

# Unsuspected functional disparity in Devonian fishes revealed by tooth morphometrics?

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Received: 17 March 2014 / Revised: 2 July 2014 / Accepted: 4 July 2014 / Published online: 31 July 2014  
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**Abstract** The shape of features involved in key biological functions, such as teeth in nutrition, can provide insights into ecological processes even in ancient time, by linking the occupation of the morphological space (disparity) to the occupation of the ecological space. Investigating disparity in radiating groups may provide insights into the ecological diversification underlying evolution of morphological diversity. Actinopterygian fishes initiated their radiation in the Devonian, a period characterized by the diversification of marine ecosystem. Although a former morpho-functional analysis of jaw shape concluded to conservative and poorly diversified morphologies in this early part of their history, fish tooth disparity evidenced here an unsuspected diversity of possible functional significance in the pivotal period of the Late Devonian (Famennian). All teeth being caniniforms, some were stocky and robust, in agreement with expectations for active generalist predators. More surprisingly, elongated teeth also occurred at the beginning of Famennian. Their needle-like shape challenges morpho-functional interpretations by making them fragile in response to bending or torsion. The occurrence of both types of fish teeth during the beginning of the Famennian points to a discrete but real increase in disparity, thus testifying a first burst of feeding specialization despite overall conservative jaw morphology. The disappearance of these needle-like teeth in the Late Famennian might have been related to a relay in dental

diversity with abundant co-occurring groups, namely conodonts and chondrichthyans (sharks).

**Keywords** Eco-morphology · Disparity · Actinopterygian fishes · Devonian · Conodonts · Sharks

## Introduction

Morphological disparity, when being of functional significance, offers an opportunity to trace ecological variety in the fossil record, for which more direct evidences of how resources were exploited and partitioned are lacking (e.g., Foote 1994; Anderson et al. 2011). This may deliver precious clues about ecological structure and dynamics in ancient times and most importantly, how ecological complexity progressively evolved and responded to environmental changes (e.g., Bellwood et al. 2014a).

Exemplifying that morphological disparity goes with ecological diversification and ability to exploit diverse resources, groups dominating the modern marine ecosystems often started as discrete members of past ecosystems, displaying low disparity and occupying marginal ecological niches (Friedman 2010; Sallan and Coates 2010). This is notably the case for actinopterygians, or bony fishes, the most speciose group of living fishes (Friedman and Sallan 2012; Nelson 2006). Their appearance and rise, as part of the jawed vertebrates (gnathostomes), during the Devonian and into the post-Devonian, is one of the key episodes in vertebrate evolution (Sallan and Coates 2010). Among jawed vertebrates, however, actinopterygian fishes exhibited during all the Devonian a low and conservative disparity, contributing only poorly to the functional disparity at that time (Anderson et al. 2011). Their rise in abundance and diversity started only after the Hangenberg crisis punctuating the end of the Devonian (Sallan and Coates 2010).

These recent studies raise several questions. First, eco-morphological disparity of fishes was assessed based on jaw

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Communicated by: Sven Thatje

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functional traits (Anderson et al. 2011), letting aside another important ecologically relevant component, namely tooth shape. Together with jaws, teeth are nowadays one of the most important traits structuring resource exploitation in fishes (e.g., Sage and Selander 1975; Motta 1989; Mittelbach et al. 1992; Norton et al. 1995; Luczkovich et al. 1995; Bellwood et al. 2014b). Focusing on jaw might ignore important and functionally relevant components of fish disparity, especially given that numerous fish remains in that remote period consist in isolated teeth only. Second, all these studies focused on long-term evolution, presenting data at the scale of the geological stage and thus pooling time interval up to 15 myrs (Sallan and Coates 2010; Anderson et al. 2011). However, evolutionary processes may go at a faster speed, and onset of diversification may be masked by such time averaging. Studying disparity at a finer time scale may evidence unsuspected trends within 10–15 kyrs (e.g., Girard and Renaud 2012).

The present study therefore aims at quantifying morphological disparity in teeth of actinopterygian fishes during a period of pivotal importance in their history, namely the Late Devonian (Famennian period, some 370 millions of years ago). This period started with one of the major extinctions in Earth's history, occurring at the Frasnian/Famennian boundary (F/F) (McGhee 1996; Walliser 1996). This extinction decimated major component of marine ecosystems and likely offered free ecological space for survivors to (re-) diversify. However, jawed vertebrates in general and actinopterygian fishes in particular were not decimated by this episode (Sallan and Coates 2010). The Late Devonian period finished with another major extinction event, the Hangenberg, which seems to have had a much more pervasive impact on vertebrate faunas and have triggered the rise of the actinopterygians (Sallan and Coates 2010). This period is also pivotal in the organization of the marine ecosystems, seeing a rise in the occupation of the free water column, to the detriment of the benthic and demersal habitats, i.e., those of swimming animals that live close to the seafloor (Klug et al. 2010).

