A new Iberian pleurosternid (Jurassic-Cretaceous transition, Spain) and first neuroanatomical study of this clade of stem turtles

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(Received XX Month XXXX; accepted XX Month XXXX)

A new Iberian pleurosternid (Jurassic-Cretaceous transition, Spain) and first neuroanatomical study of this clade of stem turtles

A partial skeleton of a pleurosternid turtle (Paracryptodira), from the Jurassic-Cretaceous transition at the Spanish locality of Ágreda (Moncayo Region, Soria Province), is presented here. Its partial skull represents the third of this lineage to be recognized in the European record, with the previously known specimens corresponding to British species. The specimen of Pleurosternidae studied here is attributed to a new species, *Pleurosternon moncayensis*. This lineage of stem turtles is identified as the most abundant and diverse group of freshwater aquatic turtles in Europe for the stages adjacent to the Jurassic-Cretaceous transition. Its presence decreased radically at post-Berriasian levels, when freshwater lineages of Eucryptodira, of Asian origin, are identified as the dominant forms at these aquatic turtle faunas. The confirmation of Pleurosternidae as freshwater inhabitants is made here, through the first neuroanatomical study for this lineage. Thus, the neuroanatomical reconstruction of *Pleurosternon moncayensis* sp. nov. is the first to be carried out for a freshwater stem turtle, and it allows us to identify convergent adaptations with freshwater members of the crown Testudines.

Keywords: Tithonian-Berriasian, European record, stem Testudines, *Pleurosternon*, new species, neuroanatomy.

Introduction

A single lineage of freshwater stem turtles (i.e., Testudinata not belonging to the crown Testudines) is identified in the Upper Jurassic to Lower Cretaceous record of Europe: Pleurosternidae (Pérez-García 2020a). Although this lineage of Paracryptodira has been known in Europe since the first half of the 19th century, only two of the European taxa defined before the 21st century are currently identified as valid forms: *Pleurosternon bullockii* (Owen 1842), currently known in uppermost Jurassic (Tithonian) and lowermost Cretaceous (Berriasian) sites in Great Britain and France (Gônet et al. 2018; Guerrero and Pérez-García 2020); and *Dorsetochelys typocardium* (Seeley 1869), identified in the lowermost Cretaceous (Berriasian) record of both Great Britain and Germany (Pérez-García 2014). However, the European diversity recognized for this Laurasian lineage has markedly increased over the last decade, through the description of three new forms in the Iberian Peninsula (Pérez-García 2017): the oldest European pleurosternid, *Selenemys lusitanica* Pérez-García and Ortega 2011, from the upper Kimmeridgian of the Lusitanian Basin in central-western Portugal; a taxon from the uppermost Jurassic (Tithonian) of the Spanish province of Teruel, *Riodevemys inumbragigas* Pérez-García, Royo-Torres and Cobos 2015a; and the youngest pleurosternid identified worldwide, *Toremys cassiopeia* Pérez-García, Espílez, Mampel and Alcalá 2015b, also from a site in Teruel Province, but from the uppermost Lower Cretaceous (Albian) (Pérez-García and Ortega 2011; Pérez-García et al. 2015a, 2015b; Pérez-García 2017). Fragmentary material of Pleurosternidae has been identified in other Tithonian to Barremian Iberian localities (see Pérez-García 2009; Pérez-García et al. 2010, 2013). However, the scarce information provided by these remains did not allow the determination of greater diversity than that represented by these three taxa

(Pérez-García 2017). Therefore, all pleurosternids currently identified in the Iberian domain correspond to endemic forms.

All the Iberian pleurosternids are exclusively represented by postcranial remains (see Pérez-García 2017 and references therein). In fact, only two skulls of this lineage have so far been recognized in the European record, both from the British Berriasian Purbeck Limestone Group (Evans and Kemp 1975, 1976), one of them corresponding to *Dorsetochelys typocardium* and the other to *Pleurosternon bullockii* (Pérez-García 2014; Joyce and Anquetin 2019; Evers et al. 2020).

[Figure 1 near here]

A partial skeleton of a pleurosternid, found in an outcrop included in the lower part of the upper Tithonian-lowermost Berriasian Matute Alloformation in Ágreda (Soria Province, Castile and León Autonomous Community, north-central Spain; Fig. 1), is presented here. It represents the first find of this clade identified in the Cameros Basin, and one of the few vertebrate remains described in the Alloformation. The specimen not only preserves elements of the shell, but also the partial skull. This specimen is not compatible with any of the taxa so far identified in the Iberian record. Therefore, its study allows us to further increase the Iberian diversity of Pleurosternidae. Its attribution to a new form exclusive to this area (closely related or not to any of the Iberian taxa described so far) or the first identification in the Iberian Peninsula of one of the two species hitherto known in other European regions, are discussed. In addition, the first neuroanatomical reconstruction of a paracryptodiran turtle is performed, and the hypothesis about the aquatic lifestyle of the pleurosternids is evaluated considering several neuroanatomical characters observed for the first time in this lineage.

Institutional abbreviations. DORCM, Dorset County Museum, Dorchester, UK; IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MPZ, Museo de Ciencias Naturales de la Universidad de Zaragoza, Zaragoza, Spain; NHMUK, Natural History Museum, London, UK; UMZC, University Museum of Zoology, Cambridge, UK.

Anatomical abbreviations. asc, anterior semicircular canal; bo, basioccipital; bs, basisphenoid; cc, crus communis; cca, cerebral carotid artery; ccv, canalis cavernosus; cnv, canalis nervi vidiani; cprnv, canalis pro ramus nervi vidiani; cr, cartilaginous ridge; cst, canalis stapedio-temporale; ct, cavum tympani; eo, exoccipital; ep, epiplastral process; epip, epipterygoid; ex, extragular scute; fnt, foramen nervi trigemini; fo, fenestra ovalis; fpccc, foramen posterius canalis carotici cerebralis; fst, foramen stapedio-temporale; gu, gular scute; hu, humeral scute; hyob, hyomandibular branch of facial nerve; ica, incisura columella auris; inf, inframarginal scute; lag, lagena; lpp, lateral process of pterygoid; lsc, lateral semicircular canal; m, marginal scute; op, opisthotic; pa, parietal; pi, processus interfenestralis; pit, pituitary fossa; pl, pleural scute; po, postorbital; pr, prootic; psc, posterior semicircular canal; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; v, vertebral scute; V, trigeminal nerve; VI, abducens nerve; VIII, vestibulocochlear nerve; X-XI, vagus and accessory nerves; XII, hypoglossal nerve.

Geological setting

The specimen studied here, MPZ 2020/53, was collected in the early 1990´s in a fossil site here named the El Pontarrón 1, located 3 km to the NE of the village of Ágreda (Soria Province, Spain) (Fig. 1). The geographical coordinates of the outcrop are: 41º

52’ 18’’N / 1º 54’ 20’’W. Geologically, it is located in the eastern part of the Cameros Basin, in the northwestern part of the Iberian Basin Rift System. The Cameros Basin, like the other basins of this tectono-sedimentary system, developed during the latest Jurassic-Early Cretaceous, as a consequence of the rifting phase linked to the opening of the Western Tethys and the Northern Atlantic (see Salas et al. 2001; Aurell et al. 2019, and references therein). The sedimentary record of the Cameros Basin includes a thick accumulation (up to 8,000 m) of Tithonian to Albian siliciclastic to carbonate units, deposited in a wide spectrum of continental (alluvial and lacustrine) to coastal environments. These thick successions were divided by Tischer (1966) into five groups (Tera, Oncala, Urbión, Enciso and Oliván), and more recently into successive genetic units or alloformations (e.g., Gómez-Fernández and Meléndez 1994; Meléndez and Gómez-Fernández 2000), and depositional sequences (e.g., Mas et al. 2004, 2019; Clemente 2010).

The more complete stratigraphic analysis of the Tithonian-Berriasian units around Ágreda was performed by Gomez-Fernández and Meléndez (1994) and Meléndez and Gómez-Fernández (2000). These authors identified three allostratigraphic units in the area (Fig. 1). The Ágreda Alloformation (unit I) unconformably overlies the Upper Jurassic (Oxfordian to lower Kimmeridgian) local shallow marine units and consists of alluvial facies interbedded with lacustrine to palustrine carbonates. The Magaña and Matute alloformations (units II and III) are dominated by clastic fluvial facies and carbonate lacustrine facies respectively (Gómez-Fernández and Meléndez 1994; Meléndez and Gómez-Fernández 2000). The collected specimen was recorded in a carbonate level located in the lower part of the Matute Alloformation (Fig. 1C). It consists of a mixed siliciclastic and carbonate succession, with a predominance of the latter lithology. Gómez-Fernández and Meléndez (1994) described four different subunits within this alloformation according to the adjacent palaeogeographical domains. The Ágreda area, located in the eastern domain, was assigned to the Subunit IIIC, mostly composed by ochreish micritic limestones, dolomites and marls, with occasional gypsum moulds and chert nodules. The Subunit IIIC, where the turtle specimen studied here was found, records a deposition in shallow carbonate lakes with intense evaporation and is characterized by a rich fossil association (charophytes, bivalves, gastropods, ostracods, fishes, and reptile remains) (Gómez Fernández and Meléndez 1994). Despite the fact that the presence of both fishes and reptile remains has been cited since this early works, few paleontological works have been published, the semionotiform actinopterygian fish *Camerichthys lunae* being one of the few main findings (Bermudez-Rochas and Poyato-Ariza 2014).

