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NEW THYREOPHORAN REMAINS WITH STEGOSAURIAN AFFINITIES FROM THE LOWER CRETACEOUS OF ARGENTINA

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Abstract. South American Mesozoic vertebrate fossils are key to contrasting the classic North American and European views of clade evolution. Over the past decades, several relevant findings of stegosaurian remains from Argentina have revealed a greater diversity than previously thought. These include the early stegosaur *Isaberrysaura* from the Los Molles Formation (Middle Jurassic) and indeterminate stegosaurian remains from the Cañadón Calcáreo (Upper Jurassic) and the La Amarga (Lower Cretaceous) formations, all from the Argentinian Patagonia. To increase the knowledge of stegosaurian presence and diversity in South America, we present here new remains from the Berriasian–Valanginian Bajada Colorada Formation of Neuquén Province (Argentina). These consist of sacral vertebrae, dorsal ribs and several osteoderm types, including stegosaurian-like spines. Overall anatomical features (*e.g.*, sacral vertebrae and ribs dorsoventrally compressed, and dorsal ribs with T-shaped proximal transverse section), shape analysis of the sacral vertebrae, and the morphological disparity of the osteoderms support an assignation to Thyreophora with affinities to Stegosauria. The finding of these remains in Bajada Colorada reinforces the presence of stegosaurs in the Argentine Patagonia during the Lower Cretaceous. Our explorations and research in Bajada Colorada support the hypothesis that the historical absence of stegosaurian remains in the southern continents was due to search and/or preservational biases, as other authors proposed. These new stegosaurian remains also support the presence of a transitional fauna in Bajada Colorada, including both Jurassic and Cretaceous components.

Key words. Stegosauria. Thyreophora. Patagonia. Argentina. Lower Cretaceous. Bajada Colorada Formation.

Resumen. NUEVOS RESTOS FÓSILES CON AFINIDADES ESTEGOSAURIANAS DEL CRETÁCICO INFERIOR DE ARGENTINA. Los fósiles de vertebrados del Mesozoico de América del Sur son importantes para contrastar las visiones norteamericanas y europeas sobre la evolución de los clados. Durante las últimas décadas, varios hallazgos relevantes de restos estegosaurianos de Argentina han revelado una diversidad mayor de la pensada. Estos incluyen al estegosaurio basal *Isaberrysaura* de la Formación Los Molles (Jurásico Medio) y restos indeterminados de Stegosauria de las formaciones Cañadón Calcáreo (Jurásico Superior) y La Amarga (Cretácico Inferior), todos ellos procedentes de la Patagonia Argentina. Con el objetivo de incrementar el conocimiento del registro fósil y diversidad de estegosaurios en América del Sur, aquí presentamos nuevos restos de la Formación Bajada Colorada (Berriasiano–Valanginiano) de la Provincia de Neuquén (Argentina). Estos consisten en vértebras sacras, costillas dorsales y varios tipos de osteodermos, incluyendo espinas de morfología estegosauriana. Caracteres anatómicos generales (*e.g.*, vértebras y costillas sacras dorsoventralmente comprimidas, y costillas dorsales con sección proximal en forma de T), la conformación de las vértebras sacras y la disparidad morfológica de los osteodermos soportan una asignación a Thyreophora con afinidades a Stegosauria. El hallazgo de estos materiales en Bajada Colorada refuerza la presencia de estegosaurios en la Patagonia Argentina durante el Cretácico Inferior. Los resultados obtenidos en Bajada Colorada son consistentes con la propuesta de otros autores de que la ausencia histórica de restos de estegosaurios en el hemisferio sur se debe a sesgos de búsqueda y/o de preservación. Se soporta la presencia de una fauna transicional en Bajada Colorada que incluye componentes jurásicos y cretácicos.

Palabras clave. Stegosauria. Thyreophora. Patagonia. Argentina. Cretácico Inferior. Formación Bajada Colorada.

INTRODUCTION

Thyreophoran (armored dinosaurs) remains from the Southern Hemisphere are much less abundant than those from the Northern Hemisphere (Pereda-Suberbiola et al., 2015; Maidment et al., 2020). However, new findings over the last decades have progressively increased their presence in southern continents, and the relevance of southern forms in the evolution of the clade.

The thyreophoran fossil record from Gondwana spans from the Lower Jurassic to the latest Cretaceous. Some relevant findings from Eastern Gondwana include stegosaurs and ankylosaurs. The stegosaur *Kentrosaurus* (Hennig, 1915) from the Upper Jurassic of Tanzania was a reference taxon for basal stegosaurs until the discovery of *Huayangosaurus* from the Upper Jurassic of China (Dong et al., 1982; see the age change in Maidment et al., 2020). Also, several recent findings from the Middle Atlas Mountains of Morocco were relevant for thyreophoran diversity. The stegosaurid *Adratiklit* (Maidment et al., 2020), from the Middle Jurassic of Morocco, suggests quick diversification and global distribution of stegosaurs after their origin. From stratigraphically near layers, the dacentrurine *Thyreosaurus* (Zafaty et al., 2024) reveals a new and unique armor configuration of recumbent plates on the back. Among ankylosaurs, these Mid-Jurassic rocks also provided the first known ankylosaur from Africa, *Spicomellus* (Maidment et al., 2021, 2025). In the Lower Cretaceous of Australia, the ankylosaurs *Minmi* (Molnar, 1980; Molnar & Frey, 1987) and *Kunbarrasaurus* (Molnar, 1996; Leahey et al., 2015) are the most relevant. The latter being an almost complete articulated specimen commonly recovered as a basal ankylosaur in most phylogenies (*i.e.*, Soto-Acuña et al., 2021). These are complemented with taxa either incomplete (*Paranthodon* from the Early Cretaceous of South Africa; Galton & Coombs, 1981; Raven & Maidment, 2018), or problematic ("*Dravidosaurus*" from the Upper Cretaceous of India; Yadagiri & Ayyasami, 1979; Chatterjee & Rudra, 1996; Maidment et al., 2008; Galton, 2012), and many indeterminate thyreophoran (Nath et al., 2002; Rauhut & López Arbarello, 2009; Ridgwell & Sereno, 2010; Ridgwell, 2011; Galton, 2012, 2019) and ankylosaurian (de Valais et al., 2003; Gasparini et al., 2015; Rozadilla et al., 2021) remains.

The last few years have shed several new findings from South America that have helped to establish the Gondwanan thyreophorans in a global context. The discovery of the Upper Cretaceous thyreophoran *Jakapil* from Argentina, closely related to *Scelidosaurus*, suggests the survival of basal thyreophorans in South America, thus spanning Jurassic–Cretaceous times (Riguetti et al., 2022b; Fonseca et al., 2024). The almost complete ankylosaur *Stegouros* (Soto-Acuña et al., 2021) from Upper Cretaceous deposits of Chile enabled the establishment of a Gondwanan ankylosaur clade, Parankylosauria, together with *Kunbarrasaurus* and *Antarctopelta* (the latter from the Upper Cretaceous deposits of the Antarctic Peninsula, and the first dinosaur found in Antarctica; Gasparini et al., 1987; Salgado & Gasparini, 2006). Conversely, the nodosaurid *Patagopelta* (Salgado & Coria, 1996; Riguetti et al., 2022a) from the Upper Cretaceous of Argentina supports both the presence of a migrant ankylosaur lineage from North America and a mixed ankylosaurian fauna in South America during the latest Cretaceous (Riguetti et al., 2024). Alternative interpretations are presented by Maidment et al. (2025).

Although very incomplete, stegosaurian remains from Argentina represent both the oldest and some of the youngest forms worldwide. The basal stegosaur *Isaberrysaura* from the Middle Jurassic Los Molles Formation represents the oldest thyreophoran record from South America (Salgado et al., 2017; see also Han et al., 2017, and Maidment et al., 2020) and the oldest record stegosaur worldwide (Sánchez-Fenollosa & Cobos, 2025, and references therein). The presence of *Isaberrysaura* in South America, together with other early stegosaurs in geographically distant regions such as Morocco and China, suggests rapid diversification of the group during the Middle Jurassic (Zafaty et al., 2024). Conversely, indeterminate remains from the Lower Cretaceous La Amarga Formation represent one of the younger members of the clade (Bonaparte, 1986; Pereda-Suberbiola et al., 2013; discussed by Maidment et al., 2008), together with some other partial remains from China and Mongolia (see Sánchez-Fenollosa & Cobos, 2025, and references therein). Additional partial stegosaurian remains from Argentina include a partial humerus from the Upper Jurassic Cañadón Calcáreo Formation (Rauhut et al., 2021), and possible osteoderms from the Lower Cretaceous Bajada Colorada Formation (Apesteguía et al., 2015; discussed by Riguetti, 2017).

The increasing number of research groups performing fieldwork in Jurassic and Lower Cretaceous Gondwanan outcrops over the last decades has resulted in new information suggesting that the apparent lack of thyreophoran fossils may reflect sampling bias rather than a true biogeographic pattern (Maidment et al., 2020). One of these recently studied areas is the Bajada Colorada Formation (Berriasian–

Valanginian) at the homonym locality in Neuquén Province, Argentina (Gallina et al., 2021a). These deposits have yielded remains of several dinosaur species, including sauropods like the diplodocid *Leinkupal laticauda* (Gallina et al., 2014), the dicraeosaurid *Bajadasaurus pronuspinax* (Gallina et al., 2019; Garderes et al., 2023), and the titanosaur *Ninjatitan zapatai* (Gallina et al., 2021b), as well as partial remains of indeterminate abelisaurid, coelurosaur, megalosaurid and noasaurine theropods (Canale et al., 2017, 2019, 2021). In this context, we present here new thyreophoran remains with stegosaurian affinities from this site. These new materials strengthen the presence of stegosaurian dinosaurs in Bajada Colorada, allowing a reevaluation of previously published remains, and provide a basis for discussing similarities between the ancient fauna from the Upper Jurassic worldwide and the Lower Cretaceous Bajada Colorada Formation.

Geological context

The type locality of the Bajada Colorada Formation is located at the northwestern margin of the Limay River, almost 200 km southwest of the city of Neuquén, Neuquén Province, Argentina (Fig. 1A). At this locality, the outcrops reach a thickness of nearly 150 m (Leanza & Hugo, 1997). More extensive and thicker outcrops of the formation occur toward the central region of the Neuquén Province and in the northwestern part of the Río Negro Province. Following stratigraphic correlations with the Mulichinco Formation (Leanza, 1981) and the Rayoso Formation within the Río Limay Group (Herrero Ducloux, 1946; Pozzo, 1956), the Bajada Colorada Formation (Roll, 1939) was finally established as a distinct unit within the Mendoza Group, based on both seismology (Foucault et al., 1987) and surface geological studies, with an estimated upper Berriasian–lower Valanginian age (Leanza & Hugo, 1997; Fig. 1B).

