

A digital redescription of the Middle Miocene (Langhian) carettochelyid turtle *Allaeochelys libyca*

Yann Rollot¹, Serjoscha W. Evers¹, Walter G. Joyce¹

¹ Chemin du Musée 6, Department of Geosciences, University of Fribourg, Fribourg, Switzerland

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Corresponding author: Yann Rollot (yann.rollot@gmail.com)

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Abstract

Allaeochelys libyca is a carettochelyid turtle from the Middle Miocene of Libya. The species is the only valid carettochelyid taxon recovered from Africa and was named based on fragmentary material that includes a partial cranium and isolated shell remains. The description of the holotype cranium was limited to external aspects, and micro-computed tomography was only performed later on that material. Here, we use these micro-computed tomography scans to reinvestigate the external and internal anatomy of the holotype cranium to document several erroneous anatomical interpretations and provide new insights into the morphology of the trigeminal foramen area, the endosseous labyrinth, and circulatory system of *Allaeochelys libyca*. The anatomical insights provided herein have the potential to be translated into new phylogenetic characters that are expected to improve the resolution among the *Anosteira* and *Allaeochelys* lineages, which are still poorly resolved.

Key Words

anatomy, Carettochelyidae, micro-computed tomography, Miocene

Introduction

Carettochelyidae is a clade of aquatic, hidden neck turtles (Cryptodira), of which the only extant representative, the pig-nosed turtle *Carettochelys insculpta*, lives as a relict species in New Guinea and Australia (Ramsay 1887; Joyce 2014; TTWG 2021). The clade used to have a wider geographic distribution and higher diversity. The oldest occurrences in the fossil record are fragmentary remains from the mid Cretaceous. Two taxa are currently recognized from that time period, *Kizylkumemys khoratensis* from the Aptian of Thailand and *Kizylkumemys schultzi* from the Cenomanian of Uzbekistan (Nesov 1976, 1977; Tong et al. 2005, 2006). More abundant remains are known from the Cenozoic with a dozen valid species having been described from deposits across Asia, North America, Europe, and Africa (Joyce 2014 and references therein; Carbot-Chanona et al. 2020; White et al. 2023). The available fossil material mostly consists of shell material, but skull remains are known for about half of the

valid carettochelyid taxa, in particular *Anosteira pulchra* (Joyce et al. 2018), *Anosteira maomingensis* (Tong et al. 2010; Danilov et al. 2017), *Allaeochelys crassesculpta* (Harrassowitz 1922), *Allaeochelys libyca* (Havlik et al. 2014), and *Carettochelys niahensis* (White et al. 2023). Several studies documented the cranial anatomy of the extant *Carettochelys insculpta* (Ramsay 1887; Baur 1889; Waite 1905; Walther 1922; Joyce 2014).

Allaeochelys libyca from the Middle Miocene (Langhian) of Libya was described based on a partial cranium and several, isolated shell fragments (Havlik et al. 2014). Although other carettochelyid remains have been reported from Egypt (Dacqué 1912; Lapparent de Broin 2000), the Democratic Republic of the Congo (Hirayama 1992), and perhaps Saudi Arabia (Thomas et al. 1982), these consist of rare, isolated shell elements that are currently not diagnostic enough to identify additional species. *Allaeochelys libyca*, therefore, is the only valid African taxon to date. The study of Havlik et al. (2014) documented all externally available aspects

of the anatomy of the cranium, but as tomographic scans were not performed at that time, internal structures and cavities, such as the inner ear, the cavum acustico-jugulare, and canals for arteries and nerves, were not described. In the meantime, this cranium was scanned using micro-computed tomography (μ CT) and the slice data alongside the 3D models of the inner ear and cranium were made publicly available on the online repository MorphoSource (Evers 2021) as part of a study on turtle inner ears (Evers et al. 2022). As part of an ongoing project that aims to document unpublished and historical carettochelyid material, we downloaded the μ CT scans of the cranium of *Allaeochelys libyca*, but noticed differences in the interpretation of some anatomical features between our three-dimensional reconstructions and the original description provided by Havlik et al. (2014). We, therefore, here present the results of the bone-by-bone segmentation of this skull, which allows us to correct said erroneous anatomical interpretations and to document additional features that could not be documented originally, such as the anatomy of the cavum acustico-jugulare or the circulatory system. The new anatomical information highlighted in the present contribution does not challenge the validity of the species *Allaeochelys libyca*, but is expected to have an impact on phylogenetic matrices, which will be explored elsewhere.

Institutional abbreviations

BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; **FMNH**, Field Museum of Natural History, Chicago, USA; **NHMUK**, Natural History Museum London, London, England.

Material and methods

The material of *Allaeochelys libyca* is housed at the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany. BSPG 1991 II 130 was scanned at the School of Earth Sciences X-ray Tomography Facility of the University of Bristol using a Nikon Metrology XT H 225 ST scanner, with a voltage of 125 kV, a current of 265 μ A, 1601 projections, and no filter. The scanning resulted in 1813 coronal slices and a voxel size of 37.8 μ m. Scans are available at MorphoSource (<https://www.morphosource.org/concern/media/000350560>; Evers 2021). BSPG 1991 II 130 was segmented in Mimics Innovation Suite 25 (<https://www.materialise.com/en/healthcare/mimics-innovation-suite>) using the lasso and interpolation tools. The segmented objects were exported as .ply files and visualized in Blender 2.79b (<https://www.blender.org>) to create high-quality illustrations and figures. 3D models were deposited at MorphoSource (<https://www.morphosource.org/projects/000570948>).

We frequently cite for comparison the cranial anatomy of *Carettochelys insculpta*. Although this species has seen several cranial descriptions (Ramsay 1887; Baur 1889; Waite 1905; Walther 1922; Joyce 2014), many of our observations are not based on these descriptions, but on a fully segmented specimen (NHMUK 1903.7.10.1), which will be described in detail elsewhere. The CT scans of that specimen as well as 3D models of its cranium and endosseous labyrinth have already been published (CT scans: <https://www.morphosource.org/concern/media/000077378>; 3D models: cranium, <https://www.morphosource.org/concern/media/000373013>; endosseous labyrinth, <https://www.morphosource.org/concern/media/000373016>), whereas the bone-by-bone segmentations will be released with the aforementioned description.

Systematic palaeontology

Testudines Batsch, 1788

Cryptodira Cope, 1868

Trionychia Baur, 1891

Carettochelyidae Gill, 1889

***Allaeochelys* Noulet, 1867**

***Allaeochelys libyca* Havlik et al., 2014**

Holotype. BSPG 1991 II 130, an incomplete cranium.

Referred material. BSPG 1991 II 96, a left hypoplastron; BSPG 1991 II 97, a left hypoplastron; BSPG 1991 II 110, a bridge peripheral; BSPG 1991 II 113, an anterior peripheral; BSPG 1991 II 114, a peripheral I; BSPG 1991 II 131, an incomplete supraoccipital.

Type locality and horizon. Gebel Zelten (Jabal Zaltan), southwestern slopes, localities “MS 2” or “Wadi Shatirat,” Al Wahat District, Libya (Wessels et al. 2003). Lower Maradah Formation, Middle Miocene, Langhian (Desio 1935; Wessels et al. 2003).

Revised diagnosis. *Allaeochelys libyca* can be diagnosed as a representative of Carettochelyidae based on its dermal ornamentation made of thick ridges separated by equally sized grooves, presence of a deep fossa on the posterior surface of the quadrate, and a reduced antrum postoticum and a member of Carettochelyinae based on the absence of carapacial and plastral scutes and the presence of a broad plastron. *Allaeochelys libyca* can be differentiated from *Carettochelys insculpta* by having a broader and shorter cranium, a secondary contact between the prefrontal and frontal within the orbit, a more posteriorly located foramen posterius canalis carotici interni close to the fenestra postotica, a larger contribution of the opisthotic to the tubercula basioccipitale, a deeper pterygoid fossa, a larger quadrate fossa, a deeper sulcus between the mandibular condyles, a reduced canalis cavernosus, and absence of the sulcus cavernosus. *Allaeochelys libyca* resembles *Carettochelys niahensis* by having a secondary contact between the prefrontal and frontal, but appears to have an even broader skull.

Description and comparisons of the cranium of *Allaeochelys libyca*

General comments. The cranium of BSPG 1991 II 130, the holotype of *Allaeochelys libyca*, lacks most of its anteroventral and ventrolateral portions (Fig. 1). The premaxillae, maxillae, jugals, vomer, epipterygoids, and squamosals are not preserved. The palatines and postorbitals are almost completely lacking as well, and only small pieces of bone belonging to the most posterior and most medial portions of the right palatine and left postorbital, respectively, remain attached to the cranium. The prefrontals, frontals, parietals, pterygoids, parabasisphenoid, supraoccipital, and opisthotics lack substantial amounts of their original anatomy, whereas the prootics, quadrates, and basioccipital suffer from minor signs of damage. The exoccipitals are the only bones that are fully preserved.

