



Paleodiversity of Late Cretaceous Ankylosauria from Mexico and their phylogenetic significance

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Abstract

Isolated bones and osteoderms of ankylosaurian dinosaurs recovered from Late Cretaceous sediments of northern Coahuila, northeastern Mexico, have been identified as remains of nodosaurids. Here, we summarize these discoveries and provide a review on Mexican Ankylosauria from a taxonomic perspective. We also present a new taxon, *Acantholipan gonzalezi* gen. et sp. nov. from the Pen Formation and provide a phylogenetic analysis integrating the new taxon. *A. gonzalezi* is the first named ankylosaur from Mexico that adds to the currently rare nodosaurid diversity from southern Laramidia.

Keywords Dinosaur · Nodosauridae · Pen Formation · Mexico · Endemism · Laramidia

Abbreviations

AMNH American Museum of Natural History, New York
CEUM College of Eastern Utah Prehistoric Museum, Price
CPC Colección Paleontológica de Coahuila, Museo del Desierto, Saltillo

FHSM Sternberg Museum of Natural History, Hays VP
INAH Instituto Nacional de Antropología e Historia, Mexico
IVPP Institute of Vertebrate Paleontology and Paleoanthropology, Beijing
MTM Magyar Természettudományi Múzeum, Budapest
MUDE Museo del Desierto, Saltillo
ROM Royal Ontario Museum, Toronto
UMNH Utah Museum of Natural History, Salt Lake City

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Introduction

Ankylosauria represent a clade of thyreophoran (shield-bearing) Ornithischia characterized by flat and wide skulls, whose roofs have been densely decorated with osteoderms. The armored bodies of these obligatory quadrupeds are barrel shaped (Carpenter 2012; Vickaryous et al. 2004). Ankylosauria are divided into two families: Ankylosauridae (Brown, 1908) and Nodosauridae (Marsh, 1890). Ankylosauridae are characterized by short and wide skulls, and tail clubs, amongst other features. Nodosauridae have an angled ischium, a body and tail covered with massive osteoderms often forming spines, and lack a tail club

(Arbour and Currie 2016). The highest diversity of Nodosauridae is reached during the Late Cretaceous in North America and Europe. Generally, however, Nodosauridae show a wide range of geographic distribution and are reported from Europe, South America, and Antarctica (Arbour and Currie 2016).

Ankylosaurs are characteristic and abundant components of dinosaur assemblages from the Late Cretaceous of western North America (Laramidia). Campanian strata have yielded numerous specimens of nodosaurids and ankylosaurids, mostly from Canada and the United States. In contrast, the record from the southern part of Laramidia is surprisingly scarce (Loewen et al. 2013; Rivera-Sylva and Carpenter 2014). Ankylosaurid remains are extremely rare in the Late Cretaceous of Mexico, contrasting with the relatively richer hadrosaurian assemblages reported from this region (Morris 1981; Gates et al. 2007; Prieto-Márquez and Serrano-Bráñas 2012; Ramírez-Velasco et al. 2012, 2014). Nevertheless, nodosaurid remains have been reported from Mexican strata, although most of these are undiagnostic (Rivera-Sylva et al. 2011a; Martínez-Díaz and Montellano-Ballesteros 2011). Here, we reexamine the material documented from the “El Gallo Formation” (Campanian) of Baja California Norte, the Aguja Formation (Campanian) of Coahuila, and the Pen Formation

(Santonian) of northern Coahuila (Fig. 1; Palomino-Sánchez 2008; Rivera-Sylva et al. 2011a).

Materials and methods

The material described here includes specimens CPC 272, and CPC 273 housed at MUDE, both comprising incomplete postcranial elements. They were collected under written authorization of INAH through the permits registered in their sections Consejo Nacional de Paleontología (Oficio 401.13-352) and Consejo Nacional de Arqueología (Oficio 401.B(4)19.2013/36/1862).

Photographs were taken with an Olympus E620 SLR camera with a Zuiko 14–42 mm 1:3.5–5.6 zoom and a Zuiko 35 mm, 1:3.5 macro lens under optimal natural light. The images were exempted from their background with GIMP GNU 2.8.22. No other manipulations were made.

For the cladistic analysis, we used the data matrix provided by Arbour et al. (2016) and the slightly modified data matrix of Arbour and Currie (2016). We added the scoring of *Acantholipan gonzalezi* and CPC 273 to this matrix using Mesquite 3.40 (Maddison and Maddison 2018). The phylogenetic analysis was conducted in TNT version 1.1 (Goloboff et al. 2008), using the Traditional Search option



Fig. 1 Geographic location of the ankylosaurid-bearing fossil sites documented here. EG: “El Gallo Formation”, Baja California; SC: San Carlos Formation, Chihuahua; Ag: Aguja Formation, Coahuila;

Pn: Pen Formation, Coahuila; Ol: Olmos Formation, Coahuila; CdP: Cerro del Pueblo Formation, Coahuila

with one random seed and 1000 replicates of Wagner trees, and the tree bisection reconnection (TBR) swapping algorithm, using space for 99,999 trees in memory, and holding ten trees in each replication. All characters were treated as unordered and of equal weight. The strict consensus tree and the majority rule tree (cut 50%) were calculated from the resulting trees. Bremer supports, consistency index (CI) and retention index (RI) were calculated in TNT using the BREMER.RUN and STATS.RUN scripts, respectively.

