

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

(Kemp 1982, 2012), dinocephalians were large-bodied animals, adapted to both carnivory (e.g., Anteosauridae) and herbivory (e.g., Tapinocephalidae, Boonstra 1963a, b). The most common dinocephalians found in the *Tapinocephalus* Assemblage Zone (Kemp 1982, 2005, 2012) are members of the Titanosuchidae (namely, *Jonkeria* and *Titanosuchus*), which may have been omnivores (Shelton et al. 2019).

Jonkeria was first named by Van Hoepan (1916) based on a well-preserved skull and associated postcranial skeleton recovered from the lower Karoo beds. Subsequently, a number of species were attributed to the *Jonkeria*, however, some of the species were synonymized by Boonstra (1969) after re-examining the *Tapinocephalus* Assemblage Zone material. Morphologically, *Jonkeria* appears to be closely related to *Titanosuchus* with the most obvious difference between the two being *Jonkeria*'s shorter limbs (Kemp 1982, 2012). Based on the presence of a long snout and a heavily built skull equipped with sharp incisors and fang-like canines, Colbert (1969) suggested that *Jonkeria* was a fierce carnivore that preyed on large animals. However, the presence of numerous, small, leaf-shaped postcanine teeth that bear serrated edges suitable for grasping/plucking plant material are suggestive of a herbivorous diet for titanosuchids (Kemp 1982, 2005; King 1988). Given this mixed dentition, it is likely that *Jonkeria* may have been omnivorous (Kemp 1982; Shelton et al. 2019) and may have used its large body size to intimidate and confiscate the prey of small carnivores (Colbert 1969). Such behaviour is commonly seen in modern opportunistic omnivores like grizzly bears (*Ursus arctos*) (Bastille-Rousseau et al. 2011; Gunther et al. 2014). In contrast to other therapsid clades, such as anomodonts, therocephalians and non-mammalian cynodonts, dinocephalians have received relatively little palaeobiological attention (Barghusen 1975; Kammerer 2011; Chinsamy-Turan 2012a). Compared to other dinocephalians, fossils of *Jonkeria* are relatively scarce and there are only a few palaeobiological studies of this genus (Boonstra 1969; Shelton et al. 2019).

Bone histology and skeletochronology are valuable tools for inferring biological information about age, lifestyle and sexual maturity of extant (e.g., Woodward et al. 2014; Montoya-Sanhueza and Chinsamy 2018; Nacarino-Meneses and Köhler 2018; Legendre and Botha-Brink 2018; Bhat et al. 2019; Chinsamy and Warburton 2020) and extinct animals (e.g., de Ricqlès 1969, 1972; Francillon-Vieillot et al. 1990;

Chinsamy 1997; Ray et al. 2004, 2005; Chinsamy-Turan 2005; Chinsamy et al. 2013, 2019, 2020; Woodward et al. 2020). Such techniques have been applied to study various vertebrate groups including dinosaurs (e.g., Chinsamy and Dodson 1995; Chinsamy et al. 1994, 1998; Horner et al. 1999, 2000; Klein and Sander 2008; Woodward et al. 2015; Handley et al. 2016; Angst et al. 2017; Cerda et al. 2017; Krupandan et al. 2018; Cullen et al. 2020), basal turtles (e.g., Scheyer and Sánchez-Villagra 2007; Scheyer and Sander 2007; Pereyra et al. 2020), mammals and their relatives (e.g., Botha and Chinsamy 2000; Ray et al. 2004; Chinsamy and Hurum 2006; Chinsamy and Abdala 2008; Hurum and Chinsamy-Turan 2012; Jasinowski and Chinsamy 2012; Shelton et al. 2013; Huttenlocker and Botha-Brink 2014; Lambertz et al. 2016; Shelton and Sander 2017; Botha-Brink et al. 2018; Huttenlocker and Shelton 2020; Botha 2020). Despite the host of information that can be revealed by vertebrate bone histology, information on dinocephalian histology has been scarce (de Ricqlès 1972; Chinsamy-Turan 2012a; Shelton et al. 2019), which has led to limited information about their biology. Although, Enlow and Brown (1956, 1957) conducted the seminal study on the bone microstructure of therapsids, de Ricqlès (1972) provided the earliest and systematic description of bone histology of a variety of therapsids including Titanosuchidae. De Ricqlès (1972) briefly described richly vascularized, dense Haversian bone in *Titanosuchus ferox* with numerous secondary osteons partially dispersed over each other, whereas the interstitial tissue is comprised of lamellar bone with poor vascularity. The most recent work on titanosuchid bone histology led to the identification of osteomyelitis in a femur of *Jonkeria parva* (Shelton et al. 2019). This pathology is characterized by the growth of radial bony spicules perpendicular to the normal unaffected fibrolamellar bone tissue of the cortex. In addition, Shelton et al. (2019) also noted an increase in localized vascularization and substantial remodeling in the vicinity of the puncture marks that may have been the cause of infection.

In the current study, we apply bone histological techniques to *Jonkeria parva* and *J. ingens*, as well as an undetermined *Jonkeria* species (Table 1). The main objectives of the current research are (i) to describe the inter-elemental and intraspecific bone histology of the genus *Jonkeria*; (ii) to shed light on the histological variation and life history information of different species of *Jonkeria*; and (iii) to expand our knowledge about their palaeobiology.

Table 1. Skeletal elements of *Jonkeria* that were studied. All the material was recovered from the *Tapinocephalus* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. Source of information: Boonstra (1955, 1969); King (1988). SAM-PK-12233a/b/c are different elements of the same individual.

Specimen number	Skeletal element	Taxon	Locality	Section type
SAM-PK-12233a	femur	<i>Jonkeria parva</i> Boonstra, 1955	Deesweesfontein Farm in Laingsburg, <i>Tapinocephalus</i> Assemblage Zone of the Karoo Basin, South Africa.	transverse
SAM-PK-12233b	radius			
SAM-PK-12233c	tarsal			
SAM-PK-11994	humerus	<i>Jonkeria ingens</i> Broom, 1923	Welgemoed, Prince Albert, <i>Tapinocephalus</i> Assemblage Zone, South Africa.	transverse core
BP/1/5409	rib	cf. <i>Jonkeria</i> sp.	Banksdrif (Koornplaas, 41), <i>Tapinocephalus</i> Assemblage Zone (Beaufort Group, Karoo Supergroup, South Africa.	transverse, longitudinal

Institutional abbreviations.—BP, Evolutionary Sciences Institute (previously Bernard Price Institute), University of the Witwatersrand, Johannesburg, South Africa; SAM, Iziko South African Museums, Cape Town, South Africa.

