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Biological and physical evidence for extreme seasonality in central Permian Pangea

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ABSTRACT

Climate models indicate increased desertification in the continental interior of Pangea during the Permian, which would have affected the composition of the flora and fauna. We present a multi-proxy paleoenvironmental reconstruction of a terrestrial ecosystem in central Pangea of Lopingian age. The reconstruction is based on biological and physical data from the Moradi Formation, located in the Tim Mersoi sub-Basin, northern Niger. Paleosols and sedimentological evidence indicate that the prevailing climate was semi-arid to very arid with marked intervals of high water availability. Carbon stable isotope data from organic matter and paleosols suggest that both the soil productivity and actual evapotranspiration were very low, corresponding to arid conditions. Histological analysis of pareiasaur bones shows evidence of active metabolism and reveals distinct growth marks. These interruptions of bone formation are indicative of growth rhythms, and are considered as markers for contrasting seasonality or episodic climate events. The macrofossil floras have low diversity and represent gymnosperm-dominated woodlands. Most notable are ovuliferous dwarf shoots of voltzian conifers, and a 25-m long tree trunk with irregularly positioned branch scars. The combined biological and physical evidence suggests that the Moradi Formation was deposited under a generally arid climate with recurring periods of water abundance, allowing for a well-established ground water-dependent ecosystem. With respect to its environment, this system is comparable with modern ecosystems such as the southern African Namib Desert and the Lake Eyre Basin in Australia, which are discussed as modern analogues.

1. Introduction

Lithological and phytogeographic data show that the region currently forming the interior of Africa experienced increased aridification from the Late Carboniferous–early Permian to the middle to late Permian (Gibbs et al., 2002; Rees et al., 2002). Climate models estimate that desert-like conditions prevailed in central Pangea during the Lopingian, with most recent models suggesting summertime high temperatures around 40–50 °C (Fluteau et al., 2001; Peyser and Poulsen, 2008; Kiehl and Shields, 2005). The change from seasonally wet Cisuralian climate to desert-like Lopingian climate must have considerably altered both the composition of the flora and fauna in the local communities, and also their potential pathways for dispersal (Sidor et al., 2005). How exactly the biota responded is difficult to assess, however, as arid climates typically do not create the best conditions for plant preservation (Gastaldo and Demko, 2010), leaving an unsatisfactory gap in our knowledge of central Pangean ecosystems.

Fortunately, rare fossil vertebrate and plant assemblages have, in the past ten years, been discovered from the upper Permian in northern Niger (Damiani et al., 2006; Sidor et al., 2003, 2005; Smiley et al., 2008; Steyer et al., 2006; Tsuji et al., 2013; Turner et al., 2015). During Lopingian times, deposition of the Moradi Formation of the Tim Mersoi sub-basin, Iullemeden Basin, occurred approximately 10° S of the paleoequator in central Pangea. Studies of vertebrate fossils from the Moradi Formation have suggested a community structure and taxonomic composition similar to those described

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from Morocco (e.g. Germain, 2010; Jalil and Dutuit, 1996; Jalil and Janvier, 2005; Sidor, 2013; Steyer and Jalil, 2009). They are, however, distinctly different from any of the better understood southern Pangean assemblages (e.g. South Africa, Tanzania, Zambia, and Malawi), which were dominated by therapsids (e.g. Angielczyk et al., 2013; Sidor et al., 2005, 2013). The faunas from Niger and Morroco both are dominated by temnospondyls, pareiasaurs, and captorhinids. The two herbivorous reptiles described from the Moradi Formation of Niger, the captorhinid *Moradisaurus* and the pareiasaur *Bunostegos*, are known only from the formation (de Ricqlès and Taquet, 1982; Sidor et al., 2003; Taquet, 1969; Tsuji et al., 2013; Turner et al., 2015). Similarly, both of the temnospondyls described, *Nigerpeton* and *Saharastega*, represent relicts, or holdovers of lineages represented in faunas thought to have gone extinct near the Pennsylvanian–Permian boundary elsewhere (Damiani et al., 2006; Sidor et al., 2005, 2013; Steyer et al., 2006). The only terrestrial predator discovered in these faunas is represented by fragmentary gorgonopsid remains, not sufficient for a generic identification (Smiley et al., 2008). Due to the lack of any obvious physical barrier between the faunas of central and southern Pangea, Sidor et al. (2005) hypothesized that climate was the factor likely responsible for the biogeographic isolation and endemism of the Moradi assemblage.

These climatic interpretations are corroborated by sedimentary, morphological, and mineralogical data from paleosol profiles in the Moradi Formation, which display evidence of prevailing arid conditions at the time of development (Tabor et al., 2011; Smith et al., 2015). The paleosols and associated sedimentary strata are characteristic of those formed under a range of conditions from well to poorly drained, and represent stable floodplains of ephemeral, anabranching fluvial depositional systems (Tabor et al., 2011). These soil types are indicative of semi-arid areas with relatively shallow water tables, and include those formed on plains surrounding ephemeral lakes or playa environments. Modern analogues of these soil types can be found in the Namib Desert (Watson, 1992) of southwestern Africa and the Lake Eyre Basin, central and eastern Australia (Tabor et al., 2011; Fielding and Alexander, 2001; Tooth and Nanson, 2000). Both fossil and extant landscapes represent Heinrich Walter's zonobiome 3, or hot and arid subtropical deserts with very little rain (Breckle, 2002).

