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BONE HISTOLOGY OF DINOCEPHALIANS (THERAPSIDA, DINOCEPHALIA): PALAEOBIOLOGICAL AND PALAEOECOLOGICAL INFERENCES

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Abstract: We investigate the bone histology of multiple skeletal elements of dinocephalian taxa from the middle Permian *Tapinocephalus* Assemblage Zone of the Karoo Basin of South Africa. The results show that the cortex is predominantly composed of fibrolamellar bone, suggesting rapid osteogenesis for these basal non-mammalian therapsids. However, in a few skeletal elements, growth marks interrupt the deposition of the fibrolamellar bone tissue, indicating periodic arrests in growth. Ontogenetic differences are observed among the specimens studied: the majority have fibrolamellar bone deposited up to the peripheral margin of the bone wall, indicating continuous fast growth right up to the time of death, while a few specimens have avascular lamellar bone tissue with multiple, closely spaced rest lines, indicating maturity and a slowing down of growth prior to death. Several taxon-specific histological variations in terms of orientation of vascular canals and primary osteons, incidence of growth marks, and extent of secondary medullary reconstruction suggest slight differences in growth trajectories between the different taxa. The skeletal elements of the herbivorous taxa (*Keratocephalus*, *Moschops* and *Struthiocephalus*) and the omnivorous *Jonkeria*, previously studied, are characterized by a thick cortex, and extensively developed medullary spongiosa, suggestive of semi-aquatic habits. In contrast, the femoral histology of the carnivorous *Anteosaurus* suggests that it was more terrestrial.

Key words: bone histology, Dinocephalia, graviportality, growth marks, Karoo Basin, Permian.

DINOCEPHALIANS were a group of large-bodied basal therapsids that radiated during the Guadalupian epoch of the Permian Period (Boonstra 1963*a*, *b*; Rubidge 1991; Nicolas & Rubidge 2010; Day *et al.* 2015). The group includes carnivores (e.g. Anteosauridae), herbivores (e.g. Tapinocephalidae) and omnivores (e.g. Titanosuchidae), with the tapinocephalids being the most abundant in the fossil record (Boonstra 1963*a*, *b*; Barghusen 1975; Nicolas & Rubidge 2010). The dinocephalians are characterized by their thick walled, ornamented skulls with interdigitating upper and lower incisors (Rubidge & Sidor 2001; Kemp 2005, 2012). *Moschops* and *Tapinocephalus* had the heaviest and thickest skulls of all the dinocephalians (Kemp 2012).

Dinocephalians experienced their first phase of diversification in the *Eodicynodon* Assemblage Zone of the Beaufort Group of the Karoo Supergroup of South Africa (Boonstra 1969; Rubidge 1991; Govender *et al.* 2002), and were abundant in the early parts of the overlying *Tapinocephalus* Assemblage Zone (TAZ, *sensu* Smith & Keyser 1995; Kemp 2012; Day & Rubidge 2020; Day & Smith 2020). The TAZ has the highest tetrapod diversity of all the Karoo biozones, with dinocephalians representing more than 30% of the total tetrapod fauna (Chinsamy-Turan 2012; Kruger *et al.* 2018). However, by the end of the TAZ they completely disappear from the fossil record leaving no known descendants (Boonstra 1971; Kemp 1982, 2012). Their disappearance near the top of the TAZ marks the base of the *Pristerognathus* Assemblage Zone (Day *et al.* 2015).

Dinocephalians are also known from the middle Permian rocks of Russia (Ivachnenko 1995, 2000), Zimbabwe (Lepper *et al.* 2000; Munyikwa 2001), Brazil (Langer 2000; Cisneros *et al.* 2012), Tanzania (Simon *et al.* 2010)

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