Material and methods

Jonkeria specimens studied here were excavated from the *Tapinocephalus* Assemblage Zone of the South African Karoo Basin (Boonstra 1969), and are housed in the Iziko Museums of Cape Town, and the Evolutionary Studies Institute (formerly the Bernard Price Institute) at the University of the Witwatersrand, Johannesburg, South Africa. For our analysis, five skeletal elements, including a femur, humerus, radius, tarsal, and partial rib, were selected to investigate both inter-elemental and intraspecific histological variability (Table 1). The femur, radius, and tarsal (SAM-PK-12233a–c) belong to *Jonkeria parva* and were collected by Lieuwe D. Boonstra and colleagues (1969) at Deesweesfontein Farm in Laingsburg, South Africa. The specimens bearing the same specimen numbers but differentiated by a/b/c indicate different elements of the same individual. It should be noted that the femur (SAM-PK-12233a) was studied by Shelton et al. (2019) wherein a pathology was reported. In the current study, several transverse sections at different levels of the femoral shaft were studied to assess histological variation along the bone. The distal part of an isolated humerus (SAM-PK-11994) recovered from Welgemoed, Prince Albert, South Africa (Boonstra 1955; King 1988) was also studied and is referred to as *Jonkeria ingens* (previously known as *Dinophoneus ingens*; Broom 1923; Boonstra, 1969; King 1988). The species description was based on a complete skull (Broom 1923) that was previously collected by M.J. van Wyk on his farm Kookfontein in Prince Albert, *Tapinocephalus* Assemblage Zone, South Africa. The final specimen included in our study is BP/1/5409, which is an isolated partial rib collected from Banksdrif (Koorndraai, 41), *Tapinocephalus* Assemblage Zone (Beaufort Group, Karoo Supergroup), and is designated as cf. *Jonkeria* sp. All the studied specimens were obtained either from the Iziko South African Museums, Cape Town, or the Evolutionary Studies Institute (formerly the Bernard Price Institute) at the University of the Witwatersrand, Johannesburg, South Africa (see Table 1). Permission to section the fossils was obtained from the South African Heritage Resources Agency (SAHRA: permits 2076, 3752-4658).

Since vertebrates display a wide range of variation in histological characteristics (e.g., Horner et al. 1999, 2000; Ray and Chinsamy 2004; Ray et al. 2004), as well as bone depositional rates (e.g., Amprino 1947; de Margerie et al. 2002, 2004; Starck and Chinsamy 2002; Botha-Brink and Angielczyk 2010), multi-element studies of individuals provide a better assessment of their growth patterns, life habits and evolutionary history (Botha and Chinsamy 2004, 2005; Chinsamy-Turan 2005, 2012b; Ray et al. 2009). The

destructive nature of histological analyses and the scarcity of the complete specimens prohibited sectioning a large number of bones; however, an optimal sample was obtained by selecting partial skeletal elements from available species. Transverse sections were prepared from midshaft levels wherever possible as these are the regions of the bone that undergo the least secondary remodeling (Enlow 1963; Chinsamy 1995; Chinsamy-Turan 2005) and limb bones were mostly selected because they represent the best track record of growth (Francillon-Vieillot et al. 1990; Chinsamy-Turan 2005; Bhat et al. 2019; Chinsamy and Worthy 2021). On the other hand, the rib was sectioned towards the proximal end as this region is considered to maintain a better growth mark record than weight bearing long bones (Stein and Sander 2009; Waskow and Sander 2014). In addition, several longitudinal sections were also prepared to record additional information about the organisation of collagen fibrils (Stein and Prondvai 2014).

Thin sections were petrographically prepared using cutting and grinding techniques following Chinsamy and Raath (1992). In addition, some of the bones were either sampled by the hydraulic coring method using a drill with a diamond encrusted coring bit or cut using a Dremel Precision Tool, following the procedures outlined in Stein and Sander (2009). Core drilling was carried out preferentially in an area that was anatomically unimportant for taxonomic identification, but yet ideal for histological analyses. After the 1 cm cores were obtained, the holes were infilled with plaster to preserve the overall morphology. The cores were embedded in an epoxy resin (EpoxyAcast 690 and/or Struers Epofix; Chinsamy and Raath 1992; Chinsamy-Turan 2005). Coring, sectioning, embedding and thin sectioning, as well as microscopy thereafter were performed in the thin sectioning laboratory of the Palaeobiology Research Group at the Biological Sciences Department at the University of Cape Town. The embedded bones were mounted on frosted glass slides, thin sectioned using a Struers Accutom-50 and thereafter ground and polished using carborundum (silicon carbide) discs of various grit sizes (400–1200 μm). This is followed by a final polish on a lap wheel with a velvet cloth using aluminium oxide (Al_2O_3) solution. The final thickness of the thin section was 50–45 μm , which proved to be optimum for our analyses. More than two sections from a single bone were prepared in case of slide breakages. All the prepared bones were studied and photographed using digital compact cameras Nikon DS-Fi1 and Axiocam 208 color mounted on a Carl Zeiss Axio Lab A1 polarizing microscope. The histological nomenclature follows Francillon-Vieillot et al. (1990) and Chinsamy-Turan (2005, 2012b). Chinsamy-Turan (2005) noted that although the orientation of canals in the bone can be used as a proxy to describe the extent and orientation of the vascular canals present in the bone, their orientation does not reflect the orientation of the actual blood vessels (Starck and Chinsamy 2002; Chinsamy and Warburton 2020) as these canals/lumens are often occupied by multiple blood vessels, as well as nerves and various other connective tis-

sues (Chinsamy-Turan 2005). However, the estimation of canal area is comparable in different skeletal elements within a single taxon or in different taxa, as well as through ontogeny (Chinsamy 1993; Chinsamy et al. 2016; Botha and Chinsamy 2004) and therefore provides a maximum estimation of vascularization in each section (Chinsamy 1993).

Results

Our observations revealed that, in general, the bone histology of the specimens is well preserved (Figs. 1–5), although, diagenesis has substantially changed the original orientation of the crystallites in some bones and in these cases obscured some of their histological characteristics. A reddish-brown staining was noticed in a few sections and has been previously attributed to fungal activity or infiltration of humic factors as seen in most archeological settings (Piepenbrink 1986; Jans et al. 2002; Nacarino-Meneses et al. 2021). However, such staining generally occurs in the outer cortex or in the zone of the bone lying in contact with the sediment and therefore suggests a physico-chemical aetiology for the sections studied here (Garland 1987; Lyman 1994; Huculak and Rogers 2009). Our results show that each *Jonkeria* species has unique histological features, which are described separately in the following section.

Jonkeria parva (Boonstra, 1955)

Femur.—Here we studied a series of cross-sections of the femoral (SAM-PK-12233a) shaft proximal to the bite marks observed on the bone surface (previously described by Shelton et al. 2019). In the current study, a detailed histological analysis was performed to assess the limit of the infection and the variation in histology at different levels. All the cross-sections of the femur show a thick compact bone wall and medullary spongiosa. The medullary region is entirely infilled by struts of bony trabeculae in which the pore spaces/openings and resorption cavities are mostly infilled with sedimentary matrix. The primary bone is composed of highly vascularized uninterrupted fibrolamellar bone. Numerous primary osteons are embedded in the interstitial woven bone matrix. Secondary osteons and growth marks are not present.

