Record of climate-driven morphological changes in 376 Ma Devonian fossils

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ABSTRACT

The Lower and Upper Kellwasser horizons represent two anoxic events that mark the mass extinction at the Frasnian-Famennian (F-F) boundary. Among other groups, conodont animals were severely affected, but the genus *Palmatolepis* survived with a complete turnover at the F-F boundary. Here the fine morphological variations of the genus *Palmatolepis* and the sea-surface temperature evolution are quantified in two F-F boundary sections using morphometrics and oxygen isotopic composition of apatite, respectively. In accordance with other F-F sections, the isotope records show two positive excursions of ~1‰ during the Lower and Upper Kellwasser anoxic events. The conodont shape and the oxygen isotopic composition of the genus *Palmatolepis* are significantly correlated within the Frasnian and Famennian Stages, suggesting a strong environmental influence on the morphology of the feeding apparatus of the conodont animal. We propose that the morphological differences are linked to changes in the trophic position of *Palmatolepis*: enhanced organic carbon burial, which is supported by global positive carbon isotope excursions in inorganic and organic carbon during both the Lower and Upper Kellwasser events altered the primary biomass production and thus, the subsequent nutrient supply to higher trophic levels. While the carbon and oxygen isotopic shifts are of similar amplitude during Lower and Upper Kellwasser events, the variation of the shape of *Palmatolepis* during the Upper Kellwasser, i.e., the F-F boundary, is more pronounced than during the Lower Kellwasser.

INTRODUCTION

The Late Devonian time interval was characterized by a series of environmental perturbations, the largest of which marks the Frasnian-Famennian (F-F) boundary. This F-F crisis primarily affected the marine community in low-latitude ecosystems (McGhee, 1996), and was consistent with two marine anoxic events known as the Lower and Upper Kellwasser horizons (Buggisch, 1991). The top of the Upper Kellwasser marks the F-F boundary and is associated with major extinction pulses.

Both events display similar depositional facies and share similar paleoenvironmental signatures. Carbon stable isotope data suggest that each Kellwasser event coincided with a phase of enhanced organic carbon burial translated in positive carbon isotope excursions of ~3‰ both in inorganic and organic fractions (Buggisch and Joachimski, 2006; Chen et al., 2005; Joachimski et al., 2001, 2002; Savage et al., 2006). For comparison, the amplitude of the inorganic and organic carbon isotope variation at the Cenomanian-Turonian boundary is only 2‰ (Arthur et al., 1988). Each Kellwasser event also coincides with increased carbonate $^{87}Sr/^{86}Sr$ ratios (Chen et al., 2005), supporting the hypothesis of intensified continental weathering and enhanced burial of marine organic carbon. Finally, each Kellwasser event records a positive oxygen isotope excursion in conodont apatite ($\delta^{18}O_p$), indicating that climatic cooling was the ultimate consequence of the organic carbon burial and lowering of atmospheric CO_2 (Joachimski and Buggisch, 2002).

The mechanisms that strongly depleted the marine biodiversity at low latitude as well as the rhythm of the extinction pulses that characterize the F-F boundary are debated (e.g., Racki, 2005). This aspect of the biotic response points to another unsolved paradox regarding this period: the paleoenvironmental signatures of the Lower and Upper Kellwasser events appear to be very similar, whereas their respective impacts on the biosphere were dramatically different (McGhee, 1996).

Conodonts, extinct animals related to early vertebrates (Briggs, 1992; Donoghue and Purnell, 1999; Purnell, 1995), are among the most common Devonian pelagic fossils. The fossilized parts of this animal are conodont elements, millimeter-sized remains composed of fluorapatite interpreted as tooth-like jaw elements (Purnell and von Bitter, 1992), which support the hypothesis that it was not a suspensivorous animal, but instead a macrophagous predator and/or scavenger. The genus *Palmatolepis* is the major representative of the Late Devonian conodont pelagic fauna (Seddon and Sweet, 1971).

This study focuses on potential correlations between geochemical and morphometric changes in the conodont genus *Palmatolepis* across the upper Frasnian and the lower Famennian, testing the hypothesis that rates of morphological changes are correlated with rates of environmental changes recorded in the $\delta^{18}O_p$ of conodonts.

