *Sauropelta*; Ford 2000; Arbour *et al.* 2011; Burns & Currie 2014; Burns 2015; Raven *et al.* 2020). Postcervical osteoderms with low keels running anteroposteriorly, like those of many ankylosaurs (e.g. *Ankylosaurus*, *Euoplocephalus*, *Edmontonia*, *Hungarosaurus*, *Kunbarrasaurus*, *Stegouros* and *Struthiosaurus*; Ford 2000; Pereda-Suberbiola & Galton 2001; Carpenter 2004; Ösi 2005; Burns 2015; Penkalski 2018; Soto-Acuña *et al.* 2021), are currently unknown in *Patagopelta*. In all pieces, the external texture is strongly rugose and ornamented with pits and furrows. Ventrally, these are smooth with an interwoven texture and some foramina, the larger ones near the edges. One postpectoral osteoderm was sectioned to study its histology (see below).

The first type is composed of one sub-conical osteoderm (MPCA-Pv-41a, Fig. 10A–C). This piece bears a

clear anterior edge from the base to the apex. The apex is both posteriorly displaced and curved towards the right side. The outline of the base is sub-quadrangular. Ventrally, the base is strongly concave, and both the anterior and posterior borders are thicker than the lateral and medial borders. The external surface is rugose and bears a large number of pits or small foramina. This osteoderm is quite similar to the caudal osteoderms in the ankylosaurine specimen MPC 100/1305, which is placed dorsally in the proximal to mid-region of the tail (Carpenter *et al.* 2011).

The second morphology is composed of five domed osteoderms with extended thin basal edges (MPCA-SM-41b, 43, 721, 724 and 725, Fig. 10D–G), resembling that of MACN-PV-RN-1149 (Murray *et al.* 2019, fig. 1A). The blunt apex is low (except in MPCA-SM-724) and posteriorly displaced, with a concave anterior edge and a convex posterior one. Although the basal edges are somewhat undulating, the osteoderm is sub-ovate in dorsal view. Ventrally, the surface is concave. Dorsally, the texture is more rugose and bears numerous pits or small foramina, and furrows. MPCA-SM-43 differs in being laterally compressed, with its thin basal edges ventrally extended. It preserves its left edge, rounded in lateral view. Ventrally, it is strongly concave. Contrasting with the other osteoderms of this type, textural striae are interwoven towards the centre and longitudinal towards the edges. The strong ventral extension of the basal edges makes a taller and ventrally deep osteoderm, suggesting a more lateral placement in the body than others of this type (Ford 2000). In overall shape these osteoderms resemble the low osteoderms of *Edmontonia* (Gilmore 1930), *Sauropelta* (Ostrom 1970; pl. 27, B–F), the type F osteoderms of *Europelta* (Kirkland *et al.* 2013) and the larger ossicles of *Polacanthus* (Blows 2015).

The third morphology is composed of nine pointed osteoderms with variable height and variable extension of the basal edges (MPCA-Pv-74, 75, 76, 716, 717, 718, 719, 722 and 723; Fig. 10H, I). These pieces bear a conical dorsal eminence with a subtly marked anterior edge from the base to the apex. The apex is posteriorly displaced in variable positions, so the anterior edge of the base is variably extended. The basal edges are expanded with a sub-ovate (rarely sub-trapezoidal) outline in dorsal view. Ventrally, the larger pieces are strongly concave in the centre, with some large central foramina (altered in some osteoderms either by a pathology or bioerosion, as bores; see Britt *et al.* 2008; Matthias *et al.* 2016), although the apex seems solid. The surface between the concavity and the radial basal edges is sub-horizontal, usually with a subtle interwoven texture and foramina. These pieces are very similar to

the osteoderms sometimes associated with articulated caudal vertebrae in ankylosaurs (Carpenter *et al.* 2011; Raven *et al.* 2020). In addition, these osteoderms are quite similar to some described by Murray *et al.* (2019, fig. 2B, C).

Caudal plate. MPCA-SM-720 (Fig. 10J–L) is a large, sub-rhomboid and strongly laterally compressed caudal plate with a blunt apex. Its distal third is more compressed than its base, and is slightly curved anteroposteriorly. The proximal two-thirds are mainly composed of the edges of the base, strongly proximally projected and therefore giving a deeply concave base. In lateral view, it is symmetrical distally and asymmetrical proximally, due to the differential extension of the basal edges. The external surface is ornamented with large furrows and foramina. The internal (basal) surface is eroded and the ventral concavity is partially filled with matrix, both losing and obscuring textural details. A probable lateral caudal osteoderm was thin sectioned to study its histology (see below). Proximal caudal plates with low to rounded apices, like that of *Patagopelta* (Fig. 10J–L), are also known in the parankylosaur *Kunbarrasaurus* (Molnar 2001); several nodosaurids such as *Europelta* (Kirkland *et al.* 2013), *Struthiosaurus* (Pereda-Suberbiola & Galton 2001) and *Sauropelta* (also with one plate being transitional between rounded and triangular, bearing a posterior small spike; Ostrom 1970; Carpenter & Kirkland 1998); and the ankylosaurid *Aletopelta* (Ford & Kirkland 2001). This contrasts with the proximodistally elongated, triangular caudal plates of basal nodosaurids, such as *Gastonia* (Kinneer *et al.* 2016), *Polacanthus* (Blows 2015; Raven *et al.* 2020) and *Dongyangopelta* (Chen *et al.* 2013), and of ankylosaurids like MPC 100/1305 (*Saichania* for Carpenter *et al.* 2011; cf. *Pinacosaurus* for Arbour & Currie 2013b) or *Zuul* (Arbour & Evans 2017). These are also unlike the triangular and thicker mid- to distal caudal osteoderms of the parankylosaurs *Antarctopelta* and *Stegouros* (Soto-Acuña *et al.* 2021).

Although the osteoderms described by Murray *et al.* (2019) are referred to *Patagopelta* in this paper, the caudal osteoderm described by the authors differs from the caudal plate described here (FR pers. obs.). This could reflect a shape variation of lateral caudal osteoderms in South American nodosaurids, where the anterior osteoderms are plate-shaped and they become more conical posteriorly along the tail.

Indeterminate osteoderm. MPCA-Pv-42b (Fig. 11) is a low spine with a marked anterior edge from the base to the apex, and transversely rounded posteriorly. In lateral view, the anterior edge of the spine is slightly convex and the posterior edge is concave to straight, with the

apex being posteriorly directed. In anterior view, the expanded base is strongly asymmetrical, stepped between the two lateral edges. The left edge is thinner and more ventrally extended than the laterally orientated thicker right edge. Although broken, the basal outline is oval-shaped in ventral view. The osteoderm base is fully solid with several short bone projections in the ventral surface that are orientated in many directions (predominantly towards the right side of the piece). Ventrally, no foramina are visible. Dorsally, the texture is rugose with some pits and furrows, similar to all other osteoderms.

The identification of MPCA-Pv-42b is problematic. Although its shape resembles that of the distal cervical osteoderms, the strongly asymmetrical, solid and irregularly textured base of MPCA-Pv-42b is very different to that of the cervical pieces. In addition, cervical osteoderms have striated boundaries around the base of the dorsal eminence, which is absent in MPCA-Pv-42b. A spine with an asymmetrical base is also known in the crescentic osteoderm of *Hungarosaurus* (Ösi 2005; Ösi & Pereda-Suberbiola 2017). Although the tall cylindrical spine of *Hungarosaurus* differs from the low conical spine of *Patagopelta*, its lateral side is more ventrally displaced than the horizontal medial one, like the stepped base of MPCA-Pv-42b. In addition, the rare base of MPCA-Pv-42b may be related to the association with such a crescent-shaped structure. In any case, this complex fused osteoderm is possibly from the pelvic-sacral region (see Ösi & Pereda-Suberbiola 2017).

Osteoderm histology. Several osteoderms (including those of the cervical rings, the large pectoral spine and several postpectoral osteoderms) show broken surfaces in different orientations (transversal, longitudinal, oblique) that expose the microstructure. All broken surfaces bear similar patterns. The external bone cortex is strongly thicker than the internal cortex, and between them there is a thick layer of spongy to trabecular bone. The sectioning of the larger pectoral spine allows us to observe that in the spine, the external cortex is somewhat thicker towards the apex than in the edges of the base.

A sample of four sectioned osteoderms of three different kinds has been obtained. The first type includes two thin sections of low osteoderms with concave bases in transverse section, similar to the postpectoral osteoderms described above. The second type includes a thin section of a higher keeled osteoderm with a deep base (a possible caudal osteoderm). Finally, the third type of osteoderm is the largest in size and belongs to a large, solid and conical osteoderm with a concave base, similar to the presacral spines described above.

In all pieces, the microanatomy shows both external and basal cortices that enclose spongy bone (Fig. 12A). The external cortex is thicker than the basal cortex

(2.5 mm vs 1 mm in the smaller osteoderms, and 3–4 mm vs 0.5–1 mm in the larger pieces), as is known in nodosaurids, and contrasting with the thin, homogeneous basal and external cortices in ankylosaurid and ‘polacanthine’ osteoderms (Burns & Currie 2014, and references therein; Brum *et al.* 2021). The external cortex is composed of two distinct tissues, an external one that is non- to poorly vascularized, and an internal more vascularized layer with prevalent longitudinal vascular canals. The cortical tissue is composed of highly ordered interwoven structural fibre bundles (ISFB), as in the osteoderms of other nodosaurids and the parankylosaur *Antarctopelta* (Scheyer & Sander 2004; Burns & Currie 2014; Cerda *et al.* 2019). The fibres are orientated at 90° to each other and at angles of approximately 45° and 135° with respect to the external surface (Fig. 12A–C). Internal to the compact cortices, there is a thick cancellous core. In the postpectoral osteoderm, it is composed of an external more finely cancellous bone and a coarse cancellous bone internally (Fig. 12A). In larger osteoderms, the coarse cancellous core is thicker and reaches the thin basal cortex (that may locally be resorbed; in Fig. 12D, the base is almost as thin as the trabeculae). There is no fine cancellous bone between the coarse cancellous bone and the basal cortex in larger osteoderms. Except in the larger osteoderm, the finely cancellous cortex bears few secondary osteons. Haversian bone is not present in any sampled osteoderm.

Phylogenetic analysis

To perform the phylogenetic analysis, we used the morphological data matrix of Soto-Acuña *et al.* (2021; modified from previous works by Arbour & Currie 2016, Arbour *et al.* 2016 and Zheng *et al.* 2018). Considering the new materials and the current redescription, we recoded the operational taxonomic unit (OTU) of *Patagopelta cristata*. We also incorporated a new character, ‘ratio between coracoid and scapula lengths (coracoid length less than a half the scapula length = 0; more than half = 1)’, modified from the diagnosis of *Peloroplites cedrimontanus* (Carpenter *et al.* 2008), which was scored for all OTUs based on the literature. The final data set includes 65 OTUs and 190 characters. To edit the data matrix, we used the software Mesquite (version 3.2, Maddison & Maddison 2019). Detailed phylogenetic information is included in the [Supplemental material](#).

We ran a phylogenetic analysis in TNT version 1.5 (Goloboff & Catalano 2016). No characters were treated as additive, nor were any weighted. The analysis was carried out with a tree search using new technologies, running 10,000 random-addition sequences under

Ratchet, Tree Fusing, Sectorial Search and Drift algorithms (under default parameters), in a space for 2,000,000 trees. The obtained most parsimonious trees (MPTs) were swapped with the tree bisection reconnection (TBR) algorithm until they filled the tree memory. The command ‘pcrprune’ was used to remove unstable taxa from the strict consensus. Bootstrap support was calculated with 1000 pseudoreplicates. In addition, implied weighting was applied to test the stability of the clades when weighed against homoplasy using a wide range of values of the *k* parameter (*k* = 1–10, 15, 20, 25, 30, 40 and 50). Searches under implied weighting were carried out in the same way as under equal weights.

