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Temporal dynamics of the geographic differentiation of Late Devonian *Palmatolepis* assemblages in the Prototethys

CATHERINE GIRARD, TA HOA PHUONG, NORMAN SAVAGE, and SABRINA RENAUD



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Throughout their history, species had to face environmental variations spatially and temporally. How both levels of variation interact will be of key importance in conditioning their response to major perturbations. We addressed this question by focusing on a period in Earth's history marked by dramatic environmental and faunal changes, the Late Devonian Frasnian/Famennian boundary. From a paleogeographic point of view, this period is characterized by a cosmopolitanism of the faunas across a large ocean, the Prototethys. We considered the biotic reaction at a seldom considered scale, namely within a single subgenus of conodont, *Palmatolepis* (*Manticolepis*). Patterns of spatial and temporal differentiation were quantified using morphometrics of its platform element. The recognized cosmopolitanism of the faunas was confirmed at this scale of variation since temporal records gathered in distant areas around the Prototethys, including the seldom documented regions located nowadays in South-East Asia, displayed similar morphological trends in response to the major F/F crisis. Beyond this overall cosmopolitanism, subtle geographic structure was evidenced but was not stable through time. Geographic differentiation was maximal shortly before the F/F crisis, suggesting that despite high sea-level, tectonics leaded to complex submarine landscapes promoting differentiation. In contrast any geographic structure was swamped out after the crisis, possibly due to a global recolonization from few favorable patches.

Key words: Conodonta, mass extinction, morphometrics, geographic differentiation, Frasnian/Famennian, Prototethys.

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Introduction

Throughout their history, species had to face and adapt to environmental variations at different scales, both spatially and temporally. Spatial variations in environmental conditions, as various as temperature, salinity, nutrient availability and productivity for the prominent factors in the marine realm, moulded the distribution area of the species depending on their preferences (e.g., Caron et al. 1987; Gaylord and Gaines 2000; Schmidt et al. 2004). These preferences condition the reactions to environmental perturbations (e.g., Schmidt et al. 2003) but these preferences can themselves evolve through time, leading to complex evolutionary patterns through time and space (Renaud and Schmidt 2003). Depending on the relative amplitude of both scales of variations, the response to peculiar local conditions may override variations due to global environmental changes (Stenseth et al. 2003). Hence, complex scenarii including together large-scale climatic trends, fluctuations in the local habitats, as well as ecological and physiological data may be necessary to decipher the distribution of some current species including marine organisms such as fishes (Buisson and Grenouillet 2009).

In turn, the spatial structure of the environmental conditions may vary through time, leading to alternations of phases characterized by enhanced geographical exchanges or restricted conditions and endemism. How these spatial variations interact with temporal changes is critical for understanding the evolutionary dynamics of species, including how they have faced past environmental crises and how they will face the ongoing climate change.

The Earth's history has been marked by several major crises that offer the opportunity to address the interaction of geographic and temporal environmental variations. Among them, the Late Devonian period is known to have experienced a drastic turn-over in the faunas, culminating at the Frasnian/Famennian (F/F) boundary. Traditionally considered as one of

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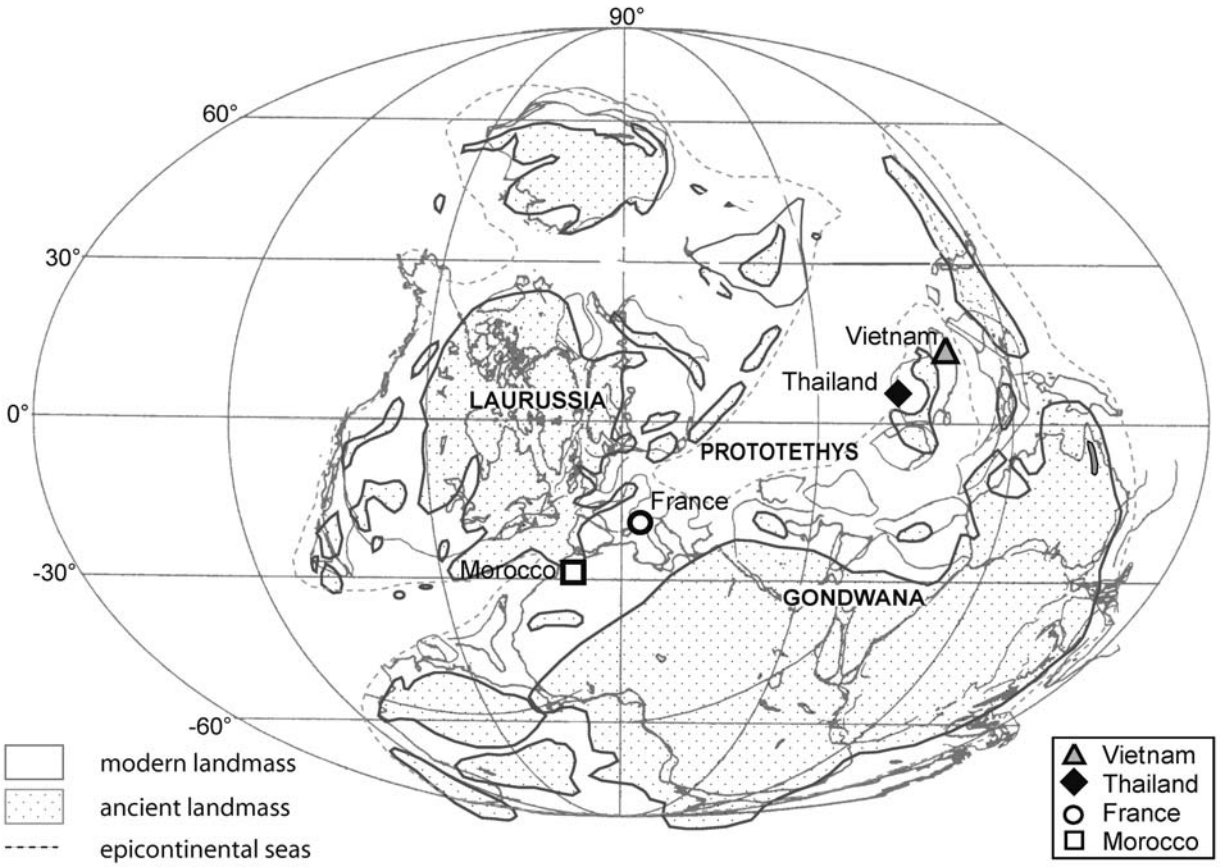


Fig. 1. Palaeogeographic map of the Late Devonian showing the location of the sections considered in the present study (after Scotese and McKerrow 1990; Scotese and Golonka 1992). Circle = Coumiac Upper Quarry (France), square = Mrirt (Morocco), triangle = Xom Nha (Vietnam), diamond = Thong Pha Phum (Thailand).

the "Big Five" mass extinctions, with the disappearance of 70% of all species and 50% of all genera (Raup and Sepkoski 1982), the processes underlying this indubitable loss in biodiversity are today debated. A deficit in speciation may be involved rather than high extinction rates (Bambach et al. 2004; Racki 2005; Alroy 2008). Drastic environmental changes seem anyway to have triggered this biotic turn-over (i.e., Algeo et al. 1998; Joachimski and Buggisch 2002).

