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Step-wise morphological trends in fluctuating environments: Evidence in the Late Devonian conodont genus *Palmatolepis*

Tendance morphologique non-progressive en environnement instable : exemple du conodonte *Palmatolepis* (Dévonien supérieur)

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Abstract

Long-term morphological changes were investigated in the conodont genus *Palmatolepis*, using a Fourier analysis of the outline of platform elements. Three time-slices and four Late Frasnian – Early Famennian sections on North Gondwana were studied. No difference existed between locations, but shape variations were recorded associated with the successive Kellwasser events. The Middle Famennian period was analyzed in a section located at the Baltica margin across the *annulata* event. Some morphological changes may be related to the deposition of the corresponding black shales, but the main feature is a heterogeneity of the populations, which can be split into two morphological types. Latest Famennian conodonts from another North Gondwanan section show only minor shape changes during this time interval, which is environmentally stable prior to the global Hangenberg event. Based on synthetic shape variations across the whole period an morphological trend towards narrower elements is observed. This morphological change happens step-wise in response to global events. The amplitude of the shape shift is proportionally related to the extend of the successive Late Devonian global events.
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Résumé

Les tendances morphologiques à long terme du conodonte *Palmatolepis* ont été étudiées par l'intermédiaire d'une analyse de Fourier du contour de l'élément plate-forme. Trois intervalles de temps et quatre coupes ont été considérés. Deux coupes du Nord Gondwana couvrent le Frasnien supérieur – Famennien inférieur. Les conodontes de ces deux coupes sont morphologiquement similaires, mais des variations de forme sont enregistrées lors des deux événements successifs du Kellwasser. Une coupe de la Baltica échantillonne l'événement *annulata* (Famennien moyen). Des changements morphologiques peuvent être reliés au dépôt des schistes noirs *annulata*, mais le résultat principal est une hétérogénéité des populations, qui peuvent être séparées en deux types morphologiques. Une dernière coupe du Nord Gondwana permet l'analyse de la période du Famennien terminal. Seuls des changements de forme mineurs sont observés durant cet intervalle de temps, qui est environnementalement stable bien que précédant l'événement global Hangenberg. Considérant les variations synthétiques de forme à travers la période dans son ensemble, une tendance morphologique vers des éléments plus étroits est observée. Ce changement morphologique se produit de manière non progressive, alternant des périodes de stase et des sauts morphologiques en réponse aux perturbations environnementales. L'ampleur des sauts morphologiques semble liée à l'importance des événements globaux successifs du Dévonien supérieur.
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Keywords: Frasnian/Famennian; Kellwasser; *Annulata*; Hangenberg; Morphometrics; Fourier analysis

Mots clés : Frasnien/Famennien ; Kellwasser ; *Annulata* ; Hangenberg ; Morphométrie ; Analyse de Fourier

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1. Introduction

The Late Devonian is characterized by a succession of anoxic events apparently coupled with global sea-level fluctuations (Johnson et al., 1985). Among them, the Upper Kellwasser (UKW) event at the Frasnian/Famennian (F/F) boundary and the Hangenberg event close to the Devonian/Carboniferous (D/C) boundary are associated with mass extinctions among both benthic and pelagic organisms (Walliser, 1996). The anoxic conditions observed worldwide during these two events seem to be synchronous at geological time-scale in off-shore environments. Rapid sea-level changes occurred during both the late Frasnian and the late Famennian (Sandberg et al., 2002). World-wide Devonian anoxic episodes include the Lower Kellwasser (LKW) approximately 2 My before the UKW and the *annulata* event some 10 My after the UKW. These events have lesser effects on the faunas than the UKW and Hangenberg events but are also correlated with sea-level fluctuations (Becker, 1993). The succession of the Lower and Upper Kellwasser events constitutes the Kellwasser crisis.

Our purpose is to investigate the morphological changes of organisms over a period of approximately 15 My, and contrast long-term patterns with short-term variations observed during three time intervals: the Late Frasnian – Early Famennian (around the F/F boundary), the *annulata* event, and during the Latest Famennian closely before the D/C boundary.

This study is based on a morphometric analysis of conodont elements. These are parts of the feeding apparatus of an extinct marine animal supposedly close to the vertebrates (e.g. Aldridge et al., 1993; Janvier, 1995). Several paired elements of different types composed a complex feeding apparatus (Purnell, 1994; Donoghue and Purnell, 1999). Among these different types of elements, we focused on platform elements, because they display the most rapid evolution, and have therefore been used extensively for biostratigraphic purposes. Among them, the *Palmatolepis* genus has been selected for this study, because it is abundant and is the best known conodont genus of the Late Devonian period. It appears at the beginning of the Frasnian and disappears at the end of the Famennian close to the D/C boundary. In order to follow its variations through time, the morphological changes have been quantified using an outline analysis based on Fourier transform.

Previous studies investigated the morphological response of *Palmatolepis* to the Kellwasser crisis in the Montagne Noire, France (Renaud and Girard, 1999; Girard et al., 2004). These studies have shown that a major morphological shift was associated with the Upper Kellwasser (F/F boundary) while a minor shape change occurred during the Lower Kellwasser. In the present study, another section documenting the Kellwasser period, M'rirt (Morocco) is compared to the Coumiac reference section. These two outcrop areas that include the Kellwasser period are compared to two additional Late Devonian sites (Fig. 1): the Effenberg section (Rhenish Massif, Germany) contains the anoxic episodes associated with the *annulata* event. The section of Puech de la Suque (Montagne Noire, France) has been chosen for the period immediately preceding the Hangenberg event (D/C boundary). All sections were characterized by similar paleoenvironments, being deposited on carbonate platforms in off-shore conditions.

According to paleogeographic reconstructions (Scotese and McKerrow, 1990), these strata were deposited in the tropical zone during the Late Devonian. The Montagne Noire (France) and the Meseta (Morocco) were probably separated by approximately the same latitudinal gradient as now (Fig. 2) and belonged to the North Gondwana margin. The Rhenish Massif (Germany) was located on Baltica, but the limited distance to North Gondwanan sections should not have hindered mixing of active swimming pelagic organisms such as conodonts.

2. Material and Method

2.1. Material

All the rock-samples have been dissolved in formic acid (10%) and the samples have been washed through a 100 µm and a 1 mm sieves. The fraction retained by the 100 µm sieve was picked for all conodont elements.

