



Disentangling allometry and response to Kellwasser anoxic events in the Late Devonian conodont genus *Ancyrodella*

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Is the ability to respond to minor perturbations a key to survival to major crisis? This idea was supported by previous studies on Late Devonian conodonts. Genera surviving the Frasnian/Famennian (F/F) crisis, at the end of the Upper Kellwasser anoxic event, had shown a response to a similar but minor event, the Lower Kellwasser (LKW). In contrast, the genus *Ancyrodella* went extinct at the F/F crisis. This study aims to assess whether this extinction was associated with the absence of response to the minor LKW event. For this purpose, the shape of the P1 platform elements of the conodont *Ancyrodella curvata* was quantified based on their 2-D outlines. Conodonts were extracted from two outcrops documenting the Late Devonian Kellwasser events, Coumiac (France) and Mriit (Morocco). *Ancyrodella curvata* is characterized by a marked allometric growth that may blur any other source of shape difference, like response to the LKW. Hence, a multivariate method was developed to disentangle size-free from size-related shape variations. No coherent temporal size variations emerged from the analysis, but allometry occurring along the growth of the element indeed appeared as the prevailing source of shape variation. By isolating size-free variations, however, we were able to evidence a morphometric response of *A. curvata* to the LKW independent from the allometric pattern. Hence, the extinction of *A. curvata* at the F/F crisis cannot be attributed to an absence of response to minor events. The amount of shape change involved in the LKW shift is, however, of minor importance in comparison with the shape variation due to allometric growth. Alternate hypotheses have been further investigated. *Ancyrodella curvata* appears as a rare species in the assemblages, and its distribution worldwide suggests a rather specialist taxon. Considering survivorship curves (i.e. frequency distribution of the conodont as a function of its size) *A. curvata* was characterized by low and constant mortality rate. This may be a clue for a long growth and progressive investment in the reproduction. These arguments support the view that *A. curvata* was a rather specialist, rare and 'K-selected' taxon. All these factors may not be exclusive and their unfavourable conjunction might have been the key to the extinction of *A. curvata*. □ *Conodonts, extinction, Frasnian, Fourier analysis, morphometrics, survival.*

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Selectivity of mass extinction is a major issue in palaeobiology. Generalist clades have been proposed to better survive environmental perturbations, causing macroevolutionary trends of recovery from rather primitive, small-size stocks diversifying into large-size, derived forms (McKinney 1990). Macroevolutionary properties of clades, such as species diversity, have also been invoked as a cause for survival (Erwin 1989; Twitchett 2006). Alternatively, the cause for preferential survival has been searched into the ecological characteristics of the taxa, such as feeding behaviour or geographical range (Jablonski & Raup 1995). In contrast, the hypothesis that the potential of response of a taxon to minor perturbation may be the key to its survival to major environmental changes has received little interest.

We investigated this aspect by comparing the fine-scale response of conodonts to Late Devonian

environmental perturbations. Conodonts were early marine vertebrates, eel-like in their body shape, documented in the fossil record by microscopic elements interpreted as part of their feeding apparatus (Purnell & Donoghue 1997). Conodonts, as well as most of the marine fauna, were severely affected by the crisis occurring at the Frasnian/Famennian (F/F) boundary. This boundary coincides with the end of the Upper Kellwasser event (UKW). Although the detailed scenario of the environmental changes causing the F/F mass extinction is still debated, a momentary decrease in temperature associated with a regressive trend is evidenced (Joachimski & Buggish 2002). The UKW is pre-dated by about 0.8 million years by the Lower Kellwasser event (LKW). This event had only a minor impact on the fauna. However, the geochemical signature of this event is apparently similar to the one of the UKW, suggesting similar environmental



Fig. 1. Three different growth stages of P1 platform elements of *Ancyrodella curvata*, illustrated by conodonts from the level M3 (Mriat, Morocco).

processes despite the major difference of impact on the fauna.

Two conodont genera surviving the F/F crisis, *Palmatolepis* and *Icriodus*, have been shown to display a response to the LKW as well as a response to the UKW (Renaud & Girard 1999; Girard *et al.* 2004a, b). Another genus, *Ancyrodella*, did not survive the crisis. The present study aims to assess whether its extinction may have been related to an absence of response to the LKW. In this purpose, the shape of the P1 platform element of the conodont apparatus was quantified using an outline analysis (Renaud & Girard 1999; Girard *et al.* 2004a, b). The hypothesis behind is that a shape change should correspond to a genetic change, and that shape variation through time would thus trace microevolution. This assumption may be flawed by low heritability of shape, or environmental components of the variation interfering with the genetic variation (Atchley & Rutledge 1980), but further testing of the hypothesis is impossible on such long extinct animals.

In the case of *Ancyrodella curvata*, the morphometric analysis had to tackle with a large allometric component in the growth of the element (Fig. 1): elements obviously changed their shape as they grew. Traditionally, ontogenetic changes in morphometric traits have been described by comparing various size-related measurements (e.g. distances, lengths and widths) according the equation of simple allometry $y = bx^k$, equivalently written as $\ln(y) = \ln(b) + k\ln(x)$ (Huxley

1924). If $k = 1$, the traits are isometric: their ratio does not change during growth. Hence, considering morphological traits, allometry implies some shape changes associated with increase in size. Conversely, the absence of size-related shape variation is isometry (Klingenberg 1998). In the context of multivariate statistics, isometry thus corresponds to the stochastic independence of size (a univariate scalar value) and shape (inherently multivariate) whereas allometry is an association between size and shape.

A possible response to environmental changes of *A. curvata* may involve shape changes related to or independent from growth; in the second case, tracing these changes may be difficult because of the overwhelming amount of shape variance related to growth in this taxon. Hence, we developed a method allowing a separation of the both component in the shape variance, based on multivariate regressions of the morphometric shape descriptors on size. This approach was applied to morphometric variations of the P1 platform elements of *A. curvata* in two outcrops documenting the time interval of the two Kellwasser events, in order to identify and compare a possible response to the LKW and UKW, and assess if the extinction of *A. curvata* at the end of the UKW had been preceded by an absence of response to the LKW. Other possible factors making *A. curvata* prone to extinction, such as relative abundance in the assemblages and patterns of survivorship, are also considered.

