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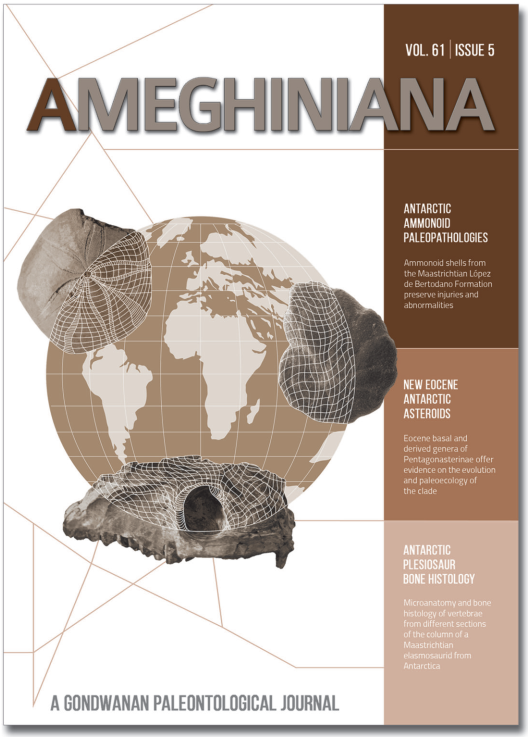

COMPARATIVE ANALYSIS OF BONE MICROSTRUCTURE AND HISTOLOGY IN DIFFERENT SECTIONS OF THE VERTEBRAL COLUMN OF *VEGASAURUS MOLYI* (PLESIOSAUR: ELASMOSAURID) FROM THE UPPER CRETACEOUS OF ANTARCTICA

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ANTARCTIC PLESIOSAUR BONE HISTOLOGY

Microanatomy and bone histology of vertebrae from different sections of the column of a Maastrichtian elasmosaurid from Antarctica

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COMPARATIVE ANALYSIS OF BONE MICROSTRUCTURE AND HISTOLOGY IN DIFFERENT SECTIONS OF THE VERTEBRAL COLUMN OF *VEGASAURUS MOLYI* (PLESIOSAUR: ELASMOSAURID) FROM THE UPPER CRETACEOUS OF ANTARCTICA

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Abstract. Elasmosaurids were the most diverse forms of plesiosaurs during the Late Cretaceous and achieved a cosmopolitan distribution. Thus, its fossils have been recorded on all continents, including Antarctica. Knowledge of paleobiological and evolutionary aspects of plesiosaurs has advanced considerably in recent years, including microstructural and paleohistological analyses of bone tissue. However, comparative analyses are still relatively scarce. To analyze how the degree of remodeling varies in the vertebral column of *Vegasaurus molyi* (MLP 93-I-5-1) from the Upper Cretaceous of Antarctica, histological sections of four vertebrae representing different sections of the column were made. The sections present a high degree of remodeling and an external fundamental system, indicating that the individual has reached skeletal maturity. The caudal vertebra shows the least degree of remodeling and retains the greatest number of lines of arrested growth. The results indicate that the degree of bone remodeling increases from the caudal region to the cervical region. When considering the middle sections of the vertebral elements, there is an increase in the compaction index from the cervical region to the caudal region. These differences in the bone microstructure are perceptible and serve as a criterion for determining which element of the vertebral column and in which part of its thin sections should be created. This will yield more information at the paleohistological level, allowing paleobiological inferences such as ontogenetic stage, differential growth of various parts of the skeleton, and blood supply, among other factors.

Key words. Paleohistology. Plesiosaur. Maastrichtian.

Resumen. ANÁLISIS COMPARATIVO DE MICROESTRUCTURA ÓSEA E HISTOLOGÍA EN DIFERENTES SECCIONES DE LA COLUMNA VERTEBRAL DE *VEGASAURUS MOLYI* (PLESIOSAURIO: ELASMOSÁURIDO) DEL CRETÁCICO SUPERIOR DE LA ANTÁRTIDA. Los elasmosáuridos fueron las formas más diversas de plesiosaurios durante el Cretácico Superior y lograron una distribución cosmopolita. Sus fósiles han sido registrados en todos los continentes, incluida la Antártida. El conocimiento de los aspectos paleobiológicos y evolutivos de los plesiosaurios ha avanzado considerablemente en los últimos años, incluidos los análisis microestructurales y paleohistológicos del tejido óseo. Sin embargo, los análisis comparativos son todavía relativamente escasos. Para analizar cómo varía el grado de remodelación en la columna vertebral de *Vegasaurus molyi* (MLP 93-I-5-1), del Cretácico Superior de la Antártida, se realizaron cortes histológicos de cuatro vértebras que representan diferentes secciones de la columna. Las secciones presentan un alto grado de remodelación y un sistema fundamental externo, lo que indica que el individuo ha alcanzado la madurez esquelética. La vértebra caudal muestra el menor grado de remodelación y conserva el mayor número de líneas de crecimiento detenido. Los resultados indican que el grado de remodelación ósea aumenta desde la región caudal hasta la región cervical. Cuando se consideran las secciones medias de los elementos vertebrales, se observa un aumento en el índice de compactación desde la región cervical hacia la caudal. Estas diferencias en la microestructura ósea sirven como criterio para determinar qué elemento de la columna vertebral y en qué parte del mismo se debe realizar secciones delgadas. Esto arrojará más información a nivel paleohistológico, permitiendo inferencias paleobiológicas como el estadio ontogenético, el crecimiento diferencial de varias partes del esqueleto y el suministro de sangre, entre otros factores.

Palabras clave. Paleohistología. Plesiosaurio. Maastrichtiano.

Plesiosauria, whose biochron extends from the Late Triassic to the Late Cretaceous, constitutes the most derived group within the Sauropterygia. Elasmosaurids were the most diverse Late Cretaceous forms within this clade and achieved a cosmopolitan distribution. Thus, their fossils have been registered on all continents, including Antarctica (Sato *et al.*, 2005; Kear, 2006; O'Gorman, 2011, 2013). The knowledge of paleobiological and evolutionary aspects of plesiosaurs has advanced considerably in recent years, including microstructural and paleohistological analyses of bone tissue. However this type of analyses have been focused on the postcranial skeleton (*e.g.*, limb bone, vertebra, and rib sections) and they oriented to the understanding of the ontogenetic trajectory, biomechanical and physiological adaptations (Kiprijanoff, 1881–1883; Biró-Bagóczky & Larraín, 1986; Wiffen *et al.*, 1995; Fostowicz-Frelik & Gazdzicki, 2001; Salgado *et al.*, 2007; Street & O'Keefe, 2010; Liebe & Hurum, 2012; Talevi & Fernández, 2011, 2015; Talevi, 2015; O'Gorman *et al.*, 2017; Ossa-Fuentes *et al.*, 2017; Wintrich *et al.*, 2017a; O'Keefe *et al.*, 2019; Sander & Wintrich, 2021).

Despite these advances, comparative analyses are still relatively scarce. Within this framework, the goal of the present contribution is to complement the growing knowledge of microanatomy and histology through the comparative analysis of the bone microstructure of vertebrae from different sections of the column (cervical, pectoral, dorsal, and caudal) of an elasmosaurid recovered from lower Maastrichtian levels of the Snow Hill Island Formation, Vega Island (Antarctica).