The Bajada Colorada Formation consists of reddish continental rocks that overlie the Picún Leufú Formation in a transitional contact and are overlain by the Agrio Formation across an erosive discordance (the Huncálica or Intravalanginiana discordance; Leanza et al., 2011). The Bajada Colorada Formation is mainly composed of reddish conglomerates, coarse sandstones, siltstones and claystones with several grayish, brownish and violet tonalities, arranged in rhythmic sequences with normal grading. At the base, there is a predominance of fine and coarse conglomerates intercalated with trough cross-stratified sandstones. In the upper portion, the layers are thinner, fine-grained and more intensely reddish, alternating with light green layers (Leanza & Hugo, 1997; Leanza et al., 2011). According to Leanza and Hugo (1997), the eastern outcrops at the type locality of the Bajada Colorada Formation are thinner and finer-grained than those of the western outcrops (near the National Route 40). The formation also preserves paleosols (Leanza & Hugo, 2001), numerous opalized tree trunks and a diverse assemblage of dinosaur remains (Leanza & Hugo, 1997; Gallina et al., 2021b).

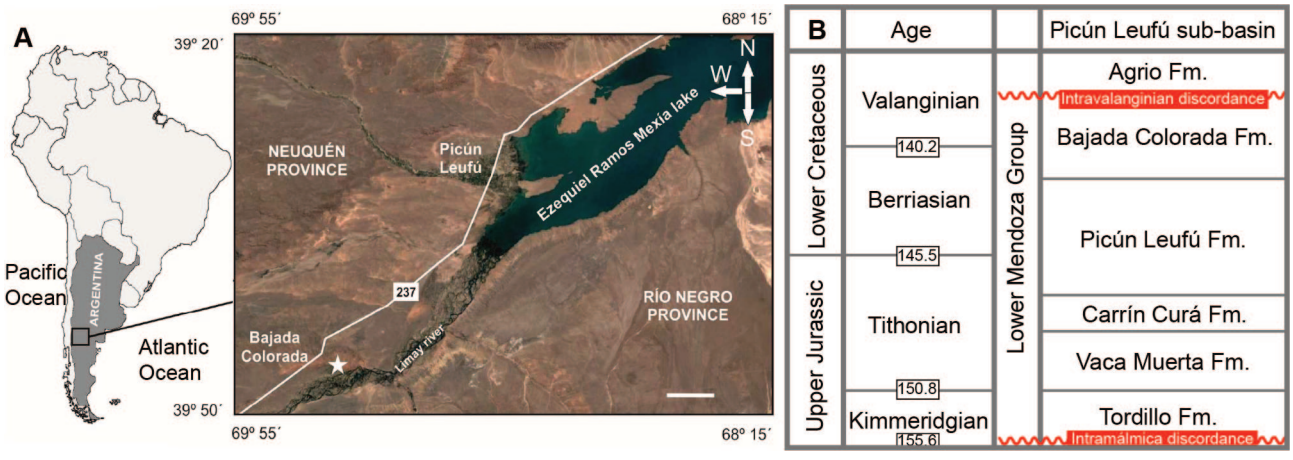

Figure 1. A, Locality of the Bajada Colorada Formation (modified from Canale et al., 2017) Scale = 10 km. B, Stratigraphic placement of the Bajada Colorada Formation at the Picún Leufú Sub-Basin, Neuquén Province, Argentina (modified from Leanza et al., 2011).

At the type locality, the main fossiliferous site studied here is located near the base of a multiepisodic bed of mid- to fine-grained (locally coarse) sandstones, with trough cross-stratification, almost 2 m thick. This bed is violet colored towards its base and reddish in the upper part. The base conformably contacts over a bed of orange to red siltstones (1.2 m thick), and the upper surface is in erosive contact with a fine-grained conglomeratic bed with trough cross-stratification (70 cm thick). The bones described here were collected near the base of this sandstone bed.

The Bajada Colorada Formation is interpreted as fluvial deposits (meandering or anastomosed types; sometimes interpreted as a deltaic system; Leanza & Hugo, 1997) formed under variable energy conditions, ranging from very high to moderate, and including intercalations of hyperconcentrated flows (Leanza et al., 2011).

MATERIALS AND METHODS

The described materials are deposited in the vertebrate paleontology collection of the Museo Municipal Ernesto Bachmann (Villa El Chocón, Neuquén Province, Argentina). These include two sacral fragments (MMCh-PV 293 and 294), four dorsal rib fragments with an associated osteoderm (MMCh-PV 291), and several isolated osteoderms (MMCh-PV 72-1, 72-2, 72-3, 72-4, 118, 153, 226, 227, 253, 249, 250, 251, 252, 254, 266 and 291). All elements were collected in several field trips between 2015 and 2022. For osteoderm orientation and identification, we follow the criteria commonly used in thyreophoran osteoderms (*e.g.*, Ford, 2000; Blows, 2001a, 2001b; Burns & Currie, 2014; Blows, 2015), complemented by direct comparisons with non-standardized osteoderm descriptions (*e.g.*, Galton, 1982; Maidment et al., 2015; Kinneer et al., 2016; Norman 2020b).

Comparisons were performed using both literature and first hand observation of several individuals, including the sauropods *Leinkupal*, *Futalognkosaurus*, *Volkheimeria*, an indeterminate Titanosauria (MLP 46-VIII-21-2), *Limaysaurus*, *Andesaurus*, indeterminate Rebbachisauridae (several remains of the MMCh-PV collection), and titanosaurian osteoderms (MACN-PV-RN-233); ornithopods such as *Macrogryphosaurus* (MUCPv-321), *Huallasaurus* (=*Kritosaurus*; MACN-PV 02), an indeterminate Hadrosauridae (several remains of the MPCA-PV collection); and theropod remains of the MMCh-PV collection (*e.g.*, *Meraxes*). This was complemented with digitized material provided by Xabier Pereda-Suberbiola, Pablo Gallina, Susannah Maidment, Ralph Molnar, the Museum für Naturkunde (Berlin), and several virtual paleontological collections (*e.g.*, AMNH and NHM). In addition, to make an accurate identification through shape analysis, we performed a Principal Component Analysis (PCA) of the sacral fragments MMCh-PV 293 and 294, complemented with a Canonical Variate Analysis (CVA) to test group discrimination comparisons, following the methods proposed by Klingenberg (2011; see also Villalobos Leiva & Benítez, 2020). Methodological details are included in the Appendix S1.

Institutional acronyms. AMNH, American Museum of Natural History, New York, USA; **CV,** Natural History Museum, Chongqing, China; **MACN-PV,** División de Paleontología, Colección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina; **MfN,** Museum für Naturkunde, Berlín, Germany; **MLP-PV,** Museo de La Plata, División Paleontología de Vertebrados, La Plata, Argentina; **MMCh,** Museo Municipal de Villa El Chocón, Argentina; **MPCA-PV,** Museo Provincial Carlos Ameghino, Colección Paleovertebrados, Cipolletti, Argentina; **MUCPv,** Museo Universidad Nacional del Comahue, Paleotología de Vertebrados, Neuquén, Argentina; **NHM,** Natural History Museum, London, England; **SM,** Smithsonian Museum, Washington, USA; **YPM,** Peabody Museum of the Yale University, New Haven, USA.

RESULTS

Taphonomic comments

Considering the geological aspects of the site and the taphonomic attributes of the bones, several inferences can be made regarding the burial history of the fossil association from Bajada Colorada. The bones exhibit low degrees of bioerosion, abrasion, surface alteration and fragmentation (and therefore low sphericity and roundness), common association of taxonomically compatible materials, and are preserved in comparable proportions of elements with different bone density and shape (*e.g.*, teeth vs vertebrae). These indices suggest a relatively rapid burial with low or

null transport of the dead assemblage. The presence of closely associated and articulated remains, as well as the azimuthal orientation of several bones in hydrodynamically stable positions, shows that although quick, the burial occurred after decomposition and disarticulation of the carcasses. A horizon of bone fragments located just above the original level of bone deposition suggests slight reworking of the deposit. As a whole, these features indicate that the recovered fossil assemblage is multispecific (*sensu* Behrensmeyer, 2007), including dicraeosaurids, diplodocids, abelisauroids, megalosauroids and thyreophorans. Thus, the hypothesis of an autochthonous to para-autochthonous paleocommunity, with associated and articulated remains of a few discrete individuals buried *in situ* with low to null transport, is better supported than the alternative hypothesis of a spatial and/or temporal fossil accumulation of many individuals (Riguetti et al., 2023). A more detailed taphonomic analysis of the site is in process.

Sacral elements

Description. The sacral elements (MMCh-PV 293 and 294; Figs. 2A–D, 3A–D, respectively) are conserved as two fragments, each one composed of two vertebral centra. MMCh-PV 294 conserves the right ribs and MMCh-PV 293 the left ones. Although both fragments lack an obvious contact or articulation between them, their similar sizes suggest they may belong to the same individual. Comparing with sacral ribs and vertebrae in the literature and considering the anterior and posterior limits of the iliosacral yoke in each fragment, respectively, the vertebrae of MMCh-PV 294 are recognized as the first and the second sacral vertebrae, and those of MMCh-PV 293 are the third and fourth. The first sacral rib is identified by its thickness and posterolateral direction in ventral view, with the anterior rib edge very extended anteromedially on the centrum (Figs. 2A, B). The fourth rib is also recognized by its thickness, the proximal anteroposterior extension, the lateral direction of the main axis in ventral view, and the anterolateral direction of the distalmost portion (Figs. 3A, B).

In both sacral fragments, the vertebral centra are dorsoventrally compressed and strongly fused to each other and with their corresponding ribs. Only the contact between vertebral centra 3 and 4 is visible. Although badly preserved, the exposed articular surfaces of vertebral centra 1 and 4 are suboval with the main axis oriented horizontally. The anterior articular surface of the first vertebral centrum is very damaged. The posterior articular surface of the last vertebral centrum is poorly preserved but appears flattened in life. The first and fourth vertebral centra are the widest, and the third is the narrowest. Ventrally, the vertebral centra are transversely convex, forming a wide, longitudinal crest in the third centrum. The posterior fragment (MMCh-PV 293) partially conserves the floor of the neural canal, which appears slightly wider in the third vertebra relative to

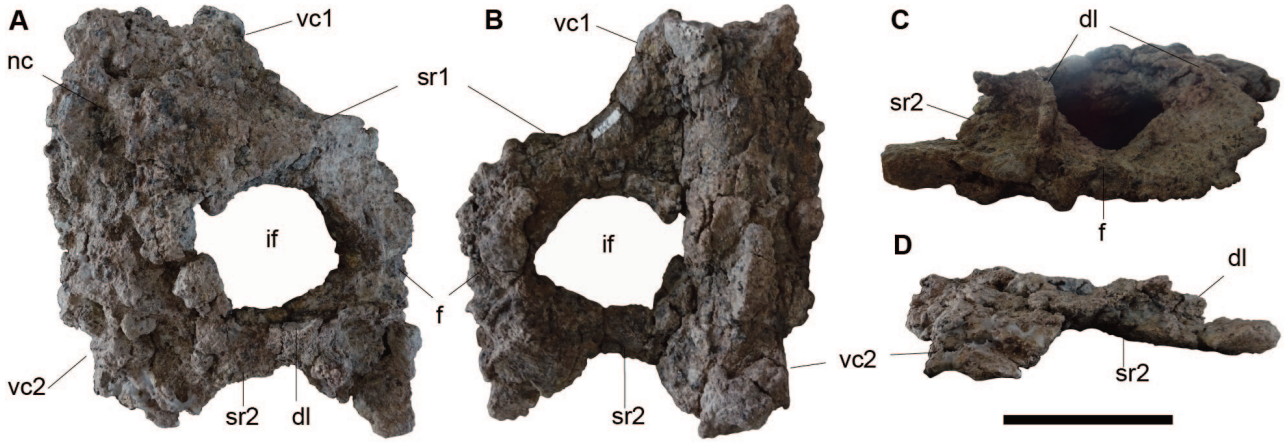

Figure 2. A–D, Sacral fragment MMCh-PV 294; A, dorsal view; B, ventral view; C, right lateral view; D, posterior view. Abbreviations: dl, dorsal lamina; f, distal rib fusion (iliosacral yoke); if, intercostal fenestra; nc, neural canal; sr1, sacral rib 1; sr2, sacral rib 2; vc1, vertebral centrum 1; vc2, vertebral centrum 2. Scale = 10 cm.