In this paper new biological and physical evidence for extreme seasonality in the Moradi Formation are presented, using a wide array of ecological proxies. The paleosol and sedimentological data are described briefly, and the stable carbon isotope compositions of paleosol calcite and co-existing organic matter are presented and discussed in terms of their relevance to interpretations of paleoclimate, biological productivity and water availability for floral and faunal communities across these paleolandscapes. Data from tetrapod bone histology is presented for evidence of seasonality, including cyclical periodic cessation of growth. The Moradi gymnosperm-dominated fossil floras, including a large tree trunk, are described for the first time, and compared to modern analogs in order to constrain the environmental circumstances under which these plants grew. Finally, the implications of the combined data on the interpretation of climate for Lopingian central Pangea are discussed.

2. Material and methods

2.1. Geological setting

The Carboniferous–Permian stratigraphy and structural evolution of the Tim Mersoi sub-basin of the Iullemeden basin in north–central Niger was recently reviewed in Tabor et al. (2011). At the time of active Permian deposition, the basin was moving northward from ~30 to ~10° S (Scotese et al., 1999), and remained at least 2000 km from the nearest open ocean. The Moradi Formation is the terminal lithostratigraphic unit of the Izegouandane Group and, in the study area, comprises ~100 m of dominantly red mudstones with secondary fluvial channel sandstones and conglomerates as well as rare coarse breccias (Fig. 1). A Lopingian age of deposition for Izegouandane Group strata is primarily based upon biostratigraphic correlations of fossil vertebrates in the Moradi Formation to contemporaneous strata in Russia and South Africa (Sidor et al., 2005; Lucas, 2004; Taquet, 1969).

The specimens described in this paper were collected from several localities located approximately 20 km west of Arlit, Agadez Department, northern Niger (see O'Keefe et al., 2005 or Damiani et al., 2006 for a map of the study area). The localities are within 1 km of each other and all fall within the upper half of the Moradi Formation. Detailed locality data are available to qualified researchers at the Musée National du Niger in Niamey (MNN) or by contacting Christian A. Sidor. The fossil material described here is housed in the paleontological collections at the MNN.

2.2. Sedimentary environment and taphonomy of plant fossil localities

The upper Moradi succession is made up of three distinctive associations of sedimentary facies, which were interpreted as having accumulated in discrete sub-environments of the Moradi alluvial plain. These are (1) high sinuosity channel fill and point bar, (2) loessic floodplain and incised distributary channels, and (3) end-point playa. The stratigraphic position and sedimentological log of the fossil localities recovered by our team in the 2003 (S) and 2006 (T) expeditions is shown in Fig. 1. The plant fossils from locality T9 occur within the loessic floodplain facies in a 0.25 m-thick bed of pale red massively-bedded calcareous siltstone ("siltite") with olive mottling along vertically orientated, downward branching root molds. This facies directly overlies a 3 m-thick conglomeratic sandstone displaying gently dipping (+/−20°) beds on its upper surface, which are interpreted as lateral accretion units of a large low-angle point bar. The fossiliferous "siltite" is immediately succeeded by a sequence of carbonate mudrock breccia and thinly-bedded micritic limestone interpreted as the accumulated deposits of a semi-permanent playa lake that most likely formed at the end-point of an ephemeral distributary channel (Smith et al., 2009, 2015). For a paleogeographic map and more information on the study area see Smith et al., 2015.

The leaf fossils occur as three-dimensional molds scattered at random orientations throughout the pale red siltstone, rather than concentrated along horizontal bedding planes. The lack of clearly-defined bedding planes within a bed of homogeneous unsorted silt-sized grains suggests that the leaf-bearing bed was deposited in a single episode and fairly rapidly as is common in windstorm-generated loess (Giles et al., 2013). The presence of root channels and the pervasive carbonate cement are indicative of incipient pedogenesis with relatively high water-tables in an evaporative setting, such as would be encountered on the sparsely-vegetated margins of an arid zone floodplain lake.

2.3. Fossil flora

Fossil plants were observed and collected from a total of three localities (Fig. 1). Two (field localities T09 and T24) produced vegetative remains and one (field locality T25) produced fossil wood. Localities T09 and T24, in the upper part of the Moradi Formation, produced vegetative and fertile plant fossils in the form of dark rust-colored carbonaceous dust in three-dimensional molds of a lighter colored fine-grained siltstone. The material was photographed using a Nikon D300 with a 60 mm macro lens. Leaf fossils were found at both localities. Ovuliferous dwarf shoots of a voltzian conifer were found only at T24. Of the sixty-one dwarf shoots collected, twenty-eight were selected for morphological measurements based on well-defined outlines and completeness. Because terminology used to describe ovuliferous cones of early conifers deviates from that for modern species, terms used herein are explained (see Hernandez-Castillo et al., 2001; Rothwell et al., 2005). "Bracts" are foliar appendages of the cone (or fertile zone) axis, these are interpreted as a modified leaves. "Ovuliferous dwarf shoots" or "dwarf shoots" are lateral branches of limited growth, arising in