Quantitative conodont-based approaches for correlation of the Late Devonian Kellwasser anoxic events

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Abstract

We present the trends of absolute conodont abundance, relative genera abundance, and conodont morphometrics across the Late Devonian Kellwasser horizons at three northern Gondwanan epicontinental seaway locations.

At three contrasting depositional settings, the Kellwasser events are characterized by a decrease in conodont abundance, high percentage of the conodont genus *Icriodus* and morphological change of the conodont genus *Palmatolepis*. These changes can be identified in sections where the events are expressed as interbedded anoxic and oxic deposits as well as in settings characterized by continuous anoxic sediment accumulation. Hence, these changes are interpreted as global and synchronous and can be thus used for event correlation.

The paradox of these results is that despite quite similar isotopic signals, faunal change during the Lower Kellwasser event was less than during the Upper Kellwasser event. We interpret that this discrepancy is due to an unconformity (including topmost Frasnian to earliest Famennian) at several F/F sections which removed the record of peak paleoenvironmental change.
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1. Introduction

Anoxic or dysoxic events are common in Earth history. Some were related to mass extinction events, such as the Cenomanian/Turonian (Kolonic et al., 2005) and the Frasnian/Famennian (McGhee, 1996) boundaries. Recently, super-anoxic events have been implicated for the largest mass extinction, the Permo/Triassic event (Grice et al., 2005). Both the Cretaceous and Devonian are marked by a numerous succession of anoxic-dysoxic

events, however just few of them were associated with mass extinction (Walliser, 1996).

During the Late Devonian, the Frasnian/Famennian (F/F) boundary is associated with a massive faunal turnover, and coincides with the top of black bituminous layers in outer shelf deposits named the Upper Kellwasser (UKW) Horizon (Schindler, 1990, 1993). This horizon is preceded by a similar horizon, the Lower Kellwasser (LKW). Biotic events, named Lower Kellwasser (LKE) and Upper Kellwasser (UKE) events, are observed during both Kellwasser horizons, and are characterized by biotic extinctions especially at the top of the UKE. The processes and timing of both events which eventually lead to the mass extinction of the F/F have been the focus of numerous studies (Bond et al., 2004; Joachimski et al., 2004; Racki, 2005; Riquier

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et al., 2005, 2006). All proposed scenarii rely on the accurate correlation of several sections, and especially a precise location of the UKW and LKW events. Though these events are easily identifiable as organic-rich anoxic horizons in many sections, uncertainty remains in sections where anoxic conditions prevailed before, between and after the two Kellwasser events. Some of these outcrops (for instance La Serre, in the Montagne Noire) are extensively studied and served as basis for proposing new environmental scenarii suggesting that both Kellwasser events were caused by different mechanisms and have different geographic extents (Bond et al., 2004; Riquier et al., 2006). Such scenarii are in disagreement with other hypotheses which are based on variations of oxygen and carbon isotopes, suggesting that both Kellwasser events were global and had similar causes (Joachimski and Buggisch, 1993, 2002; Joachimski et al., 2004).

We suggest that the discrepancy between the scenarii is due to the imprecision of the current stratigraphy that lead to misplacing the Lower Kellwasser event in sections where it is not identifiable based on facies variation. During the Devonian, the main biostratigraphic markers are conodonts, elements of the buccal apparatus of an animal related to early vertebrates (Briggs, 1992; Purnell, 1995; Donoghue and Purnell, 1999). Conodonts are mm-size phosphatic remains interpreted as tooth-like jaw elements (Purnell and von Bitter, 1992). Conodonts may react to environmental perturbations without a major change in the faunal composition, but by changes in their absolute abundance, in the relative contribution of the different genera depending on their ecological preferences (Seddon and Sweet, 1971; Sandberg et al., 1988), and/or by shape changes of a given genus (Girard et al., 2004). To propose an alternative to the traditional conodont stratigraphy, we combined several quantitative conodont-based approaches to analyse the time period preceding the F/F including both Kellwasser events. They are based on three approaches: absolute and relative abundances, and morphometric variations.

We analysed three sections from different environmental settings: (1) the F/F stratotype section of Coumiac (France), where the Kellwasser horizons are characterized by dark-grey, carbon-rich hypoxic deposits intercalated within well-oxygenated, carbonated beds. (2) The Mrirt section (Morocco), characterized by a similar environmental context to Coumiac. Considering this section allows a test of the reproducibility of our conodont-based approaches. (3) The section of La Serre (France), nearby Coumiac, where the Kellwasser horizons cannot be identified by facies differences because anoxic conditions prevailed throughout deposition.

2. Geological setting

2.1. Depositional context

The first two sections are located in the Montagne Noire, France (Fig. 1). Coumiac Upper Quarry (CUQ) is the stratotype section for the Frasnian/Famennian boundary (Klapper et al., 1993). This section is composed of oxidized sediments deposited on an outershelf submarine rise (Feist, 1985; Feist and Klapper, 1985). The Kellwasser horizons are easily identifiable by an intercalation of two dark grey, coarse limestone beds in the otherwise medium-red sequence of oxygenated deposits. Iron encrustation with well developed micro-stromatolitic cauliflower structures formed by iron-oxidizing bacteria occurs at the top of the Upper Kellwasser and indicates an interruption of the carbonate sedimentation and/or extremely low sedimentation rates (House et al., 2000).

The section at La Serre trench C (LSC) is close to the Coumiac UQ section (Fig. 1) The sequence consists of a succession of laminated dysoxic marlstones and siltstones. The Kellwasser horizons cannot be determined based on facies, because the dysoxic grey Kellwasser-like facies occurs throughout the succession. These prevailing anoxic conditions were interpreted as the result of a deposition in a small, deep restricted basin (Schindler, 1990). There is no physical evidence for condensed sedimentation, sedimentary gaps, or discontinuities, either at the F/F boundary or elsewhere in the section.

The third site considered is the Mrirt section (M), located in the Moroccan Meseta. The depositional environment was similar to that of Coumiac UQ, resulting in similar facies (Lazreq, 1992, 1999). Thus, the Kellwasser horizons can be recognized as dysoxic grey levels interbedded within an otherwise light-colored, well oxygenated succession (Fig. 1). The presence of microhardgrounds and iron-oxide horizons associated with the Upper Kellwasser horizon, as already observed in Coumiac, indicate slow submarine sedimentation.

