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Strategies of survival during extreme environmental perturbations: evolution of conodonts in response to the Kellwasser crisis (Upper Devonian)

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Abstract

The size and shape evolution of two conodont genera surviving the Kellwasser period, *Icriodus* and *Palmatolepis*, has been quantified using a Fourier analysis of the outline of platform elements. Morphological variations of both genera in response to environmental fluctuations are comparable, although slightly shifted in time, suggesting a differential sensitivity to the environmental variations due to differences in favored habitats. The period of the crisis comprises two anoxic events of increasing importance and impact on the biosphere. For each event, the post-crisis conodont elements are smaller than those found before and exhibit extreme morphs, while the recovery period is characterized by an increase in size and inverse changes in shape; morphological trends are expressed with a lower amplitude during the first anoxic event. Strategies of morphological response are different for the two genera, implying heterochronic shifts or changes in the developmental pathway. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Ecosystems have undergone major crises characterized by mass extinctions at different times in Earth's history. The causes of these crises may vary, but their consequences on ecosystems generally comprise three possible phases: extinction, survival and recovery. The consequence of such events on the biosphere has been considered mainly from a stratigraphic point of view as a sequence of extinctions

and appearances of species (Raup and Sepkoski, 1982; Sepkoski, 1982). Such an approach emphasizes the catastrophic aspect of a mass-extinction event by neglecting the possible phylogenetic relationships between the pre- and post-crisis species, and by focusing on the crisis period only.

However, understanding of how an ecosystem reacts to extreme environmental pressure requires assessment of the different possible strategies of survival and recovery. For this purpose, the detailed response of organisms to environmental variations must be studied, and compared with patterns shown during undisturbed periods. In order to assess the role of adaptation of the different species in their

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survival of any crisis, their response to the crisis should be compared to their response to an event of the same type but of less amplitude and consequence to the biosphere.

For this purpose, we have focused on the Kellwasser crisis characterizing the Frasnian/Famennian boundary. This period is known to be one of the seven most important extinction events in the Earth's history (Walliser, 1996). The Kellwasser period was characterized by global anoxic events that strongly affected the biosphere. The environmental perturbation comprises two anoxic levels, the Lower and Upper Kellwasser (Schindler, 1990). The Lower Kellwasser event seems to start the late Frasnian period of biotic crisis, with a drop in diversity in several benthic trilobites families (Feist and Schindler, 1994) as well as in other groups (Schindler, 1990; Becker, 1993). However, most of the extinctions occurred during the Upper Kellwasser and reached a maximum at the Frasnian/Famennian boundary (McLaren, 1970; Walliser, 1996).

Several studies have allowed the environmental variations that characterize the Kellwasser crisis to be assessed. The anoxic events were probably due to an episodic oscillation of the oceanic oxygen minimum associated with eustatic sea-level fluctuations, but the factors which have triggered the Upper Kellwasser mass-extinction remain controversial in spite of many studies and hypotheses (Walliser, 1996 and references therein). The duration of the Upper Kellwasser event has been estimated as about 12,500 yr (Sandberg et al., 1988), and the whole Kellwasser period would correspond to about 100,000 yr (Schindler, 1990).

In order to study the detailed response of organisms to these environmental variations, conodonts were selected because they are abundant, well known and characterized by a rapid evolution at this time (Ziegler and Sandberg, 1990). We concentrated on two conodont genera which survived the crisis with different strategies. *Icriodus* (Fig. 1A) provides one of the few examples of a genus surviving the Upper Kellwasser crisis without any major change. In contrast, all species of *Palmatolepis* (Fig. 1B) were replaced during the Upper Kellwasser crisis. These conodonts are considered to have been dependent on water depth, *Palmatolepis* being dominant in deep-water environments while the proportion

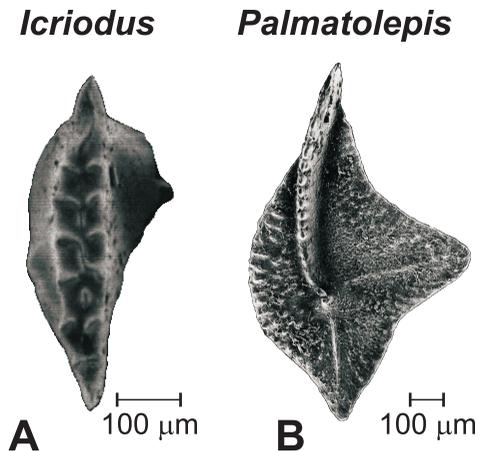


Fig. 1. Examples of the two genera considered in this study. (A) *Icriodus alternatus*. (B) *Palmatolepis praetriangularis*.

of *Icriodus* increases in shallow-water environments (Seddon and Sweet, 1971; Sandberg, 1976; Sandberg et al., 1988).

The size and shape of representatives of these genera have been quantified using an outline analysis based on a Fourier transform method, and their variations compared through the Kellwasser crisis in order to decipher evolutionary strategies of the two genera.

2. Geological setting

The Coumiac Upper Quarry in the Montagne Noire, France (Fig. 2) allows high-resolution sampling of the whole period around the Frasnian/Famennian boundary, i.e. the Kellwasser crisis and the recovery period following it. This section corresponds to an outer-shelf environment, with condensed, oxidized carbonate sedimentation deposited on a submarine rise (Feist, 1985; Feist and Klapper, 1985). The anoxic events are represented by the intercalation of two dark gray coarse limestone beds in the otherwise normally oxygenated sequence.

