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Vertebrate palaeohistology then and now: A retrospective in the light of the contributions of Armand de Ricqlès

Paléohistologie jadis et à présent : une rétrospective à la lumière des contributions d'Armand de Ricqlès

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ABSTRACT

In addition to his many contributions to the basic anatomy and nomenclature of the osteohistology of extant vertebrates, Armand de Ricqlès has been more instrumental than any other researcher of the past half century in elucidating the structure and anatomy of the bone tissues of extinct vertebrates and in guiding the field in interpreting their meaning and application to a variety of important paleobiological problems. As a result of his pioneering work, which began with his doctoral thesis and has continued through five decades of collaborative research, we are now able to answer definitively many questions about the growth, physiology, function, and paleoecology of extinct tetrapods. In some cases we can even clarify their taxonomic status in ways unavailable through gross anatomical studies. This would have been unimaginable several decades ago, and it demonstrates how, thanks largely to the work and influence of Armand de Ricqlès, palaeohistology has been thoroughly integrated into palaeobiology.

RÉSUMÉ

Outre ses nombreuses contributions à l'anatomie et à la nomenclature de base de l'ostéohistologie des vertébrés existant encore, Armand de Ricqlès a joué, plus que quiconque, un rôle décisif dans le demi-siècle passé, en élucidant la structure de l'anatomie des tissus osseux de vertébrés disparus, en étant le guide en ce domaine, par son interprétation de leur signification et leur application à nombre d'importants problèmes paléobiologiques. Le résultat de son travail de pionnier, qui a commencé par sa thèse de doctorat et qui s'est poursuivi au long de cinq décades de recherche en collaboration, est que l'on peut à présent répondre définitivement à nombre de questions sur la croissance, la physiologie, la fonction et la paléoécologie des tétrapodes disparus. Dans certains cas, il est même possible de clarifier leur statut taxonomique, ce qui n'eût pas été possible par des études anatomiques grossières. Cela eût été inimaginable quelques décades plus tôt et montre combien, en grande partie grâce au travail et à l'influence d'Armand de Ricqlès, la paléohistologie a été complètement intégrée dans la paléobiologie.

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1. Introduction

Palaeontology, like many other sciences, began to take shape during the enlightenment, and it did so in fits and starts. Fossilized objects (literally, those "dug up" from the Earth) originally included minerals, meteorites, and archaeological remains, as well as those to which we would now restrict the term "fossil". Once it was established that these were not sports of nature or works of the devil but remains of formerly living plants and animals, it was possible to begin to interpret their meaning. By the late 18th century a great many kinds of fossilized plants and animals had been brought to light and discussed – enough to establish several classes of facts. During the next century knowledge of the fossil record improved at a considerable pace, so that the progression of life through time, as it was often called, became well understood in its general outlines. As a result, the acceptance of change through time in biotas, biogeography, and climate much preceded the acceptance of the idea of the transmutation of species, or what we would now call evolution.

The field of paleohistology developed with similar fits and starts, and like the science of paleontology in general, it relied to a great extent on the actualistic assumption: that is, that extinct organisms can be understood through what is known of extant ones. Insights into the ecology and functional morphology of extinct vertebrates have historically been based on the general (and sometimes specific) resemblances of their body parts to those of extant counterparts, closely related or not (Thomason, 1997). The understanding of paleohistological anatomy and function was attendant on the development of this understanding of the tissues of living organisms, as well as on the development of microscopes and other equipment and techniques that could help to interpret them. The great 18th century English anatomist John Hunter left a collection of some 13,000 specimens to the Royal College of Surgeons, including many histological preparations (Owen, 1992). It was natural for scientists who studied fossil animals to make thin-sections of some of their tissues, because they were trained in an anatomical tradition where such preparations were in the natural course of study. So, for example, Richard Owen figured thin-sections of the dermal scutes of the dinosaur *Scelidosaurus* when he described the animal in 1861 (Owen, 1861). Pioneers such as John Quekett tried to identify and understand the structures in fossil and recent bone and to explain how different kinds of tissues were generated and grew. Unfortunately their studies could not be sufficiently comparative and systematic to avoid the pitfalls that accompany all new sciences (Quekett, 1849).

