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The role of sea-level change and marine anoxia in the Frasnian–Famennian (Late Devonian) mass extinction

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ABSTRACT

Johnson et al. (Johnson, J.G., Klapper, G., Sandberg, C.A., 1985. Devonian eustatic fluctuations in Euramerica. Geological Society of America Bulletin 96, 567–587) proposed one of the first explicit links between marine anoxia, transgression and mass extinction for the Frasnian–Famennian (F–F, Late Devonian) mass extinction. This cause-and-effect nexus has been accepted by many but others prefer sea-level fall and cooling as an extinction mechanism. New facies analysis of sections in the USA and Europe (France, Germany, Poland), and comparison with sections known from the literature in Canada, Australia and China reveal several high-frequency relative sea-level changes in the late Frasnian to earliest Famennian extinction interval. A clear signal of major transgression is seen within the Early *rhenana* Zone (e.g. drowning of the carbonate platform in the western United States). This is the base of transgressive–regressive Cycle IId of the Johnson et al. (Johnson, J.G., Klapper, G., Sandberg, C.A., 1985. Devonian eustatic fluctuations in Euramerica. Geological Society of America Bulletin 96, 567–587) eustatic curve. This was curtailed by regression and sequence boundary generation within the early *linguiformis* Zone, recorded by hardground and karstification surfaces in sections from Canada to Australia. This major eustatic fall probably terminated platform carbonate deposition over wide areas, especially in western North America. The subsequent transgression in the later *linguiformis* Zone, recorded by the widespread development of organic-rich shale facies, is also significant because it is associated with the expansion of anoxic deposition, known as the Upper Kellwasser Event. Johnson et al.'s (Johnson, J.G., Klapper, G., Sandberg, C.A., 1985. Devonian eustatic fluctuations in Euramerica. Geological Society of America Bulletin 96, 567–587) original transgression-anoxia–extinction link is thus supported, although some extinction losses of platform carbonate biota during the preceeding regression cannot be ruled out. Conodont faunas suffered major losses during the Upper Kellwasser Event, with deep-water taxa notably affected. This renders unreliable any eustatic analyses utilising changes in conodont biofacies. Claims for a latest Frasnian regression are not supported, and probably reflect poor biostratigraphic dating of the early *linguiformis* Zone sequence boundary.

1. Introduction

The Frasnian–Famennian mass extinction (F–F, Late Devonian) is one of the "big 5" faunal crises of the Phanerozoic with taxa being lost from a broad range of marine habitats (Hallam and Wignall, 1997). The precise timing of the extinctions is debated, and probably varied from group to group, but severe losses undoubtedly occurred within the latest Frasnian *linguiformis* Zone (e.g. Casier and Devleeschouwer, 1995; Casier et al., 1996; Bond, 2006), although many reef taxa may have disappeared earlier, in the *rhenana* Zones (Copper, 2002). Extinction losses of groups such as the ostracods, conodonts, and tentaculitoids are contemporaneous with the widespread deposition of the anoxic facies, most notably the Upper Kellwasser Horizon of Germany (Fig. 1), and many workers have attributed the extinction event to this phenomenon (e.g. Joachimski and Buggisch, 1993; Becker and House, 1994; Levman and von Bitter, 2002; Bond et al., 2004).

The relationship between sea-level, the Upper Kellwasser anoxic event and the contemporaneous mass extinction is a subject of conflicting opinions (e.g. Hallam and Wignall, 1999 *versus* Sandberg et al., 2002). Thus, sea-level change features in the scenarios of Buggisch (1991), Joachimski and Buggisch (1993) and Becker and House (1994), but it is not implicated as the primary kill mechanism. In contrast, others directly attribute the extinctions to sea-level change (e.g. Newell, 1967; Johnson, 1974; Johnson et al., 1985; Sandberg et al., 1988, 2002). For example, Johnson (1974) suggested that a rapid regressive–transgressive pulse occurred during the late Frasnian, eliminating "perched" faunas, which had colonised widespread shelf areas during a period of high sea-level. Johnson and colleagues subsequently produced a eustatic sea-level curve for the Devonian which has become widely accepted as a "standard" for the interval. Nonetheless, the relationship of this curve to the contemporary anoxic events and F–F mass extinction has been the subject of widely varying interpretations. This

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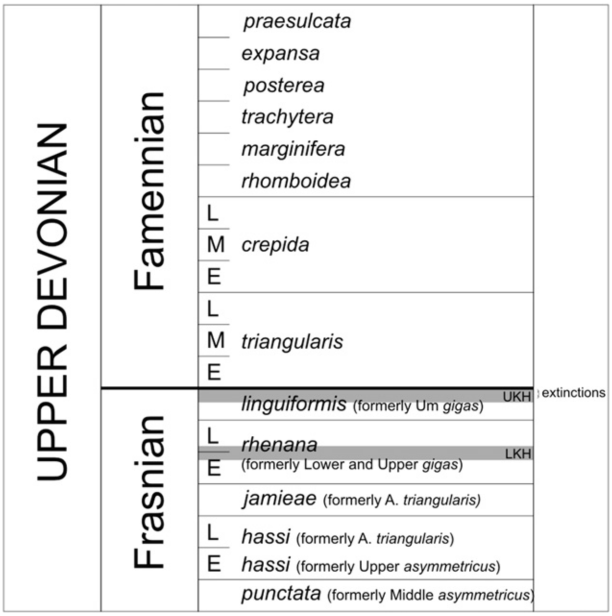

Fig. 1. The Late Devonian standard conodont zonation (after Ziegler and Sandberg, 1990). Previous zonal names are indicated where relevant. The position of the two Kellwasser Horizons (Lower and Upper) in Germany is shown by "LKH" and "UKH" respectively.

paper aims to re-examine the validity of the F–F boundary portion of this curve using facies analyses of sections studied by the authors (Section 3) and recently-published data from the literature in order to critically assess the role (if any) of sea-level change during the mass extinction and its relationship with contemporary redox changes.

2. The Devonian Euramerican sea-level curve of Johnson et al. (1985)

The Johnson et al. (1985) eustatic sea-level curve was based on a study of sections in the western United States, western Canada, New York State, Belgium, and Germany, using a combination of facies analysis and a conodont biostratigraphic scheme for correlation. Deepening events were identified from a range of lithofacies responses including the onset of black shale deposition, the inception of reef growth, inundation of muds following drowning of the carbonate platform, and onlap onto unconformities (Johnson et al., 1985, p. 570). Two major "depophases" (termed I and II) were identified within the Devonian, each consisting of 6 transgressive–regressive (T–R) cycles labelled a to f. The base of depophase I is marked by the Lochkovian/Pragian sequence boundary, whilst the base of depophases II lies within the Givetian, at the Taghanic sequence boundary. Overall the Pragian to Frasnian was a time of rising sea-level, with the late Frasnian being a period of second-order highstand, before sea-level began to fall in the Famennian.

The T–R Cycle IId is of relevance here, because this cycle begins in the Frasnian Lower *gigas* Zone and continues to the base of the Middle *triangularis* Zone, and thus straddles the F–F mass extinction interval. Johnson et al. (1985, p. 578) considered the sea-level rise component of cycle IId to be:

> "the greatest of Devonian transgressions... (because it) coincides with the West Falls Group of New York and encompasses the Kellwasser Limestone of Germany and the Matagne Shale of Belgium... (and) comprises a pair of widely recognised transgressions".

The two transgressions were separated by "a small-scale drop in sea level" (Johnson et al., 1985, p. 584) and were followed by a major regression in the Middle *triangularis* Zone. The first of the transgressions occurred within the Lower *gigas* Zone and is thus contemporaneous with the development of the Lower Kellwasser Horizon in Germany. Unfortunately, Johnson et al. (1985) provided conflicting ages for the second transgression and thus sowed the seeds of confusion in much of the subsequent literature. In their Fig. 12 the second transgression was shown as beginning at the base of the Lower *triangularis* Zone, but they state in their text that this transgression correlates with the Upper Kellwasser Horizon. This began in the Uppermost *gigas* Zone as correctly shown in their time-rock chart (Johnson et al., 1985, Fig. 2). We therefore assume that their Fig. 12 was poorly drafted and that the second transgression of T–R Cycle IId coincides with the development of the Upper Kellwasser Horizon in the Uppermost *gigas* Zone. This is the interval of the F–F mass extinction and so it is clearly important to clarify their ideas about sea-level at this time. Thus, Johnson et al. (1985, p. 581) noted that, in Europe at least, the extinctions had already occurred before regression at the top of T–R cycle IId and clearly stated that "the Frasnian–early Famennian transgressive history supports an interpretation that a succession of three rapid deepening events within and above IId, not regression, caused many of the Frasnian extinctions".

