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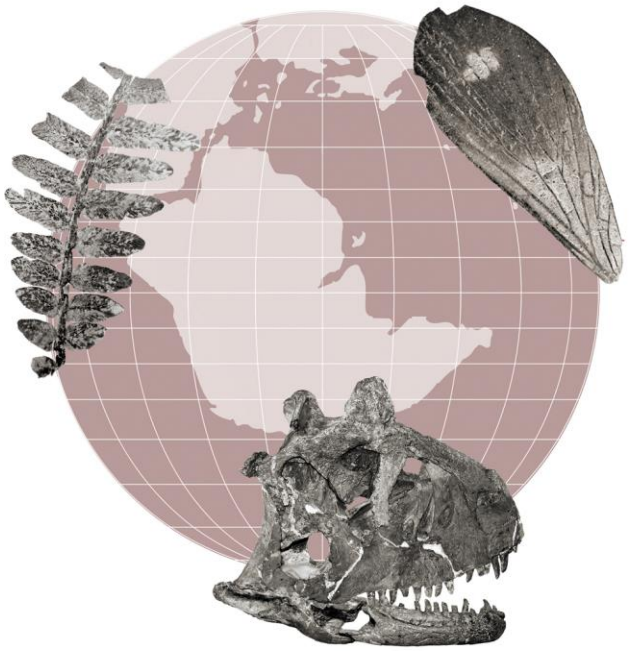

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PRELIMINARY REPORT OF ABELISAURID (DINOSAURIA, THEROPODA) TOOTH AND TOOTH ATTACHMENT TISSUES

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Short Description: We present here a study focused on the histology of tooth and tooth attachment tissue of an abelisaurid theropod.

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Abstract. Abelisauridae is a group of Late Cretaceous Gondwanan theropods characterized by their bizarre skull anatomy, including a short, high and conspicuously fused cranium ornamented with a rugose external surface. Studies of abelisaurid teeth have focused on external crown morphology, leaving aspects of microstructure of tooth and tooth attachments (i.e. periodontium) unexplored. These kinds of analyses are essential to a more complete understanding of dental anatomy, development, and evolution in theropod dinosaurs. In this contribution we study the microstructure of the tooth and periodontium of an undetermined abelisaurid (MUCPv-1151) from the Upper Cretaceous of Argentina. The histological analysis of a lower jaw fragment revealed the presence of enamel, dentine with distinct growth lines and cementum in the teeth and alveolar bone lining each alveolus. Although the dental microstructure is comparable to that described for other theropod dinosaurs, there is significant variation in the thickness of the growth lines in the dentine. Regarding periodontium histology, the data indicate that abelisaurids had a gomphosis-type implantation, with a tissue distribution comparable to that of other saurischians, including other non-avian theropods. However, differences were identified in the thickness of the cellular cementum and the degree of development of Sharpey's fibers in the cementum and alveolar bone. Histological data reveal that the pattern of tooth formation and replacement in abelisaurids is comparable with that of other amniotes. This contribution reveals that, irrespective of cranial specializations reported for abelisaurid theropods, their tooth and periodontium, alongside the pattern of tooth formation and replacement, are exhibits highly conservative patterns.

Keywords. Dental growth rate. Dental histology. Periodontum. Tooth attachment. Theropoda. Abelisauridae.

Resumen. ESTUDIO PRELIMINAR SOBRE DIENTES Y TEJIDOS DE INJERCIÓN DENTAL DE ABELISÁURIDOS (DINOSAURIA, THEROPODA). Abelisauridae es un grupo de terópodos gondwanicos del Cretácico Superior que se caracterizan por su peculiar anatomía craneal, que incluye un cráneo corto, alto y visiblemente fusionado, ornamentado con una superficie externa rugosa. Los estudios de los dientes de los abelisáuridos se han centrado en la morfología externa de la corona, dejando sin explorar aspectos de la microestructura dental y de sus tejidos de implante (ie., el periodonto). Este tipo de análisis es esencial para una comprensión más completa de la anatomía, el desarrollo y la evolución dental en los dinosaurios terópodos. En esta contribución, estudiamos la microestructura dental y del periodonto de un abelisáurido indeterminado (MUCPv-1151) del Cretácico Superior de Argentina. El análisis histológico de un fragmento de mandíbula inferior reveló la presencia de esmalte, dentina con líneas de crecimiento distintivas y cemento en los dientes, así como hueso alveolar recubriendo cada alvéolo. Aunque la microestructura dental es comparable a la descrita para otros dinosaurios terópodos, existe una variación significativa en el grosor de las líneas de crecimiento en la dentina. Con respecto a la histología del periodonto, los datos indican que los abelisáuridos tenían una implantación de tipo gonfosis, con una distribución tisular comparable a la de otros saurísquios, incluyendo otros terópodos no avianos. Sin embargo, se identificaron diferencias en el grosor del cemento celular y el grado de desarrollo de las fibras de Sharpey en el cemento y el hueso alveolar. Los datos histológicos revelan que el patrón de formación y reemplazo dental en los abelisáuridos es comparable al de otros amniotas. Esta contribución revela que, independientemente de las especializaciones craneales reportadas para los terópodos abelisáuridos, sus dientes y su periodonto, junto con el patrón de formación y reemplazo dental, exhiben patrones altamente conservativos.

Palabras clave. Tasa de crecimiento dental. Histología dental. Periodonto. Anclaje dental. Theropoda. Abelisauridae.

ABELISAURIDAE IS A GROUP OF LATE CRETACEOUS GONDWANAN THEROPODS, NAMED BY BONAPARTE AND NOVAS (1985) TO INCLUDE THE GENUS *ABELISAURUS* FROM THE ARGENTINEAN PATAGONIA. This clade includes a large number of forms found in South America, Africa, Madagascar, India, and also southern Europe (Bonaparte, 1991, 1996; Novas *et al*., 2013; Tortosa *et al*., 2014). Abelisaurids are characterized by their highly reduced forelimbs and a bizarre skull anatomy, including a short, high and conspicuously fused cranium ornamented with a rugose external surface that evolved, in some cases, horns or domes on the parietal roof (Bonaparte, 1991; Sampson, 1998; Sampson & Witmer, 2007; Novas, 2009; Novas *et al*., 2013; Zaher *et al*., 2020; Cerroni *et al*., 2022). Similar to most of the non-avian theropods (Brink *et al*. 2015), abelisaurids were carnivorous dinosaurs with polyphyodont dentitions with typical ziphodont tooth morphology inserted in distinct alveoli. Although the dental anatomy of abelisaurid theropods has been thoroughly analyzed in some taxa (*e.g.*, *Majungasaurus crenatissimus*, Smith, 2007), information regarding tooth microstructure and tooth attachment in this clade are still poorly explored.

To date, dental histology of abelisaurid theropods has been only partially studied by D'Emic *et al*. (2019), who specifically studied the incremental lines of von Ebner in *Majungasaurus crenatissimus.* Von Ebner lines are daily formed growth marks present in the dentin (Erickson, 1996a, 1996b). Combining data from CT and histology, D'Emic *et al*. (2019) analyzed the tooth formation and replacement rates in *Majungasaurus crenatissimus* using both the tooth size and the von Ebner spacing. The replacement rates in this taxon were interpreted as being higher than that of other non-avian theropods. The estimation of tooth formation rates using spacing between von Ebner lines has been also conducted in other sauropsids, including, for example, lepidosaurs,

sauropterygians and crocodyliforms (*e.g.*, Gren & Lidgren, 2013; Kear *et al*., 2017; Ricart *et al*., 2019; Navarro *et al*., 2022).