2.2. Conodont biostratigraphy

As a first basis to compare the three sections, traditional conodont biostratigraphy has been established (Fig. 1). The standard zonation of Ziegler and Sandberg (1990) was used for the Famennian. The *triangularis* zone has been recognized in all three sections. The lower and middle *triangularis* zones can be recognized at La Serre and Coumiac (Schülke, 1999), but the lower *triangularis* zone seems to be missing in the Mrirt section and only the middle and the base of the upper
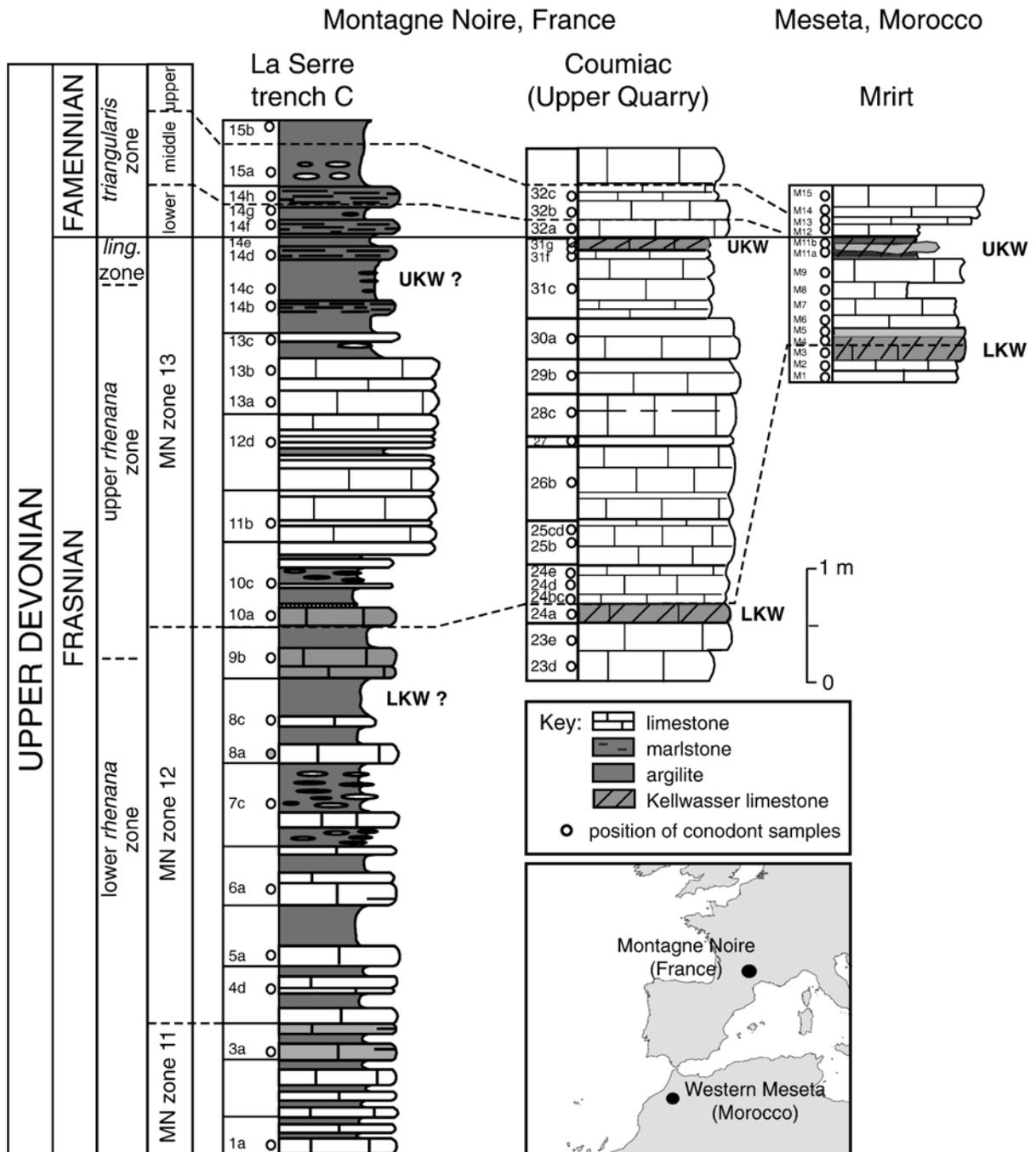
Fig. 1. Correlation of the Frasnian/Famennian (F/F) boundary beds among the La Serre, Coumiac sections (Montagne Noire, France), and the Mrirt section (Meseta, Morocco). LKW=Lower Kellwasser, UKW=Upper Kellwasser, ling.=*linguiformis*. Bed numbers at left of the stratigraphic profiles.

triangularis zone have been recognized (Lazreq, 1999). For the Frasnian, a more detailed biostratigraphic zonation, based on MN (Montagne Noire) zones (Klapper, 1989) was compared to the standard Late Devonian zonation (Ziegler and Sandberg, 1990).

At Coumiac UQ, the conodont index of the MN 13 zone *Palmatolepis bogartensis* appears in the level CUQ24bc above the Lower Kellwasser horizon (House et al., 2000). The index of the upper *rhenana* zone in the sense of Ziegler and Sandberg (1990), *P. rhenana*

rhenana, does not appear before the level CUQ 26, but the lower dark grey Kellwasser horizon (CUQ 24a) yielded *Ancyrognathus asymmetricus* which is an additional marker of the beginning of the upper *rhenana* zone in the sense of Ziegler and Sandberg (1990). As the beginning of the upper *rhenana* zone can be correlated with the top of the MN 12 zone (Klapper and Becker, 1999), the Lower Kellwasser horizon can be dated at the beginning of the upper *rhenana* zone or top of MN 12 zone.

At Mrirt, *Palmatolepis bogartensis*, the defining species for the base of MN13 zone appears within the Lower Kellwasser horizon (between bed M3 and bed M4). The Lower Kellwasser horizon yields *Ancyrognathus asymmetricus* and can be correlated with the beginning of the upper *rhenana* zone or top of MN 12 zone.