We recovered 64,260 MPTs with a score of 699. The consistency index was 0.325 and the retention index was 0.0593. The reduced strict consensus tree is shown in [Figure 13](#). The complete strict consensus tree and the majority rule (75%) consensus tree are included in [Supplemental material](#). The overall branch support is very low, as occurred in previous studies with this data set (Arbour *et al.* 2016; Zheng *et al.* 2018; Soto-Acuña *et al.* 2021), due to the high amount of missing data and homoplasy. Because of this, we performed implied weighting searches to test group stability (see below). In the strict consensus, *Patagopelta* was recovered as a Nodosaurinae (*sensu* Madzia *et al.* 2021) in a polytomy with *Ashislepelta*, *Borealopelta*, *Pawpawsaurus*, the Paw Paw scuteling and *Texasetes*. The ancestral node of Nodosaurinae is a polytomy with the clade that includes *Patagopelta*, *Niobrarasaurus*, *Nodosaurus*, *Silvisaurus*, *Sauropelta* and *Tatankacephalus*. In this way, *Patagopelta* is more closely related to the ‘mid’-Cretaceous nodosaurids of North America and the Late Cretaceous nodosaurids of Europe than to the derived Panoplosaurini of North America (*contra* Arbour *et al.* 2016; Zheng *et al.* 2018; Soto-Acuña *et al.* 2021).

Nodosaurinae is supported by the following synapomorphies: squamosal/postorbital horn base with broad triangular cross-section and overall shape pyramidal (ch. 46: 0→1; shared with *Europelta*, *Gargoyleosaurus*, *Gastonia*, *Hylaeosaurus* and many ankylosaurids), paroccipital processes directed caudolaterally (ch. 72: 1→0; shared with *Europelta*, *Animantarx*, *Gargoyleosaurus*, *Kunbarrasaurus*, *Stegouros*, and non-ankylosaurian thyreophorans), no mandibular caputegulum (ch. 86: 1→0; shared with *Hungarosaurus*, *Gargoyleosaurus*, *Cedarpelta* and few ankylosaurids), number of dentary teeth equal to or more than 25 (ch. 91: 0→1; shared with *Gargoyleosaurus* and *Ankylosaurus*), presence of longitudinal ridge at mid-height of centrum of mid and distal caudals (ch. 104: 0→1; shared with *Hungarosaurus* and *Struthiosaurus*), acromion process of scapula directed towards the scapular glenoid

(ch. 121: 0→1; shared with *Animantarx* and *Peloroplites*), radial condyle of humerus round and/or proximal end of radius circular in end view (ch. 140; shared with *Animantarx* and *Stegopelta*), angle between long axis of femoral head and long axis of shaft around 100–120° (ch. 144: 2→1; shared with *Cedarpelta* and *Peloroplites*), lateralmost osteoderms in thoracic region are solid, conical spikes (ch. 170: 2→3), and symmetrical tooth crowns (ch. 179: 0→1; shared with *Liaoningosaurus*, *Chuanqilong*, *Saichania*, *Euoplocephalus*, *Zuul* and *Dyoplosaurus*). The less inclusive polytomy that contains *Patagopelta* within Nodosaurinae is supported by the following synapomorphies: external nares hidden in dorsal view (ch. 16: 0→1; shared with ankylosaurids), 11 to 30 caputegulae in fronto-nasal and prefrontal region (ch. 21: 1→2; shared with *Gargoyleosaurus*, *Akainacephalus*, *Saichania*, *Tarchia* and *Tsagantegia*), anterior surface of the quadrate transversely concave (ch. 57: 1→0; shared with *Struthiosaurus austriacus*), coracoid glenoid half the size of scapular glenoid (ch. 116: 0→1; shared with *Animantarx* and *Hungarosaurus*), presence of an oblique ridge on the lateral femoral shaft, distal to the anterior trochanter (ch. 147: 0→1; shared with *Animantarx*, *Hoplitosaurus* and *Peloroplites*), and absence of furrows perpendicular to the basal edge of deeply excavated triangular osteoderms (ch. 169: 0→1; shared with *Europelta*, *Hungarosaurus*, *Akainacephalus*, *Euoplocephalus*, *Dyoplosaurus*, *Scolosaurus*, *Zuul* and parankylosaurs). The only autapomorphy recovered for *Patagopelta* is the presence of a poorly developed basal cortex of skeletally mature osteoderms (ch. 159: 1→2).

The whole topology is mostly similar to prior analyses (Soto-Acuña *et al.* 2021 and references therein), recovering the more inclusive clades Parankylosuria, Euankylosauria, Nodosauridae and Ankylosauridae. Also, the internal grouping of Ankylosauridae is the same as in Soto-Acuña *et al.* (2021), but the resolution within Nodosauridae is quite different. While we recover a better resolved base of Nodosauridae, the resolution of the less inclusive clades is poor. However, we recover all closely related *Struthiosaurus* species without *Borealopelta*, as occurred in previous analyses. Surprisingly, the Late Cretaceous North American *Edmontonia* and *Denversaurus* are recovered as closely related not with *Panoplosaurus*, but rather with *Mymoorapelta* (Late Jurassic of North America) and the Early Cretaceous Asian *Dongyangopelta*, *Sauropelites* and *Taohelong*. This also occurred in the analysis of Soto-Acuña *et al.* 2021 (*contra* traditional analyses that recover the clade Panoplosaurini including Late Cretaceous North American nodosaurids; see Ösi 2005; Lü *et al.* 2007; Burns 2015; Arbour *et al.* 2016). *Mymoorapelta* and the Asian taxa were previously

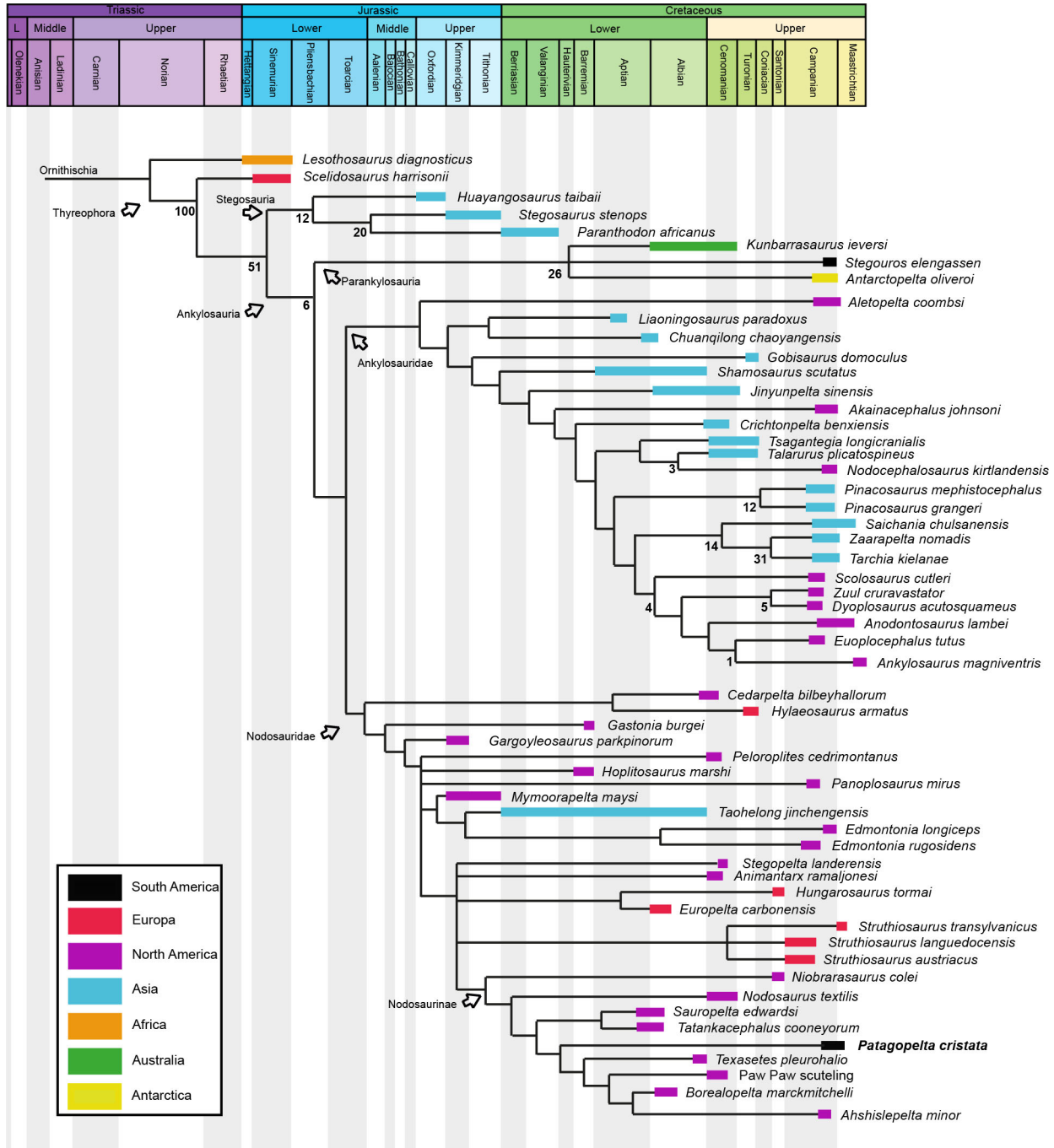


Figure 13. Time-calibrated strict reduced consensus tree. Branch supports are figured (bootstrap). The fossil record of each species is represented by a coloured line considering its continental provenance. Record ages are taken from Ostrom (1970), Jacobs (1994), Carpenter & Kirkland (1998), Arbour & Currie (2016), Brown *et al.* (2017), Zheng *et al.* (2018) and Raven *et al.* (2020).

recovered as basal ankylosaurs or basal nodosaurids (e.g. Arbour & Currie 2016). The variable placement in phylogenetic analyses would be associated with the high amount of missing data in the Asian taxa (only 6 to 13 characters coded), with strong influence of some few coded characters (e.g. ch. 172: form of pelvic

osteoderms). Also, it is worth noting that nodosaurids are usually more incomplete, and therefore less supported and collapsed, than ankylosaurids. Further information is needed to resolve this grouping.

The use of implied weighting (weight against homoplastic characters) in a wide range of k values also

supports the result recovered by the strict consensus tree without weighting. Grouping stabilizes at $k = 5$, and the range $k = 5\text{--}50$ recovers a similar major grouping, with *Patagopelta* always closely related to ‘mid’-Cretaceous North American nodosaurids. It also recovers the clade Struthiosaurinae and the same *Edmontonia*-Asian taxa grouping mentioned above (under $k = 15\text{--}30$, *Panoplosaurus* is incorporated into the group). All topologies are included in the [Supplemental material](#). Summarizing, a variation in parameters like k shows a relatively stable position of *Patagopelta*, supporting the result of the unweighted analysis (see Goloboff *et al.* 2008).

Discussion

Taxonomic remarks

Previous works agree with the assignment of the Salitral Moreno material to Nodosauridae (Salgado & Coria 1996; Coria & Salgado 2001; Arbour & Currie 2016). This work proposes to erect a new genus and species, and supports that it is a member of Nodosauridae. Also, this is the first formal statement of a new ankylosaurian taxon from Argentina (and the second from South America). Currently, nodosaurid diagnostic characters (see Coombs 1978; Carpenter & Kirkland 1998; Blows 2015; Arbour & Currie 2016) in the studied material include: an asymmetrical cingulum on the base of the tooth crown; a sub-rounded low quadratojugal osteoderm; large transverse processes conserved at least down the middle caudal vertebral series; a shallow longitudinal groove ventral to the vertebral centra of the synsacrum; a large hemispherical femoral head dorsomedially angled (more than 120° from the femoral shaft); femoral head separated from the greater trochanter by a deep fossa; a fourth trochanter placed proximally on the femoral shaft; cervical half ring composed of transversely fused osteoderms lacking a basal accessory bony band; conical spine-like osteoderms in the cervical half rings; a large-based presacral spine.

