



General Palaeontology, Systematics and Evolution

## A hypothesis of differential secondary bone formation in dinosaurs



### *Hypothèse de formation différentielle d'os secondaire chez les dinosaures*

Kevin Padian<sup>a,\*</sup>, Sarah Werning<sup>b</sup>, John R. Horner<sup>c</sup><sup>a</sup> Department of Integrative Biology and Museum of Paleontology, University of California, 94720 Berkeley, USA<sup>b</sup> Department of Anatomical Sciences, Stony Brook University, 11794 Stony Brook, USA<sup>c</sup> Museum of the Rockies, Montana State University, 59717 Bozeman, USA

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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

\* Corresponding author.

E-mail address: [kpadian@berkeley.edu](mailto:kpadian@berkeley.edu) (K. Padian).

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

stage of growth, but they are less universal than the four we list here.

Secondary bone remodeling is known to increase with biomechanical stress, age, and necessary redeployment of skeletal nutrients, and is associated with endosteal bone production (Castanet and de Ricqlès, 1986–1987; McFarlin et al., 2008). But do these factors explain every incident of secondary remodeling? Here we explore briefly a hypothesis that may be particularly relevant to animals with relatively high growth and metabolic rates and some size disparity among the long bones of the skeleton.

## 2. Skeletochronology, LAGs, and the EFS

In 1999 Horner et al. described the bone histology of the type specimen of *Hypacrosaurus stebingeri* (Museum of the Rockies, Bozeman, Montana, MOR 549), a large hadrosaurid dinosaur from the Late Cretaceous of Montana. A variety of bones in the skeleton was sectioned. A principal focus of that paper was to determine the animal's age at death, which presented a challenge because the numbers of preserved LAGs (lines of arrested growth) varied among the sampled bones. In some bones, LAGs were obscured or erased by the formation of erosion spaces in the deep cortex, the expansion of the medullary cavity, and the proliferation of secondary osteons, which usually developed first in the deep cortex and increasingly expanded toward the periphery (Francillon-Vieillot et al., 1990). We concluded at the time that it was difficult to assess skeletal age (inferred from the number of LAGs) from one bone alone, and suggested the use of several in order to arrive at the most reasonable estimates. In the present note, we offer a refinement on this suggestion, and propose a hypothesis of process to explain some of these patterns.

Two other factors affect the assessment of age, however. One is growth rate, because in very rapidly growing bones, particularly at early growth stages, annual lines may be difficult to discern (Horner et al., 2000), as is notorious for very large, rapidly growing dinosaurs such as sauropods (Sander, 2000). There has been some question whether some larger dinosaurs even deposited a visible first-year LAG, even when later ones are visible (e.g., Horner et al., 2000). This pattern is understandable according to two general classes of observation: larger species of a clade tend to grow at higher rates than smaller species (Case, 1978), and individuals grow more rapidly at earlier stages than at later ones (Amprino, 1947).

The second factor that affects the assessment of age is the interpretation of the EFS, or External Fundamental System (Cormack, 1987), a relatively avascular and acellular bone tissue that forms sub-periosteally on the bones of individuals that have essentially reached a plateau in skeletal growth (i.e., the upper asymptote of their growth curve). Although this feature was first reported in mammals, it has been found in many archosaurs, including birds, non-avian dinosaurs, crocodiles, and other extinct pseudosuchians (e.g. de Ricqlès et al., 2003; Erickson et al., 2004; Horner et al., 1999; Sander, 2000; Turvey et al., 2005; Woodward et al., 2011). It reflects asymptotic growth, which appears to be common to all vertebrates (more slowly growing taxa

**Table 1**

Skeletal elements of the type specimen of *Hypacrosaurus stebingeri* (MOR 549), providing minimum and maximum counts of LAGs in the cortex and of apparent growth marks in the External Fundamental System.