In addition to the histological features described in Shelton et al (2019), the cross-section more proximal to the bite marks (see Shelton et al. 2019: 1094, fig. 1c) shows woven bone and rich vascularization (Fig. 1A, B). The density of osteocyte lacunae within the woven bone increases towards the bite marks within the same diaphyseal section (Fig. 1B). Vascular canals have a predominantly circumfer-

ential arrangement in the inner and mid-cortex whereas reticular vascular canals dominate towards the peripheral cortex (Fig. 1A), although local patches of simple longitudinal and radial canals are visible in the compacta. Large erosion spaces are present and extensive secondary reconstruction is visible which extend to the interior of the cross-section with some of these erosion spaces enlarged enough to reach cancellous dimensions (Fig. 1A₁). Resorption cavities show varying degrees of centripetal deposition of lamellar bone (Fig. 1A₁).

In the cross-section most distal from the bite marks (Fig. 1C), the density of osteocyte lacunae within the primary bone tissue appears lower. Vascular canals are primarily circumferential and laminar in pattern but are widely spaced (Fig. 1C₁, C₂) compared to the cross-section close to the bite marks (Fig. 1A). However, all the cross-sections have reticular organization of periosteal vascular canals. Radial bony spicules present in the more proximal cross-sections closer to the bite marks (Shelton et al. 2019: 1095, fig. 2a, b) were not observed. The inner cortex is highly porous due to extensive erosional cavities (Fig. 1C₁, C₂) interconnected by laminar vascular canals which result in the formation of cancellous bone.

Radius.—The diaphyseal section of the radius (SAM-PK-12233b; Fig. 2) reveal that the cortex is entirely composed of fibrolamellar bone tissue with a reticular to plexiform arrangement of primary osteons. Reticular vascular canals are dominant in the inner-most cortex and become plexiform containing both radial and circumferential canals towards the subperiosteal cortex (Fig. 2A₁). The vascularization pattern varies within the same diaphyseal section (Fig. 2). The primary matrix consists of woven bone with a random arrangement of collagen fibers (Fig. 2A₁, B₁). An additional distinct feature of this bone is the narrow band of avascular lamellar tissue identified here as an annulus in the mid-cortical region that indicates a slowing down of bone deposition (Fig. 2A₂, A₃) despite the fact that the overall tissue is fibrolamellar associated with numerous primary osteons. Near the inner cortex, large resorption cavities are surrounded by lamellar bone tissue (Fig. 2A₁). The medullary region is occluded with secondary trabeculae (Fig. 2A₁).

Tarsal.—The cross-section of the tarsal (SAM-PK-12233c; Fig. 3) comprises a thick layer of compacted bone that surrounds a central cancellous region; the latter appears to be the secondarily infilled medullary cavity (Fig. 3A₁). The primary bone tissue is highly vascularized, and consists of uninterrupted fibrolamellar bone tissue. Secondary reconstruction occurs in the perimedullary regions of the

Fig. 1. Transverse sections of the femur (SAM-PK-12233a) of *Jonkeria parva* (Boonstra, 1955) from the middle Permian *Tapinocephalus* Assemblage Zone of the Karoo Basin of South Africa. **A.** Histological features of diaphyseal cross-section closest to bite marks; note: change in vascular pattern (dotted line) from circumferential to reticular FLB towards the outer cortex. **B.** Fibrolamellar bone with highly dense osteocyte lacunae (arrows). **C.** Histological features of diaphyseal cross-section away from the bite marks showing less dense osteocyte lacunae (arrows) in the woven bone matrix; note: change in vascular pattern (dotted line) from circumferential to reticular; canals are erosively enlarged (arrowhead in C₂) and these canals result from extensive resorption and become cancellous towards the inner cortex. Abbreviations: po, primary osteon; rc, resorption cavity; wb, woven bone. Photographs under ordinary light (A₁, A₂, B₁, C₁–C₃) and cross-polarized light with lambda compensator (B₂, C₄). →

