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Neuroanatomical Study and Three-Dimensional Reconstruction of the Skull of a Bothremydid Turtle (Pleurodira) Based on the European Eocene *Tartaruscola teodorii*

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Abstract: Bothremydidae is a successful lineage of pleurodiran turtles that lived from the Cretaceous to the Paleogene, and are found in most continents of both Laurasia and Gondwana. Despite numerous known cranial remains of this clade, no study on the complete neuroanatomical reconstruction of any of its representatives has been published so far. *Tartaruscola teodorii* is a French lower Eocene member of Foxemydina (Bothremydini), known by two skulls. It is one of the few bothremydids identified in the Cenozoic record of Europe. The present study includes the complete three-dimensional reconstruction of each of the cranial bones of both the holotype and the paratype of *T. teodorii*, increasing the anatomical information about this species. The virtual reconstruction of its neuroanatomical structures is presented here, including the cranial cavity, nerves, nasal cavity, inner ears, and carotid arteries. This analysis is the first detailed neuroanatomical study performed for a member of Bothremydidae. In addition, the virtual reconstruction of the neuroanatomical structures of some extant taxa belonging to several pleurodiran lineages (Chelidae, Pelomedusidae and Podocnemididae), are also carried out and analyzed, so that the comparative framework for Pleurodira is remarkably improved.

Keywords: Pan-Pleurodira; Bothremydidae; neuroanatomy; cranial anatomy; CTscan



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1. Introduction

The computed tomography is a very useful and non-invasive technique to known the anatomy of the inner cranial structures and cavities of the skull without damaging the specimens [1,2]. The information on the neuroanatomy of extinct species, resulting from the application of these scanning techniques and their subsequent processing, can provide relevant data on their sensory capabilities and lifestyles (e.g., [3,4]). The use of these techniques has been employed for several lineages of vertebrates since the end of the twentieth century (e.g., [5,6]), its application for the analysis of extinct turtles being more recent than for other groups of reptiles, such as crocodylians and dinosaurs [7,8]. The first virtual three-dimensional neuroanatomical reconstruction of an extinct turtle, namely the European Upper Jurassic plesiochelyid *Plesiochelys etalloni* (Pictet and Humbert, 1857) [9], was published less than a decade ago [10]. Since then, the neuroanatomy of several extinct turtles has been analyzed, including basal taxa (i.e., undisputed members of Testudinata not belonging to the crown Testudines; see Lautenschlager et al. [11] for *Proganochelys quenstedti* Baur, 1887 [12]; Paulina-Carabajal et al. [13] for Meiolaniidae; Paulina-Carabajal et al. [14] for Helochelydridae; Martín-Jiménez et al. [15] for *Kallokibotion bajazidi* Nopcsa, 1923 [16]; and Pérez-García et al. [17] for Pleurosternidae), and also representatives of the crown Testudines. Most of the studies relative to the neuroanatomy of Testudines were concerned with eucryptodiran turtles or forms probably attributable to this lineage (see Evers and Joyce [18] for Sandownidae; Mautner et al. [19] and Paulina-Carabajal et al. [13] for Testudinidae; Evers et al. [20] for Protostegidae), very few extinct members of Pan-

Pleurodira (all of them belonging to the crown Pleurodira) having been considered. In fact, although partial neuroanatomical reconstructions of scarce extant members of Pleurodira have been included in some comparative studies [11,21], only those of some extinct species, not attributable to any of the clades that are part of current biodiversity, were published. The first one is a member of the extinct clade Peiopemydidae, *Yuraramirim montealtensis* Ferreira, Iori, Hermanson and Langer, 2018 [22], a Brazilian Upper Cretaceous (Turonian–Santonian) species. Its complete neuroanatomical reconstruction has been performed, based on the almost complete skull known for this taxon. A more recent study [23] includes the reconstruction and analysis of the posterior region of the cranial cavity (including inner ears, carotids, and some nerves) of a basal member of Podocnemididae, the Brazilian Upper Cretaceous (Santonian) *Amabilis uchoensis* Hermanson, Iori, Evers, Langer and Ferreira, 2020 [23], a species only known by a partial skull. In addition, the inner ear of the Moroccan Paleocene Bothremydini bothremydid *Bothremys maghrebiana* Gaffney, Tong and Meylan, 2006 [24], the cranial cavities of the Moroccan Upper Cretaceous podocnemidid *Hamadachelys escuillei* Tong and Buffetaut, 1996 [25], the Moroccan Paleocene Taphrosphyini bothremydid *Phosphatochelys tedfordi* Gaffney and Tong, 2003 [26], and the Brazilian Lower Cretaceous araripemydid *Araripemys barretoii* Price, 1973 [27]; and the internal carotid canals of the Moroccan Upper Cretaceous Cearachelyini bothremydid *Galianemys whitei* Gaffney, Tong and Meylan, 2002 [28] and the Moroccan Eocene Taphrosphyini bothremydid *Ummulisani rutgersensis* Gaffney, Tong and Meylan, 2006 [24], were also reconstructed by these authors [23] (see Supplementary Figure S12 for *Bothremys maghrebiana*, Supplementary Figures S13 and S14 for *Hamadachelys escuillei*, Supplementary Figures S14–S16 for *Phosphatochelys tedfordi*, Supplementary Figure S15 for *Araripemys barretoii*, Supplementary Figure S17 for *Galianemys whitei*, and Supplementary Figures S18 and S20 for *Ummulisani rutgersensis*). The carotids, vidian nerves system, and inner ears of the Malagasy Upper Cretaceous (Maastrichtian) representative of Sahonachelyidae *Sahonachelys mailakavava* Joyce, Rollot, Evers, Lyson, Rahantarisoa and Krause, 2021 [29], were reconstructed, based on the complete skull known for this species.

Three clades of Pleurodira are part of the current biodiversity, being represented in intertropical regions of the southern hemisphere. However, the paleobiogeographic distribution of this lineage, as well as its diversity, were notably greater during some intervals of the Late Cretaceous and Paleogene (see [30] and references therein). Thus, the extinct clade Bothremydidae (Pelomedusoides, Podocnemidoidea) is one of the best represented lineages of Pleurodira and even of Testudinata in the Upper Cretaceous to Eocene fossil record of several Laurasian and Gondwanan countries, considering both its abundance and its diversity (e.g., [24,31,32]). By contrast, no complete reconstruction of the neuroanatomy of a member of Bothremydidae is currently available, and only two studies, published before the use of the computed tomography scans for these analyses, have considered some neuroanatomical characters of this clade. The first is the description of two artificial latex casts, each of them coming from a North American Upper Cretaceous species: *Bothremys cooki* (Leidy, 1865) [33] and *Chedighaii barberi* (Schmidt, 1940) [34,35]. The other is a subsequent study of a natural endocast of *Chedighaii barberi* [36]. Although Hermanson et al. [23] encoded several neuroanatomical characters for some bothremyids, they only figured a few of the neuroanatomical structures of some of those taxa (see above).

This is the first study to reconstruct and describe the neuroanatomy of a bothremydid in detail. It is concerned with *Tartaruscola teodorii* Pérez-García, 2016 [37] (Bothremydini, Foxemydina), from the lower Eocene (early Ypresian) record of France [37] (Figure 1). This study is based on the holotype and paratype of the taxon, which are the only skulls of Bothremydidae identified in the Cenozoic record of Europe (Figure 1A–D). In addition, the complete virtual neuroanatomical reconstructions of various extant pleurodiran species, corresponding to the three clades living today (i.e., Chelidae, Pelomedusidae, and Podocnemididae), are also presented and analyzed, expanding the poor comparative neuroanatomical framework so far available for Pleurodira. Furthermore, the detailed analysis of the cranial anatomy of *Tartaruscola teodorii* allows us to improve the knowledge

about this species, one of the last indisputable representatives of Bothremydidae known worldwide, by the characterization of several hitherto unknown characters.

Institutional abbreviations: MACV, Museo de Anatomía Comparada de Vertebrados, Universidad Complutense de Madrid, Madrid, Spain; MNHN.F, Palaeontology Collection, Muséum national d'Histoire naturelle, Paris, France; MNHN.ZA.AC, Collection of Reptiles, Comparative Anatomy, Muséum national d'Histoire naturelle, Paris, France.

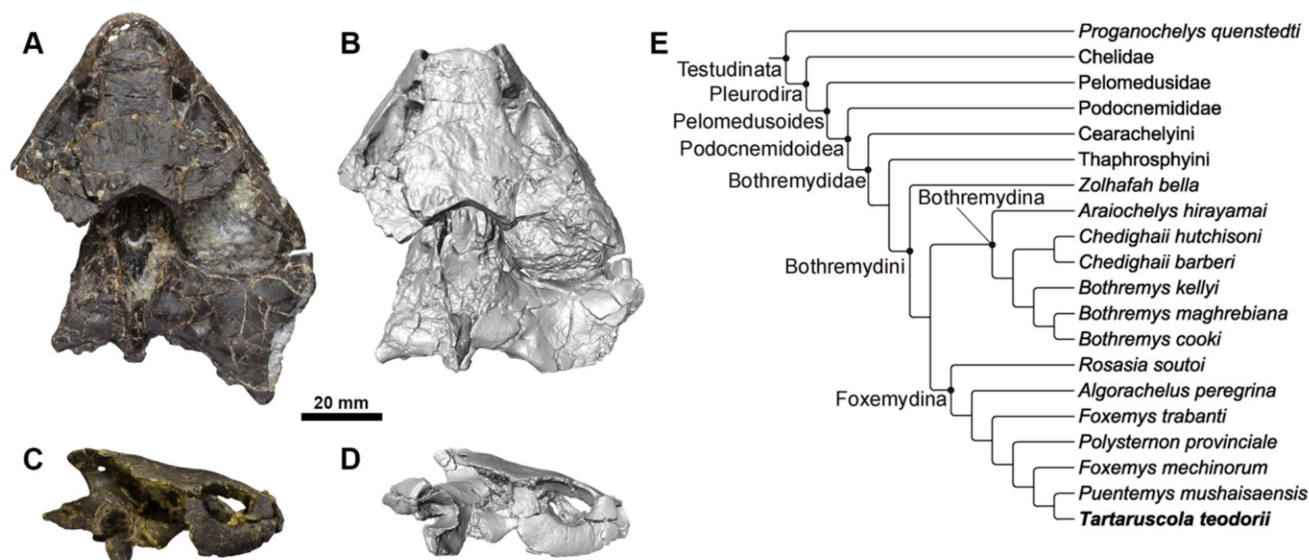


Figure 1. (A,B) Holotype (MNHN.F.SPP33) and (C,D) paratype (MNHN.F.SPP34) of *Tartaruscola teodorii* (Bothremydidae, Foxemydina), from the lower Ypresian (early Eocene) of Saint-Papoul (Aude, France), and phylogenetic position of the taxon. (A–D), photographs and (A,C) and virtual three-dimensional reconstructions of the skulls (B,D), in dorsal and (A,B), and right lateral (C,D) views. (E), Phylogenetic position of *Tartaruscola teodorii* in the single tree obtained through the phylogenetic analysis performed here, based on that proposed by Pérez-García [37].

2. Materials and Methods

Several skulls of extinct and extant representatives of the crown Pleurodira were CT-scanned and processed here. These are the holotype (MNHN.F.SPP33) and the paratype (MNHN.F.SPP34) of the French lower Eocene bothremydid *Tartaruscola teodorii* (Figures 1–5), and each of the following extant species: the chelids *Chelus fimbriata* (Schneider, 1783) [38] (MNHN.ZA.AC A9940) and *Hydromedusa tectifera* Cope, 1870 [39] (MNHN.ZA.AC 1870-9), the pelomedusid *Pelusios niger* (Duméril and Bibron, 1835) [40] (MNHN.ZA.AC 1934-371), and the podocnemidids *Podocnemis unifilis* Troschel, 1848 [41] (MACV 2667) and *Erymnochelys madagascariensis* (Grandidier, 1867) [42] (MNHN.ZA.AC 1946-71) (Figures 6 and 7).

All these skulls were scanned at the Servicio de Técnicas no Destructivas, of the Museo Nacional de Ciencias Naturales (Madrid, Spain). This process was all carried out through Nikon XT H-160 a high-resolution scanner. The parameters used to scan all these specimens and the number of images obtained in .DICOM format are indicated in the Supplementary File S1. Due to the length of the holotype of *Tartaruscola teodorii* relative to the maximum sample size admitted in this scanner, the anterior part of both premaxillae and maxillae, and the posterior part of the right opisthotic and squamosal could not be scanned (Figures 1, 2 and 4). Considering their relatively large sizes, the skulls of *Chelus fimbriata* and *Erymnochelys madagascariensis* were scanned twice (i.e., one of them applied to an area slightly greater than the anterior half of its length, and the other to an area slightly greater than the posterior, so that the middle area was scanned both times, facilitating the subsequent processing), excluding the rightmost lateral area. For the same reason, only the mid region of the skull of *Podocnemis unifilis* could be scanned using this high-resolution scanner, excluding the anteriormost, posteriormost, and both lateral regions. Due to this, the skulls of these three extant pleurodiran species were also scanned with a

scanner Optima CT600, at the Clínica Quirón Juan Bravo (Madrid, Spain), obtaining less images with a lesser resolution and higher voxel size, but allowing the processing of the complete specimens (see Supplementary File S1). The segmentation and three-dimensional reconstructions of the osseous elements and inner structures of all these skulls were carried out with the tools of the software Avizo 7.1 (VSG) obtaining three-dimensional meshes that were exported as files with a .STL format (Figures 1–7). Furthermore, in the case of both fossil skulls, each bone was individually reconstructed and figured using different colors (Figures 2 and 3). The models of the osseous elements of all the skulls and also those of the neuroanatomical structures of the extant species processed here remain unaltered, but Geomagic Studio 2014.3.0 was used to smooth the external surfaces of all reconstructed inner cavities of both specimens of *Tartaruscola teodorii*. The CT scans of the holotype and the paratype of *Tartaruscola teodorii*, as well as the cranial and neuroanatomical models, were uploaded to MorphoSource (see Data Availability Statement). The linear and angular measurements of the cavum cranii and the inner ears were obtained using the measure tools of Avizo 7.1, and the volumetric measures of the nasal and cranial cavities by the use of the Geomagic Studio 2014.3.0 tools (see Table 1 and Supplementary File S2). Bi-dimensional images of the skull and inner cavities had been achieved using the snapshot tools of Avizo 7.1. Finally, the figures were composed using Adobe Photoshop CS6. In addition to the comparison of the inner structures of *Tartaruscola teodorii* with those of the extant taxa processed here, all information available in the literature corresponding to both bothremydids [24,35,36] and other extant and extinct pleurodires [11,22,23,29], was also considered.

