Osteohistology of the Triassic archosauromorphs
Prolacerta, Proterosuchus, Euparkeria, and
Erythrosuchus from the Karoo Basin of South Africa

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OSTEOHISTOLOGY OF THE TRIASSIC ARCHOSAUROMORPHS PROLACERTA, PROTEROSUCHUS, EUPARKERIA, AND ERYTHROSUCHUS FROM THE KAROO BASIN OF SOUTH AFRICA

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ABSTRACT—The South African non-archosauriform archosauromorph Prolacerta and the archosauriforms Proterosuchus, Erythrosuchus, and Euparkeria were important constituents of the Early to early Middle Triassic Karoo ecosystem following the end-Permian mass extinction. We present new data on the osteohistology of these stem archosaurs and provide insight into their paleobiology. Bone tissues of the Early Triassic Prolacerta contain a poorly defined fibro-lamellar complex, with parallel-fibered bone in some regions, whereas the contemporaneous Proterosuchus exhibits rapidly forming uninterrupted fibro-lamellar bone early in its ontogeny, which becomes slow forming lamellar-zonal bone with increasing age. The early Middle Triassic Erythrosuchus deposited highly vascularized, uninterrupted fibro-lamellar bone throughout ontogeny, whereas the growth of the contemporaneous Euparkeria was relatively slow and cyclical. When our data are combined with those of previous studies, preliminary results reveal that Early and Middle Triassic non-crown group archosauromorphs generally exhibit faster growth rates than many of those of the Late Triassic. Early rapid growth and rapid attainment of sexual maturity are consistent with life history expectations for taxa living in the unpredictable conditions following the end-Permian mass extinction. Further research with larger sample sizes will be required to determine the nature of the environmental pressures on these basal archosaurs.

INTRODUCTION

Archosauria, which includes crocodilians, birds, and their extinct relatives diversified during the Middle Triassic to become the dominant clade of terrestrial vertebrates for the remainder of the Mesozoic Era. The stem archosaurs, i.e., non-archosaurian Archosauromorphia (sensu Gauthier, 1986), first appeared during the Late Permian, but only became abundant during the Triassic Archosauromorpha (sensu Gauthier, 1986), first appeared during the Mesozoic Era. The stem archosaurs, i.e., non-archosaurian Archosauriformes (sensu Gauthier, 1986), and non-archosaurian Archosauromorphs (sensu Gauthier, 1986), the last group comprises proterosuchids, erythrosuchids, protorochampsids, euparkeriids, and several isolated genera.

There has been much debate regarding the phylogenetic relationships of the basal Archosauromorpha (e.g., Gauthier, 1986; Benton and Clark, 1988; Sereno and Arcucci, 1990; Sereno, 1991; Parrish, 1992, 1993; Juul, 1994; Gower, 2003; Gower and Sennikov, 1996, 1997, 2000). Thus, research on this group has focused on re-examining basal archosaur morphology in order to better assess archosauromorph relationships (Gower, 2003). Relatively fewer studies have directed their efforts towards understanding the growth of these animals. As most basal archosauromorph taxa lived during the Early and Middle Triassic, they formed an important part of the recovery ecosystem immediately following the end-Permian mass extinction (Botha and Smith, 2006; Sahney and Benton, 2007). The Early Triassic was a time of severe ecological crisis and instability in both the terrestrial (Roopnarine et al., 2007) and marine realms (Payne et al., 2004; Bottjer et al., 2008). The global climate during the Triassic is characterized as being particularly harsh and arid with highly seasonal, unreliable quantities of rainfall (Smith, 1995; Smith and Ward, 2001). Animals living in unpredictable environments often respond by growing rapidly in order to reach sexual maturity as quickly as possible, a strategy that has been observed in living taxa (e.g., Cardinales and Modin, 1999; Curtin et al., 2009). Thus, exploring the biology and ecology of basal archosauromorphs can provide insight into the life histories of extinct terrestrial vertebrates living in an unpredictable, drought-prone environment. In this way, this study is a test of the application of life-history theory to extinct communities.

Here we present new data on the osteohistology of the non-archosauriform archosauromorph Prolacerta broomi Parrington, 1935, and the archosauriforms Proterosuchus fergusi Broom, 1903, Erythrosuchus africanus Broom, 1905, and Euparkeria capensis Broom, 1913, with some interpretation of the paleobiology of the basal archosaurs.

TAXA EXAMINED IN THIS STUDY

The Early Triassic non-archosauriform archosauromorph Prolacerta broomi (Fig. 1) was included in this study as an archosauriform outgroup. It is a small (80 mm skull length) archosauromorph, known from South Africa and Antarctica, that was initially thought to be the precursor of squamates (Robinson, 1967, 1973). However, more complete descriptions of the animal (Gow, 1975; Modesto and Susies, 2004) have revealed it to be the sister taxon of archosauriforms (Dilkes, 1998; Modesto and Susies, 2004).

The earliest archosauriform taxon known from South Africa is the medium-sized (approximately 2 m in body length) Proterosuchus fergusi (Reig, 1970; Welman, 1998). The lifestyle of this animal has been speculated upon by several authors. Broom (1932), Broili and Schröder (1934), Reig (1970), and Cruickshank...
(1972) proposed a semi-aquatic lifestyle for the animal, based on its body proportions and horizontal zygapophyses (which are similar to those of extant crocodilians), the supposedly wet climate in which it lived, and its association with *Lystrosaurus*, a dicynodont therapsid that was then presumed to be amphibious. However, more recent sedimentological analyses interpret the climate of this period as relatively arid, with highly seasonal unpredictable rainfall (Smith, 1995; Smith and Ward, 2001). The lifestyle of *Lystrosaurus* is also a contentious issue. Broom (1902, 1903) and Watson (1912, 1913) first proposed an aquatic lifestyle, which was recently supported by Ray et al. (2005). In contrast, King (1991), King and Cluver (1991), and Botha and Smith (2006) proposed a terrestrial lifestyle for the animal. Furthermore, Cruickshank (1972) also noted that the position of the external nares in *Proterosuchus*, the vertically oriented occipital region (which differs from typical aquatic crocodilians), and the well-ossified limbs, carpus, and tarsus indicated a terrestrial lifestyle for this taxon (Cruickshank, 1972). Similarly, Welman (1998) also observed the absence of dorsally oriented nares, a feature that Nesbitt et al. (2009) noted is typical of aquatic reptiles such as crocodilians, phytosaurs, mesosaurs, and plesiosaurs (Camp, 1930; Mazin, 2001; Modesto, 2006). Thus, the lifestyle of *Proterosuchus* remains unresolved, but the weight of evidence is for a terrestrial rather than aquatic lifestyle. *Proterosuchus* (Fig. 1) is important in Pangaeanscale reconstructions of Early Triassic paleobiogeography in that it is the first new terrestrial taxon to appear above the Permo-Triassic boundary in the Karoo-aged basins of South Africa and Russia (Benton et al., 2004; Smith and Botha, 2005). It was the most prominent predator in the main Karoo Basin during the earliest Triassic, but was supplanted in the Middle Triassic by the more derived archosauriform *Erythrosuchus africanus*.