During this Late Devonian period, most of the continental land masses were assembled in two main continents, Gondwana and Laurussia (Scotese and McKerrow 1990) that bordered a large Prototethys ocean. How oceanic circulation was organized in this past ocean and the vast epicontinental seas of the shelves is still unknown. However, the homogeneity of the composition of the faunas around the Prototethys suggests that the Late Devonian was a period of cosmopolitanism for marine species (McGhee 1996; Cooper 1998; Rode and Lieberman 2004, 2005; McNamara et al. 2009).

Among the genera surviving the crisis, and hence allowing an investigation of how the environmental perturbations affected its geographic structuration, we focused on the conodont genus *Palmatolepis*. Previous studies showed that its evolutionary response to the F/F crisis was adequately described by the morphometric variations of its platform element outline (e.g., Girard and Renaud 2007). A subtle geographic structure was also evidenced for this genus shortly before the F/F boundary (Girard et al. 2007) despite evidences of an overall cosmopolitanism of Late Devonian conodont fauna (Klapper 1995).

To investigate how this geographic structure articulates and interacts with the dramatic changes observed through the Late Devonian period, we applied the same morphometric analysis to *Palmatolepis* conodonts documenting the temporal variations through the late Frasnian and early Famennian in four outcrops, characterizing the two contrasted areas of the Western and Eastern Prototethys. The western zone was sampled at the stratotype section of Coumiac (France) and in Mrirt (Morocco). Abundant literature has been devoted to the conodont systematics and stratigraphy of these sections (Becker et al. 1989; Klapper 1989; Klapper et al. 1993; Lazreq 1992; 1999; Girard and Renaud 2007) in contrast with the poorly documented eastern sections of Xom Nha (Vietnam) (Ta 1998; Luu et al. 2007) and Thong Pha Phum (Thailand) (Savage et al. 2006).

Together with a comprehensive analysis throughout the four sections, we further focused on the geographic differentiation in three successive time-slices: the period shortly preceding the F/F boundary, and two further time-slices bracketing the crisis: one in the preceding zone and one in the following zone.

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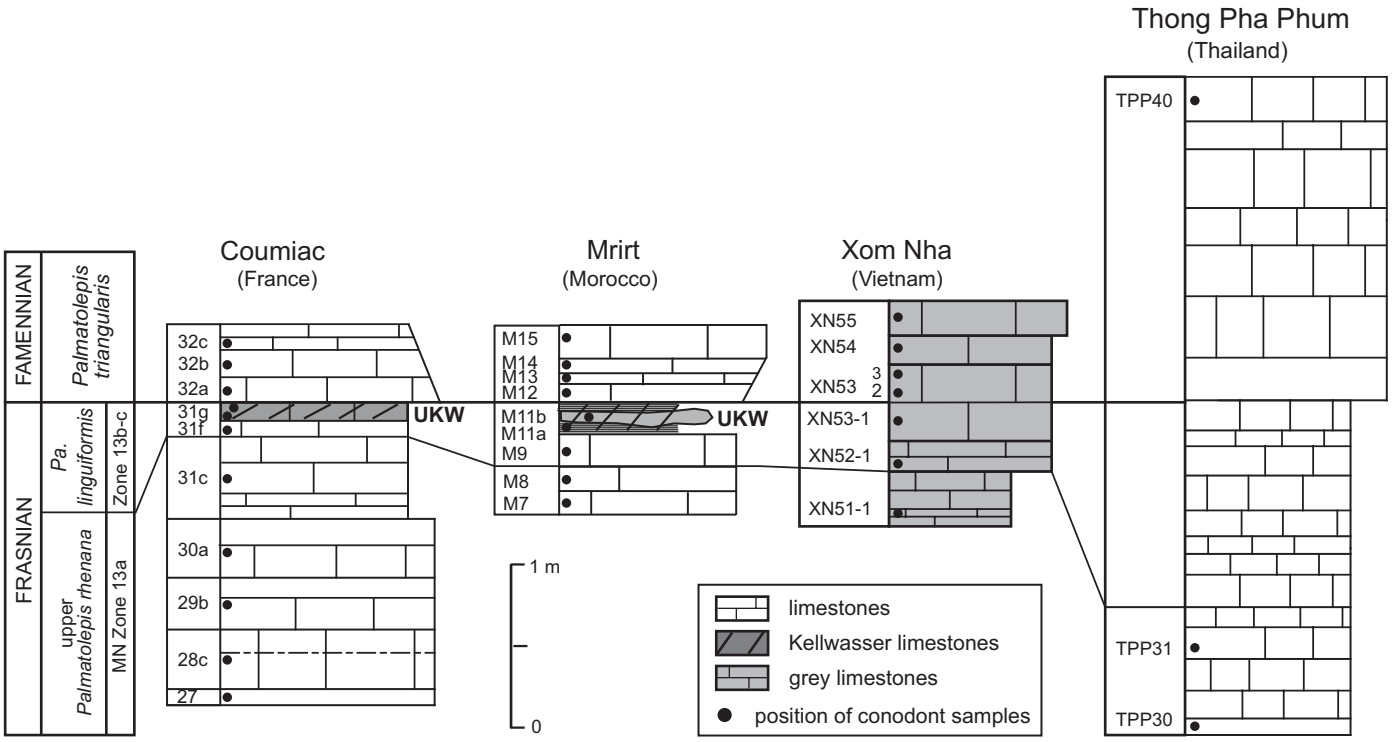


Fig. 2. Stratigraphical logs of the four compared sections, Coumiac (France), Mrirt (Morocco), Xom Nha (Vietnam) and Thong Pha Phum (Thailand). The studied levels are marked by a black circle. In gray, the dysoxic Kellwasser (UKW = Upper Kellwasser). *Pa*., *Palmatolepis*.

Abbreviations.—CUQ, Coumiac Upper Quarry; FC, Fourier Coefficient; F/F, Frasnian/Famennian; KW, Kruskal Wallis; M, Mrirt section; MM, Moroccan Meseta; MN, Montagne Noire; Pa., Palmatolepis; PC, principal component; PCA, principal component analysis; RFT, radial Fourier transform; sf, size-free; TPP, Thong Pha Phum; UKW, Upper Kellwasser; XN, Xom Nha.

Material and age of samples

Successive levels documenting the period of the latest Frasnian and the earliest Famennian throughout the four sections were sampled and compared. The first two sections are located on the Western part of the Prototethys (Fig. 1). Coumiac Upper Quarry (CUQ) is the stratotype section for the Frasnian/Famennian boundary (Klapper et al. 1993). The second site considered is the Mrirt section (M), located in the Moroccan Meseta (Fig. 1). 11 levels in Coumiac and 9 levels in Mrirt have been considered across the F/F (data from Girard and Renaud 2007). For these two sections, the F/F boundary coincides with the top of a black organic-rich level, recording anoxic conditions and called the Upper Kellwasser event (Fig. 2).