Systematic paleontology

Dinosauria Owen (1842)

Ornithischia Seeley (1887)

Thyreophora Nopcsa (1915)

Ankylosauria Osborn (1923)

Ankylosauridae Brown (1908)

Ankylosauridae indet.

(Fig. 2a–c)

Referred specimen: CPC 1867, osteoderm (Fig. 2a–c)

Horizon and Locality: The material was recovered from the Cerro del Pueblo Formation (Upper Cretaceous; Campanian); LA 14 near Las Águilas, Porvenir de Jalpa, Coahuila, northeast Mexico.

Description: CPC 1867 is the anterior fragment of an osteoderm, which is transversely broken in the middle. The lateral margin is broken, too. The coarsely pitted and wrinkled external face bears a medial blunt longitudinal keel. The ventral surface is smooth and deeply concave. The maximum length of the fragment is 57.1 mm and the maximum width is 64.1 mm. The maximum thickness is 26.4 mm. The compacta is exceedingly thin, measuring only 2 mm. The large medullar cavity is filled with a foamy irregular spongiosa.

Discussion: Because of the thin-walled compacta, the foamy spongiosa and the deeply concave internal face, the osteoderm is referred to Ankylosauridae (Carpenter, 2004).

Ankylosauridae indet.

Harley J. Garbani identified an osteoderm (LACM 29000) of an ankylosaurid from the “El Gallo Formation” in Baja California (Campanian, Upper Cretaceous) (Morris 1967). The specimen was originally housed in the Los Angeles County Museum, California, USA, and was sent to the Colección Nacional de Paleontología at the Universidad Nacional Autónoma de México (UNAM) in the 1990s. There it was lost (Perrilliat, pers. comm., 2009). However, photos of the lost specimen taken by Tracy Ford in 2000 and shown to one of us (HRS) illustrate half of an internally concave osteoderm that is evidently ankylosaurid.

In his revision of dinosaur material from Mexico, Hernández (1997) mentions the presence of cf. *Euoplocephalus* as well as Nodosauridae indet. from the “El Gallo Formation”. However, the author may simply have followed earlier data given by Morris (1967), because he neither illustrated nor described this material.

Two vertebrae and a metatarsal of an ankylosaurid were reported from the San Carlos Formation (lower Campanian) of Aldama, Chihuahua (Rivera-Sylva et al. 2011a) but were not described because the specimens are housed in a private collection and are not officially available.

Internally concave osteoderms of Ankylosauridae were described by Rivera-Sylva and Espinosa-Chávez (2006) from the Cerro del Pueblo Formation near La Parrita in southern Coahuila. Subsequently, Ramirez-Velasco and Hernández (2014) mention a conical osteoderm with concave internal surface associated with a femur fragment from an unknown locality in Coahuila. Ramirez-Velasco et al. (2014) mention the presence of a metatarsal fragment of Ankylosauria from the Olmos Formation, and a phalanx from the Cerro del Pueblo Formation, both in Coahuila, but

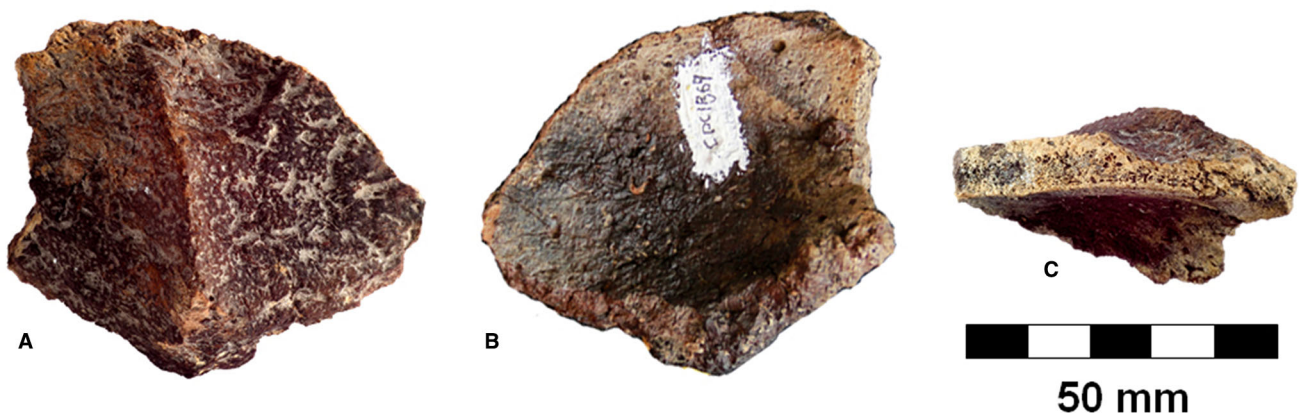


Fig. 2 Ankylosaurid osteoderm (CPC 1867) in: **a** dorsal, **b** ventral, and **c** lateral views. Scale: 50 mm

they neither illustrate the specimens nor do they provide measurements or a detailed description of the material, which can therefore not be identified.