In the case of the tooth attachment tissues (i.e., periodontium), these have not been analyzed in Abelisauridae. Furthermore, our current knowledge about the structure of the periodontium in other non-avian theropod dinosaurs is still very scarce. To date, the only contributions in this regard have been conducted on the Triassic basal neotheropod *Coelophysis bauri* and the tetanurans *Allosaurus fragilis* and *Gorgosaurus* sp. (Reid, 1996; Fong *et al*., 2016; LeBlanc *et al*., 2016a, 2017b). As reported for other dinosaurs (*e.g.*, García & Zurriaguz, 2016; LeBlanc *et al*., 2016a, 2017b; Bramble *et al*., 2017; Chen *et al*., 2018), the periodontium of non-avian theropods is composed of three specific tissues: root cementum, alveolar bone, and periodontal ligament (Reid, 1996; Fong *et al*., 2016; LeBlanc *et al*., 2016a, 2017b). This tripartite condition represents the plesiomorphic condition for Amniota (*e.g.*, LeBlanc & Reiz, 2013; LeBlanc *et al*., 2016b, 2017a, 2017b, 2018). Despite the conservative nature of the periodontal tissue histology, changes in the spatial distribution, degree of development and rates of formation of these tissues has resulted in diverse tooth attachment geometries, replacement modes, and bone architectures supporting the dentition in vertebrates (*e.g.*, LeBlanc *et al*., 2016a, 2020). In general terms, the histological study of the periodontium has yielded valuable insights into the paleoecology, palaeobiology and systematics of extinct groups (*e.g.*, Caldwell *et al*. 2003; Budney *et al*., 2006; Maxwell *et al*., 2011a, 2011b; Snyder *et al*., 2020, Dumont *et al*., 2016; LeBlanc *et al*., 2017a, 2020; 2021; 2023; Chen *et al*., 2018; Mestriner *et al*., 2021; Navarro *et al*., 2022; Cerda & Codorniú, 2023).

In this contribution we describe and interpret the microstructure of the tooth and tooth attachment tissues of an undetermined abelisaurid (MUCPv-1151) from the Upper

Cretaceous of Argentina (Porfiri, *et al*., 2006; 2009). Taking into account the current knowledge about tooth and tooth attachment histology of vertebrates, the main aims of this preliminary study are are: 1- to determine if the high growth rate of tooth formation reported for *Majungasaurus crenatissimus* is widespread in other abelisaurids; 2- to characterize the periodontal histology of abelisaurids, using MUCPv-1151 as an exemplar; 3- to examine and compare the tooth attachment of abelisaurids with other archosaurs, evaluating the hypothesis of conservatism in the microstructural and spatial distribution of the involved structures. This corresponds to the first histological study on tooth attachment tissue for Ceratosauria.

MATERIAL AND METHODS

A fragment of a lower jaw from an incomplete skull (MUCPv-1151) was sampled for histological analysis (Figure 1). The sample corresponds to a partial skeleton recovered from the Upper Cretaceous (Cenomanian) outcrops of the Candeleros Formation, at Aguada Pichana locality (170 Km nortwest from Neuquén Province, Patagonia Argentina). Taxonomical assignment of MUCPv-1151 to Abelisauridae has been provided by Lamanna *et al*. (2019). A total of five thin sections, three transversal (perpendicular to the tooth row) and two coronal (parallel to the tooth row in a labiolingual plane), were obtained for histological analysis (Figure 1). Thin sections were prepared at the petrographic laboratory of Universidad Nacional de San Luis (San Luis, Argentina), using standard methods detailed by Cerda & Chinsamy (2012). Nomenclature and definitions of histological structures used in this study follow Francillon-Vieillot *et al*. (1990) and LeBlanc *et al*. (2017b). Nomenclature for tooth implantation, attachment, and replacement follows LeBlanc *et al*., (2017b) and Bertin *et al*. (2018).

RESULTS

The sampled portion of the mandible is formed by the dentary, which has lost the most of the functional tooth crowns. The lateral (labial) wall of the dentary is higher than the medial (lingual) one due the absence of interdental plates in the sample. The teeth are deeply implanted in distinct alveoli that reach the ventral portion of the dentary (Figure 2). Each alveolus contains one functional and at least one replacement tooth. Although the roots and crowns of both functional and replacement teeth located inside the alveoli have suffered from crushing, their original position can still be determined. In this regard, the replacement teeth are located lingual to the functional teeth (Figure 3.1-3.4). The apical portion of the functional tooth roots appear to be partially resorbed. The labial margins of the alveoli at the deeper portion of the dentary (i.e. distal to the occlusal margin) exhibit shallow resorption bays, here interpreted as replacement crypts (Figure 3 .3).

Thin sections reveal a thin (32-48 μm) layer of enamel capping the tooth crowns (Figure 4.1-4.3). These measurements where mostly obtained from the crown of the replacement tooth. Enamel exhibits a strong birefringence under cross-polarized light, however the pattern is not homogeneous. In this regard, the enamel layer is formed by distinct thin and columnar structures that exhibits different pattern of birefringence (Figure 4.2, 4.3). The bulk of the teeth is formed by orthodentine (hereafter referred to as dentine), which contains long tubules that would have housed the odontoblast processes and occasional nerve filaments extending radially from the pulp cavity towards the outer surface of the tooth. Dentine tubules extend into the dentine cores of the serrations (denticles) (Figure 4.1). These tubules are less evident near the dentine-enamel junction. The dentine appearance in this region is in some cases irregular and

possibly corresponds with globular dentine (Figure 4.2) (Brink *et al.*, 2015). Globular dentine is, however, not evident in root dentine. The dentine exhibits a stratified pattern of dark and light concentric bands (Figure 4.4-4.9). Due to diagenetic alteration, these bands were only partially preserved in the sampled teeth. We measured the distance between successive bands in different points of the sectioned teeth (77 measurements). Due the banding nature of these histological structures, the thickness of successive bands was considered as the distance between the inner margins of two consecutive dark bands. We obtained an average thickness of 34 μm (SD ±14 μm) with a range of variation between 9 and 63 μm. It must be noted that the distance between bands was particularly short (*e.g.*, 10-13 μm) in some instances (*e.g.*, in the crown of the replacement tooth showed in the Figure 4.9).

The dentine of the roots is lined by cellular cementum (Figure 5.1-5.3). The same contain ovoid cementocyte lacunae. Cellular cementum is birefringent under polarized light. Extinction pattern reveals that collagenous fibers were oriented perpendicular to the root surface. The thickness of the cellular cementum is rather homogenous, ranging between 52 and 60 μm. No evident Sharpey's fibers are recorded in the cellular cementum.

A distinct band of birefringent, acellular tissue is present between the cellular cementum and the dentine (Figure 5.2, 5.3). This tissue is actually composed by two thin layers which exhibit tenuous differences with regard to the degree of birefringence. The layer adjacent to the acellular cementum is the one with a more pronounced birefringence and is interpreted as acellular cementum. The second, less birefringent layer appears to correspond with the hyaline layer of the dentine (layer or of Hopewell-Smith) (Nimoshini *et al.*, 2021).

Each alveolus is lined by a distinct layer of alveolar bone, which is separated from the jawbone by a reversal line (Figure 5.4-5.6). The alveolar bone is formed by a well vascularized woven bone matrix, with abundant and densely grouped osteocyte lacunae arranged in no recognizable pattern. Vascular canals do not exhibit a particular arrangement. The alveolar bone contains simple vascular canals and occasional primary osteons, as indicated by the presence of lamellar bone lining the canals. Distinct Sharpey's fibers are absent in the alveolar bone.

The jaw bone, dentary in this case, is composed of highly remodeled compact bone (Figure 5.7-5.10). Secondary osteons, formed during several events of resorption and new bone deposition, are mainly aligned parallel to the dentary main axis (i.e., anteroposterior/mesiodistal alignment). A slight variation to this pattern is observed in the outer cortex of the lingual side of the dentary, toward the occlusal margin. Here some groups of secondary osteons exhibits an alignment perpendicular to the dentary main axis (Figure 5.9). The labial margins show a distinct appearance which is characterized by the presence of ridges and valleys, reflecting some degree of ornamentation in this side of the element (Figure 5.10, 5.11). Primary bone is preserved in the outermost portion of the labial cortex (Figure 5.11).The same is formed by poorly vascularized parallel fibered bone and contains several lines of arrested growth. Sharpey's fibers are particularly abundant in this part of the cortex (Figure 5.11). Transversal sections reveal that each tooth is separated by an hourglass-shaped wall of interdental bone in cross-section (Figure 5.12). As occur in the lingual and labial walls of the dentary, the interdental bone is entirely remodeled. The secondary osteons constituting the interdental bone appears to be mostly arranged oblique to both mesiodistal and labiolingual axis of the dentary (Figure 5.12).