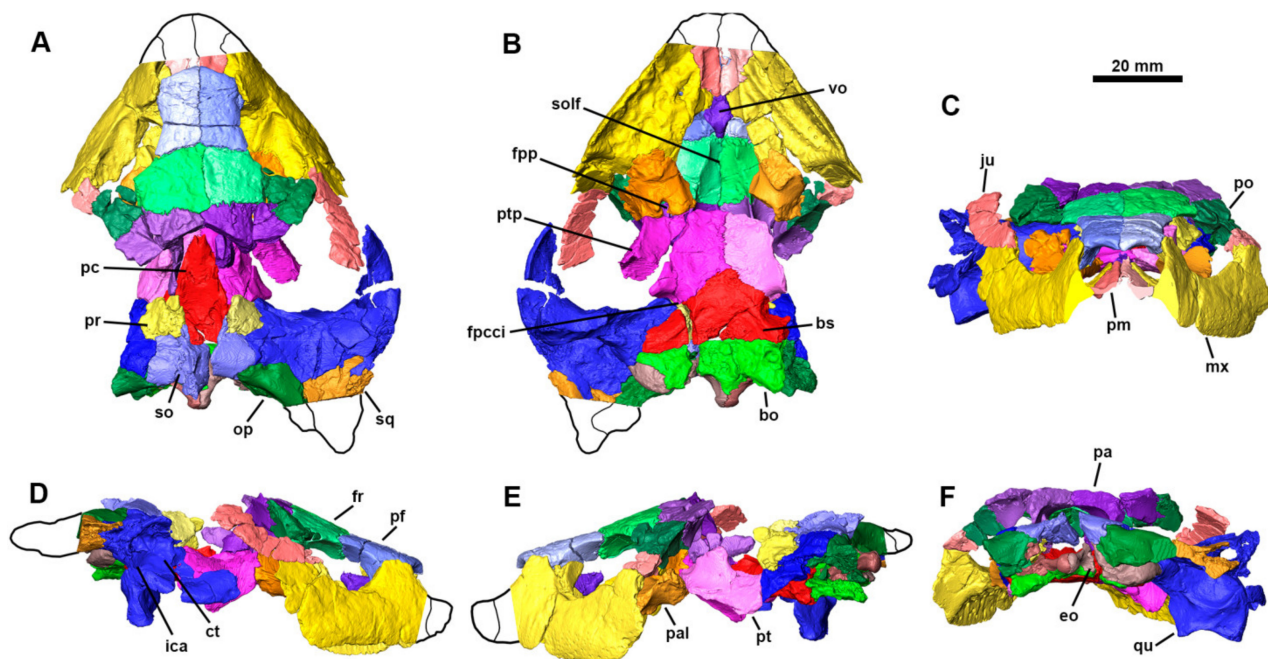


Figure 2. Virtual three-dimensional reconstruction of the specimen MNHN.F.SPP33, the holotype of *Tartaruscola teodorii* (Bothremydidae, Foxemydina), from the lower Ypresian (early Eocene) of Saint-Papoul (Aude, France), in which each bone is shown with a different color. The skull is presented in dorsal (A), ventral, (B), anterior (C), right lateral (D), left lateral (E) and posterior (F) views. Abbreviations: bo, basioccipital; bs, basisphenoid; ct, cavum tympani; eo, exoccipital; fpcci, foramen posterius canalis caroticum internus; fpp, foramen palatinum posterius; fr, frontal; ica, incisura collumela auris; ju, jugal; mx, maxilla; op, opisthotic; pa, parietal; pal, palatine; pc, processus clinoideus; pf, prefrontal; pm, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; ptp, processus trochlearis pterygoideus; qu, quadrate; so, supraoccipital; solf, sulcus olfactorius; sq, squamosal; vo, vomer.

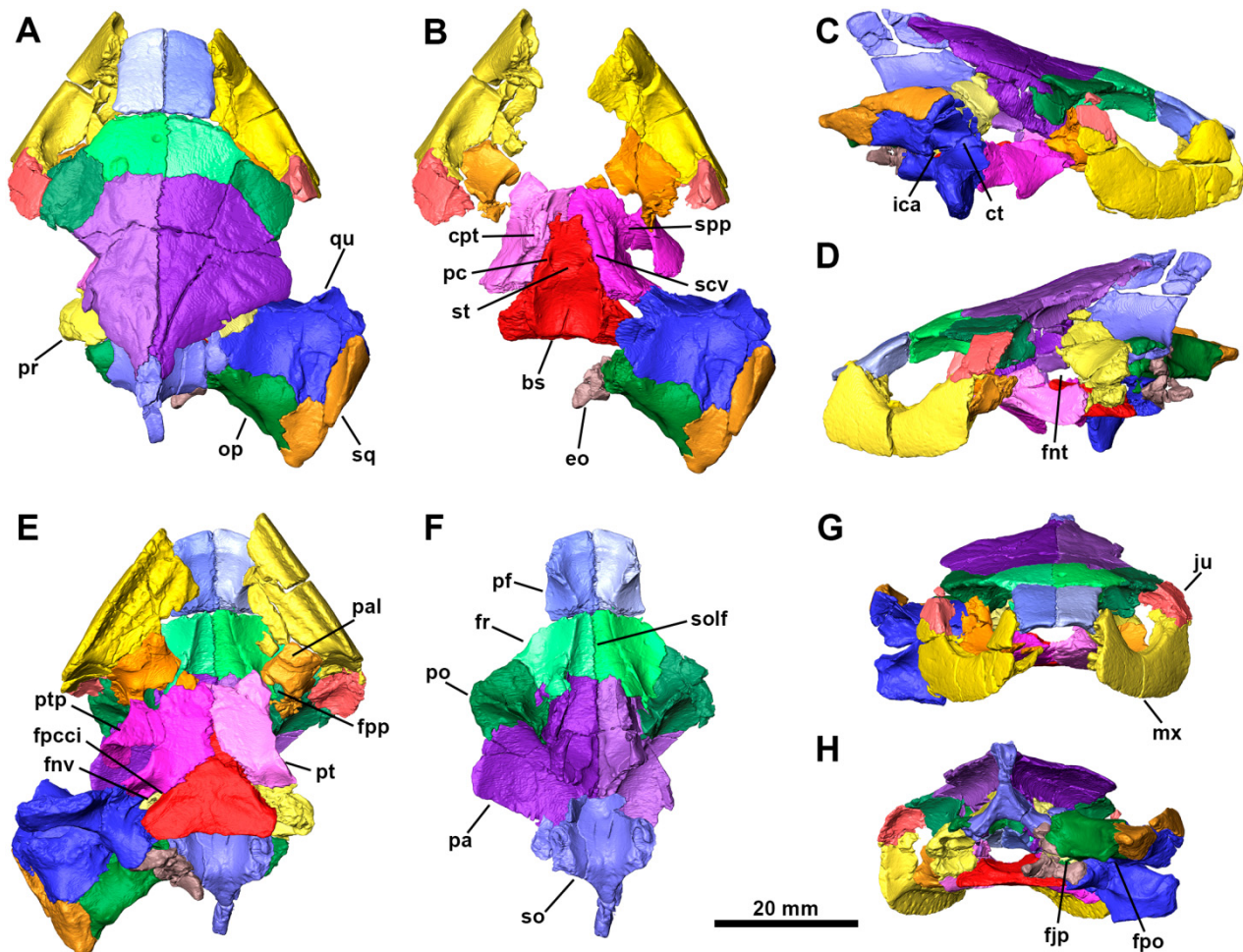


Figure 3. Virtual three-dimensional reconstruction of the specimen MNHN.F.SPP34, the paratype of *Tartaruskola teodorii* (Bothremydidae, Foxemydina), from the lower Ypresian (early Eocene) of Saint-Papoul (Aude, France), in which each bone is shown with a different color. The skull is presented in dorsal (A,B), right lateral (C), left lateral (D), ventral (E,F), anterior (G) and posterior (H) views. The bones of the cranial roof (prefrontals, frontals, parietals, postorbitals and supraoccipital) and prootics have been virtually removed in dorsal view (B) to show the dorsal surfaces of the palatal elements. All bones except the roof (prefrontals, frontals, parietals, postorbitals, and supraoccipital) have been virtually removed (F), to show the ventral view of that region. Abbreviations: bo, basioccipital; bs, basisphenoid; cpt, crista pterygoidea; ct, cavum tympani; eo, exoccipital; fjp, foramen jugulare posterius; fnt, foramen nervi trigemini; fnv, foramen nervi vidiani; fpcci, foramen posterius canalis caroticum internus; fpo, fenestra postotica; fpp, foramen palatinum posterius; fr, frontal; ica, incisura collumela auris; ju, jugal; mx, maxilla; op, opisthotic; pa, parietal; pal, palatine; pc, processus clinoideus; pf, prefrontal; pm, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; ptp, processus trochlearis pterygoideus; qu, quadrate; scv, sulcus cavernosus; so, supraoccipital; solf, sulcus olfactorius; spp, sulcus palatinopterygoideus; sq, squamosal; st, sella turcica; vo, vomer.

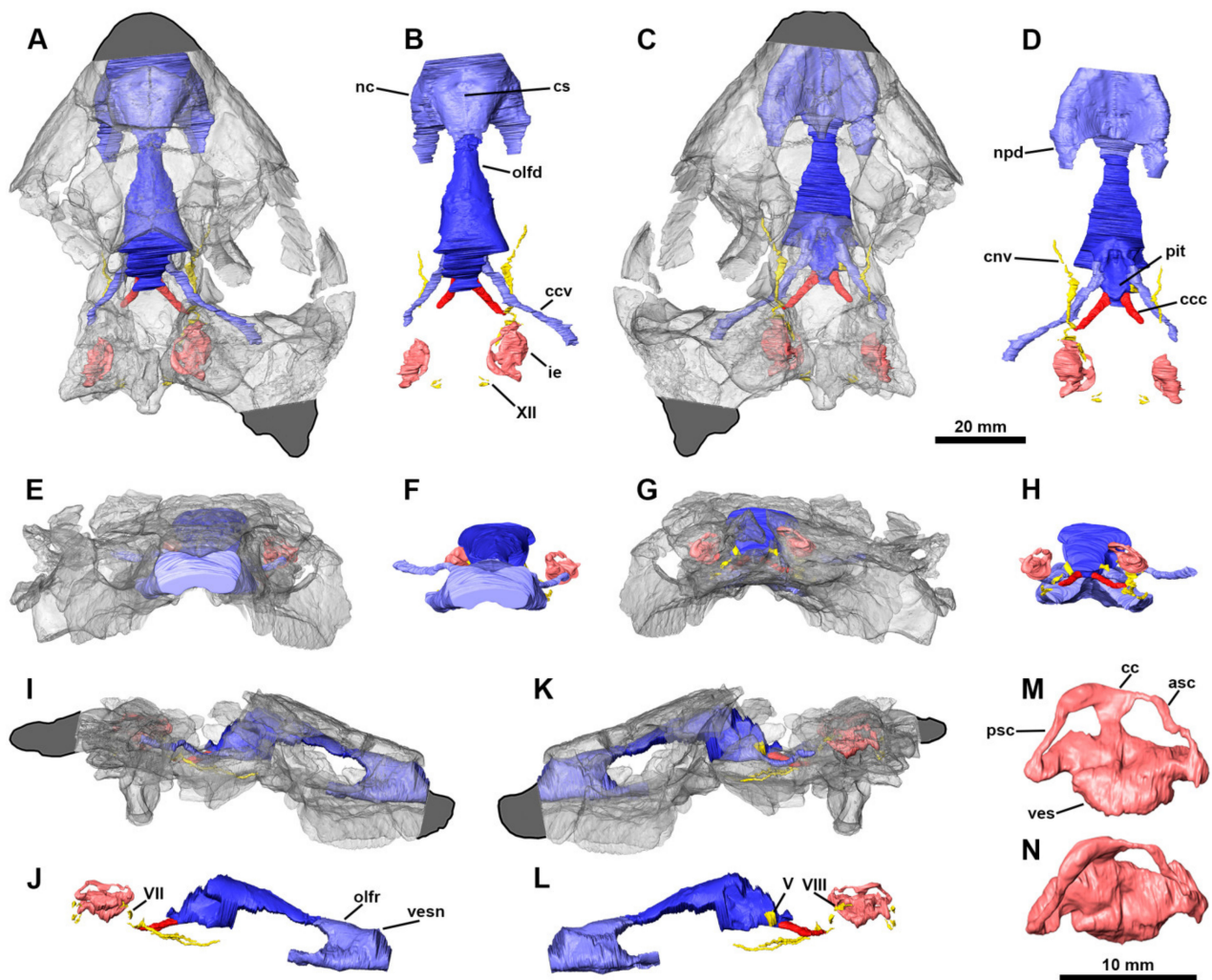


Figure 4. Osteological and neuroanatomical three-dimensional virtual reconstructions of the specimen MNHN.F.SPP33, corresponding to the holotype of *Tartaruscola teodorii* (Bothremydidae, Foxemydina), from the lower Ypresian (early Eocene) of Saint-Papoul (Aude, France). The osseous elements (in grey) have been visualized as transparent (A,C,E,G,I,K) in order to show the reconstruction of the endocast of cranial and nasal cavities (in blue) (B,D,F,H,J,L). The reconstructions are presented in dorsal (A,B), ventral (C,D), anterior (E,F), posterior (G,H), right lateral (I,J), and left lateral (K,L) views. (M,N), Right inner ear reconstruction in lateral (M) and dorsal (N) views. Abbreviations: asc, anterior semicircular canal; cc, crus communis; ccc, canalis caroticus cerebialis; ccv, canalis cavernosus; cnv, canalis nervi vidiani; cs, cartilaginous septum; ie, inner ear; nc, nasal cavities; npd, nasopharyngeal duct; olfd, olfactory duct; olfr, olfactory region; pit, pituitary fossa; psc, posterior semicircular canal; V, trigeminal nerve; ves, vestibulum; vesn, vestibulum nasi; VII, facial nerve; VIII, vestibulocochlear nerve; XII, hypoglossal nerve.

