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Towards an Integrated Approach

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UNDERSTANDING LATE DEVONIAN AND PERMIAN-TRIASSIC BIOTIC AND CLIMATIC EVENTS

Towards an Integrated Approach

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Towards an Integrated Approach
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Chapter 1
Introduction

Paul B. Wignall

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The intense interest in the nature and origin of mass extinctions shown by the scientific community and the media has now lasted for two and a half decades. Initially focussed on the end-Cretaceous catastrophe, the last decade has seen a surge of interest in the other mass extinction events of the geological record, of which the Late Devonian and end-Permian events are two of the "big 5". Numerous research programmes are currently engaged in trying to understand these events and they share many features in common, for example, in the loss of equatorial reef communities, an association with oceanic anoxia, climate change and voluminous volcanism. This last factor is clearly the case with the end-Permian event, which coincides with the voluminous outpourings of the Siberian Traps, while similar volcanism is inferred rather than proved for the Late Devonian event. This volume draws together several studies on these key times in Earth history and reflects the diverse approaches that are necessarily required to understand such critical moments. The majority of the contributions originally formed part of a thematic symposium at the annual meeting of the Geological Society of America at Seattle, Washington in November 2003.

The Devonian contributions begin with Racki's review of the current state-of-play regarding the mass extinction at the mid-Late Devonian Frasnian-Famennian boundary. Despite much recent effort, he shows that there are still many outstanding problems that need resolving. No doubt some will prove more tractable than others. Thanks to the first order highstand of sea level in the Late Devonian, marine boundary sections are plentiful, but it is a quirk of palaeogeography that most are concentrated within a narrow equatorial belt. Thus, any latitudinal selectivity to extinction losses is difficult to demonstrate. This is unfortunate because temperature selectivity is a key factor in many extinction models. As McGhee discusses in the following chapter (and see also Stock's contribution) there is substantial palaeontological evidence that the extinction coincided with a cooling event. Joachimski et al.'s (2004) recent oxygen isotope data have provided some quantification of this cooling event, although the reported excursion of 5–7°C in sea-surface temperatures from a pre-excursion high of 32°C does not really seem like the sort of cooling liable to create an environmental catastrophe. There are no indications of glaciation at this time; for example no contemporaneous tillites are known.

As the study of individual mass extinction events matures it is notable that new advances are often made as the time resolution improves. Thus, the better events are constrained within a high-resolution time frame the more it will prove possible to determine cause-and-effect relationships. For Late Devonian studies, absolute dating has improved considerably in recent years – for example, Kaufmann et al. (2004) is an important contribution – and this, combined with improvements to the biostratigraphic resolution, will help improve extinction models. In this regard Girard et al.'s contribution to this volume provides valuable data and improved resolution to the *linguiformis* Zone, the terminal Frasnian conodont biozone and a key interval of the Frasnian-Famennian extinction crisis.

With the exception of the end-Ordovician event, meteorite impact has been invoked as the causal mechanism for all the major, mass extinctions and several minor extinction events too. However, with the obvious exception of the end-Cretaceous event, this extinction cause has not been widely favoured by the scientific community. Only for the Late Devonian event could impact be reasonably regarded as a serious contender among the range of proposed extinction mechanisms. This is due to the occurrence of several large impact craters of Late Devonian age, and also some smaller ones. Thus, Schieber and Over present data here on the beautifully preserved Flynn Creek crater of Tennessee. Whether any of these impacts was responsible for the extinction events depends essentially on demonstrating a coincidence of timing and here again recent improvements of radiometric dating are crucial. Currently, it appears that the impacts are not temporally related to extinctions, although here McGhee considers the possibility that the impacts triggered long-term climatic effects that may ultimately have had disastrous consequences.

Amongst the many victims of the extinctions, the stromatoporoids are particularly noteworthy because, prior to the Late Devonian, they were the dominant framework builders of Palaeozoic reefs while by the end of this interval they had gone extinct. Stock provides a thorough review of this group and shows how their fortunes reflect the controlling interplay of changing sea level and vicariance events. The Frasnian-Famennian crisis removed much of the stromatoporoids diversity and abundance, although they persisted throughout the Famennian. However, as Stock shows, these last survivors failed to show any evolutionary exuberance prior to their ultimate demise at the end of the Devonian, a phenomenon memorably named "dead clade walking" by Jablonski (2004). Rode and Lieberman model the geographic and stratigraphic range of brachiopod and bivalve taxa from the Middle and Upper Devonian of the northern Appalachian Basin with interesting results. They show that species which increase their range during the crisis interval in the *linguiformis* Zone, showed preferential survival and that consequently broad geographic range during this crisis interval (but not before it) is seen to favour survival. It is tempting to view this range expansion as a consequence of taxa moving into vacant ecospace as incumbent taxa are lost.

