

General Palaeontology (Palaeobiology) / Paléontologie générale

## Time recording in bone microstructures of endothermic animals; functional relationships

Jacques Castanet

*Ostéohistologie comparée, FRE 2696 CNRS–MNHN–Collège de France–université Pierre-et-Marie-Curie,  
case 7077, 4, place Jussieu, 75251 Paris cedex 05, France*

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### Abstract

Because they are mineralised, skeletal tissues can record and preserve indefinitely in their microstructures the expression of various constraints and especially the passage of time. Such traces of time can be either continuous or periodic (growth marks), but when deciphered they offer a powerful tool to reconstruct life history traits and even ecological conditions of time in extant as well as extinct species. Nevertheless, the temporal message ‘printed’ in skeletal tissues can be disturbed or even destroyed by various causes that need to be understood before this ‘biological chronometer’ can be accurately used. **To cite this article: J. Castanet, C. R. Palevol 5 (2006).**

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### Résumé

**L’empreinte du temps dans les microstructures osseuses chez les animaux endothermes ; relations fonctionnelles.** Parce qu’ils sont minéralisés, les tissus squelettiques enregistrent et conservent souvent indéfiniment dans leurs microstructures l’expression des contraintes variées qu’ils subissent au cours de leur croissance, et en particulier l’empreinte du temps. Celle-ci, exprimée sous forme de variations continues, et surtout discontinues (marques de croissance périodiques), constitue, une fois décryptée, un précieux outil d’investigation chronologique, permettant potentiellement de restituer les traits et conditions d’histoire de vie impliquant le temps chez les animaux actuels ou disparus. Cependant, ce message temporel inscrit dans les tissus squelettiques peut être brouillé, voire détruit, par des causes multiples qu’il importe de bien identifier pour bénéficier d’un outil performant. **Pour citer cet article : J. Castanet, C. R. Palevol 5 (2006).**

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*E-mail address:* [castanet@ccr.jussieu.fr](mailto:castanet@ccr.jussieu.fr) (J. Castanet).

## 1. General considerations on bone structures recording time

Because they form the main support structure of the organism, bone architecture (morphology, microanatomy, and microstructure) is often regarded as the result of biomechanical constraints experienced during ontogeny and later life. More generally, bone histomorphology results from macroevolutionary adaptation (phylogenetic aspects) and developmental constraints (ontogenetic aspects), both of which have a genetic basis, modified by reversible influences during the life of an individual (phenotypic plasticity) [38]. Julius Wolff [58] was one of the first to suggest the mechanical determinism of bone microanatomy. This relationship, also documented by d'Arcy Thompson [53] and known as Wolff's law, is now generally accepted [13,14] (see also the principles of 'mechanomorphosis' [56] and of 'symmorphosis' [34]). Phosphocalcitic metabolism also plays a role in bone microstructural organization (e.g., as part of Haversian remodelling), and it can result in various pathologies (e.g. osteoporosis).

Paradoxically even though the various physical and physiological constraints that are involved at all levels of bone organization that have been identified, the expression of time (ontogenetic growth) on bone architecture, especially its microstructures, at various stages of ontogeny remains poorly understood. Nevertheless, this influence of time on bone is of great interest in organismal and populational biology. Because time is involved in many individual life history traits (age, longevity, growth rates, age at maturity), those traits and others related to ecological conditions can be potentially reconstructed from bone organization, both in extant and extinct animals (palaeobiology, palaeoenvironments), because bone microstructures can be preserved over millions of years (see [52] for a recent review).

Thus, the goal of this short synthesis is to improve our understanding of recording bone microstructures. Nevertheless, because of space limitation, we will mainly consider endothermic organisms (especially mammals) because the interpretation of histological structures that may reflect time recording are more controversial in their bones than in those of ectothermic vertebrates.

Two approaches can be sorted out when analyzing the expression of time dimension on bone organization:

- The first considers partly time-dependent bone microstructures and their continuous variations, used as a criterion for time assessment.

- The second is relevant to specific time-dependent bone structures, as a direct expression of time on the skeleton.