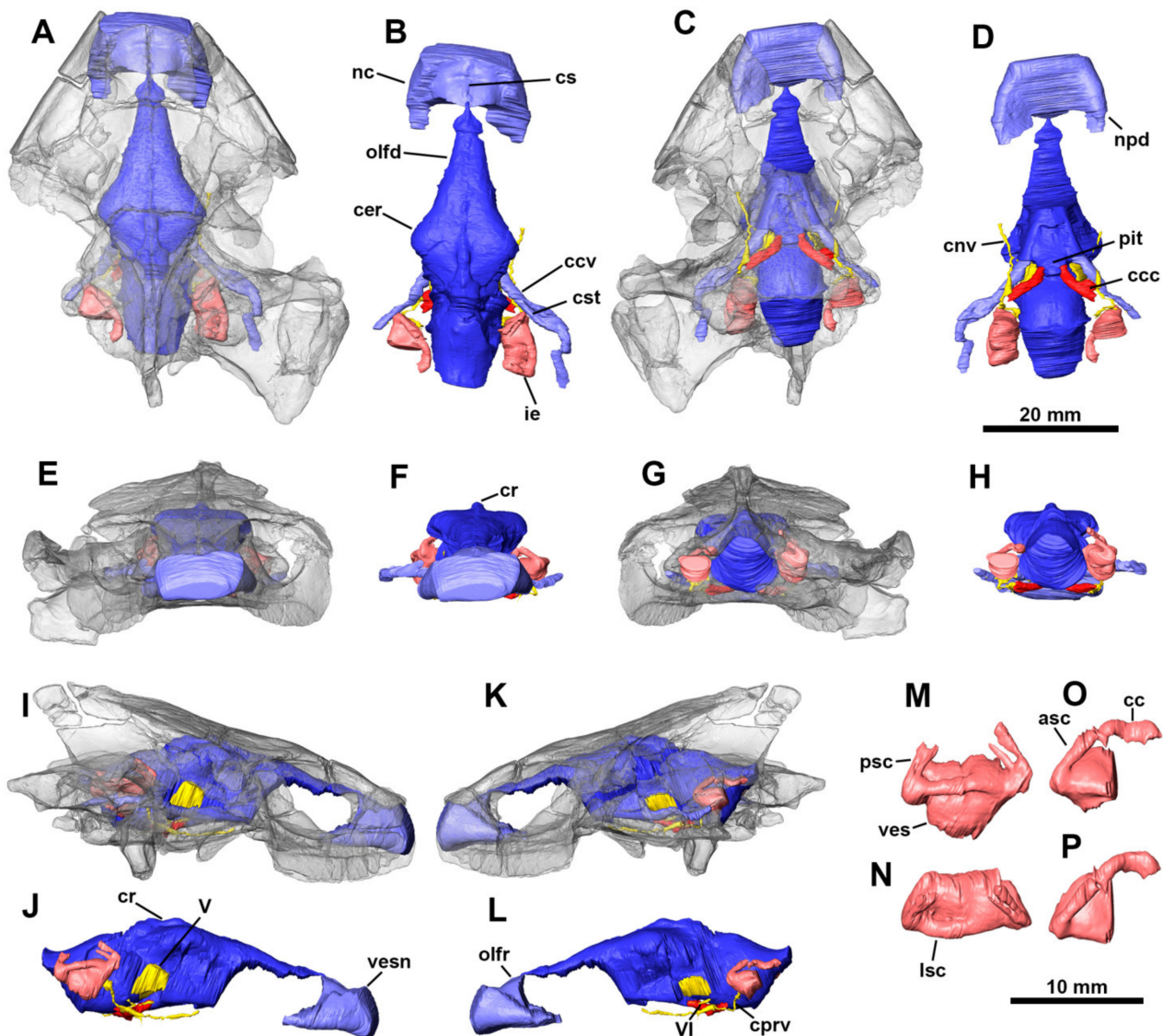


Figure 5. Osteological and neuroanatomical three-dimensional virtual reconstructions of the specimen MNHN.F.SPP34, the paratype of *Tartaruscola teodorii* (Bothremydidae, Foxemydina), from the lower Ypresian (early Eocene) of Saint-Papoul (Aude, France). The osseous elements (in grey) have been visualized as transparent (A,C,E,G,I,K) in order to show the reconstruction of the endocast of cranial and nasal cavities (in blue) (B,D,F,H,J,L). The reconstructions are presented in dorsal (A,B), ventral (C,D), anterior (E,F), posterior (G,H), right lateral (I,J), and left lateral (K,L) views. (M,N), Right inner ear reconstruction in lateral (M) and dorsal (N) views. (O,P), Left incomplete inner ear in lateral (O) and dorsal (P) views. Abbreviations: asc, anterior semicircular canal; cc, crus communis; ccc, canalis caroticus cerebialis; ccv, canalis cavernosus; cer, cerebral hemisphere; cnv, canalis nervi vidiani; cprv, canalis pro ramo vidiani; cr, cartilaginous ridge; cs, cartilaginous septum; cst, canalis stapedio-temporalis; ie, inner ear; lsc, lateral semicircular canal; nc, nasal cavities; npd, nasopharyngeal duct; olfd, olfactory duct; olfr, olfactory region; pit, pituitary fossa; psc, posterior semicircular canal; V, trigeminal nerve; ves, vestibulum; vesn, vestibulum nasi; VI, abducens nerve.

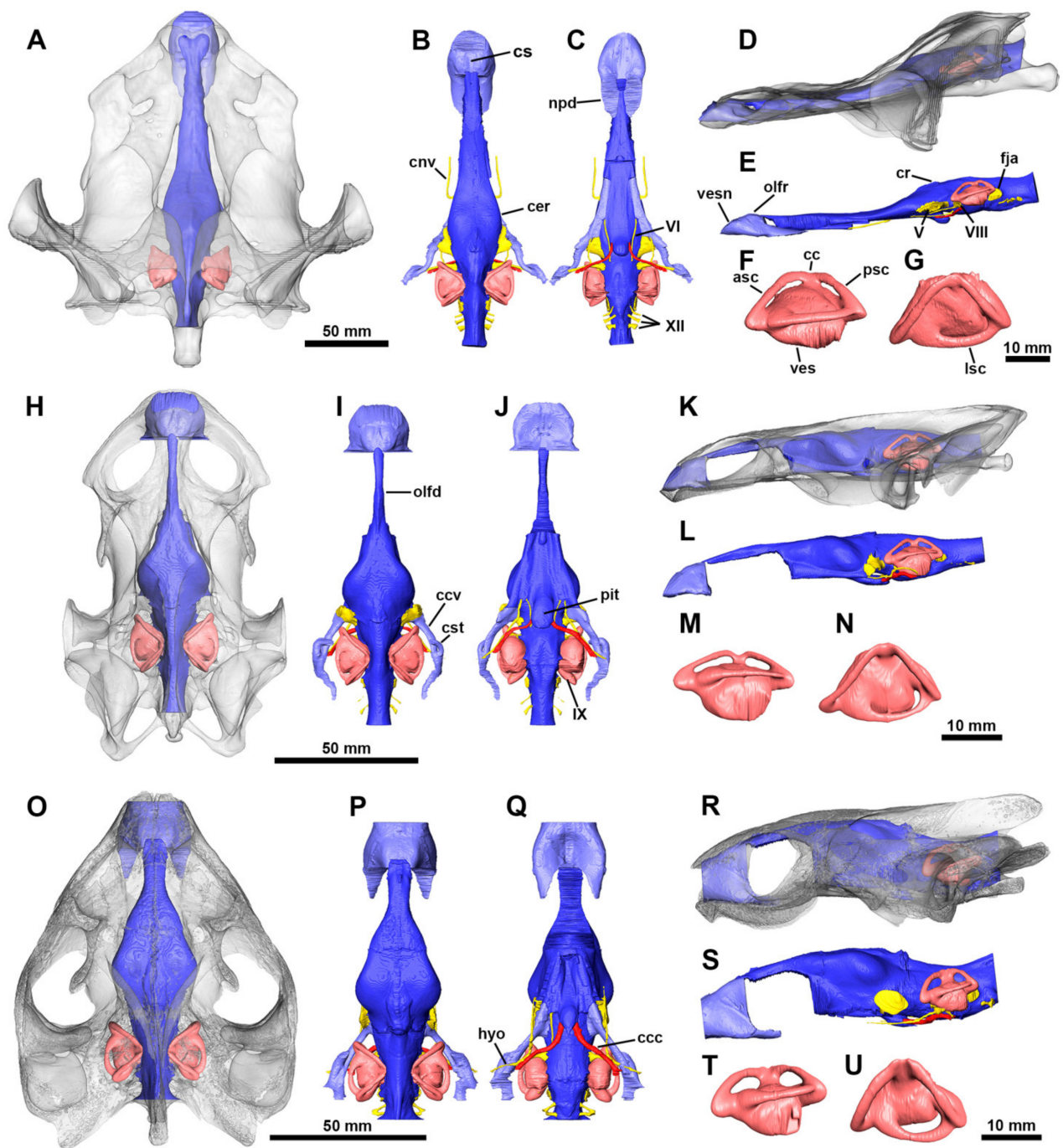


Figure 6. Osteological and neuroanatomical three-dimensional virtual reconstructions of the extant chelids *Chelus fimbriata* (MNHN.ZA.AC A9940; (A–G)) and *Hydromedusa tectifera* (MNHN.ZA.AC 1870-9; (H–N)), and the pelomedusid *Pelusios niger* (MNHN.ZA.AC 1934-371; (O–U)). The osseous elements (in grey) have been visualized as transparent (A,D,H,K,O,R) in order to show the reconstruction of the endocast of cranial and nasal cavities (in blue), and inner ears (in pink) (B,C,E,I,J,L,P,Q,S). The reconstructions are presented in dorsal (A,B,H,I,O,P), ventral (C,J,Q), and left lateral (D,E,K,L,R,S) views. Reconstruction of the left inner ears of these taxa (F,G,M,N,T,U) in lateral (F,M,T) and dorsal (G,N,U) views. Abbreviations: asc, anterior semicircular canal; cc, crus communis; ccc, canalis caroticus cerebialis; ccv, canalis cavernosus; cer, cerebral hemisphere; cnv, canalis nervi vidiani; cprv, canalis pro ramo vidiani; cr, cartilaginous ridge; cs, cartilaginous septum; cst, canalis stapedio-temporalis; fja, foramen jugulare anterius; hyo, hyomandibular branch of facial nerve; ie, inner ear; IX, glossopharyngeal nerve; lsc, lateral semicircular canal; nc, nasal cavities; npd, nasopharyngeal duct; olfd, olfactory duct; olfr, olfactory region; pit, pituitary fossa; psc, posterior semicircular canal; V, trigeminal nerve; ves, vestibulum; vesn, vestibulum nasi; VI, abducens nerve; VII, facial nerve; VIII, vestibulocochlear nerve; XII, hypoglossal nerve.