**Tableau 1**

Éléments du squelette du spécimen type *Hypacrosaurus gsteineri* (MOR 549) fournissant les comptages minimums et maximums de LAGS dans le cortex et de marques de croissance apparente dans l'External Fundamental System (EFS).

Element	Min cortex	Max cortex	Min EFS	Max EFS
Scapula	5	6	2–3	6–8
Radius	5	7	2	7–8
Metacarpal	0	1	3–4	7–8
Femur	6	8	1	1
Tibia	7	8	1	2
Fibula	5	7	1	4–5
Metatarsal	2	6	4	10
Pedal phalanx	0	0	0	0
Rib	5	6	3	5
Caudal chevron	6	6	3	5
Neural spine	3	4	2	3
Ossified tendon	6	6	3	5

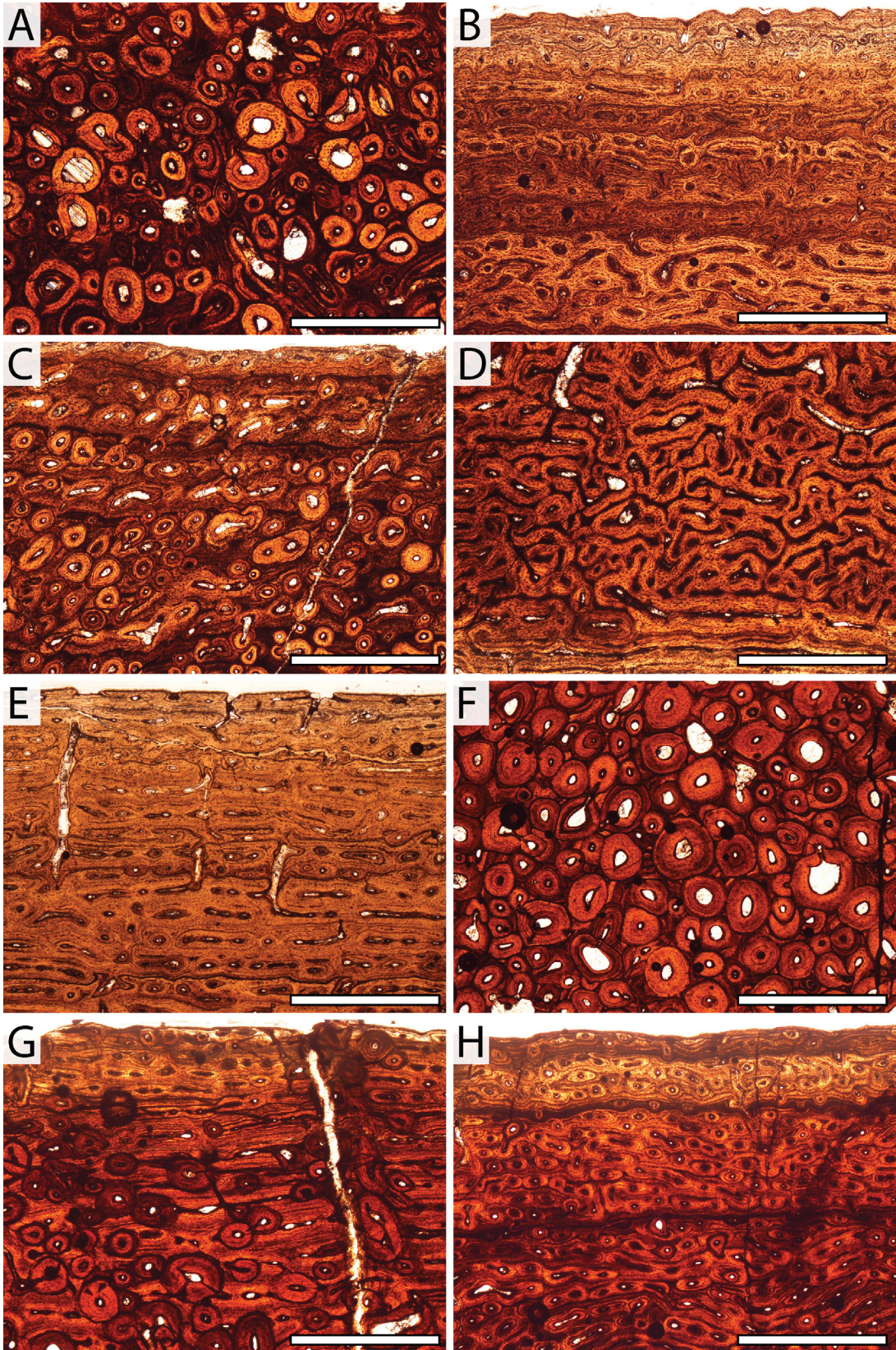
From Horner et al. (1999).