### 1.1. Partly time-dependent variations of bone microstructures

It is a truism to say that biological structures change with age. However, bone and teeth, as perennially growing tissues, are unique in that they preserve and retrieve such time-dependent modifications, even after fossilization. Bone histological (microstructural) variations mainly deal with the change of proportion between the numbers of primary and secondary vascular canals (mainly between primary and secondary osteons and their ratio) observed in the compact cortices of bones. These histological partly time-dependent variations were suspected for a long time in human bone [2,3], but, Kerley [26] was the first to propose the practical use of this continuous change in bone microstructures for aging humans. He also took into account modifications of the number of bone lamellae in the external cortex of long bones. Kerley estimated that age could be assessed with a precision of  $\pm 10$  yr in at least 85% of the individuals analysed. Many later authors tested and refined Kerley's method [1,6,16,30,36,51,54,55] (Fig. 1A and B).

Nevertheless, it appears that such histomorphometric characters used to assess the time signals encoded in bone organization are of weak resolution and sometimes even unreliable. As for all morphometric characters (bone size, bone mass, bone welding), these histological variations must be calibrated from a reference model before use. But owing to individual variation, the model has to be built from the population studied, which is circular because it would correspond to the object of the investigation itself! [20]. In practice, very few human (palaeo)populations formed by individuals of known age at death are available to calibrate the method, and this is all the more true for non-human species. Moreover, the time–bone structural correlation greatly weakens after sexual maturity, when growth more or less stops, especially in endothermic organisms. Thus some authors do not hesitate to say that time-age estimation from continuous histological variations “is art, not science” [35].

### 1.2. Specific time-dependent bone microstructures

These are called 'growth marks' (growth rings). They correspond to the histological expression of bio-

logical rhythms recorded by growing skeletal elements (bone and teeth in endothermic vertebrates). Similar time-recording structures can be non-cyclical but linked to a precise biological event, well identified in ontogeny such as hatching in lizards, metamorphosis in amphibians, or possibly weaning in mammals [8]. When they are periodic, bone growth marks are mainly the result of endogenous rhythms, reinforced and synchronized by seasonality [6]. Thus, because they are largely independent of organismal biology, the number of bone growth marks would not be affected by individual or populational variations. Accordingly, no prior sample of reference would be needed for time (age) calculation. Consequently, bone growth marks offer a direct tool to restore many life history traits and conditions of life involving time. This is the basis of the skeletochronological method [6].

With the exception of special kinds of growth marks described in the metaphysis of long bones in children by Harris in 1931 [21] (called Harris's lines) and taken into account in medical issues, the use of growth marks as a direct biological chronometer in endothermic animals begins with the Scheffer's study [50] using marks in dentine of the Northern Fur Seal, *Callorhinus ursinus*. Since that time a true 'explosion' of skeletochronological studies occurred in mammals [28,41]. In this taxon, growth marks are generally recorded from teeth (mainly from cementum), although in many species, marks also appear in the bone cortices [28] and can be used for time assessment [8]. So far more than 60 species of mammals exhibiting bone growth marks can be listed and half of them offer a good correlation between the number of marks and individual age. Surprisingly, only extant mammals are involved in such skeletochronological studies. No study dealing with bone growth cycles recorded in extinct mammalian species has yet been reported, although several archaeological studies using tooth material are currently under way (e.g., [4]). Bone growth marks also exist in birds, extant [27,29,57] (Fig. 1C) and extinct [10–12, 47] (Fig. 1D). Nevertheless, especially in birds, the special morphogenetic trajectory of bone growth (see below) makes practice of skeletochronology a difficult and controversial task [31,33,37]. Moreover, many groups of dinosaurs (considered here as endotherm-like) expressed growth marks in their long bone cortices [44] and recently an upsurge of studies has been attempted from various aspects of their bone microstructures to assess longevity, somatic maturity, growth patterns, and metabolism in those fascinating animals [9, 15,17–19,22–24,46–49]. Growth marks are also at the