The later studies of Foote, Gross, Seitz, Ørvig, and others elucidated the microscopic structure of the tissues of more and more extinct vertebrates, but special mention must be made of the landmark studies of Donald H. Enlow (Enlow and Brown, 1956–1958; Enlow, 1969; reviewed in de Ricqlès, 1975a, 1976b). Enlow's surveys of the bone tissues of extinct vertebrates were so extensive and comparative that he effectively brought the study of fossil bone tissues into the modern day. Although he did not have a legion of like-minded colleagues or graduate students to build his paleontological tradition, through his publications, in which he pioneered techniques and analyses, he influenced a great many researchers who are still working. One of them was the young Armand de Ricqlès.

2. Systematics and evolution in the study of palaeohistology

The results of Armand de Ricqlès's doctoral dissertation were published as a series of twelve papers in *Annales de Paléontologie* from 1968 to 1981, under the general title "*Recherches paléohistologiques sur les os longs des tétrapodes*." (de Ricqlès, 1968, 1969b, 1972a, 1974a, b, 1975a, 1976a, 1977a, b, 1978a, b, 1981) This work was groundbreaking for several reasons. As Enlow had done, he meticulously laid out the taxonomy of bone tissues and explained their generation, bringing in new observations and analyses. He classified them according to their structural types and how they grew in the skeleton, and explained how a single bone could express different kinds of tissues at the same time in different regions as well as through its development to maturity. He focused on the structure, generation, and development of secondary (Haversian) bone because it appeared in various kinds of extinct as well as extant tetrapods, and its distribution needed to be explained. Most influentially, he described bone tissue types in a taxonomic and evolutionary framework, so that within the major groups of tetrapods, it could be seen how tissues were distributed and how they changed phylogenetically. And he added an important level of inference to paleohistological analysis by linking local bone tissue deposition rate to its physiological underpinning.

When the bone tissue types of tetrapods were sorted by phylogenetic groups, it appeared that some types of bone were restricted to some kinds of tetrapods, and that some tetrapods seldom if ever produced certain kinds of bone tissues. Within particular major lineages, there were wholesale transitions between tissue types in the long bones that clearly reflected a rise in growth and presumably metabolic rates; these were seen in synapsids (de Ricqlès, 1974c) and diapsids (de Ricqlès, 1972c).

Armand was keenly interested in the connection between bone tissue type and metabolic physiology, even from his earliest work. One of his first papers (de Ricqlès, 1969a, 1969b) discussed how bone histology could be used as an indicator of thermal physiology. Using Amprino's (1947) dictum that local bone tissue type principally reflects growth rate, he reasoned that bone tissues with higher vascularization were growing at higher rates, which signaled higher metabolic levels than those that were growing more slowly; this became a major theme in his work (de Ricqlès, 1972b, 1974c, 1976b, 1978a, 1978b, 1979b, 1980a, 1980b, etc.). Although in his works Armand approached this topic judiciously, there are some pitfalls for investigators who do not have his level of experience, as all who have worked with him and learned from him know. One caveat is that because individuals change their growth rate through life, and because in any given section of fossil bone the complete ontogeny of the individual is rarely preserved, it is easy to be misled. A section that shows highly vascularized tissue may suggest endothermy (or, to be more precise, tachymetabolism: Batavia, 2010), but because most juvenile tetrapods grow more quickly than they do at later stages (and many slow down rapidly), all that can be said is that at that stage the animal seems to be growing at a certain rate, determined through comparisons with tissues of extant vertebrates. Similarly, tissues with low vascularization may suggest bradymetabolism (low metabolic rates), but this kind of tissue is also typical of adult individuals regardless of metabolic regime.

3. The development of integrative palaeohistology

In the late 1980s, Armand began a collaborative project with John R. Horner of the Museum of the Rockies at Montana State University, Bozeman. Jack Horner's discoveries of nests, eggs, and skeletons of embryonic and recently hatched dinosaurs in the Late Cretaceous formations of Montana had stimulated his interest in the growth and development of dinosaurs (Horner and Makela, 1979; Horner and Gorman, 1988). They decided to analyze the sequence of bone formation in these dinosaurs from embryos (where possible) to adults, and to obtain some idea of their growth rates and age, using the presumably annual lines of arrested growth (LAGs) and other features of bone tissue formation. Jack set up a laboratory to process thin-sections in the Museum of the Rockies in Bozeman, Montana, where the vast collections have been almost entirely assembled by Jack and his crews since the early 1980s. Thanks to the skills and diligence of Ellen-Thérèse Lamm, Alison Gentry, the late Diane Gabriel, and many other staff members and students, the Museum of the Rockies paleohistological collection is one of the largest and most comprehensive in the world. Armand and Jack began a collaboration of some 25 years with various colleagues who studied a range of paleohistological material in phylogenetic and ontogenetic context that had never been attempted, and resulted in dozens of monographs, papers, and reviews (see references cited).