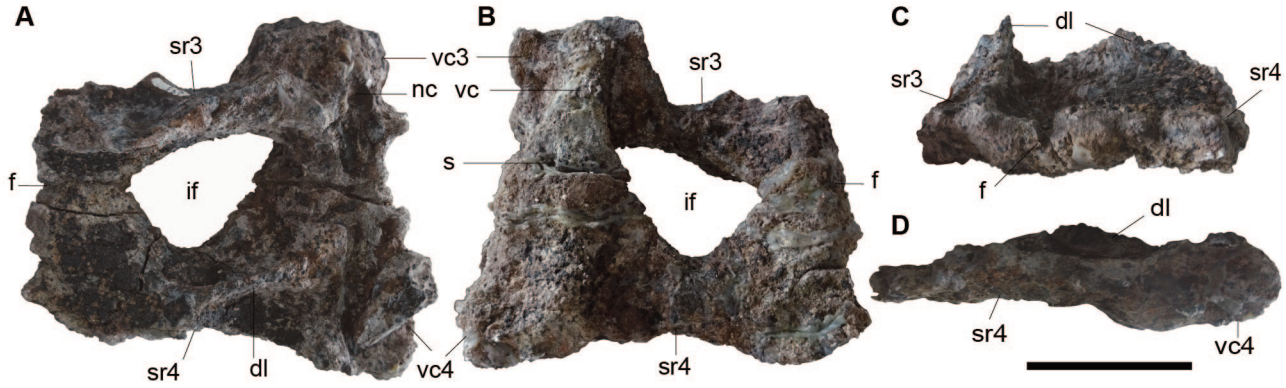

Figure 3. A–D, Sacral fragment MMCh-PV 293; A, dorsal view; B, ventral view; C, left lateral view; D, posterior view. Abbreviations: dl, dorsal lamina; f, distal rib fusion (iliosacral yoke); if, intercostal fenestra; nc, neural canal; s, vertebral suture; sr3, sacral rib 3; sr4, sacral rib 4; vc, ventral crest; vc3, vertebral centrum 3; vc4, vertebral centrum 4. Scale = 10 cm.

the fourth (Fig. 3A). In the anterior fragment (MMCh-PV 294), only vertebra 1 partially conserves the floor of the neural canal, similar in width to that in vertebra 3 (Fig. 2A).

The sacral ribs are thick, robust, and laterally oriented, in both anterior and ventral views (except the first sacral rib, which is slightly posterolaterally directed; Figs. 2, 3). In transverse section, the ribs are thicker ventrally and more laminar dorsally. In ventral view, the ribs are strongly expanded proximally (most in the first vertebra) and distally. The base of the fourth sacral rib extends anteriorly, reaching the vertebral centrum 3. Distally, the ribs expand and fuse, forming an anteroposteriorly elongated, horizontal iliosacral yoke (aligned with the vertebral centra; Figs. 2C, 3C) that would contact the ilium laterally. All ribs contact each vertebral centrum subtly below mid-height, encompassing about two-thirds of its height.

The intercostal fenestrae show different shapes. The most anterior fenestra, formed by the first and second ribs, is oval with its long axis medio-laterally directed, and with symmetrical anterior and posterior edges. The most posterior fenestra, formed by the third and fourth ribs, is strongly asymmetrical, with a gently concave anterior edge and a strongly concave posterior edge. The main axis of this fenestra is directed posterolaterally. The bad preservation of the ribs of the second and third vertebrae prevents us from knowing the shape of the corresponding fenestrae.

PCA. The most relevant morphometric results of the analyses on sacral fragments (MMCh-PV 293 and 294) are presented here. Grouping is well discriminated in the CVA, allowing for comparisons between them based on PCA shapes. All resulting graphs (Appendix S1; Figs. S1, S3), values and discussion of each analysis are included within Appendix S1. Resumed results are presented in Figure 4.

In both analyses, the principal component 1 (PC1) is mainly associated with lateral elongation of both the sacral ribs and the associated fenestrae, and the principal component 2 (PC2) represents the variations in size and position of the intercostal fenestrae relative to the sagittal plane (associated with vertebral centra width) (see deformation schemes; Appendix S1; Figs. S2, S3). In the first analysis, MMCh-PV 294 (the anterior portion of the sacrum) is recovered outside the confidence ellipses of all the sampled groups (Fig. 4A), but closer to the stegosaur individual *Huayangosaurus*. In the second analysis, MMCh-PV 293 (the posterior portion of the sacrum) is recovered within the confidence ellipses of both sauropod groups (diplodocoids and macronarians) but the closest individual is *Stegosaurus stenops* (Fig. 4B). Relative to the other individuals in the sample, MMCh-PV 293 and 294 show average PC values of lateral extension (width) of its elements, average size of the intercostal fenestrae in the anterior fragment, and large size of the intercostal fenestrae in the posterior fragment.

The placement of the Bajada Colorada elements outside all confidence ellipses in the first analysis, but close to different groups in both analyses, could suggest a new sacral shape, possibly a new group. However, systematic approximations cannot be made. Even considering the size and degree of fusion of the elements, we cannot rule

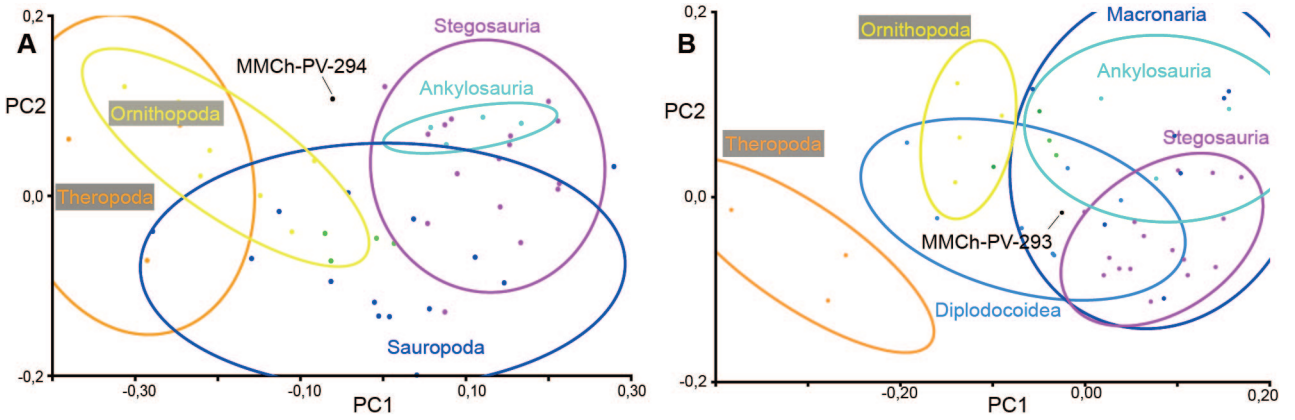

Figure 4. Simplified morphospaces of the PCA analyses. A, MMCh-PV 294; B, MMCh-PV 293. Confidence ellipses for Ankylosauria (light blue), Diplodocoidea (turquoise in B), Macronaria (blue in B), Ornithopoda (yellow), Sauropoda (blue in A), Stegosauria (violet) and Theropoda (orange) are shown. Details are in the Appendix S1. Abbreviations: PC1, principal component 1; PC2, principal component 2.

out ontogenetic and/or taphonomic shape variations. Also, the low value of the explained variance (68% and 62% accumulated by PC1 and PC2, respectively, in each analysis) gives weak support for the results. Despite the approximations and similarities with some of the analyzed groups (mainly stegosaurs and sauropods), the PCAs were not conclusive.

Anatomical comparisons. In theropod (see Gilmore, 1920; Bonaparte et al., 1990; Xu et al., 1999; Brochu, 2003; Gianechini et al., 2018) and ornithopod dinosaurs (Owen, 1854; Galton, 1981; Forster, 1990; Norman, 2002; Carpenter & Wilson, 2008; and *Macrogryphosaurus*, MUCPv-321, FJR pers. obs.; Figs. 5A, B), the sacra are narrower than in other groups, with tall (not dorsoventrally compressed) vertebral centra and short sacral ribs placed high on the vertebrae (between the vertebral centra and the neural arches). This morphology seems to be probably associated with the bipedal lifestyle of these dinosaurs (contrasting with the broad sacrum of obligate quadrupedals; Figs. 4A, B). In general, sacral ribs in these groups are not distally fused to join the ilium (Gilmore, 1920; Norell & Makovicky, 2004; Tykoski & Rowe, 2004), except for some Abelisauridae (*e.g.*, *Aucausaurus* and *Skorpiovenator*; Baiano, 2021). In sauropods (Marsh, 1896; Hatcher, 1901; Osborn & Mook, 1921; Janensch, 1929; Ostrom & McIntosh, 1966; McIntosh et al., 1996; Wilson & Sereno, 1998; Taylor, 2009; Coria et al., 2013; Xu et al., 2018; Holwerda et al., 2021; Ma et al., 2022; *Volkheimeria* and Titanosauria indeterminate, MLP 46-VIII-21-2, FJR pers. obs.; see examples in Figs. 5C, D), sacral ribs are more laterally extended, and are born more ventrally on the vertebral centra than in bipedal forms. In members of this clade, sacral ribs are lateroventrally directed in anterior (or posterior) view, often showing a strong proximodistal curvature. Vertebral centra are not (or little) dorsoventrally compressed (with few possible exceptions; see Marsh, 1896; Carballido & Sander, 2014). Intercostal fenestrae are commonly narrower (lateromedially short) than the associated vertebral centra (consistent with the PCA). Sacral ribs are generally very laminar and curved in lateral view (*e.g.*, *Dicraeosaurus*, MfN MB. R. 3688; *Cathetosaurus*; Jensen, 1988). Such features are absent in MMCh-PV 293 and 294.