Two sections have been investigated for the eastern part of the Prototethys, both belonging to the Indochina block: the section Xom Nha (central Vietnam) and Thong Pha Phum (Western Thailand) (Fig. 1). Seven levels in Xom Nha and three levels in Thong Pha Phum have been considered across the F/F boundary. These sections display continuous carbonated succession, without lithological evidence of the presence of the Kellwasser event (Fig. 2). However, a $\delta^{13}C$ positive excursion has been documented in the Thong Pha Phum section just above the bed TPP 37. This excursion has been tentatively correlated with a similar excursion already observed in Europe, North America (Joachimski et al. 2009) and China (Chen et al. 2002), just before the Frasnian/Famennian boundary, and interpreted as the signal of the Upper Kellwasser event (Savage et al. 2006).

For each stratigraphic level, a piece of 100 to 200g rock was dissolved in formic acid (10%) and rinsed through two sieves. The samples are immersed in formic acid less than 24h to avoid corrosion of the conodont elements. Empirically the abundant occurrence of gracile elements validates the use of unbuffered acid for this step. All intact *Palmatolepis* (*Manticolepis*) platform elements were picked for subsequent morphometric analyses (Table 1).

In all sections, the detailed stratigraphic framework was established based on the determination of the conodont fauna; this tentative framework was subsequently compared with patterns emerging from the morphometric analyses. Traditional stratigraphic correlations (Fig. 2) have been used based on the Late Devonian conodont zonation (Ziegler and Sandberg 1990) and compared to MN conodont zones (Klapper 1989) established in the Montagne Noire (France) but now recognized as being of worldwide significance (Girard et al. 2005). In the Coumiac section, determination of conodonts showed that beds CUQ27-31c at the base of the section belong to the late *Palmatolepis rhenana* Zone or MN 13a Zone, and

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Table 1. Number of *Palmatolepis* (*Manticolepis*) elements measured for morphometric analysis in successive beds in Coumiac (France) and Mrirt (Morocco) for the Western part of Prototethys and in beds in Xom Nha (Vietnam) and Thong Pha Phum (Thailand) for the East part of the Prototethys. In grey: the three time-slices considered in this study. Abbreviations: CUQ, Coumiac Upper Quarry; M, Mrirt; Pa_M, number of entire *Palmatolepis* (*Manticolepis*) elements measured for morphometrics; TPP, Thong Pha Phum; XN, Xom Nha.

Stages	Conodont zones		Western Prototethys				Eastern Prototethys			
			Coumiac		Mrirt		Xom Nha		TPP	
			Samples	Pa_M	Samples	Pa_M	Samples	Pa_M	Samples	Pa_M
Famennian	*Palmatolepis triangularis*				M15	98	XN55	3		
			CUQ32c	45	M14	42	XN54	34	TPP40	38
			CUQ32b	45	M13	133	XN53-3	7		
			CUQ32a	51	M12	6	XN53-2	3		
Frasnian	*Palmatolepis linguiformis*	MN13b-c	CUQ31g2	58	M11b	25				
			CUQ31g1	68	M11a	13	XN53-1	302		
			CUQ31f	94	M9	52	XN52-1	140		
	late *Palmatolepis rhenana*	MN13a	CUQ31c	481					TPP31	22
			CUQ30a	469						
			CUQ29b	350	M8	74	XN51-1	23	TPP30	83
			CUQ28c	263						
			CUQ27t	170	M7	81				

beds CUQ31f–31g to the *Palmatolepis linguiformis* Zone, corresponding to the MN 13b–c zones. The characteristic form of the zone, *Pa. linguiformis*, is, however, very seldom found in this section (less than 0.5%). Beds 32a–b–c were attributed to the *Palmatolepis triangularis* Zone. In the Moroccan section of Mrirt, the beds M7–8 are dated of late *Pa. rhenana* Zone (MN 13a Zone), and beds M9–11 to the *Pa. linguiformis* Zone (MN13b–c zones). The base of the Famennian is represented by the beds M12–15 which are attributed to the *Palmatolepis triangularis* Zone.

For the Thai section of Thong Pha Phum, conodonts from three levels (TPP 30-31-40) have been considered. Beds TPP 30-31 are of Late *Pa. rhenana* Zone age (MN 13a Zone), and Bed TPP 40 yielded numerous *Pa. triangularis* indicating the *Pa. triangularis* Zone (Savage et al. 2006).

Seven levels have been studied for the Xom Nha section. Bed 51 contains conodonts belonging to the Upper *Palmatolepis rhenana* Zone (MN 13a Zone). In beds 52 and 53-1 the index species of the *Pa. linguiformis* Zone occurs. It represents approximately 10% of the total assemblage. Beds 53-2 to 55 can be attributed to the *Pa. triangularis* Zone (Ta 1998).

This stratigraphic correlation between the different levels of the sections is presented in the Fig. 2 and the Table 1.

Methods

Morphometrics of *Palmatolepis* conodonts according to a generic approach

The traditionally used taxonomy of Late Devonian conodonts largely relies on a parataxonomic approach based on a single platform element (Pa or P1) taken as a marker of the evolution of the whole animal in a synecdoche that is frequent in paleontological studies (e.g., most interpretations of small mammal assemblages only rely on teeth remains, see for instance Michaux 1971). Multielement analyses are challenging issues (Dzik 2002) but still encounter several limitations for an extensive application to large scale studies. The reconstruction of a multi-element apparatus relies either on seldom found remains of in situ conodont apparatuses, or on assignation of elements to an apparatus of a given species based on similar frequencies in the assemblage. This approach suffers the drawback that various elements of a single apparatus may have different potential of sedimentation and preservation, that may lead to taphonomic biases hindering confident reconstructions of apparatuses (von Bitter and Purnell 2005). Hence, the taxonomy of the genus *Palmatolepis* has been established according to the current parataxonomic approach and accordingly, we based our morphometric analysis on the platform element.

The large morphological variation within this genus and particularly during the Late Devonian was traditionally tackled by splitting it into many species and subspecies. The validity of these entities for stratigraphic purposes is indubitable and in agreement, we relied on this approach to establish our tentative stratigraphic framework.

Some drawbacks emerge, however, when attempting to tackle evolutionary issues. The lack of well-defined clusters has been recognized by many authors, mentioning transitional forms between species (e.g., Ziegler and Sandberg 1990) and leaving generally more than 80% of the specimens in an open nomenclature (e.g., Sandberg et al. 1988; Schülke 1998; Morrow 2000). Furthermore the fuzzy limits between described species led to the proposition of two parallel taxonomies, partially but not fully overlapping (Klapper 1989; Ziegler and Sandberg 1990).

Since most characteristics features of *Palmatolepis* platform elements regard the shape of its platform, morpho-

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metric analyses brought additional light on how to tackle the abundant morphological variability. (i) The separate analysis of the different recognized species showed that they shared similar temporal trends, instead of being stable over time (Renaud and Girard 1999). (ii) When considering together the wealth of undetermined specimens, identified specimens appeared as end-members of a continuous morphological variation showing coherent trends through time (Girard et al. 2004). (iii) Considering all *Palmatolepis* elements together independently of any a priori identification allows the recognition of clear-cut morphological clusters whenever they occur: a study focused on the Latest Devonian period clearly evidenced two distinct groups of *Palmatolepis* (Girard et al. 2007). Subtle geographic variations within the most abundant group were further evidenced using the "generic" approach consisting in pooling all *Palmatolepis* elements into a single entity corresponding to a continuous morphological variation. We hence adopted this approach in the present study for analysing the temporal and spatial morphological variation of the conodont *Palmatolepis*.