The preserved portions of the skull roof highlight the presence of the characteristic carettochelyid skull sculpturing, made of thick ridges separated by equally sized grooves (Fig. 1). As in all carettochelyids (see Baur 1889; Harrassowitz 1922; Walther 1922; Joyce 2014; Danilov et al. 2017; Joyce et al. 2018; White et al. 2023), the upper temporal emargination is deep, the supraoccipital is posteriorly expanded by means of a well-developed crista supraoccipitalis and horizontal plate, the incisura columella auris is fully enclosed by the quadrate, the mandibular condyle is low, the palatines posteriorly contact the parabasisphenoid and fully separate the pterygoids, and the quadrate is posteriorly excavated by a fossa. The cranium is more robust and less gracile than that of *Anosteira pulchra* (Joyce et al. 2018), but broader than *Carettochelys insculpta* (Walther 1922). Although comparisons are difficult, proportions seem to be similar to *Carettochelys niahensis* (White et al. 2023). A unique feature exhibited by the cranium of *Allaeochelys libyca* is the complete reduction of the sulcus cavernosus, which is accompanied by a particular morphology of the trigeminal nerve foramen area.

The “trigeminal foramen” of turtles is somewhat of a misnomer, as only two of three of the trigeminal nerve rami exit this passage (Evers et al. 2019). The foramen instead is a lateral window from the outside into the region of the sulcus cavernosus, through which said nerve rami pass in addition to the mandibular artery of some groups of turtles (Albrecht 1967, 1976; Rollot et al. 2021a). When viewed from the side, the trigeminal foramen of *Carettochelys insculpta* is a large, diagonally arranged, oval opening. Superficially, the anterodorsal third of this opening corresponds to the trigeminal passage per se, while the posteroventral third corresponds to the passage of the mandibular artery into the lower temporal fossa. In BSPG 1991 II 130, the descending branch of the prootic is laterally displaced, perhaps obliterating the passage of the lateral head vein and visually separating passage of the trigeminal nerve rami and the mandibular artery. As preserved, only portions of the trigeminal foramen system can be observed, making it necessary to communicate

about its subparts. We here explicitly refer to the anterior foramen of BSPG 1991 II 130 as the trigeminal foramen *sensu stricto*, but the posterior foramen as the mandibular artery foramen, while recognizing that the two combined, if separated, are homologous with the trigeminal foramen *sensu lato* of *Carettochelys insculpta* (see Prootic below).

Nasal. The nasals are absent in BSPG 1991 II 130 (Fig. 1A–D), as in all carettochelyids (Waite 1905; Harrassowitz 1922; Walther 1922; Danilov et al. 2017; Joyce et al. 2018; White et al. 2023).

Prefrontal. The two prefrontals are heavily damaged. While most of the right element is missing, with only the most dorsomedial part being apparent, its left counterpart preserves the dorsal plate, but the descending process is completely missing (Fig. 1A–D). The anterior surface of the left prefrontal is smooth and an articulation facet is missing, showing that the nasal is absent (Fig. 1E). The prefrontal, therefore, forms the dorsal margin of the apertura narium externa and the dorsal roof of the fossa nasalis. The prefrontal also forms the dorsal margin of the orbit. The ventrolateral portion of the prefrontal forms the dorsal base of the descending process. The lateral half of that base forms an articulation facet, which corresponds to the ventrolateral contact of the prefrontal with the ascending process of the maxilla (Fig. 1C), while the medial half ventrally highlights a broken surface, i.e., the area where the descending process of the prefrontal is broken off. The prefrontal otherwise contacts the frontal posteriorly along a convex suture. The left prefrontal additionally exhibits a small, asymmetric, posteromedial contact with the right frontal (Fig. 1A, B).

Frontal. The two frontals are nearly complete. The right element lacks its most anterolateral portion. Additional, minor damage can be seen along the crista cranii of both bones (Fig. 1A, B). The frontal contacts the prefrontal anteriorly along a slightly concave suture, the parietal posteriorly, and the postorbital posterolaterally (Fig. 1A, B). The frontal is wider than long and anterolaterally forms a short process that forms the posterodorsal margin of the orbit (Fig. 1A). The extent of this contribution to the orbit margin is similar to that of most carettochelyids (Waite 1905; Harrassowitz 1922; Walther 1922; White et al. 2023) but not *Anosteira pulchra* and *Anosteira maomingensis*, in which this contribution is slightly broader (Danilov et al. 2017; Joyce et al. 2018). Ventrally, the frontals form low crista cranii, which jointly delimit a moderately broad sulcus olfactorius (Fig. 1B). The posterior half of the two cristae collectively encapsulate an area that is enlarged relative to the sulcus olfactorius and that contained the olfactory bulbs (Evers et al. 2019). The anteromedial part of the crista cranii is mediolaterally broadened and forms an oval articulation facet (Fig. 1B). This facet, previously not reported by Havlik et al. (2014), likely corresponds to a secondary contact between the crista cranii of the frontal and the descending process of the prefrontal. A similar arrangement is present in *Carettochelys niahensis*, where a secondary contact

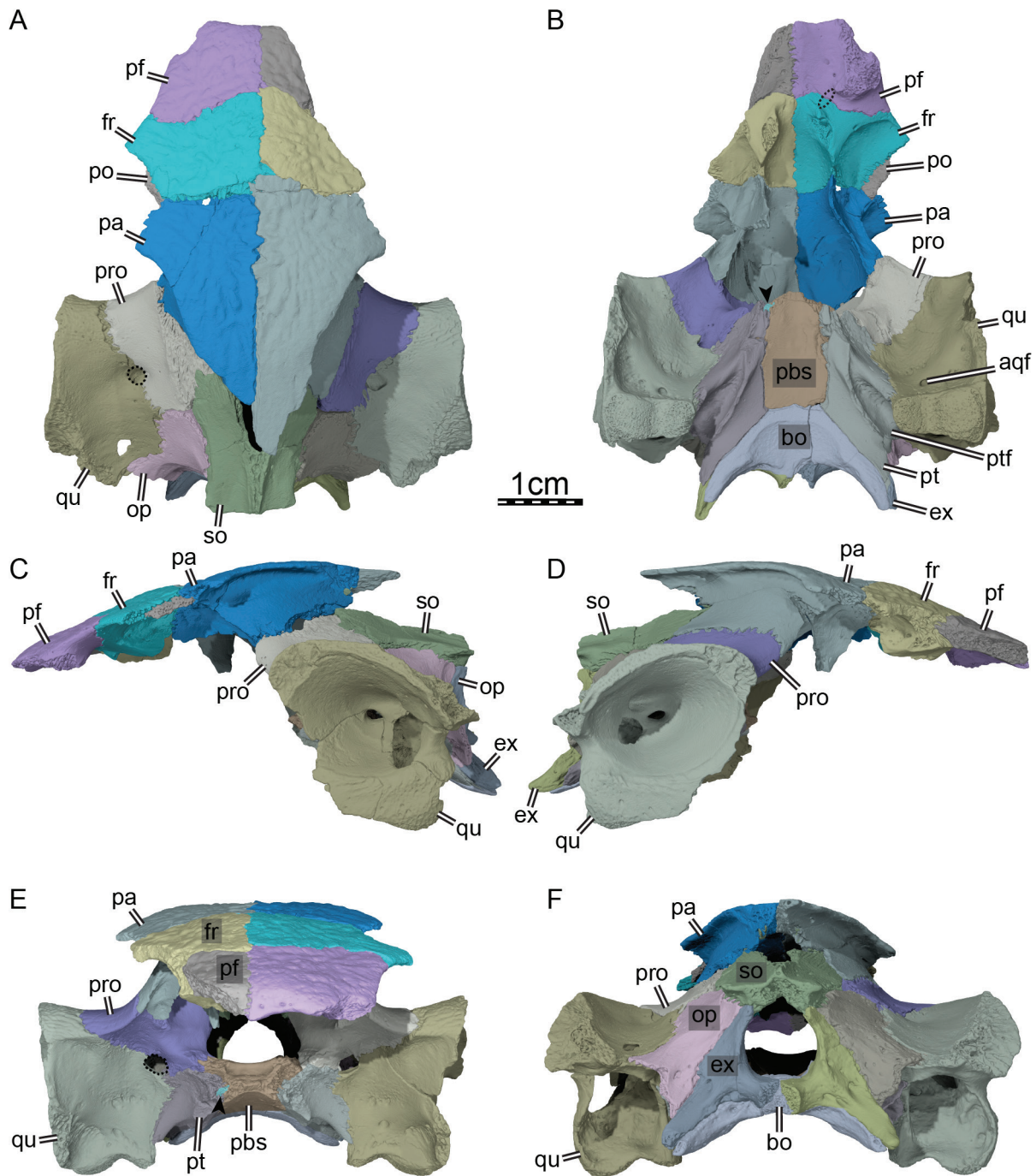


Figure 1. Three-dimensional renderings of the segmented cranium of BSPG 1991 II 113. **A.** Dorsal view; **B.** Ventral view; **C.** Left lateral view; **D.** Right lateral view; **E.** Anterior view; **F.** Posterior view. Abbreviations: aqf, anterior quadrate foramen; bo, basioccipital; ex, exoccipital; fr, frontal; op, opisthotic; pa, parietal; pbs, parabasisphenoid; pf, prefrontal; po, postorbital; pro, prootic; pt, pterygoid; ptf, pterygoid fossa; qu, quadrate; so, supraoccipital. Black arrowhead indicates the small, preserved portion of the right palatine. Dashed lines indicate the foramen stapedio-temporale in **A**, the passage between the orbit and nasal cavity in **B**, and the mandibular artery foramen in **E**.

between the frontal and prefrontal anteriorly delimits a foramen that forms a passage between the orbit and the nasal cavity (White et al. 2023). In the extant turtle *Carettochelys insculpta*, such a contact is not present, but the crista cranii closely approaches the descending process of the prefrontal, forming a slit-like passage between the orbital and nasal cavities along the most anterior portion of the foramen interorbitale (Walther

1922; Joyce 2014). The condition described for *Carettochelys niahensis* and *Allaeochelys libyca* likely highlights an extended degree of ossification of the interorbital area compared to *Carettochelys insculpta*.

