

Description of the first Cretaceous (Santonian)
articulated skeletal lungfish remains
from South America, Argentina

Karen M. PANZERI, Soledad GOIRIC CAVALLI,
Alberto L. CIONE & Leonardo S. FILIPPI



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Karen M. PANZERI

Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET),
Godoy Cruz 2290, Ciudad Autónoma de Buenos Aires (Argentina)
and División Paleontología Vertebrados, Museo de La Plata,
Paseo del Bosque s/n, W1900FWA La Plata (Argentina)
k.panzeri@fcnym.unlp.edu.ar (corresponding author)

Soledad GOUIRIC CAVALLI

Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET),
Godoy Cruz 2290, Ciudad Autónoma de Buenos Aires (Argentina)
and División Paleontología Vertebrados, Museo de La Plata,
Paseo del Bosque s/n, W1900FWA La Plata (Argentina)
sgouiric@fcnym.unlp.edu.ar

Alberto L. CIONE

División Paleontología Vertebrados, Museo de La Plata,
Paseo del Bosque s/n, W1900FWA La Plata (Argentina)
acione@fcnym.unlp.edu.ar

Leonardo S. FILIPPI

Museo Municipal Argentino Urquiza, Chos Malal 1277,
CP 8319, Rincón de los Sauces, Neuquén (Argentina)
lsfilippi@gmail.com

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ABSTRACT

The fossil record of dipnoans is mostly represented by tooth plates and jaw bones, whereas nearly complete or complete skulls are rare. Here, we describe a new dipnoan from the Santonian (Upper Cretaceous) of Patagonia (Argentina) using three-dimensional renderings generated by CT scans. It consists of a near-complete skull and postcranial material. *Rinconodus salvadori* n. gen., n. sp. is diagnosed by a combination of features, such as medial series composed of two unpaired bones, mediolateral series composed of two paired bones, lateral series with at least one bone, medial edge of tooth plates longer than the lingual edge and equally curved, upper tooth plates contiguous or close to one another with five denticulations, lower tooth plates widely separated with four denticulations, first denticulation of upper tooth plates longer and thinner than the remaining denticulations, and posteriorly curved, first denticulation of lower tooth plates relatively straight and longer than the remaining ones, among other characters. The new species is based on the first two nearly complete Santonian dipnoan skulls from South America. Moreover, the materials presented here are the geologically youngest dipnoan remains consisting of a near-complete skull and postcranium from the Cretaceous of Gondwana.

KEY WORDS

Sarcopterygii,
Dipnoi,
Ceratodontidae,
Ceratodontidae,
Cretaceous,
Santonian,
Neuquén Basin,
Argentina,
new genus,
new species.

RÉSUMÉ

Description des premiers restes squelettiques articulés de dipneuste (Dipnoi, Ceratodontidae) du Crétacé (Santonien) d'Amérique du Sud, Argentine.

Les fossiles des dipneustes sont principalement représentés par des plaques dentaires et des os de la mâchoire, alors que les crânes complets, ou presque complets, sont rares. Ici, nous décrivons un nouveau dipneuste du Santonien (Crétacé supérieur) de la Patagonie Argentine à l'aide de rendus tridimensionnels générés par des tomodensitogrammes. Il s'agit d'un crâne quasi-complet et de matériel postcrânien. *Rinconodus salvadori* n. gen., n. sp. est diagnostiqué par une combinaison de caractéristiques, telles que : série médiale composée de deux os non appariés, série médio-latérale composée de deux os appariés, série latérale avec au moins un os, bord médial des plaques dentaires plus long que le bord lingual et de même courbure, plaques dentaires supérieures contiguës ou proches les unes des autres avec cinq denticulations, plaques dentaires inférieures largement séparées avec quatre denticulations, première denticulation des plaques dentaires supérieures plus longue et plus mince que les autres denticulations, et courbée postérieurement, première denticulation des plaques dentaires inférieures relativement droite et plus longue que les autres, entre autres. La nouvelle espèce est basée sur les deux premiers crânes de dipneustes Santoniens presque complets d'Amérique du Sud. De plus, les matériaux présentés ici sont les enregistrements les plus récents d'un crâne de dipneuste presque complet et de matériel postcrânien du Crétacé du Gondwana.

MOTS CLÉS

Sarcopterygii,
Dipnoi,
Ceratodontoidei,
Ceratodontidae,
Crétacé,
Santonien,
Neuquén Bassin,
Argentine,
genre nouveau,
espèce nouvelle.

INTRODUCTION

Dipnoi is an old extant clade dating back to the Early Devonian (e.g. Schultze 1986; Clement 2019). The evolutionary history of post-Devonian lungfishes is characterized by several diversity peaks showing a decrease in diversity towards the present (Kemp *et al.* 2017). Today, dipnoans are represented only by two families restricted to the Southern Hemisphere: Neoceratodontidae and Lepidosirenidae.

Post-Paleozoic dipnoans have a particular dental apparatus composed of pairs of tooth plates. In the upper jaw, there are two pairs (pterygopalatine and vomerine tooth plates) and in the lower jaw, there is only one (prearticular tooth plates) (Clement 2019).

Post-Devonian record is mostly represented by tooth plates –which have a high fossilization potential–, while other cranial and postcranial elements are rare and mainly consist of isolated bones (e.g. Kemp 1998; Cavin *et al.* 2007; Pawlak *et al.* 2020). Most of the skull roof material is of Triassic age (Teller 1891; Teixeira 1949; Lehman *et al.* 1959; Vorobyeva 1967), whereas they are scarce for the Jurassic and Cretaceous (Schultze 1981; Cavin *et al.* 2007, 2020; Pardo *et al.* 2010; Giordano *et al.* 2017). Thus, the understanding of the systematics and the anatomy of Mesozoic lungfishes is mostly based on tooth plates.

In southern South America, the dipnoan fossil record extends from the Triassic to Eocene (Fernández *et al.* 1973; Agnolin *et al.* 2016). Argentinian dipnoans are abundant in upper Mesozoic formations deposited in estuarine and continental environments (e.g. Lago Colhue Huapí, Bajo de la Carpa, La Colonia and Allen formations) and mainly in Patagonia. These materials correspond mostly to tooth plates and jaw bones being assigned to the families Ptychoceratodontidae (only one tooth plate, Agnolin *et al.* 2016) and

Ceratodontidae (Apesteguía *et al.* 2007; Cione *et al.* 2007; Cione & Gouiric-Cavalli 2012; Panzeri *et al.* 2020). Recently, two skulls recovered from the Bajo de la Carpa Formation in Neuquén Province were reported and briefly described (see Giordano *et al.* 2017).

This contribution assesses the material studied by Giordano *et al.* (2017) from an anatomic and taxonomic approach. We also describe a postcranium found in association with a skull. In addition, we provide a comparison of the new skulls and postcranial material with other Mesozoic species.

GEOLOGICAL SETTINGS

The Neuquén Basin was a retro-arc basin developed in Mesozoic times in the Pacific margin of South America (Legarreta & Uliana 1996). It houses a near-continuous Late Triassic-early Cenozoic marine and continental succession that was deposited on the eastern side of the evolving Andean Mountain chain (Howell *et al.* 2005), located towards the northwest of the Somuncurá Massif, Patagonia, Argentina (Fig. 1A, B). The Neuquén Group was deposited in the Neuquén Basin during the Late Cretaceous (Cenomanian-Campanian) (Garrido 2010). The Neuquén Group includes three subgroups: Río Colorado, Río Neuquén and Río Limay. The Río Colorado Subgroup comprises the Bajo de la Carpa and the Anacleto formations (Cazau & Uliana 1973; Ramos 1981), and extends covering the Neuquén and Río Negro provinces in Patagonia Argentina (Fig. 1B).

The Bajo de la Carpa Formation (Fossa Mancini *et al.* 1938) is one of the most characteristic units of the Neuquén Group (Leanza *et al.* 2004). It overlies in discontinuity (of erosive nature) with the Plottier Formation and is covered in same relation by the Anacleto Formation. The Bajo de la Carpa

Formation is composed of reddish orange quartz sandstones with little matrix (Garrido 2010). The levels of quartz sandstones are interspersed with pelitic horizons accompanied by gypsum deposits (Garrido 2010). There are no absolute ages for Bajo de la Carpa Formation, but it is assigned to a Santonian age due to its paleontological content and their relation with successive formations (Leanza & Hugo 2001). The depositional environment of Bajo de la Carpa Formation corresponds to a river and flooded plains, with the participation of eolic deposits (Leanza & Hugo 2001).

Many fossilized vertebrate remains have been recovered in the Bajo de la Carpa formation: theropod, sauropod, and ornithomimid dinosaurs such as *Achillesaurus manazzoni* (Martinelli & Vera, 2007), *Tratayenia rosalesi* (Porfiri, Valieri, Santos & Lamanna, 2018), *Viavenator exxoni* (Filippi, Méndez, Juárez-Valieri & Garrido, 2016), *Llukalkan aliocranianus* (Gianechini, Méndez, Filippi, Paulina-Carabajal, Juárez-Valieri & Garrido, 2021), *Mahuidacursor lipanglei* (Cruzado-Caballero, Gasca, Filippi, Cerda & Garrido, 2019), *Bonitasaura salgadoi* (Apesteguía, 2004), *Rinconosaurus caudamirus* (Calvo & González Riga, 2003), and abelisaurid teeth (Filippi *et al.* 2015); the notosuchians *Comahuesuchus* Bonaparte, 1991, *Notosuchus* Woodward, 1896 (Pol *et al.* 2014), and *Kinesuchus overoi* (Filippi, Barrios & Garrido, 2018); and the dipnoan material described here and in Giordano *et al.* (2017). The dipnoan material come from the La Invernada locality (Fig. 1C), located southeast of the town of Rincon de los Sauces, Neuquén Province.

MATERIAL AND METHODS

MATERIAL

The studied material was recovered in the Upper Cretaceous (Santonian). All the material come from the Bajo de la Carpa Formation, at La Invernada locality and were collected in a fieldtrip carried out by the Museo Municipal Argentino Urquiza during the year 2015. The specimens are housed at the vertebrate paleontology collections of the Museo Municipal Argentino Urquiza, Rincón de los Sauces, Neuquén Province, Patagonia, under the acronym MAU-PV.

The studied material consists of two skulls (MAU-PV-LI-612, MAU-PV-LI-613), an incomplete axial skeleton (MAU-PV-LI-630), and isolated and fragmentary pterygopalatine tooth plates, some with ankylosed bones, (MAU-PV-LI-637; MAU-PV-LI-638; MAU-PV-LI-639). MAU-PV-LI-630 was found in proximity to one of the skulls, but the precise association remains unclear.

METHODS

Specimens were studied under a stereomicroscope (ZEISS Stemi 2000-C). Measurements were taken directly on the material using a Digital Caliper, and high-resolution photographs on the free software ImageJ (Schneider *et al.* 2012). The measurement of the skull was taken from the most anterior preserved portion of the snout to the most posterior preserved portion of the occipital region. Digital

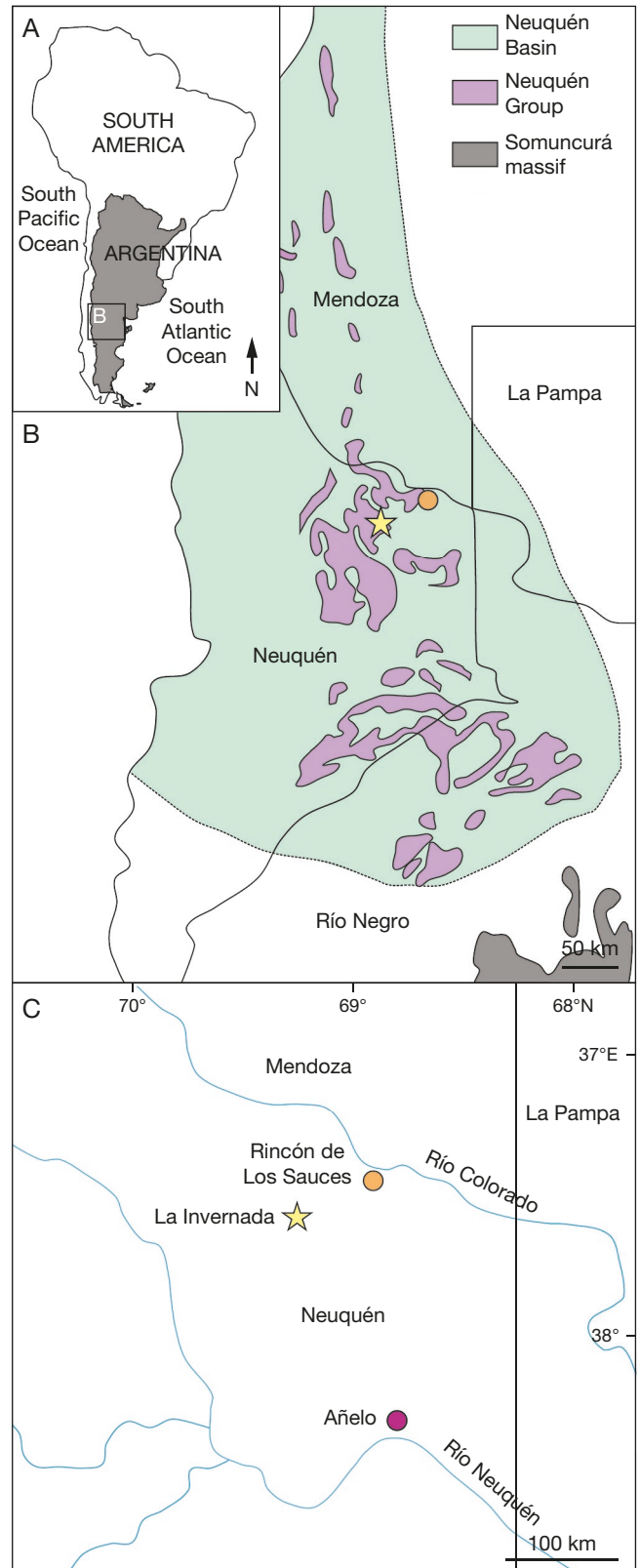


FIG. 1. — Location map: **A**, South America, in gray Argentina; **B**, detail of A. Colors: dark gray, Somuncurá massif; green, Neuquén basin; violet, Neuquén Group (modified from Garrido 2010); **C**, detail of the southeast of the Neuquén Province with the fossil locality mentioned in the text (modified from Filippi *et al.* 2016): La Invernada. The Neuquén Basin limits are in dotted line. The star indicates La Invernada locality, and the circles the nearby towns.