Regarding basal thyreophorans, the sacrum of the bipedal *Scutellosaurus* (Breeden et al., 2021) is consistent with the shapes described for theropods and ornithopods above. *Scelidosaurus*, the sister taxon of the large, quadrupedal eurypodan thyreophorans, was proposed as a facultative quadrupedal (Norman, 2021). It shows slightly dorsoventrally compressed sacral vertebrae with lateral extension of the ribs, forming a broader sacrum that approaches the eurypodan sacrum shape (Carpenter et al., 2013). However, the sacral ribs in this taxon are more robust and contact the upper half of the vertebral centra (Norman, 2020a). In eurypodans (Figs. 5E, F), sacral centra are wide and dorsoventrally compressed (Coombs, 1971; Dong et al., 1977; Maryańska, 1977; Hao et al., 2018a; Zheng et al., 2018), and most also show sacral ribs which contact the vertebral centra more ventrally than in other

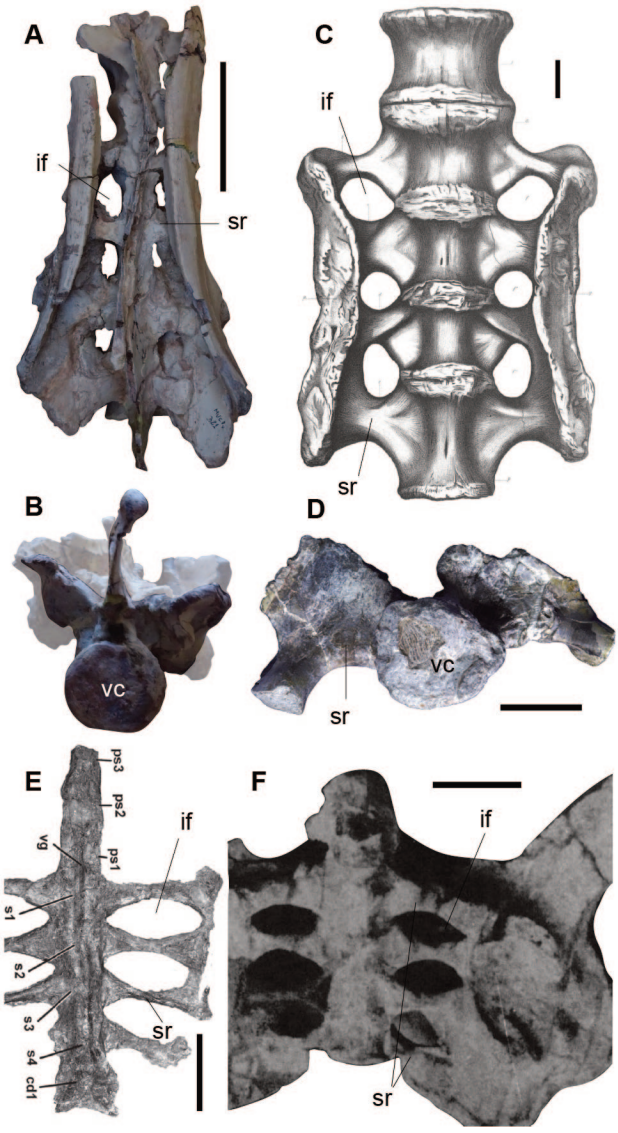

Figure 5. Sacra, comparisons 1. A–B, pelvis and sacrum of *Macrogryphosaurus*; A, dorsal view, B, posterior view (the ilia, behind, are transparented). C, Sacrum of *Brontosaurus* in ventral view (modified from Marsh, 1896). D, Sacrum of *Shunosaurus* in posterior view (modified from Ma et al., 2022). E, Sacrum of *Gastonia* in ventral view (modified from Kinneer et al., 2016). F, Pelvis of CV 721 (*Huayangosaurus* for Zhou, 1983, Stegosauria indet. for Maidment et al., 2006) in ventral view (modified from Zhou, 1983). Abbreviations: cd, sacrocaudal vertebra; if, intercostal fenestra; ps, presacral vertebra; s, sacral vertebra; sr, sacral rib; vc, vertebral centrum; vg, ventral groove. Scale = 10 cm.

groups (Gilmore, 1914; Hennig, 1925; Ostrom & McIntosh, 1966; Galton, 1982; Salgado & Gasparini, 2006; Carpenter et al., 2013; Kirkland et al., 2013; Burns, 2015; Maidment et al., 2018; Wiersma & Irmis, 2018; Raven et al., 2020; Riguetti et al., 2022a; Sánchez-Fenollosa et al., 2025), resembling the condition in MMCh-PV 293 and 294. Vertebral centra are widely convex to flattened ventrally and may bear (Burns, 2015; Galton & Carpenter, 2016; Kinneer et al., 2016; Hao et al., 2018a; also a diagnostic feature of Nodosauridae, see Lull, 1921; Coombs, 1971; Raven et al., 2020; Riguetti et al., 2022a) or lack (Gilmore, 1914; Ostrom & McIntosh, 1966; Maryańska, 1977; Galton, 1982; Dong, et al., 1983; Carpenter & Kirkland, 1998; Salgado & Gasparini, 2006; Carpenter et al., 2013; Wiersma & Irmis, 2018) a ventral longitudinal groove, also absent in MMCh-PV 293 and 294. A broad ventral crest similar to that of MMCh-PV 293 is also present in some stegosaurs, but its inconsistent occurrence within the clade may reflect intraspecific variation (Maidment et al., 2015).

Consistent with the PCA results, sacral ribs are laterally extended in thyreophorans. In stegosaurs and some basal ankylosaurs, the extension occurs in a way similar to that in MMCh-PV 293 and 294 (Gilmore, 1914; Galton, 1982; Dong et al., 1983; Zhou, 1984; Dong, 1990; Galton, 1991; Maidment et al., 2008; Carpenter et al., 2013; Maidment et al., 2015; Galton & Carpenter, 2016; Hao et al., 2018a; Norman, 2020a), while in most ankylosaurs the lateral extension of the ribs is more pronounced (Lull, 1921; Maryańska, 1977; Carpenter & Kirkland, 1998; Arbour & Currie, 2013; Kirkland et al., 2013; Burns, 2015; Kinneer et al., 2016; Wiersma & Irmis, 2018; Raven et al., 2020; Soto-Acuña et al., 2021; and *Nodosaurus* YPM-1815, virtual collection). Also, the Bajada Colorada sacral elements share with stegosaurs the presence of a first sacral rib with a slight distal curvature in posterior direction (see Gilmore, 1914; Zhou, 1984; Dong, 1990; Carpenter et al., 2013; Maidment et al., 2015; Galton & Carpenter, 2016; Hao et al., 2018b; and *Dacentrurus*, without considering the presacral rib, only present in some individuals of this taxon; Galton, 1991; Maidment et al., 2008) contrasting the straight and laterally directed first sacral rib of ankylosaurs and *Scelidosaurus* (Carpenter & Kirkland, 1998; Arbour & Currie, 2013; Carpenter et al., 2013; Burns, 2015; Norman, 2020a).

Although the PCA results suggest that the sacrum shape of MMCh-PV 293 and 294 is closer to that of stegosaurs, they do not allow a definitive identification of the elements as either sauropods or stegosaurs. Summarizing the most important features mentioned above, the vertebral centra are proportionally wider in stegosaurs

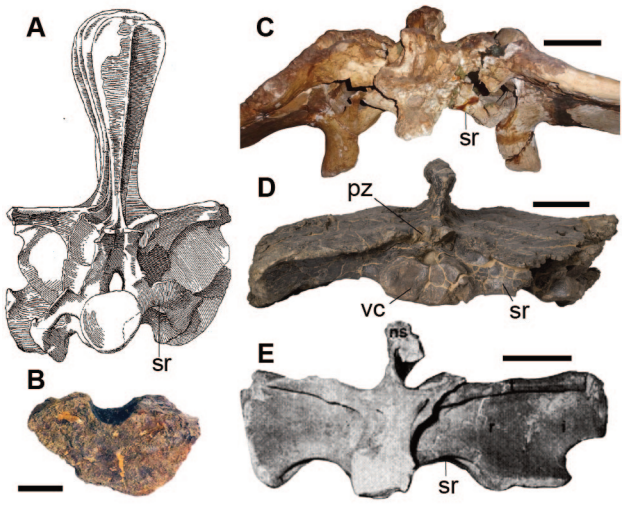

Figure 6. Sacra, comparisons 2. A, Sacrum of *Dicraeosaurus* in anterior view (modified from Janensch, 1929; not to scale). B, Sacral vertebra of *Hesperosaurus* in anterior view (modified from Maidment et al., 2018). C, Pelvis and sacrum of Titanosauria MLP–PV 46-VIII-21-2 in anterior view (see also Filippini et al, 2016). D, Sacrum of *Dacentrurus* in posterior view (modified from Sánchez-Fenollosa et al., 2025). E, Sacrum of *Kentrosaurus* in anterior view (Galton, 1988). Abbreviations: pz, postzygapophysis; sr, sacral rib; vc, vertebral centrum. Scale = 2 (B) and 10 (C–E) cm.

than in most sauropods, the latter also bearing higher sacral centra (Figs. 6A, B). On the other hand, the position and orientation of the sacral ribs also differ between groups (Figs. 6C–E). In thyreophoroids (Eurypoda+*Scelidosaurus*), the ribs are directed laterally and aligned almost horizontally in lateral view (both at their proximal and distal ends). In sauropods, the ribs are greatly expanded dorsoventrally at their distal ends, with the ventral edge directed lateroventrally, especially in the first one or two sacral ribs, whose proximal ends are located higher on the vertebrae. Posteriorly along the series, the ribs are placed lower on the centra, and become lateralized (with few exceptions, *e.g.*, *Camarasaurus* and *Europasaurus*; Osborn & Mook, 1921; Carballido & Sander, 2014). This variation in the position of the most anterior sacral ribs is reflected in the ilium, which is proportionally higher anteriorly in sauropods than in stegosaurs (Figs. 6C–E). Thus, a Stegosauria assignment for MMCh-PV 293 and 294 is supported.

Dorsal ribs

Description. MMCh-PV 291 (Figs. 7A–C) comprises four fragments of dorsal ribs and an osteoderm, all found in close association (the osteoderm is described below). The rib fragments correspond to the distal portion and all elements show a similar morphology. The body of the rib is mostly straight. One of the ribs is poorly preserved with an oval cross-section proximally that becomes lateromedially compressed distally. In the other ribs, a well-developed anterior intercostal ridge and a smaller developed posterior intercostal ridge form a rough proximal T-shape section (not as marked as that in ankylosaurs; Figs. 7B, C). These intercostal ridges house the corresponding anterior and posterior costal grooves on their medial surfaces. Distally, the ridges merge with the costal body, and the transverse rib section becomes oval to flattened distally. The anteroposterior width of the elements is relatively constant throughout their extension. The dimensions of the fragments (anteroposterior and proximodistal lengths) and the absence of curvature suggest they correspond to the mid-distal portion.

