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Histological observations of Enantiornithine bone (Saurischia, Aves) from the Lower Cretaceous of Las Hoyas (Spain)

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Abstract

New material from a small, presumably adult enantiornithine bird (Saurischia: Aves) from the Lower Cretaceous of Las Hoyas (Spain) provides new data on the bone histology of those Mesozoic birds, which became extinct at the Cretaceous–Tertiary boundary. The material is referred to cf. *Concornis lacustris.* The outer cortex of the studied long bones is formed of a rather typical parallel-fibered bone tissue, with sparse flattened osteocyte lacunae, evidence of lines of arrested growth (LAGs) and no vascularization. This structure matches the outer circumferential layer (OCL) of many extant mature, small to tiny birds and also agrees with earlier descriptions of enantiornithine cortical bone. The deeper cortex progressively contains a much more plentiful component of osteocyte lacunae, which are more plump than flat. This region is also permeated by a few vascular canals surrounded by bone lamellae that form osteonal structures. The relationship of the osteonal material to the neighbouring primary tissue strongly suggests that the osteons are secondary. In some sections, it is possible to follow those osteons as formed by outward extensions from the endosteal bone tissue into the deep primary cortex. This specimen shows more histodiversity than the few enantiornithine samples previously reported. This further suggests that although growth may have been slow when the adult size was approached, it was more rapid at earlier stages. Even if as yet not enough is known of those early stages to document just how rapid early growth may have been, and whether enantiornithines grew differently from the basal avian models known from other early birds, the new data do not necessarily suggest that they had growth regimes quite distinct from extant birds of similar body sizes nor, by implication, completely different metabolic patterns or regimes. ***To cite this article: O. Cambra-Moo et al., C. R. Palevol 5 (2006)***.

Résumé

Observations histologiques d'os d'Énantiornithe (Saurischia, Aves) du Crétacé inférieur de Las Hoyas (Espagne). Un nouveau matériel appartenant à un petit Énantiornithe (Saurischia, Aves), probablement adulte, du Crétacé inférieur de Las Hoyas (Espagne) apporte de nouvelles données sur l'histologie osseuse de ces oiseaux disparus à la fin du Crétacé. Ce matériel est rapporté à cf. *Concornis lacustris*. La corticale externe des os longs étudiés est avasculaire, formée d'une matrice osseuse à fibres

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parallèles, pourvue de lacunes ostéocytaires aplaties. Des lignes d'arrêt de croissance (LACs) sont présentes. Cette organisation correspond au « système fondamental externe » décrit chez de nombreux oiseaux adultes actuels. Elle s'accorde aussi avec la description des corticales osseuses, déjà réalisée chez un Énantiornithe adulte. En revanche, la corticale profonde comprend de nombreuses lacunes ostéocytaires, plus globuleuses qu'aplaties. Cette région est aussi pénétrée par quelques canaux vasculaires entourés par des lamelles osseuses, le tout formant des ostéones, probablement secondaires, d'après leur aspect et leur rapport au tissu osseux adjacent. Ces ostéones apparaissent constitué par des extrusions de l'os endostéal bordant la cavité médullaire. Ces données sont discutées relativement aux connaissances actuelles sur l'histologie osseuse comparée des oiseaux actuels et mésozoïques du point de vue de la dynamique de croissance et de l'évolution de la physiologie thermo-métabolique. Nos observations montrent une plus grande histodiversité, en particulier pour l'os en croissance, que dans les rares spécimens déjà décrits. Elles suggèrent que la croissance a pu être effectivement très lente, alors que la taille staturale était prête d'être atteinte, mais que la croissance était plus active à des stades plus précoces, bien que les nouvelles observations ne permettent pas d'apprécier quantitativement celle-ci. On ne peut non plus en déduire que les Énantiornithes différaient significativement, par leur mode de croissance, d'autres oiseaux basaux connus à cet égard. Les nouvelles données suggèrent à tout le moins que les Énantiornithes n'avaient pas nécessairement un régime de croissance très différent de celui des oiseaux modernes de même taille, et, par implication, des caractéristiques thermo-métaboliques profondément différentes de celles de ces derniers. ***Pour citer cet article : O. Cambra-Moo et al., C. R. Palevol 5 (2006)***.