Before examining the Johnson et al. (1985) curve in the light of more recent work it is important to note some significant changes in

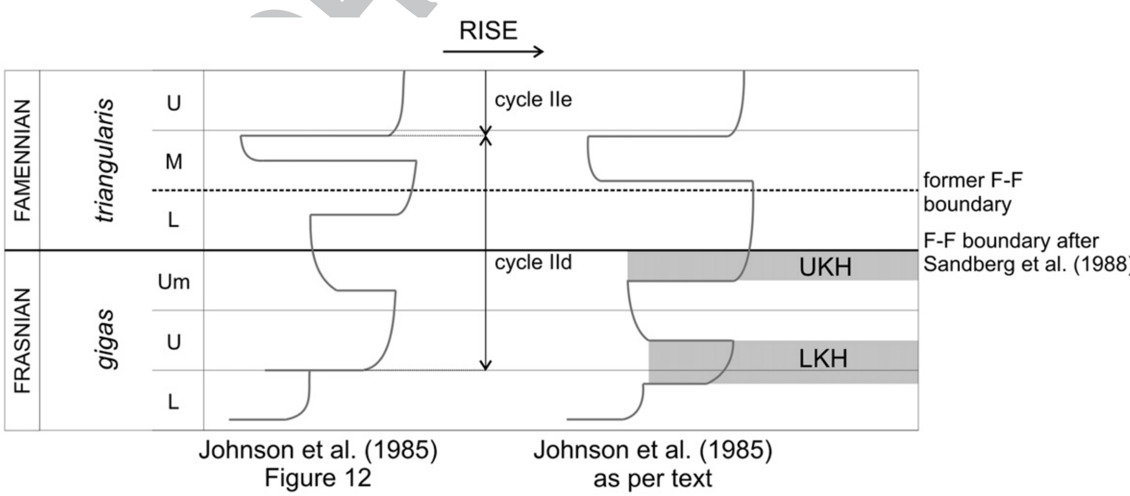

Fig. 2. The eustatic sea-level curve of Johnson et al. (1985), on the left as reproduced in their Fig. 12, and on the right as described in their text. Note Lower (L), Upper (U), and Uppermost (Um) *gigas* Zones are now replaced by Early and Late *rhenana* and *linguiformis* Zones respectively. Lower (L), Middle (M) and Upper (U) *triangularis* Zones are now more correctly termed Early, Middle, and Late *triangularis* Zones.

the Late Devonian conodont zonation scheme that have occurred since 1985. Thus, the Lower to Upper *gigas* interval is now approximated by the Early to Late *rhenana* Zones, whilst the Uppermost *gigas* Zone has become the *linguiformis* Zone (Ziegler and Sandberg, 1990). The F–F boundary has also been redefined (Sandberg et al., 1988). In 1985 it was placed at the Lower/Middle *triangularis* zonal boundary but it is now placed at the base of the Lower (now more correctly called Early) *triangularis* Zone. Thus, the second major transgression of the Johnson et al. (1985) T–R cycle IId now begins within the *linguiformis* Zone and the major regression at the top of the cycle is well within the Famennian rather than at the old F–F boundary (Fig. 2).

3. F–F boundary facies changes in the United States and Europe

Boundary sections in the western and eastern United States, and in France, Germany, and Poland, were studied by the authors for their geochemistry, faunal content, and sedimentology. The key sections of the original Johnson et al. (1985) study have been revisited and re-evaluated here. Aspects of the redox history in these sections, specifically pyrite framboid and trace metal content, has been discussed previously by Bond and Zaton (2003), Bond et al. (2004), and Bond and Wignall (2005), who presented evidence for marine anoxia during the crisis interval. The extinction record has also been assessed, and it is clear that losses culminated during the latest part of the *linguiformis* Zone (e.g. Casier et al., 1996; Bond, 2006).

3.1. Western United States

The Great Basin sections of the western United States provided a key component of Johnson et al.'s (1985) study, although as they were developed adjacent to a tectonically-active foreland basin (Sandberg et al., 2003), the region clearly has the potential for tectonic events to overprint a eustatic signature. The Upper Devonian succession has been studied by the authors in four sections in Nevada and Utah (Fig. 3). These record deposition within two basins, the Pilot and the Woodruff basins, that were separated by the proto-Antler forebulge. Deepest water sedimentation in the Late Devonian of the Woodruff basin is recorded by the Woodruff Formation, a unit dominated by laminated shales and cherts. At Whiterock Canyon, the most westerly and distal location studied, the entire section belongs to the Woodruff Formation, and pyritic, laminated siltstones and lesser shales and cherts are the only lithologies. The only signal of eustasy in such a deep-water setting may come from the grain-size fluctuations between clay and silt. Thus, the finest-grained strata are found in the early Late *rhenana* Zone and the *linguiformis* Zone (Fig. 3).

To the east of the Whiterock Canyon section an extensive series of exposures in eastern Nevada provides sections through the west-facing slope sediments of the proto-Antler forebulge. Two sections, with distinctly different slope facies, have been studied in the Northern Antelope Range and at the Devils Gate road cut (Fig. 3). The latter location is the type location for the Devils Gate Limestone Formation. This consists of two principal facies types: hemipelagic carbonates (and minor cherts) and allodapic limestones. At the base of the section, in the later part of the Early *rhenana* Zone, there is a sharp transition from fossiliferous, bioturbated micrites to finely laminated micrites. This is clearly a deepening event and it has been called the '*semichatovae* transgression' (Sandberg et al., 1997). Allodapic limestones (matrix-supported, conglomerates with a diverse shelf fauna) appear in the Late *rhenana* Zone and this, together with the development of small-scale slump features in the finer-grained strata, is clear evidence for slope progradation. There is a temporary abatement in major slope failure