The Tithonian age of the Ágreda Alloformation, which is included in the lower part of the Tera Group (Gómez-Fernández and Meléndez, 1994; Mas et al. 2019), is well-constrained by the presence of the charophtye *Dyctioclavator* aff. *fieri* (Gómez-Fernández and Meléndez 1994). Schudack and Schudack (2009) also reported the presence of the Tithonian freshwater ostracod *Cetacella armata* in the basal part of the Tera Group. However, the findings of charophytes in the Matute Alloformation have poor biostratigraphic significance (*Mesochara harrissii*, *Porochara* sp. and *Clavatorites*) and their age has been attributed to either the Tithonian or the early Berriasian (Salomon 1982, Martín-Closas 1989; Martín-Closas and Alonso Millán 1998). According to Meléndez and Gómez-Fernández (2000) and also following the stratigraphic synthesis provided by Mas et al. (2004, 2019) for the Cameros Basin, the Matute Alloformation (or Formation) is included in the upper part of the Tithonian-earliest Berriasian Tera Group (see Fig. 1B). Accordingly, the most probable age of the El Pontarrón 1 fossil site is late Tithonian-earliest Berriasian.

Materials and methods

The partial skeleton analysed here is deposited in the “Museo de Ciencias Naturales de la Universidad de Zaragoza” (Zaragoza, Spain) with the collection number MPZ 2020/53 (Canudo 2018). The comparative study of this specimen with fossil remains of all other European pleurosternids (including the type material of all of them), as well as with some North American fossils (including the type specimen of *Glyptops plicatulus* (Cope 1877)), not only takes into account the information available in the literature but is also based on the first hand observation of all of them.

The skull of MPZ 2020/53 was scanned at the “Servicio de Técnicas No Destructivas”, in the “Museo Nacional de Ciencias Naturales” (Madrid, Spain), to perform the segmentation and posterior anatomical and neuroanatomical reconstructions. This was done with a high-resolution Nikon XT H-160 scanner. The fossil was scanned with 1000 projections, using a voltage of 160 kV and a current of 64 µA, resulting in 992 images in .DICOM format, with a voxel size of 43 µm. The segmentation and three-dimensional reconstructions of the bones and the inner structures were made carried out with the tools in the software Avizo 7.1 (VSG). As a result of the segmentation, three-dimensional meshes of the complete fossil, and of each bone and neuroanatomical structure, were obtained and exported as .STL format models. The models of the isolated bones remain unaltered, but Geomagic Studio 2014.3.0 was used to smooth the external surface of all reconstructed neuroanatomical structures. Bi-dimensional images of the skull and inner cavities, and the measurements, were obtained using the snapshot and measure tools of Avizo 7.1 respectively. Finally, the figures were composed using Adobe Photoshop CS6.

The new taxon was coded in the data matrix used by Pérez-García et al. (2015b), in which the phylogenetic relationships of the pleurosternids were analysed (Appendix 1), and several changes to the coding of *Pleurosternon bullockii* have been made. The analysis employed the same procedure as in Pérez-García et al. (2015b).

Systematic palaeontology

Testudinata Klein 1760

Paracryptodira Gaffney 1975

Baenoidea Williams 1950

Pleurosternidae Cope 1868

Pleurosternon Owen 1853

Type species: Pleurosternon bullockii (Owen 1842)

Distribution: Tithonian (Late Jurassic) to Berriasian (Early Cretaceous) of Western Europe (United Kingdom, France, and Spain).

Pleurosternon moncayensis sp. nov.

(Figs. 2, 3, 4A-B, 5-6)

Holotype: Specimen MPZ 2020/53, a partial skeleton including several disarticulated elements of the carapace and the plastron (Fig. 2), as well as the partial skull (Figs. 3, 4A-B, 5-6A-F).

Type locality and horizon: El Pontarrón 1 fossil site, Ágreda, Moncayo Region, Soria Province, Castile and León Autonomous Community, north-central Spain. Lower part of the Matute Alloformation (Late Tithonian-early Berriasian), eastern Cameros Basin. (Gómez-Fernández and Meléndez 1994; Meléndez and Gómez Fernandez, 2000).

Etymology: moncayensis derives from Moncayo, alluding to the fact that the holotype and only known specimen of the new species comes from Ágreda, a Spanish town belonging to the Moncayo Region.

Diagnosis: Member of *Pleurosternon* based on the following character combination: presence of basipterygoid processes, shell size greater than 25 cm, outer surface of the shell and skull distinctly sculptured by small pits and tubercles, overlap of the marginal scutes on the costal series, absence of extragular protrusions. It differs from the other currently known species of the genus, *Pleurosternon bullockii*, by the following characters: absence of contact between the supraoccipital and the quadrates; shorter basipterygoid processes; wider than long epiplastra, with a long posterior margin, perpendicular to the axial plane; shorter gular scutes, not reaching the entoplastron.

[Figure 2 near here]

Osseous description: Four disarticulated carapacial plates of MPZ 2020/53, and two of the plastron, are preserved (Fig. 2). The outer surface of all of them is distinctly sculptured by small pits and low tubercles, generating a rough pattern (Fig. 2C', G', M'). The plates preserved of the carapace correspond to three costals and one peripheral. Considering its morphology, as well as the sulci of the scutes located on them, the almost complete costal is recognized as probably the seventh right one (Fig. 2A-B). This plate lacks the lateral margin. The complete one corresponds to the complete eighth right costal (Fig. 2E-F). The most partial costal is only represented by its lateral region (Fig. 2D). The peripheral is an almost complete plate of the bridge (Fig. 2H-K).

Comparisons with other pleurosternids allow us to interpret, based on the shape of the most posterior costal of MPZ 2020/53, that this taxon probably had more than one suprapygal (Fig. 2E-F). Based on the morphology of the adjacent plates, the width of the suprapygal series increases towards the posterior region, so that the first would be the narrowest. The lateral margin of the bridge peripheral was dorsally directed (Fig. 2H-K).

The vertebral series was composed of five scutes, and the pleural series of four pairs (Fig. 2F). The overlap of the marginal scutes on the costal series was present in this taxon (Fig. 2D, F).

The plastral elements preserved in the analyzed specimen correspond to the lateral region of probably the left hypoplastron (Fig. 2L), and the partial right epiplastron (Fig. 2N-P). The lateral margin of the epiplastron shows that the anterior plastral lobe was subrounded. It lacked extragular protrusions. The epiplastra are wider than they are long, and show a long posterior margin, perpendicular to the axial plane. A relatively small but well-developed epiplastral process or cleithra is recognized at the postero-medial end of the visceral surface of that plate (Fig. 2O-P). The epiplastra contacted each other sagittally, preventing the entoplastron from reaching the anterior plastral margin (Fig. 2N-P). Although the gular scutes were longer than the extragulars, they did not reach the contact of the epiplastra with the entoplastron (Fig. 2N). This taxon lacked sagittal contact between the extragulars. It had inframarginal scutes (Fig. 2L). The visceral overlap of the scutes on the anterior plastral lobe was short (Fig. 2O).

[Figure 3 near here]

Only the posterior region of the skull of MPZ 2020/53 is preserved (Figs. 3, 4A-B, 5, 6A-F). The outer surfaces of both the cranial roof and the lateral region of the skull show an ornamental pattern similar to that identified on the plates (Fig. 4B). The cranial roof only preserves the anterior portion of both parietals and most of the right postorbital (Fig. 5G). The right epipterygoid, the posterior fragment of the left one, and the right quadratojugal are also preserved (Fig. 5K-M). The complete quadrates, exoccipitals, squamosals, and opisthotics are also preserved in the posterior region of the skull (Fig. 5G-L), but the left cranial side and the dorsal portion of the supraoccipital are eroded (Fig. 5G, I, K). The palatal region preserves the complete basisphenoid and basioccipital, and the almost complete pterygoids, which lack the anterior portion (Fig. 5H). The otic capsules preserve the prootics and opisthotics, the left prootic being dorsally eroded (Fig. 5G).

[Figure 4 near here]

The partially preserved parietals laterally contact the postorbitals and ventrally the epipterygoids (Fig. 5G, K, M). The posterior rami of the processus inferior parietalis form the dorsoposterior margins of the foramina for the trigeminal nerves, which does not contact the prootics (Fig. 5M). The epipterygoids are small laminar bones that anteroventrally delimit these foramina. The right postorbital was ventrally displaced, partially overlapping the quadratojugal (Fig. 5H, J, L). Posteriorly, the preserved postorbital contacts the anterodorsal region of the squamosal (Fig. 5G). The quadratojugal presents a posterodorsal expansion spreading over the cavum tympani (Fig. 5L). The foramina stapedio-temporale are laterally formed by the quadrates and medially by the prootics (Fig. 5G). Most of the cavum tympani correspond to the quadrates (Fig. 5K-L). The incisura columellae auris, which are posteroventrally open, are located on these bones (Fig. 5L). The squamosals form the posterior margins of the cavum tympani. The mandibular condyles of the quadrates are relatively small, being twice as wide as long (Fig. 5H).