The Upper Coumiac Quarry (Fig. 3) has been carefully studied, but only the levels immediately adjacent to the Upper Kellwasser event have been studied in detail. The levels prior to the Upper Kellwasser seem to correspond to a progressive increase in water depth, while the end of the Upper Kellwasser can be

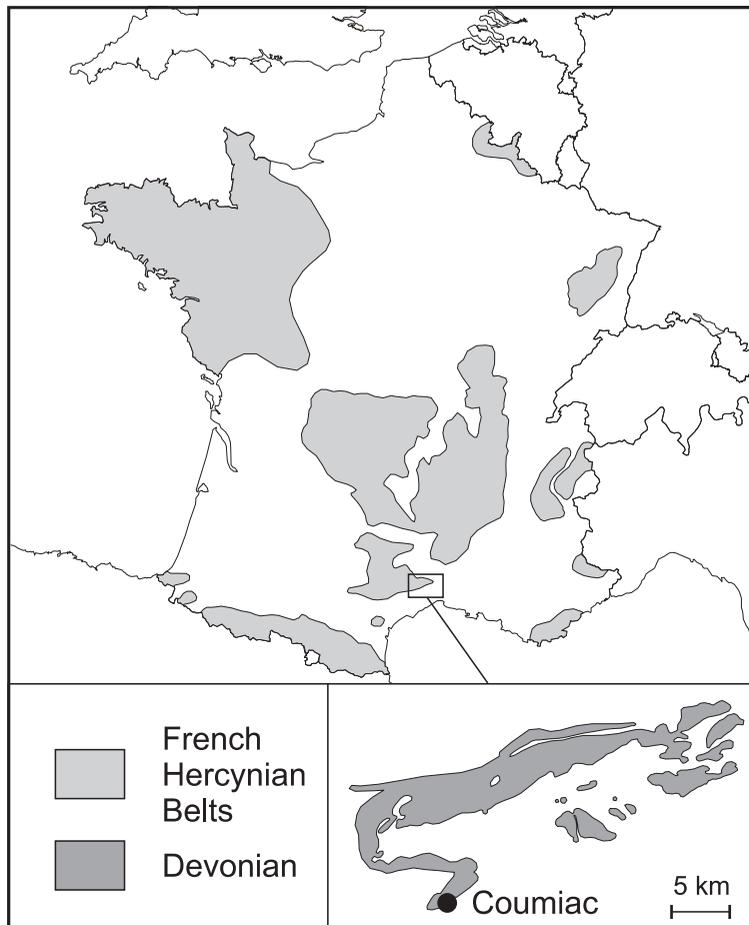


Fig. 2. Geological setting of Hercynian belts in France and location of the Coumiac Quarry.

interpreted to represent a sudden, large fall in sea level followed by a transgressive trend during the first Famennian levels (Girard and Feist, 1997). According to geochemical data, the Upper Kellwasser crisis was also associated with a reduction of exchange between deep-sea and continental margin waters and, in consequence, a nearly stagnant ocean during the crisis (Girard and Albarède, 1996).

3. Material and methods

3.1. Material

The conodont animal possessed a complex feeding apparatus composed of several paired or sym-

metrical elements of different types (Sweet, 1981; Briggs et al., 1983; Aldridge et al., 1987). Some attempts have been made to reconstruct the whole apparatus of Frasnian and Famennian species of conodonts on the basis of preserved clusters of elements and consistent associations, and base the taxonomy on these multi-elements reconstructions (e.g. Klapper and Foster, 1986, 1993; Schülke, 1997). It is, however, relevant here to focus on shape changes in the most rapidly evolving elements, the platforms (Pa elements) (see e.g. Nicoll, 1987).

For the present study, 11 levels have been sampled in the Coumiac Upper Quarry (Fig. 3), with closest sampling through the interval of maximum turnover of species. The number of conodonts collected for each genus, species, and level considered

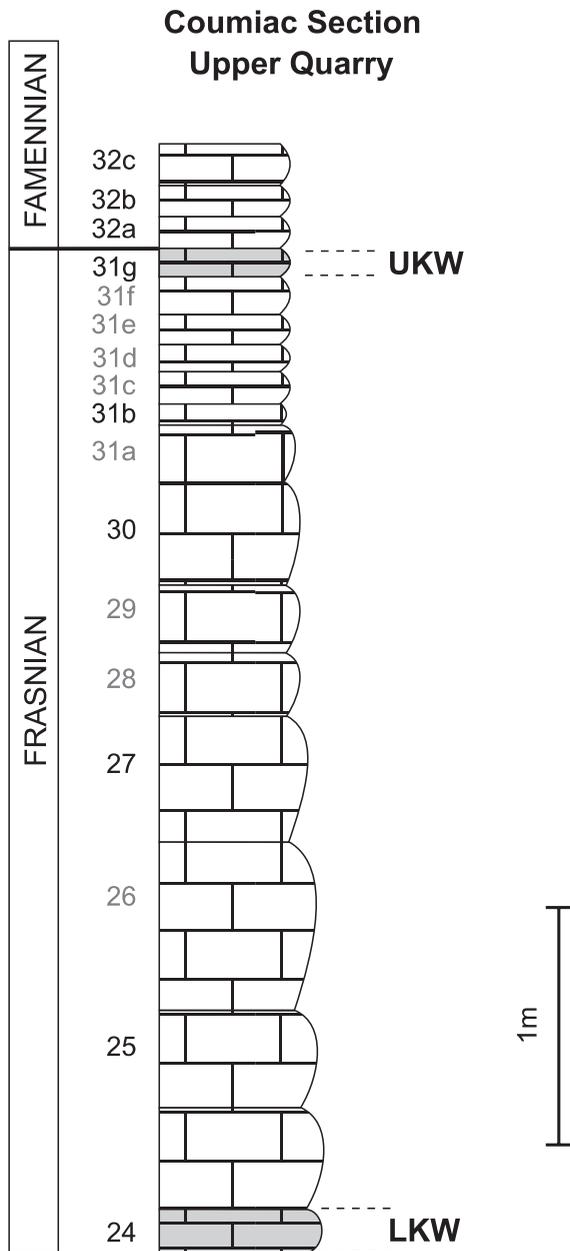


Fig. 3. Stratigraphic column of the Upper Quarry in Coumiac. Levels in grey are the two anoxic events. LKW = Lower Kellwasser; UKW = Upper Kellwasser. Numbers in grey indicate the levels that have not been sampled for this study.

here is detailed in Table 1. For *Palmatolepis*, small juveniles elements, not developed enough to be attributed to a particular species, have been collected

only at some levels. For *Icriodus*, only *I. alternatus* is present through the whole section. *I. symmetricus*, only found in the first level of the section, was not included in the present study.