Keywords: Enantiornithines; Histology; Lines of Arrested Growth (LAGs); Osteocyte lacunae

Mots clés : Énantiornithes ; Histologie ; Lignes d'arrêt de croissance (LACs) ; Logettes périostéocytaires

1. Introduction

Bone shaft histology of presumably adult Cretaceous Enantiornithe birds of fairly large body size has been described as composed of non-vascular, lamellar bone tissue with extensive occurrence of 'lines of arrested growth' or LAGs [4,6]. Taken at face value, this bone structure does not differ from that observed in lizards and other ectotherms. Accordingly, authors have suggested that Enantiornithes may have retained a plesiomorphic physiology among birds, not achieving a fully endo-homeothermic physiology. This hypothesis of a late appearance of full endo-homeothermy among birds (and by implication of ectothermy among non-avian dinosaurs) has been widely expressed [2,6,7], although it has been challenged [10,12,14]. In addition, the detailed bone histology of *Confuciusornis*, exemplifying the histological condition in an even more basal clade of Mesozoic birds, suggests high growth rates (and an endothermic physiology) as the plesiomorphic condition in birds [15]. This is also in agreement with the histological condition observed among non-avian Theropods, the outgroup condition [9,13].

Recently, evidence from hatchling (or 'embryonic' = *in ovo*) Enantiornithes [5,20] has shown that during early ontogeny, those birds shared with extant birds (and non-avian dinosaurs [9,13]) a pattern of fast growing, well-vascularized bone tissue, quite distinct from the one observed among adult Enantiornithes, whose bone apparently recorded only the late stages of slow growth (see below).

How and when did the shift from one type of bone tissue to another take place during enantiornithine ontogeny, and what is its functional significance? One possibility would be a very early shift, after hatching, to a slow, protracted growth, punctuated by numerous lines of arrested growth, along a 'reptilian-like' growth pattern, as suggested by Chinsamy et al. [4,6]. Conversely, the high initial growth rate might have been retained for a longer time, allowing a significant percentage of total body size to be reached quickly (in a matter of days, or weeks), as among most extant birds. Recent comparative studies among extant birds have demonstrated that in adults the relative amount of the cortex formed by a compact, non-vascular coating of parallel-fibered bone tissue (the outer circumferential layer, OCL) strongly depends on body size, irrespective of phylogenetic or biological (e.g., altricial vs precocial) parameters [11]. Moreover, depending on the intensity of endosteal resorption (which is usually high in birds because of their thin adult cortex), little evidence of the phase of active growth may remain in the adult cortex, which thus may mainly correspond to the OCL. This is the condition in many small birds, whereas large to very large birds with a more extended period of rapid growth retain more of the related bone tissue types and a relatively narrower OCL in their adult cortex. As a result, in most small birds, little evidence remains in the adult cortex of the early phase of very active growth experienced by young individuals, but such evidence of fast growth would be much more commonly retained in the adult skeleton of large to very large birds [1,15]. The explanation accounts for many comparative observations available for decades (e.g., [8]). In other words, the histology of the thin-walled bones of adult birds may retain only an incomplete (and deceptive) record of their actual growth trajectory, especially among the smaller species.

2. Material

An enantiornithine specimen from Las Hoyas (Lower Cretaceous, Spain) offers new data on such matters (Figs. 1 and 2). Las Hoyas is a valuable Lower Cretaceous *Konservat Lagerstätten* that has provided important specimens of algae, plants and animals. The outcrop is composed entirely of Upper Barremian continental limestone deposits of the La Huerguina Formation. Freshwater, terrestrial and aerial organisms occur together in the same sedimentary horizon [17,18]. Las Hoyas has provided exceptional evidences of Mesozoic birds: initial report on *Iberomesornis romeralli* was followed by description of *Concornis lacustris* and *Eoalulavis hoyasi* [19]. These three aves have been recently placed phylogenetically within Enantiornithes, and *Concornis* and *Eoalulavis* within Euenantiornithes [3,19]. All three specimens are almost complete skeletons. Other isolated bony elements were retrieved at Las Hoyas, such as the isolated pedal skeleton attributed to *I. romeralli* [16,18], and LH21006 a-b, a slab and counterslab with an articulated tibiotarsus and tarsometatarsus. Both elements show the posterior view of a right hindlimb.