The end-Frasnian interval has long been known to be associated with the development of two anoxic events named after the Kellwasser Horizons developed in the classic German sections. Riquier et al. and Bond and Wignall provide new data on the geochemical aspects of these anoxic events and their geographic extent respectively. Riquier et al.'s multielement data demonstrate the intensity of anoxia in sections from Morocco, France and Germany and they argue, using evidence from fluctuations in barium concentrations, for elevated primary productivity during the anoxic events. The Kellwasser events have been primarily documented from North African and European sections whereas it has been unclear if they are also developed in the well-known Great Basin sequences of the western United States. Using a combination of facies analysis and pyrite framboid assay, Bond and Wignall show that Upper Kellwasser Event of Europe corresponds to the intensification and expansion of anoxia within the Great Basin. This *linguiformis* interval therefore witnessed a peak of anoxia, both in terms of intensity and geographic spread, and it is undoubtedly significant that this time coincides with the end-Frasnian mass extinction.

The final contributions to the volume look at the end-Permian mass extinction and its aftermath. Racki and Wignall concentrate on the significance of the Siberian Traps and their high latitude locus of eruption. Such a location is unique for Phanerozoic large igneous province eruption events, and it may have contributed to the apparent severity of the environmental consequences as these authors argue. The following contributions by Fraiser and Bottjer and Pruss et al. focus on the uniquely prolonged aftermath of the end-Permian mass extinction. This interval, which spanned the entire Early Triassic, was marked by the loss of many taxa that ultimately reappeared in the Middle Triassic. It has often been suggested that the absence of such Lazarus taxa reflects the poor preservation of Lower Triassic faunas and particularly the absence of silicified specimens. Fraiser and Bottjer successfully debunk this proposition by demonstrating the presence of appreciable numbers of silicified fossils in Lower Triassic strata. In the same vein, Wheeley and Twitchett (2005) have recently shown that Lazarus gastropods are not present in an unusually diverse earliest Triassic assemblage from Oman that includes silicified specimens. The absence of fossils in the Early Triassic is therefore a real phenomenon rather than an artefact of preservation. Pruss et al. further demonstrate the unusual nature of Lower Triassic rocks by highlighting the appearance of anachronistic microbial structures more typical of Proterozoic and Cambrian strata and by recording the presence of an impoverished trace fossil assemblage. These final studies demonstrate how much there is to learn about conditions in the aftermath of mass extinctions and both show that "normal" conditions were a long time in returning. For the end-Permian event at least, the post-apocalyptic world appears to have been as stressed as that which caused the extinction. In this regard the term "aftermath" may be something of a misnomer. During much of the Early Triassic the stressful conditions that began at the end of the Permian may have persisted in a prolongation of the crisis interval.

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Chapter 2

Toward understanding Late Devonian global events: few answers, many questions

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> *"As one grows older, one realizes how little one knows: 'the more you learn, the more ignorant you become'. The joy of being a scientist is to discover this (...) As one accumulated information about how the Earth works, all the simple questions would be answered. Then the questions would have to become more intricate and harder to solve"* (Benton, 2003, p. 304)

Abstract

The Late Devonian was an epoch of dramatic evolutionary and environmental changes linked primarily with the Frasnian-Famennian (F-F) mass extinction. Current data and ideas support a prolonged, multi-causal nature of the biodiversity crisis, which favor Earth-bound mechanisms rather than a global cosmic catastrophe. The better understanding of the Late Devonian ocean-climate-biosphere system leads to several questions, and provides an agenda for future research. (1) *Magnitude and rank of biotic changes*: more detailed biodiversity studies are needed to place the end-Frasnian extinction in its Late Devonian context. In particular, the emerging severity of the end-Givetian and end-Famennian extinctions contrasts with the current overemphasis on the stepwise F–F crisis. (2) *Timing of the key boundaries*: a lack of radioisotopic dates hampers any estimation of true biodiversity dynamics, and the integrated comparison with reported ages of impact craters and magmatic events. (3) *Marine vs. terrestrial events*: insight into global ecosystem changes and correlation should be strengthened by chemostratigraphy, exemplified by the carbon isotope link between marine- and land-derived organic materials. (4) *High-resolution (bio)geochemical patterns*: isotope secular trends are poorly known at the intra-zonal and inter-basin scales, exemplified by prominent carbon isotope shifts across the Lower-Middle Frasnian passage. Further evidence is also awaited to verify cooling (vs. anoxia) pulses as the main stress factor in the F–F and end-Famennian marine settings, as well as climatic feedback with evolving weathering regimes on land and nutrient dynamic in marine realm. (5) *Near-equatorial vs. high-latitude domains*: refined data from extratropical successions, e.g. from the Kolyma Block, are still awaited. (6) *Tectonic and volcanic activity*: an integrated analysis of tectonic and igneous events, possibly triggered by superplume activity, will serve to evaluate any possible link with the Late Devonian biospheric perturbations. (7) Cyclostratigraphical perspective: includes growing research on refined magnetosusceptibility (MS) and various sea-level signatures to test whether they result from variation in Milankovitch frequency orbital variability. In addition, eustatic sea-level trends and their assumed glacioeustatic forcing have only recently been subject to discussion.