Some characters studied in *Patagopelta* seem to show a potential phylogenetic signal. In the femur, the reduced lateral condyle associated with a notch is present in several nodosaurids and absent in parankylosaurs and ankylosaurids. Also, the caudal series seem to show a reduction of the transverse processes caudally in several morphological states: basal thyreophorans, parankylosaurs and basal nodosaurids bear strong transverse processes in mid-caudal vertebrae, but these are reduced to small pointed or button-like processes, or lateral crests, in some nodosaurids (e.g. *Hungarosaurus* and *Niobrarasaurus*; Carpenter *et al.* 1995; Ósi *et al.* 2019;

in ankylosaurids the tail is greatly modified; see Arbour & Currie 2016 and references therein), probably representing several states of a continuous variation. An exhaustive revision of ankylosaurian caudal vertebrae and femora with a formal definition of the character is required to test the discussed features in a phylogenetic analysis.

The cervical osteoderms of *Patagopelta* are also very diagnostic. Osteoderm utility in ankylosaurian taxonomy and systematics has been discussed several times (i.e. Ford 2000; Arbour *et al.* 2011; Burns & Currie 2014). Features of the cervical half rings are useful at the alpha taxonomic level and higher for ankylosaurids (e.g. Arbour & Currie 2013a, 2016), and have been used to differentiate some Late Cretaceous Laramidian nodosaurids (Carpenter 1990). However, well-defined formal characters of nodosaurid cervical osteoderms are still lacking.

Palaeobiogeographical implications

Ankylosaurian remains are known from the Middle Jurassic to the latest Cretaceous. The poorly supported topologies (Fig. 13, and [Supplemental material](#); see also Arbour & Currie 2016; Soto-Acuña *et al.* 2021), along with some problematic Jurassic remains, make it difficult to elucidate the site of origin of the ankylosaurs and the divergence of nodosaurids and ankylosaurids (and some nodosaurid clades; Arbour & Currie 2016; Galton 2019; Maidment *et al.* 2020). However, during the Jurassic–Early Cretaceous they had an extensive distribution across Laurasian landmasses, and their palaeobiogeography is better understood along with the origin of the Gondwanan parankylosaur lineage (Arbour & Currie 2016; Soto-Acuña *et al.* 2021; Fig. 13).

Our phylogenetic analysis shows that not all Gondwanan ankylosaurs were closely related (see also Arbour & Currie 2016; Soto-Acuña *et al.* 2021). *Kunbarrasaurus* from the Early Cretaceous of Australia, *Stegouros* from the Late Cretaceous of South America and *Antarctopelta* from the Late Cretaceous of Antarctica are recovered as the sister taxa of all other ankylosaurs within Parankylosauria (Soto-Acuña *et al.* 2021; see also Wiersma & Irmis 2018). In contrast, *Patagopelta* was recovered deeply nested within Nodosauridae, in a clade containing primarily mid-Cretaceous North American taxa. These results suggest that at least two lineages of ankylosaurs evolved in Gondwanan landmasses (the phylogenetic position of the incomplete *Spicomellus* from the Middle Jurassic of Morocco still needs to be tested; Maidment *et al.* 2021).

Previous palaeobiogeographical hypotheses for South American ankylosaurs have suggested a Campanian–Maastrichtian migration from North America into South America (Bonaparte 1986; Coria & Salgado 2001;

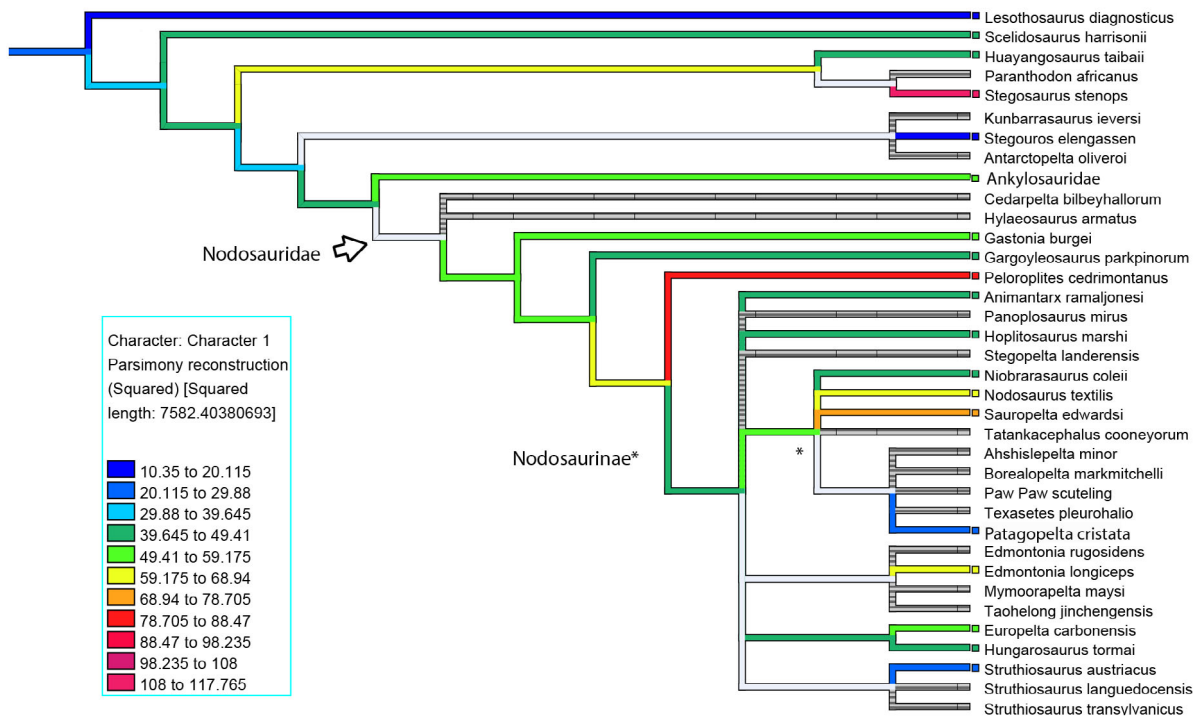


Figure 14. Colour mapping of femoral length over the strict consensus tree. Values of the colour scale are in mm. The categories in the colour scale are set by default in Mesquite.

Arbour & Currie 2016) to explain the presence of the typical Laurasian association of ankylosaurs and hadrosaurs in the Argentinian Patagonia (Leanza *et al.* 2004). Alternatively, Gasparini *et al.* (1996) and Agnolín *et al.* (2010) proposed a lineage of Gondwanan ankylosaurs that originated in the Late Jurassic, with endemic forms in Australia (Gasparini *et al.* 1996). However, our results depict a different, combined panorama, where parankylosaurs represent an early branch of the lineage present in southern continents from when Laurasia and Gondwana split apart until the latest Cretaceous, and the second branch is composed of small nodosaurid euankylosaurs related to ‘mid’-Cretaceous North American forms, supporting the allochthony of the Late Cretaceous North Patagonian ankylosaurs.

In addition, our study allows us to consider some alternative ideas. *Patagopelta* is recovered as closely related to some ‘mid’-Cretaceous nodosaurids from North America within the Nodosaurinae (*sensu* Madzia *et al.* 2021). Since *Patagopelta* is closely related to *Borealopelta*, *Pawpawsaurus* and *Texasetes* from the Albian of North America (Figs 13, 14), it is possible that the South American nodosaurid lineage could have originated during the ‘mid’-Cretaceous of North America, at least during the Albian, which is at least 40 My earlier than has been previously proposed. This

alternative proposal must be treated with caution because of the incompleteness of the Gondwanan nodosaurid fossil record (and that of related forms) and the consequent poor palaeobiogeographical information. Another Patagonian record of ankylosaurs (Paulina-Carabajal *et al.* 2021) from the Cenomanian–Santonian might support earlier dispersals from North to South America. However, it comprises only an indeterminate tooth and ossicles that might also be related to earlier ankylosaurian faunas like those of Australia.

Regarding palaeogeographical possibilities, land connections between South and North America across the Caribbean were mainly proposed for both the earlier Early Cretaceous (Pindell *et al.* 2012) and the latest Late Cretaceous (Pindell & Kennan 2009, and references therein). The latter is consistent with the biogeographical event of the Campanian–Maastrichtian known as the First American Biotic Interchange (FABI; Goin *et al.* 2012). This proposal, strongly supported by the distribution patterns of several lineages including mammals, lizards, snakes and dinosaurs (Goin *et al.* 2012, 2016b; Carneiro *et al.* 2018; and references therein), was traditionally used to explain the presence of ankylosaurs in South America (Coria & Salgado 2001). In addition, ‘mid’-Cretaceous continental vertebrate faunas from South America and Africa show a large stability in

their components during the Albian–Cenomanian with possible faunal interchange (i.e. Candeiro *et al.* 2011; Krause *et al.* 2020; and references therein), and with no allochthonous taxa until the Late Campanian (Leanza *et al.* 2004). An alternative palaeogeographical approach proposes that some possible land connections between South and North America could have occurred during the Albian–Santonian, which might support an earlier dispersal of nodosaurids (Pindell & Kennan 2001). However, this interpretation is not strongly supported (Iturralde-Vinent 2006; Goin *et al.* 2016b). Iturralde-Vinent (2006) also mentioned the presence of ornithopod remains from the Cenomanian of Honduras (Horne 1994) that support a continent-island connection about 85–95 My ago (Cenomanian–Santonian), but not a land bridge between the Americas.

As a whole, the geological evidence and the fossil record mainly support a Late Campanian–Maastrichtian land connection, and the consequent ankylosaur migration. However, we do not rule out a probable earlier time for the ankylosaur migration occurring during the Albian–Santonian time span, which should be considered in the light of further evidence.

Small-bodied ankylosaurs

The Salitral Moreno ankylosaur material is generally much smaller than comparable elements from other ankylosaur taxa. In particular, the femur length of 25.7 cm is about half the length of those of the ankylosaurids *Euoplocephalus*, *Anodontosaurus* and *Dyoplosaurus* (Arbour & Currie 2013), and the nodosaurid ankylosaur *Europelta* (Kirkland *et al.* 2013). Dorsal vertebra MPCA-SM-69 of *Patagopelta* has a centrum width of 30.40 mm and length of 47.39 mm, which are about 35–45% of the equivalent dimensions in specimens of *Euoplocephalus* (Arbour & Currie 2013) and less than half the size of those in *Europelta* (Kirkland *et al.* 2013). Material referred to *Patagopelta* is comparable in size to juvenile specimens of the ankylosaurid *Pinacosaurus* (Burns *et al.* 2015). We consider the referred *Patagopelta* material to represent a non-juvenile specimen based on a number of anatomical features. Firstly, the complete absence of visible sutures in the dorsal vertebrae and the complete fusion of synsacral vertebral elements is more consistent with a non-juvenile age for this material (Coombs 1986; see also Burns *et al.* 2015). Secondly, the presence of well-developed postcervical osteoderms points to a non-juvenile ontogenetic stage for *Patagopelta*; although its cervical and femoral dimensions are similar to those of juvenile *Pinacosaurus*, *Pinacosaurus* specimens at this size apparently lack osteoderms other than those on the cervical half rings (i.e. Maryańska 1977; Jacobs *et al.*

1994; Burns *et al.* 2011). Finally, Salgado & Coria (1996) and Coria & Salgado (2001) proposed that the strong development of muscular lines on the femur indicates an adult stage for the individual. However, adult femora of several ankylosaurian taxa lack a similar development of muscular lines as that observed in *Patagopelta cristata*; we consider this feature one of the diagnostic traits for *Patagopelta* but also acknowledge that it may be ontogenetically linked, pending further examples of this feature in other taxa.