Parietal. The parietal forms the posterior half of the skull roof, the lateral half of the upper temporal emargination, and roofs the braincase. The dorsal plate of the parietal is nearly complete, only missing its most distal

part, and contacts the frontal anteriorly, the postorbital anterolaterally, and the supraoccipital posteroventrally (Fig. 1). Within the upper temporal fossa, the parietal contacts the prootic laterally and the supraoccipital posteriorly (Fig. 1A). The descending process of each parietal is severely damaged and only preserves its most dorsal portions (Fig. 1C, D). Nevertheless, the bony contacts of the parietal around the foramen nervi trigemini *sensu stricto* can be inferred based on comparisons with the extant *Carettochelys insculpta*. In both the extant form and BSPG 1991 II 130, the posterior margin of the foramen nervi trigemini *sensu stricto* is imprinted onto the anterior surface of the prootic. The dorsal end of this imprint is formed by a small, anteroventral bump-like process of the prootic, which is well visible in the fossil on both sides. As preserved, this bump prohibits the posterior end of the descending process of the parietal to enter the dorsal margin of the foramen nervi trigemini *sensu stricto* on the right side of the fossil. This can also be appreciated on the left side, where the process is broken, but where the prootic bump and sutural contact for the descending process indicate a symmetrical morphology with the right side. In *Carettochelys insculpta*, the prootic bump serves as an articulation site for a postero-dorsal process of the epipterygoid, which prohibits the descending parietal process from entering the trigeminal foramen *sensu stricto* margin at a more anterior position. The morphology of BSPG 1991 II 130 is fully consistent with that of *Carettochelys insculpta*, and thus it is reasonable to infer that an epipterygoid–prootic contact in the anterodorsal margin of the foramen nervi trigemini *sensu stricto* precluded a parietal contribution to this opening. The preserved portion of the descending process shows that it is continuous with the crista cranii of the frontal and also forms a prominent ridge along its lateral surface that extends posteroventrolaterally from the base of the process within the upper temporal fossa (Fig. 1B, E). This ridge is continuous with the processus trochlearis oticum, and forms parts of its anteriorly overhanging margin, as in *Carettochelys insculpta* and *Anosteira maomingensis* (Walther 1922; Joyce 2014; Danilov et al. 2017). Within the braincase, the descending process of the parietal is deeply recessed and, jointly with the prootic, forms a broad cavity that housed large cerebral hemispheres, as in trionychians more generally (Fig. 1B; Ferreira et al. 2023). In the median contact of both parietals, there is an additional constriction of the brain cavity toward the supraoccipital contact, which corresponds to a median, bulge-like cartilaginous rider (Werneburg et al. 2021).

Postorbital. The postorbitals are almost completely missing. Only the most medial portion of the left element is preserved, which contacts the frontal anteromedially and the parietal posteromedially (Fig. 1A, B). The fully preserved left frontal and parietal and comparisons with *Carettochelys insculpta* also allow to infer that the postorbital contributed to the orbital margin and the upper temporal emargination.

Jugal. The jugals are not preserved in BSPG 1991 II 130.

Quadratojugal. A small part of the right quadratojugal was described by Havlik et al. (2014) as preserved in articulation with the remainder of the fossil, in a position anteroventral to the cavum tympani. This portion of the quadratojugal disarticulated along its suture with the quadrate in the specimen prior to CT scanning but was scanned alongside the rest of the fossil. The ventral margin of the quadratojugal fragment was formerly aligned with the ventral margin of the quadrate's articular process and showed no indication of a dorsal upcurving that is generally present in taxa with moderate or deep cheek emarginations. Instead, the fragment is fully consistent with the morphology of *Carettochelys insculpta*, in which the cheek emargination is minimal and limited to a more anterior portion of the quadratojugal (Waite 1905; Walther 1922; Joyce 2014). In addition, the preserved quadrates on both sides of BSPG 1991 II 130 show that the posterodorsal articulation of the quadratojugal with the quadrate was limited to the anterodorsal margin of the cavum tympani and did not extend posteriorly further along the dorsal margin. A quadratojugal–squamosal contact was certainly absent in BSPG 1991 II 130 as the articular facets of the quadratojugal and squamosal on the quadrates are widely spaced from one another, much as in *Carettochelys insculpta*.

Squamosal. The squamosals are not preserved in BSPG 1991 II 130. Nevertheless, the quadrates on both sides show well-developed articular facets for the squamosals. These facets are triangular and somewhat broader than in *Carettochelys insculpta*. However, as in the extant taxon, the facets are anteriorly clearly separated from those of the quadratojugal, showing that no contact with the quadratojugal was present. The quadrate bone surrounding the squamosal facet furthermore shows that, again as in *Carettochelys insculpta*, the squamosal of BSPG 1991 II 130 was excluded from the posterodorsal margin of the cavum tympani.

Premaxilla. The premaxillae are not preserved in BSPG 1991 II 130.

Maxilla. The maxillae are not preserved in BSPG 1991 II 130.

Palatine. The μ CT scans of BSPG 1991 II 130 reveal that a very small portion of the right palatine is preserved just anterior to the suture between the parabasisphenoid and pterygoid (Fig. 1B, E). Although this piece is so small that it barely allows making statements about the anatomy of the palatine, it nevertheless shows that a contact between the palatine and pterygoid, and palatine and parabasisphenoid was present, as in all carettochelyids (Waite 1905; Harrassowitz 1922; Walther 1922; Danilov et al. 2017; Joyce et al. 2018). The location of this fragment at the level of the sella turcica between the pterygoid and parabasisphenoid also suggests that a contact of the pterygoid with its counterpart was likely absent, again, as in all carettochelyids (Waite 1905; Harrassowitz 1922; Walther 1922; Danilov et al. 2017; Joyce et al. 2018).

Vomer. The vomer is not preserved in BSPG 1991 II 130.

Pterygoid. Only the posterior half of the pterygoids are preserved in BSPG 1991 II 130, which contact the

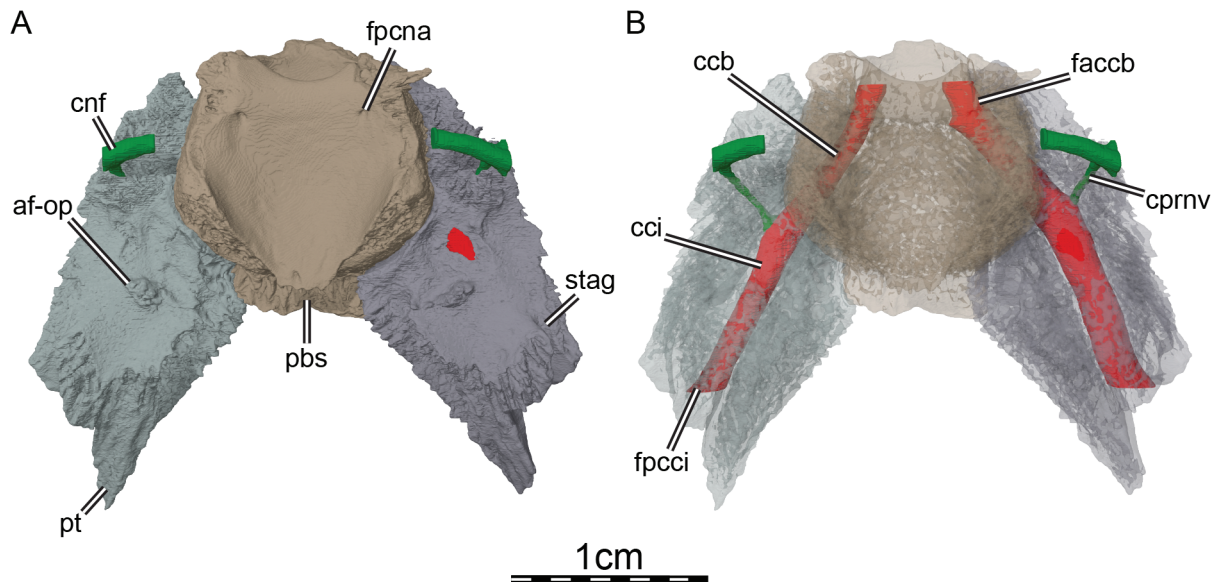


Figure 2. Three-dimensional renderings of the circulatory system of BSPG 1991 II 113. **A.** Dorsal view; **B.** Dorsal view with bones rendered transparent. Abbreviations: af-op, articulation facet for the opisthotic; ccb, canalis caroticus basisphenoidalis; cci, canalis caroticus internus; cnf, canalis nervus facialis; cprnv, canalis pro ramo nervi vidiani; faccb, foramen anterius canalis carotici basisphenoidalis; fpcci, foramen posterius canalis carotici interni; fpcna, foramen posterius canalis nervi abducentis; pbs, parabasisphenoid; pt, pterygoid; stag, stapedial artery groove.

