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The discrepancy between morphological and microanatomical patterns of anamniotic stegocephalian postcrania from the Early Permian Briar Creek Bonebed (Texas)

Distinction entre configurations morphologiques et micro-anatomiques du post-crâne de Stégocéphale anamniotique du Permien inférieur du gisement d'ossements de Briar Creek (Texas)

Dorota Konietzko-Meier^{a,*}, Christen D. Shelton^{a,c}, P. Martin Sander^a

^a Division of Paleontology, Steinmann Institute, University of Bonn, Nussallee 8, 53115 Bonn, Germany

^b Department of Biosystematics, University of Opole, Oleska 22, 45052 Opole, Poland

^c Department of Zoology, University of Cape Town, Private Bag X3, Rhodes Gift, 7700 Rondebosch, South Africa

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ABSTRACT

The histological framework of thirteen Early Permian tetrapod long bones from a single locality, the Briar Creek Bonebed in Archer County, Texas, USA, is described from a series of transverse sections through the midshafts. The bones were morphologically categorized and belong to one of three taxa: *Eryops*, *Archeria*, and *Diadectes*. However, five histotypes are recognized. The first category includes the juvenile bone. The second histotype is characterized by the presence of radial vascular canals. The third histotype is characterized by the numerous longitudinal canals arranged in regular rows. In the fourth histotype, there is strong remodeling in the deep part of the cortex, creating a distinct border with the external layer of lamellar bone. In the fifth histotype, the deep part of the cortex is progressively remodeled towards osteoporosis with distinct layers of large circumferentially arranged erosion cavities. For femora and humeri, histotypes match morphology. Histotype II is characteristic for *Diadectes* propodials, histotype III is characteristic for *Eryops* propodials, and histotype IV is characteristic for *Archeria* propodials. A discrepancy between morphology and histology is observed in the ulnae, fibula and radius. This discrepancy may be explained by interspecific or intraspecific variability.

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RÉSUMÉ

Mots clés :

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Le cadre histologique de 13 os longs du Permien inférieur en provenance d'un site unique, le gisement d'ossements de Briar Creek d'Archer County, Texas, USA, est décrit à partir d'une série de coupes transversales au travers des diaphyses d'os. Les os sont rangés par catégorie morphologique et appartiennent à l'un des trois taxons *Eryops*, *Archeria* et *Diadectes*.

* Corresponding author.

E-mail address: dorotam@uni.opole.pl (D. Konietzko-Meier).

Os longs
Eryops
Archeria
Diadectes

Cependant, on peut distinguer cinq histotypes. La première catégorie comporte l'os juvénile ; la deuxième est caractérisée par la présence de canaux vasculaires radiaux ; le troisième histotype présente de nombreux canaux longitudinaux organisés en rangées régulières. Dans le quatrième histotype, il y a un remaniement intense dans la partie profonde du cortex, créant une bordure distincte avec un feuillet externe d'os lamellaire. Dans le cinquième histotype, la partie profonde du cortex est progressivement remaniée en direction de l'ostéoporose, avec des feuillets distincts constitués de grandes cavités d'érosion, disposées de manière circulaire. Pour les fémurs et les humérus, les histotypes correspondent à la morphologie. L'hystotype II est caractéristique des propodiales de *Diadectes*, l'hystotype III, des propodiales d'*Eriops*, et l'hystotype IV, des propodiales d'*Archeria*. Une distinction entre morphologie et histologie est observée dans les ulna, fibula et radius. Cette distinction peut être expliquée par une variabilité interspécifique ou intraspécifique.

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1. Introduction

The most extensive fossil record of Early Permian tetrapods is in the southwestern United States, specifically Texas and Oklahoma. The Texas material is mostly concentrated in and around the Archer County area (Fig. 1). Evidence of Early Permian vertebrates of both terrestrial and aquatic lifestyles has been collected from the famous Texas redbeds for over a century (Case, 1915; Cope, 1878; Romer, 1928, 1957; Sander, 1987, 1989; Shelton

et al., 2013). One of the most important localities in the redbeds is the Briar Creek Bonebed, discovered by E.C. Case in 1912 (Case, 1915). Romer (1928) provided a comprehensive review of the fauna of this locality, listing the temnospondyls *Trimerorhachis* sp., *Zatrachys serratus*, *Eryops* sp., and *Aspidosaurus* sp., the lepospondyl *Diplocaulus* sp., the anthracosaur *Archeria* sp. (formerly *Cricotus* sp.), the diadectomorph *Diadectes* sp., the parareptile *Bolosaurus* sp., and the synapsids *Dimetrodon* sp., *Edaphosaurus* sp., and *Ophiacodon* sp.

