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A literature review of the spatial organization of lamellar bone

Revue bibliographique sur l'organisation spatiale de l'os lamellaire

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ABSTRACT

Identification and interpretation of bone tissue types is the primary goal of histological analysis. Lamellar bone, a fundamental tissue, is generally easily identifiable in polarized microscopy. It is important, however, to understand the formation and structure of the tissues that are being studied. Lamellae are widely accepted to form a plywood-like structure, but this hypothesis has been and continues to be contested. Here, we discuss the common interpretations provided by the scientific community as to the spatial organization of lamellar bone. The two major competing hypotheses, lamellae that have alternating tissue compositions versus lamellae that alternate in fiber orientation, are described. In addition, recent research has led to a confounding array of interpretations of lamellae, with several authors viewing the thickness, orientations and composition of lamellae differently. We conclude that a blended approach is needed, as the varying methods are not easily comparable to one another. With an integrated approach, lamellae can be better understood, improving interpretations, including histological ones.

Mots clés :
Os lamellaire
Orientation des fibres de collagène
Lamellae hétérogènes

RÉSUMÉ

L'identification et l'interprétation des types de tissu osseux constituent le but principal de l'analyse histologique. L'os lamellaire, un tissu fondamental, est généralement facilement identifiable au microscope polarisant. Il est cependant important de comprendre la formation et la structure des tissus qui sont étudiés. Il est largement admis que les « lamellae » forment une structure de type contreplaqué, mais cette hypothèse a été et continue à être contestée. Dans cet article sont discutées les interprétations courantes fournies à la communauté scientifique quant à l'organisation spatiale de l'os lamellaire. Les deux hypothèses majeures en présence sont, d'une part, que les lamellae ont des compositions de tissu alternant, d'autre part, qu'elles alternent dans l'orientation des fibres. En outre, une recherche récente a conduit à un ensemble déconcertant d'interprétations des lamellae, avec des auteurs envisageant différemment l'épaisseur, les orientations et la composition des lamellae. Nous en concluons qu'une approche combinée est nécessaire, sachant que les diverses méthodes d'étude ne sont pas facilement comparables les unes aux autres. Avec une approche intégrée, les lamellae peuvent être mieux comprises, en perfectionnant les interprétations incluant celles de type histologique.

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1. Introduction

Lamellar bone is one of the main tissue types of bone and is found throughout vertebrates. In recent years, much has come to light about the origin and structure of the lamellae. However, with new methods and approaches come re-interpretations, and a decisive explanation of the organization and composition of lamellae has not yet been established. And, although the theory of bone lamellation has been discussed for over a century with several different hypotheses proposed, a consensus is still lacking.

Histologically, lamellar bone can be either a primary or secondary tissue. In polarized light microscopy, lamellae are typically easily identifiable with organized and parallel alternating dark and light layers and elongated osteocyte lacunae. Both in primary and secondary osteons, lamellar bone centripetally infills the vascular spaces. Secondary osteons form by first resorbing bone then redepositing new lamellae (Fig. 1A, B, D, E). They are elliptical, have a cement line, separating the osteon from surrounding bone, and are oriented parallel to the main loading direction, which means they can alter the original vascular organization. Primary osteons, on the other hand, do not alter the original vascular organization and form directly on the surface of bone. Circumferential layers are lamellae with usually very elongated and thin osteocyte lacunae, which are deposited on the endosteal or periosteal edge of the cortex (Fig. 1C). Trabeculae (Fig. 1F) are frequently remodeled with scalloped regions of lamellae. Researchers rely on these observations to make assumptions about the collagen fiber organization (e.g., Ascenzi and Bonucci, 1967, 1968; Skedros et al., 2009). Even though there is support for these interpretations from the literature, alternative hypotheses have been proposed, as well as new techniques applied, which provide more complex ideas as to how collagen fibers are organized within lamellae.

When studying fossil material, however, diagenetic and fossilization processes can alter, damage, or obscure the ability to effectively observe lamellae as they were in life. We, therefore, need comparisons with modern bone to be able to say anything relevant about fossil bone. Unfortunately, however, it is not possible to make proper assessments about lamellar organization in fossil bone, if there is no consensus on its organization in modern bone. Here, we review the recent literature on lamellar bone organization with the different methods used and discuss the problems and potential solutions.