Taking advantage of a recently described outcrop offering a remarkably complete record of the Famennian (Girard et al. 2014), disparity of actinopterygian fishes was assessed by quantifying their tooth morphology using geometric morphometrics. Results were interpreted in the context of variations observed in co-occurring groups delivering teeth of similar size (mostly conodonts and chondrichthyans), and thus in potential ecological interactions with the actinopterygian fishes.

## Material and methods

### Geological setting

The material was collected from the Col des Tribes section located in the Montagne Noire, France. This is a calcareous

outcrop about 84-m thick. The depositional environment inferred here is an open marine environment of low energy along the whole outcrop (Girard et al. 2014). Based on the conodont zonation (Ziegler and Sandberg 1990), the entire latest Devonian stage, i.e., the Famennian, with its lower and upper boundaries, is represented on this section (Girard et al. 2014). All the successive nine conodont zones (thereafter called stratigraphic zones) composing the entire Famennian were recognized, allowing a study of morphological disparity at a temporal scale of about 1.5 kyrs.

### Material

Rocks samples collected on the outcrop were decalcified using 10 % formic acid. The residues were rinsed between 100 µm and 1-mm sieves. All teeth present in these samples were picked. Regarding teeth, the material almost exclusively included actinopterygian and chondrichthyan remains (Fig. 1).

Most of the conical teeth were identified as actinopterygian teeth because of the presence of a translucent hard tissue, identified as an acrodin cap at the top of the crown (Liszkowski and Racki 1993). Subsequently, they will be designed as “fish teeth”. Material from different levels was grouped by stratigraphic zones in order to have sufficient specimens per group for statistical analyses (Table 1). A dozen teeth of another “large-based” type have been found. These teeth may belong to sarcopterygians (lobe-finned fishes). Given the paucity of the record in the Col des Tribes and the lack of diagnostic features, this material has not been included in subsequent analyses.

### Methods

#### *Acquisition of morphometric data*

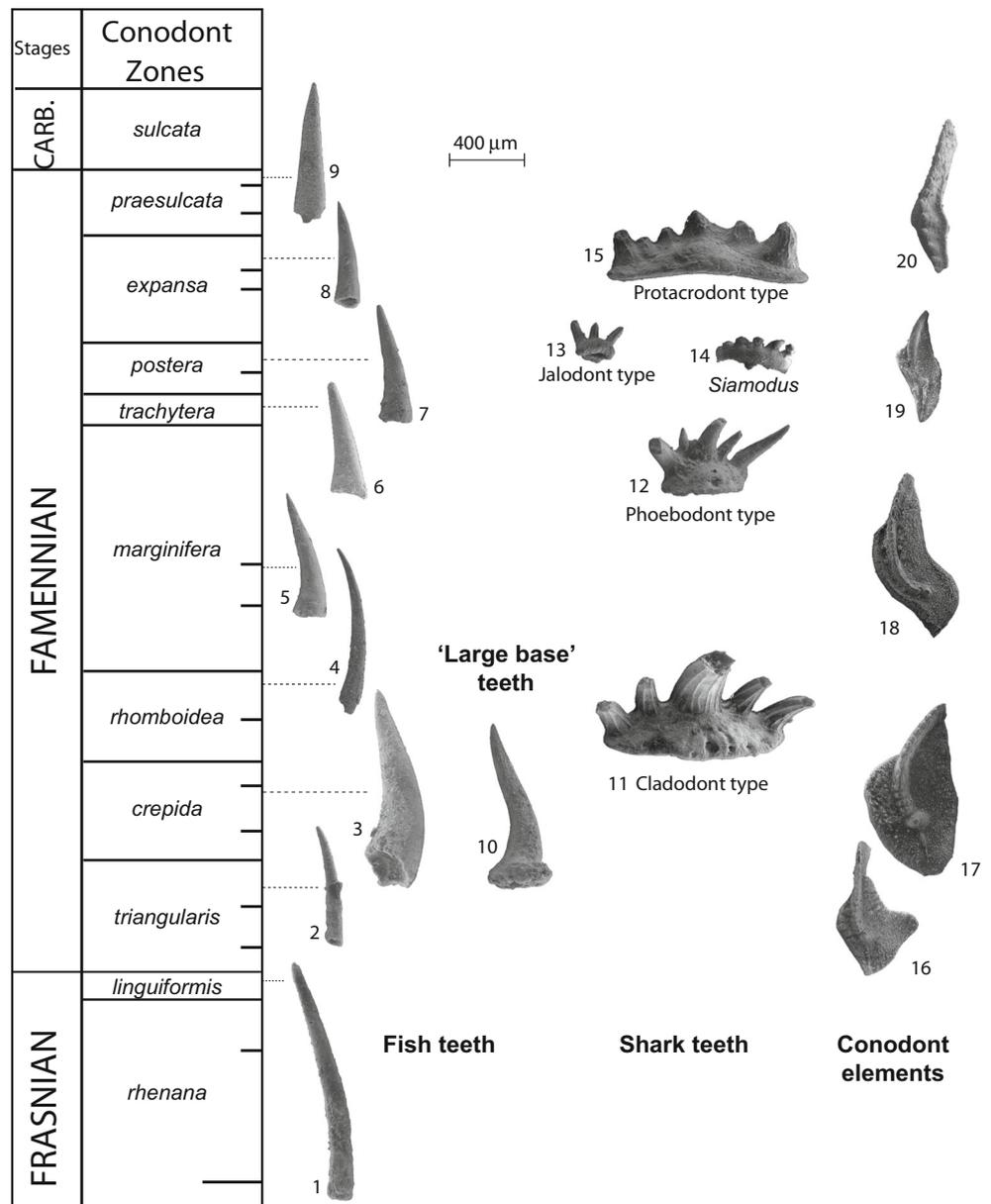
The shape of fish teeth was quantified using 2D geometric morphometrics (Bookstein 1991). Teeth were orientated in a comparable way: top above, concave side at the left, and convex side at the right. Three landmarks defined the overall shape of the tooth: the two basal points and the top. The curvature of the tooth was further documented by two series of seven sliding landmarks, one series on the concave, and one series on the convex side (Fig. 2).