An ankylosaur femur from the Olmos Formation near Sabinas, Coahuila, was mentioned by Meyer et al. (2005), but neither properly described nor depicted, because it was housed in a private collection.

Nodosauridae Marsh, 1890

***Acantholipan* gen. nov.**

urn:lsid:zoobank.org:act:BEB89092-0429-49A0-B985-FDA4225E62BE

***A. gonzalezi* sp. nov.**

urn:lsid:zoobank.org:act:4C5F0E44-9C7D-4807-B75B-657091475CFA

Fig. 3a–g

Etymology: Greek *ακανθός* (acanthus) = spine; and the Spanish contraction of *Lépai-Ndé* (gray people) *lipan*, a tribe of Apaches from northern Mexico; *gonzalezi* = in honor of Arturo H. Gonzalez González, for his outstanding support to Mexican paleontology.

Holotype (Fig. 3a–g):

One dorsal vertebra, one caudal vertebra, one rib fragment, the distal end of a left humerus, a left ulna, the distal end of a left femur, and one distal thoracic osteodermal spine. The holotype of *Acantholipan gonzalezi* has been previously figured (Rivera-Sylva et al. 2011a: Fig. 3), except for the caudal vertebra, rib and femora that are figured here for the first time (Fig. 3d, f, g). The specimen is housed at the Colección Paleontológica de Coahuila (CPC) at the Museo del Desierto, Saltillo, Coahuila, Mexico, under the collection number CPC 272.

Horizon and locality: The material was recovered from the Pen Formation (Upper Cretaceous, Santonian), at the Los Primos locality, south of the town of San Miguel (Rivera-Sylva et al. 2011a: Fig. 1), Municipality of Ocampo, Coahuila, Mexico. The exact locality information is on file at the MUDE and is supplied on request.

Diagnosis: Combination of the following characters: (1) ulna with anterolateral process prominent, tapering and truncated proximally (triangular in lateral view); (2) conical and slightly caudally curved lateral thoracic osteoderm with a longitudinal oval cross section and vascular grooves on the lateral face only.

Description: The specimen is from one individual and has previously been documented by Rivera-Sylva et al. (2011a) but had not been formally named as a new species. We refer to this publication for description of the non-diagnostic material. Here, we only reevaluate the ulna and an

◀**Fig. 3** *Acantholipan gonzalezi* gen. et sp. n., holotype, CPC 272; left ulna in: **a**₁ caudal; **a**₂ cranial; **a**₃ lateral; distal thoracic osteodermal spine in: **b**₁ right lateral; **b**₂ left lateral; **c** dorsal vertebra in cranial view; caudal vertebra in: **d**₁ cranial and **d**₂ ventral views; humerus in: **e**₁ caudal and, **e**₂ ventral views; femur in: **f**₁ right lateral; and, **f**₂ cranial views; **g** rib. Scale: 100 mm

osteodermal spine, being the only diagnostic elements of the present material.

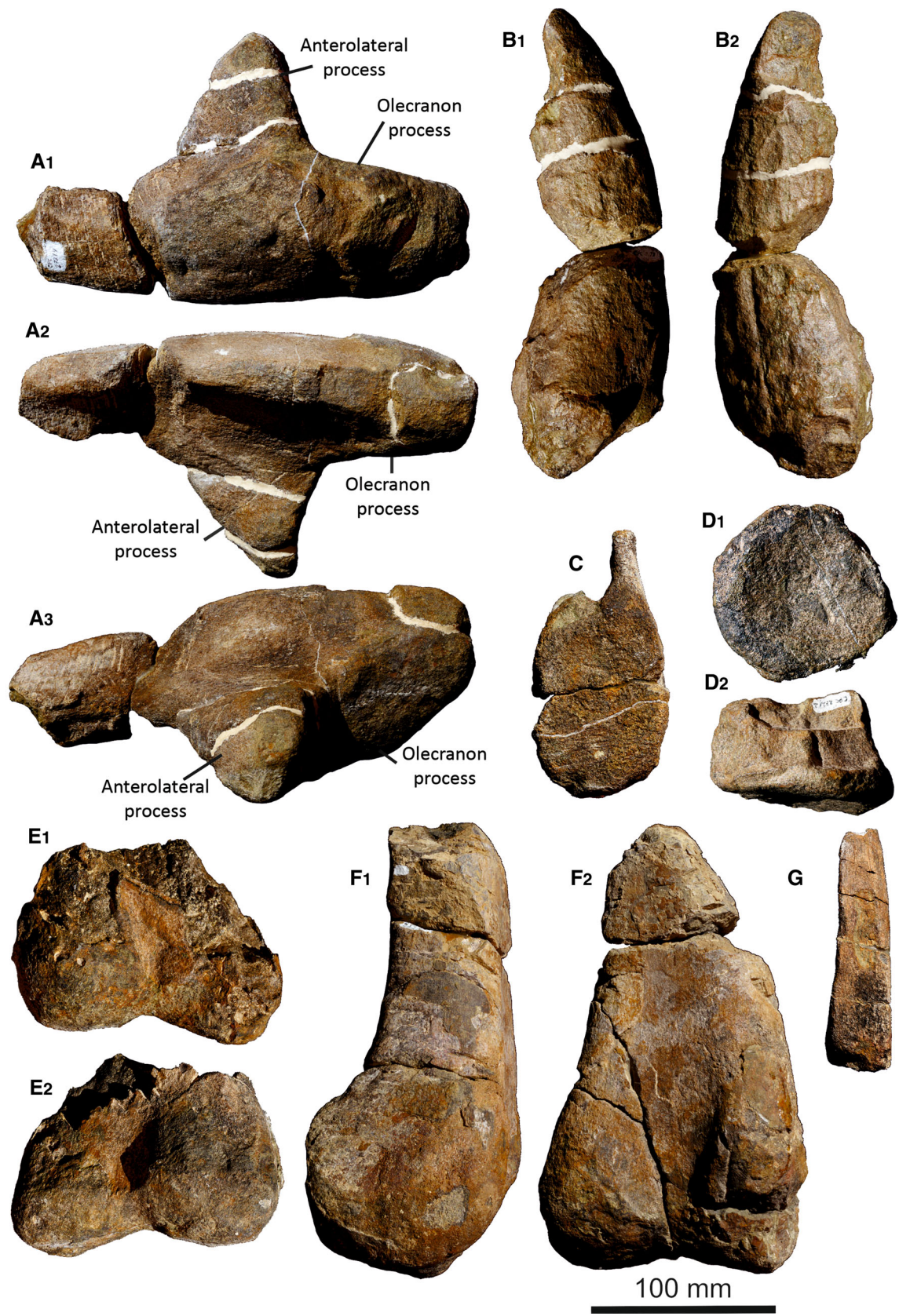
Left ulna (Fig. 3a)—the left ulna of CPC 272 lacks its distal third. The olecranon is prominent, wedge-shaped in lateral view and proximally truncated as in other ankylosaurs (Vickaryous et al. 2004), with a length/height ratio of 1:1. In anterior view, the olecranon of CPC 272 forms a broad, inverted right-angled triangle. However, its proximal end is rounded and not pointed as in *Sauropelta*. The humeral notch at the base of the olecranon is well developed and thus resembles that of *Niobrariasaurus* and *Stegopelta*, while the radial notch placed lateral to it is shallow and thus similar to that of other ankylosaurs (Rivera-Sylva et al. 2011a). The anterolateral process is unusually prominent compared with other nodosaurids; it forms an isosceles triangle in outline and is similar in length to the olecranon process.

