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Oneirosaurus caballeroi gen. et sp. nov., a new mosasaur from Colombia

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ABSTRACT

A new mosasaur specimen found in the Coniacian beds of Lebrija, Santander, Central Colombia, is here described. The new specimen represents a new genus and species of plioplatecarpine mosasaurid that we name *Oneirosaurus caballeroi* gen. et sp. nov. *Oneirosaurus* is a plioplatecarpine characterized by one character unknown in any other plioplatecarpine: the presence of two external foramina for the exit of nerves X, XI, and XII. It is also distinguished by a combination of characters that includes among others: prefrontal and postorbitofrontal separated at the roof of the orbit; broad frontal, with short triangular surface anterior to the orbits; triangular and broad anterodorsal surface of the parietal contacting the postorbital for a short distance; infrastapedial process of the quadrate robust without being fused to the suprastapedial process; small otosphenoidal crest of prootic not covering the exit of nerve VII; basioccipital canal opening into the floor of the braincase through two large foramina separated by a medial septum; lingual alveolar parapet of dentary lower than labial; marginal teeth crown with subcircular cross-section at base and with two carinae arranged at 180º; and presence of a notch in anterior border of the atlas neural arch. The morphological comparisons and the cladistic analysis show the new taxon as an intermedium plioplatecarpine with phylogenetic proximity to the Colombian species *Yaguarasaurus columbianus* from the lower Turonian and to the species *Ectenosaurus clidastoides* from the Santonian-Campanian of the USA. Our phylogenetic results shows tethysaurines and halisaurines as plesiopelvic and plesiopedal groups separated from the hydropelvic and hydropedal derived groups Tylosaurinae, Plioplatecarpinae, and Mosasaurinae.

Keywords: Mosasauridae; Plioplatecarpinae; Northern Gondwana; Coniacian.

Oneirosaurus caballeroi gen. et sp. nov., un nuevo mosasaurio de Colombia

RESUMEN

Se describe un nuevo espécimen de mosasaurio encontrado en capas del Coniaciano en Lebrija, Santander, Centro de Colombia. El nuevo espécimen representa un nuevo género y especie de mosasáurido pliopatecarpino que nosotros nombramos *Oneirosaurus caballeroi* gen. et sp. nov. *Oneirosaurus* es un plioplatecarpino que se distingue de cualquier otro plioplatecarpino por la presencia de dos forámenes externos para la salida de los nervios X, XI y XII. *Oneirosaurus* también se distingue por una combinación de caracteres que incluye entre otros: prefrontal y postorbitofrontal separados en el techo de la órbita; frontal ancho, con superficie triangular corta anterior a las órbitas; superficie anterodorsal triangular y ancha del parietal contactando el postorbital por una distancia corta; proceso infraestapedial del cuadrado robusto y sin fusionarse con el proceso supraestapedial; proótico con una pequeña cresta otosfenoidal que no cubre la salida del nervio VII; canal basioccipital abriéndose en el piso del basicráneo a través de dos grandes forámenes separados por un septo medial; dentario con parapeto alveolar lingual más bajo que el labial; corona de los dientes marginales con sección transversal subcircular en la base y con dos carenas dispuestas a 180º; y presencia de una muesca en el borde anterior del arco neural del atlas. Las comparaciones morfológicas y el análisis cladístico muestran al nuevo taxón como un plioplatecarpino intermedio con proximidad filogenética a la especie colombiana *Yaguarasaurus columbianus* del Turoniano inferior y a la especie *Ectenosaurus clidastoides* del Santoniano-Campaniano de EUA. Nuestros resultados filogenéticos muestran a los tethysaurinos y halisaurinos como grupos plesiopélvicos y plesiopedales separados de los grupos derivados hydropélvicos e hydropedales Tylosaurinae, Plioplatecarpinae, y Mosasaurinae.

Palabras clave: Mosasauridae; Plioplatecarpinae; Gondwana del Norte; Coniaciano.

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I. Introduction

Mosasaurs were Late Cretaceous cosmopolitan marine reptiles. In South America, mosasaur specimens have been found in Colombia, Venezuela, Peru, Brazil, Chile, and Argentina (Bengston and Lindgren, 2005; Caldwell and Bell, 1995; Fernández and Gasparini, 2012; Fernández and Talevi, 2015; Jiménez-Huidobro *et al*., 2015; Jimenez-Huidobro *et al*., 2017; Otero, 2016; Páramo-Fonseca, 2012; Páramo-Fonseca, 2015; Price, 1957 in Bardet *et al.*, 2005; Pierce and Welles, 1959; Sanchez-Villagra *et al*., 2008; Soto-Acuña *et al*., 2015). South American mosasaurs have shown derived forms (Fernández and Gasparini, 2012; Otero, 2016) but also basal morphologies from the early Late Cretaceous that remain poorly known globally (Páramo, 1994; Páramo-Fonseca, 2000, 2012, 2013).

The reports on Colombian mosasaurs include four specimens found in Turonian beds of the Upper Magdalena Valley, southern Colombia (Páramo 1994; Páramo-Fonseca, 1997; 2000; 2012), one specimen found in Coniacian beds of Lebrija, Santander, northern Colombia (Páramo-Fonseca, 2012), one specimen found in Campanian beds of Coello, Tolima, central Colombia (Páramo-Fonseca, 2012; 2013), one specimen found in upper Campanian – lower Maastrichtian beds of Cuítiva, Boyacá, Central Colombia (López-Rueda *et al*., 2024), and four specimens found in Maastrichtian beds of Cuítiva, Boyacá, Central Colombia (López-Rueda *et al*., 2024). The Turonian specimens, recognized as *Yaguarasaurus columbianus* Páramo 1994, correspond to two nearly complete skulls with cervical vertebrae and two specimens represented by isolated cranial remains (Páramo, 1994; Páramo-Fonseca, 2000; 2012). The Campanian specimen, a complete skeleton, was identified as *Eonatator coellensis* Páramo-Fonseca, 2013 (Páramo-Fonseca, 2012; 2013). The Coniacian specimen is the subject of this contribution; it corresponds to an incomplete skull (IGMp879524) previously reported without description, under catalog number IPN-2, by Páramo-Fonseca (2012). The Campanian and Maastrichtian specimens found in Cuítiva, are isolated fragments and were identified as *Globidens* sp., Mosasauridae indet. and Pliopatecarpinae indet. (see López-Rueda *et al*., 2024). Another two Colombian mosasaur specimens were reported in unpublished academic works. One of them, a poorly preserved incomplete skull with vertebral remains, was collected from Coniacian beds from Cucaita, Boyacá, central Colombia (Correa-Agudelo, 2016) and the other, four fragmentary vertebrae, was found in Turonian-Coniacian beds from Ortega, Tolima, south-central Colombia (Narváez-Rincón, 2018).

The material here described was extracted from Coniacian beds in the municipality of Lebrija, Santander, and comprises an almost complete skull and atlas. This material represents the first record of a mosasaur from northern Colombia. The specimen shows an enigmatic mineralization that enabled the conservation of anatomical features rarely observed in mosasaurs, as is the interorbital septum, which in this specimen is exceptionally preserved (see Páramo-Fonseca *et al*., 2024). In this contribution, we provide a detailed morpho-anatomical description of the specimen, we identified it as a new genus and species of Plioplatecarpinae (sensu Polcyn *et al*., 2023), and included it to a phylogenetic context of mosasauroids.

2. Materials and Methods

The specimen (IGMp879524), previously reported under catalog number IPN-2 (Páramo-Fonseca, 2012), was collected by the late Mr. Jaime Caballero in a quarry located near the town of Lebrija, at the site called La Azufrada, on the road leading from Bucaramanga to Barrancabermeja (Fig. 1A). In 1997, Mr. Caballero reported the find to the Servicio Geológico Colombiano (SGC) (named INGEOMINAS at that time). A few years later, after the unfortunate death of Mr. Caballero, his family voluntarily handed over the specimen to the SGC for study. In subsequent visits of the SGC to the finding site, we (M.E.P.-F.) collected vertebral fragments and ribs in the same quarry where the skull was found. Given that the precise stratigraphic origin of the skull remains is unknown, it is not possible to affirm if these postcranial remains pertained to the same individual. Therefore, in this work we will describe only the material donated by Caballero's family, which consists of a nearly complete skull (lacking the anterior end of the snout) and the atlantal elements. The skull is preserved three-dimensionally articulated with some bones slightly displaced from their original position.

The skull was prepared in the macrofossil laboratory of the SGC, using chemical methods. Once the fossil was covered with polyvinyl acrylates, it underwent successive baths in a 3% water diluted formic acid solution, followed by rinsing and drying. The preparation process revealed the presence of a gray material, indissoluble in the acid, which was found coating a large part of the bone surfaces. In many cases, this material was found firmly adhered on thin and delicate structures. In these cases, we decided to preserve the gray coverture without subjecting the specimen to mechanical preparation to avoid risking the integrity of the fossilized parts.

The taxonomic identification was based on a detailed morphological comparison with previously known Colombian mosasaurs (Páramo 1994; Páramo-Fonseca, 1997; 2000; 2013) and the recognition of mosasaurs morphological traits analyzed on Russell (1967), Bell and Polcyn (2005), Polcyn and Bell (2005), Konishi and Caldwell (2011) Makádi *et al.* (2012), Palci *et al.* (2013), Polcyn *et al.* (2023) among others.

A phylogenetic analysis was performed using the matrix of Simões *et al.* (2017) (taken from Madzia and Cau, 2017) which includes the changes proposed by different authors to the initial matrix of Bell (1997) (Jiménez-Huidobro and Caldwell, 2016; LeBlanc *et al.*, 2012; Palci *et al*., 2013). The outgroup used in the analysis was the dolichosaurid lizard *Adriosaurus suessi* Seeley, 1881, as proposed by Simões *et al*. (2017). A revision of the scoring of *Yaguarasaurus columbianus* was done, and two Colombian taxa were added to the matrix: *Eonatator coellensis* and the new taxon described in this work. The recently described taxon *Sarabosaurus dahli* Polcyn *et al*., 2023 was also added to the matrix for a second analysis, using the scoring of Polcyn *et al.* (2023) and scoring the remaining characters from their published description (see Supplemental Data 1).

We ran two cladistic analyses. The first one was run with 125 characters and 46 (OTUs), whereas the second analysis was run with 47 (OTUs) including *Sarabosaurus dahli*. Both analyses were run using TNT (v1.6) (Goloboff and Morales, 2023). All characters were treated as unordered and were equally weighted. An initial exploration for the shortest-length tree islands was performed using the new technology search options (Ratchet + Drift + Tree fusing) with 200 ratchet iterations (1 random seed) and 99,999 trees limit. The resulting trees were then used as the starting point for a Tree bisection and reconnection (TBR) branch swapping algorithm. A strict consensus was obtained and the iterPCR algorithm applied to identify unstable OTUs (Pol and Escapa, 2009). The Retention (RI) and Consistency (CI) indexes (Farris, 1989) were calculated, and Bremer Support values (Bremer 1994) were computed for the nodes in the consensus tree using the TNT tools. Finally, the resulting strict reduced consensus tree was time calibrated using the timePaleoPhy function of the package paleotree 3.4.5 (Bapst, 2012) in R 4.2.3 (R Core Team, 2022), implementing mlb calibration with a minimum branch length of 1 Ma, and plotted using the geoscalePhylo function from the R package strap 1.6-0 (Bell and Lloyd, 2015).

3. Geologic and biostratigraphic context

IGMp879524 was found in layers of the Galembo Formation (Fig. 1B). This stratigraphic unit was recently elevated to the rank of Formation by Terraza-Melo (2019), but it was previously considered the upper member (Galembo Member) of the La Luna Formation (Morales *et al.*, 1958). According to Terraza-Melo (2019) the Galembo Formation is a Coniacian-Santonian marine sedimentary succession constituted by calcareous mudstones and wackestones rich in planktonic foraminifera and organic matter. It has been interpreted as deposited in the middle to outer shelf (Terraza-Melo, 2019).