Landmarks and sliding landmarks were digitized using tpsDig2 (Rohlf 2010a). Each tooth was therefore described by a configuration of 3 landmarks and 14 sliding landmarks, i.e., by 34 x and y coordinates.

#### *Morphometric analysis of fish teeth*

These configurations were superimposed using a Procrustes procedure using tpsRelw (Rohlf 2010b). This method

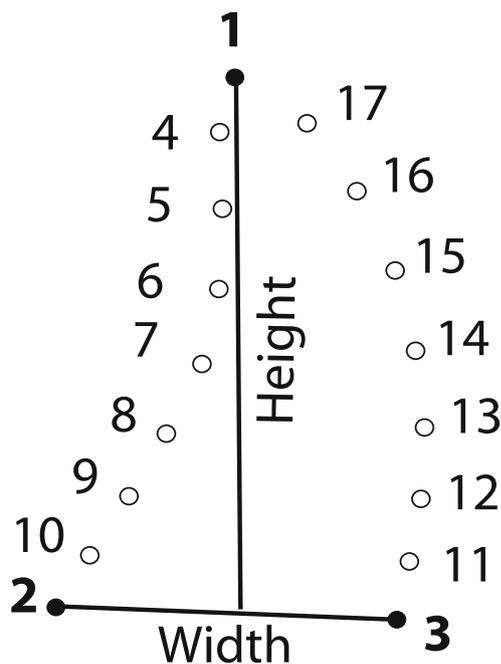
**Fig. 1** Diversity of tooth and tooth-like material in Col des Tribes section. 1–9 Actinopterygian fish teeth (*linguiformis* to *praesulcata* zones). 10 Large-based tooth probably belonging to a sarcopterygian fish (*crepida* zone). (11–15) Chondrichthyan (shark) teeth, lingual view. 11 Cladodont tooth (*Denaea* sp., *rhomboidea* zone): kidney-shaped teeth with a major central cusp surrounded by several smaller ones. 12 Phoebodont tooth (*Phoebodus limpidus*, *expansa* zone): round-shaped teeth with three major slender cusps separated by cusplets. 13 Jalodont tooth (*Jalodus australiensis*, *expansa* zone): round-shaped teeth with three thick cusps of equal size, often bearing lanceolate ornamentation. 14 *Siamodus* teeth (*S. janvieri*, *expansa* zone): crescent-shaped teeth with five or seven low rounded and well-separated cusps. 15 Protacrodont tooth (*Protacrodus* sp., *praesulcata* zone): long, thin teeth with very low cusps that can be partially fused toward the basis. (16–19) Conodont P1 elements: 16 *Palmatolepis quadrantinodosalobata* (*triangularis* zone). 17 *Palmatolepis crepida* (*crepida* zone). 18 *Palmatolepis marginifera marginifera* (*marginifera* zone). 19 *Palmatolepis perlobata postera* (*postera* zone). 20 *Palmatolepis gracilis gracilis* (*praesulcata* zone)