TABLE 1. — Alternative terminology of *Rinconodus salvadori* n. gen., n. sp. skull roof bones, following the nomenclatural criterion used here (Cavin *et al.* 2007) as well as those proposed by other authors.

Present study, following the criterion of Cavin <i>et al.</i> (2007)	Following the criterion of Goodrich (1925) and Lehman <i>et al.</i> (1959)	Following the criterion of Romer (1936) and Forster-Cooper (1937)	Following the criterion of Owen (1839) and Bemis (1986)
Anterior medial	Rostrofrontal central	EC/EQ	Dermal ethmoid
Posterior medial	Parietal central	AB/ABC	Frontoparietal
Anterior-mediolateral	Lateral Frontal	KLMN/KLM	Supraorbital
Posterior-mediolateral	Lateral Parietal	IJ	Extrascapular
?Lateral bone	?Dermosphenotic	?YZ, ?XYZ	?Dermosphenotic/Squamosal

photographs were taken with a Canon PowerShot camera attached to a stereomicroscope.

MAU-PV-LI-612 was scanned using a Cone Beam CT scan and a Kodak 9000C 3D CT scan at the Facultad de Odontología de la Universidad de Buenos Aires (FOUBA). The X-ray beam was generated with a current of 10 mA and a voltage of 70 kV, with a pixel size of 200 µm and a FOV of 100 mm. The resulting CT has 186 (coronal) slices with a thickness of 0.2 mm. MAU-PV-LI-613 were scanned using a Toshiba Activion scanner at Hospital San Martín, La Plata. The X-ray beam was generated with a current of 250 mA, a voltage of 120 kV, a pixel size of 490 µm and a FOV of 250 mm. The resulting CT scan has 224 (axial) slices with a thickness of 1.0 mm.

The resulting dataset was segmented into the free software Invesalius 3.1.1 (<https://invesalius.github.io/download.html>; De Moraes *et al.* 2011) and used to generate the 3D models. Subsequently, the 3D models were edited using the free software Blender (<http://www.blender.org>; Blender Institute; Morelli *et al.* 2015). A 3D pdf was made with the free software Design Spark Mechanical 4.0 (Gribovski 2015).

Remarks on nomenclature

Several authors proposed schemes to homologate the dipnoan skull bones with those of other vertebrates (Owen 1839; Goodrich 1925; Romer 1936) (Fig. 2A-C). Among these, some use classical bone nomenclature (Goodrich 1925), and others use letters and numbers (Romer 1936) (Fig. 2A, B). Both types of nomenclature schemes are still used, but with modifications (see Forster-Cooper 1937; Lehman 1959; Martin 1979; Bemis 1986; Campbell & Barwick 2001; Ahlberg *et al.* 2001; Schultze 2008). In most of these criteria (e.g. Goodrich 1925; Romer 1936; Forster-Cooper 1937; Kemp 1998), the determination of each bone is established by the lateral line system and the relations with other easily recognizable bones (like the B bone) (see Thomson & Campbell 1971). However, throughout the evolutionary history, dipnoans have undergone reductions, fusions, the appearance of new ossification centers and/or a greater development of certain bones over others. All these modifications can occur without a visible alteration of the lateral line path (see Jardine 1969; Miles 1977). Although these criteria are relatively consistent and useful for Paleozoic species, they are difficult to apply in Mesozoic and Cenozoic taxa due to the high degree of fusion and/or loss of bones. Thus, following

these criteria, the interpretations made on the skull bones of Mesozoic and Cenozoic species are highly variable (see Lehman 1966; Martin 1979; Schultze 1981; Kemp 1998; Kemp 1999: table 2; Cavin *et al.* 2007: table 1).

In this contribution we follow the topographic criterion proposed by Cavin *et al.* 2007 (Fig. 2C), which recommends the use of series (i.e., medial, mediolateral and lateral) for describing the skull bones (Fig. 2C). Thus, each bone is named according to their spatial arrangement respectively to the remaining bones. We decided to implement this criterion for the description since the interpretations can be replicated by anyone. Likewise, the possible determinations will be presented using other criteria (Table 1). For the nomenclature of the lateral line system, we followed Pehrson (1949). For jaw bones and tooth terminology, we followed the set of terms used in Panzeri *et al.* (2020), which is a compendium of the terminology of Kemp (1977); Churcher & De Iullis (2001); Smith & Campbell (1987), and Kemp & Berrell (2020). Palatal terminology follows Pardo *et al.* (2010) and postcranial terminology follows Arratia *et al.* (2001).

INSTITUTIONAL ABBREVIATIONS

MACN	Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires;
MAU	Museo Argentino Urquiza, Neuquén;
MCF	Museo Municipal Carmen Funes, Neuquén;
MML	Museo Municipal Héctor Cabazza, Río Negro;
MPCN	Museo Patagónico de Ciencias Naturales, Río Negro;
MPEF	Museo Paleontológico Egidio Furlong, Chubut;
MPM	Museo Padre Molina, Santa Cruz.

SYSTEMATIC PALEONTOLOGY

Class SARCOPTERYGII Romer, 1955

Order DIPNOI Müller, 1845

Suborder CERATODONTOIDEI Nikolski, 1954

Family CERATODONTIDAE Gill, 1872

Genus *Rinconodus* n. gen.

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TYPE SPECIES. — *Rinconodus salvadori* n. sp.

DIAGNOSIS. — As for type and only species (see below).

Rinconodus salvadori n. gen., n. sp.
(Figs 3; 4A-D)

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MATERIAL TYPE. — **Holotype.** MAU-PV-LI-613 (Figs 3; 4), an incomplete head which preserves several bones of the skull roof, palate, and jaw bones with their upper and lower tooth plates.

Paratypes. MAU-PV-LI-612 (Fig. 5), an incomplete head preserving bones of the skull roof, palate, upper tooth plates, and a fragment of lower tooth plate; MAU-PV-LI-637; MAU-PV-LI-638; MAU-PV-LI-639, fragmentary upper tooth plates; MAU-PV-LI-630, an incomplete vertebral column (section of the caudal region), with scales and fin rays, preserved in part counterpart.

DIAGNOSIS. — Dipnoan fish characterized by having a roughly rounded skull with a high degree of fusion and/or loss of dermal bones and a unique combination of characters. Skull roof bones organized in three series: i) medial series composed by two unpaired bones; ii) mediolateral series composed by two paired bones; and iii) lateral series with at least one bone. Anterior medial bone without sensory canals. Lateral line system partially enclosed in the anterior mediolateral bone and with pores. Anterior mediolateral bone with a descending process for articulation with the ascending pterygopalatine process of the upper jaw. Anterior mediolateral bone with an overlapping suture with the posterior mediolateral bone. Absence of pineal foramen. Upper tooth plates contiguous or close to one another with five denticulations. Lower tooth plates widely separated with four denticulations. Ridges originating postero-medially. Medial edge of tooth plates longer than the lingual edge and equally curved. First denticulation of upper tooth plates longer and thinner than the remaining denticulations, and posteriorly curved. First denticulation of lower tooth plates relatively straight and longer than the remaining. An oblong or elliptical upper symphysis and a linear lower symphysis. The pterygopalatine process is present (at level of the second denticulation). Double prearticular groove. Pattern of wear in form of circles on furrows, on mediolingual edge and over the plateau. Aspondylous vertebral column with a persistent and functional notochord in adult specimens.

ETYMOLOGY. — The generic name is due to the town of Rincon de los Sauces, near the bearing outcropping beds. The specific name is in honor of the MAU technician Salvador Palomo, who found the specimens.

TYPE LOCALITY. — La Invernada locality, Neuquén Province, Argentina (37°34'57.1"S, 69°19'16.2"W).

TYPE HORIZON. — Bajo de la Carpa Formation, Santonian (Upper Cretaceous).

DESCRIPTION

Remarks on skull preservation

Comparing both specimens, the holotype (Figs 3; 4) retains more of the original oval shape, and it is slightly deformed. MAU-PV-LI-613 measures *c.* 4.81 cm in antero-posteriorly length and the bones of its skull roof are poorly preserved (Figs 3A; 6A, B). Partially preserved bones include: the anterior and posterior medial bones of the medial series (Fig. 4A), and the anterior mediolateral bone of the mediolateral series (Fig. 4A, C). Neither bones nor its impressions are recognized in the lateral series. The preserved palatine zone of MAU-PV-LI-613 comprises the incomplete parasphenoid and pterygopalatine bones. The pterygopalatine tooth plates

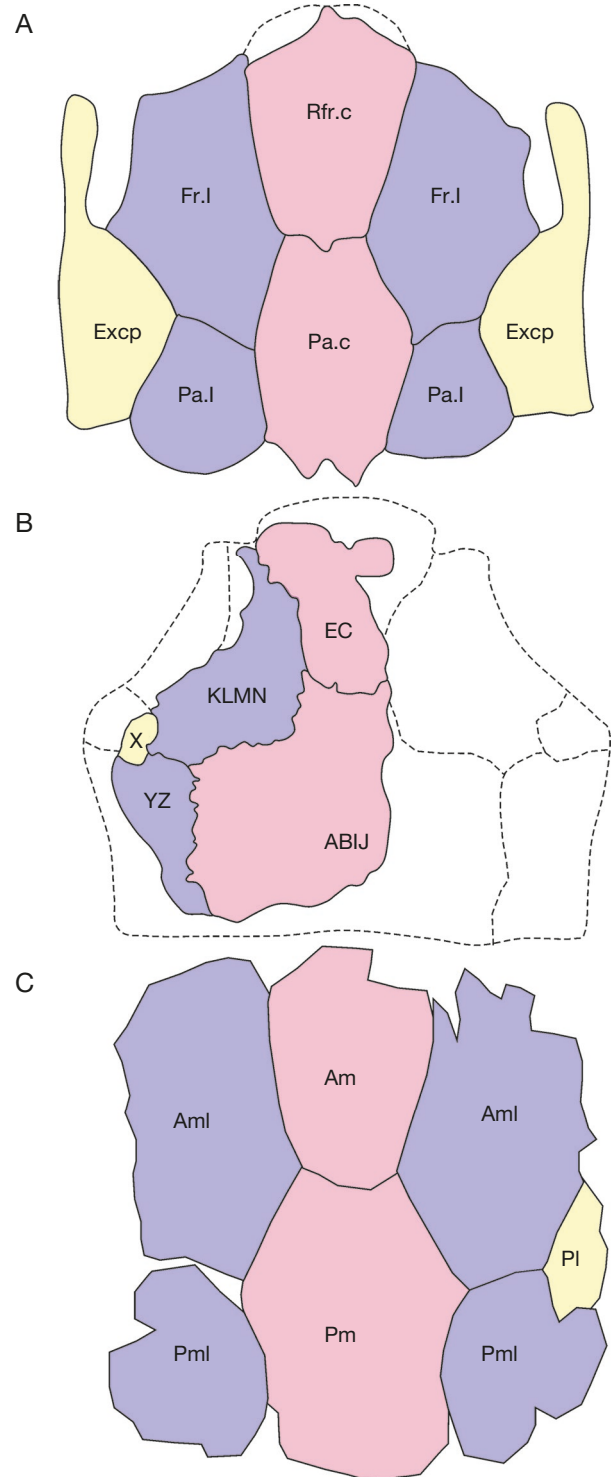


FIG. 2. — Nomenclature of the dipnoan skull bones according to criteria used in the anatomic studies: **A**, diagram of the dorsal view of the skull of *Arganodus atlantis* Martin, 1979 (and the interpretation of Kemp 1998) and following the homology criterion of Goodrich (1925); **B**, diagram of *Ceratodus sturii* (Teller, 1891) in dorsal view from Schultze (1981) and following the homology criterion of Romer (1936); **C**, diagram of the dorsal view of the skull of *Ferganoceratodus martini* Cavin, Suteethorn, Buffetaut & Tong, 2007 following the topographic criterion of Cavin *et al.* (2007). The colors follow the criterion of Cavin *et al.* (2007) used in this work: **blue**, mediolateral series; **red**, medial series; **yellow**, lateral series. Abbreviations: **Am**, anterior medial bone; **Aml**, anterior mediolateral bone; **Excp**, extraescapular; **Fl**, lateral frontal; **Fr.l**, lateral frontal; **Pa.c**, central parietal; **Pa.l**, lateral parietal; **Pl**, posterior lateral bone; **Pm**, posterior medial bone; **Pml**, posterior mediolateral bone; **Rfr.c**, central rostrofrontal.