At La Serre, a longer time interval is recognized. The MN zones 13 and 12 are fully identified, as well as the top of the MN zone 11 (Klapper in Feist, 2002). The boundary between these latter zones is defined as the appearance of *P. winchelli* (LSC3 and LSC4). The species *Ancyrognathus asymmetricus* is found in bed LSC10, resulting in the boundary between the zones 12 and 13 between LSC9 and LSC10. Since this part of section yields only very few

Table 1
Numerical analysis of conodont assemblages from successive beds at La Serre section (LSC)

Samples	Depth	Weight	Po	Pa	An	Ic	Total	Pa$_M$
	(m)	(g)						
LSC15b	890	200	0	24	0	5	29	20
LSC15a	830	200	33	138	0	28	199	79
LSC14h	814	200	57	498	0	54	609	226
LSC14g	805	350	10	19	0	7	36	9
LSC14f	795	275	30	110	0	65	205	94
LSC14d	767	500	140	30	3	54	227	13
LSC14c2	762	200	145	50	3	42	240	27
LSC14b2	719	180	51	131	7	6	195	105
LSC13c	694	220	76	513	10	4	603	264
LSC13b	683	220	812	2036	59	121	3028	930
LSC13a2	660	300	1813	1356	36	34	3239	799
LSC12d	605	210	503	497	10	59	1069	251
LSC11b	517	280	635	199	20	6	860	89
LSC10c	490	350	104	76	24	0	204	44
LSC10a	460	720	16	67	4	1	88	47
LSC9b	423	890	24	16	5	10	55	11
LSC8c	380	520	2	8	2	6	18	4
LSC8a	343	550	93	0	20	69	182	–
LSC7c	286	790	68	27	15	78	188	18
LSC6a2	252	200	170	216	96	115	597	115
LSC5a	161	120	236	19	31	105	391	11
LSC4d	151	160	139	24	19	6	188	13
LSC3a	85	170	90	42	4	26	162	28
LSC1a	0	250	46	6	11	13	76	5

Abbreviations: Po = *Polygnathus*; Pa = *Palmatolepis*, An = Ancyrogroup, Ic = *Icriodus*. Pa$_M$ = number of *Palmatolepis* measured for morphometrics.

Table 2
Numerical analysis of conodont assemblages from successive beds at Coumiac Upper Quarry section (UQ)

Samples	Depth	Weight	Po	Pa	An	Ic	Total	Pa$_M$
	(m)	(g)						
UQ32c	443	500	32	219	0	44	295	45
UQ32b	426	500	41	328	0	51	420	45
UQ32a	408	500	50	120	1	51	221	51
UQ31g2	393	500	336	65	21	100	521	58
UQ31g1	387	500	417	285	20	87	809	68
UQ31f	381	500	332	1040	59	41	1471	94
UQ31c	353	500	486	1925	129	113	2653	481
UQ30	317	500	1646	1212	29	0	2887	469
UQ29b	265	500	1739	1511	48	159	3457	350
UQ28c	224	500	1049	1175	64	217	2505	263
UQ27	204	500	1068	646	38	104	1856	170
UQ26b	149	500	390	652	43	225	1310	235
UQ25cd	122	150	104	92	26	7	229	49
UQ25b	95	500	367	239	48	37	691	48
UQ24e	77	230	87	61	20	2	170	34
UQ24d	68	200	29	43	7	22	101	19
UQ24bc	49	260	30	20	21	45	116	15
UQ24a	42	500	339	52	206	102	699	37
UQ23e	25	500	323	90	48	231	692	18
UQ23d	3	240	214	268	44	77	603	121

Abbreviations: Po = *Polygnathus*; Pa = *Palmatolepis*, An = Ancyrogroup, Ic = *Icriodus*. Pa$_M$ = number of *Palmatolepis* measured for morphometrics.

conodonts (Table 1), the precise location of the boundary between MN12 and MN13 zones remains questionable. The lack of *Palmatolepis* in LSC8a makes biostratigraphic dating of this part of the section difficult.

Table 3
Numerical analysis of conodont assemblages from successive beds at Mrirt section (M)

Samples	Depth	Weight	Po	Pa	An	Ic	Total	Pa$_M$
	(m)	(g)						
M 15	152	100	26	282	0	93	401	98
M 14	142	60	8	66	0	20	94	42
M 13	136	200	38	337	0	88	463	133
M 12	126	120	5	18	0	8	31	6
M 11b	110	85	13	49	9	1	72	25
M 11a	106	30	20	39	1	1	61	13
M 9	89	50	62	147	21	1	231	52
M 8	71	150	73	141	3	4	221	74
M 7a	58	20	60	159	3	0	222	81
M 6	47	350	183	818	44	9	1054	420
M 5	42	200	67	101	13	43	224	59
M 4	22	200	58	13	21	83	175	12
M 3	18	210	164	107	74	61	406	71
M 2	4.5	120	477	339	82	34	932	200
M 1	0	100	94	139	18	1	252	63

Abbreviations: Po = *Polygnathus*; Pa = *Palmatolepis*, An = Ancyrogroup, Ic = *Icriodus*. Pa$_M$ = number of *Palmatolepis* measured for morphometrics.

3. Sampling of conodonts

Rock samples were dissolved in dilute formic acid (10%) and rinsed through two sieves. The fraction between 100 μm and 1 mm was picked for all conodont elements. Platform elements were identified at the genus level and counted. Absolute abundances per kg of rocks were very unequal. For each sample, at least 100 platform elements have been analysed to allow a reliable estimation of relative abundances. All intact *Palmatolepis* platform elements were selected for morphometric analysis. Details are given in Table 1 (La Serre C), Table 2 (Coumiac UQ) and Table 3 (Mrirt).

4. Methods

4.1. Abundance and biofacies analyses

Absolute abundance was estimated as the number of platform elements per kg of rock. Since the variations are

very important, these data have been log-transformed. Among these platform elements, several genera can be identified and have been related to different environmental preferences. The representatives of the conodont genus *Icriodus* occur in larger proportions within shallow-marine facies. Their increase in proportion within the conodont assemblage are interpreted as a sea-level fall (Sandberg et al., 1988, 2002). Other genera like *Palmatolepis* seem to be characteristic of deeper water environments. Hence, the variations of the relative proportion of the different genera provide an indirect water depth proxy that may be correlated among sections. Such an approach is called biofacies analysis (Seddon and Sweet, 1971; Sandberg, 1976).