**Table 1** Sampling along the stratigraphic zones. Number of teeth of fishes and sharks (counting) are provided, as well as number of unbroken fish teeth used for morphometric analyses, and abundances (estimated per kg of rock) of fishes, and sharks. Stratigraphic zones: *linguiformis* (ling),

*triangularis* (triang), *crepida* (crep), *rhomboidea* (rhomb), *marginifera* (marg), *trachytera* (trach), *postera* (post), *expansa* (exp), and *praesulcata* (prae)

		Ling	Triang	Crep	Rhomb	Marg	Trach	Post	Exp	Prae	Total
Counting	Fishes	54	58	71	57	188	130	84	319	84	1045
	Sharks	2	11	11	13	0	3	0	22	8	70
	Sarcopterygians	0	1	2	2	0	0	0	2	0	7
Morphometrics	Fishes	15	16	27	37	87	58	50	156	34	480
Abundances	Fishes	30.5	90.6	33.3	39.6	47.8	40.5	91.3	114.7	41.0	
	Sharks	1.2	6	4.6	2.7	0	0.9	0	7.9	3.9	



**Fig. 2** Morphometric quantification of tooth shape: landmarks (filled circles), sliding landmarks (open circles), height and width (dotted lines)

performed a scaling, translation, and rotation of the data in order to minimize the sum of squared distances between corresponding landmarks (Rohlf and Slice 1990). The size estimator used to scale the specimens was the centroid size, i.e., the square root of the sum of squared distances between all landmarks of a configuration and their centroid. Sliding landmarks are allowed to slide along the curve in order to optimize the adjustment of the points along the curve across all specimens (Bookstein 1997).

Procrustes residuals resulting from this superimposition constitute shape variables that were analyzed using a principal component analysis (PCA). This allowed representing the shape variation on few synthetic axes. It was performed using the package FactoMineR (Husson et al. 2012) with R 3.01 (R Core Team 2013). Differences between temporal groups were further tested by multivariate analyses of variance (MANOVA) on PC axes totaling most of the variance.

Size and shape can be related by allometric relationships. This was investigated by simple regressions of each PC axis vs size, completed by a multiple linear regression between the shape variables and the log transformed centroid size using tpsRegr (Rohlf 2010b). The stability of the relationship through time was investigated using a multivariate analysis of covariance (MANCOVA), independent factors being then stratigraphic zone, centroid size, and the interaction of both. A significant interaction term would point to differences of the size/shape relationship through time.

This quantification of tooth shape includes detailed features such as the curvature of the tooth. Beyond differences in

curvature, all teeth being coniforms, a major feature describing their variation is their basic shape, opposing elongated to short teeth. A simplified description of tooth shape was further considered for focusing on these basic shape differences. The width of the tooth was evaluated as the distance between the two basal points. The height was calculated as the distance of their midpoint to the top of the tooth. The height/width ratio (H/W) provided a simple estimate of the overall tooth shape. Differences in width, height, and H/W between temporal zones were tested using a non-parametric Kruskal-Wallis test. Disparity was evaluated as the range of H/W values observed per zone. To minimize the impact of outliers, the range was estimated as the 95 %-minus the 5 %-percentile of the distribution. Finally, the robustness of the results regarding sampling size was assessed using a procedure of random rarefaction. For each stratigraphic zone, sample size was rarefied to the minimum sample size ( $N=15$ ) ten times. For each trial, mean width, height, and H/W were calculated, and Kruskal-Wallis tests were performed to test for differences along the record.