parabasisphenoid medially, the palatine anteriorly, the prootic anterodorsolaterally, the quadrate laterally, the basioccipital posteromedially, the opisthotic posterodorsally, and the exoccipital posterodorsomedially (Figs 1B, E, 2). Additionally, there was likely a contact with the epipterygoid. Ventrally, the pterygoid forms a deep pterygoid fossa and contributes to the elongate tubercula basioccipitale anterolaterally (Fig. 1B). At about mid-length between the parabasisphenoid and quadrate, the pterygoid forms a low ridge that delineates the pterygoid fossa medially (Fig. 1B). The ridge is ventrally broken, and it likely formed an enfolded structure that partially covered the pterygoid fossa ventrally, as in *Carettochelys insculpta* (Walther 1922; Joyce 2014), but likely not *Anosteira maomingensis*, in which this ridge seems to be absent (Danilov et al. 2017), and definitely not *Anosteira pulchra*, in which the ridge is clearly absent (Joyce et al. 2018). The pterygoid of BSPG 1991 II 130 ventromedially minorly enters the margin of the mandibular artery foramen (Figs 1E, 3). The ventral half of the canalis pro ramo nervi vidiani, which transmits the vidian nerve from the geniculate ganglion to the canalis caroticus internus (Gaffney 1979; Rollot et al. 2021a), is also formed by the pterygoid (Fig. 2A). The pterygoid floors the endosseous labyrinth and cavum acustico-jugulare and forms the ventral margin of the fenestra ovalis and ventromedial margin of the small fenestra postotica. Dorsally, at about mid-length, the pterygoid forms a low bulging articulation facet for contact with the processus interfenestralis of the opisthotic (Fig. 2A). This dorsal articular boss is unusual among turtles, but certainly present in *Carettochelys insculpta*. Within the cavum acustico-jugulare, the posterodorsal surface of the pterygoid forms a narrow groove, as in *Carettochelys insculpta*,

and that is interpreted as having housed the stapedial artery and/or the lateral head vein (Fig. 2A). Posteriorly, the pterygoid entirely forms the foramen posterius canalis carotici interni, the position of which differs from the early branching carettochelyids *Anosteira pulchra* (Joyce et al. 2018) and *Anosteira maomingensis* (Danilov et al. 2017), in which the foramen is located more anteroventrally and between the parabasisphenoid and pterygoid, similar to the generalized position of paracryptodires (Gaffney 1975). The foramen posterius canalis carotici interni of BSPG 1991 II 130 leads into the canalis caroticus internus, which extends anteromedially through the pterygoid (Fig. 2B) before entering the parabasisphenoid as the canalis caroticus basisphenoidalis. A canalis caroticus lateralis is absent, as in *Carettochelys insculpta* (Rollot et al. 2021a). At about mid-length, the canalis caroticus internus is slightly exposed dorsally within the floor of the endosseous labyrinth (Fig. 2). Dorsal to the foramen posterius canalis carotici interni, the pterygoid forms a bony platform that contacts the opisthotic dorsally, forming a secondary wall posterior to the processus interfenestralis, as in *Carettochelys insculpta* (Walther 1922).

Epipterygoid. A large epipterygoid was described on the left side of BSPG 1991 II 130 by Havlik et al. (2014), but the μ CT scans of that specimen show that this piece of bone anteroventral to the mandibular artery foramen actually belongs to the pterygoid (Fig. 3). The epipterygoid usually lies along the anterior and ventral margins of the foramen nervi trigemini *sensu lato* in other carettochelyids (Walther 1922; Joyce et al. 2018) and overlies the pterygoid in about the area where Havlik et al. (2014) drew their epipterygoid. In BSPG 1991 II 130, the area that was indicated as being the epipterygoid by Havlik et al. (2014) has a slightly different, somewhat rougher surface texture than

the surrounding bone surfaces exposed along the lower temporal fossa. We consider it likely, based on comparisons of a completely segmented specimen of *Carettochelys insculpta* (NHMUK 1903.7.10.1), that this area represents an articulation area for a formerly present but not preserved epipterygoid of BSPG 1991 II 130. Details of this are further given below in the context of descriptions and discussions surrounding the foramen for the mandibular artery.

Quadrate. The quadrates are nearly complete, with only minor damage along the anterior and posterior margins of the cavum tympani (Figs 1C, D, 4). The quadrate contacts the quadratojugal anteriorly, the prootic anteromedially, the opisthotic posteromedially, and the pterygoid ventromedially (Fig. 1A, B, E, F). Posterodorsolaterally, the quadrate forms a mediolaterally expanded articular facet for articulation with the

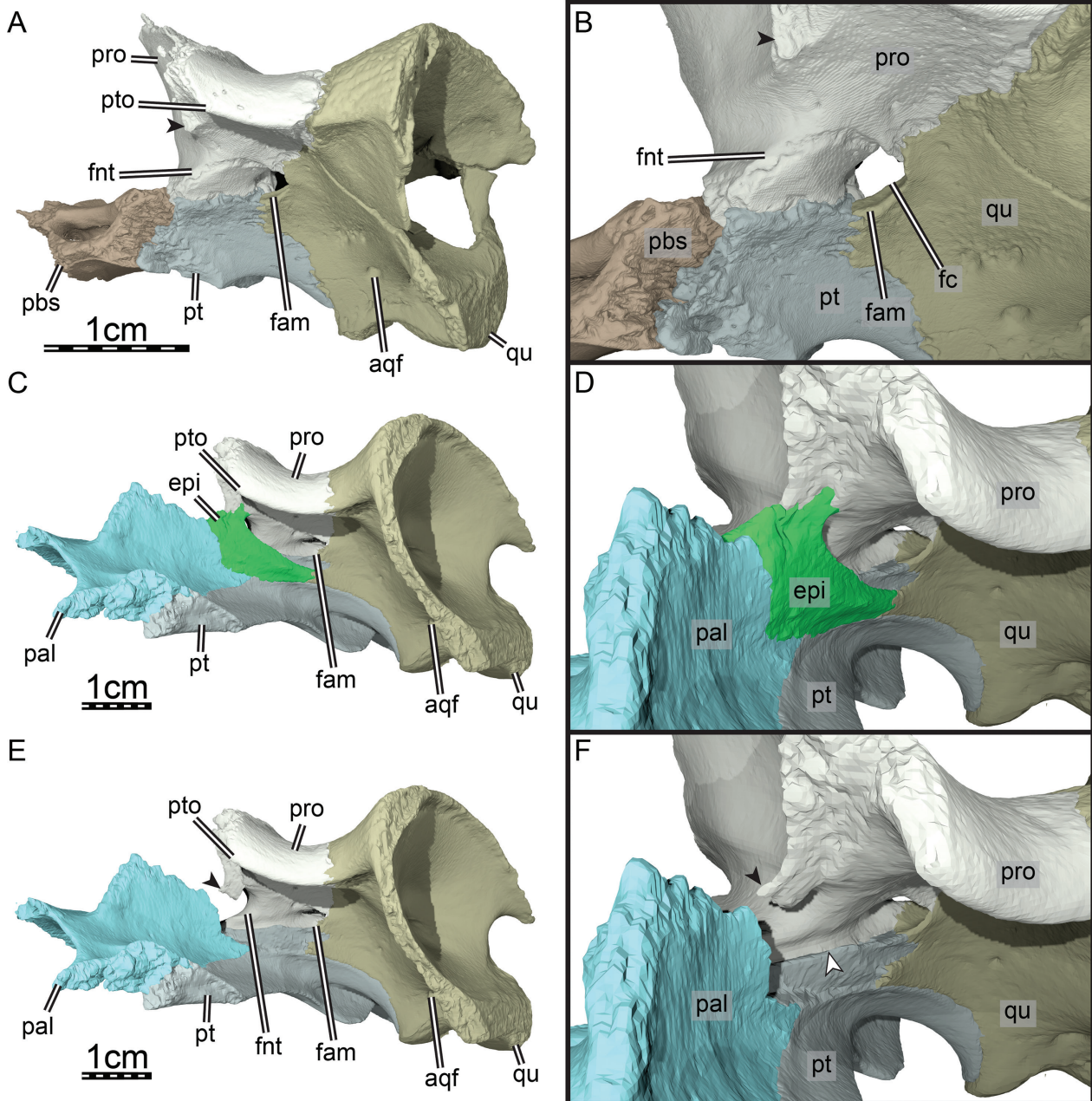


Figure 3. Three-dimensional renderings of the left trigeminal area of *Allaeochelys libyca* (BSPG 1991 II 113) and *Carettochelys insculpta* (NHMUK 1903.7.10.1). **A.** Left trigeminal area of *Allaeochelys libyca* in anterolateral view; **B.** Close-up on the left trigeminal area of *Allaeochelys libyca*; **C.** Left trigeminal area of *Carettochelys insculpta* in anterolateral view; **D.** Close-up on the left trigeminal area of *Carettochelys insculpta*; **E.** Left trigeminal area of *Carettochelys insculpta* in anterolateral view with the epipterygoid removed; **F.** Close-up on the left trigeminal area of *Carettochelys insculpta* with the epipterygoid removed. Abbreviations: aqf, anterior quadrate foramen; epi, epipterygoid; fam, foramen arteriomandibulare; fc, foramen cavernosum; fnt, foramen nervi trigemini; pal, palatine; pbs, parabasisphenoid; pro, prootic; pt, pterygoid; pto, processus trochlearis oticum; qu, quadrate. Black arrowheads indicate the anteroventral bump on the prootic that is interpreted as serving for the contact with the epipterygoid, and the white arrowhead indicates the lateral margin of the sulcus cavernosus formed by the pterygoid in *Carettochelys insculpta*.