3.2. Fourier analysis of the outline

Shape analysis has been based on the outline of the conodont elements viewed from above, as this view appeared to express most of the variability. Outlines, even complex ones, can be described in a very simple way using Fourier analysis (Foote, 1989). This method is independent of the orientation of the outline and the influence of measurement error is limited by filtering the noise occurring in the detail of the outline. A similar method has previously been applied to conodonts for taxonomic discrimination (Klapper and Foster, 1986, 1993). In order to maximize the segregation of the different species, those authors considered specific parts of the outlines where differences were especially localized. In the present study, the outline analysis is not used for taxonomic purposes but for quantifying the global morphological distance between the different samples, and therefore the outline has been analyzed globally.

The two-dimensional outline of the conodont was first digitized using an image analyzer (OPTIMAS v.4.0). For each conodont, 64 points were sampled at equally spaced intervals along the outline, the starting-point being defined at the top of the conodont. In order to compare, and eventually pool, right and left forms, left elements were subjected to a mirror image transformation and measured as right elements. From the coordinates, 64 radii were calculated corresponding to the distance of each point to the center of gravity of the conodont outline. A discrete Fourier transform was then applied to this set of 64 radii. The outline is thus expressed as a sum of trigonometric functions of decreasing wave-length, the harmonics, according to the standard formula:

$$r(s) = a_0 + \sum_{n=1}^K \left[a_n \cos\left(\frac{s}{L2\pi n}\right) + b_n \sin\left(\frac{s}{L2\pi n}\right) \right] \quad (1)$$

where r is the radius at the abscissa s along the outline, L the perimeter, K the number of points

Table 1
Sample size of the different species in each level

Levels	<i>Icriodus</i>		<i>Palmatolepis</i>							
	<i>altern.</i>	<i>subrecta</i>	<i>rotunda</i>	<i>hassi</i>	<i>gigas</i>	<i>rhenana</i>	<i>praetr.</i>	<i>triang.</i>	<i>clarki</i>	juveniles
32c	10 (6)						20 (9)	13 (4)	3 (2)	9
32b	19 (11)						17 (6)	7 (7)		21
32a2	31 (20)						14 (7)	5 (5)		13
32a1	15 (10)						11 (4)	5 (2)		3
31g3	41 (18)		5 (4)							4
31g2	22 (14)	9 (6)	6 (2)	1 (0)	4 (0)			1 (0)		
31g1	12 (4)	22 (12)		2 (2)	11 (3)			3 (1)		
31b	15 (4)	17 (7)	11 (8)							
30	9 (5)	68 (27)	17 (8)	13 (4)						
27	42 (20)	16 (6)	12 (8)		3 (0)	4 (3)				
25	8 (5)	5 (1)	1 (0)							21
24	79 (50)	6 (3)								13

In brackets: number of right elements. Abbreviations: *altern.* = *alternatus*; *praetr.* = *praetriangularis*; *triang.* = *triangularis*. Bold characters delineate the two dysoxic Kellwasser events.

along the outline, and n the rank of the harmonic. The coefficients a_n and b_n are calculated according to the formula using the complex numbers:

$$h_n = a_n + ib_n = 1/\sqrt{K} \sum_{s=1}^K r(s) e^{2\pi i(s-1)(n-1)/K} \quad (2)$$

where a_n is the real part and b_n the imaginary part of the complex Fourier coefficient h_n .

The size is then standardized by dividing all the coefficients by the zeroth harmonic amplitude, a_0 , which is the diameter of a circle with the same area as the digitized outline, and can thus be used as a measure of size (Ehrlich and Weinberg, 1970).

A reconstruction of the outline corresponding to any set of Fourier coefficients can be obtained using the Inverse Fourier Transform, following processes inverse to those used to calculate the Fourier coefficients (Rohlf and Archie, 1984).

A characteristic of the Fourier harmonics is that the higher the rank of the harmonic, the more details of the outline it describes. This property can be used to filter measurement noise as it is expected to increase with the harmonic rank (Renaud et al., 1996), and to limit the number of coefficients to be retained for subsequent statistical analyses. The Fourier coefficients have been retained up to the tenth harmonic for *Icriodus* and up to the twelfth for *Palmatolepis*, since the details on the outline of

Icriodus appear to be more sensitive to noise than those on *Palmatolepis*.

3.3. MANOVA on the Fourier coefficients

For each element, a set of Fourier coefficients was obtained, 20 and 24 Fourier coefficients for *Icriodus* and *Palmatolepis*, respectively. A MANOVA (Multivariate Analysis of Variance), associated with a canonical variate analysis, was performed on these variables in order to display the relationships between the different groups. In this analysis, the groups correspond to the different stratigraphic levels for each species. A test of significance for differences among groups relative to within-group variability is provided (Wilk's Lambda test), as well as the scores of the group means along the canonical axes (Marcus, 1993). In this space the variations in morphology and the relative positions of the samples can be visualized. In order to compare juvenile *Palmatolepis* specimens with adult ones without influencing the calculation of the among-groups relationships, the coordinates of the juveniles in the canonical space defined by the adult *Palmatolepis* were calculated afterwards using the canonical vectors.

Variations in size may be compared to the shape variations. The zeroth harmonic a_0 is proportional to the size of each conodont, and has been selected

as size variable. A one-way analysis of variance (ANOVA) has been used to test the existence of size differences.