Keywords: Late Devonian; global events; biodiversity; geochronology; geochemistry; anoxia; palaeoclimate; volcanism

1. Introduction

The Late Devonian was an epoch of dramatic evolutionary and environmental changes, but focused primarily during one of the severest Phanerozoic extinctions close to the

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Frasnian-Famennian (F-F) boundary (Figs. 1–3), extensively summarized by McGhee (1996). In particular, a rapid decline of the low latitude, stromatoporoid-coral reefs (with a carbonate production loss of >90% according to Flügel and Kiessling, 2002) reflects a crucial ecosystem perturbation. This spectacular change in the stratigraphical record inspired introduction of the cosmic-accident concept by McLaren (1970) as the prime trigger of all global bioevents, and thus the Late Devonian successions have been studied intensively since 1970s. From the outset, problems of correlation and stage terminology seriously confused matters, but these were clarified in 1993, when the International Union of Geological Sciences approved a definition of the F–F boundary at the base of the conodont *Palmatolepis triangularis* Zone (Ziegler and Sandberg, 1990, 2001), i.e. immediately above the main anoxic Kellwasser Event and at a level of major extinction (Klapper et al., 1993;

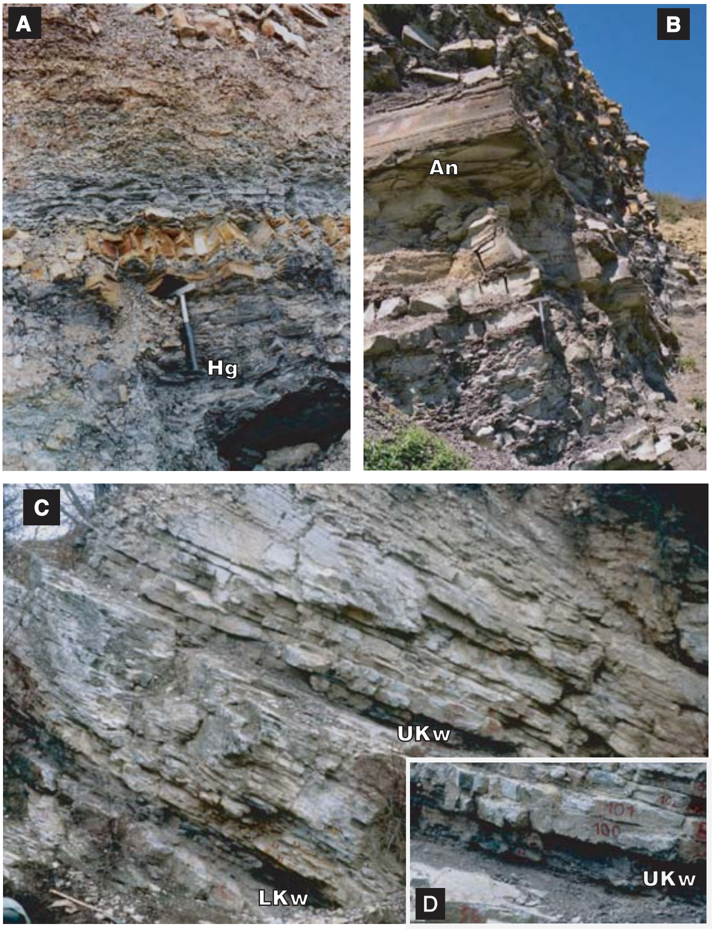

Figure 1. Field photos of Late Devonian black shale horizons recording global anoxic events (see summary in Walliser, 1996): the Famennian Hangenberg (A) and *annulata* (B) events at Kowala, Poland (see also Fig. 9), and the two Late Frasnian Kellwasser events at Steinbruch Schmidt, Germany (C). Photos taken by P. Filipiak (A–B) and E. Schindler (C–D).