squamosal (Figs 1A, 4). A contact with the supraoccipital is absent, as in other carettochelyids (Walther 1922; Danilov et al. 2017; Joyce et al. 2018). As the quadrate only forms a short epipterygoid process anteriorly, a contact between the epipterygoid and quadrate was likely absent in BSPG 1991 II 130 or minimal (Fig. 3), as in some *Carettochelys insculpta* specimens. The quadrate of BSPG 1991 II 130 forms the lateral and ventrolateral margin of the mandibular artery foramen, and less than half of the processus trochlearis oticum (Figs 1E, 3). Along its ventral surface, anterior to the condylus mandibularis, the quadrate forms a conspicuous foramen of several millimeter width, which leads into a canal that extends dorsally within the quadrate and joins the most anterior aspect of the quadrate fossa (Fig. 1B). We herein refer to this foramen as the anterior quadrate foramen. The path and location of its canal somewhat resembles that of the canalis chorda tympani quadrati (sensu Gaffney 1972), which transmits the chorda tympani branch of the facial nerve (CN VII). However, the chorda tympani canal generally opens along the posterior surface of the quadrate and connects dorsally to the incisura columella auris, which has a direct connection to the facial nerve path via the cavum acustico-jugulare. Here, we are not able to identify any connection between the quadrate canal in BSPG 1991 II 130 and the incisura columella auris or otherwise the cavum acustico-jugulare, and therefore cannot know its precise identity. However, as the foramen is also evident in the extant *Carettochelys insculpta*, but absent in the early branching carettochelyid *Anosteira pulchra* for which we have CT scans to ascertain this statement, we provide a new name for the structure as a potential shared character of derived carettochelyids. The quadrate forms a low, ventrally oriented mandibular condyle, of which the lateral articular surface is about twice the size of the medial one (Figs 1B, 4). The two articular facets are separated by a deep and relatively wide sulcus (Fig. 4B). Anterolateral to the articular process, the quadrate extends with a vertical, sheeted process that is ventrally projecting from the margin of the cavum tympani, and which effectively forms a lateral wall to the most posterior portion of the lower temporal fossa. This sheeted process anteriorly contacted the quadratojugal (Havlik et al. 2014), but the respective quadratojugal piece is now disarticulated. Within the upper temporal fossa, the quadrate forms the lateral margin of the foramen stapedio-temporale (Fig. 1A). The foramen leads into the canalis stapedio-temporalis, which is notably short, mostly oriented mediolaterally, and laterally bordered by the quadrate. The canalis stapedio-temporalis leads into the cavum acustico-jugulare, of which the quadrate forms the lateral wall. The medial surface of the quadrate forms an imprint that allows to determine the path of the stapedia artery. A large groove extends anteriorly and slightly dorsally from the fenestra postotica and, anterodorsal to the incisura columella auris, abruptly curves to extend ventrally and join the mandibular artery foramen. Dorsally and at about mid-length between the incisura columella auris and mandibular

artery foramen, the quadrate forms a low ridge, which with the prootic collectively defines a passage for the stapedia artery from the cavum acustico-jugulare to the canalis stapedio-temporalis. It is likely that the split between the stapedia and mandibular artery occurred at that level, with the stapedia artery extending laterally through the canalis stapedio-temporalis and the mandibular artery curving ventrally to exit the skull by means of the foramen cavernosum. Laterally, the quadrate forms most of the cavum tympani, to the exception of the most anterior margin that is formed by the quadratojugal (Figs 1C, D, 4A), as in other carettochelyids (Walther 1922; Danilov et al. 2017; Joyce et al. 2018). The quadrate also completely encloses the incisura columella auris and forms a small antrum postoticum (Figs 3A, 4A), which extends posterodorsolaterally through the quadrate and squamosal, as in *Anosteira pulchra* (Joyce et al. 2018) and *Anosteira maomingensis* (Danilov et al. 2017). Along its posterior surface, the quadrate forms the quadrate fossa (Fig. 4B), as in other carettochelyids (Harrassowitz 1922; Walther 1922; Danilov et al. 2017; Joyce et al. 2018). The quadrate fossa is broad and deep, as in more derived members of the clade (Joyce 2014).

Prootic. The prootics are intact in BSPG 1991 II 130. Within the upper temporal fossa, the prootic contacts the parietal anteromedially, the supraoccipital posteromedially, the quadrate laterally, and the opisthotic posteriorly, and forms the medial margin of the foramen stapedio-temporale (Fig. 1A). Ventrally, the prootic contacts the parabasisphenoid medially, the pterygoid ventrally, the quadrate laterally, and, likely, the epipterygoid anteroventrolaterally (Figs 1B, E, 3). The prootic forms the greater half of the processus trochlearis oticum, which is medially continuous with a prominent ridge formed by the descending process of the parietal (Figs 1B, E, 3). The anterior margin of the process overhangs the lower temporal fossa and forms a broadly concave surface for the adductor musculature and associated tendons. Within the lower temporal fossa, the prootic forms the posterior margin of the foramen nervi trigemini *sensu stricto*, i.e., the opening through which the maxillary and mandibular nerve rami of the trigeminal nerve system pass (“external trigeminal foramen” of Evers et al. 2019), and the medial margin of the mandibular artery foramen, which was labelled as the “posterior” foramen nervi trigemini by Havlik et al. (2014) (Figs 1E, 3). These foramina and the associated canalis cavernosus are described in conjunction further below, as the morphology seen in *Allaeochelys libyca* is quite unusual. Within the braincase, the prootic anteriorly forms the posterior portion of a deep cavity, which collectively with the parietal encapsulates the cerebral hemisphere, which appears to be notably large, as has also been reported for extant trionychids (Ferreira et al. 2023). Posterior to the foramen nervi trigemini *sensu stricto* of BSPG 1991 II 130, and ventral to the cerebral hemisphere imprints, the course of the trigeminal nerve tissue can be inferred to pass along the anteromedial surface of the prootic, which walls a broad cavum epiptericum. On its medial surface, the prootic forms the fenestra acustico-facialis, but the latter is

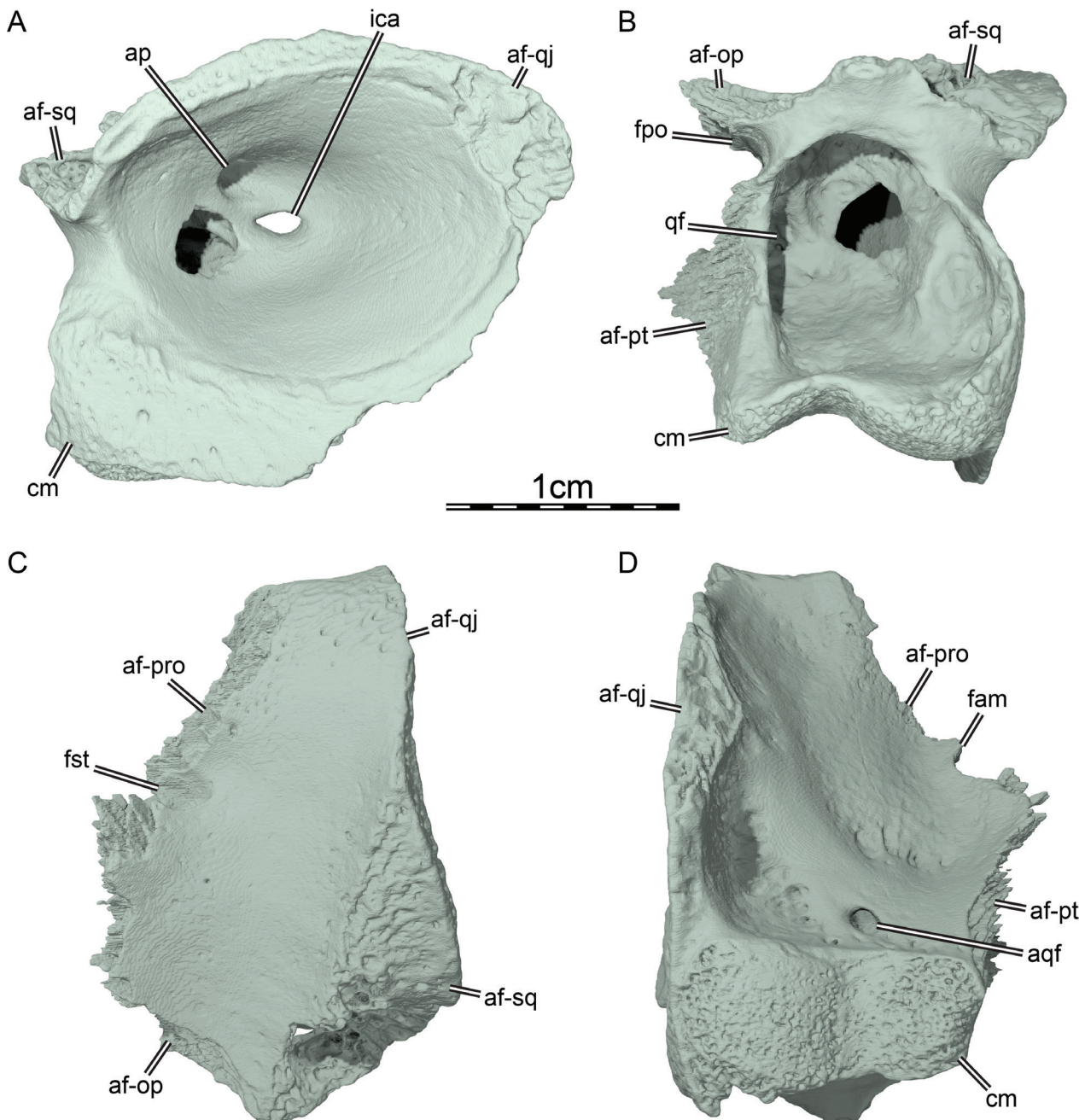


Figure 4. Three-dimensional renderings of the right quadrate of BSPG 1991 II 113. **A.** Lateral view; **B.** Posterior view; **C.** Dorsal view; **D.** Ventral view. Abbreviations: af-op, articulation facet for opisthotic; af-pro, articulation facet for prootic; af-pt, articulation facet for pterygoid; af-qj, articulation facet for quadratojugal; af-sq, articulation facet for squamosal; ap, antrum postoticum; aqf, anterior quadrate foramen; cm, condylus mandibularis; fam, foramen arteriomandibulare; fpo, fenestra postotica; fst, foramen stapedio-temporalis; ica, incisura columella auris; qf, quadrate fossa.