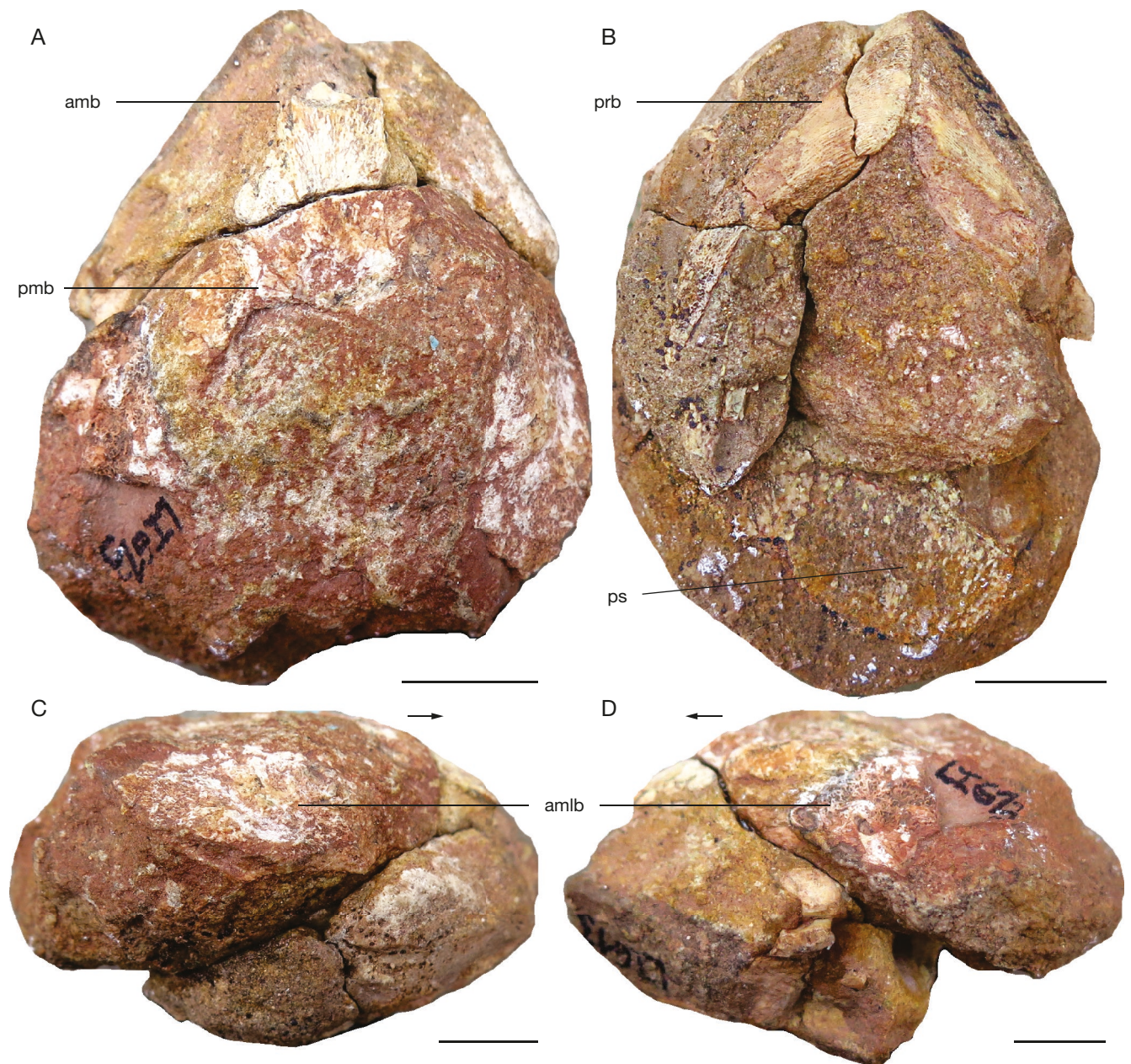


FIG. 3. — Skull of *Rinconodus salvadori* n. gen., n. sp. MAU-PV-LI-613: **A**, skull in dorsal view; **B**, skull in ventral view; **C**, skull in right view; **D**, skull in left view. Abbreviations: **amb**, anterior medial bone; **amlb**, anterior mediolateral bone; **ps**, parasphenoid; **pmb**, posterior medial bone; **prb**, prearticular bone. **Arrows** point anteriorly. Scale bars: 1 cm.

of MAU-PV-LI-613 are almost complete (i.e., with broken first denticulations). The lower jaw preserves the prearticular bones with the almost complete tooth plates (the first denticulation of the right tooth plate is broken).

MAU-PV-LI-612 shows a more pronounced post-mortem deformation. The skull is dorsoventrally compressed, and the ascending process of the pterygopalatine bone and the descending process of the anterior mediolateral bone are broken and displaced. The skull of MAU-PV-LI-612 (Fig. 5) has 5.57 cm in length and is partially preserved. Though the preserved skull roof bones of MAU-PV-LI-612 are less than those of the holotype (MAU-PV-LI-613), they are in better condition (Fig. 6C, D). Partially preserved bones of the skull roof comprise: the

anterior and posterior medial bones of the medial series; the anterior mediolateral bones, and the impression in sediment of the right posterior mediolateral bone of the mediolateral series; and a fragment of bone of the lateral series. The preserved palatine zone comprises the incomplete parasphenoid and the upper jaw with the pterygopalatine bones. The pterygopalatine tooth plates are complete but broken. The lower jaw is represented by a fragment of the prearticular bone with a partially preserved right prearticular tooth plate (Fig. 9).

Skull roof

The medial series of *Rinconodus salvadori* n. gen., n. sp. has two bones, a small anterior medial bone and a larger posterior

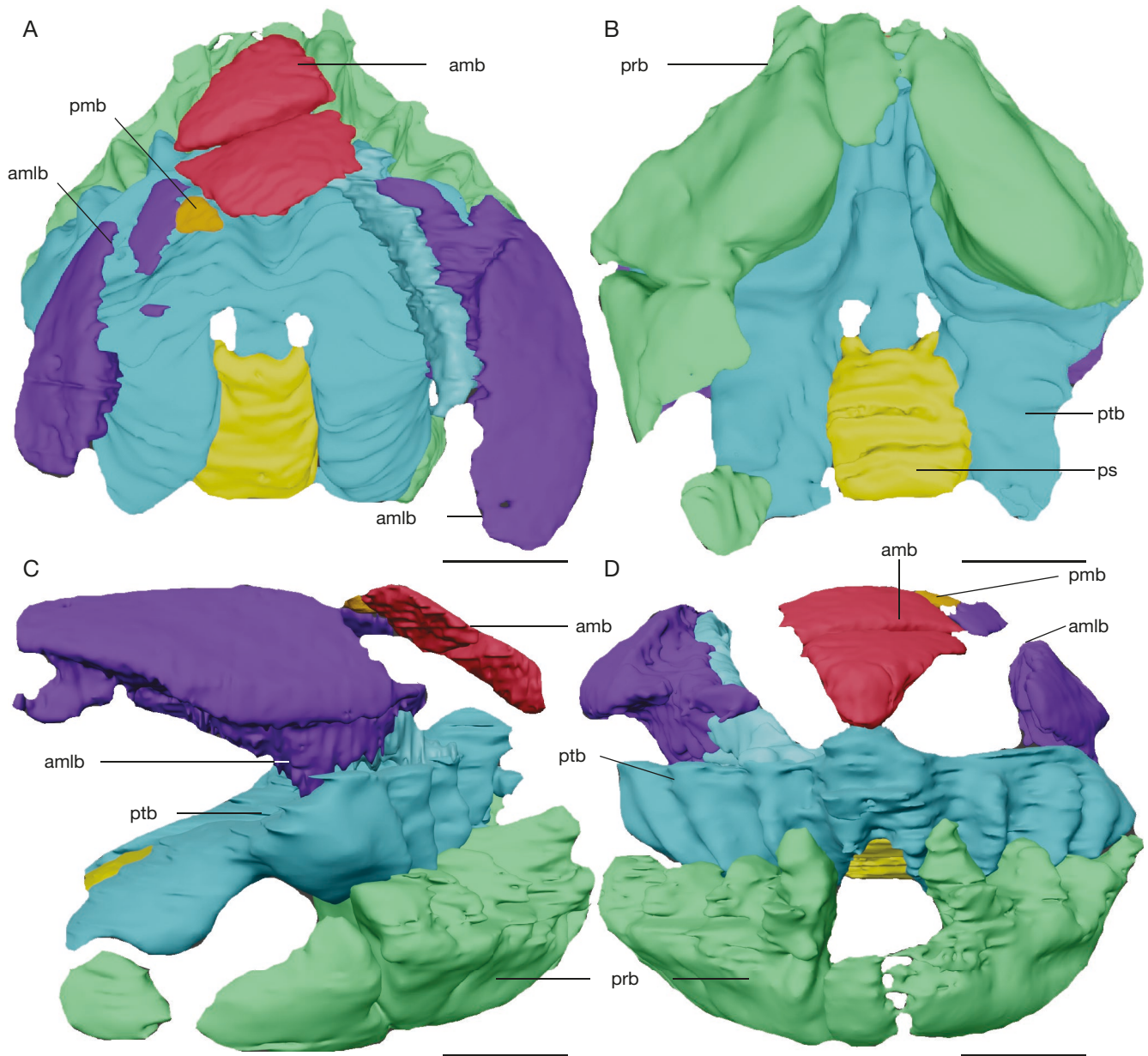


FIG. 4. — Three-dimensional rendering of the skull of *Rinconodus salvadori* n. gen., n. sp. MAU-PV-LI-613: **A**, rendering in dorsal view; **B**, rendering in ventral view; **C**, rendering in right view; **D**, rendering in frontal view. Abbreviations: **amb**, anterior medial bone; **amlb**, anterior mediolateral bone; **pmb**, posterior medial bone; **prb**, prearticular bone; **ps**, parasphenoid; **ptb**, pterygopalatine bone. **Arrows** point anteriorly. Scale bars: 1 cm.

medial one. The anterior medial bone is pentagonal, slightly longer than wider and tapering forward (Figs 3A; 4A; 5A; 6). According to Kemp (1998) and Cavin *et al.* (2007), the anterior medial bone forms the so-called snout. Both, MAU-PV-LI-612 and MAU-PV-LI-613, have the anteriormost portion of this region broken, making it impossible to know how large the snout is (Fig. 6). Ornamentation of the anterior medial bone consists of grooves with pits that radiate from the center of ossification located near the posterior edge. The anterior medial bone is sutured posteriorly to the posterior medial bone and to the sides with the anterior mediolateral bones.

The posterior medial bone is partially preserved in both skulls, and its morphology is difficult to assess with certainty

(Figs 3A; 4A). However, its outline is based on bone impression in sediment surface (Fig. 5). Posterior medial bone is longer than wider tapering forward. The posterior edge is sinuous being concave in the midline (Fig. 6). Based on the inferred outline, the posterior medial bone seems to be the largest bone of the skull roof. It is sutured anteriorly with the anterior medial bone and towards the sides to the bones of the mediolateral series. No lateral line canals or pores are observed in bones of the medial series.