4.2. Morphometrical analyses

During the considered time interval, *Palmatolepis* is the most abundant conodont genus. Previous studies have shown that the shape of its platform element
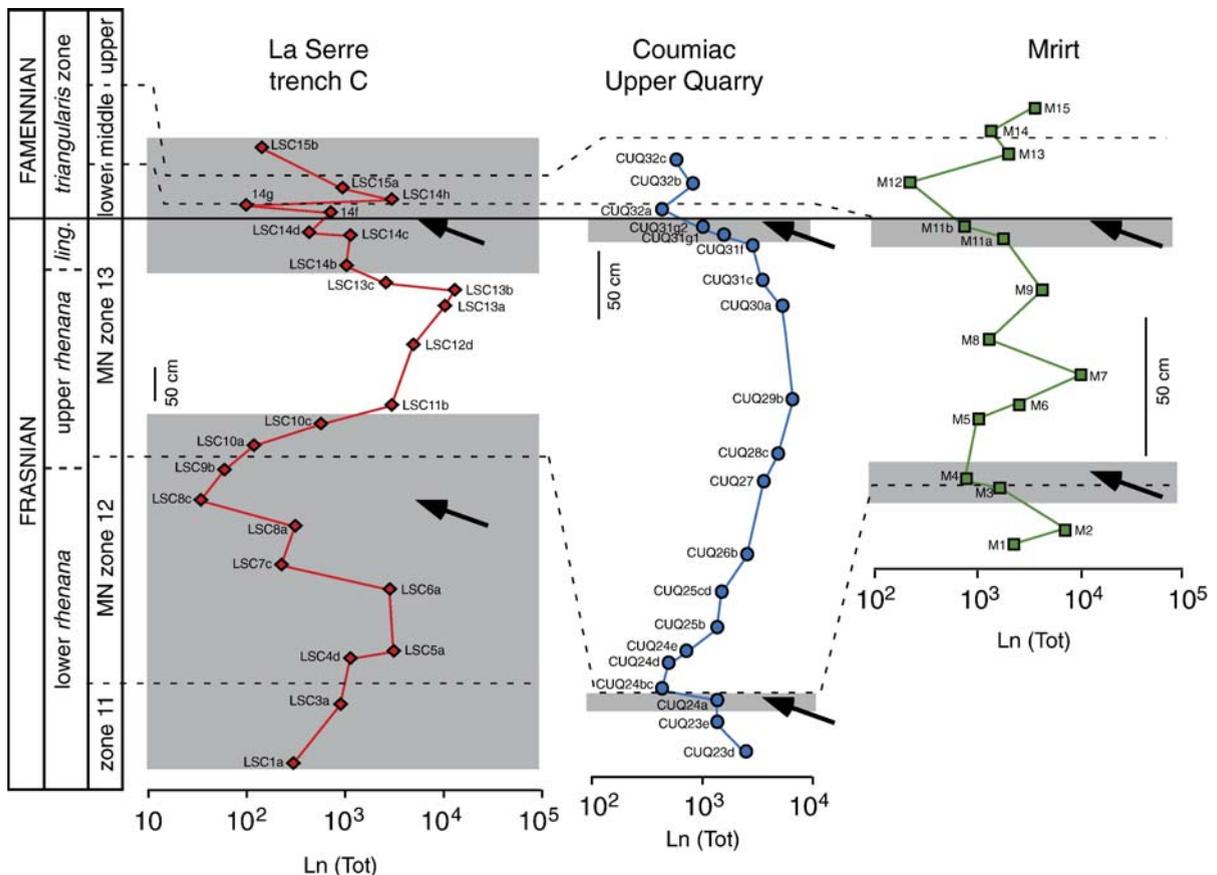

Fig. 2. Total number of platform conodonts per kilogram across the Frasnian/Famennian boundary of the La Serre and Coumiac sections (Montagne Noire, France) and the Mrirt section (Meseta, Morocco). The anoxic levels are in grey. The black arrows indicate the position of the top of the Lower and Upper Kellwasser events.

varies through time, especially during the Kellwasser events (Renaud and Girard, 1999; Girard et al., 2004). A morphometric quantification of its shape variations may thus provide a powerful tool for locating and correlating the events among sections.

The shape of each platform element was quantified using a Fourier analysis of its outline. A set of radii (i.e., the distance of each point to the center of gravity of the outline) is extracted from the x, y coordinates of equally spaced points along the outline. This set is expressed as a function of the distance along the circumference. This function is decomposed in successive trigonometric functions of decreasing wavelength (the harmonics) using Fourier methods (Renaud and Girard, 1999; Renaud and Michaux, 2003). The rank of the last harmonic to be considered has been estimated as the eleventh harmonic, corresponding to a good compromise between measurement error, the amount of information and the number of variables to be considered in subsequent analyses (Girard et al., 2004). Since each harmonic is weighted by two Fourier coefficients, each conodont outline is described by a set of 22 variables. Multivariate analyses are used to summarize these variables on few synthetic axes. In order

to best express the shape changes through time, a canonical analysis was computed. This procedure standardize the within-group variance and maximize the expression of the among-group variance, the group being the stratigraphic levels of the different sections. Associated with the canonical analysis, a multivariate analysis of variance (MANOVA) provides a test (Wilks Lambda) of whether these shape variations are significant.

5. Results

5.1. Absolute abundance

Conodont abundance is high during the Late Frasnian (Fig. 2) with more than 1000 platform conodont elements per kilogram. At the top of the MN zone 13, an abrupt decrease occurs in all sections, reaching a minimum in the lowermost Famennian, just above the top of the Upper Kellwasser horizon (grey band on Fig. 2) in Mrirt and Coumiac.