DISCUSSION

Dentinal growth marks

An evident stratified pattern of dark and light concentric bands was recorded in the dentine of the sectioned teeth of MUCPv-1151. At first instance, the bands appear to correspond to the increment lines of von Ebner. However the variation in their thickness (i.e. distance between the inner margins of two consecutive dark bands) raises doubts about their nature. The thickness of the increment lines has been reported for numerous vertebrate groups (*e.g.*, Erickson, 1996a, 1996b, Gren & Lidgren, 2013; García & Zurriaguz, 2016; D'Emic *et al*., 2013, 2024; Kear *et al*., 2017; Chen *et al*., 2018, 2023; Whitney & Sidor, 2020; Navarro *et al*., 2022; Maho & Reiz, 2024), including non-avian theropods (Erickson, 1996b; Button *et al*. 2017; D'Emic *et al*., 2019; Heckeberg & Rauhut, 2020) and toothed birds (Dumont *et al*., 2016). In abelisaurids, the thickness of the increment lines reported by D'Emic *et al*. (2019) for *Majungasaurus crenatissimus* is 18 ± 5μm, which fall within the range of other archosaurs. This value does not differ significantly from the obtained for *Ceratosaurus* (14 ± 3μm), the only non-abelisaurid ceratosaur for which incremental lines of von Ebner lines have measured. Button *et al*. (2017) indicated that the average of dentine deposition in Dinosauria resides within a narrow range between 10-20 μm per day. Since incremental lines of von Ebner are formed daily, this range can be considered as a direct indicator of dentine incremental rates for dinosaurs. These values depart from the obtained from MUCPv-1151, which has a higher thickness average (34 μm), with an important standard deviation (± 14 μm). Furthermore, while the minimum thickness value in MUCPv-1151 (9 μm) resembles the expected values, the maximum (63 μm) far exceeds it. This discrepancy may be due to different, non-mutually exclusive factors. First, while the most closely grouped marks could indeed correspond to von Ebner lines, the thicker increments possibly represent

Andresen lines. Andresen lines have been described in several vertebrates (*e.g.*, Scheyer & Moser, 2011; Gren & Lidgren, 2013; Kear *et al*., 2017) and correspond to long-period growth marks regularly deposited after several days (*e.g.*, 6-10 in humans) (Berkovitz & Shellis, 2016). Since most thickness measurements tend to cluster within two distinct intervals (10-19 μm and 34-43 μm), these could correspond to the average thickness between von Ebner lines and Andresen lines, respectively. However, it should be noted that in those cases where Andresen lines are reported, these are superimposed on the von Ebner lines (*e.g.*, Scheyer & Moser, 2011; Gren & Lidgren, 2013; Kear *et al*., 2017), something that is not evident in MUCPv-1151. The section plane is another factor that could influence the strong variation regarding growth line thickness in the specimen here analyzed. Kosch & Zanno (2020) showed that the section plane not only affects the count of dentin increment lines, but can also affect their spacing. Given the enormous variation in the growth marks thickness and the lack of certainty regarding their nature (i.e., whether they are all von Ebner lines or if Andresen lines are also included), we refrain from make inferences regarding the rate of tooth formation in MUCPv-1151.

Tooth attachment tissues

The existence of a periodontal space between the cellular cementum and the alveolar bone in MUCPv-1151 indicates that, similar to most archosaurs (*e.g.*, García & Zurriaguz, 2016; Fong *et al*., 2016; LeBlanc *et al*., 2017b; Chen *et al*., 2018), tooth attachment in abelisaurids corresponds to gomphosis. Gomphosis is characterized by the presence of three attachment tissues: cementum (cellular and acellular), alveolar bone and periodontal ligament (Bertin, 2016; LeBlanc *et al*., 2017b). Although this type of implantation is highly conserved in terms of the tissue types involved, the amount and arrangement of these tissues can generate highly specialized patterns within lineages

(*e.g.*, LeBlanc *et al*., 2017b; Bramble *et al*., 2017; Navarro *et al*., 2022). In the case of non-avian theropods, the few studies conducted on the subject show a basic condition in which the roots are symmetrically covered by cellular and acellular cementum and the alveolus is lined by alveolar bone (*e.g.*, Reid, 1996; Fong *et al*., 2016; LeBlanc *et al*., 2017). This condition is reported here in MUCPv-1151, revealing that, irrespective of cranial specializations reported for abelisaurid theropods, their tooth implantation exhibits a conserved pattern with respect to Theropoda more broadly.. Despite the general resemblance regarding tooth implantation tissues among non-avian theropods, some differences are recorded in specific features. In this regard, the cellular cementum thickness in MUCPv-1151 (52-60 µm) is comparable with the reported for *Coelophysis* (50-55 µm) but noticeably thinner than the described for *Gorgosaurus* (150-175 µm) (Fong *et al*., 2016; LeBlanc *et al*., 2017b). Since serial sections through the tooth roots of these theropods revealed no detectable differences in cementum thickness along the roots (Fong *et al*., 2016; LeBlanc *et al*., 2017b), the recorded variation among different taxa does not appear to be related with the position of the root examined. Instead, the cellular cementum thickness could be just tooth size-dependent, given the large size of *Gorgosaurus* in comparison with *Coelophysis* and MUCPv-1151. This possible causal relationship is supported by the reports of toothed birds as *Hesperornis regalis*, where the cellular cementum thickness is less than 20 µm (figure 7.c in Dumont *et al*., 2016). It must be noted, however, that the cellular cementum thickness is possibly related with other factors than tooth size in other archosaurs lineages. For example, Navarro *et al*. (2022) considered that the relatively thicker cellular cementum found among Mesoeucrocodylia, at least in comparison with other archosaurs, is possible related with the increased bite forces.

Regarding alveolar bone, the distribution and fine structure of this tissue in MUCPv-1151 are comparable not only with that reported for other non-avian theropods, such as *Allosaurus*, *Coelophysis* and *Gorgosaurus* (Reid, 1996; Fong *et al*., 2016; LeBlanc *et al*., 2017b), but also sauropod dinosaurs (García & Zurriaguz, 2016). The presence of highly vascularized woven fibered bone forming the alveolar bone is not a feature restricted to saurischian dinosaurs, since the same has been reported even for non amniote tetrapods (LeBlanc & Reiz, 2013).

As previously mentioned, in gomphosis, a non-mineralized periodontal ligament anchors into root cementum coating each tooth and into the alveolar bone forming each tooth socket (Bertin *et al*., 2018; LeBlanc, *et al*., 2017b). The portion of the periodontal ligament inserted into the cementum and the alveolar bone is mineralized, commonly leaving distinct extrinsic Sharpey's fibers in the matrix (*e.g.*, LeBlanc, *et al*., 2017b). These extrinsic fibers, however, are not as evident in MUCPv-1151 as in other archosaurs as notosuchian crocodyliforms (Navarro *et al*., 2022) or early dinosauriforms (Mestrimer *et al*., 2021). Whereas Sharpey's fibers are not recorded in the alveolar bone of MUCPv-1151, they appear to be faintly grouped in the cellular cementum, as evidenced by the extinction pattern observed in this tissue under polarized light. This pattern is similar to the observed in the cellular cementum and alveolar bone of *Coelophysis* (figure 3d in Fong *et al*., 2016; figure 1a, b in LeBlanc *et al*., 2017b) but differs from the reported for *Gorgosaurus*, where the Sharpey's fibers are much more evident in these tissues (figure 1c and d in LeBlanc *et al*., 2017b). Although these variations could be due to preservations artifacts, this seem rather improbable since Sharpey's fibers, possibly related with the periosteum of dermal tissue, are well preserved in the jaw bone (Figure 411). The poor development of Sharpey' fibers in MUCPv-1151 (and possibly *Coelophysis*) is then possibly related to the intrinsic nature

of the periodontal ligament and the mineralization processes of the same. On this regard, it must be noted that in some cases Sharpey' fibers are not clearly evident in the cementum even when the non-mineralized portion of the periodontal ligament are distinct in the section (*e.g.*, LeBlanc *et al*., 2017a).