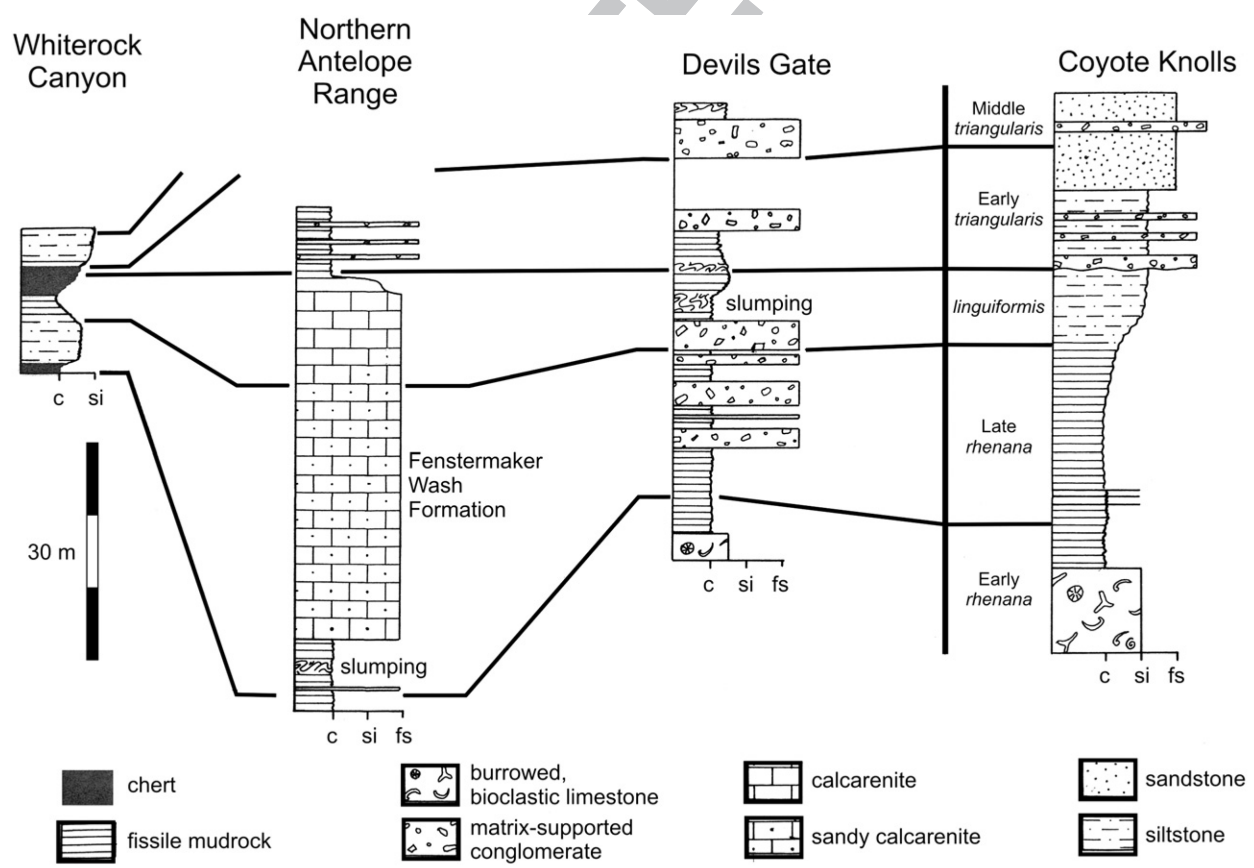

Fig. 3. Correlation panel of Upper Devonian sections from the Great Basin, western USA. Locality details are given in Bond and Wignall (2005). Conodont zonation is from Sandberg et al. (1988, 1997) and Morrow (2000).

during the late part of the *linguiformis* Zone coinciding with the development of intensely anoxic conditions (Bond and Wignall, 2005), probably a consequence of sea-level rise.

The Northern Antelope Range section also provides a record of slope deposition and, like the Devils Gate section, this began in the Late *rhenana* Zone with the development of an expanded section of sandy, calcarenites that rest on fine-grained strata of the Woodruff Formation (Fig. 3). This is the upper tongue of the Fenstermaker Wash Formation and Sandberg et al. (2003) attribute its onset to the migration of the forebulge. Within the *linguiformis* portion of the calcarenites there is a gradual loss of the quartz sand component (Bond and Wignall, 2005) that possibly constitutes a signal of transgression causing the supply of terrigenous material to become more distal from this slope setting. The decline in terrigenous supply may alternatively be explained by switching supply directions and thus deciphering any sea-level signal in this expanded slope sections is difficult.

Much clearer depth changes are seen in the Coyote Knolls section of western Utah. This is from the Pilot Basin and provides an example of a coarsening and shallowing-up cycle in the late Frasnian–earliest Famennian interval (Fig. 3). Initial flooding occurred late in the Early *rhenana* Zone when the thoroughly bioturbated and highly fossiliferous limestones of the Guilmette Formation were replaced by the laminated shales of the Pilot Shale Formation. In its lower part the Pilot Shale contains a few, thin siltstone turbidites but, by the late *linguiformis* Zone persistent siltstone deposition was established. These coarsen-up into sandstones in the late Early *triangularis* Zone (Fig. 3). The Famennian portion of this section is also characterised by calcirudites often composed of flat pebbles.

In summary, the best potential eustatic sea-level signal in the Great Basin record is the '*semichatovae* transgression' in the later part of the Early *rhenana* Zone. This is the regional expression of the flooding at the base of cycle IId in the Johnson et al. (1985) eustatic curve. The "small-scale drop in sea level" (Johnson et al., 1985, p. 584) in the early *linguiformis* Zone is only weakly manifest in this region although, as shown below, it is a much more significant event elsewhere. The second transgression of cycle IId is displayed as a decreased clastic input in the *linguiformis* Zone of the Woodruff Basin and an intensification of basinal anoxia, the regional manifestation of the Upper Kellwasser Event (Bond and Wignall, 2005). This is seen in both the basinal White Rock Canyon section and the Northern Antelope Range slope section. At Devils Gate the later part of the *linguiformis* Zone records a temporary cessation of slope failure and the development of anoxia, both evidence of sea-level rise. In contrast, the Pilot Basin record of Coyote Knolls shows no evidence for base-level rise at this time, rather the F–F interval is a single progradational cycle following the *semichatovae* transgression.

3.2. Eastern United States

Late Devonian sediments are well known from the Appalachian Basin of Virginia, West Virginia, Ohio, Pennsylvania, and New York (e.g. Rickard, 1975; Filer, 2002), and record a series of five transgressive–regressive cycles during this interval (Filer, 2002). The sections have been the focus of both conodont and platinum group element studies (e.g. Over, 1997, 2002), and the F–F boundary has now been placed accurately at Beaver Meadow Creek, a base-of-slope section, which has been visited for this study. The most notable lithological change occurs in the upper part of the Early *rhenana* Zone (MN Zone 12 of Over, 1997) when the pale, coarse, siltstones of the Nunda Sandstone (of the Nunda Formation) are sharply overlain by black, finely laminated, silty shales of the Pipe Creek Shale Member of the Java Formation (Fig. 4). The Pipe Creek Shale continues up to the base of the Late *rhenana* Zone, which marks the base of the Hanover Shale. This comprises shales and siltstones which continue across the F–F boundary. The shales vary in their colour, from green to black, and degree of bioturbation, reflecting varying oxygen levels during the Late *rhenana* to *linguiformis* Zones. The lower part of the *linguiformis* Zone records more siltstone beds and fewer black shales suggestive of a slight shallowing event. The upper part of the *linguiformis* Zone is characterised by numerous finely laminated black shales, including a 0.8 thick example, which extends across the F–F boundary and into the Early *triangularis* Zone (Over, 1997). Filer's (2002) study of subsurface data in the northeast USA reveals a contemporaneous significant increase in gamma-ray values throughout Ohio and West Virginia, which reflects onlap onto the basin margin, and widespread shale deposition, and provides evidence for significant deepening. Above this, a 2.5 thick pale grey, bioturbated siltstone is overlain by further organic-rich shales and siltstones of the Dunkirk Formation.

As in the western United States, the most obvious potential eustatic sea-level signal in the New York record occurs in the later part of the Early *rhenana* Zone, at the boundary between the Nunda Sandstone and the Pipe Creek Shale (Fig. 4). This is clearly the regional expression of the flooding at the base of cycle IId in the Johnson et al. (1985) eustatic curve. Furthermore, there is potential evidence for regression and subsequent transgression during the *linguiformis* Zone but there is no evidence for regression at the F–F boundary. Over (1997, p. 165) states, "if significant sea-level drop occurred, it did not interrupt black shale deposition [across the F–F boundary]". The development of pale grey siltstones in the Early *triangularis* Zone may be evidence for regression at the top of T–R cycle IId. Over (1997) interprets the transgressive base of the Dunkirk Shale, in the Early *triangularis* Zone as the base of T–R Cycle IIe.

Based on detailed isopach and lithofacies maps (derived from gamma-ray logs) from a wider study of the Appalachian basin sections, Filer (2002) recognised 11 fourth-order progradational–retrogradational cycles from the late Frasnian. The two cycles of greatest amplitude correlate with the base of the Pipe Creek Shale (Filer's cycle 7), and the upper part of the Hanover Shale (late *linguiformis* Zone, Filer's cycle 11, see Fig. 4). Filer (2002) interprets this later retrogradation as the onset of a major third-order transgression, which begins in the latest Frasnian and ultimately results in deposition of the Dunkirk Shale in the Famennian. This major transgression across the boundary could thus be correlated with the upper transgression in Johnson et al.'s (1985) cycle IId. Unfortunately, Filer's (2002) Fig. 8 reproduced the poorly drafted Fig. 12 of Johnson et al. (1985, see above) with the result that there is no apparent correlation of the two major sea-level rises in the Johnson et al. (1985) study. However, the sea-level history discussed in the text of Johnson et al. (1985) shows a somewhat better correlation (Figs. 2 and 4), but the sharp, Early *triangularis* Zone regression is not seen in the Filer (2002) curve.