*Erythrosuchus* (Fig. 1) represents the first of many radiations of large carnivores during the Middle Triassic (Parrish, 1992). It was larger than *Proterosuchus* (up to 5 m in length) with a disproportionately large head (Hughes, 1963; Gower, 2003). Earlier researchers proposed an aquatic mode of life to support the large head (von Huene, 1911; however, later researchers consider it to be completely terrestrial (e.g., Tatarinov, 1961; Parrish, 1992).

Another well-known archosauriform from the Middle Triassic of South Africa is the smaller (<1 m in length), but more derived *Euparkeria capensis* (Fig. 1) (Sereno, 1991). Once included within the Archosaurus as a basal ‘ornithosuchian’ (Gauthier, 1984), it is now considered to be an archosauriform (Parrish, 1992; Juul, 1994; Gower and Wilkinson, 1996) and is widely accepted as being closely related to the common ancestor of dinosaurs and crocodilians (Gower and Wilkinson, 1996).

**Previous Studies**

The morphology of the skulls and postcrania of *Prolacerta*, *Proterosuchus*, and *Euparkeria* have been described in detail (e.g., Broom, 1903, 1913; Ewer, 1965; Gow, 1975; Welman, 1998; Gower, 2003; Modesto and Sues, 2004) and although the postcranial skeleton of *Erythrosuchus* has yet to be adequately described (due to fragmentary material), the skull, ankle, and isolated postcranial elements have been described (e.g., von Huene, 1911; Brink, 1955; Cruikshank, 1978; Parrish, 1992; Gower, 1996, 2003). To date, very little is known about the growth patterns of these animals because, due to their rarity, complete ontogenetic series are not available for any of these taxa.

The study of bone histology (microstructure) is a well-established technique for analyzing the growth of extinct animals. By comparing the bone tissues of extant animals with those of living taxa, the growth patterns, ontogenetic status, and, indirectly, aspects of the physiology of fossil taxa can be inferred (Amprino, 1947; Enlow and Brown, 1956, 1957; de Ricqlès, 1976). Gross (1934) and later de Ricqlès (1976) briefly described the bone microstructure of *Erythrosuchus* as rapidly forming azonal fibro-lamellar bone, and their results were recently confirmed by de Ricqlès et al. (2008). These authors assessed the bone histology of 12 Triassic archosaurs, including a range of non-dinosaurian archosauriforms and dinosaurs, in a phylogenetic context. *Euparkeria* was also briefly mentioned in this study, but the description was based only on a possible humerus, osteoderms, and rib fragments (de Ricqlès et al., 2008). This sizeable contribution provided an important foundation from which further research could develop.

**MATERIALS AND METHODS**

The study material consists of 20 limb bones and ribs from four Early to Middle Triassic archosauriform taxa from the Karoo Basin of South Africa (Table 1). These include one individual of *Prolacerta broomi* (NMQR 3763), three individuals of *Proterosuchus fergusi* (SAM-PK-K140, SAM-PK-11208, NMQR 880), three individuals of *Erythrosuchus africanus* (SAM-PK-K10025, SAM-PK-1118, NMQR 3675), and three individuals of *Euparkeria capensis* (SAM-PK-K10010, SAM-PK-13666, SAM-PK-K10548). Limb bones were preferentially selected because they contain the least secondary remodeling in the midshaft regions and hence exhibit the most complete growth record of the animal (Chinsamy, 1990, 1991, 1995; Francillon-Vieillot et al., 1990; Horner et al., 1999). However, ribs and other fragments were also examined to provide further data. Histological analysis is a destructive sampling technique and limb bones of these taxa are relatively rare, which poses difficulties in obtaining enough material for this type of study. Despite this, we were fortunate in obtaining various associated limb bones from single individuals as well as homologous elements from multiple specimens, allowing us to consider inter- elemental and inter-individual variation when documenting the growth patterns of these taxa.

In South Africa, *Prolacerta* and *Proterosuchus* are known from the Lower Triassic *Lystrosaurus Assemblage Zone* and *Erythrosuchus* is restricted to the overlying Middle Triassic *Cynognathus Assemblage Zone* (*Cynognathus* zone B; Hancox et al., 1995) (Table 1). The study material of all these taxa was positively identified through the association of the elements with skull material. *Euparkeria* is known from a single locality on the outskirts of the town Aliwal North from the Middle Triassic *Cynognathus Assemblage Zone* (also *Cynognathus* zone B). The material includes several similar-sized adult individuals (Ewer, 1965) preserved on a number of sandstone blocks intermingled with three specimens of the rhynchosaur *Mesosuchus browni* (Dilkes, 1998). The study

**FIGURE 1.** Phylogenetic relationships of the archosauromorph taxa examined in this study (in bold). Phylogeny taken from Sues (2003), Dilkes and Sues (2009), and Nesbitt et al. (2009).
material taken from these blocks was positively identified as *Euparkeria capensis* by comparing the limb bone morphology to the associated articulated skeletons with skulls. This allowed for conclusive species identification, something that has not been done previously with *Euparkeria capensis*.

All elements were measured and photographed prior to thin sectioning. An estimate of ontogenetic age was also calculated for each element using skull lengths and associated limb bone measurements from the largest known specimens of each genus. As the mid-diaaphysis experiences the least secondary remodeling and thus provides the most complete information about the life history of the animal, elements were thin-sectioned in this region wherever possible. The thin-sectioning process was conducted at the National Museum, Bloemfontein, following procedures outlined by Chinsamy and Raath (1992). The bone microstructure was viewed and photographed using a Nikon Eclipse 50i Polarizing microscope and DS-Fi1 digital camera. Bone histology terminology follows that of Francillon-Vieillot et al. (1990) and Reid (1996).

The organization and density of the vascular canals in cortical bone is closely related to bone apposition rate (e.g., Amprino, 1947; Margerie et al., 2002). Quantifying the relative area occupied by the vascular canals in a given section of bone provides a quantitative method for comparing relative vascular density between different taxa. This process reflects the maximum possible vascularization for each element, as the channels would have included lymph and nerves as well as blood vessels (Starck and Chinsamy, 2002). The relative vascular area or cortical porosity was quantified using the image analysis program NIH ImageJ. It was calculated by taking the total canal area and dividing it by the total cortical area for each thin section and then multiplying by 100 to obtain a percentage. A completely solid, avascular bone would have a cortical porosity of 0%, whereas a completely porous bone would have a cortical porosity of 100%.