Institutional abbreviations. CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Ciudad Autónoma de Buenos Aires, Argentina; **IIPG,** Instituto de Investigación en Paleobiología y Geología, General Roca, Río Negro, Argentina; **MLP,** Museo de La Plata, La Plata, Argentina; **UNRN,** Universidad Nacional de Río Negro, Río Negro, Argentina.

MATERIALS AND METHODS

Samples used for histological analysis consist of ten cross-sections of four vertebral centra of different parts of the column of a single specimen (MLP 93-I-5-1) recovered from the lower Maastrichtian Cape Lamb Member of the Snow Hill Island Formation (Crame *et al.*, 1991; Pirrie *et al.*, 1997), Antarctica. The Snow Hill Island Formation belongs to the Marambio Group (Rinaldi, 1982), which is exposed in the James Ross Archipelago, northeastern Antarctic Peninsula. At Vega Island, the Cape Lamb Member of the Snow Hill Island Formation is interpreted as a shallowing and coarsening upward succession characterized by basal offshore mudstones and very fine-grained silty sandstones that pass gradationally upwards into proximal, nearshore marine, clean sandstone beds (Pirrie *et al.*, 1991; Olivero *et al.*, 2008; Marenssi *et al.*, 2001). Sections of this specimen were preliminarily reported as part of an unpublished doctoral thesis (Talevi, 2011) and subsequent work by Talevi (2015). In 2015, the specimen was described by O'Gorman *et al.* as proposed as the holotype of the new taxon *Vegasaurus molyi* O'Gorman, Salgado, Olivero & Marenssi, 2015.

The paleohistological analysis presented herein is based on the transversal (anterior, middle, and posterior) thin sections of cervical, dorsal, and caudal vertebrae. In the case of the pectoral vertebrae, only the transversal middle section is described (Fig 1). The thin sections were obtained according to Chinsamy and Raath's (1992) protocol at the Laboratorio de Secciones Delgadas of the Instituto de Investigación en Paleobiología y Geología of Universidad Nacional de Río Negro-CONICET (Argentina) and Laboratorio de Cortes del Departamento de Geología de la Universidad Nacional de San Luis, San Luis, Argentina. They were examined under a microscope in normal and polarised light. The slides obtained were analyzed with a petrographic microscope (ZEISS Axio Imager) under the plane and cross-polarised light. Images of each thin section were captured by a digital camera (ZEISS Axiocam 105) and processed with Adobe Photoshop 2020, and Adobe Illustrator 2022. The compaction was estimated using the compactness index (**CI**) calculated using the software ImageJ (Abramoff *et al.*, 2004) for all sections as the area occupied by bone multiplied by 100 divided by the total sectional area. In the case of the dorsal centrum, as it presents fractures resulting from the taphonomic processes, the CI was calculated in two different ways. The first one contemplates the entire section, including the spaces generated by fractures (IC-1). The second excludes them (IC-2). The latter was determined by calculating the average of the two parts that made up the section. The external (fusion of the neural arch to the vertebral body) and internal (substantial remodeled tissue and development external fundamental system (**EFS**)) characteristics indicate the specimen was an adult-late adult.

RESULTS

Microanatomical organization

The microanatomical organization in all thin sections displays a consistent pattern characterized by a layer of compact tissue in the cortical region and compacted cancellous bone in the medullary region. Towards the innermost part of the medullary region, the tissue becomes more compact in both anterior and posterior sections. In the posterior section of the dorsal vertebra, the cancellous bone is less compact compared to the other posterior sections. The medullary cavity is not observed; however, all middle sections and posterior sections of the caudal vertebra are distinguished by the presence of a central cavity. This central cavity does not represent a true medullary cavity. However, rather than confluence of artery canals (Fig. 1). These artery canals extend from the base of the vertebra to the dorsal margin and branch into canals of smaller caliber, radiating from the central region to the laterals and dorsal region. The pectoral section exhibits the highest number of smaller-caliber canals among all the vertebral elements analyzed. Sedimentary fill infiltrates these canals, allowing the identification of their continuity throughout the section (Fig. 1).

Histological features

Cervical vertebra (Fig. 2). The development of a zonal bone is observed on the dorsal margin of the cortical tissue. The zones exhibit a pseudolamellar bone matrix, while the annuli

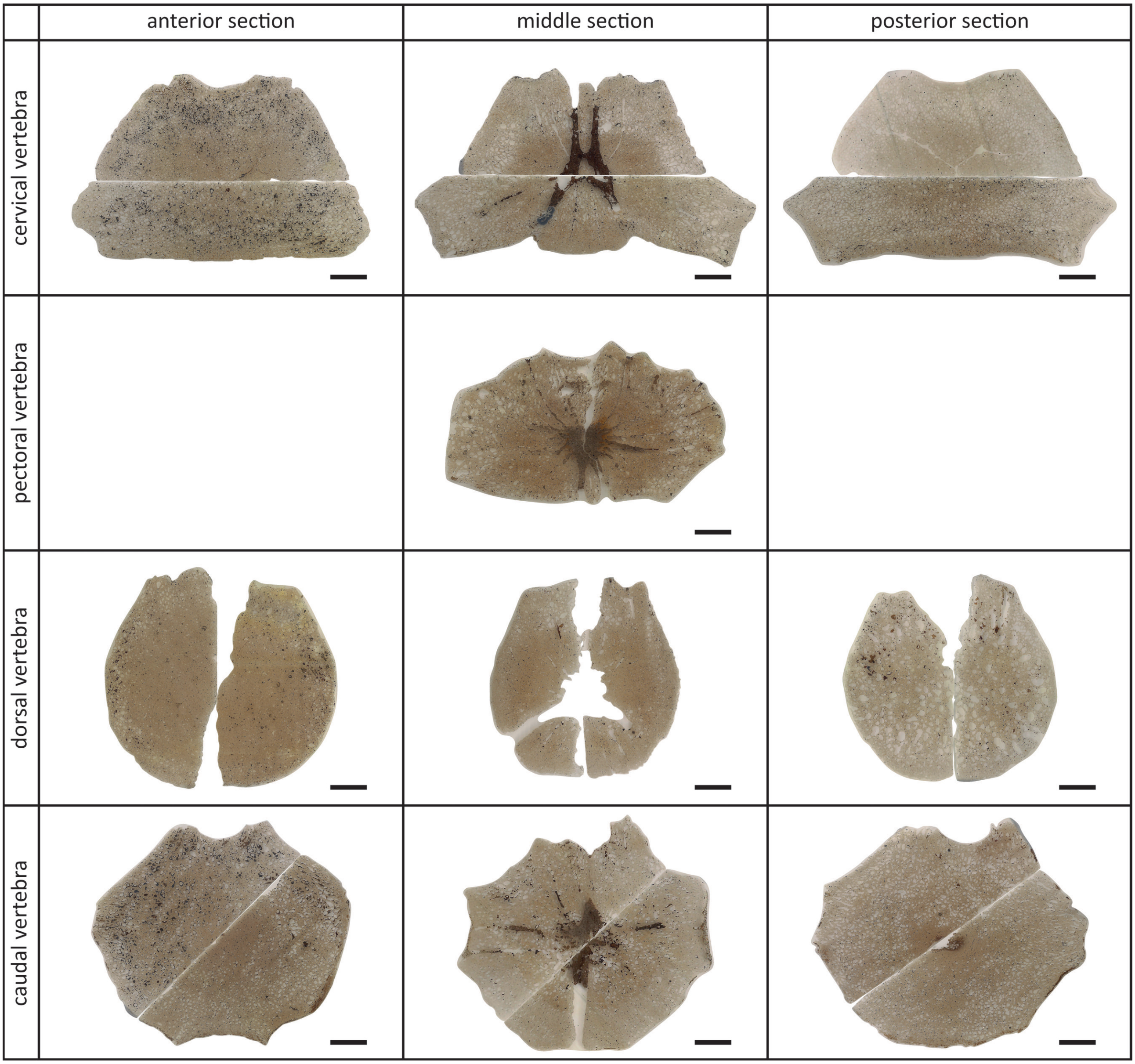

Figure 1. Transverse sections (anterior, middle, and posterior) of the vertebral elements (cervical, pectoral, dorsal, and caudal). Scale bar 1 cm.