For these two sections, a similar decrease in abundance is observed at the top of the Lower Kellwasser horizon which coincides with the top of the LKE, at the
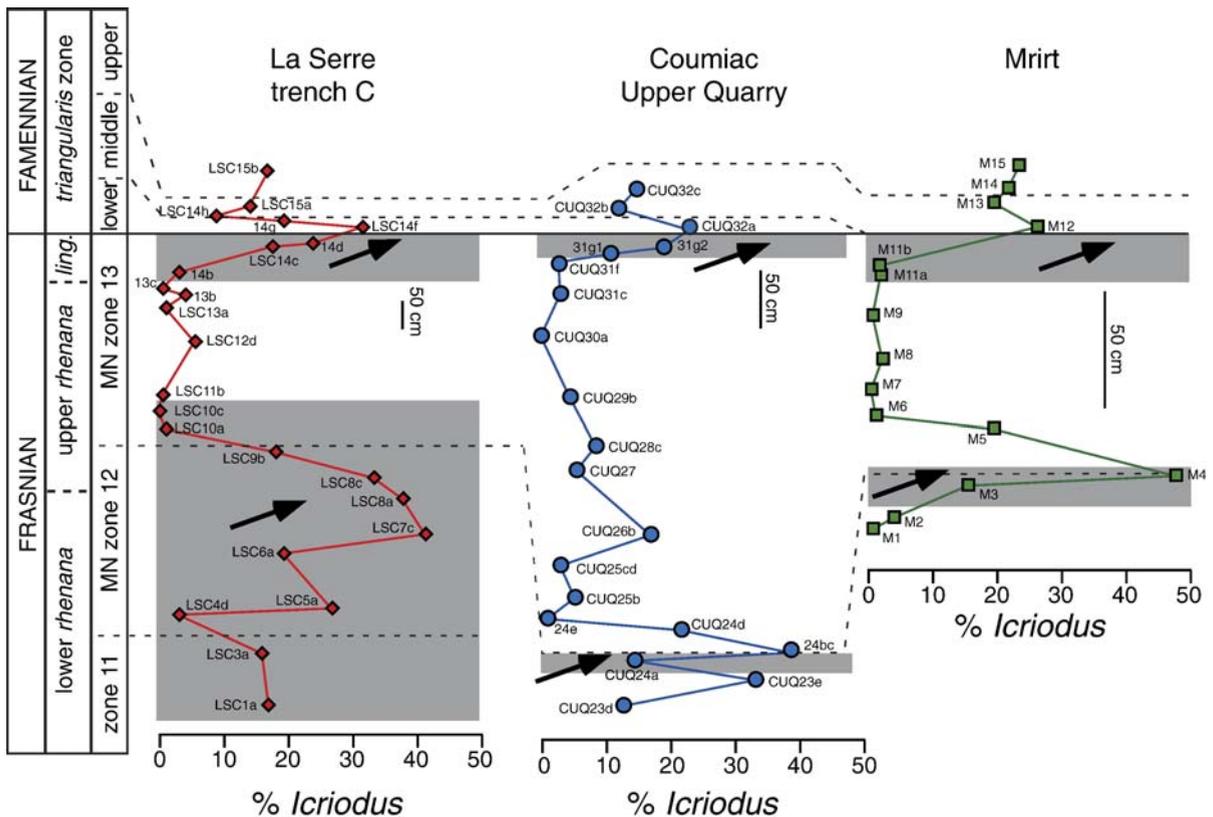

Fig. 3. Percentage of the genus *Icriodus* across the Frasnian/Famennian boundary of the La Serre and Coumiac sections (Montagne Noire, France) and the Mrirt section (Meseta, Morocco). The anoxic levels are in grey. The black arrows indicate the position of the top of the Lower and Upper Kellwasser events.

MN 12 - MN 13 boundary. At the La Serre section, a decrease in the platform conodont abundance occurs during the MN zone 12, reaching a minimum at the top of the MN zone 12 (LSC8c).

Based on these results, we tentatively correlated the events in the three sections as follows. The UKE (black arrows on Fig. 2) terminates just before the minimum in conodont abundance above the Frasnian/Famennian boundary. This interpreted end of the UKE coincides with the top of the Upper Kellwasser horizon in the two sections where it is identifiable based on facies changes (Coumiac UQ and Mrirt).

For these two sections, a minimum abundance is also observed just above the termination of the Lower Kellwasser horizon. Hence, we interpret the minimum of abundance at La Serre (between beds LSC8a and LSC8c) as the end of the LKE. Based on this correlation, a stratigraphic discrepancy emerges, the top of the LKE (LSC8c) occurring before the MN 12/13 boundary. This discrepancy may be due to the paucity of conodonts at La Serre C (Table 1), rendering the traditional conodont biostratigraphy unreliable. We tested the validity of this tentative correlation with other conodont-based approaches, described below.

5.2. Relative abundance

Four genera occur during the considered time interval, but most variations in relative abundance are due to the balance between the shallow-water *Icriodus* vs the other, deeper water genera. Hence, only the variations in the percentage of *Icriodus* are presented and discussed in detail. Complete data are shown in Tables 1, 2, and 3.

A peak in *Icriodus* percentage occurs at the F/F boundary and is associated with the end of the UKE at the F/F boundary in the three sections (Fig. 3).

Similarly, the LKE is associated with an earlier peak of *Icriodus* at Coumiac (peak at the end of the LKW horizon) and Mrirt (peak during the LKW horizon). This increase in the percentage of *Icriodus* is synchronous with the decrease in total abundance (Fig. 2) and can be used as an another marker signaling the end of the Lower Kellwasser event.