4. Size and shape variations of the conodont elements

4.1. Comparison of right and left elements

The difference between right and left elements has finally been tested within each population. Because of the small size of most samples (Table 1), testing the shape difference by MANOVA was impossible, so ANOVA was used for size as well as for each Fourier coefficient. Left–right asymmetry of size appears to be negligible (significant result of the ANOVA on a_0 : *Icriodus*, 0%; *Palmatolepis*, 6%) and asymmetry of shape a minor phenomenon (significant results of the ANOVA on Fourier coefficients: *Icriodus*, 6%; *Palmatolepis*, 11%), which may be due either to slight directional asymmetry or to uneven distribution of right and left elements because of taphonomic biases. Asymmetry between right and left sides has thus been considered as a part of the within-group variance in the MANOVA, since pooling right and left elements allows consideration of a larger sample size, especially important during the anoxic events. The first canonical vectors of the MANOVAs effected on right and left elements were compared to those of MANOVAs effected on right elements alone. This procedure allows testing of the stability of the canonical vectors obtained (Reyment, 1991).

4.2. *Icriodus*

The MANOVA on the Fourier coefficients of the conodonts from the successive levels indicates that a significant morphological variation through time exists in *Icriodus alternatus* (Wilk's Lambda = 0.165, degrees of freedom: $df_1 = 220$, $df_2 = 2660$, probability $P < 0.001^{***}$). The canonical vectors obtained on right elements alone are highly correlated (CA1: $r^2 = 0.738$, $P < 0.001^{***}$; CA2: $r^2 = 0.562$, $P = 0.005^{**}$), suggesting that the results are stable and non sensitive to a possible difference between right and left sides. The plot of the group means in canonical space (Fig. 4) allows visualization of

the morphological relationships between the different groups. Surprisingly, the most divergent group corresponds to the youngest one (32c), at the top of the Coumiac section. Along the first canonical axis the levels 32c and 31g1, corresponding to the beginning of the Upper Kellwasser, are opposed to the groups corresponding to the levels immediately post-Upper Kellwasser (32a1, 32a1, and 32b), while the other groups are intermediate between these two poles.

Theoretical outlines corresponding to the scores on the canonical axes can be reconstructed using the Inverse Fourier transform method, and illustrate shape variations represented along the canonical axes. The first canonical axis, the most important since it represents 36% of the among groups variation, corresponds to a shape difference in the top part of the conodont: more pointed on one side of the diagram, more rounded on the other side. The second canonical axis, representing 21% of the variance, opposes narrow elements and broader ones, the latter corresponding to the Famennian species.

The first canonical axis can be used as a synthetic shape variable in order to represent shape variations along the section, which can be compared to size variations (Fig. 5). Size exhibits significant variations through time ($F = 13.9$, $df = 11$, $P < 0.001^{***}$), and size and shape appear to vary simultaneously. A first shift occurs just above the first anoxic event, with a trend toward more pointed and smaller conodonts. Thereafter *Icriodus alternatus* becomes larger and more rounded up to the first level of the Upper Kellwasser. Subsequently the conodonts become smaller and more pointed in shape with the most dramatic changes in size as well as in shape occurring at the end of the anoxic event. The highest level again displays important size and shape variations. *Icriodus alternatus* becomes rounded again, and increases in size up to the size of the last Frasnian conodonts.

The concomitant variations in size and shape can be better visualized on a plot of shape as a function of size (Fig. 6). Globally, size and shape are significantly correlated (coefficient of correlation $r^2 = 0.61$, $P = 0.003^{**}$), but the relationship is much stronger when restricted to the youngest levels of the section (levels 30 to 32c: $r^2 = 0.95$, $P < 0.001^{***}$). It seems that the three first points are aligned according to the same direction, but shifted

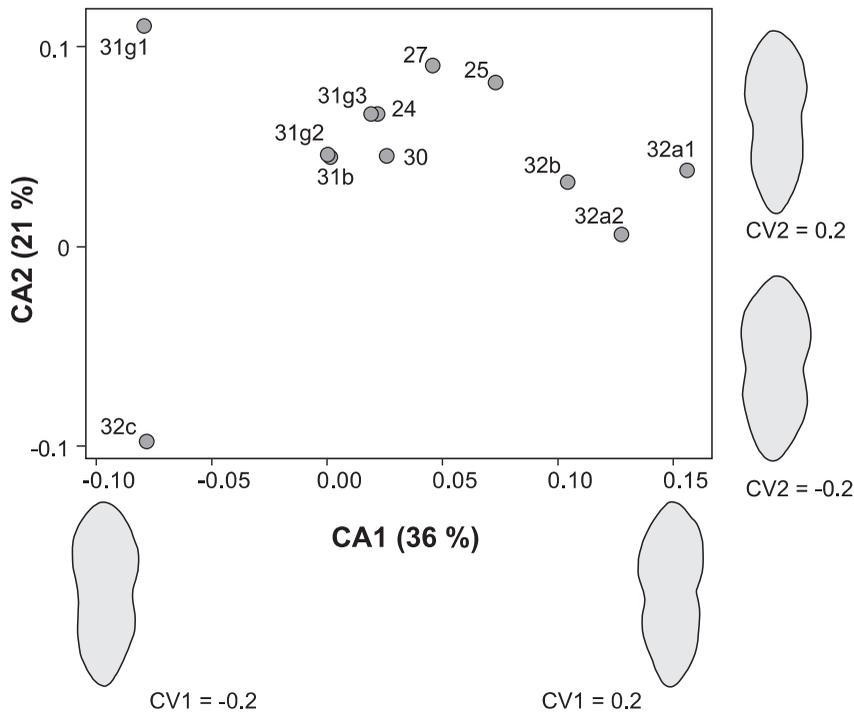


Fig. 4. First two canonical axes and corresponding outlines for *Icriodus*. The labels correspond to the numbering of the levels. The reconstructions are obtained using inverse Fourier transform on sets of coordinates along the canonical vectors.

towards smaller size. This pattern can be interpreted as a global allometric relationship linking size and shape of *Icriodus alternatus*, with a shift occurring between the two Kellwasser events, the conodonts becoming larger for the same shape between levels 27 and 30.

4.3. *Palmatolepis*

A second type of response to the crisis is represented by the genus *Palmatolepis*, which survived the Upper Kellwasser crisis by a replacement of species.