MATERIAL AND METHODS

Two F-F boundary sections (376.1 ± 3.6 Ma; Kaufmann, 2006) were studied in the Montagne Noire (southern France). The Coumiac section represents the stratotype for the F-F boundary and exposes light-colored micritic limestones. The Kellwasser horizons are represented by two dark gray limestone horizons, the F-F boundary coinciding with the top of the Upper Kellwasser (Klapper et al., 1993). In contrast, anoxic conditions prevailed during most of the period at the La Serre trench C section. This resulted in a prolonged deposition of black organic carbon–rich limestones and marls. As a consequence, the Kellwasser horizons cannot be identified lithologically at the La Serre section. The F-F boundary is recognized based on the faunal turnover, and top of the Lower Kellwasser horizon has been identified using quantitative conodont-based approaches (Girard and Renaud, 2007). The undisturbed, thinly laminated, fine-grained sediments indicate a quiet poorly oxygenated depositional environment.

All *Palmatolepis* elements present in the rock samples were considered independently of their taxonomic assignment (Girard et al., 2004). The platform shape was considered as a valuable description of the element overall shape. The corresponding outline was quantified using a radial Fourier transform (Renaud and Girard, 1999). Each conodont outline is described by a set of 22 Fourier coefficients that, once standardized by size, represent shape descriptors.

Multivariate analyses were conducted on these variables in order to express the morphological variance on a small number of axes. Canonical analyses were chosen in order to focus on the variation among

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stratigraphic levels. Multivariate analyses of variance allowed testing of the statistical significance of these changes.

Oxygen isotope analyses were performed on conodont apatite following the methods described in Joachimski et al. (2004). All values are reported in the conventional delta notation in per mil relative to Vienna standard mean ocean water. The overall reproducibility determined by replicate analyses of standards and conodont samples was better than ±0.2‰ (1σ).

RESULTS

Conodont shape varies significantly in both sections and through time ($P < 0.001$; Fig. 1). The patterns of variation are remarkably similar in both sections. A major morphological shift marks the F-F boundary. This change corresponds to a transition from elongated to triangular conodont elements (Fig. 1). In contrast, the Frasnian period preceding the F-F boundary is marked by a relative stability in shape with a minor shift associated with the Lower Kellwasser horizon.

Oxygen isotope composition of conodont apatite shows similar trends in both sections (Fig. 1), but the $\delta^{18}O_p$ values from the Coumiac section are always higher than those from La Serre (i.e., by ~3 °C). The difference is on average +1‰, but decreases to +0.5‰ in the early Famennian. The $\delta^{18}O_p$ values at the Coumiac section show that the Lower and Upper Kellwasser horizons are characterized by an increase of 1.1‰ and 0.8‰, respectively. The $\delta^{18}O_p$ values at the La Serre section increase by 1.5‰ at the Lower Kellwasser and 1‰ at the Upper Kellwasser. Between the two Kellwasser horizons, $\delta^{18}O_p$ values gradually decrease and reach a minimum at the base of the Upper Kellwasser.

Three features emerge from the comparison of both data sets (Fig. 2). (1) The results of both sections are comparable. (2) Conodont shape during the Famennian was different from that of the Frasnian. (3) During each time interval the morphometrical data vary linearly with the oxygen isotope ratios. Linear regression indicates a significant correlation for the Frasnian ($n = 34$, $R = 0.504$, $P = 0.002$) and a correlation close to the significant probability of 0.05 for the Famennian despite the limited number of samples ($n = 7$, $R = 0.740$, $P = 0.06$). The relationships are confirmed using a nonparametric test (Kendall test of concordance; Kendall, 1962) that provides more robust results for small samples (Frasnian: $P < 0.001$; Famennian: $P = 0.008$).

DISCUSSION

The $\delta^{18}O_p$ of conodonts, as for fish apatite, is a function of the seawater temperature during mineralization and the oxygen isotope composition of seawater (Kolodny et al., 1983; Luz et al., 1984; Trotter et al., 2008). However, the interpretation of $\delta^{18}O_p$ in terms of paleotemperature ultimately requires that the primary isotopic signal did not reequilibrate (even partially) with burial pore fluids or meteoritic water during diagenesis. At Coumiac and La Serre, the rare earth elements of conodonts are bell shaped (Girard and Albarède, 1996), a pattern interpreted by Reynard et al. (1999) as a consequence of extensive diagenesis. Here, the relationship between the conodont morphology and the $\delta^{18}O_p$ values cannot be explained by any known diagenetic process. Moreover, while it cannot be ascertained that the $\delta^{18}O_p$ values were not slightly shifted by diagenesis, we consider that the overall trend of $\delta^{18}O_p$ is still preserved.