are not sampled or die before reaching maximum size, and grow very slowly as they approach it: Sebens, 1987).

It is now universally accepted that LAGs are annually deposited, although their interpretation in individual taxa with aberrant histological features (double and triple LAGs, polish lines, etc.) may be complicated, and environmental or physiological conditions may affect their production (Castanet, 1986–1987). In the EFS, growth marks may appear that are more or less continuous around the periphery of a bone, much like LAGs; but they are often difficult to trace for much of the periphery. There is also reason to think that the lines of the EFS may not be annual, or at least have not been shown to be annual. Horner et al. (1999; see Table 1) found that they varied in number more than cortical LAGs did in a single skeleton of the hadrosaurid dinosaur *Hypacrosaurus*. Castanet et al. (1988) found that the number of lines in the EFS in the tuatara, (*Sphenodon*) varied between the phalanges and the femur of the same individual. The femur had more lines overall, in both the cortex and EFS, and they inferred that the cause was the longer growing period of the femur. Martinez-Maza et al. (2014) treated EFS lines in the metapodials of the Miocene horse *Hipparion* as potentially annual, although they admitted that there is no experimental evidence that validates this assumption. Horner et al. (1999) found it particularly problematic to interpret the skeletochronology of the metapodials in *Hypacrosaurus* (see Table 1), and that throughout the skeleton the lines in the EFS provided no consistent signal.

We hypothesize that much of the variation in the expression of skeletochronological indicators (and potential indicators) is often a function of growth rates of individual bones, especially in large, rapidly growing animals. These growth rates are in turn underpinned by metabolic rates. The difficulty of counting growth lines in the cortex of the limb bones of giant sauropods presents an example.







### 3. Limb size, growth rates, and secondary bone tissue

In addition to the presence of LAGs and the EFS, another feature often considered a manifestation of age is the proliferation of secondary (Haversian) osteons in cortical bone. When these structures appear only in one region of a bone or along a single axis, this suggests an association with mechanical stress, cortical drift, or repair of microdamage, rather than a pure reflection of absolute age (Frost, 1994; McFarlin et al., 2008). Secondary osteons that form as a result of age rather than biomechanical processes generally appear first in the deep cortex of long bones and spread centrifugally through ontogeny (Alquist and Damsten, 1969; Francillon-Vieillot et al., 1990; Kerley, 1965). This general relationship between the extent of secondary remodeling and age has been noted in dinosaur growth series (e.g., Horner et al., 2000; Klein and Sander, 2008; Werning, 2012), and has been used to infer relative ontogenetic stages among conspecifics (e.g., Scannella and Horner, 2010, although this involved cranial remodeling).

Notably, however, the amount of secondary remodeling often differs among elements. For example, Werning (2012) found that in the bipedal ornithomimid dinosaur *Tenontosaurus*, the forearm elements always showed greater secondary remodeling than the femur or tibia of the same individual. Furthermore, the remodeling of the forelimb began at earlier ontogenetic stages, and thus these elements appeared to be histologically “older” than the larger elements. This is also the case in the ornithomimids *Hypacrosaurus* (Horner et al., 1999; Fig. 1) and *Maiasaura* (Horner et al., 2000), and the prosauropod *Plateosaurus* (Klein and Sander, 2007).