For the Kellwasser period (Late Frasnian – Early Famennian), 15 levels have been sampled in the M'rirt section (western Meseta, Morocco) and compared to 8 levels from the Coumiac section (Montagne Noire, south France). Stratigraphic dating and correlation between sections have been based on Lazreq (1992, 1999) and Klapper (1989).

The Middle Famennian *annulata* event has been investigated in the Effenberg section, Rhenish Massif, Germany, whose stratigraphy and sedimentological setting have been described by Korn and Luppold (1987). Seven samples provided enough material for statistical analyses. In the Late Famennian sequence preceding the Hangenberg event, 19 levels have been sampled at the Puech de la Suque section (Montagne Noire, France). The samples analyzed in this study are the same as those used for biofacies by Girard (1994) but some of them have been pooled in order to obtain enough *Palmatolepis* for morphometrics (Table 1).

It should be noted that whereas conodonts were present in the anoxic levels characterizing the Kellwasser events, conodonts were not recovered from the black shales characterising the *annulata* and Hangenberg events.

2.2. Fourier analysis of the outline

Conodont animals have a bilateral symmetry. Both right and left *Palmatolepis* elements are found in a population. 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 morphometric

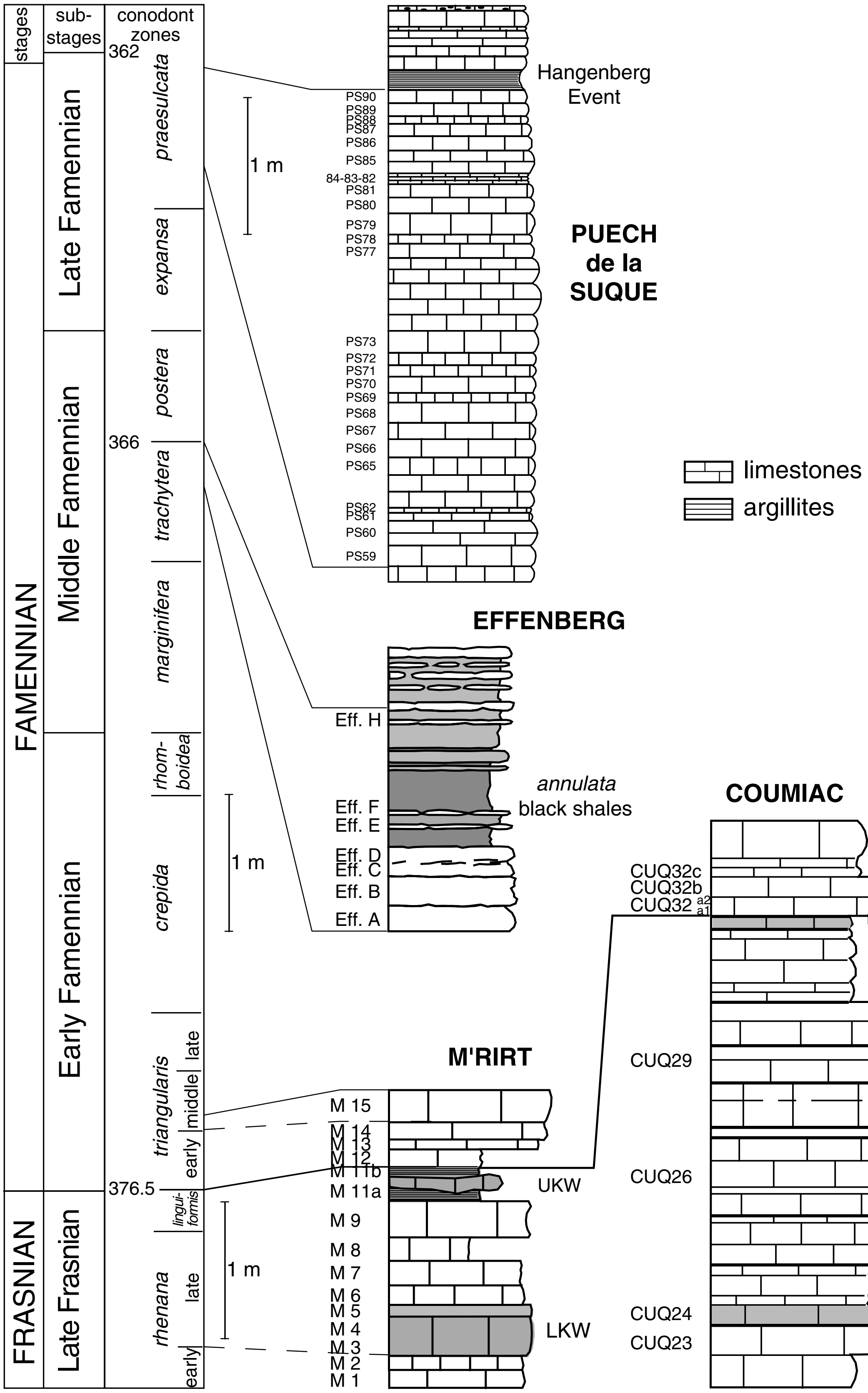

Fig. 1. Stratigraphical logs of the sections, chronologically positioned along the Frasnian and Famennian conodont zonation (Sandberg et al., 2002). Approximate ages after Tucker et al. (1998). In gray the anoxic deposits. LKW: Lower Kellwasser, UKW: Upper Kellwasser.

Fig. 1. Logs stratigraphiques des coupes, positionnés en fonction de la zonation basée sur les conodontes du Frasnien et du Famennien (Sandberg et al., 2002). Âges approximatifs d'après Tucker et al. (1998). En gris les niveaux anoxiques. LKW : Kellwasser inférieur, UKW : Kellwasser supérieur.