This approach is only challenged during the Latest Frasnian (*Palmatolepis linguiformis* Zone) when as mentioned, two distinct groups coexist. They correspond to two subgenera: (1) *Palmatolepis* (*Palmatolepis*), including *Pa.* (*Pa.*) *linguiformis*, the index species of the zone; (2) *Palmatolepis* (*Manticolepis*) which includes all other specimens (Girard et al. 2007). Because of the transient occurrence *Pa.* (*Palmatolepis*) that only exists during the Latest Devonian, and of its rarity even during this time interval, we focused the subsequent morphometric analyses on *Pa.* (*Manticolepis*) only, being considered as a single evolutionary unit.

Fourier analysis

The morphometric analysis was focused on *Palmatolepis* platform elements (Fig. 3), which have already shown clear morphological responses to the Frasnian/Famennian global environmental perturbation in the Western Prototethys (Renaud and Girard 1999; Girard and Renaud 2007) and a geographic differentiation in the *Palmatolepis linguiformis* (late Frasnian) time slice (Girard et al. 2007). All the intact *Palmatolepis* platform elements of a level were considered.

Conodonts having a bilateral symmetry, both right and left elements are found in an assemblage. Left elements were subjected to a mirror transformation and measured as right elements. The two-dimensional outline of each conodont was automatically digitized using an image analyzer (Optimas), using the same magnification for all elements irrespective of their size. 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 dorsal (or anterior) tip of the platform. A radial Fourier transform (RFT) was applied to this data set. From the *x*, *y* coordinates of the 64 points, 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 is thus expressed as a finite sum of trigonometric functions of decreasing wavelength (harmonics), weighted by two Fourier Coefficients A_n and B_n (Renaud and Girard 1999). The zero harmonic, A_0, is proportional to the size of each conodont and was used to standardize all the Fourier coefficients, in order to retain shape information only. Eleven harmonics were retained, considered as a good compromise between information content and number of variables.

Statistics

Conodont size.—The size of each conodont element was estimated using the zero harmonic (A_0) based on the analysis of its outline. This size estimator was chosen because directly related to the shape analysis and because it is highly related to other, more intuitive size estimators (as an example, A_0 was compared in the level CUQ32c to a range of size estimators using linear regression and was highly correlated to all of them: Area: $R^2 = 0.974$; $\sqrt{\text{Area}}$: $R^2 = 0.995$; Perimeter: $R^2 = 0.981$; Maximum Length: $R^2 = 0.986$; Maximum Breadth: $R^2 = 0.964$).

For the three time-slices differences in size between samples as well as size differences between the sections and between the Eastern part and Western parts of the Prototethys were investigated using analyses of variance (ANOVA). Given the non-normal distribution of conodont size, the analyses were completed by Kruskal Wallis (KW) tests. This is a non-parametric analog of a one-way analysis of variance which tests for differences in the center of the distribution of the groups. Differences in distribution of conodont size may further be related to differences in variance instead of differences in mean values. Hence, a comparison of variance was performed using a Levene's test that tests for the equality of variance in different samples.

Conodont shape.—The shape of each conodont element was described by a set of 22 Fourier Coefficients (FCs), cor-

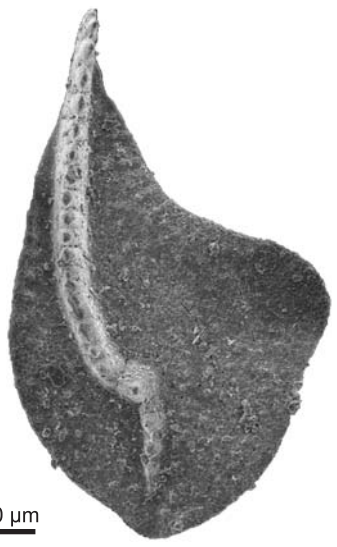


Fig. 3. Upper view of a *Palmatolepis* (*Manticolepis*) element.

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responding to 2 FCs per 11 harmonics. These FCs have been standardized by size, estimated by A_0, and retain shape information only.

A principal component analysis (PCA) was first performed on the data set corresponding to the 22 FCs of the conodonts in all sections and levels, in order to display the total morphological variance on a few synthetic axes without any a priori hypotheses. This allowed a visualization of the differentiation pattern through time and space and of the global relationship with size. The PCA was performed on the correlation matrix in order to balance the weight given to the different FCs. This procedure tends to give a similar importance to local and global shape differences.

Patterns of shape differentiation were thereafter tested using multivariate analyses of variance (MANOVA). Differences were investigated among levels for each section, and among sections for each of the three time-slices, as well as geographic differences between the Eastern and Western part of the Prototethys, and between sections within a given geographic area. A limit in the interpretation of MANOVA results is its sensitivity to sample size: the more specimens, the higher the chance of detecting significant differences among groups (Michaux et al. 2007).

Within each time-slice, we further investigated the distribution of the morphotypes following the procedure developed for size analysis, the first axis of a PCA per time-slice being considered as synthetic shape axis. Differences in shape between the Eastern and Western part of the Prototethys, and between sections within each area, were tested by an ANOVA on the scores on PC1 axis, completed by Kruskal Wallis and Levene's tests .

Size-shape relationship and size-free shape estimates.— Despite their standardization by the zeroth harmonic, the Fourier coefficients may still include size-related, allometric shape variation. Although less obvious than in other genera like *Ancyrodella* (Girard and Renaud 2008), a significant component of allometric variation has been evidenced in *Palmatolepis* (*Manticolepis*) conodonts of the Latest Devonian (Girard et al. 2007). The existence of such a relationship between size and shape of the conodonts was first investigated in our data set using a linear regression between A_0, considered as size estimator, and the first axis of the principal component analysis, considered as a synthetic shape axis. This provides a first insight into the relationship between size and shape, and a visualisation of this relationship.

This method provides a straightforward visualization, shape being summarized along a synthetic axis. This is, however, a simplification of the multivariate data set. Hence, this approach was complemented by a multiple regression of one variable (the size of the conodont element estimated by the first Fourier Coefficient A_0) upon all other Fourier Coefficients (FCs), that consider the relationship of a pool of dependent variables (here the FCs) with another independent variable (here the size of the conodonts). This approach provides "size-free" shape variables that appeared efficient in disentangling sources of shape variations related to allometric growth from those related to environmental fluctuations in the conodont *Ancyrodella* (Girard and Renaud 2008).