The supraoccipital is dorsally eroded, lacking the area corresponding to the crest (Fig. 5G, I). The preserved processus externus pterygoideus (i.e., the right one) is slightly displaced in relation to the rest of that bone, through a fracture (Fig. 5H, J, M). This process is laterally expanded (Fig. 5H). The most anterior area of the process is absent. However, the margin that contains the canalis nervi vidiani is partially present (Fig. 5J). The posterior processes of the pterygoids are short (Fig. 5H, M). They show a short posteromedial contact with the basioccipital. In ventral view, the basisphenoid is an elongated triangular bone (Fig. 5H). The ventral surface of the rostrum basisphenoidale is exposed. The dorsum sellae is formed by a short ridge which dorsally covers the posterior end of the sella turcica. The retractor bulbi pits (sensu Evers et al. 2020) are located lateral to the base of the clinoid processes. Only the right pit is completely preserved, and it is posteriorly deep. The pit is separated from the sella turcica by a short anterolateral ridge. The basipterygoid processes are located at the mid length of the basisphenoid. Laterally, they contact the pterygoids. The posterolateral processes of the basisphenoid overlap the anteroventral surface of the basioccipital. The basioccipital presents a pair of poorly developed tubercules (Fig. 5H). The occipital condyle is completely formed by the basioccipital (Fig. 5I). The exoccipitals have long lateral expansions along the paroccipital processes of the opisthotics. The exoccipitals do not contact in the sagittal plane.

In lateral view, the fenestra ovalis is anteriorly formed by both the ventroposterior processes of the prootics and posteriorly by the processus interfenestralis of the opisthotics. Ventrally, it is completely enclosed by these bones (Fig. 5M). The ventral processes of the prootics and opisthotics are ventrally covered by the pterygoids and the basisphenoid. The processus interfenestralis are ventrally directed and separate the cavum tympani from the recessus scalae tympani. The fenestra perilymphatica is a small opening in the ventral region of the interfenestral process of each opisthotic. These processes are ventrally expanded, forming a footplate. The posterior surfaces of the paroccipital processes are dorsoventrally flat (Fig. 5I).

[Figure 5 near here]

Neuroanatomical description: MPZ 2020/53 preserves the distal region of the cranial cavity, including the posterior portion of the cerebral hemispheres. Some neuroanatomical structures could be reconstructed, including those corresponding to the sella turcica, inner ears, canalis caroticus cerebralis, canalis cavernosus, canalis stapedio-temporalis and some cranial nerves (Fig. 6).

The distal area of the cartilaginous ridge is present behind the cerebral hemispheres (Fig. 6G, I-J). This structure corresponds to a low protuberance, located at the level of the contact between the parietals and the supraoccipital. The sella turcica, which contained the pituitary gland, is small and short, lacking a posterior expansion (Fig. 6H-J). The ventral surface of the pituitary fossa does not reach the ventral margin of the cranial cavity. The dorsum sellae is an anteroposterior short ridge that covers the posterior end of the sella turcica in the region where the foramina anterius canalis carotici cerebralis are located. Posterolaterally, the cerebral carotid arteries exited from the cranial cavity through these foramina (Fig. 6H). The dorsal surface of the medulla oblongata is concave (Fig. 6I-J). Its distal region is dorsally directed. Its ventral surface is flat.

The foramina nervi trigemini are anteroventrally delimited by the epipterygoids and posterodorsally by the posterior processes of the parietals (Figs. 6G). The branches of the trigeminal nerves presented short trajectories, reaching the canalis cavernosus (Fig. 6G-H). The canalis cavernosus are ventrally formed by the pterygoids, dorsally by the prootics, and laterally by the quadrates. These canals are posterolateraly directed, contacting the cavum acustico-jugulare (Fig. 6H-I). Only the right canalis nervi abducentis could be reconstructed (Fig. 6H, J). The anterior foramen of this channel has its origin at the bulbi retractor pits, in the ventrolateral surface of the processus clinoideus. The canalis nervi abducentis runs in a posteromedial trajectory through the basisphenoid, dorsolaterally reaching the middle length of this bone. The trajectory of this canal is straight and short. The facial and vestibulocochlear nerves exited from the cranial cavity, posteriorly to the foramina nervi trigemini, through two foramina located in the fossa acustico-facialis (Fig. 6H-J). This fossa is located in the medial surface of the prootics. The distal hyomandibular branches of the facial nerves were posterolaterally projected, reaching the dorsal surface of the canalis cavernosus. The canals of these nerves split and the vidian branches are anteroventrally curved through the canalis pro ramus nervi vidiani, piercing the pterygoids and exiting close to the suture with the basisphenoid. The vidian nerves reached the canalis carotici interni and entered the cranial cavity through anterolateral canals, located in the pterygoids (Fig. 5J). The vestibulocochlear nerves exited posterior to the facial nerves and innervated the labyrinth of the inner ears (Fig. 6H-J). The glossopharyngeal nerves could not be reconstructed because of the poor preservation of the opisthotic region. The foramina jugulare anterius correspond to the vagus and accessory nerves, which exited from the cranial cavity (Figs. 6G-J). These foramina are anteriorly formed by the opisthotics and posteriorly by the exoccipitals, and they are posteromedially located relative to the cavum labyrinthicum. The hypoglossal nerves are formed by two canals that pierced the exoccipitals and flow into lateral fossae. The anterior canals are more ventrally located than the posterior ones, and both are slightly more ventrally located than the foramina jugulare anterius.

The left inner ear is better preserved than the right one; its crus communis and semicircular canals being less deformed (Fig. 6K-N). The left anterior semicircular canal does not preserve its dorsal apex (Fig 6L). The vestibular eminences of the specimen are open to the cranial cavity so, in life, they were formed by cartilaginous walls. The inner ears present rounded and low anterior and posterior semicircular canals (i.e., the vertical canals), which not reach the dorsal level of the medulla oblongata (Fig. 6I-J). The anterior canal is longer and higher than the posterior, both canals being anteroposteriorly elongated (Fig. 6L, N). The crus communis is anteroposteriorly wide, and dorsally low (Fig. 6L). The dorsal surfaces of both canals slightly exceed the dorsal level of the crus communis, giving the labyrinth an M-shape appearance in lateral view (Fig. 6L, N). The anterior and posterior ampullae are well developed. The lateral semicircular canal, which is wider than the vertical ones, is not completely closed. In dorsal view, the angle formed by the vertical semicircular canals is about 85º (Fig. 6K, M). The inner ears display a small and globose lagena, representing almost 30% of the total height of the cavum labyrinthicum (Fig. 6L, N).

The canalis carotici cerebralis contained the cerebral branches of the carotid arteries. These canals enter the cranial cavity through the foramina anterius canalis carotici cerebralis, located at the posterior end of the sella turcica (Fig. 6H-J). Posterolaterally, these paired channels run, in a short and straight trajectory, to the foramina posterius canalis carotici cerebralis, located in the suture between the basisphenoid and the pterygoids, at the level of the basipterygoid processes (Fig. 6B). The ventral surface of the pterygoids preserves shallow grooves that contained the carotid arteries. There is no evidence of the anterior palatine branches of the carotid arteries. The foramina posterius canalis carotici palatinum cannot be properly identified. Due to the absence of foramina posterius canalis carotici internus, the carotid arteries enter the skull, to reach the posterior foramina of the cerebral carotid canals, without an osseous covering.

[Figure 6 near here]

Discussion

Systematic attribution of the taxon from Ágreda

The specimen studied here can be identified as a member of Pleurosternidae considering the following character combination: foramen posterius canalis carotici cerebralis located along the contact between the pterygoids and the basisphenoid; short contact between the pterygoids and the basioccipital; small fenestra perilymphatica; distinctly sculptured outer surface of both the skull and the shell; presence of epiplastral processes; relatively short gulars; presence of inframarginal scutes (Pérez-García et al. 2015a; Joyce and Anquetin 2019). However, it cannot be attributed to either of the two pleurosternids so far recognized in the uppermost Jurassic to lowermost Cretaceous record of the Iberian Peninsula: *Selenemys lusitanica* and *Riodevemys inumbragigas*. Thus, the presence of well-developed visceral dorsal epiplastral processes contrasts with the markedly reduced development of these structures in *Selenemys lusitanica* (Pérez-García and Ortega 2011). The taxon from Ágreda does not share with *Riodevemys inumbragigas* the development of a long overlap of all pleural scutes on the peripheral plates, this condition being recognized as exclusive to that taxon (Pérez-García et al. 2015a). It also cannot be attributable to the younger Iberian taxon *Toremys cassiopeia* considering the notably larger size of the taxon from Ágreda, the Albian species being a very small form, with an estimated carapace length of the larger individuals close to 15 cm (Pérez-García et al. 2015b).

MPZ 2020/53 differs from the British Lower Cretaceous *Dorsetochelys typocardium* in characters such as the overlap of the tenth pair of marginal scutes on the eighth costal (Pérez-García 2014). All these shell characters that allow the distinction of the Ágreda taxon from the cited European forms are compatible with those of the synchronic (Tithonian to Berriasian) *Pleurosternon bullockii* (recently recognized as the only valid species of the genus *Pleurosternon*, see Guerrero and Pérez-García 2020), sharing a combination of characters until now recognized as exclusive with this form, including those indicated above (overlap the marginal scutes on the costal series; well-developed visceral dorsal epiplastral processes; shell size greater than 25 cm), as well as the presence of small pits on the outer surface of the shell (which is also shared with *Selenemys lusitanica*); and the absence of well-developed extragular protrusions (as in all pleurosternids except in the North American *Dinochelys whitei* Gaffney 1979). However, it cannot be attributed to the species *Pleurosternon bullockii*, but is recognized as a form probably close to it, since its gular scutes do not reach the entoplastron (which is not shared with any other pleurosternid so far defined), and its epiplastra are wider than long (as in *Riodevemys inumbragigas*), and show a long posterior margin, perpendicular to the axial plane (which generates an epiplastral shape exclusive to the taxon from Ágreda).