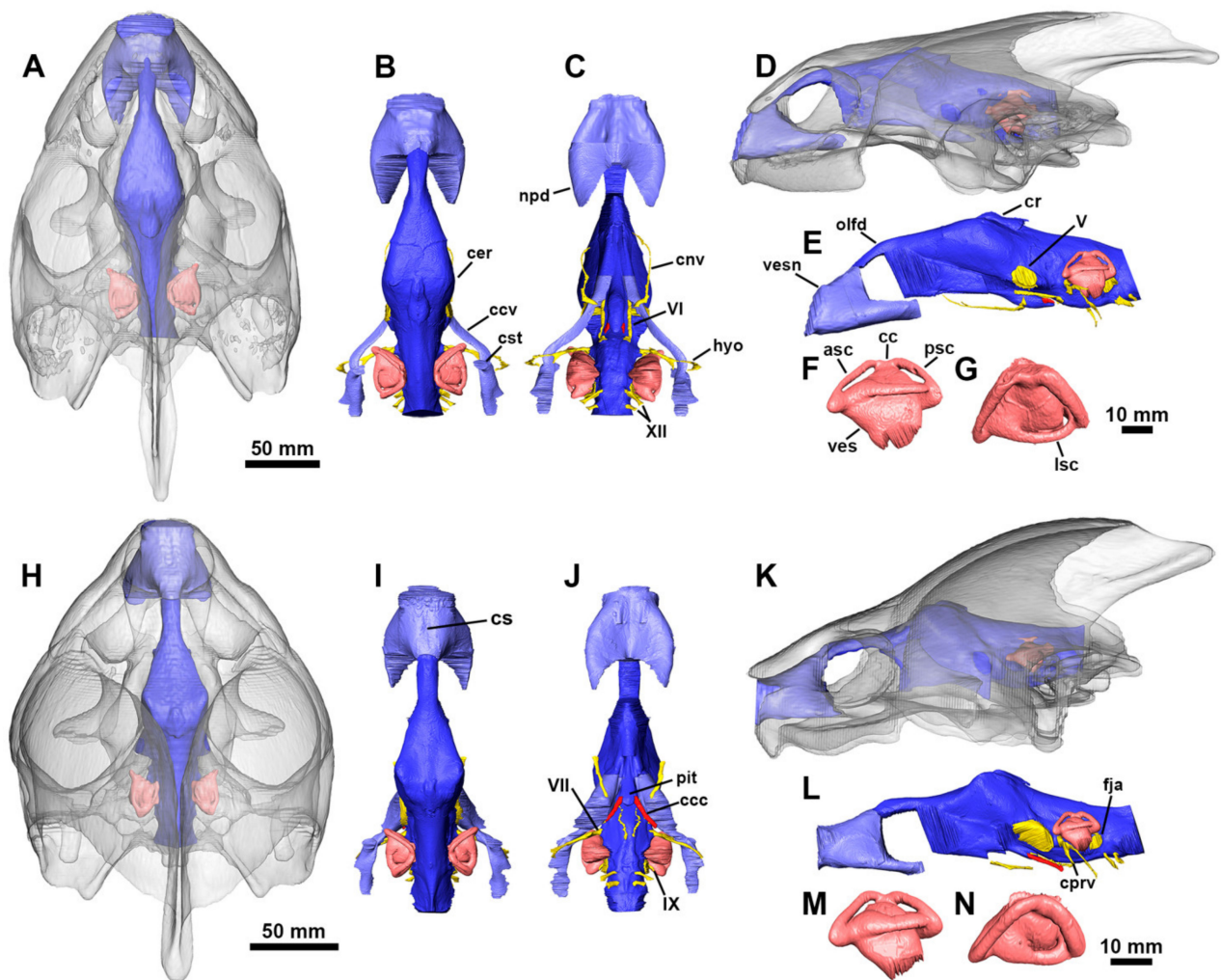


Figure 7. Osteological and neuroanatomical three-dimensional virtual reconstructions of the extant podocnemidids *Podocnemis unifilis* (MACV 2667; (A–G)) and *Erymnochelys madagascariensis* (MNHN.ZA.AC 1946-71; (H–N)). The osseous elements (in grey) have been visualized as transparent (A,D,H,K) in order to show the reconstruction of the endocast of cranial and nasal cavities (in blue) (B,C,E,I,J,L). The reconstructions are presented in dorsal (A,B,H,I), ventral (C,J), and left lateral (D,E,K,L) views. Reconstruction of the left inner ears of these taxa (F,G,M,N) in lateral (F,M) and dorsal (G,N) views. Abbreviations: asc, anterior semicircular canal; cc, crus communis; ccc, canalis caroticus cerebialis; ccv, canalis cavernosus; cer, cerebral hemisphere; cnv, canalis nervi vidiani; cprv, canalis pro ramo vidiani; cr, cartilaginous ridge; cs, cartilaginous septum; cst, canalis stapedio-temporalis; fja, foramen jugulare anterius; hyo, hyomandibular branch of facial nerve; ie, inner ear; IX, glossopharyngeal nerve; lsc, lateral semicircular canal; nc, nasal cavities; npd, nasopharyngeal duct; olfd, olfactory duct; olfr, olfactory region; pit, pituitary fossa; psc, posterior semicircular canal; V, trigeminal nerve; ves, vestibulum; vesn, vestibulum nasi; VI, abducens nerve; VII, facial nerve; VIII, vestibulocochlear nerve; XII, hypoglossal nerve.

In order to confirm the previous systematic identification of *Tartaruscola teodorii* as a member of Foxemydina, it was coded in the data matrix of [43], which was similar to that used in the paper where this taxon was defined (i.e., that in [37], based on the data matrix proposed by [24]), but that included a larger number of characters (based on [44]), modifications in the character states of some taxa, and the inclusion of the Spanish Cenomanian (Late Cretaceous) bothremydid *Algorachelus peregrina* Pérez-García, 2016 [43]. As in [43], *Proganochelys quenstedtii* was considered as the outgroup taxon; the data matrix was analyzed by a heuristic tree search, using TNT 1.5 [45], corresponding to a traditional search with 1000 replications of Wagner trees (using random addition sequences) followed by tree bisection recognition (TBR) as a swapping algorithm, saving 100 trees per replication; implied weighting was performed ($K = 3.0$); and a pruned strict consensus tree

was generated (*Bothremys arabicus* (Zalmout, Mustafa and Wilson, 2005) [46] being also identified here as a wild card taxon).

Table 1. Angles and ratios corresponding to the measurement of the pleurodiran taxa studied here.

Taxa	CavC An	MW/TL	OlfD/TL	L/Wpit	%NC	ASC/PSC An	PSC/ASC	Car An
<i>Tartaruscola teodorii</i> (MNHN.F.SPP33) ¹	-	-	-	0.8	-	81	0.9	98
<i>Tartaruscola teodorii</i> (MNHN.F.SPP34)	145	37.6	21.6	0.8	22.8	-	-	109
<i>Chelus fimbriata</i> (MNHN.ZA.AC A9940) ¹	172	20.2	20.4	1.0	16.8	80	0.8	113
<i>Hydromedusa tectifera</i> (MNHN.ZA.AC 1870-9)	170	25.8	30.3	1.4	14.1	93.5	0.8	110
<i>Pelusios niger</i> (MNHN.ZA.AC 1934-371)	171	33.2	22.1	1.7	19.7	81.5	0.9	95
<i>Podocnemis unifilis</i> (MACV 2667)	149	28.0	24.5	2.5	23.6	81.5	0.8	81
<i>Erymnochelys madagascariensis</i> (MNHN.ZA.AC 1946-71)	146	27.5	23.7	1.7	26.3	80.5	0.8	84

Abbreviations: CavC An, angle formed between the dorsal surface of the olfactory bulbs region and the dorsal end of the medulla oblongata; MW/TL, ratio between the maximum width (i.e., corresponding to the cerebral hemispheres) and the total length of the cavum cranii; OlfD/TL, ratio between the olfactory duct length and the total length of the cavum cranii; L/Wpit, ratio between the length and the width of the endocast of the pituitary fossa; %NC, ratio between the volume occupied by the nasal cavity and the total volume of the endocast; ASC/PSC An, angle formed by the anterior and posterior semicircular canals in dorsal view; PSC/ASC, ratio between the length of the posterior semicircular canal and that of the anterior semicircular canal; Car An, angle formed by the carotid arteries between the foramina posterius canalis carotici interni and the foramina antierius canalis caritici cerebri. ¹ The values of the inner ears represent the average of the two inner ears in all taxa except in *Chelus fimbriata*, in which the values correspond to the left inner ear, and in the holotype of *Tartaruscola teodorii*, in which the values correspond to the right inner ear.

3. Results

3.1. New Osteological Information and Phylogenetical Implications

The new osteological information obtained for the skull of *Tartaruscola teodorii* allows to identify some character states previously unknown for this taxon (see [37], and Supplementary File S3): state 1 (absence of parietal-squamosal contact) for character 15 (see Figure 3A); state 0 (jugal reaching the orbital margin) for character 20 (see Figure 2C–E or Figure 3C,D,G); state 0 (orbitonarial bar width roughly equal to or slightly less than diameter of orbit) for character 40 (see Figure 2D,E or Figure 3C,D); state 1 (presence of a posteroventral flange in the pterygoid, along its lateral edge, and medial to the processus trochlearis pterygoidei) for character 71 (see Figure 2B, or Figure 3E); state 1 (absence of foramen caroticum laterale) for character 76 (see Figure 2B or Figure 3E); state 1 (hyomandibular branch of the facial nerve lying in its own canal) for character 90; state 1 (fenestra ovalis very close to the vertical plane) for character 97; and state 1 (processus interfenestralis expanded ventrally) for character 98. In addition, the coding of two characters can be modified relative to that in the data matrix of the paper where this taxon was defined [38]: character 95 is recoded from state 0 (complete prootic exposure or exposure absent) to state 1 (small prootic exposure, surrounded by pterygoid, basisphenoid, and quadrate, the foramen nervi facialis being exposed) (see Figure 3E); and character 107, previously encoded as 0, is identified here as unknown (?) (see Figure 2A or Figure 3B). This character considered the presence of the processus clinioideus and the possession of

canals for the abducens nerves (state 0), or absence of processus clinoides and presence of grooves lateral to the basisphenoid (state 1) [24]. The processus clinoides is present in *Tartaruscola teodorii* (a condition shared with the state 0), but this taxon shows lateral grooves for the nerves (a condition not shared with the state 0, but with the state 1).

As a result of the phylogenetical analysis performed here, the identification of *Tartaruscola teodorii* as a member of Foxemydina is confirmed by the only tree obtained (CI: 0.696; RI: 0.770; 18.3131 steps) *Algorachelus peregrina* and *Rosasia soutoi* Carrington da Costa, 1940 [47] are identified as members of this clade rather than as representatives of Bothremydina (see Figure 1E).

3.2. Neuroanatomical Descriptions

3.2.1. *Tartaruscola teodorii*

The lack of the posterior part of the skull roof of the skull of the holotype of *Tartaruscola teodorii* (MNHN.F.SPP33), only the anterior half of its cavum cranii could be reconstructed, including the olfactory duct, olfactory bulbs and pituitary fossa (Figure 4). The nasal cavities, inner ears, complete right and partial left canalis cavernosus, carotid arteries, and some cranial nerves were also reconstructed. The cavum cranii of the paratype of the taxon (MNHN.F.SPP34) was completely reconstructed, but not the ventral end of the cavity posterior to the inner ears due to the basioccipital not being preserved (Figure 5). Nasal cavities, inner ears, right canalis cavernosus, carotid circulatory system, and some cranial nerves were also reconstructed.

The shape of the cavum cranii is usually defined by the angle formed between the anterior (i.e., the forebrain and midbrain) and the posterior (i.e., the hindbrain) regions of the dorsal surface of the cranial cavity, measured in the area corresponding to the cartilaginous ridge, which defines the dorsalmost point (see Table 1 and Sections S2.1 and S2.2 in the Supplementary File S2). For *Tartaruscola teodorii*, this angle could only be measured in MNHN.F.SPP34, its value being about 146° (Figure 5J–L; see Table 1). In both specimens, the anterior region of the cranial cavity is almost straight, being posterodorsally directed (Figure 4J,L or Figure 5J,L) to reach the cartilaginous ridge in MNHN.F.SPP34. The posterior region presents a concave surface (Figure 5J,L). In *Tartaruscola teodorii*, the olfactory tract reaches almost 22% of the total length of the cavum cranii in the paratype (Figure 5B,J–L; see Table 1). The olfactory duct is observed in both specimens, being housed at the sulcus olfactorius, in the ventral surface of the frontals (Figure 2B or Figure 3E,F). Posteriorly, the olfactory nerve contacts the olfactory bulbs, which are poorly expanded laterally. The mid and posterior dorsal region of the cavum cranii could not be reconstructed in MNHN.F.SPP33, the lateral expansion of the cerebral hemispheres is unknown (Figure 4B). The cerebral hemispheres of the paratype present a well-developed lateral expansion (Figure 5B; see Table 1). Dorsally, the endocast of the cavum cranii of MNHN.F.SPP34 has an elongated longitudinal dorsal ridge, located at the level of the hemispheres. This ridge originates at the mid-length of the ventral surface of the parietals, and is posteriorly expanded until reaching the contact between the parietals and the supraoccipital (Figure 5B,F,J,L). Ventrally, a small pituitary gland, housed in a shallow sella turcica, is recognized in both specimens (Figure 4D or Figure 5D). The dorsum sellae is low and its anterior edge does not overhang the sella turcica. The pituitary fossa is more expanded laterally rather than anteroposteriorly (see Table 1 and Section S2.3 in the Supplementary File S2). The posterior ventral surface of the cranial cavity remains unknown in MNHN.F.SPP34, but the dorsal surface of the basioccipital observed in MNHN.F.SPP33 suggests a flat ventral surface for this region of the cavum cranii (Figure 2A).