Tooth replacement sequence

The thin sections obtained from MUCPv-1151 allow us to infer the sequence of tooth development and mode of replacement in an abelisaurid theropod. The position of the functional and replacement teeth within the same alveolus reveals that, as reported for most other amniotes, including non-avian dinosaurs (*e.g.*, Edmund, 1960; Fong *et al*., 2016; Chen *et al*., 2018), newly formed teeth develop lingual to the functional teeth (Figure 3). Distinct resorption spaces located in the lingual side of the dentary are here interpreted as replacement crypts and correspond to the spaces where the new replacement teeth began to form. Replacement crypts in the lingual side of the tooth bearing bone have been described in other non-avian saurischians (Reid, 1996; Fong *et al*., 2016; Leblanc *et al*., 2017b). Following the pattern inferred by Fong *et al*. (2016) and LeBlanc *et al*. (2017b) for non-avian theropods, it appears that the developing tooth in MUCPv-1151 first forms within the replacement crypt. As the replacement tooth matured, it migrated labially, resorbing the lingual surface of the functional tooth root. In a more advanced stage of development, the replacement tooth occupies fully the pulp cavity of the functioning tooth, which is followed by shedding of the older tooth. An exception to this pattern has been reported for crocodilians, where, except for hatching individuals, the replacement crypts are positioned underneath the roots of the functional teeth, albeit very slightly lingual to the midline of the functional tooth root (LeBlanc *et*

al., 2017b). The pattern of tooth replacement sequence in abelisaurids appears to be conservative regarding not only non-avian theropods, but also amniotes in general.

CONCLUSIONS AND FUTURE PERSPECTIVES

In this study, we present results on tooth and tooth attachment histology of an abelisaurid theropod. Although the dental microstructure is comparable to that described for other theropod dinosaurs, there is significant variation in the thickness of the growth lines in the dentine. It is not clear whether these lines correspond to incremental lines of von Ebner or Andresen lines. We consider that new thin sections analyses on abelisaurid theropod teeth are necessary for the accurate interpretation of these lines and the cause of their thickness variation. These new analyses should be performed from sections oriented in a mesiodistal plane, since these have proven to be the most reliable for the study of these lines in theropod dinosaurs (*e.g.* D'Emic *et al*., 2019). Furthermore, thin sections obtained from mesiodistal plane will allow the adjustment of the proposed models for tooth replacement rates proposed for non-avian theropods (D'Emic *et al*., 2019). Regarding tooth attachment histology, the data indicate that abelisaurids, like other dinosaurs, had a gomphosis-type implantation, with a tissue distribution comparable to that of other saurischians. However, differences were identified in the thickness of the cellular cementum layer and the degree of development of Sharpey's fibers in the cementum and alveolar bone. The hypotheses proposed here to explain these variations should be tested in new studies that not only include more individuals assigned to Abelisauridae, but also to other saurischian dinosaurs. Inclusion of specimens of different ontogenetic stages is also desirable. Finally, although histological data reveal that the pattern of tooth formation and replacement in abelisaurids is comparable with that of other amniotes, new data based on CT analyses will allow for a more in-depth and precise analysis of this.

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Figure captions

Figure 1. Fragment of the lower mandible of Abelisauridae indet. MUCPv-1151 sampled for histological analysis in **1,** labial; **2,** lingual; and **3,** occlusal views. Dashed lines indicate the location and orientation of the thin sections. Inset numbers correspond with the images showed in Figure 2. Abbreviations: **nvf,** neurovascular foramen. Scale bar equals 10 mm.-PLANED FOR A SINGLE COLUMN-

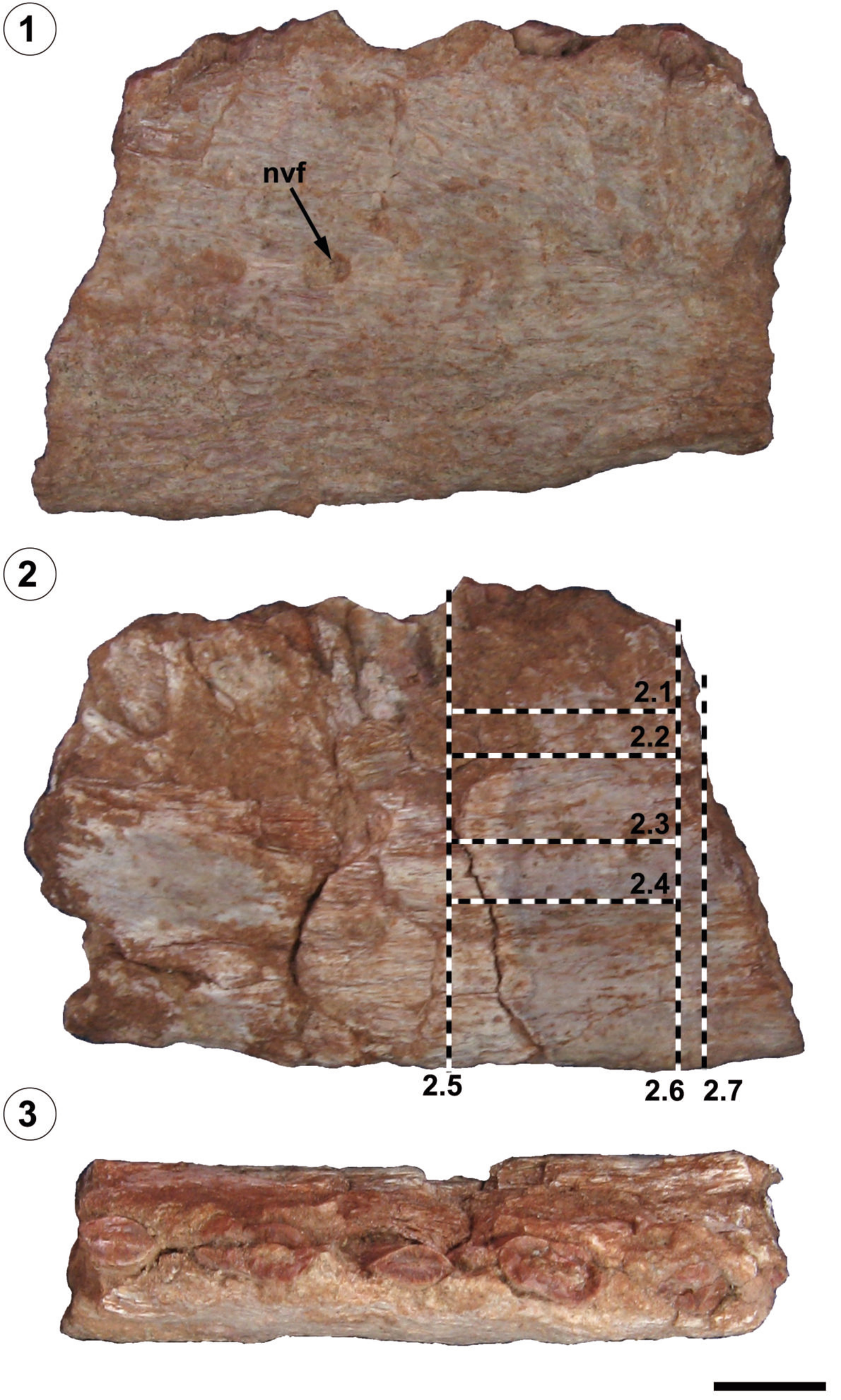
Figure 2. Complete histological sections of Abelisauridae indet. MUCPv-1151. **1-4,** transversal sections (anterior/mesial is to the left, and lingual towards the top of the images). **5-7,** coronal sections (labial is to the left, and occlusal toward the top of the images). The location of each section is indicated in the Figure 1. Numbered boxes indicate the position of the images showed in the Figures 4 and 5. Scale bars equal 5 mm. -PLANED FOR A SINGLE COLUMN-

