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Research paper

Growth patterns as deduced from bone microstructure of some selected neotherapsids with special emphasis on dicynodonts: Phylogenetic implications

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Abstract

Osteohistological analysis of the dicynodonts *Endothiodon*, *Diictodon*, *Lystrosaurus* and *Wadiasaurus* reveals distinctly different growth patterns within a framework of an overall fast growth. The late Permian endemic taxon from India, *Endothiodon mahalanobisi* and the South African *Diictodon feliceps* had periodic fast growth. The early Triassic *Lystrosaurus murrayi* and the middle Triassic *Wadiasaurus indicus* had an initial fast growth followed by a relatively slow growth later in ontogeny as is observed from the presence of peripheral parallel fibred bone. Although all examined dicynodont genera had an indeterminate growth strategy, the bone microstructure of *Wadiasaurus* suggests that its growth was much slower than that of other dicynodonts examined. Mapping of osetohistological character states on a cladogram depicting the inter-relationship between available neotherapsid genera shows that fibrolamellar bone tissue, overall fast growth and indeterminate growth strategy were plesiomorphic for the neotherapsids. A considerable reduction in developmental plasticity and evolution of apparently independent growth trajectories from environmental conditions are evident within the non-mammalian cynodonts, with the advanced tritylodontids achieving almost a mammalian growth trajectory.

Keywords: Bone microstructure; Dicynodont; Paleobiology; Osteohistology; Therapsid

1. Introduction

Dicynodontia, an extinct group of non-mammalian therapsids, diversified into numerous genera and species during middle and late Permian (e.g., Lucas, 2002) to become the dominant terrestrial herbivores of that time. Apart from Russia, Scotland, Laos and China, these middle-late Permian forms are known from the Gondwanan countries such as South Africa, Tanzania, Zambia, Mozambique, Madagascar, Brazil and India. During the Triassic period, dicynodonts had almost a worldwide distribution but their generic and specific diversity decreased markedly at the onset of Triassic. They eventually became extinct by the end of late Triassic, though Thulborn and Turner (2003) reported some fragmentary dicynodont remains from Cretaceous deposits of Australia. The dicynodonts are considered as the first successful terrestrial herbivores and had various roles as browsers and foragers (King, 1993). The cranial morphology of the dicynodonts suggests that they had a propalinal movement of the lower jaw that resulted in efficient mastication, whereas postcranial anatomy suggests that dicynodonts exhibited a postural dichotomy, which consisted of abducted forelimbs and nearly adducted hindlimbs (Watson, 1960; Cox, 1972; Cluver, 1978; King, 1981a; Ray and Chinsamy, 2003; Ray, 2006).

Following the initial work by Owen (1845, 1859), Seeley (1889) and Broom (1913, 1932), taxonomy, osteology and functional morphology of the dicynodonts have been studied extensively (e.g., Camp and Welles, 1956; Watson, 1960; Crompton and Hotton, 1967; Cluver, 1971, 1978; Cluver and Hotton, 1981; King, 1981a,b, 1988, 1993; Cluver and King, 1983; Ray, 2000, 2001; Angielczyk, 2001; Surkov and Benton, 2004; Vega-Dias et al., 2004; Surkov et al., 2005; Ray, 2006). In comparison, there are few studies on dicynodont paleobiology, especially on their life history strategies and growth patterns.

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Bone histology provides valuable information on several aspects of an animal's life such as growth strategy, biomechanics and lifestyles as histological and morphological integrity is generally preserved during fossilization (e.g., Chinsamy and Dodson, 1995; Ray and Chinsamy, 2004; Chinsamy, 2005; Steyer et al., 2004; Sanchez et al., 2008). Early work on dicynodont bone microstructure was mainly based on isolated bone material, which could only be identified to the generic level (e.g., de Ricqlès, 1972, 1976). Although some later works rectified the situation and were based on positively identified multiple skeletal elements of different dicynodont genera such as *Oudenodon* (Botha, 2003), *Diictodon* (Ray and Chinsamy, 2004) and *Lystrosaurus* (Ray et al., 2005), there has been no attempt at a comparative analysis of the dicynodont bone histology except for that by Chinsamy and Rubidge (1993) or to evaluate the bone histology of the dicynodonts and/or neotherapsids from a phylogenetic perspective.

This paper presents a comparative study of the bone microstructure of four Permian and Triassic dicynodonts, including a detailed osteohistological description of a new Indian endemic taxon; the late Permian *Endothiodon mahalanobisi*, in order to elucidate growth patterns and lifestyle adaptations. In addition, the osteohistology of the available neotherapsids were assessed in a phylogenetic context to document the evolutionary signatures within the bone microstructure of the neotherapsids.