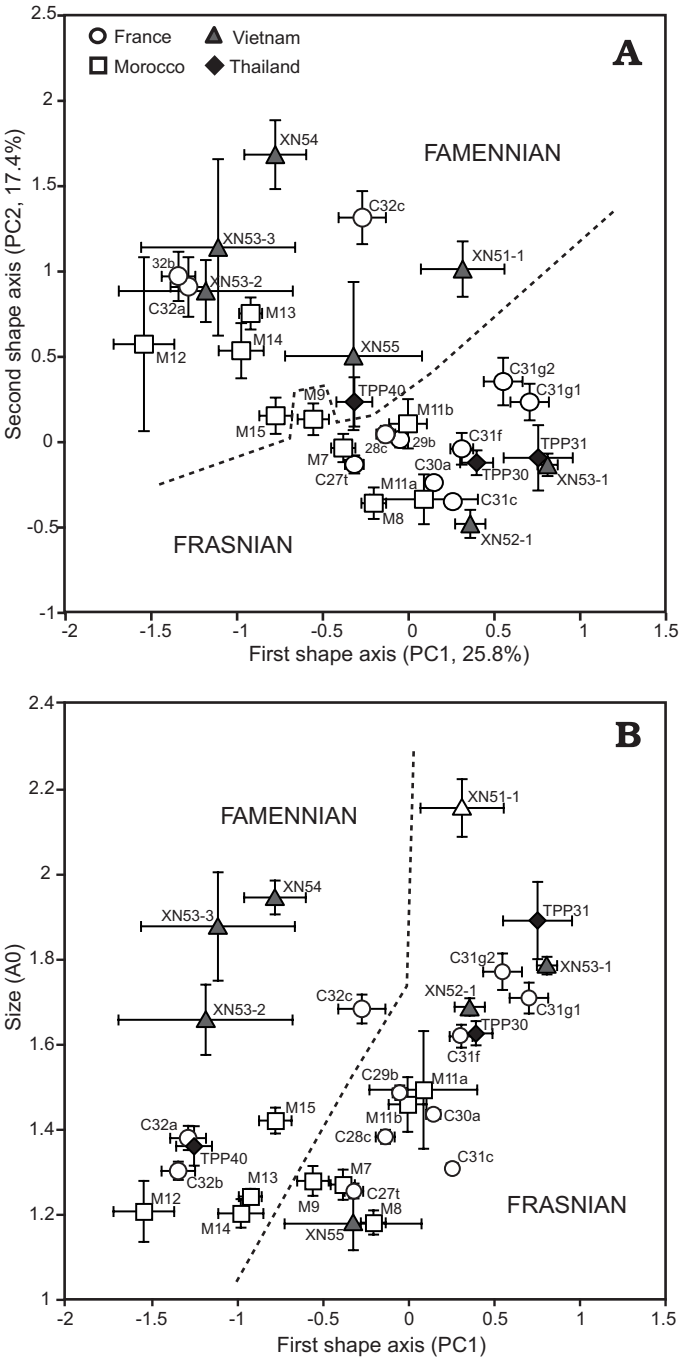


Fig. 4. Geographical and temporal variations between levels/localities based on the shape analysis of *Palmatolepis* elements. **A**. Morphological space defined by the first two axes of the principal component analysis (PC1, 25.8% and PC2, 17.2%) which explain almost half of the total variance. **B**. Relationship between average size and shape values in all considered levels. Size is estimated by A_0, shape by scores on PC1. The symbols represent the average value per level; error bars correspond to the 95% confidence interval. Open symbols: Frasnian; grey and black symbols: Famennian; circles = Coumiac, squares = Mrirt, triangles = Xom Nha, diamonds = Thong Pha Phum.

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Table 2. Tests for size and shape differences for the three time-slices. Size is estimated by the zeroth harmonic (A_0) derived from the outline analysis. Shape estimators are the first axes of a principal component analysis either on raw shape variables (Fourier coefficients, FCs) (PC1) or on size-free shape variables (residuals after regression of the FCs vs size) (PC1sf). Size and shape differences in mean values were tested by analyses of variance (ANOVA) completed by Kruskal Wallis tests, and differences in variance were tested using Levene's tests. Abbreviations: CUQ, Coumiac Upper Quarry; KW, Kruskal-Wallis; P, probability; sf, size-free; TPP, Thong Pha Phum; XN, Xom Nha.

			East/West			CUQ-Mrirt			TPP-XN		
			ANOVA	KW	Levene	ANOVA	KW	Levene	ANOVA	KW	Levene
			P	P	P	P	P	P	P	P	P
Famennian	*Palmatolepis triangularis*	A_0	0.038	0.057	0.155	0.000	0.000	0.794	0.000	0.000	0.210
		PC1	0.092	0.059	0.718	0.000	0.000	0.092	0.000	0.000	0.023
		PC1sf	0.001	0.001	0.680	0.008	0.002	0.155	0.134	0.131	0.262
Frasnian	*Palmatolepis linguiformis*	A_0	0.000	0.000	0.000	0.000	0.000	0.865			
		PC1	0.000	0.000	0.000	0.000	0.000	0.716			
		PC1sf	0.000	0.000	0.000	0.000	0.000	0.097			
Frasnian	*Palmatolepis rhenana*	A_0	0.000	0.000	0.352	0.000	0.000	0.005	0.000	0.000	0.143
		PC1	0.000	0.000	0.020	0.024	0.039	0.011	0.536	0.568	0.090
		PC1sf	0.000	0.002	0.000	0.382	0.230	0.192	0.003	0.009	0.004

In order to discard the global size-related effect, but retain geographic and temporal variations, a new data set was obtained as the residuals of multivariate regression of the FCs vs. size. A similar approach was applied for each time-slice.

These new "size-free" data-sets were analysed as the raw data sets using multivariate statistics, including visualisation by a PCA and tests of the geographic structure by MANOVA. Distribution of the first axis of each of these PCA, considered as synthetic size-free shape axis, was further investigated for each time-slice using ANOVA, Kruskal-Wallis and Levene's tests.

Results

Patterns of size and shape differentiation.—Variations in size and shape were first addressed by considering together all *Manticolepis* conodonts from the four sections across the time period considered (Fig. 4). Regarding shape (Fig. 4A), the major differentiation opposes Frasnian and Famennian conodonts whatever their geographic origin. This opposition does not hold true for size (Fig. 4B) that fails to show clear patterns. Noteworthy, samples from the Vietnamese outcrop (Xom Nha) tend to be larger on average whereas those from the Moroccan section (Mrirt) tend to be the smallest.

We further tested how much size and shape varied in the different sections. Temporal variations in size were significant in CUQ and TPP but not in XN and Mrirt. Temporal variations in shape were documented in all four sections (MANOVA: $P < 0.001$).

We further investigated how much size may drive shape variations due to allometric relationship. Indeed, size and shape appear overall related (Fig. 4B). This relationship is highly significant both when considering PC1 as synthetic shape estimator (PC1 vs. A_0: $P < 0.001$) and when considering a multivariate regression of all shape variables (FCs) vs. size ($P < 0.001$).