As in all Testudines, the absence of an osseous laterosphenoid in *Tartaruscola teodorii* does not allow the reconstruction of the canals of the cranial nerves of the optic region (i.e., optic, oculomotor and trochlear nerves). The proximal extent of the trigeminal (cranial V) nerves were reconstructed in MNHN.F.SPP34 (Figure 5J,L), but only the left one was partially reconstructed in the holotype (Figure 4L). The foramen of the trigeminal nerve of *Tartaruscola teodorii* is formed by the parietal and the pterygoid, with a small participation of the prootic (Figure 2D,E or Figure 3C,D or Figure 4K,L or Figure 5I–L). This nerve

originates in the cavum cranii posteroventral to the cerebral hemispheres. The canalis cavernosus is formed by the pterygoid anteroventrally, and the prootic and the quadrate posterolaterally, overpassing the level of the canalis stapedio-temporalis (Figure 4B,D or Figure 5B,D). The foramen stapedio-temporalis is located in the anterior region of both the prootic and the quadrate (Figure 5B). The abducens (cranial VI) nerves were reconstructed in the specimen MNHN.F.SPP34 (Figure 5D,J,L). The canal for this nerve is relatively short. The canal is anteriorly directed, running into a groove lateral to the weakly-developed processus clinoideus. This nerve reaches the canalis cavernosus ventrally to the trigeminal nerve. The right facial (cranial VII) and vestibulocochlear (cranial VIII) nerves and the left vidian branches of both specimens, as well as the partial left facial nerve of MNHN.F.SPP34, were reconstructed (Figure 4D,J,L or Figure 5D,J,L). The facial and the vestibulocochlear nerves exit from the cranial cavity through the fossa acustico-facialis, located in the medial surface of the prootic. The facial nerve exits anteroventrally to vestibulocochlear one. The facial nerve splits, posterior to a short lateral trajectory, in the geniculate ganglion. The canal of the proximal hyomandibular branch is short and reaches the canalis cavernosus laterally. The vidian branch of the facial nerve is anteroventrally directed through the canalis pro ramo vidiani of the prootic (Figure 5L). This branch enters the internal carotid arteries, posterolaterally to the foramen canalis carotici interni, through the foramen nervi vidiani (Figure 3E or Figure 4C,D or Figure 5C,D). The canal of the anterior vidian nerve pierces the pterygoid to reach the foramen palatinum posterius (Figure 4C or Figure 5C). The vestibulocochlear nerve presents short lateral trajectory, innervating a great part of the anterior region of the labyrinth. The cranial nerves IX–XI could not be reconstructed in any skull of *Tartaruscola teodorii*. The hypoglossal (cranial XII) nerves of MNHN.F.SPP33 were reconstructed (Figure 4B,D). Those nerves pierced the exoccipital through two canals, and exit in the medial edge of the foramen jugulare posterius. The anterior canal of the hypoglossal nerves is thinner than the posterior one.

The nasal cavities of MNHN.F.SPP33 and MNHN.F.SPP34 were completely reconstructed (Figures 4 and 5). They are well-developed structures, with a wide posterior portion of the vestibulum nasi. The anteriormost region could not be reconstructed in neither of the skulls. The nasal cavities of the paratype MNHN.F.SPP34 represent 23% of the total volume of the endocast (i.e., including the volume of the nasal cavities and that of the cavum cranii, see Table 1). The value for the nasal cavity could be lightly lesser than that measured due the incomplete preservation of the posterior region of the cavum cranii. These cavities present a medial separation corresponding to the medial cartilaginous septum (Figure 4B,D or Figure 5B). The nasal cavum proprium presents a low dorsal medial expansion, located just behind the vestibulum nasi (Figure 4J,L or Figure 5J,L). This enlargement of the nasal cavity, which contacts posteriorly with the olfactory nerve, included the olfactory region. The nasopharyngeal ducts are laterally expanded, and present almost straight and posteriorly directed trajectories (Figure 4D or Figure 5D).

Due to the poor preservation of the otic region of MNHN.F.SPP33, its inner ears show a strong dorsoventral compression affecting both semicircular canals and vestibulum (Figure 4M,N). MNHN.F.SPP34 preserved the anterior half of the left inner ear, including the crus communis, but also the vestibulum and lateral semicircular canal of the right inner ear (Figure 5M–P). The vertical semicircular canals of the right inner ear (both the anterior as the posterior) are displaced from their original positions due the ventral displacement of the supraoccipital. The semicircular canals of *Tartaruscola teodorii* are low dorsoventrally, and their height is equal to more than 70% of the total inner ear height (see Section S2.4 in the Supplementary File S2). The anterior semicircular canal is formed by the prootic and the supraoccipital. The posterior semicircular canal runs between the supraoccipital and the opisthotic. The lateral semicircular canal is mainly formed by the opisthotic, with a small anterior participation of the prootic. The angle formed by the anterior and the posterior semicircular canals can only be measured in the right inner ear of MNHN.F.SPP33, and its value is about 81° (Figure 4N; Table 1). The anterior semicircular canal is the longest canal of the inner ear in *Tartaruscola teodorii*, and the lateral canal is the shortest due to

its conjunction with parts of the posterior canal through a secondary crus communis (see Section S2.5 in the Supplementary File S2). The preserved lateral semicircular canal of MNHN.F.SPP34 is almost round in the cross section, and the anterior and the posterior canals are oval. The maximum cross-sectional diameter of the anterior semicircular canal is 1.2 mm. The width of the lateral semicircular canal is 1.3 mm. The internal spaces, formed between the anterior and the posterior semicircular canals and the crus communis and dorsal surface of the vestibulum (observed in the right inner ear of MNHN.F.SPP33), are apparently wide, being recognized as almost oval in lateral view due to the ventrally curved appearance of the vertical canals (Figure 4M; see Section S2.6 in the Supplementary File S2). The space formed by the lateral semicircular canal and the vestibulum is observed in the right inner ear of MNHN.F.SPP34, and it presents a small diameter (Figure 5N). Dorsally, the vertical semicircular canals (i.e., the anterior and posterior semicircular canals) slightly exceed the height of the crus communis. The crus communis is longer than high (see Section S2.6 in the Supplementary File S2). The vestibulum is dorsoventrally compressed in MNHN.F.SPP33. This structure is rounded and weakly-expanded dorsoventrally in MNHN.F.SPP34. The vestibulum height is equal to 80% of the inner ear total height in MNHN.F.SPP33 (see Section S2.4 in the Supplementary File S2). The relative height of the vestibulum could not be measured in the paratype because the total height of the inner ear remains unknown.

The carotid canals of the paratype of *Tartaruscola teodorii* have been completely reconstructed (Figure 5D), but the distal end of the left canal and the foramen posterius canalis carotici internus of the holotype are not preserved (Figure 4D). Lateral to the foramen posterius canalis carotici interni, the quadrate shows ventral and posterolaterally directed groove, which housed the posterior portion of the internal carotid (Figure 2B or Figure 3E or Figure 4B or Figure 5E). The foramen posterius canalis carotici interni is formed by the basisphenoid and the pterygoid. The cerebral branches of the carotids pierce the basisphenoid and reach the posterior end of the sella turcica (Figure 4C,D or Figure 5C,D), forming an obtuse angle of almost 110° (Figure 5D; Table 1). Laterally, the foramina anterius canalis carotici cerebri (sensu [48]) are clearly separated between them, showing a relatively wide distance from each other (Figure 4D or Figure 5D). The anterolateral foramina observed in the pterygoids correspond to the vidian branches of the facial nerves. Thus, neither the palatine branches of the carotids nor the foramina for them are recognized.

3.2.2. *Chelus fimbriata*

The shape of the cavum cranii of *Chelus fimbriata* is almost flat, with a value of the angle formed by the dorsal surface of midbrain and hindbrain of 172° (Figure 6E; see Table 1). The dorsal surface of the posterior region remains almost straight, being subparallel to the ventral one. The dorsal anterior surface of the cranial cavity is concave in lateral view. The olfactory nerve is straight and short, being equal to 20% of the cranial cavity length (Figure 6B; see Table 1). The olfactory bulbs are poorly-demarcated. Anteriorly, they lack a clear limit with the olfactory nerve. The optic region of *Chelus fimbriata*, together the olfactory duct, are very elongated posteriorly, reaching the cerebral hemispheres at a level equivalent to the mid-length of the cranial cavity. The hemispheres are poorly expanded laterally (their maximum width is equal to 20% of the total length of the cranial cavity; see Table 1). The dorsal cartilaginous ridge is low and short (Figure 6B,E). The sella turcica contains a short pituitary gland, which is posteroventrally directed (Figure 6C,E). The endocast of the pituitary fossa is oval, and its anterodorsal axis is slightly longer than the mediolateral (see Table 1 and Section S2.3 in the Supplementary File S2). The low dorsum sellae overhangs the posterior end of the sella turcica.

The trigeminal nerve exits laterally, from the cavum cranii through large and antero-posteriorly long foramen (Figure 6B,C,E). This foramen is formed by the pterygoid, the parietal, and the prootic. The canalis cavernosus is formed by the pterygoid anteroventrally, the parietal anterodorsally, and the prootic and quadrate posteriorly, reaching the level of the canalis stapedio-temporalis (Figure 6B). The foramen stapedio-temporalis is

formed by the quadrate and the prootic. This foramen is dorsally located. The abducens nerve pierces the basisphenoid anteroposteriorly, running parallel to the sella turcica, and reaching the base of the posterior area of the sulcus cavernosus (Figure 6C). The fossa acustico-facialis of the prootic contain the foramina of the facial and vestibulocochlear nerves. The proximal facial nerve pierces the lateral area of the prootic, reaching the geniculate ganglion, which is located dorsally to the canalis caroticus cerebialis (Figure 6C,E). The proximal hyomandibular branch of the facial nerve runs posterolaterally from the geniculate ganglion, reaching the canalis cavernosus behind the canalis stapedio-temporalis. The distal hyomandibular branch crosses the canalis cavernosus and continues piercing the quadrate laterally. The vidian branch is anteroventrally directed, running into the canalis cavernosus, and anteriorly reaching the sulcus palatinoptyergoideus (Figure 6B,C). The vestibulocochlear nerve has short lateral trajectory, and pierces the prootic through three canals. The glossopharyngeal nerve pierces the opisthotic to reach the posterior region of the cavum labyrinthicum. The foramen jugulare anterius is formed by the opisthotic and the exoccipital, and corresponds to the exit of the vagus and accessory nerves (Figure 6B,C,E). The hypoglossal nerve pierced the exoccipital through three canals that contact the foramen jugulare posterius.

The nasal cavities are small, reaching 17% of the endocast total volume (Figure 6B,C,E; see Table 1). The vestibulum nasi is long and narrow. The cavities are divided by a medial cartilaginous septum, inferred by the presence of a groove (Figure 6B,C). The posterodorsal olfactory region is a low and small expansion, medially divided by a longitudinal depression (Figure 6B). The nasopharyngeal ducts are long and straight structures. They are postero-medially directed, contacting the buccal cavity through the internal nares (Figure 6C).

The semicircular canals are dorsally low, but the anterior and the posterior canals are ventrally expanded, reaching more than 70% of the total inner ear height (Figure 6F; see Section S2.4 in the Supplementary File S2). The anterior semicircular canal is formed by the prootic and the supraoccipital, the posterior semicircular canal by supraoccipital and the opisthotic, and the lateral semicircular canal by the opisthotic and the prootic. The angle between the vertical canals is about 80° (Figure 6G; see Table 1). The cross sections of both the anterior and the posterior semicircular canals are elliptical, but the lateral semicircular canal shows a rounded cross section in its central area. The anterior semicircular canal is the longest and thinnest canal of the labyrinthic system (see Section S2.5 in the Supplementary File S2). The posterior semicircular canal is the shortest. The vertical canals of the labyrinthic system are almost straight, so the internal spaces of the vertical canals are very narrow, and anteroposteriorly elongated (Figure 6F; see Section S2.6 in the Supplementary File S2). The space between the lateral semicircular canal and the vestibulum is wide and long (Figure 6G). Dorsally, the vertical canals slightly exceed the crus communis. This structure is wide anteroposteriorly, but it shows a poor dorsoventral development. Ventrally, the vestibulum is weakly-expanded (80% of the inner ear total height; see Section S2.4 in the Supplementary File S2).

The carotid artery enters the skull through the foramen posterius canalis carotici interni, which is formed by the prootic (Figure 6C). The carotid arteries pierce the basisphenoid through paired canals that form an obtuse angle of about 110°, and reach the lateral rim of the pituitary fossa (see Table 1). Laterally, the foramina anterius canalis carotici cerebialis show a relatively wide distance from each other. The palatine branches of the carotids and the foramina for them are not recognized from them.

3.2.3. *Hydromedusa tectifera*

The value of the angle formed by the dorsal surfaces of the midbrain and hindbrain in *Hydromedusa tectifera* is 170°, conferring a subhorizontal layout of the dorsal area of this cavity a subhorizontal layout (Figure 6L; see Table 1). The cross section of the cranial cavity becomes narrow posteriorly. The olfactory nerve is a straight, long and very narrow duct, constituting almost a third of the total length of the cranial cavity (Figure 6I; see

Table 1). The olfactory bulbs are poorly expanded laterally. The cerebral hemispheres show a weak lateral expansion (i.e., its width being equal to 26% of the total length of the cranial cavity; see Table 1). The cartilaginous ridge is low and short (Figure 6I,L). The sella turcica is a short structure, longer than wide (Figure 6J; see Table 1 and Section S2.3 in the Supplementary File S2). The dorsum sellae is low. It covers the posterior end of the pituitary fossa.