The diaphyseal cortical thickness of the limb bones was also calculated where possible. Several factors, including phylogeny, biomechanics, ontogeny, body size, and environmental fluctuations, influence the microstructure of bones (e.g., Cubo et al., 2005; Kriloff et al., 2008). However, numerous studies have shown that lifestyle preferences affect the bone microstructure of an animal as well (Wall, 1983; Stein, 1989; Bou et al., 1990; Fish, 1993; Germain and Laurin, 2005; Kriloff et al., 2008; Canoville and Laurin, 2010). For example, a relatively thick cortex (>30% of the average diameter) may indicate an aquatic or fossorial lifestyle (Wall, 1983; de Buffrénil et al., 1990; Hua and de Buffrénil, 1996; Botha, 2002, 2003), because thick bone walls counteract buoyancy while in the water and provide extra strength and support while swimming or digging. In extreme cases, aquatic animals exhibit particularly thick, compact cortices (e.g., the manatee, *Dugong dugong*) or completely infilled medullary cavities with broad transition zones between the compacta and medullary cavity (e.g., the dolphin, *Delphinus delphis*) depending on the extent of the aquatic lifestyle (Canoville and Laurin, 2010).

<table>
<thead>
<tr>
<th>Genus, Element</th>
<th>Accession number</th>
<th>Locality</th>
<th>Assemblage zone</th>
<th>Skull length</th>
<th>Total mid-shaft width</th>
<th>Total proximal width</th>
<th>Total distal width</th>
<th>% adult</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Prolacerta broomi</em></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rib</td>
<td>NMQR 3673</td>
<td>Fairdale, Bethulie</td>
<td><em>Lystrosaurus</em></td>
<td>76</td>
<td>4.8</td>
<td>12.2</td>
<td>95</td>
<td></td>
</tr>
<tr>
<td>Femur</td>
<td>SAM-PK-K140c</td>
<td>Visag, Conway</td>
<td><em>Lystrosaurus</em></td>
<td>266</td>
<td>139.2</td>
<td>14.8</td>
<td>25.4</td>
<td>67</td>
</tr>
<tr>
<td>Fibula</td>
<td>NMQR 880</td>
<td>Kruislelie, Winburg</td>
<td><em>Lystrosaurus</em></td>
<td>331.5</td>
<td>13.9</td>
<td>26.2</td>
<td>82</td>
<td></td>
</tr>
<tr>
<td>Femur</td>
<td>SAM-PK-11208a</td>
<td>Barendskaal, Middelburg</td>
<td><em>Lystrosaurus</em></td>
<td></td>
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</tr>
<tr>
<td>Fibula</td>
<td>SAM-PK-11208b</td>
<td>Barendskaal, Middelburg</td>
<td><em>Lystrosaurus</em></td>
<td></td>
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The % adult size was estimated using the largest known specimens for each genus.
In this study, both the thickness of the cortex and the overall compactness of the bone were measured. The cortical thickness (or ‘k,’ according to Currey and Alexander, 1985) was recorded by measuring the ratio between the inner diameter and outer diameter of the bone. Cortical thickness is thinnest when k tends towards 0 (i.e., no bone walls) and thickest when k tends towards 1 (i.e., solid bone) (Currey and Alexander, 1985). Secondly, a bone compactness profile (defined as “the ratio between the surface occupied by bone tissues and the total bone surface” [Germain and Laurin, 2005:337]) was obtained for each element (where possible) using the computer program Bone Profiler for Windows (Girondot and Laurin, 2003). This method involves converting an image of the bone cross-section to a simple black and white image, where the black areas represent bone and the white areas the medullary spaces and channels within the cortex. Bone Profiler then calculates the ratio between the mineralized tissue surface and the total cross-sectional surface (Girondot and Laurin, 2003; Laurin et al., 2004; Germain and Laurin, 2005; Canoville and Laurin, 2010). Compactness is lower towards 0 and higher towards 1. The method of Currey and Alexander (1985) is easy to implement, but it assumes that transverse bone sections have perfectly circular profiles and a sharp distinction between the medullary cavity and cortex. This is not always the case, thus the compactness method of Girondot and Laurin (2003) was also used because it is more biologically appropriate. However, the latter method also requires completely preserved transverse sections. Because some thin sections revealed broken or fragmentary cortices and because the cortical channels were not always clear throughout the entire cross-section in all study elements, only the bones of Euparkeria, a tibia (SAM-PK-K140b) and fibula (NMQR 880) of Proterosuchus, and a section of an Erythrosuchus radius (NMQR 3675) could be assessed using this method.

**Institutional Abbreviations—BP.** Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; NMQR, National Museum, Bloemfontein; SAM-PK, Iziko South African Museum, Cape Town.

**RESULTS**

**Prolacerta broomi**

NMQR 3763 is a tibia from a single individual. *Prolacerta* specimens are rare and thus it is not known how large this animal grew. However, the neurocentral sutures of the cervical vertebrae of NMQR 3763 are fused and the skull length measures 76 mm in length, which is close to the largest specimen known (80 mm maximum skull length). Thus, it is likely that NMQR 3763 represents an adult.

Transverse sections through the midshaft of the tibia reveal a relatively compact cortex ($k = 0.54$; compactness 0.69) and enlarged resorption cavities in the perimedullary region. The endosteal lamellae form a ring around the inner cortex and do not extend into the medullary cavity, leaving it relatively free of bony trabeculae. The compacta contains small vascular canals ($17 \ \mu m$ in diameter) arranged as longitudinally oriented primary osteons (cortical porosity 2.2%), distributed haphazardly throughout the cortex (Fig. 2A–C). The osteocyte lacunae are globular and mostly arranged haphazardly throughout the cortex and around the primary osteons, suggesting a fibrolamellar complex. However, there are patches, in the absence of primary osteons, where the osteocyte lacunae form a more organized, parallel arrangement (Fig. 2D). Under polarized light, the fibers are arranged in a single direction, apart from those surrounding the primary osteons, but there are regions showing a woven-fibered bone matrix. A weakly developed fibrolamellar complex, with regions of parallel-fibered bone in the innermost and outermost regions of the bone. Several small secondary osteons are observed on the posterolateral side of the bone. The vascular canals extend to the subperiosteal surface without decreasing in size or abundance. Canaliculi are not preserved and growth rings are absent.

**Proterosuchus fergusi**

The skull of the largest specimen known for this genus, SAM-PK-K10603, measures 400 mm in length and is regarded as having reached somatic maturity. This specimen was taken to represent 100% adult size against which specimen SAM-PK-K140 was measured and is estimated to be 67% of the maximum size known for this genus (as defined by skull length and associated limb bones). A complete skull was available for NMQR 880 and is estimated to be 82% the size of SAM-PK-K10603. SAM-PK-11208 does not comprise a complete skull, but using comparable limb bone measurements it is estimated to be 100% adult (Table 1).