The non-amniote bones reported here belong to large stegocephalians, which can grow up to two meters in length: *Eryops*, *Archeria*, and *Diadectes*, representing various lifestyles and phylogenetic positions among early Tetrapoda.

Of particular interest is the iconic temnospondyl *Eryops*, whose habitat preference has been debated. Case (1915) considered *Eryops* an aquatic animal based on the dorsal position of its nostrils and orbits. Conversely, Romer (1947) and Pawley and Warren (2006) argued that *Eryops* was a terrestrial animal because of its well-ossified limbs (including a well-ossified carpus and tarsus) and a highly ossified vertebral column. Despite the well-ossified skeleton, the spongy structure observed in the long bones of *Eryops* resembles that of aquatic animals (Quémeneur et al., 2013; Ricqlès and Buffrénil, 2001; Sanchez et al., 2010). Sanchez et al. (2010) pointed out that high torsional resistance of the long bones suggested that *Eryops*, even though hypothesized to have mostly dwelt on lake bottoms, may have had the ability to venture into the terrestrial environment.

Archeria was an elongate aquatic predatory anthracosaur (Romer, 1957). Some authors (Laurin and Reisz, 1997; Marjanović and Laurin, 2013) placed embolomeres among stem-tetrapods, rather than in their traditional position in Reptiliomorpha (e.g. Ruta et al., 2003), so the affinities of embolomeres are currently contentious.

The bone histology of the *Archeria* femur midshaft was illustrated by de Ricqlès (1975, 1978). According to these papers, the cortex is highly remodeled, resembling Harversian bone (Ricqlès, 1978), and the medullary region is filled with spongiosa (Ricqlès, 1978).

Diadectes belongs to Diadectomorpha, which is generally placed as the sister taxon to the crown amniotes (sauropsids + synapsids), together forming

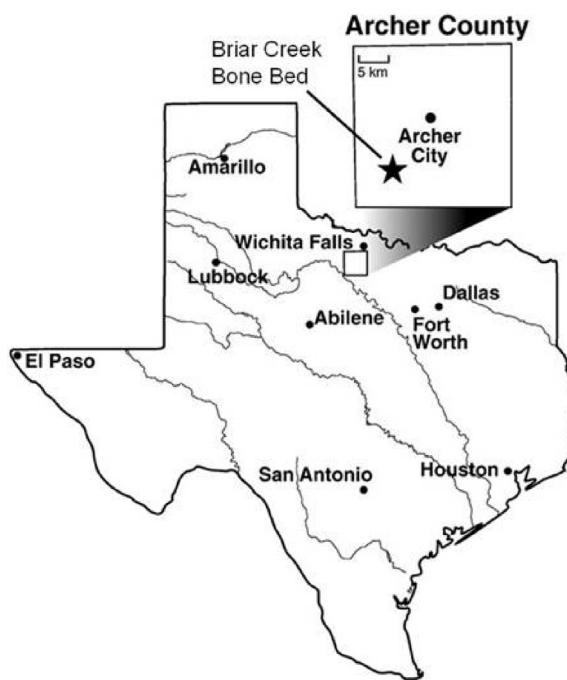


Fig. 1. Location of Archer County, Texas, USA. This map shows the location of the Briar Creek Bonebed, the site of the 2010 and 2011 excavations that yielded the material for this study. This bonebed is in the Nocona Formation (Lower Permian, Artinskian).

Fig. 1. Localisation d'Archer County, États-Unis. La carte indique la localisation du gisement d'ossements de Briar Creek, le site des fouilles de 2010 et 2011 qui ont fourni le matériel de l'étude ici présentée. Le lit qui contient les os se trouve dans la formation Nocona (Permien inférieur, Artiskien). Modifié d'après Labandeira et Allen (2007).

Modified from Labandeira and Allen (2007).

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