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# Dorsal rib histology of dinosaurs and a crocodylomorph from western Portugal: Skeletochronological implications on age determination and life history traits

## *Histologie des côtes dorsales de dinosaures et d'un crocodile de l'Ouest du Portugal : implications squelettochronologiques sur la détermination de l'âge et des traits d'histoire de vie*

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ABSTRACT

Bone histology is an important tool for uncovering life history traits of extinct animals, particularly those that lack modern analogs, such as the non-avian dinosaurs. In most studies, histological analyses preferentially focus on long bones for understanding growth rates and determining age. Here we show, by analyzing ornithischians (a stegosaur and an ornithopod), saurischians (a sauropod and a theropod), and a crocodile, rib histology is a suitable alternative. The estimated age for all sampled taxa ranges between 14 to 17 years for *Lourinhanosaurus antunesi* and 27 to 31 years estimated for *Draconyx loureiroi*. The theropod *Baryonyx* was skeletally mature around 23–25 years of age but showed unfused neurocentral sutures, a paedomorphic feature possibly related to aquatic locomotion. Our results show that ribs can contain a nearly complete growth record, and reveal important information about individual age, point of sexual maturity, and, in some cases, sex. Because ribs are more available than long bones, this method opens new possibilities for studying rare and incomplete fossils, including holotypes.



RÉSUMÉ

L'histologie osseuse révèle d'importantes informations sur les traits d'histoire de vie des animaux éteints n'ayant pas d'analogues modernes, comme les dinosaures non aviens. En général, les os longs sont préférés pour les analyses histologiques. En collectant des données histologiques sur les côtes de différents taxons de vertébrés fossiles tels que des ornithischiens (un stégosaure et un ornithopode), des saurischiens (un sauropode et un théropode) et un crocodile, nous montrons que l'histologie des côtes est un outil approprié pour l'étude des traits d'histoire de vie. Nos résultats montrent que les côtes renferment un enregistrement de la croissance presque complet et, avec cela, d'importantes informations

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sur l'âge individuel, l'âge de maturité sexuelle et parfois le sexe de l'animal. L'âge estimé de tous les spécimens échantillonnés varie entre 14 et 17 ans (*Lourinhanosaurus antunesi* ; subadultes) et 27 et 31 ans (*Draconyx loureiroi* ; adultes). Le théropode *Baryonyx* a atteint sa maturité squelettique vers 23–25 ans, mais montre des sutures du neurocentre non fusionnées, une stratégie pédomorphique qui pourrait être liée à la locomotion aquatique. Les côtes étant plus accessibles que les os longs, cette méthode ouvre de nouvelles perspectives pour l'étude de spécimens rares et incomplets, ou même d'holotypes.


## 1. Introduction

Non-avian dinosaurs are the best-known extinct taxa. Unfortunately, these large creatures lack modern analogs, making it difficult to reconstruct their age and growth. Osteological features like neurocentral fusion are often used to estimate the ontogenetic age of archosaurs. However, even if the closure of neurocentral sutures in pseudosuchians seems to be a plesiomorphic feature (Brochu, 1996; Ikejiri, 2012), the reliability of this diagnosis in other archosaurs is still controversial (Fronimos and Wilson, 2017; Irmis, 2007). Therefore, to obtain information about their life history, the growth record preserved in hard tissues can be used (Castanet, 1994; Castanet et al., 1993). Within the fields of bone histology and skeletochronology, important data can be obtained concerning growth rates, individual age, longevity, skeletal-, and, in some cases, sexual maturity (e.g., Curry, 1999; Enlow and Brown, 1956, 1957, 1958; Griebeler et al., 2013; Horner et al., 1999; Klein and Sander, 2007, 2008; Klein et al., 2009; de Ricqlès, 1975, 1976; de Ricqlès et al., 2001; Sander, 2000; Sander et al., 2011; Woodward et al., 2011a, 2011b). The majority of paleo-histological studies focus on the long bone diaphysis (caused by their nearly circumferential shape, making it possible to infer growth curves). A few former studies, however, have used rib histology of extinct vertebrates (e.g., D'Emic et al., 2015; Erickson et al., 2004; Houssaye and Bardet, 2012; Waskow and Sander, 2014). In contrast to extant reptiles and other non-avian dinosaurs, sauropod long bone histology lacks a skeletochronological significant growth record; thus, rib histology is needed to obtain information about their age, growth, and life cycles. In their histological study on the ribcage of the nearly complete and articulated *Camarasaurus* sp. (SMA 0002), Waskow and Sander (2014) determined that the proximal end of a rib shaft contains the most complete growth record within sauropods. Fossil ribs are generally more frequently preserved and not as important for exhibitions as long bones; thus, they are more easily accessible for analyses. The current study focuses on rib histology of different Portuguese vertebrate taxa (mainly non-avian dinosaurs) to determine whether ribs provide sufficient histological data on life history traits of dinosaurs and other vertebrates.

### 1.1. Growth record preservation in primary bone tissue

Growth in bone tissue is recorded by the formation of annuli. Each annulus represents the bone tissue that was deposited during one year. The most important features concerning annularity used in this study are lines of arrested growth (LAGs), which are clearly developed thin, continuous, dark lines completing the single annuli. These LAGs represent the former surface of the bone where growth was interrupted. Another form of growth lines are polish lines. These more diffuse structures are not observable under the microscope, but they are only visible by tilting a polished bone surface, in order to reflect light. They are easy to see with the naked eye (Sander, 2000). Interpretations of the annual nature of the cyclicity preserved in primary bone tissues of several skeletal elements, like the humerus and femur, have been controversial in the past (e.g., Chinsamy and Hillenius, 2004; Padian and Horner, 2004). Nevertheless, annularity of growth cycles has been demonstrated in long bones, as well as other skeletal elements such as the scapula, coracoid, and ribs of extant and extinct reptiles such as *Alligator mississippiensis* or varanid squamates (e.g., Erickson et al., 2003; Garcia, 2011; Smirina and Ananjeva, 2007; Smirina and Tsellarius, 1996; Woodward et al., 2014) and extant mammals (e.g., several ruminants) with very similar histology to that of non-avian dinosaurs (Köhler et al., 2012). Furthermore, counting lines of arrested growth (LAGs) is a standard method of aging both ectothermic (actinopterygians, lissamphibians, squamates and crocodillomorphs) and endothermic (mammals) vertebrates (e.g., Altunişik et al., 2014; Caetano, 1990; Castanet and Smirina, 1990; Castanet et al., 1993, 2004; Hutton, 1986; Pancharatna and Kumbar, 2013; Snover et al., 2013). Therefore, the annual cyclicity of growth marks is generally accepted for non-avian dinosaurs (Erickson, 2005; Sander et al., 2011). Also, it is well-established that the presence of an External Fundamental System (EFS) indicates skeletal maturity (Chinsamy-Turan, 2005; Erickson, 2005; Sander, 2000; Sander et al., 2011; Turvey et al., 2005). The annularity of LAGs within the EFS is, however, controversial. The close spacing of the LAGs with no significant histological elements like osteons or vascular canals in between can be interpreted in different ways: either as a shorter timeframe (more than one LAG deposited in a year) or a longer timeframe (LAGs deposited only every second or third year) (Horner et al., 1999). Additionally, some LAGs might be more distinct than others, and some might be partly erased by the remodeling process.

In some cases, cyclicity only appears as a polish line, which is defined as a growth line in fibrolamellar bone that is visible in a polished section but not in a thin section (Sander, 2000), or as a modulation of bone tissue