Taking into account femoral size, an adult individual of *Patagopelta cristata* would have been a very small-bodied ankylosaur. Regarding other nodosaurids, *Hungarosaurus tormai* is estimated to have a body length of 4.0 m with a femoral maximum length of 47.0 cm (11.8% of body length; Ősi & Makádi 2009); similarly, the femoral length of *Europelta carbonensis* (50.3 cm) is ~11.2% of the ~4.5 m body length (Kirkland *et al.* 2013); in *Struthiosaurus* the femoral length (26.5 cm) is 8.8–13.3% of the 2–3 m body length (Pereda-Suberbiola 1992; Pereda-Suberbiola & Galton 2001; Ősi & Prondvai 2013); in *Edmontonia* the femoral length (66 cm) is 9.4–11% of the 6.0–7.0 m body length (Vickaryous *et al.* 2004; Paul 2010; femur length 66 cm, Carpenter 1990); and in *Sauropelta* the femoral length (70 cm) is 13.5% of the 5.2 m body length (Carpenter 1984). Using these measurements (femoral/body size ratio ~11–13%), the femoral length of 25.7 cm for the *Patagopelta cristata* holotype individual yields an estimated body length of 2.0–2.3 m, similar to *Struthiosaurus* (as previously mentioned by Salgado & Coria 1996).

Nodosaurids from the Aptian–Cenomanian of North America show a variety of estimated body lengths (e.g. 3 m in *Animantarx* to 5–6 m in *Sauropelta*; Carpenter & Kirkland 1998 and references therein; Vickaryous *et al.* 2004), but derived Late Cretaceous lineages followed different trends in body length. Struthiosaurini (*sensu* Kirkland *et al.* 2013) were relatively small, whereas Late Cretaceous North American nodosaurids (*Edmontonia*, *Denversaurus* and *Panoplosaurus*, commonly grouped within the Panoplosaurini but recovered as polyphyletic in our analysis) had large body lengths. The body mass estimations made by Benson *et al.* (2018) also reflect this pattern. Within Struthiosaurini, body mass ranges between 128.20 kg in *Struthiosaurus transylvanicus* and 688.18 kg in *Hungarosaurus tormai*. In Panoplosaurini the mean body mass is larger: 2256.71 kg for *Edmontonia longiceps*, 1530.51 kg for *E. rugosidens* and 1372.85 kg for *Panoplosaurus*. The other Cretaceous North American nodosaurids are more variable in body mass, including *Animantarx* (764.11 kg), *Niobrarasaurus* (1231.08 kg), *Nodosaurus* (1231.08 kg) and *Sauropelta* (3010.16 kg). Unfortunately, the absence of a humerus precludes our

ability to estimate body mass in *Patagopelta*, but based on femur dimensions *Patagopelta* likely had a mass comparable to that of *Struthiosaurus*, in the 100–400 kg range (Pereda-Suberbiola 1992; Benson *et al.* 2018), and almost certainly well under 1000 kg.

The small body size of *Patagopelta* does not seem to reflect a phylogenetic trend towards a reduction in body size within Nodosauridae overall or within our least inclusive clade containing *Patagopelta* (*Texasetes*, *Pawpawsaurus*, *Borealopelta* or *Ahshislepelta*, where femoral information is still lacking). The mapping of the femoral length (as a proxy for body length) in our strict consensus tree is shown in Figure 14 (the complete strict consensus tree and femoral measurements are incorporated into the Supplemental material). Testing the evolution of body size, the node reconstruction shows a 50–60 cm femoral length at the base of Nodosauridae (also for Ankylosauridae). The nodosaurid clade excluding *Peloroplites* and the ‘polacanthines’ reduced the femoral length to 40–50 cm at its base, but there is not a clear trend in femoral length within the subgroups. In fact, each internal clade shows both specimens with larger, similar and small femoral length, relative to the mentioned node. Thus, a non-phyletic (autapomorphic) dwarfism may explain the size variation in *Patagopelta*. However, the lack of resolution within the less inclusive clade containing *Patagopelta* precludes a conclusive statement regarding the small size of some closely related taxa (*Pawpawsaurus* and *Texasetes*), based on measurements other than femoral length.

Small body sizes in the sauropod *Magyarosaurus*, the ornithomimid *Zalmoxes* and the nodosaurid ankylosaur *Struthiosaurus* (Pereda-Suberbiola & Galton 2009; Benton *et al.* 2010; Stein *et al.* 2010; Ősi *et al.* 2012, 2014) from the Late Cretaceous Hateg Island (today Romania) has been attributed to the island rule by some authors (Pereda-Suberbiola & Galton 2009; Benton *et al.* 2010; Stein *et al.* 2010; Ősi *et al.* 2012, 2014), although others (i.e. Meiri *et al.* 2008; Itescu *et al.* 2014) have proposed alternate explanations. It is interesting that *Stegouros* also had a very small body size for an ankylosaur, with a femur length of approximately 15 cm and estimated body length of 2 m, despite not being closely phylogenetically related to *Patagopelta* in our analysis.

Although we cannot confirm that *Patagopelta* lived on an island archipelago, several marine transgressions from the Atlantic Ocean flooded the southern region of South America (e.g. the Kawas Sea), resulting in an archipelago-like configuration with a mixture of marine and continental faunas during the Cretaceous–Palaeogene transition (Riccardi 1988; see also Gasparini *et al.* 2001; Wilson & Arens 2001; Rougier *et al.* 2009; Malumíán &

Náñez 2011; Goin *et al.* 2016a, b; and references therein). In addition, considering that South American ankylosaurs may have migrated from North America during the Late Cretaceous (see Palaeobiogeographical implications, above), both the Caribbean archipelago and the isolated landmasses from the northern region of South America (Macotay *et al.* 2003; Iturralde-Vinent 2006) were obligatory paths towards southern latitudes. Perhaps the small body size of *Patagopelta* can be attributed to a reduction in body size of its ancestors crossing into South America. The insular dwarfing hypothesis was also proposed for the small-sized saltosaurine sauropods from the Late Cretaceous North Patagonian Allen Formation (Apesteguía 2002; see also Klein *et al.* 2012). In fact, the saltosaurine *Rocasaurus* (Salgado & Azzpilueta 2000) was found in the same quarry as the femur and tooth of *Patagopelta* in Salitral Moreno (LS pers. obs.).

Alternative hypotheses concerning the small size of South American ankylosaurs (and within the struthiosaurines) include competitive exclusion against hadrosaurids and the endemic diversity of Late Cretaceous sauropods (Salgado & Azzpilueta 2000), which includes small-sized forms (de Jesus Faria *et al.* 2014; Aranciaga-Rolando *et al.* 2021, and references therein). Paedomorphic dwarfism has also been discussed previously (Pereda-Suberbiola & Galton 2009). In any case, all these hypotheses need to be tested by expanding the ankylosaurian fossil record from Central and South America and the corresponding histological studies.

Conclusions

Revised materials allow the erection of the new genus and species *Patagopelta cristata*, a small nodosaurid ankylosaur from the Late Cretaceous of Salitral Moreno (Argentinian Patagonia). This taxon bears diagnostic features in the anatomy of the cervical half rings and the femur, that are unique among ankylosaurs. Our phylogenetic analysis improves the nodosaurid topology of prior studies and recovered *Patagopelta* within Nodosaurinae, along with other ‘mid’-Cretaceous nodosaurids from North America. This phylogenetic position is also supported by anatomical features not established as formal characters. The ~2 m body length estimated for *Patagopelta* is surprisingly small, and is comparable to that of the nodosaurid *Struthiosaurus* from the Late Cretaceous of Europe. As in the case of *Struthiosaurus* from the Hateg Island (Cretaceous of Europe), the decrease in size of the Argentinian nodosaurid may be related to the presence of an archipelago in southern South America in the context of the Kawas Sea transgressive event. *Patagopelta* represents a lineage of South

American nodosaurids that migrated into South America during the Late Cretaceous, most probably during the Campanian–Maastrichtian, although an older migration of this lineage closely related to the older ‘mid’-Cretaceous North American nodosaurids could not be completely rejected.

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Supplemental material

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References

- Agnolín, F. L., Ezcurra, M. D., Pais, D. F. & Salisbury, S. W. 2010.** A reappraisal of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand: evidence for their Gondwanan affinities. *Journal of Systematic Palaeontology*, **8**(2), 257–300. doi:10.1080/14772011003594870
- Andreis, R. R., Iñiguez Rodríguez, A. M., Lluch, J. A. & Sabio, D. A. 1974.** Estudio sedimentológico de las Formaciones del Cretácico Superior del área del lago Pellegrini (Provincia de Río Negro, República Argentina). *Revista de la Asociación Geológica Argentina*, **29**, 83–104.
- Apesteguía, S. 2002.** Successional structure in continental tetrapod faunas from Argentina along the Cretaceous. Boletim do 6º Simpósio sobre o Cretáceo do Brasil / 2º Simposio sobre el Cretácico de América del Sur. São Pedro, Brasil, pp. 135–141. UNESP-IGCE-DGA, São Pedro, Brasil. ISSN 1516-8239.
- Aranciaga Rolando, M., García Marsa, J. A., Agnolín, F. L., Motta, M. J., Rozadilla, S. & Novas, F. E. 2021.** The sauropod record of Salitral Ojo del Agua: An Upper Cretaceous (Allen Formation) fossiliferous locality from northern Patagonia, Argentina. *Cretaceous Research*, **129**, 105029. doi:10.1016/j.cretres.2021.105029
- Arbour, V. M. 2009.** Estimating impact forces of tail club strikes by ankylosaurid dinosaurs. *PLoS ONE*, **4**, e6738. doi:10.1371/journal.pone.0006738
- Arbour, V. M., Burns, M. E. & Currie, P. J. 2011.** A review of pelvic shield morphology in ankylosaurs (Dinosauria: Ornithischia). *Journal of Paleontology*, **85**, 298–302. doi:10.1666/10-071.1
- Arbour, V. M. & Currie, P. J. 2013a.** *Euoplocephalus tutus* and the diversity of ankylosaurid dinosaurs in the Late Cretaceous of Alberta, Canada, and Montana, USA. *PLoS ONE*, **8**, e62421. doi:10.1371/journal.pone.0062421
- Arbour, V. M. & Currie, P. J. 2013b.** The taxonomic identity of a nearly complete ankylosaurid dinosaur skeleton from the Gobi Desert of Mongolia. *Cretaceous Research*, **46**, 24–30. doi:10.1016/j.cretres.2013.08.008
- Arbour, V. M., Currie, P. J. & Badamgarav, D. 2014.** The ankylosaurid dinosaurs of the Upper Cretaceous Baruungoyot and Nemegt formations of Mongolia. *Zoological Journal of the Linnean Society*, **172**, 631–652. doi:10.1111/zoj.12185
- Arbour, V. M. & Currie, P. J. 2016.** Systematics, phylogeny and palaeobiogeography of the ankylosaurid dinosaurs. *Journal of Systematic Palaeontology*, **14**(5), 385–444. doi:10.1080/14772019.2015.1059985
- Arbour, V. M., Zanno, L. E. & Gates, T. 2016.** Ankylosaurian dinosaur palaeoenvironmental associations were influenced by extirpation, sea-level fluctuation, and geodispersal. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **449**, 289–299. doi:10.1016/j.palaeo.2016.02.033
- Arbour, V. M. & Evans, D. C. 2017.** A new ankylosaurine dinosaur from the Judith River Formation of Montana, USA, based on an exceptional skeleton with soft tissue preservation. *Royal Society Open Science*, **4**, 161086. doi:10.1098/rsos.161086
- Armas, P. & Sánchez, M. L. 2011.** Análisis estratigráfico secuencial (Cretácico Superior) en el borde nororiental de