At La Serre, the peak of *Icriodus* is observed between LSC6a and LSC8c. These results corroborate the tentative correlation based on the peaks in total abundance rather than the biostratigraphic zonation, further invalidating the position of the previously defined MN 12–13 boundary.
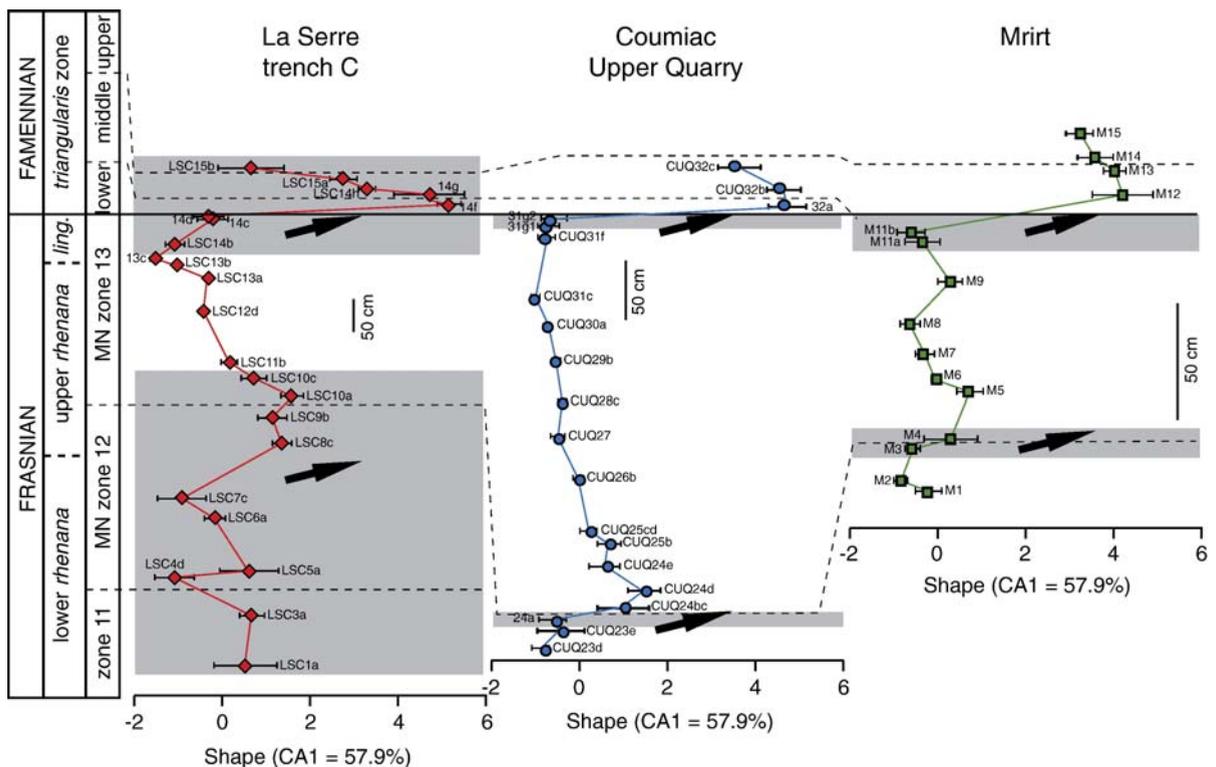

Fig. 4. Shape variability of the genus *Palmatolepis* represented by the first canonical axis (CA1) across the Frasnian/Famennian boundary of the La Serre and Coumiac sections (Montagne Noire, France) and the Mrirt section (Meseta, Morocco). The anoxic levels are in grey. The black arrows indicate the position of the top of the Lower and Upper Kellwasser events.
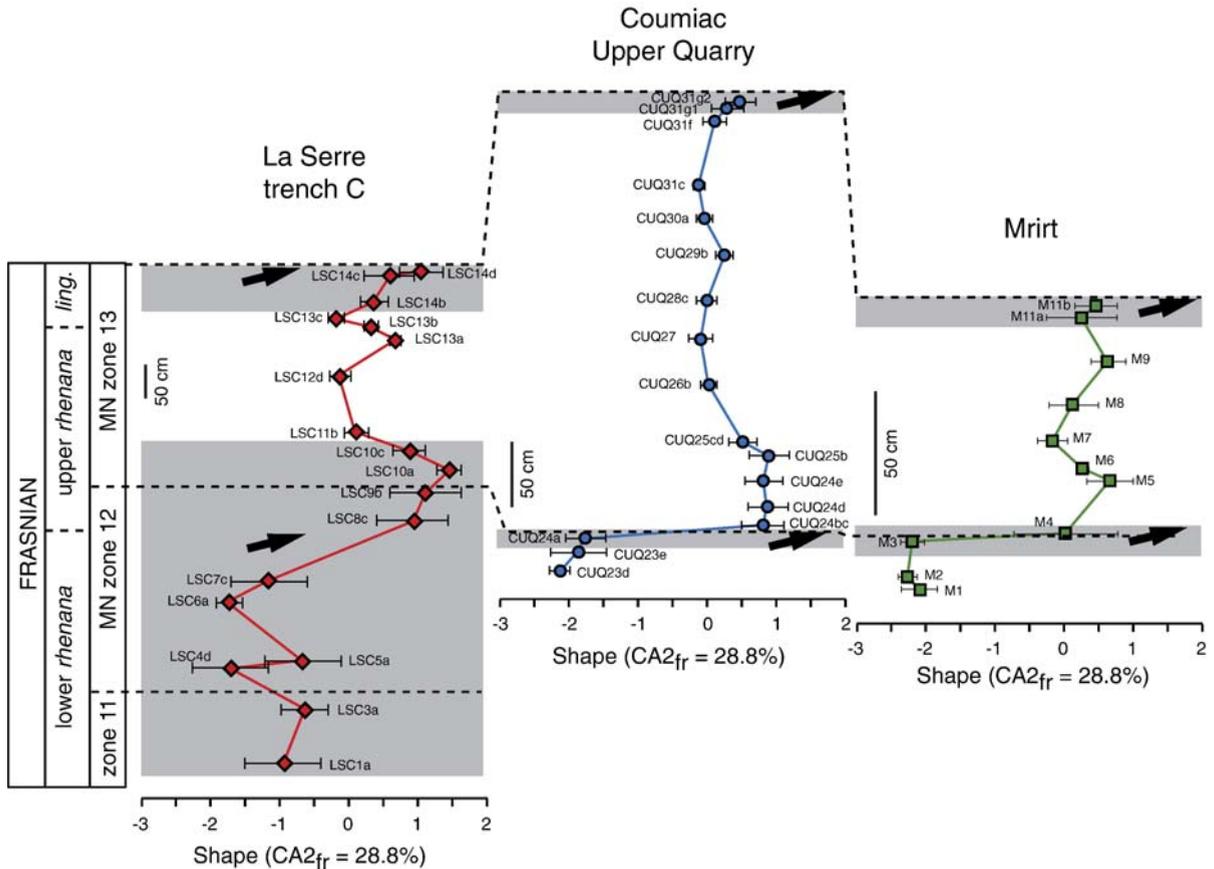
Fig. 5. Morphological variation of the genus *Palmatolepis* represented by the second canonical axis (CA2) for the Late Frasnian at the La Serre and Coumiac sections (Montagne Noire, France) and the Mrirt section (Meseta, Morocco). The anoxic levels are in grey. The black arrows indicate the position of the top of the Lower and Upper Kellwasser events.