Geological setting and conodont samples

The two sections of Coumiac (Montagne Noire, France) and Mrirt (Western Meseta, Morocco) were sampled. Coumiac Upper Quarry (CUQ) is the stratotype section for the F/F boundary (Klapper *et al.* 1993). This section is composed of oxidized sediments deposited on an outerself submarine rise (Feist 1985; Feist & 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. At Mrirt, the Frasnian is composed of well bedded grey limestones with rich pelagic and some benthic faunas. The Frasnian sequence contains two levels of dark micritic limestones, noted M3-4 and M11a-11b. They correspond to the LKW and UKW events (Lazreq 1992).

Estimating sedimentation rates are quite difficult given the imprecision of the datations. However, sedimentological evidences suggest that if some variations occurred, no systematic trends would have biased the sampling of given time intervals relative to other. By default, further representations along the sections have been plotted as a function of rock thickness.

Rock samples have been dissolved in dilute formic acid and all specimens of *A. curvata* have been picked from 17 levels from the Coumiac section (south France) and 10 levels in the Mrirt section (Morocco) (Table 1). Only one species of *Ancyrodella* composed the genus during this time period: *A. curvata*.

Outline and statistical analyses

Outline analysis

Conodonts having a bilateral symmetry, both right and left *A. curvata* elements, are found in an assemblage. Left elements were subjected to a horizontal mirror transformation and measured as right elements, in order to take both right and left elements into account in the morphometrical analysis. The validity of this assumption was checked *a posteriori* on a few samples. Following the method developed by Renaud & Girard (1999), the 2-D outline of each conodont was automatically digitized using an image analyser (Optimas v. 6.0). For each conodont, maximum length, area, and 64 equally spaced points were digitized from the outline, the starting point being defined at the top of the free blade of the conodont element. A radial Fourier transform was applied to

Table 1. Number of the specimens of *Ancyrodella curvata* measured in each level for the Coumiac Upper Quarry (CUQ) and Mrirt (M) sections.

Section	Level	Number	Depth (cm)
Coumiac	CUQ31g2	15	365
Coumiac	CUQ31g1	10	360
Coumiac	CUQ31f	118	350
Coumiac	CUQ31e	35	325
Coumiac	CUQ31c	8	300
Coumiac	CUQ30	3	275
Coumiac	CUQ29b	16	245
Coumiac	CUQ28c	16	210
Coumiac	CUQ27	5	180
Coumiac	CUQ26b	14	145
Coumiac	CUQ25c	3	100
Coumiac	CUQ25b	7	90
Coumiac	CUQ24e	3	70
Coumiac	CUQ24bc	4	35
Coumiac	CUQ24a	39	25
Coumiac	CUQ23e	11	15
Coumiac	CUQ23d	11	0
Mrirt	M11b	6	125
Mrirt	M11a	1	120
Mrirt	M9	25	100
Mrirt	M7	20	70
Mrirt	M6	15	55
Mrirt	M5	6	45
Mrirt	M4	9	35
Mrirt	M3	27	25
Mrirt	M2	18	15
Mrirt	M1	6	0

Depth = position of the samples in the section.

the set of radii. From the x , y coordinates of the points, 64 radii corresponding to the distance of each point to the centre of gravity of the outline were calculated. A Fourier transform was then applied to this set of 64 radii. The outline was thus expressed as a finite sum of trigonometric functions of decreasing wavelength, the harmonics. Each harmonic is weighted by two Fourier coefficients (FCs). The zero harmonic (A_0) corresponds to the average of the radii for a given outline. It is thus a linear dimension that was used to standardize all other FCs in order to eliminate isometric size effects.

A characteristic of the Fourier harmonics is that the higher the rank of the harmonic, the more details of the outline it describes. The Fourier coefficients have been retained up to the eleventh for the genus *A. curvata* in order to filter the measurement noise, as it is expected to increase with the harmonic rank (Renaud 1999).

Statistical analyses

The size of each conodont element was estimated by several univariate parameters: maximum length, area, and the zero harmonic of the radial Fourier transform. The relationships between these different size

Table 2. Relationships between size measures of the conodont elements from Coumiac (CUQ) and Mriit (M).

	X	Y	N	R	Slope	± SE	Intercept	± SE
CUQ + M	ML	A_0	452	0.992	2.735	0.017	-0.207	0.012
CUQ			318	0.993	2.797	0.019	-0.233	0.014
M			134	0.994	2.616	0.026	-0.166	0.019
CUQ + M	$\sqrt{\text{Area}}$	A_0	452	0.997	4.326	0.015	0.177	0.006
CUQ			318	0.998	4.302	0.016	0.181	0.006
M			134	0.996	4.385	0.033	0.166	0.012
CUQ + M	$\ln(\text{ML})$	$\ln(A_0)$	452	0.992	1.138	0.007	0.930	0.004
CUQ			318	0.992	1.153	0.008	0.945	0.005
M			134	0.993	1.107	0.011	0.896	0.007

X, independent variable; Y, dependent variable; N, number of specimens; R, coefficient of regression; SE, standard error; ML, maximum length; $\sqrt{\text{Area}}$, square root of the outline area; A_0 , zero harmonic of the Fourier analysis of the outline. For all regressions probability $P < 0.001$.

parameters were investigated using linear regression. Differences in size between samples were investigated using analyses of variance and the non-parametric Kruskal–Wallis test, which controls the absence of differences between the centre of the groups; it corresponds to a non-parametric analogue of a one-way analysis of variance and accounts for the highly unequal sample sizes.

The shape of each conodont was described by a set of 22 FCs, corresponding to 2 FCs per 11 harmonics. Note that these FCs have been standardized by size and retain shape information only. The data set including the FCs of the conodonts of both sections was analysed using multivariate statistics. A principal component analysis (PCA) was performed in the first place, in order to display the total variance on a few synthetic axes without any *a priori* hypotheses. The PCA was performed on the correlation matrix in order to balance the weight given to the different FCs.

Because of the allometric growth of *Ancyrodella curvata*, the relationship of size and shape had to be addressed. Despite their standardization by the zero harmonic, the FCs still include size-related, allometric shape variation. In order to disentangle the factors causing size and shape variations, a multivariate regression was applied that regressed the FCs (dependent variables) upon an independent variable, here the relevant size estimator. In this case, the multivariate regression corresponds to the set of all single regressions of the FCs upon the independent variable (Monti *et al.* 2001). The residuals of the multivariate regression constituted a new data set where the allometric effect was removed.