Although the exact stratigraphic origin of the described mosasaur remains is unknown, we (M.E.P.-F.) collected some ammonoids from the same quarry where the mosasaur remains were found. Four of these ammonoids were selected to assess the age of the mosasaur. They were determined by Fernando Etayo-Serna (pers. comm.) as follows: the specimen Az-7 (Fig. 1C) was identified as *Gauthiericeras* aff. *listeri* (van Hoepen, 1965), and according to Wright *et al.* (1996) this genus indicates the upper Coniacian; the specimens Az-5, Az-11 and Az-12 (Figs. 1D-F respectively) were identified as *Barroisiceras* aff. *subtuberculatum* (Gerhardt, 1897), and according to Wright *et al.* (1996) this genus indicates the upper Turonian-lower Coniacian. During preparation, we recovered a couple of small ammonoid specimens from the surrounding sediment. According to Fernando Etayo-Serna (pers. comm.) the ammonoids specimens are juvenile individuals and cannot be taxonomically placed with certainty, nonetheless, their features concur with those of Coniacian ammonoids.

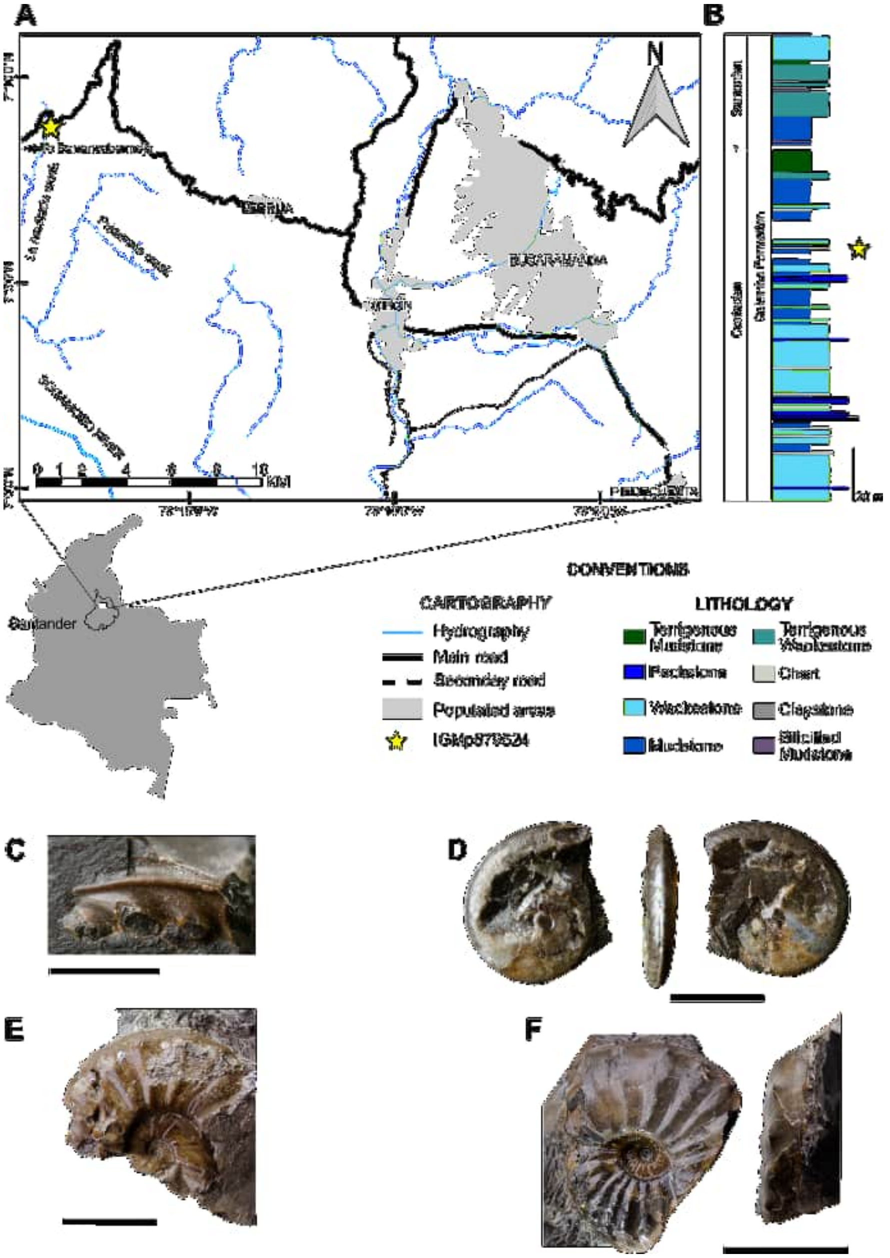

Figure 1. Geographic and Stratigraphic origin of the studied specimen (IGMp879524). **A**, map of Lebrija, Santander region with geographical location of the finding site (yellow star). **B**, generalized stratigraphic column of the Galembo Formation cropping out at the Lebrija region (modified from Terraza-Melo, 2019), showing the probable occurrence of the specimen (yellow star). **C-F**, ammonites collected in the quarry where the specimen was found; **C**, specimen Az-7, *Gauthiericeras* aff. *listeri* (von Hoepen, 1965). **D-F**, *Barroisiceras* aff. *subtuberculatum* (Gerhardt, 1897) (**D**: Az-5, **E**: Az-11, **F**: Az-12). Scale bars **C-D** = 1 cm; **E-F** = 5 cm.

The postcranial fragmentary remains of mosasaur found in the same quarry were collected in a sector of the outcrop close to where the ammonoids Az-7, Az-11 and Az-12 were collected. Without knowing the precise stratigraphic origin of the mosasaur specimen here described, the available information only allows us to suggest a Coniacian age for the mosasaur.

Nomenclatural Acts

This publication, and the nomenclatural act contained herein, has been registered in ZooBank, the ICZN online registration system for new taxa. The ZooBank Life Science Identifier (LSID) for this publication is urn:lsid:zoobank.org:pub:1131B0E0-7603-4881-AF76-5A8E6F130282 The LSIDs for the new taxon are given under the Systematic Paleontology section (below).

4. Systematic Paleontology

REPTILIA Linnaeus, 1758
SQUAMATA Oppel, 1811
MOSASAURIDAE Gervais, 1853
PLIOPLATECARPINAE Dollo, 1884 (sensu Polcyn *et al.*, 2023)
Oneirosaurus gen. nov.
urn:lsid:zoobank.org:act:FFEC38C0-51F7-499E-A1DE-0CFC2962F7A0
Type and only species: *Oneirosaurus caballeroi*, sp. nov.

Type Locality: La Azufrada locality, Barancabermeja-Bucaramanga highway, Lebrija municipality, Santander, Colombia; coordinates: 7°8'56''N, 73°18'24''W; Plate 109-II-D of the Instituto Geográfico Agustín Codazzi.

Stratigraphic horizon: Galembo Formation. Coniacian, Upper Cretaceous (Figure 1B)

Derivation of name: From greek *Oneiro* (όνειρο), dream and *Saurus* (σαύρος), lizard. "Dream reptile" referring to the exceptional preservation of its delicate structures.

Diagnosis: As for type and only known species.

Oneirosaurus caballeroi sp. nov.
(Figs. 2–6)
urn:lsid:zoobank.org:act:EEEF4FA3-0016-4FBE-97DC-6A700918A7FB

Holotype: IGMp879524 (old catalog number: IPN-2), nearly complete skull with articulated mandible, lacking its anterior end, and disarticulated atlas. Paleontological collections of the Museo Geológico Nacional José Royo y Gómez of the Servicio Geológico Colombiano (SGC) (formerly INGEOMINAS), Colombia.

Derivation of name: *caballeroi,* is proposed in honor of the late Mr. Jaime Caballero, who collected and reported the specimen. After his death his family handed the specimen to the Museo Geológico Nacional José Royo y Gómez of the SCG.

Diagnosis: *Oneirosaurus caballeroi* (IGMp879524) is a plioplatecarpine having one character unknown in any other plioplatecarpine: the presence of two external foramina for the exit of nerves X, XI and XII (Fig. 3C). *Oneirosaurus caballeroi* is also defined by the following unique combination of characters: prefrontal and postorbitofrontal separated at the roof of the orbit (differing from *Platecarpus* Cope, 1869, *Plioplatecarpus* Dollo, 1882, and *Latoplatecarpus* Konishi and Caldwell, 2011); broad frontal (almost 70% of its length), with short triangular surface anterior to the orbits (differing from *Yaguarasaurus*, *Russellosaurus* Polcyn and Bell, 2005, *Tethysaurus* Bardet *et al.*, 2003, *Ectenosaurus* Russell, 1967 and *Sarabosaurus* Polcyn *et al.*, 2023); triangular and broad anterodorsal surface of the parietal (as in *Yaguarasaurus*, *Russellosaurus*, *Tethysaurus*, *Angolasaurus* Telles-Antunes, 1964, and *Selmasaurus* Wright and Shannon, 1988), contacting the postorbital for a short distance (differing from *Yaguarasaurus*); suspensory rami of parietal anteriorly broad (as in *Yaguarasaurus*) originating below the narrowest part of the longitudinal dorsal table and posteriorly short (differing from *Yaguarasaurus*); parietal foramen small and located entirely in the parietal (as in *Yaguarasaurus*, *Russellosaurus*, *Tethysaurus*, *Angolasaurus*, and *Selmasaurus*); infrastapedial process of the quadrate robust without being fused to the suprastapedial process (as in *Platecarpus* and *Selmasaurus*); distal condyle of the quadrate saddle-shaped (as in *Yaguarasaurus*, *Russellosaurus*, *Tethysaurus*, and *Pannoniasaurus* Makádi *et al.*, 2012); small otosphenoidal crest of prootic not covering the exit of nerve VII (differing from *Yaguarasaurus*, *Russellosaurus*, *Tethysaurus*, *Platecarpus*, and *Latoplatecarpus*); basioccipital canal opening into the floor of the braincase through two large foramina separated by a medial septum (as in *Plesioplatecarpus* Konishi and Caldwell, 2011 and *Angolasaurus*); pterygoid anterior teeth not distinctly smaller (differing from *Sarabosaurus*); lingual alveolar parapet of dentary lower than labial (as in *Yaguarasaurus*, *Russellosaurus*, and *Romeosaurus* Palci *et al.*, 2013); marginal teeth crown with subcircular cross-section at base (differing from *Tethysaurus*) and with two carinae arranged at 180º, one mesial and the other distal (differing from *Yaguarasaurus* and *Angolasaurus*); presence of a notch in anterior border of the atlas neural arch (also in *Ectenosaurus* and *Sarabosaurus*).

5. Preservation features

The skull is incomplete; its anterior and posterior ends, as well as most of the external surface of the anterior dorsal bones, have been lost due to fracture during extraction. The skull is preserved articulated in three-dimensions, with some bones slightly displaced from their original position. The quadrates are rotated towards the skull roof. The atlas was found with its elements disarticulated, with the intercentrum rotated below the paraoccipital process of the left opisthotic, the centrum (odontoid) in the left temporal fenestra near the lateral wall of the parietal and separated from it by the spinous process of the left atlantal neural arch, which is directed forward, and the right atlantal neural arch rotated with the spinous process directed backwards and missing its basal portion.

The general arrangement of the bones, with a slight rotation of the mandibles and the displacement of the quadrates and atlas components towards the cranial roof, suggests that the skull was deposited face up. The displacements concur with pre-fossilization accommodation by gravity from the face-up position of the skull. This condition suggests a low-energy depositional environment in which the mosasaur carcass remained undisturbed during the processes of decomposition, burial, and mineralization.

The fossilized bones are dark brown in color, and many are covered by a thin layer of a gray mineralization. This mineralization is composed of microcrystalline quartz and calcite (Páramo-Fonseca *et al.*, 2024). The mineralization thinly covers cartilaginous surfaces facilitating the preservation of structures that are not usually conserved in mosasaurs, such as the chondrocranial elements (see Páramo-Fonseca *et al.*, 2024). According to Páramo-Fonseca *et al.* (2024) this mineralization was produced by a partial silicification process promoted by lower pH microenvironments associated with bacterial breakdown of non-biomineralized tissues during early diagenesis.

6. Anatomical description

Premaxilla: The premaxilla is almost entirely lost, only a small fragment of the most posterior end of the internarial bar has been preserved in contact with the frontal (Figs. 2A, 3A, 4A). It does not reach the posterior border of the external nares. The suture with the frontal shows a sharp posterior medial extension. Below the preserved fragment of the premaxilla, on the left side, a horizontal nasal lamina extends posteriorly bordering lateroventrally the anterior half of the frontal internarial process.