Herein we describe LH21006 a-b, a rather poorly preserved specimen with patchy bone preservation and impressions (see Fig. 1), in which some specific anatomical features can nevertheless be recognised. In the specimen the tarsometarsus (**Tmt**) is broken at its distal condylar area. The maximum length of **Tmt** is 22.9 mm. On the other hand, the tibiotarsus (**Tit**) has its proximal end broken and eroded, with a maximum preserved length of 23.5 mm. The skeleton of LH21006 recall *Concornis lacustris* in its proportions (**Tmt** = 22 mm and **Tit** = 35.36 mm), but these elements are smaller in *Iberomesornis* (**Tmt** = 11–14 mm; **Tit** = 20 mm). The equivalent size of LH21006 and *Concornis* suggests that the specimen is an adult individual of about 70 g body mass.

The specimen apparently has a true tibiotarsus, with proximal tarsals fused to the tibia. The tarsometatarsus is slender (straight and long) as in *Concornis* and the unfused metatarsals II and IV are situated in the same plane. They have sub-equal shaft diameters, being thinner than metatarsal III. The central portion of metatarsal III is rather convex and slightly more anterior to the other two. This new avian specimen shows an intercondylar sulcus (character #152 from [3]), an Ornithothoracine feature. The impression of a deep condylar area, divided by an intercondylar groove that is filled by sediment, can be observed on the specimen. No definite apomorphy shared with Enantiornithes can be demonstrated. However, the lack of fusion between metatarsals II to IV, a primitive character otherwise absent in Ornithuromorpha, suggests an enantiornithine affinity. Therefore, the specimen could be phylogenetically placed within Ornithothoraces, but not among Ornithuromorpha, which implies an enantiornithine assignment. This conclusion is strongly supported by the general similarity that the specimen has with *Concornis lacustris*, to which it is tentatively referred here. Given the fully ossified epiphyseal regions and the compact, smooth surface of the bone shafts, the material is presumed to belong to an adult individual.

3. Methods

After careful recording of the selected bone, including measurements, photographs and casting, slab and counter-slab were reunified in their original relative position in order to benefit from the total bone material available on both. The slabs were embedded in a polyester resin according to current practice (e.g., [21]) and allowed to polymerize slowly under controlled temperature. After hardening, excesses of resin and stone were sawed away from the block. The trimmed block was then subserially cut at slow speed with a circular diamond saw (Isomet Buehler LTD Company). Nineteen cross-sections were processed from the tarsometatarsal shafts: they offer a reasonably consistent picture of their structural pattern. In addition, tiny bone splinters from the same material were carefully collected, lined up and embedded together, to allow additional cross sections in more cortical material.

4. Histological description

Casual observation would suggest a primary cortex entirely composed of an OCL, with clear evidence for at least two (and perhaps three) LAGs, and a free marrow cavity surrounded by a well-defined centripetal coating of endosteal bone (Fig. 3). This suggests a structural situation very similar to the one already described in larger Enantiornithes [4–6], including the occurrence of LAGs. However, close observation reveals a more complex situation. The outer cortex is indeed formed of a rather typical parallel-fibered bone, with