2. Material and methods

The late Permian dicynodont species considered here are *Endothiodon* (*E. mahalanobisi*) and *Diictodon* (*D. feliceps*) whereas the Triassic genera involved are *Lystrosaurus* (*L. murrayi*) and *Wadiasaurus* (*W. indicus*). The skull size of the adult specimens ranged from ca. 100 mm to 400 mm, and the specimens were collected from different stratigraphic horizons and geographic regions (Table 1). In addition, *Oudenodon* (Botha, 2003) was also used for comparative purposes. Although an ideal data set for osteohistological analysis should incorporate multiple skeletal elements from a number of individuals, the destructive nature of the analysis does not allow for such an ideal data set. In the current work, we generated histological data for the late Permian dicynodont *Endothiodon mahalanobisi*, and supplemented these data with that of the dicynodonts, *Diictodon* (Ray and Chinsamy, 2004), *Oudenodon* (Botha, 2003), *Lystrosaurus* (Ray et al., 2005), *Wadiasaurus* (Ray et al., in press), and the other neotherapsids (Ray et al., 2004; Botha and Chinsamy, 2000, 2004, 2005; Chinsamy and Hurum, 2006).

The four dicynodont genera (Fig. 1) examined here are represented by a number of skeletal elements (Table 1) comprising various limb bones (humerus, femur, radius, ulna and fibula) along with several dorsal ribs, centra and scapulae. The skeletal elements mostly belonged to adult individuals as deduced from gross skeletal morphology, relative size and bone microstructures (e.g., Ray and Chinsamy, 2004). All the specimens of *E. mahalanobisi*, *W. indicus* and a few specimens of *L. murrayi* are housed in the Geology Museum, Indian Statistical Institute, Kolkata, India whereas the material of *D. feliceps* and other *L. murrayi* material are stored in the South African Museum, Cape Town, South Africa. Additional information was drawn from de Ricqlès (1972, 1976), Chinsamy and Rubidge (1993), Ray and Chinsamy (2004), and Ray et al. (2004, 2005).

All the specimens were photographed, morphological variations were noted, and standard measurements were recorded. Wherever possible, several serial sections (transverse and longitudinal) from the same element were processed following the techniques outlined by Chinsamy and Raath (1992). The thin sections were studied under normal and polarized light by using a petrographic polarizing microscope. The relative bone wall or cortical thickness (RBT) was measured across the transverse sections and is expressed as a percentage of the diameter (Bühler, 1986; Ray and Chinsamy, 2004). Measurements were taken along two perpendicular directions at 2.5× magnification. Histological terminology and definitions generally followed that of Francillon-Vieillot et al. (1990), de Ricqlès et al. (1991), and Reid (1996).

3. Bone histology

3.1. General features

All the bones examined contain a well-differentiated central medullary cavity surrounded by an outer relatively compact cortex. Most of the vascular channels show centripetally deposited osteonal bone and form primary osteons. These primary osteons are usually embedded in a woven fibered bone matrix, resulting in fibrolamellar bone tissue. Although most of the primary osteons are isolated and discrete, they vary in orientation and are often circularly and longitudinally oriented, having radial and circumferential anastomoses. The primary osteons are larger in the deeper cortex in comparison to those near the periphery. In general, vascularity decreases towards the periphery. In most of the elements, the perimedullary region contains numerous erosionally enlarged resorption cavities and a few secondary osteons. Apart from these general features, each skeletal element of the different dicynodont genera examined has certain distinct characteristics which are given separately in details in the following section.

3.2. *Endothiodon mahalanobisi*

Limb bones examined included a humerus (ISIR771/1), a tibia (ISIR771/2) and a fibula (ISIR771/3). The humerus (ISIR771/1) contains a small medullary cavity surrounded by a thick cortex (RBT = 30.65%) and a regularly outlined periosteal periphery in the diaphyseal section. The cortical bone tissue is fibrolamellar with the primary osteons arranged in a reticular to plexiform pattern (Fig. 2A and B). Vascularization is generally moderate. A line of arrested growth (LAG) is present in the mid-cortical region (Fig. 2B). Irregular resorption cavities are present in the inner cortex (Fig. 2B, Rc).

The fibula and tibia are poorly preserved because of diagenetic alteration. However, as in the case of the humerus, these also have thick cortices. RBT of the fibula is 31.5% whereas that of the tibia is 26.6%. The outer cortex of the fibula contains dis-