Pleurosternon bullockii is one of the few pleurosternids of which the skull is known. Thus, only two skulls from this lineage had so far been published for the European fossil record: that attributable to *Pleurosternon bullockii* (UMZC T1041. See Evans and Kemp 1975; Evers et al. 2020) and the holotype of *Dorsetochelys typocardium* (DORCM G.23. See Evans and Kemp 1976; Pérez-García 2014). Not only the ornamental pattern (Fig. 4), but also most of the anatomical characters recognized in the skull from Ágreda (Fig. 5) are compatible with those of *Pleurosternon bullockii* (see

Evans and Kemp 1975; Evers et al. 2020). In fact, the presence of basipterygoid processes of the basisphenoid is shared with *Pleurosternon bullockii* (and also with the North American *Glyptops plicatulus*) but not with *Dorsetochelys typocardium*. However, the processes are larger in *Pleurosternon bullockii* and *Glyptops plicatulus* than in the taxon from Ágreda. A small contact between the supraoccipital and each quadrate is present in *Pleurosternon bullockii*, posterior to the foramen stapedio-temporale (Evers et al. 2020). This character was unknown in the other pleurosternids hitherto defined. However, the contact between these bones is absent in the taxon from Ágreda. Taking into account all these characters, it is recognized as attributable to a new species. The relatively limited availability of characters in both the shell and the skull of the specimen from Ágreda suggests its identification as a form probably closely related to *Pleurosternon bullockii*. Therefore, we opted for its attribution to this genus, *Pleurosternon moncayensis* sp. nov. being defined.

The limited information provided by the skull fragment of the holotype of the new species, *Pleurosternon moncayensis*, does not allow us to recognize any character state that differs from those encoded for any of the other pleurosternids in the most complete matrix of anatomical characters currently available for the analysis of the phylogenetic relationships between the members of this lineage (see Pérez-García et al. 2015b; and Appendices 1 and 2). The only differences in the coding of the species from Ágreda and those of some of the other pleurosternids in that data matrix correspond to two shell characters: shell ornamented by small, regular, and clearly defined pits (character 89, state 3: exclusively shared with *Pleurosternon bullockii* and *Selenemys lusitanica*); and location of the pleuro-marginal sulcus in contact with the costal-peripheral sutures or on the costal plates (character 117, state 1: shared with all pleurosternids except *Riodevemys inumbragigas*). Therefore, taking into account the relatively small number of characters in this matrix that can be encoded for the new taxon (22 of 123, see Appendix 1), and especially that most of them correspond to states shared with most pleurosternids in which they are known, the phylogenetic analysis does not offer a robust position for that new species. Thus, following the methodology indicated by Pérez-García et al. (2015b), the taxon from Ágreda is obtained as part of a polytomy (both in the strict consensus and in the majority rule trees), in which it is grouped with *Pleurosternon bullockii*, but also with *Riodevemys inumbragigas* and *Selenemys lusitanica*. However, this node (also obtained as part of a polytomy with the other pleurosternids: *Dinochelys whitei*, *Glyptops plicatulus*, *Dorsetochelys typocardium*, and *Toremys cassiopeia*) is characterized by three synapomorphies, but only one of these characters is known for the new taxon: the one indicated above referring to the ornamental pattern (character 89), shared with *Pleurosternon bullockii* and *Selenemys lusitanica*, but not with *Riodevemys inumbragigas*. The other two corresponded to the maximum plastron length in relation to that of its lobes (character 108) and to the overlap of the second marginals on the first costals (character 118).

Diversity and distribution of Pleurosternidae in Europe

The presence of *Pleurosternon* had been confirmed in the Upper Jurassic (upper Tithonian) and Lower Cretaceous (Berriasian) records of both Great Britain and France (Gônet et al. 2018; Joyce and Anquetin 2019; Guerrero and Pérez-García 2020), the species *Pleurosternon bullockii* being the only one identified in the two regions (Guerrero and Pérez-García 2020). The specimen analyzed here allows us to recognize the presence of a form closely related to *Pleurosternon bullockii* in the Iberian record, expanding the palaeobiogeographic distribution of the genus *Pleurosternon*, and describing a second representative, *Pleurosternon moncayensis* sp. nov.

Recently Joyce and Rollot (2020) considered that the Belgian Barremian or Aptian *Peltochelys duchastelii* Dollo 1885 could be a member of Paracryptodira. Thus, these authors reviewed the coding of this taxon in two data matrices that included representatives of different lineages of Testudinata, indicating that the result of these analyses suggested paracryptodire relationships for this species in a global context. However, these authors pointed out that most of the character states modified or added by them were based on their interpretation of problematic regions (with fractures, slight displacements of some elements with respect to the original position, and details hidden by the paint used by previous researchers to highlight the margins interpreted for the plates and scutes), so that the possibility that these observations were erroneous could not be ruled out. Personal observation of the lectotype of this taxon (IRSNB Ct. R. 16), on which the coding of Joyce and Rollot (2020) as well as those in previous works (e.g., Joyce 2007; Pérez-García 2011) were based, is equally unable to confirm the encoding of most of these characters, so they should be considered as unknown, as their encoding is doubtful (i.e., they should have been recoded as "?"). Thus, the coding of this taxon should hardly vary with respect to that proposed in previous works (see Pérez-García 2011), so that its position as a member of Paracryptodira cannot be supported. In fact, the detailed observation of the visceral area of the anterior region of the carapace does not allow us to observe an equivalent suture to that interpreted by Joyce and Rollot (2020) for the dorsal region, between the nuchal and the putative first peripheral. Thus, the encoding of problematic characters such as those related to the number of peripherals, the contact between the first peripheral and the first costal or the contribution of the nuchal to the shell margin is not methodologically appropriate. In this sense, as indicated by Joyce and Rollot (2020), the discovery of new and better-preserved material of *Peltochelys duchastelii* would be necessary to confirm the encoding of these characters. In fact, the absence of mesoplastra in *Peltochelys duchastelii* is shared, among others, with the members of Pan-Cryptodira, differing from the condition known for all paracryptodires (Pérez-García et al. 2015a.). The ornamental pattern of *Peltochelys duchastelii* is also radically different from that of any representative of Paracryptodira but resembles that of some members of Cryptodira (see Meylan 1988; Pérez-García 2011). Furthermore, the reinterpretation of the putative presence of a single gular scute in *Peltochelys duchastelii*, made by Joyce and Rollot (2020), contrasts with the condition in the members of Paracryptodira, the presence of two scutes being recently confirmed for *Pleurosternon bullockii*, a condition shared with all other pleurosternids (Guerrero and Pérez-García 2020). Taking all this into account, the Joyce and Rollot's (2020) reconsideration of some Mesozoic European members of Pleurosternidae as representatives of Compsemydidae,exclusively as a result of the inclusion of *Peltochelys duchastelii* in a matrix of Paracryptodira, cannot be supported here. In fact, the redefinition proposed by those authors for that clade (in which they included *Riodevemys inumbragigas*, *Selenemys lusitanica*, *Peltochelys duchastelli*, *Compsemys victa* Leidy 1856 and *Berruchelus russelli* Pérez-García 2012; Pleurosternidae having been restricted to *Dorsetochelys typocardium*, *Glyptops plicatulus*, *Pleurosternon bullockii* and *Toremys cassiopeia*), based exclusively on shell characters, was problematic. Thus, they characterized Compsemydidae by the presence of a finely textured shell, sutured bridge, sinuous plastral midline sulcus, absence of a contact between the first pair of peripherals and the first of costals, and withdrawal of the nuchal from the anterior margin of the shell, resulting from a midline contact of the peripherals of the first pair. The first-hand study of all these taxa shows that each of these two putative groups does not possess a unique ornamental pattern shared between its members and different from those of the other. Thus, the pattern of *Selenemys* *lusitanica* is different from that of *Riodevemys inumbragigas*, *Peltochelys duchastelli* and the indisputable members of Compsemydidae (*Compsemys victa* and *Berruchelus russelli*), but it is shared with *Pleurosternon bullockii* (see Pérez-García and Ortega 2011; Guerrero and Pérez-García 2020). A sutured bridge is present in all those paracryptodiran taxa. A sinuous plastral midline sulcus can be identified in both putative clades. For example, some specimens of *Pleurosternon bullockii*, such as DORCM G14 and NHMUK R 1889, show this condition. The absence of a contact between the first pair of peripherals and the costal series is not shared among all putative members of Compsemydidae, since the contact is present in *Riodevemys inumbragigas* (Pérez-García et al. 2015a). The nuchal of this species has a wide anterior margin, generating a wide separation between the plates corresponding to the first pair of peripherals. However, these plates are medially very close to each other in *Toremys cassiopeia*, since the anterior margin of the nuchal is very narrow (Pérez-García et al. 2015b). Taking into account all these problems, generated by the consideration of *Peltochelys duchastelii* as a member of Paracryptodira owing to the coding of badly known character states, which cannot be confirmed, the biogeographic considerations proposed by Joyce and Rollot (2020) relative to Compsemydidae and Pleurosternidae are not supported here. In fact, the presence of Compsemydidae in Europe is not identified in the Mesozoic record, but exclusively in Palaeocene levels (Pérez-García 2012, 2020b).

