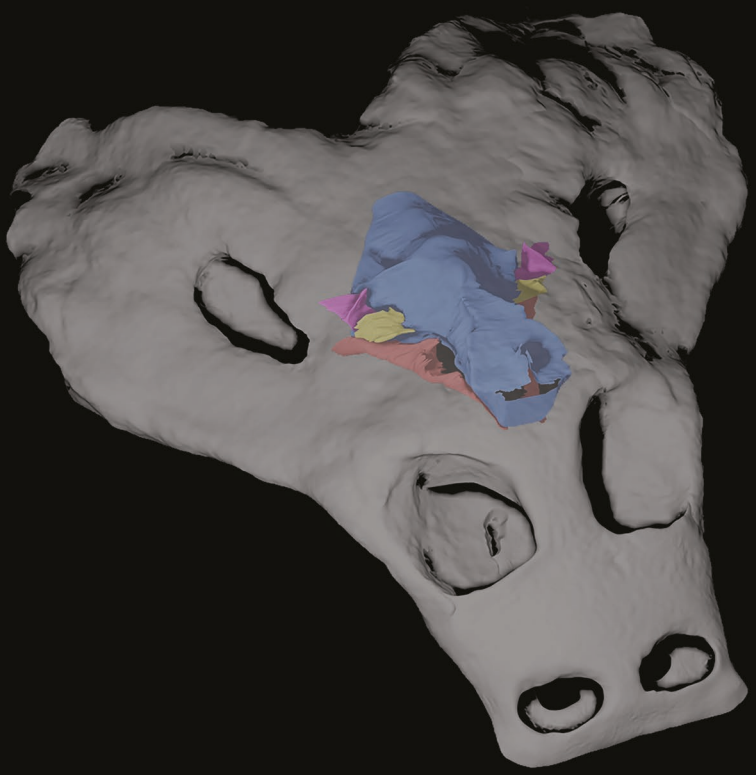
comptes rendus
palevol
2020 • 19 • 10

Braincase and endocranium of the Placodont *Parahenodus atancensis* de Miguel Chaves, Ortega & Pérez-García, 2018, a representative of the highly specialized clade Henodontidae

Carlos DE MIGUEL CHAVES, Alejandro SERRANO, Francisco ORTEGA & Adán PÉREZ-GARCÍA



art. 19 (10) — Published on 7 December 2020
www.cr-palevol.fr

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Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

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ISSN (imprimé / *print*) : 1631-0683/ ISSN (électronique / *electronic*) : 1777-571X

Braincase and endocranium of the Placodont *Parahenodus atancensis* de Miguel Chaves, Ortega & Pérez-García, 2018, a representative of the highly specialized clade Henodontidae

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Submitted on 31 August 2019 | Accepted on 29 November 2019 | Published on 7 December 2020

urn:lsid:zoobank.org:pub:B90B8231-C8AA-40C0-8737-F2A3CD2B6143

De Miguel Chaves C., Serrano A., Ortega F. & Pérez-García A. 2020. — Braincase and endocranium of the Placodont *Parahenodus atancensis* de Miguel Chaves, Ortega & Pérez-García, 2018, a representative of the highly specialized clade Henodontidae. *Comptes Rendus Palevol* 19 (10): 173-186. https://doi.org/10.5852/cr-palevol2020v19a10

ABSTRACT
Parahenodus atancensis de Miguel Chaves, Ortega & Pérez-García, 2018 is a recently described bizarre cyamodontoid placodont, based on a partial but well-preserved Spanish Upper Triassic skull. It was identified as the sister taxon of the German highly specialized *Henodus chelyops* Huene, 1936. The use of micro-computed tomography has been able to significantly increase knowledge of the cranial anatomy of *Parahenodus atancensis* by the characterization of several bones and structures previously unknown for this taxon, as well as to obtain a partial reconstruction of its brain endocast and associated endocranial structures, poorly known in most Triassic sauropterygians. In addition, we identify several synapomorphies of the braincase of Cyamodontoidea so far unknown in Henodontidae, improving knowledge about this clade. The study of the endocranium and neurosensory structures of *Parahenodus atancensis* suggests a relatively lower reliance on vision, the pineal system and the pituitary than in other Triassic sauropterygians.

KEY WORDS
Sauropterygia,
Upper Triassic,
El Atance,
Europe,
neuroanatomy.

RÉSUMÉ
La boîte crânienne et l'endocrâne du Placodont Parahenodus atancensis *de Miguel Chaves, Ortega & Pérez-García, 2018, un représentant du groupe hautement spécialisé Henodontidae.*
Parahenodus atancensis de Miguel Chaves, Ortega & Pérez-García, 2018 est un placodonte cyamodontoïde récemment décrit à partir d'un crâne partiel mais bien préservé du Trias supérieur d'Espagne.

Il a été identifié comme le groupe-frère du taxon allemand hautement spécialisé *Henodus chelyops* Huene, 1936. L'utilisation de la micro-tomographie permet d'améliorer considérablement les connaissances sur l'anatomie crânienne de *Parahenodus atancensis* par la caractérisation de plusieurs os et structures auparavant inconnues chez ce taxon, ainsi que d'obtenir une reconstruction partielle de son cerveau et des structures endocrâniennes associées, peu connus chez les sauroptérygiens du Trias. De plus, nous identifions plusieurs synapomorphies de la boîte crânienne de Cyamodontoidea jusque-là inconnues chez les Henodontidae, améliorant ainsi la connaissance du clade. L'étude du cerveau et des structures neurosensorielles de *Parahenodus atancensis* suggère une dépendance relativement moindre de la vision, du système pinéal et de l'hypophyse par rapport aux autres sauroptérygiens du Trias.

MOTS-CLÉS
Sauropterygia,
Trias supérieur,
El Atance,
Europe,
neuroanatomie.

INTRODUCTION

Placodonts were a clade of mostly-durophagous Triassic sauropterygians that inhabited shallow waters of the Paleotethys Sea; their fossil record ranging from the Anisian (Middle Triassic) to the Rhaetian (Late Triassic) (Rieppel 2000; Neenan *et al.* 2013, 2015; Klein *et al.* 2015). Thus, remains of placodonts have been recovered in Europe (e.g. Rieppel 2000; Klein & Scheyer 2014; Neenan & Scheyer 2014; de Miguel Chaves *et al.* 2018, 2020), the Middle East (Haas 1975; Rieppel *et al.* 1999; Vickers-Rich *et al.* 1999; Rieppel 2002a; Kear *et al.* 2010) and China (Li 2000; Li & Rieppel 2002; Jiang *et al.* 2008; Zhao *et al.* 2008; Neenan *et al.* 2015; Wang *et al.* 2018, 2019). The members of Placodontia show two morphotypes: unarmored placodonts or placodontoids, and armored placodonts or cyamodontoids. Whereas the monophyly of Cyamodontoidea is well established, the phylogenetic relationships within Placodontoidea are still object of debate, being currently considered monophyletic by several authors (Neenan *et al.* 2015; de Miguel Chaves *et al.* 2018), but paraphyletic by others (Wang *et al.* 2018, 2019).

Henodus chelyops Huene, 1936 is a bizarre cyamodontoid placodont exclusively found in the Carnian (Upper Triassic) of Tübingen (Germany) (Huene 1936). It presents some exclusive adaptations that suggest a very specialized trophic niche (i.e., herbivory and filter-feeding), very different to the durophagy of the other members of Placodontia (Reif & Stein 1999; Rieppel 2002b; Naish 2004), and therefore its phylogenetic position has traditionally been problematic. A recently described cyamodontoid placodont from the Upper Triassic fossil site of El Atance (Guadalajara, Spain), *Parahenodus atancensis* de Miguel Chaves, Ortega & Pérez-García, 2018, has been recognized as the sister taxon of *Henodus chelyops* (de Miguel Chaves *et al.* 2018). *Parahenodus atancensis* shares some highly derived characters with *Henodus chelyops*, but it also presents some primitive conditions for other characters, shared with other less derived members of Cyamodontoidea. Thus, the find of *Parahenodus atancensis* provided relevant information about the acquisition of these autapomorphic characters in *Henodus chelyops* and the evolution of the clade Henodontidae (de Miguel Chaves *et al.* 2018).

