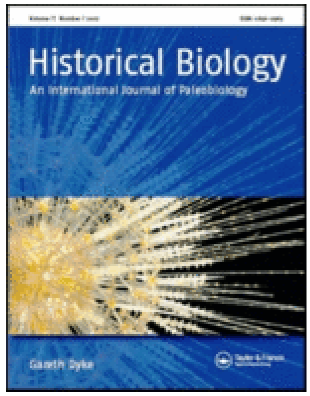

Extreme vascularisation in the dentary of an early-diverging iguanodontian dinosaur

Journal:	*Historical Biology*
Manuscript ID	GHBI-2023-0041.R1
Manuscript Type:	Research Article
Date Submitted by the Author:	02-Jun-2023
Complete List of Authors:	Rotatori, Filippo Maria; Universidade NOVA de Lisboa Faculdade de Ciências e Tecnologia, Earth Sciences Quaranta, Mattia; Universita degli Studi di Bologna, BiGeA Bertozzo, Filippo; Royal Belgian Institute of Natural Sciences, Paleontology Hübner, Tom; Not Applicable, Earth Sciences Silva, Bruno; Sociedade de Historia Natural, Earth Sciences Mateus, Octávio; Universidade NOVA de Lisboa Faculdade de Ciências e Tecnologia, Earth Sciences Moreno Azanza, Miguel; Universidad de Zaragoza Facultad de Ciencias, Ciencias de la Tierra
Keywords:	Vascularisation, Tooth replacement, Ornithischia, Homeostasis, Iguanodontia, Jurassic

Extreme vascularisation in the dentary of ~~a~~an ~~basal~~ early-diverging iguanodontian dinosaur

Filippo Maria Rotatori [a,b*], Mattia Quaranta [c], Filippo Bertozzo[d,e], Tom Hübner [f], Bruno Camilo [a,e,g], Octávio Mateus [a,b], Miguel Moreno-Azanza [a,b,h]

[a] GEOBIOTEC, Department of Earth Sciences, NOVA School of Science and Technology, Campus de Caparica, 2829 516 Caparica, Portugal.

[b] Museu da Lourinhã, Rua João Luis de Moura 95, 2530-158, Lourinhã, Portugal

[c] Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Alma Mater Studiorum, Università di Bologna, Bologna, Italy

[d] Operational Directorate Earth and History of Life, Royal Belgian Institute of Natural Sciences, Brussels, Belgium

[e] CI2Paleo/Sociedade de História Natural (SHN), Travessa Florêncio Augusto Chagas, nº8B, 2560-230 Torres Vedras, Portugal

[f] Stiftung Schloss Friedenstein Gotha, Schlossplatz 1, D-99867, Germany

[g] European Centre of Paleontology, Institute of Biology, Laboratory of Paleobiology, University of Opole, ul.Oleska 48, 45-052 Opole, Poland.

[h] Aragosaurus_ Reconstrucciones Paleoambientales-IUCA, Facultad de Ciencias, Universidade de Zaragoza, 50009, Zaragoza, Spain

*corresponding author: filippo.rotatori.93@gmail.com

Abstract

Virtual palaeontology is a growing field~~s~~, leading palaeontologists to better understand the microanatomy of many extinct species. The application of techniques such as CT~~t~~ and µ~~Ct~~CT-scanning allows the researchers to study micro-anatomical features in a non-invasive way and make inferences on the palaeobiology of~~ the~~ animals. Dinosaurs have been extensively studied using ~~with~~ these techniques, with particular focus on the micro~~-~~anatomy of the ~~dorsal part of the skull~~cranium, whereas~~. On the other hand,~~ relatively little is known of~~n~~ other cranial elements, such as the lower jaw. Here we ~~contribute~~ aim to fill this gap, describing the micro-anatomy of the specimen ML 768, an isolated dentary belonging to a dryosaurid iguanodontian dinosaur from the Upper Jurassic of Lourinhã Fm. The dentary ML 768 was subjected to ~~µCt~~µCT-scanning and subsequently the data were segmented in Avizo and rendered in Blender. We ~~managed to identify~~identified functional and replacement teeth, recognising ~~identifying~~ remnants of old replacement cycles. Furthermore, we mapped a rich neurovascular network present in the dentary and compared it with reference literature. We found that the high vascularization is shared ~~consistent~~ with other cerapodan dinosaurs with high tooth replacement rates, ~~and we hypothesize that it played a role in maintaining the homeostasisanimals homeostasis~~although homeostasis may have also played a role in the development of this condition~~-~~. Further evidence is needed to appreciate the macroevolutionary significance of these findings. ~~To better understand vascular patterns in the clade, more µCt data from other iguanodontians are needed.~~