3.3. France

The Montagne Noire region of southern France exposes several Late Devonian sequences, including the stratotypes for the F–F boundary at Coumiac (Klapper et al., 1993) and the Devonian–Carboniferous boundary at La Serre (Paproth et al., 1991). Both are condensed limestone sections, considered to have formed on intrabasinal submarine rises (e.g. Schindler, 1990; Becker and House, 1994). The Coumiac section is almost entirely comprised of massive, pink micrites of the Upper Coumiac Formation. These are interbedded with two discrete dark grey beds — the first is an 18 cm-thick finely laminated micrite in the lower part of the Late *rhenana* Zone, and the second is a 7 cm-thick homoctenid-ostracod packstone, deposited during the latest *linguiformis* Zone (Fig. 5). Pyrite framboid and trace metal data reveal these beds, particularly the latter, to be discrete anoxic events within an otherwise well-oxygenated sequence (Bond et al., 2004). The top surface of the Coumiac Formation is a hardground, with numerous borings. The base of the succeeding Lower Griotte Formation lies within the Late *triangularis* Zone, and records a distinct change in facies to bright red, nodular

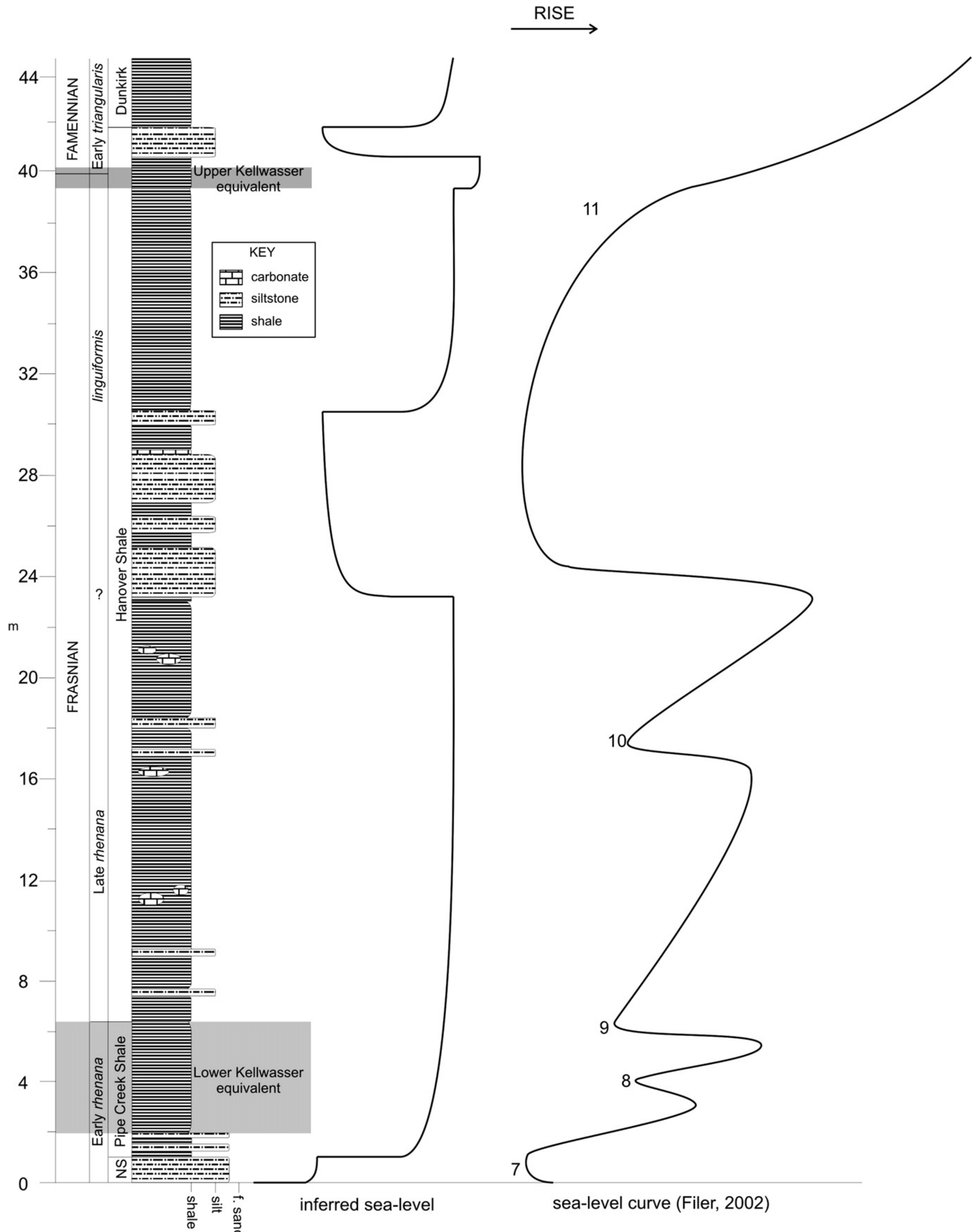

Fig. 4. Log of Beaver Meadow Creek, New York State. Conodont zonation is from Over (1997). NS = Nunda Sandstone. Lower and Upper Kellwasser equivalents are shown as shaded beds. The inferred sea-level history is shown (left) together with that of Filer (2002) for the northeastern United States. The numbers on Filer's (2002) curve refer to the base of his cycles. Note that the Filer (2002) curve has been adjusted to fit the thickness of this section.

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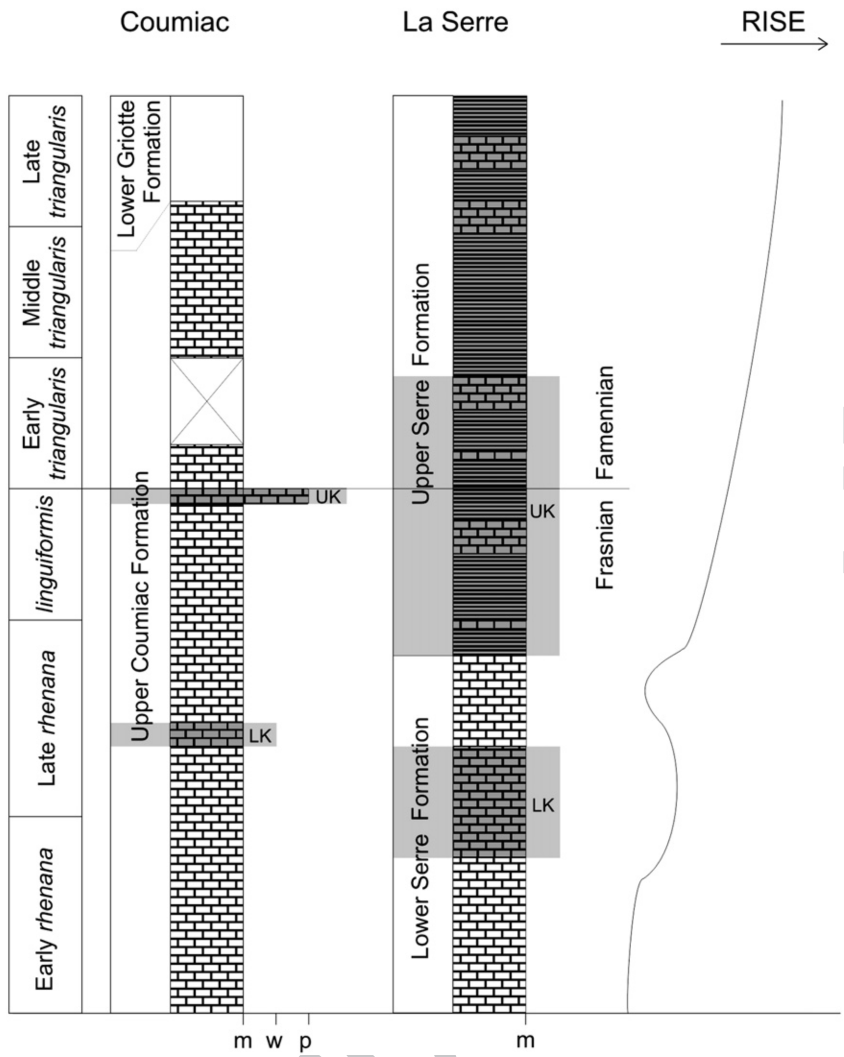

Fig. 5. Logs of Coumiac and La Serre sections, France, with inferred sea-level history. Conodont zonation is from Schindler (1990) and Becker and House (1994). Position of the Lower Kellwasser (LK) and Upper Kellwasser (UK) equivalents is shown by shaded bands. Lithologic key as in Fig. 4. Note that shaded lithologies represent dark grey to black limestones/shales. m = mudstone, w = wackestone, p = packstone.

limestones. Anoxic facies are highly characteristic of transgressions (e.g. Wignall, 1991, 1994), and thus the two pulses of anoxia recorded in this otherwise lithologically monotonous sequence may reflect deepening events.