Although some nothosaurian endocasts were cited but not described at the end of the nineteenth century (Koken 1890, 1893a, b), the first work on the neuroanatomy of the Triassic members of Sauropterygia goes back to the study and description of an endocast of *Nothosaurus mirabilis* Münster, 1834 (Edinger 1921). Several works have focused on the study of the braincase and neurosensory structures of Triassic sauropterygians for almost a century, including nothosauroids (Gorce 1960; Rieppel 1994) and placodonts (Edinger 1925; Hopson 1979; Nosotti & Pinna 1993, 1996; Rieppel 2001; Nosotti & Rieppel 2002). In addition, the use of computed and micro-computed tomographic scanning has been incorporated into the study of the cranial morphology and braincase of this group in recent years (Neenan *et al.* 2013, 2014, 2015; Neenan & Scheyer 2014; Marquez-Aliaga *et al.* 2019; Wang *et al.* 2019). However, a detailed study and reconstruction of the brain and neurosensory and neurovascular structures has only been carried out in the placodont *Placodus gigas* Agassiz, 1833 (Neenan & Scheyer 2012), and in the nothosaur *Nothosaurus marchicus* Koken, 1893 (Voeten *et al.* 2018). The use of micro-computed tomographic scanning has also been recently applied to the reconstruction of the labyrinth of several sauropterygian taxa (Neenan *et al.* 2017).

Thus, we present a detailed description of the skull and braincase of *Parahenodus atancensis* using micro-computed tomography, providing new abundant information on the cranial anatomy of this taxon, highlighting those characters that are not observable in an external view. We also provide a reconstruction of the cranial endocast of *Parahenodus atancensis*, corresponding to the first published three-dimensional reconstruction of a cyamodontoid placodont endocranium and neurosensory structures.

Institutional abbreviation

MUPA–ATZ El Atance collection, Museo de Paleontología de Castilla–La Mancha, Cuenca, Spain.

MATERIAL AND METHODS

The material studied here is the holotype and only known specimen of *Parahenodus atancensis*, MUPA ATZ0104, housed in the Museo de Paleontología de Castilla-La Mancha (Cuenca, Spain). It was found in the Upper Triassic (Carnian to Norian) fossil site of El Atance, in the Municipality of Sigüenza (Guadalajara, Spain) (de Miguel Chaves *et al.* 2018).

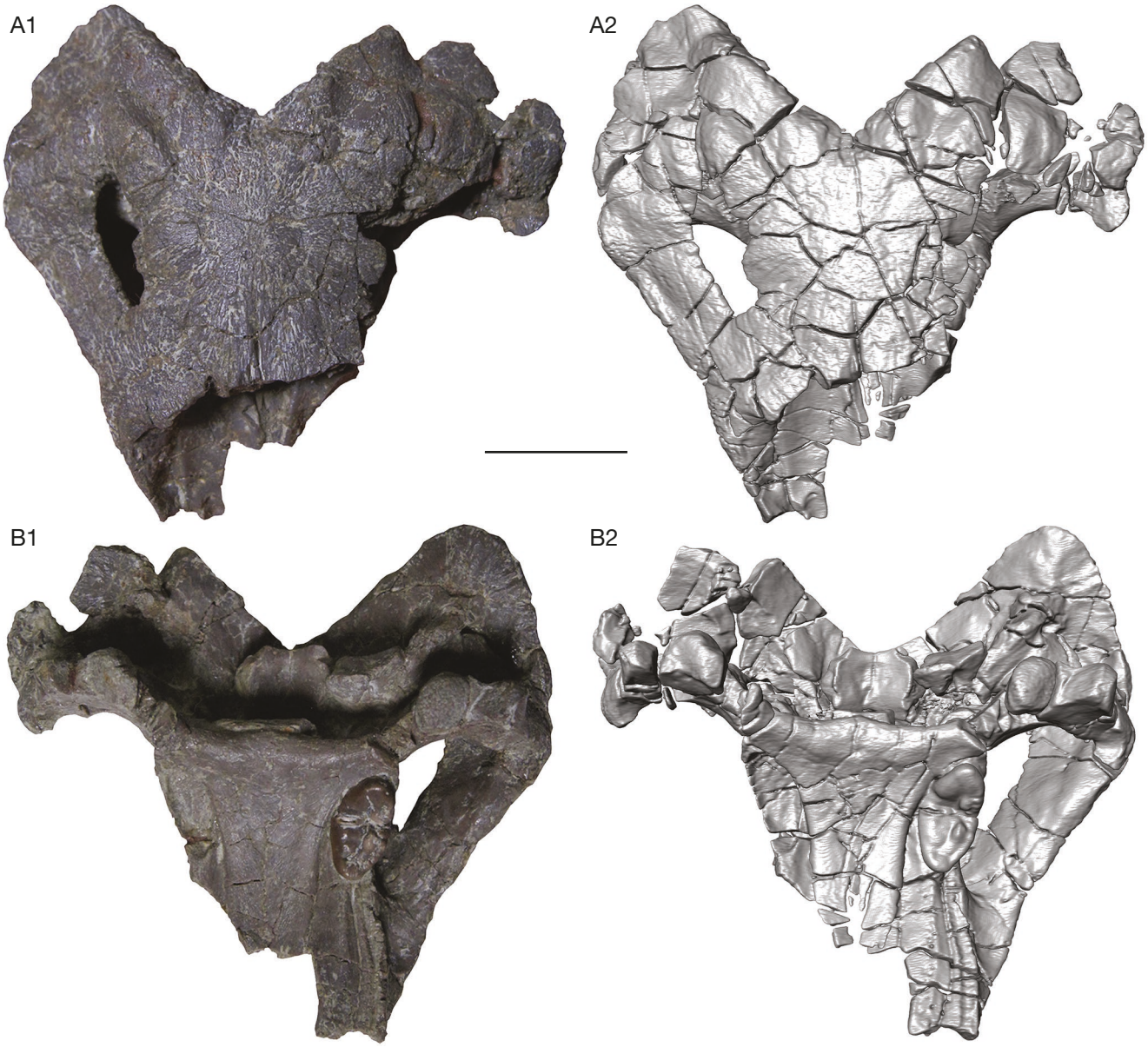

Fig. 1. — MUPA ATZ0104, holotype skull of *Parahenodus atancensis* de Miguel Chaves, Ortega & Pérez-García, 2018, from the Upper Triassic fossil site of El Atance (Guadalajara, Spain): **A1**, photograph of the dorsal view; **A2**, dorsal view of the digital rendering of the skull; **B1**, photograph of the ventral view; **B2**, ventral view of the digital rendering of the skull. Scale bar: 2 cm.

MUPA ATZ0104 is an undeformed partial skull 63 mm long and 73 mm wide, which preserves the parietal table, and the partial right orbit, palate and occiput (Fig. 1). However, it lacks the rostrum, most of the orbits and the left side of the skull table. The skull is internally filled with marl.

MUPA ATZ0104 was scanned with a high resolution scanner Nikon XT H-160, in the Servicio de Técnicas No Destructivas: Microscopía Electrónica y Confocal y Espectroscopía ct-Scan, of the Museo Nacional de Ciencias Naturales (Madrid, Spain). The scanning used a voltage of 152 kV and a current of 49 µA. The inter-slice spacing was 0.08 mm. The raw data were imported to a segmentation and 3D editor software for segmentation, visualization and analysis. An interactive 3D PDF of the skull bones, brain and associated structures is included as Electronic Supplementary Material (Appendices).