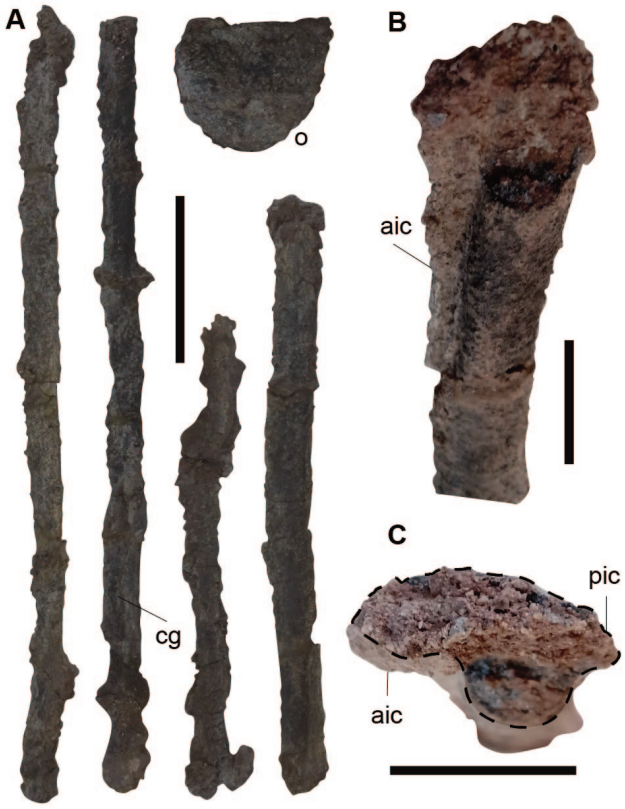

Figure 7. MMCh-PV 291, composed of four dorsal rib fragments and an associated osteoderm. A, Dorsal view of the elements (except that showing the costal groove). B, Rib detail in proximal oblique view. C, Proximal view of the same rib in B (dashed line delimits the transverse section of the rib). Abbreviations: aic, anterior intercostal crest; cg, costal groove; o, osteoderm; pic, posterior intercostal crest. Scale = 10 (A) and 2 (B–C) cm.

Comparisons. Sauropod dorsal ribs bear a subtriangular, L-shaped or oval proximal section, which becomes flattened to ovate distally and anteroposteriorly elongated (Osborn & Mook, 1921; Janensch, 1929, 1950; Upchurch et al., 2004; Coria et al., 2013; Waskow & Sander, 2014; Tschopp & Mateus, 2017; Windholz & Cerda, 2021; Rebbachisauridae indet. MMCh-PV 49, FJR pers. obs.; *Patagosaurus*, FJR pers. obs.; Fig. 8A). In theropods, the dorsal ribs are rod-like with a subtriangular or L to T-shaped proximal section (Gilmore, 1920; Madsen, 1976; Harris, 1998; O'Connor, 2007; Waskow & Mateus, 2017; Gianechini et al., 2018; Baiano, 2021). When a T-section is conserved (*e.g.*, *Wiehenvenator*, Rauhut et al., 2016; *Tyrannosaurus*, Brochu, 2003), this is limited to the proximal third or half portion of the axis. The distal end usually retains an oval section. In non-styracosternan ornithopods, the ribs are generally short, broad and transversely compressed distally, without a T-shaped proximal section (Carpenter & Wilson, 2008, and *Camptosaurus* SM-7406, virtual collection; Cerda & Chinsamy, 2012; Waskow & Mateus, 2017; Cruzado-Caballero et al., 2019; Rozadilla et al., 2019; *Tenontosaurus* YPM 5459 and 5472, virtual collection; and *Macrogryphosaurus* MUCPv-321, FJR pers. obs.; Figs. 8B, F). In Styracosterna, intercostal ridges are prominent in the proximal third and decreases distally, and the transverse section of the rib becomes oval to compressed mid-distally (Owen, 1854; Norman, 1980; McDonald et al., 2012; Campione, 2015; Norman, 2015; Lockwood et al., 2021; Hadrosauridae indet. YPM-VPPU-1878, 2560, 23255 and 28659, virtual collection; *Iguanodon* NHM-PV-OR-10514, virtual collection; *Huallasaurus* MACN-PV 02, and Hadrosauridae indet. unnumbered material, MPCA-PV collection, FJR pers. obs.; see *Eolambia* in Fig. 8C).

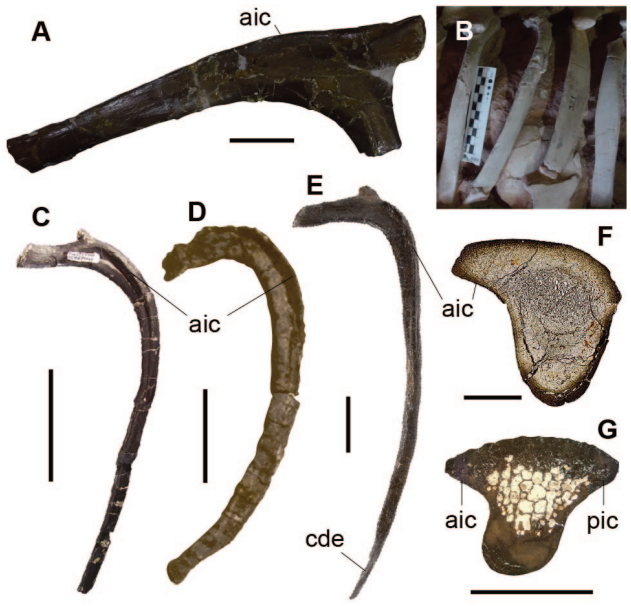

Figure 8. Dorsal ribs, comparisons. A, *Patagosaurus* MACN-CH-238 in anterior view. B, *Macrogryphosaurus* in lateral view. C, *Eolambia* in anterior view (modified from McDonald et al., 2012). D, *Animantarx* in anterior view. E, *Stegosaurus* in anterior view (modified from Maidment et al., 2015). F, proximal transverse L-shaped section of the rib of *Draconyx* (modified from Waskow & Mateus, 2017). G, proximal transverse T-shaped section of the rib of *Jakapil.* Abbreviations: aic, anterior intercostal crest; cde, compressed distal end; pic, posterior intercostal crest. Scale = 0.5 (G), 1 (F) and 10 (A–E) cm.

Thyreophorans bear a T or L-shaped rib section in the proximal third or up to the middle of the costal body, but they differ distally between groups (Molnar & Wiffen, 1994; Raven et al., 2020). In basal thyreophorans and ankylosaurs, the distal portion is rod-shaped, with a subquadrangular to subovate section (Figs. 8D, G) (Gilmore, 1930; Ostrom, 1970; Haubold, 1990; Kirkland et al., 2013; Blows, 2015; Kinneer et al., 2016; Wiersma & Irmis, 2018; Norman, 2020a; Riguetti et al., 2022b; and *Antarctopelta*, FJR pers. obs.). On the other hand, the distal rib section in stegosaurs is oval to lateromedially compressed, especially in the longest ribs (Gilmore, 1914; Hennig, 1925; Zhou, 1983; Maidment et al., 2015; Costa & Mateus, 2019; Fig. 8E). Therefore, the proximal L/T-shaped section and the distal lateromedial compression of the elements in MMCh-PV 291 are more consistent with a stegosaurian identification.

Osteoderms

In general, they preserve complete edges with poor preservation of the external bone cortex. Therefore, it is not possible to identify superficial structures characteristic of osteoderms such as grooves or foramina. Recovered osteoderms bear large morphological disparity, allowing us to classify them into (at least) four groups: spines with asymmetric bases, flat scutes, conical scutes, and irregular osteoderms. Some elements previously described as plate-like osteoderms (Apesteguía et al., 2015; Riguetti et al., 2022c) are not considered osteoderms here. These elements lack diagnostic features of stegosaurian plates (see Blows, 2001b; Galton, 2016, and references therein) and cannot be differentiated from vertebral fragments of

the sauropod vertebrae found in the site. Also, the presence of longitudinal striation and a longitudinal bone lamina in some elements is not compatible with stegosaurian features related to plate growth. Stegosaurian plates grow from the base, with the ontogenetically oldest tissue located distally and the youngest at the base, developing symmetrical proximodistally oriented bone fibers on both sides of the plate (de Buffrénil et al., 1986).

Spines

Description. MMCh-PV 153 (Figs. 9A–C), MMCh-PV 227 (Figs. 9D–G) and MMCh-PV 118 (Figs. 9H–J) are spines that lack their apex. The elements are mostly lateromedially compressed, with sharp anterior and posterior edges and an oval transverse section. In lateral view, they display a gradual morphological transition, with MMCh-PV 227 subromboidal in outline, MMCh-PV 118 subtriangular, and MMCh-PV 153 subtriangular but more elongated. The apex is posteriorly offset relative to the base in all spines. In ventral view, the base is anteroposteriorly oval, with the posterior edge being more laterally compressed in MMCh-PV 118 and MMCh-PV 227. The base is strongly inclined, asymmetrical in anterior view, with the lateral edge extending further ventrally (so the spine would lean to the right in anterior view if the base is oriented horizontally). Although the base is the widest portion of these elements, the basal edges are not extended. The basal surface is slightly concave (MMCh-PV 227 displays a longitudinal groove). In all cases, the lateral surface is convex, and the medial surface is flattened to gently convex. In dorsal view, MMCh-PV 227 bears two exposed surfaces of broken bone separated by sediment, suggesting the presence of two apices, the posterior one being larger (Fig. 9G). The broken distal section of MMCh-PV 153 (and probably also MMCh-PV 118) shows sediment filling, possibly filling the central vascular cavity (see Hayashi et al., 2012). However, the preservation of the elements does not allow greater precision.

MMCh-PV 250 (Figs. 9K–M) is a pyramidal and slightly lateromedially compressed element. In lateral view, the element is triangular, with the blunt apex posteriorly displaced and the posterior edge vertically oriented. The base is strongly asymmetrical, with the medial edge very extended proximally and continuous with the medial side of the apex, so that in medial view the surface is homogeneously flat (without an interruption between the spine and the base). The lateral edge of the base is much shorter and runs laterally. Therefore, the lateral and medial edges of the base form an angle of approximately 90° in anterior view. Both basal edges are anteroposteriorly rounded. The anterior edge of the element is not laterally compressed but transversely rounded, while the posterior surface is flattened. In anterior view, the medial surface is slightly convex to flattened, the lateral surface is slightly concave, and they show a slight convergence towards the apex, resulting in a wide, uniform apex without an acute tip or a widened base.

Comparisons. To recognize stegosaur spines, Galton (2016) used the following characters: the base is not deeply concave and has rounded edges (1), absence of a longitudinal (apicobasal in this contribution) groove on the lateral or medial surfaces (2), the spine is straight in medial and lateral views (3), absence of a posterior groove for the next spine (as in "polacanthines") (4), and the cross-section bears a thick cortical bone (5) and a central canal (6). The spines identified in Bajada Colorada show the characters 1 (equivocal in 118), 2 (equivocal in 118), 3 (partially, due to the absence of the apex in all cases), and 4. The preservation of the material makes it difficult to recognize the characters 5 and 6, although 5 seems visible in MMCh-PV 293, and 6 in MMCh-PV 153.