The mediolateral series of *Rinconodus salvadori* n. gen., n. sp., is composed by two bones: the anterior mediolateral bone and the posterior mediolateral bone. Anterior mediolateral bone represents $\frac{3}{4}$ of the total length of the skull, being

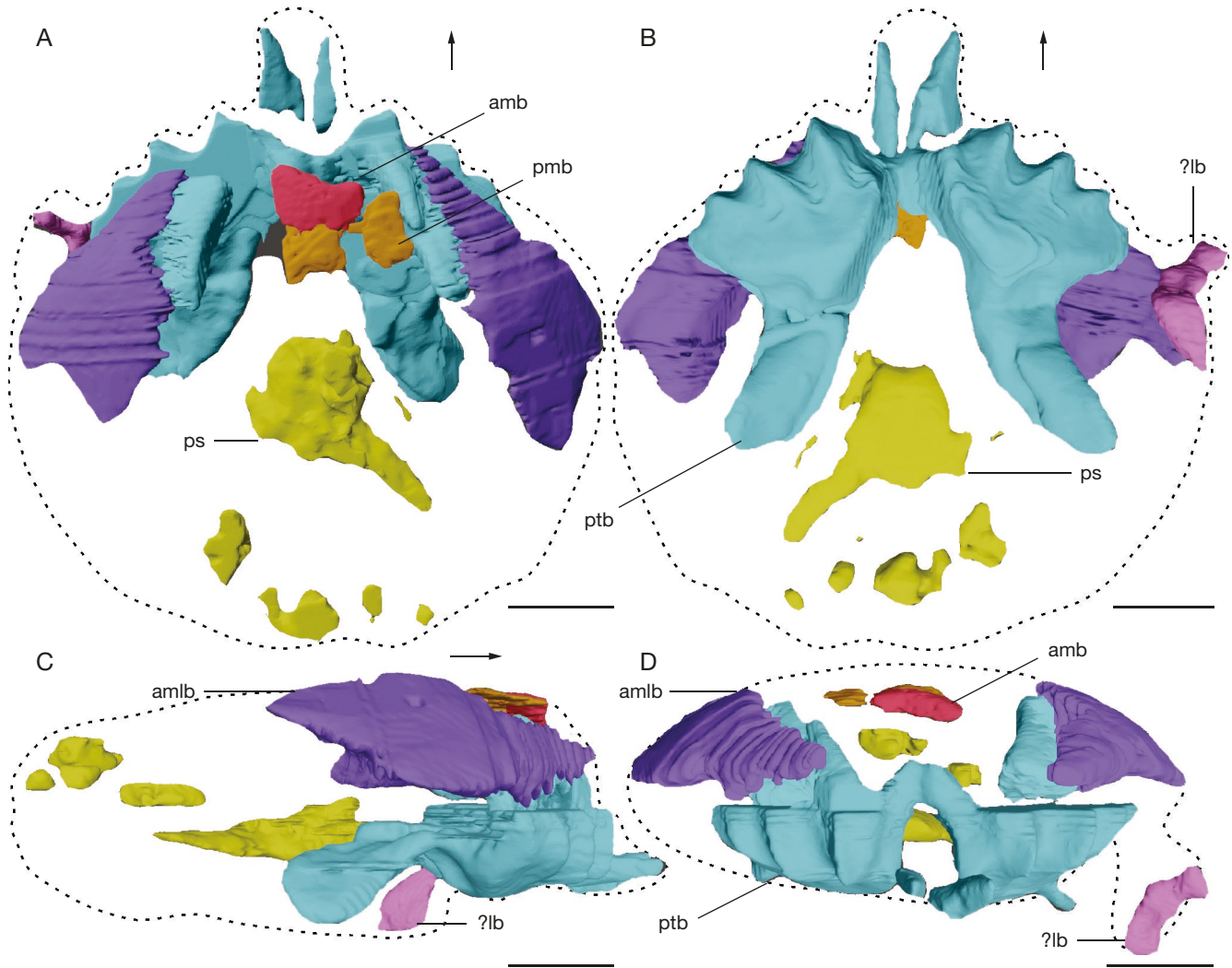


FIG. 5. — Three-dimensional rendering of the skull of *Rinconodus salvadori* n. gen., n. sp. MAU-PV-LI-612: **A**, rendering in dorsal view; **B**, rendering in ventral view; **C**, rendering in right view **D**, rendering in frontal view. Abbreviations: **amb**, anterior medial bone; **amlb**, anterior mediolateral bone; **ps**, parasphenoid; **ptb**, pterygopalatine bone; **pmb**, posterior medial bone; **?lb**, lateral bone?. **Arrows** point anteriorly. **Dotted line** indicates the preserved outline of skull. Scale bars: 1 cm.

longer than wider (Figs 5A, C; 7A-D). The anterior edge is sutured with the anterior medial bone and, the medial edge, with the posterior medial bone.

The concave dorsal margin of the orbit is anteriorly delimited by the anterolateral edge of the anterior mediolateral bone and, posteriorly, by the lateral process of the same bone (Fig. 7A). Posteriorly to the lateral process, there is a small facet for the overlapping suture between the two bones of the mediolateral series (Fig. 7A).

The external surface of the anterior mediolateral bone bears the supraorbital sensory canal of the head lateral-line system. The supraorbital sensory canal has pores and is partially enclosed on the bone (Fig. 7E, F, H-J). The external surface of the anterior mediolateral bone is completely preserved only on the right side of MAU-PV-LI-612 (Fig. 5).

The inner surface of the anterior mediolateral bone bears the descending process that articulates with the ascending process of the pterygopalatine bone, and with the olfactory capsules. The descending process is a mediolateral compressed bone, which is ventro-medially directed

towards the pterygopalatine (Fig. 7G). The descending process is completely preserved only on the right side of MAU-PV-LI-613.

The posterior-mediolateral bone is inferred based on the impression over the sediment. Only MAU-PV-LI-612 preserves fragments of the anterior region of the posterior-mediolateral bone (Fig. 7A).

The lateral series is poorly preserved in both specimens. However, we observed a bone in lateral view of MAU-PV-LI-612 interpreted here as part of the lateral series (Fig. 7B).

Palatine zone and ankylosed upper tooth plates (synonym of pterygopalatine tooth plates)

The upper tooth plates are ankylosed to the pterygopalatine bone (Fig. 8A, B). The upper jaw symphysis is positioned close to the first denticulation of the tooth plates and its surface is oblong in shape. Thus, upper tooth plates are close together (Fig. 8A). Upper tooth plates have five denticulations, and their surface is covered by punctations without a clear pattern of distribution (Fig. 8C).

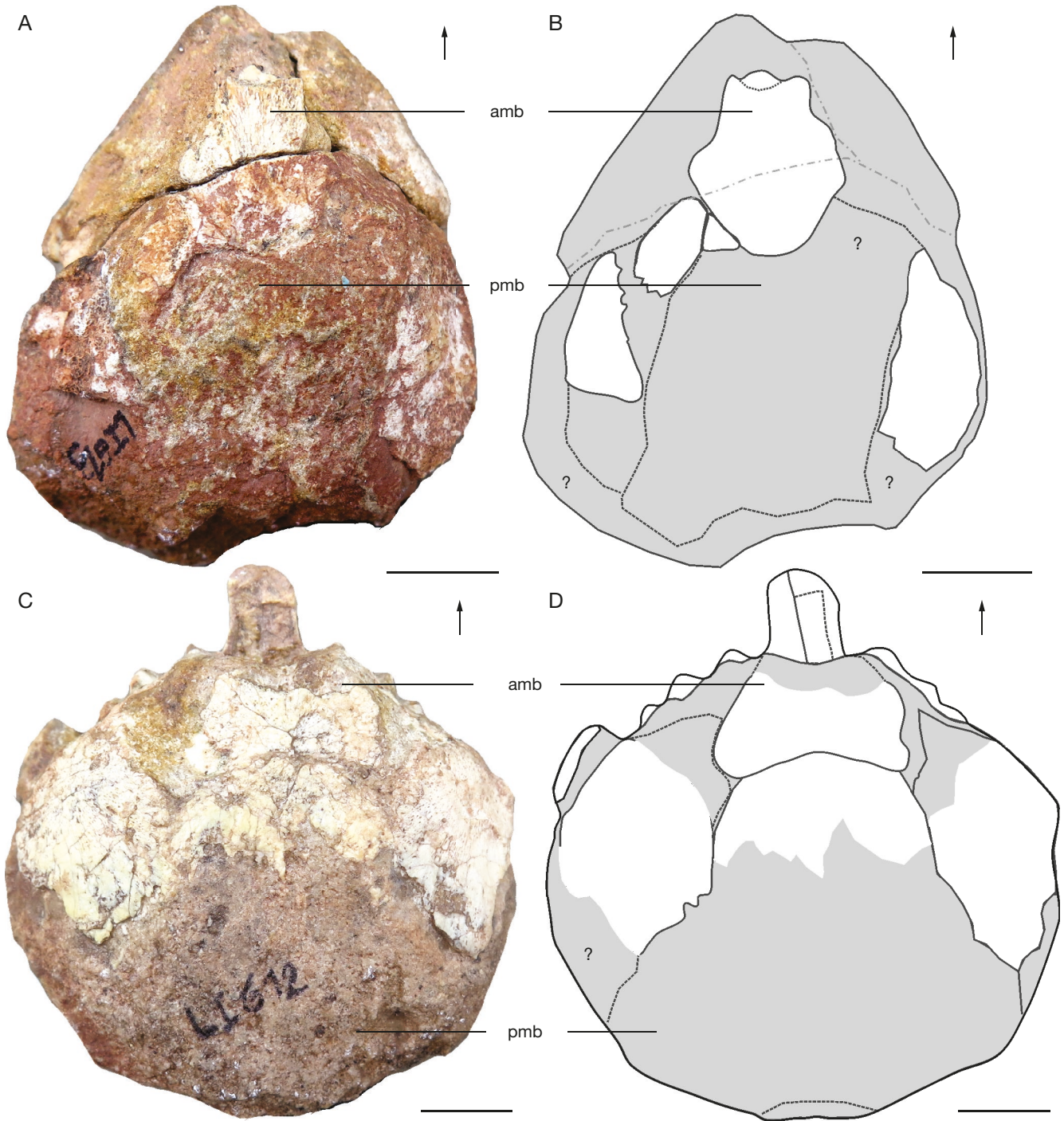


FIG. 6. — Dorsal view of skull roof showing the bones of the medial series of *Rinconodus salvadori* n. gen., n. sp. Original specimens (A, C) and its reconstructions (B, D): **white**, preserved bones; **gray**, sediment; **dark gray**, fractures; **dotted line**, inferred outlines of the bones. **A**, MAU-PV-LI-613, skull in dorsal view; **B**, reconstruction of MAU-PV-LI-613; **C**, MAU-PV-LI-612, skull in dorsal view; **D**, reconstruction of MAU-PV-LI-612. Abbreviations: **amb**, anterior medial bone; **pmb**, posterior medial bone. Question mark (?) bone difficult to interpret. **Arrows** point anteriorly. Scale bars: 1 cm.

The first denticulation is the largest, and it curves laterally (Fig. 8A). The remaining denticulations decrease in size posteriorly and their anterior edges are inclined ventromedially towards the symphysis (Fig. 8A, D). The second cleft is the deepest.

The inner angle of the pterygopalatine tooth plates is located at the level of the second cleft and does not coincide with the posterior tip of the pterygopalatine symphysis

(Fig. 8A). The medial edge of the pterygopalatine tooth plates is longer than the lingual edge and equally curved. While on the medial edge this curvature is homogeneous, on the lingual edge there is a concavity close to the inner angle (Fig. 8F, G).

The enamel, when present, is located over the edges (at the base of the denticulations and clefts) and disposed in bands. The enamel bone junction is leveled around the tooth plate.