RESULTS

New insights into the osseous anatomy of the *Parahenodus atancensis* skull

A detailed description of the external morphology of the holotype of *Parahenodus atancensis* was provided by de Miguel Chaves *et al.* (2018). However, the application of CT technology has allowed us to complete that description by the characterization of the inner morphology of the braincase, in addition to performing the three-dimensional reconstruction of each of the osseous elements preserved in this specimen (Fig. 2).

New osseous information relative to the skull of *Parahenodus atancensis* is described in this section. The quadratojugals contact the complete lateral and dorsolateral surfaces of the quadrates (Fig. 2A, C, E, F). In ventral view, the contact

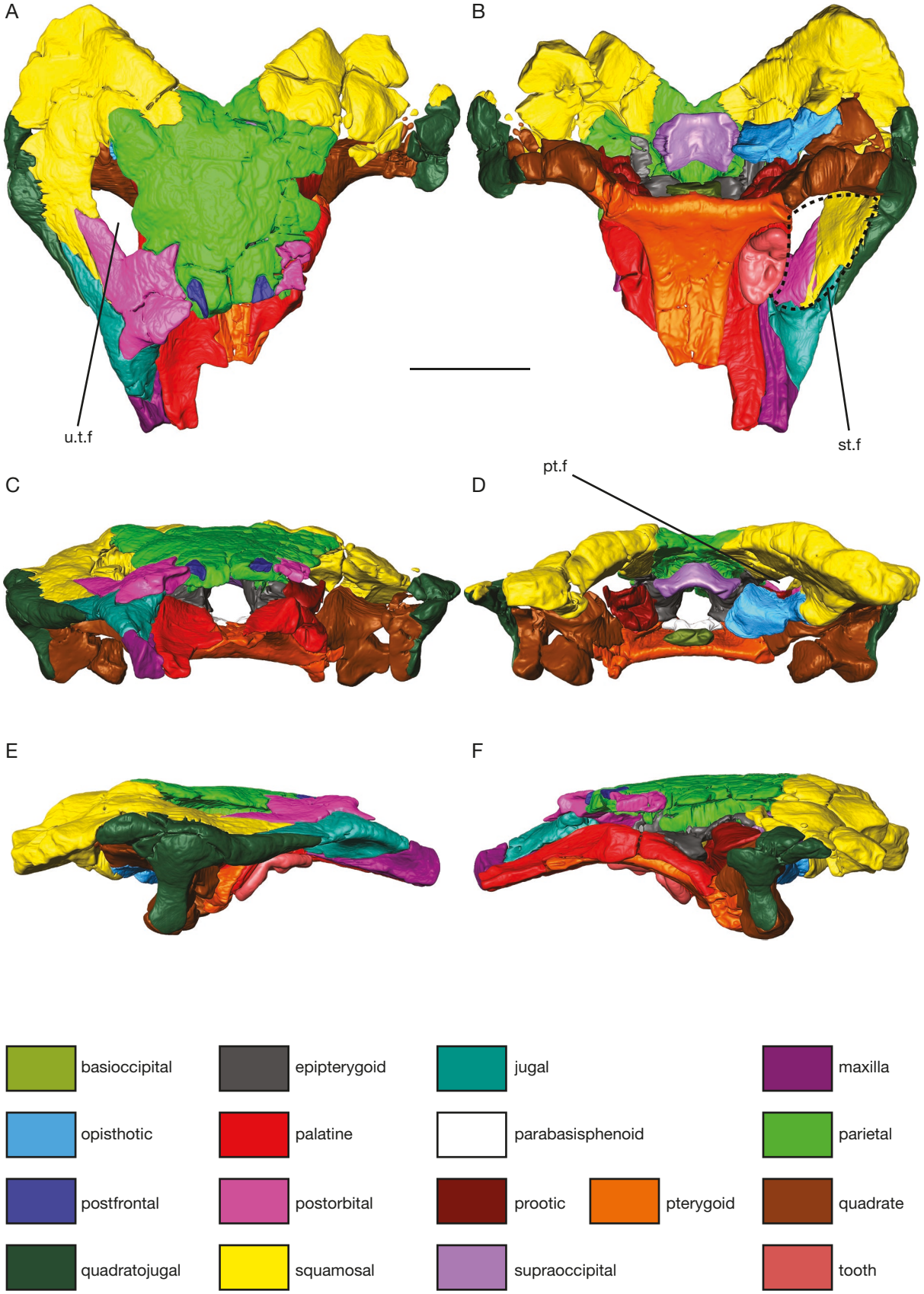

Fig. 2. — Three-dimensional digital model of the holotype of *Parahenodus atancensis* de Miguel Chaves, Ortega & Pérez-García, 2018 (MUPA ATZ0104), from the Upper Triassic of El Atance (Guadalajara, Spain), where the bones have been individualized by different colors, in dorsal (**A**), ventral (**B**), anterior (**C**), posterior (**D**), right lateral (**E**), and left lateral (**F**) views. Anatomical abbreviations: **pt.f**, post-temporal fenestra; **st.f**, subtemporal fossa; **u.t.f**, upper temporal fossa. **Dashed lines** indicate the contour of the subtemporal fossa. Scale bar: 2 cm.

Fig. 3. — Detail of the three-dimensional digital model of the holotype of *Parahenodus atancensis* de Miguel Chaves, Ortega & Pérez-García, 2018 (MUPA ATZ0104), from the Upper Triassic of El Atance (Guadalajara, Spain), in dorsolateral view. The parietal has been removed in this image. Color captions as in Figure 2. Anatomical abbreviations: **bo**, basioccipital; **ept**, epipterygoid; **o**, opisthotic; **o.p**, otic process of the squamosal; **p**, palatine; **pb**, parabasisphenoid; **po**, prootic; **po.f**, pteroccipital foramen; **pt**, pterygoid; **pt.f**, post-temporal fenestra; **ptf**, postfrontal; **pto**, postorbital; **q**, quadrate; **so**, supraoccipital; **sq**, squamosal. **White dashed lines** indicate the contour of the anterior part of the post-temporal fenestra, and **black dashed lines** the contour of the pteroccipital foramen. Scale bar: 1 cm.

between the preserved jugal and maxilla is located near the external margin of the palate (Fig. 2B), being confirmed as caused by a medial expansion of the jugal, as suggested by de Miguel Chaves *et al.* (2018). This medial expansion of the right jugal also contacts ventromedially with the palatine. This study allows a detailed characterization of the jugals of this taxon. In ventral view, the jugal posterolaterally contacts the quadratojugal, posteromedially the postorbital, and the squamosal between both sutures. Furthermore, the jugal defines the anterior margin of the preserved subtemporal fossa (Fig. 2B). The medial margin of the subtemporal fossa is formed by the pterygoid, the palatine and the medial projection of the jugal. Due to breakage, the contact between the palatines and the quadrates cannot be accurately defined.

The occiput and the posterior part of the braincase of MUPA ATZ0104 are badly damaged. Thus, part of the supraoccipital, the exoccipitals and most of the basioccipital, including the condyle, are lost, and most of the foramina present in the posterior surface of the skull cannot be observed either (Fig. 2D). The supraoccipital defines the dorsal margin of the foramen magnum, and it is in contact with the parietals. The supraoccipital would also have been in contact with the opisthotic but due to the preservation of the fossil this area of contact is missing. The preserved right opisthotic forms the paroccipital process, which includes a ventral tuber. The opisthotic also presents a lateral ascendant ramus that contacts a descendent process of the squamosal (Fig. 2D). It also contacts the quadrate. The anterior surface of the opisthotic is not well preserved.

The squamosals possess a small projection that expands anteriorly, the otic process (*sensu* Nosotti & Pinna 1993), which contacts the posterolateral region of the prootics (Fig. 3). Another small medioventral projection of the squamosals contacts the posterodorsal expansion of the epipterygoids (Fig. 3).

