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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

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

tetrapodomorphs (Gess and Hiller, 1995a; Gess and Coates, 2008). These are preserved alongside both phaeophyte and charophyte aquatic algae (Gess and Hiller, 1995b; Hiller and Gess, 1996). Non-aquatic biota from the Waterloo Farm locality have also been reported including diverse flora (Gess and Hiller, 1995a), lycopsid roots (Prestianni and Gess, 2014) and scorpion remains, representing the earliest evidence of a terrestrial animal from Gondwana (Gess, 2013).

Upper Devonian faunal and floral elements from the Waterloo Farm locality, being located near the top of the Famennian aged Witpoort Formation (Gess, 2016), immediately predate the time of the Hangenberg event and, therefore will have been directly affected by the biotic crisis. From other studies, it is well documented that in consequence of the Hangenberg event gnathostome vertebrate diversity was reduced by 50% (Sallan and Coates, 2010) and the body sizes of vertebrates became reduced for at least 36 Ma in the aftermath of this crisis (Sallan and Galimberti, 2015). The effects on the invertebrate fauna, however, seem to be less understood. The present study explores the pre-Carboniferous origin of naiaditid bivalves and their changing known geographic distribution across the Devonian-Carboniferous boundary. Presented here is the oldest known record of the family Naiaditidae, which is widespread in Carboniferous to Upper Permian strata (e.g., Tchernyshev, 1931; Bennison, 1960; Rogers, 1965; Eagar and Weir, 1971; Vasey, 1984; Guirdham et al., 2003; Falcon-Lang et al., 2006; Bennett et al., 2012; Amler and Schöllmann, 2012; Urazaeva et al., 2015). Its first reported occurrence in the Upper Devonian (herein reported) may contribute to a better understanding of bivalve response to the end-Devonian mass extinction event.

2. Geologic setting

The Waterloo Farm locality exposed in 1985 by roadworks south of Grahamstown, South Africa is part of a package of black shale lenses inter-bedded within quartz arenites of the uppermost Witpoort Formation (Gess, 2011), a Famennian subdivision of the Witteberg Group (Cape Supergroup) (Gess, 2016) (Fig. 1). A Famennian age for the Witpoort Formation was initially proposed by Cooper (1986) as part

of a study correlating sea level changes in the Cape Supergroup with Laurasian sea level curves (Cooper, 1986). Significantly he correlated the arenaceous (quartz sand dominated) Witpoort Formation with the Famennian regression. He interpreted the abrupt change to thick fine argillaceous deposits, which comprise the overlying Kweekvlei Formation (Lake Mentz Subgroup), with onset of the Tournaisian transgression, marking the end of the Famennian. A Frasnian age for the underlying Weltevrede Subgroup is supported by presence of the Givetian to Frasnian brachiopod, *Tropidolepis* in strata near the top of the Weltevrede Subgroup, including in the Grahamstown area (Boucot et al., 1983). A Tournaisian to Visean palynological age was established for the Waaipoort Formation, the uppermost of three units comprising the Lake Mentz Subgroup which overlies the Witpoort Formation (Streel and Theron, 1999). This was consistent with a Visean age estimate for a diverse actinopterygian fauna described from the same unit (Marais, 1963; Gardiner, 1969, 1973).

Recent study of early vertebrate remains from the Witteberg Group highlights a distinct vertebrate faunal turnover at the top of the Witpoort Formation. Faunas dominated by placoderms and other typically Devonian taxa come to an abrupt end at this level and are replaced by others comprised chiefly of characteristically Carboniferous actinopterygians (Gess, 2016). This is consistent with the internationally observed vertebrate faunal turnover associated with the Hangenberg extinction event, at the end of the Famennian, in which placoderms became extinct (Gess, 2016). The diverse flora recovered from Waterloo Farm, including the generally Frasnian to Famennian (Algeo et al., 2001) genus *Archaeopteris* (Anderson et al., 1995) provides additional, more indirect, support for the dating of the Witteberg Group units by Cooper (1986). The Waterloo Farm locality, which hosts a diverse fauna of placoderms and large sarcopterygians (Gess and Coates, 2008), is situated near the stratigraphic top of the Witpoort Formation and is therefore considered to be of late to latest Famennian age (Gess, 2011).

The sediments of the uppermost Witpoort Formation are interpreted as having been deposited in a barrier island complex along the shore of the high-latitude Agulhas Sea (Taylor and Hiller, 1993). The black shale
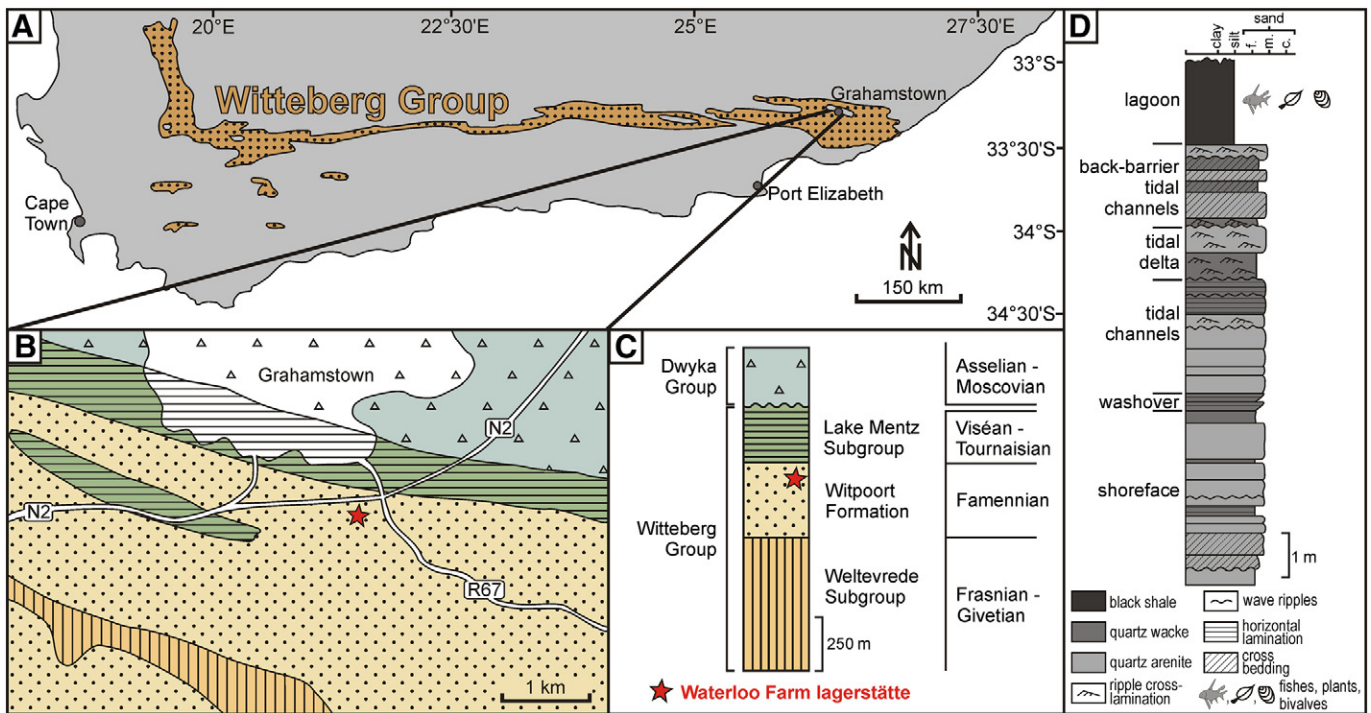