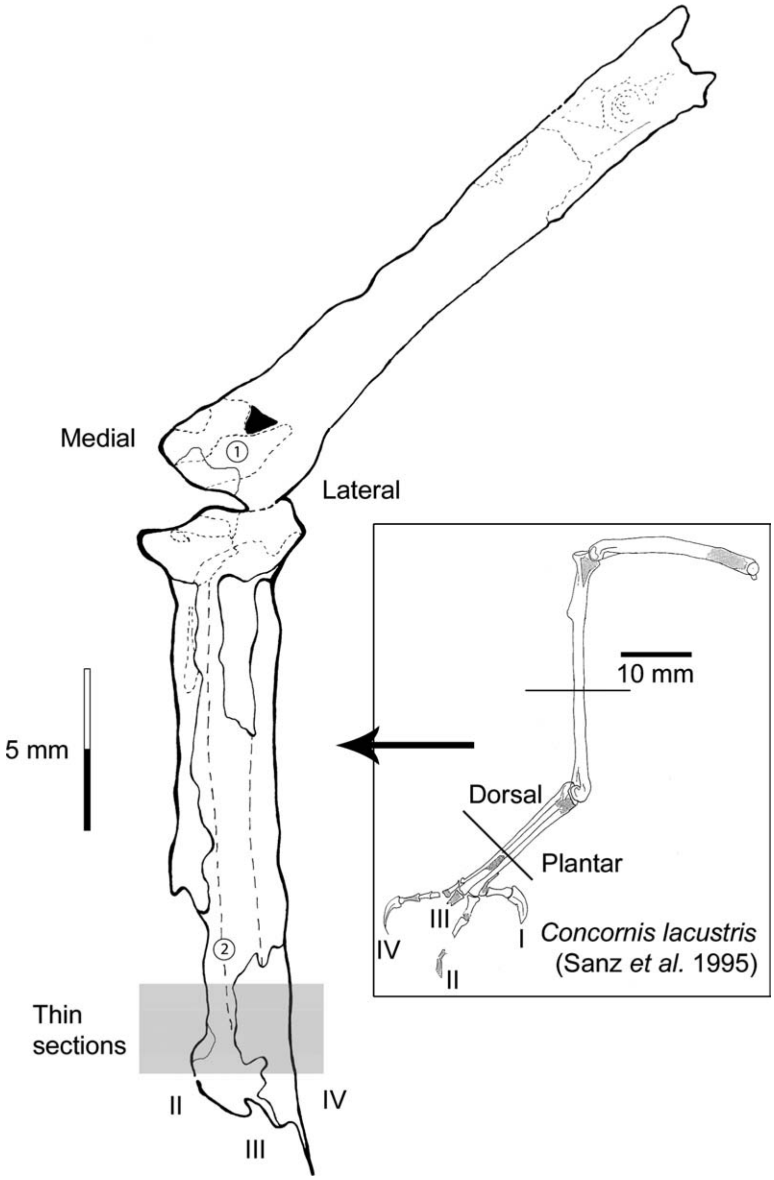

Fig. 1. Posterior view of the right tibiotarsus and tarsometatarsus of avian specimen LH21006a-b cf. *Concornis lacustris* from the Upper Barremian of Las Hoyas (Cuenca, Spain). For comparison *Concornis lacustris* right hindlimb is placed in a box. The two lines drawn on *Concornis* indicate an equivalent area to the one of LH21006. The specimen shares some special similarities with *Concornis*: presence (1) of narrow, deep intercondylar sulcus on tibiotarsus that proximally undercut the condyles (#152 from [3]). Circle 1: filled intercondylar groove on the counter slab. Circle 2: absence (0) of fusion of metatarsal II to IV (#156 from [3]). Compare to Fig. 2.

Fig. 1. Vue postérieure du tibiotarse et du tarsométatarse droits de LH21006a-b, un spécimen avien cf. *Concornis lacustris* du Barrémien supérieur de Las Hoyas (Cuenca, Espagne). On a représenté dans un cadre le membre postérieur droit de *Concornis lacustris* pour comparaison. Sur ce dessin, les deux traits limitent les régions conservées chez LH21006. Ce spécimen présente quelques similitudes particulières avec *Concornis*, soit (1) la présence d'un sulcus intercondylaire étroit et profond au tibiotarse qui sépare proximalement les condyles (caractère 152 de [3]). Cercle 1: le sulcus intercondylaire rempli de sédiment sur la contre-empreinte, cercle 2: absence (0) de fusion des métatarsiens II à IV (caractère 156 de Chiappe [3]). À comparer à la Fig. 2.