Pleurosternidae is the only group of freshwater turtles recognized in the Upper Jurassic record of both North America and Europe (Gaffney 1979; Pérez-García 2017; Joyce and Anquetin 2019). The North American record of Pleurosternidae is restricted to the Upper Jurassic, whereas these stem turtles are recognized in both Upper Jurassic and Lower Cretaceous levels in Europe, from the Kimmeridgian to the Albian (Pérez-

García et al. 2015b). Thus, this group experienced a vicariant biogeographical distribution as a consequence of the opening of the North Atlantic Ocean (Pérez-García and Ortega 2011; Pérez-García et al. 2015b). In Europe, relatively wide diversity is recognized for Pleurosternidae between the last stage of the Jurassic (Tithonian) and the first of the Lower Cretaceous (Berriasian), so that it was not affected by the faunal turnover across the Jurassic-Cretaceous boundary as seen in other vertebrate groups (e.g., Tennant et al. 2017). In fact, the species *Pleurosternon bullockii* is recognized both before and after the boundary (Guerrero and Pérez-García 2020). The species described in this paper, the Tithonian or Berriasian *Pleurosternon moncayensis* sp. nov, increases the diversity identified for this group in that time period, in which the Tithonian *Riodevemys inumbragigas*, Tithonian remains of *Selenemys* sp., the Tithonian and Berriasian *Pleurosternon bullockii*, and the Berriasian *Dorsetochelys typocardium*, are also recognized. In this context, the problematic German taxon '*Desmemys bertelsmanii*' Wegner 1911, exclusively identified by a juvenile individual whose shell is considered lost, could represent another European Berriasian pleurosternid, but it is currently recognized as a *nomen dubium* (see Joyce and Anquetin 2019). Thus, the pleurosternids are identified as the clearly predominant group of freshwater turtles in Europe during the Jurassic-Cretaceous transition, considering both the abundance of remains and the diversity represented (Pérez-García 2017).

Several lineages of freshwater turtles, attributable to the crown Testudines (all or most of them basal representatives of Eucryptodira) reached Europe, from Asia, during the Early Cretaceous (see Pérez-García 2017, and references therein). Although their presence has been confirmed since the Valanginian, they were especially abundant around the Barremian. For this interval, several representatives of Xinjiangchelyidae (the Hauterivian or Barremian *Larachelus morla* Pérez-García and Murelaga 2012a and

Camerochelys vilanovai Pérez-García and Murelaga 2013, the Barremian *Brodiechelys royoi* Pérez-García, Gasulla and Ortega 2014, and the Barremian or Aptian *Brodiechelys brodiei* (Lydekker 1889)), as well as other eucryptodires whose precise systematic position is unknown (the Barremian *Galvechelone lopezmartinezae* Pérez-García and Murelaga 2012b and *Hoyasemys jimenezi* Pérez-García, de la Fuente and Ortega 2012, and the Barremian or Aptian *Chitracephalus dumonii* Dollo 1885 and *Peltochelys duchastelii*), have been identified. Although the pleurosternids were present in Europe until the last stage of the Lower Cretaceous (i.e., the Albian, when *Toremys cassiopeia* lived, which corresponds to the only representative of this group defined at post-Berriasian levels), their abundance and diversity in post-Berriasian levels are recognized as markedly lower than in previous stages (Krebs 1995; Buscalioni et al. 2008; Canudo et al. 2010; Pérez-García et al. 2013), probably due to the arrival of those successful Asian lineages.

The absence of a known record of Pleurosternidae after the Albian coincides with the disappearance of many other groups of European reptiles, an important faunal replacement, strongly conditioned by climate changes, reported for the end of the Early Cretaceous (see Pérez-García et al. 2020 and references therein). None of the freshwater eucryptodiran lineages of Asian origin that represented a successful fauna of turtles in the Lower Cretaceous record of Europe are also recognized in the Upper Cretaceous (Lapparent de Broin 2001; Pérez-García 2017).

Neuroanatomical implications

Pleurosternids are generally proposed as freshwater aquatic turtles, mainly considering the riverine and lacustrine origin interpreted for many of the sites and facies in which remains of this clade have been found (Joyce and Anquetin 2019; Pérez-García et al.

2015a). This is also in accordance with the lacustrine origin of the El Pontarron 1 site where *Pleurosternon moncayensis* sp. nov. was found. The first characterization of the neuroanatomy of the pleurosternid turtles, performed here, allows the comparison of their inner ears with those of other extinct and extant freshwater taxa, providing new arguments to evaluate this hypothesis.

The labyrinthic system shows a relatively low degree of morphological variation among the different members of Testudinata (Paulina-Carabajal et al. 2017; Lautenschlager et al. 2018). The study of the inner cranial cavities of the skull of the stem taxon *Pleurosternon moncayensis* allows us to interpret, for the first time, that the angle formed by the anterior and posterior semicircular canals in Pleurosternidae (about 85º in the new species) was more acute than those in the terrestrial stem taxa, in which the values exceeded 100º (Lautenschlager et al. 2018; Martín-Jiménez et al. 2021; Paulina-Carabajal et al. 2017). No reconstruction of the inner ear of any indisputable aquatic stem turtle had been performed so far. However, both the marine sandownids and the coastal plesiochelyids, generally identified as members of Eucryptodira (Joyce 2007; Tong and Meylan 2013; Anquetin et al. 2014; Cadena 2015; Pérez-García, 2017), have recently been suggested as not attributable to the crown Testudines (Evers and Benson 2019), and neuroanatomical studies of both taxa have been published (see Paulina-Carabajal et al. 2013; Evers and Joyce 2020). The values for the angle between the anterior and posterior semicircular canals of the sandownids (reconstructed for *Sandownia harrisi* Meylan, Moody, Walker and Chapman 2000, to be of about 73º following Evers and Joyce 2020) and plesiochelyids (reconstructed for *Plesiochelys etalloni* (Pictet and Humbert 1857), to be about 80º following Paulina-Carabajal et al. 2013), are lower than the angle identified here for the pleurosternids. Therefore, the values of this angle in the three mentioned clades (i.e., Pleurosternidae, Sandownidae and Plesiochelyidae) are compatible with the range of variability observed for the aquatic forms of the crown Testudines (between 79º and 98º; see table 1 in Paulina-Carabajal et al. 2017, and table 1 in Lautenschlager et al. 2018), with more acute angles than those of the terrestrial turtles.

The diameters of the semicircular canals of stem and derived terrestrial turtles, and also those of indisputable cryptodiran marine turtles (i.e., the members of Pan-Chelonoidea, corresponding to pelagic forms), are thicker than those of the aquatic freshwater turtles (both cryptodires and pleurodires) (Georgi 2008; Neenan et al. 2017). The thinner diameter present in the aquatic freshwater turtles and also identified here for the pleurosternids, together with the anteroposteriorly more elongated vertical canals (i.e., the anterior and posterior semicircular canals) in all of these than in the terrestrial and pelagic forms, confers them a more slender appearance for these structures. Considering both conditions, the labyrinthic system of the coastal plesiochelyids resembles more closely that of the freshwater taxa than that of the pelagic marine turtles (Paulina-Carabajal et al. 2013). The semicircular canals of the sandownids are slightly narrower and slightly more elongated than in the pelagic marine turtles, for which a marine lifestyle with diving restrictions has been interpreted (Evers and Joyce 2020).

The M-shape of the dorsal section of the labyrinth of *Pleurosternon moncayensis*, observed in lateral view, is shared with most aquatic taxa (including marine and freshwater forms), but not with the terrestrial turtles (including both stem taxa and the members of the crown Testudines), which display less dorsal development relative to the crus communis, as they are almost horizontal (Paulina-Carabajal et al. 2017; Ferreira et al. 2018; Lautenslager et al. 2018; Hermanson et al. 2020). Although the sandownids show the condition recognized for most aquatic taxa, the plesiochelyids display low vertical canals, similar to those of the terrestrial turtles (Paulina-Carabajal et al. 2013).

The presence of a markedly longer anterior semicircular canal than the posterior in the pleurosternids coincides with the condition recognized in all freshwater forms (Georgi 2008; Ferreira et al. 2018; Hermanson et al. 2020), and in the sandownids (Evers and Joyce 2020). This condition differs from those in the stem and derived terrestrial forms, the pelagic marine taxa and also the coastal plesiochelyids, in which the vertical canals are sub-equal in size or the anterior canal is only slightly longer than the posterior (Paulina-Carabajal et al. 2013, 2017; Neenan et al. 2017; Lautenschlager et al. 2018; Evers et al. 2019; Martín-Jiménez et al. 2021).

Considering all this information, several arguments, obtained through the first neuroanatomical reconstruction of a pleurosternid, and specifically through the reconstruction of its labyrinthic system, allow us to evaluate the lifestyle of this clade of stem turtles. Thus, the combination of characters observed in the semicircular canals of their inner ears confirms the interpretation of the pleurosternids as freshwater aquatic turtles: narrow and anteroposteriorly elongated canals, with a dorsal development exceeding the level of the crus communis, and showing an acute angle between the vertical canals, of which the anterior is markedly longer than the posterior.