MMCh-PV 153 and 118 are spines with a strongly asymmetric base. The relatively low profile and lateromedial compression of these spines is reminiscent of the osteoderms of *Huayangosaurus* (Fig. 10A; Zhou, 1984) and *Tuojiangosaurus* (Dong et al., 1977) rather than the elongated, cylindrical spines of *Kentrosaurus* (Hennig, 1925; Galton, 1982), *Miragaia* (Costa & Mateus, 2019), *Dacentrurus* (Galton, 1985) and *Stegosaurus* (Maidment et al., 2015; Galton, 2016). However, the strong inclination of the base in MMCh-PV 153 relative to the spine suggests a parascapular placement. In fact, the profile of the complete element is strongly reminiscent of the parascapular spine proposed for *Loricatosaurus* (Galton, 2016). Maidment et al. (2008) recognize this element as a caudal spine; however, caudal spines commonly present a posterior inclination relative to

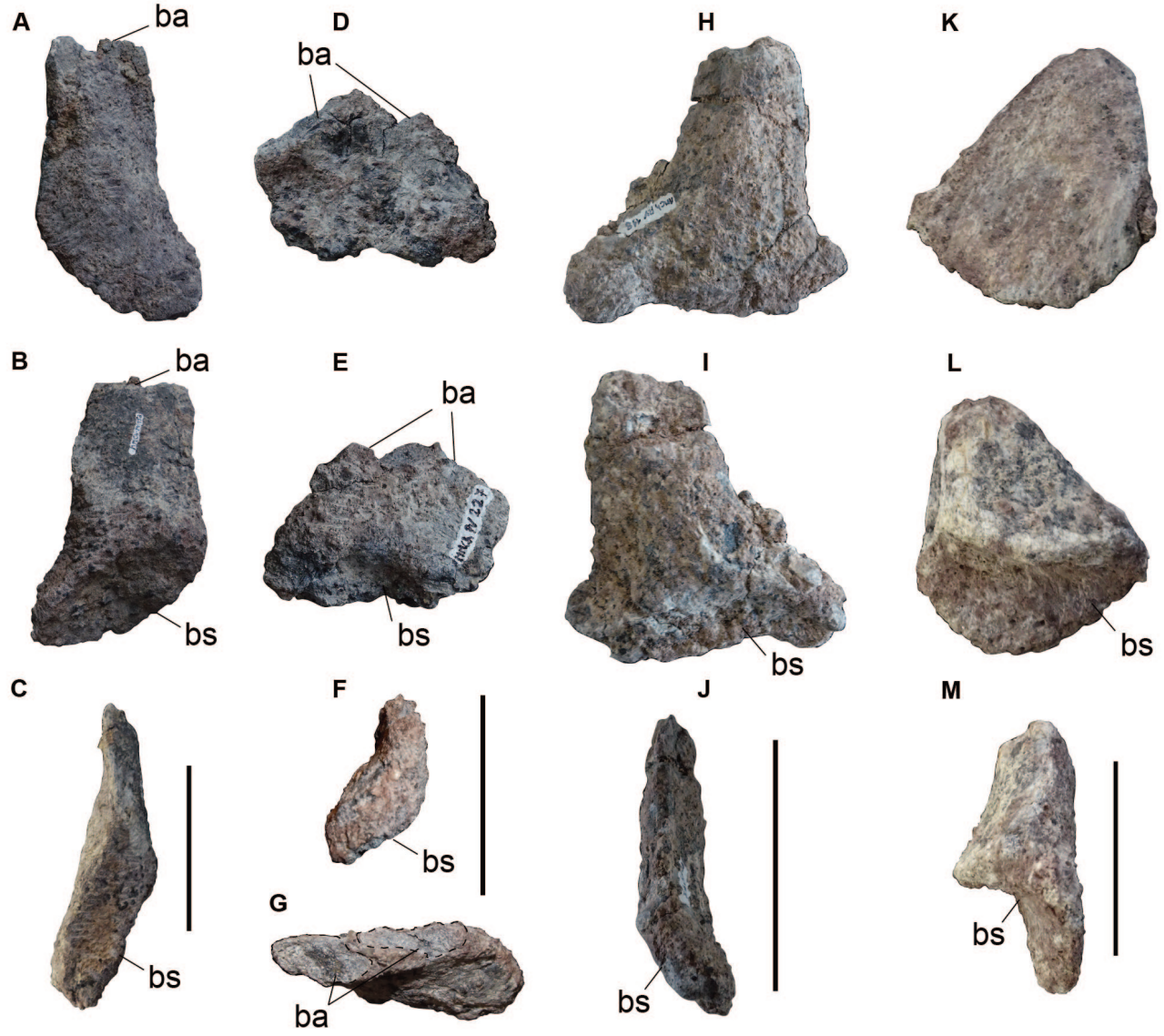

Figure 9. Dermal spines from Bajada Colorada locality. A–C, MMCh-PV 153; A, lateral view; B, medial view; C, anterior view. D–G, MMCh-PV 227; D, lateral view; E, medial view; F, anterior view; G, apical view. H–J, MMCh-PV 118; H, lateral view; I, medial view; J, anterior view. K–M, MMCh-PV 250; K, lateral view; L, medial view; M, anterior view. Dashed lines in G outline the two broken surfaces separated by rock. Abbreviations: ba, broken apex; bs, basal surface. Scale = 5 cm (for clusters D–G and H–J) and 10 cm (for clusters A–C and K–M).

the base. In *Loricatosaurus*, the base of the spine is very inclined but is not as expanded as occurs in the parascapular spines of other stegosaurs, a difference proposed as sexual dimorphism (Galton, 2016). Although roughly similar in shape to MMCh-PV 153, MMCh-PV 118 and 227 bear some features (*e.g.*, compressed anterior and posterior edges of the spine in MMCh-PV 118 and two apices in MMCh-PV 227) that suggest a different identification than parascapular spines. In MMCh-PV 227, the little asymmetrical base and the two apices are reminiscent of the distal cervical spines of some ankylosaurs such as *Edmontonia* (Fig. 10D; Gilmore, 1930). MMCh-PV 118 shows the typical paramedial fashion (Galton, 2016).

Without reaching the extreme morphology of the parascapular spines, the paramedial spines of stegosaurs usually display strongly asymmetrical bases. The asymmetric base of MMCh-PV 250, where the medial edge is ventrally projected and the lateral edge is laterally directed, resembles those of the sixth plate of *Kentrosaurus* (Galton, 1982; Figs. 10E, F), the cervical plates of *Miragaia* (Mateus et al., 2009),

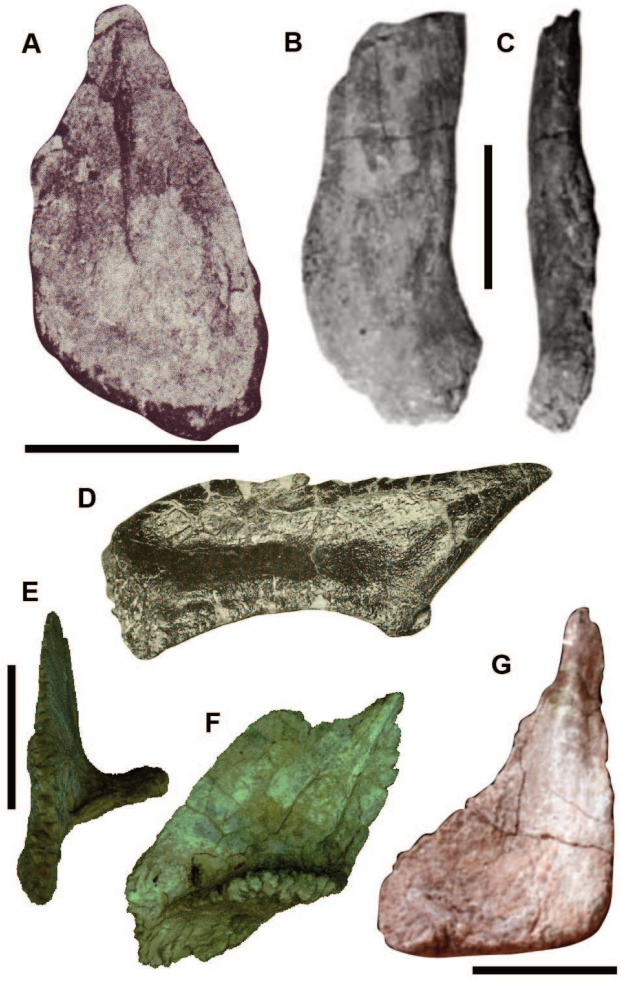

Figure 10. Dermal spines, comparisons. A, Spine of *Huayangosaurus* in lateral view (modified from Zhou, 1984). B–C, Parascapular spine of *Loricatosaurus* (modified from Galton, 2016); B, lateral view; C, posterior view. D, Pectoral spine of *Edmontonia* (modified from Gilmore, 1930; not to scale). E–F, Sixth plate/spine of *Kentrosaurus* (MfN digital collection); E, anterior view; F, lateral view. G, Caudal spine of *Spinophorosaurus* in lateral view (modified from Remes et al., 2009). Scale = 10 cm.

and the anterior caudal spines of *Stegosaurus sulcatus* (Gilmore, 1914; Galton, 2016).

Caudal spines are also present in some sauropod dinosaurs (*e.g.*, *Spinophorosaurus* from the Middle Jurassic of Niger; Remes et al., 2009; Fig. 10G). However, these differ from those of Bajada Colorada in that they have a widened, rounded base, and a concave medial surface.

Flat scutes

Description. MMCh-PV 226 and 291 (Figs. 11A–C) are dorsoventrally compressed elements with variable outline in dorsal view. MMCh-PV 226 has a subovate morphology in dorsal view, with straight lateral margins, and well-rounded anterior and posterior margins, one of which (anterior?) is slightly narrower than the opposite. Dorsally, it is slightly convex and bears a very low and wide crest displaced towards one of the sides (medial?). The dorsal texture is superficially altered (possibly corrasion, *sensu* Brett & Baird, 1986) and is only preserved in a few areas. No obvious ornamentation is visible. Ventrally, the piece is slightly concave, although the outermost layer of cortical bone is not visible (either by erosion or natural absence).

MMCh-PV 291 is a scute found closely associated with the dorsal rib fragments. It bears a D-shaped outline in dorsal view, with a presumed straight medial edge and a rounded lateral edge. Dorsally, it has an eccentric, low and narrow crest, which is more pronounced than that of MMCh-PV 226. In dorsal view, the crest is subparallel to the straight edge of the scute, and is displaced towards the more rounded edge (lateral?). Assuming that the crest is located posteriorly, as is usually the case in thyreophoran scutes, the transverse section of the osteoderm gradually thickens anteriorly, except for the most anterior central portion, which is thinner. The dorsal surface of the bone is better preserved than in MMCh-PV 226, and is mostly smooth, although some grooves are preserved. Ventrally, the texture is rough and irregular, but lacks the outermost layer of bone (either by erosion or natural absence).