sparse flattened osteocytic lacunae and no vascularization (Fig. 4). This structure matches what is observed as forming the OCL in most extant small to tiny birds at somatic maturity [11]. It also agrees with earlier descriptions of presumably adult enantiornithine cortical bone [4,6]. However, the deeper cortex is rather different: it progressively contains a much more plentiful component of osteocyte lacunae with plump, rather than flat shapes (Fig. 4). This region is also permeated by a few vascular canals surrounded by bone lamellae,

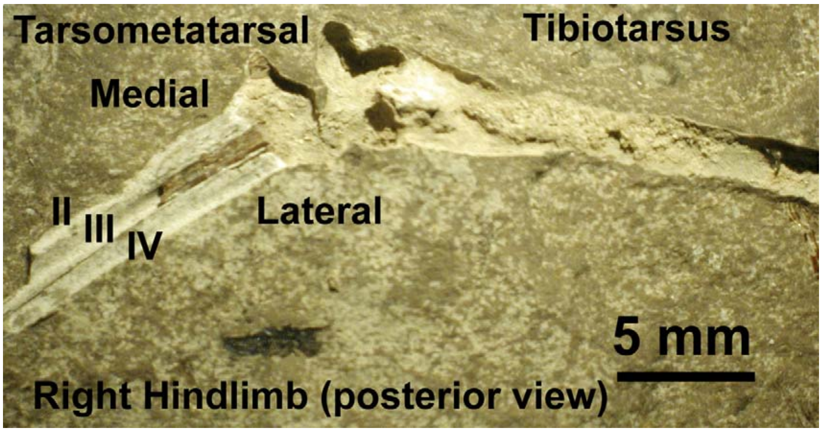

Fig. 2. Photograph of specimen LH21006 (counterslab) showing the intratarsal joint.
Fig. 2. Photo de la contre-empreinte du spécimen LH21006, montrant l'articulation intratarsienne.

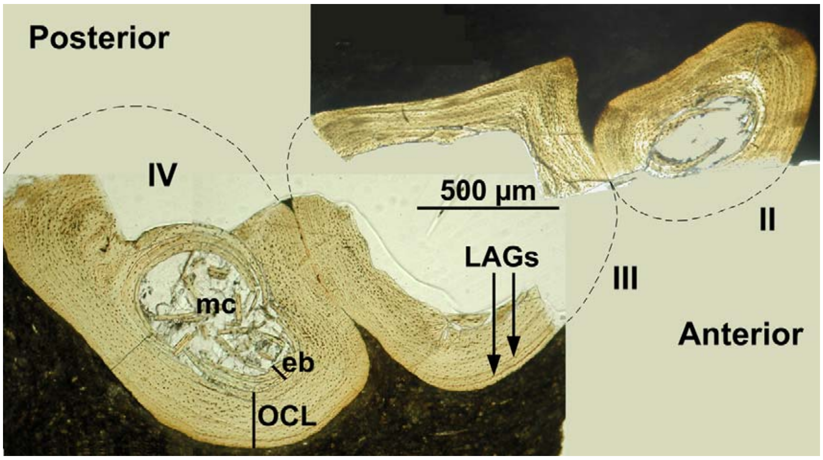

Fig. 3. General view of the three metatarsal shaft cross-sections from slab plus counter-slab. Cortex mostly composed by an OCL showing at least two LAGs and a free marrow cavity surrounded by a centripetal coating of endosteal bone. Abbreviations: eb: endosteal bone; LAGs: lines of arrested growth; mc: medullary cavity; OCL: outer circumferential layer.
Fig. 3. Vue générale de la section transversale diaphysaire des trois métatarsiens à partir du spécimen total (« empreinte » et « contre-empreinte », voir § Méthodes). Le cortex est principalement formé par une couche circonférentielle externe avasculaire (*outer circumferential layer* ou OCL), montrant au moins deux lignes d'arrêt de croissance (LAG) et une cavité médullaire libre entourée d'une couche d'os endostéal à dépôt centripète. Abréviations: eb: os endostéal, LAG: lignes d'arrêt de croissance, mc: cavité médullaire, OCL: couche circonférentielle externe.

giving them an osteonal structure (Fig. 5). Relationships of the osteonal material to the neighbouring primary tissue strongly suggest erosion/reconstruction cycles: hence the osteons would be secondary (Fig. 5). In some sections, it is possible to follow extensions from the endosteal bone tissue into the deep cortex, where they form the secondary osteons (Fig. 6).