Using the equation of Kolodny et al. (1983), the positive $\delta^{18}O$ shifts at the Lower and Upper Kellwasser horizons translate into cooling at low latitudes by 4–7 and 3–4 °C, respectively. The $\delta^{18}O$ records reported in this study compare particularly well with the results published by Joachimski and Buggisch (2002) for two F-F sections in Germany (Fig. 3). The $\delta^{18}O$ values of the *P. linguiformis* zone as well as the amplitudes of the $\delta^{18}O$ excursion during the Lower Kellwasser are comparable in the four sections, whereas the amplitudes of the $\delta^{18}O$ excursion during the Upper Kellwasser are lower at La Serre and Coumiac than at Beringhausen and Vogelsberg (Fig. 3). The amplitude of temperature of these two cooling events is comparable to the range of sea-surface temperatures recorded during the last glacial-interglacial transition at low to

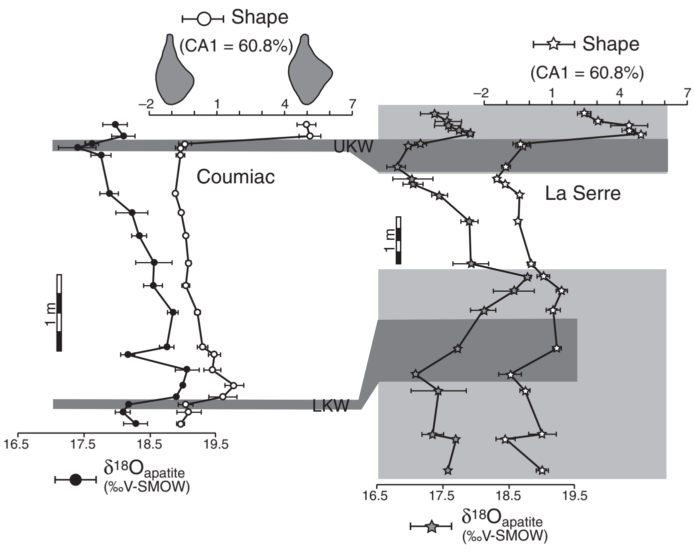

Figure 1. Shape changes of conodont *Palmatolepis* and variation of apatite phosphate oxygen isotope ratios through time at Coumiac (left) and La Serre (right) sections. The $\delta^{18}O$ of seawater is set at –1‰ (Joachimski and Buggisch, 2002). Shapes of conodont elements were quantified using Fourier analysis of platform outline. Synthetic shape axis is the first canonical axis (CA1, 60.8% of the among-group variance) of analysis on Fourier coefficients (grouping factor in canonical analysis: stratigraphic level per section). Symbols represent average value per level; error bars correspond to 95% confidence interval. Reconstructed outlines allow a visualization of shape changes along CA1 and correspond to CA1 = –1 (left) and CA1 = 5 (right). Anoxic levels are in dark gray; anoxic facies are in light gray. LKW—Lower Kellwasser; UKW—Upper Kellwasser; V-SMOW—Vienna standard mean ocean water.