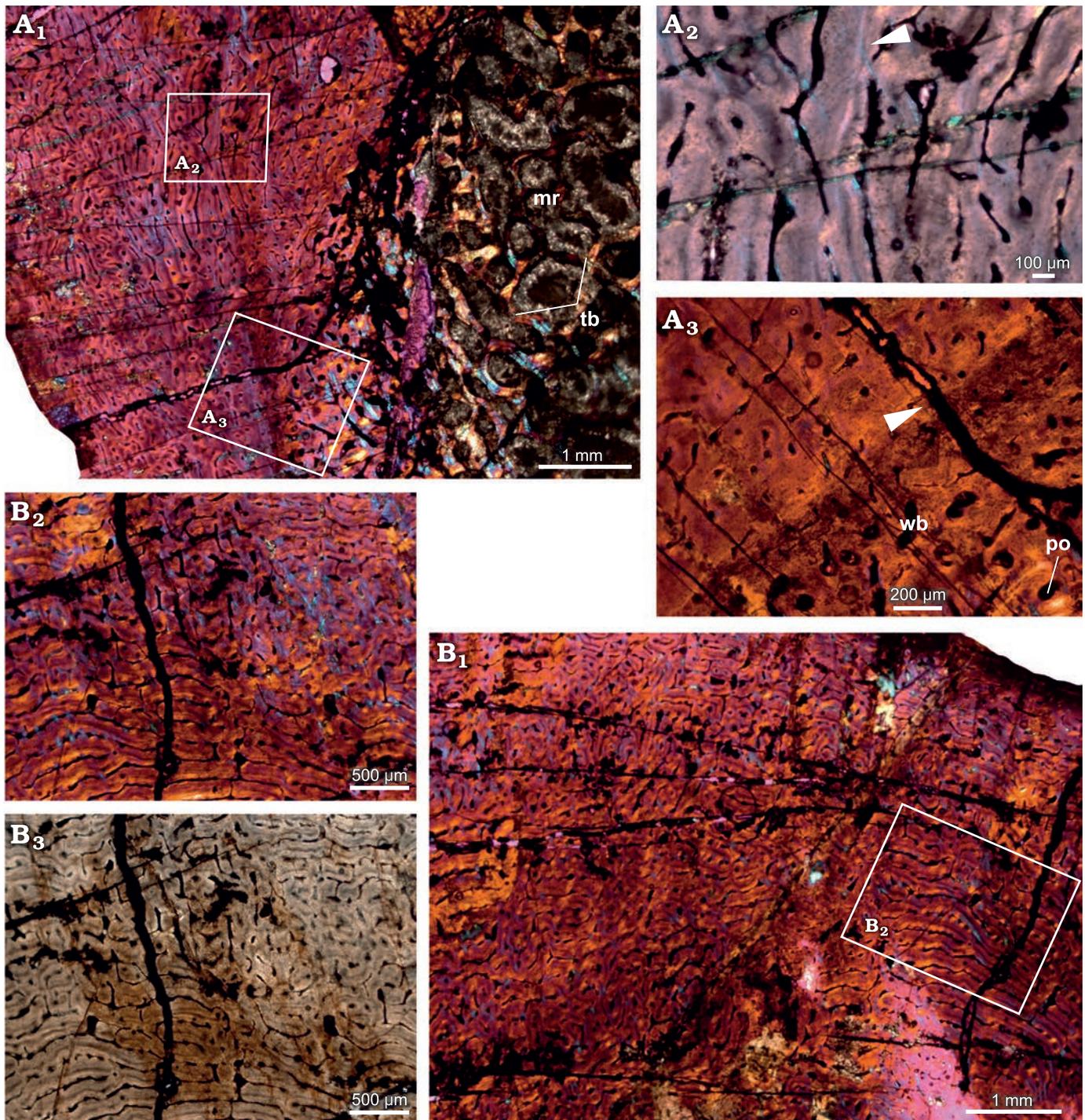


Fig. 2. Transverse sections of the radius (SAM-PK-12233b) of *Jonkeria parva* (Boonstra, 1955) from the middle Permian *Tapinocephalus* Assemblage Zone of the Karoo Basin of South Africa. A₁, diaphyseal cross-section showing highly vascularized fibrolamellar bone tissue in the outer cortex and the medullary cavity filled with bony trabeculae; note: the numerous enlarged resorption cavities in the perimedullary region. A₂, detail showing an annulus with lamellar bone (arrowhead). A₃, detail showing extension of an annulus in the cortex (arrowhead). B₁, fibrolamellar bone tissue with woven matrix in the outer cortex showing circumferential and reticular organization of the vascular canals; B₂, B₃, detail showing the change to a reticular organization of the vascular canals. Abbreviations: mr, medullary region; po, primary osteon; tb, trabeculae; wb, woven bone. Photographs under cross-polarized light with lambda compensator (A₁–A₃, B₁, B₂) and ordinary light (B₃).

cross-section, and several large erosion cavities with a dense network of bony trabeculae are visible (Fig. 3A₁). Vascularization varies throughout the cross-section and decreases in density from the inner to outer cortex

(Fig. 3A₂). Simple longitudinal and reticular vascular canals are observed throughout the cortex (Fig. 3A₃–A₆). Vascular canals are largely reticular laterally (Fig. 3A₅, A₆) and longitudinal canals occur dorsally (Fig. 3A₃, A₄).

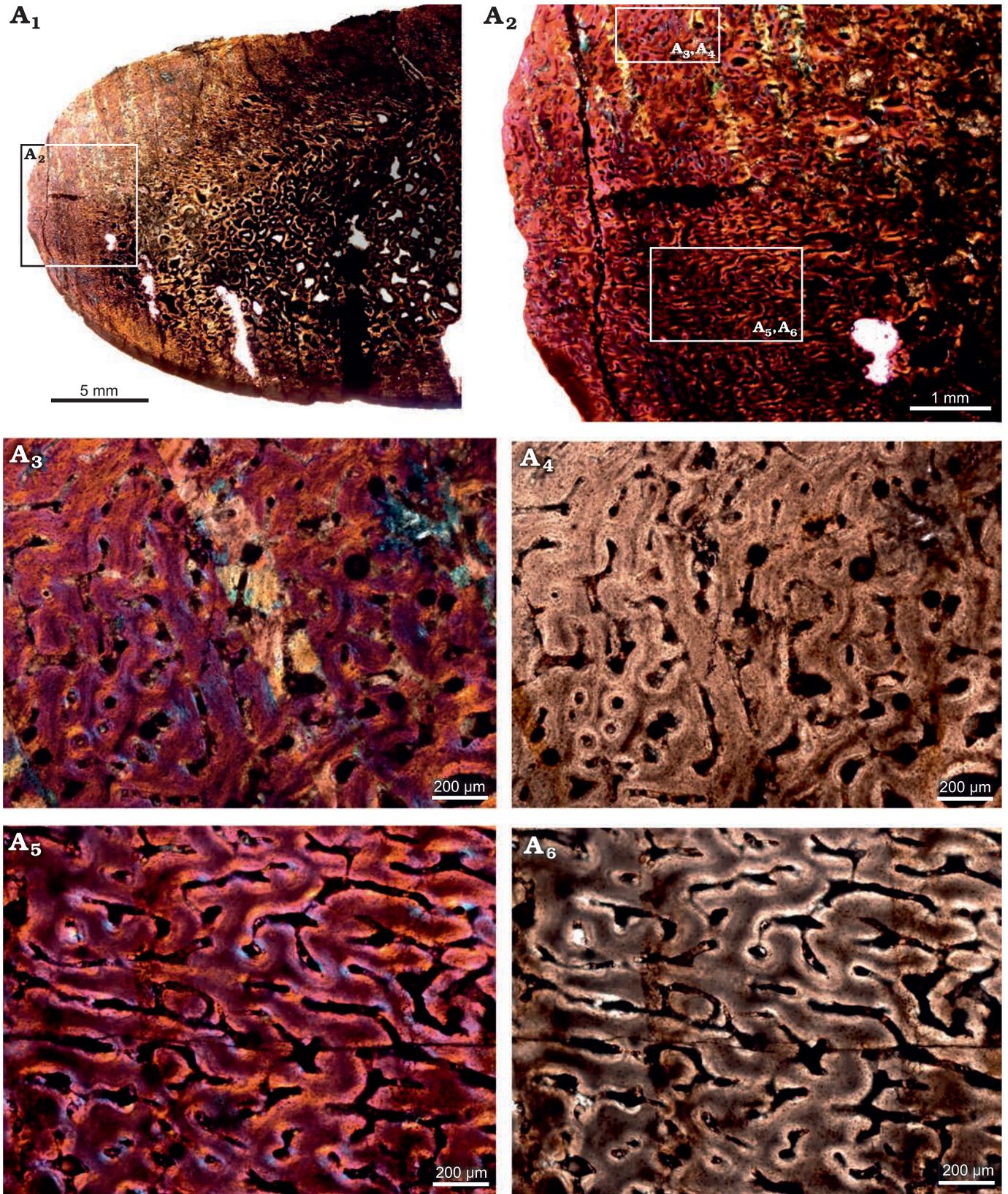


Fig. 3. Transverse sections of the tarsal (SAM-PK-12233c) of *Jonkeria parva* (Boonstra, 1955) from the middle Permian *Tapinocephalus* Assemblage Zone of the Karoo Basin of South Africa. A₁, diaphyseal cross-section showing highly vascularized fibrolamellar bone tissue in the outer cortex and cancellous bone tissue with extensively developed bony trabeculae in the medullary cavity; note: numerous enlarged resorption cavities in the perimedullary region. A₂, detail showing highly vascularized reticular FLB. A₃, A₄, detail showing simple longitudinal vascular canals. A₅, A₆, detail showing reticular vascular canals. Photographs under cross-polarized light with lambda compensator (A₁–A₃, A₅) and ordinary light (A₄, A₆).



Fig. 4. Thin section of a core of the humerus (SAM-PK-11994) of *Jonkeria ingens* (Broom, 1923) from the middle Permian *Tapinocephalus* Assemblage Zone of the Karoo Basin of South Africa. A₁, overall view of humerus showing laminar fibrolamellar bone in the outer cortex and the increasingly cancellous nature of the bone towards the medullary cavity; note: numerous enlarged resorption cavities in the perimedullary cavity, and the layer of indurated sediments at the top of the section. A₂, A₃, highly vascularized laminar fibrolamellar bone. A₄, A₅, details showing a few isolated simple longitudinal vascular canals and primary osteons. A₆, A₇, detail showing large resorption cavities lined by narrow deposit of lamellar bone (arrows). Abbreviations: po, primary osteons; rc, resorption cavity; wb, woven bone. Photographs under ordinary light (A₁, A₂, A₄, A₆), and cross-polarized light with lambda compensator (A₃, A₅, A₇).