The shape analysis performed on the *Palmatolepis* data is similar to the analysis on *Icriodus* but includes several species (Table 1). The MANOVA shows that globally a shape differentiation exists between the different samples (Wilk's Lambda = 0.003, $df_1 = 696$, $df_2 = 5283$, $P < 0.001^{***}$). As for *Icriodus*, the canonical vectors obtained on right elements alone are highly correlated (CA1: $r^2 = 0.895$, $P < 0.001^{***}$; CA2: $r^2 = 0.885$, $P < 0.001^{***}$).

In canonical space (Fig. 7), the Frasnian species, i.e. *Pa. rotunda*, *subrecta*, *hassi*, *gigas*, and *rhenana*,

appear to be very well separated from the Famennian ones, i.e. *Pa. praetriangularis*, *triangularis*, and *clarki*. One exception can be noted: one of the first samples of *Pa. praetriangularis*, which appears during the Upper Kellwasser event, is closer to the Frasnian species than to the Famennian ones.

Within the Frasnian species, *Pa. subrecta* and *rotunda* are well segregated along the second canonical axis. One exception can be noted again, corresponding to both samples from the level 25. This level is just above to the Lower Kellwasser event, where *Pa. rotunda* and *subrecta* are shifted towards the positive side of the first canonical axis. The species that occur in small numbers, i.e. *Pa. gigas*, *hassi*, and *rhenana*, appear to be rather intermediate in shape between the two predominant Frasnian species *Pa. rotunda* and *subrecta*.

Within the Famennian group, no differentiation exists between *Pa. praetriangularis* and *triangularis*. The only group of *Pa. clarki*, a species appearing in the highest level of the section, is close to this ensemble, but slightly shifted towards the negative side of the first canonical axis.

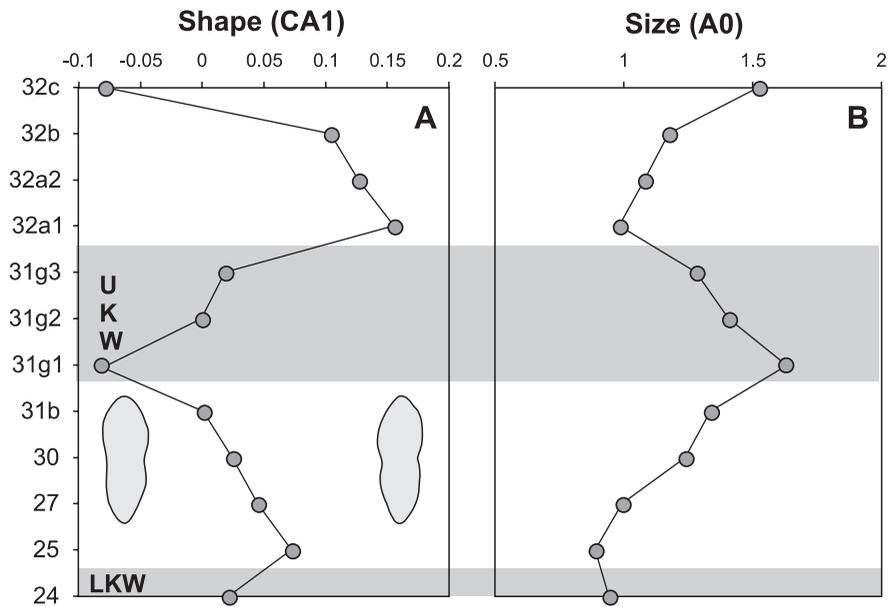


Fig. 5. Morphological variations of *Icriodus* through the Coumiac Quarry section. (A) Shape, represented by the first canonical axis. (B) Size, estimated by the zeroth harmonic. In grey, the two anoxic events.

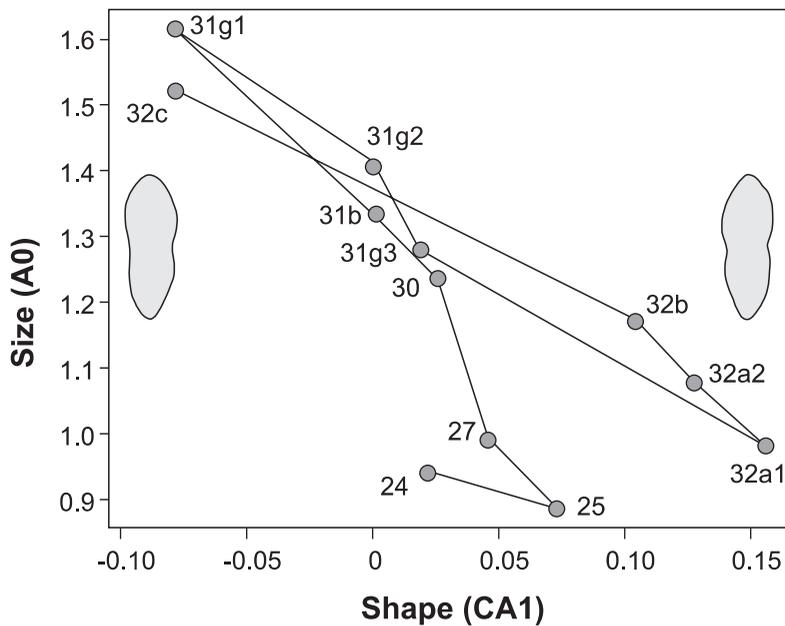


Fig. 6. Relationship between size and shape in *Icriodus*. The labels correspond to the numbering of the levels. The line between the dots denotes the time relationship.