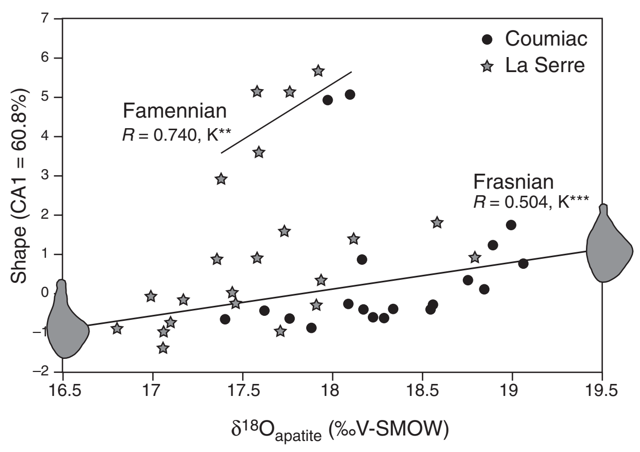

Figure 2. Relationship between $\delta^{18}O$ and shape variations of conodont elements for Coumiac and La Serre sections. Solid lines correspond to linear regressions of $\delta^{18}O$ versus CA1 (first canonical axis) for Frasnian ($P = 0.002$) and Famennian ($P = 0.057$). Coefficient of linear regression is indicated (R) as well as significance threshold given by Kendall (1962) coefficient of concordance (K). Shape changes involved along Frasnian correlation are visualized using multivariate regression of Fourier coefficients on oxygen isotope values ($P = 0.0008$). V-SMOW—Vienna standard mean ocean water.

middle latitudes (deMenocal et al., 2000; Pahnke et al., 2003; Weldeab et al., 2007). Nevertheless, the new oxygen isotope data further support the earlier interpretation of two global cooling pulses during the latest Frasnian. Enhanced burial of organic carbon and subsequent lowering of atmospheric CO_2 levels during the deposition of the Kellwasser horizons as suggested by the positive excursions in $\delta^{13}C$ of carbonate (Fig. 3) have probably been at the onset of these cooling episodes. The compilation of $\delta^{13}C$ data through the F-F boundary (Fig. 3) shows that the maximum of the $\delta^{13}C$ excursion during the Lower Kellwasser corresponds to the upper part of the anoxic event. In spite of the uncertainties on the duration of the upper *P. rhenana* zone, it can be deduced that the maximum of the Lower Kellwasser $\delta^{13}C$ excursion took place ~500 k.y. after the beginning of the anoxic event. However, the shift in the shape change of conodonts seems to have occurred before the $\delta^{13}C$ excursion (Fig. 3).

We propose that the shape evolution of the conodont *Palmatolepis* during both Kellwasser events was not driven by a modification of the seawater temperature, which was the consequence of the organic carbon burial, but instead by a change of the nutrient availability. Accelerated continental runoff due to the spread of rooted plants to upland areas (Berner, 1997), leading to a turnover in the structure of the phytoplankton community, eutrophication, and further anoxia (Fig. 3), constitute a commonly accepted scenario for the Kellwasser events (Joachimski et al., 2002; Murphy et al., 2000, 2001; Racki and Wignall, 2001; Schwark and Empt, 2006). However, productivity variations can have profound effects on the abundance and the structure of higher trophic levels. As predicted by food chain models (Abrams, 1993) and verified using mesocosm, i.e., experimental marine enclosure (e.g., Hulot et al., 2000; Leibold and Wilbur, 1992), the increase of productivity before the Kellwasser events most probably affected nutrient transfers up to autotroph organisms, primary consumers, and conodonts, i.e., secondary consumers. Because conodont elements were part of a feeding apparatus, slight changes in the composition of the diet might have initiated subtle changes in the shape of the elements. Such effects have been demonstrated for various modern organisms (Streelman et al., 2003; Ward-Campbell et al., 2005).

A progressive and reversible shape change is observed in response to gradual environmental changes around the Kellwasser events recorded by carbon and oxygen isotopes. Such back and forth shape changes may be interpreted as a plastic response. The nature of the response, however, seems to have been very different for the Lower and Upper Kellwasser horizons, suggesting various underlying evolutionary processes. It is likely that a profound change occurred in the *Palmatolepis* genetic background at the F-F boundary, a hypothesis in agreement with the complete turnover of the taxonomic entities recognized within this genus. A morphological response was also observed concerning the conodont genus *Icriodus* (Girard and Renaud, 2007). However, the response of these genera to minor perturbations was not the key to their survival to the F-F crisis, because the genus *Ancyrodella*, which also underwent small morphological changes during the Lower Kellwasser, went extinct at the F-F boundary (Girard and Renaud, 2008).