Jonkeria ingens (Broom, 1923)

Humerus.—The core sample from the humerus (SAM-PK-11994; Fig. 4) shows a thick, compact cortex surrounding a region of cancellous bone which appears to infill the medullary cavity. Due to intense remodeling in the inner cortex, the transition between the medullary region and cortical bone is progressive. The periosteal bone margin is crushed

and is encrusted by indurated sediments (Fig. 4A₁). The cortical bone is entirely composed of highly vascularized fibrolamellar bone tissues with circumferential vascular canals. These vascular canals form a laminar arrangement with their major axis approximately parallel to the cortical periphery where these canals become closely spaced (Fig. 4A₂, A₃). Several isolated vascular canals show cen-

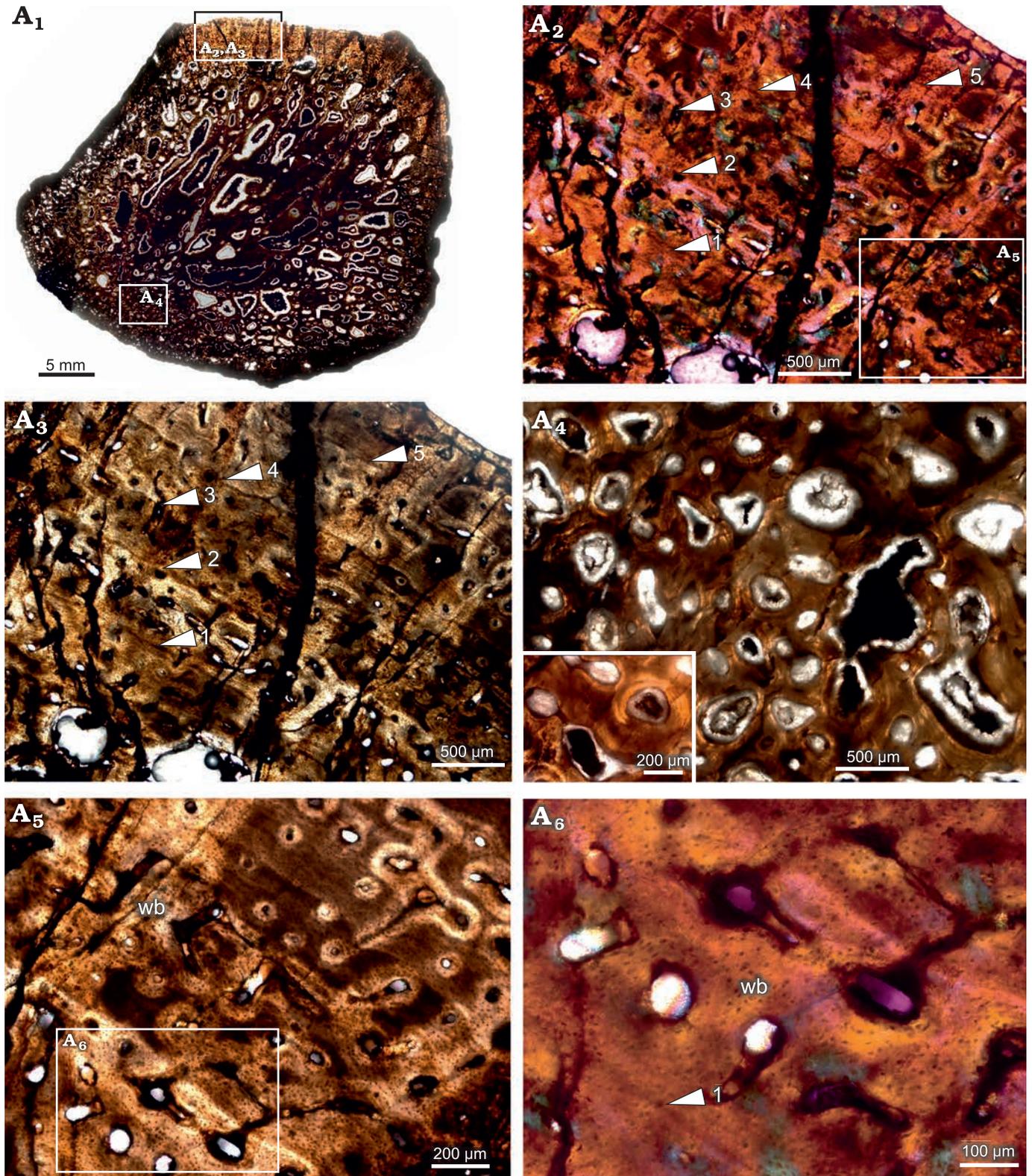


Fig. 5. Transverse section of the rib (BP/1/5409) of *cf. Jonkeria* sp. from the middle Permian *Tapinocephalus* Assemblage Zone of the Karoo Basin of South Africa. A₁, overall view of the rib showing the highly cancellous nature of the cortex; note that only the top area of the section preserves the compact cortical bone tissue. A₂, A₃, detail showing slight change in the tissue type around the lines of arrested growths but overall matrix is woven; note: numbers associated with arrowheads indicate lines of arrested growth (LAGs) in ascending order from the medullary region to periosteal periphery. A₄, detail showing enlarged erosional cavities (inset). A₅, detail showing fibrolamellar bone between lines of arrested growth. A₆, detail showing dense woven matrix; note the change in the density of osteocyte lacunae around the LAG (number associated with arrowhead indicates LAG). Abbreviation: wb, woven bone. Photographs under ordinary light (A₁, A₃, A₄, A₅), and cross-polarized light with lambda compensator (A₂, A₆).