But what causes these differences? Why do some bones remodel more extensively or earlier in ontogeny? Without casting doubt on the validity of the biomechanical processes discussed above, we suggest the hypothesis that in large animals with high growth rates, the onset and pace of secondary bone formation can be largely a function of the size of the bone, and of the growth strategies of individual bones.

Dinosaurs are among the largest animals for which we have a reasonable sense of growth rates (Padian and Lamm, 2013). Some, such as tyrannosaurs, are obligate bipeds; some, such as sauropods, are obligate quadrupeds; and some, such as hadrosaurs, may have been facultatively

quadrupedal or bipedal (Coombs, 1978). In animals with serially homologous long bones of the same approximate size (e.g., humerus and femur, ulna and tibia), the development of secondary osteons should be similar in serially corresponding bones, unless there is a biomechanical reason that complicates this (for example, regional variation near a muscle attachment site). Such animals will normally be quadrupeds, and their long bones are sharing the weight-bearing and the locomotory impetus (Alexander et al., 1979; Anderson et al., 1985; Campione and Evans, 2012). In quadrupeds with more disparity between the fore and hind limbs, the situation may be somewhat different: the hind limbs, being larger, are thought to bear greater responsibility for weight-bearing and locomotion (Anderson et al., 1985; Campione et al., 2014). We further hypothesize that in bipedal (and possibly facultatively bipedal) animals, in which there is a particularly strong limb disparity, the development of secondary osteons will be greater in the smaller bones than in larger bones, even if they support little or no weight.

This disparity in growth begins with eclosion (hatching). When embryonic reptile skeletons are contained in eggs, their long bones are of more similar lengths than later in ontogeny, because their maximum lengths are constrained by the geometry of the egg. For example, pterosaur long bones are longer than axial skeletal elements in adult forms, and also much differently proportioned among themselves. But in the egg, the length differences among the bones are inconsiderable. Jenkins et al. (2001, Table 1) described a very young post-hatchling pterosaur and compared its proportions to those of other juvenile and adult Triassic pterosaurs (*Eudimorphodon* and *Peteinosaurus*). They showed that there was much less difference among the long bone elements in juveniles than in adult forms. Upon hatching, differential growth commences.

Our hypothesis centers on the problem of differential growth after eclosion. As many animals grow, different bones assume different functional roles, and their sizes and proportions grow accordingly. To achieve allometric growth, smaller elements must either grow more slowly than larger ones, or reach their adult (maximum) proportions earlier than larger ones. Each element experiences its own growth trajectory, which may differ from those of the other elements, and from the rate of accumulation of body mass. In the absence of other biomechanical

**Fig. 1.** (Color online.) Cross-sections of various bones of *Hypacrosaurus stebingeri* (MOR 549), an ostensible adult based on the presence of an External Fundamental System (Horner et al., 1999). A. Internal cortex of the femur, showing extensive remodeling (including several generations of secondary osteons in places). B, C. External cortex of the femur in two different areas, showing contrasts in the degree of secondary remodeling (virtually none to considerable but still less than in the internal cortex). D, E. Internal and external cortex (respectively) of the tibia, showing almost no remodeling. F–H. Internal (F) and two external areas (G, H) of the fibula; the inner cortex is reworked by several generations of secondary osteons, but these are only sparse and scattered to virtually absent in the outer cortex. All scales = 1 mm. For details see Horner et al. (1999). High resolution versions of these images can be accessed at Morphobank (O’Leary and Kaufman, 2012), Project P2121 (<http://morphobank.org/permalink/?P2121>).