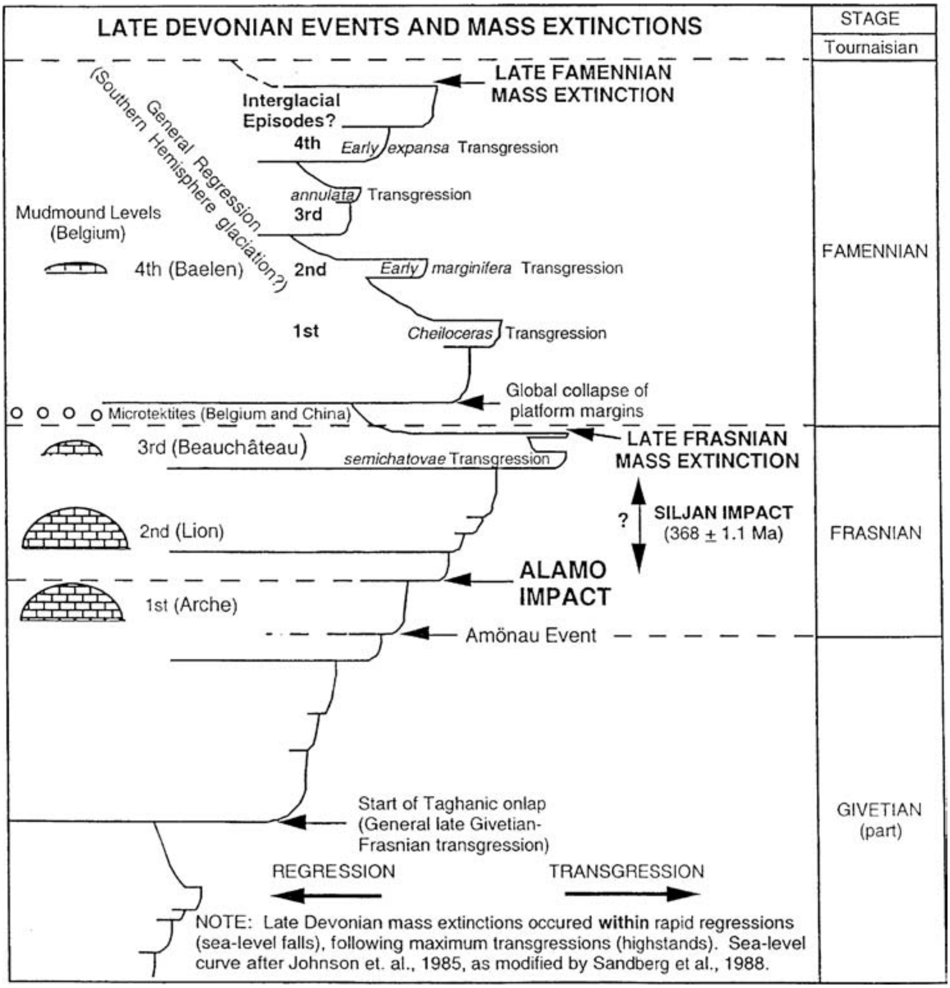

Figure 2. Late Devonian event stratigraphy, with reference to sea-level eustatic cyclicity (after Sandberg et al., 2000).

Walliser, 1996; House et al., 2000). In fact, studies of the eventful Late Devonian sedimentary and biotic record began as early as the 1980s as a paradigm of global changes and event stratigraphy, when Walliser (1981) and Eder and Franke (1982) linked widespread marker facies such as black shales (see Fig. 2) and reef extinction, respectively, with a global oceanographic trigger.