This new data set was analysed using multivariate statistics. Considering the unbalanced number of conodonts in the different samples, a PCA did not appear as appropriate because giving too much importance to the within-group variation of the largest samples. Hence, the differences among groups were investigated using a multivariate analysis of

variance (MANOVA, test considered: Wilks' lambda). Associated with the MANOVA, canonical axes were estimated that displayed the among-group shape variation on a few synthetic axes.

The interpretation of these axes relies on a visualization of the shape changes they describe. These reconstructions can be obtained from a set of FCs corresponding to scores on the synthetic axes, thereafter using an inverse Fourier transform. This set of coefficients was obtained by calculating the multivariate regression parameters of FCs (dependent variables) upon the relevant synthetic axis (independent variable) (Monti *et al.* 2001). In the same way, a visualization of the allometric shape change was obtained by regressing FCs on size.

Results

Relationships between size parameters

Size is an intuitively simple variable but concretely its estimation can rely on various measurements like maximum length and area of the outline, or on a size estimator like the zero harmonic (A_0) derived from the Fourier analysis. We thus investigated the relationships among these different size variables. Considering the square root of the area in order to get a linear measurement, all size variables appeared as highly correlated (Table 2), with comparable results among both sections. Maximum length is an easily measured size variable and its relationship to A_0 was further investigated using the allometric equation $\ln(y) = \ln(b) + k\ln(x)$. The regression was highly significant with a slope (allometric coefficient b) close to 1 (Table 2) indicating an isometric relationship between both size variables. A_0 was nevertheless chosen as size estimator thereafter, because length only measures size variation of the conodont element along one direction, whereas A_0 estimates size variations of the whole platform.

Table 3. Tests for size variations through the sections. Size estimators considered are the zero harmonic (A_0) derived from the outline analysis, and $\ln(A_0)$.

		ANOVA			Kruskal-Wallis	
		d.f.	F-ratio	P	Test statistic	P
Coumiac	A_0	16	2.640	0.001	32.951	0.008
	$\ln(A_0)$	16	2.269	0.004	32.951	0.008
Mrirt	A_0	9	1.504	0.154	11.000	0.276
	$\ln(A_0)$	9	1.334	0.226	11.000	0.276

d.f., degree of freedom; P, probability (in bold significant probabilities $P < 0.05$).

Test of the bilateral symmetry

The conodont animal had a bilateral symmetry but occlusion among conodont elements seems to have been complex (Donoghue & Purnell, 1999) and might have caused directional asymmetry between right and left elements. Since during measurements, left elements were subjected to a horizontal mirror transformation and measured as right elements, the existence of an asymmetry was tested prior to further investigations on two levels of the Coumiac quarry (CUQ 31e: 17 right/18 left elements; CUQ 31f: 37 right/31 left). In none of the case a difference in size was reported (Kruskal-Wallis test on A_0 : CUQ 31e, $P = 0.531$; CUQ 31f, $P = 0.868$). Results on shape indicated the existence of a significant but weak asymmetry (MANOVA on FCs: CUQ 31e, $P = 0.0009$; CUQ 31f, $P = 0.0106$).

Such a result is similar to those found on *Icriodus* and *Palmatolepis* (Renaud & Girard 1999). Because the amount of asymmetry seemed limited compared with differences among levels (all MANOVA delivering $P < 0.0001$), and because of the poor sampling in some levels, right and left conodont were nevertheless pooled together within each level.

Size variations through time

Size varies significantly among samples through Coumiac but not in Mrirt (Table 3). Minimal average size is reached in both sections at the top of the LKW (Fig. 2). No other clear temporal trend emerges and the variations rather correspond to fluctuations in the time interval bracketed by the two Kellwasser events.

Allometry as the major cause of shape variation

The PCA performed on the raw FCs provided synthetic axes for a first inspection of the major sources of shape variations. The scores on the first axis (PC1,

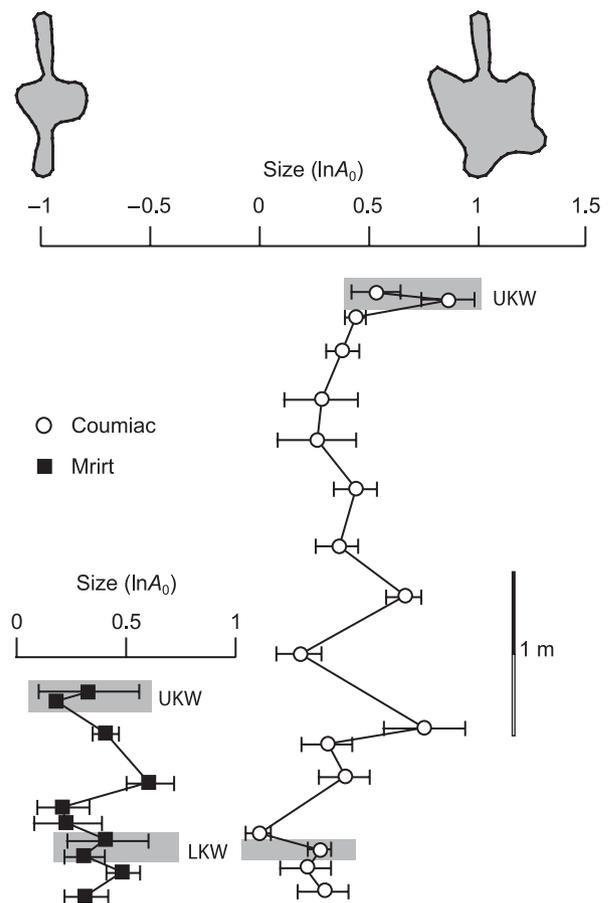


Fig. 2. Size variations of *Ancyrodella curvata* through Coumiac and Mrirt sections. Size is estimated by the logarithm of the zero harmonic of the Fourier analysis. Symbols represent the average value per level; error bars are the 95% confidence interval. Symbols: open circles for Coumiac; black squares for Mrirt. The reconstructed outlines visualize the allometric shape changes associated to size variation. Being obtained using a multivariate regression of the Fourier coefficients on the size estimator ($\ln A_0$), they correspond to the shape of a conodont of size $\ln(A_0) = -1$ (left) and $\ln(A_0) = 1$ (right). These size values are equivalent to a P1 element length of ~ 0.2 mm and ~ 1.1 mm, respectively. The grey boxes represent the Lower (LKW) and Upper (UKW) Kellwasser events.