incompletely preserved as portions of the prootic are missing posteromedially. Within the fenestra acustico-facialis, only the medial foramen of the canalis nervus facialis is fully preserved. The canalis nervus facialis extends laterally through the prootic and joins the medial margin of the cavum acustico-jugulare. The canal is extremely large in BSPG 1991 II 130. The canalis pro ramo nervi vidiani branches off the canalis nervus facialis just medial to the latter contact and extends ventromedially through the prootic and pterygoid to join the canalis caroticus internus (Fig. 2), which is the common condition in carettochelyids (Joyce et al. 2018; Rollot et al. 2021a). In BSPG 1991 II

130, a likely vidian nerve canal splits from the canalis caroticus internus at the level of its contact with the canalis pro ramo nervi vidiani and extends anteroventrally through the pterygoid. The preserved portion of this proposed vidian canal is, however, extremely short because of the damage that affects the anteroventral region of the cranium. The location of this canal within the pterygoid in that area of the cranium is nevertheless highly indicative of a canalis nervus vidianus. The preserved aspects of the facial nerve pattern in *Allaeochelys libyca* are nevertheless very similar to that of other carettochelyids (Joyce et al. 2018; Rollot et al. 2021a). Canals and foramina for the vestibulocochlear

nerves (CN VIII) are mostly lacking and only the ventral margin of one foramen remains preserved within the fenestra acustico-facialis, just anterodorsal to the medial foramen for the facial nerve canal. The prootic otherwise forms the anterior half of the endosseous labyrinth, the anterior half of the anterior semicircular canal, and the anterior half of the fenestra ovalis. The anterior half of the lateral semicircular canal is not fully enclosed by bone, and the prootic only forms the lateral margin of a groove that contained the anterior portion of the lateral semicircular duct. Lateral to the fenestra ovalis, there is no posterior recess in the prootic, as in *Carettochelys insculpta*. The prootic also forms the anteromedial wall of the cavum acustico-jugulare and the medial half of the canalis stapedio-temporalis. The foramen nervi trigemini *sensu stricto* (see above) is not truly preserved in BSPG 1991 II 130. Although there is an anteriorly concave notch in the anterior surface of the prootic, this likely represents parts of the prootic surface that forms the cavum epiptericum. The remainder of the foramen was likely formed by the epipterygoid, and not by the parietal. This can be inferred as the posterior end of the descending process of the parietal is completely preserved on the right side of BSPG 1991 II 130. Here, the epipterygoid articulated with a small antero-ventrally protruding bump of the prootic (Fig. 3A, B), which currently prohibits the parietal to enter the trigeminal foramen margin. In the extant *Carettochelys insculpta*, an exact same bump-like process serves as an articular process for a posterodorsal process of the epipterygoid, which excludes the parietal from the foramen nervi trigemini *sensu stricto*. Below, we argue that the trigeminal foramen *sensu stricto* was likely confluent with an opening for the mandibular artery, which is closely associated with the canalis cavernosus. This canal of turtles is a result of their basicranial evolution: Testudines have modified their cranioquadrate space during their early basicranial evolution (e.g., Gaffney 1990; Sterli and Joyce 2007; Anquetin et al. 2009; Sterli and de la Fuente 2010; Rabi et al. 2013; Ferreira et al. 2020), thereby trapping the lateral head vein in a canal called the canalis cavernosus (Gaffney 1979), which extends from the anterior aspect of the cavum acustico-jugulare between the pterygoid, quadrate and prootic into the secondary braincase of turtles, where the lateral head vein continues medial to the secondary braincase wall that is generally formed by the pterygoid and parietal (Gaffney 1979; Evers et al. 2019; Rollot et al. 2021a). BSPG 1991 II 130 has a morphology of the “cavernous” area that differs strongly from this generalized testudine bauplan. Our examination of comparative material shows that the morphology of BSPG 1991 II 130 is, however, also mirrored in *Carettochelys insculpta*, but the distinctness of this morphology has, to our knowledge, not been noticed or described before. In BSPG 1991 II 130, the most anterior aspect of the cavum acustico-jugulare does not become constricted to a broad canalis cavernosus as is the general condition in turtles. Instead, there is an anteriorly directed, large, circular opening that exits from the cavum acustico-jugulare directly into the vicinity of the mandibular artery foramen. Havlik et al. (2014) identified this opening

as the “posterior” trigeminal nerve foramen. However, the opening cannot be directly associated with the trigeminal nerve, because it is connected to the cavum acustico-jugulare, and not the cavum cranii, which houses the brain from where the cranial nerves stem. Instead, the opening is likely associated with the mandibular artery, which in many turtle groups passes from the cavum acustico-jugulare into the canalis cavernosus, from where it has different courses it can take to reach the mandible. In many turtles, the mandibular artery passes laterally through the trigeminal foramen (Albrecht 1976), but it can also pass through the interorbital foramen as in *Dermatemys mawii* (Evers et al. 2022), or it can pass through a separate foramen opening from the canalis cavernosus into the temporal fossa, as in some testudinids like gopher tortoises, but also as in *Chelonia mydas* (e.g., McDowell 1961; Crumly 1982, 1994; Evers and Benson 2019; Rollot et al. 2021a). In *Carettochelys insculpta*, there is no separate mandibular artery foramen, but the trigeminal foramen is posteroventrally elongated (Fig. 3C, D). Instead of being a nearly circular or slightly oval foramen, the trigeminal opening is stretched and slightly curved. Hereby, the posteroventral aspect of the foramen essentially opens into the canalis cavernosus. This morphology suggests that the elongated trigeminal foramen of *Carettochelys insculpta* essentially incorporates a mandibular foramen. Herein, we call this morphology the “trigeminal foramen *sensu lato*”. The opening from the cavum acustico-jugulare of BSPG 1991 II 130 likely represents the posteroventral part of an incompletely preserved trigeminal foramen *sensu lato*. In BSPG 1991 II 130 and *Carettochelys insculpta*, the trigeminal foramen *sensu lato* is formed largely by the quadrate and prootic, with a ventral contribution of the pterygoid. Whereas in the incompletely preserved BSPG 1991 II 130 it looks like a canalis cavernosus is entirely reduced, the morphology of *Carettochelys insculpta* shows otherwise: in the extant form, the epipterygoid forms a bony bridge from the pterygoid region of the trigeminal foramen *sensu lato* to the descending process of the parietal (Fig. 3C, D). Hereby, the epipterygoid forms the anterolateral wall of a tightly constricted space between the epipterygoid, pterygoid and prootic, which clearly corresponds to a strongly size-reduced canalis cavernosus. In BSPG 1991 II 130, the epipterygoid is not preserved, so that the impression of a complete absence of the canalis cavernosus is given. However, a small process of the prootic in the dorsal margin of the partly preserved trigeminal foramen *sensu lato* of BSPG 1991 II 30 (Fig. 3A, B) suggests that an epipterygoid with similar contacts and shape as in *Carettochelys insculpta* (Fig. 3C–F) was once present. Thus, the large, circular foramen of BSPG 1991 II 130 likely corresponds to the part of the trigeminal foramen *sensu lato* through which the mandibular artery would pass into the temporal cavity, and the likely confluence with the trigeminal foramen is not evident due to the missing epipterygoid, which would have encased a size-reduced canalis cavernosus. An alternative interpretation of the region in BSPG 1991 II 130 would be that the sulcus cavernosus indeed is entirely reduced, and that the mandibular artery and lateral head vein both exit

into the temporal fossa. If the morphology of *Allaeochelys libyca* is informative about the plesiomorphic state of carettochelyid evolution, this scenario would require a complete loss of the canalis cavernosus in *Allaeochelys* and then the re-evolution of a size-reduced canalis cavernosus in *Carettochelys insculpta*, which we think is less likely.

Opisthotic. The two opisthotics are damaged and lack their most anteromedial portion, which contributes to the hiatus acusticus, and most of the processus interfenestralis. The opisthotic contacts the prootic anteriorly, the supraoccipital medially, the quadrate laterally, the exoccipital posteroventromedially, and the pterygoid posteroventrolaterally (Fig. 1A, F). A small contact between the basioccipital and processus interfenestralis of the opisthotic might have been present, but is obscured by damage. The opisthotic forms the posterior half of the endosseous labyrinth, the lateral semicircular canal, and the posterior half of the posterior semicircular canal. The most lateral aspect of the left processus interfenestralis is preserved, which allows assessing that the opisthotic forms the posterior half of the fenestra ovalis and that

the processus interfenestralis ventrally contacts the pterygoid. The amount of damage that affects the processus interfenestralis, however, prevents us to observe any other structure to which the process usually contributes in carettochelyids. We are therefore unable to provide any anatomical details about the fenestra perilymphatica or the foramina associated with the glossopharyngeal nerve course. The processus interfenestralis forms the anterior wall of the recessus scalae tympani, which is notably large in BSPG 1991 II 130. Posteriorly, the opisthotic forms the posterior wall to the recessus scalae tympani that ventrally contacts the pterygoid and forms the medial margin of the fenestra postotica (Fig. 5A). At the level of the suture with the pterygoid, the opisthotic forms alongside the latter bone a small canal that extends posterolaterally and joins the back of the cranium by means of a foramen formed by these two bones (Fig. 5A). The canal and foramen may have served as a passage for the glossopharyngeal nerve, as the latter is known to extend posterolaterally within the recessus scalae tympani and through the fenestra postotica in turtles (Soliman 1964; Gaffney 1979).