The prootics are short elements with a convex lateral surface and a deeply concave medial one, where they possess a cavity where the endosseous labyrinths (inner ear) are located. A posterolateral projection of the prootics contacts the otic process of the squamosals (Fig. 3). This projection of the prootics also defines the medial margin of the palatoquadrate cartilage recess, and has a groove for this cartilage (see below). This groove for the palatoquadrate cartilage is also present in the quadrates (Fig. 4). The prootics are located anterior to the opisthotics (Fig. 3). However, due to the bad preservation of the anterior surface of the preserved right opisthotic, the limits of the otic capsule cannot be well defined. The prootics also contact the quadrates ventrolaterally, and are located posterior to the epipterygoids (Fig. 4).

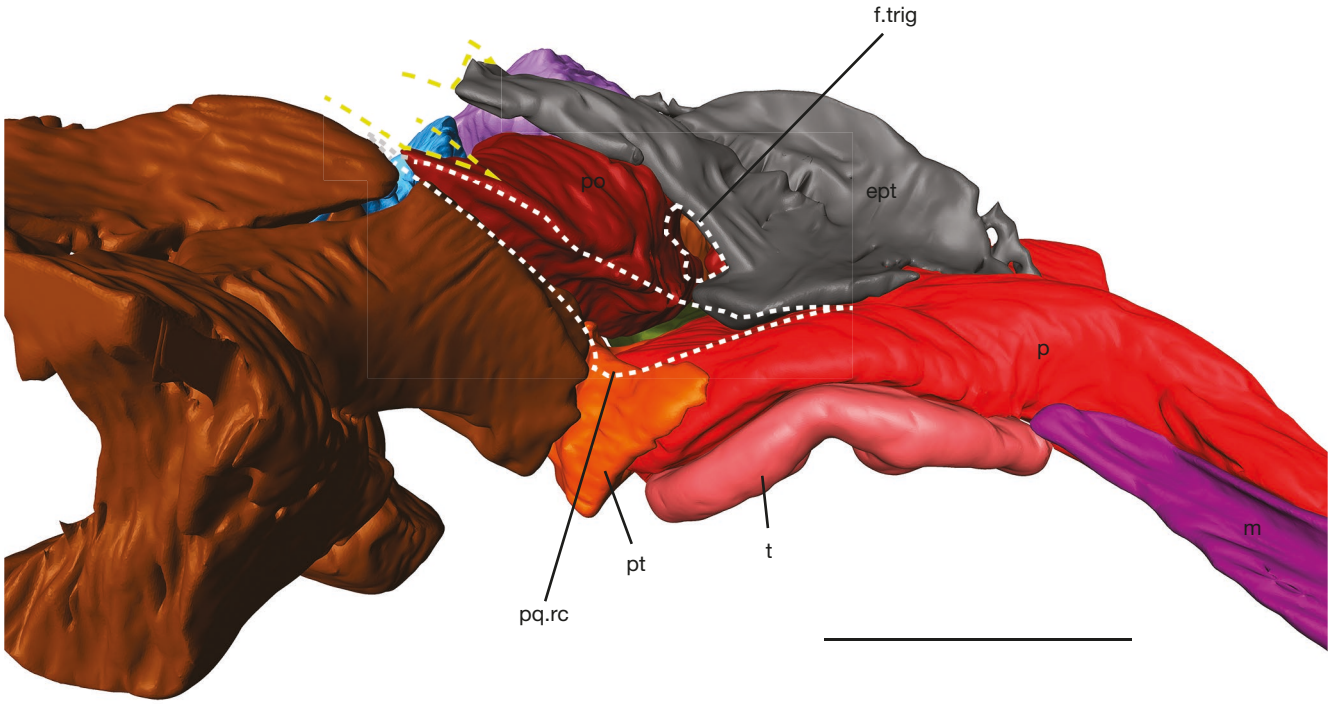

Fig. 4. — Detail of the three-dimensional digital model of the holotype of *Parahenodus atancensis* de Miguel Chaves, Ortega & Pérez-García, 2018 (MUPA ATZ0104), from the Upper Triassic of El Atance (Guadalajara, Spain), in right lateral view. The parietal, squamosals, quadratojugals, jugals, postorbitals and postfrontals have been removed in this image. Color captions as in Figure 2. Anatomical abbreviations: **ept**, epipterygoid; **f.trig**, trigeminal foramen; **m**, maxilla; **p**, palatine; **po**, prootic; **pq.rc**, palatoquadrate cartilage recess; **pt**, pterygoid; **q**, quadrate; **t**, tooth. **White dashed lines** indicate the contour of the trigeminal foramen and the palatoquadrate cartilage recess. **Yellow dashed lines** indicate the contact of the squamosal with the prootic and the epipterygoid. Scale bar: 1 cm.

The epipterygoids are complex elements that form most of the lateral walls of the preserved braincase (Fig. 3). They are anteriorly convex, and strongly concave posteriorly, with a lateroventral expansion that extends over the palatines (Fig. 4). The epipterygoids have a longitudinal furrow that receives a descending process of the parietals (Fig. 3). A well-developed posterodorsal projection of the epipterygoids contacts a medioventral expansion of the squamosals (Fig. 3). The epipterygoids contact the fused parietal dorsally, the prootics and the squamosals posteriorly, and the palatines, the pterygoids and the parabasisphenoid ventrally.

The parietals are fused into a single element, and they enclose the braincase dorsally (Fig. 2A). This unpaired parietal possesses two descending processes that are received by the epipterygoids. These descending processes become posteriorly a ventral thickening of the bone, where the parietal contacts the supraoccipital.

The right post-temporal fenestra has been identified in *Parahenodus atancesis* (Figs 2D; 3). It is defined posteroventrally by the opisthotic; posterodorsally, posteromedially, posterolaterally, dorsally and laterally by the squamosal; anterodorsally and anteromedially by the epipterygoid; and anteroventrally by the prootic (Figs 2D; 3). A foramen is present at the anterior region of the preserved right post-temporal fenestra, the pteroccipital foramen, which opens ventrally to a short passage of the stapedial artery, anterior to the paroccipital process (Fig. 3). This pteroccipital foramen is delimited posteriorly by the opisthotic, laterally by the otic process of the squamosal, anteriorly by the prootic, and laterally by the squamosal and the epipterygoid.

A pair of palatoquadrate cartilage recesses has also been identified in the holotype of *Parahenodus atancensis* (Fig. 4). They are triangular cleavages that would have been filled with cartilage in the living animal, connecting the quadrate and the epipterygoid. They are defined mostly by the palatines and the medial wing of the quadrates laterally; medially by the squamosals, the prootics and the epipterygoids; and ventrally by the quadrates, the palatines and the pterygoids. A groove for the cartilage is observed in the quadrates and the prootics.

The prootics and the epipterygoids also define the trigeminal foramina, which allow the exit of the trigeminal nerves (Fig. 4). The trigeminal foramina are limited anteriorly by the epipterygoids and posteriorly by the prootics.

Most of the small parabasisphenoid complex is also preserved, being located anteriorly to the basioccipital (Fig. 5). It closes the braincase ventrally in the preserved area. It is V-shaped, with its lateral projections contacting the pterygoids and the epipterygoids. The *sella turcica* is small and shallow, being square-shaped in dorsal view. Two small cerebral carotid foramina are also present. A poorly developed *dorsum sellae* is observed in the posterior margin of the *sella turcica*.

Morphology of the reconstructed brain, inner ear, and neurosensory and neurovascular structures

Due to the preservation of MUPA ATZ0104, only a small portion of the endocast can be identified (Fig. 6). The antorbital region of the skull is missing, so most of the forebrain (including the olfactory structures) could not be reconstructed.