Osteodermal spine (Fig. 3b)—a long and conical horn-like spine with slight caudal curvature is here interpreted as a posterior thoracic osteoderm (Rivera-Sylva et al. 2011a). In cross section, it is longitudinally oval with a length/width ratio of 1:3. Vascular grooves are present on its entire lateral face only, thus somewhat resembling a ceratopsian horn-core. CPC 272 is identified as a nodosaurid osteodermal spine because of its conical outline and longitudinal oval cross section.

Comments and comparisons: Nine nodosaurids are presently identified from the Late Cretaceous of North America: *Panoplosaurus*, *Edmontonia*, *Glyptodontopelta*, *Niobrariasaurus*, *Nodosaurus*, *Silvisaurus*, *Stegopelta*, *Aletopelta*, and *Denversaurus* (Carpenter, 2012).

While *Acantholipan gonzalezi* is of Santonian age, *Stegopelta*, *Silvisaurus*, and *Nodosaurus* are Cenomanian in age, *Niobrariasaurus* is a Coniacian taxon, and *Panoplosaurus*, *Glyptodontopelta*, and *Denversaurus* are Maastrichtian in age (Carpenter 2004, 2012; Burns 2008). Only *Edmontonia* and *Aletopelta* are of Campanian age and thus closer with *A. gonzalezi* from the Pen Formation.

The anterolateral process of the ulna of *A. gonzalezi* differs from that of *Edmontonia*, *Aletopelta*, *Peloropiltis*, *Hungarosaurus*, and UMNH VP 19473 where the olecranon is half the length of the anterolateral process, while in *A. gonzalezi* it has a 1:1 ratio in its prominence compared with the olecranon, with its truncated proximal end similar