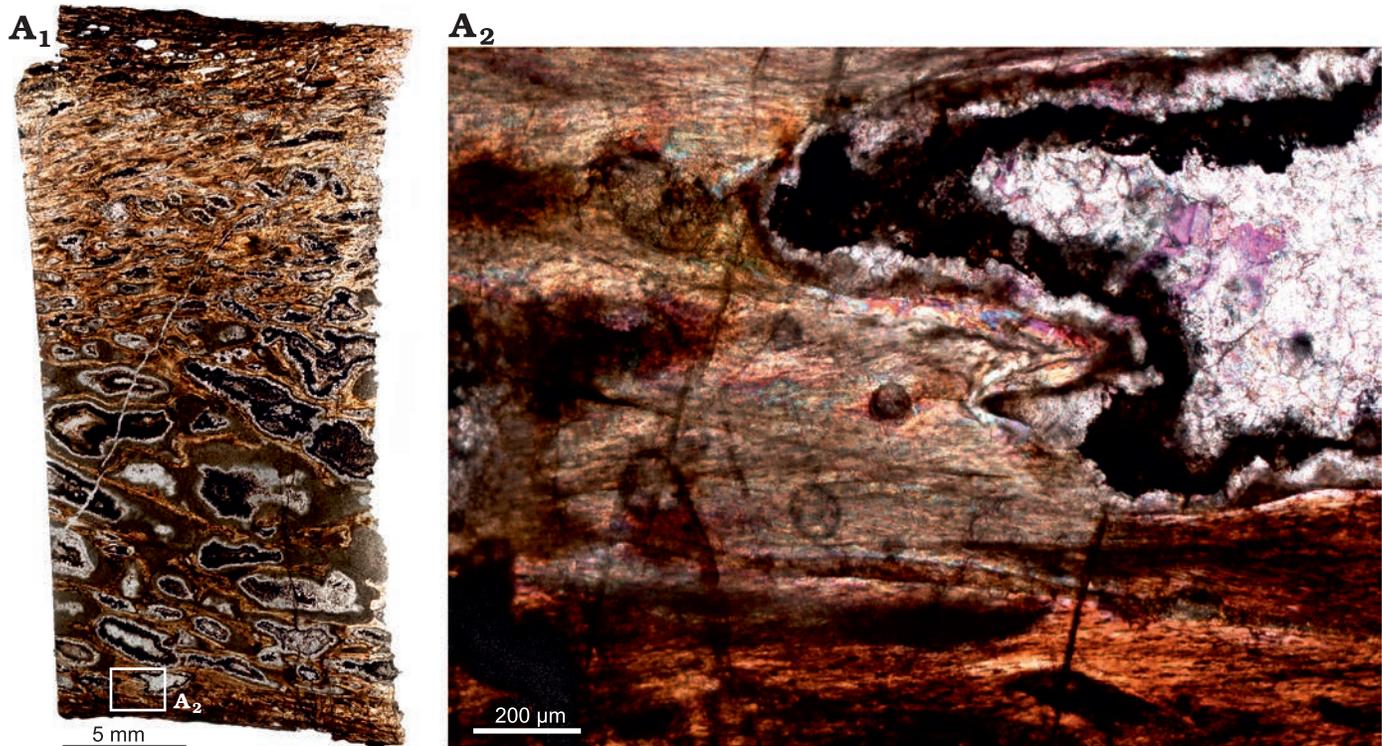


Fig. 6. Longitudinal section of the rib (BP/1/5409) of cf. *Jonkeria* sp. from the middle Permian *Tapinocephalus* Assemblage Zone of the Karoo Basin of South Africa. A₁, overall view of the rib showing highly secondarily remodeled cortex; note: numerous enlarged resorption cavities. A₂, detail showing woven bone and enlarged resorption spaces. Photographs under ordinary light (A₁) and cross-polarized light with lambda compensator (A₂).

tripetal deposition of lamellar bone (Fig. 4A₄, A₅) forming the primary osteons. The medullary region is highly cancellous in nature with large erosional cavities and mostly concentric lamellar deposits along their endosteal surfaces (Fig. 4A₆, A₇). The compact cortex does not exhibit any growth marks.

cf. *Jonkeria* sp.

Rib.—The cross-section of the rib (BP/1/5409; Fig. 5A₁) appears to have a thin outer layer of compacta and a thick inner region consisting of highly remodeled cancellous bone. The amount of cancellous bone varies within a single cross-section and at places, it penetrates the cortex leaving behind only a thin lining of compact bone wall. Overall, the cortical bone is composed of highly vascularized fibrolamellar bone tissue (Fig. 5A₂, A₃), although the tissue surrounding the growth marks indicates slight slowing down of bone deposition (Fig. 5A₅, A₆). Longitudinally organized vascular canals are prevalent, but an occasional reticular canal is observed. Secondary reconstruction is extensive throughout the cortex resulting in large resorption cavities (Fig. 5A₁, A₄). Many of these cavities are infilled by centripetally deposited lamellar bone (Fig. 5A₄). The primary cortex exhibits five widely spaced growth marks (Fig. 5A₂, A₃). It should be noted here that there is a slight change in the tissue type and texture surrounding growth marks, but overall, the matrix is woven. In longitudinal sections the predominant tissue appears to be fibrolamellar with a woven texture (Fig. 6).

Discussion

Although the early research on dinocephalian bone histology (de Ricqlès 1972) was conducted on mostly fragmented bones at a generic level, it provided an important basis for subsequent study (Chinsamy-Turan 2012b; references therein). Fibrolamellar bone tissue dominates the limb bone histology of various therapsids and implies that this fast-growing tissue appeared early in the evolution of therapsids (de Ricqlès 1972; Chinsamy and Rubidge 1993; Ray et al. 2004, 2009; Chinsamy-Turan 2012a, b). This supposition was supported by the subsequent finding of fibrolamellar tissue in the postcrania of the more basal late Carboniferous and early Permian pelycosaur-grade, non-mammalian synapsids (Shelton and Sander 2017). Classically pelycosaurs were first reported as having slowly formed, lamellar-zonal bone tissue with fibrolamellar bone reported in the extended neural spines of some species (Enlow and Brown 1956, 1957, 1958; Enlow 1969; de Ricqlès 1974; Huttenlocker et al. 2010). However, Huttenlocker et al. (2010) reported extensive parallel-fibered bone in addition to lamellar and fibrolamellar bone in the neural spines of *Sphenacodon* and *Dimetrodon*. Even though fibrolamellar bone tissue occur in the herbivorous tapinocephalids, de Ricqlès (1972) reported an overall lamellar bone matrix with a richly vascularized dense Haversian system within *Titanosuchus*, the sister taxon of *Jonkeria*. Shelton et al. (2019) first reported the presence of

highly vascularized, uninterrupted fibrolamellar tissue in a femur of *Jonkeria parva*.

In the current study, all the sectioned *Jonkeria* bones exhibit highly vascularized fibrolamellar bone, which indicates rapid rates of bone deposition (Amprino 1947; Francillon-Vieillot et al. 1990; de Margerie et al. 2002; Starck and Chinsamy 2002; Chinsamy-Turan 2005). In addition, the presence of vascular canals at the peripheral margin of the bone wall indicates that periosteal growth was still ongoing at the time of death (Botha and Chinsamy 2004; de Margerie et al. 2004; Bhat et al. 2019). Except for the rib (BP/1/5409), there is no direct evidence of slowing down or termination of growth in the external cortex of the sectioned bones. This implies that skeletal elements from two individuals are from young animals (e.g., Ray et al. 2005). However, the occurrence of an annulus in the radius (SAM-PK-12233b) suggests a temporary slowing down of growth during adverse environmental conditions (Hutton 1986; Chinsamy et al. 1998, 2020; Botha and Chinsamy 2005; Ray et al. 2005; Chinsamy-Turan 2005; Köhler et al. 2012; Chinsamy and Warburton 2020; Chinsamy and Worthy 2021). A slight change in tissue type was noticed in the rib (BP/1/5409) with five lines of arrested growth (LAGs, *sensu* Francillon-Vieillot et al. 1990; Castanet et al. 1993; Chinsamy et al. 1995) interrupting woven bone, suggesting that this element is from an ontogenetically older individual that had experienced periodic pauses in bone deposition and hence growth. The presence of multiple growth lines/marks indicates a flexible growth strategy (Starck and Chinsamy 2002) and directly suggests that this individual grew in an interrupted manner (Chinsamy-Turan 2005). This growth strategy is plesiomorphic for extant and extinct mammals (Chinsamy and Rubidge 1993; Botha and Chinsamy 2000; Ray et al. 2004; Chinsamy and Hurum 2006; Ray et al. 2009, 2010; Buffrénil and Lambert 2011; Hurum and Chinsamy 2012; Montoya-Sanhueza and Chinsamy 2017, 2018; Nacarino-Meneses and Orlandi-Oliveras 2021; Nacarino-Meneses et al. 2021; Chinsamy and Warburton 2021). Such LAGs have also been found in several dinosaur species (e.g., Chinsamy 1990; Starck and Chinsamy 2002; Chinsamy-Turan 2005; Klein and Sander 2008; Chinsamy and Tumarkin-Deratzian 2009; Köhler et al. 2012; Krupandan et al. 2018; Woodward 2019; Cullen et al. 2020), including fossil birds (e.g., Angst et al. 2017; Chinsamy et al. 2020; Chinsamy and Worthy 2021).