Figure 3. Location of replacement and functional teeth in Abelisauridae indet. MUCPv-1151. **1-4,** Diagrammatic illustration of the complete transversal sections showed in Figure 3.1-3.4 (anterior/mesial is to the left, and lingual towards the top of the images). Whereas the jaw bone is represented in light gray, replacement and functional teeth are in black and dark gray respectively. Black asterisk signal the position of a replacement crypt. Roman numbers denote each individual alveolus. Scale bars equal 5 mm. -PLANED FOR A SINGLE COLUMN-

Figure 4. Tooth histology of Abelisauridae indet. MUCPv-1151. **1-3,** general view (1) and details (2, 3) of the tooth in transveral sections. Note the particular pattern of birefringence of the enamel. The box inset in 1 represents the position of the detailed

612 view showed in 2. **4-9,** detailed view of the dentine in both transversal (4-7) and coronal
613 (8, 9) sections. The images inset at the upper right corner correspond to the
614 enlargements of the areas indicated in each withe box. White arrowheads signal the
615 position of successive marks in the dentine. For ease of comparison, both the general
616 images and the details are shown on the same scale. 1, 4-9, 12: plane polarized light. 2,
617 3; cross polarized light with lambda compensator. Abbreviations: **de,** dentine; **dt,**
618 dentine tubules; **en,** enamel; **gd,** globular dentine; **td,** tooth denticle. Scale bars equal
619 0.2 mm (1, 4-9), 0.1 mm (2, 3). -PLANED FOR A DOUBLE COLUMN-
620
621 **Figure 5.** Histology of tooth and tooth attachment tissues of Abelisauridae indet.
622 MUCPv-1151. **1-3,** general view (1) and details (2, 3) of the tooth attachment tissues in
623 transversal section. The area showed in 2 and 3 correspond to the large box inset in 1. **4-**
624 **6,** alveolar bone preserved in different areas of the sample, including both transversal
625 (4, 6) and coronal (5) sections. The detailed view showed in 6 correspond to the small
626 inset box in 1. **7-9,** Haversian bone tissue in transversal (7) and coronal (8, 9) sections
627 of the dentary. Note the predominance of longitudinally oriented secondary osteons.
628 White arrowhead in 9 signals the position of a group of secondary osteons with a
629 different orientation. **10, 11,** general view (10) and detail (11) of the outer lateral cortex
630 showing remains of primary bone tissue. Note the irregular appearance of the external
631 surface, which exhibits ridges and valleys. **12,** transversal section showing strongly
632 remodeled tissue in the interdental bone. Note the irregular orientation of the secondary
633 osteons. 1, 2, 4, 5, 7-9, 12: cross polarized light with lambda compensator. 3, 6, 10, 11:
634 plane polarized light. Abbreviations: **ab,** alveolar bone; **ac,** acelular cementum; **cc,**
635 cellular cementum; **cl,** cementocyte lacuna; **de,** dentine; **Hb,** Haversain bone; **hl,**
636 hyaline layer; **ol,** osteocyte lacuna; **pc,** pulpar cavity; **po,** primary osteon; **ps,**