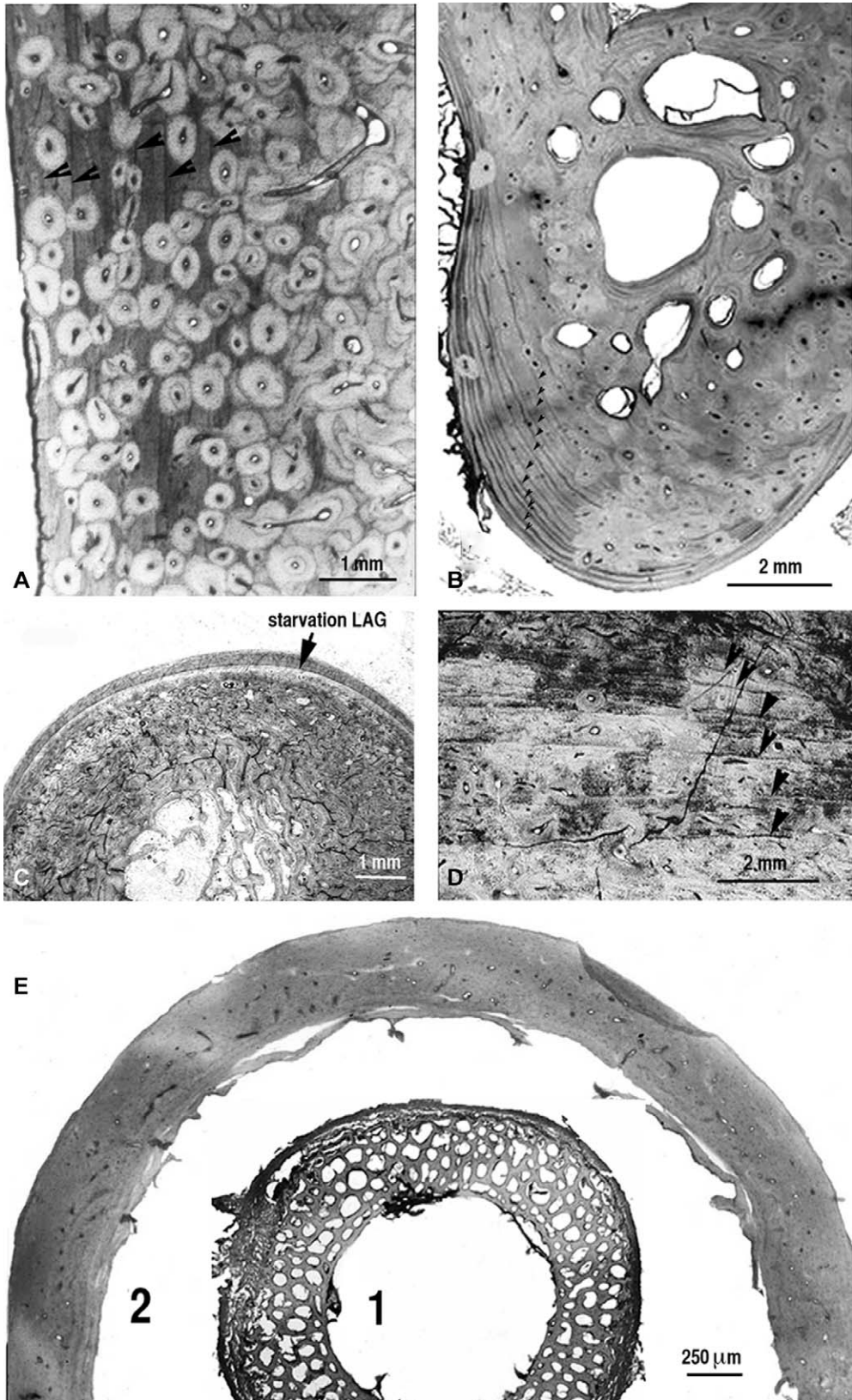
heart of biological inferences regarding 'Therapsids' or 'mammal-like reptiles', the 'ancestors' of mammals [43].

In endothermic animals, bone growth marks are similar to those of ectotherms. Their histological features and spatial organization directly result from local and general rates and rhythms of bone growth. Most often in mammals, birds and dinosaurs, thin Lines of Arrested Growth (LAGs) alternate with wide bony layers sometime called 'zones' *sensu* Peabody [40] linked to active periods of osteogenesis. Annuli are thin bone layers, mostly made of a few lamellae, deposited in place of LAGs when osteogenesis is slow but not stopped. In general, one LAG (or annulus) plus one zone make an annual growth cycle. LAGs appear as strongly chromophilic, birefringent and slightly hypermineralized structures. Zones can be made up of all the categories of avascular and vascularized bone tissue matrix. Hence, classically growth marks are typical of the lamellar-zonal category [45], but they also can be expressed in the fibrolamellar complex. Such an arrangement, called the fibrolamellar-zonal complex [7], can be observed in many dinosaur bones [15,17–19,22–24,39, 48] and in non-mammalian Therapsids [43]. More attention need to be paid to that bone category in mammals where primary vascularized bone can be well preserved in adult skeletons, as for instance among artiodactyls.