Fig. 1. Geological setting of the Upper Devonian (Famennian) Waterloo Farm lagerstätte located south of Grahamstown, South Africa. A–B, geographic position and geological map of the wider study area. C, stratigraphic subdivision of the Middle Devonian to Lower Permian succession in the study area. D, vertical section of the eastern part of the road cutting at Waterloo Farm revealing strata near the top of the Witpoort Formation (after Taylor and Hiller, 1993). The layer, from which the bivalve specimens have been collected, is situated at the top.

represents anaerobic muds deposited in a back barrier lagoon, with both marine and fresh water inputs (Hiller and Taylor, 1992; Gess and Hiller, 1995a). This shale lens and a few lesser adjacent shales constitute the only known Famennian locality in southern Africa from which faunal remains have been reported (Gess, 2011). Fine black anaerobic muds deposited in still portions of the lagoon accumulated a huge mixed assemblage representing the life of marine and fresh water influenced parts of the lagoonal system, as well as that of adjacent terrestrial environments (Gess and Hiller, 1995a). The Waterloo Farm lagerstätte represents an important biogeographic outlier. Whereas Upper Devonian faunas and floras found in North America, Europe, China, Australia and Eastern Antarctica were tropical, that found at Waterloo Farm was situated within the Antarctic circle (Gess, 2011) (Fig. 2). Systematic excavation over many years has resulted in a very large collection of material which allows for reconstruction of a fairly complete ecological system. Relationships are determinable from, for example, stomach contents within certain vertebrates, numerical analysis of size ranges present, the presence or absence of vertebrate hatchlings and growth of aquatic algae on terrestrially derived axes. Ongoing research is creating a unique holistic picture of high-latitude continental life in Gondwana immediately predating the end-Devonian extinction event.

3. Material and methods

Material has been collected by RWG from the Waterloo Farm locality (and shale samples rescued therefrom during roadworks) intermittently between 1985 and 2015. The most common faunal component comprises naiaditid bivalves, which though common are generally poorly preserved, their thin shells often only partially preserved and lacking full outlines or clear growth rings. A sample of 138 large (4–17 mm) specimens has been collected. In addition numerous small valves are noted, ranging between 1 and 5 mm in length, though their state of preservation precludes unequivocal identification as juveniles of the same species. A set of 13 large specimens, which were exceptionally well preserved, were selected for analysis. These were microscopically drawn and photographed by using both the mirror tube of a stereomicroscope and a motor controlled camera image stacking system. The morphology of the valve has been described according to literature by previous workers on bivalves of similar morphology (e.g., Řehoř, 1972; Huwe, 2006). For objective and reproducible descriptions of the morphological elements a terminology according to Fig. 3 was used.
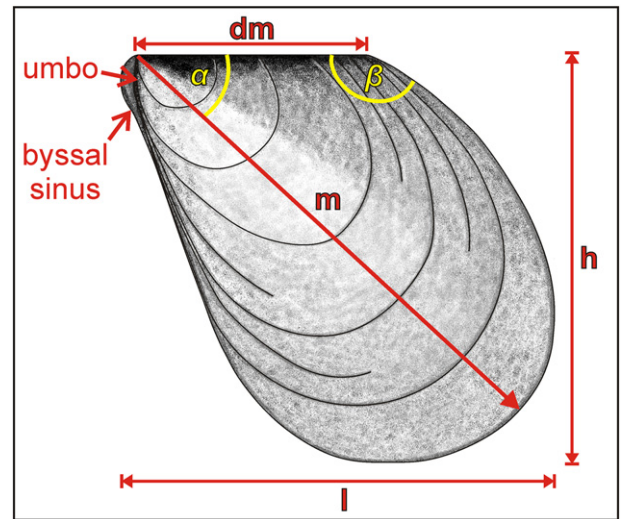

Fig. 3. Morphological measurements of a naiaditid bivalve shell (parameters and terminology modified after Huwe, 2006): l, total length of the valve; h, total height of the valve; dm, length of the dorsal margin; m, maximum oblique distance; α, angle of obliquity; β, angle between dorsal margin and posterior margin.

For general taxonomical classification the bivalve systematic of Carter et al. (2011) was used in the present study. The taxonomic determination was conducted by literature-based comparison with anthraconauti-form bivalves (i.e., *Anthraconauta*, *Curvirimula* and *Naiadites*) of similar morphology, from Devonian (e.g., Amler, 1995) and Carboniferous (e.g., Rogers, 1965; Eagar and Weir, 1971; Vasey, 1984) occurrences. All specimens figured here are stored in the Albany Museum in Grahamstown, South Africa (collection number "AM7507" to "AM7520").

4. Results

4.1. Preservation and sedimentology

The bivalve-bearing slabs consist of slightly metamorphosed shaley mudstone with fine, horizontal, internal lamination. These carbonate-free, fine-grained mudstones are dark grey to medium grey. Weakly
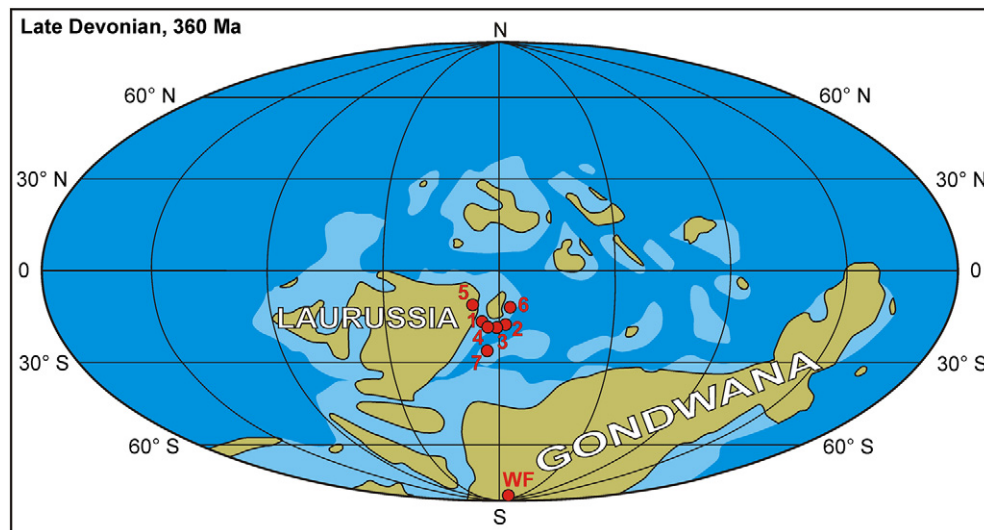

Fig. 2. Latest Devonian plate tectonic situation (map modified from Kaiser et al. [2015] and references cited therein) and the geographic distribution of *Naiadites*. "WF" marks the palaeogeographic position of the Waterloo Farm lagerstätte ("WF") with the occurrences of *Naiadites* forma Devonicus of the present study. Red points mark occurrences of *Naiadites* of Carboniferous age based on the following records: 1, Scotland (Leitch, 1941; Bennett et al., 2012); 2, Czechia (Řehoř, 1972); 3, Germany (Huwe, 2006; Amler and Schöllmann, 2012); 4, England (Dix and Trueman, 1932); 5, Canada (Dawson, 1860; Falcon-Lang et al., 2006); 6, Donetsk Basin (Tchernyshev, 1931); 7, Spain (Eagar and Weir, 1971).

developed foliation planes are secondarily enriched with 0.5–1 mm muscovite-like mica crystals. The bivalves were embedded horizontally and are preserved either as internal sediment-filled casts (steinkerns) or as slightly glossy, dark brown to grey coloured impressions in the sediment. The primarily calcareous shells became dissolved during diagenetic processes, which require further study. In two specimens remnants of a yellowish grey shell pseudomorphosis was observed. The bivalves are associated with compacted, slightly coalified plant detritus of 4–25 mm in size and of light grey colour.