Keywords: ~~v~~Vasculari~~s~~zation, T~~t~~ooth replacement, O~~o~~rnithischia, H~~h~~omeostasis, I~~i~~guanodontia, Jurassic ~~Virtual palaeontology, 3D modelling, micro-anatomy, Archosauria, mandible~~

Introduction

Virtual palaeontology, ~~as defined by Sutton~~following Garwood et al (2014) is a field which experienced an exponential growth in the last few decades, thanks to its non-invasive nature (Conroy & Vannier 1984). In recent years, the application of imaging technologies using computed tomography (Ct-scan) (e.g., Witmer et al., 2008), microtomography (μC~~t~~T-scan) (e.g. Simões et al., 2022) and synchrotron analyses (e.g., Cau et al., 2017) to vertebrate palaeontology~~,~~ has improved our understanding of the internal~~ner~~ anatomy of extinct species. The high resolution and level of detail~~s~~ that these techniques ~~reach~~ can achieve nowadays ~~can~~ has shed new insights onto their behaviour (e.g., Witmer et al., 2003; Walsh et al., 2009), and life history (e.g. Wang et al., 2017) ~~or~~ and answered questions regarding ~~on~~ form and function (Sereno et al. 2007; Yoshida et al. 2023).

The lower jaws of extant and extinct archosaurs have been scanned in the past years, allowing the reconstruction ~~to reconstruct~~ of ~~the~~their neurovascular system ~~(Porter et a., 2016; Lessner, 2021;~~ (Porter & Witmer 2016; Lessner 2021; Bouabdellah et al. 2022; Kawabe & Hattori 2022)~~)~~, an important feature that can inform about metabolism ~~(Porter and Witmer, 2019)~~ (Porter & Witmer 2016), ~~and~~ diet and feeding strategies (Lessner~~,~~ 2021) in these animals. Unfortunately, the amount of comparable data available in the literature is scarce and not yet sufficient for proper comparative analyses between different dinosaurian taxa ~~yet~~.

Rotatori et al. (2020) described the specimen ML 768, ~~-~~a dentary from a small Dryosauridae indet. from Praia do Zimbral (Portugal), which “preserves seven tooth positions and one isolated tooth, two erupting teeth and six roots of already worn-down teeth” (Rotatori et al., 2020, pg. 39). The authors reported the presence of seven individual foramina on the lateral side of the bones, which appear to be in a good state of preservation. Here, we further develop the description of this specimen by including the virtual reconstruction of the neurovascular system that led to the opening of these seven foramina. We aim to identify the size of the vascular canal, the possible ramifications along the alveoli and their spatial relationships with the dentary teeth. Finally, our results are compared with other reconstructed neurovascular canals in dinosaurian dentaries to determine analogies and homologies.

Material and methods

The specimen ML 768 is a small right dentary housed at Museu da Lourinhã (Portugal) belonging to a dryosaurid iguanodontian. Its systematic affinities, gross anatomy, and geological context were previously described by Rotatori et al.~~,~~ (2020). To investigate its internal microanatomy, the specimen was subjected to µCT~~t~~-scanning at the Centro de Evolucion Humana (CENIEH) in Burgos, Spain. ML 768 was scanned with V|Tome|X s 240 by GE Sensing & Inspections Technologies Phoenix, with a constant voltage of 120 KV and current ranging from 90 to 275 µA. We obtained 1661 slices in total, with a voxel size of 20 µm. The segmentation was performed in the software Avizo v.2019 (Scientific 2019), and the resulting meshes were exported and rendered in Blender v.3.4.1 (Hess 2013). Detailed micro-anatomical description and comparison were carried out, following the one adopted by Bouabdellah et al., (2022).