Maxilla and septomaxilla: Both maxillae lack the anterior end and have lost their external surface. The right one also lacks its posterior end. The absence of the external surface prevents an accurate description of the sutures of the maxillae with the prefrontals, lacrimals and jugals, as well as the lateral border of the external nares. Nevertheless, it can be established that the posterior end of the left maxilla is covered laterally by the anterior ramus of the jugal (Fig 4A). Due to a complete lack of the external surface on the right maxilla the medial contact with the palatine is visible (Fig 3C). This contact begins anteriorly with a short longitudinal suture that then curves posterolaterally reaching the inner dorsal border of the dentate ramus of the maxilla. The position of the palatine in contact with the maxilla at the level of the last four alveoli in the specimen under study is equivalent in *Y. columbianus*. The posterior border of the external nares is located at the level of the fifth posterior alveolus (counted from back to front), as in *Y. columbianus*. The absence of the ascending lamina in the left maxilla exposes the canal for the maxillary artery, which extends longitudinally above the alveoli (see Figure 4A). In lateral view, the alveolar border of the maxilla is straight (Figs. 3A, 4A). In the left maxilla there are eight alveoli or teeth, while in the right maxilla only seven are present. The preserved alveoli are of uniform size, except for the most posterior ones which are smaller. The lingual alveolar ridge is slightly shorter than the labial. The replacement teeth occupy a posteromedial position regarding the functional teeth.

Although most of the septomaxillae are missing with the anterior end of the snout, a fragment of septomaxilla is found over the maxillae on each side of the external nares (Figs. 2A, 3A, 4A). These fragments are placed between the seventh and eighth posterior teeth (counted from back to front). The posterior edge of the septomaxillae exhibits a similar position in *Yaguarasaurus columbianus* (see Páramo, 1994).

Nasal: Posterior to the septomaxilla, below the internarial bar, a small broken fragment of bone is found on the medial wall of each naris. Given its location, these fragments are here recognized as portions of nasals (Figs. 3A, 4A).

Frontal: The frontal is incomplete; it lacks its most posterior part and almost all the right dorsal surface. The general shape of the frontal is anteriorly triangular and posteriorly rectangular (Fig. 2A). A low medial ridge is evident on the anterior region of the dorsal surface of the frontal. This ridge is reduced in the posterior region, where the surface of the bone becomes slightly concave. The contact between the frontal and the premaxilla is visible dorsally at the most anterior end of the preserved internarial bar and is V-shaped. The frontal forms the only conserved portion of the internarial bar, and its edges are not emarginated in the posterior edge of the nares. At the posterior end of the nares, the frontal meets the prefrontal (Fig. 2A). The suture between these two bones extends diagonally backward to the anterodorsal border of the orbit. From this point, the frontal shows straight lateral margins, parallel to the longitudinal axis of the skull and form the roof of the orbits separating the prefrontal from the postorbitofrontal. On the left side of the skull, the posterolateral end of the frontal extends into a semicircular process enclosed by the postorbitofrontal (Fig. 2A). Although the almost dorsal surface of the posterior end of the frontal has been lost, the suture with the parietal can be inferred from the textural difference between the two bones. This suture describes a slightly undulating straight line with a medial posterior concavity.

Prefrontal: The prefrontals have lost almost all their external surface, only a small portion has been preserved in the right prefrontal. The descending rami of the two prefrontals are well-preserved and can be clearly seen in contact with the palatines, constituting the anterior wall of the orbits. The prefrontal forms a small portion of the posterolateral border of the external naris (Fig. 2A). Posteriorly, the prefrontal extends, overlapped by the frontal, to the anterodorsal border of the orbit; it does not contact the postorbitofrontal below the orbit (Fig. 4A).

Lacrimal: Both lacrimals are poorly preserved. The lacrimal is a small rhomboid-shaped bone. It contacts dorsally the prefrontal and ventrally the maxilla (Figs. 2A, 3A, 4A).

Jugal: The left jugal is completely preserved (Fig. 4A), and only the postorbital bar of the right jugal is present (Fig. 3A). The jugal is L-shaped, with a thick vertical bar and a longer, thinner horizontal ramus that is gently curved and compressed dorsoventrally (Fig. 4A). The joining between the two rami is a gentle curve that shows a slightly developed posterior protuberance at the starting point of the vertical ramus.

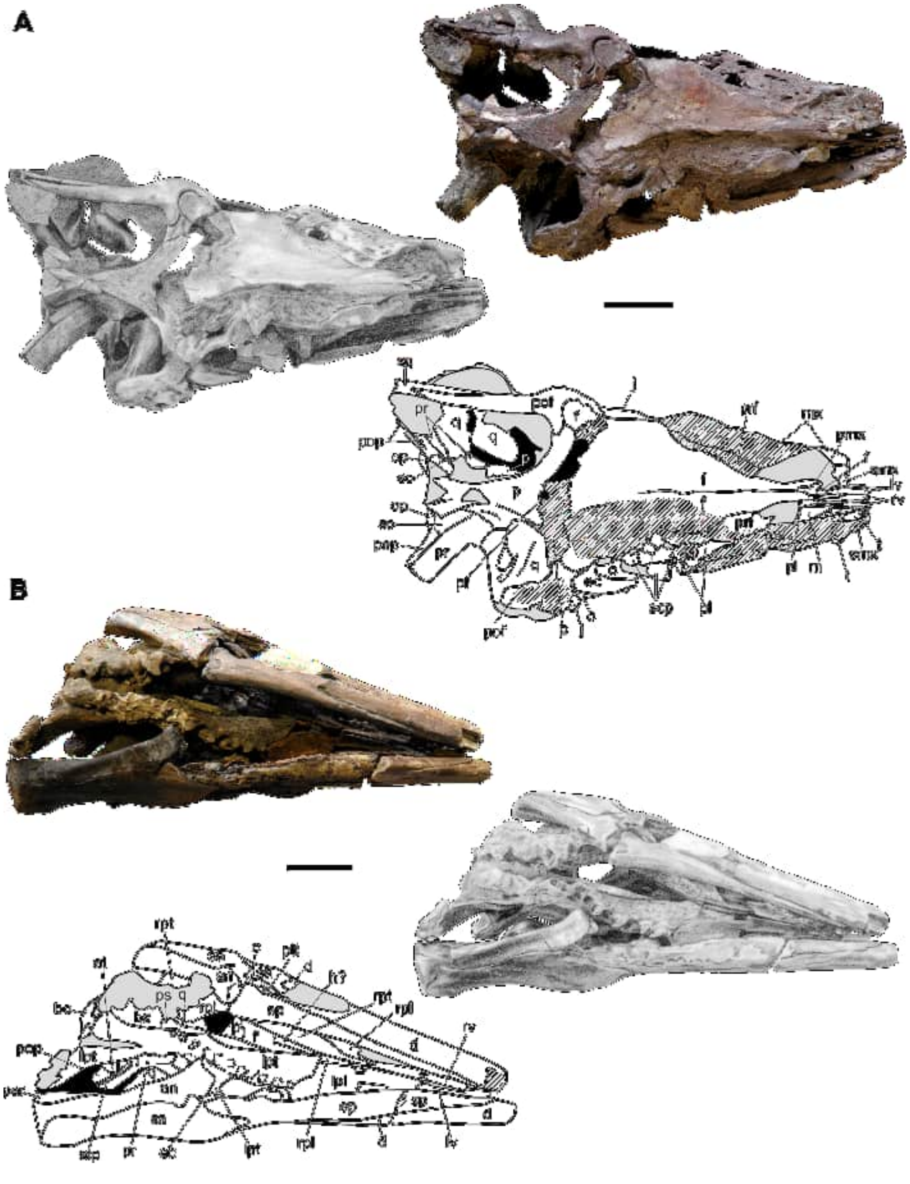

Figure 2. *Oneirosaurus caballeroi* gen. et sp. nov., holotype IGMp879524. Photograph, drawing and interpretative sketch of the specimen in **A**, dorsal without left mandibular ramus and **B**, ventral views. Gray fill, sediment; pattern fill, broken bone surface; black, empty space. Scale bars = 50 mm. **Abbreviations**: **an**, angular; **at**, atlas; **bo**, basioccipital; **bs**, basisphenoid; **c**, coronoid; **d**, dentary; **ec**, ectopterygoid; **f**, frontal; **h**, hyod; **j**, jugal; **la**, lacrimal; **lpl**, left palatine; **lpt,** left pterygoid; **lv**, left vomer; **m**, mandible; **mx**, maxilla; **op**, opisthotic-exoccipital; **p**, parietal; **par**, prearticular ; **pf**, parietal foramen; **pl**, palatine; **pmx**, premaxilla; **pof**, postorbitofrontal; **pop**, paraoccipital process of the opisthotic; **pr**, prootic; **prf**, prefrontal; **ps**, parasphenoid; **ptt**, pterygoid tooth; **q**, quadrate; **rpl**, right palatine; **rpt**, right pterygoid; **rv**, right vomer; **sa**, surangular; **scp**, sclerotic plate; **smx**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **stp**, stapes; **t**, tooth.

Parietal: The parietal is partially preserved; its anterior border and most of the suspensory rami have been lost (Fig. 2A). The dorsal surface of the parietal has a large triangular anterior table that narrows posteriorly between the temporal fenestrae forming a medial subrectangular surface, which tightens posteriorly. The parietal foramen is small and lies entirely on the anterior triangular surface of the parietal. The contact with the frontal is almost straight, with symmetrical undulations. Anterolaterally, the parietal joins the postorbitofrontal in a semicircular suture (Fig. 2A). This joint is not completely closed suggesting a non-ossified union. In the preserved posterior part of the parietal, the suspensory rami originate below the medial rectangular table, where this table is narrower. The suspensory rami project posteriorly becoming dorsoventrally compressed. On the lateral surface of the parietal, below the beginning of the suspensory rami several foramina are observed.

Postorbitofrontal: The left postorbitofrontal is preserved in its entirety, while only part of the anterior region of the right postorbitofrontal is present. Dorsally, the postorbitofrontal encloses the posterolateral extension of the frontal in an anteriorly concave semicircle and contacts the parietal by a suture describing an anteromedially convex semicircle (Fig. 2A). Behind the junction with the frontal and the parietal, the postorbitofrontal shows a faint line with parallel striae, that seems to correspond to vestiges of the suture between the postfrontal and the postorbital, suggesting a not completely ossified union (a feature of probable juvenile stage). In lateral view, the postorbitofrontal has an elongated triangular shape, with an anterior rounded protuberance that projects downward in an acuminate extension, overlapping the posterior part of the ascending ramus of the jugal (Fig. 4A). The posterior process of the postorbitofrontal borders the temporal fenestra and inserts into the squamosal (Figs. 2A, 4A).

Supratemporal: Only the anterior ventral process of the supratemporal is preserved on both sides of the skull. It is covered medially and dorsally by the paraoccipital process of the opisthotic and laterally by the prootic (Figs. 5A, D).

Squamosal: Only the anterior part of the left squamosal is preserved. It shows the regular shape of the squamosal in mosasaurids. It embraces the postorbitofrontal dorsolaterally and ventrally along a large section of the temporal arcade (Fig. 4A).

Quadrate: Both quadrates are rotated towards the temporal fenestrae, with the condyles oriented towards the midline of the skull (Fig 2A, 5A). Although the surfaces of the quadrates are covered by a thin layer of indissoluble material, the morphology of these bones is perfectly distinguishable (Fig. 4B). In anterior view, the quadrate is rectangular, convex in its latero-dorsal region and concave in its mid-ventral region; the condyle is distinguished from the body by a sinusoidal line. In medial view, the shaft of the quadrate shows a central vertical ridge, which is more compressed in its lower part; the suprastapedial process almost completely closes the meatus (stapedial notch), giving it an inverted drop shape, without being fused to the infrastapedial process (sensu Palci *et al.*, 2013, p. 603) nor to the ascending posteroventral border of the tympanic ala, but extending medially below them; between the vertical ridge and the antero-dorsal edge of the meatus there is an elongated fossa (stapedial pit) that becomes deep ventrally (Fig. 4B). In posterior view, the suprastapedial process descends sub-parallel to the quadrate shaft; it has parallel edges and diagonal ventral end, forming a tip that projects medially to below the infrastapedial process; an indentation for the depressor mandibularis muscle is found on the medial diagonal surface of the suprastapedial process; the infrastapedial process is robust; the condyle is little exposed with a ventral border slightly concave (Fig. 4B). In lateral view, the quadrate is seen as a circular cavity formed by the suprastapedial process and the tympanic ala, which has a well-developed posteroventral ascending edge, almost contacting the suprastapedial process; the shaft of the quadrate projects ventrally for a short distance, forming the condyle, which is well exposed and ventrally convex (Fig. 4B). The quadrate condyle develops perpendicular to the tympanic expansion and to the axial plane of the skull; it is lateromedially elongated and has two slightly pronounced heads, the external larger than the internal. None of the tympanic operculum is preserved. In neither of the quadrates the alar crest is completely exposed.