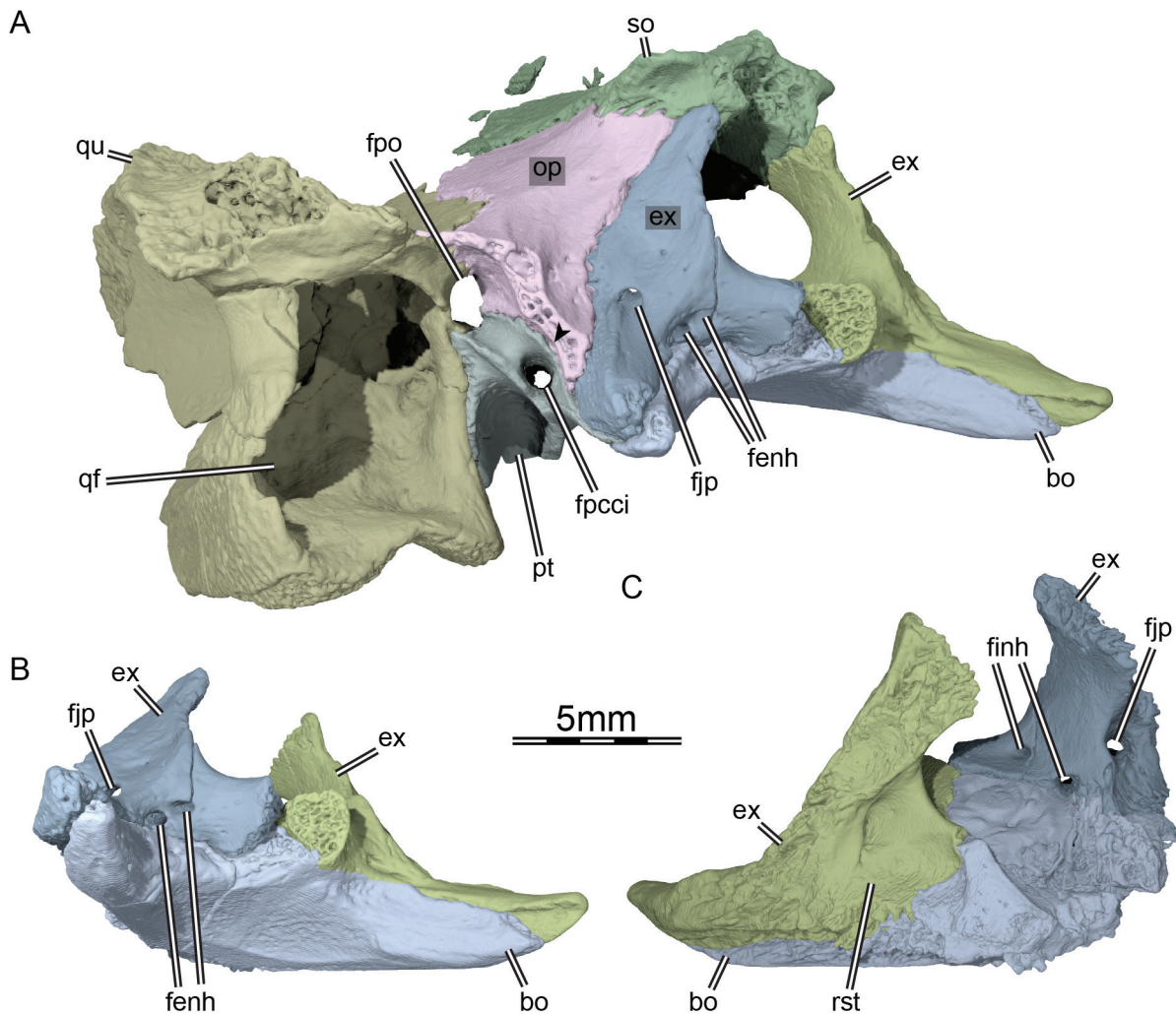


Figure 5. Three-dimensional renderings of the left posterior portion of BSPG 1991 II 113. **A.** Posterolateral view; **B.** Posteroventrolateral view; **C.** Anterodorsolateral view. Abbreviations: bo, basioccipital; ex, exoccipital; fenh, foramen externum nervi hypoglossi; finh, foramen internum nervi hypoglossi; fjp, foramen jugulare posterius; fpcci, foramen posterius canalis carotici interni; fpo, fenestra postotica; op, opisthotic; pt, pterygoid; qp, quadrate fossa; qu, quadrate; rst, recessus scalae tympani; so, supraoccipital. Black arrowhead indicates the position of the foramen oropharyngeale.

Supraoccipital. The supraoccipital is incomplete, lacking its most anterior and anterodorsal parts and the crista supraoccipitalis almost completely. The supraoccipital contacts the parietal anteriorly, the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipital posteroventrolaterally (Fig. 1A, F). The supraoccipital forms the posterior half of the braincase roof, the posterior half of the anterior semicircular canal, the anterior half of the posterior semicircular canal, the dorsal margin of the hiatus acusticus, and the dorsal margin of the foramen magnum. Although the crista supraoccipitalis is broken off, a small portion of the mediolaterally expanded plate usually seen in carettochelyids is preserved (Fig. 1A). The expanded plate starts posterior to the level of the prootic-opisthotic contact, just medial to the contact between the supraoccipital and opisthotic. In dorsal view, it is apparent that the lateral margins of the preserved portion of the expanded plate are slightly concave, and seem to slightly broaden again towards the posterior (Fig. 1A), suggesting that the expanded plate of the crista supraoccipitalis was broader posteriorly, as in *Carettochelys insculpta* (Joyce 2014), but not *Anosteira pulchra* (Joyce et al. 2018).

Basioccipital. The basioccipital is almost complete, only lacking a small portion around the occipital condyle. The basioccipital can generally be differentiated in the CT scans from the exoccipitals, although the suture between the basioccipital and right exoccipital fades away slightly within the right tuberculum basioccipitale. The basioccipital contacts the parabasisphenoid anteriorly, the pterygoid laterally, and the exoccipital posterodorsolaterally and posterodorsally (Figs 1B, F, 5). The contact of the basioccipital with the parabasisphenoid is mediolaterally elongate in ventral view, but is actually restricted to the most central aspect of the two bones more dorsally. This creates a depression lateral to the basioccipital-parabasisphenoid contact that expands the endosseous labyrinth ventrally. A crista basis tubercula basalis is likely absent, although this may be the result of the light damage that affects the anterodorsal surface of the basioccipital (Fig. 5C). In ventral view, the central part of the basioccipital forms a shallow depression that laterally reaches the tubercula basioccipitale, and posteriorly extends up to the occipital condyle (Fig. 1B). The tubercula basioccipitale are posteriorly elongate (Figs 1B, 5), as in *Carettochelys insculpta* (Walther 1922; Joyce 2014) and *Allaeochelys crassesculpta* (Harrassowitz 1922), but different from the short processes seen in *Anosteira pulchra* (Joyce et al. 2018). The occipital condyle is greatly damaged and only the base of the exoccipital lobes is preserved (Figs 1F, 5A, B). The preserved portion neither allows to determine with confidence to which extent each bone contributed to the condyle, nor how many lobes were actually forming the condyle. Although the basioccipital is exposed ventromedially between the exoccipitals, a slight reduction in width of the basioccipital towards the posterior is apparent in the μ CT image stack, but our observations are not sufficient to determine with confidence the morphology of the occipital condyle in BSPG 1991 II 130.

Exoccipital. The exoccipitals are almost complete, only the portion around the occipital condyle is damaged. The exoccipital contacts the supraoccipital dorsally, the opisthotic laterally, the pterygoid ventrolaterally, and the basioccipital ventrally (Figs 1F, 5). The exoccipital forms the posterolateral wall of the braincase and the lateral margin of the foramen magnum. Within the braincase, the exoccipital forms two internal foramina for the hypoglossal nerve (Fig. 5C). The more anterior foramen is smaller and located just above the suture between the exoccipital and basioccipital. The other foramen is larger and located more posteriorly, at the level of the foramen magnum. Both foramina lead into separate canalis nervi hypoglossi that extend posterolaterally through the exoccipital. The exterior foramina nervi hypoglossi are separate but close to one another, located in a shallow cavity that lies lateral to the occipital condyle and just dorsal to the exoccipital-basioccipital suture (Fig. 5A, B). Our interpretation differs from that of Havlik et al. (2014), who identified three external foramina for the hypoglossal nerve. Cross-examination of the μ CT scans available to us reveals that the most ventral of the three foramina identified by the latter authors actually corresponds to some porosity that is externally exposed, and that only two sets of internal and external foramina are present in *Allaeochelys libyca*, as in *Carettochelys insculpta* (Walther 1922) and *Anosteira pulchra* (FMNH PR966). The anteromedial surface of the exoccipital is concave and smooth and forms parts of the posterior wall of the recessus scalae tympani. Within the recessus scalae tympani, the exoccipital forms a moderately large but short canal that extends posterolaterally and joins the posterior surface of the exoccipital by means of the foramen jugulare posterius, which is located just dorso-lateral to the foramina externum nervi hypoglossi (Fig. 5). Medially, the exoccipital forms the posterior margin of the foramen jugulare anterius, i.e., the internal opening between the recessus scalae tympani and the braincase. The exoccipital also forms the dorsal part of the elongate tubercula basioccipitale with an elongated posterolateral process (Figs 1F, 5).