The reconstructed outlines illustrate the shape changes associated with these differences. The first canonical axis opposes Frasnian to Famennian

species. The negative side, corresponding to Frasnian species, is characterized by globally elongated outlines, with a rounded platform located towards the

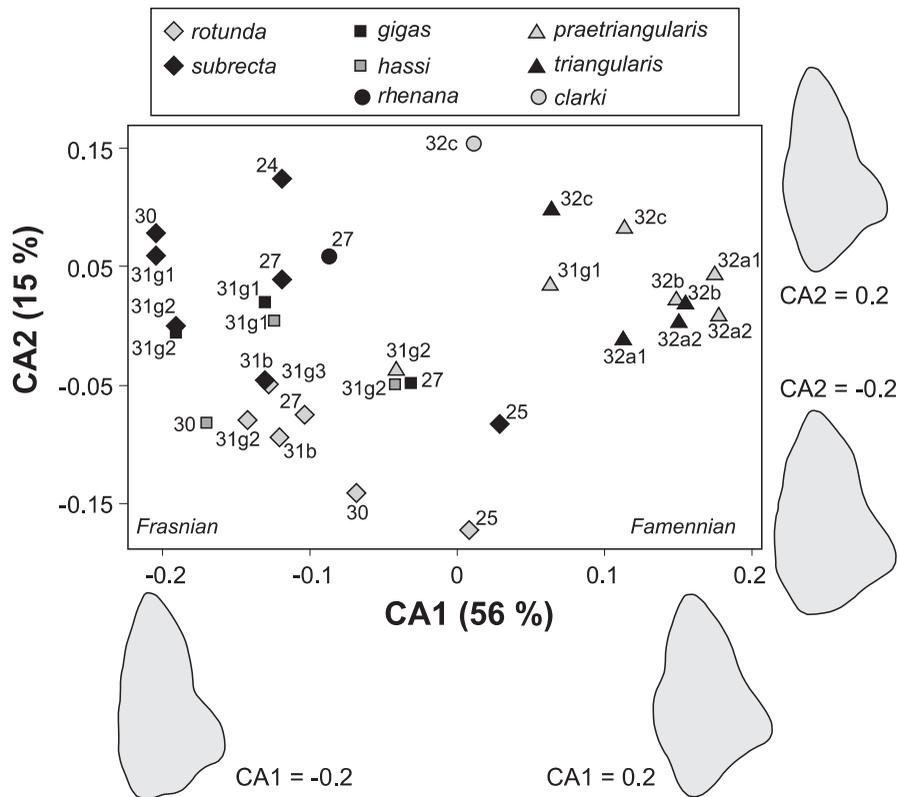


Fig. 7. First two canonical axes and corresponding outlines for *Palmatolepis*. The labels correspond to the numbering of the levels. The reconstructions are obtained using inverse Fourier transform on sets of coordinates along the canonical vectors.

back. The opposite side of the first canonical axis, corresponding to the Famennian species, is characterized by a broader platform with a pointed shape to the platform and to the rear. The second canonical axis mainly opposes outlines with an elongated rear to outlines with a rounded posterior part.

As for *Icriodus*, the first canonical axis, representing 56% of the among group variance, can be selected as synthetic shape variable, and its variations through time compared to size variations (Fig. 8). The size differentiation is globally significant ($F = 11.09$, $df = 29$, $P < 0.001^{***}$).

The Frasnian species *Pa. rotunda* and *subrecta* seem morphologically relatively stable (Fig. 8A), except for a shift towards pointed outlines just after the Lower Kellwasser event. During the Upper Kellwasser crisis, no shape change seems to occur in these species. The main change at this time is the appearance of the first *Pa. praetriangularis*, shifted towards more pointed outlines. However,

these first *Pa. praetriangularis* are closer to the Frasnian species than subsequent specimens. A strong shift towards pointed outlines occurs at the end of the Upper Kellwasser event. The first three Famennian levels are characterized by morphological stability, and extreme morphs along the first canonical axis. A change takes place in the highest level, with *Pa. praetriangularis* and *triangularis* slightly shifted towards the elongated, rounded outlines, and the appearance of a new species morphologically close to Frasnian species.

The shape variations of the poorly represented Frasnian species, *Pa. gigas*, *hassi*, and *rhenana*, are difficult to interpret, but it can be noted that they are located on the same side of the first canonical axis as the other Frasnian species.

The variations in size (Fig. 8B) broadly parallel the variations in shape. The levels during and after the Lower Kellwasser event are characterized by small *Pa. rotunda* and *subrecta*, which increase

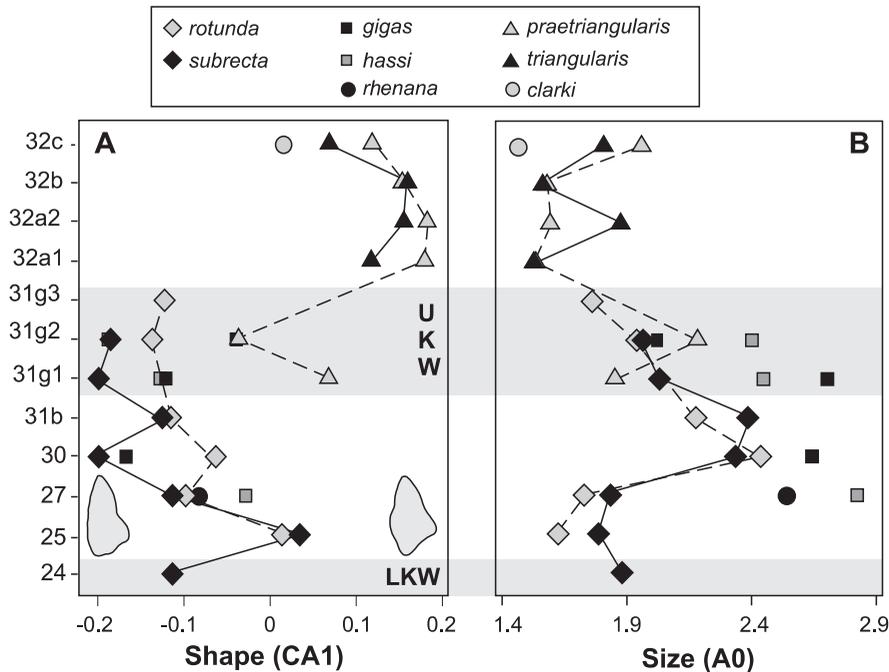


Fig. 8. Morphological variations of *Palmatolepis* through the Coumiac Quarry section. (A) Shape, represented by the first canonical axis. (B) Size, estimated by the zeroth harmonic. In grey, the two anoxic events.

in size between the two anoxic events. These two species experience a major decrease in size at the beginning of the Upper Kellwasser event. The first *Pa. praetriangularis* seem to have approximately the same size as these two species at this time, and this species decreases in size just above the Upper Kellwasser event. The poorly represented Frasnian species, *Pa. gigas*, *hassi*, and *rhenana*, seem to be essentially characterized by a large size, but even for these species, the Upper Kellwasser specimens tend to be smaller than the previous ones.