- Cuenca Neuquina, Argentina. *Andean Geology*, **38**, 119–155.
- Armas, P. & Sánchez, M. L. 2013.** Sedimentología y arquitectura de las dunas costeras de la Formación Allen, Grupo Malargüe, cuenca Neuquina – Río Negro, Argentina. *Revista Mexicana de Ciencias Geológicas*, **30**(1), 65–79.
- Aslan, A. & Behrensmeyer, A. K. 1996.** Taphonomy and time resolution of bone assemblages in a contemporary fluvial system: the East Fork River, Wyoming. *Palaios*, **11**, 411–421. doi:10.2307/3515209
- Barrio, C. A. 1990.** Paleogeographic control of Upper Cretaceous tidal deposits, Neuquén Basin, Argentina. *Journal of South American Earth Sciences*, **3**, 31–49. doi:10.1016/0895-9811(90)90016-T
- Benson, R. B. J., Hunt, G., Carrano, M. T. & Campione, N. E. 2018.** Cope's rule and the adaptive landscape of dinosaur body size evolution. *Palaeontology*, **61**, 13–48. doi:10.1111/pala.12329
- Benton, M. J., Csiki, Z., Grigorescu, D., Redelstorff, R., Sander, P. M., Stein, K. & Weishampel, D. B. 2010.** Dinosaurs and the island rule: the dwarfed dinosaurs from Hateg Island. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **293**, 438–454.
- Bertels, A. 1969.** Estratigrafía del límite Cretácico/Terciario en Patagonia septentrional. *Revista de la Asociación Geológica Argentina*, **24**(1), 41–54.
- Blows, W. T. 2015.** *British polacanthid dinosaurs – observations on the history and palaeontology of the UK polacanthid armoured dinosaurs and their relatives*. Siri Scientific Press, Manchester, 220 pp.
- Bonaparte, J. F. 1986.** History of the terrestrial Cretaceous vertebrates. *Actas del IV Congreso Argentino de Paleontología y Bioestratigrafía*, Mendoza, **4**, 63–95.
- Britt, B. B., Scheetz, R. D. & Dangerfield, A. 2008.** A suite of dermestid beetle traces on dinosaur bone from the Upper Jurassic Morrison Formation, Wyoming, USA. *Ichnos: An International Journal for Plant and Animal Traces*, **15**(2), 59–71. doi:10.1080/10420940701193284
- Brown, C. M. 2017.** An exceptionally preserved armored dinosaur reveals the morphology and allometry of osteoderms and their horny epidermal coverings. *PeerJ*, **5**, e4066; doi:10.7717/peerj.4066
- Brown, C. M., Henderson, D. M., Vinther, J., Fletcher, I., Sistiaga, A., Herrera, J. & Summons, R. E. 2017.** An exceptionally preserved three-dimensional armored dinosaur reveals insights into coloration and Cretaceous predator-prey dynamics. *Current Biology*, **27**, 2514–2521. doi:10.1016/j.cub.2017.06.071
- Brum, A., Simões, T. R., Eleutério, L. H., Souza, G. A., Sayão, J. M. & Kellner, A. W. 2021.** Microstructure of new Antarctic ankylosaur osteoderms and comments on structural variation in dinosaurian osteoderm. *Jornadas Argentinas de Paleontología de Vertebrados Abstracts*, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), Mendoza. Vol. 21 Núm. 2(R), pp. 28–29.
- Bunzel, E. 1871.** Die Reptil fauna der Gosau-Formation in der Neuen Welt bei Wiener Neustadt. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt Wien*, **5**, 1–18.
- Burns, M. E. 2015.** *Intraspecific variation in the armoured dinosaurs (Dinosauria: Ankylosauria)*. Unpublished PhD thesis, University of Alberta, Edmonton, 285 pp.
- Burns, M. E., Currie, P. J., Sissons, R. L. & Arbour, V. M. 2011.** Juvenile specimens *Ornithosaurus grangeri* Gilmore, 1933 (Ornithischia: Ankylosauria) from the Late Cretaceous of China, with comments on the specific taxonomy of *Pinacosaurus*. *Cretaceous Research*, **32**, 174–186. doi:10.1016/j.cretres.2010.11.007
- Burns, M. E. & Currie, P. J. 2014.** External and internal structure of ankylosaur (Dinosauria, Ornithischia) osteoderms and their systematic relevance. *Journal of Vertebrate Paleontology*, **34**(4), 835–851. doi:10.1080/02724634.2014.840309
- Burns, M. E., Tumanova, T. A. & Currie, P. J. 2015.** Postcrania of juvenile *Ornithosaurus grangeri* (Ornithischia: Ankylosauria) from the Upper Cretaceous Alagteeg Formation, Alag Teeg, Mongolia: implications for ontogenetic allometry in ankylosaurs. *Journal of Paleontology*, **89**, 168–182. doi:10.1017/jpa.2014.14
- Candeiro, C. R. A., Fanti, F., Therrien, F. & Lamanna, M. C. 2011.** Continental fossil vertebrates from the mid-Cretaceous (Albian–Cenomanian) Alcântara Formation, Brazil, and their relationship with contemporaneous faunas from North Africa. *Journal of African Earth Sciences*, **60**, 79–92. doi:10.1016/j.jafrearsci.2011.02.004
- Carneiro, L. M., Oliveira, É. V., & Goin, F. J. 2018.** *Austropediomys marshalli* gen. et sp. nov., a new Pedomyoidea (Mammalia, Metatheria) from the Paleogene of Brazil: paleobiogeographic implications. *Revista Brasileira de Paleontologia*, **21**, 120–131. doi:10.4072/rbp.2018.2.03
- Carpenter, K. 1984.** Skeletal reconstruction and life restoration of *Sauropelta* (Ankylosauria: Nodosauridae) from the Cretaceous of North America. *Canadian Journal of Earth Science*, **21**, 1491–1498. doi:10.1139/e84-154
- Carpenter, K. 1990.** Ankylosaur systematics: example using *Panoplosaurus* and *Edmontonia* (Ankylosauria: Nodosauridae). Pp. 281–298 in K. Carpenter & P. J. Currie (eds) *Dinosaur systematics: approaches and perspectives*. Cambridge University Press, Cambridge.
- Carpenter, K. 2001.** Phylogenetic analysis of the Ankylosauria. Pp. 455–483 in K. Carpenter (ed.) *The armored dinosaurs*. Indiana University Press, Bloomington.
- Carpenter, K. 2004.** Redescription of *Ankylosaurus magniventris* Brown 1908 (Ankylosauridae) from the Upper Cretaceous of the Western Interior of North America. *Canadian Journal of Earth Sciences*, **41**, 961–986. doi:10.1139/e04-043
- Carpenter, K. 2012.** Ankylosaurs. Pp. 505–528 in M. K. Brett-Surman, T. R. Holtz & J. O. Farlow (eds) *The complete dinosaur*. Second Edition. Indiana University Press, Bloomington.
- Carpenter, K., Dilkes D. & Weishampel, D. B. 1995.** The dinosaurs of the Niobrara Chalk Formation (Upper Cretaceous, Kansas). *Journal of Vertebrate Paleontology*, **15**, 275–297. doi:10.1080/02724634.1995.10011230
- Carpenter, K. & Kirkland, J. I. 1998.** Review of Lower and middle Cretaceous ankylosaurs from North America. *New Mexico Museum of Natural History and Science Bulletin*, **14**, 249–270.
- Carpenter, K. & Everhart, M. J. 2007.** Skull of the ankylosaur *Niobrarasaurus coleii* (Ankylosauria: Nodosauridae) from the Smoky Hill Chalk (Coniacian) of western Kansas. *Transactions of the Kansas Academy of Sciences*, **110**, 1–9. doi:10.1660/0022-8443(2007)110 [1:SOTANC]2.0.CO;2

- Carpenter, K., Bartlett, J., Bird, J. & Barrick, R. 2008.** Ankylosaurs from the Price River Quarries, Cedar Mountain Formation (Lower Cretaceous), east-central Utah. *Journal of Vertebrate Paleontology*, **28**(4), 1089–1101. doi:10.1671/0272-4634-28.4.1089
- Carpenter, K., Hayashi, S., Kobayashi, Y., Maryanska, T., Barsbold, R., Sato, K. & Obata, I. 2011.** *Saichania chulsanensis* (Ornithischia, Ankylosauridae) from the Upper Cretaceous of Mongolia. *Palaeontographica Abteilung A*, **293**, 161.
- Carpenter, K., DiCroce, T., Kinneer, B. & Simon, R. 2013.** Pelvis of *Gargoyleosaurus* (Dinosauria: Ankylosauria) and the origin and evolution of the ankylosaur pelvis. *PLoS ONE*, **8**(11), e79887. doi:10.1371/journal.pone.0079887
- Casadío, S. 1994.** *Estratigrafía y paleontología del intervalo Maastrichtiano–Daniano en el occidente de la provincia de La Pampa, Argentina*. Unpublished PhD thesis, Universidad Nacional de Córdoba, 420 pp.
- Casamiquela, R. M. 1978.** La zona litoral de la transgresión Maastrichtiense en el norte de la Patagonia. Aspectos ecológicos. *Ameghiniana*, **15**, 137–146. <https://ameghiniana.org.ar/index.php/ameghiniana/article/view/1550>
- Cerda, I. A., Gasparini, Z., Coria, R. A., Salgado, L., Reguero, M., Ponce, D. A., Gonzalez, R., Jannello, J. M. & Moly, J. 2019.** Paleobiological inferences for the Antarctic dinosaur *Antarctopelta oliveroi* (Ornithischia: Ankylosauria) based on bone histology of the holotype. *Cretaceous Research*, **103**, 104171. doi:10.1016/j.cretres.2019.07.001
- Cerda, I. A., Pereyra, M. E., Garrone, M., Ponce, D., Navarro, T. G., González, R., Militello, M., Luna, C. A. & Jannello, J. M. 2020.** A basic guide for sampling and preparation of extant and fossil bones for histological studies. *Publicación Electrónica de la Asociación Paleontológica Argentina*, **20**(1), 15–28. doi:10.5710/PEAPA.07.04.2020.314
- Chen, R., Zheng, W., Azuma, Y., Shibata, M., Lou, T., Jin, Q. & Jin, X. 2013.** A new nodosaurid ankylosaur from the Chaochuan Formation of Dongyang, Zhejiang Province, China. *Acta Geologica Sinica*, **87**, 801840. doi:10.1111/1755-6724.12077
- Coombs, W. P. 1971.** *The Ankylosauria*. Unpublished PhD thesis, Columbia University, 487 pp.
- Coombs, W. P. 1978.** The families of the ornithischian dinosaur Order Ankylosauria. *Palaeontology*, **21**, 143–170.
- Coombs, W. P. 1986.** A juvenile ankylosaur referable to the genus *Euoplocephalus* (Reptilia, Ornithischia). *Journal of Vertebrate Paleontology*, **6**(2), 162–173. doi:10.1080/02724634.1986.10011608
- Coombs, W. P. 1995a.** A new nodosaurid ankylosaur (Dinosauria: Ornithischia) from the Lower Cretaceous of Texas. *Journal of Vertebrate Paleontology*, **15**, 298–312. doi:10.1080/02724634.1995.10011231
- Coombs, W. P. 1995b.** Ankylosaurian tail clubs of middle Campanian to early Maastrichtian age from western North America, with description of a tiny club from Alberta and discussion of tail orientation and tail club function. *Canadian Journal of Earth Sciences*, **32**, 902–912. doi:10.1139/e95-075
- Coombs, W. & Maryanska, T. 1990.** Ankylosauria. Pp. 456–483 in D. Weishampel, P. Dodson & H. Osmolska (eds) *The Dinosauria*. Second Edition. University of California Press, Berkeley.
- Coria, R. A. & Salgado, L. 2001.** South American ankylosaurs. Pp. 159–168 in K. Carpenter (ed.) *The armored dinosaurs*. Indiana University Press, Bloomington and Indianapolis.
- Cruzado-Caballero, P. & Coria, R. A. 2016.** Revisiting the hadrosaurid (Dinosauria: Ornithopoda) diversity of the Allen Formation: a re-evaluation of *Willinakaqe salitralensis* from Salitral Moreno, Río Negro Province, Argentina. *Ameghiniana*, **53**, 231–237. doi:10.5710/AMGH.25.09.2015.2943
- 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. doi:10.1080/02724634.2017.1289381
- Currie, P. J., Badamgarav, D., Koppelhus, E. B., Sissons, R. & Vickaryous, M. K. 2011.** Hands, feet, and behaviour in *Pinacosaurus* (Dinosauria: Ankylosauridae). *Acta Palaeontologica Polonica*, **56**, 489–504. doi:10.4202/app.2010.0055
- de Jesus Faria, C. C., Gonzalez Riga, B., AnjosCandeiro, C. R. dos b, SilvaMarinho, T. da, Ortiz David, L., Medeiros Simbras, F., Barboza Castanho, R., Pereira Muniz, F. & Gomes da CostaPereira, P. V. L. 2014.** Cretaceous sauropod diversity and taxonomic succession in South America. *Journal of South American Earth Sciences*, **61**, 154–163. doi:10.1016/j.jsames.2014.11.008
- de Valais, S., Apesteuguía, S. & Udrizar Sauthier, D. 2003.** Nuevas evidencias de dinosaurios de la Formación Puerto Yeruá (Cretácico), Provincia de Entre Ríos, Argentina. *Ameghiniana*, **40**(3), 507–511. doi: <https://www.ameghiniana.org.ar/index.php/ameghiniana/article/view/991>
- Eaton, T. H. 1960.** A new armored dinosaur from the Cretaceous of Kansas. *The University of Kansas Palaeontological Contributions: Vertebrata*, **8**, 124.
- Everhart, M. 2014.** *Niobrarasaurus colei: remains of a planteating dinosaur from the Smoky Hill Chalk*. Updated at: <http://oceansofkansas.com/Dinosaur.html>, accessed 3 August 2014.
- Ford, T. L. 2000.** A review of ankylosaur osteoderms from New Mexico and a preliminary review of ankylosaur armor. *New Mexico Museum Natural History Sciences Bulletin*, **17**, 157–176.
- Ford, T. L. & Kirkland, J. I. 2001.** Carlsbad ankylosaur (Ornithischia, Ankylosauria): an ankylosaurid and not a nodosaurid. Pp. 239–260 in K. Carpenter (ed.) *The armored dinosaurs*. Indiana University Press, Bloomington.
- Galton, P. M. 2019.** Earliest record of an ankylosaurian dinosaur (Ornithischia: Thyreophora): dermal armor from the lower Kota Formation (Lower Jurassic) of India. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **291**, 205–219. doi:10.1127/njgpa/2019/0800
- García, G. & Pereda-Suberbiola, X. 2003.** A new species of *Struthiosaurus* (Dinosauria: Ankylosauria) from the Upper Cretaceous of Villeveyrac (Southern France). *Journal of Vertebrate Paleontology*, **23**, 156–165. doi:10.1671/0272-4634(2003)23%5B156%3AANSOSD%5D2.0.CO%3B2
- García, R. A. & Salgado, L. 2013.** The titanosaur sauropods from the late Campanian–early Maastrichtian Allen Formation of Salitral Moreno, Río Negro, Argentina. *Acta*