Comparisons. Oval and polygonal scutes are widespread among thyreophorans. The flat scutes from Bajada Colorada lack strong dorsal ridges, therefore resembling those of *Jakapil* (Riguetti et al., 2022b), the stegosaur *Thyreosaurus* (Zafaty et al., 2024), and some basal ankylosaurs, such as the thoracic scutes of *Gastonia* (Kinneer et al., 2016) and *Gargoyleosaurus* (Kilbourne & Carpenter, 2005). Both the lack of features suggesting fusion to other osteoderms (which is common in cervical osteoderms of thyreophorans) and its close association with dorsal ribs, support a thoracic (or nearby) position of MMCh-PV 291.

MMCh-PV 291 is different from the typical costal plates found in several ornithischians (*e.g.*, non-hadrosauroid ornithopods and some thyreophorans, including *Huayangosaurus*, *Scelidosaurus* and *Saichania*; Maryańska, 1977; Zhou, 1984; Dong, 1990; Peng et al., 2005; Maidment

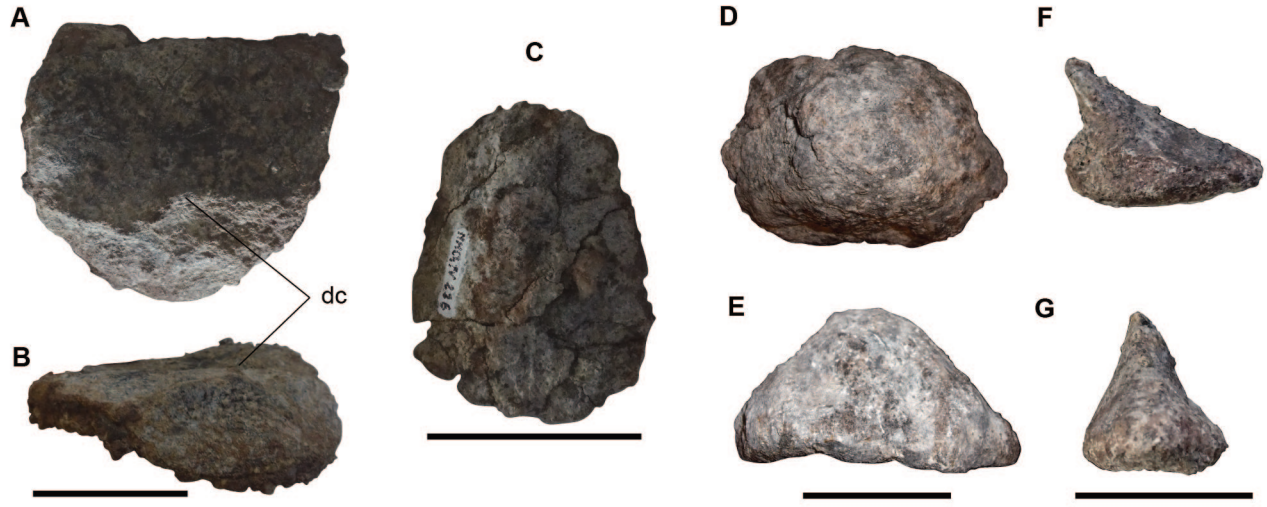

Figure 11. Dermal scutes from Bajada Colorada locality. A–B, Flat scutes MMCh-PV 291; A, dorsal view; B, lateral view. C, Flat scute MMCh-PV 226 in dorsal view. D–E, Conical scutes MMCh-PV 72-1; D, dorsal view; E, lateral view. Conical scutes MMCh-PV 249; F, lateral view; G, anterior view. Abbreviation: dc, dorsal crest. Scale = 5 cm.

et al., 2006; Butler & Galton, 2008; Brown et al., 2011; Norman, 2020a; Park et al., 2021). These plates are mostly tall elements, about 1–3 mm thick, with rough textures (possibly formed by calcification of cartilage or other mineralized tissue). They are arranged parallel to the main axis of the dorsal ribs, and usually in contact with the posterior intercostal edge. MMCh-PV 291 is thicker than the thin intercostal plates (10–20 mm, except the much thinner lateral and anterior edges), with well-defined edges lacking obvious contact structures on both scute and ribs. On the other hand, unlike the irregular and elongated intercostal plates, MMCh-PV 291 is more equidimensional, as commonly occurs in the flat osteoderms of thyreophorans (Kinneer et al., 2016; Riguetti et al., 2022b; Zafaty et al., 2024).

Conical scutes

Description. MMCh-PV 72-1 (Figs. 11D, E) bears a low conical morphology. The apex is blunt and slightly displaced (probably posteriorly). The dorsal surface is homogeneous, without obvious anterior or posterior edges. In ventral view, the base has a slightly hexagonal, anteroposteriorly elongated outline. The edges of the base are formed by 7 or 8 rounded and irregular bumps. These are arranged in two parallel rows of 3 bulges, one larger and triangular at the ?anterior end, and the opposite end is partially broken. Ventrally, the base is concave, and its texture is altered, possibly as a result of corrasion (*sensu* Brett & Baird, 1986). There are no obvious ornamentations.

MMCh-PV 249 (Figs. 11F, G) is a small scute with a spine-like dorsal prominence (it is not categorized as a spine since its height is lower than twice the width of the base, according to Blows, 2001a, 2015). In lateral view, the element is subtriangular and asymmetrical, with the apex directed posteriorly. The anterior edge rises gradually, and the posterior edge is subvertical. The anterior edge of the apex and the edges of the base are transversely rounded. The posterior edge is slightly compressed just below the spine. In anterior view, the element is mostly symmetrical and widens at its base, but without extension of the basal edges. In ventral view, the base is oval, with the long axis in an anteroposterior direction. The base is solid, and the ventral surface is flat. Although the external surface is better preserved than other elements, no ornamentation is present.

Comparisons. Unlike the stegosaurian affinities proposed by Apesteguía et al. (2015), conical osteoderms are common in ankylosaurs (see Ostrom, 1970; Maryańska, 1977; Ford, 2000; Carpenter et al., 2011; Kinneer et al., 2016; Murray et al., 2019). However, these mostly bear a marked anterior edge (or both edges; see also the character 2 for osteoderm identification of Blows, 2001b) and a concave or hollow base (not solid). Exceptions similar to MMCh-PV 72-1 and

MMCh-PV 249 are the conical ossicles of the ankylosaurs *Hylaeosaurus* (Blows, 2015, fig. 7.40c) and *Polacanthus* (NHM-PV-OR 36516, virtual collection). Similar elements were also present in the thoracic region of the basal stegosaur *Huayangosaurus* (Zhou, 1984, pl. XII, fig. 3).

Irregular elements

Description. MMCh-PV 72-4 (Figs. 12A–C), 251 (Figs. 12D–F) and 252 (Figs. 12G–I) are very asymmetrical elements, and unequally compressed dorsoventrally (in increasing order of compression: MMCh-PV 72-4, 251, 252). They show a subquadrangular to hexagonal outline, somewhat elongated in MMCh-PV 252 and 251. In lateral view, the peripheral edges show a sigmoidal fashion. All edges are transversely rounded. These bear one asymmetric ridge on each side. The dorsal crest is low and broad, and is obliquely oriented relative to the longer axis of the elements. It is displaced posterolaterally (inferred by the highest point of the crest). The ventral crest is slightly higher and narrower (stronger in MMCh-PV 251 and 252). These are subcentral and merge laterally with the peripheral edge, defining a concavity on its internal side. These asymmetric ridges give a rhomboid cross-section for the elements. In MMCh-PV 251, the ventral concavity is located on the same side relative to the dorsal crest, while in MMCh-PV 72-4 and 252 it is located on the opposite side, suggesting the location of these elements on opposite sides of the body in life. MMCh-PV 251 (the smaller) is externally smooth, and MMCh-PV 252 is homogeneously rough. In MMCh-PV 72-4, the ventral concavity is smooth and coincides with a dorsal surface similar in size and texture (but flattened to convex), both forming the thinnest portion of the element. The rest of the element is much rougher and thicker. None of these elements bears obvious foramina or grooves typical of osteoderms.

Comparisons. These are complete elements (not bone fragments) and lack the typical features and texture of endochondral elements, therefore reinforcing the potential assignment to osteoderms. These irregular elements are quite different from the osteoderms of thyreophorans, sauropods, pseudosuchians and theropods (the osteoderm-bearing Mesozoic continental vertebrates).

Since its first assignment to stegosaurian osteoderms (Apesteguía et al., 2015), MMCh-PV 72-4 had problematic interpretation, placement and orientation on the animal's body in life. The new elements MMCh-PV 251 and 252 do not solve the problem, but give support to the identification of a novel type of element.

Osteoderms with dorsal and ventral crests have been described in some Cretaceous titanosaur sauropods (*e.g.*, Dodson et al., 1998; Molnar, 2011; Vidal et al., 2014). However, these are more symmetrical and lack the ventral concavity. Considering that the titanosaur *Ninjatitan* has been found in Bajada Colorada (Gallina et al., 2021b), in levels closer to MMCh-PV 72-4, 251 and 252, an assignment to this sauropod group cannot be ruled out.

DISCUSSION

Morphometry and identification of sacral elements

Anatomy, morphogeometrics, and phylogenetics are often used as independent sources of information in taxonomic studies (*e.g.*, Zhang et al., 2020). Although the limited available material precludes a formal phylogenetic analysis, both the anatomical and morphogeometric information support an assignment to Stegosauria for MMCh-PV 293 and 294. This assignment is also supported by the anatomy of the dorsal ribs, their association with an osteoderm, and the wide disparity of osteoderm shapes. In addition to PCA results, the anatomy of the osteoderms, reminiscent of the spines and scutes of the Huayangosauridae *Huayangosaurus*, might also suggest some affinities to this taxon. The use of a large number of landmarks and semi-landmarks to outline the entire element (*e.g.*, 3D morphometry used for phylogenetic approximations; Páramo et al., 2020) would give a more robust taxonomic approach for this material.