Geographic differences in size.—In the earliest time-slice (*Palmatolepis rhenana*), a significant difference in mean size was found between the Eastern and the Western part of the Prototethys (Fig. 5A). Variances of the distribution were, however, similar on both sides of the ocean. Local differences in size were involved within both area, the two sections documenting the Western part (CUQ and Mrirt) and Eastern part (XN and TPP) being significantly different from each other in mean size (Table 2). Differences in size variance were more reduced, being only significant on the Western part of the ocean (Table 2).

In the following time-slice shortly preceding the Kellwasser event and the F-F boundary (*Palmatolepis linguiformis*), the East-West difference was marked on mean size as well as on size variance. A difference among sections documenting the Western area was also evidenced but these assemblages shared similar patterns of variance (Table 2).

In the latest time-slice corresponding to the beginning of the Famennian (*Palmatolepis triangularis*), Eastern and Western assemblages do not differ anymore in mean size nor size variance (Table 2). Differences in mean size however locally exist but size variances are similar between these two sections (Fig. 5A, Table 2).

Geographic differences in shape.—During the *Pa. rhenana* time-slice, conodonts from the Eastern and Western part of the Prototethys differ in shape (MANOVA on FCs: $P < 0.001$; Fig. 5B). They also slightly differ in shape variance as estimated on PC1 (Table 2). This difference in shape distribution was even more marked during the *Pa. linguiformis* time-slice (Tables 2 and 3). This shape difference fades out during the subsequent time-slice *triangularis* (Tables 2 and 3).

Within each time-slice, this global geographic pattern is, however, blurred by local differ-

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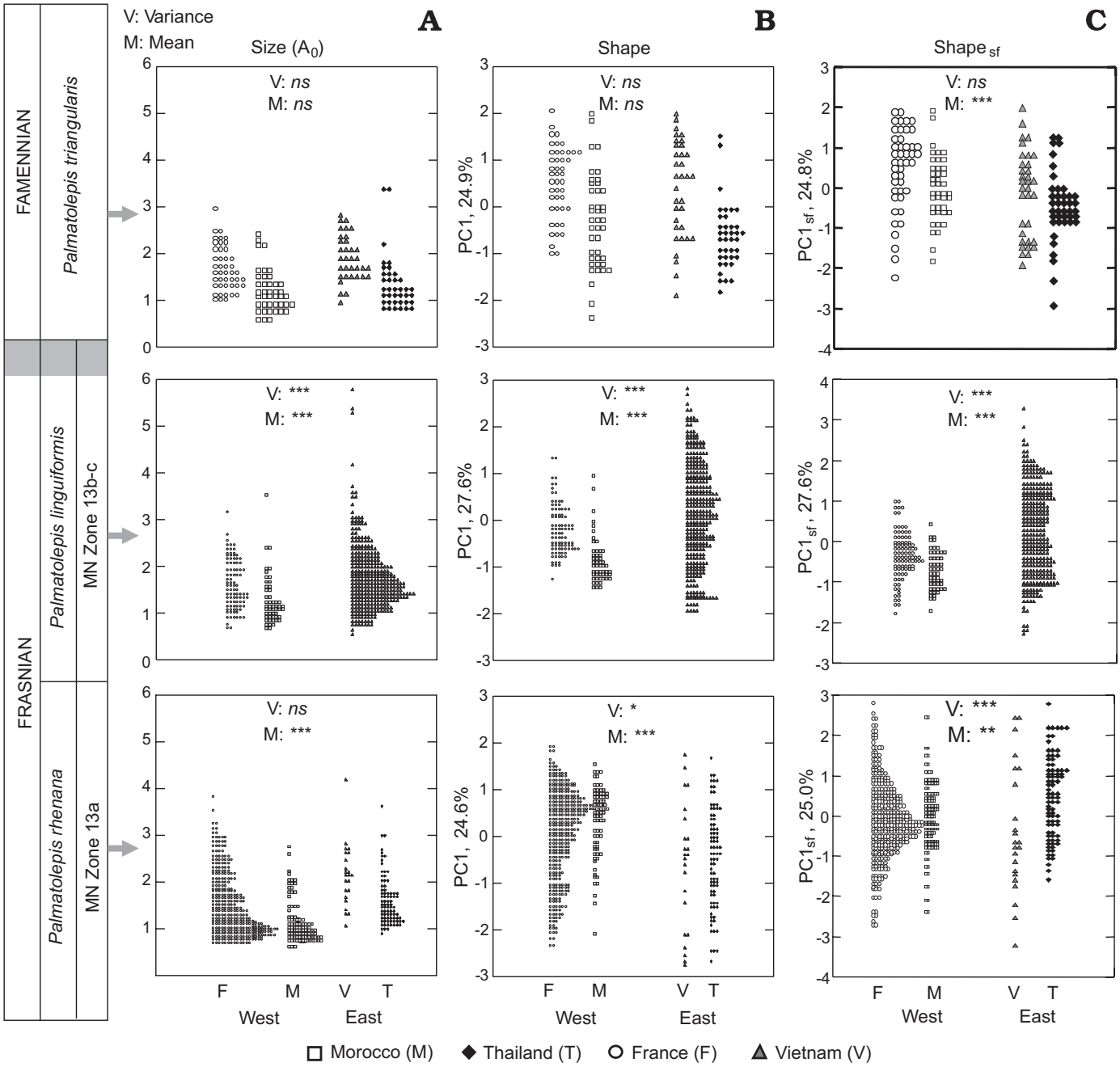


Fig. 5. Differences in size and shape variance through time and space. **A**. Size distribution of the *Palmatolepis* (*Manticolepis*) elements per geographical region and per time slice. Each dot corresponds to a value. Size is estimated by the zeroth harmonic of a Fourier analysis of the platform outline. **B**. Shape distribution, of the *Palmatolepis* (*Manticolepis*) elements per geographical region and per time slice. Shape is estimated by the scores on PC1. Each dot corresponds to a value. **C**. Distribution of the size-free shape, estimated by the scores on $PC1_{sf}$, of the *Palmatolepis* (*Manticolepis*) elements per geographical region and per time slice. Each dot represents single specimen; the grey beld corresponds to the Upper Kellwasser (UKW). Abbreviations: M, mean (Kruskall-Wallis); V, variance (Levene test).

ences are not highly pronounced during the *Pa. rhenana* time-slice (Tables 2 and 3), but are more marked during the *Pa. linguiformis* time-slice within the Western area (Table 3) and during the *Pa. triangularis* time-slice (Tables 2 and 3).

Geographic differences in size-free shape (Fig. 5C).— Considering size-free shape estimates instead of raw FCs for each time-slice separately, there was little change in the pattern of shape differentiation during the *Palmatolepis rhenana* time-slice between Eastern and Western area (Tables 2 and 3) but the difference in shape variance increased (Table 2). Local differences were less marked in the Western area (Tables 2 and 3) but more pronounced in the Eastern area (Tables 2 and 3).