Chondrocranial elements: In the internal midline of the skull, the specimen preserves some chondrocranial elements, from which the complete interorbital septum is recognized (Fig. 3A). Such a complete structure has never been recorded in any mosasaur. A detailed description of the chondrocranial elements was recently published by Páramo-Fonseca *et al.* (2024)

Sclerotic plates: In the anterodorsal region of both orbits, accumulated fragments of the ossified sclerotic plates are found. Ten fragments can be identified in the right orbit and seven in the left orbit (Figs. 3A, 4A). None of the plates is completely exhibited, so the shape of their outline cannot be established. The largest fragments are 15 x 15 mm. These plates are very thin and show a very fine radial striation.

Palate

Palatine-vomer: The palatine-vomers lack their most anterior portion. The palatine forms the posterior medial and the posterior border of the internal nares (Fig. 2B). The anterior end of the palatine is covered dorsally and ventrally by the vomer, but is not fused to it, suggesting a juvenile stage of the individual (Fig. 4C). The vomerine processes of the palatines, together with the preserved vomers form a longitudinal sub-vertical lamina dorsally and ventrally concave, differing from the more horizontal position of these bones illustrated by Camp (1942, fig 14) for *Plotosaurus* Camp, 1951. This arrangement concurs with that found in *Yaguarasaurus columbianus* (see Páramo 1994, fig 12). Posteriorly, the palatine widens forming a surface that diagonally separates the pterygoid from the maxilla. The posterior portion of the palatine has a dorsal thickening that contacts the descending ramus of the prefrontal, forming the anterior wall of the orbits.

Pterygoid: Both pterygoids are almost completely preserved; only the most posterior end of the right one is missing. Anteriorly, they contact each other in the midline forming an acuminate extension that covers ventrally the palatines (Fig. 2B, 4C). At approximately the middle of their length, the pterygoids separate widely and project, laterally at a right angle, to the ectopterygoid process. This process receives dorsally the ectopterygoid at its anterolateral end. The ventral surface of the central region of each pterygoid has a row of teeth arranged in a curved line that extends from the antero-lateral junction with the palatine to the base of the basisphenoid process. Posteriorly, the pterygoids approach medially again via the basisphenoid processes, and then diverge posteriorly projecting outward to the quadrates. The basisphenoid process projects posteriorly from the tooth-bearing surface, forming a long, slender process that extends beneath the basisphenoid and basioccipital to the level of the basal tubera of the latter. The elongated quadrate process is aliform. Thirteen tooth positions are counted on the dentate surface. The pterygoid teeth are smaller than the mandibular and maxillary teeth. Their shape is recurved, with the apex directed posterolaterally. The posterior teeth are very small, and the intermediate teeth are the largest. Given that the teeth are covered by the gray mineralization, it is not possible to determine the texture of the teeth crowns.

Ectopterygoid: Both ectopterygoids are well-preserved (Fig. 2A, 3A). The ectopterygoid is relatively large and forms a bridge between the lateral process of the pterygoid and the jugal. The anterolateral process of the ectopterygoid extends longitudinally for 3 cm, bordering dorsally the coronoid (Fig. 3A, 4A). The medial process expands above and anterior to the lateral process of the pterygoid.

Epipterygoid: Both epipterygoids are preserved, but neither are in their anatomical position. The left one rests sub-horizontally on the ventrolateral surface of the frontal and the right one is diagonally embedded between the two pterygoids (Fig. 3A). Their complete morphology cannot be observed. The visible portion is a straight bar with a slightly expanded end towards the frontal (Figs. 3A, 5C).

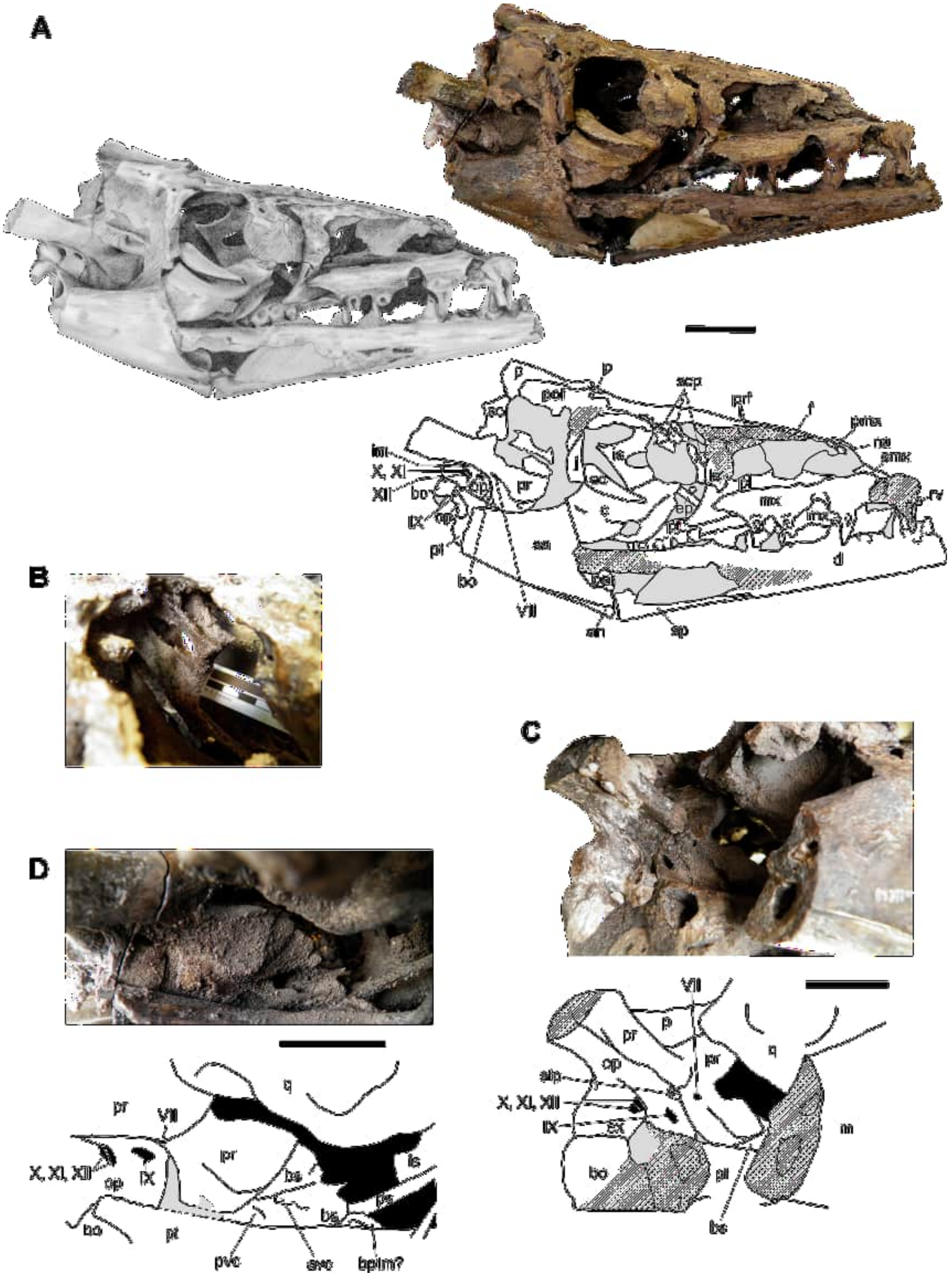

Figure 3. *Oneirosaurus caballeroi* gen. et sp. nov, holotype IGMp879524. **A**, photograph, drawing and interpretative scheme of the specimen without left mandibular ramus, in right lateral view. **B**, photograph of the interorbital septum in oblique postero-dorsal view (scale in centimeters). **C**, basicranial region in right external view, showing the broken stapes. **D**, Detail of the prootic and basisphenoid in right lateral view. Gray fill, sediment; pattern fill, broken bone surface; black, empty space. Scale bars: A = 50 mm; C-D = 30 mm. **Abbreviations**: **an**, angular; **avc,** anterior aperture of the vidian canal; **bo**, basioccipital; **bptm**, basipterygoid meniscus; **bs**, basisphenoid; **c**, coronoid; **d**, dentary; **ec**, ectopterygoid; **ep**, epipterygoid; **ex**, exoccipital; **f**, frontal; **im**, internal auditory meatus; **is**, interorbital septum; **j**, jugal; **la**, lacrimal; **m**, mandible; **mx**, maxilla; **na**, nasal; **op**, opisthotic-exoccipital; **p**, parietal; **par**, prearticular; **pl**, palatine; **pmx**, premaxilla; **pof**, postorbitofrontal; **pr**, prootic; **prf**, prefrontal; **ps**, parasphenoid; **pt**, pterygoid; **pvc,** posterior aperture of the vidian canal **q**; quadrate; **rv**, right vomer; **sa**, surangular; **scp**, sclerotic plate; **smx**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **stp,** stapes; **VII, IX-XII**, exit of cranial nerves.