The trigeminal nerve exits from the cranial cavity through large foramen, formed by the pterygoid, the parietal, and the prootic (Figure 6I,L). The canalis cavernosus is formed by the pterygoid, the prootic, and the quadrate (Figure 6I,J). The abducens nerve runs anteroposteriorly, being located parallel to the sella turcica and dorsal to the cerebral branch of the carotid artery (Figure 6J). The anterior foramen of the abducens nerve canal is located in the basisphenoid, lateral to the anterior limit of the sella turcica and medial to the sulcus cavernosus. The foramina of the facial and vestibulocochlear nerves exit from the fossa acustico-facialis. The geniculate ganglion of the facial nerve dorsally contacts the carotid artery (Figure 6J,L). The proximal hyomandibular branch of the facial nerve runs posterolaterally. This canal reaches the canalis cavernosus at the level of the cavum tympani. The vidian branch is anteroventrally directed, being located lateral to the cerebral carotid artery (Figure 6J). The most anterior vidian nerve pierces the pterygoid and exits lateral to the anterior foramen of the abducens nerve. The vestibulocochlear nerve runs in a short lateral trajectory, innervating the cavum labyrinthicum. The foramen formed at the exit of the glossopharyngeal nerve from the cavum cranii is not discernible, but the distal branch of this nerve exits from the ventral surface of the posterior ampulla of the labyrinth. The foramen jugulare anterius is located in the contact surface between the opisthotic and the exoccipital (Figure 6I,J,L). The hypoglossal nerve pierced the exoccipital through two canals that flow into the foramen jugulare posterius.

The nasal cavities are small, making up 14% of the total volume of the endocast (Figure 6I,J,L; see Table 1). The vestibulum nasi in *Hydromedusa tectifera* is wide. There is no evidence of a medial cartilaginous septum in the reconstruction of the nasal cavities. The dorsal expansion of the olfactory region is low and short (Figure 6L). The nasopharyngeal ducts are posteriorly directed, with short trajectories to flow into greatly enlarged internal nares (Figure 6J).

The semicircular canals are low, reaching more than 60% of the total inner ear height (Figure 6M; see Section S2.4 in the Supplementary File S2). The anterior semicircular canal is formed by the prootic and the supraoccipital, the posterior semicircular canal by the supraoccipital and the opisthotic, and the lateral semicircular canal by the prootic and the opisthotic. The angle between the anterior and the posterior semicircular canals exceeds 90° (corresponding to 96° in the case of the left inner ear and 91° in the right one; see Table 1; Section S2.5 in the Supplementary File S2) (Figure 6N). The anterior semicircular canal is the longest canal of the labyrinth system (see Section S2.5 in the Supplementary File S2). The posterior and the lateral semicircular canals present similar lengths to each other. The vertical canals are almost circular in cross section, but that of the lateral semicircular one is elliptical, due to this canal being dorsoventrally compressed. The lateral semicircular canal is narrower in the region close to the posterior ampulla. As the anterior and posterior semicircular canals are almost straight, the internal spaces of the vertical canals are narrow and elongated anteroposteriorly (Figure 6M; see Section S2.6 in the Supplementary File S2). The space formed by the lateral canal and the vestibulum is long anteroposteriorly (Figure 6N). Dorsally, both the anterior and the posterior semicircular canals exceed the crus communis height. The crus communis shows a dorsal notch. This structure is longer than high. All semicircular canals are thin and present a sub-equal maximum width. The vestibulum is rounded and expanded ventrally, reaching between 80 and 90% of the total height of the inner ear.

The carotid artery enters the skull ventrolaterally, through the foramen posterius canalis carotici interni (Figure 6J). This foramen, formed by the prootic, is located close to the suture of this bones with the quadrate. The canal of the carotid pierces the prootics

and the basisphenoid. The carotid canals form an angle of 110° (see Table 1). The cerebral branch reaches the lateral rim of the pituitary fossa. The foramina anterius canalis carotici cerebialis show a relatively wide distance between them. The palatine branches of the carotids and the foramina for them are not recognized from them.

3.2.4. *Pelusios niger*

The midbrain and the hindbrain delimit an angle of about 171° , with the anterior part of the cranial cavity being slightly convex, but the posterior being clearly concave (Figure 6S; see Table 1). The posterior end of the medulla oblongata is posterodorsally directed. The olfactory nerve is a short duct (i.e., its length is equivalent to 22% of the total cranial cavity length; see Table 1), which shows an anterior end slightly expanded laterally (Figure 6P). The olfactory bulbs are poorly expanded laterally. The cerebral hemispheres present a well-developed lateral expansion (their maximum width is equal to 33% of the total length of the cranial cavity; see Table 1). The cartilaginous ridge is low, but wide and long, with a deep concavity in the dorsal surface (Figure 6PS). The sella turcica is short and deep, with a posterior thin expansion covered by the dorsum sellae. The pituitary fossa is longer than wide (Figure 6Q; see Table 1 and Section S2.3 in the Supplementary File S2).

The trigeminal nerve exits laterally to the cavum cranii through oval and large foramen, formed by the pterygoid, the parietal and the prootic (Figure 6P,Q,S). The canalis cavernosus emerges from the cavum cranii and it is formed by the prootic and the quadrate (Figure 6P,Q). The abducens nerve canal runs parallel to the sella turcica (Figure 6Q). The anterior foramen of the abducens nerve canal is located in the basisphenoid, lateral to the pituitary fossa and medial to the contact between the sulcus cavernosus and the foramen of the trigeminal nerve. The facial and vestibulocochlear nerves exit from the cavum cranii, piercing the prootic. Dorsally, the geniculate ganglion contacts the canalis caroticus internus (Figure 6Q,S). The proximal hyomandibular branch of the facial nerve runs laterally, reaching the canalis cavernosus (Figure 6Q). The distal hyomandibular nerve exits through the posteromedial surface of the articular process of the quadrate. The vidian branch is anteroventrally directed, piercing the pterygoid to reach the sulcus palatinoptyergoideus. The vestibulocochlear nerve enters through a single canal, anteroposteriorly wide, to innervate the labyrinth. The glossopharyngeal nerve pierces the processus interfenestralis of the opisthotic, goes across the cavum labyrinthicum, and exits at the recessus scalae tympani. The foramen jugulare anterius is formed by the opisthotic and the exoccipital (Figure 6P,Q,S). The vagus and accessory nerves reach the recessus scalae tympani. The hypoglossal nerve pierced the exoccipital through two canals. These canals are laterally convergent, and exit posterior to the foramen jugulare posterius.

The nasal cavities are small, constituting almost 20% of the total volume of the endocast (Figure 6P,Q,S; see Table 1). The vestibulum nasi is laterally expanded. The nasal cavities do not show evidence of the presence of a medial cartilaginous septum. The olfactory region of the nasal cavities presents a medial dorsal expansion that contacts posteriorly the contacts olfactory duct (Figure 6S). Anteriorly, the nasopharyngeal ducts are laterally expanded. These ducts are posteriorly directed, by straight and short trajectories (Figure 6Q).

The semicircular canals are low. They reach 60% of the total inner ear height (Figure 6T; see Section S2.4 in the Supplementary File S2). The anterior semicircular canal is formed by the prootic and the supraoccipital, and the posterior canal runs between the supraoccipital and the opisthotic. The lateral semicircular canal is formed by the prootic and the opisthotic. The angle formed by the vertical canals is about 80° (Figure 6U; see Table 1). The anterior semicircular canal is longer than the posterior one (see Section S2.5 in the Supplementary File S2). The lateral semicircular canal is the shortest canal of the labyrinth. All canals are almost circular in cross section, in the mid shaft of them, but are elliptical close to the crus communis and the ampullae. The anterior semicircular canal is the thinnest, and the posterior and the lateral ones present a sub-equal maximum width between them. The lateral semicircular canal is enlarged posteriorly towards the contact surface with the posterior ampulla. The vertical canals are slightly curved ventrally, and present oval and

wide internal spaces (Figure 6T; see Section S2.6 in the Supplementary File S2). The space between the lateral semicircular canal and the vestibulum is wide (Figure 6U). Dorsally, the vertical canals slightly exceed the height of the crus communis. The crus communis is relatively high, and shows a dorsal notch. The vestibulum is ventrally expanded, making up 70% of the total height of the inner ear.

The internal carotid artery enters the skull posteroventrally, through the foramen posterius canalis carotici interni (Figure 6Q). This foramen is formed by the prootic, being located close to the suture of this bone with the quadrate. The canal of the carotid pierces the prootic and crosses the basisphenoid to reach the posterolateral area of the sella turcica. The angle formed between these canals is slightly obtuse (95° ; see Table 1). The foramina anterius canalis carotici cerebralis are clearly separated between them. The palatine branches of the carotids and the foramina for them are not recognized from them.

3.2.5. *Podocnemis unifilis*

The midbrain and hindbrain regions are set at an angle of 149° (see Table 1). The dorsal surface of the contact between the olfactory duct and the olfactory bulbs is convex (Figure 7E). The surface of the cranial cavity posterior to the dorsal crest is straight and ventrally directed. The olfactory nerve is 18 mm long (representing 24% of total cranial cavity length; see Table 1), with the anterior end being slightly expanded laterally and strongly curved ventrally (Figure 7B,E). The olfactory bulbs are poorly expanded laterally (Figure 7B). The cerebral hemispheres are moderately expanded laterally (their width being equal to 27% of the total length of the cavum cranii; see Table 1). The dorsal cartilaginous ridge is long, becoming wider posteriorly than anteriorly, and showing a shallow concavity in its dorsal surface (Figure 7B,E). The sella turcica is long and deep, being twice as long as wide (Figure 7C; see Table 1 and Section S2.3 in the Supplementary File S2). The dorsum sellae covers the posterior end of the sella turcica.

The trigeminal nerve exits laterally from the cavum cranii, through an oval, large foramen formed by the pterygoid, the parietal, and the prootic (Figure 7B,E). The canalis cavernosus is posterolaterally directed, and it is formed by the pterygoid, the prootic, and the quadrate (Figure 7B,C). This canal reaches the canalis stapedio-temporalis, which wherein the dorsal foramen is formed by the prootic and the quadrate. The abducens nerve runs parallel to the sella turcica (Figure 7C,E). This nerve enters inside an enlarged cavity formed by the pterygoid and the basisphenoid (i.e., the cavum pterygoidei), and anteriorly reaches the medial surface of the sulcus cavernosus. The foramina of the facial and vestibulocochlear nerves are located in the fossa acustico-facialis. The facial nerve splits in the geniculate ganglion located between the cavum cranii and the canalis cavernosus. The proximal hyomandibular branch runs laterally to this ganglion and enters the canalis cavernosus (Figure 7C). The corda tympani branch of the facial nerve exits at the ventromedial surface of the articular process of the quadrate. The vidian branch is anteroventrally directed, crossing the cavum pterygoidei. The canalis nervi vidiani reaches the sulcus palatinopterygoideus at the level of the rostrum basisphenoidale. The vestibulocochlear nerve innervates the cavum labyrinthicum through two lateral and short canals. The glossopharyngeal nerve pierces the dorsal region of the processus interfenestralis of the opisthotic and enters the cavum labyrinthicum. The foramen jugulare anterius is located at the contact between the opisthotic and the exoccipital (Figure 7C,E). The vagus and accessory nerves reach the recessus scalae tympani, and exit through the foramen jugulare posterius. The hypoglossal nerve pierced the exoccipital through two canals located in the posterior region of the foramen jugulare posterius.

The nasal cavities are small, representing almost 24% of the total volume of the endocast (Figure 7B,C,E; see Table 1). The vestibulum nasi is short and wide. The nasal cavities do not show any evidence of the presence of a medial septum. Immediately posterior to the vestibulum, the nasal cavities are dorsolaterally expanded, forming a low dorsal expansion for the olfactory region. The nasopharyngeal ducts are posteriorly directed, with straight trajectories (Figure 7C).

The semicircular canals are low, making up almost 60% of the total inner ear height (Figure 7F; see Section S2.4 in the Supplementary File S2). The anterior semicircular canal is formed by the prootic and the supraoccipital, while the posterior canal pierces the supraoccipital and the opisthotic. The lateral semicircular canal is formed by both the prootic and the opisthotic. The value of the angle between the vertical canals is about 80° in both labyrinths (Figure 7G; see Table 1). The anterior semicircular canal is the longest and thinnest canal of the labyrinthine system (see Section S2.5 in the Supplementary File S2). The posterior and the lateral semicircular canals are sub-equal in both length and width. All canals are elliptical in the cross section, with the lateral canal being almost rounded in its medial length. The posterior semicircular canal is dorsally enlarged close to the contact with the crus communis. The anterior and posterior canals are almost straight conferring an anteroposteriorly narrow and elongated appearance of the internal spaces of the vertical canals (Figure 7F; see Section S2.6 in the Supplementary File S2). The space between the lateral canal and the vestibulum is enlarged anteroposteriorly (Figure 7G). The vertical canals slightly exceed the height of the crus communis. The crus communis is very low relative to its length. The vestibulum is ventrally expanded, reaching almost 90% of the total height of the inner ear.

The foramen posterius canalis carotici interni is lacking in the specimen analyzed here. The internal carotid artery enters through the cavum pterygoidei, and reaches the posterolateral surface of the sella turcica, piercing the basisphenoid. The canals of the cerebral branches are short (Figure 7C), forming an acute angle, with a value of 81° (see Table 1). The foramina anterius canalis carotici cerebri present a wide distance between them. The palatine branches of the carotids and the foramina for them are not recognized from them.