periodontal space; **rl,** resorption line; **Sf,** Sharpey's fibers, **vc,** vascular canal. Scale bars equal 0.2 mm (1, 4, 5, 11), 0.1 mm (2, 3, 6, 8), 0.5 mm (7, 9, 10), 1 mm (12). -PLANED FOR A SINGLE COLUMN-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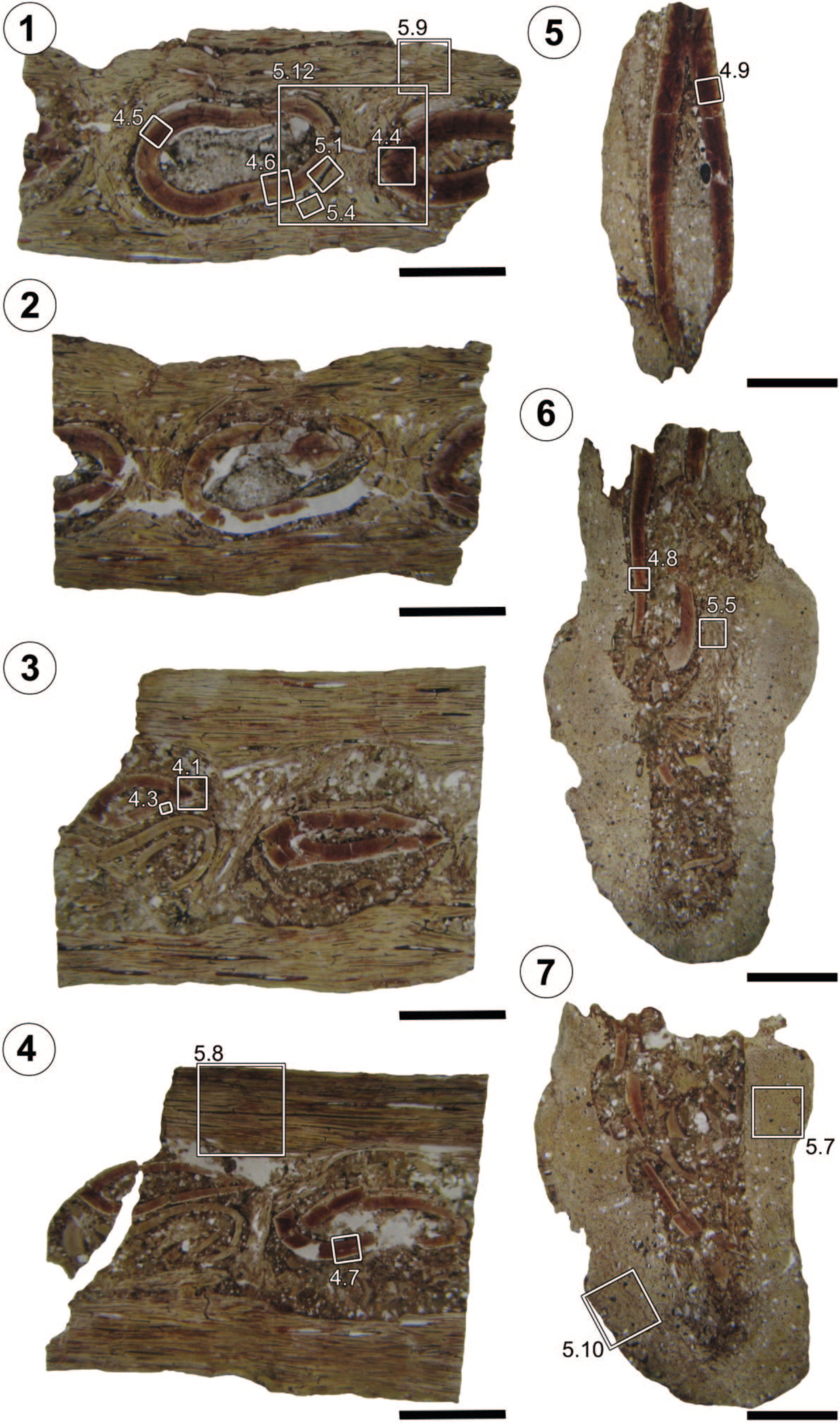
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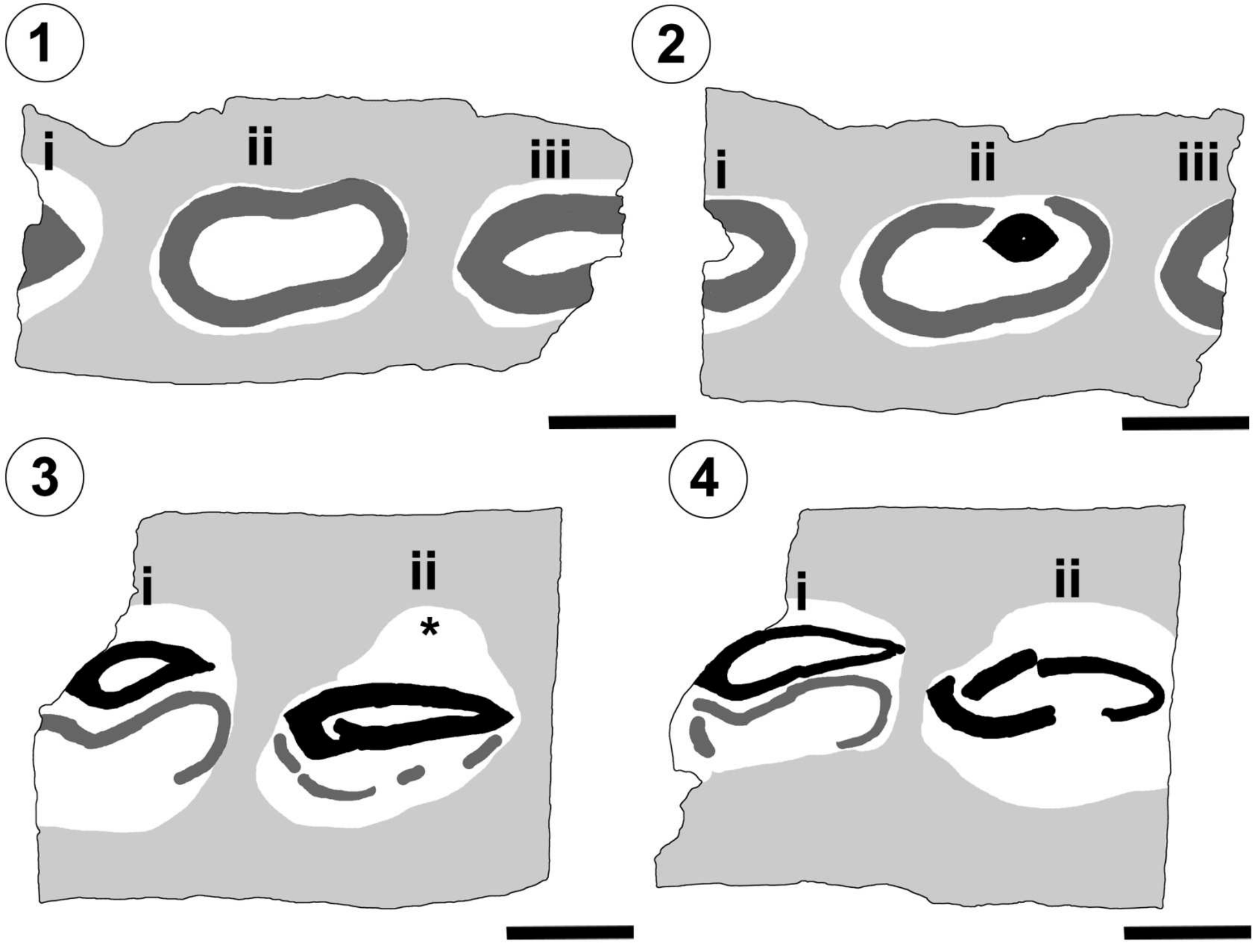
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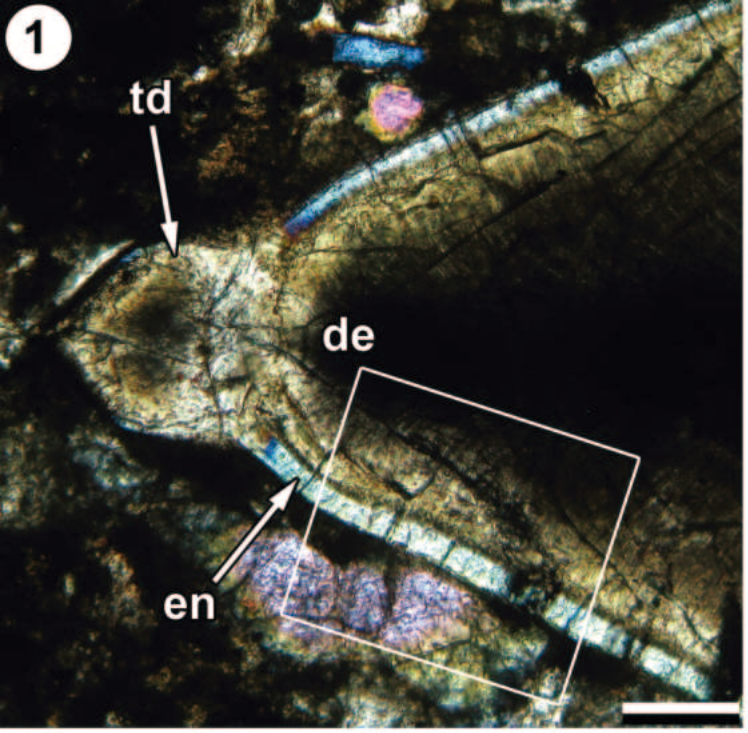