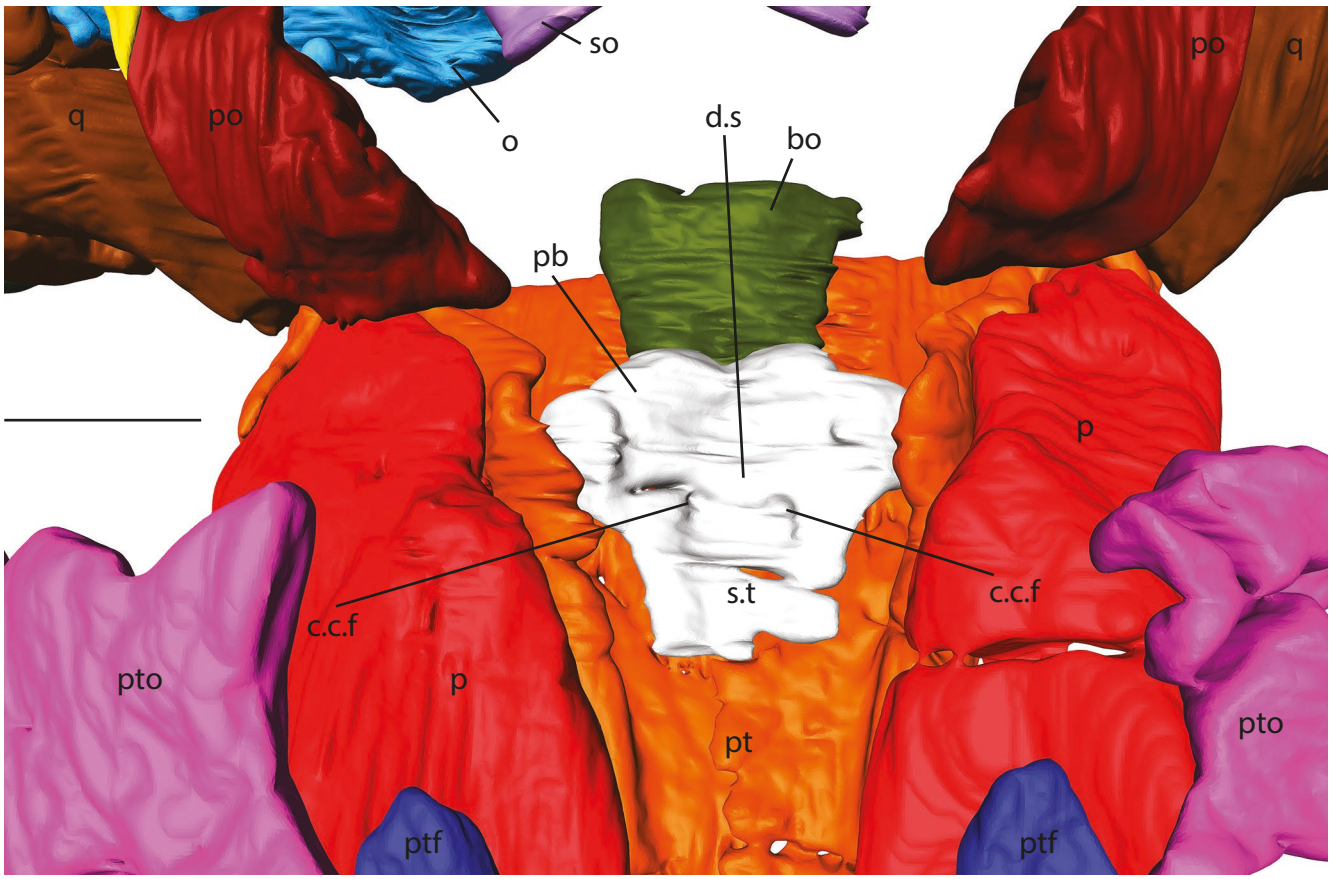

Fig. 5. — Detail of the three-dimensional digital model of the holotype of *Parahenodus atancensis* de Miguel Chaves, Ortega & Pérez-García, 2018 (MUPA ATZ0104), in dorsal view. The fused parietal and the epipterygoids have been removed in this image. Color captions as in Figure 2. Anatomical abbreviations: **bo**, basioccipital; **c.c.f**, cerebral carotid foramina; **d.s**, *dorsum sellae*; **o**, opisthotic; **p**, palatine; **pb**, parabasisphenoid; **po**, prootic; **pt**, pterygoid; **ptf**, postfrontal; **pto**, postorbital; **q**, quadrate; **s.t**, *sella turcica*; **so**, supraoccipital. Scale bar: 0.5 cm.

In the same way, the skull lacks most of the bones in the occipital region (i.e., the exoccipitals, part of the supraoccipital, the left opisthotic and most of the basioccipital). Thus, the reconstruction of the endocast of MUPA ATZ0104 includes the posterior area of the forebrain or prosencephalon, most of the midbrain or mesencephalon, and the anterior part of the hindbrain or rhombencephalon.

Only the posteriormost region of the forebrain of MUPA ATZ0104, where the pineal system is located, could be reconstructed (Fig. 7). The cerebrum has a flat dorsal surface, and a trapezium-shape section, the dorsal surface being longer than the ventral one (Fig. 7C, D). The pineal system in *Parahenodus atancensis* is represented by a very thin and laterally compressed passage, which connects the dorsal surface of the brain with a longitudinally narrow pineal foramen located anteriorly in the fused parietal (Fig. 7A, C, D).

The area where the pituitary (or hypophysis) would have been is identified as a weakly developed rectangular structure, located in the posteroventralmost part of the prosencephalon (Fig. 7B). It is settled over the *sella turcica* of the parabasisphenoid. It has two small lobes that lead to the two small cerebral carotid foramina of the *sella turcica*.

The reconstructed mesencephalon of *Parahenodus atancensis* exhibits a pair of strong lateral and symmetric compressions (Fig. 7A). These lateral compressions of the midbrain are well defined by the medial ascendant wall of the epipterygoids. Each of these strong compressions could correspond to the *cava epipterica*. Optic lobes could not be clearly distinguished in the endocast of the midbrain of MUPA ATZ0104. Posterior to the *cava epipterica*, the mesencephalon expands laterally (Fig. 7A). The morphology of the mesencephalon and rhombencephalon in the area posterior to this point cannot be defined.

Only the anteriormost part of both right and left endosseous labyrinths could be reconstructed (Fig. 7), due to the poor preservation of the right opisthotic and the lack of the left one, the otic capsules being incomplete. Both endosseous labyrinths are slightly distorted and medially rotated. Thus, only part of the anterior semicircular canal can be reconstructed, as well as part of the vestibule of the inner ear (Fig. 7E, F). They seem to be dorsoventrally short and anteroposteriorly elongated. However, the morphology of the anterior semicircular canal cannot be observed in detail due to the collapse of these canals and the poor preservation of the prootics.

Although most of the areas where the cranial nerves of MUPA ATZ0104 were located are lost, the canal for the trigeminal nerve (V) can be identified (Fig. 7). This canal is located anterior to the endosseous labyrinth, being enclosed between the epipterygoids and the prootics. The trigeminal nerve would emerge from the braincase through the trigeminal foramen (see above).