show a lamellar matrix. Bone remodeling extends to the cortical margin, where secondary osteons differentiated by cement lines are also observed, along with some erosion bays. In the anterior section, three lines of arrested growth (**LAGs**) were identified within an avascular lamellar matrix, constituting the EFS (Fig. 2.1). Conversely, 11 LAGs were observed in the middle and posterior sections, predominantly distributed in pairs along the zonal bone and the EFS (Fig. 2.2–2.3). In addition, Sharpey's fibers were observed on the cortical tissue along margins near the neural canal and

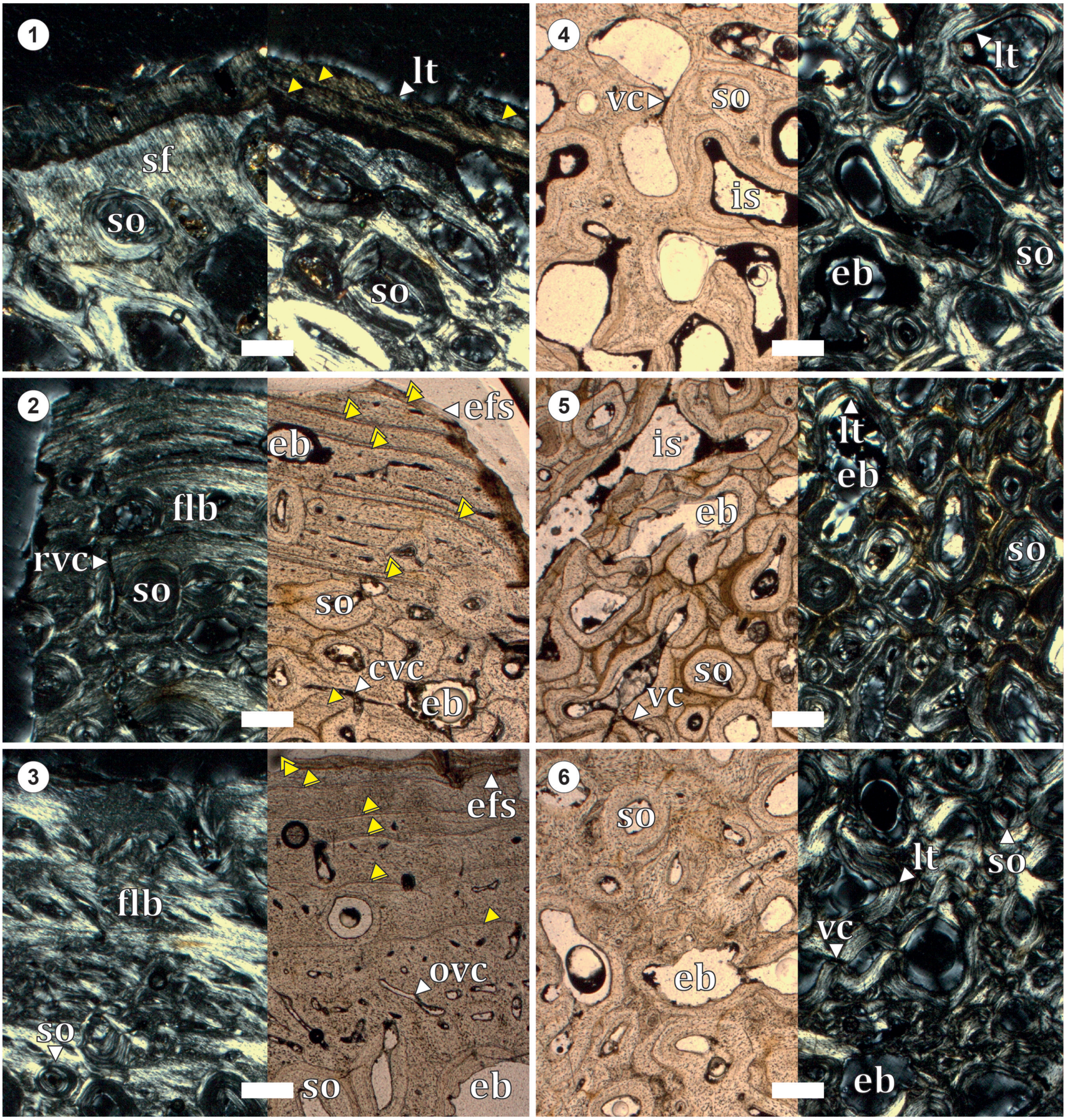

Figure 2. Cervical vertebra. **1, 4,** anterior section; **2, 5,** middle section; **3, 6,** posterior section. **1–3,** cortical region; **4–6,** medullary region. Abbreviations: **eb,** erosion bay; **efs,** external fundamental system; **flb,** fibrolamellar tissue; **is,** intertrabecular spaces; **lt,** lamellar tissue; **ovc,** oblique vascular canals; **rvc,** radial vascular canal; **sf,** Sharpey's fibres; **so,** secondary osteon; **vc,** Volkmann's canals; **yellow triangle,** lines of arrested growth. Scale bar 200 µm.

neural arch. In general terms, Sharpey's fibers, also known as "extrinsic fibers, they are anchored to a bone, tissue or organ external to the bone. The thickness, density, and length of Sharpey's fibers vary depending on their location (Aaron, 2012; Buffrénil & Quilhac, 2021). In the medullary region, a predominantly secondarily compacted trabecular tissue with erosion bays and secondary osteons prevails (Fig. 2.4–2.6). Intertrabecular spaces are surrounded by lamellar tissue distributed centripetally (Fig. 2.4–2.5). These spaces are irregular and do not have a specific orientation, although these cavities expand slightly to the cortical region. In the most internal area of the medullary region, compact tissue predominates with the presence of secondary osteons interconnected by Volkmann's canals (Fig. 2.5). Although vascularization is primarily longitudinal, some circumferential channels parallel to growth marks were observed. Osteocyte lacunae are oval-shaped and align according to the distribution of fibres. Bone remodeling is more pronounced in the anterior section.