Institutional abbreviations – ML, Museu da Lourinhã, Lourinhã, Portugal; SMNS, Staatliches Museum fur Naturkunde, Stuttgart, Germany.

Results

Description - ML768 is a ~~nearly~~ fairly complete dentary missing only the symphyseal end anteriorly and most of its posterior end including the coronoid process. Due to the uncertainty of the ontogenetic stage of the specimen, is not possible to better locate the position of the preserved portion. In fact, Hübner and Rauhut (2010) showed a progressive lengthening of the antorbital region in the skull of *Dysalotosaurus lettowvorbecki*. As we identified the symphysis region and the splenial articular suture, we may conclude that ML 768 represents a relatively young individual as seen in SMSN 52348. On the lateral surface (Figure ~~1~~2 A), at least six, possibly seven, neuro-vascular foramina arranged in two different rows are well distinguishable. In medial view (Figure 3 A), the articular surface for the splenial starts anteriorly approximately below the second preserved tooth position. Ventrally to that surface, a deep Meckelian sulcus runs for the entirety of the preserved length of the ~~jaw~~ dentary (Figure 3 A). On the ~~medioventral~~ ventromedial edge of the bone, some porosity is present as possible signs of further vascularization. ~~Furthermore, the~~The CT-images highlight seven functional teeth (ft) which do not preserve the crowns, two replacement teeth (rt) in an early stage of development and a worn-out crown (wc) (Figures 1-3 C). The functional teeth are located lateral to the two replacement teeth (Figure 1). ~~As can be observed in Figure 1 A, the functional teeth are arranged in a row which formed the mastication surface. Furthermore, it is possible to distinguish a total of eight tooth positions (Figure 1 A), contrarily from what is observed by Rotatori et al (2020).~~ The functional teeth are located lateral to the two replacement teeth (Figure 1), arranged in a row, which formed the occlusal surface. A total of eight tooth positions (Figure 1 A) were identified contra Rotatori et al. (2020).The functional teeth do not preserve the crown, but the root is complete in ft-V and ft-VII, slightly fractured at the base in ft-III, while the root is broken ~~it is not preserved~~ in various degrees in the others (Figure 3 C). There is no sign of resorption at the bases of the roots of the functional teeth, which indicates that the replacement cycle had not started yet in most of the tooth positions (tp). The absence of replacement teeth in those same tooth positions ~~of replacement teeth~~ supports this interpretation. The ~~only exception~~ exceptions are~~is~~ ~~constituted by the~~ two replacement teeth crowns ~~mentioned~~ discussed above (rt-I and rt-II, Figures 1-3) and the small worn-out crown (wc) lateral to ft VI (Fig 1 C). Rt-I is medial to ft-II (Figure 1 C) but it appears to have not started any resorption in the latter, since the root is intact, despite broken on the apical surface. Rt-II is medial to ft-IV (Figure 1 C), and a small pit along the base of the ft-IV root is observed, indicating how the resorption had just started~~ at the moment of death~~. The position of the wc, within~~in~~ respect to ft VI, indicates that it is probably the remnant of an older replacement cycle. The leaf-shaped crowns of rt-I and rt-II do not have a root yet formed, although the marginal denticles and the primary ridge are well developed. The crowns of the replacement teeth do not display any wear facets indicating that they were not functional antemortem~~do not display any wearing facets, indicating that there were not yet functional teeth when the animal died.~~