It has really only been in the past two decades that access to materials for paleohistological study has been anything but strictly limited. There is a simple reason for this. Until the recent series of papers by Armand and his colleagues, with their insights into the growth rates and skeletochronology of bones and their implications for many aspects of the biology of fossil tetrapods, palaeohistology attracted very little interest. It could still be said that most colleagues in the field are generally innocent of its basic principles and insights, and that not much attention is given to them in the training of vertebrate paleontologists. This is nothing new: since the mid 19th century, there has seldom been more than one or a very few specialists in this field, from Owen and Quekett to Foote, Seitz, Gross, Ørvig, Enlow, and of course de Ricqlès. Consequently, few curators in charge of fossil vertebrates have had much sympathy with the prospect of seeing their prize specimens destroyed under the rock saw for the arcane benefit of paleohistological shamans and their obscure and trivial stores of knowledge. At best a researcher could hope for an isolated long bone of good quality to section; at worst, a fragment of a rib or shaft of sometimes ambiguous provenience. The advantage of the collaboration between Armand and Jack was that Jack had collected all his dinosaurs and was very sympathetic to the goal of understanding their growth, so he had no reservations about sectioning them as needed. Paleohistological research could thus proceed systematically.

The importance of this advance cannot be overestimated, because for the first time a comprehensive study of the ontogeny of a group of extinct vertebrates could be undertaken with the assurance that researchers could control the exact skeletal element and location of sections taken in individuals from the earliest growth stages to adults, and that they could be compared with their relatives and with other taxa under the same controlled conditions. Before this, even in the classical paleohistological literature, plates of photographs typically presented sections taken from a femur here, an ulna here, a rib there, and all from various positions within the bone.

By the early 1990s the two researchers had sketched out a plan to study the growth and evolution of bone tissues in dinosaurs – not simply individual dinosaur taxa, but the entire group, as well as their extinct relatives among the archosaurs. They identified four major signals (or "factors" or "influences") on the appearance of bone tissue in any region of a skeleton at any given time. These were ontogeny, which, echoing the great insight of Rodolfo Amprino (1947), should reflect the growth stage of a taxon and how rapidly the tissue is being deposited; phylogeny, which reflects modes and rates of growth that are inherited; mechanics, which reflects physical influences on the bone that can include adaptations for modes of life as different as flying and diving; and environment, which tends to reflect direct effects of stress, injury, disease, and other factors on individuals. These factors are not mutually exclusive, of course: phylogeny is common to most features, and characteristics involved with physiology reflect both ontogeny and phylogeny (and sometimes environmental stress). In addition to the Museum of the Rockies resources, de Ricqlès and Horner were able to form collaborations with curators of other collections complementary to theirs that were essential to the phylogenetic and ontogenetic studies that they planned.

Other workers such as Robin Reid and Anusuya Chinsamy were beginning to make valuable contributions to the histological knowledge of individual dinosaurs, and to formulate hypotheses to explain the distribution of bone tissue types among taxa. Chinsamy (1993), with her study of size and growth in a set of ontogenetic stages of the sauropodomorph *Massospondylus*, had produced one of the first quantitative estimates of growth in a dinosaur, at least for a considerable part of its ontogeny.