During the *Pa. linguiformis* time-slice, the pattern of geographic differentiation was as marked on size-free shape parameters as for raw data. Significant differences

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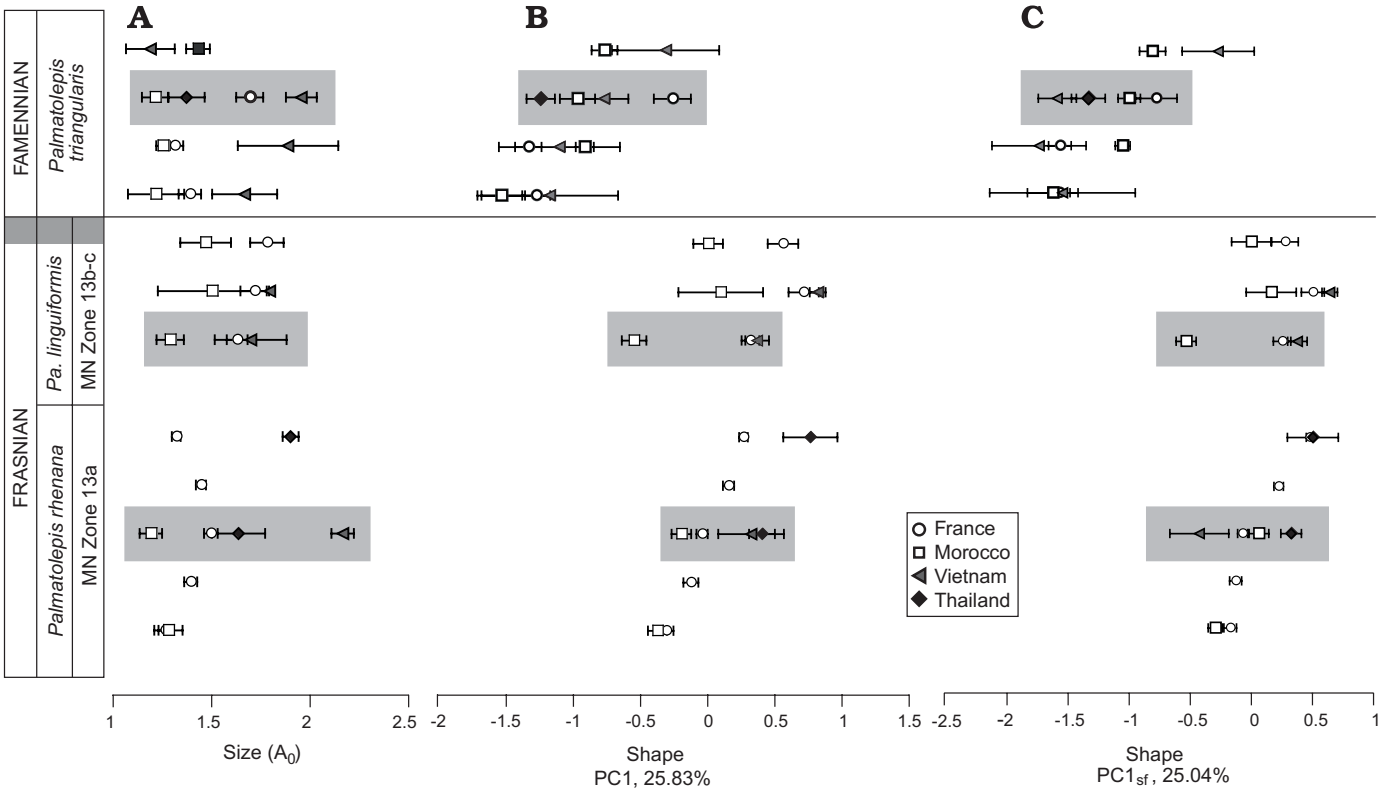


Fig. 6. Size (estimated by the zeroth harmonic of a Fourier analysis of the platform outline) and shape variations of *Palmatolepis* (*Manticolepis*) through Coumiac (France), Mrirt (Morocco), Xom Nha (Vietnam) and Thong Pha Phum (Thailand). Shape is estimated by the score on PC1 (25.5%) and by the score on $PC1_{sf}$ (24.4%). The symbols represent the average value per level; error bars correspond to the 95% confidence interval. The grey beld corresponds to the Upper Kellwasser (UKW). Open symbols: Frasnian; grey and black symbols: Famennian; circles = Coumiac, squares = Mrirt, triangles = Xom Nha, diamond = Thong Pha Phum. Grey boxes = the 3 time-slices.

between East and West emerged (Tables 2 and 3). Local differences within the Western area were also pronounced (Tables 2 and 3).

Considering the size-free shape estimates increased the differentiation between East and West during the *Pa. triangularis* time-slice (Tables 2 and 3) although differences in shape variance are still not significant (Table 2). In contrast, local differences are attenuated (Table 3).

Table 3. Tests for shape differences for the three time-slices tested using multivariate analyses of variance (MANOVA). Shape estimators are the Fourier Coefficients (FCs) and the residuals of a multivariate regression of the FCs vs. size (Res-sf). Abbreviations: CUQ, Coumiac Upper Quarry; P, probability; sf, size-free; TPP, Thong Pha Phum; XN, Xom Nha.

		MANOVA	East/ West	CUQ-Mrirt	TPP-XN
			P	P	P
Famennian	*Palmatolepis triangularis*	A1-B11	0.000	0.000	0.000
		Res-sf	0.000	0.000	0.004
Frasnian	*Palmatolepis linguiformis*	A1-B11	0.000	0.001	
		Res-sf	0.000	0.000	
Frasnian	*Palmatolepis rhenana*	A1-B11	0.000	0.001	0.000
		Res-sf	0.001	0.010	0.000

Summary of size and shape variations through time and space.—The patterns of differentiation detailed above per time-slice can be integrated into a broader framework showing temporal and spatial variations (Fig. 6). Temporal and spatial trends in size are quite fuzzy (Fig. 6A) and especially, no clear response to the major step represented by the F/F boundary can be identified consistently. Local characteristics seem to be of prime importance, with conodonts being on average the smallest in the Moroccan section (Mrirt) and the largest in the Vietnamese outcrop (Xom Nha), to the exception of the latest sample.

Patterns of shape variations are much more coherent (Fig. 6B). Especially, the major morphological shift characterising the F/F, already recognized in Western samples (e.g., Girard and Renaud 2007) appears to occur in a similar way in the Eastern locations. Eastern samples, especially from Xom Nha, appear close to the reference outcrop Coumiac but slightly shifted towards positive values, whereas conodonts in Mrirt appear to be characterized by the reverse trend. This may be due to an allometric covariation with size, Xom Nha and Mrirt being characterized by the largest and smallest conodont size, respectively. Considering size-free shape variations (Fig. 6C) allowed removing any blurring effects of local size differences. Indeed, the gap between Vietnamese and Coumiac samples disappeared, providing very coherent trends across, before and after the F/F boundary.