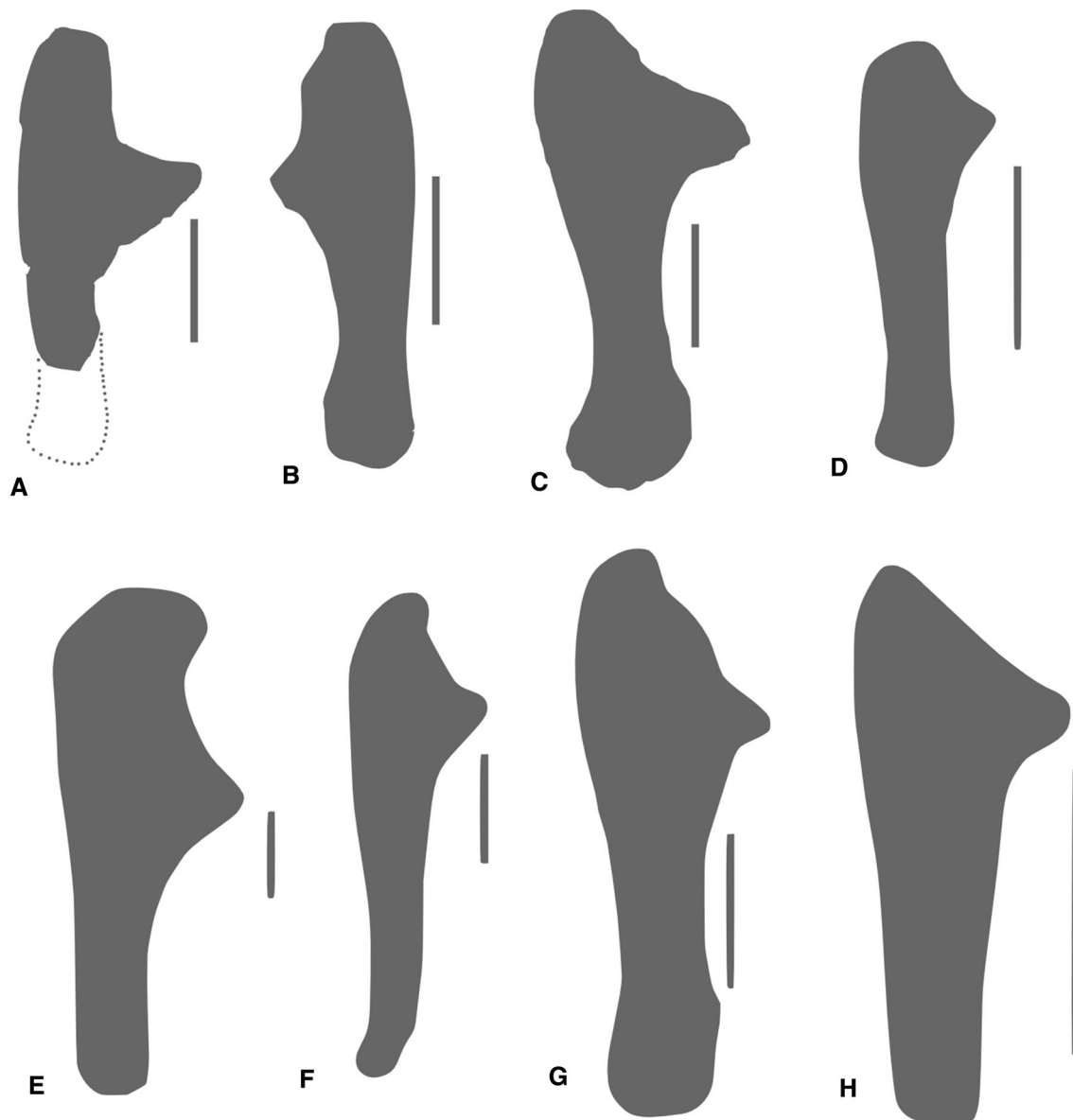


Fig. 4 Comparison of outline drawings of ankylosaur ulnae. **a** *Acantholipian gonzalezi* (CPC 272), left ulna in medial view; **b** *Edmontonia rugosidens* (ROM 1215), left ulna in anterior view; **c** UMNH VP 19473, ulna in lateral view; **d** *Liaoningosaurus paradoxus* (IVPP V12560), left ulna in medial view; **e** *Peloroplites cedrimontanus* (CEUM 11347), right ulna in lateral view; **f** *Hungarosaurus tormai*

(MTM 2007.25.2), right ulna in lateral view; **g** *Niobrarsaurus coleii* (FHSM VP-14855), right ulna in lateral view; **h** *Minmi* sp. (QMF 18101), left ulna in medial view. Scale bars in **a–c**, **e–h** equal 10 cm; scale bar in **d** equals 1 cm After: Carpenter et al. (1995), Han et al. (2014); Russell (1940)

to *Niobrarsaurus coleii* (FHSM VP-14855) (Fig. 4) and *Stegopelta* (Carpenter and Kirkland, 1998).

Ford (2000), Burns (2008) and Burns and Currie (2014) stated that osteoderms of nodosaurids bore diagnostic characters, which is corroborated here in *A. gonzalezi*. With a width-length ratio of 1:3, the osteodermal spine of *A. gonzalezi* is longer, with respect to its width, than in both *Edmontonia* and *Aletopelta* where the ratio is 1:2. In *Edmontonia*, the thoracic spines are slightly transversely compressed and straight, terminating in a blade (Sternberg

1928). In *Aletopelta* they are much more laterally compressed, being three to four times longer than wide, with blunt anterior and posterior keels (Coombs and Deméré 1996). The osteodermal spine of *A. gonzalezi* closely resembles those reported for the Santonian *Hungarosaurus* and *Struthiosaurus* from Europe (Ősi and Pereda-Suberbiola 2017), but the grooves of *A. gonzalezi* are wider than those reported for the European taxa. The osteodermal spine is interpreted as a distal thoracic spine because it was found near the femur and the caudal vertebra.