SAM-PK-K140 includes a tibia and femur from one individual. These elements, which both contain large, free medullary cavities, are surrounded by relatively narrow cortices (tibia $k = 0.6$; compactness 0.573; femur $k = 0.58$). The osteocyte lacunae are globular, abundant, and arranged haphazardly in a woven-fibered bone matrix. Canaliculi are not preserved. The vascular canals in the tibia ($22 \ \mu m$ in diameter; cortical porosity 9%) and femur ($39 \ \mu m$ in diameter; cortical porosity 15%) are numerous and either radiate out from the medullary cavity or are arranged as longitudinally oriented primary osteons in radial rows (Fig. 3A, B). The tibia also exhibits patches of randomly distributed longitudinally oriented primary osteons. There are several resorption cavities on one side of the bone in the tibia, but they are not extensive and secondary osteons were not observed in either limb bone. There is a thin layer of circumferential endosteal lamellae surrounding the medullary cavities in both elements. The orientation of the osteocyte lacunae becomes more organized at the subperiosteal surface of the tibia, suggesting a slight decrease in growth rate, but growth rings are absent in both elements.

The bone tissue of fibula NMQR 880 ($k = 0.37$; compactness 0.778) consists of a moderately vascularized (cortical porosity 4.1%), poorly developed fibro-lamellar complex in the innermost cortex, which changes into clearly defined lamellar-zonal bone towards the periphery (Fig. 3C, D). Annuli (representing a temporary decrease in growth rate) are absent from the inner cortex, but appear in the peripheral lamellar-zonal region. The vascular canals ($27 \ \mu m$ in diameter) in the inner cortex comprise mostly simple longitudinally oriented canals, but also poorly defined primary osteons. The osteocyte lacunae in this region are abundant and globular, but become flattened in the peripheral lamellar region. Canaliculi are preserved in patches and radiate out in all directions from the osteocyte lacunae. A clear medullary cavity is surrounded by multiple, thick layers of endosteal circumferential lamellae that contain flattened osteocyte lacunae. Enlarged resorption cavities surround the medullary cavity in the perimedullary region and extend into the mid-cortex in the region of a ridge that runs longitudinally down the side of the bone shaft. Sharpey’s fibers are observed on the medial side of the bone.

SAM-PK-11208 includes a femur and fibula from a single individual. The femur (Fig. 3E), which was sectioned below the midshaft region towards the distal end, comprises a large, free medullary cavity that is surrounded by a narrow cortex (cortical thickness could not be quantified due to incomplete preservation of the cortex). Secondary remodeling in the perimedullary region is extensive, with large erosion cavities extending periosteally (close to the periosteal surface in places), but no secondary osteons were observed. The primary bone tissue comprises lamellar-zonal bone with highly organized osteocyte lacunae arranged parallel to one another (Fig. 3E). Vascularization is poor (cortical porosity 2.3%) and changes from radially oriented canals ($16 \ \mu m$ in diameter) in the innermost cortex, to a
mixture of these and longitudinally oriented simple vascular canals in the outer cortex. There are fewer vascular canals at the subperiosteal surface. Multiple annuli and lines of arrested growth (LAGs; which represent a periodic, but complete cessation in growth) interrupt the bone tissue from the mid- to outer cortex. Sharpey’s fibers, for the attachment of muscles, are present in some regions.

The fibula of SAM-PK-11208 consists of a relatively narrow cortex \((k = 0.73)\) that surrounds a large, clear medullary cavity. Secondary remodeling extends into the mid-cortex. Although large erosion cavities surround the medullary cavity, secondary osteons are absent. The primary bone tissue consists of a parallel-fibered bone matrix with radiating vascular canals (23 \(\mu\)m in diameter) (Fig. 3F) interspersed with longitudinally oriented primary osteons (cortical porosity 7%). The bone tissue becomes poorly vascularized lamellar-zonal bone with sparse longitudinally oriented simple canals and multiple annuli towards the periphery. A small section of circumferential endosteal lamellae bordering the medullary cavity is present and Sharpey’s fibers were observed in places.

**Erythrosuchus africanus**

Complete skulls are not available for any of the study specimens and, thus, identifications were based on partial skull material. Charig et al. (1976) report 960 mm as the maximum skull length for this taxon. Specimen NMQR 3675 comprises an almost complete articulated skeleton and two-thirds of the skull is preserved. Thus the length of the complete skull could be approximated and is estimated to be 63% of the maximum size known for this genus. Using limb bone measurements, specimen SAM-PK-K10025 is estimated to be 56% maximum size. SAM-PK-1118 does not include any limb bones that could be compared with the other specimens and only skull fragments of this individual are preserved, thus the ontogenetic status of this individual could not be estimated using gross measurements.

The *Erythrosuchus* material includes a tibia and rib from one individual (SAM-PK-K10025), a rib and unidentified fragment from another individual (SAM-PK-1118), and a radius and three rib fragments from a third individual (NMQR3675). All elements...
FIGURE 3. Bone histology of the Early Triassic Proterosuchus fergusi. A, tibia SAM-PK-K140b showing uninterrupted fibro-lamellar bone with radially oriented vascular canals; B, femur SAM-PK-K140c showing uninterrupted fibro-lamellar bone with a thin layer of circumferential endosteal lamellae (arrow) surrounding the medullary cavity; C, fibula NMQR 880 showing longitudinally oriented vascular canals in the mid-cortex and lamellar-zonal bone towards the periphery (arrowhead). An annulus (arrow) is present in the lamellar-zonal region; D, high magnification of the lamellar-zonal region (arrowhead) of fibula NMQR 880; E, F, femur SAM-PK-11208a and fibula SAM-PK-11208b showing a change to lamellar-zonal bone towards the periphery (arrowheads). Scale bars equal 1000 µm in A, B, and C; 100 µm in D; 500 µm in E and F.
contain numerous vascular canals in a woven-fibered bone matrix. The tibia of SAM-PK-K10025 (Fig. 4A) has undergone some diagenesis, particularly in the inner and mid-cortex, and is thus not well preserved. Similarly, the outer cortex of the rib from the same individual has also been diagenetically altered. It is clear, however, that the tibia consists of a thick cortex ($k = 0.35$). A region of cancellous bone with large erosion cavities in the perimedullary region results in a small free region in the center of the bone. The primary bone tissue consists of moderate to highly vascularized fibro-lamellar bone in a plexiform network, similar to that seen in the femur/humerus in Gross (1934) and the fibula in de Ricqlès et al. (2008). The canals are slightly smaller periosteally, and longitudinally oriented primary osteons are more common in the perimedullary and mid-cortical regions than at the subperiosteal surface. The osteocyte lacunae are only preserved in patches and appear to be globular in shape. Canaliculi are not preserved. Growth rings are absent. The rib of SAM-PK-K10025 has also been diagenetically altered, but is somewhat better preserved than the tibia. It contains a small medullary cavity that is filled with bony trabeculae. Resorption cavities are observed in the perimedullary region. The fibro-lamellar bone of the rib is highly vascularized, similar to the condition seen in the rib of de Ricqlès et al. (2008) and contains numerous large ($67 \mu m$ in diameter) longitudinally oriented primary and secondary osteons randomly dispersed throughout the cortex. Anastomoses are absent and there is no decrease in vascular density towards the periphery. Osteocyte lacunae are only preserved in patches and are globular in shape, and canaliculi are not preserved.