Parabasisphenoid. The parabasisphenoid is broken at the anterior limit of the sella turcica. The anterior parts of the otherwise broad and flat rostrum basisphenoidale are therefore missing. The area around the clinoid process and retractor bulbi pits is damaged as well and we are not able to describe these structures. The parabasisphenoid contacts the palatine anteriorly, the pterygoid laterally, the prootic anterodorsolaterally, and the basioccipital posteriorly (Fig. 1B, E). The dorsal surface of the parabasisphenoid is concave and floors the braincase. The parabasisphenoid posteriorly forms a short, thin sheet of bone that underlies the basioccipital and gives the impression of a broad contact between the two bones, but the contact is dorsally limited to the most central portion of both the parabasisphenoid and basioccipital. The parabasisphenoid forms the dorsum sellae, which anteriorly projects to cover the sella turcica. The foramina anterius

canalis carotici basisphenoidalis are located within the lateral corners of the sella turcica and lead into the canalis caroticus basisphenoidalis, which in BSPG 1991 II 130 are the anterior continuation of the canalis caroticus internus (Fig. 2B). The foramina posterius canalis nervi abducentis are located along the dorsal surface of the parabasisphenoid, posterolateral to the dorsum sellae (Fig. 2A). The foramen posterius canalis nervi abducentis leads into the canalis nervus abducentis, which extends anteriorly through the parabasisphenoid. The anterior path of the canal and bony contributions to the foramen anterius canalis nervi abducentis remain unknown as this area is damaged in BSPG 1991 II 130.

Endosseous labyrinth. The semicircular canals are thick, with the anterior semicircular canal being the longest of the three and that anteriorly joins the vestibule at the level of the anterior ampulla (Fig. 6). The posterior semicircular canal is shorter than the anterior canal and its posterior third is ventrally confluent with the posterior portion of the lateral semicircular canal, forming a large secondary common crus (Fig. 6B). The common crus is low and dorsally forms an embayment between the anterior and posterior semicircular canals, as in many other turtles (Fig. 6A; see Evers et al. 2019; Martín-Jiménez and Pérez-García 2021, 2022, 2023a, 2023b; Rollot et al. 2021b; Smith et al. 2023). The lateral semicircular canal is the shortest of the three, only forming a proper canal along the posterior half of the labyrinth that is barely detached from the vestibule, which results in a narrow, dorsoventral opening between the lateral canal and the vestibule (Fig. 6C). Anteriorly, the lateral canal merges with a large lateral ampulla. The morphology of the endosseous labyrinth of BSPG 1991 II 130 is extremely similar to that of NHMUK 1903.7.10.1 (*Carettochelys insculpta*). We are only able to identify two very subtle differences between the two endosseous labyrinths, namely a slightly thicker anterior semicircular canal in BSPG 1991 II 130 and a slightly more excavated dorsal embayment of the common crus appears BSPG 1991 II 130.

Discussion and conclusions

The availability of μ CT scans and complete segmentation of BSPG 1991 II 130 allows us to reinterpret several features that were originally misinterpreted by Havlik et al. (2014). The opening originally interpreted as the “posterior” foramen nervi trigemini actually corresponds to the posterior end of a trigeminal foramen *sensu lato*, i.e. the confluent foramina for the trigeminal nerve and mandibular artery. The mandibular artery is inferred to pass directly into the lower temporal fossa by reference to the circulatory system described for *Carettochelys insculpta* by Rollot et al. (2021a). The foramen nervi trigemini *sensu lato* is incompletely preserved in BSPG 1991 II 130, as the epipterygoid is absent. Havlik et al. (2014) identified an epipterygoid beneath the processus trochlearis oticum and between the mandibular artery foramen and foramen nervi trigemini *sensu stricto*. The μ CT scans of BSPG 1991 II 130 show that the sutures of this purported epipterygoid with the surrounding bones, i.e., the quadrate, prootic, and pterygoid, actually correspond to a crack, and that the epipterygoid is not preserved. Ironically, we infer that an epipterygoid would have likely sat in a similar area, forming a narrowly constricted and size-reduced canalis cavernosus, as in *Carettochelys insculpta*. This highly unusual ‘cavernous’ area seems to be a derived feature of at least *Carettochelyinae*. The μ CT scans and three-dimensional reconstructions also allowed us to confirm the presence of two internal and external hypoglossal foramina with their associated canals, versus the three external foramina labeled by Havlik et al. (2014) in the figures of their contribution. We also reinterpret the suture between the exoccipital and basioccipital, which is nearly horizontal and located more ventrally than interpreted by Havlik et al. (2014), but we note that in the μ CT scans, this suture fades away towards the posterior, which likely made its identification on the specimen without back-up from tomographic data difficult. Finally, we identify a small piece of bone located anterior to the right pterygoid-parabasisphenoid suture as a remnant of

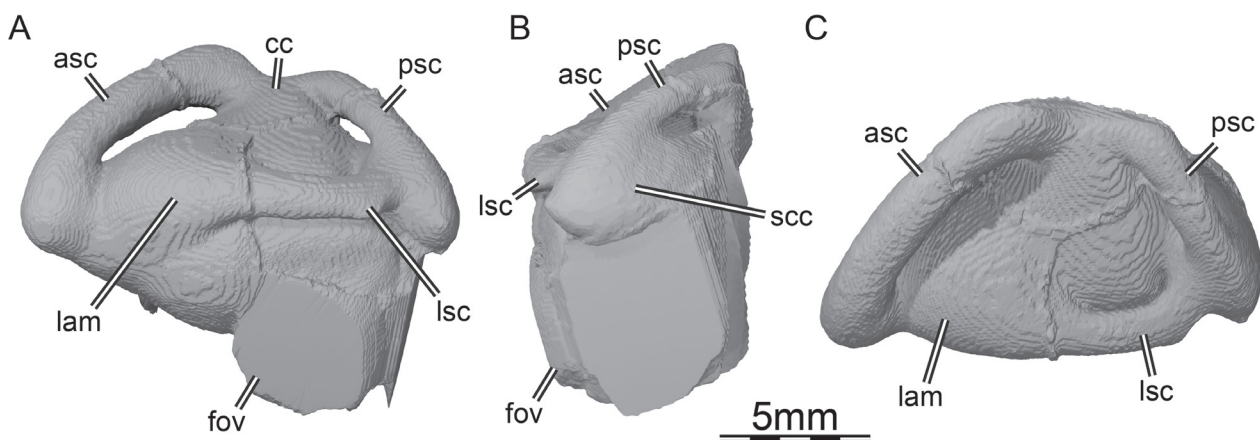


Figure 6. Three-dimensional renderings of the left endosseous labyrinth of BSPG 1991 II 113. **A.** Lateral view; **B.** Posterior view; **C.** Dorsal view. Abbreviations: asc, anterior semicircular canal; cc, common crus; fov, fenestra ovalis; lam, lateral ampulla; lsc, lateral semicircular canal; psc, posterior semicircular canal; scc, secondary common crus.

the palatine, but acknowledge that the identification of this bone was only possible thanks to the μ CT scans. Our reconstructions of the preserved portions of the facial nerve and internal carotid artery canals also show that the circulatory and innervation systems of *Allaeochelys libyca* are likely identical to that of *Anosteira pulchra* (Joyce et al. 2018) and *Carettochelys insculpta* (Rollot et al. 2021a). Despite differences in the location of the foramen posterius canalis carotici interni, all three taxa share the absence of the canalis caroticus lateralis and the location of the split of the facial nerve into its subordinate branches, i.e., the vidian and hyomandibular nerves, that is located within the prootic. Although the circulatory and innervation systems remain unknown for the most early branching carettochelyids *Kizylkumemys khoratensis* and *Kizylkumemys schultzi*, current knowledge suggests that all carettochelyids likely have very similar systems.

Despite the reinterpretation of several anatomical features and the new information provided in the present contribution, the differences we highlighted between our study and the original work of Havlik et al. (2014) do not challenge the validity of *Allaeochelys libyca*. The insights provided herein will nevertheless be reflected in phylogenetic matrices, as scorings of several characters will have to be updated accordingly (e.g., subdivision of the foramen nervi trigemini). We also believe that some of our observations have the potential to be transcribed into new phylogenetic characters, such as the presence versus absence of a contact between the crista cranii of the frontal and the descending process of the prefrontal, the presence versus absence of an additional canal and associated foramina in the opisthotic for the glossopharyngeal nerve, or the short versus elongate tubercula basioccipitale. Even if scoring changes and new characters are not expected to drastically change the phylogenetic relationships of carettochelyids, they might allow a better resolution within some subclades of carettochelyids. *Anosteira* spp. and *Allaeochelys* spp. are commonly retrieved as unresolved subclades (Havlik et al. 2014; Danilov et al. 2017; Carbot-Chanona et al. 2020), and the inclusion of new characters might allow a better resolution within the latter. The inclusion in phylogenetic matrices of the newly described *Carettochelys niahensis* (White et al. 2023), even if the reported material is fragmentary, might provide novel insights as well.

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