The neurovascular canal consists of one main~~ ramus~~ canal~~-~~ which runs anteroposteriorly, which we identified as the mandibular canal as described in other taxa (Bouabdellah et al. 2022; Kawabe & Hattori 2022). Anteroventrally to the second preserved tooth position (ft-II), this ramus deflects ventrally following the descending position of the teeth from here towards the symphysis (Figure 2 C). In archosaurs, including dinosaurs, this canal hosts a complex network of nerves and lymphatic ~~vases~~ vessels (Witmer 1995; Porter et al. 2016; Lessner 2021). This network is thought to include ~~includes~~ part of the trigeminal innervation, the ventral-alveolar nerve and the mandibular artery (Bouabdellah et al. 2022; Mateus & Estraviz-López 2022; Kawabe & Hattori 2022). From the mandibular canal~~its main ramus~~, at least seven ~~rami~~ branches depart dorsally (d-I – d-VII), ~~connecting to the~~expanding in the bony walls that enclose the alveoli (Figure 2 B). On their dorsal-most end, they form ~~globular~~ complex ~~networks~~dendritic network ~~modelling a complicated and dense~~ system in proximity to the tooth crowns (Figure 2B, C). The dorsally projecting ~~rami~~ branches (d-I – d-VII),~~-~~ become closer to one another anteriorly in proximity to the ventral deflection of the mandibular canal ~~as well as their internal vascularization network, increase in density towards the anterior part of the dentary~~ (Figure 2). Laterally, three thick canals project perpendicular to the dental roots and crowns from the main ~~ramus~~ canal (l-I – l-III) and connect with the large lateral foramina (Figure 2 A, C). At least three additional neuro-vascular canals depart ventrally (v-I – v-III) from the main ~~ramus~~ canal, almost reaching ~~almost~~ the ventral surface of the dentary.

Discussion

Despite the extensive use of C~~t~~T-scan~~-D~~ data in palaeontology ~~in the~~during the last few decades, few studies have focused on the internal micro-anatomy of lower jaws in dinosaurs. Recent studies have highlighted a dense neurovascular system in *Tyrannosaurus rex* ~~similar~~ considered comparable to the ones ~~of~~ found in crocodilians (Bouabdellah et al. 2022; Kawabe ~~&~~and Hattori 2022). On the other hand, in their comparative study, Kawabe ~~and~~ and Hattori (2022) remarked how in the cerapodan ornithischian dinosaurs *Triceratops horridus*, *Edmontosaurus annectens*, and *Fukuisaurus tetoriensis*, the mandibular ~~ramus~~ canal is ~~differently~~ arranged differently ~~than into~~ *Tyrannosaurus*~~.~~ *rex*. In these ~~latter~~cerapodan taxa, instead of a ~~dense~~thick dendritic vascular structure (Lessner 2021), there is one dense thick main ~~ramus~~ canal with several smaller ~~branching~~ ~~smaller rami~~ branches as in ML 768. Furthermore, the density of vascularization that seems to increase anteriorly towards the predentary contact in the studied dryosaurid dentary is also present in the other cerapodan taxa (Kawabe ~~&~~and Hattori 2022). On the contrary, the heterodontosaur *Fruitadens haagarorum* shows a proportionally thinner vascular canal, in relation with the development of the dental roots (Butler *et al.* 2012). The dentary ML 768, which represents an undetermined species of Dryosauridae (Rotatori et al. 2020), follows the pattern present within Cerapoda. The striking difference between the cerapodan taxa and *Fruitadens haagarorum* is the increase of dental replacement rates in the former taxa with respect to the latter (Norman 2004). We ~~may~~ hypothesize that this ~~augment of size~~ size increase of vascular canals within

Cerapoda may be~~is~~ linked to the increase in dental replacement rates. In the specimen ML 768 this is clearly evident by the presence of the three canals (I-I – I-III) perpendicular to the dental structures~~ which have been linked to direct supply of nutrients to fast replacement teeth (Edmund 1957)~~. Interestingly, this character seems to ~~happen~~ at least ~~at the base of~~in the early evolution of Dryomorpha, suggesting that the evolutionary trend leading to the development of hadrosaur dental batteries started already in the Jurassic. Among Cerapoda, dental batteries evolved at least twice: once in the lineage leading to Hadrosauridae and another time in the lineage to Ceratopsidae (Hailu ~~&~~and Dodson 2004; Horner et al. 2004). Earlier diverging representatives of both lineages do not present batteries (Hailu ~~&~~and Dodson 2004; Norman 2004), and the transformation occurring in the neurovascular system has never been documented so far in literature.