The elements of SAM-PK-1118 are better preserved. Both the rib (cortical porosity 13%) and fragment consist of highly vascularized fibro-lamellar bone where vascular density remains constant up to the subperiosteal surface. The vascular canals are mostly primary osteons with short anastomoses and form a reticular network in places. They are smaller in diameter (average $33 \mu m$) than those of rib SAM-PK-K10025. The rib contains a large medullary cavity that is filled with broken fragments of trabeculae. Some secondary remodeling is apparent in the perimedullary region in the form of enlarged resorption cavities. Small secondary osteons are common throughout the cortex. The osteocyte lacunae are globular and abundant, but canaliculi are not preserved. Two faint annuli were observed in each element near the subperiosteal surfaces.

FIGURE 4. Bone histology of the Middle Triassic *Erythrosuchus africanus*. A, B, radius NMQR 3675 and tibia SAM-PK-K10025 showing uninterrupted fibro-lamellar bone; C, D, rib NMQR 3675c showing longitudinally oriented primary and secondary (arrows) osteons in a fibro-lamellar complex. Arrowhead indicates an annulus near the periphery. Scale bars equal 500 $\mu m$ in A; 1000 $\mu m$ in B and C; 100 $\mu m$ in D.
The bone tissue of radius NMQR 3675 (Fig. 4B) is similar to tibia SAM-PK-K10025, but is a little better preserved. A relatively thick cortex \((k = 0.2;\) compactness 0.856) surrounds a large medullary cavity. A few broken fragments of trabecular bone lie within the medullary cavity but two-thirds of the region preserves a thin layer of circumferential endosteal lamellae and erosion cavities are largely absent, suggesting that the medullary cavity was probably relatively free of bony trabeculae during life. The cortex consists of uninterrupted highly vascularized (cortical porosity 9%) fibro-lamellar bone. The vascular canals are arranged either in a plexiform network or they radiate out towards the subperiosteal surface. There is no decrease in channel density toward the periphery. The vascular canals are relatively narrow (27 \(\mu m\) in diameter). Numerous canaliculi are preserved and radiate out from the abundant, globular osteocyte lacunae in all directions. Small secondary osteons are observed in the perimedullary region.

Endosteal trabeculae extend into the medullary cavities of all three ribs of NMQR 3675. The cortex is relatively compact and comprises a highly vascularized woven-fibered bone matrix. A mixture of large (43 \(\mu m\) in diameter) longitudinally oriented primary and secondary osteons are arranged haphazardly throughout the cortex. A few isolated enlarged resorption cavities are observed in the mid-cortex. Canaliculi are preserved in patches and radiate out from the abundant, globular osteocyte lacunae, which are distributed randomly throughout the cortex. One of the ribs contains an annulus near the subperiosteal surface (Fig. 4C, D). New bone containing large primary osteons was deposited after this annulus.

**Euparkeria capensis**

Ewer (1965) described all of the *Euparkeria* individuals as adults, although there is some variability with complete skulls ranging from 69 to 100 mm in length. This latter measurement was used along with comparable limb bone measurements to estimate the ontogenetic status of the *Euparkeria* material in this study. All study material has been assigned an adult status because estimates range from 88% to 96% of the maximum known size of this genus (Table 1).

SAM-PK-13666 is a humerus that comprises a relatively thick cortex \((k = 0.44;\) compactness 0.771). The small medullary cavity is devoid of trabecular infilling. Secondary remodeling is almost non-existent; one enlarged resorption cavity is present on the posteromedial side of the bone. The primary bone tissue consists of highly organized (the osteocyte lacunae are arranged parallel to one another in places) parallel-fibered bone. The vascular canals (cortical porosity 5.4%) are arranged as longitudinally oriented primary osteons and some regions also have short anastomoses forming a subreticular pattern (Fig. 5A). The abundant globular osteocyte lacunae radiate short canaliculi. Two indistinct wide annuli interrupt the bone tissue and a layer of circumferential endosteal lamellae surrounds the medullary cavity. Calcified cartilage was observed in the proximal epiphysial region.

SAM-PK-K10010 includes a femur, tibia, and fibula from a single individual. As femur SAM-PK-K10010a was not complete, thin sections had to be taken slightly proximal to the midshaft region. In all three elements, a narrow cortex (compactness: femur 0.448, tibia 0.738, fibula 0.692) surrounds a large free medullary cavity \((k: \text{femur 0.73, tibia 0.48, fibula 0.51})\). The primary bone tissue is poor to moderately vascularized (depending on the element), highly organized parallel-fibered bone (Fig. 5B, C, D). The osteocyte lacunae are globular in shape and abundant, but canaliculi are not preserved in any element. Cortical porosity is 3.3% in the femur, 3.5% in the tibia, and 5% in the fibula. The canals mostly consist of longitudinally oriented simple canals, with a few randomly distributed primary osteons. The tibia contains more canals with short anastomoses forming a subreticular pattern in places (Fig. 5C). Cortical porosity remains constant throughout the cortex. Two LAGs interrupt the bone tissues of both the femur and fibula. Multiple LAGs and annuli are present in the tibia. Secondary remodeling is more extensive in the femur, on the posterolateral side of the bone (Fig. 5B), probably because it was thin-sectioned closer to the metaphysis than the other elements. In the tibia and fibula, enlarged resorption cavities are present only in a small region on the anterior and posterolateral sides of the bone, respectively. A fairly substantial layer of circumferential endosteal lamellae surrounds the medullary cavity in the fibula (Fig. 5D). Calcified cartilage was observed in the distal epiphysial region of the tibia.

The femur SAM-PK-K10548 (Fig. 6) consists of a relatively narrow cortex \((k = 0.53;\) compactness 0.661) that surrounds a large free medullary cavity. The moderately vascularized (4.4%), highly organized parallel-fibered bone contains mostly longitudinally oriented simple canals with a few primary osteons and short anastomoses in places (Fig. 6A, B). The osteocyte lacunae vary between globular and flattened, and canaliculi are not preserved. The vascular density remains constant throughout the cortex (Fig. 6A). A few enlarged resorption cavities are present on the anteromedial side of the bone, but they are not extensive. A thin layer of inner circumferential endosteal lamellae surrounds most of the medullary cavity. Calcified cartilage was observed in the distal epiphysial region (Fig. 6C).