**Fig. 1.** (Couleur en ligne.) Coupes dans différents os de *Hypacrosaurus stebingeri* (MOR 549), apparemment adulte d’après la présence d’un *External Fundamental System* (Horner et al., 1999). A. Cortex interne de fémur, montrant de vastes remaniements (incluant plusieurs générations d’ostéons secondaires par endroits). B, C. Cortex externe de fémur dans deux zones différentes, montrant des contrastes dans le degré de remaniement secondaire (virtuellement nul à considérable, mais encore moins que dans le cortex interne). D, E. Cortex interne et externe (respectivement) de tibia ne montrant presque aucun remaniement. F–H. Zone interne (F) et deux zones externes (G, H) de fibula ; le cortex interne est remanié par plusieurs générations d’ostéons secondaires, mais ces derniers sont seulement rares et dispersés, jusqu’à virtuellement absents dans le cortex externe. Toutes échelles = 1 mm. Pour plus de détails, voir Horner et al. (1999). Les versions Haute Résolution de ces images sont accessibles sur la Morphobank (O’Leary et Kaufman, 2012). Projet P2121 (<http://morphobank.org/permalink/?P2121>).

pressures, larger bones (especially the main mass-bearing elements) may experience both higher growth rates and longer durations of growth than smaller bones. These elements should also record histological signals of higher growth rates than the more slowly growing elements (e.g., higher canal density, more disorganized collagen fibers, wider spacing between LAGs; [Amprino, 1947](#); [Francillon-Vieillot et al., 1990](#)).

It could be, as a reviewer suggested, that this pattern may be explained by Von Baer's Law. In this case, the long bones would be of more similar lengths early in ontogeny because general characteristics of the group develop before special ones, so isometric growth would prevail before allometric growth in the developing embryo.

We hypothesize that the degree of secondary remodeling in such animals is not mainly a function of biomechanical stress or the animal's age, but of different growth trajectories among elements. Under this hypothesis, the largest long bones would be growing too rapidly to deposit secondary tissues, because the nutrients delivered to them would largely be used in primary periosteal bone deposition. This reflects their role in support; these bones must pace their growth with that of the animal's increasing body mass. On the other hand, smaller bones, especially if they do not bear weight, will experience considerable secondary remodeling as a means of slowing their element-specific growth rates.

Secondary remodeling may serve as the mechanism of slowed growth in two ways. First, remodeling reduces the overall porosity of the element relative to the faster-growing primary tissues, which have greater canal density and connectivity. Reducing the total number of canals and their anastomoses in turn reduces nutrient supply from the blood. Second, remodeling diverts resources from periosteal expansion. The available nutrient content contained within the blood will be similar whether flowing through smaller or the larger bones (which still need additional nutrients to accommodate continued rapid growth). Rather than using the nutrients to increase circumference, smaller bones use them to rework existing tissues. This would account for the preponderance of secondary bone tissue in these smaller bones that do not bear weight or experience significant strain. This is a different situation from that of smaller weight-bearing bones such as the fibula and metatarsals, which may experience considerable reworking because they take on substantial biomechanical stress.

Our hypothesis suggests that high metabolic rates may be forcing bone tissue development, which is uncontroversial; but it further suggests that secondary bone tissue deposition is greater in the smaller long bones of animals with high metabolic rates than in the larger bones, because the smaller bones may not “refuse,” in a sense, the metabolites carried by the blood. Here, for convenience, we are using somewhat metaphorical language in order to make a point. Because they do not “want” to grow, in a vitalistic sense (mediated by genetic and epigenetic factors), these bones remodel their tissues in order to expend the energy and metabolites. In other words, our hypothesis reduces to this: in some taxa with disparate limb proportions, the smaller bones don't “want” to get bigger, so they have to

remodel their tissues because they can't refuse the supply of metabolites that the vascular system brings to all bones in the body. We think that this largely explains the disproportionate distribution of secondary osteons in large and small bones in these animals, regardless of weight-bearing.

