BONE HISTOLOGY OF THE MIDDLE TRIASSIC LONG-NECKED REPTILES TANYSTROPHEUS AND MACROCNEMUS (ARCHOSAUROMORPHA, PROTOROSAURIA)

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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Tanystropheus and Macrocnemus are two Middle Triassic representatives of the Protorosauria (Archosauromorpha; Fig. 1A). Their cervical vertebrae are elongated, a trait characteristic for protorosaurs but particularly pronounced in Tanystropheidae, including the name-giving taxon Tanystropheus (Peyer, 1931). The morphology of Macrocnemus is in accordance with a terrestrial habit (Rieppel, 1989). In contrast, the lifestyle of Tanystropheus is not clearly identifiable and osteological analyses have not yet been able to settle the issues of the anatomically correct posture of the neck and the habit of Tanystropheus.

Besides historical (phylogenetic) aspects, bone histology is now widely used to trace biological, environmental, and mechanical factors that an animal is subject to during its life span (e.g., Horner et al., 1999; Ricqlès, 2001; Canoville and Laurin, 2010; Houssaye, 2013; Padian and Lamm, 2013; Klein et al., 2016). Here we performed a bone histological analysis of selected postcranial bones (including cervical vertebrae and ribs, and long bones) of Tanystropheus and Macrocnemus in order to infer their paleoecology and mode of growth.

Institutional Abbreviations—MHI, Muschelkalk Museum Hagdorn Ingelfingen, Ingelfingen, Germany; PIMUZ, Paleontological Institute and Museum of the University of Zurich, Zurich, Switzerland; SMNS, State Museum of Natural History, Stuttgart, Germany.

MATERIALS AND METHODS

The sampled specimens of Macrocnemus and Tanystropheus are held in museum collections in Switzerland (PIMUZ) and Germany (MHI, SMNS) and include cervical vertebrae and ribs as well as limb bones. In addition, a postcloacal bone, previously misidentified as a cervical rib of Tanystropheus, was sampled (Fig. 1B–E). For the complete list of sampled specimens, see Table 1.

Long bones were cut at mid-diaphysis to ensure a maximally preserved growth record. The fossil samples were processed using the methodology described in Chinsamy and Raath (1992). For the paleohistological description, we follow the terminology established in Francillon-Vieillot et al. (1990).

Lifestyle can potentially be inferred by the compactness of the bone and the compactness profile over a bone cross-section. To this end, three sections were analyzed using the program Bone Profiler (Girondot and Laurin, 2003; Canoville and Laurin, 2010) and the bone compactness parameters S (width of transitional zone between medullary and cortical region), P (position of transitional zone between medullary and cortical region), Min (compactness at section center), and Max (compactness at outermost cortex) were calculated.

For long bones, the femur SMNS 54622 (Tanystropheus) was chosen because it represents the only long bone preserved well enough three-dimensionally to conduct the analysis. The mid-vertebral section of MHI 1104 (Tanystropheus) was also analyzed. A femur (PIMUZ T 4926) assigned to the aquatic sauropthygian nothosaurid Larosaurus was analyzed for comparison.

We used Adobe Photoshop Elements 9 for image editing and Bone Profiler for the analysis, as well as the Excel file (appendix S10) accompanying Canoville and Laurin (2010) for life history inference. The methodology and details of the analysis are described in the aforementioned references.

RESULTS

The thin sections of Tanystropheus and Macrocnemus exhibit a common basic bone tissue; namely, lamellar-zonal compact bone consisting of a primary compact lamellar to parallel-fibered matrix of periosteal origin, with extensive evidence for cyclical growth (Figs. 1–3). This bone type contains longitudinal simple primary vascular canals. The number of vascular canals is smaller in the more compact sections of the cortex within a single cross-section. Small variations in the vascularization can occur locally in one section or between different bones. Below we describe a general comparison of the different skeletal elements sampled; for a more detailed description, see Supplemental Data.

All limb bones show a relatively isometric accretion rate of the bone lamellae, only varying in thickness and organization due to the shape of the bone. In SMNS 54622 (Tanystropheus), the largest femur, the medulla contains a spongiosa made of secondary trabeculae surrounding a central hollow cavity (Fig. 2A; see also Fig. S1 in Supplemental Data). In contrast, the vertebrae exhibit a strongly anisometric deposition of bone. The general shape of the centrum in cross-section is oval to rectangular (Fig. 2C, D; see also Fig. S1). The lateral and ventral cortices are more parallel-fibered compared with that of limb bones, whereas the dorsal cortex is almost lamellar. The neural canal is sheathed by a layer of secondary endosteal lamellar bone. The spinous process deeply impacts the dorsal morphology and histology of a vertebra. At mid-length of the centrum, roughly the outer half of the dorsal cortex is separated from the inner layers by a cluster of secondary osteons (Fig. 2C),