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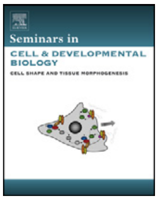

Review

Developmental palaeontology of Reptilia as revealed by histological studies

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ABSTRACT

Among the fossilised ontogenetic series known for tetrapods, only more basal groups like temnospondyl amphibians have been used extensively in developmental studies, whereas reptilian and synapsid data have been largely neglected so far. However, before such ontogenetic series can be subject to study, the relative age and affiliation of putative specimens within a series has to be verified. Bone histology has a long-standing tradition as being a source of palaeobiological and growth history data in fossil amniotes and indeed, the analysis of bone microstructures still remains the most important and most reliable tool for determining the absolute ontogenetic age of fossil vertebrates. It is also the only direct way to reconstruct life histories and growth strategies for extinct animals. Herein the record of bone histology among Reptilia and its application to elucidate and expand fossilised ontogenies as a source of developmental data are reviewed.

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1. Introduction

To understand modern life, it is essential to study its evolutionary past. Fossils allow us to assess the breadth of bone biology and development in evolutionary history, because many fossil bones present tissue structures and developmental pathways not known in extant species. A fossil specimen however represents only a glimpse of the complete ontogenesis from fertilization to death. In order to better understand the evolution of extinct life history in a fossil species, it is important to analyse as much ontogenetic data as possible. There is continued and heightened interest to incorporate ontogenetic aspects in palaeobiological but also in phylogenetic studies, and vice versa, to also include fossils in studies of evolutionary developmental biology.

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During the past two decades, major advances in the study and phylogenetic analyses of skeletal developmental events were achieved [1]. Studying fossil growth series has largely been restricted to basal groups among Vertebrata (e.g., tetrapodomorphs, temnospondyl amphibians), basically because of the abundance and exceptional preservation of fossils in these groups ([2,3] this issue).

Fossil embryos and juvenile specimens, although rare faunal elements in the fossil record, are known from a variety of amniote lineages ([4] this issue), however, because of preservation and abundance of fossils, dinosaurs and marine reptiles from the Triassic strata of Europe and China are especially well suited to increase the scope of these studies into the amniote record. However, even in the UNESCO site of Monte San Giorgio, one of the most important fossil Lagerstätten of marine reptiles from the Middle Triassic, the discovery of well based developmental series including embryos, juveniles and adults, is a rare circumstance. Ichthyosaurs and the small sauropterygian pachypleurosaurs yielded so far the best growth series, but additional taxa, including for example other marine sauropterygians or archosauromorphs might also be suited to provide valuable data in the future. With the exponential output of descriptions of closely related and well preserved fossils from China [5–10], developmental data for comparison are steadily increasing.

For over a century, comparative histological research of fossil vertebrate bones has been established as a complementary venue of research next to gross morphology and osteology [11–13]. In contrast to the developmental studies which were dominated so far by fossil non-amniote taxa, the field of bone histology of fossil tetrapods was, until recently [14,15], dominated by amniote lineages [16–20].

Bone histology permits to access data about palaeoecology and phylogeny [21–23], as well as growth and life history (Fig. 1) and individual age of extinct taxa [24–27], the latter being important in appraising the ontogenetic age of individuals within a fossil series. In this regard, it was aptly stated that "bone tissues throughout the skeleton should be described at as many stages of growth as can be made available in taxa whose phylogenetic relationships are established on the basis of other characters" ([28]: p. 351). Herein, the skeletochronological aspect of bone histology in Reptilia (*sensu* [29]) is summarised, and the importance of bone histology to potentially reveal and expand fossil ontogenetic series is outlined. Bone histological terminology and classification of bone tissues follows Francillon-Vieillot et al. [25] and Sander et al. [30].

Fossil reptilian groups for which life history data based on bone microstructures are available are shown in Fig. 2. Note that the taxonomic position of some taxa, i.e., turtles and ichthyosaurs, is still under debate. A comprehensive list of studies and sampled taxa using bone histology in amniotes is available under http://www.developmental-palaeontology.net.

2. Bone histology applied to fossilised ontogenies

The assessment of individual age in extant and fossil vertebrates is for a large part based on the counting of periodically deposited growth marks, i.e., annuli or lines of arrested growth (LAGs) or growth cycles in primary bone tissue, a method known as skeletochronology [27,31–37]. In poikilotherms, LAGs mainly occur due to annual cessation of bone growth, although they are also known from bones of homoeothermic animals (as summarised in Refs. [36–38]). The annularity of these cyclical growth marks has been validated for several vertebrate groups using extant examples [39–43], however, the mechanism of LAG deposition and identification of LAGs in fossils are still debated [44–47]. Possible reasons discussed for annual growth marks in bone are environmental changes (seasonal changes in light intensity, temperatures, or related to wet and dry seasonal patterns), nutrition and diet, disease, as well as migratory and reproductive cyclicity [27,32,48].

Where the growth record was lost because of internal remodelling processes of the bone, i.e., through the centrifugal expansion of the marrow cavity, potential growth cycles have to be retrocalculated. Given the intrinsic connection of bone structures and rate of bone deposition known as Amprino's rule [46,49–51], bone deposition rates can corroborate age estimates based on cyclical growth marks [52–54]. Similarly, the analysis of the isotope composition, i.e., changing $\delta^{18}O$ values within the cortical regions of the bone, may contribute to infer cyclical or seasonal growth patterns [55]. Many of these methods have been recently developed, and thus their assets to the growing field of skeletochronology still have to be critically evaluated.

Several studies on dinosaurs [30,54,56–58] have demonstrated that histological sections of fossil bone samples can be used to establish the relative age/ontogenetic stage of specimens. Because bones are usually affected by remodelling processes a single bone does not reveal the complete growth of an individual, and overlapping histological records of younger and older individuals must be combined to elucidate the full ontogenetic growth trajectory for the species. Once we have the necessary sufficient phylogenetic and ontogenetic control for the interpretation of histological data, "it is becoming possible to see how growth strategies change throughout the evolution of an extinct clade, and how they allow animals to exploit new evolutionary opportunities" ([59]: p. 144).

3. Parareptilia

Among Parareptilia, a diverse group of Palaeozoic and Early Mesozoic reptiles [60], descriptions of bone histology are available basically only for mesosaurs, pareiasaurs and procolophonids [17,61], with newer studies focusing more on functional and phylogenetic aspects of bone microstructures than on aspects related to growth and aging [62,63]. Skeletochronological or life history studies using several specimens of different ontogenetic stages have, up to our knowledge, never been attempted in any parareptile.

4. Eureptilia

4.1. Basal Eureptilia and Basal Diapsida

With the exception of the more diverse and widespread basal eureptilian Captorhinidae, and the diapsid Younginiformes and *Claudiosaurus germaini* (Late Permian of Madagascar), for which bone histological data are partly also available [17,21,32,61,64], the fossil record of basal eureptiles and basal diapsids (small to medium sized terrestrial lizard-like animals) is poor. Those specimens sectioned for histology usually exhibit periosteal lamellar-zonal bone suitable for growth studies [64]. Good growth series are also known from some of the marine Younginiformes, e.g., *Hovasaurus* and *Tangasaurus* [65,66].

4.2. Ichthyopterygia and Thalattosauriformes

Growth series including embryos were mainly known for ichthyosaurs and thalattosaurs from the Lower Jurassic Posidonia Shale [67] and Middle Triassic Besano Formation, Monte San Giorgio [68], respectively, but exceptional growth series as evidenced by abundant embryonic to adult specimens were recently reported also for the small sized ichthyosaur *Qianichthyosaurus* and the tha-