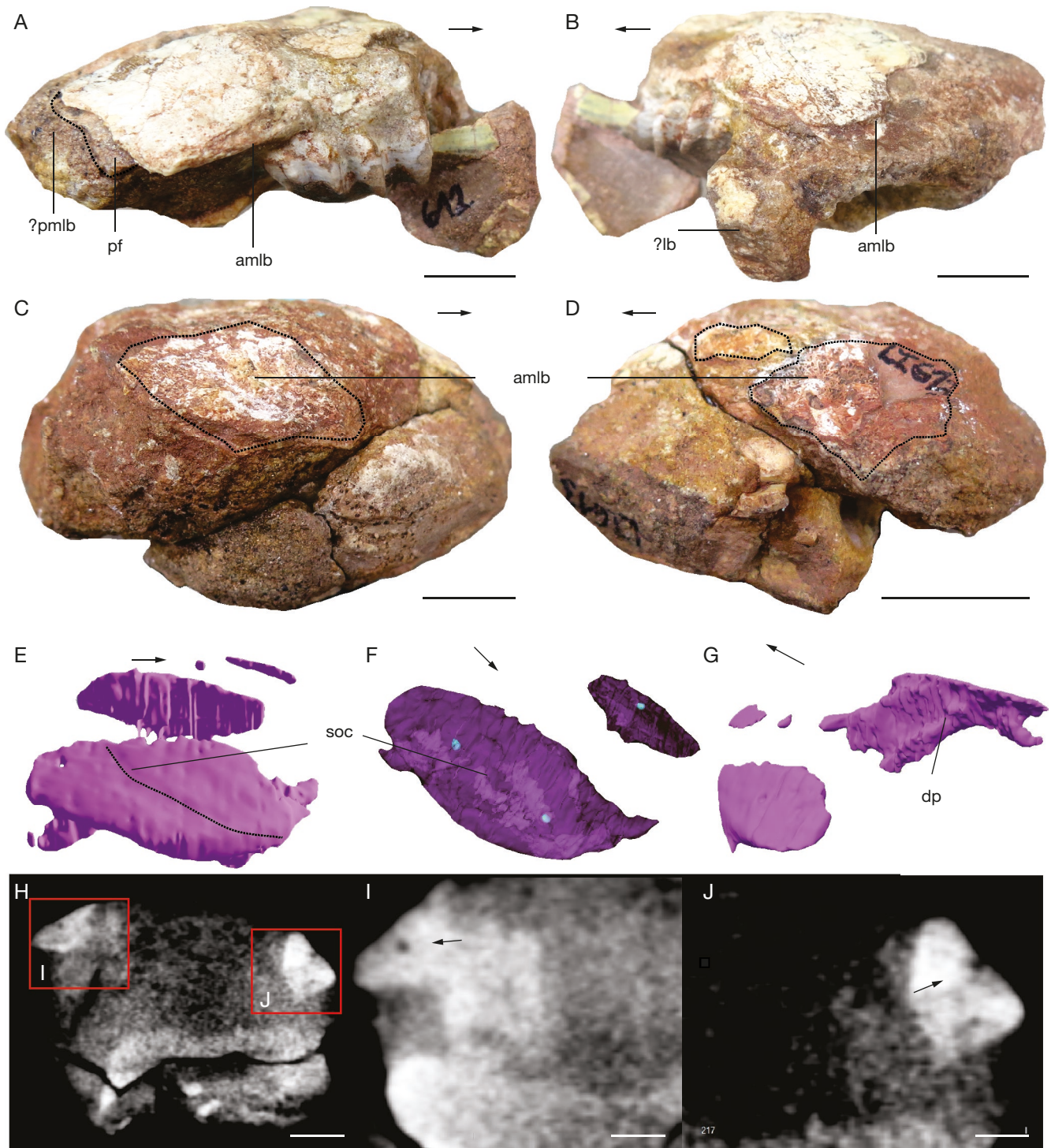


FIG. 7. — Skull roof bones of the mediolateral and lateral series of *Rinconodus salvadori* n. gen., n. sp.: **A**, MAU-PV-LI-612, skull in left view; **B**, MAU-PV-LI-612, skull in lateral right view; **C**, MAU-PV-LI-613, skull in left view; **D**, MAU-PV-LI-613, skull in right view; **E**, mediolateral bone showing the external surface with the supraorbital canal; **F**, mediolateral bone with transparency showing in light-blue parts of the canal pores; **G**, descending process of the mediolateral bone; **H**, tomogram showing the supraorbital sensory canal, red squares are showed in I and J; **I**, amplified area of **H** showing the sensory canal (arrow); **J** amplified area of **H** showing the sensory canal (arrow) partially open. Abbreviations: **amlb**, anterior mediolateral bone; **dp**, descending process of the anterior mediolateral bone; **pf**, posterior facet; **soc**, supraorbital sensory canal; **?lb**, lateral bone of uncertain position; **?pmlb**, impression in sediment of the posterior mediolateral bone. Dotted line indicates the preserved limits of the bones. Arrows point anteriorly. Scale bars: A-H, 1 cm; I, J, 0.2 cm.

In the specimen MAU-PV-LI-612, the enamel extends over the pterygopalatine bone (towards the posterior margin of the medial edge) forming a projection (Fig. 8E). The specimen MAU-PV-LI-613 and the incomplete pterygopalatine

tooth plate MAU-PV-LI-638 do not have such projection. In these (MAU-PV-LI-613 and MAU-PV-LI-638), the area of the inner angle is more prominent due to a concavity on the lingual edge (Fig. 8F, G).

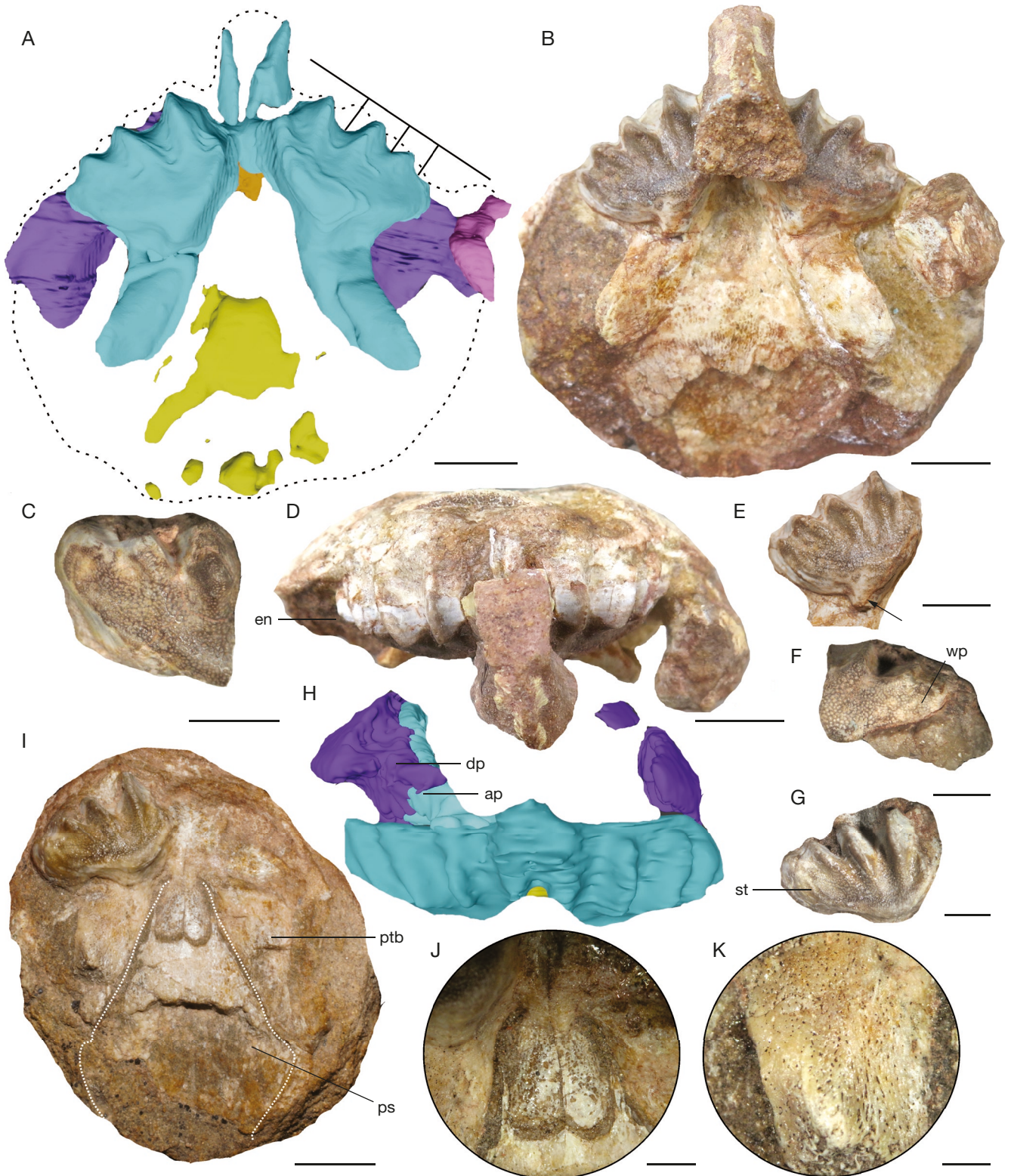


FIG. 8. — Skull roof and palate views of *Rinconodus salvadori* n. gen., n. sp.: **A**, rendering of MAU-PV-LI-612 in palatal view, the lines show the deep of the clefts; **B**, palatal view of MAU-PV-LI-612; **C**, MAU-PV-LI-637 pterygopalatine tooth plate with punctuations; **D**, MAU-PV-LI-612 in frontal view showing the enamel over the tooth plates and the denticles of the tooth plates; **E**, detail of MAU-PV-LI-612 showing the overgrowth of the enamel (arrow) over the pterygopalatine bone; **F**, MAU-PV-LI-638 incomplete pterygopalatine tooth plate showing the wear pattern on the step area; **G**, MAU-PV-LI-613 detail of pterygopalatine tooth plate showing the step; **H**, MAU-PV-LI-613 rendering of pterygopalatine bones and tooth plates in frontal view, note that the ascending process is evident at the base of the second denticulation; **I**, MAU-PV-LI-613 in palatal view; **J**, detail of MAU-PV-LI-613 showing the bilobed structure; **K**, detail of MAU-PV-LI-613 showing the ornamentation of the pterygopalatine bone. Abbreviations: **ap**, ascending process; **dp**, descending process of the anterior mediolateral bone; **en**, enamel; **ps**, parasphenoid; **ptb**, pterygopalatine bone; **st**, step; **wp**, wear pattern. Scale bars: A, B, D, E, I, 1 cm; C, F, G, 0.5 cm; J, K, 0.25 cm.

The wear produced during life is evident on: i) the occlusal surface (as wear patterns); ii) the plateau area; and iii) the posterior surface of the ridges (as wear facets). The wear pattern over the occlusal surface is represented by small circumferences on the posterior area of the tooth plate (Fig. 8F). On the plateau area, wear generates a concavity, where a positive structure of the lower tooth plates occludes. Due to this concavity, the mediolingual edge and the area of the ridges are elevated (Fig. 8B, G). In the specimen MAU-PV-LI-613, the fifth ridge forms an incipient step (Fig. 8G).

The crests in profile are rounded and may have denticles (Fig. 8D). The presence of denticles shows earlier ontogenetic stages in relation to individuals who do not possess them. Denticles are observed in MAU-PV-LI-612.

The ascending pterygopalatine process is located at the level of the second denticulation. The ascending pterygopalatine process is caudally directed as in many dipnoans (see Kemp 1998) and located medially to the descending process. It is observed complete only in the segmentation of MAU-PV-LI-613 (Fig. 8H).

The pterygopalatine bone curves slightly at its medial edge. The curving forms an acute angle in relation to the lingual edge of the tooth plate. The pterygopalatine bone shows ornamentation over the surface in the form of grooves with pits (Fig. 8I-K).

Caudal to the symphysis of the pterygopalatine bone there is a bilobated lamina of bone. Between the two lobes there is a suture which is continuous to the symphysis of the pterygopalatine bones (Fig. 8I-J). On the sides of the lobes there are two long and narrow concavities filled with sediment (Figs 4B; 8I, J). The bilobated ossification is observed only in MAU-PV-LI-613.

The parasphenoid is located medially to the pterygopalatine bones and in contact with them; it is part of the base of the braincase forming most of the bony palate. The preserved anterior portion has a rhomboidal shape (Fig. 8B, I).

Lower jaw and ankylosed lower tooth plates (synonym of prearticular tooth plates)

The lower tooth plates are ankylosed to the pterygopalatine bone (Fig. 9A, B). The lower jaw symphysis is narrow and straight, and has a well-developed anterior symphyseal process. Thus, lower tooth plates are distant from each other (Fig. 9A). The prearticular bone has the prearticular canal divided by the Ruge's ridge, which delimits a shallower anterior and a deeper posterior concavity (Fig. 9B, C).

Externally, and covering the posterior area of the prearticular, there are small fragments of bones that are difficult to interpret (Fig. 7D). However, by position, they could be fragments of the angular bone. The bones of the lower jaw have the same ornamentation present on the bones of the upper jaw (Fig. 9J, K).

The lower tooth plates have four denticulations, and their occlusal surface is covered by punctations with no pattern of distribution (Fig. 9D, E). Denticulations decrease in length posteriorly, being the first one straight and thin (Fig. 9A, D). The inner angle of the prearticular tooth plates is located at the level of the first denticulation (Fig. 9A), the second cleft

seems to be the deepest. The medial edge is longer than the lingual edge, both equally curved (Fig. 9A). The enamel is located over the edges and arranged in bands (Fig. 9F). The enamel bone junction is leveled.

The wear produced during life is evidenced on: i) the occlusal surface (as wear patterns); ii) the plateau area; and iii) the anterior facets of the ridges. The first ridge has a wear facet on its anterior side (Fig. 9E). This generates a concavity and an elevated flange towards the medial edge. The anterior sides of the denticulations have facets product of wear. Due to wear, the enamel of the anterior surface of the denticulation is reduced, while the posterior surface of the denticulation retains the enamel (Fig. 9G, H). On the plateau area, wear generates a convex surface that occludes on the concavity of the pterygopalatine tooth plates (Fig. 9I). This surface is not markedly convex as in other Argentinian dipnoans. The patterns of wear during life are in form of small circles evidenced on the mediolingual edge and on the furrows (Fig. 9I).

The fourth ridge generates the spur. This structure is formed by the wear of the fourth ridge leaving the lingual edge elevated. The spur occludes against the step of the upper tooth plates (Fig. 9A, B).

