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GROWTH STRATEGIES INFERRED FROM THE PALEOHISTOLOGICAL STUDY OF RIBS OF ORNITHOPOD DINOSAURS FROM THE MAESTRAZGO BASIN (TERUEL, SPAIN)

JUAN MAÍLLO[1*], JEROME HIDALGO-SANZ[1], JOSÉ MANUEL GASCA[1,2], MIGUEL MORENO-AZANZA[1,3]

ABSTRACT

A paleohistological comparison has been made between the dorsal ribs of two iguanodontid ornithopod specimens from the Azud Aliaga (Aliaga) and Pepe (Ladruñán) sites, both from the Barremian (Lower Cretaceous) of the Maestrazgo Basin (Teruel, Spain). Both specimens share a similar histological development in early stages of ontogeny, while in more advanced stages they elaborate different growth strategies. The specimen from Pepe shows homogeneous growth over time, while the one from Azud Aliaga modifies its development in more advanced ontogenetic stages. In relation to the paleobiology of the ornithopods from the Maestrazgo, these results may reflect different physiological requirements and/or a variable susceptibility to extrinsic paleoecological factors.

Keywords: Osteohistology, Ornithopoda, Ribs, Ontogeny, Growth.

1. INTRODUCTION

The skeletochronological study of dinosaur remains has been primarily focused on long bone samples, whose uninterrupted and symmetrical growth throughout the animal's ontogeny favours the preservation of growth marks. However, multiple studies have reevaluated the potential of axial skeleton bones, such as ribs, as a skeletochronological proxies in numerous dinosaur clades (Erickson *et al.*, 2004; Waskow & Sander, 2014; Waskow & Mateus, 2017; Hedrick *et al.*, 2020). These studies have shown

1. Aragosaurus-IUCA: Recursos Geológicos y Paleoambientes, Departamento de Ciencias de la Tierra, Universidad de Zaragoza, Zaragoza, España. *maillojuan150@gmail.com

2. Departamento de Geología, Universidad de Salamanca, Salamanca, España.

3. GEOBIOTEC, Department of Earth Sciences, NOVA School of Science and Technology, Campus de Caparica, Caparica, Portugal.

that these bones preserve growth primary tissue and growth marks in certain segments. This enables the paleohistological study of ribs to become a plausible alternative when it comes to studying specimens of incomplete dinosaur skeletons such as those found in the Maestrazgo Basin.

In this contribution, a paleohistological analysis of the dorsal ribs of an ornithopod dinosaur found in the vicinity of Aliaga is carried out, as well as a comparison with the results obtained in previous studies carried on ribs from another approximately coeval ornithopod from the Maestrazgo Basin (Maíllo *et al.*, 2023). The final goal aims to identify common patterns between both specimens during their histological development, as well as their divergences and possible implications regarding their growth strategies.

2. GEOLOGICAL SETTING

The fossils studied here were collected in two sites found in the Lower Cretaceous Maestrazgo Basin: Azud Aliaga, close to the town of Aliaga, in the El Castellar Formation (Galve sub-basin, latest Hauterivian early Barremian in age), and Pepe, close to the town of Ladruñán, in the Mirambel Formation (Morella sub-basin, Barremian in age).

Both fossil sites have yielded single associated disarticulated skeletons of undetermined iguanodontian ornithopods, found in continental fine-grained facies. Azud Aliaga outcrops in the lower part of El Castellar Formation, in a violet marly lutitic level representing a poorly drained flood plain deposit (Melendez *et al.*, 2009), while Pepe is found in a siliciclastic series in the uppermost part of Mirambel Formation, representing a fluvial floodplain deposit (Gasca *et al.*, 2017).

3. MATERIALS AND METHODS

The described material comprises four incomplete dorsal ribs attributed here to Iguanodontia Indet. All materials are housed in the Museo de Ciencias Naturales de la Universidad de Zaragoza.

Four thin sections with a thickness of 70-100 µm were prepared at Servicio General de Apoyo a la Investigación (SAI) of the Universidad de Zaragoza. Each rib was transversally cut at proximal points under the tuberculum, following standard methods (Chinsamy & Raath, 1992). They were examined using an Olympus BX53M petrographic microscope housed at IUCA-UNIZAR, and to obtain singular images, OLYMPUS Stream Basic was executed together with an Olympus DP27 coupled camera.

4. RESULTS

The Azud Aliaga ribs are well preserved, showing a cortical formation of variable thickness and remodeling along the different anatomical planes, as well as a scarcely porous medullary region. As for Pepe ribs, their cortical

Zubía | *núm. 42 (2024), pp. 197-202*
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tissue also shows variable thickness and remodeling, but their medullary region is larger in diameter and porosity, presenting wide remodeling chambers in the space adjacent to the endosteal surface.

All samples show the preferential remodeling of the medial and especially lateral sides, developing dense haversian tissue until the periosteal border. The proximal and anterior areas show small spaces of primary tissue, composed of fibrolamellar tissue with primarily longitudinally oriented canals organised in circumferentially oriented bundles. Lines of arrested growth (LAG) or subdivisions of split LAGs can also be identified, which are relatively evenly spaced endosteally, and more closely spaced periosteally.