The bone histology of multiple skeletal elements of different species of *Jonkeria* shows a predominance of highly vascularized uninterrupted fibrolamellar bone tissue in the cortices, while the medullary regions were completely infilled by cancellous bone tissue. Based on the bone histology documented in different taxa, we conclude that *Jonkeria* had an overall fast growth rate. However, it appears that adverse environmental conditions may have interrupted or even ceased growth as shown by the occurrence of an annulus in the mid-cortical region of the radius, as well as multiple growth marks in the periosteal cortex of the sampled rib.

It is also possible that the interrupted growth of the rib may reflect a difference in rib growth during late ontogenetic stages.

Comparative bone histology of *Jonkeria*.—Several taxon-specific histological variations were noticed in the skeletal elements of the studied taxa, which reflects slight differences in growth trajectories. However, it should be noted that the different bones of the different species were recovered from different localities, and individuals from these different species possibly experienced different environmental conditions. Specimens of *Jonkeria parva* and *J. ingens* are characterized by having a thick cortex of primary fibrolamellar bone with numerous primary osteons. Both lack any evidence of slowing down of growth. *J. ingens* has a thick cortex with a predominantly laminar fibrolamellar bone organization, whereas *J. parva* shows a reticular to plexiform fibrolamellar bone tissue, although the femur (SAM-PK-12233a; Fig. 1) has mostly circumferential vascular canals in the interior cortex and reticular canals in the peripheral cortex. In both species, the medullary regions are highly remodeled and completely infilled with cancellous bone tissue (Figs. 1–4). The latter has large erosional cavities which are lined by lamellar bone tissue (Fig. 4A₆, A₇). The amount of cancellous bone tissue varies in both species. Another similarity between the two species is the absence of bone growth marks/LAGs (Peabody 1961; Smirina 1974; Castanet 1982; Castanet and Baez 1991; Castanet et al. 1988, 1993; Francillon-Vieillot et al. 1990; Chinsamy et al. 1995). However, a narrow strip of poorly vascularized lamellar bone tissue was noticed in the radius of *J. parva*. Of all the specimens, the rib of cf. *Jonkeria* sp. was most different since it showed five LAGs in the outer cortex which represent temporary pauses in growth (Chinsamy-Turan 2005).

Histovariation.—Apart from the presence or absence of annuli and bone growth marks, differences in the degree of vascularization, secondary reconstruction and tissue organisation were observed among the different skeletal elements of a single individual. Variations in the site-specific orientation of the primary vascular canals and tissue organisation are noted within the same diaphyseal section. As bone histology is affected by phylogenetic, ontogenetic, functional and biomechanical constraints, inter-elemental and intraskeletal variations are not surprising within the single skeleton or between individuals (e.g., Starck and Chinsamy 2002; Chinsamy-Turan and Ray 2012; Bhat et al. 2019; Chinsamy and Warburton 2020).

One of the noteworthy features with regards to the pathological femur (SAM-PK-12233a) is that the density of osteocyte lacunae is higher (Fig. 1B) and there is a closer spacing between vascular canals nearer to the site of the bite marks. In addition, further away from the site of infection, such as in the midshaft region there are no radial spicules (see Shelton et al. 2019). Most of the canals within this section are erosionally enlarged; they result from an extensive resorption, become cancellous towards the inner cortex

(Fig. 1C₁, C₂) and when present in large numbers represent haemopoiesis (sensu Ray et al. 2009, 2010). Thus, based on the histological features observed in the femur shaft, we believe that the infection was localised in nature.

Although our sample size was small, inter-elemental histological variation within the same taxon were noted. A marked variation between the femur, radius and tarsal of *J. parva* is the degree of vascularization and orientation of vascular canals. In contrast to the femur which has laminar and reticular fibrolamellar bone in the inner and outer cortex, the radius and tarsal have a large amount of reticular fibrolamellar bone surrounding cancellous medullary regions. Isolated radial and longitudinal canals are scattered throughout the cortex. It may be also noted that the different types of organization of the vascular canals suggest slight differences in the rate at which fibrolamellar bone was deposited in the different skeletal elements. A single annulus is present in radius SAM-PK-12233b (Fig. 2A₂, A₃). Bone growth marks are absent in both *J. parva* and *J. ingens*. The humerus of *J. ingens* has circumferential vascular canals in the mid- and outer-cortex. The amount of cancellous bone tissue varies across the cross-section and it appears that the primary compact bone was resorbed to reach such cancellous proportions. The absence of lines of arrested growth and the presence of highly vascularized woven bone in the limb bones of both *Jonkeria* species suggests uninterrupted, rapid growth (Peabody 1961; Smirina 1974; Castanet 1982; Castanet and Baez 1991; Castanet et al. 1988, 1993; Francillon-Vieillot et al. 1990; Chinsamy et al. 1995) at least during early ontogeny. On the other hand, the rib fragment of cf. *Jonkeria* sp. has five equally spaced growth marks which indicate periodic cessation of growth during some adverse environmental conditions (Chinsamy-Turan 2005). This finding further suggests that the rib may have come from an older individual as compared to the other skeletal elements studied.

Lifestyle adaptations.—It is well known that bone density and cortical thickness are correlated with mode of life (Wall 1983; Chinsamy 1997; Germain and Laurin 2005; Gray et al. 2007; Laurin et al. 2011; Houssaye et al. 2016; Canoville and Chinsamy 2017). A semi-aquatic lifestyle requires an increase in bone density to counterbalance hydrological buoyancy (Chinsamy 1991; Gray et al. 2007; Hayashi et al. 2013) and often leads to a greater bone wall thickness (Wall 1983). However, burrowing/fossorial animals also have thick bone walls (Bramble 1982; Ultsch and Anderson 1988; Lips 1991; Magwene 1993; Ray and Chinsamy 2004; Botha and Chinsamy 2004, 2005; Chinsamy and Abdala 2008; Lyson et al. 2016; Montoya-Sanhueza and Chinsamy 2017; Legendre and Botha-Brink 2018; Bhat et al. 2019) as compared to terrestrial animals which have lower relative bone thickness (RBT) values (<30%; sensu Wall 1983). In this situation it is important to consider other morphological adaptations for burrowing (e.g. *Cistephalus*, Nasterlack et al. 2012; *Bathyergus*, Montoya-Sanhueza and Chinsamy

2017), as well as other morphological features that might aid in deducing their lifestyle habits (Houssaye et al. 2016). In addition to peculiar cranial and postcranial characteristics of *Jonkeria* (e.g., a long snout, a heavily built skull and shorter limbs), there is no record of their association with burrows; therefore, it is unlikely that *Jonkeria* were fossorial.