Vertebral column and associated structures

MAU-PV-LI-630 consists of an incomplete specimen representing a section of the caudal region (Fig. 10A, B), measuring 15 cm in length. The space occupied by the functional notochord is preserved and centra are represented only by arcocentra (Arratia *et al.* 2001).

The neural arches are badly preserved, and they articulate distally with the supraneural bones. The supraneurals have their proximal ends expanded, and articulate distally with the thicker dorsal radials (Fig. 10B). Both, supraneurals and dorsal radials, have a general rod shape and are ornamented with grooves and pits.

Ventrally to the notochord a bone is interpreted, following Arratia *et al.* 2001, as the haemal arches fused with the haemal spines. Distally, the haemal arches articulate with the infrahaemal bones. Although all the haemal arches and the infrahaemal bones are incomplete, fragments and impressions in sediment allow the interpretation of the morphology of these elements. The haemal arches and the infrahaemal bones are rod shaped and have their proximal and distal ends widened. The segmented fin rays are preserved in certain areas of the counterpart material (Fig. 10C).

Scales

Body scales are badly preserved, and their actual morphology remains unclear. Body scales appear to have two types of ornamentation. These consist of: i) a reticulated pattern of ridges separated by interconnected grooves with pores (Fig. 10D, E); and ii) isolated tubercles (Fig. 10D, F). The presence of tubercles is consistent with the overlapped anterior field of the scale, while the reticulated pattern is consistent with the exposed posterior field of the scale (see Cavin *et al.* 2007; contra Marshall 1988 and Mondéjar-Fernández & Clément 2012) (Fig. 10D).

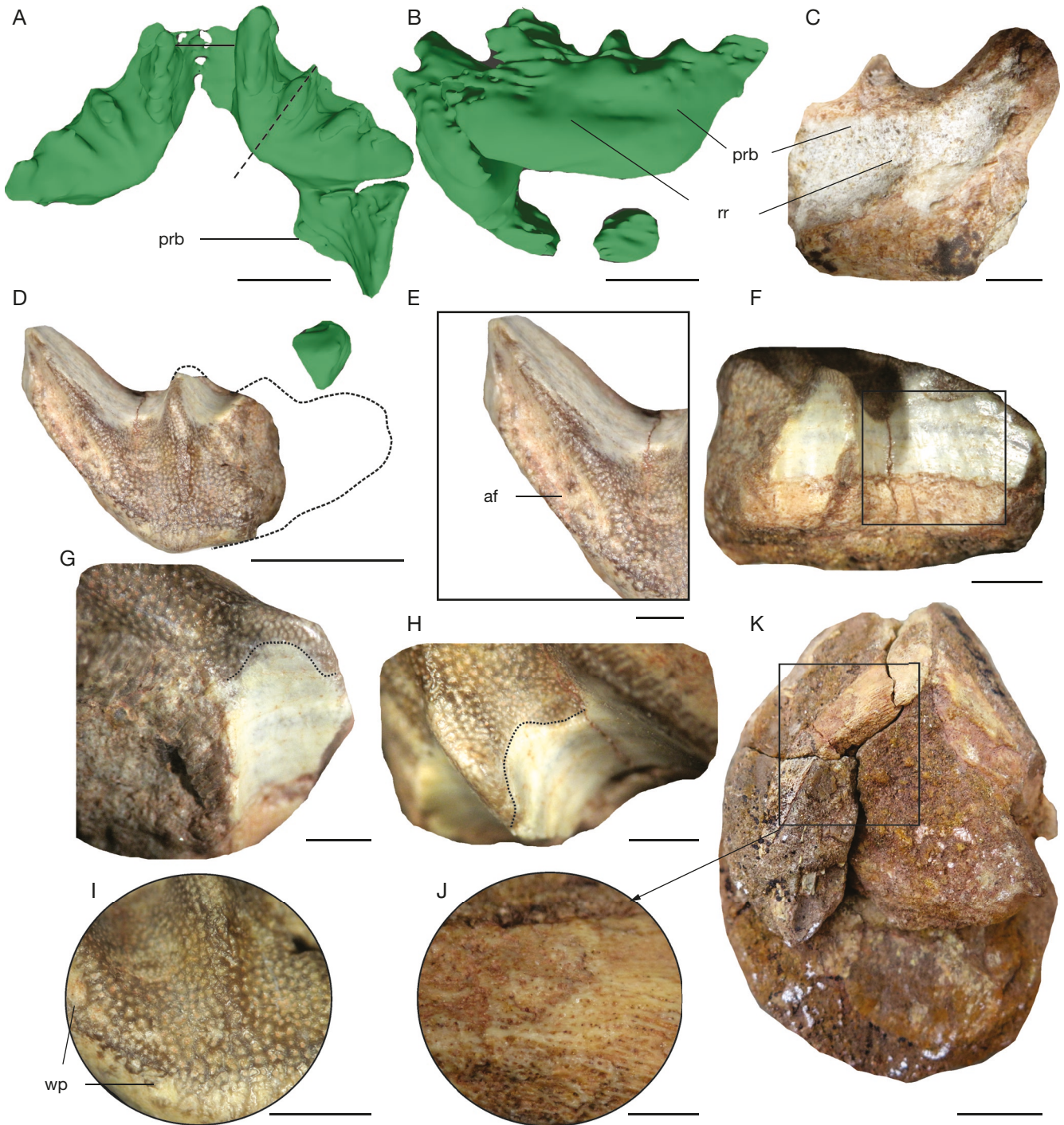


FIG. 9. — Lower jaw bones and prearticular tooth plates of *Rinconodus salvadori* n. gen., n. sp.: **A**, MAU-PV-LI-613, rendering of the prearticular bone with tooth plates: in **discontinuous line**, the level of the inner angle; in **continuous line**, the width separation between tooth plates; **B**, MAU-PV-LI-613 rendering of the prearticular bone in labial view with the prearticular canal divided by the Ruge's ridge; **C**, MAU-PV-LI-612 prearticular tooth plate in labial view with the prearticular canal divided by the Ruge's ridge; **D**, detail of MAU-PV-LI-612 lower tooth plate with ankylosed bone showing the base first denticulation; **E**, MAU-PV-LI-612, detail showing the anterior facet of the first ridge; **F**, detail of MAU-PV-LI-612 showing the bands of enamel in labial view; **G**, detail of MAU-PV-LI-612 showing the posterior facet of the second denticulation, with enamel; **H**, detail of MAU-PV-LI-612 showing the anterior facet of the second denticulation without enamel; **I**, MAU-PV-LI-612 detail of the wear pattern on the mediolingual edge and over the furrows; **J**, MAU-PV-LI-613 detail of the prearticular bone showing the ornamentation; **K**, MAU-PV-LI-613 in ventral view. Abbreviations: **af**, anterior facet; **prb**, prearticular bone; **rr**, ridge of Ruge's ridge canal; **wp**, wear pattern. Scale bars: A, B, D, K, 1 cm; C, E-J, 0.2 cm.

DISCUSSION

The anatomical studies allow to assign the material from Bajo de la Carpa Formation to a new genus and species, *Rinconodus*

salvadori n. gen., n. sp. Following Martin 1982a, b, this new taxon belongs to the family Ceratodontidae due to its long posterior bone in the medial series, and its rounded denticulations in the tooth plates. However, this family has not been

recovered as a monophyletic group in recent phylogenetic analyses (Kemp *et al.* 2017).

The new species exhibits a unique combination of morphological characters among other ceratodontid dipnoans (e.g. medial series with two bones, mediolateral series with two bones and at least one bone in the lateral series, anterior medial bone without sensory canals, upper tooth plates with five denticulations, lower tooth plates with four denticulations, medial edge of tooth plates longer than the lingual edge and equally curved). Being aware of the difficulty of establishing homologies between the skull roof bones of dipnoans (see material and methods section), comparisons will be made following the topographic criterion of Cavin *et al.* 2007.

Rinconodus salvadori n. gen., n. sp. has two bones in the mediolateral series and two bones in the medial series. As an evolutionary trend, dipnoans tend to reduce the number of skull roof bones and lose paired bones (Westoll 1949; Miles 1977; Clack *et al.* 2011) towards recent species. Thus, Paleozoic and some Triassic species (Lehman 1966; Kemp 1993) have many bones in their series with some bones of the medial series being paired, while in the cranial roof of Cenozoic species there are less bones and they are unpaired in the medial series (Kemp 1998: figs 1-9).

The skull roof of *Rinconodus salvadori* n. gen., n. sp. has a roughly rounded general shape, similar to that of *Ceratodus sturii* Teller, 1891; *Namatozodia pitikanta* Kemp, 1993, and *Potamoceratodus guentheri* (Marsh, 1878). The previously mentioned species (and putative in *R. salvadori* n. gen., n. sp.) share a rostrum (or pseudorostrum) due to the narrowing of the most anterior skull bones. A different condition is observed in dipnoans with a square skull roof, like the species *Ptychoceratodus serratus* Schultze, 1981, *Feragnoceratodus martini* Cavin, Suteethorn, Buffetaut & Tong, 2007; *Ferganoceratodus annekepa* Cavin, Deesi & Chanthasi, 2020, and *Arganodus atlantis* Martin, 1979, where no rostrum is observed.

The dipnoan Mesozoic reports include specimens from the Lower Triassic from Africa, Asia, and Australia, and from the Upper Triassic to Upper Cretaceous from Africa, Asia, Europe, and North America. Most of the Argentinian dipnoans, including the skull here described, come from Cretaceous deposits. In previous works, Patagonian dipnoans have been related to Cretaceous species of Madagascar (Martin 1981b, 1982b; Schultze 1991; Cione *et al.* 2007) but, as most of the dipnoan skull roofs known so far, those of Madagascar come from Triassic deposits. These are: the ceratodontid *Paraceratodus germaini* Lehman, Chateau, Laurain & Nauche, 1959, and the gnathorhizid *Beltanodus ambulobensis* Schultze 1981, both from the Lower Triassic of Sakamena Formation. Contrary to *R. salvadori* n. gen., n. sp., *Paraceratodus germaini* has three bones in the medial series and five in the mediolateral series (Fig. 11A, B), while *Beltanodus ambulobensis* has paired bones in the medial series and more than two bones in the mediolateral series (Martin 1981b: fig. 1c, d) (Fig. 11C).

The ceratodontid *Microceratodus angolensis* Teixeira, 1949, from the Lower Triassic of the Cassange series, Lutoa (Angola), has the bones of the skull roof ornamented with fine tubercles (Martin 1981a, b). *M. angolensis* differs from *Rinconodus*

salvadori n. gen., n. sp. in having more bones (three) in the medial and mediolateral series. Both species have no paired bones in the medial series (Lehman 1966; Antunes *et al.* 1990) (Fig. 11D).

Other dipnoans with skull material come from the Lower Triassic of Australia. These are: *Gosfordia truncata* Woodward, 1890 from the Gosford Formation, New South Wales, *Ariguna formosa* Wade, 1935 from deposits at Brookvale, New South Wales, *Aphelodus anapes* from the Blina Formation, Western Australia and *Namatozodia pitikanta* from the Arcadia Formation, Western Australia. Kemp (1994) described the first two species, which consist of cranial and postcranial material. Compared to *Rinconodus salvadori* n. gen., n. sp., *G. truncata* has more bones (three) in the mediolateral series and a longer anterior medial bone (Kemp 1994: fig. 1) (Fig. 11E). *Rinconodus salvadori* n. gen., n. sp. has two bones of different size in the medial series. Contrary to that, the ceratodontid *A. formosa* has the posterior part of the skull (reaching the posterior area of the orbits) covered by scales and at least two oval bones (possibly more) similar in size in the medial series (Kemp 1994: fig. 2).

The gnathorhizid *Namatozodia pitikanta* is a dipnoan with a rounded short skull (7 mm in length) and fragile bones. *Namatozodia pitikanta* is similar to juveniles of the species *Neoceratodus forsteri*, but the skull is well mineralized and completely developed (Kemp 1993: figs 3, 4). *Namatozodia pitikanta* has three bones (one of them paired) in the medial series and a more rounded skull than *R. salvadori* n. gen., n. sp. The other Triassic species from Western Australia is the sagenodont *Aphelodus anapes* Kemp, 1993, represented by tooth plates with associated jaw bones and isolated bones of the medial series of the skull roof. Compared to *Rinconodus salvadori* n. gen., n. sp., *Aphelodus anapes* has at least two rounded and similar-sized bones in the medial series (Kemp 1993: fig. 2).

The species *Asiatoceratodus sharovi* Vorobyeva, 1967 from the Lower Triassic Madygen Formation (Kyrgyzstan), is an asiaticoceratodontid with two bones in the medial series and two bones in the mediolateral series (Vorobyeva 1967). *Asiatoceratodus sharovi*, shares the same number of bones in the medial and mediolateral series with *R. salvadori* n. gen., n. sp. However, *A. sharovi* has a bigger anterior medial bone and the anterior portion of the posterior medial bone narrower than that present in *R. salvadori* n. gen., n. sp. (Fig. 11F).