Furthermore, as already noted by some ~~workers~~ researchers (Porter et al. 2016; Porter ~~&~~and Witmer 2020), the anterior region of the skull of dinosaurs is a key-area for thermoregulation. We cannot exclude that, given the relatively high metabolic rates of dryosaurids (Hübner 2012), this enlargement of the neurovascular canals played a role in maintaining the ~~animals~~ homeostasis. More specifically, Porter and~~and~~ Witmer (2020) showed how cephalic circulation in dinosaurs ~~is~~ was arranged in two different patterns, according to their specific thermoregulatory strategy. Indeed, the authors identified (i) a distributed thermoregulatory strategy and (ii) a focused thermoregulatory strategy. The former is characterized by a balanced vascular pattern, and there is not a specific area in the skull where this vascularis~~z~~ation is more emphasized. On the contrary, the latter is characterized by a strongly unbalanced vascular patterns, and the vascularis~~z~~ation is strongly emphasized in ~~some~~ certain areas of~~in~~ the skull. Overall, small~~-~~-sized ~~species~~ taxa are found to adopt (i), while (ii) is preferred by larger species, and the preference of one over the other does not appear to be phylogenetically constrained (Porter ~~&~~and Witmer 2020). Unfortunately, Porter ~~and~~ and Witmer (2020) considered only the dorsal part of the skull, overlooking the role of the dentary in such strategies. We cannot exclude, and it is quite likely indeed, that the lower jaw played a role in such thermoregulatory systems, as in other archosaurs. In fact, the density of vascularization in ML 768 seems to increase towards the tip of the lower jaw, where thermic exchange happens in *Crocodylus* sp. and ~~aves~~birds~~.~~ (Porter et al. 2016; Porter ~~&~~and Witmer 2016). Finally, it is worth noting ~~hy to note~~ ~~how~~ that in ornithischians the development of a ~~ramphothecar~~hamphotheca requires a dedicated nutrient supply, which also increases the ~~neuro-vascular size~~vascular demand (Norman et al. 2004).

In short, the highly developed neurovascular system observed in the dentary ML 768 can be explained in terms of:

1. Increased tooth replacement rates: as mentioned above, the increased replacement rates respect to early diverging ornithischian dinosaurs. As this increase appeared at least twice within Ornithischia, in the lineages that lead to the appearance of both Ceratopsidae and Hadrosauridae, we predict that major re-arrangements in the neurovascular system of the jaws is likely to have occurred.
2. Thermoregulation strategy: as mentioned above, small-sized animals should adopt a diffuse thermoregulation strategy. Since relative small size~~d~~ is the basal condition for iguanodontians (Norman et al. 2004), we expect a shift from diffuse strategy (i) to unbalanced ~~stratefy~~strategy (ii) occurring within Iguanodontia, possibly related ~~with~~ increase in size~~.~~ ~~(Porter *et al.* 2016)~~Since the sampling of Porter et al.~~,~~ (2016) has been so far limited, investigating the evolution of thermoregulatory system in different clades of dinosaurs can help untangle their various adaptive landscapes through Mesozoic.

We cannot exclude a complex interplay between the two-abovementioned hypotheses, and future testing will help to entangle this matter. ~~In order to~~To ~~corroborate~~ test the hypotheses presented here, more data on the mandibular neuro-vascular system of several other basal iguanodontians is needed, ~~.~~in order to better understand the evolution of these traits in a phylogenetic framework.

Conclusions

We describe~~d~~ the micro~~-~~anatomy of a small, fractured isolated dentary of a dryosaurid dinosaur. Micro-CT scans revealed the presence of two rows of teeth, with two replacement crowns present. The crowns of the functional teeth are not preserved, although the integrity of the roots indicate that these teeth did not begin the resorption cycle at the moment of death. The neurovascular system present in the dentary strongly differs from the one described ~~presented~~ in *Tyrannosaurus rex* and the heterodontosaur *Fruitadens haagarorum,* while perfectly matching the pattern described in certain cerapodan dinosaurs. The proportionally large canals are consistent with high dental replacement rates, thermoregulation system and ramphoteca development. CT~~t~~ ~~-~~scanning of more complete ornithopod specimens is needed to test ~~the hypotheses here presented.~~ if the relative enlargement of blood vessels in the dentary ML 768 can be explained in terms of (1) increased tooth-replacement rates, (2) thermoregulation strategy or a complex interplay between the two of them.