The relationship between size and shape (Fig. 9) is less obvious than for *Icriodus* (Fig. 6). Globally, a significant relationship exists between size and shape ($r^2 = 0.38$, $P = 0.001^{***}$), but the variation within each species does not appear to follow any allometric relationship, and the observed relationship could be due to the smaller size of the Famennian species. Also, in contrast with *Icriodus*, the samples do not include young individuals as they are not attributable to a given species. To test the hypothesis of a heterochronic mechanism leading to the shape difference between the Frasnian and Famennian species, some juvenile samples have been added to this plot. Three

clear main groups emerge: the Frasnian adults, the Frasnian juveniles, and the Famennian adults. The Frasnian juveniles appear to be intermediate in shape between Frasnian and Famennian adults, and much smaller than both groups.

5. Discussion

5.1. Some comments about the notion of species in conodonts

The paleobiological interpretation of the size and shape variations of the conodonts in response to the environmental perturbations of the Kellwasser depends on the biological significance of a conodont species. The results of the size and shape analysis have shown that *Icriodus* displays variations comparable to *Palmatolepis* variations. The importance of size and shape differentiation within *Palmatolepis* between the different species has been tested by ANOVA on size estimated by a_0 and MANOVA on Fourier coefficients within each level (Table 2). Since outline of platform conodont elements can be

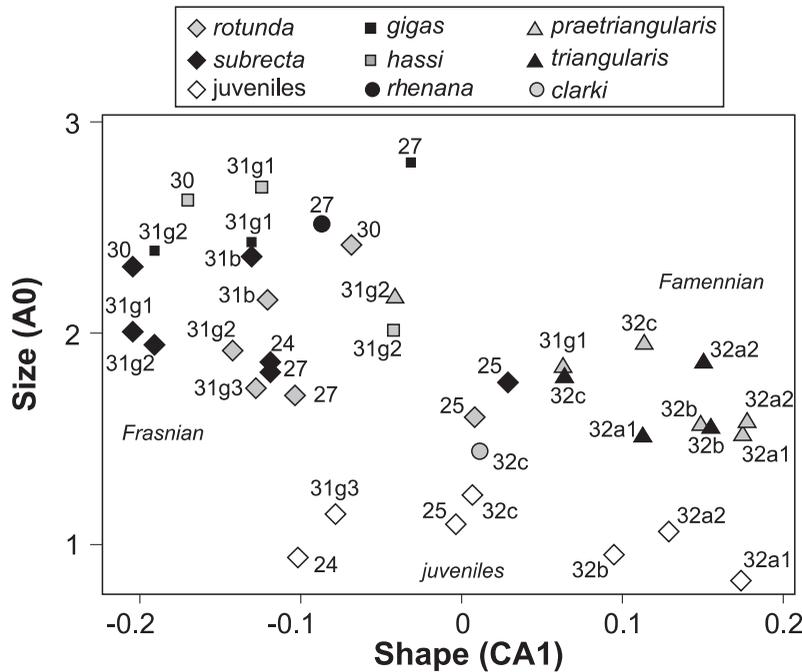


Fig. 9. Relationship between size and shape in *Palmatolepis*. The labels correspond to the numbering of the levels.

Table 2

Probabilities and significance of the size and shape differentiation of *Palmatolepis* species in the different levels

Levels	Composition	Size		Shape		Harmonics
		<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	
32c	CPT	0.168	ns	0.445	ns	10
32b	PT	0.852	ns	0.141	ns	10
32a2	PT	0.183	ns	0.218	ns	8
32a1	PT	0.972	ns	0.620	ns	7
31g3	R	–	–	–	–	–
31g2	RSHGP	0.030	*	0.402	ns	8
31g1	SHGP	0.001	***	0.001	***	10
31b	RS	0.216	ns	0.052	ns	10
30	RSH	0.017	*	0.000	***	10
27	RSGN	0.000	***	0.032	*	10
25	RS	0.443	ns	0.693	ns	2
24	S	–	–	–	–	–

* *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001; ns = non significant.

Composition: abbreviations of the species present in the level: C = *clarki*; P = *praetriangularis*; T = *triangularis*; R = *rotunda*; S = *subrecta*; G = *gigas*; H = *hassi*; N = *rhenana*. Size: probabilities of the ANOVAs. Shape: Wilk's Lambda probabilities of the MANOVAs performed on the Fourier coefficients. Harmonics: number of harmonics considered in the MANOVA. Bold characters delineate the two dysoxic Kellwasser events.

considered as crucial for the separation of morphologically similar species (Klapper and Foster, 1993), and the differences between the Famennian species are never significant, these species may therefore be considered as morphotypes. The differentiation between Frasnian species is more important, especially in the levels containing more than the two main species. However, *Pa. rotunda* and *subrecta* appear to be comparable in size and shape in several levels. The parallel variations in size and shape of these two species (Fig. 8) further support the hypothesis that the different species of *Palmatolepis* might be considered as morphotypes, more or less differentiated, rather than as true, separate biological species. The pool of *Palmatolepis* could thus be separated into only two species, corresponding to the Frasnian and to the Famennian conodonts. The existence of intermediate morphs between these two species, such as the *Pa. rotunda* and *subrecta* from the level 25, and the *Pa. praetriangularis* from level 31g2, suggests that the Frasnian and Famennian species are closely related and may be linked by an ancestor–descendent relationship. According to this hypothesis, the variations of *Icriodus* and *Palmatolepis* can be compared

since they both represent the response of a genetic pool to the same environmental variations.