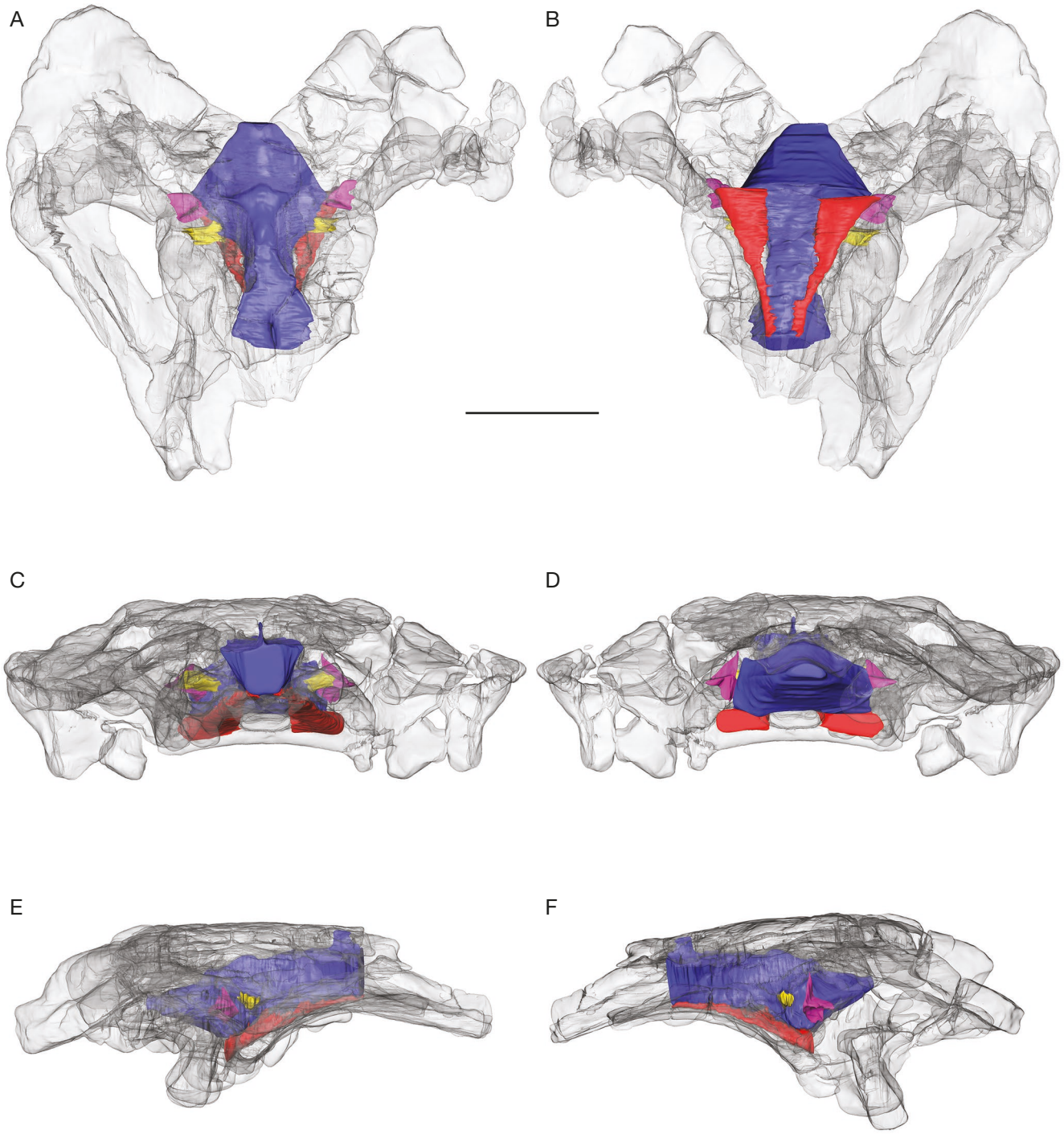

Fig. 6. — Digital reconstruction of the endocranial structures of the holotype of *Parahenodus atancensis* de Miguel Chaves, Ortega & Pérez-García, 2018 (MUPA ATZ0104), located within the rendered semi-transparent skull, in dorsal (**A**), ventral (**B**), anterior (**C**), posterior (**D**), right lateral (**E**) and left lateral (**F**) views. Scale bar: 2 cm.

Ventrally to the brain, the paired carotid branches are recognized, corresponding to two long neurovascular canals that run longitudinally to the occipital foramina, not preserved in MUPA ATZ0104 (Fig. 7B, E, F). In fact, because of the loss of most of the occiput in the holotype of *Parahenodus atancensis*, we cannot reconstruct the morphology of the carotid arteries posterior to the pterygoids. The canals for the carotid branches are ventrally and laterally delimited by the pterygoids, medially by the basioccipital and the parabasisphenoid, and dorso-anteriorly by the parabasisphenoid. The carotids would emerge from the brain ventrally to the pineal organ (Fig. 7E, F). Posterior to this point, they

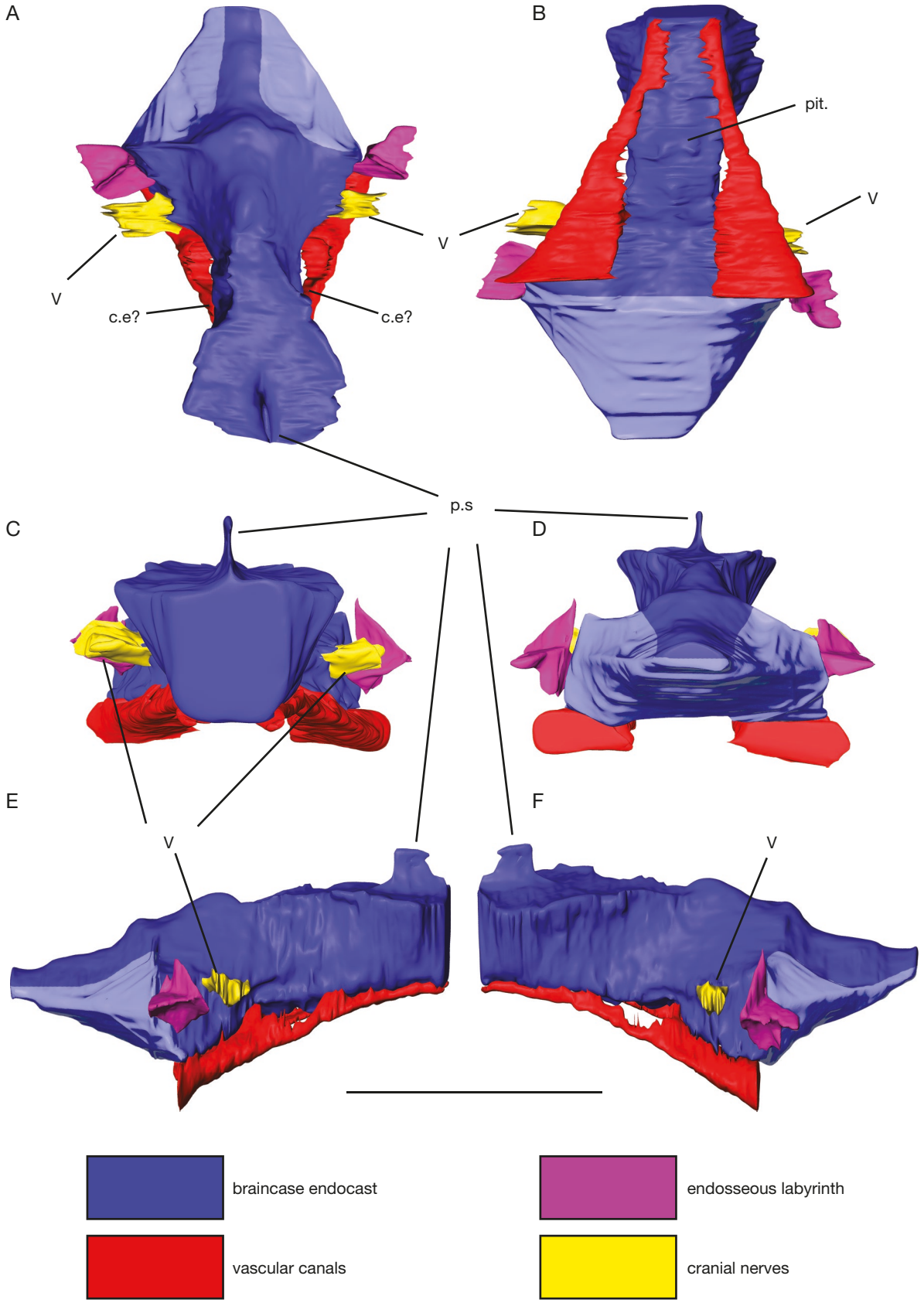

Fig. 7. — Digital reconstruction of the brain and associated endocranial structures of the holotype of *Parahenodus atancensis* de Miguel Chaves, Ortega & Pérez-García, 2018 (MUPA ATZ0104), in dorsal (**A**), ventral (**B**), anterior (**C**), posterior (**D**), right lateral (**E**) and left lateral (**F**) views. Anatomical abbreviations: **c.e**, cavum epiptericum; **p.s**, pineal system; **pit.**, pituitary; **V**, trigeminal nerve. **Light blue** corresponds to the areas in which the morphology of the brain cannot be reconstructed due to the loss of the adjacent bones of the skull. Scale bar: 2 cm.

would reach the *sella turcica* in the parabasisphenoid and, although it cannot be clearly observed due to the preservation, they would contact the pituitary through the small carotid foramina of the *sella turcica*.