The F–F section at La Serre presents clear evidence for sea-level change. The base of the sequence comprises massive, pink and grey sparites of the Lower Serre Formation. Within the upper part of the Early *rhenana* Zone, there is a transition to medium grey to black micrites and marly micrites, some of which are finely laminated (Fig. 5). This transition is suggestive of deepening at the time of transgression at the base of T–R cycle IId of Johnson et al. (1985). Above these dark beds, pale pink micrites extend to the top of the Lower Serre Formation, in the Late *rhenana* Zone. Further deepening is evident at the base of the Upper Serre Formation in the upper part of the Late *rhenana* Zone, which is marked by a distinct facies change to black, finely laminated shales, interbedded with black, argillaceous limestones. This may be the regional manifestation of the upper transgression of T–R cycle IId, although if so, the transgression began slightly earlier in France. The late Frasnian anoxic facies continues well up into the Famennian *crepida* Zone and records no evidence for regression. According to Becker (1993), the Upper Serre Formation is overlain by the grey, nodular limestones of the Griotte Limestone Formation, beginning in the earliest *rhomboidea* Zone.

3.4. Germany

Late Devonian sequences in the Rhine Slate Mountains and Harz Mountains of Germany record the drowning of carbonate platforms and the development of a basin-and-rise topography (Buggisch, 1972). F–F boundary sections are characterised by the widespread development of two well-known black, argillaceous limestone beds, known as the “Kellwasser Horizons”, the term used in the eponymous section, but widely applied to similar facies of (approximately) the same age observed in many parts of the world (see Bond et al., 2004). The Steinbruch Benner section is remarkably similar to that at Coumiac. It is a condensed sequence, largely composed of pale grey micrites and microsparites, with notable exceptions. At the base of the Late *rhenana* Zone, finely laminated, organic-rich, black limestones and shales develop, which extend into the middle part of this zone. These beds are overlain by pale grey micrites and sparites which extend to the top of the Late *rhenana* Zone. During the middle part of the *linguiformis* Zone, anoxic facies develop again, with finely laminated, black shale and micrite extending to the top of the Frasnian. The Early to Late *triangularis* Zones record a return to pale grey micrite deposition. Thus, the Benner section records two discrete anoxic events during the late Frasnian, manifest as the “Kellwasser Horizons”. These provide evidence for deepening, and as such the two transgressions

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of T–R cycle IId of Johnson et al. (1985) can be recognised in Germany. The diachronous nature of the Lower Kellwasser Horizon has been demonstrated by Crick et al. (2002) based on magnetostratigraphic susceptibility, and later by Bond et al. (2004), and thus the basal transgression of T–R cycle IId occurs at the base of the Late *rhenana* Zone at Steinbruch Benner, slightly later than it occurs elsewhere.

3.5. Poland

The Late Devonian of the Holy Cross Mountains records deposition in a carbonate platform and basin system, which formed part of a large equatorial carbonate shelf (Szulczewski, 1995; Racki et al., 2002). Facies evidence from two boundary sections is presented here: the well-known Kowala Quarry sequence which records base-of-slope to basinal deposition within the intrashelf Chęciny–Zrbza basin; and the Psie Górki section, which records shallow-water deposition of the Dyminy reef complex immediately to the north.

At Kowala Quarry, the succession is dominated by micrites, interbedded with thin beds of calcareous, dark grey shales and calcarenites (pelbiosparites, grainstones). The *jamiae* to Early *rhenana* Zone sequence comprises generally massive, pale-to-dark grey, marly micrites with thin interbeds of shales and calcarenites. During the Early *rhenana* to Late *rhenana* Zone, the frequency of calcarenite input decreased, and the succession becomes dominated by beds of pale-to-dark grey micrites, sometimes finely laminated, with rare, thin shale interbeds. This style of deposition continued into the Famennian, with periodic fluctuations in redox conditions. Thus, in the upper part of the Late *rhenana* Zone a distinctive, dark grey to black, finely laminated shale is seen, and this contains pyrite framboids and trace metals indicative of intensely anoxic conditions (Bond et al., 2004). This facies is repeated in the upper part of the *linguiformis* Zone, where it is the regional manifestation of the Upper Kellwasser Horizon (e.g. Joachimski et al., 2001). The F–F boundary itself has been placed by Racki (1999) in the upper of two distinctive, thin chert beds, both of which have a crinoidal hash at their base. In the Famennian, the thickness of the shale interbeds increases to the point where they dominate the sequence in the Late *triangularis* Zone.

The interpreted relative sea-level changes at Kowala begins with transgression in the late Frasnian that caused the source of calcarenite to become more distal and thus lost from this basinal setting. This was perhaps followed by regression in the later part of the *triangularis* Zone that caused the clastic content of the section to increase. There is no clear evidence for the higher frequency sea-level changes of Johnson et al. (1985) or Filer (2002) in this section.

The Psie Górki section exposes shallow-water fore-reef sediments that provides a particularly sensitive record of sea-level change near the F–F boundary, although the *rhenana* Zone is not exposed. The *linguiformis* Zone consists of packstones and biomicrites composed of reef debris (mostly stromatoporoid, coral and dasycladacean clasts). The *triangularis* Zone sediments comprise grainstones, composed of crinoids (in the lower part) and algal mat intraclasts, but no Frasnian reef fauna is present (Casier et al., 2002). The F–F boundary itself is placed within an 8 cm-thick bed of finely laminated micropelsparite which separates the two principal lithologies described above. The facies either side of the F–F boundary are broadly similar and indicate very shallow-water deposition. However, the finely laminated bed, enriched in redox sensitive trace metals (Bond et al., 2004), at the stage boundary is suggestive of anoxic, deeper-water deposition and therefore a brief, high amplitude transgression. This interpretation contrasts with previous work which has suggested that the reef development was terminated by a brief end-Frasnian regression (Racki, 1990; Casier et al., 2002). However, there is no clear meteoric diagenetic evidence in the top Frasnian, which one might expect if there had been exposure. Other evidence for a late *linguiformis* regression in Poland includes a bloom of icriodid conodonts (Szulczewski, 1989). However, conodont biofacies evidence is controversial as outlined below. More tangible evidence for regression includes detrital intercalations, local conglomerates and breccias (Matyja and Narkiewicz, 1992), but the biostratigraphic control on these occurrences needs improving.

4. Comparison with other regions

Studies of F–F boundary sections in other regions provide evidence to support, and refine, several aspects of the Johnson et al. (1985) sea-level curve.

4.1. South China

In southern China (Guangxi province) the *linguiformis* Zone sediments comprise shales and mudstones overlain by bioclastic limestones of the *triangularis* Zone. Muchez et al. (1996) derived a Late Devonian sea-level history for this region based on facies analysis and produced a curve that resembles the Johnson et al. (1985) curve as depicted in their Fig. 12 (our Fig. 2). This included two transgressions in the Late *rhenana* and *linguiformis* Zones, separated by regression with a second regression and sequence boundary formation occurring at the F–F boundary. The subsequent sea-level rise in the Middle *triangularis* Zone is then presumably the onset of T–R cycle IIe of Johnson et al. (1985). The Muchez et al. (1996) sea-level history differs from that implied by Johnson et al. (1985) in their text in the crucial F–F boundary and extinction interval, in that no sequence boundary is developed here. Indeed little facies evidence was provided by Muchez et al. (1996) in support of their interpretation.