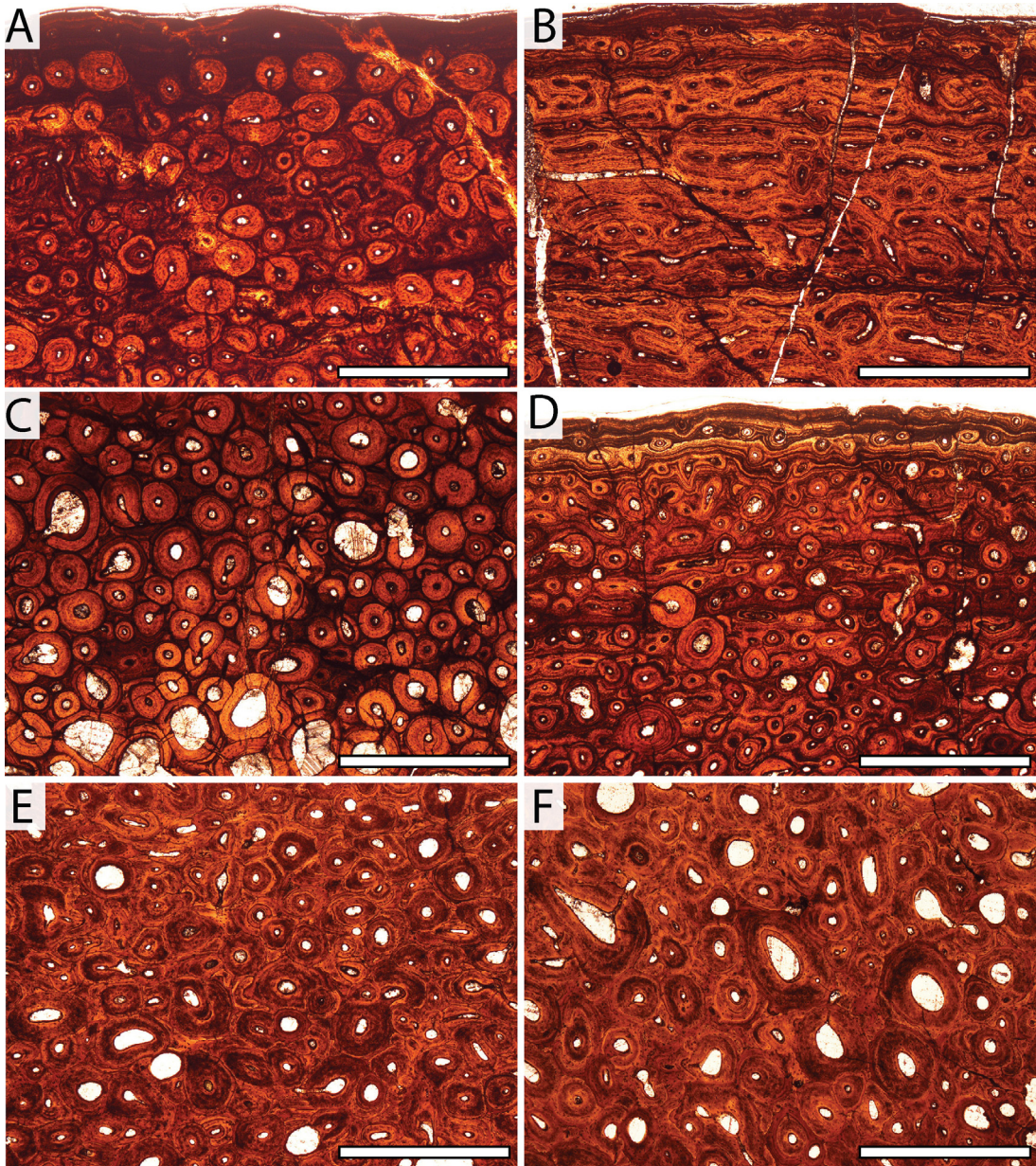
To use another metaphor, it is like constantly constructing a house: larger bones such as the femur and tibia make new tissue, like adding on rooms of a house, whereas smaller bones such as the radius and ulna are doing what amounts to interior remodeling of a house, in both cases using the same rate of flow of materials.