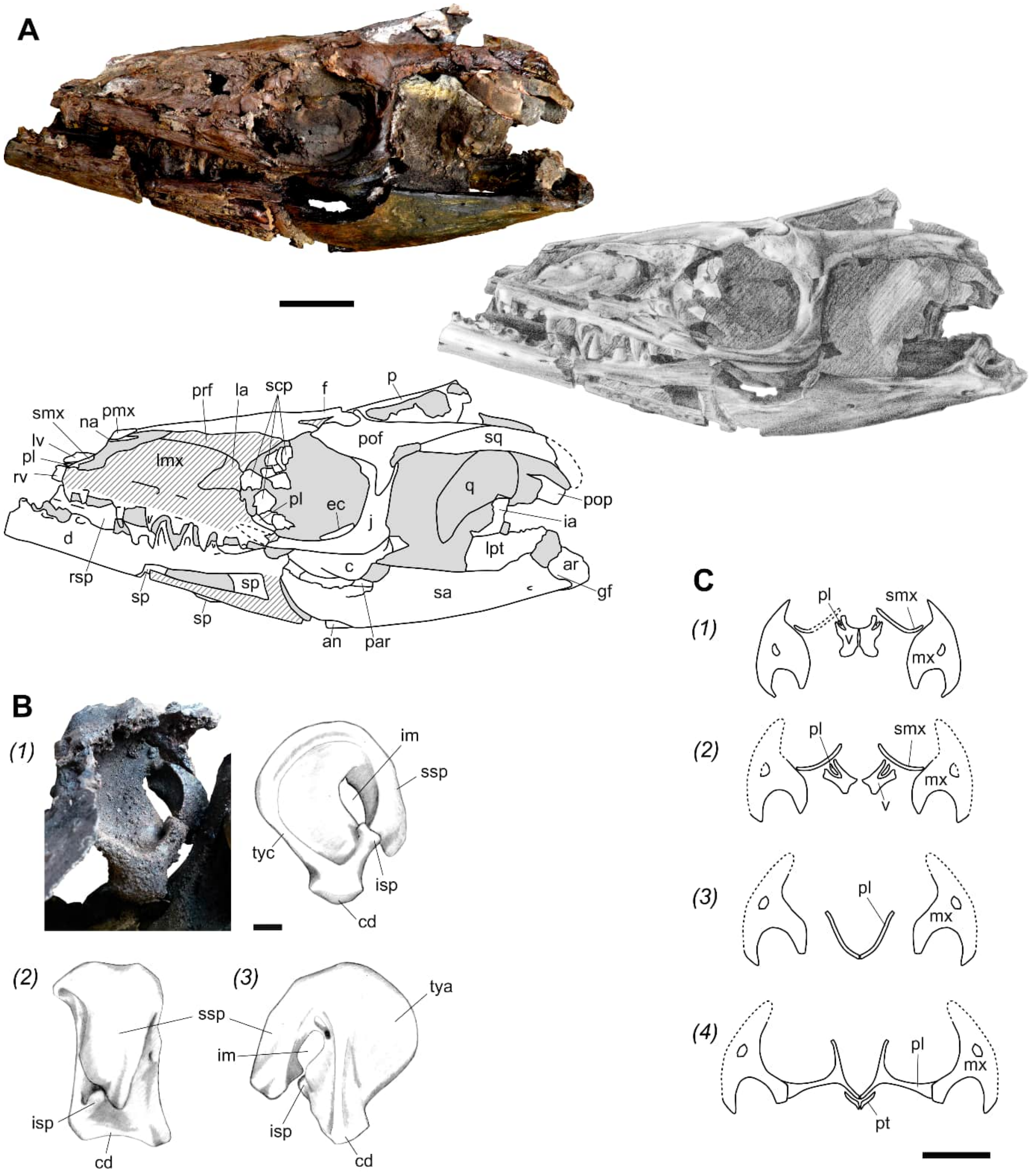

Figure 4. *Oneirosaurus caballeroi* gen. et sp. nov., holotype IGMp879524. **A**, Photograph, drawing and interpretative scheme of the specimen in left lateral view. **B**, Left quadrate; photograph and interpretative sketch in lateral view *(1)*; sketches in posterior *(2)* and medial *(3)* views. **C**, interpreted cross-sections based on the observation of the palatal region at the level of the following alveoli counted from back to front: ninth or preserved anterior end *(1)*, eighth *(2)*, sixth *(3)* and fifth *(4)*. Gray fill, sediment; pattern fill, broken bone surface; black, empty space. Scale bars: A = 50 mm; B-C = 20 mm. **Abbreviations**: **ai**, atlas intercentrum; **an**, angular; **ar**, articular; **c**, coronoid; **cma**, canal for the maxillary artery; **cd**, condyle; **d**, dentary; **ec**, ectopterygoid; **f**, frontal; **gf**, glenoid fossa; **im**, internal auditory meatus; **isp**, infrastapedial process; **j**, jugal; **la**, lacrimal; **lmx**, left maxilla; **lpt**, left pterygoid; **lv**, left vomer; **mx**, maxilla; **na**, nasal; **p**, parietal; **par**, prearticular; **pl**, palatine; **pmx**, premaxilla; **pof**, postorbitofrontal; **pop**, paraoccipital process of the opisthotic; **prf**, prefrontal; **pt**, pterygoid; **q**, quadrate; **rsp**, right splenial; **rv**, right vomer; **sa**, surangular; **scp**, sclerotic plate; **smx**, septomaxilla; **sp**, splenial; **sq**, squamosal; **ssp**, suprastapedial process; **tya**, tympanic ala; **tyc**, tympanic crest; **v**, vomer.

Unidentified elements probably associated to pterygoquadrate: On each side of the parasphenoid, just anterior to the basipterygoid process of the basisphenoid and over each pterygoid, there is a small, Y-shaped element with distally expanded rami (Fig. 5C). Both are covered by gray mineralization and therefore their cartilaginous or bone origin cannot be established. The antero-medial ramus contacts the parasphenoid, rising and forming a ridge that surpasses vertically the level of the parasphenoid. The other two rami are horizontally flattened and follow the curved lateral border of the pterygoid (Fig. 5C). No equivalent elements have been reported on mosasaurs. The fact that they are symmetric paired elements, not displaced by gravity to the skull roof, suggests that these elements are in anatomical position and are more probably related to paired structures than to the medial sphenoidal series. These elements are located where the epipterygoids should have rested, suggesting each could be part of a pterygoquadrate as illustrated for the lacertid *Acanthodactylus boskianus* (Daudin, 1802) by Bellairs and Kamal (1981, fig. 14), and represent probably the basipterygoid meniscus or the pterygoid process of the pterygoquadrate of lizards (following Bellairs and Kamal, 1981).

Unidentified element probably associated to hyobranchial apparatus: Posterior to each ectopterygoid and medial to each jugal and coronoid, a straight bar-shaped ossicle, thinner than the epipterygoid is located vertically. These ossicles do not articulate with any other bone. Their thin bar morphology and their spatial location suggest these ossicles could be part of the hyobranchial apparatus, probably the ceratobranchial, which generally ossify in lizards (Bellairs and Kamal, 1981).

Occipital region

Supraoccipital: The supraoccipital lacks its posterior dorsal end, but its ventral portion contributing to the roof of the foramen magnum is well preserved (Fig. 5A). In posterior view, the supraoccipital shows a central vertical ridge as in *Y. columbianus* (see Páramo, 1994, fig.8). Anteriorly, the supraoccipital extends over the opisthotic and prootic on each side of the skull.

Opisthotic-exoccipital: The opisthotic and exoccipital are fused. The opisthotic-exoccipitals have been preserved without their posterior end of the paraoccipital process. They form the lateral walls of the foramen magnum and the latero-dorsal ends of the occipital condyle (Fig. 5A, B). In the lateral wall, there are two foramina for the exit of nerves X, XI and XII, separated by a thin lamina and, in front of these, there is a larger foramen for the perilymphatic sac and nerve IX (following Russell, 1967) (Figs. 3C, D). On the medial wall, anterior to the foramen magnum, the opening for the nerves X and XI (jugular foramen) is clearly visible and, anterolaterally and very close to it, the foramen for nerve IX is distinguished. The distribution of the foramina for nerve XII, on the inner wall of the cranial cavity, is sub-parallel to the ventral edge of the jugular foramen, as illustrated by Russell for *Clidastes propython* Cope, 1869 (Russell, 1967, fig. 13). In the paraoccipital process, the opisthotic-exoccipital and the prootic are joined by slightly interdigitated, but open sutures, suggesting the presence of cartilage, as a probable juvenile condition. Posteriorly, the ventro-medial end of the supratemporal is observed between these bones (Fig. 5D).

Prootic: Both prootics are preserved almost in their entirety, with only the most posterior end of the right missing. In lateral view the prootic has a shape of a lying "Y", with two anterior and one posterior rami (Fig. 3C). In the antero-ventral ramus (inferior process), the otosphenoidal crest is seen poorly pronounced, and posteriorly to it, the foramen for the exit of nerve VII opens on the surface of the bone (Figs. 3C-D). The posterior ramus of the prootic forms the lateral wall of the suspensorium. In the anterior region of this ramus, each prootic borders the exoccipital, forming the fenestra ovalis, where the columella exits the otic capsule toward the quadrate (Fig. 3C). Posteriorly, the prootic borders the paraoccipital process of the opisthotic dorsally and the supratemporal medially (Fig. 5D). The prootic covers laterally the anterior extension of the supratemporal for a substantial length.

Stapes: Both stapes are preserved in their original position, the right one is broken. The stapes is an elongated and slender small bone that extends along and against the preserved portion of the paraoccipital process. The right stapes is broken close to the fenestra ovalis showing a circular cross-section (Fig. 3C).

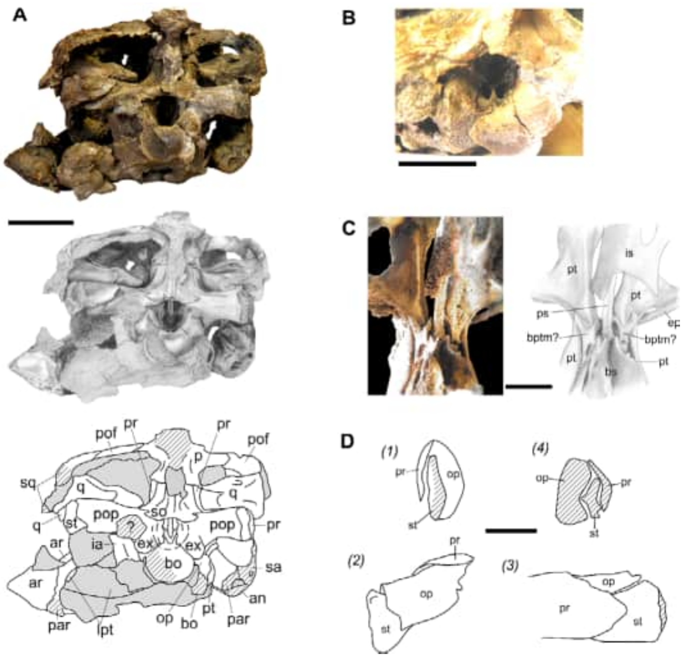

Figure 5. *Oneirosaurus caballeroi* gen. et sp. nov., holotype IGM879524. **A**, Photograph, drawing and interpretative scheme of the specimen in posterior view. **B**, basioccipital floor in posterior view. **C**, photograph and interpretative drawing of the anterior basicranial region in dorsal view, showing the presence of non-identified bones (probably basipterigoyd meniscus). **D**, schematic details of the paraoccipital bars; left paraoccipital bar in posterolateral *(1)*, dorsally oblique posteromedial *(2)*, and anterolateral *(3)* views; the incomplete right paraoccipital bar in the broken section *(4)*. Gray fill, sediment; pattern fill, broken bone surface; black, empty space. Scale bars: **A** = 50 mm; **B- C =** 30 mm; **D** = approximately 20 mm. **Abbreviations**: **ai**, atlas intercentrum; **an**, angular; **ar**, articular; **bo**, basioccipital; **bptm**, basipterygoid meniscus; **bs**, basisphenoid; **ep**, epipterygoid; **ex**, exoccipital; **is**, interorbital septum; **lpt**, left pterygoid; **op**, opisthotic; **p**, parietal; **par**, prearticular; **pof**, postorbitofrontal; **pop**, paraoccipital process of the opisthotic; **pr**, prootic; **ps**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **sa**, surangular; **so**, supraoccipital; **sq**, squamosal; **st**, supratemporal.

Basioccipital: The basioccipital has lost a portion of the condyle and part of the right basal tubercle. The ventral surface is completely covered by insoluble material, preventing the observation of its details. The occipital condyle is barely wider than it is tall, and the basal tubera are long, extending ventrally for a distance approximately one-half the height of the occipital condyle. The floor of the medullary cavity is pierced by two large foramina for the basilar artery, separated by a thin septum (Fig. 5B). The floor narrows anteriorly forming a "V" shaped bottom of the anterior medullary cavity (Fig. 5B).

Basisphenoid: The basisphenoid is complete, but its ventral surface is poorly observable given that it is thickly covered by insoluble material. The dorsal ala is moderately developed. In the lateral wall of the basisphenoid is the vidian canal, which has a short lateral wall (Fig. 3D). Dorsal and slightly posterior to the anterior aperture of the vidian canal, there is an aperture that enters medially. This dorsal aperture should house the medial ramus of the internal carotid artery (following Camp, 1942) or represents the exit of the basilar artery (sensu Russell, 1967). The groove for conducting the internal jugular vein is narrow and runs ventral and anterior to the vidian canal. The anterior end of the basisphenoid is projected in the parasphenoid rostrum, where the parasphenoid is fused. At this point, the lateral walls of the basisphenoid are elevated and show a little thin dorsal process pointing forward. Beneath this dorsal process, the anterior edge of the lateral wall shows a concavity that should have held the anterior ramus of the basilar artery (Fig. 5C). The floor of the cerebral cavity is narrowly "V" shaped. Differing from the dorsum sellae illustrated by Russell for *Platecarpus* (see Russell, 1967, fig. 10), in the internal cavity the dorsum sellae is not clearly demarcated. However, the slope of the floor increases posteriorly, differentiating the sella turcica space from the medullary cavity of the basioccipital. In the sella turcica area there are two medial elongated slits where the foramen for the internal carotid ramus is housed. On each side of the internal cavity, the canal for the nerve VI opens near the dorsal end of the dorsal ala.

Parasphenoid: This bone is completely preserved in anatomic position. It projects a slender rostrum (cultriform process) from the base of the basisphenoid which extends anteriorly slightly inclined dorsally (Figs. 2B, 3D). The rostrum is somewhat dorsoventrally compressed and has a regular thickness, except in its anterior end where it thins and ends in a point.

Mandible

The mandibular rami are gracile. Both rami lack the anterior end and have lost part of its external surface. The right mandibular ramus also lacks its posterior end (Figs. 3A, 4A, 6A).