Acknowledgements

We deeply thank all the workers and volunteers of Museu da Lourinhã, where the specimen is deposited. This work is funded by national funds through the Fundação para a Ciência e a Tecnologia (FCT), I.P., through the Research Unit ~~under the project~~ GeoBioTec UIDB/04035/2020; ~~, and~~ the project BioGeoSauria PTDC/CTA-PAL/2217/2021 and the fellowship SFRH/BD/146230/2019 PhD fellowship (FMR); MMA is supported by the MCIN/AEI/10.13039/501100011033 and co-financed by the NextGeneration EU/PRTR, Ramón y Cajal contract RYC2021-034473-I. We thank the Ct-scan crew at CENIEH for the assistance during data acquisition.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Orcid

Filippo Maria Rotatori: 0000-0002-7084-1919

Mattia Quaranta: 0000-0003-3344-0101

Filippo Bertozzo: 0000-0002-0917-9989

Bruno Camilo: 0000-0003-3202-5010

~~Tom Hübner:~~

Octàvio Mateus: 0000-0003-1253-3616

Miguel Moreno-Azanza: 0000-0002-7210-1033

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FIGURE CAPTIONS

Figure 1: ML 768. Dryosauridae indet. Right dentary ML 768 in dorsal view. (A) rendering of all the elements together: bone, neurovascular systemsystem, and teeth; (B) rendering of the elements with the mesh of the bone in transparencey; (C) detail of the neurovascular system and dentary teeth. Scale: 1 cm. Abbreviations: l, lateral canal; ft, functional teeth; tp, tooth position; wc, worn out crown. Roman numbers identify the position of the anatomical structures according to anteroposterior axis.Roman numbers identify the position according antero-posterior axis. Arrow indicates anterior side.

Figure 2: Dryosauridae indet. Right dentary ML 768 ML 768. Dryosauridae indet. Right dentary in lateral view. (A) rendering of all the elements together: bone, neurovascular system and teeth; (B) rendering of the elements with the mesh of the bone in transparencetransparency; (C) detail of the neurovascular system and dentary teeth. Scale: 1 cm. Abbreviations: d, dorsal canal; l, lateral canal; fo, foramina; ft, functional teeth; v, ventral canals; wc, worn out crown. Roman numbers identify the position of the anatomical structures according to antero-posterior axis. Arrow indicates anterior side.

Figure 3: Dryosauridae indet. Right dentary ML 768 ~~ML 768. Dryosauridae indet. Right dentary~~ in medial view. (A) rendering of all the elements together: bone, neurovascular system and teeth; (B) rendering of the elements with the mesh of the bone in ~~transparence~~transparency; (C) detail of the neurovascular system and dentary teeth. Scale: 1 cm. Abbreviations: d, dorsal canal; ft, functional teeth; mk, Meckelian sulcus; spl, splenial contact. Roman numbers identify the position of the anatomical structures according to anteroposterior axis~~Roman numbers identify the position according antero-posterior axis~~. Arrow indicates anterior ~~side~~.