**DISCUSSION**

**Growth Patterns of the Studied Taxa**

Table 2 provides a summary of the quantifiable characters and bone tissue patterns of the taxa examined in this study. The bone tissue pattern of *Prolacerta* is characterized by parallel-fibered bone with longitudinal primary osteons and localized woven bone matrix. Some regions contain primary osteons and haphazardly arranged globular osteocyte lacunae, suggesting relatively rapid growth, and others contain fewer primary osteons and more organized bone tissue, with flattened osteocyte lacunae arranged parallel to one another, suggesting relatively slow growth. The bone matrix of *Prolacerta* can thus best be described as intermediate between parallel fibered (Fig. 7A) and woven (Fig. 7B). Transitions between these categories are known in other taxa (e.g., some 'pelycosaurs' and dinosaurs [Enlow and Brown, 1957; Redelstof and Sander, 2009; Huttenslocher and Rega, in press], and some extant squamates and proboscidiens [de Ricqles et al., 1991]) and can even appear within the same section (Francillon-Vieillot et al., 1990). The individual studied is close in size to the largest *Prolacerta* specimen known and the neurocentral sutures of the cervical vertebrae are fused, suggesting that this animal had reached adult status at time of death. However, there is no indication of a decrease in growth rate towards the periphery and growth rings are absent. The closure of the cervical neurocentral sutures has been found to be a reliable indicator of maturity in extant crocodilians (Brochu, 1996) and squamates (Maisano, 2002), but does not necessarily indicate that maximum size has been reached. Although it is possible that *Prolacerta* grew considerably larger than is currently known, it is clear from both gross morphology and the bone microstructure that specimen NMQR 3673 was not a juvenile. Experiments on extant reptiles have shown that growth rings, which represent a temporary slowing down or cessation in growth, are deposited annually, during the unfavorable growing season. Because the climate of the Early Triassic Karoo is characterized by highly seasonal rainfall and possibly drought conditions, it is noteworthy that either the growth of *Prolacerta* (at least during early to mid-ontogeny) did not temporarily slow down or cease during the unfavourable growing season or adult status was attained within one year.
The presence of abundant radiating vascular canals in a fibrolamellar complex and absence of growth rings in *Proterosuchus* SAM-PK-K140 (67% maximum size) suggests that this individual was growing relatively rapidly at time of death (Fig. 7C). In contrast, the bone tissue patterns of the ontogenetically older specimens, NMQR 880 and SAM-PK-11208 (82% and 100% maximum size, respectively), reveal a dramatic change in growth from rapidly forming fibro-lamellar bone to slowly forming lamellar-zonal bone tissue (Fig. 7D). This change in tissue type indicates that sexual maturity had probably already been reached. Sexual maturity has been shown to be associated with a dramatic change to a slowly forming bone tissue type (parallel-fibered or lamellar bone matrix) in living taxa (e.g., amphibians and reptiles [Castanet and Smirina, 1990; Castanet and Baez, 1991] and walrus *Odobenus rosmarus* [Klevezal, 1996]) and the association has also been proposed for several fossil taxa (non-avian dinosaurs [Reid, 1996; Sander, 2000] and non-mammaliaform cynodont therapsids [Botha and Chinsamy, 2005]). Lee and Werning (2008) demonstrated that sexual maturity in dinosaurs may have occurred with a decrease in bone deposition rate, but prior to the onset of a different bone tissue type. The growth patterns of *Proterosuchus* are interpreted as relatively rapid continuous growth until fairly late in ontogeny (at least until 67% adult size), with a transformation to slow, interrupted growth once sexual maturity was reached. The appearance of growth rings in the peripheral lamellar-zonal region indicates that growth became intermittent late in ontogeny and either decreased or ceased temporarily during the unfavourable growing season.

The growth of *Erythrosuchus* is characterized by rapid, uninterrupted growth, as revealed by relatively highly vascularized fibro-lamellar bone (Fig. 7E), and supports previous observations of earlier studies (Gross, 1934; de Ricqlès, 1976; de Ricqlès et al., 2008). Growth rings have not been reported previously for *Erythrosuchus*, nor were they observed in the limb bones in this study. However, annuli were observed in a fragment and two ribs, indicating that *Erythrosuchus* was capable of varying its growth
The general absence of growth rings, however, until at least 63% adult size (Table 1), indicates early rapid growth to at least the subadult stage. De Ricqlès et al. (2008) noted a decrease in growth rate and a poorly defined external fundamental system or EFS (as defined by Cormack, 1987) in a rib (BP/1/4680), which indicates the attainment of maximum size and thus a virtual cessation in growth (although an increase in mass may still occur). Interestingly, the authors noted that growth rings were absent in all study elements, including the rib containing the EFS, contrary to our findings. It is possible that the change in bone tissue towards the periphery in their rib represented a temporary decrease in growth rate, but not necessarily an EFS, or this difference may be the result of individual variation (caused by either genetic or environmental differences).

All the *Euparkeria* elements used in this analysis were considered to be adult a priori and the bone microstructure of all the limb bones supports this assumption. The presence of parallel-fibered bone and prominence of annuli and LAGs indicates a comparatively slow growth rate for this genus (Fig. 7F). These observations differ from what was noted by de Ricqlès et al. (2008). They examined an unidentified limb bone (a possible humerus or femur), osteoderms, and rib fragments of *Euparkeria*. The authors noted that growth rings were absent and the bone tissue consisted of a poorly defined fibro-lamellar complex. It is possible that the limb bone in their study belonged to a juvenile individual and growth rings were absent early in ontogeny (although Ewer [1965] noted that the *Euparkeria* material consisted of an aggregate of adults based on gross morphology), or that the element may belong to *Mesosuchus* and not *Euparkeria*. Fossils of these taxa are closely associated on the sandstone blocks in which they are preserved. The growth of *Euparkeria* differs markedly from the other taxa studied, in the presence of poorly vascularized parallel-fibered bone throughout the entire cortex and prominence of annuli and LAGs. It was a relatively small animal (approximately 1 m body length) and considerably smaller than *Proterosuchus* (2 m body length) or *Erythrosuchus* (5 m body length). Within a given clade, large taxa often grow absolutely faster than smaller ones do (Case, 1978; Padian et al., 2004), and the slower growth in *Euparkeria* may simply be size related.

The compactness values of all the studied taxa range from 0.448 in a *Euparkeria* femur SAM-PK-K10010a to 0.856 in the *Erythrosuchus* radius NMQR 3675. Femur SAM-PK-K10010a was sectioned slightly below the mid-diaphysis towards the metaphyseal region (and thus accounts for the lower compactness because metaphyses are more spongy than the diaphysis), but the rest of the *Euparkeria* values range from 0.661 in femur SAM-PK-K10548 to 0.771 in humerus SAM-PK-13666. The *Prolacerta* and *Proterosuchus* compactness values are similar to those of *Euparkeria*. The k values indicate moderately thick cortices in *Prolacerta* (0.54), *Proterosuchus* (average 0.57), and *Euparkeria* (average 0.54). These results agree with Cubo et al.’s (2005) findings; these authors described the last common ancestor of archosaurs as having moderately thick cortices (0.476). In contrast, *Erythrosuchus* has a relatively thicker cortex (average 0.28), similar to that of living crocodilians (0.22; Cubo et al., 2005).