Three comprehensive summaries of the 'state-of-art' were published in the 1990s: McGhee (1996), Walliser (1996) and Hallam and Wignall (1997). Further progress is notable over the millennium crossroad, shown in two thematic 2002 issues of *Palaeogeography, Palaeoclimatology, Palaeoecology* (Racki and House, 2002) and *Acta Palaeontologica Polonica* (Baliński et al., 2002), which display the multidisciplinary efforts of international cooperation in Late Devonian studies. Other programs resulted in a series

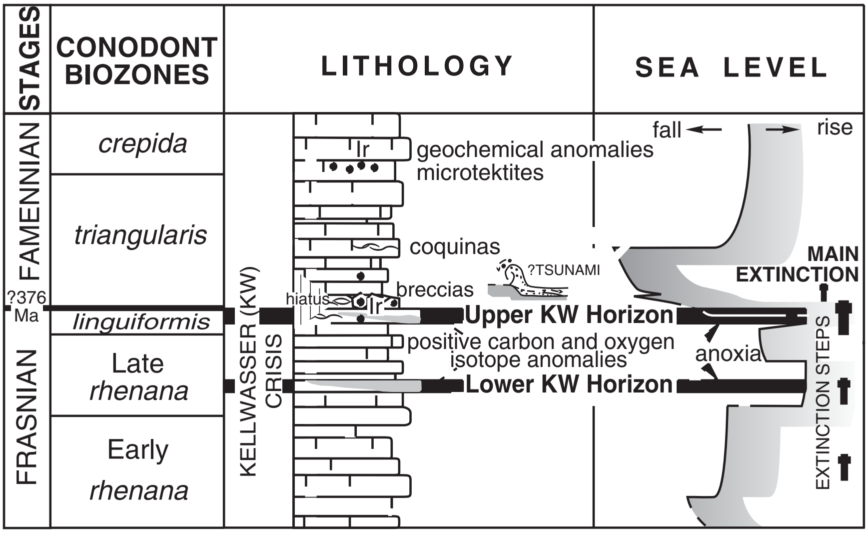

Figure 3. Diagram showing composite sedimentary and geochemical record across the F–F transition, and major eustatic and biotic events (modified Fig. 1 from Racki, 1999b; based on Fig. 3 in Joachimski and Buggisch, 1993; see also Figs 1 and 2).

of important papers by mainly Chinese-British (e.g. Chen et al., 2001, 2002, 2005; Chen and Tucker, 2003, 2004) and American (e.g. Murphy et al., 2000; Sageman et al., 2003) research groups. Some recent works have emphasized a gradual stepdown decline of many faunal groups, and the term "Kellwassser (KW) Crisis" that merges the effects of both anoxic KW events (Schindler, 1993), has entered the literature (Figs 2c and 3). Thus, more and more evidence has been accumulated for a prolonged nature of the F–F biosphere perturbation, and for an Earth-bound biodiversity crisis instead of a worldwide cosmic cataclysm resembling the end-Cretaceous event (see summary in Racki, 1999b; Copper, 2002).

Several new questions and strategic matters for future research emerged simultaneously with growing insight into the convoluted terrestrial processes. A better understanding of the Late Devonian ocean–climate–biosphere system leads to seven key frontiers, still waiting for extensive exploration, that were also raised in many presentations during the Geological Society of America Technical Session "Understanding Late Devonian and Permian–Triassic Biotic and Climatic Events: Towards an Integrated Approach" in Seattle in 2003. A subjective account of their coverage is a basic goal of this introductory article, with some references to continued polemics on primary extraterrestrial vs. Earth-bound causes as applied to the Late Devonian records (e.g. Alvarez, 2003; McGhee, this volume). Several joint research matters with the Permian–Triassic (P–Tr) boundary crisis are also outlined.

2. Magnitude and rank of biotic changes

The Late Devonian mass extinction was not a single instantaneous ("bedding-plane") killing event, as originally proposed by McLaren (1970) in his catastrophic impact scenario, but instead it consisted of a series of 'extinction pulses' (McGhee, 1996, 2001, this volume) occurring over several million years (ca. 5 Ma according to timescale of Kaufmann et al., 2004). As noted by McGhee (1996, pp. 44–46) and stressed recently by Bambach et al. (2004), *lowered origination* contributed more than elevated extinction to the F–F mass depletion of marine diversity that occurred during times of generally high extermination (see crustacean example in Rode and Lieberman, 2002). This is a different situation when compared to other globally distinct, 'true' mass extinctions, i.e. end-Ordovician, end-Permian, and end-Cretaceous. Alternatively, statistical analysis of pure taxonomic numbers is criticized as a straightforward proxy of the magnitude of ecological rebuilding in the ranking of mass extinction by McGhee et al. (2004). In fact, carbonate production by reefs appears to be not stabilized by their diversity over the long timescales (Kiessling, 2005).