24.3% of the total variance) are clearly related to the size of the conodont element (Fig. 3). A linear regression between PC1 and A_0 is significant ($N = 451$, $P < 0.001$, $R^2 = 0.547$) despite a non-linear pattern (Fig. 3A), suggesting that a log transformation may be relevant. Note that the log transformation is used in the context of allometric studies for two reasons. First, it allows to express the relationship between two size variables ($y = bx^k$) as a linear relationship. Second, it puts the size variables on a multiplicative (logarithmic) scale, which is relevant for the interpretation of most size data since growth is a multiplicative process (Warton *et al.* 2006). On the contrary, shape axes are not multiplicative and a shift of one

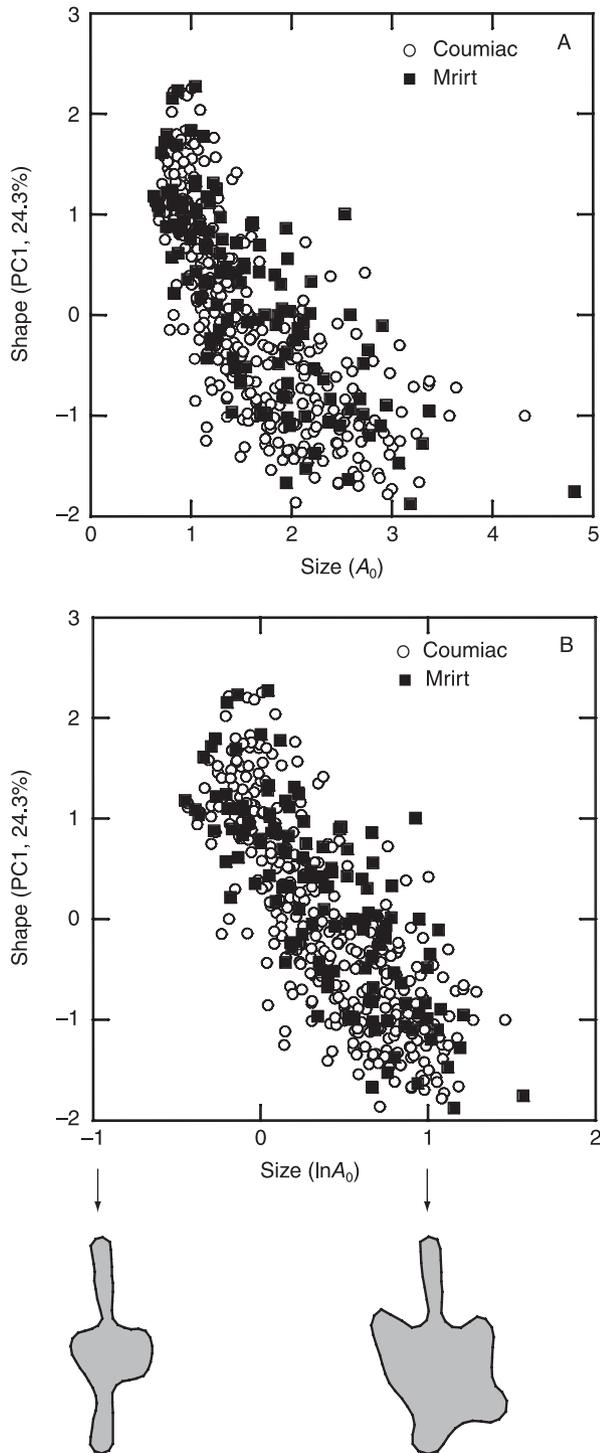


Fig. 3. Shape, estimated by scores on PC1, versus size estimated by A_0 (A) and $\ln A_0$ (B). Open circles = conodonts from Coumiac; black squares = conodonts from Mrirt. The reconstructed outlines visualize the allometric shape changes associated to size variation. Being obtained using a multivariate regression of the Fourier coefficients on the size estimator ($\ln A_0$), they correspond to the shape of a conodont of size $\ln(A_0) = -1$ (left) and $\ln(A_0) = 1$ (right).

unit along PC1 corresponds to the same amount of shape change whatever the position on the axis. Hence, the log transformation was considered relevant for the size estimator A_0 but not for the shape variables (PC1 and FCs, which are not proportional to size). Consequently, the allometric relationship was investigated by considering $PC1 = k \ln(A_0) + \ln(b)$, but the allometric coefficient k cannot be compared with usual values derived from the comparison of two size-related measurements.

Using this equation provided a linear size–shape relationship (Fig. 3B) and increased the amount of variance explained by the regression ($R^2 = 0.617$). Hence, thereafter, $\ln(A_0)$ was considered as the size variable to be compared with shape. This highly significant relationship between size and shape evidences the existence of a strong allometry, the definition of this concept being an association between shape and size (Klingenberg 1998).

The size–shape relationship was quite similar between the two outcrops, the slope and the intercept being slightly different as shown by their estimated standard error (Table 4). The paucity of specimens in most of the levels hindered a robust estimate of the regression and hence to test if the size–shape relationship was stable over time, results based on the few well-sampled levels suggest that some variations occur among levels without clear temporal pattern (Table 4).

In order to analyse the allometric pattern of growth in a fully multivariate way, a regression of the FCs upon $\ln(A_0)$ was performed. It confirmed the highly significant size–shape relationship corresponding to allometric growth (Wilks' lambda $P < 0.0001$). Based on this analysis, sets of FCs corresponding to given size values were calculated, providing a visualization of the multivariate allometric shape changes along the growth of *A. curvata* (Fig. 2). In agreement with the pictures of real specimens (Fig. 1), conodonts of small size are characterized by an elongated blade relative to a reduced platform. The larger grows the conodont, the larger the platform, which becomes more and more asymmetrical and star-shaped.