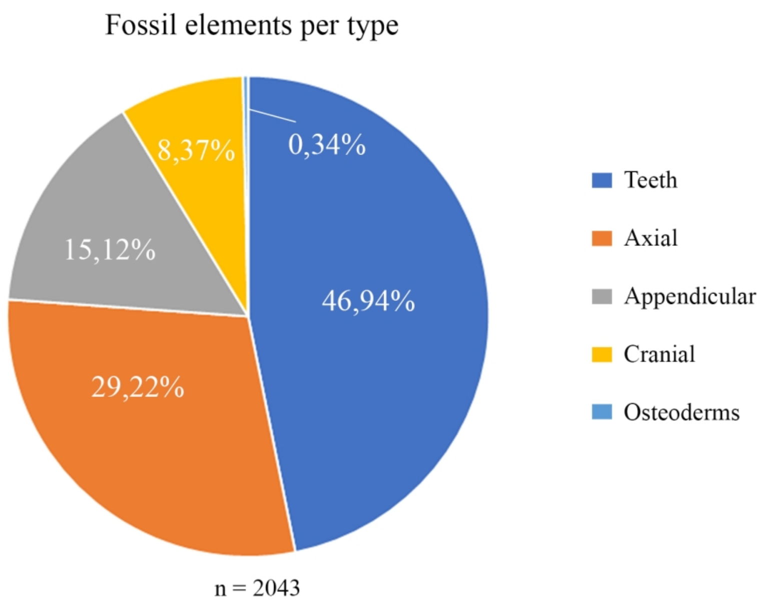

Figure 1

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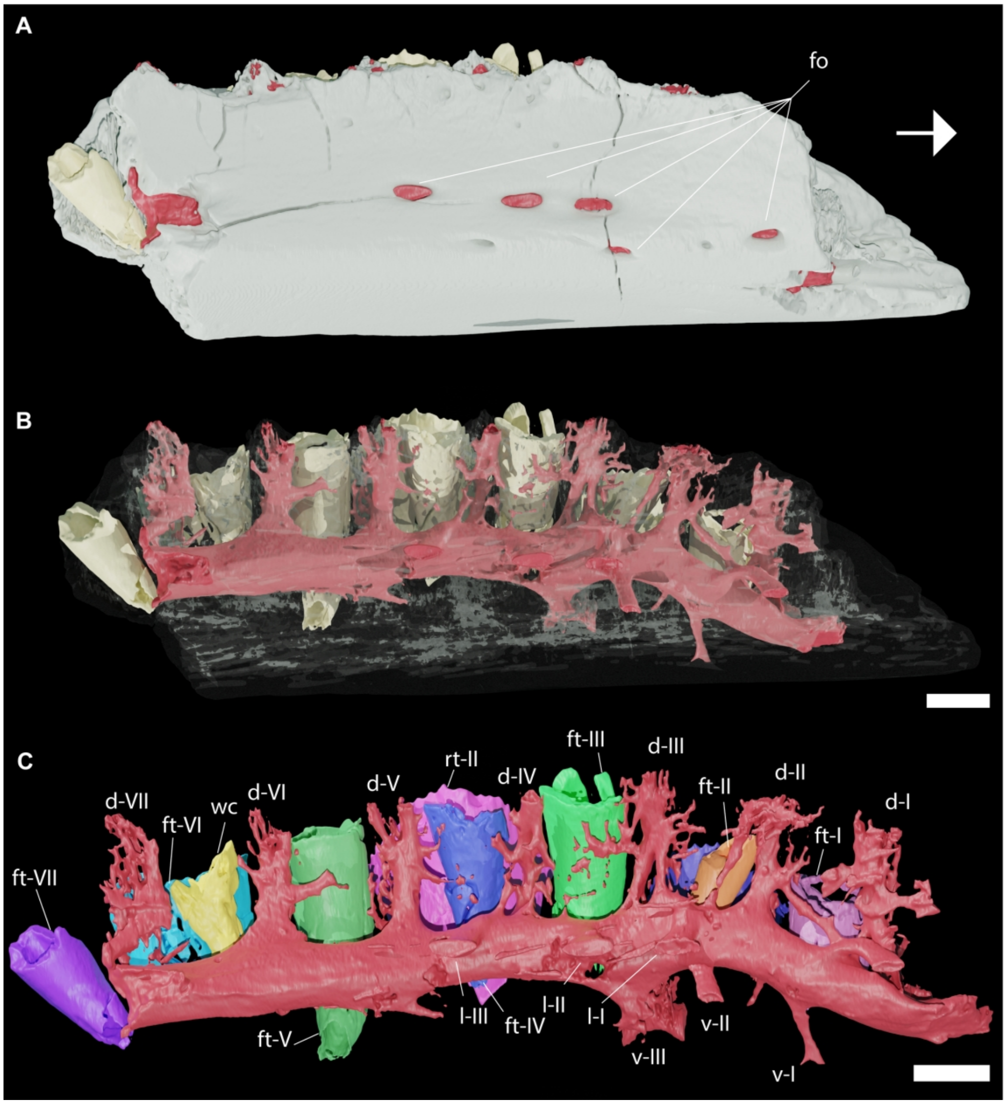