- Palaeontologica Polonica*, **58**(2), 269–284. doi:10.4202/app.2011.0055
- Gasparini, Z., Pereda-Suberbiola, X. & Molnar, R. E.** 1996. New data on the ankylosaurian dinosaur from the Late Cretaceous of the Antarctica Peninsula. *Memoirs of the Queensland Museum*, **39**, 583–594.
- Gasparini, Z., de la Fuente, M., Fernández, M. & Bona, P.** 2001. Reptiles from Late Cretaceous coastal environments of northern Patagonia. *VII International Symposium on Mesozoic Terrestrial Ecosystems, Buenos Aires. Asociación Paleontológica Argentina publicación especial*, **7**, 101–105.
- Gasparini, Z., Sterli, J., Parras, A., O’Gorman, J. P., Salgado, L., Varela, J. & Pol, D.** 2015. Late Cretaceous reptilian biota of the La Colonia Formation, central Patagonia, Argentina: occurrences, preservation and paleoenvironments. *Cretaceous Research*, **54**, 154–168. doi:10.1016/j.cretres.2014.11.010
- Gasulla, J. M., Ortega, F., Pereda-Suberbiola, X., Escaso, F. & Sanz, J. L.** 2011. Elements of la armadura dermica del Dinosaurio Anquilosaurio *Polacanthus* Owen, 1865, en el Cretácico Inferior de Morella (Castellon, Espana). *Ameghiniana*, **48**, 508–519. doi:10.5710/AMGH.v48i4(276)
- Gilmore, C. W.** 1914. Osteology of the armored Dinosauria in the United States National Museum, with special reference to the genus *Stegosaurus*. *United States National Museum Bulletin*, **89**, 1136.
- Gilmore, C. W.** 1930. On dinosaurian reptiles from the Two Medicine Formation of Montana. *Proceedings of the United States National Museum*, **77**, 139.
- Goin, F. J., Gelfo, J. N., Chornogubsky, L., Woodburne, M. O. & Martin, T.** 2012. Origins, radiations, and distribution of South American mammals: from greenhouse to icehouse worlds. Pp. 20–50 in B. D. Patterson & L. P. Costa (eds) *Bones, clones, and biomes: an 80-million year history of recent Neotropical mammals*. University of Chicago Press, Chicago. doi:10.7208/9780226649214-003
- Goin, F. J., Woodburne, M. O., Zimicz, A. N., Martin, G. M. & Chornogubsky, L.** 2016a. Dispersal of vertebrates from between the Americas, Antarctica, and Australia in the Late Cretaceous and Early Cenozoic. Pp. 77–124 in P. Blondel, E. Guilyardi, J. Rabassa & C. Horwood (eds) *A brief history of South American metatherians*. Springer, Dordrecht. doi:10.1007/978-94-017-7420-8_3
- Goin, F. J., Woodburne, M. O., Zimicz, A. N., Martin, G. M. & Chornogubsky, L.** 2016b. Evolutionary contexts. Pp. 125–154 in *A brief history of South American metatherians: evolutionary contexts and intercontinental dispersals*. Springer Earth System Sciences. doi:10.1007/978-94-017-7420-8_4
- Goloboff, P. A., Carpenter, J. M., Arias, J. S. & Esquivel, D. R. M.** 2008. Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics*, **24**, 1–16. doi:10.1111/j.1096-0031.2008.00209.x
- Goloboff, P. & Catalano, S.** 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, **32**, 221–238. doi:10.1111/cla.12160
- Horne, G. S.** 1994. A mid-Cretaceous ornithopod from central Honduras. *Journal of Vertebrate Paleontology*, **14**(1), 147–150. doi:10.1080/02724634.1994.10011548
- Huene, F.** 1929. Los Saurisquios y Ornitisquios del Cretaceo Argentino. *Anales del Museo de La Plata*, **3**, 196.
- Hugo, C. A. & Leanza, H. A.** 2001a. Hoja Geológica 3969-IV, General Roca, provincias del Neuquén y Río Negro. *Instituto de Geología y Recursos Naturales, SEGEMAR, Boletín* **308**, 1–71. <http://repositorio.segemar.gov.ar/handle/308849217/126>
- Hugo, C. A. & Leanza, H. A.** 2001b. Hoja Geológica 3966-III, Villa Regina, provincia Río Negro. *Instituto de Geología y Recursos Naturales, SEGEMAR, Boletín* **309**, 1–58. <http://repositorio.segemar.gov.ar/handle/308849217/196>
- Itescu, Y., Karraker, N. E., Pritchard, P., Raia, P. & Meiri, S.** 2014. Is the island rule general? Turtles disagree. *Global Ecology and Biogeography*, **23**, 689–700. doi:10.1111/geb.12149
- Iturralde-Vinent, M. A.** 2006. Meso–Cenozoic Caribbean paleogeography: implications for the historical biogeography of the region. *International Geology Review*, **48**, 791–827. doi:10.2747/0020-6814.48.9.791
- Jacobs, L. L., Winkler, D. A., Murray, P. A. & Maurice, J. M.** 1994. A nodosaurid scuteling from the Texas shore of the Western Interior Seaway. Pp. 337–346 in K. Carpenter, K. F. Hirsch & J. R. Horner (eds) *Dinosaur eggs and babies*. Cambridge University Press, Cambridge.
- Juarez-Valieri, R., Haro, J., Fiorelli, L., Calvo, J.** 2010. A new hadrosauroid (Dinosauria: Ornithopoda) from the Allen Formation (Late Cretaceous) of Patagonia, Argentina. *Revista del Museo Argentino de Ciencias Naturales nueva serie*, **12**(2), 217–231.
- Kilbourne, B. & Carpenter, K.** 2005. Redescription of *Gargoyleosaurus parkpinorum*, a polacanthid ankylosaur from the Upper Jurassic of Albany County, Wyoming. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **237**, 111–160. doi:10.1127/njgpa/235/2005/111
- Kinneer, B., Carpenter, K. & Shaw, A.** 2016. Redescription of *Gastonia burgei* (Dinosauria: Ankylosauria, Polacanthidae), and description of a new species. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **282**, 37–80. doi:10.1127/njgpa/2016/0605
- Kirkland, J. I. & Carpenter, K.** 1994. North America’s first pre-Cretaceous ankylosaur (Dinosauria) from the Upper Jurassic Morrison Formation of west Colorado. *Brigham Young University Geology Studies*, **40**, 25–42.
- Kirkland, J. I., Alcalá, L., Loewen, M. A., Espilez, E., Mampel, L. & Wiersma, J. P.** 2013. The basal nodosaurid ankylosaur *Europelta carbonensis* n. gen., n. sp. from the Lower Cretaceous (Lower Albian) Escucha Formation of Northeastern Spain. *PLoS ONE*, **8**(12), e80405. doi:10.1371/journal.pone.0080405
- Klein, N., Sander, P. M., Stein, K., Le Loeuff, J., Carballido, J. L. & Buffetaut, E.** 2012. Modified laminar bone in *Ampelosaurus atacis* and other titanosaurs (Sauropoda): implications for life history and physiology. *PLoS ONE*, **7**(5), e36907. doi:10.1371/journal.pone.0036907
- Krause, J. M., Ramezani, J., Umazano, A. M., Pol, D., Carballido, J. L., Sterli, J., Puerta, P., Cúneo, R. N. & Bellosi, E. S.** 2020. High-resolution chronostratigraphy of the Cerro Barcino Formation (Patagonia): paleobiologic implications for the mid-Cretaceous dinosaur-rich fauna of South America. *Gondwana Research*, **80**, 33–49. doi:10.1016/j.gr.2019.10.005