One of the first projects de Ricqlès and Horner and their colleagues undertook was a small one, but it underscored the potential of bone histology to approach paleobiological problems. Bob Harmon of the Museum of the Rockies had collected the wing skeleton of a Late Cretaceous pterosaur about 2 m in wing span. Its morphology showed that it belonged to the Azhdarchidae, a group of Late Cretaceous pterodactyloids that included *Quetzalcoatlus*, the largest known pterosaur (wing span approaching 12 m). Was this skeleton a juvenile of *Quetzalcoatlus*? Some wing bone fragments of *Quetzalcoatlus* were borrowed from the

University of Texas, including the largest known specimen and another half that size, and these were thin-sectioned. Although the largest specimen was degraded by bacterial action, the smaller specimen showed by its dense vascularization that it was still in a very active stage of growth. In contrast, the specimen from Montana showed few blood vessels and considerable secondary reworking, all of which suggested very slow growth and perhaps the near-cessation of size increase. These observations showed that the Montana specimen could not have been a juvenile of *Quetzalcoatlus* or another known taxon. And so, for the first time that we know among archosaurs, a new taxon, *Montanazhdarcho minor*, was established on the basis of long bone histology (Padian et al., 1995). A more recent paper (Knoll et al., 2010) established that the two Early Jurassic South African ornithischians *Lesothosaurus* and *Stormbergia* are probably merely ontogenetic stages of each other. These two papers demonstrate how histology can be used to determine whether two or more taxa are more likely distinct or conspecific.

Armand's vast knowledge of bone tissue structure, development, and evolution formed the basis for a research program that would realize the vision that he and Jack Horner shared for understanding the life history strategies of dinosaurs. They determined to study the bone histology of as many archosaurian taxa as possible in their ontogenetic and phylogenetic frameworks. Although researchers from Quekett (1849) to Houde (1987) had hoped to use bone histology to make taxonomic identifications,[1] it was clear from a variety of studies on the development of bone, from Foote (1916) to Amprino (1947), that the overriding factor that explained the appearance of bone tissue at any given place in the skeleton was its developmental rate. It was also known from the comparative work of many scholars, notably Jacques Castanet and his colleagues that the features of bone tissues in a given skeletal region change through growth, again as a reflection of the change in developmental rate with age. These facts, plus the ability to use annual growth lines to quantify age of specimens in an ontogenetic series, encouraged them to piece together a general picture of the life histories of dinosaurs and their relatives.

To establish which bones were best for histological analysis, sections from all of the major long bones of the hadrosaurid dinosaur *Hypacrosaurus* were taken (Horner et al., 1999). Different bones preserved different numbers of LAGs, which might be seen as a conflicting result; however, the different sizes of these bones also reflected their different growth rates, and some bones had undergone more erosion and secondary reworking than others, so the number of LAGs could not be expected to be constant among elements. The largest bones, the femur and tibia, showed the clearest development and the least reworking, because they grew faster than the other bones, so further skeletochronological studies were based on these elements. Although other workers have used various elements, including fibulae and ribs, these bones are often more subject to reworking and possibly to other growth rhythms that make them unsuitable for skeletochronological use and of very little utility for understanding the growth rates of tissues in the skeleton.

The preservation of a nearly complete growth series, from embryo to adult, of the hadrosaur *Maiasaura* provided a superb opportunity to document how tissue types changed in the major limb bones through ontogeny (Horner et al., 2000). It was important to establish this baseline data because even at that time, characterizations of growth regimes had been based by some workers on single sections of bones, with no ontogenetic or phylogenetic context, and inferences had been drawn about metabolism, physiology, and ecology of certain extinct animals on very incomplete material as well.

In later years de Ricqlès, Horner, and their colleagues extended their research to a comparison of embryonic bone tissues in dinosaurs and a variety of living and fossil reptiles (including birds); the evolutionary changes in growth rates during the evolution of birds from dinosaurs and during the early history of birds; and in the evolution of trends in growth rates and size in theropod and ornithischian dinosaurs, including some "bizarre structures" in thyreophorans (de Ricqlès et al., 2001, 2003a; Horner et al., 2001; Main et al., 2005; Padian et al., 2001). They also compared growth in dinosaurs to growth in pterosaurs (de Ricqlès et al., 2000; Padian et al., 2004) and Triassic pseudosuchians (de Ricqlès et al., 2003b, 2008).

In addition to many works on the bone histology of archosaurs, Armand had a strong interest in all tetrapods, as his dissertation research indicates. Some of the principal groups that attracted his interest include temnospondyls (de Ricqlès, 1964, 1965, 1975b, 1981; Steyer et al., 2004) and a variety of secondarily aquatic tetrapods, which manifest unusual histological features of pachyostosis and other kinds of bone thickening (de Ricqlès, 1969c, 1989a, 1989b; de Ricqlès and de Buffrénil, 1995, 2001; Wiffen et al., 1995; De Buffrénil et al., 1987).