Dentary: The dentaries are incomplete; the posterior eight alveoli or teeth are preserved in the left dentary, while in the right one only seven teeth positions are present. The dentary is relatively slender; the alveolar border is straight (Fig. 3A). The lingual alveolar edge is shorter than the labial alveolar edge, so the dental roots of the teeth are more exhibited lingually (Fig. 6A). All the alveoli are similar in size. In the anterior preserved end, the dentary is low, its height is equivalent to the distance occupied by two alveoli (3 cm). The lateral anterior surface of the dentary has 4 elongated foramina parallel to the alveolar edge, at 1 cm from this edge (Fig. 4A). Posterior to the last alveolus, the dentary forms the dorsal portion of the mandible for a distance equivalent to three alveoli. Its posterior dorsal end contacts loosely the coronoid, and its posterior lateral end meets with the surangular. In this region, the dentaries of both mandibular rami are strongly fractured and have lost part of its exterior surface, showing a broad mandibular canal, in which a slender lamina of the prearticular extends. Ventrally, the dentary is embraced by the splenial. In medial view, the ventral border of the dentary is exhibited from the level of the sixth posterior alveolus (Fig. 6A).

Splenial: The splenial forms the internal face of the mandible, covering the anterior lamina of the prearticular (Fig. 6A). The splenial decreases in height anteriorly. In lateral view the splenial appears exposed ventrally from the level of the fifth posterior alveolus, and posteriorly its lateral exposure increases forming a low sloping suture with the dentary (Fig. 3A). The posterior end of the splenial has the articular facet for the angular, which is sub-triangular to oval in outline and vertically elongated.

Coronoid: Both coronoids are complete and faintly displaced dorsally from its original position. The coronoid is robust, longitudinally short, and ventrally curved. Its posterior process is small. The lateral descendent ala is relatively short, whereas the medial one is large (Fig 3A, 4A).

Surangular: The surangulars are incomplete. They constitute most of the lateral surface and the dorsal medial region of the posterior mandible (Figs. 3A, 4A, 6A). The surangular forms the anterior and lateral walls of the glenoid fossa, without prolonging behind it. The dorsal edge of the surangular is inclined; it anteriorly rises as a fine lamina to form a coronoid buttress. In lateral view, the ventral edge of the surangular contacts the angular anteriorly, and posteriorly it contacts the articular in a curved suture that reaches the lateral edge of the glenoid fossa near its posterior end. Dorsally, this suture turns forward crossing laterally the glenoid fossa. In the posterior lateral surface, near the anterior margin of the glenoid fossa, the surangular bears a foramen (Fig.4A). In medial view, the surangular contacts the prearticular by a long subhorizontal suture (Fig. 6A).

Angular: Both angulars are preserved, but the posterior part of the left one is lost. The angular is an elongated bone that widens anteriorly to form the articulation with the splenial (Fig. 2B, 3A). The anterior articular surface, to receive the splenial, is triangular and has a dorsal "V" shaped concavity. The angular extends posteriorly forming the ventral edge of the mandibles. Its posterior lateral end reaches the level of the beginning of the glenoid fossa. Latero-dorsally the angular is covered by the surangular. Medially, the angular is posteriorly covered by the prearticular, but anteriorly it partially covers the prearticular, without reaching the coronoid (Fig. 6A).

Prearticular-articular: The posterior end of the mandible is only preserved in the left mandibular ramus (Fig. 4A, 6A). Here, the suture between the prearticular and the articular is noticeable, suggesting an unfused contact between these bones and a juvenile stage of the individual. In lateroventral view, this suture is a slightly sinuous curved line that extends from the posterior end of the angular to the posterior lower mandibular edge. In the medial face of the mandible, this suture ascends diagonally to reach the medial edge of the glenoid fossa (Fig. 6A). Both prearticulars have partially lost their anterior laminae due to their extreme thinness. Posteriorly, the prearticular is more robust; it forms the ventral portion of the medial face of the mandible and the medial edge of the glenoid fossa (Fig. 6A). The articular forms the posterior end of the mandible. In the ventrolateral face of the mandible, it forms an elongated subtriangular surface that extents forward covered by the surangular laterally and by the prearticular medially, reaching the posterior edge of the angular. The lateral suture with the surangular descends from the glenoid fossa and near the ventral edge of the mandible it curves anteriorly. Dorsally, the articular forms almost all the floor of the glenoid fossa and posteriorly a very short retroarticular process which is feebly inflected (Fig. 4A). It shows a triangular dorso-medial surface with wrinkled texture, that served as an important muscular insertion area. In its anterior medial end, the articular forms, with the prearticular, a slight tuberosity in the lower edge of the glenoid fossa (Fig. 6A). The surface of the lateral posterior end of the retroarticular process is porous and at least one large foramen can be identified, however, the poor preservation of this region hinders us to affirm that no other foramina were present.

Marginal Teeth

All the teeth in the alveoli are broken; they lack their labial surface. Only one disarticulated tooth is complete (Fig. 6B) This tooth is 3 cm from the base of the root to the crown apex. The root is bulbous and 1.2 cm in height. The crown is circular in section at its base and oval to its apex. The ratio of its height and basal diameter is 2.0. The crown of the teeth is curved backwards and slightly inwards. It has two smooth carinae well-defined, 180° from each other, one mesial and the other distal. The lingual surface of the crowns is finely and densely striated. The labial surface, which is preserved in the complete tooth, shows wider striae more spaced than those of the lingual surface.

Postcranial elements

The preserved postcranial elements are restrained to the atlas components. They were found disarticulated and displaced from their original position. During the preparation, the centrum and the neural arches were extracted and prepared individually. The intercentrum remains in its preserved position, near the paraoccipital process of the left opisthotic (Fig. 4A, 5A).

The atlas centrum (odontoid) has an octagonal contour in anterior and posterior views. Anteriorly, it shows a slightly concave medial subtriangular surface limited laterally by the articular facets for the neural arches (Fig. 6C). The posterior surface of the atlas centrum has two well-defined flat faces separated by a medial vertical crest, and the dorsal surface is concave (Fig. 6C). The shape of the neural arches concurs with that illustrated by Russell (1967; fig. 39) for *Clidastes propython* Cope, 1869. The synapophyseal process of the neural arch is large (Fig. 6D). The spinous process is separated from the surface for the articulation with the occipital condyle by a groove. Behind the base of the spinous process there is a concavity housing a foramen. The intercentrum is not completely exposed; the posterior surface, subtriangular in outline, and the articulation facet for the left neural arch can be identified. The surface for the articulation with the basioccipital is concave.

7. Morphological comparisons

Two Colombian mosasaurs have been described to date: the halisaurine *Eonatator coellensis* from the Campanian of Tolima (central Colombia) (Páramo-Fonseca, 2013) and the plioplatecarpine (sensu Polcyn *et al.*, 2023) *Yaguarasaurus columbianus* from the Turonian of the Upper Magdalena Valley (southern Colombia) (Páramo, 1994). The new specimen here described (IGMp879524), was found in the Coniacian of northern Colombia and its cranial morphology is closer to that of *Y. columbianus* than to that of *E. coellensis*.

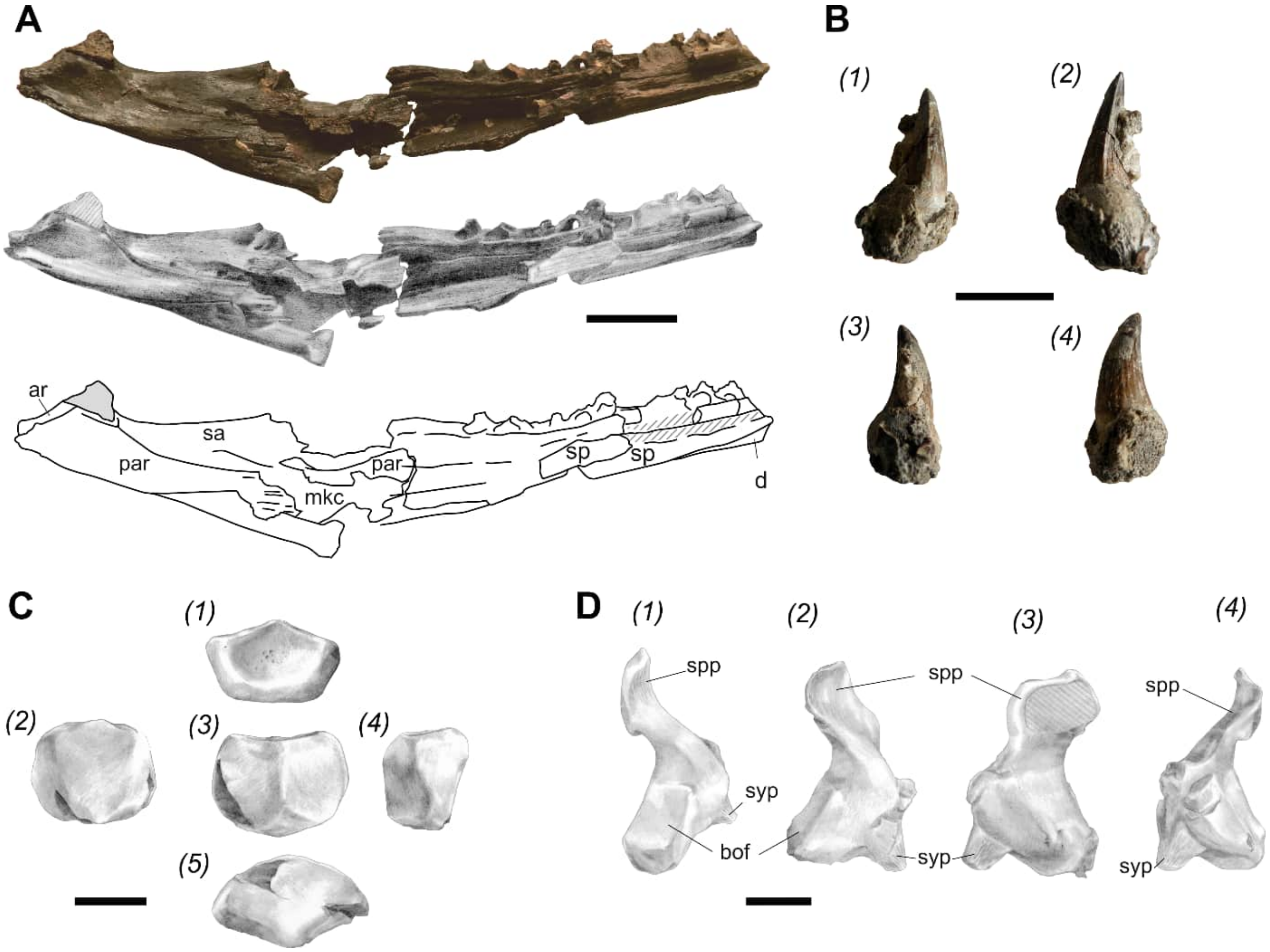

Figure 6. *Oneirosaurus caballeroi* gen. et sp. nov., holotype IGMp879524. **A**, Photograph, drawing and interpretative scheme of the left mandibular ramus without the coronoid in medial view; **B**, disarticulated tooth in anterior *(1)*, posterior *(2)*, lingual *(3)* and labial *(4)* views. **C**, Atlas centum in dorsal *(1)*, anterior *(2)*, posterior *(3)* right lateral *(4)*, and ventral *(5)* views. **D**, Left atlas neural arch in anterior *(1)*, lateral *(2)*, medial *(3)* and posterior *(4)* views. Gray fill, sediment; pattern fill, broken bone surface. Scale bars: **A** = 50 mm; **B-D** = 20 mm. **Abbreviations**: **an**, angular; **ar**, articular; **bof**, facet for the basioccipital; **d**, dentary; **mkc**, Meckel's canal; **par**, prearticular; **sa**, surangular; **sp**, splenial, **spp**, spinous process; **syp**, synapophyseal process.

The morphology of IGMp879524 is coincident with the diagnoses of two different groups considered monophyletic and exclusive: Plioplatecarpinae sensu Konishi and Caldwell (2011) and Tethysaurinae sensu Makádi *et al.* (2012). Recently, Polcyn *et al.* (2023) synonymized Yaguarasaurinae (sensu Palci *et al.*, 2013), Tethysaurinae (sensu Makádi *et al.*, 2012), Plioplatecarpinae (sensu Konishi and Caldwell, 2011) and Pioplatecarpini (sensu Russell, 1967) under a more inclusive group Plioplatecarpinae in a new sense, based on a particular basicranial vascularization shared by some russellosaurines. Tethysaurinae was proposed by Makádi *et al.* (2012) based on a cladistic analyses of mosasauroids. In contrast, in the cladistic analyses of Konishi and Caldwell (2011) and that of Polcyn *et al.* (2023) the ingroup was limited to 17 russellosaurine mosasaurs. To determine the morphological affinities of IGMp879524 with these groups, we compare its morphological features with the characters included in the diagnosis of each of these groups.