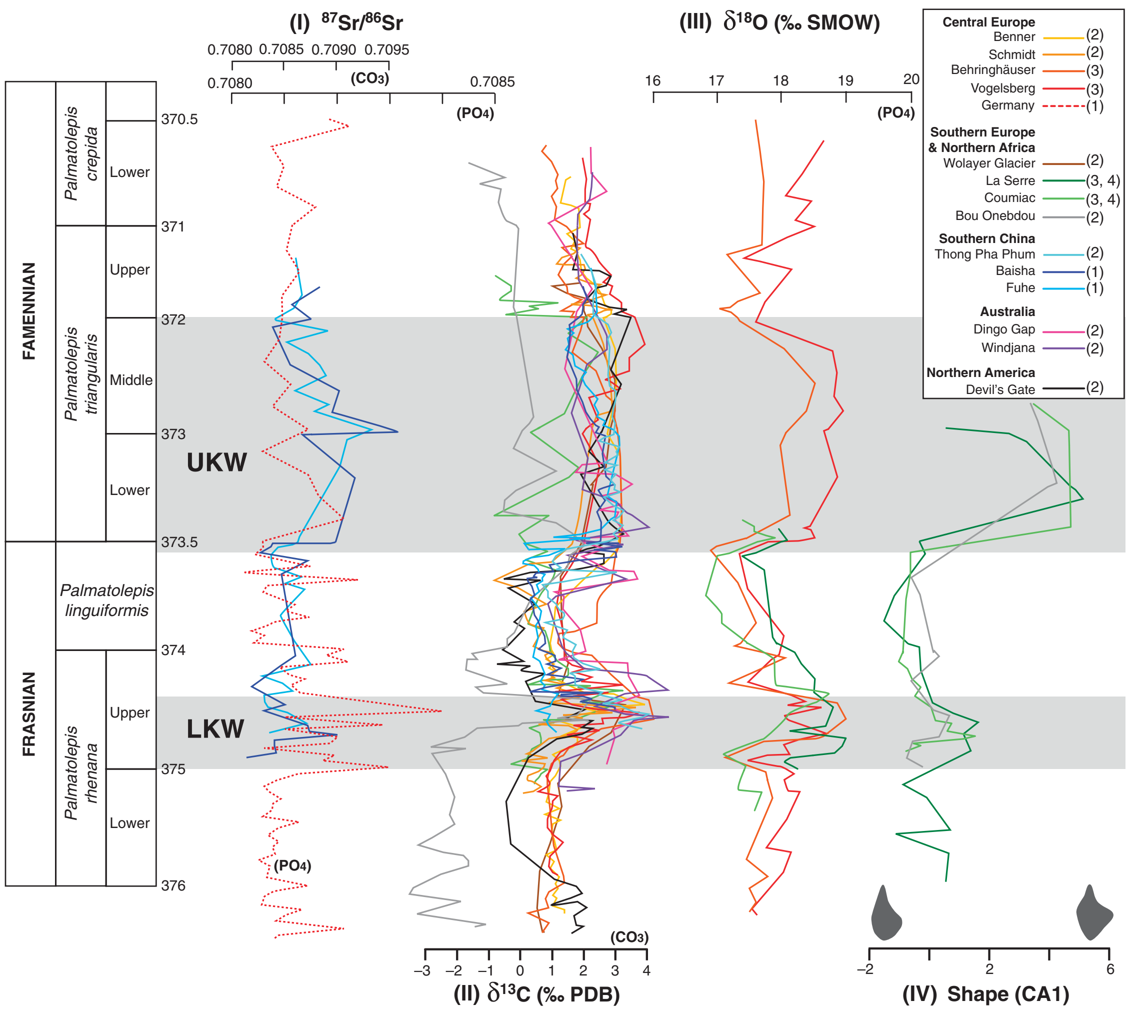

Figure 3. Comparison of variations in (I) calcite and apatite strontium isotope composition, (II) inorganic carbon isotope composition, (III) apatite oxygen isotope composition, and (IV) shape of conodont *Palmatolepis* during Late Devonian, illustrating enhanced continental runoff and organic carbon burial, decreasing seawater temperature, and morphological changes during Lower and Upper Kellwasser events (LKW and UKW, respectively). Time scale with equivalent intervals used for reference is from Buggisch and Joachimski (2006). Data that do not include both Kellwasser events are not considered. Dashed lines indicate phosphate, whereas solid lines indicate carbonate. (1) Data are from Veizer et al. (1999) and Chen et al. (2005). (2) Data are from Joachimski and Buggisch (1993, 2002), Joachimski et al. (2002), Stephens and Sumner (2003), Chen et al. (2005), and Savage et al. (2006). (3) Data are from Joachimski and Buggisch (2002) and this work. (4) Data are from this work. SMOW—standard mean ocean water; PDB—Peedee belemnite.

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