Conclusions

A partial skeleton of a turtle attributable to Pleurosternidae (Paracryptodira, Baenoidea), found in a late Tithonian- earliest Berriasian outcrop at the Spanish locality of Ágreda (Moncayo Region, Soria Province), is studied here. No remains of this group of turtles had been found so far in that region, being one of the few vertebrate remains described there. This individual corresponds to the oldest turtle fossil identified in the Cameros Basin. In addition to several disarticulated plates of the shell (both carapacial and plastral elements), the specimen preserves the partial skull. It corresponds to the first cranial remain of a pleurosternid found in Spain, and to the third identified in Europe, the previously known skulls having been found in the United Kingdom.

In the last decade, several representatives of Pleurosternidae have been identified in the Jurassic-Cretaceous transition levels of the Iberian Peninsula. The specimen from Ágreda cannot be attributed to any of them. It is here recognized as a new species, possibly closely related to the British Tithonian to Berriasian pleurosternid *Pleurosternon bullockii*. Therefore, the new species *Pleurosternon moncayensis* is defined. The diversity of this lineage for the European record is reviewed. Five species that lived between the Kimmeridgian and the Berriasian are recognized (i.e., *Selenemys lusitanica*, *Riodevemys inumbragigas*, *Dorsetochelys typocardium*, *Pleurosternon bullockii*, and *Pleurosternon moncayensis* sp. nov.), but so far no defined species had been identified between the Valanginian and the Aptian. Thus, there is a gap in the pleurosternid record until the only defined post-Berriasian pleurosternid, the Spanish Albian species *Toremys cassiopeia*.

The first neuroanatomical reconstruction of a pleurosternid is performed here, based on the high-resolution computed tomography scanning of the partial skull of *Pleurosternon moncayensis* sp. nov. The combination of characters observed in the labyrinthic system of its inner ears allows us to confirm the interpretation of the pleurosternids as freshwater aquatic turtles. Therefore, the neuroanatomical reconstruction of *Pleurosternon moncayensis* sp. nov. is the first one so far performed for a freshwater stem turtle. These results agree with the lacustrine palaeoenvironmental reconstruction inferred for the unit (Matute Alloformation) where the specimen was found.

Acknowledgements

The authors thank Félix Pérez Lorente (Universidad de La Rioja) and Gloria Cuenca Bescós (Universidad de Zaragoza) for the administrative procedures related to the discovery and deposit of the holotype of the new taxon; José Manuel Gasca (Universidad de Zaragoza) and Penelope Cruzado-Caballero (Universidad de La Laguna) for their participation in some of the tasks related to its storage, conservation, and access; and the editor Gareth J. Dyke and the reviewers Pedro M. Callapez and Ignacio Maniel for comments and suggestions. DC is supported by the Beatriu de Pinós postdoctoral programme (BP2017-00195) of the Government of Catalonia's Secretariat for Universities and Research of the Ministry of Economy and Knowledge. This study was subsidized in part by the Project CGL2017-85038-P of the Spanish Ministerio de Economía y Competitividad-ERDF, as well as by the Aragón Regional Government ("grupo de Referencia Aragosaurus: reconstrucciones paleoambientales y recursos geológicos").

Disclosure statement

No potential conflict of interest was reported by the authors.

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Figure 1. Geographical and geological setting of El Pontarrón 1 site (Ágreda, Moncayo Region, Soria Province, Spain) (indicated by red star in B-D), where the holotype of the late Tithonian- earliest Berriasian pleurosternid *Pleurosternon moncayensis* sp. nov. was found, in the Matute Alloformation. A, Geographical setting in the Iberian Peninsula context. B, Geological map of the area (redrawn from Gómez-Fernández and Meléndez, 1994). C) Ortoimage including the El Pontarrón 1 outcrop in the lower part of the Matute Alloformation, which is dominated by thick-bedded micritic to skeletal lacustrine limestones. D) Field view of the well-bedded lacustrine carbonates of the

lower part of the Matute Alloformation, indicating the position of El Pontarrón 1 outcrop (image taken from GoogleMaps).

Figure 2. Shell remains of the holotype of the pleurosternid *Pleurosternon moncayensis* sp. nov., MPZ 2020/53, from the late Tithonian- earliest Berriasian of Ágreda (Moncayo Region, Soria Province, Spain). A-C, probably seventh right costal, in ventral (A) and dorsal (B) views, and detail of its outer surface (C’). D, lateral region of a costal, in dorsal view. E-G, eighth right costal, in ventral (E) and dorsal (F) views, and detail of its outer surface (G’). H-K, bridge peripheral, in lateral (H), ventral (I), anterior (J) and posterior (K) views. L-M, lateral area of the probably left hypoplastron, in ventral view, and detail of its outer surface (M’). N-P, right epiplastron, in ventral (N), dorsal (O) and medial (P) views.

Figure 3. Partial skull of the holotype of the pleurosternid *Pleurosternon moncayensis* sp. nov., MPZ 2020/53, from the late Tithonian- earliest Berriasian of Ágreda (Moncayo Region, Soria Province, Spain), in dorsal (A), ventral (B), posterior (D), anterior (E), left lateral (F), and right lateral (G) views.

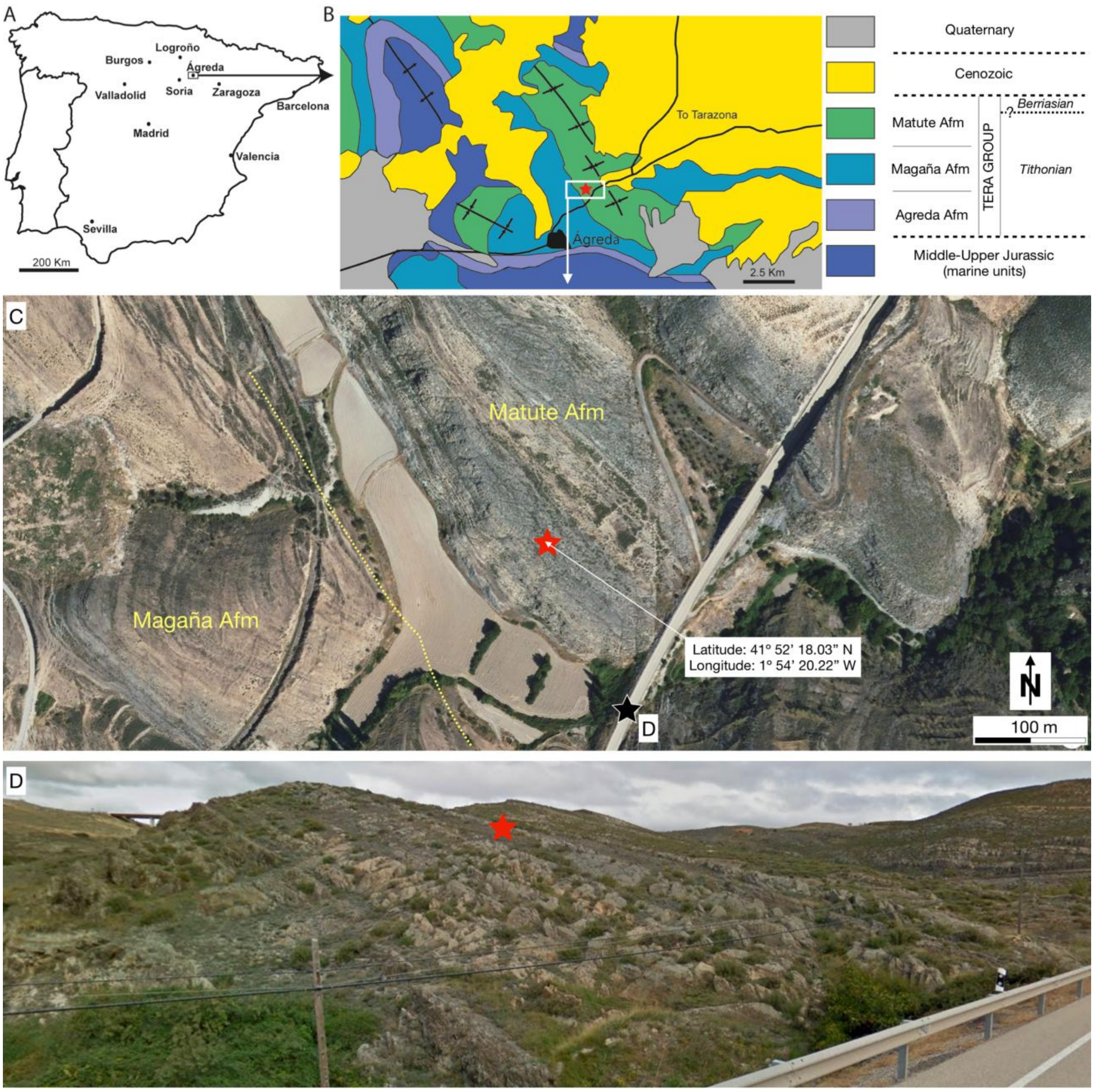
Figure 4. Detail of the ornamental pattern on the outer surface of the postero-lateral region of the skull of the pleurosternid *Pleurosternon moncayensis* sp. nov., MPZ 2020/53, from the late Tithonian- earliest Berriasian of Ágreda (Moncayo Region, Soria Province, Spain) (A-B), and on the only known skull of *Pleurosternon bullockii*, UMZC T1041, from the Berriasian of Durlston Bay (Dorset, England, UK) (C-D).