The evolutionary dynamics across the F–F extinction horizon is overall still far from reliably documented (see summaries in Bultynck, 2000). Many palaeontological studies have provided a picture of biodiversity and ecologic changes across the major stage boundary in several regions and fossil groups, as exemplified particularly by the comprehensive work undertaken on the ostracods by Lethiers and Casier (summarized in Casier and Lethiers, 2001; also Groos-Uffenorde and Schindler, 1990; Olempska, 2002; Casier, 2003). However, lack of the high-resolution (bed-by-bed) documentation in reference or other biostratigraphically complete successions usually precludes a precise chronostratigraphical control needed to determine timing of the events occurring within the boundary interval itself (House, 1996; see examples in Blieck et al., 2000 and Streel et al., 2000). In fact, it is difficult to quantitatively assess of the biodiversity change during the F–F bioevent (and all other mass extinctions) so long as ancestor-descendant and biogeographical relationships in many fossil groups remain, to some extent, vague (MacLeod et al., 1997; Lieberman, 2002; Wood, 2004). Nevertheless, a progress is exemplified by Rode and Lieberman (2004), and increased resistance is postulated for shelly faunas that populated extensive offshore habitats.

Another hard matter is related to the poorly known survival-zone biota in the aftermath the F–F extinction that might potentially yield clues to the Late Palaeozoic biodiversity recovery (e.g. Erwin, 2001; Jablonski, 2002; Wood, 2004). A significant unbalanced excess of bacterially controlled productivity (Joachimski et al., 2001; Gong et al., 2002; see also Ormiston and Oglesby, 1995), coupled with frequent opportunistic marine algal blooms and suppression of major pelagic consumers (conodonts, ammonoids, sharks), is a remarkable feature in marine habitats (Paris et al., 1996; Ginter, 2002; Dzik, 2002; Chen and Tucker, 2003); however, a stronger effect in phytoplankton is not observed (Streel et al., 2000; see also Casier, 2003). These signatures from the photic zone could indicate a highly disorganized 'biological pump', seen during other mass extinction events, particularly the end-Cretaceous crisis (D'Hondt et al., 1998). Twitchett (2001) has suggested that the Lilliput effect – the small size of survivors in the immediate post-extinction aftermath – is a principal character of all recoveries after mass extinctions, confirmed by the F–F conodont and brachiopod response (Schülke, 1998; Renaud and Girard, 1999; Baliński, 2002). He relates this to a temporary decrease in food supply, with a resultant drop in the biomass and size in extreme oligotrophic settings. Thus, the major interruption episode of the trophic web due to large-scale destabilization events awaits more serious survey (Racki et al., 2002; Vermeij, 2004), especially that evidence to eutrophication is far more common (*cf.* Racki, 1999a; Joachimski et al., 2001, 2002; Tribovillard et al., 2004; Averbuch et al., 2005). A post-extinction acme of microbial reef communities (see below) could be expression of fertility pulses, related to oceanic anoxia, on carbonate platform biota (as shown in the Aptian Tethyan margin; Immenhauser et al., 2005).

More importantly, it appears that detailed study is required for a longer interval than just across the Frasnian-Famennian boundary. The emerging severity of the end-Givetian and end-Famennian extinctions contrasts with a possibly overvalued significance, at least in *relative* terms, of the end-Frasnian biotic events (House, 2002), as demonstrated for echinoderms, bryozoans and radiolarians (Afanaseeva and Morozova, 1995; Webster et al., 1998; Głuchowski, 2002; Wang et al., 2003; Waters et al., 2003) and, probably, gastropods (Amler and Heidelberger, 2003). This demand is clear especially from biodiversity compilations of Copper (2002; in Brice et al., 2000) for Devonian atrypids and corals (see also terebratulid data; Garcia-Alcalde in Brice et al., 2000). Accordingly, the mid-Palaeozoic reef maximum in size and biodiversity corresponds to early-middle Givetian, and, by contrast, the Frasnian represents a late stage in a 'dying' episode that extinguishes development of the lower-diversity stromatoporoid-coral reef ecosystems in the calcite epeiric seas (Copper, 2002; Tapanila, 2005). Nevertheless, the end-Givetian biotic turnover remains conjectural in important aspects, and its detailed correlation with well-proved events in pelagic successions, which record a complex sequence of sedimentary events and faunal changes known as the Taghanic Biocrisis (see summary in Aboussalam and Becker, 2001), has not been achieved. In fact, a two-step collapse of Givetian stromatoporoid-coral bank biota is reported from the southern Laurussian carbonate shelf (Racki, 1993). In addition, Marshall et al. (2003) considered the aridity-driven changes in epeiric ecosystems as a trigger for the very significant Taghanic extinctions in both the marine and terrestrial realms. Hence, a greatly refined and time-constrained study of taxon stratigraphical ranges is required, particularly related to the many deepening pulses and reef decimations known during the Frasnian (House, 2002).