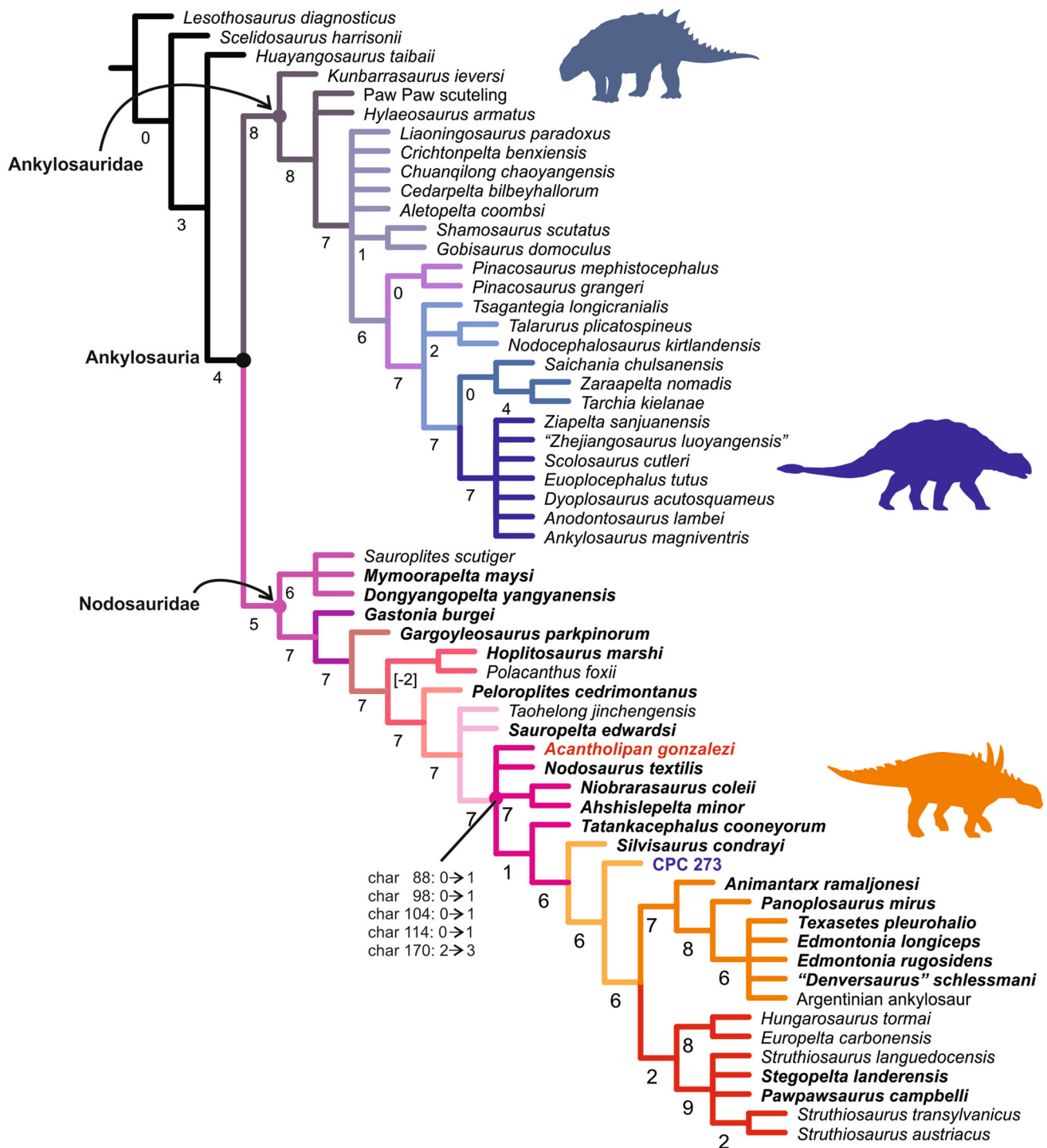


Fig. 5 Strict consensus tree of Ankylosauria, illustrating the phylogenetic position of *Acantholipan gonzalezi* and CPC 273 (TL: 573, CI: 0.396, RI: 0.648). North American nodosaurids are marked in bold. Numbers below line are Bremer Support

The remains of *A. gonzalezi* were discovered in coastal to shallow marine sediments, like those of other nodosaurids (e.g., *Aletopelta*, *Borealopelta*, *Nodosaurus*, *Stegopelta*, *Pawpawsaurus*, and *Niobrarasaurus*, Carpenter

and Kirkland 1998; Carpenter et al. 1995; Ford and Kirkland 2001; Arbour et al. 2016; Brown et al. 2017).

Nodosauridae indet.