This hypothesis can be directly tested by examination of the histology of the long bones of a variety of bipedal and quadrupedal tetrapods with high growth rates. Among bipeds, we predict that the smaller bones of the forelimb (1) will show a different ontogenetic trajectory (i.e., growth will cease before it does in the larger bones, or we will see disproportionately slower growth with age); (2) will acquire greater development of secondary bone tissues, even though they bear little or no weight; and (3) will show the appearance of secondary osteons that will coincide with (earlier) growth cessation in smaller elements, or with their transition to slower growth than in larger elements. Animals that are facultative quadrupeds may be expected to show different results, but this will require careful testing.

This prediction is borne out histologically in obligate and facultative bipeds such as *Hypacrosaurus*, *Maiasaura*, *Tenontosaurus*, and *Plateosaurus*. In these taxa, the largest long bones are the femur and tibia, which typically experience little or no remodeling until growth slows considerably, in what would be called the “late juvenile” or “sub-adult” stage, depending on the taxon. However, in all cases the forelimb elements begin remodeling much earlier in terms of the animal's ontogeny (e.g., [Horner et al., 1999, 2000](#); [Klein and Sander, 2007](#); [Werning, 2012](#)). However, this is not always the case. For example, the ornithomimid *Dysalotosaurus* shows no difference in the onset or extent of secondary remodeling between forelimb and weight-bearing elements ([Hübner, 2012](#)).

Caution will need to be exercised. For example, this hypothesis may be less applicable depending on the adult size of the taxon (more remodeling often occurs in smaller taxa, because they have lower growth rates than larger related species: [Padian et al., 2001](#)). Additionally, in animals with high metabolic rates that secondarily grow slowly, secondary bone growth should be much more prevalent in their bones than in the bones of related animals that grow quickly. Humans, for example, have high metabolic rates like other mammals but they grow relatively slowly; as a result, the long bones of adults and sub-adults have extensive development of secondary osteons. Compare, for example, the secondary bone development recorded in the humerus and femur of the green monkey, the gibbon, and the chimp—all slowly growing primates of small to medium size ([McFarlin et al., 2008](#))—with that of *Hypacrosaurus* ([Horner et al., 1999](#)). The latter taxon has less Haversian remodeling, especially in its larger elements, largely a function of growth rates (even though all these taxa have relatively higher metabolic rates than most reptiles and amphibians).





**Fig. 2.** (Color online.) Continuation of Fig. 1. A, B. Cortex of the metatarsal near opposite sides of the periosteal surface, showing very little to very extensive remodeling. C, D. Internal and external cortex of the radius. Similar pattern to that of the fibula, but the outer cortex is considerably more reworked unto the most recent depositional layers. E, F. Cortex of the metacarpal near opposite sides of the periosteal surface. The entire cortex is completely secondarily remodeled. All scales = 1 mm. For details see Horner et al. (1999). High resolution versions of these images can be accessed at Morphobank (O'Leary and Kaufman, 2012), Project P2121 (<http://morphobank.org/permalink/?P2121>).

**Fig. 2.** (Couleur en ligne.) Suite de la Fig. 1. A, B. Cortex de métatarsaire proche des côtés opposés de la surface périostique, montrant des remaniements de peu nombreux à très vastes. C, D. Cortex interne et externe de radius. Figure similaire à celle de la fibula, mais le cortex externe est beaucoup plus remanié vers les feuillettes de dépôt les plus récents. E, F. Cortex de métacarpe proche des côtés opposés de la surface périostique. Le cortex entier est complètement remanié secondairement. Toutes échelles = 1 mm. Pour plus de détails, voir Horner et al. (1999). Les versions HauteRésolution de ces images sont accessibles sur la Morphobank (O'Leary et Kaufman, 2012). Projet P2121 (<http://morphobank.org/permalink/?P2121>).