Even if metazoan reef ecosystems were impacted on a global scale (Copper, 2002), Webb (1996) claimed that the cyclical Middle–Late Devonian reef construction was continuous through the F–F extinction boundary, and without evident consequence for framework rigidity until the Devonian-Carboniferous (D–C) boundary (or Hangenberg) extinction event (*cf.* Shen and Webb, 2004). In north-western Australia, the most dramatic ecological changes caused by the F–F extinction are limited to back-reef habitats, while complex post-extinction microbial-sponge reef biotas represent a continuation of novel ecologies established already in the latest Frasnian (Wood, 2004; see also Reitner et al., 2001). Shallow-water buildups, marked by a calcimicrobial and stromatolitic framework with a few skeleton-dominated (stromatoporoid) examples, were widely distributed during the Famennian (Shen and Webb, 2004), but greatly constricted geographically mostly owing to a fall of northern hemisphere reefs after the D–C boundary (Kiessling, 2001); in fact, low-diversity reefs were particularly prone to environmental perturbations (Kiessling, 2005). A decoupling between reef construction and carbonate-platform development is emphasized by Kiessling et al. (2003, Fig. 15 therein) for the mid-Palaeozoic, because non-reefal carbonate production was particularly prolific during times of depressed reef growth (see the Famennian example in Peterhansel and Pratt, 2001).

In contrast to evolutionary pattern of several benthic groups (e.g. bivalves and gastropods; Amler, 1999; Amler and Heidelberger, 2003), the importance of Hangenberg environmental degradation is emphasized currently in radiolarians (Umeda, 2001) and plants

(Streel et al., 2000). In any case, the D–C extinction event could be more profound than previously thought (see summary in Walliser, 1996 and Caplan and Bustin, 1999).

3. Timing of the key boundaries

The second prominent uncertainty in Late Devonian event stratigraphy is tied to doubtful timing of the key boundaries. Almost all the Devonian ages are in flux, and appropriate time calibration is urgently needed. This is a principal goal of the Subcommission on Devonian Stratigraphy, but the progress is very slow. As shown in Figure 4, the numerical age of the F–F boundary remains highly controversial and has ranged from 376.5 Ma (Tucker et al., 1998) to 364 Ma (Compston, 2000) to 374.5 Ma (Gradstein et al., 2004; see also Gehmlich et al., 2000). However, a date around 376 Ma appears more probable after new U-Pb zircon analysis from a bentonite layer, intercalated between the two KW horizons at Steinbruch Schmidt, provided a date of 376.1 ± 1.6 Ma (Kauffmann et al., 2004).

A lack of consistent numerical dates hampers any estimation of true rates of biodiversity changes across the key intervals, as e.g. estimated ages for the Famennian Stage still range from 5.3 to 14.7 Ma (Fig. 4). This hindrance also precludes a definitive acceptance or rejection of the impact vs. volcanism models for extinction. For example, the central point in the impact discussion remains the timing of the Siljan crater, determined as 368 ± 1 Ma (see McGhee, 1996, Table 8.3). As stressed by Racki (1999b, p. 620): "although this crater is real, we cannot say exactly whether the documented impact occurred near the F–F