DISCUSSION

The virtual reconstruction of the skull of the henodontid pladocont *Parahenodus atancensis*, based on its holotype and so far only known specimen, provides new information about this taxon and improves our knowledge of the highly specialized clade Henodontidae. The ventral contact between the jugal and the maxilla of *Parahenodus atancensis* is recognized here as caused by a medial expansion of the jugal (Figs 2B; 8). This suture has not been described in any specimen of the other representative of Henodontidae currently known, *Henodus chelyops*, due to preservation issues (Rieppel 2001). A contact between the process of the squamosals and the posterodorsal process of the epipterygoids is present in *Parahenodus atancensis* (Fig. 3), this contact being also present in *Cyamodus rostratus* Münster, 1839, and *Placochelys placodonta* Jaekel, 1902 (Rieppel, 2001), but unknown in the other cyamodontoids. The otic process of the squamosal *sensu* Nosotti & Pinna (1993) is present in MUPA ATZ0104, being in contact with the prootic (Fig. 3). This neomorphic process is also observed in other cyamodontoids such as *Placochelys placodonta*, *Cyamodus rostratus* and *Cyamodus orientalis* Wang, Li, Scheyer & Zhao, 2019 (Rieppel 2001; Wang *et al.* 2019), but is unknown in *Henodus chelyops*. The epipterygoids of *Parahenodus atancensis* are identified as large and complex elements that define the braincase laterally (Fig. 3). Due to the preservation, the morphology and disposition of these bones in *Henodus chelyops* cannot be well defined, but the morphology in MUPA ATZ0104 is shared with that of other cyamodontoids. Thus, a broad dorsal process, the contact with the squamosal at the dorsal margin of post-temporal fenestra, and the large suture with the palatines are shared amongst all of them (Rieppel 2001; Neenan *et al.* 2015). The presence of the palatoquadrate cartilage recess in the holotype of *Parahenodus atancensis* (i.e., a cleft filled with cartilage in the living animal that would connect the quadrate with the epipterygoid; Fig. 4), is shared with the other cyamodontoids, being considered as a synapomorphy of Cyamodontoidea (Rieppel 2001; Neenan *et al.* 2015). It was also identified in Specimen I of *Henodus chelyops* (Rieppel 2001). The presence of a pteroccipital foramen (*sensu* Rieppel 2001) delimited by the opisthotic, the prootic, the squamosal and the epipterygoid (Fig. 3), is also a synapomorphy of Cyamodontoidea (Rieppel 2001; Neenan *et al.* 2015; Wang *et al.* 2019). It is indeed identified in Specimen I of *Henodus chelyops* (Rieppel 2001). The exit for the trigeminal nerve (V) (the trigeminal foramen *sensu* Rieppel 2001; the prootic fenestra *sensu* Neenan & Scheyer 2012 and Wang *et al.* 2019; or the prootic foramen *sensu* Neenan & Scheyer 2014), recognized here for the first time in Henodontidae (being unknown for *Henodus chelyops*) as delimited by the epipterygoid anteriorly and by the prootic posteriorly (Fig. 4), has been identified in a similar position and defined by the same bones in other cyamodontoid taxa (Nosotti & Pinna 1996; Rieppel 2001; Neenan & Scheyer 2014; Wang *et al.* 2019). By contrast, this foramen is totally enclosed by the prootic in the non-cyamodontoid placodont *Placodus gigas* (Neenan & Scheyer 2012). Information about the parabasisphenoid complex in cyamodontoid placodonts is limited, this complex having been only described in detail in *Placochelys placodonta* (Rieppel 2001) and *Psephoderma alpinum* Meyer, 1858 (Neenan & Scheyer, 2014). Its morphology in *Parahenodus atancensis* is similar to those of both taxa, with a shallow *sella turcica*, small cerebral carotid foramina and a poorly developed *dorsum sellae* (Fig. 5). However, it is larger and more complex in the non-cyamodontoid *Placodus gigas* (Neenan & Scheyer 2012). In fact, an unusual character in the latter is the notable distance between the *sella turcica* and the *dorsum sellae* (Nosotti & Rieppel 2002; Neenan & Scheyer 2012), which are usually located close to one another in cyamodontoid placodonts.

Scarce information is so far available about the brain and senses of the placodonts and other Triassic sauropterygians. However, in spite of the fragmentary nature of MUPA ATZ0104, some information can be provided about the neuroanatomy of *Parahenodus atancensis*. The preserved region of MUPA ATZ0104 shows a long and tubular brain endocast (Fig. 7), as is the case in the eosauropterygian genus *Nothosaurus* (Koken, 1893; Edinger, 1921; Voeten *et al.*, 2018), whereas the brain in *Placodus gigas* is bulkier (Nosotti & Rieppel 2002; Neenan & Scheyer 2012). The morphology of the skull can be related with those of the braincase and the brain (as suggested by Voeten *et al.* 2018), since the skulls of both nothosaurians and cyamodontoid placodonts are much more dorsoventrally compressed than that of *Placodus gigas*. As in the case of *Nothosaurus marchicus* (Voeten *et al.* 2018), *Parahenodus atancensis* lacks well-developed cerebral lobes, but unlike this small nothosaur, no optic lobes are distinguishable in the endocast of MUPA ATZ0104. The absence of well recognizable optic lobes in the midbrain of *Parahenodus atancensis* suggests a poorer vision than those of the nothosaurs and plesiosaurs, where these structures are well developed (Allemand *et al.* 2019). No optic lobes have been identified in *Placodus gigas* so far. The reconstructed pineal system in *Parahenodus atancensis* is very narrow (Fig. 7A, C, D), especially when compared with those of the Triassic sauropterygians *Placodus gigas* (Neenan & Scheyer 2012) and *Nothosaurus marchicus* (Voeten *et al.* 2018). This structure is much more developed in these two taxa, which suggests a lower dependence on the pineal organ in *Parahenodus atancensis* than in those forms, as well as a lower photoreceptive capability. Although the morphology of this pineal organ is unknown in *Henodus chelyops*, the pineal foramen is also mediolaterally compressed (e.g. Rieppel 2001), so a similar development of the pineal organ in this taxon is also expected.

The reconstructed pituitary in *Parahenodus atancensis* is weakly developed (Fig. 7B). A poorly developed