The dark grey colour of the matrix indicates an enrichment of organic carbon, while the internal lamination and the fine grain size points to a subaquatic deposition under relatively quiet water conditions, with sediment settling out from suspension. The environment has been sedimentologically interpreted as that of a brackish, semi-enclosed, coastal estuarine lagoon with significant freshwater inputs. This is supported by (for example) the presence of abundant charophyte algal remains (Gess and Hiller, 1995a, 1995b). Bivalves are found abundantly throughout the deposit, associated with both charophyte algae as well as more marine algae and vertebrates. Some degree of tolerance of salinity is therefore likely.

4.2. Taxonomy

For systematic palaeontology the bivalve classification of Carter et al. (2011) is used here. This assessment is based on 13 specimens of *Naiadites* Dawson, 1860 (family Naiaditidae Scarlato and Starobogatov, 1979; infraclass Pteriomorphia Beurlen, 1944), which have been selected for their large valve size and unusually good preservation. Genera of the Naiaditidae in the sense of Carter et al. (2011), are known for their high degree of morphological variability, as discussed for fresh water bivalves *Anthraconauta*, *Curvirimula* and *Naiadites* (e.g., Dix and Trueman, 1932; Wehrli, 1933; Řehoř, 1972; Amler and Schöllmann, 2012). This is also apparent in the current samples. Due to the limited number of well-preserved specimens a full analysis of intraspecific variability has not been conducted. Therefore, the taxonomic determination is realized up to the genus level, and a form-based open taxonomy is used instead of the species level.

The genus *Naiadites* was first defined by Dawson (1860) from the Upper Carboniferous coal-measures of Nova Scotia in Canada. The type species *Naiadites carbonarius* was described by Dawson (1860: p. 43–44) as showing a nearly straight hinge line longer than one half of the total valve length, an abruptly rounded anterior margin, nearly straight ventral margin, broad and regularly rounded posterior margin, and a thin shell with distinct growth lines. The definition of *Naiadites* has been refined in successive studies (e.g., Rogers, 1965; Warth, 1967) and a comprehensive morphological description by Huwe (2006) is followed here. Material in the current study is diagnosed as belonging to the genus *Naiadites* on the basis of: a myaliniform and more or less U-shaped contour; a straight dorsal margin; obtuse angle between the dorsal margin and the posterior margin; curved or straight posterior margin partially forming a wing; ventral margin obliquely curved; straight or slightly concave, rarely slightly convex anterior margin; anterior and posterior margins partially parallel; maximal convex curvature of the valve located slightly below the umbo in the upper third of the valve. The morphological differences between *Naiadites* and similar mytiliform bivalves such as *Posidoniella*, *Posidonia*, *Myalina*, *Septimyalina*, and *Selenimyalina* were fully summarized and discussed by Huwe (2006: her Table 3). Only *Curvirimula* and *Anthraconauta* closely resemble *Naiadites*. *Curvirimula* generally differs by having a more rounded contour. Additionally, Řehoř (1972: p. 53) mentioned fine, concentric sculptures, while the external side of *Naiadites* show more rough, concentric wrinkles. *Anthraconauta* and *Naiadites* were in cases synonymously used by previous workers as discussed by Řehoř (1972). Although the shape of *Anthraconauta* is similar to *Naiadites* the latter genus tends to have higher height/length ratio values and a longer dorsal margin in relation to the total valve length. Additionally, a byssal

sinus (see Fig. 3) is present in *Naiadites* (e.g., Huwe, 2006), while it is absent in the *Anthraconauta* (e.g., Warth, 1967).

Based on 13 specimens (AM7507 to AM7520) of different types of preservation, all collected from the uppermost Witpoort Formation (Witteberg Group, Cape Supergroup; Famennian) at the Waterloo Farm locality (Grahamstown, Eastern Cape Province, South Africa), we define *Naiadites* forma Devonicus (Fig. 4, Table 1) according to the morphology of the valve: Height of the valve 4–14 mm; dorsal margin almost straight, 4.2–17.1 mm long; maximum oblique distance 6.6–22.4 mm; position of the point of maximal curvature of the anterior margin above and of the posterior margin below a horizontal midline of the valve; position of the point of maximal curvature of the ventral margin behind a vertical midline of the valve; up to 46 growth lines; α (angle of obliquity) 20–25°; β (angle between dorsal margin and posterior margin) 35–65°; some specimens show an anterior wing with a concavely recurvation of the uppermost posterior margin below the dorsal margin.

By its inframarginal position the umbo of *Naiadites* forma Devonicus differs from the morphologically similar *Naiadites carbonarius* (figured by Cox et al., 1969: their Fig. C31/4) from the Pennsylvanian (Upper Carboniferous) of Nova Scotia in Canada. *Naiadites* forma Devonicus morphologically strongly resembles *Naiadites phillipsi* figured by Wehrli (1933: his Plate VII, Figs. 7–9) (="*Anthraconauta phillipsii*" in Weier, 1959) from the Westphalian B–C (Lower–Middle Pennsylvanian) of the Ruhr area in western Germany. The morphological variability of *Naiadites* forma Devonicus is in conformity with the variability of *Naiadites phillipsi* recorded by Wehrli (1933: his Fig. 2), in that the latter also includes forms with concave recurvature of the upper posterior margin below the dorsal margin. The slightly subquadratic shape of *Naiadites* forma Devonicus differs from the more modioliform shapes of *Naiadites moravicus*, *Naiadites alius*, and *Naiadites truemani* (all figured by Řehoř, 1972: his Plates 5–10) from the Namurian A (Upper Mississippian–Lower Pennsylvanian) in the Upper-Silesian basin in eastern Czechia. Relative to the valves measured by Řehoř (1972), *Naiadites* forma Devonicus entirely or partially lies within the size ranges of *Naiadites truemani* (length 5.6–20.8 mm) or *Naiadites moravicus* (length 4.7–33.7 mm), respectively, while *Naiadites alius* (18.7–28.3 mm) is larger than *Naiadites* forma Devonicus.

The myaliniform and U-shaped contour of *Naiadites* forma Devonicus is very similar to the valve morphology of the Late Carboniferous species *Naiadites carbonarius*, which was defined by Dawson (1860) as the type species of *Naiadites*. However, drawings and photographs (e.g., Rogers, 1965; Cox et al., 1969; Huwe, 2006) of *Naiadites carbonarius* show a carina running from the umbo to the ventral margin of the valve, which is not observed in *Naiadites* forma Devonicus. Additionally, *Naiadites carbonarius* is larger (length 17.8–29.8 mm; Rogers, 1965) than *Naiadites* forma Devonicus.

Valves of *Naiadites obesa* and *Naiadites tumida* from the Mississippian in Scotland range between 17 mm and 33 mm (Leitch, 1941) and are larger than *Naiadites* forma Devonicus. *Naiadites vorhallensis* from the Pennsylvanian (Namurian B) of western Germany (Huwe, 2006) ranges between 1 mm and 24 mm, but differs from *Naiadites* forma Devonicus in having a U-shaped contour which is more obliquely elongated towards the posteroventral margin of the valve. *Naiadites flexuosa*, which was described by Dix and Trueman (1932) based on Pennsylvanian (Westphalian) specimens from England, has a similar umbonal area to that of *Naiadites* forma Devonicus. A concave recurvature of the posterior margin below the dorsal margin can be observed in both species but the valves of *Naiadites flexuosa*, which are 36 mm in length (Dix and Trueman, 1932), are larger than valves of *Naiadites* forma Devonicus.