Figure 2

182x199mm (300 x 300 DPI)

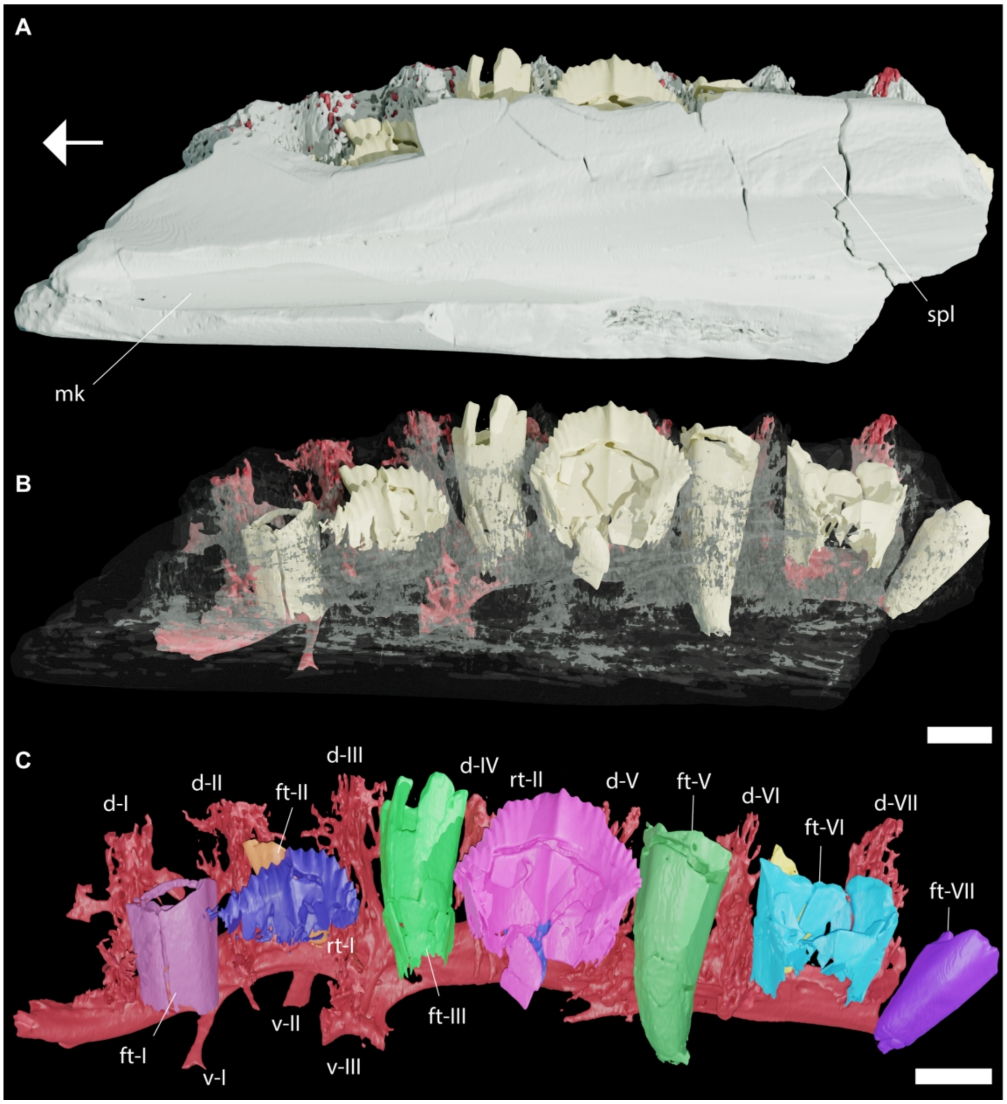

Figure 3

182x199mm (300 x 300 DPI)