Pectoral vertebra (Fig. 3). On the dorsal margin of the cortical tissue, a zonal bone with five/six LAGs is observed (Fig. 3.1). The zones exhibit a fibrolamellar bone matrix with some longitudinal and radial vascular channels. At the same time, the annuli have a lamellar matrix and contain growth lines. In the cortical region, Sharpey's fibres were observed distributed in bundles along the section, and some fibres even extend into the extensions of the blood channels (Fig. 3.2–3.3). The medullary region presents a well-developed, secondarily compacted trabecular tissue, where intertrabecular spaces are surrounded by lamellar tissue. These spaces expand to the cortical region of the vertebral centre and are elongated and distributed radially. In the innermost area of the medullary region can be identified compact tissue with the presence of secondary

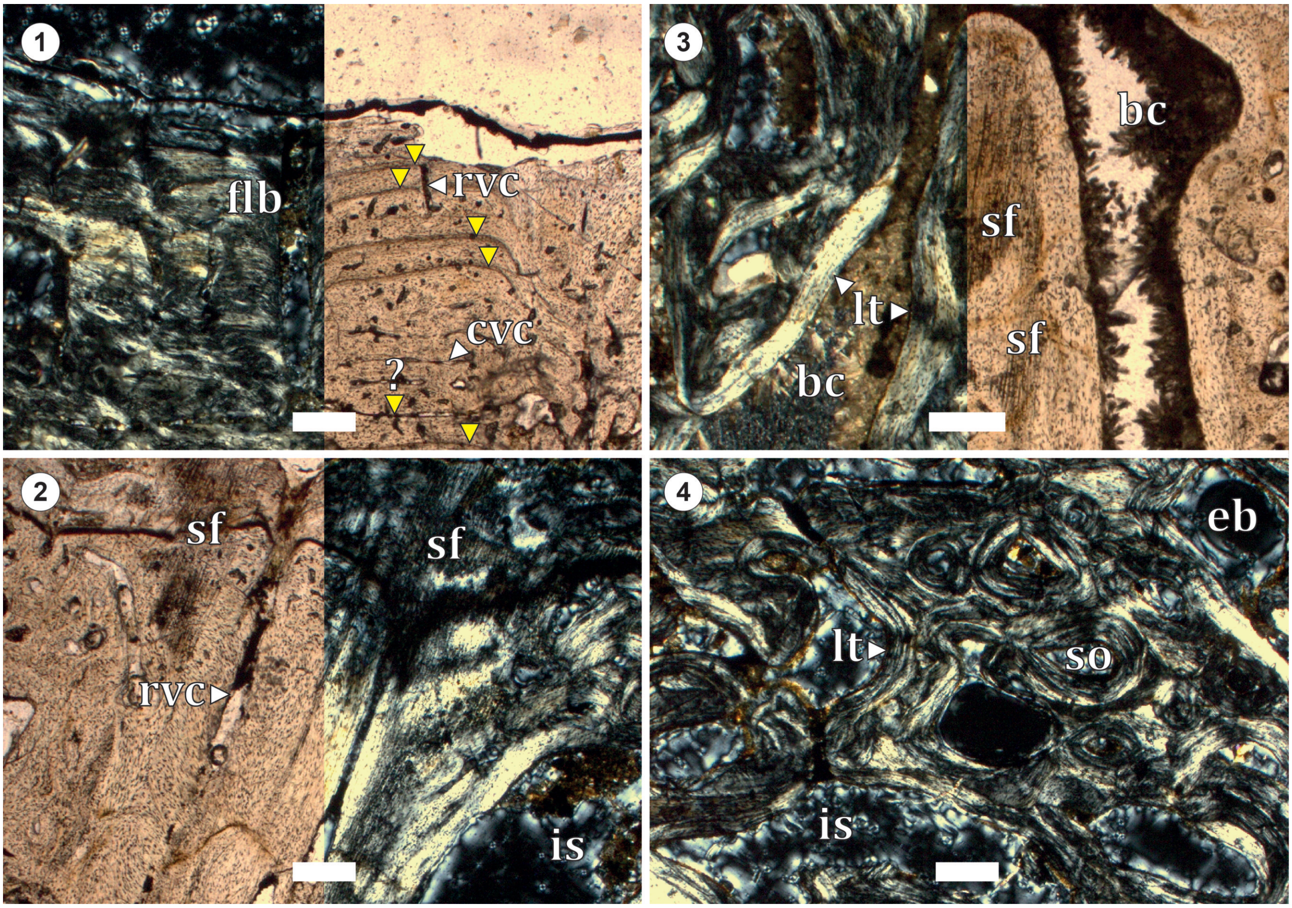

Figure 3. Pectoral vertebra. **1–4,** middle section; **1–3,** cortical region; **4,** medullary region. Abbreviations: **bc,** blood channel; **cvc,** circular vascular canal; **eb,** erosion bay; **flb,** fibrolamellar tissue; **is,** intertrabecular spaces; **lt,** lamellar tissue; **rvc,** radial vascular canal; **sf,** Sharpey's fibres; **so,** secondary osteon; **yellow triangle,** lines of arrested growth. Scale bar 200 μm.

osteons defined by clear cementation lines (Fig. 3.4). Vascularization is plexiform, with a large number of longitudinal vascular channels and, to a lesser extent, circular and radial. Osteocyte lacunae are discoidal, have limited development of canaliculi, and are oriented according to the distribution of lamellae. Bone remodeling is high, with numerous secondary osteons invading both cortical and medullary tissues. Blood channels are surrounded by lamellar tissue.

Dorsal vertebra (Fig. 4). In the cortical region, the development of zonal bone strongly remodeled by dense secondary osteon tissue is observed. In the anterior section,

