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Theropod dinosaurs and their Role in the Evolution of Endothermy

Perceptions of dinosaur lifestyle have been greatly changed over time, and one of the most contentious issues in dinosaur paleobiology during the past several decades has been their metabolic status. Portrayed as sluggish, ectotherm reptiles since their discovery in the early 18^{th} century, the "renaissance" view of dinosaurs as dynamic, endotherm creatures occurred in the 1970s when the similarities between theropods and birds were emphasized. Although recent discoveries of feathered dinosaurs in China suggest that some coelurosaurian theropods had some degree of endothermy, absence of respiratory turbinates as well as an extensive abdominal air-sac system in many theropods indicate that they did not have a highly derived, endothermic metabolic status. In the past 30 years, bone microstructure has been used to deduce various aspect of the physiology of the dinosaurs. Since paleohistology offers good evidences on growth rate and metabolism, new investigation on bone histology in saurischian dinosaurs, which are phylogenetically bracketed by (ectothermic) crocodilians and (endothermic) birds, have been done during a short visit at the Steinmann Institut für Geologie, Mineralogie und Paläontologie at the University of Bonn (Germany) in March 2010. This visit was part of a group project together with Emanuel Tschopp and Dr. Octavio Mateus (Universidade Nova the Lisboa, Portugal) in which one of the purposes was to learn about different histological characteristics of various saurischian taxa. Since the Paleontological Institute of the University of Bonn offers one of the most important collection of thin sections of sauropod bones of different ontogenetic stage, the main focus of the visit was on sauropod dinosaurs, with emphasis on changes in bone structures from very young juveniles to old adults.

The short visit was initiated by a 3-days course on paleohistology*, including lab work, presentations and discussion groups. Basic knowledge on bone structure in general and dinosaurian

* The course included an introduction to hard tissues and bone histology and a section on how to reconstruct life history and ecology from bone histology.

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bone microstructure in particular was presented, and their implications on growth rate and metabolism have been discussed in the class. Examination of various thin sections of several sauropod taxa of juvenile and adult stages allowed investigation of changes in bone structure of sauropods through their ontogeny. Thin sections in sauropod bones were then compared to those of known endo- and ectotherm animals.

Research into bone histology has shown that bone as a living tissue can exhibit various patterns, allowing them to grow and change their shape during ontogeny. Two main types of primary bone structures can be observed: lamellar-zonal bone (LZB) and fibrolamellar bone (FLB). In extant animals, these two bone types show a very clear correlation with thermophysiological strategies. Lamellar-zonal bone is present in modern exothermic reptiles and grows slowly and often intermittently, producing growth rings, or lines of arrested growth, when food supplies are limited or climates are unfavorable. On the other hand, fibrolamellar bone is a type of primary compact bone that grows quickly, without formation of growth rings, and can be found in large fast growing mammals and birds, which are endothermic animals. Fibrolamellar bone implies a high growth rate, as well as a high metabolic rate, since the organism needs to have a high metabolism (of which heat is the waste product) for supporting such a fast growth. However, it remains unclear whether the development of a new type of bone tissue was first induced by a high metabolism or a high growth rate.

The comparison of sauropod bones with those of extant animals has revealed that they are virtually indistinguishable from mammalian bones, having the very typical dense secondary Haversian bone structure. Juvenile sauropods grew at a similar rate as recent mammals and birds, which supports the assumption that they had a high metabolic rate. Growth slowed down during ontogeny, but not as much as in mammals. Changes in the bone structure from early juveniles to old adults are best visible in longbones and show that vascularization of the bone decreases during ontogeny, whereas organization increases. In young specimen, the bone is laid down very fast and irregularly, with large vascular space for blood supply and no growth marks. Getting older, the vascular space is

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becoming thinner. The canals start to be filled in with bone and to be mainly oriented circumferentially, and the enlargement of the medullar cavity starts replacing the vascular bones. In very old adults, shortly before growth ceases, a thin layer of lamellar-zonal bone was laid down, indicating slow growth in the last years of their life. Whereas this might imply also a change of the thermophysiological strategy, one has to take into account that also mammals decrease their growth rate without changing from endo- to ectothermy. Furthermore, in sauropods, this change seems to appear only in the very last ontogenetic stage, and sexual maturity is interpreted to be reached much earlier. In contrast to mammals, sauropods therefore continue to grow quite fast as adults.

Histology as one line of evidence on thermophysiological strategies thus implies a high metabolic rate for sauropods. However, based on histology alone, it remains arguable to draw conclusions on thermophysiological strategies, especially regarding the fact that there might have been strategies among saurischians, which are not seen anymore in extant organisms, what makes comparisons difficult. Further studies are therefore needed before being able to publish satisfying results. Since also all clades of dinosaurs show fibrolamellar bone, further research would have to focus on the first vertebrates to show this type of bone tissue. Therefore, no publication will result from this visit alone in the near future. However, we plan to continue investigating this important evolutionary step from ecto- to endothermy in different ways, and will of course acknowledge the ESF for their support in a final publication.