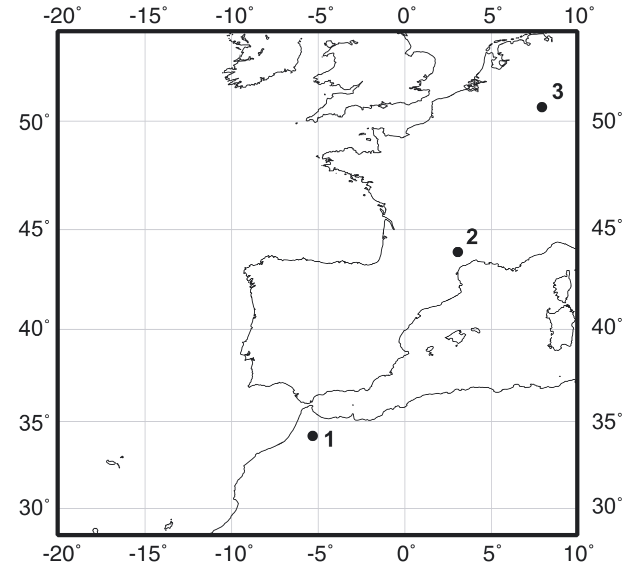

Fig. 2. Approximate location of the sections. 1 = M'rirt (Morocco), 2 = Coumiac and Puech de la Suque (France), 3 = Effenberg (Germany).
Fig. 2. Localisation approximative des coupes. 1 = M'rirt (Maroc), 2 = Coumiac et Puech de la Suque (France), 3 = Effenberg (Allemagne).

analysis since the asymmetry between right and left elements has been determined to be negligible (Renaud and Girard, 1999). The two-dimensional outline of each conodont was automatically digitized using an image analyzer (Optimas v. 6.0). For each conodont, *x*- and *y*-coordinates of 64 points were sampled at equally spaced intervals along the outline. The starting point was defined at the top of the conodont (tip of the anterior carina). From the coordinates, 64 radii were calculated corresponding to the distance of each point to the center of gravity of the conodont outline. A Fourier transform was then applied to this set of 64 radii. The outline is thus expressed as a finite sum of trigonometric functions of decreasing wave-length (harmonics) according to the formula:

$$r(s) = a_0 + \sum_{n=1}^{K} [a_n \cos(2\pi n \ s/L) + b_n \sin(2\pi n \ s/L)]$$

where r is the radius at the abscissa s along the outline, L the perimeter, K the number of points along the outline, and n the rank of the harmonic. The outline is therefore described by the set of Fourier coefficients a_n and b_n. A reconstruction of the outline corresponding to any set of Fourier coefficients can be obtained using an Inverse Fourier Transform. The zeroth harmonic, a_0, is proportional to the size of each conodont element and was used to standardized all the Fourier coefficients, in order to retain shape information only.

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

2.3. Multivariate analysis of the Fourier coefficients

For each conodont, a set of 24 Fourier coefficients (i.e. twelve harmonics characterized by two coefficients a_n and

Table 1
Number of elements considered per section and per level. In gray the location of the anoxic events. Approximates ages after Tucker et al. (1998)
Nombre d'éléments mesurés par coupe et par niveau. En gris localisation des événements anoxiques. Âges approximatifs d'après Tucker et al. (1998)

		My		samples	measured *Pa.*		samples	measured *Pa.*
LATE DEVONIAN	Famennian		Puech de la Suque					
		362,0		PS90	13			
				PS88-89	14			
				PS87	8			
				PS86	6			
				PS85	10			
				PS84	23			
				PS83	52			
				PS82	6			
				PS81	44			
				PS80	27			
				PS79	52			
				PS78	44			
				PS77	71			
				PS73	49			
				PS69-72	39			
				PS65-67	11			
				PS62	7			
				PS61	11			
				PS59-60	33			
			Effenberg		type1/type 2			
				Eff. H	7 / 8			
				Eff. F	2 / 1			
		366,0		Eff. E	3 /12			
				Eff. D	32 / 12			
				Eff. C	6 / 29			
				Eff. B	4 / 11			
				Eff. A	24 / 15			
			M'rirt	M15	98	Coumiac (Upper Quarry)	CUQ32c	45
				M14	42		CUQ32b	45
				M13	133		CUQ32a2	32
				M12	6		CUQ32a1	19
	Frasnian	376,5		M11b	25			
				M11a	13			
				M9	52		CUQ29	350
				M8	74			
				M7	81			
				M6	420		CUQ26	235
				M5	59			
				M4	12			
				M3	71		CUQ24	37
				M2	200		CUQ23	18
				M1	63			

b_n) was obtained. Multivariate Analysis of Variance (MANOVA) were performed on these variables in order to evaluate the importance of the among-group differentiation relative to within-group variations, where groups are the different stratigraphic levels of the different sections, and eventually the different *Palmatolepis* populations within some levels. A test of significance for among-group differences (Wilk's Lambda test) is provided. Associated with the MANOVA, canonical functions are estimated. The morphological variability can be visualized in the space defined by the first two canonical axes, which are usually sufficient to account for all important group differences (Marcus, 1993). In order to further visualize the shape changes involved through time, theoretical outlines can be reconstructed corresponding to the mean values of some samples, and to variations along the canonical axes.

3. Results

Several statistical analyses have been performed to investigate patterns of morphological variations, three analyses focused separately on the periods of the Kellwasser, *annulata*, and pre-Hangenberg events. Additionally, a global analysis including all samples has been performed. In all cases, the morphological differentiation was highly significant (Wilk's Lambda test: $P < 0.0001$).

3.1. Structure of the conodont populations in the three time-slices

Several species, both contemporary and successive in geological time, have been described within the genus *Palmatolepis*. During the Late Frasnian / Early Famennian period, however, the different *Palmatolepis* species varied similarly through time (Renaud and Girard, 1999). Therefore, the morphological variations of the genus were efficiently described by an outline analysis pooling all the *Palmatolepis* of a sample (Girard et al., 2004). This approach is only valuable if the population is homogeneous. The patterns of morphological variability per sample were therefore investigated in the different sections (Fig. 3) using a MANOVA grouped by stratigraphic level. In both Late Frasnian / Early Famennian sections all conodonts belonging to the genus *Palmatolepis* could be considered as part of a homogeneous paleopopulation. At the end of the Famennian, just before the Hangenberg event, which coincides with the extinction of the genus *Palmatolepis*, the paleopopulations are composed of only one species, *Pa. gracilis*. This is confirmed by the homogeneous distribution of the conodonts in each sample. Hence, all *Palmatolepis* have been taken together as for the Kellwasser period.

Conversely, *Palmatolepis* paleopopulations around the *annulata* event cannot be considered homogeneous (Fig. 3(B)). According to the phylogenetic *Palmatolepis* reconstructions of Sweet (1988), different Famennian *Palmatolepis* lineages diverged from the single stock species *Pa. triangularis* that survived the Kellwasser crisis. Accordingly, the paleopopulations observed across the *annulata* event segregate in two different groups along the canonical axes: elements with well-developed platform (type 1) *vs*. narrow elements (type 2).

3.2. Late Frasnian - Early Famennian (Kellwasser events)

Patterns of shape variations in palmatolepid platform elements across the two successive anoxic Kellwasser events have been investigated and compared in the two sections of M'rirt and Coumiac. The first two canonical axes are sufficient to describe a large proportion of the among-group variance (CA1 = 64.8%, CA2 = 16.8%). The subsequent axes have a contribution of less than 10%.