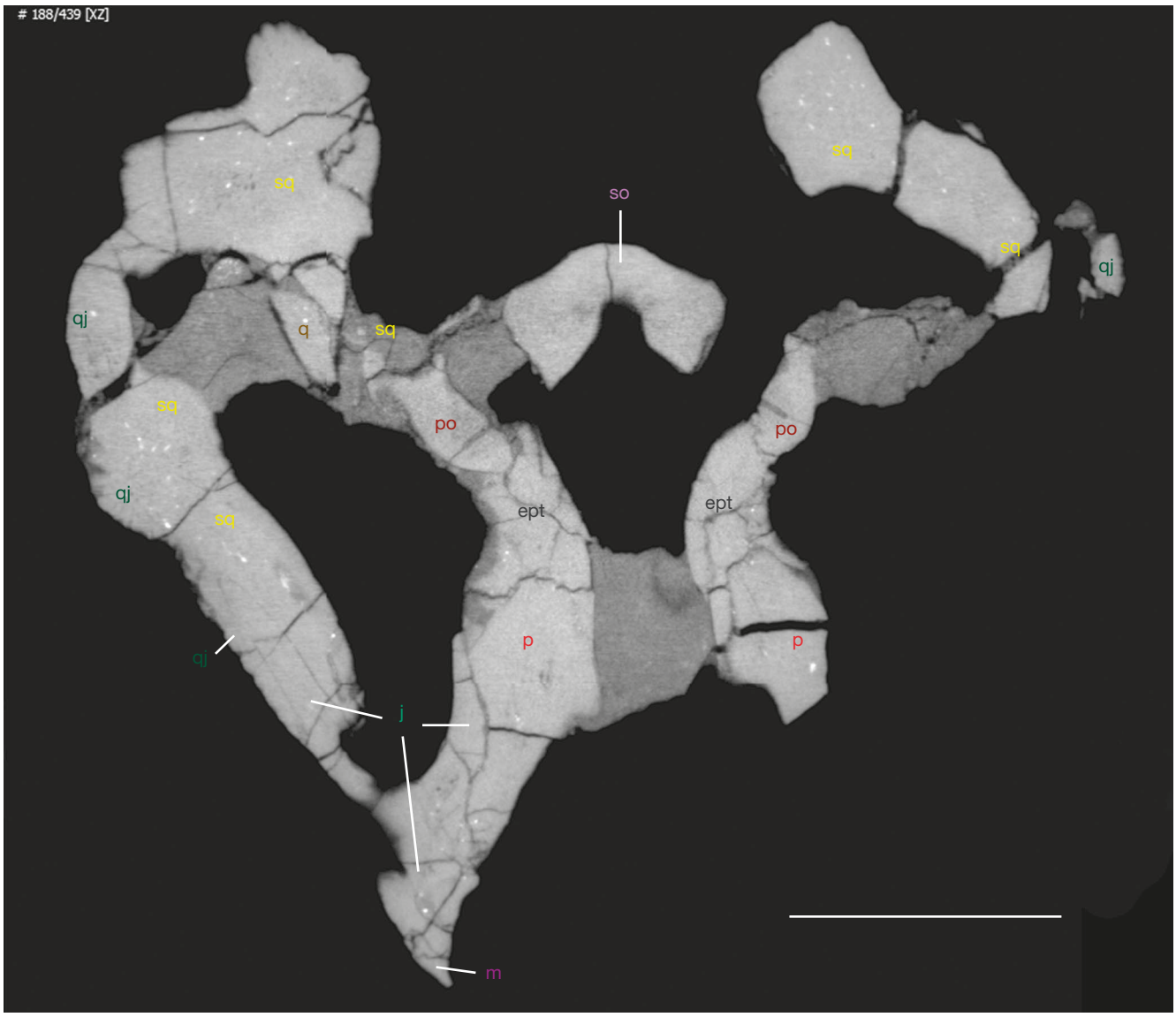

Fig. 8. — Axial CT-scan slice of the holotype of *Parahenodus atancensis* de Miguel Chaves, Ortega & Pérez-García, 2018 (MUPA ATZ0104), from the Upper Triassic of El Atance (Guadalajara, Spain). Anatomical abbreviations: **ept**, epipterygoid; **j**, jugal; **m**, maxilla; **p**, palatine; **po**, prootic; **q**, quadrate; **qj**, quadratojugal; **so**, supraoccipital; **sq**, squamosal. Scale bar: 2 cm.

pituitary can be inferred also in *Placochelys placodonta* and *Psephoderma alpinum*, based on the morphology of the parabasisphenoid complex (Rieppel 2001; Neenan & Scheyer 2014). A weak development of this structure has also been observed in *Nothosaurus marchicus* (Voeten *et al.* 2018). This contrasts with the identification of an unusually well-developed hypophysis in the placodont *Placodus gigas* (Neenan & Scheyer 2012), whose morphology could therefore be uncommon among Triassic sauropterygians, and also with the well-developed pituitary of such other Sauropterygia linages as the plesiosaurs (Otero *et al.* 2018; Allemand *et al.* 2019).

In spite of its incompleteness, the holotype of *Parahenodus atancensis* also provides some information relative to its bony labyrinth (Fig. 7). This structure is recognized as slightly dorsoventrally flattened and anteroposteriorly enlarged (Fig. 7E, F). This morphology is shared with *Placodus gigas* (Neenan & Scheyer 2012) and *Nothosaurus marchicus* (Voeten *et al.* 2018), as well as with other Triassic sauropterygians like *Simosaurus gaillardoti* Meyer, 1842 (Neenan *et al.* 2017), all of which were inhabitants of nearshore and shallow waters. Whereas the bony labyrinth of the plesiosaurs is more derived as an adaptation to pelagic lifestyles, being similar to those of most of the cryptodiran marine turtles (see some exceptions in Evers *et al.* 2019), the morphology of this element in the Triassic sauropterygians resembles that of several extant aquatic reptiles, including crocodylians, freshwater turtles and marine squamates (Neenan *et al.* 2017). This implies that the reconstructed morphology of the bony labyrinth of Henodontidae (only known for *Parahenodus atancensis*) is similar to that of both extinct and extant shallow-water semi-aquatic reptiles, whose movement is strongly based on lateral undulations of the trunk and tail (Neenan *et al.* 2017).

CONCLUSIONS

The use of micro-computed tomography for the study of MUPA ATZ0104, a partial skull corresponding to the holotype and only known specimen of the Spanish Upper Triassic *Parahenodus atancensis*, provides the first three-dimensional reconstruction of a cyamodontoid placodont braincase and neural system. This virtual reconstruction allows the identification of several osseous elements of the skull so far unpublished or poorly known, such as the epipterygoids, the prootics, the parabasisphenoid complex, the otic process of the squamosal, the palatoquadrate cartilage recess, the trigeminal foramen and the pteroccipital foramen. Several synapomorphies of the braincase of the clade Cyamodontoidea, some of them so far unknown in Henodontidae, are recognized in *Parahenodus atancensis*, including the large and complex epipterygoids contacting the squamosal at the dorsal margin of the post-temporal fenestra and the palatines in their ventral surfaces; the presence of the palatoquadrate cartilage recess; and the presence of a pteroccipital foramen defined by the opisthotic, the prootic, the squamosal and the epipterygoid.

The reconstruction of the brain endocast and the associated structures of *Parahenodus* shows a lower reliance on vision and the pineal complex than in other known Triassic sauropterygians, as well as a weakly developed hypophysis; these characters were so far unknown for the highly specialized clade Henodontidae. The partial reconstruction of the bony labyrinth shows a similar morphology to that of other Triassic sauropterygians and several extant shallow-water semi-aquatic reptiles, which suggests that *Parahenodus atancensis* was a nearshore inhabitant, which is compatible with the lifestyle proposed for the members of Placodontia.

Acknowledgements
We thank Marcos Martín (UNED) for his comments and suggestions, and for his invaluable help during the preparation of this manuscript. We thank the editor Hans-Dieter Sues, the reviewer James Neenan and an anonymous reviewer for their kind comments, which have helped to improve this paper.

Funding
This work was supported by the Ministerio de Ciencia, Innovación y Universidades (IJCI-2016-30427); the Consejería de Educación, Cultura y Deportes of Castilla-La Mancha (SBPLY/15/180601/000044); and a FPI UNED Grant (Ref. 0271864713 Y0SC001170).

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Submitted on 31 August 2019;
accepted on 29 November 2019;
published on 7 December 2020.

APPENDICES — ELECTRONIC SUPPLEMENTARY MATERIAL

Appendix 1. — Interactive PDF with the digital reconstruction of the bones of MUPA ATZ0104, the holotype of *Parahenodus atancensis*, from the Upper Triassic of El Atance (Guadalajara, Spain): http://sciencepress.mnhn.fr/sites/default/files/articles/pdf/comptes-rendus-palevol2020v19a10_s1.pdf

Appendix 2. — Interactive PDF with the digital reconstruction of the brain and associated structures of MUPA ATZ0104, the holotype of *Parahenodus atancensis*, from the Upper Triassic of El Atance (Guadalajara, Spain): http://sciencepress.mnhn.fr/sites/default/files/articles/pdf/comptes-rendus-palevol2020v19a10_s2.pdf