Size-free shape variation

The residuals of the multivariate regression of the FCs upon $\ln(A_0)$ were considered as size-free shape estimators that were analysed using multivariate statistics (Fig. 4). Significant differences emerged among samples (MANOVA: $P < 0.001$). The first canonical axis (26.7% of the among-group variance) was considered as a synthetic size-free shape axis. It represented twice as much variance as the following axis (not shown, 14.1%) that only corresponds to the divergence of poorly sampled levels (e.g. M11a).

Table 4. Regression between size (independent variable, estimated by $\ln(A_0)$) and shape (dependent variable, estimated by scores on PC1).

		N	P	R	Slope	± SE	Intercept	± SE
Coumiac + Mrirt	Total	451	0.000	0.785	-1.879	0.070	0.763	0.041
	Coumiac	318	0.000	0.793	-1.931	0.083	0.721	0.049
Coumiac	CUQ24a	39	0.000	0.743	-2.163	0.321	0.744	0.143
	CUQ31e	35	0.000	0.898	-2.456	0.209	1.073	0.120
	CUQ31f	118	0.000	0.784	-1.774	0.130	0.601	0.083
	Total	133	0.000	0.778	-1.743	0.123	0.859	0.071
Mrirt	M03	27	0.000	0.831	-1.187	0.159	0.681	0.088
	M09	25	0.000	0.837	-2.608	0.355	0.980	0.180
	Total	52	0.000	0.834	-1.947	0.255	0.830	0.100

N, number of specimens; P, probability; R, coefficient of regression; SE, standard error.

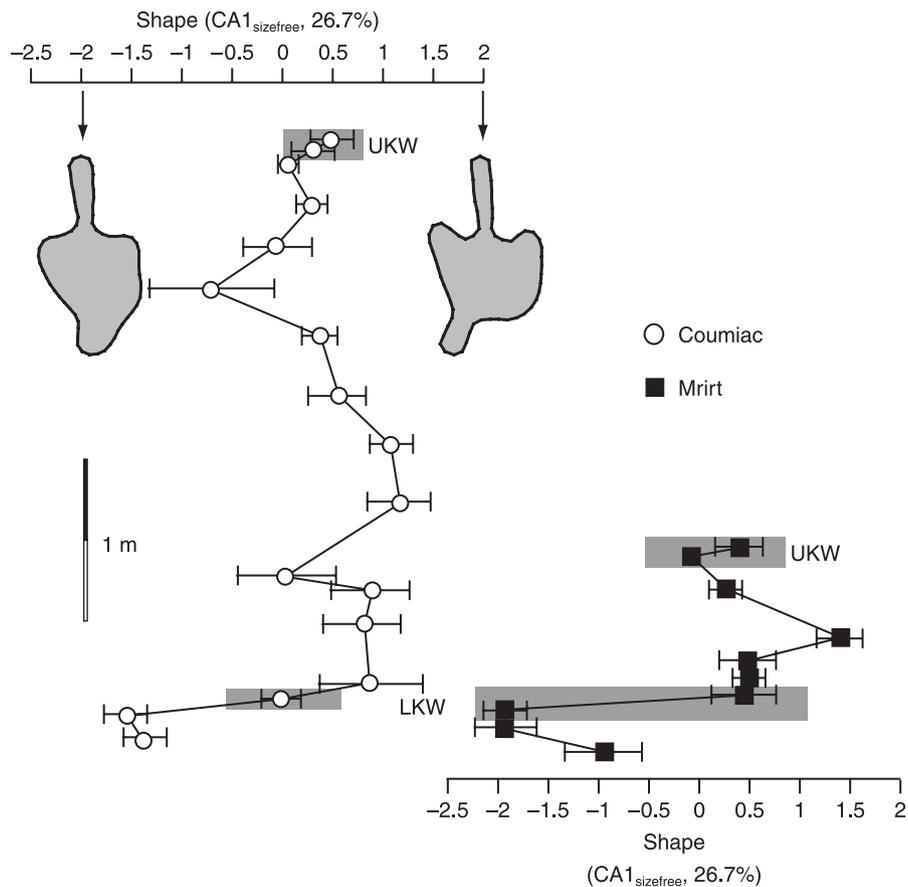


Fig. 4. Size-free morphological variations of *Ancyrodella curvata* estimated by the first canonical axis ($CA1_{size-free}$, 26.7% of the variance) through time in the two sections. Symbols correspond to the average value per level; error bars to the 95% confidence interval. Symbols: black squares for Mrirt; open circles for Coumiac. The reconstructed outlines visualize the shape changes involved along $CA1_{size-free}$. They correspond to $CA1_{size-free} = -2$ (left) and $CA1_{size-free} = 2$ (right). The grey boxes represent the Kellwasser events (LKW = Lower Kellwasser; UKW = Upper Kellwasser).

Coherent temporal trends emerge on $CA1_{size-free}$, comparable among sections (Fig. 4). The most important morphological shift occurs around the LKW, from negative $CA1$ values preceding the LKW to positive values following it. Samples documenting the LKW itself delivered intermediate values (CUQ section) or values similar either to the pre- or the post-LKW situation (Mrirt section).

Maximal values along $CA1$ are reached in the middle of the interval between the two Kellwasser events.

Values decrease before the beginning of the UKW, and slightly increase again during the event. $CA1_{size-free}$ opposes on the negative side, straight conodonts with a rather triangular platform, to star-shaped conodonts with a curved blade on the positive side.

Looking at the distribution of the scores across levels (Fig. 5), the shape variation through time does not correspond to a distribution shifting its mode within a stable range of morphologies. Rather, the end of the LKW is marked by the occurrence of new