- Leahey, L. G., Molnar, R. E., Carpenter, K., Witmer, L. M. & Salisbury, S. W. 2015. Cranial osteology of the ankylosaurian dinosaur formerly known as *Minni* sp. (Ornithischia: Thyreophora) from the Lower Cretaceous Allaru Mudstone of Richmond, Queensland, Australia. *PeerJ*, **3**, e1475. doi:10.7717/peerj.1475
- Leanza, H. A., Apesteguía, S., Novas, F. E. & de la Fuente, M. S. 2004. Cretaceous terrestrial beds from the Neuquen Basin (Argentina) and their tetrapod assemblages. *Cretaceous Research*, **25**(1), 61–87. doi:10.1016/j.cretres.2003.10.005
- Lü, J., Ji, Q., Gao, Y. & Li, Z. 2007. A new species of the ankylosaurid dinosaur *Crichtonsaurus* (Ankylosauridae: Ankylosauria) from the Cretaceous of Liaoning province, China. *Acta Geologica Sinica*, **81**, 883–897. doi:10.1111/j.1755-6724.2007.tb01010.x
- Lull, R. S. 1921. The Cretaceous armored dinosaur, *Nodosaurus textilis* Marsh. *American Journal of Science, Fifth Series*, **1**, 97–126.
- Macsotay, O., Erlich, R. N. & Peraza, T. 2003. Sedimentary structures of the La Luna, Navay and Quercual Formations, Upper Cretaceous of Venezuela. *Palaos*, **18**, 334–348. doi:10.1669/0883-1351(2003)018 <0334:SSOTLL>2.0.CO;2
- Maddison, W. P. & Maddison, D. R. 2019. *Mesquite: a modular system for evolutionary analysis. Version 3.61*. Updated at: <http://www.mesquiteproject.org>, accessed August 2021.
- Madzia, D., Arbour, V. M., Boyd, C. A., Farke, A. A., Cruzado-Caballero, P. & Evans, D. C. 2021. The phylogenetic nomenclature of ornithischian dinosaurs. *PeerJ*, **9**, e12362. doi:10.7717/peerj.12362
- Maidment, S. C. R., Raven, T. J., Ouarhache, D. & Barrett, P. M. 2020. North Africa's first stegosaur: implications for Gondwanan thyreophoran dinosaur diversity. *Gondwana Research*, **77**, 82–97. doi:10.1016/j.gr.2019.07.007
- Maidment, S. C. R., Strachan, S. J., Ouarhache, D., Scheyer, T. M., Brown, E. E., Fernandez, V., Johanson, Z., Raven, T. J & Barrett, P. M. 2021. Bizarre dermal armour suggests the first African ankylosaur. *Nature Ecology & Evolution*, **5**(12), 1576–1581. doi:10.1038/s41559-021-01553-6
- Mallon, J. C. & Anderson, J. S. 2014. The functional and palaeoecological implications of tooth morphology and wear for the megaherbivorous dinosaurs from the Dinosaur Park Formation (Upper Campanian) of Alberta, Canada. *PLoS ONE*, **9**(6), e98605. doi:10.1371/journal.pone.0098605
- Malumíán, N. & Nández, C. 2011. The Late Cretaceous–Cenozoic transgressions in Patagonia and the Fuegian Andes: Foraminifera, palaeoecology, and palaeogeography. *Biological Journal of the Linnean Society*, **103**, 269–288. doi:10.1111/j.1095-8312.2011.01649.x
- Marsh, O. C. 1889. Notice of gigantic horned Dinosauria from the Cretaceous. *American Journal of Science*, **38**, 173–175.
- Marsh, O. C. 1890. Additional characters of the Ceratopsidae, with notice of new Cretaceous dinosaurs. *American Journal of Science*, **39**, 418–426.
- Martin, R. E. 1999. *Taphonomy, a process approach*. Cambridge University Press, Cambridge, 508 pp.
- Martinelli, A. G. & Forasiepi, A. M. 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). *Revista del Museo Argentino de Ciencias Naturales*, **6**, 257–305.
- Maryńska, T. 1977. Ankylosauridae (Dinosauria) from Mongolia. *Palaeontologia Polonica*, **37**, 85151.
- Matthias, A. E., McWhinney, L. & Carpenter, K. 2016. Pathological pitting in ankylosaur (Dinosauria) osteoderms. *International Journal of Paleopathology*, **13**, 82–90. doi:10.1016/j.ijpp.2016.02.006
- McHugh, J. B., Drumheller, S. K., Riedel, A. & Kane, M. 2020. Decomposition of dinosaurian remains inferred by invertebrate traces on vertebrate bone reveal new insights into Late Jurassic ecology, decay, and climate in western Colorado. *PeerJ*, **8**, e9510 doi:10.7717/peerj.9510
- Mehl, M. G. 1936. *Hierosaurus coeii*: a new aquatic dinosaur from the Niobrara Cretaceous of Kansas. *Journal of the Scientific Laboratories Denison University*, **31**, 1–20.
- Meiri, S., Cooper, N. & Purvis, A. 2008. This island rule: made to be broken? *Proceedings of the Royal Society B*, **245**, 141–148. doi:10.1098/rspb.2007.1056
- Molnar, R. E. 1980. An ankylosaur (Ornithischia: Reptilia) from the Lower Cretaceous of Southern Queensland. *Memoirs of the Queensland Museum*, **20**, 77–87.
- Molnar, R. E. 1996. Preliminary report on a new ankylosaur from the Early Cretaceous of Queensland, Australia. *Memoirs of the Queensland Museum*, **39**(3), 653–668.
- Molnar, R. E. 2001. Armor of the small ankylosaur *Minni*. Pp. 341–362 in K. Carpenter (ed.) *The armored dinosaurs*. Indiana University Press, Bloomington.
- Murray, A., Rigueti, F. & Rozadilla, S. 2019. New ankylosaur (Thyreophora, Ornithischia) remains from the Upper Cretaceous of Patagonia. *Journal of South American Earth Sciences*, **96**, 102320. doi:10.1016/j.jsames.2019.102320
- Nopcsa, F. 1915. Die Dinosaurier des Siebenbürgischen Landesteile Ungarns. *Mitteilungen aus dem Jahrbuche der Königlich Ungarischen Geologischen Reichsanstalt, Budapest*, **23**, 3–24.
- Nopcsa, F. 1929. Dinosaurierreste aus Siebenbürgen V. *Geologica Hungarica, Series Palaeontologica*, **4**, 1–76.
- Norman, D. B. 2020a. *Scelidosaurus harrisonii* Owen, 1861 (Dinosauria: Ornithischia) from the Early Jurassic of Dorset, England: cranial anatomy. *Zoological Journal of the Linnean Society*, **188**, 1–81. doi:10.1093/zoolinnean/zlz074
- Novas, F. E. 2009. *The age of dinosaurs in South America*. Indiana University Press, Bloomington, 452 pp.
- O’Gorman, J., Salgado, L. & Gasparini, Z. 2011. Plesiosaurios de la Formación Allen (Campaniano–Maastrichtiano) en el área del Salitral de Santa Rosa (Provincia de Río Negro, Argentina). *Ameghiniana*, **48**, 129–135. doi:10.5710/AMGH.v48i1(308)
- Osborn, H. F. 1923. Two Lower Cretaceous dinosaurs of Mongolia. *American Museum Novitates*, **95**, 1–10.
- Ósi, A. 2005. *Hungarosaurus tormai*, a new ankylosaur (Dinosauria) from the Upper Cretaceous of Hungary. *Journal of Vertebrate Paleontology*, **25**, 370–383. doi:10.1671/0272-4634(2005)025%5B0370%3AHTANAD%5D2.0.CO%3B2
- Ósi, A. & Makadi, L. 2009. New remains of *Hungarosaurus tormai* (Ankylosauria, Dinosauria) from the Upper Cretaceous of Hungary: skeletal reconstruction and body mass estimation. *Palaontologische Zeitschrift*, **83**, 227–245. doi:10.1007/s12542-009-0017-5

- Ósi, A., Prondvai, E., Butler, R., & Weishampel, D. B. 2012. Phylogeny, histology and inferred body size evolution in a new rhabdodontid dinosaur from the Late Cretaceous of Hungary. *PLoS ONE*, 7(9), e44318. doi:10.1371/journal.pone.0044318
- Ósi, A. & Prondvai, E. 2013. Sympatry of two ankylosaurs (*Hungarosaurus* and cf. *Struthiosaurus*) in the Santonian of Hungary. *Cretaceous Research*, 44, 58–63. doi:10.1016/j.cretres.2013.03.006
- Ósi, A., Prondvai, E. & Csiki-Sava, Z. 2014. New ankylosaurian material from the Upper Cretaceous of Transylvania. *Annales de Paléontologie*, 100, 257–271. doi:10.1016/j.annpal.2014.02.001
- Ósi, A., Prondvai, E., Mallon, J. & Bodor, E. R. 2016. Diversity and convergences in the evolution of feeding adaptations in ankylosaurs (Dinosauria: Ornithischia). *Historical Biology*, 29, 539–570. doi:10.1080/08912963.2016.1208194
- Ósi, A., Pereda-Suberbiola, X. 2017. Notes on the pelvic armor of European ankylosaurs (Dinosauria: Ornithischia). *Cretaceous Research*, 75, 11–22. doi:10.1016/j.cretres.2017.03.007
- Ósi, A., Botfalvai, G., Albert, G. & Hajdu, Z. 2019. The dirty dozen: taxonomical and taphonomical overview of a unique ankylosaurian (Dinosauria: Ornithischia) assemblage from the Santonian Iharkút locality, Hungary. *Palaeobiodiversity and Palaeoenvironments*, 99(2), 195–240. doi:10.1007/s12549-018-0362-z
- Ósi, A., Magyar, J., Rosta, K. & Vickaryous, M. 2021. Cranial ornamentation in the Late Cretaceous nodosaurid ankylosaur *Hungarosaurus*. *PeerJ*, 9, e11010. doi:10.7717/peerj.11010
- Ostrom, J. H. 1970. Stratigraphy and palaeontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin Area, Wyoming and Montana. *Peabody Museum of Natural History, Yale University, Bulletin*, 35, 1234. doi:10.12987/9781933789439
- Owen, R. 1842. Report on British fossil reptiles. Part 2. *Report of the British Association for the Advancement of Science (Plymouth)*, 11, 60–204.
- Parsons, W. L. & Parsons, K. M. 2009. A new ankylosaur (Dinosauria: Ankylosauria) from the Lower Cretaceous Cloverly Formation of central Montana. *Canadian Journal of Earth Sciences*, 46, 721–738. doi:10.1139/E09-045
- Paul, G. S. 2010. *The Princeton field guide to dinosaurs*. Princeton University Press, Princeton, 320 pp.
- Paulina-Carabajal, A., Barrios, F. T., Méndez, A. H., Cerda, I. A. & Lee, Y.-N. 2021. A Late Cretaceous dinosaur and crocodyliform faunal association – based on isolate teeth and osteoderms – at Cerro Fortaleza Formation (Campanian–Maastrichtian) type locality, Santa Cruz, Argentina. *PLoS ONE*, 16(9), e0256233. doi:10.1371/journal.pone.0256233
- Penkalski, P. & Blows, W. T. 2013. *Scolosaurus cutleri* from the Dinosaur Park Formation of Alberta, Canada. *Canadian Journal of Earth Sciences*, 50, 171–182. doi:10.1139/cjes-2012-0098
- Pereda-Suberbiola, X. 1991. Nouvelle évidence d'une connexion terrestre entre Europe et Amérique du Nord au Cretace inferieur: *Hoplitosaurus*, synonyme de *Polacanthus* (Ornithischia: Ankylosauria). *Comptes Rendus de l'Academie de Sciences de Paris* (ser. II), 313, 971–976.
- Pereda-Suberbiola, X. 1992. A revised census of European Late Cretaceous nodosaurids (Ornithischia: Ankylosauria): last occurrence and possible extinction scenarios. *Terra Nova*, 4, 641–648. doi:10.1111/j.1365-3121.1992.tb00613.x
- Pereda-Suberbiola, X. 1993a. *Hylaeosaurus*, *Polacanthus*, and the systematics and stratigraphy of Wealden armoured dinosaurs. *Geological Magazine*, 130, 767–781. doi:10.1017/S0016756800023141
- Pereda-Suberbiola, X. 1993b. Armoured dinosaurs from the Late Cretaceous of southern France: a review. *Revue de Paléobiologie Volume Special*, 7, 163–172.
- Pereda-Suberbiola, X. 1994. *Polacanthus* (Ornithischia, Ankylosauria), a transatlantic armoured dinosaur from the Early Cretaceous of Europe and North America. *Palaeontographica, Abteilung A*, 232, 133–159.
- Pereda-Suberbiola, X. & Galton, P. M. 2001. Reappraisal of the nodosaurid ankylosaur *Struthiosaurus austriacus* Bunzel from the Upper Cretaceous Gosau Beds of Austria. Pp. 173–210 in K. Carpenter (ed.) *The armored dinosaurs*. Indiana University Press, Bloomington.
- Pereda-Suberbiola, X. & Galton, P. M. 2009. Dwarf dinosaurs in the latest Cretaceous of Europe? Pp. 263–272 in Colectivo Arqueológico-Paleontológico Salense (ed.) *Actas, IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*. Salas de los Infantes, Burgos, Spain.
- Pereda-Suberbiola, X., Díaz-Martínez, I., Salgado, L. & de Valais, S. 2015. Síntesis del registro fósil de dinosaurios tireóforos en Gondwana. Pp. 90–107 in M. Fernández & Y. Herrera (eds) *Reptiles Extintos – Volumen en Homenaje a Zulma Gasparini. Publicación Electrónica de la Asociación Paleontológica Argentina*, 15(1), 90–107. doi:10.5710/PEAPA.21.07.2015.101
- Penkalski, P. 2018. Revised systematics of the armoured dinosaur *Euoplocephalus* and its allies. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 287, 261–306. doi:10.1127/njgpa/2018/0717
- Pindell, J. L. & Kennan, L. 2001. Processes and events in the terrane assembly of Trinidad and eastern Venezuela. Pp. 159–192 in R. H. Fillon & N. C. Rosen *et al.* (eds) *Transactions of the 21st GCSSEPM annual Bob F. Perkins research conference: petroleum systems of deep-water basins*. SEPM, Texas USA. doi:10.5724/gcs.01.21.0159
- Pindell, J. L. & Kennan, L. 2009. Tectonic evolution of the Gulf of Mexico, Caribbean and northern South America in the mantle reference frame: an update. Pp. 1–55 in K. James, M. A. Lorente & J. Pindell (eds) *Origin and evolution of the Caribbean Region*. Geological Society of London, London, Special Publication, Volume 328. doi:10.1144/SP328.1
- Pindell, J. L., Maresch, W. V., Martens, U. & Stanek, K. 2012. The Greater Antillean Arc: Early Cretaceous origin and proposed relationship to Central American subduction mélanges: implications for models of Caribbean evolution. *International Geology Review*, 54, 131–143. doi:10.1080/00206814.2010.510008
- Ponce, D. A. & Cerda, I. A. 2017. Microestructura osea de osteoderms de Ankylosauria (Dinosauria, Ornithischia) de la Formación Allen (Campaniano–Maastrichtiano) de la localidad de Salitral Moreno, Río Negro, Argentina. Pp. 83 in *Libro de Resúmenes, Publicación Electrónica de la*