None of the taxa in this study exhibit pachyostosis (thickening of the cortex with no medullary cavity) as seen in aquatic animals such as plesiosaurs, nor do they have particularly thick compact cortices with tiny medullary cavities (to counteract buoyancy) as seen in shallow water aquatic animals such as *Dugong dugong* (manatee) or *Ornithorhynchus anatinus* (duckbilled platypus) (Germain and Laurin, 2005). Completely infilled medullary cavities with broad transition zones between the compacta and medullary cavity as is typical of aquatic diving animals (such as the dolphin *Delphinus delphis* and the southern elephant seal *Mirounga leonina*; Germain and Laurin, 2005; Kriloff et al., 2008) are also absent (Fig. 8). *Prolacerta*, *Euparkeria*, and

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**FIGURE 6.** Bone histology of the Middle Triassic *Euparkeria capensis*, femur SAM-PK-K10548. **A, B,** showing parallel-fibered bone with longitudinally oriented simple canals, interrupted by annuli and LAGs (arrowheads). A thin layer of circumferential endosteal lamellae (arrow) surrounds the medullary cavity (mc); **C,** high magnification of the epiphyseal region showing calcified cartilage (arrow). Scale bars equal 1000 µm in **A;** 100 µm in **B** and **C.**
Erythrosuchus africanus is the only taxon in this study whose lifestyle is still actively debated. The cortical thickness values of Proterosuchus are similar to (Proacerta, Euparkeria) or less than (Erythrosuchus) those of the other taxa. Moreover, the femoral cortical thickness of Proterosuchus is 0.58, whereas the amphibious Nile crocodile (Crocodylus niloticus) has a femoral cortical thickness of 0.22 (Cubo et al., 2005). Similarly, the cortical compactness value of Proterosuchus (0.573) is also lower than that of Alligator mississippiensis, which exhibits a tibial compactness value of 0.78 (Kriloff et al., 2008). Given the difference in these values and the observation that Proterosuchus does not exhibit any of the aquatic histological features listed above, we conclude that the bone microstructure of Proterosuchus does not support an aquatic lifestyle. Interestingly, the cortical thickness of Erythrosuchus (radius k = 0.2; tibia k = 0.35) is similar to that of the semi-aquatic Alligator mississippiensis (0.22; Cubo et al., 2005). However, Currey and Alexander (1985) found that although shallow water aquatic animals (i.e., non-divers) such as the alligator and manatee revealed low k values (i.e., thick cortices), they also found that larger animals also have low k values (e.g., the sloth bear Melursus ursinus, k = 0.26). Because Erythrosuchus exhibits no morphological features suggesting that it was aquatic or even semi-aquatic, we attribute the low k values of this animal to its large size, because thick cortices are stronger under localized impact than thinner ones (Currey and Alexander, 1985).

Archosauroomorph Growth Patterns in a Phylogenetic Context

Although early studies (e.g., Seitz, 1907; Gross, 1934; Enlow and Brown, 1957; de Ricqlès, 1976) set a solid foundation on which further research could develop, several recent studies on archosauroomorph bone histology have begun to provide more comprehensive information about the growth patterns of this group (e.g., de Ricqlès et al., 2008; Nesbitt et al., 2009; Werning and Irmis, 2010). These new data have shed light on the evolutionary relationships between archosauroomorph taxa and with the archosaur crown group in a histological context (Ricqlès et al., 2008; Werning and Irmis, 2010).

Werning and Irmis (2010) recently revealed a slow overall growth pattern for the Late Triassic basal archosauroomorph Trilophosaurus buettneri. They described the bone microstructure of this taxon as low to moderately vascularized, lamellar-zonal bone. This type of bone tissue, in association with sometimes multiple LAGs, was evident throughout ontogeny and indicates an overall slow and cyclical growth rate (Werning and Irmis, 2010). Similarly, Nesbitt et al. (2009) recently described the adult femoral bone histology of the Late Triassic archosauriform Vancleavea campi as slow, noting a poorly vascularized lamellar-zonal bone tissue with distinct LAGs throughout the cortex. These authors also noted a particularly thick cortex and infilled medullary cavity and suggested, in association with gross morphological features, that Vancleavea was semi-aquatic (Nesbitt et al., 2009). De Ricqlès et al. (2008) also examined several Middle–Late Triassic indeterminate rhynchosaurs archosauroomorph limb bones and found slowly forming lamellar-zonal bone tissue with distinct growth cycles, typical of extant reptiles. They also studied the Middle Triassic semi-aquatic proterochampsid archosauroomorph Chananaresuchus and noted an early rapid growth rate (based on an inner thick region of fibro-lamellar bone), which decreased dramatically later in ontogeny (based on the presence of peripheral lamellar-zonal bone: de Ricqlès et al., 2008).

When the data obtained in these studies is added to this study and examined in a phylogenetic context, a mixture of bone tissue patterns emerges. The basal archosauroomorph Trilophosaurus and the rhynchosaur archosauromorphs (including Scaphonyx; see Enlow and Brown, 1957) display slow, cyclical growth similar to living reptiles (de Ricqlès et al., 2008; Werning and Irmis, 2010). Proacerta, a slightly more derived archosauroomorph, reveals relatively faster, uninterrupted growth. If we assume that the cortex of Proacerta was deposited in a single year (based on the absence of growth rings), we estimate the bone deposition rate to have been approximately 2.1 µm/day (using a year of 380 days), which is similar to extant crocodilians (2.48 µm/day; Montes et al., 2010), and faster than extant varanid lizards (1.18 µm/day; Montes et al., 2010). The more derived archosauroomorphs reveal progressively increasing growth rates, with Proterosuchus (11.3 µm/day) and Chananaresuchus (de Ricqlès et al., 2008)

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**TABLE 2. Quantifiable characters and bone tissue patterns for the specimens examined in this study.**

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<th>Genus, Element</th>
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<th>Vascular canal diameter (µm)</th>
<th>Bone tissue type</th>
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**Abbreviations:** FLB, fibro-lamellar bone; LZB, lamellar-zonal bone; PFB, parallel-fibered bone.
FIGURE 7. Transverse sections in polarized light. A, *Prolacerta* NMQR 3673, tibia showing parallel-fibered bone; B, *Prolacerta* NMQR 3673, tibia showing woven-fibered bone; C, *Proterosuchus* SAM-PK-K140b tibia showing woven-fibered bone; D, *Proterosuchus* NMQR 880 fibula showing lamellar-zonal bone towards the periphery; E, *Erythrosuchus* NMQR 3675 radius showing woven-fibered bone; F, *Euparkeria* SAM-PK-K10548 femur showing parallel-fibered bone. Scale bars equal 100 µm in A, B, C, and F; 500 µm in D and E.
FIGURE 8. Mid-diaphyseal cross-sections of the study taxa showing the relative cortical thickness and cortical compactness (apart from D). A, Prolacerta tibia; B, Euparkeria tibia; C, Proterosuchus tibia; D, Erythrosuchus tibia; and E, Erythrosuchus radius. Bone shaded in black. The vascular canals in D are not shown due to patchy preservation, but E gives an indication of the size of the vascular canals in Erythrosuchus. Images are not to scale. Abbreviation: mc, medullary cavity.