Despite hopeful expectations, the time signal expressed by bone growth marks is not always easy to assess. Clearly, the design of growth marks depends on the modulations of the external rhythms due to the specific biology of the organism and the organ that records them. Thus deciphering the causes of the diversity of the expression of growth marks, of their removal or even of their absence, it is essential in practice, to use the functional relationships between time and bone microstructural organization. Most of these causes have been analyzed already [6]. Here I will emphasize some of them, dealing mainly with endothermic organisms.

### 1.2.1. Shortened post-hatching osteogenesis

If we accept the annual periodicity of bone growth marks, the clear consequence is that individuals completing their growth in one year or less could have at the maximum one LAG (if they hatch some months before the resting period for instance). Also, depending on the species and the bone studied, when osteogenesis stops, whatever the longevity, no more growth marks will be recorded [5] (Fig. 1E2). Thus many species of



birds and mammals, especially the smallest ones that reach somatic maturity in a year or less with no further bone deposition, would clearly have no growth marks. In such species the whole cortex of long bones only corresponds at most to one year of bone deposition. Conversely, if osteogenesis continues beyond a year, even only locally and at a low growth rate, LAGs can be recorded. They can form the ‘Outer Circumferential Layer’ (see [42] for other names of this OCL). Moreover, owing to allochronic bone growth processes, the various bones of the same individual will not display the same number of LAGs [5,23]. Recent experimental data exemplified the bone growth dynamic and the design of bone growth marks in the small primate *Microcebus murinus* [8]. Individuals of that species live 7–8 years on the average and are able to reach 11 years. Sexual maturity is reached between 6–8 months. At this age, most of the cortices, made of primary vascular bone tissue, are already laid down and never show LAGs. Beyond this, a thin outer layer of non-vascular bone including annual LAGs is present. Nevertheless, the maximum LAG number is 5–6 (exceptionally 7) even when the individuals studied are known to be 8, 9 and 11 years old. It clearly means that osteogenesis definitely stops after 5–6 (exceptionally 7) years in this species. Thus the number of LAGs only gives a minimum age (a minimum longevity). This possible limitation of the method occurs in many species of tetrapods

[5] and must be taken into account in any skeletochronological study [19,22].

### 1.2.2. Bone morphogenesis and bone remodelling

Two processes achieve the transformation of bone morphology associated with bone growth during ontogeny: differential growth rate/drift and bone remodelling. Differential growth does not remove growth marks. It can only change their spatial organization, or prevent their deposition (see above). Nevertheless, at the bone periphery when osteogenesis locally stops before starting again, rest lines can appear. Histologically speaking, these lines are similar to annual LAGs, but without any obvious periodicity. They are often manifested locally as split and/or double LAGs, including supplementary LAGs [6,28]. These lines can cause difficulties in applied skeletochronology, because they can be confused with cyclical (yearly) LAGs and even with lamellae if the outer circumferential layer is made of a lamellar matrix.

On the other hand, bone remodelling, a resorption–reconstruction process that changes primary to secondary bone, does remove growth marks. First, especially in birds and mammals, endosteal resorption can destroy a broad part of the inner cortex and the LAGs it can contain. In that situation, time estimation –for instance the individual age– would be underestimated. However, in many cases a special technique allows us to retro-

Fig. 1. (A) *Cervus elaphus*. Adult of unknown age. Cross section from the mandible at the M2 level, stained by Ehrlich’s haematoxylin. Primary bone with LAGs (arrows) is locally present. Secondary osteons and dense Haversian tissue on the right. Kerley’s method (cf. text) mainly contrasts the density of secondary osteons to the density of primary osteons for individual age assessment. (B) *Macaca arctoides*. A 15-year-old male. Cross-section from the mandible at the M3 level, stained by Ehrlich’s haematoxylin. Primary bone, locally remodelled, displays approximately 12 LAGs (arrows). (C) *Aptenodytes patagonicus* (King penguin). Juvenile about one year old. Unstained cross-section from the femoral diaphysis. A clear LAG close to the bone periphery obviously appears linked to the loss of weight during winter starvation (May to September), which begins about three months after hatching (pers. commun. J.-P. Robin). (D) *Dinornis* sp. (Fossil bird– Moa – from New Zealand). Unstained cross-section from femoral diaphysis. Primary bone with low remodelling displays clear LAGs (arrows). Picture: A. de Ricqlès and K. Padian. (E) *Columba livia*. Cross-sections from femoral diaphysis stained by Ehrlich’s haematoxylin. (1) Juvenile, a few weeks old. Bone cortex with many enlarged vascular cavities. (2) Adult with compact cortex. Few primary blood vessels, weakly anastomosed, mainly longitudinally oriented and located in the inner half of the bone. Owing to strong endosteal resorption, all the juvenile bone (1) has been removed. Thus, adult bone only displays a truncated picture of bone tissue organisation that does not necessarily reveal bone organization from the different life stages.