Although the results of the PCA were not conclusive, it is important to mention that there may be some biases resulting from the figures used. We mostly used figures and/or diagrams from the literature, but these are not always accurate. In sauropods, the large size of the elements makes manipulation difficult, and the point of view may be altered. Photographs are few, and the diagrams can often alter spatial relationships and perspectives. Thus, this could explain the wide morphospace represented by the group. As an example,

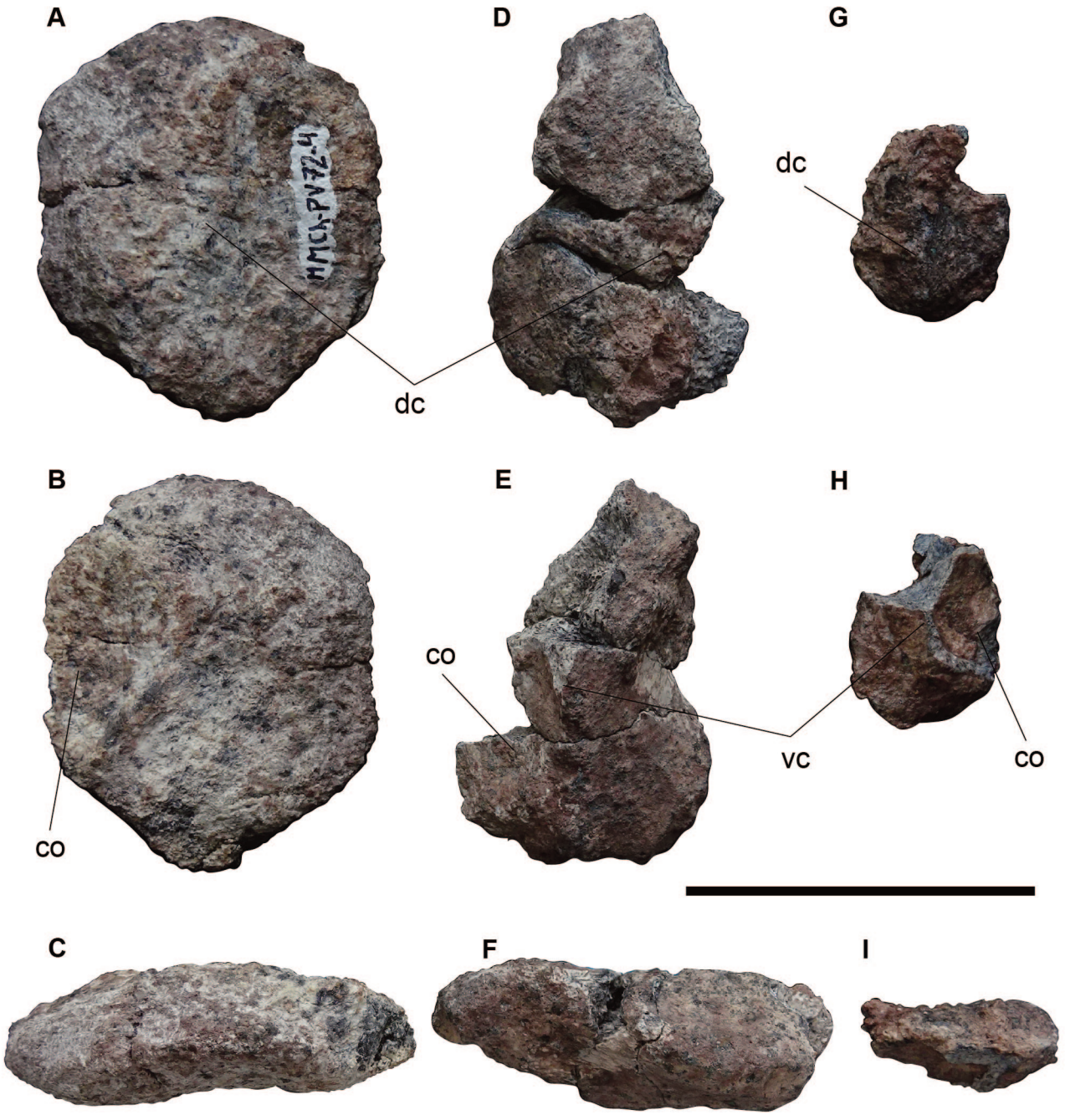

Figure 12. Irregular elements from Bajada Colorada locality. A–C, MMCh-72-4; A, dorsal view; B, ventral view; C, lateral view. D–F, MMCh-PV 251; D, dorsal view; E, ventral view; F, lateral view. G–I, MMCh-PV 252; G, dorsal view; H, ventral view; I, lateral view. Abbreviations: co, concavity; dc, dorsal crest; vc, ventral crest. Scale = 5 cm.

although diplodocids are sauropods with narrower sacra than other sauropods, the specimen DipI2 of *Diplodocus* is exaggeratedly displaced, both entering the confidence ellipse of Theropoda and very close to that of Ornithopoda in each analysis (Appendix S1, Figs. S2, S3). Nevertheless, the morphogeometric information of the different groups is consistent with the anatomical descriptions, reducing the biases incorporated by the respective figures.

South American stegosaurs

Stegosaurian remains from the Early Cretaceous of Argentina (La Amarga and Bajada Colorada formations) not

only reinforce the presence of the clade in South America but also suggest the possibility of novel lineages of thyreophorans in the region (Soto-Acuña et al., 2021; Riguetti et al., 2022b; Riguetti, 2023). The morphological representation of osteoderms from Bajada Colorada is compatible with that observed in stegosaurs from the Middle and Upper Jurassic. The spine MMCh-PV 153 is reminiscent of the spines in *Loricatosaurus* from the Middle Jurassic of England and France, which show problematic taxonomic affinities (Stegosaurinae in Maidment et al., 2020; basal Stegosauridae in Rauhut et al., 2021). The presence of either lateral scutes or flat osteoderms has been documented in the basal Stegosauria *Huayangosaurus* from the Upper Jurassic of China (Maidment et al., 2020) and the early Dacentrurinae *Thyreosaurus* from the Middle Jurassic of Morocco (Zafaty et al., 2024), respectively. In the PCAs, the shape of the sacrum was recovered as closer to that of *Huayangosaurus* (the anterior portion) and *Stegosaurus* (the posterior portion). Therefore, it is difficult to approximate the identification of the Bajada Colorada materials to any known group of stegosaurs.

In the same way, the Stegosauria remains from the Cañadón Calcáreo (Upper Jurassic of the Chubut Province, Argentina; Rauhut et al., 2021) and the La Amarga Formation (Barremian–Aptian of the Neuquén Province, Argentina; Pereda-Suberbiola et al., 2013) are very scarce, and also present problems for taxonomic identification. The former includes only a fragment of a left humerus, which supports a Stegosauridae identification. This fragment is 25 cm in length, but is estimated at 30–35 cm for the complete element, similar to humeral dimensions found in the African material of *Kentrosaurus* (Hennig, 1925) than to most other stegosaurs (Dong et al., 1983; Zhou, 1984; Hao et al., 2018a; Mateus et al., 2009; Maidment et al., 2015, 2020). The material from La Amarga included cervical vertebrae that show considerable similarity with those of *Kentrosaurus*, *Dacentrurus* and *Stegosaurus* (Pereda-Suberbiola et al., 2013). These bear a large neural canal in posterior cervical as in stegosaurs as a whole, and lateral fossae in the vertebral centrum, diagnostic for *Dacentrurus* according to Galton and Upchurch (2004; the reviews of Maidment et al. [2008] and Costa and Mateus [2019] did not mentioned this). These vertebrae are about 5–6 cm wide, similar in size to those of *Kentrosaurus*, therefore suggesting an approximate 4–5 m body length for the La Amarga individual. On the other hand, the sacral elements MMCh-PV 293 and 294 have intermediate widths between those of *Kentrosaurus* and the holotype of *S. stenops* (see Gilmore, 1914; Paul, 2010), which is estimated at 6.5 m body length. This would lead to a body length of about 5–6 m for the material from Bajada Colorada.

In addition to all these remains, it is worth noting that one of the oldest known stegosaurs in the world, *Isaberrysaura mollensis* (originally considered a Neornithischia, but today reinterpreted as a Stegosauria; Han et al., 2017; Maidment et al., 2020; Zafaty et al., 2024), was also found in the Argentinian Patagonia (Los Molles Formation, Middle Jurassic of Neuquén Province). This species includes an almost complete skull with basal features for a stegosaur (Salgado et al., 2017). Thus, despite the scarcity of the remains, stegosaur fossils are represented in Patagonia from its origin and throughout the biochron of the group (Apesteguía, 2002; Leanza et al., 2004). More material is needed to make an accurate taxonomic identification and to understand the anatomical trends of stegosaurian faunas from Patagonia (also true for Gondwanan stegosaurs; Rauhut et al., 2021).

The fossil association of Bajada Colorada

The observed taphonomic attributes suggest that the Lower Cretaceous fossil assemblage of the Bajada Colorada Formation at the main excavation site on the banks of the Limay River represents an autochthonous to parautochthonous association, currently represented by a few specimens from different groups of dinosaurs. This allows for comparisons with fossil associations from other Jurassic and Cretaceous localities worldwide (Canale et al., 2017; Gallina et al., 2021a, 2021b; and references therein). The Upper Jurassic Morrison (Kimmeridgian–Tithonian of North America), Tendaguru (Kimmeridgian–Tithonian of Tanzania), Lourinhã-Alcobaça (Kimmeridgian–Tithonian of Portugal) and (possibly) Guará-Batoví (Kimmeridgian–Tithonian of Brazil) formations display a great similarity in terms of their dinosaur diversity. This reflects an extensive distribution of several groups during the Late Jurassic, including Diplodocidae, non-Titanosauria Macronaria, Megalosauridae,

Ceratosauridae and Stegosauridae, among others (Mateus, 2006; Canale et al., 2017; Francischini et al., 2018; Gallina et al., 2021a, 2021b). In South America, the Cañadón Calcáreo Formation (Upper Jurassic of Central Patagonia) shares some components of this Jurassic fauna, mainly in terms of sauropod content (Gallina et al., 2021b). Also, other Lower Cretaceous fossil associations with similar dinosaur content have been described in the Mulichinco (Valanginian of Argentina) and Kirkwood (Berriasian–Valanginian of South Africa) formations. The former provided remains of dicraeosaurid and diplodocid sauropods, while the Kirkwood Formation preserves basal tetanurans, dicraeosaurids, brachiosaurids, a stegosaurid and a possible diplodocid (Gallina et al., 2021b). Recent quantitative analyses of the fossil association of these formations showed stronger similarities between the Gondwanan formations (Bajada Colorada, Mulichinco, Tendaguru and Kirkwood formations) relative to those from Laurasia, considering the more important ornithischian component in the latter (Garderes, 2023).

In this way, the presence of stegosaurs in the Lower Cretaceous Bajada Colorada Formation proposed here reinforces the faunal similarities with the aforementioned Upper Jurassic and Lower Cretaceous formations. Therefore, the fossil content of the Lower Cretaceous Bajada Colorada, Mulichinco and Kirkwood formations represents transitional faunas, including typically Jurassic forms (showing the decline of several groups, such as the Stegosauria, Diplodocidae, Dicraeosauridae and Megalosauridae) and the rise of new groups that diversified during the Cretaceous. (*e.g.*, Titanosauria and Abelisauridae; Gallina et al., 2021b). This strong Jurassic component in Lower Cretaceous faunas has been discussed by Apesteguía (2002) and interpreted as "relics of widespread global Jurassic faunas", identifying a 'Basal Neosauropod-Basal Tetanuran-Stegosaur Global Dinosaur Domain' that persisted into the earliest Cretaceous. These were also called Pangean relics or "Late Pangean", by Leanza et al. (2004) for the "Amargan" association of fossil tetrapods (Barremian–early Aptian). Finally, Gallina et al. (2021a) recognized the even earlier "Bajadan" association (Berriasian–early Hauterivian) in the Bajada Colorada Formation.

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