3.2.6. *Erymnochelys madagascariensis*

The midbrain and the hindbrain form an angle of 146° (see Table 1). The anterior region of the dorsal surface of the cranial cavity is concave due the dorsal expansion of the anterior portion of the olfactory nerve (Figure 7L). The dorsal surface of the cranial cavity posterior to the cartilaginous ridge is straight, being posteroventrally directed. However, the posterior area of the medulla oblongata is posterodorsally directed. The olfactory nerve is a short duct (its length is 23% of the total cranial cavity length; see Table 1), its anterior region being dorsally expanded (Figure 7I,L). The olfactory bulbs are poorly expanded laterally (Figure 7I). The cerebral hemispheres are moderately expanded laterally (its maximum width being equal to 27% of the total length of the cranial cavity; see Table 1). The dorsal ridge is relatively wide and long, its maximum width being reached at the posterior region (Figure 7I,L). The sella turcica is almost two times as long as wide (Figure 7J; see Table 1 and Section S2.3 in the Supplementary File S2), but the dorsum sellae does not cover the complete dorsal region of this fossa.

The trigeminal nerve exits laterally to the cavum cranii through an oval and large foramen, formed by the pterygoid, the parietal, and the prootic (Figure 7I,L). The canalis cavernosus is formed by the pterygoid, the prootic, and the quadrate, and it reaches the canalis stapedio-temporalis (Figure 7I,J). The abducens nerve runs through a long and straight anteriorly directed and slightly divergent canal, parallel to the sella turcica (Figure 7J). The anterior foramen of the abducens nerve canal is located in the lateral surface of the processus clinoides of the basisphenoid. The facial and vestibulocochlear nerves exit from the cavum cranii through the fossa acustico-facialis. The geniculate ganglion is located between the cavum cranii and the canalis cavernosus. The proximal hyomandibular branch pierces the prootic and reaches the ventral surface of the canalis cavernosus. The corda tympani branch of the facial nerve exits the skull through the posteromedial surface of the articular process of the quadrate. The vidian branch is anteroventrally directed through the cavum pterygoidei. Anteriorly, it reaches the sulcus palatinoptyergoideus at the level of the rostrum basisphenoidale. The vestibulocochlear nerve is formed by two canals that contact the cranial cavity and the anterior region of the cavum labyrinthicum.

The glossopharyngeal nerve pierces the processus interfenestralis of the opisthotic and enters the cavum labyrinthicum. The foramen jugulare anterius is located at the contact between the opisthotic and the exoccipital (Figure 7J,L). The vagus and accessory nerves reach the recessus scalae tympani. The hypoglossal nerve pierced the exoccipital through two canals, exiting in the medial surface of the foramen jugulare posterius.

The nasal cavities are small, representing almost 26% of the total volume of the endocast (Figure 7I,J,L; see Table 1). The vestibulum nasi is long and wide. The dorsal surface of the vestibulum presents a shallow longitudinal groove, corresponding to the medial cartilaginous septum (Figure 7I). The olfactory region is a small and low posterodorsal medial expansion, located in the nasal cavities (Figure 7L). The nasopharyngeal ducts are laterally expanded, and posteriorly directed, with straight trajectories (Figure 7J).

The semicircular canals are low, almost 60% of total inner ear height (Figure 7M; see Section S2.4 in the Supplementary File S2). The anterior semicircular canal is formed by the prootic and the supraoccipital, and the posterior canal runs between the supraoccipital and the opisthotic. The lateral canal is formed by the prootic and the opisthotic. The vertical canals form an angle of 80° (Figure 7N; see Table 1 and Section S2.5 in the Supplementary File S2). The semicircular canals are robust. The anterior semicircular canal is the longest and thinnest canal of the inner ear (see Section S2.5 in the Supplementary File S2). The posterior and the lateral semicircular canals are sub-equal in length. The vertical canals are elliptical in cross section, but the lateral canal is less compressed. The lateral semicircular canal is the most robust. The internal spaces formed by the straight vertical canals, the crus communis, and the vestibulum are narrow and anteroposteriorly elongated (Figure 7M; see Section S2.6 in the Supplementary File S2). The space formed by the lateral semicircular canal and the vestibulum is long but narrow mediolaterally (Figure 7N). The vertical semicircular canals slightly exceed the height of the crus communis. The crus communis is relatively low, with a notch in the dorsal surface. The vestibulum is ventrally expanded, almost 90% of the total height of the inner ear.

The foramen posterius canalis carotici interni is lacking in the specimen analyzed here. The carotid artery enters the cavum pterygoidei, and the canal of the cerebral branch is formed by the basisphenoid (Figure 7J). The cerebral carotid canals form an acute angle, of 84° (see Table 1). The foramina anterius canalis carotici cerebri are located in the posterolateral sides of the sella turcica, and they show a relatively wide distance from each other. The palatine branches of the carotids and the foramina for them are not recognized from them.

4. Discussion

4.1. Cranial Cavity and Nerves

The first description based on three-dimensional reconstructions of the cavum cranii, nasal cavity, inner ears, and cranial nerves for a bothremydid turtle has been performed here, based on the European Eocene *Tartaruscola teodorii*. The circulatory cranial system has also been reconstructed for the first time for a member of Foxemydina. The angle formed between the anterior (i.e., the forebrain and midbrain) and the posterior (i.e., the hindbrain) regions of the dorsal surface of the cranial cavity, measured in the area corresponding to the cartilaginous ridge is more obtuse in *Tartaruscola teodorii* than in the member of Bothremydina *Bothremys cooki* (about 133° based in the latex cast of the taxon, see Figure 21 of [35]). Both species also differs in the posterior portion of the cavum cranii, being almost straight and ventrally directed in the North American taxon, as in the Maastrichtian form *Chedighaii barberi* (see [36]), but being concave, with the dorsally directed posterior end of the medulla oblongata, in the European one. The anterior dorsal region of the cavum cranii is eroded in the natural endocast known for *Chedighaii barberi*, so this area cannot be compared with *Tartaruscola teodorii* and any other bothremydid. The angle formed by the anterior and posterior regions of the cranial cavity in *Tartaruscola teodorii* is more acute than that in extant chelids, such as those studied here (i.e., *Chelus fimbriata* and *Hydromedusa tectifera*), and others, such as *Chelodina reimanni* (see Figure 2 in [11]), in which the

dorsal anterior and posterior surfaces of the cranial cavity form an angle of almost 180° . However, the cranial cavity of the extant chelid *Emydura subglobosa* differs from that of all these chelids by the strong ventral curvature of the anterior portion of the olfactory and a concave dorsal surface of the medulla oblongata (see Figure 2 in [11]). Thus, the values of 145° observed in *Tartaruscola teodorii* and that measured in *Bothremys cooki* are lower than those in most extant chelids, except *Emydura subglobosa*, with an angle similar to that in *Tartaruscola teodorii*. All extant pelomedusoid taxa of which a neuroanatomical reconstruction is available (i.e., *Pelusios niger*, *Podocnemis unifilis* and *Erymnochelys madagascariensis*) present values for that angle closer to that in *Tartaruscola teodorii* than to those recognized for the chelids (see Table 1). Thus, the presence of a straight and dorsally directed anterior dorsal surface of the cranial cavity of *Tartaruscola teodorii*, and that of a concave posterior surface of this cavity, are similar to those observed for Pelomedusidae, as highlighted by the neuroanatomical reconstruction of *Pelusios niger* performed here. However, the concave shape of the posterodorsal surface of the cranial cavity of *Tartaruscola teodorii* differs from the almost straight surface observed here for the podocnemidids. The anterior region of the olfactory bulbs of the podocnemidid *Erymnochelys madagascariensis*, between the dorsal expansion of the duct and the cerebral hemispheres, presents a concave surface, contrasting with the almost straight trajectory recognized for both *Podocnemis unifilis* and *Tartaruscola teodorii*. The shape of the posterior dorsal surface of the cranial cavity observed in those podocnemidids is shared with those of the members of Podocnemididae *Yuraramirim montealtensis* (Figure 4 in [22]) and *Amabilis uchoensis* (Figure 6 in [23]). The dorsal surface of the cranial cavity of *Yuraramirim montealtensis* is more similar to that in *Podocnemis unifilis* than in *Erymnochelys madagascariensis*, being almost straight. The measurement of the angle between the olfactory bulbs region and the end of the medulla oblongata proposed here is a quantitative method to measure the general shape of the cavum cranii. The relative position of the cerebral hemispheres relative to that of the medulla oblongata proposed by [23] allows to observe the curvature of the pontine flexure in the hindbrain. However, the angle between the anterior portion of the cavum cranii and the posterior hindbrain, not only allows to measure the position of the hemispheres relative to that of the medulla oblongata, but also considering the position of the olfactory bulbs region.

The wide lateral expansion of the cerebral hemispheres of *Tartaruscola teodorii*, considering the ratio between the width of the cerebral hemispheres and the total length of the cranial cavity (see Table 1 and Section S2.1 in Supplementary File S2), is shared with the two bothremydids in which this region is known, *Bothremys cooki* (see [35]) and *Chedighaii barberi* (see [36]). Considering this ratio, the cerebral hemispheres in the other taxa of Pleurodira studied here and in those for which these neuroanatomical regions have so far been characterized show less lateral expansion than in the bothremydids. Thus, while the ratio between the width of the cerebral hemispheres and the total length of the cranial cavity spans between 34% and a 39% in the case of those bothremydids, it is recognized as about 20–25% in chelids, 27% in podocnemidids and 33% in pelomedusids (see Table 1). Hermanson et al. [23] considered the lateral expansion of the cerebral hemispheres the ratio between the width of the hemispheres and that of the medulla oblongata. In this case, the value obtained for *Tartaruscola teodorii* (1.87) is equivalent to that recognized by [23] for several members of Bothremydidae (ratio less than 2.25), but not for other representatives of this lineage (ratio greater than 2.25). In fact, both character states were also recognized for these authors in other lineages of Pleurodira such as, for example, Chelidae or Podocnemididae. Although they characterized the Pelomedusidae by a ratio less than 2.25, the presence of both states is also recognized here for this clade (the ratio for the specimen of *Pelusios niger* MNHN.ZA.AC 1934-371 analyzed here, is obtained as 3.13).

The presence of a well-developed dorsal cartilaginous ridge had been recognized for Bothremydina [35,36], and Taphrosphyini [23]. The three-dimensional reconstruction of *Tartaruscola teodorii* allows us to identify a similar development of this structure in another lineage of Bothremydidae: Foxemydina. This dorsal crest is extremely reduced in the chelids analyzed here, and also in the others representatives of this clade in which this

structure was previously described (i.e., *Emydura subglobosa* and *Chelodina reimanni*; see Figure 2 in [11]). The cartilaginous ridge is also identified here as reduced in Pelomedusidae (based on *Pelusios niger*) relative to the condition observed here for Bothremydidae. The ridge is weakly developed in Peiopemydidae (based on *Yuraramirim montealtensis*, see [22]). In podocnemidids, the dorsal ridge presents a variable range of development. The cartilaginous ridge of *Erymnochelys madagascariensis* is more expanded than in basal forms of Podocnemididae such as *Yuraramirim montealtensis*, but the ridge of *Erymnochelys madagascariensis* does not reach the high degree of development observed here for Bothremydidae. The specimen of *Podocnemis unifilis* here presented exhibits a well-developed ridge, more similar to that in bothremydids than in *Erymnochelys madagascariensis*. However, the specimen of *Podocnemis unifilis* figured by [11] (Figure 2) presents a very low cartilaginous ridge, almost inexistent. Therefore, this character, observed for the adult specimens, is identified here as intraspecifically variable, at least for this species.

The three-dimensional reconstruction of the endocast of the pituitary fossa in *Tartaruscola teodorii* reveals a particular morphology of this structure relative to those in other pleurodires. In the chelids *Chelus fimbriata* and *Hydromedusa tectifera*, the pelomedusid *Pelusios niger*, and the podocnemidid *Podocnemis unifilis*, the dorsum sellae overhangs the sella turcica. The absence of this feature in *Tartaruscola teodorii* is shared with *Erymnochelys madagascariensis*. However, the extremely shortness of the pituitary fossa of *Tartaruscola teodorii* differs from the condition in that podocnemidid (see Table 1). The length/width ratio of the endocast of the pituitary fossa in *Tartaruscola teodorii* reveals a structure more expanded laterally than anteroposteriorly. In contrast, the length of the pituitary fossa of all the other pleurodires known by this structure exceeds its width, ranging from a length slightly greater than the width in *Chelus fimbriata* (1.0) to more than twice as long as wide in *Podocnemis unifilis* (2.5) (see Table 1).

The length of the olfactory duct relative to the total length of the cranial cavity could be measured in the latex casts of *Bothremys cooki* and *Chedighaii barberi* [35], and in the natural endocast of *Chedighaii barberi* [36]. This ratio for the latex casts (see Figure 21 in [35]) exceed the value in *Tartaruscola teodorii* (27.9% in *Bothremys cooki* and 29% in *Chedighaii barberi*). However, the olfactory duct of the natural endocast of *Chedighaii barberi* could be shorter (less than 19% of the total length of the cranial cavity, see Figure 1 in [36]), but this should be taken with caution as this can be a result of the poor preservation of the anterior region of the dorsal surface of its cavum cranii. The olfactory duct length of the peiopemydid *Yuraramirim montealtensis*, which is about 23.9% of the cranial cavity length (see Figure 4 in [22]), is relatively longer than that in *Tartaruscola teodorii*. A relatively wide range of variation for this character is recognized in Chelidae, with the length of the olfactory duct being equivalent to 30.3% of the cranial cavity length in *Hydromedusa tectifera*, but only 12.2% in *Emydura subglobosa* (see Table 1; and Figure 2 in [11]). The ratio in *Tartaruscola teodorii* is close to that of the pelomedusid *Pelusios niger*, in neither of these taxa exceeding 23% (see Table 1). Thus, the ratio in these taxa is lower than that in *Podocnemis unifilis* and *Erymnochelys madagascariensis*, being the 23–25% (see Table 1). The proportion of the olfactory duct ratio within these taxa is directly related with the morphology and the relative length of the skulls.

