



General palaeontology, systematics and evolution

Vertebrate palaeohistology: Past and future[☆]

Paléohistologie des vertébrés : passé et futur

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ABSTRACT

Vertebrate palaeohistology has been considered for a long time as a modest subdivision of Palaeontology. Starting in the 1930s and 1940s, comparative bone tissue histology and palaeohistology progressively demonstrated the multiple correlations between bone tissue distribution and numerous biological variables, such as ontogenetic origin, growth, size, shape, biomechanics, physiology, and ecology. During the last three decades, Palaeohistology has focussed on deciphering the numerous, complex causes explaining the patterns and processes of Vertebrate evolution. Palaeohistology is a powerful tool, in connection with Biology, for the reconstruction of fossil Vertebrates as living organisms.

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RÉSUMÉ

La paléohistologie des Vertébrés a été longtemps considérée comme une sous-discipline modeste de la Paléontologie. Mais à partir des années 1930 et 1940, elle a peu à peu permis de démontrer les corrélations entre la typologie et la variabilité du tissu osseux et de nombreux facteurs biologiques tels que l'origine ontogénétique, la croissance, la taille, la forme, la biomécanique, la physiologie et l'écologie. Depuis les trois dernières décennies, la Paléohistologie s'est surtout employée à décrypter les causalités complexes et multifactorielles, à l'œuvre dans les « patterns » et les mécanismes de l'évolution des Vertébrés. Elle apparaît actuellement comme un outil de choix, en liaison avec la biologie, pour la reconstruction des Vertébrés fossiles en tant qu'organismes vivants.

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La paléohistologie des vertébrés est demeurée pendant longtemps une sous-discipline modeste et quelque peu ésotérique de la Paléontologie. Son intérêt pratique pour la Paléontologie a d'abord été reconnu dans le fait que le squelette dermique des vertébrés « inférieurs » montre des caractères tissulaires diagnostiques. Cela permet donc

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d'identifier des fragments comme appartenant aux nombreux et divers groupes de vertébrés sans mâchoires et de gnathostomes du Paléozoïque. Une orientation semblable des recherches, visant à diagnostiquer des restes de tétrapodes à partir de la diversité de leurs tissus squelettiques a aussi été tentée depuis longtemps. En dépit des résultats douteux et souvent trompeurs de cette approche en ce qui concerne les tétrapodes, cet « agenda » pour la recherche demeure d'actualité, en se fondant désormais sur l'idée que tout état de caractère du phénotype et génétiquement déterminé, devrait être porteur d'un « signal phylogénétique ».

À partir des années trente et quarante du vingtième siècle, une autre approche de l'interprétation de l'histologie osseuse comparative et de la paléohistologie a été de s'intéresser aux corrélations structuro-fonctionnelles du tissu osseux et à leurs significations pour rendre compte de sa variabilité et de sa diversité, plutôt qu'aux explications pointant la situation systématique ou la phylogénie. Cette approche s'est révélée féconde en permettant de démontrer les corrélations entre la typologie du tissu osseux et de nombreuses variables biologiques telles que l'origine ontogénique, la croissance, la taille, la forme, la biomécanique, la physiologie et l'écologie.

Au cours des trois dernières décennies, ces interprétations fonctionnelles de la diversité du tissu osseux des organismes actuels ont été de plus en plus appliquées à un corpus grandissant de données paléohistologiques, fournissant de nombreuses inférences paléobiologiques intéressantes. Les résultats récents ont trait aux différentes « stratégies » des tétrapodes s'adaptant secondairement à la vie en milieu aquatiques ou marins, aux « traits d'histoire de vie » et à la physiologie des dinosaures et des ptérosaures, à l'apparition de divers caractères fonctionnels des mammifères, etc.

La paléohistologie a été fondamentale pour mettre l'accent sur les causalités complexes, multifactorielles, à la base des « patterns » et des mécanismes de l'évolution des vertébrés, et a développé de nouvelles méthodes d'analyse de l'influence et de l'interaction de divers facteurs causaux à la base de la diversité et de la variabilité de l'os en tant que tissu.

La paléohistologie constitue aujourd'hui un outil puissant pour reconstituer les vertébrés fossiles en tant qu'organismes vivants et devient une approche de plus en plus pratiquée par les chercheurs en évolution des vertébrés les plus orientés vers la paléobiologie. La paléohistologie ne peut être séparée de très nombreux domaines de la biologie expérimentale ou comparative des vertébrés vivants actuels et s'affirme ainsi comme un domaine transdisciplinaire réactif, où des coopérations entre paléobiologistes et biologistes de l'Actuel permettent le progrès de la biologie évolutionniste dans son ensemble.

