



Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Oldest known naiaditid bivalve from the high-latitude Late Devonian (Famennian) of South Africa offers clues to survival strategies following the Hangenberg mass extinction

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ARTICLE INFO

Article history:

Received 18 August 2016

Received in revised form 12 January 2017

Accepted 15 January 2017

Available online 21 January 2017

Keywords:

Witpoort Formation

Witteberg Group

Gondwana

Waterloo Farm

Naiadites

Pteriomorphia

ABSTRACT

A phased mass extinction event (which culminated in the Hangenberg event) marked the end of the Devonian period and had a significant impact on the palaeoecology and faunal diversity of vertebrate and invertebrate communities. In the present study the taxonomy of bivalves from the Waterloo Farm lagerstätte of the Upper Devonian, Famennian, Witpoort Formation (Witteberg Group, Cape Supergroup) was studied and compared with known Carboniferous examples. For the first time, Devonian bivalves of the Naiaditidae are described from a high-latitude palaeogeographic setting of Gondwana. The presented data suggests a high-latitude origin for post-Hangenberg event Naiaditidae, found at lower latitudes during the Early Carboniferous. This may have resulted from migration to lower latitudes in response to reduced global temperatures, which were associated with climatic perturbation at the time of the Hangenberg event, and which persisted into the Early Carboniferous. Taxa that were adapted to temperature ranges existing at high latitudes during the Late Devonian are likely to have followed these temperature ranges towards lower latitudes with decreasing global temperatures. Here they may have occupied free ecospace available in the aftermath of the Late Devonian extinction event.

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1. Introduction

The Late Devonian is marked by massive extinction and faunal turnover, occurring as a number of different extinction phases, including the Kellwasser and Hangenberg events (e.g., House, 2002). Together these amount to one of the five biggest mass extinctions in Earth's history (e.g., Raup and Sepkoski, 1982). Whilst invertebrates were decimated by the Kellwasser event, this had little impact on vertebrate diversity, which suffered one of its greatest reductions during the Hangenberg event (Sallan and Coates, 2010). Precise U-Pb zircon dating of volcanic ash beds of 358.97 ± 0.11 Ma to 358.89 ± 0.20 Ma (Myrow et al., 2014) constrained the Hangenberg event to a latest Famennian (latest Devonian) age. In the Famennian 20–24% of marine and continental families went extinct (Benton, 1995). Debates about the cause of the Late Devonian extinction include sea level changes (e.g., Carmichael et al., 2016), oceanic or atmospheric anoxia (e.g., Marynowski and Filipiak, 2007; Racka et al., 2010), global cooling (e.g., Caplan and Bustin, 1999) or multiple causes (e.g., Kaiser et al., 2011; Matyja et al.,

2015). In particular, the Hangenberg event has been linked to a rapid sea level change caused by glaciation and glacial melt in the southern hemisphere, at the end of the Devonian (e.g., Sandberg et al., 2002). An increase in terrestrial plant cover has been related to increased nutrient supply in rivers, which may have led to eutrophication and algal blooms in semi-restricted epicontinental seas (e.g., Algeo et al., 2001). Increased Carbon sequestration resulting from the emergence of the first true forests, through both increased biomass and changes in the chemical decomposition of bedrock, are likely to have helped precipitate global cooling (Algeo et al., 2001).

In the present study, bivalves of the family Naiaditidae were described according to the valve morphology and compared with the stratigraphic ranges of other known naiaditid taxa to provide insights into biotic responses to the environmental perturbations of the Late Devonian extinction event. The studied material was obtained from the Waterloo Farm locality (Eastern Cape Province, South Africa), situated near the top of the Witpoort Formation (Witteberg Group, Cape Supergroup). This locality has become known for its aquatic vertebrate fauna represented by various groups including lampreys (Gess et al., 2006), placoderms (e.g., Long et al., 1997), acanthodians (Gess and Hiller, 1995a; Gess, 2001), chondrichthyans (Gess and Coates, 2015a), and sarcopterygians such as actinistians (e.g., Gess and Coates, 2008; Gess and Coates, 2015b), dipnoans (Gess and Hiller, 1995a), and

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