5.3. Morphological changes of Palmatolepis

Significant shape change characterize the platform elements of *Palmatolepis* through the time interval (MANOVA: $P < 0.0001$). The first canonical axis (CA1) displays the most important morphological signal, representing 57.9% of the total among-group variance (Fig. 4). The strong similarity in trends among the three sections stresses that the shape changes occur through time rather than being the result of local, paleogeographic changes. The most obvious shift along CA1 occurs at the F/F boundary, synchronous to peaks in minimum of total abundance and maximum in *Icriodus* percentage.

At Coumiac and Mrirt, a shift occurs at the top of the LKW followed by a progressive return to pre-LKW values. At La Serre section, a similar morphological shift is also present between the levels LSC7c-8c. This supports the tentative location of the end of the LKE based on the conodont abundance (Fig. 2) and percentage of *Icriodus* (Fig. 3). However, the signal

associated with the F/F boundary is so strong that it overwhelms any other variation and largely obliterates the shape changes associated with the LKE.

These data were reanalysed excluding the Famennian levels to remove their effects. As expected, a signal associated with the LKE emerges on the first canonical axis (CA1$_{fr}$) representing 36.8% of the total variance. On the second canonical axis (CA2$_{fr}$), representing 28.8% of the total variance, the response to the LKE is more clearly expressed, with a shift towards positive values at the end of the Lower Kellwasser event (Fig. 5).

6. Discussion

6.1. Evidence of a synchronous LKE based on combined quantitative methods

High resolution stable isotope proxies are powerful tools for deciphering paleoenvironmental change including the processes leading to mass extinctions. Their

use, however relies on a robust biostratigraphy allowing accurate worldwide correlation. The traditional cono-dont biostratigraphy may not provide a timeframe accurate enough for the interpretation of these high resolution proxies and challenges the development of new methods for the correlation of Devonian sections.

An alternative to biostratigraphy is to correlate trends in the proxies themselves, an approach developed for the Late Devonian by Joachimski and Buggisch (1993, 2002) and Joachimski et al. (2004). They established the co-occurrence of the Kellwasser horizons and peaks in carbon isotopes in numerous sections and used this observation to correlate sections where the events were not identifiable by facies changes.

The limit of this approach is that it is based on a single geochemical proxy that may be locally altered by dia-genesis. More robust results may be obtained by combining different proxy trends. Our approach uses three trends based on conodont absolute abundance, relative abundance of genera, and morphometrics of one genus. The three methods provide very coherent results that allow the tentative location of the LKE at a section (La Serre) where the event cannot be identified by facies changes. All sections considered are located on the shelf of the north Gondwana, but data from the literature suggest that the approach may be valid worldwide. Biofacies data are available for the Upper Kellwasser in Laurentia (North America [Sandberg et al., 1988; Morrow, 2000], Baltica (South Poland [Racki et al., 2002]) and for other Gondwana sections (German Harz Mountains [Hüneke, 1995]). All sections yielded a maximum in *Icriodus* percentage just above the Frasnian/Famennian boundary, in agreement with our observations.

The three methods rely on the indirect response of organisms to environmental changes, which affect both absolute and relative abundance of genera with different environmental preferences. Shape changes of buccal elements are also likely related to environmental changes, although indirectly. Trophic disturbances have been suggested to explain the Kellwasser events (Racki et al., 2002). The resulting altered food chain might result in different prey for the conodont animal and hence select for different feeding apparatus shape (Streelman et al., 2003; Ward-Campbell et al., 2005). If so, our conodont-based changes should correlate with geochemical proxies and the combination of all should offer both, a robust basis for correlating outcrops in different environmental settings, and the potential for a better insight into the environmental processes responsible for the Kellwasser and F/F events.

Stable isotope trends of Joachimski and Buggisch (1993, 2002) and Joachimski et al. (2004) record an initial carbon and oxygen isotope shift near the base of

the upper *rhenana* zone (top of the MN12 zone) and a later shift at the end of the *linguiformis* zone (equivalent to top of MN 13). In sections where the Kellwasser horizons are lithologically expressed, the carbon and oxygen isotopes shifts coincide with anoxic facies changes (Joachimski and Buggisch, 1993; Joachimski et al., 2002) and agree with our conodont-based approaches.

This congruence suggests a need to reconsider previous results at La Serre. The $\delta^{13}C$ of organic carbon excursion at the Frasnian/Famennian boundary coin-cides with shifts in conodont-based proxies; all can be interpreted as marking the top of the Upper Kellwasser event. A second shift in carbon isotope (Joachimski, pers. com.) occurs from bed LSC7 to bed LSC10. This coincides with our data and supports the location of the LKE in this interval.

Geochemical and conodont-based approaches are thus congruent. Combining all the data shows that both, the LKE and the UKE occurred in various depositional contexts worldwide, since shifts either in isotopes or conodont-based estimators have been documented on the northwestern (this study; Joachimski et al., 2004) and northeastern (South China, Chen et al., 2005; Australia, Joachimski et al., 2002) shelves of the Gondwana, and on the Laurussia (Joachimski et al., 2002). The Kellwasser events appear thus to be the product of environmental perturbations in epicontinen-tal seas that were global and synchronous.

6.2. Implications for the proposed scenarios of the Kellwasser events

Our results have important implications for reconsi-dering scenarii proposed for the Kellwasser events be-cause the environmental scenario rely on biostratigraphic interpretations. Outcrops like La Serre have often been sampled because of close proximity to the stratotype in a different environmental setting. In such depositional environment, however, some sections are very poor in conodonts making it difficult to constrain the stratigraphic position of the base of the upper *rhenana* zone.

There are numerous consequences of the biostrati-graphic mismatch. Bond et al. (2004) located the LKE during the upper *rhenana* zone (LSC 11–12–13), placing it in carbonate deposits. They concluded that this event coincided with an increase in oxygenation levels in basins such as La Serre and Kowala (Poland) sections. This correlation lead to the idea that the LKE was not expressed in basinal environments and that the event was limited to shallow water environments (Riquier et al., 2006). The apparent geographically limited extent of the Lower Kellwasser event would

explain its minor impact on the fauna (Bond et al., 2004).

An alternative interpretation, supported by our results and those from the carbon isotope trends (Joachimski et al., 2002, 2004) is to locate the LKE in anoxic deposits (LSC8). According to this interpretation, environmental and faunal shifts associated with both Kellwasser events were similar in the different depositional settings (oxygenated platforms and basins).