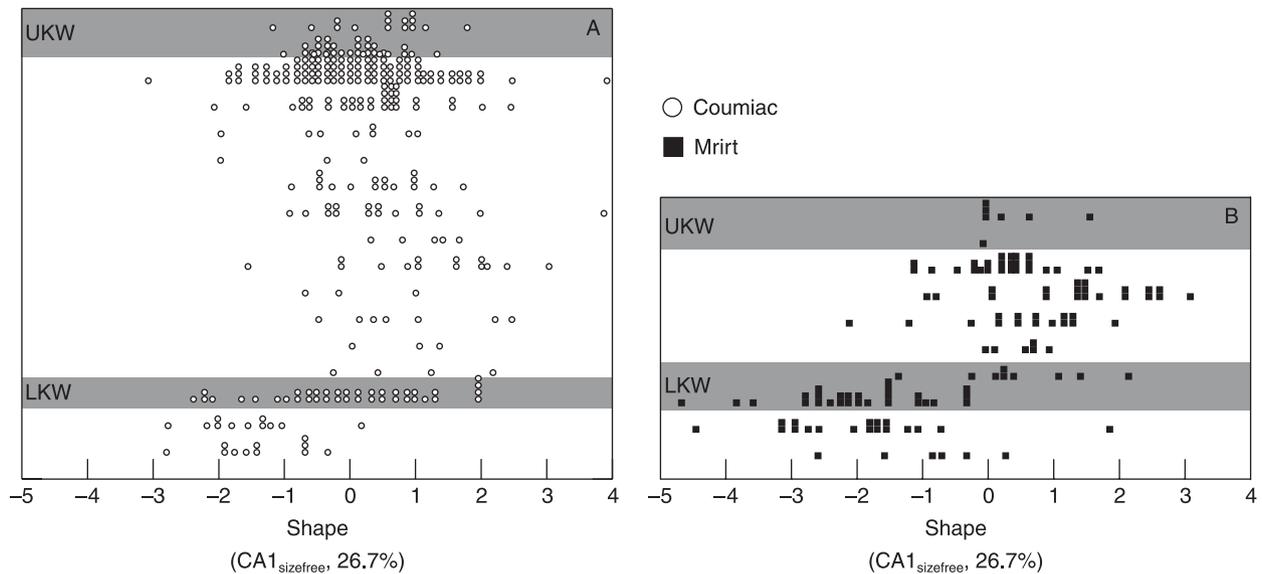


Fig. 5. Dot density of scores along CA1_{size-free}: each dot represents a specimen. Dots are plotted separately for each level in (A) Coumiac and (B) Mrirt. Symbols: open circles for Coumiac, black squares for Mrirt. The grey boxes show the Kellwasser events. LKW, Lower Kellwasser; UKW, Upper Kellwasser.

morphotypes towards the positive values of CA1_{size-free} and the disappearance of extreme morphotypes on the other side of the distribution (negative side of the range). The trend between the two Kellwasser events corresponds to a progressive re-appearance of morphotypes with negative CA1_{size-free} values, whereas the upper range remained approximately stable.

Abundance and survivorship

Ancyrodella curvata was part of an ecosystem where other conodont genera managed to survive the F/F crisis. Characterizing the ecology of long extinct taxa is difficult and remains hypothetical, but we compared the genus *Ancyrodella* with two successful survivors *Palmatolepis* and *Icriodus* on two respects: their relative abundance in the deposits and their survivorship along growth.

Four types of conodonts composed the assemblages during the considered time interval: ancyrodellids (comprising morphologically similar platform genera such as *Ancyrodella* with few *Ancyrognathus* and *Ancyroides*), *Icriodus*, *Palmatolepis* and *Polygnathus*. The composition of the Late Frasnian assemblages in Coumiac and Mrirt (Fig. 6) mostly depends on the balance between *Icriodus* and *Palmatolepis*. The genera *Icriodus* and *Palmatolepis* contributed on average for 10% and 50% of the assemblages, respectively. Maximal abundances reach more than 40% for *Icriodus* and more than 80% for *Palmatolepis*. In contrast, ancyrodellids were minor parts of the conodont fauna, contributing for 0–10% of the assemblages.

Some insights into the life history traits can be gained from the analysis of 'survivorship' (i.e. the percentage

of animals reaching a given size). Such analysis is relevant only if focused on a single species. For two genera in our assemblages, the genus included only or dominantly a single species in the documented sections: *Ancyrodella* with the single species, *A. curvata*; and *Icriodus*, mostly composed of *I. alternatus*. Many species have been described within the genus *Palmatolepis* but morphometric analysis during the time interval considered suggested that they may document extreme morphotypes of a variable scatter of morphologies, and that considering together all elements of the genus *Palmatolepis* may be closer to the biological entity (Girard *et al.* 2004b, 2007). Hence, in the three cases, considering the genus approximates to focus on single species.

In order to compare genera reaching very different size, the size (estimated in all cases by A_0) was standardized to the upper limit of the distribution, taken as the 95% percentile of the distribution in order to limit the impact of very rare, extremely large conodonts. To take into account variations between outcrops and levels, survivorship was estimated for different samples providing a large number of specimens. Curves appeared to be different among the three taxa, but relatively consistent within each taxon (Fig. 7). *Ancyrodella curvata* displayed rather straight curves indicating a mortality rate constant throughout the life of the animal (Fig. 7A). In contrast, curves of *Palmatolepis* are concave towards the bottom, indicating high mortality rates for small-sized conodonts and a stabilization thereafter (Fig. 7B). Curves of *Icriodus* are sigmoid and suggest that mortality was particularly important for conodont of intermediate size (Fig. 7C).