5. Discussion

Some histology-independent characters already noted (see § *Material*) suggest an adult or nearly somatically adult condition for the specimen, in agreement with the histological structure of the OCL-like external cortex. Nevertheless, the inner cortex (also labelled as OCL on Figs. 3–6) still records a phase of the bird's ontogeny when radial bone apposition was more active. This phase is represented by the bone tissue vascularized by secondary osteons and much richer in plump-shaped bone cells than the external (slow-growing) cortex. Indeed, extensive comparative considerations among primary bone tissue types suggest this [1,9,13, 14]. This structure represents evidence of the transition from the fast growth phase in hatchlings, as already documented by Chinsamy and Elzanowski [5], to the slow growth phase in adult Enantiornithes [4,6]. Be-

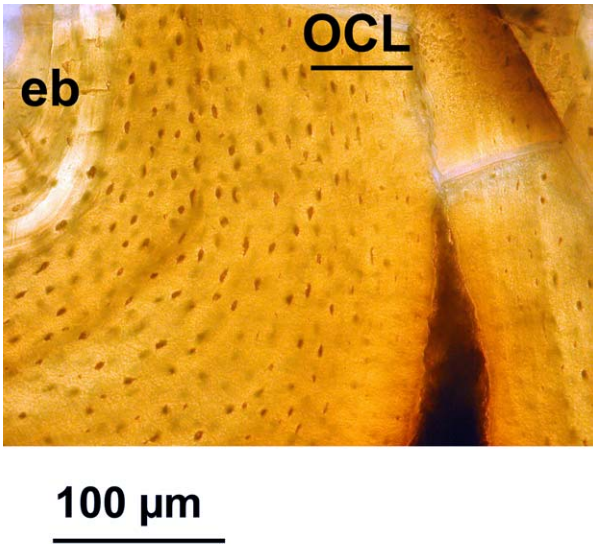

Fig. 4. Close-up of the cortex of two adjacent (unfused) metatarsals. The outer cortex has sparse flattened osteocyte lacunae. In contrast, the deeper cortex contains much more plentiful osteocyte lacunae, with fairly plump, rather than flat shapes. Abbreviations as in Fig. 3.

Fig. 4. Détail du cortex de deux métatarsiens adjacents (non soudés). Le cortex externe contient des logettes périostéocytaires dispersées et aplaties. Le cortex profond contient une plus forte population de logettes périostéocytaires globuleuses. Abréviations: cf. Fig. 3.

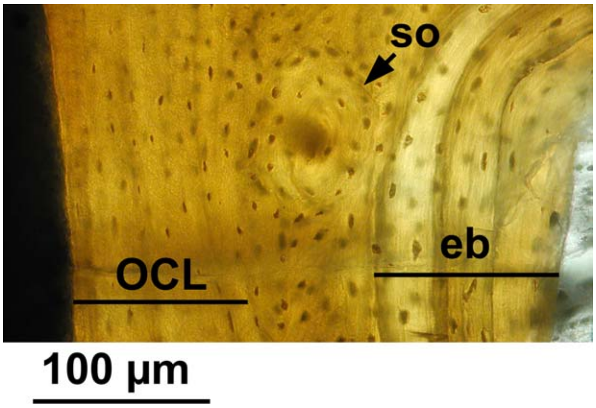

Fig. 5. Vascular canal surrounded by bone lamellae. Relationships of this structure to the neighbouring primary tissue strongly suggest an erosion/reconstruction cycle (secondary osteon). Other abbreviations as in Fig. 3.

Fig. 5. Canaux vasculaires dans le cortex profond, entourés de lamelles osseuses. La relation de ces structures avec le tissu primaire encaissant suggère fortement des cycles d'érosion/reconstruction (so: ostéones secondaires, autres abréviations comme pour la Fig. 3).