These works have generally laid the groundwork for placing palaeohistology in broad ontogenetic and phylogenetic context, in combination with many other contemporary researchers such as Jacques Castanet, Anusuya Chinsamy, Jorge Cubo, Kristina Curry Rogers, Greg Erickson, Michel Laurin, Martin Sander, and Torsten Scheyer. The review here of course does not encompass the full scope of his work in paleontology; for other references please consult the bibliography of Armand de Ricqlès's works prepared for this volume and Laurin (2011).

4. Summary works and reviews of palaeohistology and actualism of bone tissues

From his earliest work, Armand de Ricqlès incorporated analysis and review of major evolutionary concepts into his work. The value of bone histology in interpreting thermal physiology (de Ricqlès, 1969a, 1972b, 1972c, 1976b) was the subject of many papers as well as the concluding

[1] This line of research may have been inspired, in part, by the successful use of histology in the taxonomy of Paleozoic finned vertebrates, whose dermal skeleton includes, at least in some cases, a variety of tissues (enamel or enameloid, dentine, spongy and compact bone), some of which form complex structures (isolated odontodes, ridges, cosmine, etc.) (Quekett, 1849).

section of his series of papers in *Annales de Paléontologie* (1968–1981). Equally notable are his series of papers summarizing the evolution of bone tissues in tetrapods (de Ricqlès, 1979a, 1979b, 1980a, 1980b, etc.). Although most of his primary work was published in French, notable summaries in English made his work accessible to a broad Anglophonic audience (e.g., de Ricqlès, 1976b, 1980b, 1993, 2007, and most of his work with J.R. Horner and colleagues).

The perspective from his work on fossil tetrapods brought substantial insight to collaborative reviews on the bone microstructure of extant tetrapods. In particular, the kinds of bone tissues and their distribution among extant tetrapods show a disjunct distribution, but when actualistic data are complemented with information from extinct taxa, gaps are bridged and other possibilities not seen in the living fauna are revealed. Four papers necessary to the education of every bone histologist are those by Francillon-Vieillot et al. (1990) on the microstructure and mineralization of vertebrate skeletal tissues, de Ricqlès et al. (1991) on the comparative microstructure of bone, Castanet et al. (1993) on bone and individual aging, and de Ricqlès (1993) on palaeohistology of bones in a comparative evolutionary perspective. Together these works form a foundation for the interpretation of most later histological research by de Ricqlès, his colleagues, and their students.

It would be remiss not to consider Armand de Ricqlès's contributions to evolutionary theory through his understanding of palaeobiology and macroevolution. Particularly in France, where the Modern Synthesis of Evolution did not have as strong a reception as in America and Britain, his papers have informed and educated the French scientific community as well as the public. He wrote a great many papers in popular French science magazines and journals, as well as in professional venues (e.g., de Ricqlès, 1972a, 1972b, 1979b, 1983a, 1983b, 1995, 1997, 2000, 2001, 2002, 2008; Devillers and de Ricqlès, 1982; de Ricqlès and Padian, 2009; de Ricqlès and Cubo, 2010). We are reminded that he was named to the Collège de France, the rarest honor for a scholar in Europe, not as an histologist or a paleontologist but as an evolutionary biologist (see also Laurin, this volume).

5. Conclusion

Armand de Ricqlès has left an unparalleled legacy in French biology, and his legacy has extended worldwide through his work in many aspects of paleontology and palaeobiology, including the description of specimens, the analysis of tooth replacement patterns, the evolution of dermal skeletal elements, the secondary return of tetrapods to an aquatic existence, and the evolution of mineralized tissues in general. But his greatest body of work, of course, is in deciphering the ontogenetic, phylogenetic, physiological, and mechanical signals left in bone tissues, both fossil and extant. He has taught generations of students and colleagues how to decipher these signals, and in so doing has made the palaeohistology of bone a more popular, fruitful, understood, and integrated field of study than ever before. Future advances in this field will be laid pre-eminently at his doorstep.

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