The main morphological difference discriminates Frasnian and Famennian palmatolepids along the first canonical axis (Fig. 4). This change corresponds to the impact of the Upper Kellwasser event (UKW). Temporal segregation is further expressed along CA2. On the first hand, a Frasnian shape variability exists, separating the oldest palmatolepid taxa up to the beginning of Lower Kellwasser event (LKW) from the youngest Frasnian samples. On the other hand, shape differences within the Early Famennian period are also expressed along CA2. While the palmatolepids immediately following the Frasnian/Famennian boundary are clustered together, the youngest samples of both sections diverge along CA2 (M15 and CUQ32c). These variations among the Frasnian and Famennian are nevertheless of limited importance compared to the shift associated with the F/F boundary, as shown by the small amount of among-group variance expressed on CA2 (16.8%) compared to CA1 (64.8%). Noteworthy, no difference among the two sections can be identified. Samples of the same age appear to be of the same shape, and morphological shifts occur simultaneously at both locations.

Most morphological shifts observed using the present population-level approach can be related to changes in the taxonomic composition of the genus *Palmatolepis*, on which the stratigraphic zonation is based (Fig. 1). The main shift at the F/F boundary corresponds to a major turnover in the *Palmatolepis* fauna where only one species survives the F/F crisis. A stage boundary (F/F) has been based on this turnover. The shift observed between the oldest and the youngest Famennian samples corresponds to the end of the recovery period, where diversification of the *Palmatolepis* described fauna corresponds to a change in conodont subzones (Early *triangularis* / Middle *triangularis*). The shift associated with the LKW is also related to a change in the taxonomic composition of the *Palmatolepis* fauna (subzones Early *rhenana* / Late *rhenana*).

*3.3. Middle Famennian (*annulata *event)*

Since two morphological types can be recognised around the *annulata* event, conodonts were grouped per level and per

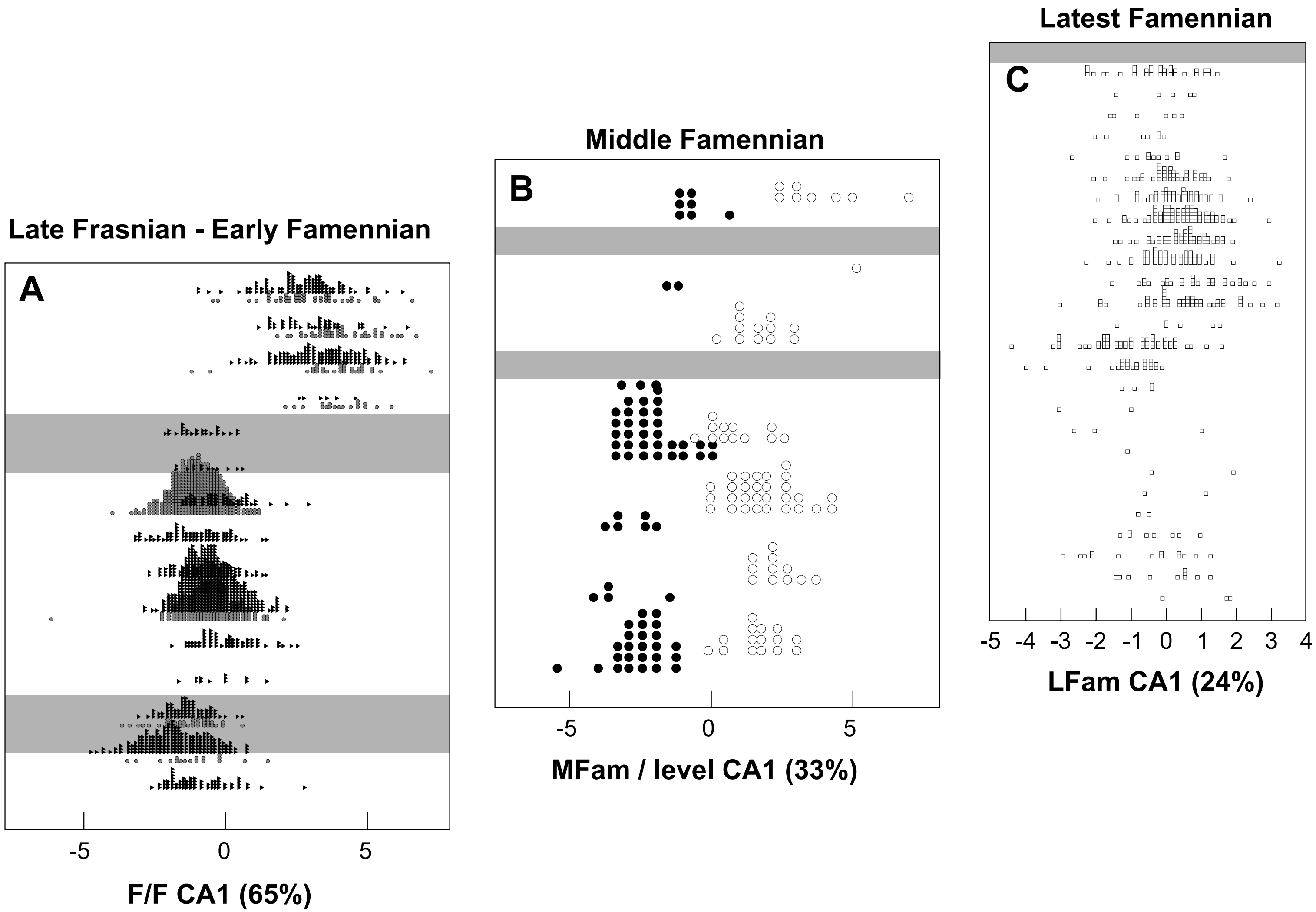

Fig. 3. Distribution per level of the shape of all *Palmatolepis*. Shape is estimated by scores on the first canonical axis and plotted according to the stratigraphical order. **A**. Late Frasnian / Early Famennian. **B**. Middle Famennian. **C**. Latest Famennian. Symbols are gray circles (Coumiac), filled triangles (M'rirt), filled circles (Effenberg - type 1), open circles (Effenberg - type 2), open squares (Puech de la Suque). In gray the anoxic events.

Fig. 3. Distribution par niveau de la forme de tous les *Palmatolepis*. La forme est estimée par les coordonnées sur le premier axe canonique, et représentée selon l'ordre stratigraphique. **A**. Frasnien supérieur / Famennien inférieur. **B**. Famennien moyen. **C**. Famennien terminal. Les symboles sont : cercles gris (Coumiac), triangles noirs (M'rirt), cercles noirs (Effenberg - type 1), cercles blancs (Effenberg - type 2), carrés blancs (Puech de la Suque). En gris les événements anoxiques.