Conchostracans (Crustacea: Branchiopoda) are also recorded from silica clastic deposits and their chitinous carapace could theoretically resemble the shells of bivalves. Although the fossil record of Devonian conchostracans from Gondwana is so far poor, Tasch (1987) reported several species with valve lengths between 3.2 mm and 5 mm. Besides
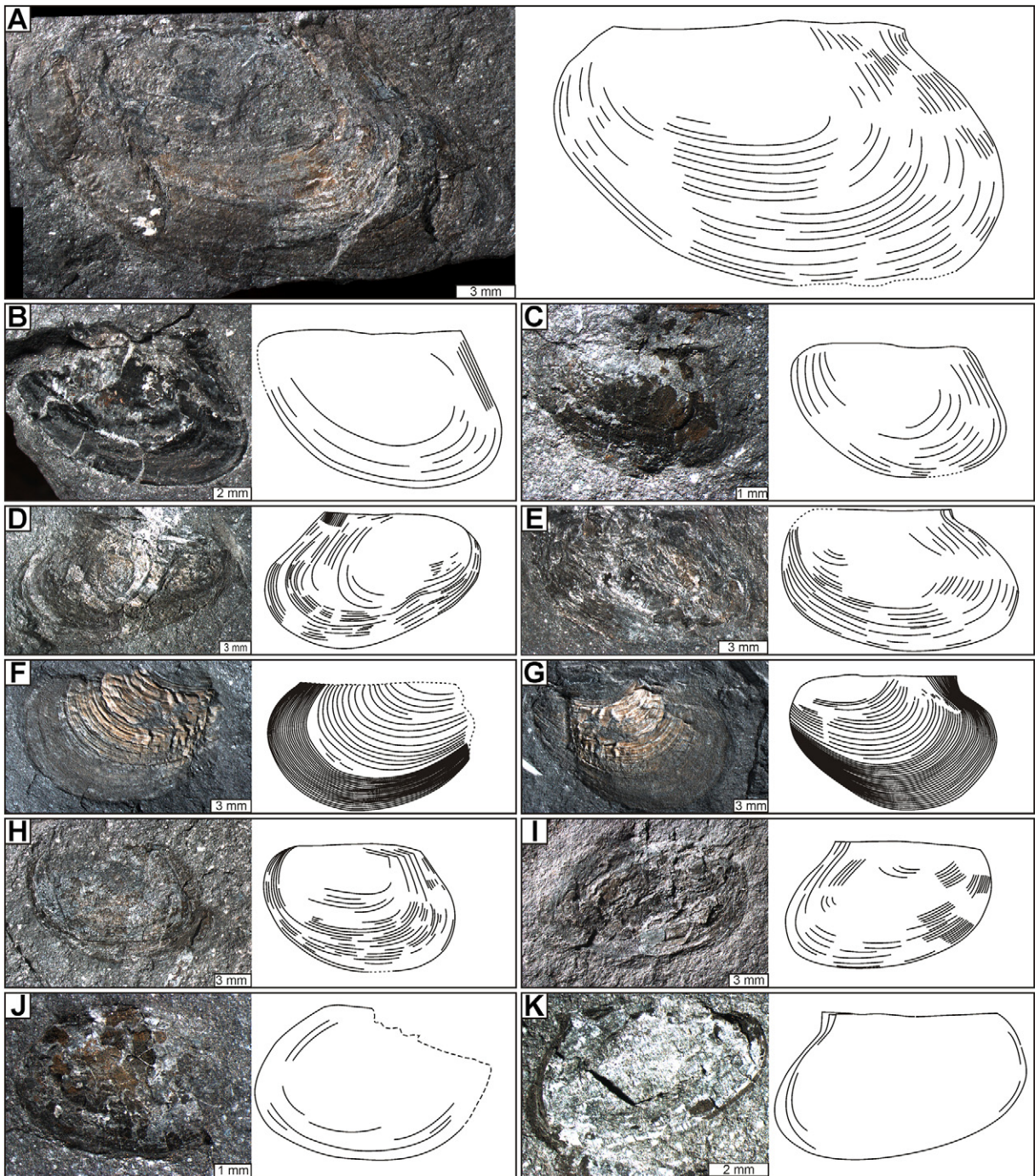
Fig. 4. *Naiadites* forma Devonicus from the Upper Devonian (Famennian) of the Waterloo Farm locality, Grahamstown, Eastern Cape Province, South Africa. A, cast of a left valve (AM7507); B, imprint of a right valve (AM7508); C, cast of a left valve (AM7509); D, cast of a right valve (AM7510); E, cast of a left valve (AM7511); F, imprint of a right valve with remnants of shell substance (AM7512); G, cast of a left valve with partially preserved shell substance (AM7513) H, partially preserved cast of a left valve (AM7514); I, imprint of a left valve (AM7515; counterpart of E); J, cast of a right valve (AM7517); K, imprint of a left valve with white coloured pseudomorphosis of the shell substance (AM7516).

these conchostracans being smaller in size than *Naiadites* forma Devonicus, the latter also has a valve morphology that is distinct from that of conchostracans. Since the growth of the conchostracan shell is realized by moulting of the crustacean animal, the chitinous valve consists of growth bands separated by distinct growth lines, each representing a single moulting (e.g., Scholze and Schneider, 2015). Such characteristic growth bands are not present in *Naiadites* forma Devonicus. Rather, it shows morphologies varying between partially smooth surfaces and the presence of more or less dense concentric lines or wrinkles (Fig. 4).

5. Discussion

5.1. Biostratigraphy

The genus *Naiadites* was defined on its holotype of *Naiadites carbonarius* Dawson, 1860 from non-marine deposits of Pennsylvanian age in Nova Scotia (Cox et al., 1969). The present study indicates that the genus *Naiadites* ranges from the Late Devonian (Famennian) to the Late Carboniferous (Pennsylvanian; e.g., Wehrli, 1933). For a higher stratigraphic resolution, the use of *Naiadites* forma Devonicus seems to

Table 1

Valve measurements of *Naiadites* forma Devonicus from the Upper Devonian (Famennian) Waterloo Farm locality (Grahamstown, Eastern Cape Province, South Africa).