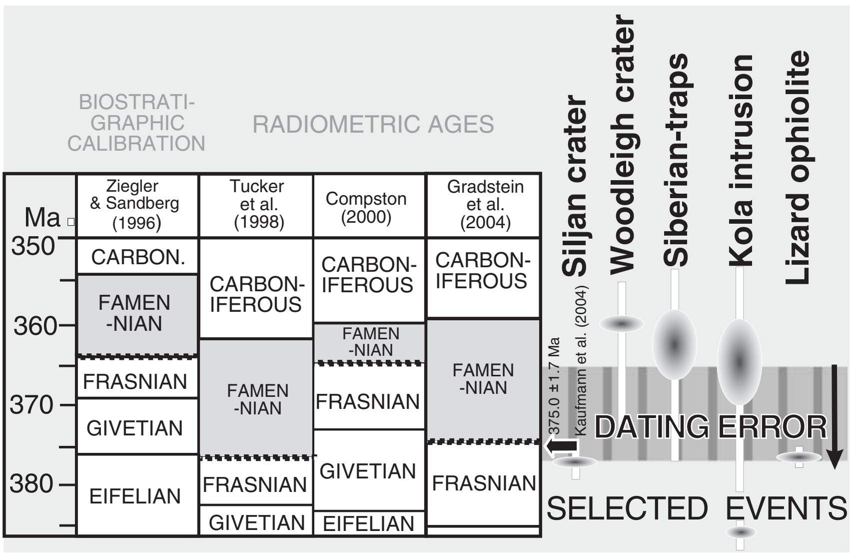

Figure 4. Comparison of four most recent Devonian time scales, and the selected Earth-bound and extraterrestrial event signatures to show their ambiguous absolute timing within established dating errors of the F–F boundary. Ages compiled from Kramm et al. (1993), Beard et al. (1996), Kravchinsky et al. (2002), Courtillot and Renne (2003), Vaughan and Scarrow (2003), Pervov et al. (2005), Reimold et al. (2005) and Uysal et al. (2005).

boundary, in the late Famennian or in the earlier Frasnian". However, the recently revised Siljan date (372 ± 2 Ma; Reimold et al., 2005) is again close to the currently proposed age for the F-F boundary, and only biostratigraphical dating of undoubted Siljan impact ejecta will be decisive. On the other hand, catastrophic volcanic paroxysm of the Devonian Siberian (Viluy) traps (see below), as highlighted by Courtillot and Renne (2003) for causation of the KW biotic crisis, could be temporally coupled both with the F–F as well as D–C extinction boundaries in the known range of dating errors (see Fig. 4).

Noteworthy, even in the case of P-Tr boundary and potentially coeval Siberian Traps, serious discrepancy and uncertainties in range of 3 Ma are evident between U-Pb and/or $^{40}Ar/^{39}Ar$ system dates (Wignall, 2001; Courtillot and Renne, 2003). In Late Devonian studies, similar doubts pertain even to the stratigraphical position of zircon-bearing ash levels sampled by Tucker et al. (1998) (see Streel et al., 2000; Over, 2002). The limiting factor in the geochronological calibration, based on high-resolution ion microprobe (SHRIMP) zircon $^{206}Pb/^{238}U$ ages, remain the origin and nature of the dated zircons; a crucial question of inherited grains is demonstrated by reallocation of a 381.1 Ma age to 367.6 Ma age for the Frasnian Little War Gap bentonite (Comptson, 2000, 2004).

4. Marine vs. terrestrial events

Ecosystem changes and event correlation between the marine and terrestrial realms are poorly known for the F–F extinction event, although it is assumed to affect both marine and terrestrial ecosystems; this is demonstrated by the diversity record of marine invertebrates, land-plant spores and macroflora (e.g. McGhee, 1996; Raymond, 2003; Raymond and Metz, 2004; but see more careful conclusion in Streel et al., 2000). A positive feedback scenario envisages the coupling of vegetation-promoted intensification of continental weathering, i.e. spread of rooted upland vascular plants and soil formation, with episodic increases of marine bio-productivity and promoted anoxic events (Kasig and Wilder, 1983; Wilder, 1994; Algeo et al., 1995; Ormiston and Oglesby, 1995; Algeo and Scheckler, 2003). Furthermore, the rise of trees probably had consequently a major effect on rapidly dropping levels of atmospheric CO_2 at that time, causing global cooling that led to South American glaciation (Berner, 2003; also Cox et al., 2001 and Raymond and Metz, 2004). On the other hand, the climatic response to mountain building-enhanced continental weathering and organic carbon burial is emphasized as well (Joachimski and Buggisch, 2002; Averbuch et al., 2005).

Pedogenic weathering rates are indeed a primary control on nutrient availability and, hence, may underscore an important influence on marine biotas, especially during anomalous greenhouse intervals (*cf.* Bambach, 1999). It is questionable, however, whether the palynological record supports any "vegetational revolutions" and land ecosystem overturns (see summary in Edwards et al., 2000 and Streel et al., 2000), rather than just a gradual, global increase of weathering rate, nutrient levels and bioproductivity during this epoch (Bambach, 1999; Racki, 1999b, p. 623; Martin, 2003; Sageman et al., 2003, p. 256). A scenario of river-borne nutrient flux is also generally disputed for eutrophication pulses beyond nearshore, especially near-estuarine, domains (*cf.* Sageman et al., 2003; Erba, 2004), although the surface waters may have been fertilized by solubilized nutrients from distant land sources (Tribovillard et al., 2004) and/or aeolian input (see Hladil, 2002). The