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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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A B S T R A C T

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.


R É S U M É

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 18$^{th}$ 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