Konishi and Caldwell (2011) provide a revised diagnosis of Plioplatecarpinae (including *Platecarpus*; *Plioplatecarpus*; *Angolasaurus*; *Ectenosaurus Selmasaurus*; plus *Latoplatecarpus* and *Plesioplatecarpus*) containing 16 diagnostic characters. They differentiate this clade from the basal russellossaurines *Yaguarasaurus*, *Russellosaurus* and *Tehysaurus*, which they included in a group informally termed the "Primitive 'tethysaur' clade".

The cranial morphology of the specimen under study (IGMp879524) matches, with a single exception, the revised diagnosis proposed by Konishi and Caldwell (2011) to define Plioplatecarpinae. The only differing character in IGMp879524 is the suprastapedial process of the quadrate, which ends in an acute end and not in a blunt end as is common in plioplatecarpines (according to Konishi and Caldwell, 2011). The almost complete conccur of the morphology of the specimen under study with the revised diagnosis of Plioplatecarpinae presented by Konishi and Caldwell (2011) would show IGMp879524 as an undoubted plioplatecarpinae. However, a careful comparison of the traits used by those authors in their cladistic analysis shows IGMp879524 with cranial features that are common to the morphology of non-plioplatecarpine russellosaurines and that of basal plioplatecarpines, placing it in an intermediate position between these two groups. Given these conditions and the morphological proximity of IGMp879524 to *Yaguarasaurus columbianus* (considered non-plioplatecarpine by Konishi and Caldwell, 2011), we consider that the high coincidence of the cranial morphology of the specimen under study with the diagnosis of Plioplatecarpinae presented by Konishi and Caldwell (2011) should be evaluated in detail. The following observations are derived from this evaluation.

First, we found that the character states scored by Konishi and Caldwell (2011) for *Y. columbianus* as (1(1)), (13(1)) and (28(1)) are inaccurate and should be rescored as (1(0)), (13(0)) and (28(2)). In addition, characters (25), (32), (34), (41), (48) and (54) coded as (?) are visible and can be scored as (25(1)), (32(0)), (34(1)), (41(0)), (48(1)) and (54(0)).

IGMp879524 shares some primitive cranial features with the so-called "primitive 'tethysaur' clade", differing from plioplatecarpines. These features (the scoring given by Konishi and Caldwell (2011) indicated in parentheses) are: 1- in dorsal view, the parietal shows a broad triangular anterior surface, anterolaterally extended in the manner of an equilateral triangle (19 (0)); 2- the lingual alveolar parapet of the dentary is lower than the labial (54(0)); 3- the quadrate stapedial pit is sub-reniform in shape (41(0)), not in *Tethysaurus*).

On the other hand, there are numerous features that IGMp879524 shares with basal russellosaurines as well as with most basal plioplatecarpines differing from the more derived plioplatecarpines. These features include: 1- frontal with weak ridge in the anterior region (11(0) different in *Ectenosaurus clidastoides* (Merriam, 1894)); 2- prefrontal and postorbitofrontal separated over the orbit (15(1) different in *Selmasaurus* spp.); 3- and 4- parietal foramen located entirely on the parietal and of small size (18(0)), (20(0) different in *Selmasaurus russelli* Wright and Shannon, 1988); 5- postorbital process of the parietal visible dorsally and forming the anteromedial border of the supratemporal fenestra (23(0) different in *Plesioplatecarpus*); 6- medial ridge of the quadrate sharpened in its central region (44(0)); and 7- marginal teeth root poorly exposed, constituting less than 25% of tooth height (90(0) different in *Selmasaurus johnsoni* Polcyn and Everhart, 2008).

In addition, IGMp879524 has some features, mainly of the quadrate, which are present or are similar in plioplatecarpines and are not found in members of the "primitive 'tethysaurian' clade". These features are 1- wide and short frontal (9(0)); 2, 3 and 4- quadrate with thin wing, with low medial ridge in its dorsal region and no flange in its central region (34(0)), (43(1)), (45(0)) and 5- basioccipital canal opening into the floor of the brain cavity by means of two large foramina separated by a medial septum (97(2)) (shared with *Angolasaurus* and *Plesioplatecarpus planifrons* (Cope, 1874), different from all other plioplatecarpines).

The conditions discussed above show the cranial features of IGMp879524 close to the morphology of basal plioplatecarpines, mainly *Angolasaurus* and *Plesioplatecarpus*, and also to the "primitive 'tethysaurian' clade". This condition places it in an intermediate position between the non-plioplatecarpine russellosaurines and Plioplatecarpines (sensu Konishi and Caldwell, 2011).

The three genera of the group named by Konishi and Caldwell (2011) "Primitive 'tethysaur' clade" are subsequently recovered by Makádi *et al.* (2012), together with *Pannoniasaurus* (from the Santonian of western Hungary), into a group that they named Tethysaurinae. Most cladistic analyses involving the taxa of this group have been based on the character matrix of Bell (1997) and Bell and Polcyn (2005) and in all of them, these taxa have been recovered as a monophyletic group (Caldwell and Palci, 2007; LeBlanc *et al.*, 2012; Palci *et al.*, 2013; Jiménez-Huidobro and Caldwell, 2016; Jiménez-Huidobro *et al.*, 2016; Madzia and Cau, 2017).

The cranial morphology of IGMp879524 is also concordant with the diagnosis of Tethysaurinae proposed by Makádi *et al.* (2012). These authors established a mosaic of primitive characters to define Tethysaurinae, all coded in their cladistic analysis. Of this mosaic, eight characters are cranial, six of which are observable in the specimen IGMp879524. Five of these characters share the state defined for Tethysaurinae as follows (the coding given by Makádi *et al.* (2012) for the clade is indicated in parentheses): 1- almost straight fronto-parietal suture (15(0)); 2- quadrate stapedial pit elongate, being more than three times longer than wide (46(2)); 3- and 4- saddle-shaped quadrate condyle without anterior upward deflection (53(0)), (54(0)) and 5- lateral surangular-articular suture behind the condyle (70(0)). The sixth character "quadrate alar concavity shallow" (50(1)), is here considered subjective to determine: in the holotype of *Yaguarasaurus*, the concavity is covered by the in-place preserved tympanic membrane and can only be inferred from the medial view of the quadrate. In this view, the ala forms a more or less pronounced convexity, which is apparently absent in the holotype of *Russellosaurus*, suggesting that the alar concavity is greater in *Yaguarasaurus* than in *Russellosaurus*. However, the holotype of *Russellosaurus* shows plastic deformation and fracture (Polcyn and Bell, 2005), while the holotype of *Y. columbianus* is preserved in excellent three-dimensional condition. This feature should be coded as (50(0)) for *Yaguarasaurus*, and probably also for *Russellosaurus*, differing from *Romeosaurus* and *Pannoniasaurus*. In IGMp879524 the quadrate ala forms a wide concavity, sharing the state (0) with *Yaguarasaurus* and *Russellosaurus*.

The morphology of IGMp879524, coincident with the diagnoses of two groups considered monophyletic and exclusive (Plioplatecarpinae sensu Konishi and Caldwell, 2011 and Tethysaurinae) raises two explanations: 1- The two groups are mutually exclusive and there are shortcomings in the formulation of their diagnoses or 2- The two groups are not mutually exclusive, and the character matrices should be revised.

Recently, Polcyn *et al.* (2023) reevaluated the clade Plioplatecarpinae based on a particular basicranial vascularization that they affirm is present in some russellosaurines and absent in all other mosasaurids. Differences in the cranial vascularization in mosasaurids had been previously noted by Russell (1967), who also conferred taxonomic value to them. Polcyn *et al.* (2023) propose a new interpretation of the cranial vascularization of the plioplatecarpines, built on traits that are partially exposed externally or can only be visualized by tomographic scanning. Their phylogenetic analysis used the plioplatecarpines data matrix of Konishi and Caldwell (2011), adding three new characters (98, 99 and 100) to test the differences of the basicranial vascularization among plioplatecarpines. Unfortunately, the scoring of the new characters 99 and 100 is difficult to understand, since some taxa are coded with a stage 2, which is not included in the description of the stages of these characters.

The emended diagnosis proposed by Polcyn *et al.* (2023) for defining the most inclusive taxon Plioplatecarpinae contains eleven characters. In IGMp879524, six of the eleven diagnostic characters can be compared, and all are concurrent with the diagnosis of Plioplatecarpinae. These characters are (the coding from the phylogenetic analysis of Polcyn *et al.* (2023) in parentheses): 1- small to medium size; 2- canals for basilar artery entering basisphenoid below abducens nerve exits and above internal carotid artery path (98(1)); 3- quadrate suprastapedial process elongate, reaching mid-height; 4-6- marginal tooth crown with sub-circular basal cross-section (91(1)), medially finely striated (92(0)) and laterally fluted. Nevertheless, IGMp879524 shows features not found in any or almost any other plioplatecarpinae, but in other mosasaur groups, as is the presence of two external foramina for the exit of nerves X, XI and XII, distinctive of Mosasaurinae (following Russell, 1967) and the presence of a notch in anterior border of the atlas neural arch, which is only found in some mosasaurines and *Ectenosaurus* and *Sarabosaurus* (see Russell, 1967; Polcyn *et al.*, 2023).

The morphological comparisons discussed above show IGMp879524 as a plioplatecarpinae in the sense of Polcyn *et al.* (2023), differing from the more primitive genera (*Tethysaurus*, *Romeosaurus*, *Russellosaurus* and *Yaguarasaurrus*) in several features (see above) but also from the primitive plioplatecarpine genera *Angolasaurrus*, *Ectenosaurus* and *Selmasaurus* and from the derived plioplatecarpine genera *Platecarpus*, *Plioplatecarpus* and *Latoplatecarpus* (sensu Konishi and Caldwell, 2011), in some other features (see above).

Among the plioplatecarpines, the greater morphological affinities of IGMp879524 are found with *Yaguarasaurus* spp. (*Y. columbianus* and *Y. regiomontanus* Rivera-Sylva *et al.*, 2024) and *Angolasaurus*. Nevertheless, some differences separate IGMp879524 from these taxa. Based on Páramo-Fonseca, 1997, Rivera-Sylva *et al*., 2024 and personal observation (M.E.P.-F.) for *Yaguarasaurus*, Telles-Antunes, 1964 for *Angolasaurus*, and the scoring of Simões *et al.*, 2017, we found the following differences: in IGMp879524 the suprastapedial process of the quadrate is long and extends to the level of the infrastapedial process whereas in *Yaguarasaurus* and *Angolasaurus* the suprastapedial process ends above the infrastapedial; the infrastapedial process of the quadrate is more robust and better defined than in these taxa. The carinae on marginal teeth are arranged at 180º, one mesial and the other distal, whereas in *Y. columbianus* (unknown in *Y. regmontanus* see Rivera-Sylva *et al*., 2024) and in *Angolasaurus* the carinae are mesially and labiodistally oriented. IGMp879524 differs from *Yaguarasaurus* also by the following features: the triangular surface of the frontal, anterior to the orbits, is longer in *Y. columbianus*; the suspensory branches of the parietal originate more anteriorly in *Yaguarasaurus* spp.; the dorsal exposure of the parietal-postorbitofrontal suture is long and has a straight diagonal trajectory in *Yaguarasaurus* spp., whereas it is short and has a semicircular trajectory in IGMp879524; the frontal of IGMp879524 has a smooth anterior dorsal ridge whereas in *Yaguarasaurus* spp. there is no ridge; the protrusion of the ventral-posterior border of the jugal is less pronounced in IGMp879524 than in *Y. columbianus* and its position is more dorsal; the otosphenoidal crest of the prootic does not cover laterally the exit of nerve VII as it covers in *Y. columbianus*; the carinae in the marginal teeth are weaker in *Yaguarasaurus* spp; the labial surface of the crowns has wider and more separated striae than the lingual surface in IGMp879524, differing from the smooth labial surface of the crown in *Y. columbianus*.

