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A hypothesis of differential secondary bone formation in dinosaurs

Hypothèse de formation différentielle d'os secondaire chez les dinosaures

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ABSTRACT

We propose the hypothesis that in the long bones of large, rapidly growing animals, secondary osteons may form to a greater degree in smaller bones than in larger ones for reasons that may have more to do with the interplay between element-specific growth rates and whole-body metabolic rates than with mechanical or environmental factors. We predict that in many large animals with rapid growth trajectories and some disparity in size in the long bones and other skeletal elements, the largest bones will show less secondary remodeling than smaller ones. The reason is that, whereas the largest bones are increasing their dimensions too rapidly to accommodate much secondary reworking (until they approach full size), the smaller bones that are not increasing in size as rapidly must still process the flow of metabolites through their elements, and this is manifested in secondary remodeling. This hypothesis does not contradict or undermine other explanations, but rather adds an additional one that focuses more on growth and metabolic rates with respect to bones of different size in the same skeleton. Because the timing of onset of remodeling and the pace of its progression both vary by element, caution must be taken when using secondary remodeling to infer the overall ontogenetic stage of the animal.

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RÉSUMÉ

Nous proposons l'hypothèse que, dans les os longs des animaux de grande taille à croissance rapide, des ostéones secondaires puissent se former plus abondamment dans les os plus petits que dans les os plus grands, car ils ont plus à faire dans les interactions entre les taux de croissance d'éléments spécifiques et les taux métaboliques pour le corps tout entier que les facteurs mécaniques et environnementaux. Nous prévoyons que chez de nombreux animaux de grande taille, ayant des modes de croissance rapide et une certaine disparité de taille entre les os longs et d'autres éléments du squelette, les os les plus grands présenteront moins de remaniements secondaires que de plus petits. La raison en est que, tandis que les plus grands os augmentent leurs dimensions trop rapidement pour accommoder plus de remaniements secondaires (jusqu'à ce qu'ils approchent de leur taille définitive), les plus petits os dont la taille n'augmente pas aussi rapidement, doivent gérer le flux des métabolites au travers de leurs éléments et ceci se manifeste dans les remaniements secondaires. Cette hypothèse ne contredit pas ou n'invalide pas d'autres explications, mais en

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apporte plutôt une supplémentaire qui se focalise plus sur les taux métaboliques et de croissance relatifs aux os de différentes tailles dans un même squelette. En raison du temps que prend la mise en place des remaniements et de leur vitesse de progression qui varient selon l'élément considéré, il est recommandé d'être prudent lorsqu'on utilise ces remaniements secondaires pour en tirer des conclusions sur le stade ontogénétique d'ensemble de l'animal.

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1. Introduction

Why are some bones of the skeleton more heavily imbued with secondary osteons than others? Does it have to do with biomechanical stresses, phylogenetic legacy, environmental conditions, growth dynamics, or some other factor? Perhaps the most generally accepted hypothesis is that remodeling is tightly linked with mechanical demands, either to repair strain-induced microdamage or to accommodate changing biomechanical needs (e.g., as bone changes in shape and size through ontogeny: Frost, 1994). This idea was first proposed in a general sense by Wolff (1986), who hypothesized that differences in mechanical stimuli or loading should be reflected in bone microstructural differences, a concept now known as Wolff's Law. Gebhardt (1906) provided the first test of Wolff's Law with reference to secondary osteons in the cortex, and established that secondary (Haversian) reworking of bone tissue progressively increased the mechanical resistance of the tissue, and was initiated by mechanical stimuli. Since then, numerous studies have demonstrated greater remodeling in regions that experience higher mechanical loads and (or) strains, or will experience them as the bone changes shape (e.g., Bouvier and Hylander, 1996; Carter, 1984, 1987; Currey, 1984; Enlow, 1962; Frost, 1987, 1990).

But this cannot be the only explanation. Amprino (1948) found that resistance was not always increased by Haversian replacement, although its production was also regulated by mechanical influences. In fact, he found that when secondary tissue replaced primary tissue in the ossified tendons and ligaments of birds, the mechanical resistance of the bone to traction (stretching) was lowered. That such tissue would form under tension falsified the hypothesis that bone formed as a mechanical response only to pressure. Amprino (1948: 298) offered a second hypothesis about the drivers of secondary osteon formation, positing that "the structural rearrangement of the matrix of bone (or of any calcified body tissue) depends largely on the necessity of continued mobilization (through resorption) of the mineral salts" that are stored, in his view temporarily, in these tissues, to be used for other physiological purposes during life, including later growth. Several experimental studies have since found that this type of remodeling mainly occurs in regions of trabecular bone that experiences low levels of mechanical strain (e.g., Bouvier and Hylander, 1996; Frost, 1987). However, temporary but intense calcium demands, such as those that occur during egg-laying or pregnancy, may also result in secondary cortical remodeling (e.g., Parfitt, 1994; Schweitzer et al., 2007). Today it is widely accepted that

bone remodeling has both biomechanical and metabolic functions.

A third hypothesis was developed by Enlow (1962, 1963, 1976), namely that secondary remodeling in the cortex is predictably correlated with regions that are undergoing endosteal growth, notably with the development of compacted coarse cancellous bone (possibly related to mechanical stress, mineral redistribution, muscle attachment, and necrotic replacement). McFarlin et al. (2008) sustained his correlation, and noted that, as many workers have observed, secondary bone development tends to occur more extensively in the deep cortex than in the outer cortex. But they added the caveat that the degree of endosteal development, which may be related to the dynamics of shape change during bone growth and therefore to cortical drift, may be correlated as well. Readers are referred to McFarlin et al. (2008) for a good overall survey of the various hypotheses that may explain secondary reworking of bone tissues in various contexts.

Secondary remodeling also reflects, at least in part, the age of the individual. The cortical area occupied by secondary osteons, as well as the number of generations (determined by the number of overlapping canals), both increase with age (e.g., Alquist and Damsten, 1969; Kerley, 1965). Secondary osteons are used to assess age in extant mammals, especially in humans and other animals associated with archaeological remains, and also has been evaluated in other taxa (e.g., ranid frogs: LeClair, 1990). However, the absolute rates of secondary replacement vary taxonomically and by element, and must be determined by observation in animals of known age (Mulhern and Ubelaker, 2003; Stover et al., 1992). A general relationship between the extent of secondary remodeling (secondary osteons plus erosion rooms) and both taxon size and individual age has been noted in extinct taxa (e.g., Horner et al., 1999, 2000; Klein and Sander, 2008; Werning, 2012), but has not been quantified.

Here we propose a new hypothesis, not intended to be universal, but to situate secondary bone formation in some animals (mainly large and rapidly growing ones) in the context of overall growth rates and relative sizes of bones. Horner et al. (2000: 115) framed the overall problem in this way:

We begin with the generalization that four principal factors determine the type and form of hard tissues that are deposited in the skeletons of vertebrates at any given time. These factors are phylogeny, ontogeny, mechanical, and environmental. There are, of course, other factors (e.g., chance, injury, illness, starvation, and individual differences) that can affect the formation of bone in specific regions of a skeleton at any particular

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