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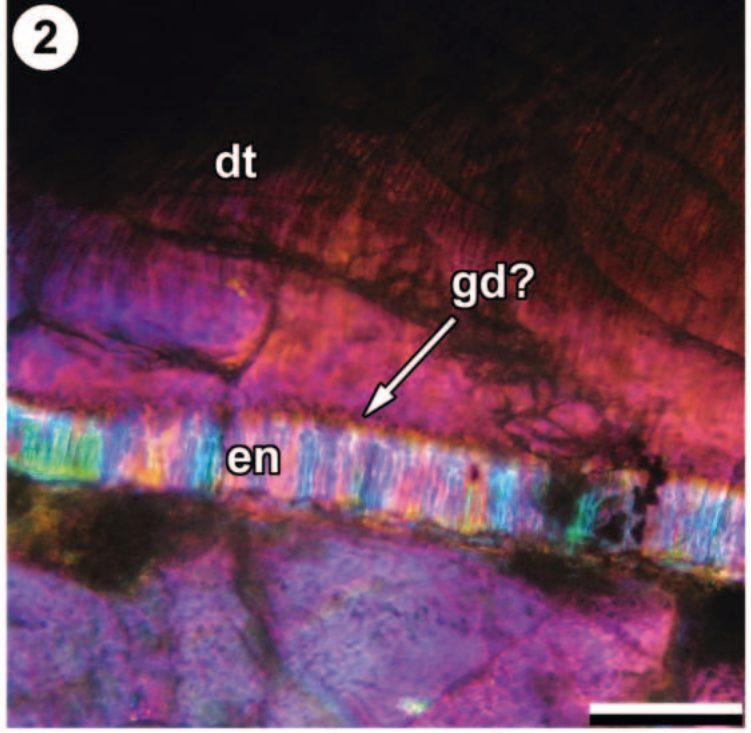
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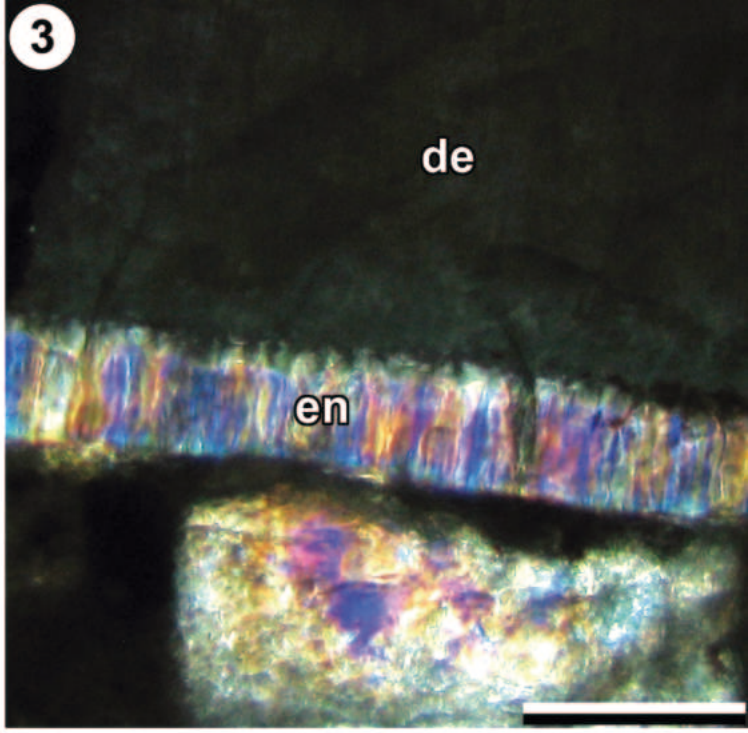
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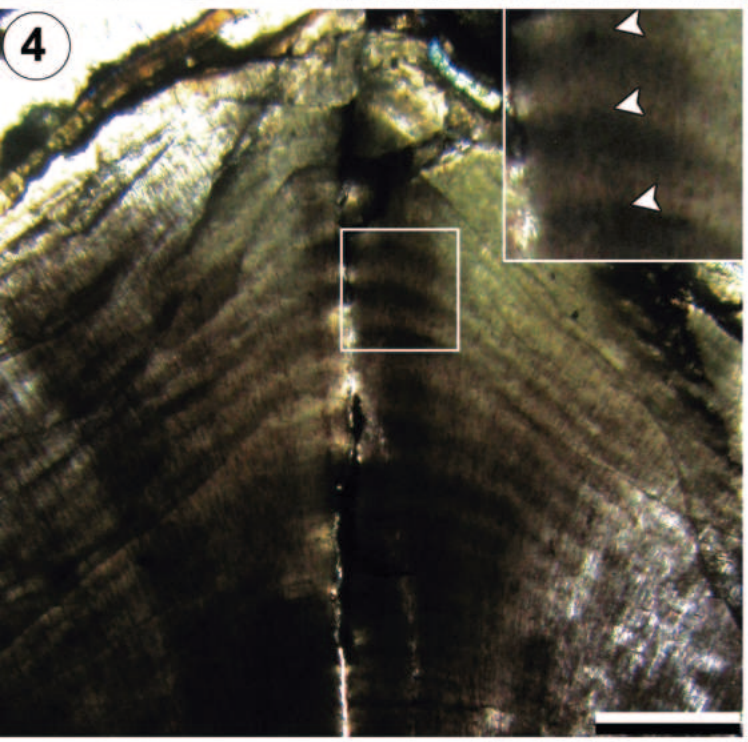
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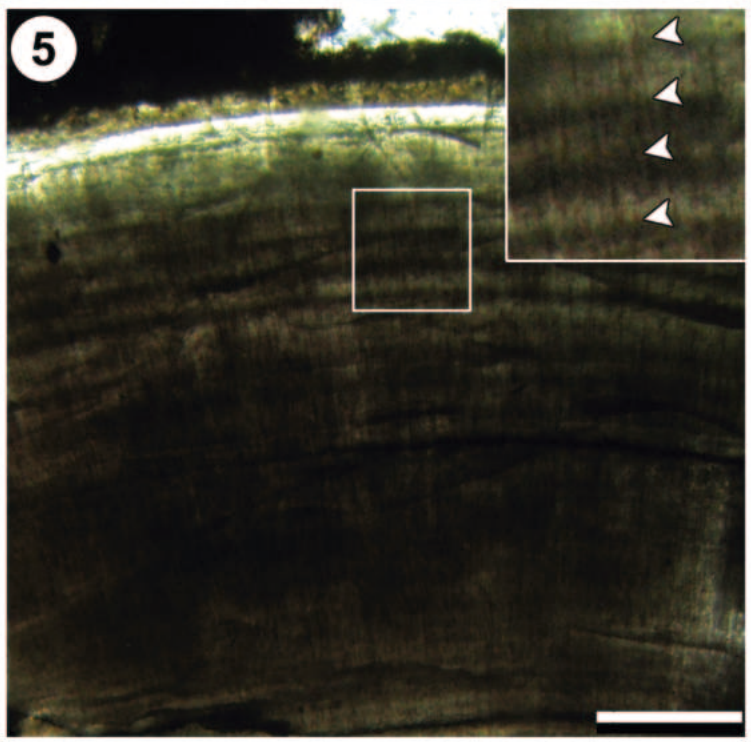
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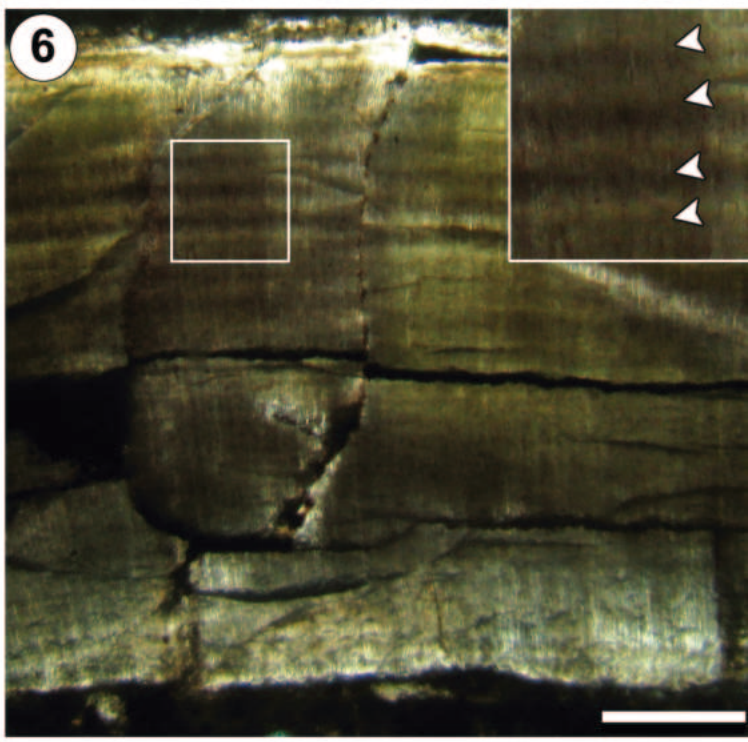