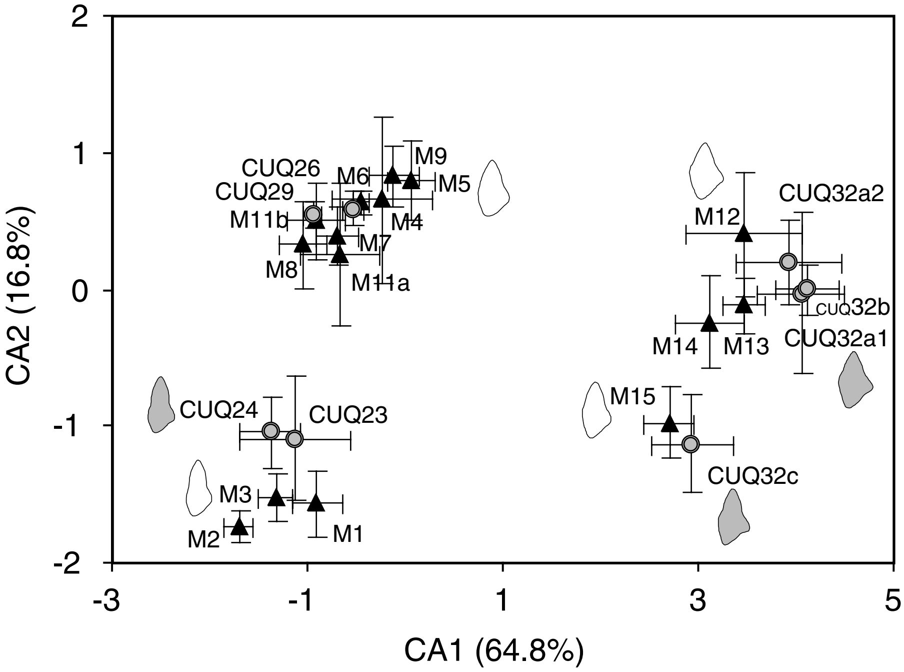

Fig. 4. Late Frasnian / Early Famennian shape differentiation. Mean scores per level are represented on the first two canonical axes calculated on all specimens per level at M'rirt (black triangles) and at Coumiac (gray circles). Error bars are the 95% standard error. Labels correspond to the level in the section (M: M'rirt, CUQ: Coumiac). Reconstructed outlines correspond to the mean values of some levels.

Fig. 4. Différenciation de forme au Frasnien supérieur / Famennien inférieur. Les moyennes par niveau sont représentées sur les deux premiers axes canoniques calculés sur tous les spécimens de chaque niveau à M'rirt (triangles noirs) et à Coumiac (cercles gris). Les barres d'erreur correspondent à l'erreur standard à 95%. Les labels correspondent au niveau dans la coupe (M : M'rirt, CUQ : Coumiac). Les contours reconstitués correspondent aux valeurs moyennes de quelques niveaux.

type for the multivariate analyses. As for the study that focused on the F/F boundary, the first two canonical axes display a large amount of among-group variance (CA1 = 60.5%, CA2 = 10.5%). The main signal expressed along CA1 supports the distinction drawn between conodont elements with a well-developed platform (type 1) and narrow elements (type 2), since it clearly separates the two groups of samples (Fig. 5). The variability displayed along CA2 is of much less importance (only 10.5% of the among-group variance). A temporal variability may be recognized within each conodont group. Youngest type 1 elements are plotted towards more positive CA1 and CA2 values, whereas youngest type 2 elements are shifted towards more positive CA1 and negative CA2 values. In both cases the main shift occurs between the E and F levels, i.e. during the deposition of the *annulata* black shales between the two main anoxic levels.

3.4. Latest Famennian period

The latest Famennian period investigated precedes the anoxic Hangenberg event, an interval devoid of preserved conodonts, during which the genus *Palmatolepis* disappears. In spite of a significant morphological differentiation, no obvious temporal pattern emerges (Fig. 6). The first two canonical axes display only a limited amount of among-group variance (CA1 = 24%, CA2 = 16.9%), due to the absence of any clear morphological shift through the section.

This relative morphological stability could be related to the absence of any environmental perturbation important

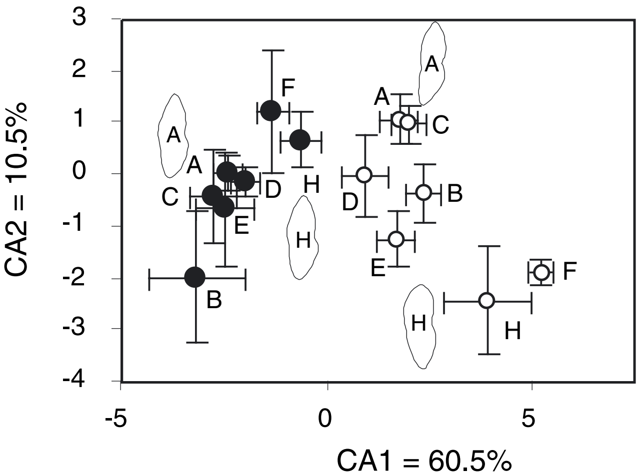

Fig. 5. Middle Famennian shape differentiation. Mean scores per level and per morphological type on the first two canonical axes, calculated on *Palmatolepis* specimens from Effenberg (Germany). Error bars are the 95% standard error. Labels correspond to the level in the section. Filled circles: elements with a well-developed platform (type 1), open circles: narrow elements (type 2). Reconstructed outlines correspond to the mean values of some levels.

Fig. 5. Différenciation de forme au Famennien moyen. Les moyennes par niveau et par type morphologique sont représentées sur les deux premiers axes canoniques calculés sur tous les spécimens d'Effenberg (Allemagne). Les barres d'erreur correspondent à l'erreur standard à 95%. Les labels correspondent au niveau dans la coupe. Cercles noirs : éléments avec une plate-forme bien développée (type 1) ; cercles blancs : éléments étroits (type 2). Les contours reconstitués correspondent aux valeurs moyennes de quelques niveaux.