Chen and Tucker (2003, 2004) have also studied the sections of Guangxi, in this case the area around Guilin. They presented a sequence stratigraphic analysis of several F–F boundary sections from deep-water and carbonate platform settings and identified cycle IId of Johnson et al. (1985) with a transgressive–regressive sequence beginning during the Early *rhenana* Zone and culminating in a major lowstand in the Late *triangularis* Zone (Fig. 6). This cycle is composed of two third-order cycles, SFr and SFa separated by a sequence boundary that Chen and Tucker (2003, 2004) place in the late *linguiformis* Zone. Field evidence for this boundary consists of a prominent palaeokarst surface in peritidal sediments, filled with dark grey limestones. The infilling limestones record a rapid, third-order sea-level rise during the latest part of the *linguiformis* Zone, which Chen and Tucker (2003) noted was synchronous with the Upper Kellwasser Horizon of Germany. This observation led Chen and Tucker (2003, p. 103) to suggest that "the rapid sea-level rise (third order) of sequence SFa starting from the latest Frasnian seems to have been synchronous worldwide", and that the associated development of marine anoxia led to a massive faunal decline in communities already severely depleted by the preceding sea-level fall. In fact their latest *linguiformis* age for the South China sequence boundary, transgressed only 16–18 kyr before the F–F boundary is significantly younger than that seen in the Johnson et al. (1985) curve where it occurs at the base of this zone. As shown above, the sequence boundary prior to the Upper Kellwasser anoxic event is generally found in the base or middle of this zone (e.g. Fig. 4). Chen and Tucker's (2003) evidence for a latest *linguiformis* age is based on the assumption that absolute durations for sedimentation can be obtained by assuming the cycles are the result of orbital forcing. On the whole this is a reasonable assumption, but transgressive sediments are typically condensed and we consider it likely that the thin package of sediment atop the *linguiformis* Zone sequence boundary could represent a significant portion of this zone. By assuming constant sedimentation rate, Chen and Tucker (2003) place the sequence boundary late in the *linguiformis* Zone at a time when, elsewhere in the world, base-level was rising rapidly, and as a result, the Guangxi record becomes out of kilter with the eustatic curve.

4.2. Australia

It has proved difficult to establish conodont biostratigraphic dating in the celebrated reef sections of the Canning Basin of Western Australia,

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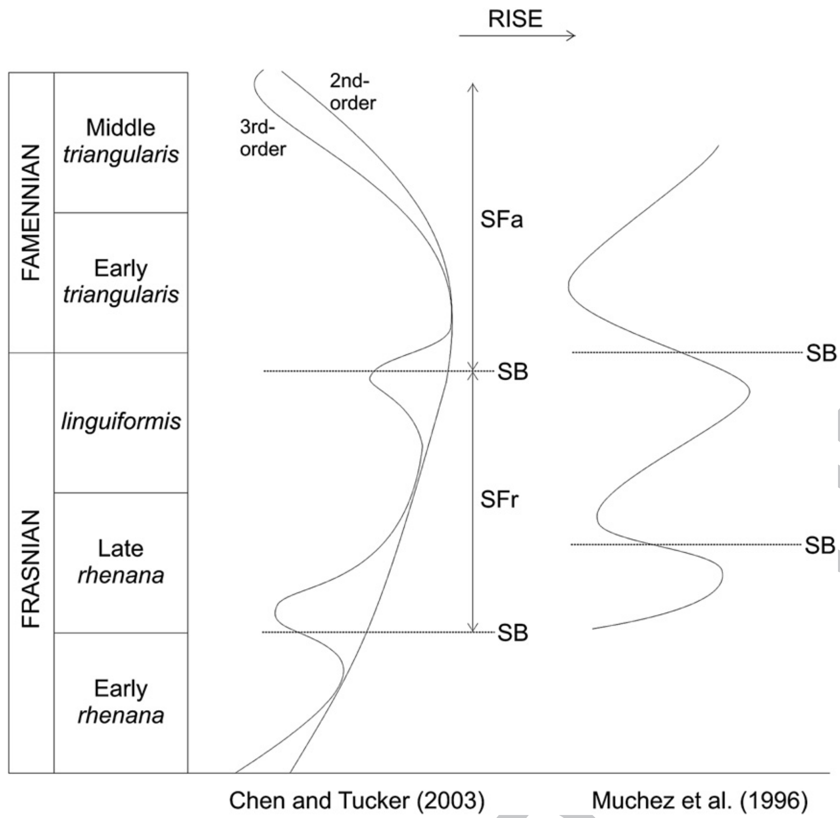

Fig. 6. Comparison of sea-level histories for South China (Chen and Tucker, 2003) and South China and Belgium (Muchez et al., 1996). SB = sequence boundary. SFr = Frasnian sequence, and SFa = Famennian sequence of Chen and Tucker (2003).

although an abundant ammonoid fauna has facilitated global correlation (Becker and House, 1997). The reefs of the region are terminated by a karstic surface that has been dated as F–F boundary age (Playford et al., 1989; Holmes and Christie-Blick, 1993; Playford, 2002). This lies between the Pillara Sequence and the Nullara Sequence and marks a long-term change from retrogradational stromatoporoid reefs to progradational stromatolite reefs (Becker and House, 1997). However, both the origin and age of the sequence boundary are contentious. Some workers favour a tectonic control with footwall uplift leading to local emergence (Southgate et al., 1993; Chow et al., 2004), whereas others favour eustatic regression (Becker and House, 1997; Playford and Hocking, 2006). The more local development of hiatuses is supported by Becker and House's (1997, p. 138) observation that sections in "a range of facies settings in the marginal-slope or in algal-sponge bioherms cross the [F–F] boundary and there is evidence of considerable facies fluctuations but *no sedimentary breaks are developed* (our italics)". In the more basinal sections they note "No lithological change at all is recognizable at the boundary" (Becker and House, 1997, p. 138). Despite these observations, Becker and House (1997) favour eustatic regression at the stage boundary. Pertinently, they also record evidence for "a brief but widely recognizable shallowing episode at the base of the *linguiformis* Zone." (Becker and House, 1997, p. 138). This is the same age as the widespread regression seen within cycle IId of the Johnson et al. (1985) curve.

Stephens and Sumner (2003) studied Canning Basin reef complexes, using carbon isotope stratigraphy as a basis for correlation. A $\delta^{13}C$ curve has been well established in Europe and North America, where two positive excursions coincide with the Kellwasser anoxic events (Joachimski and Buggisch, 1993; Wang et al., 1996; Joachimski et al., 2002). By identifying these excursions Stephens and Sumner (2003) were able to date two late Frasnian transgressions in the Oscar Range as coincident with the Kellwasser transgressions. These saw the development of upper marginal-slope facies in reef-margin settings at a time of backstepping stratal geometry. The development of a lowstand reef (i.e. progradation of the reef margin) in the Oscar Range in the inferred earliest *linguiformis* Zone indicates regression between the two transgressive intervals. This regression has also been inferred in subsurface data, where a prominent *linguiformis* Zone sequence boundary is identified (Kennard et al., 1992; Southgate et al., 1993). Thus, there is compelling evidence for eustatic control in the Canning Basin succession with the fluctuations of the Johnson et al. (1985) curve readily identifiable, but with possible tectonic complications.

4.3. Canada

Sea-level history in Canadian sections indicates substantial oscillations around the F–F boundary although a paucity of conodont biostratigraphic evidence makes comparison with the Johnson et al. (1985) curve somewhat difficult. In the Northwest Territories, two minor hiatuses are inferred close to the boundary (Geldsetzer et al., 1993). The first hiatus is recorded by karstification and brecciation of the top surface of the Kakisa Formation. A lack of conodont evidence only makes it possible to date this hiatal surface to somewhere between the Late *rhenana* and Early *triangularis* zones. It could be the early *linguiformis* regression seen in many other regions. Neptunian dykes within the Kakisa Formation are infilled with Mid *triangularis* wackestones indicating that sea-level had risen by this time. Angular fragments of this wackestone in the basal Trout River Formation, are interpreted to record a second hiatus, which probably straddled the Middle/Late *triangularis* zonal boundary (Geldsetzer et al., 1993).