Collection number	Valve length [mm]	Valve height [mm]	Height/length	Dorsal margin length [mm]	Dorsal margin length/valve length	maximum oblique distance [mm]	α	β
AM7517	6.5	4.4	0.68			6.4	22°	140°
AM7509	7.4	4.5	0.61	5.1	0.69	6.6	22°	118°
AM7520	9.0	5.2	0.58			7.9	25°	
AM7508	12.8	8.3	0.65	8.5	0.66	12.5	25°	120°
AM7518	17.1	11.1	0.65	11.1	0.65	16.2	24°	129°
AM7514	16.5	11.0	0.67	10.5	0.63	15.0	23°	128°
AM7507	23.6	13.6	0.58	15.2	0.64	22.4	23°	132°
AM7516	9.1	5.4	0.59	6.3	0.69	8.4	24°	
AM7512	17.0	11.5	0.68			16.5		
AM7513	18.6	12.0	0.64	17.1	0.92	18.3	20°	
AM7510	20.0	13.9	0.60	13.6	0.68	19.7	24°	128°
AM7511	14.8	8.8	0.59	8.8	0.59	14.8	23°	147°
AM7515	16.0	9.8	0.61	11.3	0.71	16.5	22°	

be limited, since this form is only known from a small number of well-preserved individuals which display a high degree of morphological variability. Based on current literature (e.g., Amler and Schöllmann, 2012), the different genera (i.e., *Anthraconauta*, *Curvirimula* and *Naiadites*) of anthraconauti-form bivalves, which have overlapping stratigraphic ranges in the Carboniferous, are difficult to taxonomically separate on both genus and species levels, due to the subjectivity of early workers. For example, Vasey (1984) noted that the holotypes of both *Naiadites mytiloides* and *Curvirimula corvosa* from the Pennsylvanian of Nova Scotia occurred on the same slab, and reinterpreted poorly preserved *Naiadites mytiloides* as *Curvirimula*. Similarly, Rogers (1965) re-studied numerous species of *Naiadites* and reassigned them to *Anthraconauta*, *Curvirimula* or other non-marine Carboniferous bivalve genera. In light of the high degree of morphological variability of anthraconauti-form bivalves (i.e., *Anthraconauta*, *Curvirimula* and *Naiadites*) taxonomical revision of this group, using standardized morphometrics, is overdue. Since this first report on *Naiadites* forma Devonicus is based on a limited number of well-preserved specimens displaying pronounced morphological variability, its use for fine-scale biostratigraphy seems limited.

5.2. Palaeoenvironment and biogeography

Both freshwater and marine bivalves are generally indicators of aquatic conditions, since they can respire, feed, and remain active exclusively in an aqueous medium (Cox, 1969). The respective palaeoenvironments with occurrences of Carboniferous anthraconauti-form bivalves (i.e., *Anthraconauta*, *Curvirimula* and *Naiadites*) have often been described as 'non-marine', but accounts generally lack detailed sedimentary facies analyses. In previous studies, occurrences of *Naiadites* were interpreted as being from an 'intra-continental terrestrial ecosystem' (Falcon-Lang et al., 2006) or less-specifically mentioned to be 'non-marine' (e.g., Bennison, 1960; Rogers, 1965; Eagar and Weir, 1971; Amler and Schöllmann, 2012); however, the possibility of brackish environments was not excluded and even previous reports on marine occurrences from literature have been reviewed by Řehoř (1972: p. 10ff). Adding to these reports, occurrences of *Naiadites* forma Devonicus in a fresh to brackish, semi-enclosed, coastal estuarine lagoon with significant freshwater input, suggest that *Naiadites* though preferentially inhabiting fresh water, may have tolerated some degree of salinity.

Whereas all previously known (Carboniferous) *Naiadites* species are known from low palaeolatitude (0–30°) Laurussian deposits, forma Devonicus is recorded from a high-palaeolatitude Gondwanan setting (Figs. 2, 5). Significantly, movement between these two settings may have resulted from changing climatic conditions. The Late Devonian was characterized by gradual climatic cooling, which led to a short Late Devonian glaciation in Gondwana (e.g., Algeo and Scheckler, 1998; Caplan and Bustin, 1999; Joachimski and Buggisch, 2002; Kaiser et al., 2015). A widespread episode of cool climatic conditions is evidenced from northwestern Africa (e.g., Kaiser et al., 2011), central Europe (e.g., Kaiser et al., 2006), South America (e.g., Caputo, 1985), and North America (e.g., Brezinski et al., 2010). Reduced temperatures in low latitudes at the time of the Hangenberg event may have facilitated the migration of naiaditid bivalves, already tolerant of cold water conditions, to lower latitudes. As *Naiadites* forma Devonicus represents the oldest occurrence of this lineage, it is likely that naiaditids arose in cool high-latitude waters and subsequently migrated towards lower latitudes as global oceanic conditions cooled. There, they may have occupied free ecospace available in the aftermath of the end-Devonian mass extinction event.

Bivalves occupying free ecospace following a major extinction has been demonstrated following the end-Permian mass extinction, when widespread extinction of rynchonelliform brachiopods enabled rapid colonization by Early Triassic bivalves (Fraiser and Bottjer, 2007). On the contrary, invasive species occupying ecological niches has been interpreted as a trigger, rather than a consequence of the Late Devonian biodiversity crises (i.e., Rode, 2004; Stigall, 2010). It has been suggested that spread of ecologically generalist, invasive, Late Devonian species of bivalves, brachiopods, and arthropods, potentially resulted in a dramatic reduction in speciation rates during the Late Devonian biodiversity crises (Stigall, 2010, 2012). In order to further assess the ecological impact of an invasion of cold tolerant species from high latitudes, successive studies should compare pre- and post-Hangenberg extinction event invertebrate and vertebrate faunas from high and low palaeolatitudes.

Data on other bivalve groups is currently inadequate to establish whether or not they demonstrate similar palaeogeographic shifts at this time. Amler (1996: p. 58–59) has observed that Devonian and Carboniferous bivalve faunas are insufficiently investigated and therefore general statements of species-level provincialism may be misleading. Similarly, lack of Devonian *Naiadites* at low latitudes could reflect inadequate sampling. This is however a common problem in palaeontology and it is hoped that the currently proposed hypothesis may stimulate more rigorous sampling at low latitudes.

Migration between high-latitude Gondwanan settings and low-latitude Laurussian ones likely followed a pathway from South to North along the shoreline of western Gondwana (Figs. 2, 5). Closure or reduction of the Rheic Ocean towards the end of the Devonian has been postulated as an explanation for breakdown of vertebrate faunal provincialism (Young, 1993), and would have helped facilitate dispersal. Shorter distances between continents will have allowed transport of pelagic bivalve larvae by ocean surface currents (Kříž, 1979). Consequently, future field studies are expected to provide further records of *Naiadites* along this palaeogeographic migration route.