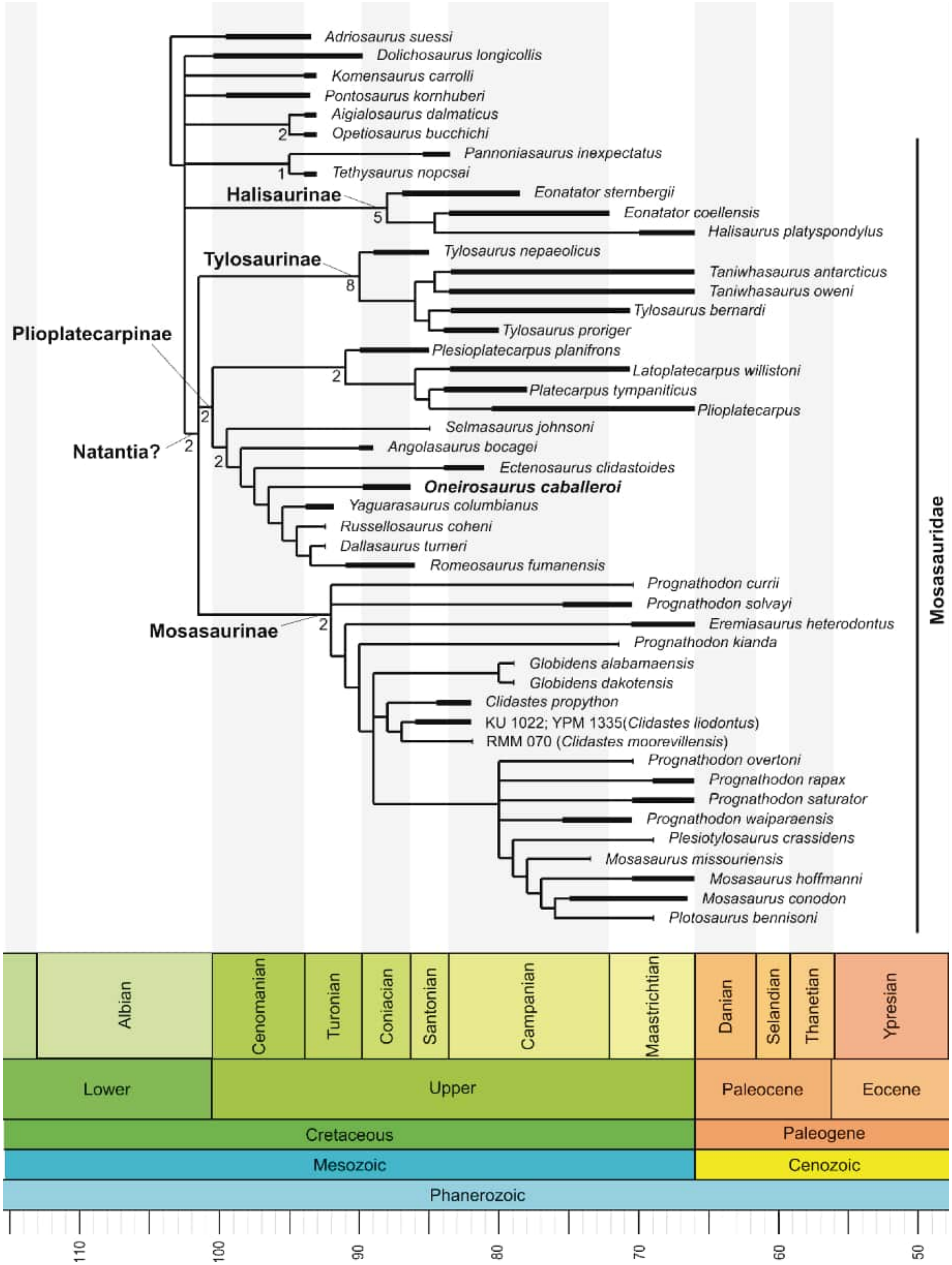

Figure 7. Phylogeny of Mosasauridae showing the position of *Oneirosaurus caballeroi* gen. et sp. nov. Time calibrated strict consensus from 72 most parsimonious trees (501 steps) with 46 OTUs and 125 characters (see Materials and Methods) recovered from the analysis of the full dataset. Bremer support values are shown in some branches.

IGMp879524 differs from *Angolasaurus* as follows. In *Angolasaurus* the quadrate stapedial pit is subcircular (reniform in IGMp879524); there is no groove on the anterolateral edge of the quadrate ala (dorsal groove in IGMp879524); the quadrate medial ridge is single, thin and high (low and rounded in IGMp879524); the quadrate condyle is convex (saddle-shaped in IGMp879524); the foramina for nerves X and XII are externally fused (separated in IGMp879524); the basioccipital tubera are short (long in IGMp879524); the medial dentary parapet is more elevated than in IGMp879524; the coronoid is slightly curved, without expanded posterior wing (concave and with expanded posterior wing in IGMp879524); the lateral surangular-articular suture is found at the middle of glenoid (behind the glenoid in IGMp879524); and the tooth replacement is sub-dental (in shallow excavations in IGMp879524).

The recently described monospecific plioplatecarpine *Sarabosaurus dahli* proposed by Polcyn *et al.*, 2023 also differs from IGMp879524 in some features. In IGMp879524 the supradental portion of the maxilla at the external naris is transversely as broad as tall (it is broader than tall in *Sarabosaurus*); there is no dermal sculpting on the dorsal surface of the frontal supraorbital region as there is in *Sarabosaurus*; the pterygoid bears 13 tooth positions (at least 14 in *Sarabosaurus*); the infrastapedial process and the posteroventral ascending alar rim of the quadrate are robust (both are poorly developed in *Sarabosaurus*); the dentary is thin (robust in *Sarabosaurus*) and its medial ridge covers part of the tooth root (exposes nearly entire tooth root in *Sarabosaurus*) (Polcyn *et al.*, 2023).

In summary, the combination of primitive and derived characters found in the new specimen IGMp879524 is unique among Plioplatecarpinae. The morphological differences with each of the genera included in Plioplatecarpinae are numerous and unquestionable (see data matrix) and support the erection of a new genus and species: *Oneirosaurus caballeroi*.

8. Phylogenetic analyses

According to our revisions, we change the following scores from the matrix of Madzia and Cau (2017): For *Yaguarasaurus columbianus* [11(0→1); 43(0→1); 44(1→0); 46(0→2)], for *Russellosaurus coheni* [11(0→1); 44(1→0)]; for *Angolasaurus bocagei* [18(1→2)] and *Sarabosaurus dahli* [8(1→?)].

First analysis (without *Sarabosaurus dahli)*

From the first analysis (without *Sarabosaurus dahli*) a strict consensus of 72 most parsimonious trees with 501 steps (RI= 0.704 and CI= 0.323) was obtained from TBR branch swapping (Fig. 7). *Oneirosaurus caballeroi* was recovered within a monophyletic clade which includes all Plioplatecarpinae *sensu* Polcyn *et al.*, 2023, except *Tethysaurus nopcsai* Bardet *et al.*, 2003. In our results, not all the groups previously included within Mosasauridae are found interrelated as a monophyletic clade; the halisaurines (*Eonatator sternbergii* + (*Eonatator coellensis* + *Halisaurus platyspondylus*)) and a branch containing *Tethysaurus nopcsai* + *Pannoniasaurus inexpectatus*, appear in an unresolved polytomy with all the basal mosasauroids and with a branch containing Tylosaurinae, Mosasaurinae and Plioplatecarpinae, each as a monophyletic clade. The three synapomorphies defining the branch Tylosaurinae + Mosasaurinae + Plioplatecarpinae refer to the locomotor skeleton: (89(1)) sacral vertebrae no more than one; (117(1)) elongated ilium crest not articulating with sacral ribs; and (123(1)) hyperphalangy present. Although certain of these characters are unknown in some of the "mosasaurid" taxa excluded from that branch, it is interesting to note that these features are related to locomotion functions showing a change from plesiopelvic and plesiopedal conditions to hydropelvic and hydropedal conditions representing the adaptation to a full-aquatic lifestyle in the derived mosasauroids. This branch is comparable to the Natantia clade of Bell (1997) and represents full-aquatic mosasauroids. Another uncommon finding in the recovered topology is the place of *Dallasaurus turneri* within the clade Plioplatecarpinae, close to *Russellosaurus* and *Romeosaurus*, a position not recovered in previous works (Jiménez-Huidobro and Caldwell, 2016; Jiménez-Huidobro and Caldwell, 2019; Madzia and Cau, 2017; Palci *et al.*, 2013; Simões *et al.*, 2017). In our resulting topology, the clade Yaguarasaurinae, as recovered in previous works, is not supported. In general, the obtained Bremer supports (see Fig. 7) show that most of the recovered branches are not well-supported with Bremer values of 2. The only two branches that are better supported are the Tylosaurinae branch and the Halisaurinae branch, with Bremer values of 8 and 5 respectively.

The clade Plioplatecarpinae, containing *Oneirosaurus caballeroi*, is supported by the following synapomorphies: (12(1)) very short descending processes from the sides of the olfactory canal surrounding and almost or totally enclosing the olfactory nerve; (18(1)) parietal table triangular in shape, with sides contacting in front of suspensorial rami; (28(1)) presence of a postorbitofrontal transverse dorsal ridge; (53(5)) 12 dentary teeth; (59(1)) absence of a coronoid posteromedial process; (66(1)) one to three large foramina present in the retroarticular process of the articular; and (70(1)) tooth fluting present.

Plioplatecarpinae was recovered with two branches, one containing *Plesioplatecarpus*, *Latoplatercarpus*, *Platecarpus,* and *Plioplatecarpus* and supported by the following synapomorphies: (15(0)) lateral sutural flange of frontal posteriorly extended and (19(1)) large parietal foramen. The second branch within Plioplatercapinae contains *Selmasaurus johnsoni*, *Angolasaurus bocagei, Ectenosaurus clidastoides*, *Russellosaurus coheni*, *Romeosaurus fumanensis*, *Dallasaurus turneri*, and the Colombian taxa *Oneirosaurus caballeroi* and *Yaguarasaurus columbianus*. This branch is supported by the following synapomorphies: (9(0)) frontal not invaded by posterior end of nares; (15(2)) lateral and medial sutural flange of frontal posteriorly extended; (18(2)) parietal table triangular shape with posterior portion forming parasagittal crest; and (48(0)) quadrate anterior ventral condyle without upward deflection of its anterior edge.

Second analysis (with *Sarabosaurus dahli*)

From the second analysis (with *Sarabosaurus dahli*) a strict consensus of 871 most parsimonious trees with 505 steps (RI= 0.701 and CI= 0.321) was obtained from TBR branch swapping (Supplemental data 2, Fig. S1). *Oneirosaurus caballeroi* was recovered within a large polytomy. The plioplatecarpines sensu Polcyn *et al.* (2023) were not recovered as a monophyletic group. The Tylosaurinae and the Mosasaurinae were found as differentiated branches, but they are not internally resolved, showing also large polytomies. When we applied the IterPCR algorithm, *Oneirosaurus caballeroi*, *Romeosaurus fumanensis*, *Russellosaurus coheni*, *Yaguarasaurus columbianus*, *Dallasaurus turneri* and *Komensaurus carrolli*, and the nodes containing *Halisaurus* and *Eonatator* were identified as unstable taxa. As the goal of the phylogenetic analyses in this contribution was to determine the phylogenetic relationships of the new taxon *Oneirosaurus caballeroi* we did not prune the unstable OTUs identified with this algorithm. However, the results of this second analysis shows that the inclusion of *Sarabosaurus dahli* produces great instability. This might be due to the presence of derived and primitive characters present in the scarce known material of *S. dahli.*

9. Conclusions

A new plioplatecarpine mosasaurid (IGMp879524) is described. Its morphology shows a combination of primitive and derived characters placing the specimen in an intermediate position between the non-plioplatecarpine russellosaurines and plioplatecarpines (sensu Konishi and Caldwell, 2011). The morphology of IGMp879524 is also unique among the more inclusive clade Plioplatecarpinae (sensu Polcyn *et al.*, 2023). It is the only plioplatecarpine having two external foramina for the exit of nerves X, XI and XII, a feature previously considered distinctive of mosasaurines. The special combination of characters of IGMp879524 allow us to determine it as a new genus and species of Plioplatecarpinae: *Oneirosaurus caballeroi.*

The results of the phylogenetic analysis support our morphological comparisons recovering *Oneirosaurus caballeroi* as a basal plioplatecarpine. In contrast to previous works *Dallasaurus* were recovered among the Plioplatecarpinae clade. Moreover, in our results, the plesiopelvic and plesiopedal "mosasaurids" (tethysaurines and halisaurines) were recovered in an unresolved polytomy with the basal mosasauroids and a branch containing the derived hydropelvic and hydropedal mosasurids (tylosaurines, plioplatecarpines and mosasaurines).

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