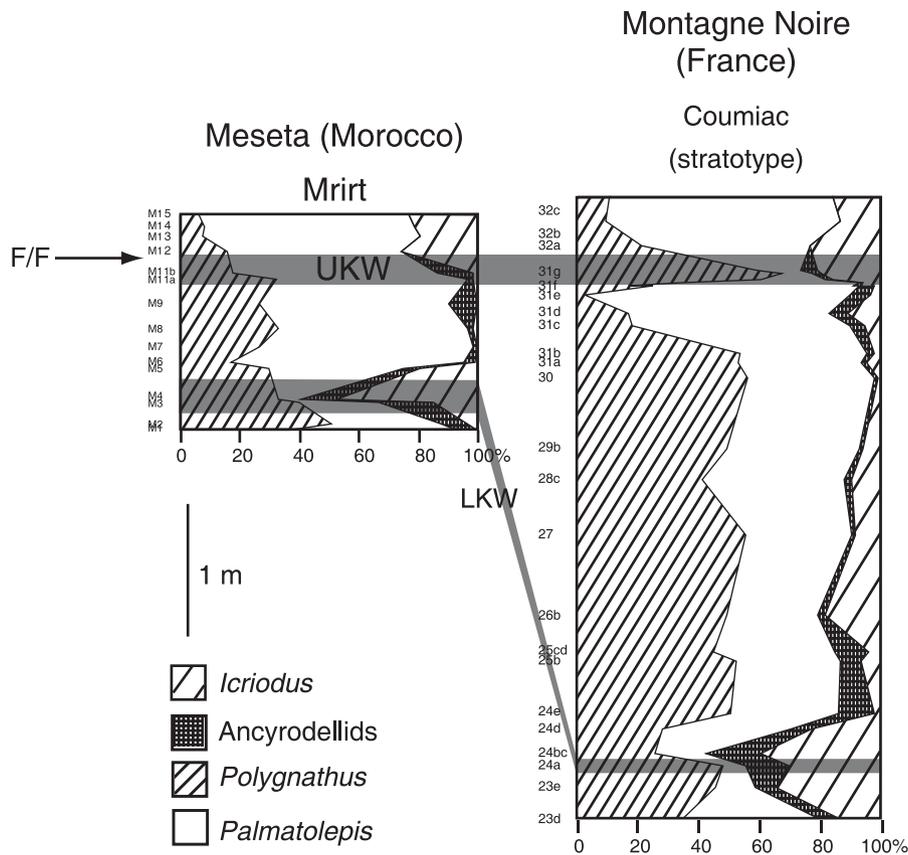


Fig. 6. Variations in relative proportion of the conodont genera composing the total assemblage in the two sections. F/F: Frasnian/Famennian boundary. In grey, the anoxic events: Lower Kellwasser (LKW) and Upper Kellwasser (UKW).

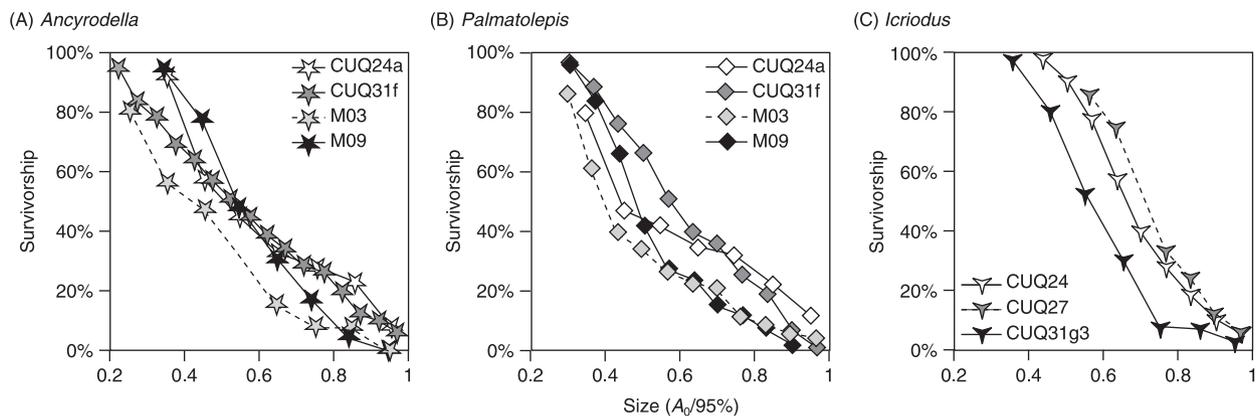


Fig. 7. Survivorship curves for (A) *Ancyrodella*, (B) *Palmatolepis*, and (C) *Icriodus*. Size estimator was A_0 , standardized within each level by the 95% percentile value of the size distribution. □A. CUQ 24a: 39 specimens, CUQ 31f: 118; M03: 27; M09: 25. □B. CUQ 24a: 37 specimens, CUQ 31f: 94; M03: 71; M09: 52 (data from Girard & Renaud 2007). □C. CUQ 24: 79 specimens; CUQ 27: 42; CUQ 31g3: 41 (data from Renaud & Girard 1999).

Discussion

Disentangling size-related and size-free shape variation

Although taken together, size and shape constitute the form of a biological object such as a conodont

element, their palaeobiological meaning can be quite different. Body size is related to growth and numerous factors, such as local conditions and life history traits, can affect this feature in extant animals. Body size is such a labile trait because it can vary without major genetic modifications, by changes in the expression of growth hormones (Bünger & Hill 1999). The

relationship between body size of the conodont animal and the size of the conodont element is not well assessed, but each element grows by accretion of concentric lamellae. The size reached by the elements thus likely increased with the age of the animal. This relationship between body and element size is confirmed by the few conodont body trace that indicate that larger conodonts bore larger elements (Purnell 1994; Donoghue & Purnell 1999). In contrast, the size-free component of shape should be less malleable than size, and despite complex developmental pathways such shape changes should be ultimately related to genetic modifications (Tucker & Sharpe 2004).

The conodont *A. curvata* exemplifies a case where the important allometric component in the growth of the element can interfere with other sources of shape variation, like evolutionary changes through time. Applying a multivariate regression of morphometric estimators vs. size allowed getting size-free shape parameters and disentangle the two aspects of shape variation: size-related and size-free shape changes. The first aspect should generate variation within and among levels, due to the size distribution of the elements in each level. The second aspect may include two parts: it can correspond to variations of the allometric relationship among levels and sections, or to changes in the shape of the elements independently of the growth. This may correspond to a difference in the shape of the nucleus, or of the zones of preferential accretion during the subsequent growth. In both cases, we can assume that these changes will have a genetic origin and hence document evolution through time.

Different conodont genera, different processes of response to the Kellwasser events

A microevolutionary response, traced by morphometric variations, to the Kellwasser anoxic events had been evidenced so far in two other conodont genera, *Icriodus* and *Palmatolepis* (Renaud & Girard 1999). Size and shape of the platform elements of *Icriodus* are related, evidencing an allometric source of shape variation. In this genus, however, size displays coherent patterns of temporal variations, levels just posterior to both the LKW and UKW clustering towards small size and being opposed to large-sized conodonts found during the inter-Kellwasser interval and at the end of the recovery period following the F/F crisis (Renaud & Girard 1999). Shape changes are observed in response to the Kellwasser events but they can be attributed to the size variations, suggesting that *Icriodus* responded to the successive events by shifts in its life history traits and that the

shape changes merely resulted from an allometric relation with size.

A response of *Palmatolepis* to both Kellwasser events was traced as well (Renaud & Girard 1999; Girard *et al.* 2004a, b). However, the shape response was not related to size by any allometric relationship. It has been interpreted as an evolutionary change affecting the shape of the nucleus and the zone of preferential accretion during the subsequent growth, possibly in response to selective pressures related to diet changes (Girard *et al.* 2007).