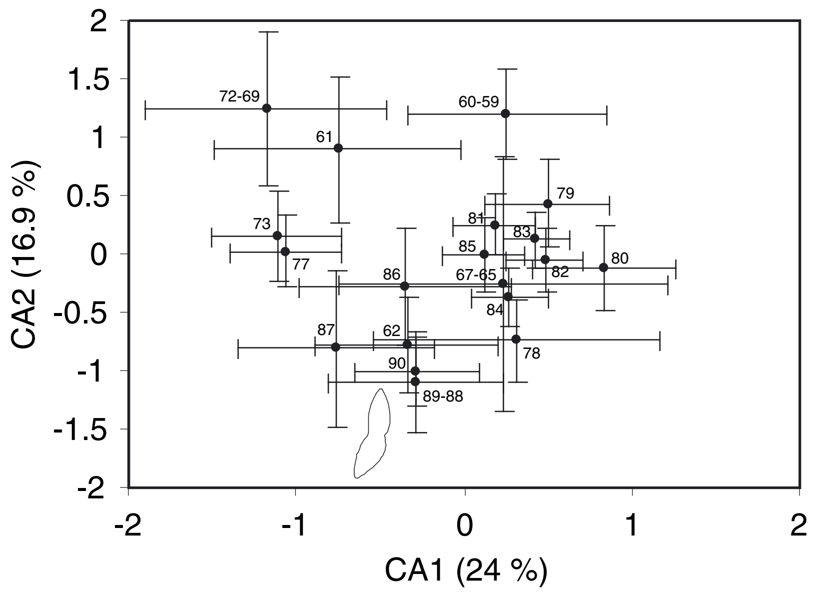

Fig. 6. Latest Famennian shape differentiation. Mean scores per level on the first two canonical axes calculated on all *Palmatolepis* specimens at Puech de la Suque (France). Error bars are the 95% standard error. Labels correspond to the level in the section. The reconstructed outline corresponds to the mean value of the level PS90.

Fig. 6. Différenciation de forme au Famennien terminal. Les moyennes par niveau sont représentées sur les deux premiers axes canoniques calculés sur tous les spécimens de *Palmatolepis* au Puech de la Suque (France). Les barres d'erreur correspondent à l'erreur standard à 95%. Les labels correspondent au niveau dans la coupe. Le contour reconstitué correspond à la valeur moyenne du niveau PS90.

enough to be marked by a change in facies deposits. Yet, environmental changes of limited importance likely occurred during this period, as suggested by variations in conodont biofacies (Girard, 1994). Morphological variations of *Palmatolepis* platform elements, estimated by scores on CA1, are significantly correlated with relative abundance of the genera *Palmatolepis* (P = *0.038**), *Branmehla* (P = *0.002***) and *Polygnathus* (P = *0.035**).

3.5. Synthetic trend through the Late Frasnian and the Famennian

The previous analyses were focused on time slices and allowed the investigation of short-term response of the genus *Palmatolepis* to environmental variations. In order to address the long-term change of the genus, all samples were thereafter considered in a combined analysis.

The long-term morphological differentiation appears to be of overriding importance, since it is displayed on CA1, expressing 87.0% of the among-group variance (Fig. 7). Along this axis, oldest samples from the Late Frasnian and Early Famennian are opposed to the youngest ones (latest Famennian). Conodonts from the Middle Famennian (*annulata* event) are split into two morphological groups. Whereas the conodonts with well-developed platforms (type 1) are located at intermediate scores on CA1, according to their intermediate age, the narrow *gracilis*-like (type 2) elements appear close in shape to the latest Famennian populations. Overall, a long-term trend towards an elongation of the element associated with a reduction of the platform is observed. At the *annulata* period, this trend is more pronounced within the *gracilis*-like (type 2) populations, whereas around the F/F boundary and during the latest Famennian, paleopopulations were more homogeneous in their variation.

The second canonical axis is of very limited importance (5.4% of the variance) compared to CA1. Yet, it might be of paleobiological significance since patterns of variation can be recognized that have been observed on the short-term analyses. Morphological shifts associated with the successive Kellwasser events can be observed along CA2, corresponding to more triangular outlines from pre-LKW to post-UKW samples. Furthermore, CA2 separates the type 2 narrow elements of the Middle Famennian from the populations of the Latest Famennian.

In order to better visualize the chronological development of these morphological trends, the shape variations have been represented according to the stratigraphical order of the different samples from the latest Frasnian to the latest Famennian (Fig. 8). The most important morphological shift along CA1 occurs between the samples associated with the F/F boundary and the Middle Famennian populations. Within these latest ones, the type 1 (well-developed platform) and type 2 (narrow elements) are well separated. The narrow elements (type 2) are closer to the latest Famennian populations, which display a very stable morphology. Along CA2 (5.4% of variance), the shifts associated with the LKW and UKW (F/F boundary) are well expressed. Once again, the latest Famennian period is characterized by a very stable morphological record.

4. Discussion

The morphometric population approach used in the present study seems suitable to describe the short and long-