1. Early palaeohistology, early vertebrates, new developments

In recent years, anatomical descriptions of new important fossil vertebrates have been increasingly complemented by more or less detailed histological descriptions (e.g., Nesbitt et al., 2009). This trend suggests that it

may be a good time to review the utility of histological knowledge of bone (and other hard tissues) for vertebrate palaeontology, and more generally, its importance for our understanding of vertebrate evolution.

For a long time, the pioneers of palaeohistology were those rare specialists of the so-called “lower vertebrates”, and specifically of the numerous clades of mostly Palaeozoic jawless and early gnathostome aquatic vertebrates (Janvier, 1996). The names of Walter Gross (e.g., 1934, 1935) and of Tor Ørvig (e.g., 1951) come immediately to mind for the first half of the twentieth century, but those major contributors were following a research tradition that can be traced back through personages such as Goodrich (e.g., 1913) and Williamson (e.g., 1849) to Owen (1840–1845) and Agassiz (1833–1844). In early Heterostracans, Osteostracans, Chondrichthyans, Placoderms, Acanthodians, Sarcopterygians and Actinopterygians, specialized dental and bony hard tissues (or particular associations of them) in the dermal skeleton are specific to those varied systematic groups. Therefore, it is not surprising that palaeohistology first developed in this domain: it offered diagnostic characters, useful for recognizing and sorting out fossils in taxonomic contexts, irrespective of any palaeobiological implications (e.g., Janvier, 1996; Ricqlès et al., 2004).

Fundamental biological issues are now linked to palaeohistological studies of early vertebrates. These include the evolution of the interactions of neural crest cells with other tissues, the genetic control of the regionalization and differentiation of skeletal tissues, and the early origins and localization of endoskeletal versus dermal skeletal tissues (e.g., Delgado et al., 2001; Donoghue and Sansom, 2002; Sire et al., 2009; Smith and Coates, 1998; Zimmer, 2000). This “early” or “lower” vertebrate palaeohistology is thriving today, because there is an ever-increasing need for expertise in the histology of the numerous clades of Early Palaeozoic vertebrates, put in modern phylogenetic perspective (Janvier, 1996).

A good example of the importance of palaeohistological data to this field of research is the current controversy on the interpretation of the hard tissues of Conodonts, whether one admits or not their homology with those of vertebrates (e.g., Blicek et al., 2010; Donoghue, 2001; Kemp, 2002; Schultze, 1996).

Other evolutionary developments among more recent “lower vertebrate” clades offer equally fascinating problems for palaeohistology. For instance, the evolution of the dermal skeleton of Actinopterygians, which can be continuously followed from the Early Devonian ganoine-bearing thick scales to the current tremendous diversity of teleost elasmoid scales, raises interesting questions about the evolution of epidermal-dermal interactions (e.g., Meunier, 1981; Sire et al., 2009).

Among tetrapods, beginning in the Upper Devonian, the apparent disappearance of any dental tissues as components of the extraoral dermal skeleton restricted comparative palaeohistology either to the study of teeth themselves, or to the study of bony and cartilaginous tissues. This evolutionary trend started much earlier, because the Frasnian tetrapodomorph *Eusthenopteron* lacks dentine and enamel/enameloid in its dermal scales (Zylberberg

et al., 2010). Because the last common ancestor of *Eusthenopteron* and stegocephalians lived in the Middle Devonian (Laurin et al., 2007, Fig. 1), the loss of dentine and enamel in tetrapodomorphs may hark back that far as well. Nevertheless, the issue of dermal-epidermal interactions and even the occurrence of non-bony hard tissues in the osteoderms of tetrapods remain active objects of study (Vickaryous and Sire, 2009).