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Discussion

Global trends of *Palmatolepis* (*Manticolepis*) shape over time.—A first striking result emerging from the present analysis was actually to show how little geographic differentiation occurred within *Palmatolepis* (*Manticolepis*) during the investigated Late Devonian period. In contrast, very coherent and homogeneous temporal trends emerge throughout the time interval in all sections considered. This corroborates previous results suggesting that shape trends in *Palmatolepis* (*Manticolepis*) were comparable among sections and might serve for stratigraphic correlations (Girard and Renaud 2007). These results, however, were only based on outcrops from the Western margin of the Prototethys; the present results show that they can be generalized to the whole Prototethysian domain. In the Western area, the temporal shape trends in *Pa.* (*Manticolepis*) have been further shown to parallel environmental variations, suggesting that shape variations might have been triggered by subtle variations in their diet, in turn triggered by changes in the trophic chain (Balter et al. 2008). The geographic homogeneity of the response of *Pa.* (*Manticolepis*) to this environmental forcing suggests that on this respect, global change had an impact largely overcoming local environmental differences. This assertion seems trivial for the F/F crisis, known to have been global and of tremendous impact on the fauna on a world-wide scale; it is less intuitive, however, for the trends occurring during the late Frasnian and the early Famennian.

Geographic differentiation and eustatic trends.—The present study failed to identify clear-cut morphotypes characteristic of the Western vs. Eastern Prototethys, all assemblages largely overlapping in size and shape. Still, thanks to the impressive sampling allowed by conodonts for morphometric analyses, we evidenced some subtle differentiation between these two biogeographic areas, in the way (mean and variance) the size and shape values were distributed. This differentiation was not constant over time: being quite subtle in the late Frasnian interval (*Pa. rhenana* Zone), it appeared maximal just before the crisis during the *Pa. linguiformis* Zone, to decrease to almost no geographic differences in the early Famennian.

Several factors may explain this temporal dynamics of the biogeographic pattern. Eustatic trends seem to be good candidates to modify the patterns of water mixing and affect the distribution of marine organisms, although evidences of their impact on the geographic structure of the fauna are conflicting. On the one hand, transgression may be invoked to increase water mixing, and hence long-term dispersal and cosmopolitanism. On the other hand, high sea-level increases the areas of epicontinental seas, possibly providing more complex landscapes favorable to geographic differentiation. Accordingly, increased diversity were observed during global rises of sea-levels in ammonoids (Klug 2002) and trilobites (McNamara and Feist 2006; McNamara et al. 2009). The more complex the marine landscapes, the more the rise in diversity associated with transgressive conditions should be pronounced.

How to interpret the temporal dynamics of geographic differentiation of *Palmatolepis* conodonts in this context? The late Frasnian *Pa. rhenana* Zone was characterized by low sea-level, followed by a transgression shortly before the F/F crisis, probably culminating at the base of the Upper Kellwasser deposit. This transgressive episode was followed by a regressive trend at the top of the Kellwasser event, which continued during the early Famennian (Sandberg et al. 2002; Racki 2005; Girard and Renaud 2007). Our results to a maximal geographic differentiation during the transgressive episode of the Latest Frasnian, an observation apparently discrepant with the long-term observation that the overall cosmopolitanism of the conodonts increased through the Frasnian (Klapper 1995) together with a global sea-level rise (Johnson et al. 1985; Haq and Schutter 2008).

This discrepancy may be due to particular tectonic conditions during the Latest Frasnian, a period suggested to be marked by extensive synsedimentary tectonics and block movements leading to complex shelf topography (Racki 1998; Averbuch et al. 2005). In addition, long-term dispersal does not necessarily prevent geographic differentiation, if the ecological conditions are contrasted enough to promote local adaptation (e.g., Norris and de Vargas 2000; de Vargas et al. 2001). Indeed, the geographic restriction of *Pa. linguiformis* during the same Latest Devonian time interval on the Eastern shelf of the Prototethys already suggested contrasted ecological conditions (Girard et al. 2007) that may have promoted subtle geographic differentiation within the apparently cosmopolitan *Pa. (Manticolepis*).

The F/F crisis swamping biogeographic differences.—Geographic differentiation within *Pa.* (*Manticolepis*) appeared overall subtle throughout the record, but for a similarly low sea-level, geographic differentiation between Eastern and Western part of the Prototethys seems to have been even lower during the early Famennian, i.e., the recovery period following the F/F crisis, than during the preceding late Frasnian *Palmatolepis rhenana* time-interval.

This suggests that the occurrence of a major biotic crisis swamped out geographic differentiation. This matches a pattern already documented for several extinctions events (Cocks and Fortey 1990; Hallam and Wignall 1997). A possible explanation is that, even for animals surviving the crisis such as *Pa.* (*Manticolepis*), survival occurred in favorable patches from which a global recolonization by forms adapted to the new environmental conditions occurred.

Overall cosmopolitanism and local differences.—Beyond these trends in temporal response to environmental changes and in biogeographic differentiation, a further striking feature is the frequent occurrence of local geographic differences between conodonts from outcrops located on the same area of the Prototethys margin. How to reconcile an overall cosmopolitanism of *Pa.* (*Manticolepis*), widely distributed without clear differentiation at a global scale, and such local differences?

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Two, not mutually exclusive, ranges of explanation can be invoked. First, marked local differences persisting throughout the record regard size differences, with for instance conodonts being on average larger in the Xom Nha section and smaller in the Mrirt section. This might be due to different taphonomic processes, favoring deposition of conodonts of various size range (McGoff 1991). Size distributions in the various sections (Fig. 5), however, document the occurrence of the whole range of conodont size in all sections, differences being rather due to distributions more or less skewed towards small-sized conodonts. Since the size of the conodont element is related to growth, the distribution of the size value can point to the pattern of survivorship of the conodonts at this time and space (e.g., Girard and Renaud 2008). Geographic structure in conodont size may thus be due to differences in life-history traits due to local ecological conditions.

It is difficult to explain geographic shape differentiation, however, by differences in growth only, especially once allometric influences have been retrieved by considering size-free variables. Shape differences, even subtle, are more commonly the phenotypic expression of an underlying genetic differentiation as shown in various marine organisms (e.g., Cadrin 2000; de Vargas et al. 2001; Borsa 2002; Kassahn et al. 2003; Turan 2004). The local morphometric differences evidenced in *Palmatolepis* (*Manticolepis*) would thus point to a genetic structure despite an overall cosmopolitanism. This raises the question of how to mix populations of marine organisms on a global and local scale. Marine organisms, especially with planktic life stages, are expected to be capable of long distance dispersal (e.g., Kyle and Boulding 2000). Indeed, long distance genetic mixing has been shown in planktic organisms such as foraminifera (Darling et al. 2000) and fishes (e.g., Grant and Bowen 1998). Such long distance dispersal is not inconsistent, however, with a structure between distant populations (Graves 1998), depending on the amount of gene flow. Geographic differences between populations may even occur at a finer scale, depending on the complexity of marine landscapes and currents, even in animals capable of long-range dispersal such as marine fishes (e.g., Roques et al. 2002; Jørgensen et al. 2005). Hence, the cosmopolitism of *Pa.* (*Manticolepis*) is compatible with both the occurrence of a large scale geographic pattern, although transient in time, and the occurrence of subtle local differentiations. This points to the potential of such fine scale morphometric analyses to decipher the population dynamics in extinct organisms; in a reassuring way, however, such biogeographic signature remains discrete compared with global signals, allowing for correlations of morphometric trends in *Pa.* (*Manticolepis*) conodonts on a global scale.

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