An intriguing discrepancy remains when comparing both events; despite quite similar isotopic signals, faunal change during the LKE was less than during the UKE, as pointed by the global faunal turn-over at the Frasnian/Famennian boundary, and the dramatic shift in *Palmatolepis* shape.

The paradox can be explained in two ways. First, despite oxygen and carbon isotope signals of similar amplitude and common trends in detritialinput, nutrient availability and hydrothermal activity (Pujol et al., 2006),

the LKE and UKE might have been the results of different processes (Riquier et al., 2006).

Alternatively, based on the similarity of the isotope signature of both events both the LKE and the UKE could have resulted from the same environmental changes, namely a climatic cooling (Joachimski and Buggisch, 2002). In this case, the paradox of a higher impact of the UKE on the faunas despite similar environmental perturbations remains. We propose that part of the environmental signal at the end of the Upper Kellwasser event might be missing (Fig. 6). The Kellwasser events are not only characterized by repeated and significant temperature changes, but are also known to be associated with rapid sea-level changes (Johnson et al., 1985). Fe-oxide crusts, representing reduced sedimentation rates, occur at several F/F boundary sections including Coumiac (Girard and Feist, 1996), Mrirt (Lazreq, 1992), Germany (Devleeschouwer et al., 2002; Piecha, 2002), Poland (Racki et al., 2002). They may represent extreme
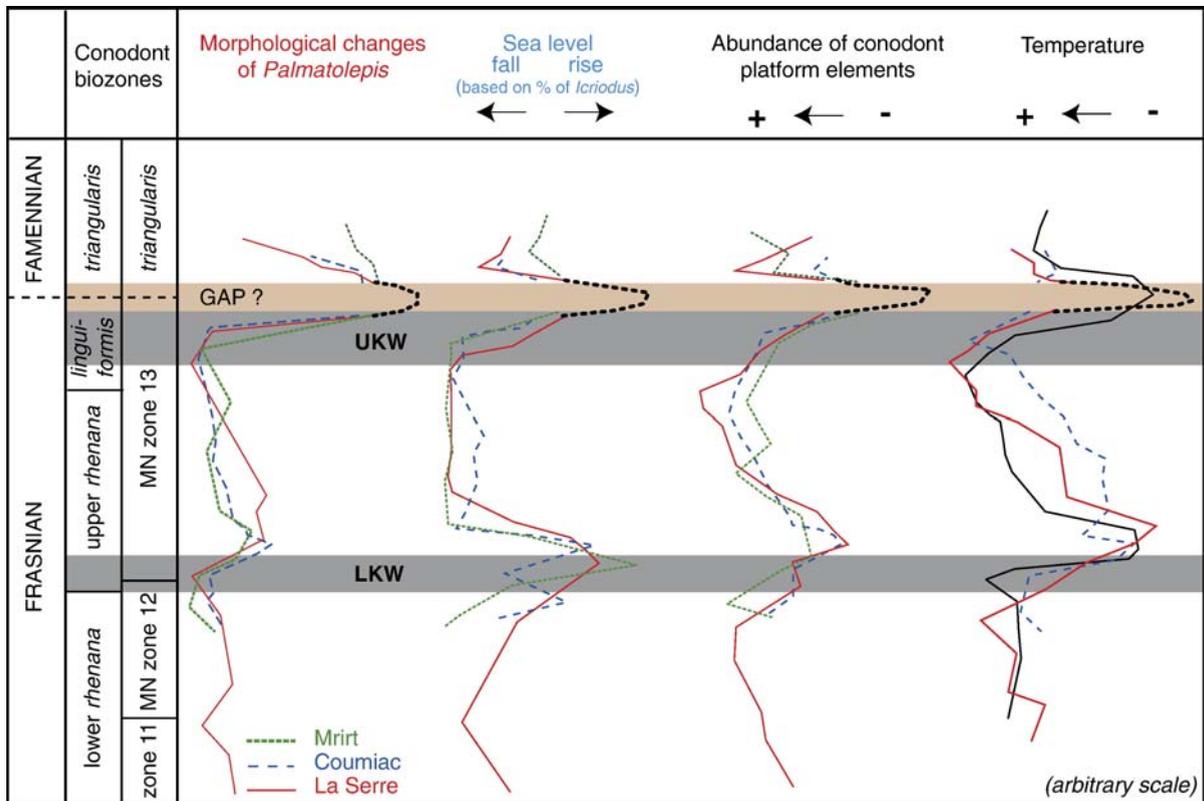

Fig. 6. Schematic variations of proxies for environment and biological response during the Kellwasser period. Black thick dotted lines=hypothetical Upper Kellwasser maximum excursion supposedly obscured by a gap in the record. From left to right (1) simplified morphometric variation of the conodont genus *Palmatolepis*, (2) variation of sea level based on the percentage of the conodont genus *Icriodus*, (3) total number of conodont platform elements (inverse scale), (4) variation in sea-surface temperature based on conodont apatite $\delta^{18}O$ (black line: composite data from Joachimski and Buggisch (2002); red and dashed blue lines: unpublished data of La Serre and Coumiac respectively). The anoxic levels are in grey. UKW=Upper Kellwasser, LKW=Lower Kellwasser. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

sedimentary condensation but slowed and microstromatolitic (Préat et al., 1998) submarine sedimentation continues during crust formation. At Coumiac the origin of the crust at the F/F boundary is controversially discussed (Sandberg et al., 1988: subaerial; House et al., 2000: submarine), but always associated with an abrupt sea-level fall suggesting that the sea-level changes were more important during the UKE than the LKE, eventually leading to a hiatus at the end of the UKE. In the La Serre section, the crucial LSC14e level (just before the Frasnian/Famennian boundary) is devoid of well preserved conodonts, which hindered morphometric and conodont-based geochemical analyses. This same lack of conodonts, however, suggests modified depositional conditions.

In conclusion, we suggest that the Late Devonian Lower and Upper Kellwasser events were global and synchronous. Whether they resulted from similar environmental perturbations of different amplitudes, or from different processes, remains to be elucidated. Further detailed paleoenvironmental studies are needed, whose interpretation will rely on a reliable and accurate stratigraphic correlation. In this context, our approach combining several quantitative conodont-based estimators may constitute a powerful tool.

Acknowledgments

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