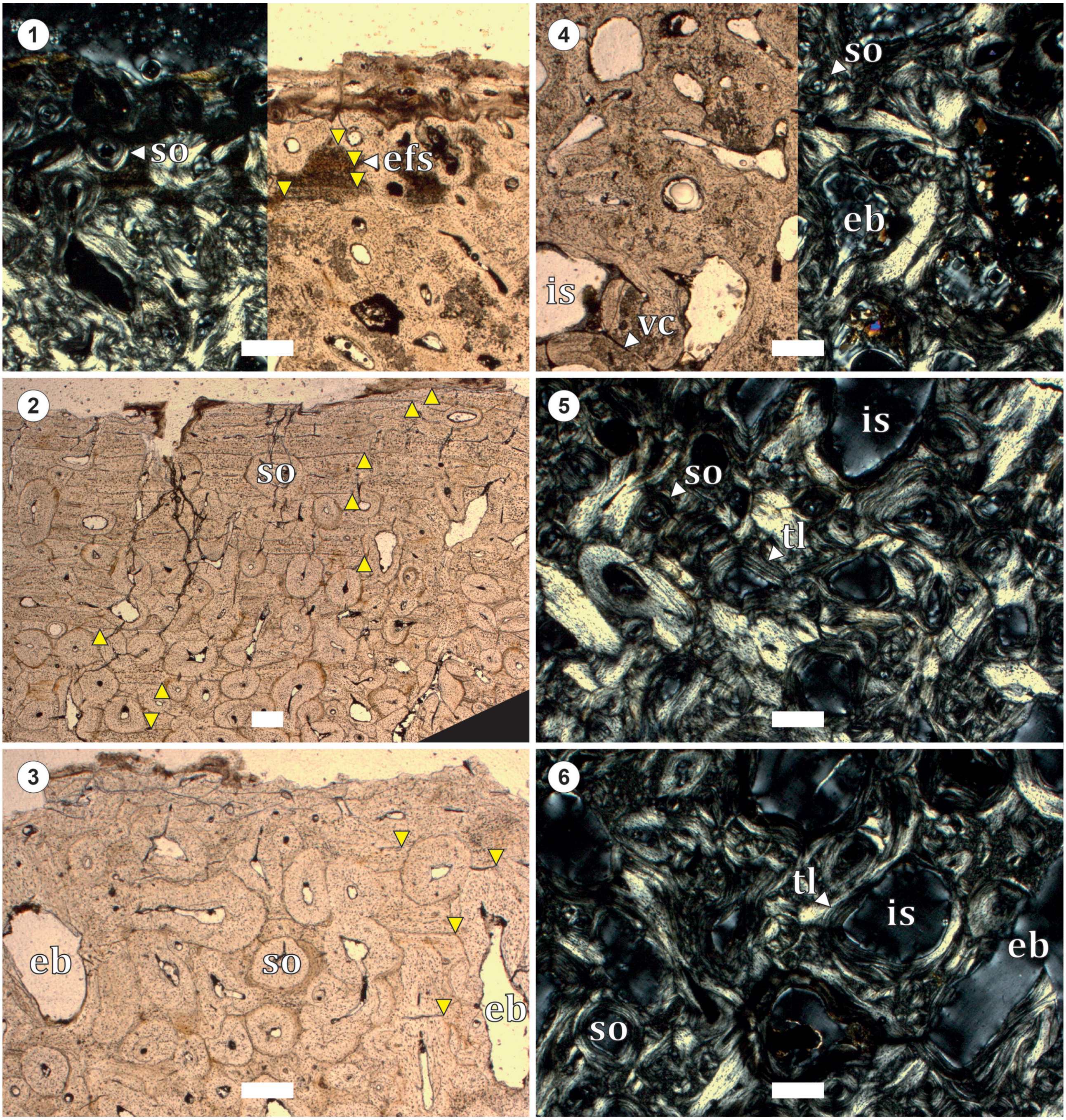

Figure 4. Dorsal vertebra. **1, 4,** anterior section; **2, 5,** middle section; **3, 6,** posterior section. **1–3,** cortical region; **4–6,** medullary region. Abbreviations: **eb,** erosion bay; **efs,** external fundamental system; **is,** intertrabecular spaces; **lt,** lamellar tissue; **so,** secondary osteon; **vc,** Volkmann's canals; **yellow triangle,** lines of arrested growth. Scale bar 200 μm.

a small segment of the EFS is seen, exhibiting four LAGs along its extension (Fig. 4.1). On the other hand, in the middle and posterior sections, eight and four LAGs, respectively, were observed, distributed within a zonal bone (Fig. 4.2–4.3). In the medullary region, a secondarily compacted trabecular tissue predominates, and intertrabecular spaces are surrounded by lamellar tissue (Fig. 4.4–4.6). Erosion bays are also observed on the medullary and perimedullary margins (Fig. 4.3–4.6). In the middle section, intertrabecular spaces have a radial distribution within the vertebral centre and expand towards the dorsal and ventral margins of the cortex. In the most internal area of the medullary region, compact bone with abundant secondary osteons exhibiting a longitudinal pattern is observed (Fig. 4.4–4.6). Vascularization is primarily longitudinal. Osteocyte lacunae are oval-shaped, align according to the distribution of fibres, and show limited development of canaliculi. All sections exhibit a high degree of bone remodeling, with the most pronounced remodeling in the anterior and posterior sections. The remodeling front crosses the entire tissue, reaching even the cortical margin (Fig. 4.1–4.3). In addition, in the middle section, remodeling is lower in the ventral margin, allowing one to observe in greater detail the zonal bone and growth marks. No Sharpey's fibres in any of the sections were observed.

Caudal vertebra (Fig. 5). The cortical region presents several lamellae of a lamellar bone matrix with many lines of arrested growth, which are part of an EFS. In the anterior, middle, and posterior sections, 15, 12, and 27 LAGs were observed, respectively (Fig. 5.1–5.3). Some secondary osteons with a longitudinal pattern were observed on the cortical margin, remodeling the primary bone matrix. In addition, Sharpey's fibres were observed at the level of the neural arch, caudal ribs, and the ventral margin of the cortical tissue. In the medullary region, a secondarily compacted trabecular tissue with irregularly shaped intertrabecular spaces was observed (Fig. 5.4–5.6). These spaces have an irregular form, except at the height of the transverse processes and the neural arch, where these spaces expand in the direction of these structures. Moreover, intertrabecular spaces are surrounded by lamellar tissue (Fig. 5.4–5.6). In the innermost area of the medullary region, there is a compact bone with extensive development of secondary osteons connected using Volkmann channels, giving a dense and compact appearance. Vascularization is primarily longitudinal (Fig. 5.1–5.6). Osteocyte lacunae are elongated, distributed according to the orientation of the fibres, and show limited development of canaliculi. In the posterior section, bone remodeling is less pronounced on the ventral margin than on the dorsal, accompanied by the highest number of LAGs. In the ventral margin of the middle section, there is a nutritional foramen that continues through a canal to the dorsal region of the section. The canal is delimited by lamellar tissue and exhibits abundant Sharpey's fibres.

Compactness index

The degree of compaction of the vertebral centra is varied, observing differences in the values of the compaction index (IC) at inter and intravertebral levels (Fig. 6). In the cervical vertebra, the CI is 44.16%, 48.40%, and 50.55% in the anterior, middle, and posterior sections respectively. In the pectoral vertebra, the CI is 53.08% in the middle section. In the dorsal vertebra, the IC-1 is 59.02%, 58.78%, and 45.50% in the anterior, middle, and posterior sections correspondingly, while the CI-2 is 64.88%, 58.58%, and 49.71% respectively. In the caudal vertebra, the CI is 83%, 78%, and 78.36% for the anterior, middle, and posterior, respectively Talevi (2015).

DISCUSSION

Ontogenetic stage

A common problem in vertebrate paleontology, and especially in plesiosaur studies, is generating taxonomic divisions or diagnosing higher-order clades by considering anatomical variations that are due to ontogenetic differences (Welles, 1952; Persson, 1963; Carpenter, 1999; O'Gorman, 2013). This problem is often due to the scarcity of diagnostic material, the existence of important ontogenetic changes, and the absence of more or less complete ontogenetic series (Welles, 1952, 1962; Brown, 1981; Carpenter, 1996; O'Keefe & Hiller, 2006). On the other hand, paedomorphosis is very common in marine reptiles, which also makes it difficult to establish criteria for determining ontogenetic stages (Rieppel, 1989; O'Keefe, 2006; Araújo *et al.*, 2015; Wintrich *et al.*, 2017a). Nonetheless, ontogenetic variation in plesiosaur bone morphology is known and well-documented (Brown, 1981;

O'Keefe & Hiller, 2006). In the particular case of plesiosaurs, Brown (1981) proposed a series of anatomical/osteological criteria for determining the age classes of individuals, such as the degree of fusion of the neural arch to the vertebral centrum. According to what was proposed by this author, age classes (growth stages) can be used to name the stages of ontogenetic development of an individual. The age classes that Brown proposed:

(1) Juvenile: one in which the neural arches of the vertebrae are not fused to the centra.

(2) Adult: one in which the fusion of the neural arches has taken place.