Fig. 1. (A) *Cervus elaphus*. Adulte d’âge inconnu. Coupe transversale dans la mandibule au niveau de la M2. Coloration par l’hématoxyline d’Ehrlich. De l’os primaire contenant des LACs (flèches) reste localement visible. Des ostéones secondaires forment un tissu haversien dense dans l’os le plus anciennement déposé (droite). C’est sur la densité en ostéones secondaires (complets et fragments) relativement à celle des canaux vasculaires simples et ostéones primaires qu’est fondée la méthode de Kerley pour estimer l’âge individuel (cf. texte). (B) *Macaca arctoides*. Mâle âgé de 15 ans. Coupe transversale de la mandibule au niveau de la M3. Coloration par l’hématoxyline d’Ehrlich. L’os primaire, non entièrement remanié, montre environ une douzaine de LACs (flèches). (C) *Aptenodytes patagonicus* (Manchot royal). Juvénile âgé de près d’un an. Coupe transversale dans la diaphyse fémorale. Lame mince non colorée. Une LAC nette près de la périphérie osseuse témoigne à l’évidence de l’amaigrissement consécutif au jeûne hivernal (mai à septembre), qui débute environ trois mois après l’éclosion (commun. pers. J.-P. Robin). (D) *Dinornis* sp. (oiseau fossile – Moa – de Nouvelle-Zélande). Coupe transversale dans la diaphyse fémorale. Lame mince non colorée. L’os primaire vascularisé, mais encore peu remanié, montre des LACs nettes (flèches), (photo A. de Ricqlès, K. Padian). (E) *Columba livia* (Pigeon biset). Coupes transversales au niveau de la diaphyse fémorale. Coloration par l’hématoxyline d’Ehrlich. (1) Juvénile, quelques semaines après l’éclosion. La corticale comporte de nombreuses et vastes lacunes vasculaires. (2) Adulte, avec une corticale compacte. Vascularisation réduite formée d’ostéones primaires peu anastomosés, majoritairement longitudinaux. Ces derniers sont surtout concentrés dans la moitié interne de l’os. Par suite d’une résorption endostale intense, tout l’os juvénile (1) a disparu. L’os adulte fournit donc une image tronquée, qui n’est pas nécessairement révélatrice de l’organisation osseuse construite aux différentes étapes de la vie.

calculate the number of LAGs removed so far [22,32]. Second, inside the cortex, when vascularized, bone remodelling leads to the Haversian system removing growth marks previously deposited in the primary bone tissue. Also, growth marks can be removed at the bone periphery by lateral bone drift, although this phenomenon is not very frequent or extensive.

Thus, after remodelling takes place, the time structures recorded in bone tissue are disturbed or even completely removed. Assessing time is difficult if not impossible in such cases. Nevertheless that does not affect the ability of bone tissues to record time.

## 2. Concluding remarks

Finally, although it may seem paradoxical and sometimes even not acknowledged [25], the occurrence of growth marks is not limited to ectothermic animals. They also appear as a general phenomenon in highly derived ('evolved') endothermic organisms, even though periodic growth is regarded as a plesiomorphic condition of animal life [46]. Their absence in endothermic species can be due to primary causes, such a short-bone growth in thickness (around one year), continuous growth or a loss of developmental plasticity, as suggested by Ray et al. [43]. It also can be the result of secondary phenomena linked to bone remodelling, bone morphogenesis, and more generally to the specific dynamics and ontogenetic strategies of the individual bone and general body growth (i.e. the growth curve profile), which are largely species-specific. Owing to (i) the duration of the rapid growth phase during juvenile stages, (ii) the total growth duration, and (iii) the bone morphogenetic processes (remodelling, differential growth rates, drift), the bone tissues observed at a given stage of ontogenesis, for instance in adult individuals, can be only a part, i.e. a 'window', of the whole bone tissue diversity potentially built during ontogenesis (Fig. 1E1 and 2). In other words, at a given age, the actual bone microstructures only retrieve to the observer a truncated picture of the individual's life history, with or without growth marks. Hence one must take care when extrapolating from it and providing 'definite' conclusions on issues such as, say, the thermo-metabolic physiology of the taxon studied. Longitudinal (ontogenetic) survey studies are needed as far as possible [24] to circumvent such problems of variability and the bias they may introduce in interpretations.