The ceratodontid *Ceratodus sturii* Teller, 1891 from the Upper Triassic, Lunz Formation, Lunz (Austria), differs from *Rinconodus salvadori* n. gen., n. sp. in having strong ornamented bones and crenulated sutures (Lehman 1975; Martin 1982c; Teller 1891: fig. 2) (Fig. 11G). Both species share the same number of bones in the medial (two) and mediolateral (two) series.

The arganodontid *Arganodus atlantis* from the Upper Triassic Timezgadiouine Formation, Argana Valley (Morocco), also shares the number of bones (two) in the medial and mediolateral series with *Rinconodus salvadori* n. gen., n. sp. (Martin 1979: fig. 1). Compared to *R. salvadori* n. gen., n. sp., *A. atlantis* has the bones of the medial series of similar

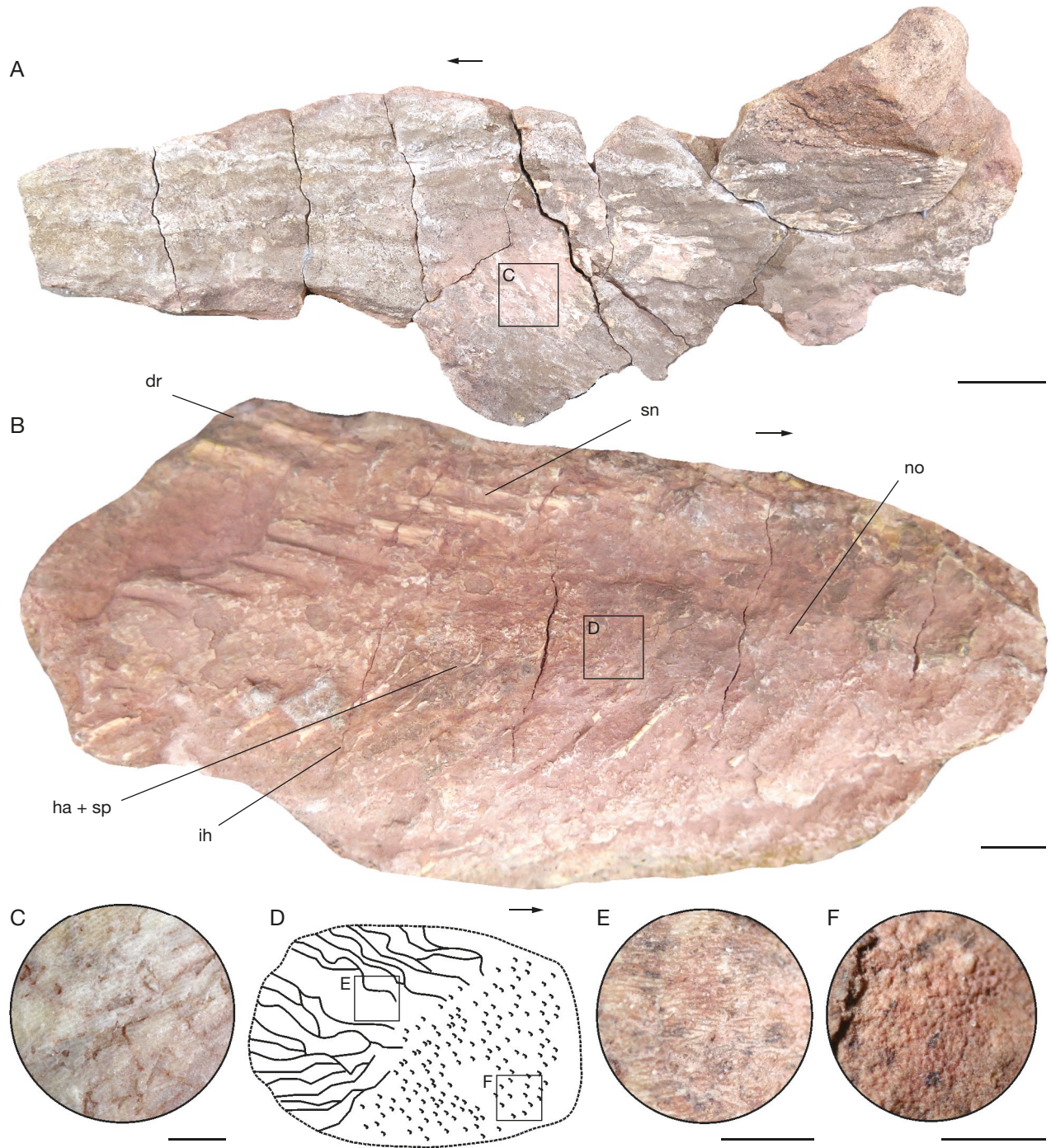


FIG. 10. — Caudal region of the vertebral column of *Rinconodus salvadori* n. gen., n. sp.; the **arrows** point anteriorly: **A, B**, MAU-PV-LI-630 preserved caudal region; **C**, detail of MAU-PV-LI-630 showing the fin rays; **D**, interpretative scheme of a scale showing the anterior overlapped (**F**) and the posterior exposed areas (**E**), modified from Cavin *et al.* 2007; **E**, MAU-PV-LI-630 scale posterior exposed area, note the ornamentation consisting of grooves; **F**, MAU-PV-LI-630 anterior overlapped area, note the ornamentation of tubercles. Abbreviations: **dr**, dorsal radial element; **ha + sp**, haemal arch with the fused haemal spine; **ih**, infrahaemal bones; **no**, notochord; **sn**, supra-neural. Scale bars: A, B, 1 cm; C, E, F, 0.1 cm.

size, with the anterior bone being slightly larger (Martin 1979: fig. 1) (Fig. 11H).

Within the ptychoceratodontids with preserved skull roof material, *Ptychoceratodus serratus* and some *Ferganoceratodus* species are known. *Ptychoceratodus serratus* Agassiz, 1838 from the Lower Keuper of Kupferzell (Germany), differs from *Rinconodus salvadori* n. gen., n. sp. in having a skull

roof with three similar-sized bones (with a fenestra) in the medial series (Schultze 1981: fig. 7; Kemp 1998) (Fig. 11I), and three bones in the mediolateral series.

Ferganoceratodus species with skull roof material comprise: *Ferganoceratodus jurassicus* Nessov & Kaznyshkin, 1985 from the Middle Jurassic of (Kyrgyzstan), *Ferganoceratodus annekeempae* from the Upper Jurassic Phu Kradung Forma-

tion, Phu Noi, (Thailand) and *Ferganoceratodus martini* from the Upper Jurassic, Lower Cretaceous Phu Kradung Formation, Phu Nam Jun, (Thailand). *Ferganoceratodus* species have two bones in the medial series and two bones in the mediolateral series (Cavin *et al.* 2007: fig. 4) (Fig. 11J, K). Compared to *Rinconodus salvadori* n. gen., n. sp., *F. martini* and *F. annekeampe* have the anterior and posterior bone of the medial series more quadrangular in shape (Cavin *et al.* 2007, 2020: fig. 2), and the posterior bone in *F. jurassicus* has a pentagonal shape (the anterior bone in *F. jurassicus* is broken, making it impossible to define the shape, Nessov & Kaznyshkin 1985: fig. 1). Like *R. salvadori* n. gen., n. sp., the species *P. serratus*, *Ferganoceratodus martini*, *Ferganoceratodus jurassicus*, and *Ferganoceratodus annekeampe*, have skull roof bones with faint lines radiating from the ossification center (Schultze 1981; Cavin *et al.* 2007).

The ceratodontid *Potamoceratodus guentheri* (Marsh, 1878) from the Upper Jurassic Morrison Formation, Colorado (United States) has two bones in the medial series with a small rostrum, and two bones in the mediolateral series (Pardo *et al.* 2010: fig. 1b; Fig. 11L). *Potamoceratodus guentheri* differs from *R. salvadori* n. gen., n. sp. in having the anterior medial bone elongated and the posterior medial bone more laterally expanded at the posterior end. Also, *Potamoceratodus guentheri*, has the base of the pterygopalatine process bilobated, while in *R. salvadori* n. gen., n. sp. it is circular (Kirkland 1987: fig. 4a). However, *Rinconodus salvadori* n. gen., n. sp. is more similar to *P. guentheri* than to other Mesozoic dipnoans with preserved skull roof in: the rounded shape of the skull, the two bones in the medial series and the two bones in the mediolateral series, the narrowing of the anterior bone of the medial series which forms a rostrum (possible in *R. salvadori* n. gen., n. sp.), and the number of denticulations in the tooth plates (five in pterygopalatine tooth plates and four in prearticular tooth plates).

Palatine zone and tooth plates

In the palatine zone of *Rinconodus salvadori* n. gen., n. sp. (only in MAU-PV-LI-613) there is a bilobated ossification in front the parasphenoid and behind the pterygopalatines. Similar structures in both fossil and extant dipnoans have not been found. In *Lepidosiren paradoxa* and *Protopterus* species the area of the pterygopalatine symphysis extends slightly posteriorly (Criswell 2015: fig. 21a-d). Here we interpret the bilobated structure as a marked posterior prolongation of the pterygopalatine symphysis. However, other interpretations cannot be excluded until new specimens are found. Regarding the overgrowth of enamel in the tooth plate of MAU-PV-LI-613, here it is interpreted as an hyperplasia. Similar anomalies have been recorded in dipnoan tooth plates from Australia and the Cretaceous of Patagonia (Kemp 2005: fig. 8D; Panzeri & Muñoz 2022).

Rinconodus salvadori n. gen., n. sp. has subtriangular tooth plates with five denticulations in upper tooth plates and four denticulations in lower tooth plates. This condition differs from that observed in other dipnoan species such as *Arganodus atlantis*, *Ceratodus sturii*, *Paraceratodus germaini*, and

Ptychoceratodus serratus (Teller 1891; Lehman *et al.* 1959; Martin 1979; Schultze 1981). The species *Potamoceratodus guentheri* and *Ceratodus molossus* Frederickson & Cifelli, 2017 from North America, have an equal number of denticulations as *R. salvadori* n. gen., n. sp. (Frederickson & Cifelli 2017: fig. 2.2; Kirkland 1987: fig. 4a). However, the medial edge of these species is longer than the observed in *Rinconodus salvadori* n. gen., n. sp. The same denticulation number is present in several species (i.e., *Asiatoceratodus sharovi* Vorobyeva, 1967, *Ceratodus shenmuensis* Liu & Yeh, 1960, *Ceratodus szechuanensis* Liu & Yeh, 1960, *Ferganoceratodus annekeampe*, *Ferganoceratodus martini*, *Ferganoceratodus jurassicus* Nessov & Kaznyshkin, 1985, *Ferganoceratodus madagascariensis* Priem, 1924 and *Ptychoceratodus roemeri* Skrzycki, 2015). However, *Rinconodus salvadori* differs from the previous ones in having a longer first denticulation and the medial edge of the upper tooth plates longer than the lingual edge and equally curved.

Regarding the inner angle of tooth plates, *Rinconodus salvadori* n. gen., n. sp. has an acute inner angle, similar to that of *Ceratodus molossus*, *Potamoceratodus guentheri* (Kirkland 1987: fig. 4a; Frederickson & Cifelli 2017: fig. 2.2) and *Ferganoceratodus* species (Cavin *et al.* 2007, 2020). Whereas the species *Ceratodus sturii*, *Arganodus atlantis* and *Ptychoceartodus serratus* (Teller 1891; Martin 1979; Schultze 1981) have upper tooth plates with a more open inner angle than in *Rinconodus salvadori* n. gen., n. sp.

Being the first Argentinian material recovered with an almost complete skull, the comparisons with the remaining species of Argentinian dipnoans are limited to the pterygopalatine, and the prearticular bones, and the ankylosed tooth plates. Since certain traits (e.g. wear during life and variation in angles) may vary during ontogeny, tooth plates of similar ontogenetic stages (established according to the criterion of Kemp (2005)) are compared here. *Rinconodus salvadori* n. gen., n. sp. differs from the remaining Argentinian dipnoans by having a unique combination of characters, e.g. tooth plates that reach medium size; rounded crests and ridges but slender denticulations; medial edge longer than the lingual edge; first ridge of the upper tooth plates slenderer than the lower one, and slightly curved; straight first ridge of the lower tooth plates straight with a marked anterior facet.