Nine hundred kilometres to the south of the Trout River locality, at Medicine Lake, Alberta, the Jasper Basin provides a continuous record of Late Devonian sedimentation (Geldsetzer et al., 1987). Here, the extinction is associated with an abrupt facies shift from bioturbated sediments, to laminated dark shales, the result of flooding of the basin by anoxic waters. Thus, Geldsetzer et al. (1987) invoke an anoxic kill

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mechanism during highstand as the cause of the F–F extinction. Orchard (1988) notes that the basin was later filled with siliciclastics, beginning in the *triangularis* Zone. This may reflect shallowing above the F–F boundary, and the top of T–R cycle IId, but regression and karstification in the region has generally been dated to the stage boundary (Copper, 2002), although detailed conodont biostratigraphic constraint is lacking.

Excellent conodont biostratigraphic control is available from the Moose River Basin of northern Ontario where the F–F boundary interval is recorded in a mudrock succession (Levman and von Bitter, 2002). At the Abitibi River section the *rhenana* Zone sediments consist of green mudstones with two thin dolostone layers. The upper of these dolostones is capped by a hardground and thin lag layer, and overlain by 4 m of black shale. Conodonts of the *linguiformis* Zone occur in the basal 2–3 cm of the black shale and basal *triangularis* conodonts occur above this (Levman and von Bitter, 2002). Once again, a basal *linguiformis* regression was succeeded by a rapid rise of sea-level, associated with the spread of anoxic facies, that continued into the *triangularis* Zone.

5. Conodont biofacies analysis

Many studies of sea-level change during the F–F mass extinction have used changes in conodont assemblages to infer a eustatic history. The results are often in conflict with the interpretations derived from facies and sequence stratigraphic analysis. Early work by Sandberg (1976) identified 11 biofacies along a nearshore-basinal transect. In particular, the genera *Palmatolepis* and *Polygnathus* were used to indicate deep and/or open waters, whilst *Icriodus* indicated shallow-water. Thus, Sandberg et al. (1988) demonstrated a progressive increase in the proportion of *Icriodus* elements from the *linguiformis* to the *triangularis* zones in two European sections (Hony, Belgium, and Steinbruch Schmidt, Germany) and inferred “an abrupt eustatic fall immediately preceded the late Frasnian mass extinction and that the fall continued unabated into the early Famennian” (Sandberg et al., 1988, p. 267). This conclusion is in stark contrast to the transgression-related anoxia and mass extinction inference of Johnson et al. (1985), published only three years before.

Sandberg et al. (1989, 2002) further developed their techniques to produce a series of palaeobiogeographic lithofacies maps and an event history, largely based on the concept of conodont biofacies, but now also supported by a study of the sediments that contain these conodonts. Their event history includes the major transgression during the Early *rhenana* Zone which saw the rapid evolution and dispersal of the deep-water conodont *Palmatolepis semichatovae* (hence the “*semichatovae* transgression” — see Section 3.1 above). This is followed by an abrupt eustatic fall which occurred still within the Early *rhenana* Zone. The fall had little effect on sedimentation in the western United States, but resulted in the cessation of carbonate platform sedimentation in other areas (e.g. the Jefferson Formation of Montana, Sandberg et al., 1989). A major transgression then occurred during the Late *rhenana* and *linguiformis* Zones, leading to the widespread establishment of basinal anoxia (Events 5 and 6 of Sandberg et al., 2002, see Fig. 7). This transgression was succeeded by Events 7 and 8 of Sandberg et al. (2002), two pulses of regression that began in the *linguiformis* Zone and continued into the Early *triangularis* Zone (Fig. 7). This regression is again based upon changes in conodont percentages and is also supported by an increase in the clastic content in all four lithofacies described in map 4 of Sandberg et al. (1989). However, this lithofacies map corresponds to the Early *triangularis* Zone and so it is unclear why the onset of regression is placed within the Frasnian. The subsequent transgression begins in the Middle *triangularis* Zone. Sandberg et al.'s (1988, 1989, 2002) sea-level history recognises two F–F transgressive–regressive cycles, as per the original Johnson et al. (1985) curve, but it differs from that of Johnson et al. (1985) in the timing of these eustatic changes. The association of the mass extinction with regression at the F–F boundary is the fundamental and key difference with the Johnson et al. (1985) curve which clearly linked the mass extinction to a phase of anoxia that spread during a transgression in the late *linguiformis* Zone.

So why is there such a discrepancy in these sea-level interpretations? Sandberg et al. (1988) rely heavily on the assumption that

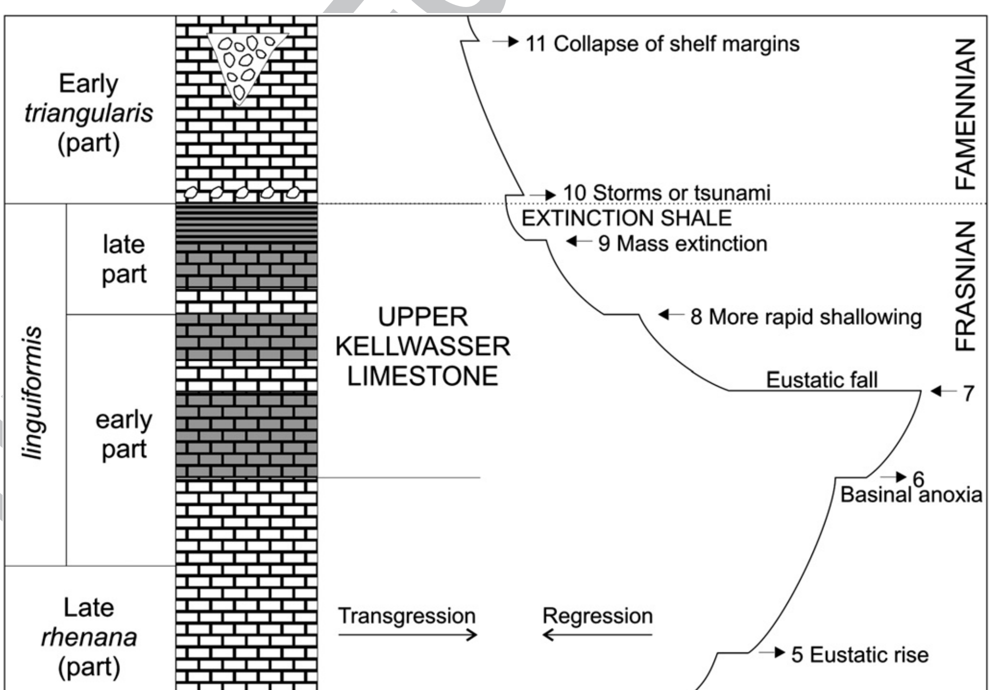

Fig. 7. Detailed sea-level history across the F–F boundary, reproduced from Sandberg et al. (2002). Lithologic key as in Fig. 4. Note that shaded lithologies represent dark grey to black limestones.

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variations in conodont assemblages reflect sea-level change. However, this assumption is potentially flawed, because the F–F mass extinction was particularly severe for conodonts, with many species and genera becoming extinct. It is possible that the increase in the supposedly shallow-water genus *Icriodus* merely reflects the near-total loss of all deep-water conodonts at this time, allowing the opportunistic expansion of the survivors (Hallam and Wignall, 1999). Certainly the increase in importance of *Icriodus* is not reflected as an increase in their abundance, as can be seen in the original data of Sandberg et al. (1988, Tables 1–3), but is a function of the extinction of species of other genera.

The water-depth significance of *Icriodus* is also not clear. Belka and Wendt (1992) studied the conodont palaeoecology of the F–F interval in Morocco, and found that in samples of Late *rhenana* Zone age, obtained from the margins of the Tafilalt Basin, *Icriodus* accounted for as much as 20% of the total conodont population. According to their Fig. 10, *Icriodus* makes up 81% of the total population from a basinal sample of the same age. Belka and Wendt (1992) note that this sample is characterised by high clastic input, but rule out sedimentary reworking of the icriodid elements because they are not contained within turbiditic layers. In any case, palmatolepid elements should be preferentially reworked by sedimentary transport because they are more abundant than icriodids along the margin of the Tafilalt platform. Belka and Wendt (1992) also found that three species of *Icriodus*, including *I. alternatus alternatus* and *I. alternatus helmsi* are randomly distributed throughout the whole Tafilalt and Mader area, and thus show no particular water-depth dependence. These two species form the vast majority of icriodids recovered by Sandberg et al. (1988) in their study.