The original purpose of palaeohistology was to discover diagnostic characters in the bony tissues of tetrapods that could be used to sort out fossil fragments and classify them correctly, which had been more or less successfully done for early vertebrates (see above). Such inquiries began early, by the middle of the 19th century, with investigators such as Queckett (1849), and later Gervais (see Ricqlès et al., 2009) and Kiprijanoff (1881–1883). However, it slowly became apparent that bone histological characters did not hold great interest for systematics (e.g., Enlow, 1963; Ricqlès et al., 2004). Nevertheless, it was the naïve incentive to discover histological characters “diagnostic” of the synapsid (mammalian) lineage that made me start my own palaeohistological works during the 1960s, a hope that vanished quickly (Ricqlès, 1975–1978). Nevertheless, new research programs continue to try to extract systematic criteria from bone tissue (e.g., Cuijpers, 2006). This is theoretically sensible because, like any intrinsic character of the semaphoront, bone tissue should convey a “phylogenetic signal” along with other structural and functional signals. (e.g., Cubo et al., 2005, 2008; Ricqlès et al., 2004). Actually, a phylogenetic signal has been demonstrated in some bone histological characters (Cubo et al., 2005), but given how few these characters are, their systematic implications are limited. Nevertheless, it is not impossible that such research programs could succeed, at long last, in deciphering significant systematic signals in bone histology, at least at some levels of the vertebrate hierarchy. But this will probably require a tremendous investment in cell and tissue morphometry and statistics. Such breakthroughs may be made easier by current improvements and advances in technology.

2. At the dawn of a technological revolution

New techniques of virtual image analysis and 3D reconstructions are currently pervading palaeontological sciences at the anatomical and microanatomical levels, and their precision has now reached the histological level (Clément and Geffard-Kuriyama, 2010). Very soon, such techniques will pervade it. Already, it is often not necessary to sacrifice a specimen if there is access to a light synchrotron line. Virtual imaging can also easily add the third dimension, so painfully gained so far, through serial sectioning or preparation of orthogonally oriented thin sections. Aside from these new techniques, which will also allow a smooth and continuous “zooming” from the histological to the micro- and macronatomical levels of structural organization, the more traditional thin sections, observed in ordinary or polarizing light with the compound microscope, will hold an important place for quite a while, especially for large objects. But new techniques may not necessarily phase out more traditional ones. A

case in point is the current development of new statistical tools that help to extract ecological and phylogenetic signals from bone tissue structures and microanatomy, either from actual thin sections, or from virtual tomographic slices (Laurin, 2004; Laurin et al., 2004). More generally, current progress in computer sciences and statistical methods are now increasingly helping us to recover and distinguish the various (ecological, biomechanical, phylogenetic) “signals” carried by bone microanatomy and histology (Cubo et al., 2005, 2008; Laurin, 2004; Laurin et al., 2004; Ricqlès and Cubo, 2010). This vindicates a long-held contention that the variability of bone tissues expresses a highly complex, multifactorial causality that can be deciphered, and hence can bring us a very rich amount of biological (and palaeobiological) information (Ricqlès, 1975–1978, 2008). Of course, such endeavors should be always set within proper phylogenetic contexts and practices.

The increasing number of palaeohistological publications and the growing collections of thin sections will soon make it necessary to create and manage histological data banks or “histothèques” that will require extensive computer resources for use online or on site (Canoville and Laurin, 2010; Kriloff et al., 2008; Ricqlès et al., 2004, 2009).

3. A strong link with extant vertebrate biology

In my view, it is impossible to separate palaeohistology from purely biological research on extant vertebrates, whether developmental biology, comparative morphology, histophysiology, microevolutionary ecology, or other fields. Such research, whether experimental or comparative, offers the actualistic models that are absolutely necessary for the interpretation of fossil hard tissues in functional rather than purely systematic terms. Living animals, amenable to experimental research, also comprise the basis to demonstrate causal relationships among various factors, whereas working on fossils restricts us to a comparative method that can at best demonstrate correlations but cannot generally show causal evidence (e.g., Harvey and Pagel, 1991). Recent work (Canoville and Laurin, 2010; Laurin, 2004; Kriloff et al., 2008) is also relevant in that regard because it uses the actualistic approach to bone microanatomy and draws palaeobiological inferences. During my early career my mind was influenced by works such as those of Amprino (1947) and Enlow (1963), who proposed various approaches to functional interpretations of what I have called bone histovariability and histodiversity (Ricqlès, 2008). Bone tissue differences produce patterns that express the numerous factors that interact in bone biology (Ricqlès, 1975–1978). Whether one considers ontogenetic differences among different bones, local or general growth dynamics, biomechanical adaptations, life-spans, or various environmentally-induced constraints such as climatic cycles, all those factors interact in forming the characters of bone as a tissue.

Actually, because it is a hard tissue deposited over significant ontogenetic time, bone comprises a “stratigraphy”, or a time/space record of its deposition and change. It is the task of comparative histologists and palaeohistologists to learn how to decipher the message recorded by bone during its own ontogeny and its fuller adaptive history.