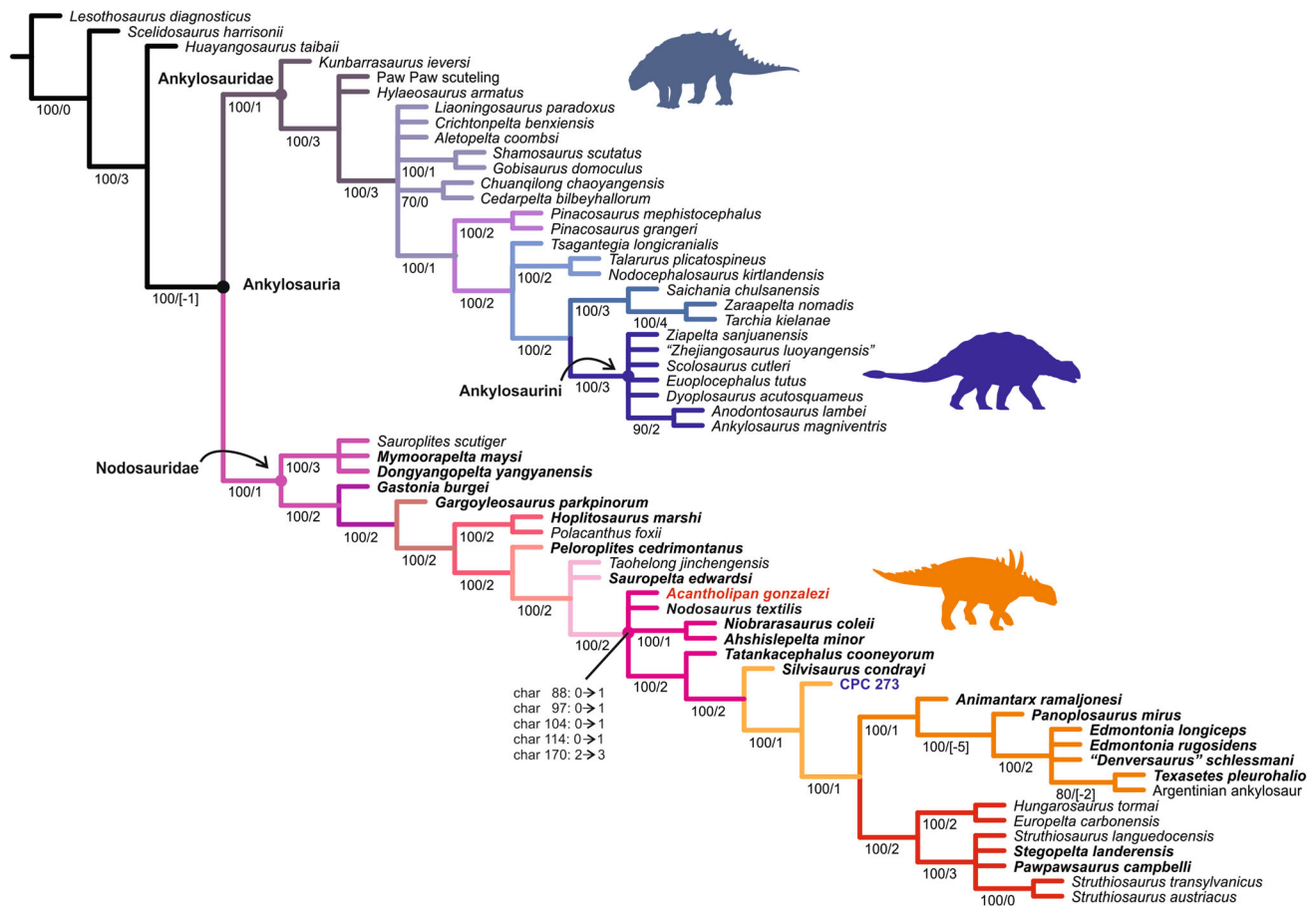


Fig. 6 Majority rule tree (cut 50%) of Ankylosauria, showing the position of *Acantholipan gonzalezi* and CPC 273 (TL: 569, CI: 0.399, RI: 0.652). North American nodosaurids are here marked in bold. Numbers below line frequency/Bremer

Evidence for Nodosauridae comes from the El Jabón Creek locality, “El Gallo Formation” (Campanian), El Disecado member, Baja California, Mexico. This material includes a tooth (UABC FCM 2625) (Rivera-Sylva et al. 2011a), which resembles those of the nodosaurid *Aletopelta coombsi* from the Campanian of California (Ford and Kirkland 2001; Rivera-Sylva and Carpenter 2014), which is of similar stratigraphic range. Martínez-Díaz and Montellano-Ballesteros (2011) mention a vertebra from the Campanian Aguja Formation at Los Altares, northeast Chihuahua, and four osteoderms from the El Rebaje locality, northern Coahuila, that were originally referred to *Panoplosaurus* by Martínez-Díaz and Montellano-Ballesteros (2011). However, ankylosaurian vertebrae are only diagnostic at family level (Vickaryous et al. 2004). Rivera-Sylva et al. (2011a) describe a nodosaurid caudal vertebra from the Cerro del Pueblo Formation, and Martínez-Díaz and Montellano-Ballesteros (2011) mention the presence of nodosaurid osteoderms and a tooth from the same formation, but the “osteodermal spine” in their description was

later identified as the nasal horn of a ceratopsian, because the core has a thick cortical layer with a spongy center (Carpenter, pers. comm., 2016).

Rivera-Sylva et al. (2011a: Fig. 4) described Specimen C (CPC 273) as ‘Nodosauridae indet.’. In this individual, the external ornamentation of the osteoderm most closely resembles that reported by Burns (2008) for *Glyptodontopelta* in showing large smooth areas interrupted by a moderate amount of randomly distributed small pits and vascular grooves that radiate from the keel. In contrast to the osteoderms of *Glyptodontopelta*, the external texture of the CPC 273 is less extensive and shallower.