On the other hand, it is now clear that the presence of growth marks (LAGs) in bone microstructures only

reveals periodic interruptions of bone growth (or of local osteogenesis) regardless of the average growth rate – low or high – or the thermal metabolism of the organism. In other words, endothermic animals can express periodic bone growth, as do ectothermic ones. Of course, everything else being equal, when growth is periodically interrupted, the overall individual growth rate will be lower, in comparison to species with continuous growth. Nevertheless, in both cases, instantaneous growth rates can be very high, and, in fact, a given organism with its osteogenesis periodically interrupted could grow almost as fast as an organism with sustained low or high osteogenesis, although growth 'strategies' would be different. Such an hypothesis recently proposed for extinct endotherm-like tetrapods viewed as fast growing organisms with high metabolism but with temporary annual decrease and/or cessation of growth [39,43] is perfectly tenable, according to the presence of growth marks (LAGs) inside the fibro-lamellar matrix of their bones.

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## References

- [1] J. Ahlquist, O. Damsten, A modification of Kerley's method for the microscopic determination of age in human bones, *J. Forensic Sci.* 14 (1969) 205–217.
- [2] R. Amprino, A. Bairati, Processi di ricostruzione e di riassorbimento nella sostanza compatta della ossa dell'uomo, *Z. Zellforsch. Mikrosk. Anat.* 24 (1936) 439–511.
- [3] V. Balthazard, L. Lebrun, Les canaux de Havers aux différents âges, *Ann. Hyg. Publ. Méd. Lég.* XV (1911) 144–152.
- [4] A. Burke, J. Castanet, Histological observations of cementum growth in horse teeth and their application to archaeology, *J. Archaeol. Sci.* 22 (1995) 479–493.
- [5] J. Castanet, D.G. Newman, H. Saint-Girons, Skeletochronological data on the growth, age and population structure of the tuatara, *Sphenodon punctatus*, on Stephens and Lady Alice Islands, New Zealand, *Herpetology* 44 (1988) 25–37.
- [6] J. Castanet, H. Francillon-Vieillot, F.J. Meunier, A. de Ricqlès, in: B. .K. Hall (Ed.), *Bone and individual aging*, Bone, CRC Press, Boca Raton, Ann Arbor, Boston, London, 1993, pp. 245–283.
- [7] J. Castanet, J. Cubo, E. de Margerie, Signification de l'histodiversité osseuse : Le message de l'os, in: *Biosystema*, n° 19, *Systématique et Paléontologie*, 2001, pp. 133–147.