In contrast to the samples from Pepe, on the periosteal margin, the Azud Aliaga samples develop a striking pattern of alternating low and high birefringence that deviances from the isotropic homogeneity of the rest of the tissue (Fig. 1). The thickness and number of iterations of this pattern varies depending on the anatomical plane.

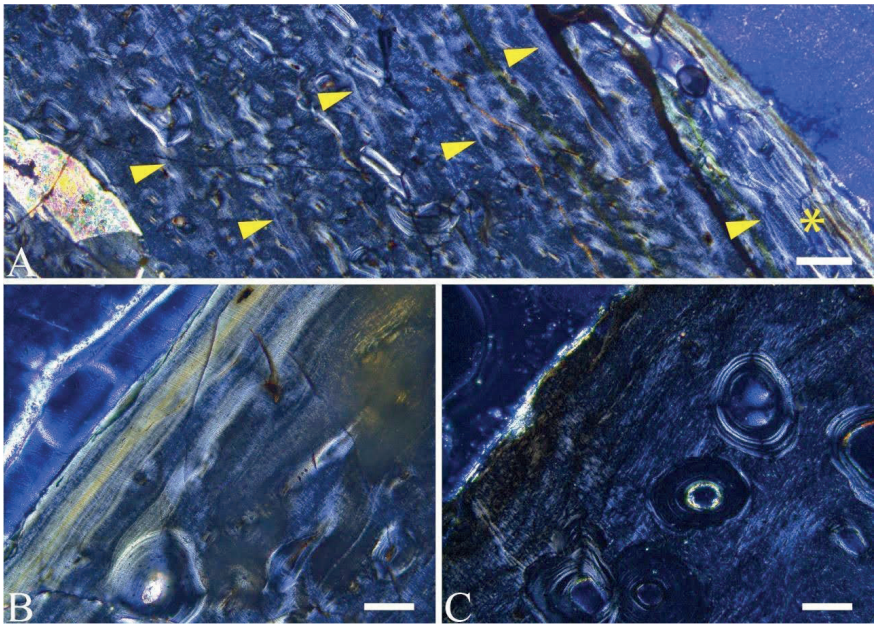

Figure 1. [A] Posterior periosteal surface of a sample from Azud Aliaga showing the dispersion of LAGs (yellow arrowheads) and the change of birefringence in the tissue (asterisk). Scale bar: 200 µm. [B] Birefringent pattern seen on the periosteal margin of Azud Aliaga samples. Scale bar: 100 µm. [C] Periosteal margin of a sample from Pepe. Its tissue remains isotropic even though it has developed a much greater number of LAGs. Scale bar: 100 µm. All photographs have been taken under polarized light.

5. DISCUSSION

The presence in all samples of a greater amount of primary tissue and LAGs in the posterior area seems to indicate that these spaces are the most

suitable ones for the preservation of growth marks on ribs, as was previously observed in other ornithopods of the Iberian Peninsula (Waskow & Mateus, 2017). As for the birefringent pattern seen in the samples from Azud Aliaga, the alternation between stripes of tissue with greater or lesser birefringence seems to suggest intervals of acceleration and deceleration during its production, or at least some type of cyclic alteration that influences the orientation of the structural fibers. Besides, the development of LAGs between some of these stretches could indicate that they could represent yearly intervals, perhaps corresponding to an effect of environmental stress associated with the transition between seasons, or the beginning of migrations (Hübner, 2012). Considering that the tissue production decreases dramatically as soon as this birefringent pattern is expressed, reaching sexual maturity could be another plausible alternative (Erickson *et al.*, 2007).

Regarding the Pepe samples, it is significant that their fibrolamellar tissue remains homogeneous and isotropic over time, despite preserving a much greater number of LAGs than those identified in the Azud Aliaga samples. Taking into account the skeletochronology inferred by Maíllo *et al.* (2023), the growth strategy of the Pepe iguanodontian seems to be invariable over time, not expressing fluctuations in the organization of the tissue, even after reaching sexual maturity. On the other hand, the Azud Aliaga iguanodontian seems to present a growth strategy that is much more susceptible to environmental factors or changes related to the ontogenetic stage. Further studies are needed to clarify if this observed differences are related to taxonomy, or if are caused by slightly different paleoenvironments in which these dinosaurs lived.

6. CONCLUSIONS

The comparative analysis of the rib pairs of both specimens allows inferring a similar histological development in early stages of development, which diverged as the animals reached more advanced ontogenetic stages. The ribs of both iguanodontians present preferential remodeling areas (medial and especially lateral), and during early stages of their development they generate an isotropic fibrolamellar tissue with LAGs. However, as both iguanodontians reach more advanced ontogenetic stages, they express different growth strategies. The iguanodontian from Pepe presented a fibrolamellar tissue of low birefringence throughout all its growth trajectory, expressing a homogeneous development and little variability against possible external factors. Conversely, the iguanodontian from Azud Aliaga developed as well fibrolamellar tissue of low birefringence and LAGs at early stages, but as its development progressed, it experienced an alteration in the arrangement of its fibrolamellar tissue that seems to suggest a greater susceptibility to paleobiological requirements (sexual maturity) and/or paleoecological factors (environmental stress or migrations).

Zubía | *núm. 42 (2024), pp. 197-202*
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ZUBÍA

42

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