6. Conclusions

The present study on *Naiadites* forma Devonicus contributes to a better understanding of the faunal diversity of the Waterloo Farm
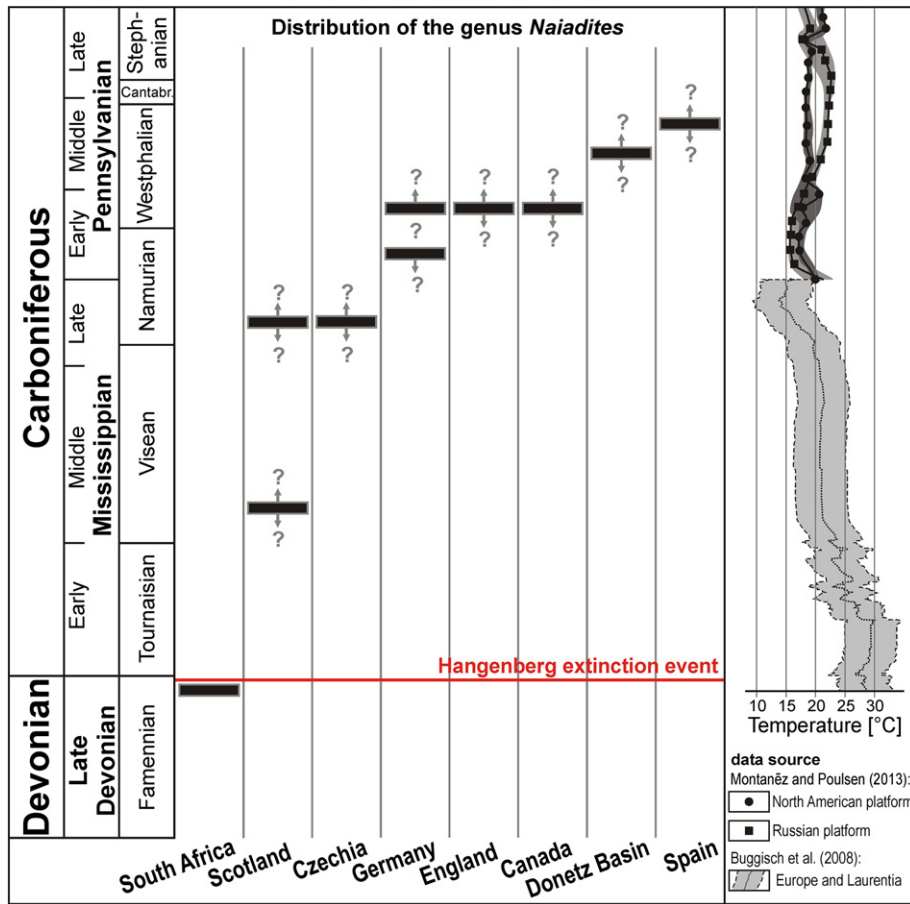
Fig. 5. Relative stratigraphic ranges of *Naiadites* plotted against its occurrences in different regions. The summarized distribution supports a proposed high-latitude origin of *Naiadites* and its subsequent migration to lower palaeolatitudes (cf. Fig. 2). The data is based on occurrences of *N. obesa, N. tumida, N. obesus, N. crassus* reported from Scotland (Leitch, 1941; Bennett et al., 2012); *N. moravicus, N. alius, N. truemani* from Czechia (Řehoř, 1972); *N. vorhallensis, N. hindi, N.* cf. *productus, N.* cf. *quadratus, N.* cf. *subtruncatus, N.* cf. *obliquus, N. quadratus, N.* cf. *alatus* from Germany (Warth, 1967; Huwe, 2006; Amler and Schöllmann, 2012); *N. triangularis, N. carinata, N. quadrata, N. modiolaris, N. producta, N. flexuosa, N. obliqua, N. daviesi* from England (Dix and Trueman, 1932); *N. carbonarius, N. elongata, N. laevis, N. arenaceus, N. ovalis, N. angulata* from Canada (Dawson, 1860; Falcon-Lang et al., 2006); *N. modiolaris, N. carinata, N. quadrata, N. triangularis, N. elongata, N. excavata* from the Donetsk Basin (Tchernyshev, 1931); and *N. obliquus* and *N.* sp. aff. *obliquus* from Spain (Eagar and Weir, 1971). Arrows and question marks indicate uncertainties of the respective stratigraphic ranges (vertical thickness is not for scale). Palaeotemperature values for the Mississippian were calculated from $\delta^{18}O$ of conodont apatite (curves modified from Buggisch et al., 2008). Palaeotemperature values for the Pennsylvanian are based on $\delta^{18}O$ of brachiopods from the Russian platform and central North America (data from Grossman et al., 2008; curves modified from Montañéz and Poulsen, 2013).

lagerstätte. Due to both the limited number of well-preserved specimens and their pronounced morphological variability, an open taxonomy is proposed at species level in order to avoid producing synonymies. Ongoing excavations at Waterloo Farm may be expected to provide a greater sample of well-preserved *Naiadites* forma Devonicus which would permit a thorough analysis of the intraspecific variability of *Naiadites* forma Devonicus.

Previous recorded occurrences of *Naiadites* are all Carboniferous and include examples from Scotland, Spain, Canada, and Germany, all of which were situated in the palaeotropics during the Carboniferous. The presence of Late Devonian (Famennian) *Naiadites* at high palaeolatitude contrasts strongly with all previous reports. It is here suggested that this reflects biotic turnover and response to climatic change initiated during the end-Devonian mass extinction event. Due to global cooling at the end of the Devonian and during the Early Carboniferous many tropical fauna may have become extinct, due to loss of habitats consistent with their preferred water temperature range, resulting in unoccupied ecological niches at low latitudes. Conversely cold water adapted taxa that had occupied niches at high palaeolatitudes were able to avoid extinction during ice-cap formation, through gradual migration to lower latitudes –– that were now characterized by water temperature within their preferred range. We predict that this may be found to account for the apparent sudden appearance of low-latitude recovery taxa in the Lower Carboniferous of Laurussia.

Acknowledgments

References

Algeo, T.J., Scheckler, S.E., 1998. Terrestrial-marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events. Philos. Trans. R. Soc. Lond. B 353, 113–130.

Algeo, T.J., Scheckler, S.E., Maynard, J.B., 2001. Effects of the Middle to Late Devonian spread of vascular land plants on weathering regimes, marine biotas, and global climate. In: Gensel, P.G., Edwards, D. (Eds.), Plants Invade the Land. Evolutionary and Environmental Perspectives. Columbia University Press, New York, pp. 213–236.

Amler, M.R.W., 1995. Die Bivalvenfauna des Oberen Famenniums West-Europas. 1. Einführung, Lithostratigraphie, Faunenübersicht, Systematik 1. Pteriomorphia. Geol. Palaeontol. 29, 19–143.

Amler, M.R.W., 1996. Die Bivalvenfauna des Oberen Famenniums West-Europas. 2. Evolution, Paläogeographie, Paläoökologie, Systematik 2. Palaeotaxodonta und Anomalodesmata. Geol. Palaeontol. 30, 49–117.

Amler, M.R.W., Schöllmann, L., 2012. Nicht-marine Bivalven aus dem Pennsylvanium von West-Deutschland. Geol. Palaeontol. 44, 75–92.

Anderson, H.M., Hiller, N., Gess, R.W., 1995. Archaeopteris (Progymnospermopsida) from the Devonian of southern Africa. Bot. J. Linn. Soc. 117, 305–320.

Bennison, G.M., 1960. Lower Carboniferous non-marine lamellibranchs from East Fife, Scotland. Palaeontology 3 (2), 137–152.

Bennett, C.E., Siveter, D.J., Davies, S.J., Williams, M., Wilkinson, I.P., Browne, M., Miller, C.G., 2012. Ostracods from freshwater and brackish environments of the Carboniferous of the Midland Valley of Scotland: the early colonization of terrestrial water bodies. Geol. Mag. 149 (3), 366–396.

Benton, M.J., 1995. Diversification and extinction in the history of life. Science 268, 52–58.

Beurlen, K., 1944. Beiträge zur Stammesgeschichte der Muscheln. Mathematisch-Naturwissenschaftlichen Abteilung der Bayerischen Akademie der Wissenschaften zu München Sitzungsberichte. 1944 (1–2) pp. 133–145.

Boucot, A.J., Brunton, C.H.C., Theron, J.N., 1983. Implications for the age of South African Devonian rocks in which Tropidolepis (Brachiopoda) has been found. Geol. Mag. 120, 51–58.

Brezinski, D.K., Cecil, C.B., Skema, V.W., 2010. Late Devonian glacigenic and associated facies from the central Appalachian Basin, eastern United States. GSA Bull. 122 (1/2), 265–281.

Buggisch, W., Joachimski, M.M., Sevastopulo, G., Morrow, J.R., 2008. Mississippian δ13Ccarb and conodont apatite δ18O records — their relation to the Late Palaeozoic Glaciation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 268, 273–292.

Caplan, M.L., Bustin, R.M., 1999. Devonian–Carboniferous Hangenberg mass extinction event, widespread organic-rich mudrock and anoxia: causes and consequences. Palaeogeogr. Palaeoclimatol. Palaeoecol. 148, 187–207.