FIGURE 9. Stratocladogram of archosauromorph bone histology studied to date. White shading indicates lamellar-zonal bone, black shading indicates fibro-lamellar bone, and grey shading indicates parallel-fibered bone tissue. Phylogeny taken from Sues (2003), Dilkes and Sues (2009), and Nesbitt et al. (2009). Histological information taken from de Ricqlès et al. (2008), Nesbitt et al. (2009), Werning and Irmis (2010), and this study. Time scale taken from Walker and Geissman (2009). Numbers indicate million years ago. Abbreviations: Chsn, Changhsingian; Olkn, Olenekian; PTB, Permo-Triassic boundary.

exhibiting rapid early growth, but slow, cyclical late growth, and Erythrosuchus, uninterrupted rapid growth (21 µm/day) throughout ontogeny. Montes et al. (2010) found that the last common ancestor of archosaurs had a bone deposition rate of approximately 13.5 µm/day (Montes et al., 2010). Non-avian dinosaurs ranged from 3 to 24 µm/day (Sander and Tückmantel, 2003; Cooper et al., 2008). Thus, the growth rates of Proterosuchus and Erythrosuchus are relatively high, with Erythrosuchus exhibiting a growth rate similar to the fastest-growing dinosaurs. It should be noted, however, that these rates are mere estimates and several assumptions were made in order to calculate these rates; for example, the number of days in a Triassic year (380 days) and the active growth period of these animals in one year (i.e., annual growth may have been restricted to a 6-month period during the more favorable growing months). Substantial variation exists both among different elements of a single individual and within a single bone type. For example, Starck and Chinsamy (2002) found that the depositional rates of fibro-lamellar bone in Japanese quail varied from 10 to 50 µm/day. In general, however, there appears to be an increase in the predominance of rapidly forming fibro-lamellar bone within the archosauromorphs, as previously noted by de Ricqlès et al. (2008). However, Euparkeria (estimated bone deposition rate of 1.4 µm/day) and Vancleavea deviate from this pattern. There may be several possible reasons for their relatively slower growth strategies, such as differences in body size or nutrient availability. Ontogenetic variation is unlikely to be the cause of these differences as all these specimens are considered to be adults.

The bone tissue patterns of these basal archosaurs differ from those of many non-archosauromorph reptiles, which predominantly contain slowly forming lamellar bone that is usually cyclical in nature. The Permian basal eureptiles Captorhinus, Moradosaurus (de Ricqlès, 1976), and Claudiosaurus (de Buffrénil and Mazin,
1989), as well as the basal diapsid eureptile Youngina (pers. observ., 2010), all reveal a slowly forming lamellar bone matrix, which, in Cladosaurus, is cyclical in nature. Triassic sauropet-
gian eureptiles such as Pachypleurosaurus, Neusticosaurus, and Nothosaurus also contain slowly forming lamellar-zonal bone (Enlow and Brown, 1957; Sander, 1990; Hua and Buffrénil, 1996; Scheyer et al., 2010). In contrast, the bone tissues of the Triassic aquatic ichthyosaurs Omphalosaurus, Stenopterygius, and Ichthyosaurus reveal rapidly forming fibro-lamellar bone, which has been attributed to their active predatory, aquatic lifestyles (de Buffrénil and Mazin, 1989). Chelonia appear to exhibit lamellar-zonal bone as a group (e.g., Enlow and Brown, 1957; de Ricqlès, 1976; Castanet and Cheylan, 1979). Few parapet-
tiles, which forms the sister group of Eupeliona, have been studied; however, de Ricqlès (1976) and Scheyer and Sander (2009) found slowly forming lamellar-zonal bone in Permian pareiasaurs. More research on parapetiles is needed, particularly on Triassic parapetiles, in order to elucidate the bone tissue pat-
ters of this group and to compare them with archosaurs.

De Ricqlès et al. (2008:72, 74) suggested that the ability to “reach and maintain” rapid growth rates during at least early and mid-ontogeny was plesiomorphic for archosauromorphs and that the Triassic was a “time of experimentation in growth strategies.” Although archosauromorph growth patterns do appear to re-
fect a phylogenetic signal, in that rapidly forming fibro-lamellar bone becomes increasingly more prominent, derived taxa such as Vancleavea and Euparkeria, which are considered to be re-
latively closely related to crown group archosaurs, deviate from this pattern and suggest that a relatively weak phylogenetic signal was present and that factors other than phylogeny must be con-
idered when interpreting the observed growth patterns of archosauromorphs; something which de Ricqlès et al. (2008) also emphasized.

Archosauromorph Growth Patterns in an Ecological Context

Stem archosaurs that lived during the Early Triassic (e.g., Pro-
lacerta, Proterosuchus) and Middle Triassic (e.g., Erythrosuchus, Chanaresthes) exhibit relatively rapid growth rates that were faster than many of those that lived during the Late Triassic (e.g., Trilophosaurus, Scaphonyx, Vancleavea). It is interesting to note that although the Early Triassic Prolacerta is similar in body size to the Middle Triassic Euparkeria, it grew relatively more quickly. The climate of the Early Triassic Karoo Basin is characterized by unreliable monsoonal-type torrential rainfall in-
terspersed with extreme drought (Smith and Botha, 2005). The relatively rapid continuous growth seen in some of these non-
dinosaurian archosaurs may have allowed these taxa to reach sexual maturity relatively quickly (Fig. 9). Early rapid, uninter-
ruped growth strategies have been observed in other taxa such as the dicynodont Lystrosaurus (Botha-Brink and Angielczyk, 2010) and the therocephalian Moschorhinus (Huttonlocker et al., 2010), both of which survived the end-Permian mass extinction and formed an important part of the Early Triassic fauna. At-
taining sexual maturity relatively quickly is advantageous in un-
predictable environments and has been observed in living taxa (e.g., Cardinale and Modin, 1999; Curtin et al., 2009). Fast early growth and rapid attainment of sexual maturity are considered to be evolutionary adaptations against low juvenile survivorship and a significantly shorter life span in unpredictable, stressful en-
vironmental conditions (e.g., Tinkle, 1969; Gasser et al., 2000; Curtin et al., 2009). Rapid early growth in Early Triassic verte-
brates is consistent with life history theory and we therefore sug-
ject that early attainment of sexual maturity was advantageous in the unpredictable rainfall regime during this time period when juvenile (as well as adult) mortality was high. As the climate later ameliorated, some animals (such as Vancleavea and Euparkeria) returned to slow early growth (and possibly delayed sexual ma-
turity). However, rapid early growth (i.e., rapidly forming fibro-
lamellar bone) was retained by the early crown group archosaurs and the later, more derived ornithodirans throughout the Late Triassic into the Jurassic (de Ricqlès et al., 2008).

As our sample size is small, this hypothesis must remain preliminary. However, future research may be able to test the environmental stress theory by increasing the Triassic archosauromorph sample size, including Permian eureptiles and Triassic parapetiles, and analyzing the bone microstructure of various vertebrate clades (i.e., other than reptiles) across the Permo-Triassic boundary to determine if rapid early growth was an important factor in the Early Triassic recovery.

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