Thus, histological differences locally recorded in a skeleton, or among homologous bones in different species, are not only the consequences – and expressions – of growth, bone modeling and remodeling. Rather, they show us the actual biological causes of growth specificity in action, and of the formation of local morphology during development (Enlow, 1963). In other words, histological analysis of bone diversity demonstrates the effect of biological factors acting in space and time as the *proximal and efficient causes of the shape and size differences* (anatomical end results) recorded among organs and species (Ricqlès, 1975–1978). Those biological factors are rather easily amenable to observation and quantification: vascular density, cell shape, size, orientation and number per unit cube of tissue, organization of extracellular collagenic matrices, and so on (e.g., Organ et al., 2010). What has been called “Amprino’s rule” (Castanet et al., 1996) expresses the histophysiological or structural-functional correlations within bone tissue, analyzed comparatively or experimentally among extant vertebrates.

All of the foregoing points to the complex, multifactorial causality of bone tissue distribution at every level of perception. Rather than opposing historicism to structuralism or functionalism, and hence putting forward univocal causation where e.g., phylogeny, topology, or biomechanics are viewed as the unique efficient cause (or explanation, or constraint) of the observed data, we have favored an approach to causality that is multifactorial and tries to take into account simultaneously the relevant factors, their interactions, and their integration (e.g., Cubo et al., 2008; Padian, 2004; Ricqlès and Cubo, 2010; Ricqlès et al., 2004).

The comparative study of bone as a tissue has thus revealed itself as a remarkable interdisciplinary crossroad, integrating developmental biology, biomechanical adaptation, histophysiology, ecophysiology and microevolution. It offers interesting possibilities to decipher the life history traits of various extant vertebrates. Over the years, in our Paris research group, some colleagues have largely deciphered, under the banner of skeletochronology, the time dimension of life history traits recorded in bone and have extensively applied it to the study of extant teleosts, amphibians, reptiles, birds, and mammals. This approach has been extended to fossils (e.g., Steyer et al., 2004). It could be also possible to use comparative bone histology along different pathways, for instance to study comparatively, among closely related species, the differentiation during ontogeny of species-specific character states of interest for taxonomic or functional purposes. The possibilities of using bone histology of extant vertebrates for various fundamental or applied research, whether on life history traits, ecology, or microevolution, are simply boundless (Ricqlès et al., 2004).

4. The “post modern” dinosaur

The general principles of uniformitarianism and parsimony allow us (*mutatis mutandis*) to extend to fossil forms the functional interpretations of bone histodiversity gained from the study of extant vertebrates (e.g., Ricqlès, 1976; Steyer et al., 2004). Accordingly, studies of the bone histology of fossil tetrapods have blossomed

during the last thirty years or so, proposing a new and independent approach to the life history traits, and generally speaking, to the palaeobiology of numerous fossil tetrapods (e.g., Canoville and Laurin, 2010; Chinsamy, 2005; Erickson, 2005; Houssaye et al., 2008; Krilloff et al., 2008; Laurin et al., 2004; Organ et al., 2010; Reid, 1996; Ricqlès and Buffrenil, 2001; Stokstad, 2004). Some of them may be more or less closely related phylogenetically, or appear to be more or less similar functionally, to extant forms. Others, perhaps more fascinating, appear to be without direct analogs in the extant world. Such are the “reptilian” synapsids or the Pterosaurs. Obviously, the dinosaurs also stand pre-eminently among this second category, although their close phylogenetic relationships to birds may warn us against their apparent “isolation” or “uniqueness” (Padian and Ricqlès, 2009).

Several current works deal more or less with the famous problem of dinosaur thermometabolism, a question I raised in 1968 directly from palaeohistological data (e.g., Bakker, 1986; Ricqlès, 1975–1978, 1976, 1980). Since then, arguments have blossomed and have become more refined and complex, even as the objective knowledge of bone histology of various dinosaurs and related groups experienced astonishing progress worldwide (e.g., Chinsamy, 2005; Reid, 1996; Ricqlès et al., 2001). I wish to say a word, in that context, of the exciting and long-lasting cooperation with my colleagues and friends Jack Horner (Bozeman, Montana) and Kevin Padian (Berkeley, California) in the exploration of archosaurian bone histology (e.g., Horner et al., 2001; Main et al., 2005; Padian, 2004).

