

Bone histology of the graviportal dinocephalian therapsid *Jonkeria* from the middle Permian *Tapinocephalus* Assemblage Zone of the Karoo Basin of South Africa

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Here we examine the bone histology of multiple skeletal elements of three individuals of *Jonkeria* from the middle Permian *Tapinocephalus* Assemblage Zone of the Karoo Basin of South Africa. Our histological results reveal a predominance of highly vascularized, uninterrupted fibrolamellar bone tissue, which suggests rapid periosteal bone deposition and an overall fast growth. However, in a rib, the periosteal bone deposition periodically stops abruptly, resulting in the deposition of several lines of arrested growth. The absence of bone growth marks in the limb bones (except for an annulus in a radius) suggests a young ontogenetic status for all specimens of the studied sample. All the skeletal elements are characterized by thick bone walls, extensive secondary reconstruction and the complete infilling of the medullary cavity by bony trabeculae. The latter condition is different to observations of contemporaneous graviportal terrestrial pareiasaurs, but similar to the observations in the modern semi-aquatic *Hippopotamus*, and suggests a possible semi-aquatic lifestyle for *Jonkeria*. On the basis of our histological findings, we assert that during early ontogeny *Jonkeria* experienced rapid sustained rates of growth, whereas later in ontogeny they experienced cyclical rates of growth.

Key words: Therapsida, Synapsida, bone microstructure, middle Permian, Beaufort Group, Abrahamskraal Formation, South Africa.

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Introduction

Jonkeria is an omnivorous dinocephalian therapsid belonging to the family Titanosuchidae (Van Hoepen 1916; Boonstra 1936, 1963a, b; Colbert 1969), whose remains have been found in the middle Permian of the *Tapinocephalus* Assemblage Zone of the Beaufort Group, Karoo Supergroup of South Africa (Boonstra 1969). The *Tapinocephalus* Assemblage Zone (sensu Smith and Keyser 1995) is the second oldest tetrapod biozone of the Beaufort Group, sandwiched biostratigraphically between the underlying *Eodicynodon* Assemblage Zone characterized by the small- to medium-sized dicynodont *Eodicynodon oosthuizeni* and the overlying *Endothiodon* Assemblage Zone characterized by *Endothiodon bathystoma* (Day and Rubidge 2020; Day and

Smith 2020). The Karoo Basin is world renowned for its extensive record of non-mammalian synapsids (e.g., Boonstra 1963a; Fordyce et al. 2012) and dinocephalians form one of the most successful therapsid lineages which flourished during the middle Permian between 265 and 260 million years ago (Boonstra 1963a, 1968). They were the most diverse and dominant group of the time, but became extinct by the end of the middle Permian *Tapinocephalus* Assemblage Zone, leaving no known descendants (Boonstra 1971; Kemp 1982, 2012; Day and Rubidge 2020). Dinocephalians are characterized by their pachyostotic skulls and pleisomorphic cranial features similar to the ancestral late Carboniferous and early Permian pelycosaur-grade synapsids (Boonstra 1963b, 1971; King 1988; Rubidge and Sidor 2001). Although they retained their basic therapsid structure