Another example may be provided by dwarf sauropods (e.g., Benton et al., 2010; D'Emic and Wilson, 2012; Stein et al., 2010) whose long bones show extensive secondary remodeling. Biomechanical stresses could have been involved, but because all bones tend to be substantially affected by Haversian remodeling, and the long bones

of much larger related sauropods (with much higher proportional stresses) are less so, we find no support for a biomechanical hypothesis. On the contrary, we suspect that secondary dwarfing of these small sauropods resulted in bones that grew to adult size at somewhat lower rates than their larger relatives as a consequence of phylogenetic

legacy, but continued to be remodeled extensively because they retained more or less their relatively high ancestral metabolic rates (Fig. 2).

#### 4. Conclusion

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, freed from the weight-bearing constraints of pacing body size, must slow or cease growth earlier to achieve allometry despite high metabolic rates and a continued flow of metabolites. Secondary remodeling forces slower growth both by reducing overall porosity (i.e., the available blood supply) and by diverting resources from growth to replacement of existing bone tissue.

We stress that it is the smaller bones, and the non-weight-bearing bones, that are at issue here, because they can test patterns of remodeling seen in larger, weight-bearing bones in both the forelimb and hindlimb. Explicit tests of this hypothesis will require sampling the same series of several elements in individuals comprising a growth series, in order to confirm different growth rates and trajectories, and the exact timing of secondary osteon appearance among elements. As Horner et al. (2000) noted, sampling different elements from the same skeleton may result in different estimates of the animal's overall ontogenetic stage. Notably, if smaller elements had much different ontogenetic trajectories compared to larger ones or to the animal's overall growth, it would reduce their utility in reconstructing the animal's overall ontogeny. In these cases, we would recommend using larger, weight-bearing elements whose growth paced mass to estimate the animal's age-mass trajectory.

This hypothesis is about a process, and it attempts to predict some of the patterns outlined in the paragraphs above. It does not attempt to undermine or replace other circumstances in which secondary bone tissue is produced. In each case, hypotheses have to be tested. Ours can be wrong in a given case for a variety of reasons related to functional load or growth and metabolic rates, or to the sequestration of tissues through the life of the animal, as outlined by the alternative hypotheses discussed above. This hypothesis is mostly confined to the explanation of differential development of tissue in animals of high rates of growth and metabolism, in which some long bones show differential size and mechanical load.

Sauropod dinosaurs can be particularly instructive here because all their limb bones bear weight. According to our hypothesis, the zeugopodial bones should be relatively more reworked than the propodials. (To our knowledge, the histology of these bones has not been assessed in a single individual sauropod) In contrast, bipedal dinosaurs would be differently instructive. The smaller, non-weight bearing bones of the forelimb (propodials and zeugopodials) might be more reworked than the corresponding larger, weight-bearing bones of the hindlimb. (This could be productively

tested in theropods and bipedal ornithopods, for example.) Many other taxa could be recruited to test this hypothesis.

Our general aim is to put forward a hypothesis that might help to discriminate between phylogenetic or mechanical effects and those related to the size of the bone and the rate of its growth, given its underlying metabolic regime. If our hypothesis stimulates further productive work, then it will have done its job.

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In the past three decades the study of bone histology in extinct organisms has become firmly established internationally as a field of vital research, a strong unified philosophy, and sophisticated methods and concepts (reviewed in Padian and Lamm, 2013). Much of this is due to the pioneering work of Armand de Ricqlès (see Padian (2011) and other articles in *Comptes Rendus Palevol* 11 [5–6], 2011). Armand perfectly bridged the gap between the classical histologists of the first half of the 20thC, such as Marcel Prenant and Yves François, and the new generation of colleagues who took their places in the second half, such as Louise Zylberberg, Jacques Castanet, Jean-Yves Sire, François Meunier, Hélène Francillon-Vieillot, Vivian de Buffrénil, and others who elucidated the anatomy and development of the bony tissues of what were then fondly called the “lower” vertebrates. Armand's interests bridged fossil and living tetrapods, and his work was instrumental in drawing the international attention of paleobiologists to the incredible research of the “Paris school” that would otherwise have been overlooked. To all these people we owe our greatest thanks and admiration.

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