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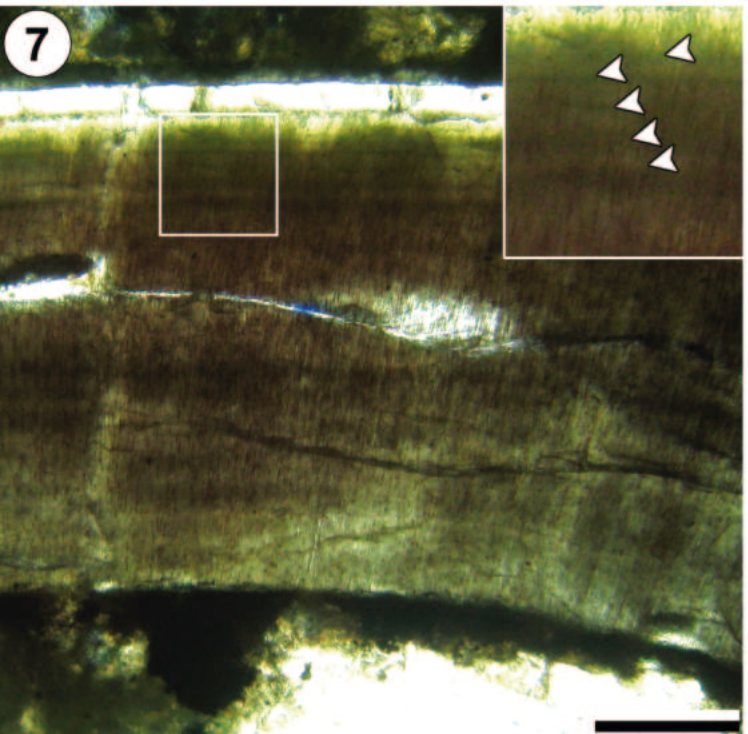
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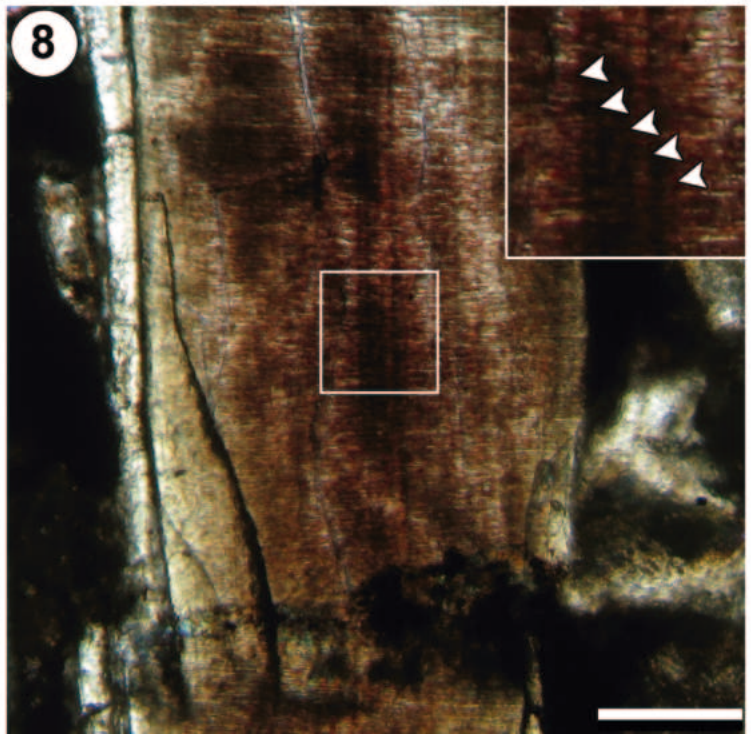
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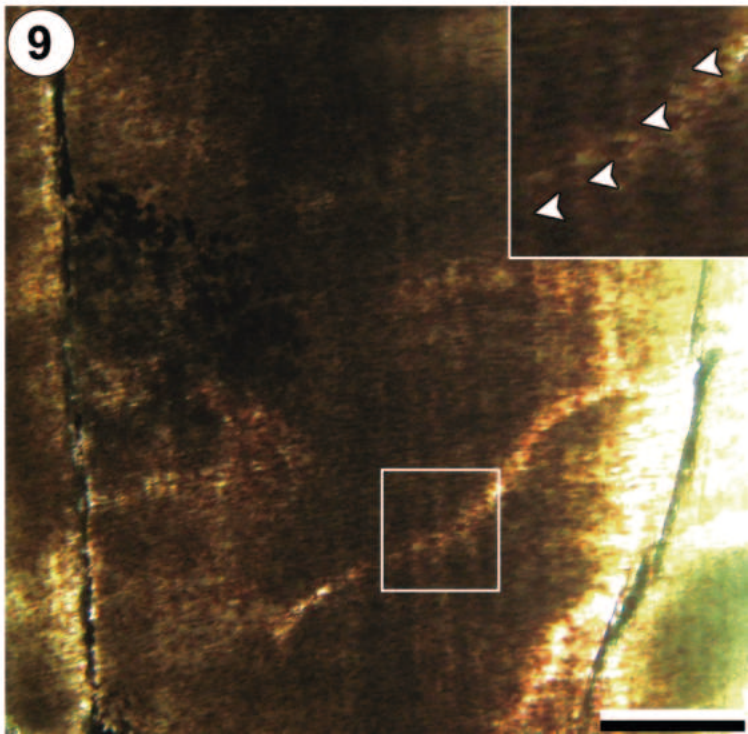
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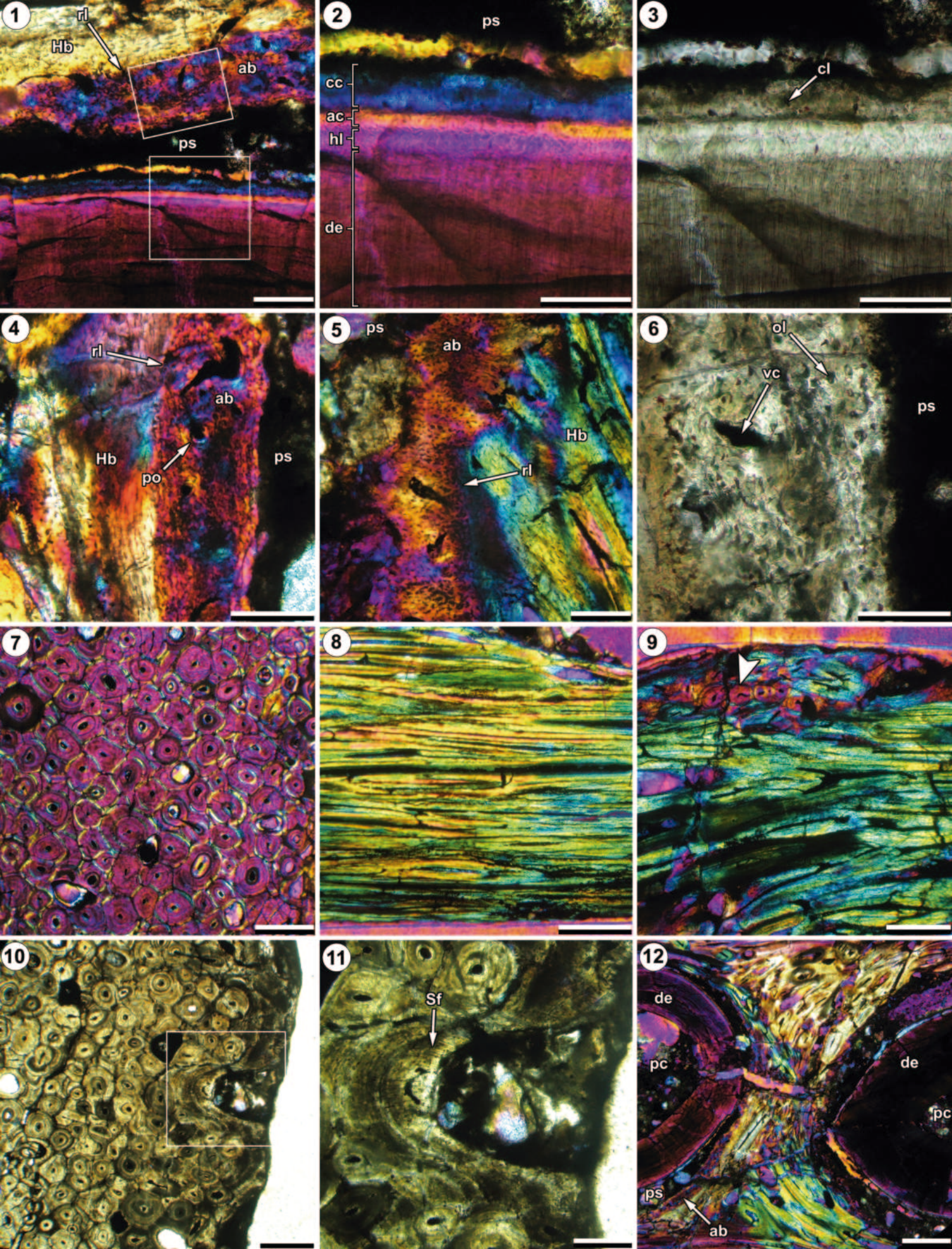
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