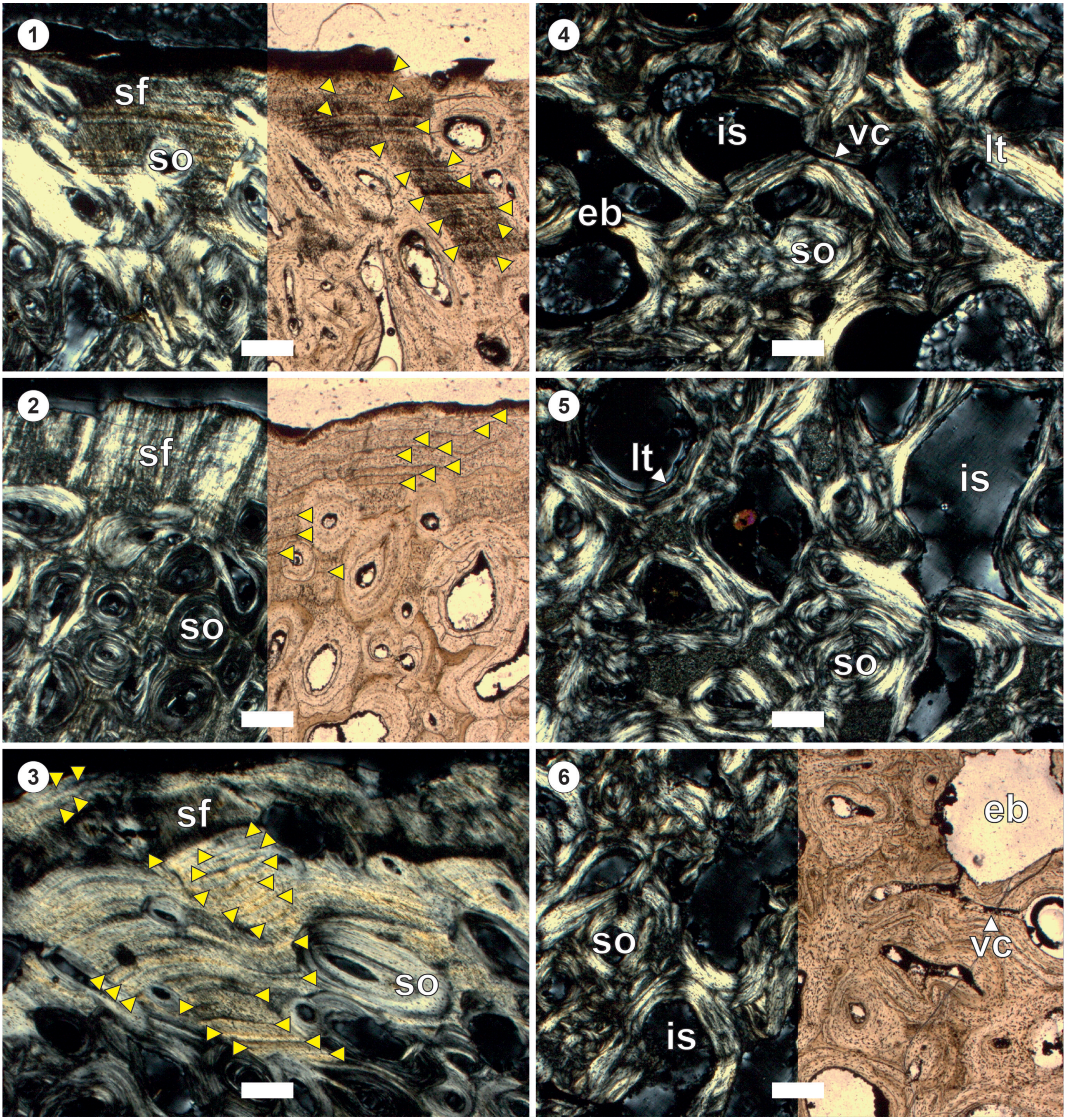

Figure 5. Caudal vertebra. **1, 4,** anterior section; **2, 5,** middle section; **3, 6,** posterior section. **1–3,** cortical region; **4–6,** medullary region. Abbreviations: **eb,** erosion bay; **is,** intertrabecular spaces; **lt,** lamellar tissue; **sf,** Sharpey's fibres; **so,** secondary osteon; **vc,** Volkmann's canals; **yellow triangle,** lines of arrested growth. Scale bar 200 µm.

(3) Senile: in which the neural arch and vertebral centrum are fused, and additionally, other characters of advanced ossification are observed.

However, the application of this system presents some difficulties. Not all neural arches fuse at the same time (Welles, 1943; Gasparini *et al.*, 2003; O'Gorman, 2011, 2013), and in cases of partial fusion, they should not be considered juvenile individuals according to Brown's classification (1981) but not adults either, since the merger is not complete.

On the other hand, Brown's age class definitions do not allow working directly with isolated materials. If the neural arches do not all fuse to the vertebral centra simultaneously, the record of a single fused vertebrae does not ensure that the other vertebrae of the column have been fused. Even in some vertebrae, the neural arch does not fuse until a very late ontogenetic stage (O'Gorman, 2013). According to O'Gorman (2013), in these cases, the age classes of Brown (1981) can be used. However, with but with some considerations: the characteristics of an element can be described (*e.g.*, a vertebra can have juvenile or adult characteristics) with some degree of independence from the state of the whole individual. In the case of the analyzed material, all the vertebrae, representing different sections of the vertebral column, show the neural arch fused to the vertebral centra, thus being able to determine that it would be an adult specimen.

In this context, the bone microstructure can be a useful tool for determining the relative ontogenetic stage. Traditionally, it has been suggested that the degree of bone compaction varies throughout the ontogeny of plesiosaurs (Wiffen *et al.*, 1995), differentiating a typically juvenile pattern, characterized by an increase of compaction of the internal structure and in the bone mass (dense tissue= pachyostotic *sensu stricto*, Houssaye, 2009, 2013), and an adult pattern characterized by a highly spongy and remodeled adult pattern (light tissue= osteoporotic, *e.g.*, Cruickshank *et al.*, 1996; Gasparini & Salgado, 2000; Fostowicz-Frelik & Gazdzicki, 2001; Salgado *et al.*, 2007). However, later contributions indicated that the degree of compaction alone would not be a good indicator of the relative osteological maturity of the individual (Street & O'Keefe, 2010; Liebe & Hurum, 2012; Talevi & Fernández, 2015).

On the other hand, other features like a higher degree of bone remodeling would be expected in adult individuals rather than in juvenile stages (Francillon-Vieillot *et al.*, 1990; Chinsamy-Turan, 2005). In turn, an external fundamental system would indicate that the individual has reached skeletal maturity (Mitchell & Sander, 2014; O'Keefe *et al.*, 2019). The existence of this layer has historically been used as an indicator of the cessation of development in organisms with determined growth (Reid, 1996; Chinsamy-Turan, 2005).

Sander and Wintrich (2021) defined eight histologic ontogenetic stages (**HOS**) and their corresponding biological ontogenetic stages for plesiosaurs: HOS 1, fetus; HOS 2, neonate; HOS 3, juvenile; HOS 4, late juvenile; HOS 5, subadult; HOS 6, early adult; HOS 7, adult; and HOS 8, late adult.

In the case of MLP 93-I-5-1, the presence of a high degree of remodeling, with well-developed secondary osteons in the cortical region (even reaching this remodeling front to the bone surface in all the vertebrae) (Figs. 2.1–2.3; 3.1; 4.1–4.3; 5.1–5.3), together with the presence of secondary trabecular tissue in the medullary region (Figs. 2.4–2.6; 3.4; 4.4–4.6; 5.4–5.6) and the presence of a EFS in all the vertebrae explored, suggests that the specimen had reached skeletal maturity at the time of death. In the same way, the histological pattern indicates that it corresponds to an intermediate between stages HOS 7 (Adult) and HOS 8 (Late Adult). Thus, the development of a woven bone with radial and plexiform vascularization, fibrolamellar bone tissue followed by an EFS with substantial Haversian replacement, and an initial cancellous medullary region is consistent with a HOS stage 7. In contrast, the Haversian replacement (although incomplete in the sample analyzed) with a spongy medullary region indicates an HOS stage 8.