- Asociación Paleontológica Argentina*, Buenos Aires. Volume 18, 2(R).
- Powell, J. E.** 1987. Hallazgo de un dinosaurio hadrosáurido (Ornithischia, Ornithopoda) en la Formación Allen (Cretácico Superior) de Salitral Moreno, Provincia de Río Negro, Argentina. *Ameghiniana*, **23**(3–4), 154.
- Raven, T. J., Barrett, P. M., Pond, S. B. & Maidment, S. C. R.** 2020. Osteology and taxonomy of British Wealden Supergroup (Berriasian–Aptian) ankylosaurs (Ornithischia, Ankylosauria). *Journal of Vertebrate Paleontology*, doi:10.1080/02724634.2020.1826956
- Riccardi, A. C.** 1988. The Cretaceous system of southern South America. *Geological Society of America Memoir*, **168**, 1–161.
- Rigueti, F. J.** 2018. Nuevos restos de Ankylosauria del Salitral Moreno y consideraciones sistemáticas sobre su armadura. Pp. 44 in *Libro de Resúmenes, Publicación Electrónica de la Asociación Paleontológica Argentina*, Buenos Aires. Volume 19, 1(R).
- Rivera-Sylva, H. E., Frey, E., Stinnesbeck, W., Carbot-Chanona, G., Sanchez-Uribe, I. E. & Guzmán-Gutiérrez, J. R.** 2018. Paleodiversity of Late Cretaceous Ankylosauria from Mexico and their phylogenetic significance. *Swiss Journal of Palaeontology*, **137**(1), 83–93. doi:10.1007/s13358-018-0153-1
- Rodríguez, M. E.** 2011. El grupo Malargue (Cretácico Tardío-Paleógeno Temprano) en la Cuenca Neuquina. Pp. 245–264 in *Geología y recursos naturales de la Provincia del Neuquén. Relatorio del XVIII Congreso Geológico Argentino, Neuquén*. Asociación Geológica Argentina. ISBN: 978-987-22403-3-2.
- Rogers, R. R. & Kidwell, S. M.** 2007. A conceptual framework for the genesis and analysis of vertebrate skeletal concentrations. Pp. 1–64 in R. R. Rogers, D. A. Eberth & A. R. Fiorillo (eds) *Bonebeds: genesis, analysis, and paleobiological significance*. University of Chicago Press, Chicago and London.
- Rougier, G. W., Chornogubsky, L., Casadio, S., Arango, N. P. & Gaillombardo, A.** 2009. Mammals from the Allen Formation, Late Cretaceous, Argentina. *Cretaceous Research*, **30**, 223–238. doi:10.1016/j.cretres.2008.07.006
- Rozadilla, S., Agnolín, F., Manabe, M., Tsuihiji, T. & Novas, F. E.** 2021. Ornithischian remains from the Chorrillo Formation (Upper Cretaceous), southern Patagonia, Argentina, and their implications on ornithischian paleobiogeography in the Southern Hemisphere. *Cretaceous Research*, **125**, 104881. doi:10.1016/j.cretres.2021.104881
- Salgado, L. & Coria, R. A.** 1993. El género *Aeolosaurus* (Sauropoda, Titanosauridae) en la Formación Allen (Campaniano–Maastrichtiano) de la Provincia de Río Negro, Argentina. *Ameghiniana*, **30**(2), 119–128.
- Salgado, L. & Coria, R. A.** 1996. First evidence of an ankylosaur (Dinosauria, Ornithischia) in South America. *Ameghiniana*, **33**(4), 367–371.
- Salgado, L. & Azpilicueta, C.** 2000. Un nuevo saltasaurino (Sauropoda, Titanosauridae) de la provincia de Río Negro (Formación Allen, Cretácico Superior), Patagonia, Argentina. *Ameghiniana*, **37**, 259–264. <https://www.ameghiniana.org.ar/index.php/ameghiniana/article/view/2144>
- Salgado, L. & Gasparini, Z.** 2006. Reappraisal of an ankylosaurian dinosaur from the Upper Cretaceous of James Ross Island (Antarctica). *Geodiversitas*, **28**(1), 119–135.
- Scheyer, T. M. & Sander, P. M.** 2004. Histology of ankylosaur osteoderms: implications for systematics and function. *Journal of Vertebrate Paleontology*, **24**(4), 874–893. doi:10.1671/0272-4634(2004)024%5B0874%3AHOAIOIF%5D2.0.CO%3B2
- Seeley, H. G.** 1881. On the reptile fauna of the Gosau Formation preserved in the Geological Museum of the University of Vienna. *Quarterly Journal of the Geological Society*, **37**, 620–707. doi:10.1144/GSL.JGS.1881.037.01-04.49
- Seeley, H. G.** 1887 [1888]. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London*, **43**, 165–171.
- Sereno, P.** 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **210**, 41–83. doi:10.1127/njgpa/210/1998/41
- Simón, M. E.** 2006. Cáscaras de huevos de dinosaurios de la Formación Allen (Campaniano–Maastrichtiano), en Salitral Moreno, provincia de Río Negro, Argentina. *Ameghiniana*, **43**(3), 513–528. <https://ameghiniana.org.ar/index.php/ameghiniana/article/view/776>.
- Soto-Acuña, S., Vargas, A. O., Kaluza, J., Leppe, M. A., Botelho, J. F., Palma-Liberona, J., Simon-Gutstein, C., Fernández, R. A., Ortiz, H., Milla, V., Aravena, B., Manríquez, L. M. E., Alarcón-Muñoz, J., Pino, J. P., Trevisan, C., Mansilla, H., Hinojosa, L. F., Muñoz-Walther, V. & Rubilar-Rogers, D.** 2021. Bizarre tail weaponry in a transitional ankylosaur from subantarctic Chile. *Nature*, **600**(7888), 259–263. doi:10.1038/s41586-021-04147-1
- Stein, K., Cziki, Z., Curry Rogers, K. C., Weishampel, D. B., Redelstorff, R., Carballido, J. L. & Sander, P. M.** 2010. Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). *Proceedings of the National Academy of Sciences*, **107**, 9258–9263. doi:10.1073/pnas.1000781107
- Sternberg, C. M.** 1921. A supplemental study of *Panoplosaurus mirus*. *Transactions of the Royal Society of Canada*, **15**, 93–102.
- Thompson, R. S., Parish, J. C., Maidment, S. C. R. & Barrett, P. M.** 2012. Phylogeny of the ankylosaurian dinosaurs (Ornithischia: Thyreophora). *Journal of Systematic Palaeontology*, **10**, 301–312. doi:10.80/14772019.2011.569091
- Tumanova, T. A.** 2000. Armoured dinosaurs from the Cretaceous of Mongolia. Pp. 517–532 in M. J. Benton, M. A. Shishkin, D. M. Unwin & E. N. Kurochkin (eds) *The age of dinosaurs in Russia and Mongolia*. Cambridge University Press, Cambridge.
- Uliana, M.** 1979. *Geología de la región comprendida entre los ríos Colorado y Negro, Provincias de Neuquén y Río Negro*. Unpublished PhD thesis, Universidad Nacional de La Plata, 117 pp. <http://sedici.unlp.edu.ar/handle/10915/5080>
- Vickaryous, M. K., Russell, A. P. & Currie, P. J.** 2001. Cranial ornamentation of ankylosaurs (Ornithischia: Thyreophora): reappraisal of developmental hypotheses. Pp. 318–340 in K. Carpenter (ed.) *The armored dinosaurs*. Indiana University Press, Bloomington.
- Vickaryous, M. K., Maryañska, T. & Weishampel, D. B.** 2004. Ankylosauria. Pp. 363–392 in D. B. Weishampel, P.

- Dodson & H. Osmólska (eds) *The Dinosauria*. Second Edition. University of California Press, Berkeley.
- Wichmann, R.** 1927. Sobre la facies lacustre Senoniana de los estratos con Dinosaurios y su fauna. *Boletín Academia Nacional de Ciencias, Córdoba*, **30**, 383–405.
- Wiersma, J. P. & Irmis, R. B.** 2018. A new southern Laramidian ankylosaurid, *Akainacephalus johnsoni* gen. et sp. nov., from the upper Campanian Kaiparowits Formation of southern Utah, USA. *PeerJ*, **6**, e5016. doi: [10.7717/peerj.5016](https://doi.org/10.7717/peerj.5016)
- Wilson, G. P. & Arens, N. C.** 2001. The evolutionary impact of an epeiric seaway on Late Cretaceous and Paleocene palynofloras of South America. *Asociación Paleontológica Argentina Publicación Especial*, **7**, 185–89. <https://peapaleontologica.org.ar/index.php/peapa/article/view/241>
- Zheng, W., Jin, X., Azuma, Y., Wang, Q., Miyata, K. & Xu, X.** 2018. The most basal ankylosaurine dinosaur from the Albian–Cenomanian of China, with implications for the evolution of the tail club. *Scientific Reports*, **8**, 3711. doi: [10.1038/s41598-018-21924-7](https://doi.org/10.1038/s41598-018-21924-7)

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