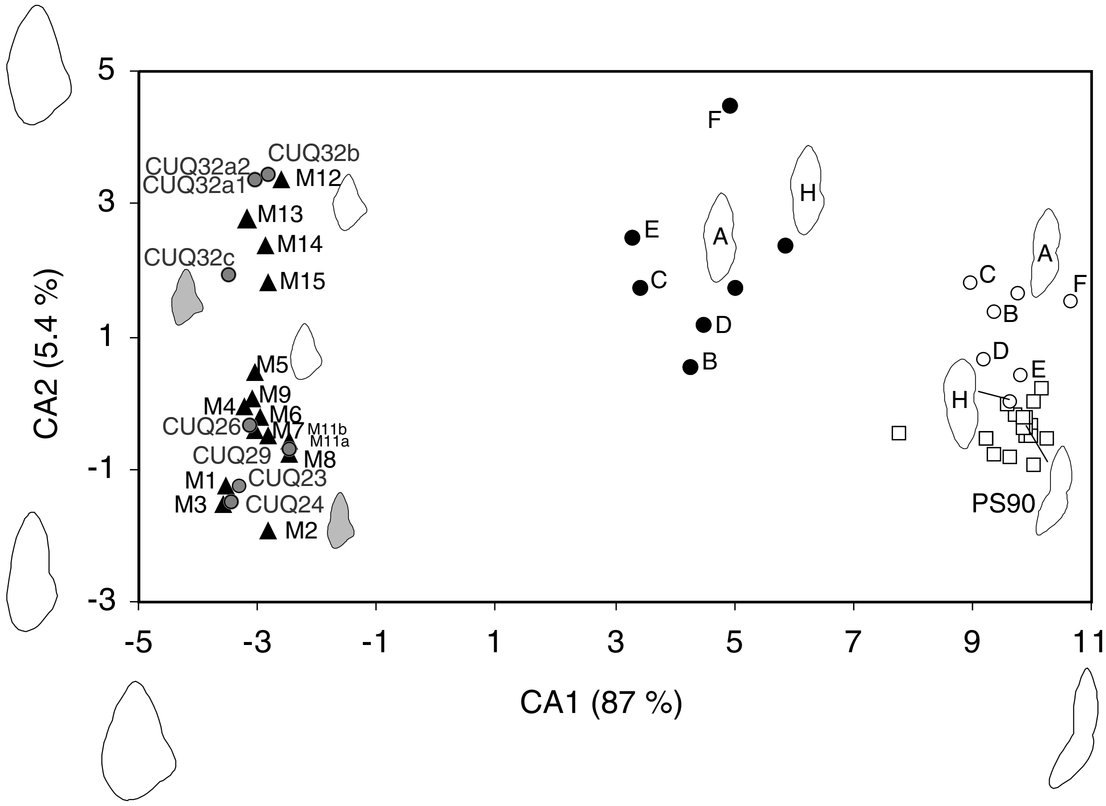

Fig. 7. Late Frasnian / Late Famennian synthetic shape differentiation. Mean scores per level and per morphological type on the first two canonical axes calculated on all *Palmatolepis* elements from the four sections previously considered. Labels correspond to the level in M'rirt (M), Coumiac (CUQ) and Effenberg sections (labels for Puech de la Suque omitted). Reconstructed outlines correspond to the mean values of some levels, and to magnified variations along the canonical axes.

Fig. 7. Différenciation synthétique de forme du Frasnien terminal au Famennien terminal. Les moyennes par niveau et par type morphologique sont représentées sur les deux premiers axes canoniques calculés sur tous les éléments *Palmatolepis* des quatre coupes précédemment considérées. Les labels correspondent au niveau à M'rirt (M), Coumiac (CUQ) et Effenberg (labels omis pour le Puech de la Suque). Les contours reconstitués correspondent aux valeurs moyennes de quelques niveaux, et aux variations amplifiées le long des axes canoniques.

term changes of the genus *Palmatolepis*. Furthermore, it supports previous evolutionary studies based on taxonomic description of species within the genus. Compared to this latter approach, which forms the basis of the stratigraphic conodont zonation of the Late Devonian, the morphometric approach provides the advantage for paleobiological studies of including all specimens, independently of their size, and discards the problem of potentially numerous unidentified specimens (up to 95% of the *Palmatolepis* populations; Morrow, 2000; Girard et al., 2004).

This approach also provided the possibility of a quantitative comparison of synchronous populations at different locations. No morphological differences have been detected between the two North Gondwanan sections of M'rirt (Morocco) and Coumiac (France). This result supports the observed cosmopolitanism of the conodont fauna at this period (Belka and Wendt, 1992).

4.1. Short-term shape variations

4.1.1. Response to the Kellwasser events

A major extinction with a huge impact on the fauna occurred during the period of the Late Frasnian / Early Famennian, associated with the UKW event. The resulting species turnover in *Palmatolepis* can be recognized using the morphometric population approach as a major morphological shift between Late Frasnian and Early Famennian populations.

This period is further characterized by the LKW, an anoxic event that preceded the UKW and of less impact on the faunas. This small-scale environmental variation seems also to trigger a morphological change of the conodonts, although of less magnitude than the response to the UKW, suggesting that the amplitude of the morphological response might be related to the extent of the perturbation. The response to a perturbation such as the UKW further involves a period of recovery, corresponding to a re-diversification of the *Palmatolepis* fauna and a morphological shift during the Earliest Famennian.

4.1.2. *Variations associated with the* annulata *event*

The Middle Famennian *Palmatolepis* populations can be split into two types (Fig. 3): elements with well-developed platform (type 1) and narrow *gracilis*-like elements (type 2).

Considering a canonical analysis per level and per morphological type, the main difference separates the two mor-