In the current study, all the bones are characterized by thick bone walls and an extensive development of cancellous bone in the medullary regions. Similar bone tissues have been reported in *Lystrosaurus murrayi* (Ray et al. 2005; Botha 2020). Based on this type of bone histology, Ray and Chinsamy (2005) proposed a semi-aquatic/aquatic lifestyle for *Lystrosaurus*. However, more recently using the same histological features, Botha (2020) proposed a fully terrestrial mode of life for *Lystrosaurus*. Botha (2020) further suggested biomechanical constraints to support the large body weight as the cause of the extensive development of medullary spongiosa. However, in a study of graviportal and aquatic tetrapods Houssaye et al. (2016) reported that the humeri, femora, and ribs change their shape and internal bone microanatomy (i.e., increasing bone compactness and reducing medullary cavities). In particular, ribs show stronger changes in compactness in aquatic taxa as compared to graviportal taxa, which is in accordance with a role in buoyancy and body trim control in shallow waters (Chinsamy 1991; Gray et al. 2007; Hayashi et al. 2013; Houssaye et al. 2016) rather than a role in weight-bearing on land (Ray et al. 2010; Houssaye et al. 2016), contra Botha (2020).

It is also worth noting that middle Permian pareiasaurs, which were similarly large extinct tetrapods contemporaneous with dinocephalians, exhibited spongy stylopod diaphyses and thin compact cortices, though not to the same extent as dinocephalians (Canoville and Chinsamy 2017). Isotopic analysis of the teeth of dinocephalians, pareiasaurs and therocephalians has shown that these large graviportal animals inhabited different ecological niches during middle and late Permian times, with pareiasaurs and therocephalians sharing a terrestrial habitat (Canoville et al. 2014). Furthermore, contra Botha (2020), elephants (Houssaye et al. 2016), giraffes (Smith 2020), and bison (Sander and Andrassy 2006; Houssaye et al. 2016; Canoville et al. 2016), which are large, graviportal terrestrial animals do not have medullary cavities infilled with spongy bone tissue as a biomechanical adaptation for their bulk. In addition, as in *Jonkeria*, the ribs of the known aquatic reptile, *Claudiosaurus* (Buffr enil and Mazin 1989) show a complete infilling of the medullary region by cancellous bone and, are considered pachyostotic as an adaptation for a semi-aquatic lifestyle (de Ricql es and Buffr enil 2001). Given these similarities, we cautiously propose that the bone histology of *Jonkeria* is indicative of a semi-aquatic habitat, though we note that further sampling and more data would be needed to further test this hypothesis.

Other physiological inferences.—Following earlier work (e.g., Reid 1987; Chinsamy 1990; Chinsamy-Turan 2005; Chinsamy and Hillenius 2004), we believe that bone tissue types cannot be used to differentiate between endothermic and ectothermic tetrapods. However, it is evident that the different types of tissues provide valuable information about the rate at which the bone was deposited (Amprino 1947; Reid 1987; Chinsamy 1990; Starck and Chinsamy 2002; Chinsamy-Turan 2005; Chinsamy and Hillenius 2004). Since the bone histology of *Jonkeria* is dominated by fibrolamellar bone with abundant primary osteons it directly suggests that this bone was laid down rapidly (Amprino 1947; Francillon-Vieillot et al. 1990; de Margerie et al. 2002; Starck and Chinsamy 2002; Chinsamy-Turan 2005). In addition, the extensive development of vascular canals is commensurate with rapid rates of bone formation irrespective of whether the animal is ectothermic or endothermic (e.g., Reid 1987, Chinsamy and Hillenius 2004). More recently, using phylogenetic eigenvector maps Faure-Brac and Cubo (2020) proposed an ectothermic metabolism for the synapsid *Ophiacodon uniformis* and an endothermic metabolism for the anomodonts (e.g., *Lystrosaurus* sp.) although both have fibrolamellar bone tissue (Shelton and Sander 2017; Botha 2020). Indeed, if *Jonkeria* were included in the Faure-Brac and Cubo (2020) study, it would likely also be considered endothermic. Thus, it is apparent that deciphering the thermal physiology of an extinct animal on the basis of its histology is highly contested (see for example, Chinsamy and Hillenius 2004). Furthermore, despite some suggestions of a correlation between osteocyte lacunae size and thermophysiology (Huttenlocker and Farmer 2017), more evidence is needed. On the basis of our histological findings, we can assert that during early ontogeny *Jonkeria* experienced rapid sustained rates of growth, whereas later in ontogeny (as seen in the rib) they experienced cyclical rates of growth. Like large sauropodomorph dinosaurs (e.g., Cerda et al. 2017), the varying rates of growth during ontogeny are probably related to the attainment of large body size, i.e., during early ontogeny they experienced sustained uninterrupted growth to reach a large body size, whereas in later stages of ontogeny (perhaps once sexual maturity was attained), they experienced slower cyclical growth patterns.

Conclusions

- Histological assessment of multiple skeletal elements of the dinocephalian *Jonkeria* from the middle Permian of South Africa reveals that the cortex is predominantly composed of uninterrupted fibrolamellar bone. Most of the vascular canals are circumferentially oriented with inner laminar and peripheral reticular patterns. However, site-specific variation in vascular pattern is noticed in different skeletal elements. Predominance of fibrolamellar bone suggests rapid osteogenesis and an overall fast rate of bone deposition and growth for *Jonkeria*.

- In the rib of cf. *Jonkeria* sp., five growth marks were observed, suggesting periodic interruptions in growth during later stages of ontogeny.
- Several taxon-specific histological variations were noticed in the skeletal elements of the studied taxa, which reflects slight differences in growth trajectories.
- Inter-elemental histological variation was noted in terms of the orientation of the vascular canals and primary osteons, incidence of annuli and bone growth marks, and extent of secondary medullary reconstruction.
- The bone histology of the *Jonkeria parva* femur (SAM-PK-12233a) reveals that the pathology/bone infection was localized, restricted to the vicinity of the bite marks (Shelton et al. 2019) and that the rest of the shaft was unaffected.
- All the skeletal elements are characterized by a thick cortex and extensively developed medullary spongiosa, which is highly suggestive that *Jonkeria* may have been semi-aquatic like the graviportal *Hippopotamus* (Houssaye et al. 2016). A good test of this hypothesis would be to assess the bone microstructures of larger sample of skeletal elements for each studied species.
- This histological study of *Jonkeria* suggests that during early ontogeny, individuals grew rapidly and uninterruptedly, whereas later in ontogeny they grew in an interrupted manner.

Authors' contributions

AC developed the initial concept for the research. AC, CDS, and MSB devised and planned the research strategy. CDS performed the original histological sectioning. MSB polished the histological sections, performed data collection and analysis, and wrote the first draft of the manuscript. AC assisted with the sample selection and supervised the histological work and reviewed the drafts of the manuscript. CDS read and contributed to the final draft.

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