Growth marks

Skeletochronology is a method used to determine an individual's age or the cycles of bone deposition that indicate seasonal changes. This is achieved through the study of growth lines retained in bone tissue. These growth marks are also used to estimate growth rates and the age of maturation of an organism (Snover *et al.*, 2007). The quantification of growth lines in long bones has been applied to various groups of marine reptiles (*e.g.*, Castanet & Smirina, 1990; Sander, 1990; Snover, 2002; Pellegrini,

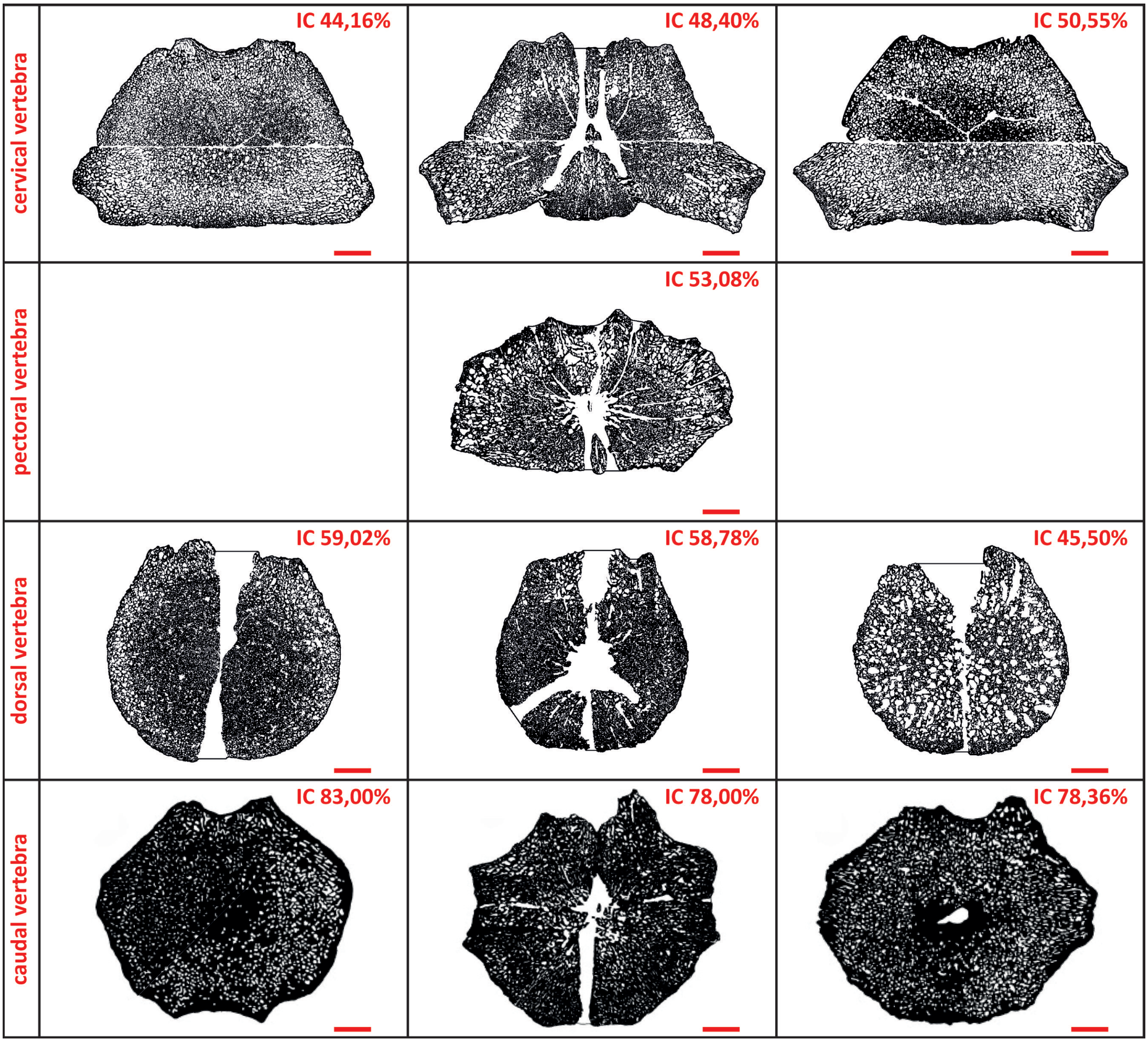

Figure 6. General view and microanatomy of cross sections. Compactness index of the cervical, pectoral, dorsal, and caudal sections. Scale bar 1 cm. Figures of the caudal vertebra taken from Talevi (2015).

2007; Snover *et al.*, 2007; Talevi, 2011; Klein, 2012; Klein *et al.*, 2015). However, it is crucial to note that new bone tissue can be formed in the center of the bone through the remodeling of existing bone, including growth marks, rendering this approach impractical. The internal parts of highly vascularized bones also make growth marks less apparent. Therefore, the cortical region of a bone, less exposed to remodeling, is more suitable for observing these marks. A growth cycle comprises a period of rapid bone growth followed by a period of decreased growth rate, sometimes resulting in complete temporary cessation. Growth periods manifest in the bone as relatively wide growth zones interspersed by thin annuli bands or LAG, representing periods when bone growth decreases (Castanet *et al.*, 1993). The growth mark method assumes that the lines of cyclical growth in cortical bone are annual, with each line in a long bone cross-section representing one year of life. The thin line or zone (annuli) is composed of avascular tissue. It represents the amount of bone deposited during the period of non-growth, usually in winter, while the thickest zone reflects growth achieved during the growing season. In some cases, growth nearly halts during the nongrowing season, reducing the annuli to a single line known as the LAG or rest line (Francillon-Vieillot *et al.*, 1990).

Starck and Chinsamy (2002) suggested that histovariability is expected in different skeleton elements. Therefore, this study is valid when applied to neutral regions of long bones. Despite questioning its application as an indicator of absolute age (Reid, 1990), it is a reliable indicator of relative age among different specimens of the same species (Pellegrini, 2007).

Regarding MLP 93-I-5-1, although appendicular bones were not analyzed, the vertebrae exhibit growth marks. Different elements (bones) have shown varying growth rates (Castanet *et al.*, 1996) and degrees of remodeling (Talevi & Fernández, 2015). Our findings suggest that caudal vertebrae, with lower degrees of remodeling, less evidence of resorption, and greater preservation of growth marks, provide an auxiliary criterion for skeletochronology studies in the absence of appendicular elements. This contribution indicates that, at least in elasmosaurid plesiosaurs, caudal vertebrae are the most useful elements of the vertebral column for skeletochronology, closely reflecting the minimum age of the individual.