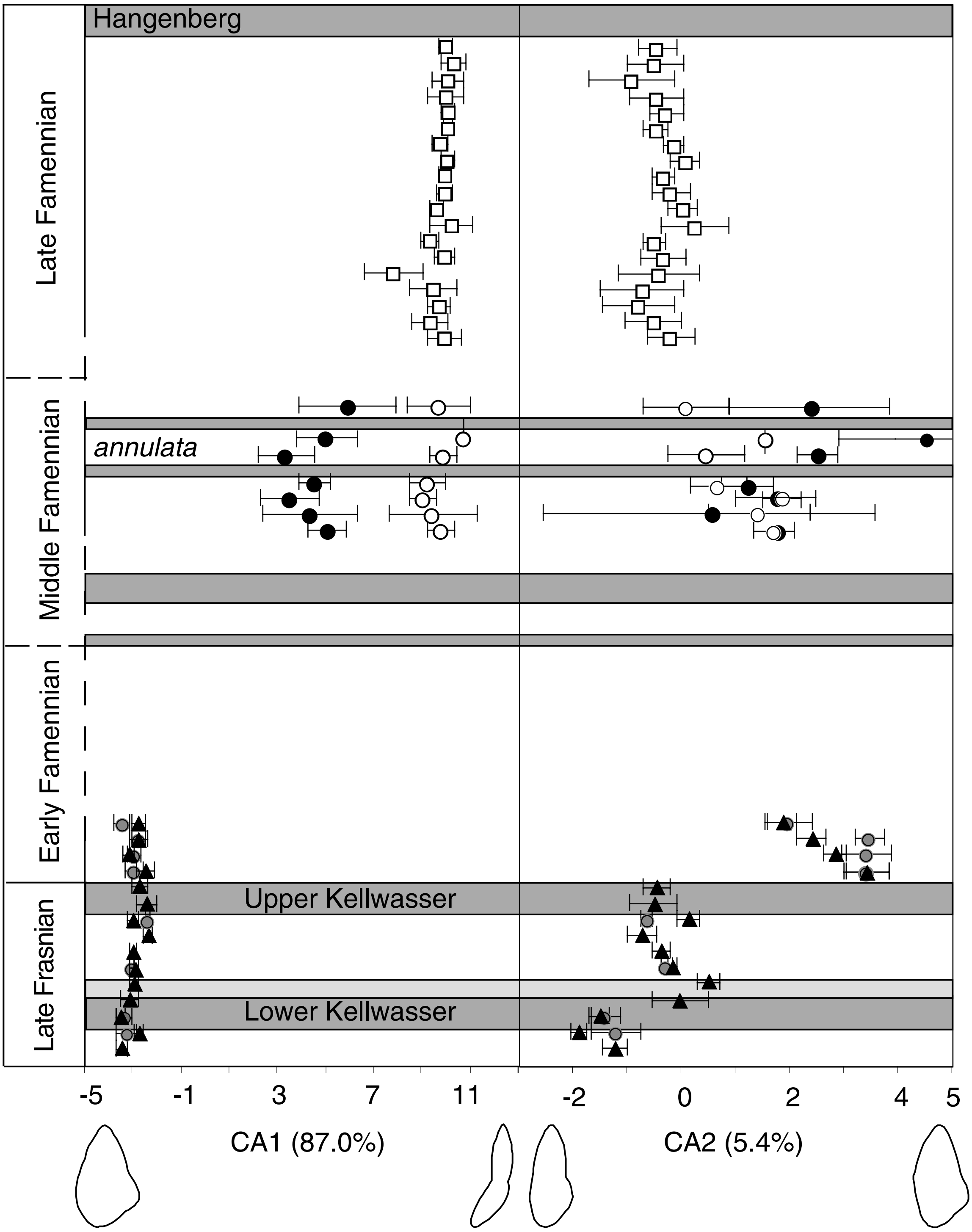

Fig. 8. Synthetic shape variations through time. Shape is estimated by the first (left) and second (right) canonical axes. Vertical axis: stratigraphic superposition order, arbitrary scale. Error bars are the 95% standard error. Symbols as in Fig. 3. Reconstructed outlines correspond to magnified variations along the canonical axes.

Fig. 8. Variations synthétiques de forme à travers le temps. La forme est estimée par le premier (à gauche) et le second (à droite) axes canoniques. L'axe vertical représente l'ordre de superposition stratigraphique (échelle arbitraire). Les barres d'erreur correspondent à l'erreur standard à 95%. Symboles voir Fig. 3. Les contours reconstitués correspondent aux variations amplifiées le long des axes canoniques.

phological types along the first canonical axis (60.5% of variance). Temporal shape variations displayed on CA2 (10.5% of variance) are comparatively of limited importance. Nevertheless, a shift occurs in both types between E and F levels between the two main anoxic levels. Hence, morphological variations might be related to the environmental changes associated with the deposition of the *annulata* black shales. This weak impact of the anoxic event on conodont shape may be due to the nature of the *annulata* event. It is known to have an impact on some components of the benthic and pelagic faunas (Walliser, 1996) but conodonts are not affected by this environmental change since no obvious change in their fauna has been recorded associated with the event (Sandberg et al., 2002).

4.1.3. Latest Famennian shape variability

The latest Famennian has been investigated because it shortly precedes the extinction of the genus *Palmatolepis* at the D/C boundary. Minor fluctuations in conodont biofacies suggest an environmental instability in a progressively transgressive context (Girard, 1994), as indicated by the slow increase of deep-sea conodont indicators such as *Palmatolepis* although no drastic environmental variations occurred during this latest Famennian period.

Environmental conditions during the latest Famennian therefore appear to be stable compared to the time intervals focused on the Kellwasser and *annulata* events. Accordingly, *Palmatolepis* taxa display only limited morphological variations during this time interval (Fig. 6). Minor shape variations occurred, which can be related to relative abundances of the genera *Palmatolepis, Branmehla*, and *Polygnathus*. The results of the latest Famennian analysis therefore support the idea of shape changes usually occurring as a response to environmental variations, the amplitude of the morphological change being related to the extent of the perturbation. Global events of the Late Devonian can be ranked according to their impact on the fauna (Walliser, 1996). Within the periods considered in the present study, UKW, LKW, *annulata* event are of decreasing importance, the latest Famennian period being characterized by even smaller environmental fluctuations. Our results show that the importance of the shape shifts observed ranked in the same order (Fig. 8).

4.2. Long-term morphological trend

Morphological changes of the *Palmatolepis* populations may be due to evolutionary processes, migrations or changes in the average taxonomic composition. These different factors are difficult to disentangle from each other especially for extinct animals without modern analogues, such as conodonts. However a synthetic analysis, including the previously discussed time intervals, could provide some insight into the patterns of changes of *Palmatolepis* through the Late Devonian.

A long-term morphological trend emerges on the first synthetic canonical axis, corresponding to a progressive narrowing of the element. This trend is of overwhelming importance compared to the short-term variations observed in response to the various events (Fig. 7). Small-scale shape variations, especially those associated with LKW and UKW, seem to be uncoupled from the long-term trend since they are displayed on the second canonical axis, independent of CA1.

Both along the synthetic shape axes CA1 and CA2 (Fig. 7), morphological changes seem to happen step-wise. Periods of limited variability alternate with morphological shifts apparently associated with environmental perturbations. Moreover, the amplitude of the shape variation seems to be related to the extent of the perturbation. The UKW, LKW, and *annulata* event have a decreasing impact on the faunas (Walliser, 1996) and are associated in our study with morphological changes of decreasing importance. Corroborating the hypothesis of an association between environmental perturbation and shape change, the most stable period considered, i.e. the latest Famennian, displays the most limited shape variations. Still, these weak shape changes also might be related to minor environmental variations.

The most important morphological shift observed occurs during a gap of our sampling, between the Kellwasser and *annulata* events. During this time interval, two global events are recorded, the Condroz and Enkeberg events (Walliser, 1996). They are interpreted as intermediate in extent between the LKW and the UKW events. Based on the observation of step-wise morphological changes as a response to environmental perturbation, we might suppose that the morphological shift between the Kellwasser and *annulata* event constitutes the cumulated effect of the response to the Condroz and Enkeberg events. This interpretation should be tested by an analysis focused on these events.

The Late Devonian appears as a period of recurrent environmental perturbations, six global events occurring over an interval of approximately 12 myr, no more than 3.5-4 myr separating successive events. A model of relationship between such variations of abiotic parameters and evolutionary patterns has been proposed by Sheldon (1996) as the *Plus ça change, plus c'est la même chose* model. According to his model, widely fluctuating environments should favor stasis, since successive opposite environmental variations should be unfavorable to adaptations to previous conditions. From time to time, a threshold in the environmental conditions might occur and trigger evolutionary changes (e.g. Renaud et al., 1999). According to this model, the step-wise morphological pattern observed in the genus *Palmatolepis* may be interpreted as a response to the widely fluctuating environmental conditions characterizing the Late Devonian period.

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