Girard and Renaud (2007) have also inferred F–F boundary eustasy based on the assumption of a shallow-water habit for *Icriodus* and deeper-water affinity of other genera such as *Palmatolepis*. Girard and Renaud (2007, p. 120) note that "a peak in *Icriodus* percentage occurs at the F–F boundary and is associated with the end of the UKE (Upper Kellwasser Event)". This increase can be more simply attributed to the drastic losses amongst *Palmatolepis* and *Polygnathus* rather than sea-level change. Furthermore, their data reveals that this "*Icriodus* spike" actually occurs within the *triangularis* Zone, and thus any inferred sea-level fall post-dates the F–F extinction. It is noteworthy that peaks in absolute number of *Icriodus* elements are rather diachronous and occur in better oxygenated strata at different levels within the Early and Late *rhenana* Zone at both the Coumiac and La Serre sections in France. For example, at La Serre, Girard and Renaud (2007) inferred a decrease of conodonts within the Early *rhenana* Zone (bed 8), a level they suggested was the Lower Kellwasser Event, which they assume to be isochronous. In fact pyrite petrographic data indicates that the most intense anoxia at this level occurs in bed 9 (uppermost Early *rhenana* Zone) at La Serre, the most likely level for the Lower Kellwasser Event (Bond et al., 2004). Even in the latest Frasnian and earliest Famennian beds, when the relative abundance of *Icriodus* is high, their absolute abundance is actually rather low. This serves to further highlight that great care should be taken using conodonts to interpret sea-level changes.

6. Discussion

6.1. Sea-level and extinction

Sea-level change figures in nearly all mass extinction scenarios for the F–F event. Most workers are in agreement that this interval falls in the later part of a major transgression, with regression and sequence boundary generation in the early part of the Famennian Stage. Although these higher order events are contentious, the interpretation of the shorter-term (third order) changes of eustasy have proved particularly controversial. No workers attribute the F–F extinction directly to transgression, although the associated spread of anoxic waters is a clearer kill mechanism (see below). However, many workers link the extinction to cooling and an associated (glacioeustatic?) regression (e.g. Copper, 1975, 2002; Playford et al., 1989; Becker and House, 1997; Chen and Tucker, 2003, 2004). For some, this severe phase of regression occurred during the development of the euxinic facies of the Upper Kellwasser Event (e.g. Sandberg et al., 2002, Fig. 5), but most proponents of regression highlight the presence of karstic surfaces in carbonate sections as evidence for this regression–extinction link (e.g. Canadian Rockies, Canning Basin, Australia, Guangxi, China). Dating a karstification event is difficult but it most likely formed during the earliest *linguiformis* Zone, before the Upper Kellwasser Event, and not at the F–F boundary. This does not invalidate a regression–extinction link but implies that the F–F extinction was spread over the duration of the *linguiformis* Zone. However, in those few sections where Frasnian reefs survived until the late *linguiformis* Zone (e.g. Psie Górki, Poland) the reef taxa clearly survived the early *linguiformis* regressive phase. In the more offshore, basinal sections the extinction losses (of groups such as tentaculitoids, ammonoids, conodonts, and ostracods) are clearly associated with late transgression or maximum Highstand Systems Tract.

6.2. Anoxia and extinction

The close association of the development of anoxic facies and the Late Devonian mass extinction has lead many authors to attribute a cause-and-effect relationship (e.g. Buggisch, 1972; House, 1985; Casier, 1987; Geldsetzer et al., 1987; Goodfellow et al., 1989; Walliser et al., 1989; Buggisch, 1991; Becker, 1993; Joachimski and Buggisch, 1993; Becker and House, 1994; Joachimski et al., 2001, 2002; Levman and von Bitter, 2002; Chen and Tucker, 2003; Bond et al., 2004; Tribovillard et al., 2004; Bond and Wignall, 2005; Riquier et al., 2005; Bond, 2006; Pujol et al., 2006). The link has been criticised by Copper (2002, p. 46–47) who notes that "A major problem with the anoxia hypothesis is that it is difficult to imagine how 'giant megaburps' of CO_2 (and SO_2)-enriched waters, brought up from below the CCD, could simultaneously spill over all the world's tropical shelf areas". This criticism rests on the assumption that only one mechanism – global oceanic upwelling – can produce widespread anoxia. In fact, analysis of the distribution of anoxic waters shows that they were best developed within the interiors of epicontinental basins, and expanded their extent during the transgressive episodes of cycle IId. There is little evidence for anoxia in oceanic margin settings and a 'megaburp' upwelling model is therefore inappropriate for the Upper Kellwasser Event (Bond et al., 2004).

A more compelling argument against the anoxia–extinction link may be the observation that "There is no evident, direct relationship between black shale horizons and reef disappearances in any sections" (Copper, 2002, p. 47). The demise of the Psie Górki reef may be an exception, but Copper's (2002) general point is a good one and it reiterates the point made by Becker et al. (1991, p. 183) that there is "no evidence for the organic-rich dark Kellwasser limestone facies" associated with the demise of the Canning Basin reefs. However, there has been no attempt to analyse redox variations in the Australian sections. Often the evidence for such changes can be rather cryptic, particularly in deeply-weathered desert sections. For example, Bratton et al. (1999) concluded, on the basis of trace metal geochemistry, that there was no evidence for the Upper Kellwasser Event in the desert sections of the Great Basin, USA. However, the Event was discovered using petrographic analysis of the same sections (Bond and Wignall, 2005). This revealed an intense phase of euxinia, based on pyrite framboid data. The framboids had been oxidised to iron oxyhydroxides, but still retained their form, whereas the geochemical signature had been lost due to intense oxidation of the samples in a desert climate. Similar studies in the Canning Basin may yet reveal a role for anoxia in the reef extinctions.

The transgression-anoxia–extinction scenario invoked here and by those authors cited above appears to be a pattern which was repeated

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several times during the Devonian. Brett and Baird (1995) recognised six Ecological–Evolutionary (E–E) subunits in the Early Devonian to Frasnian interval, at least five of which were apparently terminated by widespread hypoxic highstands. Thus, there were probably several lesser extinctions during the Devonian, and the Frasnian–Famennian event was merely a more intense manifestation of this scenario.

7. Conclusions

Similar relative sea-level changes near the Frasnian–Famennian boundary are recorded in many sections worldwide, which implies a eustatic control. The details of this eustatic history were first outlined in cycle IId of Johnson et al. (1985), although the discrepancy between their text and their Fig. 12 has led to confusion in subsequent studies.

Cycle IId begins with a major transgression in the Early *rhenana* Zone that is clearly seen in many sections. The subsequent regression in the early *linguiformis* Zone was considered a minor one by Johnson et al. (1985). This is supported by its weak manifestation in many basinal and base-of-slope sections where its impact was either minor (e.g. in the Woodruff and Pilot basins of the Great Basin, USA) or undetectable (e.g. in the Kowala section, Poland). In contrast this apparently minor regression appears to have caused the emergence and karstification of carbonate platform deposition over wide areas (Canadian Rockies, Guangxi, China).

Transgression during the *linguiformis* Zone is associated with the spread of anoxic facies (Upper Kellwasser Event) and major extinction losses, a more intense manifestation of a scenario that may have repeated several times during the Devonian. The *linguiformis* Zone deepening persisted across the F–F boundary and was terminated by subsequent sea-level fall in the *triangularis* Zone. The report of a spectacular eustatic regression at the F–F boundary (e.g. Sandberg et al., 2002) may be a miscorrelation of the early *linguiformis* sequence boundary. Nonetheless, the links of regression and extinction cannot be discounted because this emergence event removed much of the platform carbonate habitat area.

Sea-level does not change in isolation within the earth-surface system and it is likely that the major eustatic changes associated with F–F mass extinction indicate destabilisation of the climate and C cycle (e.g. Copper, 1986; Buggisch, 1991; Joachimski and Buggisch, 1993; Becker and House, 1994; Algeo et al., 1995; Algeo and Scheckler, 1998; Streel et al., 2000; Joachimski et al., 2002; Goddéris and Joachimski, 2004; Averbuch et al., 2005; Chen et al., 2005; Riquier et al., 2005). The role of volcanism, often regarded as a key triggering factor during other global environmental perturbation events, also needs further evaluation (Racki, 1998).

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