- [8] J. Castanet, S. Croci, M. Perret, J. Cubo, E. de Margerie, Lines of arrested growth in bone and age estimation in a small primate: *Microcebus murinus*, *J. Zool.* 263 (2004) 31–39.
- [9] A. Chinsamy, Image analysis and physiological implications of the vascularisation of femora in Archosaurs, *Modern Geol.* 19 (1993) 101–108.
- [10] A. Chinsamy, A.J. Elzanowski, Evolution of growth pattern in birds, *Nature* 412 (2001) 402–403.
- [11] A. Chinsamy, L.M. Chiappe, P. Dodson, Growth rings in Mesozoic birds, *Nature* (1994) 368.
- [12] A. Chinsamy, L.M. Chiappe, P. Dodson, Mesozoic avian bone microstructure: physiological implications, *Paleobiology* 21 (1995) 561–574.
- [13] J.D. Currey, The structure of Bone, in: J.D. Currey (Ed.), *The mechanical adaptations of bones*, Princeton University Press, Princeton, NJ, USA, 1984.
- [14] J.D. Currey, *Bones. Structure and mechanics*, Princeton University Press, Princeton and Oxford, 2002.
- [15] K.A. Curry, Ontogenetic histology of *Apatosaurus* (Dinosauria: Sauropoda): new insights on growth rates and longevity, *J. Vertebr. Paleontol.* 19 (1999) 654–665.
- [16] M.F. Ericksen, Histologic estimation of age at death using the anterior cortex of the femur, *Am. J. Phys. Anthropol.* 84 (1991) 171–179.
- [17] G.M. Erickson, T.A. Tumanova, Growth curve of *Psittacosaurus mongoliensis* Osborn (Ceratopsia: Psittacosauridae) inferred from long bone histology, *Zool. J. Linn. Soc.* 130 (2000) 551–566.
- [18] G.M. Erickson, K.A. Curry, K.A.S.A. Yerby, Dinosaurian growth patterns and rapid avian growth rates, *Nature* 412 (2001) 429–432.
- [19] G.M. Erickson, P.J. Makovicky, P.J. Currie, M.A. Norell, S.A. Yerby, C.A. Brochu, Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs, *Nature* 430 (2004) 772–775.
- [20] T.R. Halliday, P.A. Verrel, Body size and age in Amphibians and Reptiles, *J. Herpetol.* 22 (1988) 253–265.
- [21] H.A. Harris, Lines of arrested growth in long bones in childhood, *Br. J. Radiol.* 4 (1931) 561–640.
- [22] J.R. Horner, K. Padian, Age and growth dynamics of *Tyrannosaurus rex*, *Proc. R. Soc. Lond. B. Biol. Sci.* 271 (2004) 1875–1880.
- [23] J.R. Horner, A. de Ricqlès, K. Padian, Variation in dinosaur skeletochronology indicators: implications for age assessment and physiology, *Paleobiology* 25 (1999) 295–304.
- [24] J.R. Horner, A. de Ricqlès, K. Padian, Long bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements, *J. Vertebr. Paleontol.* 20 (2000) 115–120.
- [25] K.V. Kardong, *An Introduction to Biological Evolution*, McGraw Hill, Higher Education, 2005.
- [26] E.R. Kerley, The microscopic determination of age in human bone, *Am. J. Zool. Anthropol.* 23 (1965) 149–163.
- [27] G.A. Klevezal, Determination of age in birds by layers in the periosteal bone, *Zool. Zh. LVII* (1972) 917–922.
- [28] G.A. Klevezal, Recording structures of mammals. Determination of age and reconstruction of life history, A. A. Balkema, Rotterdam, Brookfield, 1996.
- [29] N.I. Klomp, R.W. Furness, A technique which may allow accurate determination of the age of adult birds, *Ibis* 134 (1992) 245–249.
- [30] V. Kurzawski, Mise au point sur les méthodes de détermination de l'âge par voie histologique osseuse, *Bull. Mem. Soc. Anthropol. Paris* 10 (1983) 413–424.
- [31] M. Lapena, M. Paton, F. Hernandez, F. de Lope, Z. Juarranz, Two examples showing contradictory results by using skeletochronology in birds, *Archeofauna* 2 (1993) 175–179.
- [32] R. Leclair, J. Castanet, A skeletochronological assesment of age and growth in the frog *Rana pipiens* Schreber (Amphibia, Anura) from southwestern Quebec, *Copeia* 2 (1987) 361–369.
- [33] J.C. Lewis, Periosteal layers do not indicate ages of sandhill cranes, *J. Wildl. Manage.* 43 (1979) 269–271.
- [34] D. Lieberman, A.W. Crompton, Responses of bone to stress, in: E. Weibel, C.R. Taylor, L. Bolis (Eds.), *Principles of Biological Design: The Optimization and Symmorphosis Debate*, Cambridge University Press, Cambridge, 1998, pp. 78–86.
- [35] W.R. Maples, The practical application of age estimation techniques, in: M.Y. Iscan (Ed.), *Age Markers in the Human Skeleton*, Charles C. Thomas, Springfield, IL, 1989, pp. 319–324.
- [36] D.M. Mulhern, D.H. Ubelaker, Histological examination of bone development in juveniles chimpanzees, *Am. J. Phys. Anthropol.* 122 (2003) 127–133.
- [37] R.C. Nelson, T.A. Bookhout, Counts of periosteal layers invalid for aging Canada geese, *J. Wildl. Manage.* 44 (1980) 518–521.
- [38] K. Padian, A. de Ricqlès, J.R. Horner, Dinosaurian growth and bird origins, *Nature* 412 (2001) 405–408.
- [39] K. Padian, J.R. Horner, J.R.A. de Ricqlès, Growth in small dinosaurs and pterosaurs: the evolution of archosaurian growth strategies, *J. Vertebr. Paleontol.* 24 (2004) 555–571.
- [40] F.E. Peabody, Annual growth zones in living fossil vertebrates, *J. Morphol.* 108 (1961) 11–62.
- [41] W.F. Perrin, A.C. Myrick, Age determination of toothed whales and sirenians, in: W.F. Perrin, A.C. Myrick (Eds.), *Int. Whaling Comm., Rep. of the I.W.C.*, Cambridge, 1980 (Special issue 3, La Jolla, CA, USA, 1978).
- [42] F. Ponton, A. Elzanowski, J. Castanet, A. Chinsamy, E. de Margerie, A. de Ricqlès, J. Cubo, Variation of the outer circumferential layer in the limb bones of birds, *Acta Ornithol.* 39 (2004) 137–140.
- [43] S. Ray, J. Botha, A. Chinsamy, Bone histology and growth patterns of some nonmammalian therapsids, *J. Vertebr. Paleontol.* 24 (2004) 634–648.
- [44] R.E.H. Reid, Zonal 'growth rings' in dinosaurs, *Modern Geol.* 15 (1990) 19–48.
- [45] A. de Ricqlès, Recherches paléohistologiques sur les os longs des tétrapodes. VII. Sur la classification, la signification fonctionnelle et l'histoire des tissus osseux des tétrapodes. Partie 1, *Ann. Paléontol. (Vertebr.)* 61 (1975) 51–129.
- [46] A. de Ricqlès, L'origine dinosaurienne des oiseaux et de l'endothermie avienne : les arguments histologiques, *Annee Biol.* 39 (2000) 69–100.
- [47] A. de Ricqlès, K. Padian, J.R. Horner, The bone histology of basal birds in phylogenetic and ontogenetic perspectives, in: J. Gauthier, L.F. Gall (Eds.), *New Perspectives on the Origin and Early Evolution of Birds: Proc. Int. Symp. in Honor of John H. Ostrom*, Peabody Mus. Nat. Hist., Yale University, New Haven, 2001, pp. 411–426.