Figure 5. Virtual three-dimensional reconstruction of the skull of the holotype of the pleurosternid *Pleurosternon moncayensis* sp. nov., MPZ 2020/53, from the late Tithonian- earliest Berriasian of Ágreda (Moncayo Region, Soria Province, Spain), in dorsal (A, G), ventral (B, H), posterior (C, I), anterior (D, J), left lateral (E, K), and right lateral (F, L-M) views. The bones are represented in black and the sediment in pink in A-F, and the sediment has been virtually removed and each bone is represented with a different color in G-M. The bones of the right lateral side (quadrate, quadratojugal, postorbital and squamosal) have been virtually removed in M.

Figure 6. Osseous and neuroanatomical three-dimensional virtual reconstructions of the skull of the holotype of the pleurosternid *Pleurosternon moncayensis* sp. nov., MPZ 2020/53, from the late Tithonian- earliest Berriasian of Ágreda (Moncayo Region, Soria Province, Spain). The osseous elements (in grey) have been made transparent (A-F) to show the reconstruction of the endocast (in blue), cranial nerves (yellow), labyrinthic system (pink), and arterial system (red) (A-J). The reconstructions correspond to the dorsal (A, G), ventral (B, H), posterior (C), anterior (D), left lateral (E, I) and right lateral (G, J) views. K-N, details of the left (K-L) and right (M-N) inner ears, in dorsal (K, M) and lateral (L, N) views.

Appendix 1. Scored characters for the holotype of the pleurosternid *Pleurosternon moncayensis* sp. nov., MPZ 2020/53, from the late Tithonian- earliest Berriasian of Ágreda (Moncayo Region, Soria Province, Spain), in the data matrix used by Pérez-García et al. (2015b): ?????????? ?????????0 ????????00 ?0???????? ??????01?0 000??????? 0???0??0?? ?11??????? ??????113? ???????????????????? ?1??1?1?1? ???

Appendix 2. Changes of the coding of the European late Tithonian- earliest Berriasian pleurosternid *Pleurosternon bullockii* with respect to that proposed by Pérez-García et al. (2015b), based on both the personal observation of the only known skull of this species, UMZC T1041, and the information provided by Evers et al. (2020) on it: The species is recoded as 1 for character 16 (frontal contribution to the orbit reduced to a small process); as 1 for character 18 (reduced jugal contribution to the orbit); as 0 for character 32 (opisthotic excluded from the stapedial foramen); and as ? for character 65 (unknown shape of the posterior portion of basioccipital tubercles).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Cenozoic
Matute Afm
Magaña Afm
Agreda Afm
TERA GROUP
Berriasian
?
Tithonian
Middle-Upper Jurassic (marine units)
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Figure 1.

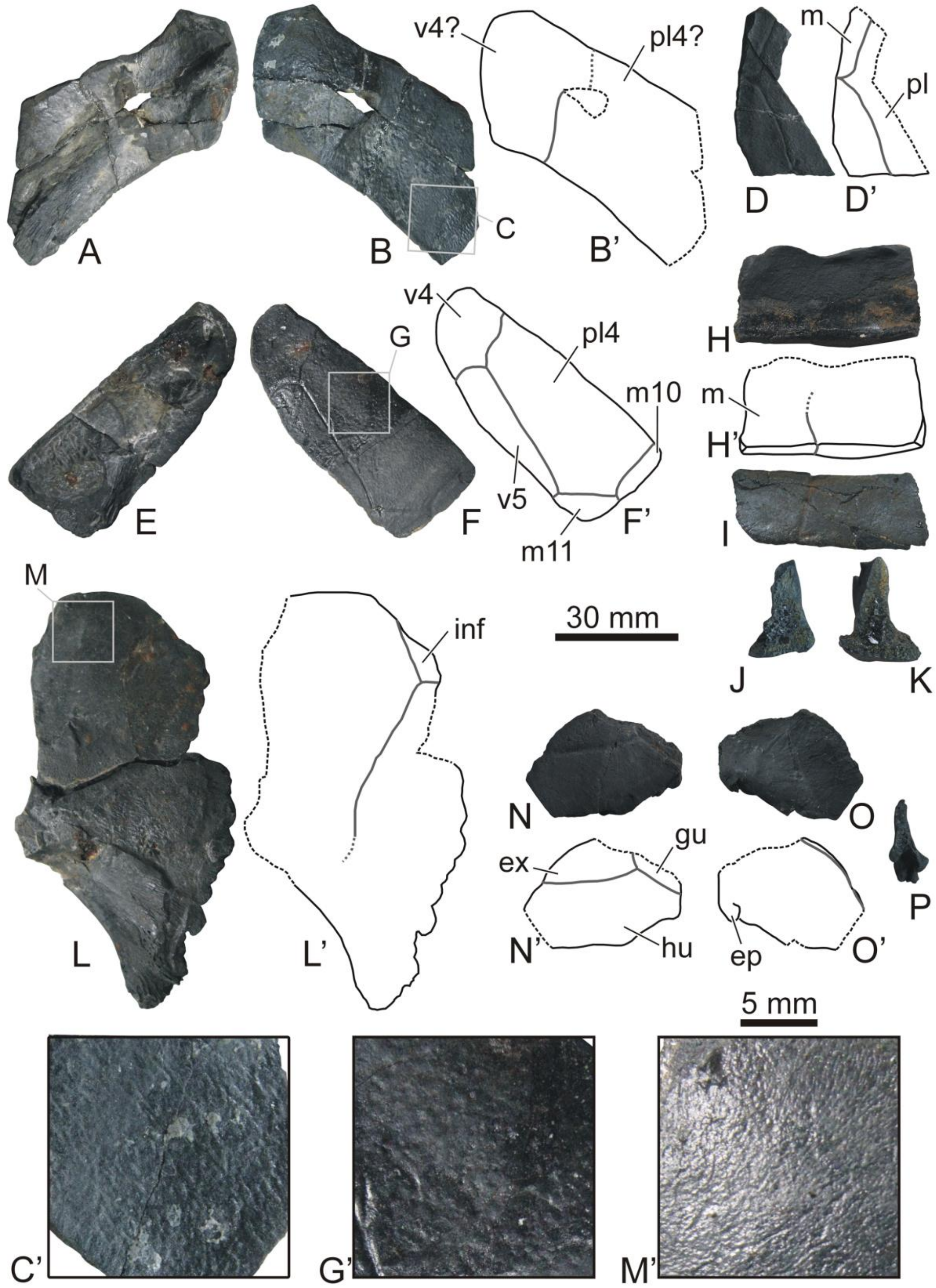
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Figure 2.

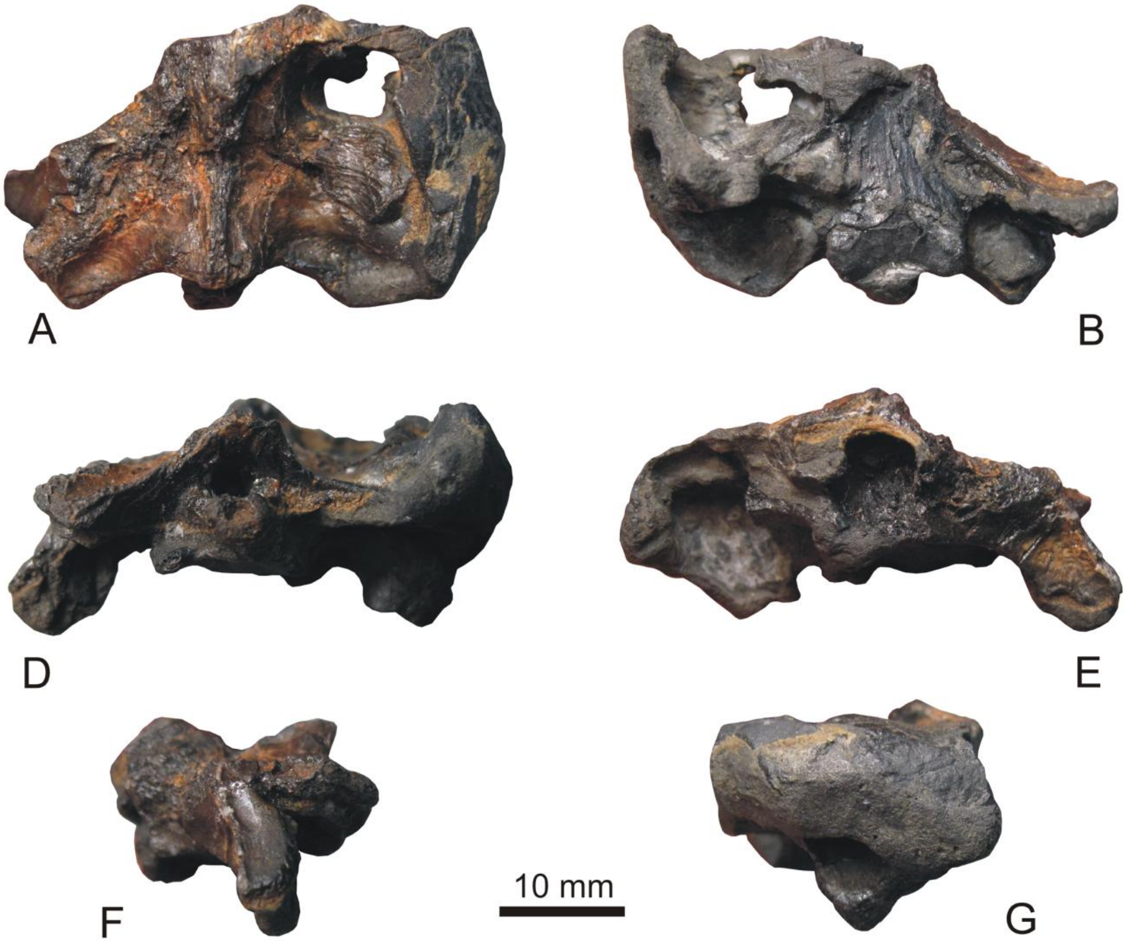

Figure 3.