Like the other species in Argentina, *Rinconodus salvadori* n. gen., n. sp. has five denticulations in upper tooth plates and four denticulations in lower tooth plates (Fig. 11M) (Apesteguía *et al.* 2007; Cione *et al.* 2007; Cione & Gouiric-Cavalli 2012; Panzeri *et al.* 2020). The upper tooth plates of *Rinconodus salvadori* n. gen., n. sp. have an acute inner angle. The other species from the Río Colorado subgroup of the Neuquén Group is *Metaceratodus kaopen* Apesteguía, Agnolin & Claeson, 2007 (Fig. 11N). Contrary to *R. salvadori* n. gen., n. sp., *M. kaopen* has upper tooth plates reaching values of an inner angle (R1-RN) of 100 degrees. Regarding the patterns product of wear, *Rinconodus salvadori* n. gen., n. sp., has tooth plates with small circles on the heel area, the furrows, and the mediolingual border. This wear pattern reflects the inner arrangement of tooth tissues that varies between species (Kemp 2001; Panzeri *et al.* 2022). In most

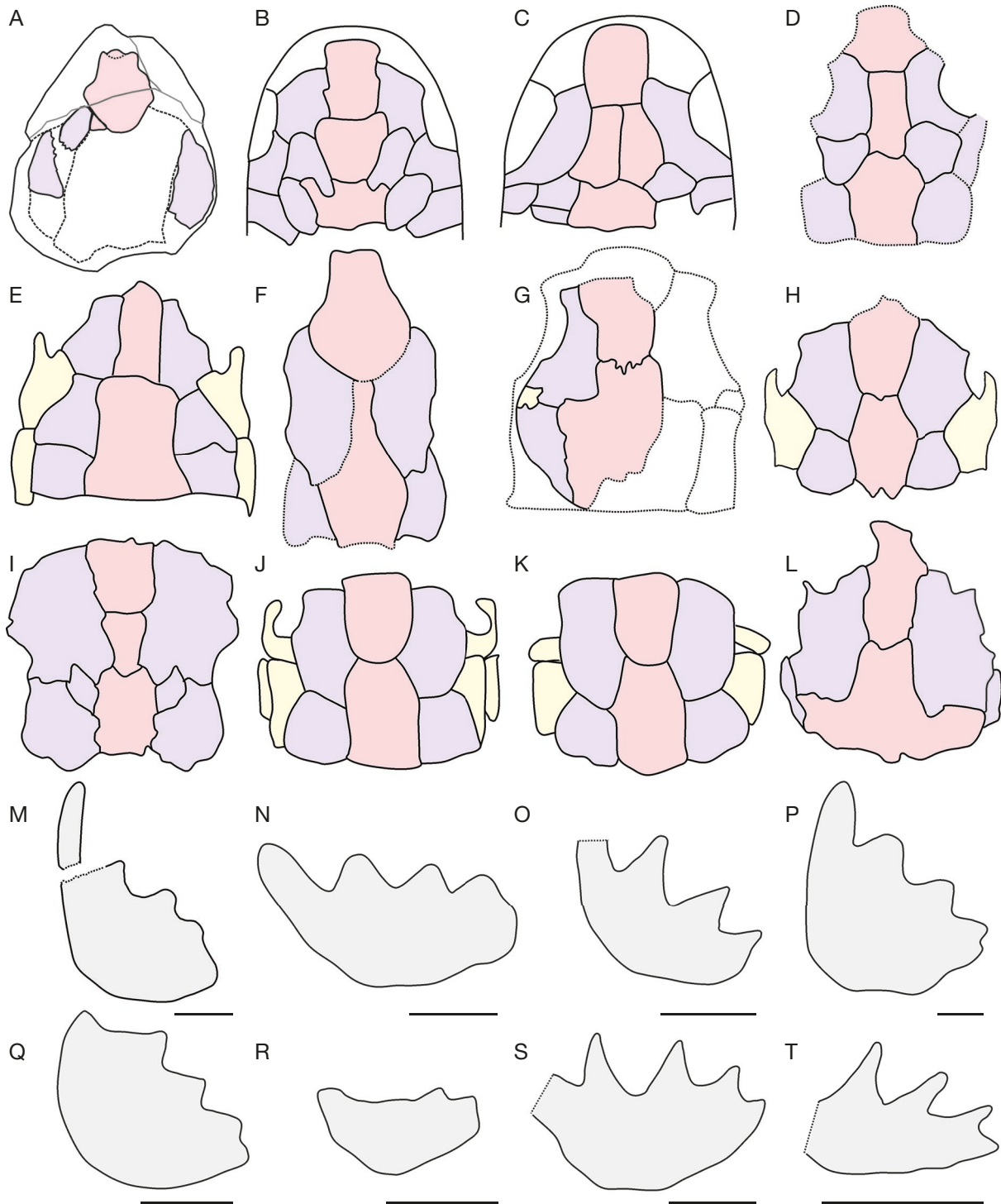


FIG. 11. — Outlines of Argentinian dipnoan tooth plates and diagrams of skull roofs of species mentioned in the text. **Dotted lines** imply the extent of the preservation of incomplete bones, no sensory canals are drawn; **blue**, mediolateral series; **red**, medial series; **yellow**, lateral series. **A**, MAU-PV-LI-613, *Rinconodus salvadori* n. gen., n. sp. skull roof; **B**, *Paraceratodus germaini* Lehman, Chateau, Laurain & Nauche, 1959 skull roof, modified from Martin 1981b; **C**, *Beltanodus ambilobensis* Schultze, 1981 skull roof, modified from Martin 1981b; **D**, *Microceratodus angolensis* (Texeira, 1947) skull roof, modified from Antunes *et al.* 1990; **E**, *Gosfordia truncata* Woodward, 1890, modified from Kemp 1994; **F**, *Asiatoceratodus sharovi* Vorobyeva, 1967 skull roof, modified from Vorobyeva 1967; **G**, *Ceratodus sturii* Teller, 1891 skull roof, modified from Martin 1982c; **H**, *Arganodus atlantis* Martin, 1979 skull roof, modified from Kemp 1998; **I**, *Ptychoceratodus serratus* (Agassiz, 1838) skull roof, modified from Schultze 1981; **J**, *Ferganoceratodus jurassicus* Nessov & Kaznyshkin, 1985 skull roof, modified from Cavin *et al.* 2007; **K**, *Ferganoceratodus martini* Cavin, Suteethorn, Buffetaut & Tong, 2007 skull roof, modified from Cavin *et al.* 2007; **L**, *Potamoceratodus guentheri* (Marsh, 1878) skull roof, modified from Pardo *et al.* 2010; **M**, MAU-PV-LI-612, *Rinconodus salvadori* n. gen., n. sp., left upper tooth plate; **N**, MPCN PV-1-1, *Metaceratodus kaopen* (Apesteguía, Agnolin & Claeson, 2007) right upper tooth plate, the outline was mirrored; **O**, MACN PV RN 157, *Metaceratodus wichmanni* (Apesteguía, Agnolin & Claeson, 2007) left upper tooth plate; **P**, MPEF-PV 11422, *Metaceratodus baibianorum* Panzeri, Gouiric-Cavalli, Muñoz & Cione, 2020 left upper tooth plate; **Q**, *Ceratodus argentinus* Apesteguía, Agnolin & Claeson, 2007 left upper tooth plate; **R**, MCF-PVPH-373, *Chaococeratodus portezuelensis* Apesteguía, Agnolin & Claeson, 2007 right lower tooth plate; **S**, MML 196, *Atlantoceratodus patagonicus* Agnolin, 2010 left upper tooth plate, the outline was mirrored; **T**, MPM-PV-1160-2, *Atlantoceratodus iheringi* (Ameghino, 1899) left upper tooth plate. Scale bars: 1 cm.

of the dipnoans described for Patagonia, this pattern is also observed (on the area of the furrows and mediolingual border as in *Metaceratodus baibianorum* Panzeri, Gouiric-Cavalli, Muñoz & Cione, 2020; mostly on the mediolingual border as in *M. kaopen* (Apesteguía *et al.* 2007) or over the entire surface as in *M. wichmanni* (Apesteguía, Agnolin & Claeson, 2007).

The shape of the first denticulation in upper tooth plates is a unique trait of *Rinconodus salvadori* n. gen., n. sp., which differs from the rest of Argentinian dipnoans. The first denticulation is slightly wide at the base, but towards the tip it becomes thinner and curves towards the back. Contrary, in most Patagonian dipnoans, the first denticulation is wider at the base (see *M. wichmanni*, Fig. 11O) or wider and with a rounded tip (see *M. kaopen*, Fig. 11N, *M. baibianorum*, Fig. 11P, and *Ceratodus argentinus* Apesteguía, Agnolin & Claeson, 2007, Fig. 11Q).

The first denticulation in prearticular tooth plates of *Rinconodus salvadori* n. gen., n. sp. is straight with a deep anterior wear facet. In most of Argentinian dipnoans, the first denticulation is curved, and the tip is sigmoidal with a shallow anterior wear facet (see *Chaoceratodus portezuelensis* Apesteguía, Agnolin & Claeson, 2007 [Fig. 11R], or *Metaceratodus baibianorum*).

On the lingual edge of the tooth plates of *Rinconodus salvadori* n. gen., n. sp., close to the last denticulations, is a resorption or loss of dental material. This is also evident in several remaining species from Argentina, like *Atlantoceratodus patagonicus* Agnolin, 2010 (Fig. 11S), and *Atlantoceratodus iheringi* (Ameghino, 1899) (Fig. 11T). However, the previous species differs from *Rinconodus salvadori* n. gen., n. sp. in having deeper clefts (Fig. 11F-H).

The ornamentation of the pterygopalatine and prearticular bones of *Rinconodus salvadori* n. gen., n. sp. is similar to that present in other species. In *Metaceratodus baibianorum*, the ornamentation forms a framework with positive features that delimits deep negative areas (Panzeri *et al.* 2020). Regarding the form, the pterygopalatine is similar to that present in *Ptychoceratodus cuyanus* Agnolin, Bogan, Egli, Novas, Isasi, Marsicano, Zavattieri & Mancuso, 2016, being elongated and forming a homogeneous curvature along its entire lingual edge.

Vertebral column and associated structures

The vertebral column of *Rinconodus salvadori* n. gen., n. sp. has three bones (neural arch, supraneural and dorsal radial) above the unpreserved notochord and two bones (haemal arch and infrahaemal) below it in each segment. A different number of bones is observed in the species *Gosfordia truncata*, and *Paraceratodus germaini*. The species *Gosfordia truncata* has a caudal section of the vertebral column with probably three bones above and below the unpreserved notochord (Ritchie 1981: fig. 2B). The species *Paraceratodus germaini* shows a more similar condition with the caudal portion of the vertebral column with two bones above the neural arch and the unpreserved notochord (in some areas it has less or more bones), and two bones below it (Lehman *et al.* 1959).

In the species *Asiatoceratodus sharovi*, the most caudal section of the vertebral column was not described in detail (Vorobyeva 1967), but in the reconstruction of the species, the author

interpreted two bones above the unpreserved notochord and three or two below it (Vorobyeva 1967: fig. 3). *Ariguna formosa* is another dipnoan with preserved postcranial material. There is no detailed description of the most caudal bones of the vertebral column and it is not possible to discern them in the figures (Kemp 1994: fig. 3). Finally, *Ferganoceratodus martini*, preserves part of the most anterior portion of the vertebral column. It has numerous ribs and some vertebrae but no haemal arches or infrahaemal bones (Cavin *et al.* 2007).

The outline of the scales of *Rinconodus salvadori* n. gen., n. sp. could not be delimited. However, two patterns of ornamentation (tubercles and reticulum) are observed. As in *R. salvadori* n. gen., n. sp., the scales of the species *Gosfordia truncata* and *Paraceratodus germaini*, have an ornamentation with a reticulated pattern (Ritchie 1981; Lehman *et al.* 1959). In *Ferganoceratodus martini* the scales have both patterns of ornamentation: reticulated and with tubercles (Cavin *et al.* 2007). A different condition is observed in other dipnoans: in *Ariguna formosa* the scales have an ornamentation with fine parallel lines, while in *Asiatoceratodus sharovi* they have longitudinal ridges and growth rings (Vorobyeva 1967: fig. 4).

CONCLUSIONS

The combination of characters observed in the Argentinian material (medial series with two bones, mediolateral series with two bones and at least one bone in the lateral series, an anterior medial bone without sensory canals, faint ornamentation of dermal skull bones, upper tooth plates with five denticulations, lower tooth plates with four denticulations, medial edge of tooth plates longer than the lingual edge and equally curved, among others), allowed us to define and characterize the taxon as belonging to a new species, *Rinconodus salvadori* n. gen., n. sp. This study is relevant because it is the youngest record of a dipnoan from the Mesozoic of Gondwana (and the first record for Argentina) with an almost complete preserved skull roof and postcranial material. In addition, it could have relevance in future phylogenetic studies since tooth plates and skull roof bones are preserved in the same specimen, which is not frequent in the Cretaceous record of dipnoans. As a preliminary result of the comparisons, we conclude that *R. salvadori* n. gen., n. sp. is more similar to *Potamoceratodus guentheri* (both in the configuration of the skull roof and in the shape of the ossifications) than to other Mesozoic dipnoans. However, future phylogenetic analysis may clarify the affinities between *R. salvadori* n. gen., n. sp. and other dipnoans.

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