The issue of dinosaurian thermometabolism cannot be satisfactorily solved as long as it is framed in simplistic terms (the “hot” versus “cold blooded” dichotomy of the media), or by opposite physiological typologies akin to Owenian essentialism (Padian, 2004). Rather, it should be integrated into the transformationist view of the Darwinian theory of evolution, an intellectual framework itself now well-analyzed and embodied in cladistic methodology (e.g., Padian, 2004; Padian and Ricqlès, 2009; Ricqlès and Padian, 2009). Accordingly, when set into this proper phylogenetic perspective, the traditional dichotomy of endo- versus ectothermy reveals its built-in epistemological fallacy because it opposes an apomorphic condition to a plesiomorphic one. Indeed, the tachymetabolic endothermy of extant birds defines the most derived (apomorphic) condition among archosaurs, and ectothermy thus covers any plesiomorphic condition relative to bird endothermy, which can encompass many distinct physiological regimes (e.g., Padian and Horner, 2004; Ricqlès, 1992). Most non-avian dinosaurs may not have been like birds physiologically, but they certainly shared with them important anatomical and physiological apomorphies (Schweitzer and Marshall, 2001). It seems to me that this minimalistic point of view is nowadays widely shared and that some kind of current scientific consensus now interprets non-avian dinosaurs as living beings, as something quite different than the “just good reptiles” image, merely blown up by a factor of 10 to 20. Besides, even this simple scaling change in itself could not fail to make dinosaurs, as “living machines”, quite different animals than anything close to

the image carried in our brain by the consideration of the extant reptilian fauna (Padian, 2004; Padian and Horner, 2004).

Whatever the final outcome of the debate, the “unconventional” interpretations of dinosaurian physiology that have developed from palaeohistological data have demonstrated their high heuristic value (Erickson, 2005, Stokstad, 2004). This is obvious in the worldwide revival of dinosaur studies that, well beyond “classical” palaeontology, have now been pervaded by other disciplines such as ecology, geochemistry, and physiology, that otherwise would not have been involved. All this has also contributed to overhaul the popular image of dinosaurs as living organisms, an image now forged by the media, and especially by the astounding and dynamic computer-processed movies, from “Jurassic Park” and beyond.

The “new dinosaur” has thus come of age, from the seventies until now, with its procession of media histrionics, wrong claims, and also just plain genuine wonder (Ricqlès, 1992). What remains of Science in all that? Have we slipped into the domain of pure wonder and fiction? Were not Bob Bakker and (more discreetly) myself “apprentice wizards,” unable to keep the endothermic dinosaur in its scientific enclosure (Bakker, 1986; Parsons, 2001; Ricqlès, 1980)? In the end, it does not matter: societies build up the myths they deserve, and all that could be expected from the current “dinomania” would be that a decent amount of its profits would support serious scientific palaeontological research. Unfortunately, we are far from this goal, as far as I know.

5. Concluding remarks

Vertebrate palaeohistology has long been a modest and rather esoteric sub-discipline of palaeontology. Its practical use for palaeontology was first linked to the taxon-specific characteristics of the dermal skeleton, which allowed diagnosis and recognition of fragmentary remains as pertaining to various taxa, especially of jawless or jawed “early vertebrates” of the Palaeozoic. Similarly oriented research on the diversity of bony tissues among fossil tetrapods has been also attempted early and, in spite of its poor and often deceptive results, remains an ever present quest in current research agendas, now framed in the belief that any intrinsic character-state of the phenotype, genetically determined, should convey some phylogenetic signal or even diagnostic character states.

Starting in the 1930s and 1940s, another approach in comparative bone tissue histology and palaeohistology has been to focus on the functional, rather than the phylogenetic-taxonomic, correlates and significance of hard tissue variability and diversity.

This approach proved rewarding as far as it could demonstrate correlations among bone tissue distributions and numerous biological variables such as ontogenetic origin, growth, size, shape, biomechanics, and ecology.

During the last three decades, functional interpretations of extant bone tissue diversity have been more and more applied to a growing corpus of palaeohistological descriptions, resulting in several interesting palaeobiological inferences. Current results deal with the various

strategies of tetrapods secondarily evolving aquatic adaptations, dinosaur and pterosaur lifestyles and physiology, evolution of mammalian functional characters, and so on. Palaeohistology has been instrumental in focusing on the complex, multifactorial causalities at work in the patterns and processes of vertebrate evolution, and has developed new ways to analyze the influences and interactions of several factors that shape the variability and diversity of bone tissue.

Palaeohistology now stands as a powerful tool to reconstruct fossil vertebrates as living organisms, and accordingly, it is becoming a more and more popular approach for the more palaeobiologically-oriented students of vertebrate evolution.

Palaeohistology cannot be set apart from many fields of research dealing with the biology of extant vertebrates. It has become a fruitful interdisciplinary domain where varied and intensive collaborations among biologists and palaeobiologists will contribute significant progress in evolutionary biology as a whole.

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