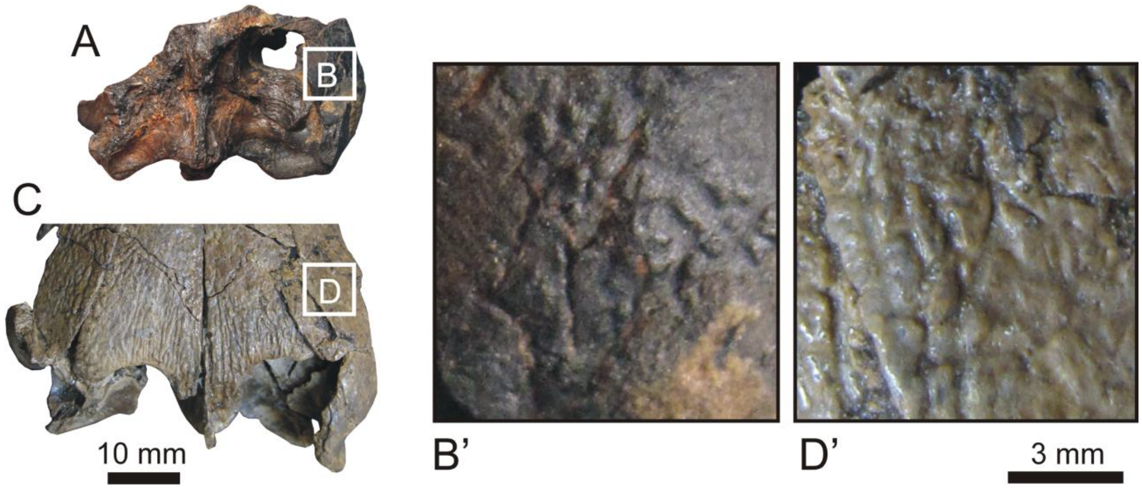

Figure 4.

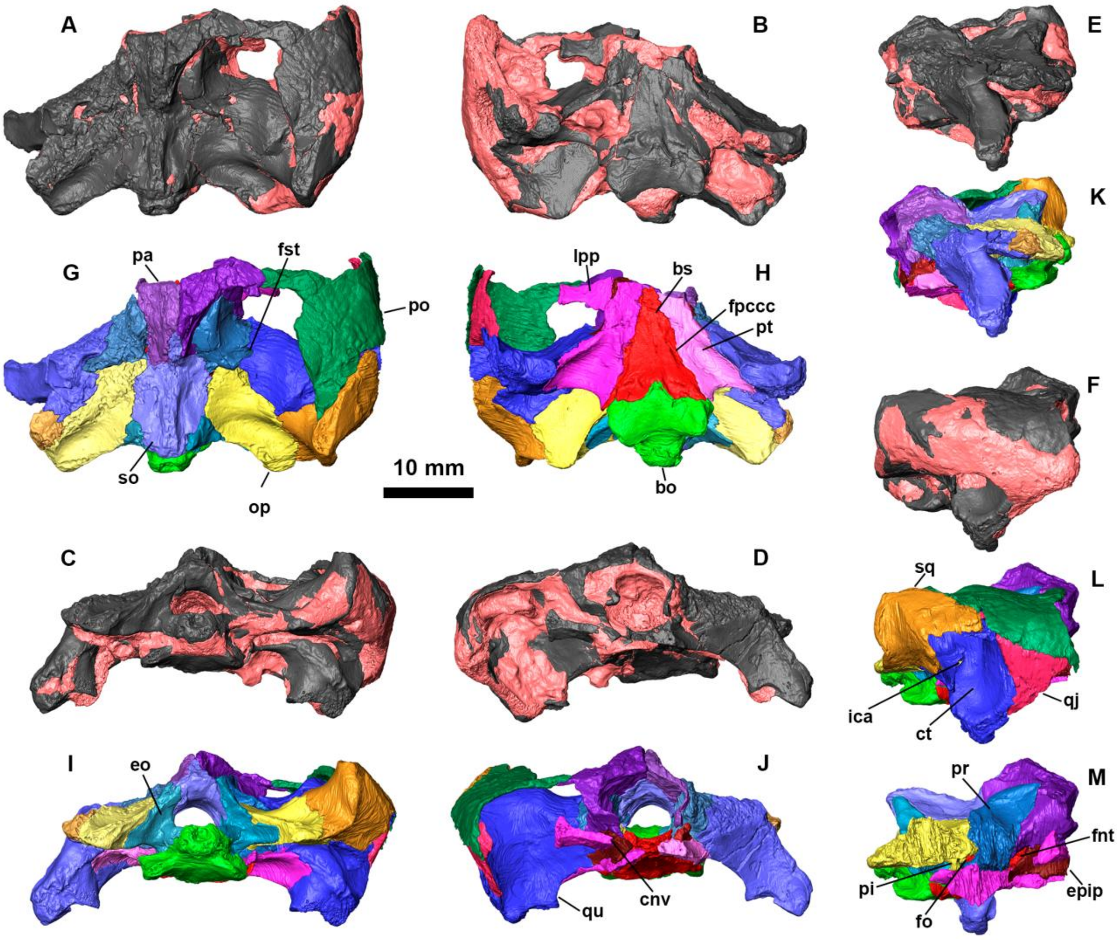
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Figure 5.

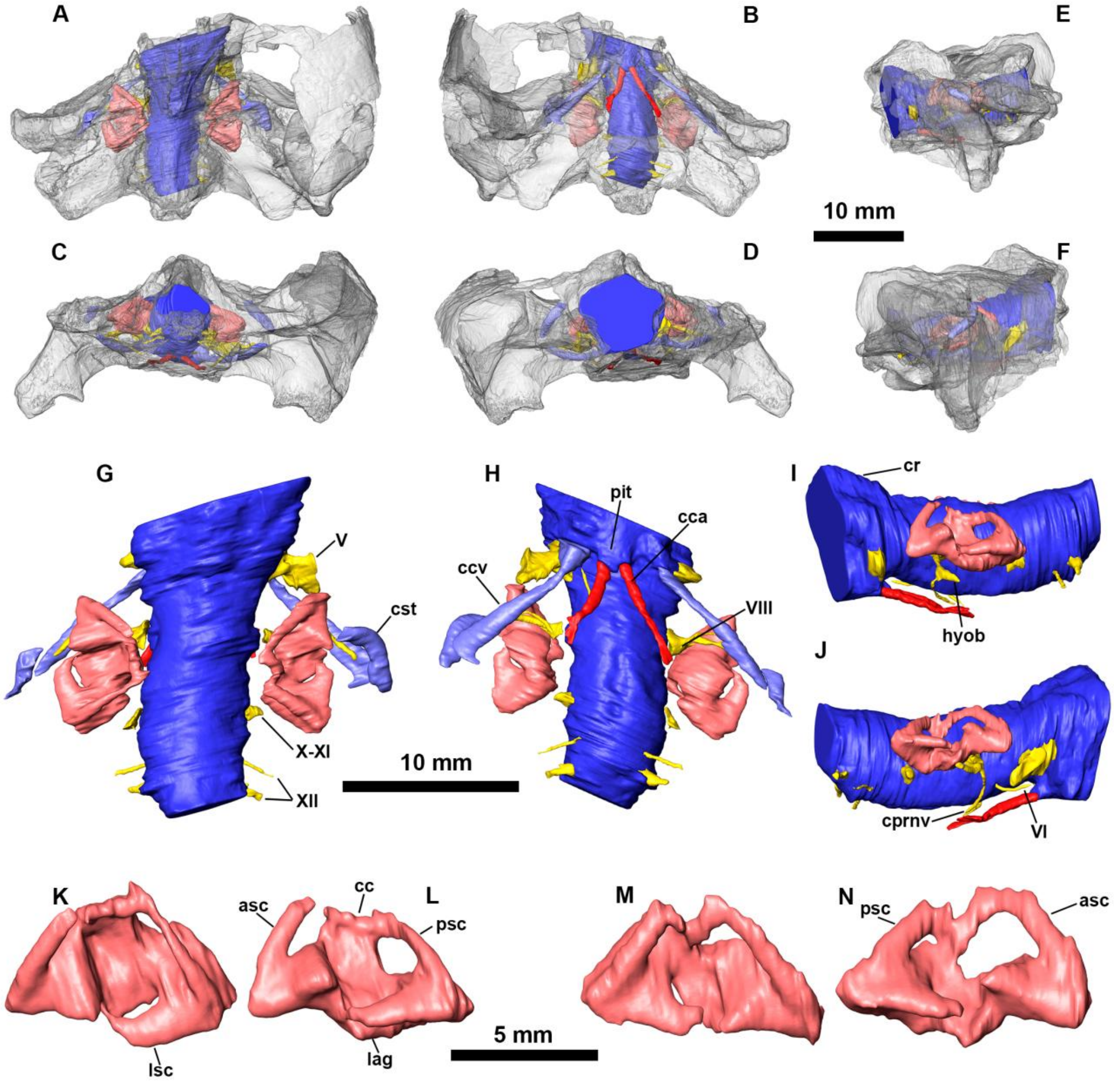
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Figure 6.