1.1. Lamellar bone formation

Lamellar bone forms from dynamic osteogenesis (Ferretti et al., 2002; Marotti et al., 1999), a process that involves osteoblasts moving away from the osteogenic surface as they deposit osteoid. Osteoblasts secrete a collagenous matrix in an organized and parallel fashion on a preexisting hard surface (e.g., cartilage or bone) (Prondvai

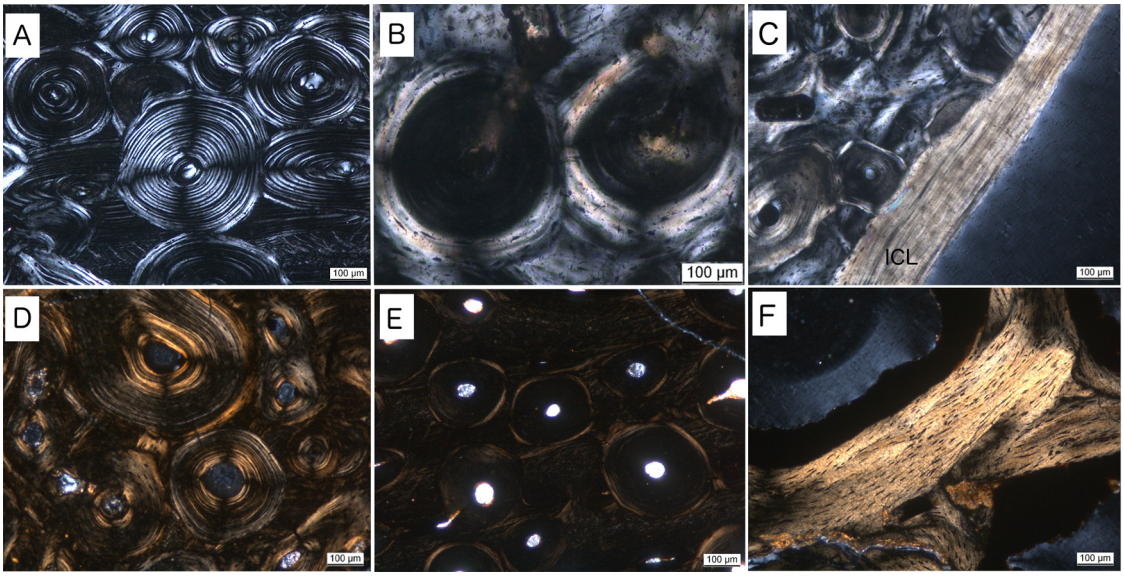

Fig. 1. Polarizing light microscopic images of lamellae in recent (A–C) and fossil (D–F) bone. **A**. Elephant humerus showing the distinctive alternating dark and light lamellar layers in secondary osteons. **B**. Elephant showing secondary osteons with almost all lamellae appearing dark, except the cement line. **C**. Giraffe tibia showing very bright inner circumferential layers (ICL) (also known as endosteal lamellae). **D**. Alternating pattern of bright and dark layers in secondary osteons of a long bone of nodosaurid *Hungarosaurus*. **E**. Mostly dark secondary osteons with a bright cement line in a sauropod humerus *Alamosaurus*. Secondary osteons that are predominantly dark are common in many fossil sections and can be in some cases attributed to diagenetic effects. **F**. Bright secondary lamellae forming trabeculae of an indet. nodosaurid.

Fig. 1. Images au microscope polarisant de lamellae dans des os récents (A–C) et fossiles (D–F). **A**. Humérus d'éléphant montrant les feuillets de lamellae distincts, alternativement noirs et blancs dans les ostéones secondaires. **B**. Ostéones secondaires d'os d'éléphant montrant que presque tous les feuillets apparaissent sombres, excepté la ligne de cimentation. **C**. Tibia de girafe montrant les feuillets internes circulaires très brillants (CL) (connus aussi en tant que lamellae endostéennes). **D**. Réseau à alternance de feuillets brillants et sombres dans des ostéones secondaires d'un os long de nodosauridé *Hungarosaurus*. **E**. Ostéones secondaires sombres pour la plupart, avec une ligne de cimentation brillante dans un humérus de sauropode *Alamosaurus*. Les ostéones secondaires, sombres de manière prédominante, s'observent couramment dans de nombreuses coupes d'os d'animaux fossiles et sont à rapporter, dans de nombreux cas, à des effets diagénétiques. **F**. Lamellae secondaires brillantes formant des trabécules chez un nodosauridé indéterminé.

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