The description of the facial nerves of *Tartaruscola teodorii* based in the three-dimensional reconstruction allows the comparison of the hyomandibular and vidian branches of a representative of this clade with those in other pleurodiran turtles. The facial nerves in the pleurodiran turtles split between the cavum cranii and the canalis cavernosus, and two patterns are recognized. As described for the specimens of Chelidae and Pelomedusidae analyzed here, and the Malagasy Maastrichtian sahonachelyid *Sahonachelys mailakavava* [29], the bifurcation of the facial nerves of these clades occurs in the geniculate ganglion that contacts dorsally with the canalis caroticus internus. However, the facial nerve of the podocnemidids presents short trajectory anterior to reaching the geniculate ganglion, located between the cavum cranii and the canalis cavernosus, without contact the carotid canal (see [21]). The pattern identified here for the bothremydids is the same observed for

the podocnemidids. The presence of canalis pro ramo vidiani where the vidian branches anteroventrally run, observed here for *Tartaruscola teodorii*, is shared with the podocnemidids, but these canals are absent in both chelids, pelomedusids, and sahonachelyids. The canalis nervi vidiani reconstructed in *Tartaruscola teodorii* confirms their anterior trajectory through the pterygoids in Bothremydidae, previously suggested based on the presence of foramina nervi vidiani anterior to the foramina posterius canalis carotici interni [23,24]. The vidian canals in the bothremydids differ from those in the podocnemidids because those of this last clade enter the cavum pterygoidei in a position anterior to that where they reach the foramina nervi vidiani of the pterygoids.

4.2. Nasal Cavities

The restoration of the nasal cavity of *Tartaruscola teodorii* is the first reconstruction of this structure in Bothremydidae, allowing comparison with those in other extinct and extant taxa. The nasal cavities of the endocast of *Chedighaii barberi* preserve the ventral surface, but the anterior and dorsal portions are masked by sediment [36]. Due to its preservation, the presence of a distinct vestibulum nasi and the dorsal development of the olfactory region could not be verified for that taxon. The nasopharyngeal ducts of *Chedighaii barberi* show a straight posteriorly directed trajectory (see Figure 1 in [36]), being more laterally directed than in *Tartaruscola teodorii*. Only the volume of the nasal cavities of *Tartaruscola teodorii* had been measured within Bothremydidae, from the three-dimensional models performed here. The long and narrow vestibulum observed in *Chelus fimbriata* differs from those of *Hydromedusa tectifera* and all pelomedusoids studied here (i.e., including *Tartaruscola teodorii*), in which this structure is wider and shorter. The nasopharyngeal ducts of *Tartaruscola teodorii* differ from those of the extant chelid *Chelus fimbriata*, in which they are more medially directed, and of *Hydromedusa tectifera*, in which they are shorter. All pelomedusoids share an anterior lateral expansion between the vestibulum and the nasopharyngeal ducts, confirmed here for the bothremydids based on the three-dimensional reconstructions performed for *Tartaruscola teodorii*. In all these forms, the ducts are posteriorly directed, defining a straight trajectory. The volume of the nasal cavities in the pleurodiran turtles studied here, including for the first time those of a bothremydid turtle, represents less than 25% of the total endocast cavities (see Table 1), as also occurs in the freshwater aquatic cryptodires [11]. The nasal cavities are more developed in extinct and extant terrestrial forms, with values over 30% [11,13].

4.3. Inner Ear

The first description of the inner ear of a bothremydid turtle, performed here (for measurements of the inner ears in the taxa analysed here see Table 1 and Sections S2.1, S2.4–S2.6 in the Supplementary File S2), shows, as in all Testudines, low dorsoventrally semicircular canals, subequals in length, and a globose vestibulum (e.g., [10,22]). As occurs in all freshwater turtles, the semicircular canals of all pleurodires studied here are longer in relation to the inner ear than in the marine and the terrestrial forms, the anterior semicircular canal is higher and longer than the posterior one, and the vertical canal is M-shaped in lateral view [49,50]. The space defined between the vertical canals, the crus communis and the vestibulum, recognized as oval in lateral view for *Tartaruscola teodorii*, is identified as probably dorsoventrally wider in this species than in the chelids and podocnemidids analyzed here, and in the extinct clade Sahnachelyidae [29]. The shape of this space in *Tartaruscola teodorii* is more similar to that of *Pelusios niger*, being apparently wider in both taxa than in these other pleurodires, because the vertical canals are higher and more curved. The fossil members of Podocnemidoidae *Yuramirim montealtensis* and *Amabilis uchoensis* present an intermediate condition for these spaces (Figure 4 in [22]; Figure 6 in [23]), being wider than in the sahonachelyid *Sahnachelys mailakavava*, the chelids *Chelus fimbriata* and *Hydromedusa tectifera*, and in the podocnemidids *Podocnemis unifilis* and *Erymnochelys madagascariensis*; but narrower than in *Tartaruscola teodorii* and *Pelusios niger*. In addition, a small space formed by the lateral semicircular canal and the vestibulum

was observed for Taphrosphyini and Bothremydini [23], as occurs in *Tartaruscola teodorii*. Contrary to these lineages, other pleurodires, including the Cearachelyini bothremydids, but also Chelidae, Pelomedusidae and Podocnemididae, present a larger space. The preserved canals of *Tartaruscola teodorii* are more robust than in chelids and pelomedusids, presenting a width/length ratio similar to that in podocnemidids (see Section S2.5 in the Supplementary File S2). However, the length of the posterior semicircular canal relative to that of the anterior one in is close to 0.9 in *Tartaruscola teodorii*, as occurs in other representatives of Bothremydini and in Taphrosphyini, but not in Cearachelyini and other lineages of Pleurodira excluding Stereogenyini [23]. The angle formed by the vertical canals is acute in all pleurodires studied here, except in the chelid *Hydromedusa tectifera*, which present a value over 90° (see Table 1). A similar condition is known for other extant chelids as *Emydura subglobosa* and *Chelodina reimanni* (90° and 98° respectively; see [11]). As it occurs in most chelids, the angle formed by the vertical semicircular canals in *Sahonachelys mailakavava* reaches 90° [29], showing a higher value than in *Tartaruscola teodorii*. The extinct representatives of Podocnemidoidae *Yuraramirim montealtensis* and *Amabilis uchoensis* present angles of 87.8° and 82° respectively [22,23]. The development of acute angles in the canals of the labyrinth is a common condition in aquatic turtles (e.g., [10,20,23]), contrasting with the obtuse angles known for the terrestrial forms [11,13,15].

4.4. Circulatory System

The internal carotids enter the skull ventrally in all pleurodiran turtles, including bothremydids [24,51]. In chelids, pelomedusids and bothremydids, the entrance of the arteries to the skull is carried out through the foramina canalis carotici interni [48]. However, the carotids enter ventrally into the cavum pterygoidei in podocnemidids, and then pierce the basisphenoid to reach the foramina anterius canalis carotici cerebralis in the posterolateral edge of the sella turcica [21]. The participation of the palatal bones in the formation of the foramen posterius canalis carotici interni is variable within the lineage of Bothremydidae [24,43,52]. That of the pterygoids and the basisphenoids, observed in *Tartaruscola teodorii*, is shared with taxa such as the Cearachelyini *Galianemys whitei*, the Taphrosphyini *Arenila krebsi* Lapparent de Broin and Werner, 1998 [53], and the Bothremydini *Foxemys mechinorum* Tong, Gaffney and Buffetaut, 1998 [54], *Polysternon provinciale* Matheron, 1869 [55], *Rosasia soutoi*, and *Algorachelus peregrina* [24,43]. Contrary to the condition in *Tartaruscola teodorii*, the quadrates participate in these foramina in most Bothremydini taxa [24,52]. The presence of canalis carotici lateralis for the palatine branches of the carotid arteries in Pleurodira was discussed, identifying these canals in Chelidae, but not in other lineages [56]. Subsequently, some authors [23] supported the presence of lateral canals in this lineage, identifying them as the palatine carotid arteries. However, in later studies these lateral canals had been interpreted as corresponding to the canalis nervi vidiani [21]. The presence of lateral canals observed in the currently available reconstructions of the extant chelids, allow confirmation that these canals are continuous with the geniculate ganglions, and they probably correspond to the vidian canals (see Section 4.4. Cranial cavity and nerves). The absence of the palatine carotid foramina described here for *Tartaruscola teodorii* is shared with the pleurodiran condition [21,24,51]. The reconstruction of the carotid canals of *Tartaruscola teodorii* reaching the foramina anterius canalis carotici internus is performed here for the first time in a member of Foxemydina. The obtuse angle formed by the carotid canals of this species is shared with the condition recognized for the other members of Taphrosphyini (based in the reconstructions of *Labrostocheilus galkini* Gaffney, Tong and Meylan, 2006 [24], *Taphrosphys ippolitoi* Gaffney, Tong and Meylan, 2006 [24], *Phosphatocheilus tedfordi* and *Ummulisani rutgersensis*), but the angle in these forms is more obtuse than that in *Tartaruscola teodorii*, exceeding 140° [23]. However, the angle observed in the representatives of *Galianemys* (Cearachelyini) is more acute than that in *Tartaruscola teodorii* [23], a condition also observed in the reconstructions of the carotid arteries presented here for the podocnemidids *Podocnemis unifilis* and *Erymnochelys madagascariensis* (see Table 1). This condition is also shared with other podocnemidids (see

Figure 8 in [23], and Figure 4 in [21]), and also with extinct members of Podocnemididae as *Yuramirim montealtensis* [22] or *Amabilis uchoensis* [23]. Thus, the angle value of the carotid canals of *Tartaruscola teodorii* shows an intermediate value between the more acute angle in Podocnemididae and basal Cearachelyini bothremydids, and the more obtuse angle identified in Taphrosphyini, being close to that observed in the chelids studied here, *Chelus fimbriata* and *Hydromedusa tectifera*. The extant pelomedusids (based in *Pelusios niger*, studied here, and the specimen of *Pelusios subniger* in Figure 5 of [21]) present more acute angles than that in *Tartaruscola teodorii*, but are more obtuse than in podocnemidids.

5. Conclusions

The extinct Bothremydidae was one of the most geographically distributed and diverse clades of Pleurodira. Their representatives were aquatic turtles, but they inhabited different environments, freshwater forms but also coastal taxa are recognized. The first three-dimensional reconstruction of the only bothremyd from the European Cenozoic record recognized by the skull is performed here. It corresponds to the French lower Eocene species *Tartaruscola teodorii*. This study is based on the analysis of both its holotype and its paratype, these being the only specimens indisputably attributable to this taxon currently known. As a result, the information about its cranial anatomy is improved, its attribution to the clade Foxemydina within Bothremydini being confirmed.

Despite the relatively large number of skulls reported for Bothremydidae, the neuroanatomy of this group is quite unknown. In this way, the first detailed description based on three-dimensional reconstruction of neuroanatomical structures in a bothremyd turtle is performed here in form of the new study of *Tartaruscola teodorii*. The angle formed by the anterior and posterior surfaces of the cavum cranii of this species, the presence of prominent cartilaginous ridge, and the great development of the cerebral hemispheres considering the ratio between their maximum width and the total length of the cavum cranii, are identified as characteristic features for Bothremydidae. Thus, the last trait is recognized as exclusive to this lineage, and the angle between the midbrain and the hindbrain is identified as similar to that in other pelomedusoids, being more acute than in the chelids. The presence of a well-developed ridge in the dorsal surface of the cranial cavity is identified within Podocnemidoidea, with a variable development of this structure in the clade Podocnemididae, but being characterized by a well-developed dorsal expansion at the posteromedial level of the cerebral hemispheres in Bothremydidae. A conservative pattern is recognized here for the cranial nerves in Bothremydidae. Within this lineage, the morphology of both the sella turcica and the dorsum sellae of *Tartaruscola teodorii* are more similar to those observed in the basal clade Cearachelyini, than in other members of Bothremydini. The angle formed by the carotid canals of *Tartaruscola teodorii* shows an intermediate condition between the more acute angle observed for Cearachelyini and the more obtuse angle in Taphrosphyini.

The first detailed description of a reconstructed inner ear of a bothremyd turtle shows the presence of characters shared with extant forms adapted to aquatic environments, such as the anteroposteriorly elongated semicircular canals and the low angle between the anterior and the posterior semicircular canals, the first one being the longest. The shape of the internal spaces between the vertical canals and the height of the crus communis recognized here for the bothremydids are more similar to the conditions on the pelomedusids than those in extant chelids and podocnemidids, and in the extinct sahonachelyids.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/d13070298/s1>, Supplementary File S1: Parameters of the scan and data obtained from each of the specimens scanned at the MNCN and the Clínica Quirón. Supplementary File S2: Linear and angular measurements of the pleurodiran specimens and taxa studied in this manuscript. Supplementary File S3: Data matrix based on that proposed by Pérez-García [43].

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