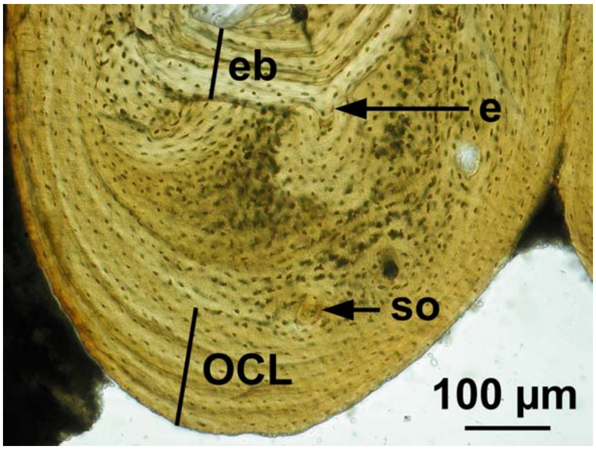

Fig. 6. External extension (e) from the endosteal bone tissue lining the marrow cavity into the deep primary bone tissue of periosteal origin, where they form the secondary osteons. Other abbreviations as in Figs. 3 and 5.

Fig. 6. Extension externe (e) à partir de l'os endostéal bordant la périphérie de la cavité médullaire jusque dans le tissu primaire périostique constituant le cortex profond, où ce matériel osseux constitue les ostéones secondaires. Autres abréviations : cf. Figs. 3 et 5.

cause the structures still retained here in the deep cortex of a presumably sub-adult to adult specimen would record this intermediate phase in growth dynamics, their very presence also suggests that all the earlier phases of growth (not present here because of endosteal bone resorption followed by endosteal centripetal deposition) were also characterized by a fairly high rate, perhaps during a short time, during the juvenile stage of this enantiornithine. In connection with the above, it is noteworthy that Chinsamy et al. [4,6] already noticed and described two populations of osteocyte lacunae in their enantiornithine bones, namely a majority of flattened cell spaces and a few larger plump cell spaces. Apparently these two kinds of cell lacunae were not clearly set apart spatially in the cortex, but rather mixed up in their material. They would likely match the 'plump' and 'flat' cell lacunae that in our material are much better set apart spatially, in the deep and external cortex respectively, and that in our view suggest a progressive change in radial growth dynamics of the bone. Qualitatively, the number of cell spaces per volume unit of tissue in the deep and external parts of the cortex also concurs with this interpretation. The development of a rather extensive amount of finely fibered endosteal bone tissue around the marrow cavity and the occurrence of vascular canals organized as secondary osteons in the deep cortex of those small bones both concur with the anatomical data and occurrence of LAGs, suggesting at least a nearly adult somatic condition for the specimen.

6. Conclusion

Taken at face value, the data reported here suggest that in some small Enantiornithes a high initial growth rate could have been retained after hatching, allowing a significant percentage of total body size to be reached quickly (in a matter of days or weeks), while later growth could have been much slower and protracted, possibly during several years, taking into account the several LAGs and assuming them to be annual (which remains a debatable issue among birds [12]). Nevertheless, the non-vascularized OCL amounts to at least 50% of the cortical thickness, a high relative and absolute value for a bird [11]. It suggests (a) that growth speed could have decreased significantly when the bird had reached only half of its maximal body size (1/8 in body mass), and (b) that compact bone tissue thickness without vascularization could have been higher among Enantiornithes than among extant birds, an issue which deserves further inquiries. Although these conclusions are obviously tentative, they could nevertheless be tested if additional material of a morphologically more juvenile specimen from the same origin ever became available for histological analysis. Currently, very little is known about the growth dynamics of Enantiornithes. They did differ from extant birds but the few bone histological descriptions now available (and the interpretation of the adult bone cortex organization in light of the bird-specific bone growth dynamics and growth trajectories) do not necessarily suggest that Enantiornithes should have had a growth regime quite distinct from extant birds of commensurate body size–nor, by implication, completely different metabolic patterns or regimes, as previously suggested [2,4,6,7].

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