5.2. *Timing and trends of the response to the Upper Kellwasser event*

For both *Icriodus* and *Palmatolepis*, the response to the Upper Kellwasser crisis comprises two stages. First, there is a strong decrease in size which may correspond to a ‘Lilliput effect’ (Urbanek, 1993; Schülke, 1995; Girard and Renaud, 1996) characteristic of the post-crisis fauna, and associated with a strong differentiation in shape. The timing of this morphological response seems to be slightly different in the two genera. The major decrease in size occurs as early as the beginning of the anoxic event for *Palmatolepis* (Fig. 8) but only during the event for *Icriodus* (Fig. 5) at the onset of the regressive trend characterizing the Frasnian/Famennian boundary (Girard and Feist, 1997). This difference in timing might be the consequence of a differential sensitivity to the environmental variations associated with the crisis due to a difference in favored habitats. The deep-water *Palmatolepis* would be affected by the rise of the oxygen minimum onto the continental shelf before the shallow-water *Icriodus*, which in turn would be more strongly affected by sea-level fall. The second stage of the response to the crisis occurs later (level 32c), with an increase in size associated with variations in shape which are the inverse of those occurring during the previous stage. These variations seem to correspond to the stage of recolonization in other groups (Feist and Schindler, 1994) and may characterize the recovery phase of the ecosystem. This recovery period seems not to be associated with important environmental variations (Girard and Albarède, 1996) except the beginning of the early Famennian transgressive trend. These results suggest that size and shape variations of the conodont elements, and especially those of *Icriodus*, could be strongly influenced by environmental variations associated with sea-level fluctuations.

5.3. *The Lower Kellwasser: same trends with a lower amplitude*

The Lower Kellwasser is an anoxic event of lower amplitude than the Upper Kellwasser, but with

some disturbance of communities (Schindler, 1990; Becker, 1993; Feist and Schindler, 1994). Variations in size and shape characterizing the response of the conodonts to the Lower Kellwasser are the same as those associated with the Upper Kellwasser, but expressed with a lower amplitude. Pa elements of *Icriodus* and *Palmatolepis* are small after this event and increase in size between the two events, i.e. a period comparable to the recovery phase following the Upper Kellwasser crisis. The shape variations are also similar to the trends characterizing the Upper Kellwasser (Figs. 5 and 8).

These similar variations associated with both anoxic events suggest that the mechanisms of response to this type of event are repeatable and that the amplitude of the biological response will vary according to the importance of the event. The repetition of the response emphasizes the strong genetic control on morphological variations as well as the adaptive success of this response. The response to each environmental crisis appears to be a gradual process where the evolutionary potential of a species will determine its ability to overcome the environmental perturbation. Such mechanisms of response are possible during the Kellwasser period since this crisis, due to fluctuations of oceanic conditions, is long enough in terms of generation time to allow evolutionary processes.

The adaptive significance of shape changes observed in *Icriodus* and *Palmatolepis* is difficult to assess, since the detailed functional morphology of conodont elements is still not fully understood. Size decrease can be more easily interpreted. Similar Lilliput effects associated with an environmental crisis have been observed in graptolites (Urbanek, 1993) and regarded as the result of a selection for new, smaller phenotypes better adapted to disturbed environments (Jaeger, 1991). Two ranges of selection pressure favouring smaller conodonts can be envisaged. Smaller conodont animals, allometrically associated with smaller elements, could have been advantaged because of a selection for new life history traits, e.g. shorter growth and earlier sexual maturation. The size decrease in conodont elements could also be a response to variation in the prey that the animal was feeding upon. Either the conodont animal was microphagous, with the elements acting as sieves to select or reject prey (Nicoll, 1987), or it

was macrophagous with the elements breaking and shearing small prey (Purnell, 1995). In both cases, the decrease in size of the elements should correspond to a decrease in size of the prey, and possibly to more fragile tests. In such a hypothesis, one could expect to observe a coeval Lilliput effect on small micro-organisms which may have been preyed upon by conodonts. Finally, both ranges of selection may be combined since the change to smaller, and possibly, rarer prey may have favoured smaller animals.

5.4. Strategies of morphological change

In *Icriodus*, size and shape are highly correlated, especially when considering the levels around the Upper Kellwasser event. The response of the conodonts to the crisis seems thus to correspond to a displacement along an allometric trajectory characteristic of the species. Such a pattern suggests that the response to the crisis may involve heterochronic mechanisms, such as dwarfism or progenesis, due to shifts of the life-history traits (Girard and Renaud, 1996). Shifts along the growth allometric trajectory can be interpreted as the consequence of a developmental flexibility (Raff, 1996), which should allow a rapid and successful response to the environmental perturbation. Such a hypothesis is confirmed by the fact that no decrease in absolute abundance of *Icriodus* is recorded during or after the crisis (Girard and Feist, 1997). The evolutionary potential of this species could explain its success in overcoming the Kellwasser crisis.

In contrast to *Icriodus*, the response of *Palmatolepis* to the crisis apparently does not involve a heterochronic process. Frasnian juveniles are clearly separated in the morphospace defined by size and shape from the Frasnian as well as from the Famennian adults (Fig. 9). The direction of ontogenetic change is thus very different from the evolutionary trajectory leading from the Frasnian to the Famennian adults, and a mere heterochronic process cannot explain the observed evolution. This interpretation is supported by the fact that juveniles seem to be affected by the same morphological shift as the adults, as shown by the post-event juveniles from the levels 25, 32a1, 32a2, and 32b, shifted along the shape axis in the same way as the adults from these levels. Such an evolutionary response allowed *Palmatolepis*

to survive the crisis, but nevertheless appears as less successful than the heterochronic response of *Icriodus*, since a strong decrease in the absolute abundance of *Palmatolepis* is associated with the Upper Kellwasser period (Girard and Feist, 1997).

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