- [48] P.M. Sander, Life history of *Tendagurus* sauropods as inferred from long bone histology, *Mitt. Mus. nat. kd. Berl. Geowis. Reihe 2* (1999) 103–112.
- [49] P.M. Sander, N. Klein, E. Buffetaut, G. Cuny, V. Suteethorn, J. Le Lœuff, Adaptive radiation in sauropod dinosaurs: bone histology indicates rapid evolution of giant body size through acceleration, *Organisms Diversity Evol.* 4 (2004) 165–173.
- [50] V.B. Scheffer, Growth layers on the teeth of Pinnipedia as an indicator of age, *Science* 112 (1950) 309–311.
- [51] I.J. Singh, D.L. Gunberg, Estimation of age at death in human males from quantitative histology of bone fragments, *Am. J. Phys. Anthropol.* 33 (1970) 373–382.
- [52] E. Stokstad, Dinosaurs under the knife, *Science* 306 (2004) 962–965.
- [53] W. D’Arcy, Thompson, *On Growth and Form*, Cambridge University Press, 1917 and 1948.
- [54] D.D. Thompson, The core technique in the determination of age at death of skeleton, *J. Forensic Sci.* 24 (1979) 902–915.
- [55] D.D. Thompson, Age changes on bone mineralization cortical thickness and Haversian canal area, *Calcif. Tissue Int.* 31 (1980) 5–12.
- [56] M.C.H. Van der Meulen, G.S. Beaupre, D.R. Carter, Mechanobiologic influences in long bone cross-sectional growth, *Bone* 14 (1993) 635–642.
- [57] R.W.M. Van Soest, W.L. Van Utrecht, The layered structure of bones of birds as a possible indication of age, *Bijdragen tot de Dierkunde* 41 (1971) 61–66.
- [58] J.D. Wolff, *Das Gesetz der Transformation der Knochen*. Hirschwald, Berlin, 1892 (English translation by P. Maquet, R. Furlong, *The law of bone remodeling*, Springer Verlag, Berlin, New York, 1986).