The present study evidenced that *A. curvata* reacted to the LKW event, as did *Icriodus* and *Palmatolepis*. Despite a strong allometric component of its growth, size-related shape changes were not involved in this response, in contrast to *Icriodus*. The changes affected the shape of the platform, independently of the growth pattern. The shape change at the end of the LKW corresponds to the apparition of new star-shaped morphotypes. We thus interpret this pattern of morphometric variation as a hint for an evolutionary response of *A. curvata* to the environmental conditions prevailing at the time. Because of the poor knowledge regarding the occlusion of *Ancyrodella* elements within the feeding apparatus, it is difficult to go further and bring an adaptive interpretation to this shape change.

Our results anyway evidence a response of *A. curvata* to the LKW. Hence, the extinction of *A. curvata* at the F/F crisis cannot be attributed to the inability to react to minor events.

Potential of response to a minor event is not a key to survival to major events

Several works suggested that biotic factors enhancing survivorship during times of environmental perturbations of limited impact were ineffectual during mass extinctions (Jablonski & Raup 1995). Our results support this assertion since the ability of *A. curvata* to respond in response to the minor event of the LKW is demonstrated; yet, this potential of response was ineffective to avoid its extinction at the end of the next anoxic event.

However, the potential of response of *A. curvata* could have been less than the one of *Icriodus* and *Palmatolepis*. It remains a signal of secondary importance compared with the amount of size-related shape change. Furthermore, the apparently important response of *A. curvata* to the LKW may be an artefact of the extinction of *Ancyrodella* at the F/F boundary, depriving the analysis of Famennian samples. The record of *Palmatolepis* and *Icriodus* shows that the morphological shift at the F/F boundary is of overwhelming importance compared with the shift associated to the LKW. Focusing the *Palmatolepis*

analysis on the Frasnian period evidenced a clear LKW shift (Girard & Renaud 2007) similar to the pattern observed for *A. curvata*.

Alternative factors increasing risks of extinction

The genera *Ancyrodella*, *Icriodus* and *Palmatolepis* demonstrated a potential of response to the minor event of the LKW that may have been a prerequisite for survival to background variations in temperature, sea level, and/or oxygen conditions in the water column. Alternatively, the survival to major perturbations may be conditioned by other factors (Jablonski & Raup 1995; McKinney 1997; Twitchett 2006). Groups with a restricted distribution area seem more prone to extinction than cosmopolitan ones, but this range of explanation does not seem relevant in the present case, since all Late Devonian conodont genera do share a similar, tropical/subtropical range.

Other ecological characteristics may have influenced the differential response of *Ancyrodella* vs. *Icriodus* and *Palmatolepis* to the crisis. A first factor is the relative abundance of the taxa within the assemblages. The Late Frasnian assemblages at Coumiac and Mrirt were highly dominated by *Polygnathus* and *Palmatolepis*, together often contributing to more than 80% of the total assemblage except during the deposition of the Kellwasser events marked by an obvious increase of *Icriodus* (Fig. 6). This dominance is not only a local characteristic of the Coumiac and Mrirt outcrops, but it is also found in many other locations (Sandberg *et al.* 1988; Morrow 2000). It is the result of eustatic variations favouring in turn *Icriodus*, which was confined in the upper photic zone, or the deeper water *Palmatolepis* (Seddon & Sweet 1971). In contrast, *A. curvata* appears as a minor component of the fauna at Coumiac and Mrirt, hardly reaching 10% of the assemblage in the levels where it is the most abundant (Fig. 6). Indeed, *A. curvata* is overall a rare species, only reaching up to 40% of the assemblages in restricted environments corresponding to moderately shallow, high energy environment around mudmounds (Sandberg *et al.* 1992).

The role of abundance as favouring survival, however, has been challenged (Lockwood 2003). Another factor that may influence the probability of extinction is the demographic structure characterizing the species: a specialist, K-selected species may be more prone to extinction than an opportunist r-selected species (Southwood *et al.* 1974). Although such inferences on long extinct taxa are very hypothetical, the distribution of the conodont frequency as a function

of its size may provide a clue about the pattern of mortality of the considered taxon (Tolmacheva & Purnell 2002). Isolated conodont elements may have fallen to the sea floor from floating carcasses, thereafter disrupted by current activity and bioturbation on sea floor; alternatively, the remains may have been the product of predators (Tolmacheva & Purnell 2002). Hence, survivorship curves expressed either the effect of predation or natural mortality.

Palmatolepis is characterized by an early high mortality (Fig. 7), a survivorship pattern corresponding to assemblages dominated by small-sized conodonts (Girard *et al.* 2004b). This suggests that this taxon invested much in early reproduction, allowing a rapid turnover, all traits that characterize opportunistic taxa. Differently, *Icriodus* appeared to have a low 'juvenile' mortality, but to suffer a high selective mortality at intermediate size. This suggests that this taxon reached similar ages. Finally, *A. curvata* exhibits constant rates of mortality. This may imply that the species had a long growth, as supported by the frequent occurrence of very small to very large specimens in the assemblages (Fig. 1); this further suggests that the reproductive effort was progressive along life. This demographic characteristic may have been unfavourable in perturbed environments compared with the rapid turnover inferred for *Palmatolepis* populations.

Conclusions

The morphometric study of *A. curvata* allowed a quantification of the allometric growth of its platform elements. The size-related and size-free shape variations were disentangled from each other using a multivariate regression approach. This method evidenced a morphometric response of *A. curvata* to the LKW anoxic event independent of the allometric growth characterizing the genus.

Other conodont genera (*Palmatolepis*, *Icriodus*) have also been shown to display response to the LKW. Since *Palmatolepis* and *Icriodus* survived the F/F crisis punctuating the next anoxic event (UKW), whereas *Ancyrodella* went extinct at this crisis, the potential of response to the minor LKW event is not a key to successful survival of the major UKW event.

Alternative factors may have contributed to the extinction of *Ancyrodella*: overall low abundance, specialized habitat preferences, and low and constant mortality along life suggesting a K-selected demographic strategy. If none of these factors seem to be a sufficient explanatory factor, their unfavourable conjunction might have been the key to the extinction of *Ancyrodella*.

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