Caputo, M.V., 1985. Late Devonian glaciation in South America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 51, 291–317.

Carmichael, S.K., Waters, J.A., Batchelor, C.J., Coleman, D.M., Suttner, T.J., Kido, E., Moore, L.M., Chadimová, L., 2016. Climate instability and tipping points in the Late Devonian: detection of the Hangenberg event in an open oceanic island arc in the Central Asian Orogenic Belt. Gondwana Res. 32, 213–231.

Carter, J.G., Altaba, C.R., Anderson, L.C., Araujo, R., Biakov, A.S., Bogan, A.E., Campbell, D.C., Campbell, M., Chen, J.-h., Cope, J.C.W., Delvene, G., Dijkstra, H.H., Fang, Z.-j., Gardner, R.N., Gavriolva, V.A., Goncharova, I.A., Harries, P.J., Hartmann, J.H., Hautmann, M., Hoeh, W.R., Hylleberg, J., Jiang, B.-y., Johnston, P., Kirkendale, L., Kleemann, K., Koppka, J., Kříž, J., Machado, D., Malchus, N., Márquez-Aliaga, A., Masse, J.-P., McRoberts, C.A., Middelfart, P.U., Mitchell, S., Nevesskaja, L.A., Özer, S., Pojeta, J., Polubotko, I.V., Pons, J.M., Popov, S., Sánchez, T., Sartori, A.F., Scott, R.W., Sey, I.I., Signorelli, J.H., Silantiev, V.V., Skelton, P.W., Steuber, T., Waterhouse, J.B., Wingard, G.L., Yancey, T., 2011. A synoptical classification of the Bivalvia (mollusca). Paleontol. Contrib. 4, 1–47.

Cooper, M.R., 1986. Facies shifts, sea-level changes and event stratigraphy in the Devonian of South Africa. S. Afr. J. Sci. 82, 255–258.

Cox, L.R., 1969. General features of Bivalvia. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part N, Mollusca 6. The University of Kansas and The Geological Society of America, Lawrence, pp. N2–N129.

Cox, L.R., Newell, N.D., Branson, C.C., Casey, R., Chavan, A., Coogan, A.H., Dechseaux, C., Fleming, C.A., Haas, F., Hertlein, L.G., Keen, A.M., LaRocque, A., McAlester, A.L., Perkins, B.F., Puri, H.S., Smith, L.A., Soot-Ryen, T., Stenzel, H.B., Turner, R.D., Weir, J., 1969. Systematic descriptions. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part N, Mollusca 6. The University of Kansas and The Geological Society of America, Lawrence, pp. N225–N907.

Dawson, J.W., 1860. Supplementary Chapter to "Acadian Geology". Oliver & Boyd, Edinburgh.

Dix, E., Trueman, A.E., 1932. Some observations on the genus Naiadites. Ann. Mag. Nat. Hist. 9, 1–20.

Eagar, R.M.C., Weir, J., 1971. Some Spanish Upper Carboniferous non-marine bivalve faunas: a preliminary statement with emphasis on facies in north-west Spain and in Britain. Trab. Geol. 3, 87–99.

Falcon-Lang, H.J., Benton, M.J., Braddy, S.J., Davies, S.J., 2006. The Pennsylvanian tropical biome reconstructed from the Joggins Formation of Nova Scotia, Canada. J. Geol. Soc. Lond. 163, 561–576.

Fraiser, M.L., Bottjer, D.J., 2007. When bivalves took over the world. Paleobiology 33 (3), 397–413.

Gardiner, B.G., 1969. New palaeoniscoid fish from the Witteberg series of South Africa. Zool. J. Linnean Soc. 48, 423–452.

Gardiner, B.G., 1973. New palaeoniscoid fish remains from Southern Africa. Palaeontol. Afr. 15, 33–35.

Gess, R.W., 2001. A new species of Diplacanthus from the Late Devonian (Famennian) of South Africa. Ann. Paléontol. 87, 49–60.

Gess, R.W., 2011. High Latitude Gondwanan Famennian Biodiversity Patterns – Evidence from the South African Witpoort Formation (Cape Supergroup, Witteberg Group). (PhD thesis). University of the Witwatersrand, Johannesburg.

Gess, R.W., 2013. The earliest record of terrestrial animals in Gondwana: a scorpion from the Famennian (Late Devonian) Witpoort Formation of South Africa. Afr. Invertebr. 54, 373–379.

Gess, R.W., 2016. Vertebrate biostratigraphy of the Witteberg Group and the Devonian Carboniferous boundary in South Africa. In: Linol, B., de Wit, M.J. (Eds.), The Origin and Evolution of the Cape Mountains and Karoo Basin. Springer International Publishing, Regional Geology Reviews:pp. 131–140 http://dx.doi.org/10.1007/978-3-319-40859-0_13.

Gess, R.W., Coates, M.I., 2008. Vertebrate Diversity of the Late Devonian (Famennian) Deposit near Grahamstown, South Africa. J. Vertebr. Paleontol. 28 (3), 83 (conference supplement).

Gess, R.W., Coates, M.I., 2015a. High-latitude Chondrichthyans from the Late Devonian (Famennian) Witpoort formation of South Africa. Paläontol. Z. 89, 147–169.

Gess, R.W., Coates, M.I., 2015b. Fossil juvenile coelacanths from the Devonian of South Africa shed light on the order of character acquisition in actinistians. Zool. J. Linnean Soc. 175, 360–383.

Gess, R., Hiller, N., 1995a. A preliminary catalogue of fossil algal, plant, arthropod, and fish remains from a Late Devonian black shale near Grahamstown, South Africa. Ann. Cape Provincial Mus. Nat. Hist. 19, 225–304.

Gess, R.W., Hiller, N., 1995b. Late Devonian charophytes from the Witteberg Group, South Africa. Rev. Palaeobot. Palynol. 89, 417–428.

Gess, R.W., Coates, M.I., Rubidge, B.S., 2006. A lamprey from the Devonian period of South Africa. Nature 443, 981–984.

Grossman, E.L., Yancey, T.E., Jones, T.E., Bruckschen, P., Chuvashov, B., Mazzullo, S.J., Mii, H.-s., 2008. Glaciation, aridification, and carbon sequestration in the Permo-Carboniferous: the isotopic record from low latitudes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 268, 222–233.

Guirdham, C., Andrews, J.E., Browne, M.A.E., Dean, M.T., 2003. Stratigraphic and palaeoenvironmental significance of microbial carbonates in the Asbian Sandy Craig Formation of Fife. Scott. J. Geol. 39 (2), 151–168.

Hiller, N., Gess, R.W., 1996. Marine algal remains from the Upper Devonian of South Africa. Rev. Palaeobot. Palynol. 91, 143–149.

Hiller, N., Taylor, F.F., 1992. Late Devonian shoreline changes; an analysis of Witteberg Group stratigraphy in the Grahamstown area. S. Afr. J. Geol. 95 (5–6), 203–214.

House, M.R., 2002. Strength, timing, setting and cause of mid-Palaeozoic extinctions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 181, 5–25.

Joachimski, M.M., Buggisch, W., 2002. Conodont apatite δ18O signatures indicate climatic cooling as a trigger of the Late Devonian mass extinction. Geology 30 (8), 711–714.

Kaiser, S.I., Steuber, T., Becker, R.T., Joachimski, M.M., 2006. Geochemical evidence for major environmental change at the Devonian–Carboniferous boundary in the Carnic Alps and the Rhenish Massif. Palaeogeogr. Palaeoclimatol. Palaeoecol. 240, 146–160.