Compaction index

As mentioned above, it has been proposed that the degree of compaction can be a good proxy for the ontogenetic stage in plesiosaurs (Wiffen *et al.*, 1995; Fostowicz-Frelik & Gazdzicki, 2001). However, Street and O'Keefe (2010) found an increase in the size of the gastralia and a particular distribution of compact tissue (pachyostosis) in an adult specimen of a cryptoclidid plesiosaur, *Tatenectes laramiensis*. They concluded that in this case, the bone structure is more indicative of the environment than the ontogenetic stage. In the same sense as Street and O'Keefe (2010), Liebe and Hurum (2012) analyzed the internal bone structure of the limb of four Jurassic plesiosaurs and observed that not all of them followed the proposed ontogenetic trajectory, so they failed to find a direct correlation between the ontogenetic stage and the degree of compaction.

Talevi and Fernández (2015) analyzed the degree of compaction between different elements of the same skeleton of an elasmosaurid plesiosaur. Their results showed that the compaction index varies markedly according to the bone analyzed and even within the same element. On the other hand, Talevi (2015) analyzed a plesiosaur caudal vertebra in different sections, showing that the degree of compaction did not vary significantly along the vertebral centrum, at least in the caudal vertebrae. Both the centrum's anterior, middle, and posterior regions present similar compaction that varies between 78 and 83%, evidencing, as a whole, a compact element. Although only one element was analyzed in this study, the results obtained indicate that, contrary to what is traditionally proposed, the element shows a high compaction index but with histological (high degree of remodeling) and anatomical characteristics (fusion of the neural arch at the vertebral body) adults.

In the samples analyzed in this work (Fig. 6), we observed that the CI does not vary significantly throughout the same element, in agreement with that analyzed by Talevi (2015). However, it is possible to observe significant differences in the CI throughout the vertebral column. These differences are readily observable in the middle sections of the vertebrae. Thus, the middle section of the cervical vertebra has a CI of 46.51%, and the middle section of the caudal vertebra has a CI of 78%. Considering the middle section of the vertebrae, we observed an increase in the CI from the cervical region to the caudal region (46.51% - 53.08% - 58.78% - 78.00%).

Blood supply

All cervical vertebrae of plesiosaurs show a pair of large foramina on the ventral surface of the vertebral centrum, called subcentral foramina or subcentralia (Romer, 1956), and are autapomorphy of the clade (Storrs, 1991; O'Keefe, 2001; Benson & Druckenmiller, 2014; Noè *et al.*, 2017; Wintrich *et al.*, 2017b). Storrs (1991) interpreted them as nutritional foramina. This peculiar vascular supply of plesiosaur vertebrae provided them with a large supply of blood, such that the occlusion of a vessel would not compromise nutrition in these bones. For this reason the vertebrae of plesiosaurs do not usually show signs of avascular necrosis. Furthermore, these nutritional foramina subcentralia and blood vessels in the vertebrae of plesiosaurs would favour the diving habits of these forms (Rothschild & Storrs, 2003). On the other hand, Wintrich *et al.* (2017b) interpreted these structures not as nutritional channels but as intersegmental arteries not reabsorbed during ontogeny and persist in their post-embryological stages, constituting a paedomorphic characteristic of the group. According to Wintrich *et al.* (2017b), in the cervical vertebrae of plesiosaurs, the process of obliteration of the cervical intersegmental arteries did not occur, so these arteries remained in position and remained functional, extending (following the direction of blood flow) through the vertebral centrum. In favor of this hypothesis, these authors point out that, in the case of nutritional canals, the vascular system spreads throughout the bone tissue while the blood vessels are continuous, extending dorsoventrally. The bone tissue surrounds the arteries, forming a lasting structure. The presence of paired canals running through the vertebral centrum implies that these structures originally housed continuous arteries traversing the vertebral centrum in a dorsoventral direction. The location and bilateral symmetry of these paired canals reflect embryological vascular characteristics that were integrated into the early development of the vertebral centra during the re-segmentation of the embryonic axial skeleton. This could be associated with the increased number of cervical vertebrae, the neck's rigidity, and the adaptive expansion into pelagic environments seen in plesiosaurs compared to other sauropterygians. Another potential adaptive advantage of retaining intersegmental arteries could be preventing blood vessel compression during deep dives (Wintrich *et al.*, 2017b).

In the midsection of the cervical vertebra analyzed in this study, it is observed that the ventral and dorsal subcentral foramina (right and left) are interconnected by a canal passing through the ossification centre of the vertebral centrum. These canals do not terminate at the ossification centre but pass through it, as depicted in Figure 2. In cross-section, the general appearance of the two canals is X-shaped, as they gradually diverge from each other towards both sides without connecting inside the vertebral centrum. The trajectory of these paired canals through the vertebral centrum aligns with the suggestion made by Wintrich *et al.* (2017b) that these structures contained persistent intersegmental arteries. Additionally, four smaller caliber canals emerge from the interior of the vertebral centrum: one pair oriented towards the neural arch and another towards the transverse processes.

Noteworthy that Wintrich *et al.* (2017b) examined cervical vertebral sections exclusively. The authors noted the absence of subcentral or nutritional foramina in dorsal vertebrae and mentioned the lack of published information on pectoral vertebrae. In this study, middle sections of pectoral, dorsal, and caudal vertebrae were scrutinized, revealing subcentral foramina extending in channels from the ventral to the dorsal portion, passing through the ossification centre.

In the middle section of the pectoral vertebra, two ventral foramina and two dorsal foramina are discernible (Fig. 2). Similar to the cervical vertebra, a dorsoventral canal interconnects these foramina. Unlike the cervical vertebra, a space is evident in the vertebral centrum, interpreted not as a true medullary cavity but as part of the ossification centre. In this case, the larger spaces may result from the loss of trabeculae during ossification or the thin section preparation, creating an apparent connection between the canals. Smaller caliber channels (subcanals) emerge from the vertebral centrum, with some extending to the cortical region. This section exhibits the highest number of subchannels among all analyzed vertebral elements. In the middle section of the dorsal vertebra (Fig. 2), two ventrolateral foramina are observable, and a dorsal foramen is challenging to distinguish due to a mechanical fracture. The absence of sedimentary fill makes it impossible to identify smaller caliber channels. In the caudal vertebra, only a ventral foramen and a dorsal foramen are visible (Fig. 2). Additionally, six subcanals emerge from the ossification centre, with two pairs oriented towards the transverse processes and one pair towards the neural arch. The canals and subcanals are enveloped in lamellar tissue, and some Sharpey's fibres are noted lining these spaces in the pectoral vertebra. Similar to the interpretation proposed by Wintrich *et al.* (2017b) for cervical vertebrae, these foramina and canals throughout the entire vertebral column are conceivable to follow a similar pattern. Further investigations with new specimens will contribute to a more comprehensive understanding of the plesiosaur vertebral vascular system.

CONCLUSIONS

All vertebrae exhibit a high degree of remodeling and an external fundamental system, indicating that the specimen MLP 93-I-5-1 has reached skeletal maturity (somatic).

Among all the samples analyzed, the caudal vertebra displays the least degree of remodeling. It retains the largest number of lines of arrested growth. This element more accurately reflects the minimum age of the individual.

The pectoral vertebra shows more canals and subcanals within the vascular system.

When considering the middle sections of the vertebral elements, there is an increase in CI from the cervical region to the caudal region.

These differences in bone microstructure are discernible and serve as a criterion when determining which element of the vertebral column and in which portion of it to create thin sections. This will yield more information at the paleohistological level, enabling paleobiological inferences such as ontogenetic stage, differential growth of various parts of the skeleton, and blood supply, among other factors.

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