The basal plates of the thoracic osteoderms of CPC 273 are round (Rivera-Sylva et al. 2011a). The keel is prominent and directed laterally. It emerges from the craniomedial margin and continues in oblique direction caudolaterally; it ends at the caudal margin of the osteoderm. The external surface is ornamented with shallow radiating dendritic grooves. This ornamentation differs from both *Panoplosaurus* and *Glyptodontopelta*, which

lack a dendritic surface on their osteoderms, being rather smooth. According to Rivera-Sylva et al. (2011a), CPC 273 preserves one of the lateral-most osteoderms of the anterior-most cervical ring and one spine that closely resembles those projecting anterolaterally from the neck of *Stegopelta* (Carpenter and Kirkland 1998). The large oval low-keeled osteoderm of CPC 273 resembles the medial osteoderms of *Edmontonia rugosidens* (AMNH 5665).

Phylogenetic analysis

Ten most parsimonious trees were recovered from our phylogenetic analysis with a best score of 555 (TBR). Both strict and majority rule trees are similar in their general topology. The strict consensus tree shows a CI of 0.396, RI of 0.648 and TL of 573 (Fig. 5). The majority rule tree presents a CI of 0.399, RI of 0.652 and TL of 569 (Fig. 6).

Although few characters could be scoring to *Acantholipan gonzalezi* and CPC 273, they give an idea of the phylogenetic position of the analyzed specimens and the results show that both taxa are nested within Nodosauridae.

In our analysis, *Sauroplices scutiger*, *Mymoorapelta maysi* and *Dongyangopelta yangyanensis* form a polytomy and are considered as the basal-most clade of nodosaurs. *Acantholipan gonzalezi* is recovered in polytomy comprising *Nodosaurus textilis*, but also with *Ahshislepelta* + *Niobrarsaurus* and a large unnamed clade comprising *Tatankacephalus* and more nested taxa. Within nodosaurs, CPC 273 is definitely more deeply nested among ankylosaurid OTUs than *A. gonzalezi*, and is positioned as sister taxon to the clade composed of two lineages, one predominately North American and the second largely being Eurasian in taxic scope. The North American group, which comprises *Animantrax*, *Panoplosaurus*, *Edmontonia* spp., “*Denversaurus*”, *Texastes*, and the Argentinian ankylosaur, could bear the label Panoplosaurinae. The unnamed second clade contains the Eurasian forms *Hungarosaurus*, *Europelta*, and *Struthiosaurus*, and the North American *Stegopelta* and *Pawpawsaurus*. The indeterminate juvenile nodosaurid from the Paw Paw Formation is identified as a basal ankylosaur, contrary to the analysis of Arbour et al. (2016) in which this OTU was interpreted to be a derived nodosaurid close to *Ahshislepelta minor* and *Niobrasaurus coilei*.

Our consensus tree by majority rule is slightly different from that obtained by Arbour et al. (2016), mainly in the resolution of Nodosauridae. These differences are less evident when *Acantholipan gonzalezi* and CPC 273 are included.

Discussion

The presence of the new nodosaurid from northeastern Mexico, *Acantholipan gonzalezi*, provides further evidence for an isolated local endemism, which has been similarly reported for other coeval dinosaurs of southern Laramidia (Lehman 1987, 1997, 2001; Sankey 2008; Prieto-Marquez et al. 2012; and Rivera-Sylva et al. (2011b, 2017)). On a global scale, ankylosaur diversity appears to be correlated with the diversification of specific food plants (Ösi et al. 2017). In America, this diversification of vegetation may have depended on climate, resulting in a north–south gradient. It was likely characterized by periodic semi-arid to arid intervals occurring earlier in the south than in the north and resulting in a vicariation of vegetation regimes. Ankylosaurs reacted to these climatic and vegetation changes with diversification, resulting in a climatic and floral decoupling of North and South Laramidia and an allopatric separation of species of herbivore dinosaurs such as ankylosaurs (Loewen et al. 2013).

The likely endemism of the two ankylosaurids of northeastern Mexico, *Acantholipan gonzalezi* and CPC 273, is consistent to that seen in other coeval dinosaurs from the area (i.e., tyrannosaurids, hadrosaurids, and ceratopsians), which have also been interpreted as endemic to this particular region as a result of the ecological separation of northern and southern Laramidia (Sampson et al. 2004; Sampson and Loewen 2010; Sampson et al. 2010; Gates et al. 2012). A hitherto unknown geographical or climatic barrier may consequently have separated northeastern Mexico and thus the southern shoreline of Laramidia, from areas located to the north of the subcontinent. This barrier must have existed long enough to allow for an allopatric diversification of northern and southern Laramidian faunal regimes (Rivera-Sylva et al. 2011b).

Conclusions

Here, we present the first diagnosable nodosaurid ankylosaur from Mexico and the southernmost North American thyreophoran: *Acantholipan gonzalezi*. The phylogenetic analysis of this Santonian taxon supports the inclusion of this new genus and species within Nodosauridae.

Significant faunal differences existed between Late Cretaceous dinosaur assemblages of North and South Laramidia and were likely triggered by climatic belts across the continent resulting in a diversification of floral regimes. This interpretation is consistent with the high degree of endemism of Late Cretaceous dinosaurs in northeastern Mexico, including the one described here. Although the diagnostic material of Mexican Thyreophora

is presently limited, the discovery of more complete specimens in the future may allow us to better understand the reasons for an allopatric diversification of Thyreophora and other dinosaur groups in the Late Cretaceous of Laramidia.

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