Kaiser, S.I., Becker, R.T., Steuber, T., Aboussalam, S.Z., 2011. Climate-controlled mass extinctions, facies, and sea-level changes around the Devonian–Carboniferous boundary in the eastern Anti-Atlas (SE Morocco). Palaeogeogr. Palaeoclimatol. Palaeoecol. 310, 340–364.

Kaiser, S.I., Aretz, M., Becker, R.T., 2015. The global Hangenberg Crisis (Devonian–Carboniferous transition): review of a first-order mass extinction. Geol. Soc. Lond., Spec. Publ. 423. http://dx.doi.org/10.1144/SP423.9.

Kříž, J., 1979. Devonian Bivalvia. Spec. Pap. Palaeontol. 23, 255–258.

Leitch, D., 1941. Naiadites from the Lower Carboniferous of Scotland: a variation study. Geol. Soc. Glasgow Trans. 20, 208–223.

Long, J.A., Anderson, M.E., Gess, R., Hiller, N., 1997. New Placoderm fishes from the Late Devonian of South Africa. J. Vertebr. Paleontol. 17, 253–268.

Marais, J.A.H., 1963. Fossil fishes from the Upper Witteberg beds near Lake Mentz, Jansenville District, Cape Province. Ann. Geol. Surv. S. Afr. 2, 193–198.

Marynowski, L., Filipiak, P., 2007. Water column euxinia and wildfire evidence during deposition of the Upper Famennian Hangenberg event horizon from the Holy Cross Mountains (central Poland). Geol. Mag. 144 (3), 569–595.

Matyja, H., Sobień, K., Marynowski, L., Stempień-Sałek, M., Małkowski, K., 2015. The expression of the Hangenberg event (latest Devonian) in a relatively shallow-marine succession (Pomeranian Basin, Poland): the results of a multi-proxy investigation. Geol. Mag. 152 (3), 400–428.

Montañéz, I.P., Poulsen, C.J., 2013. The Late Paleozoic Ice Age: an evolving paradigm. Annu. Rev. Earth Planet. Sci. 41, 629–656.

Myrow, P.M., Ramezani, J., Hanson, A.E., Bowring, S.A., Racki, G., Rakociński, M., 2014. High-precision U–Pb age and duration of the latest Devonian (Famennian) Hangenberg event, and its implications. Terra Nova 26, 222–229.

Prestianni, C., Gess, R.W., 2014. The rooting system of Leptophloeum Dawson: new material from the Upper Devonian, Famennian Witpoort Formation of South Africa. Rev. Palaeobot. Palynol. 209, 35–40.

Racka, M., Marynowski, L., Filipiak, P., Sobstel, M., Pisarzowska, A., Bond, D.P.G., 2010. Anoxic Annulata events in the Late Famennian of the Holy Cross Mountains (Southern Poland): geochemical and palaeontological record. Palaeogeogr. Palaeoclimatol. Palaeoecol. 297, 549–575.

Raup, D.M., Sepkoski, J.J., 1982. Mass extinctions in the marine fossil record. Science 215, 1501–1503.

Řehoř, F., 1972. Die Süsswassermuscheln der Gattungen Curvirimula Weir, Naiadites Dawson und Carbonicola McCoy aus dem Tschechoslowakischen Teil des Oberschlesischen Beckens. Sammelschriften der Pädagogischen Fakultät in Ostrau 23, 1–139.

Rode, A.L., 2004. Phylogenetic revision of Leptodesma (Leiopteria) (Devonian: Bivalvia). Postilla 229, 1–26.

Rogers, M.J., 1965. A revision of the species of nonmarine bivalvia from the Upper Carboniferous of eastern North America. J. Paleontol. 39 (4), 663–686.

Sandberg, C.A., Morrow, J.R., Ziegler, W., 2002. Late Devonian sea-level changes, catastrophic events, and mass extinctions. GSA Spec. Papers 356, 473–487.

Sallan, L.C., Coates, M.I., 2010. End-Devonian extinction and a bottleneck in the early evolution of modern jawed vertebrates. PNAS 107 (22), 10131–10135.

Sallan, L., Galimberti, A.K., 2015. Body-size reduction in vertebrates following the end-Devonian mass extinction. Science 350, 812–815.

Scarlato, O.A., Starobogatov, Y.I., 1979. General evolutionary patterns and the system of the class Bivalvia. In: Starobogatov, Y.I. (Ed.), Morphology, Systematics and Phylogeny of Mollusks. Trudy Zoologiceskogo Instituta, Akademija Nauk SSSR 80, Saint Petersburg, pp. 5–38 (English translation: Boss, K.J., Jacobson, M.K., 1985, Special

Occasional Publication 5, Department of Mollusks, Harvard University, Cambridge, pp. 1–66).

Scholze, F., Schneider, J.W., 2015. Improved methodology of 'conchostracan' (Crustacea: Branchiopoda) classification for biostratigraphy. Newsl. Stratigr. 48, 287–298.

Stigall, A.L., 2010. Invasive species and biodiversity crises: testing the link in the Late Devonian. PLoS One 5 (12), e15584. http://dx.doi.org/10.1371/journal.pone.0015584.

Stigall, A.L., 2012. Speciation collapse and invasive species dynamics during the Late Devonian "mass extinction". GSA Today 22, 4–9.

Streel, M., Theron, J., 1999. The Devonian-Carboniferous boundary in South Africa and the age of the earliest episode of the Dwyka glaciation: new palynological evidence. Episodes 22, 41–44.

Taylor, F.F., Hiller, N., 1993. A new Devonian fossil plant locality in the eastern Cape Province, South Africa. S. Afr. J. Sci. 89, 565–568.

Tasch, P., 1987. Fossil Conchostraca of the southern hemisphere and continental drift. Geol. Soc. Am. Mem. 165, 1–290.

Tchernyshev, B., 1931. Carbonicola, Anthracomya and Najadites of the Donetz Basin. Trans. Geol. Prospecting Serv. U.S.S.R. 72, 1–125 (in Russian).

Urazaeva, M.N., Silantiev, V.V., Usmanova, R.R., 2015. Revision of Late Permian nonmarine bivalves of the genus *Verneuilunio* Starobogatov, 1987 and its type species *Naiadites verneuili* Amalitzky, 1892. Paleontol. J. 49 (11), 1174–1183.

Vasey, G.M., 1984. A note on the Upper Carboniferous bivalve *Curvirimula Corvosa* Rogers from Chimney Corner, Nova Scotia, Canada. Marit. Sediments Atl. Geol. 20 (1), 57–60.

Warth, M., 1967. Die nichtmarinen Muscheln des Westfal A unter besonderer Berücksichtigung des Ruhrkarbons und einige grundlegende Erkenntnisse zur Taxonomie. Forschungsberichte des Landes Nordrhein-Westfalen 1846, 1–125.

Wehrli, H., 1933. Die carbonische Süßwasserfauna der Zeche Baldur (Westfalen). Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B, Abhandlungen, Beilage-Band 69, 172–187.

Weier, J., 1959. A Monograph of British Carboniferous Non-marine Lamellibranchia. Part X. Palaeontological Society, London, pp. 273–320.

Young, G.C., 1993. Vertebrate faunal provinces in the Middle Palaeozoic. In: Long, J.A. (Ed.), Palaeozoic Vertebrate Biostratigraphy and Biogeography. Bellhaven Press, London, pp. 293–323.