## Results

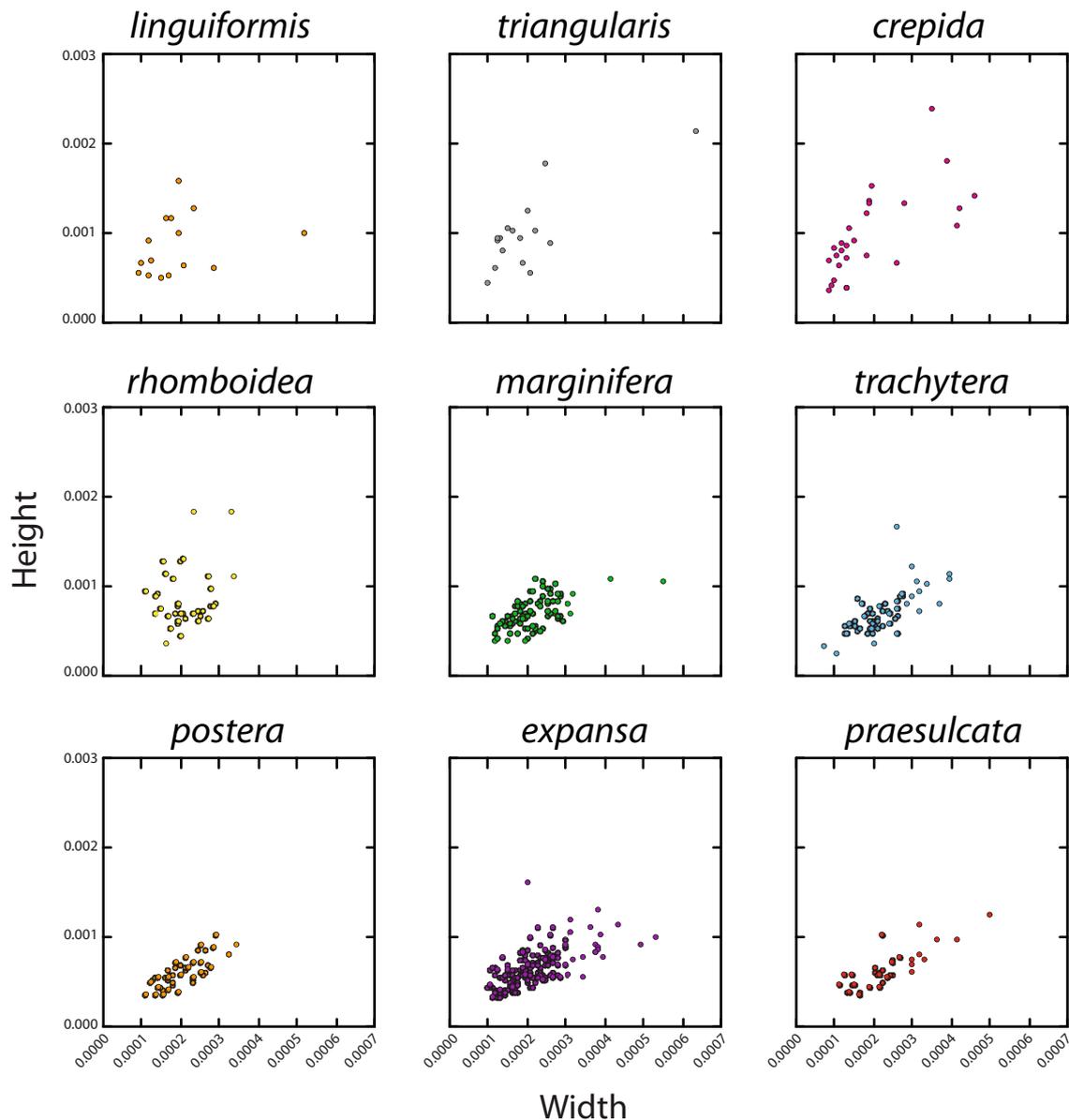
### Morphometric variations of fish teeth through time

The morphometric analysis was performed on the fish teeth from the Col des Tribes outcrop, based on the set of landmarks and sliding landmarks. It provided two axes totaling almost 90 % of the total variance (Fig. 3). No clear cluster could be identified in the distribution of the specimens in this morphospace. Nevertheless, the occupation of the morphospace seems to change through time, with an occupation of the first quarter of the morphospace (PC1 and PC2 positive) early in the record (*linguiformis* to *rhomboidea*), progressively fading away during the *marginifera* zone. Later on, this part of the morphospace remains empty, leading to a significant difference in shape between the first and later parts of the record (MANOVA on PC1-PC2, *linguiformis* to *rhomboidea* vs. *marginifera* and later zones:  $P<0.0001$ ).

The variation explained by the two axes share a similar shape feature, opposing slender teeth (PC1 and PC2 positive) to more robust ones. The temporal shift in the occupation of the morphospace seems therefore related to this change in the basic shape of the tooth. Further differences between PC1 and PC2 regard the curvature of the teeth, which seems highly variable within all samples without clear structure.

### Size-related shape variation in fish teeth

The possible importance of size-related variation in driving the overall shape variation was investigated in two ways. First,



**Fig. 3** Morphospace of fish teeth from the end-Frasnian to the end-Famennian. The morphospace was defined by the first two axes of a PCA analysis on Procrustes residuals. The representation has been split

by temporal zones. Tooth reconstructions visualizing extreme scores along the axes are provided (position along their axis pointed by an arrow, the value along the other axis being equal to zero)

each PC axis was compared to size. In both cases, the progressive elongation of the tooth described by increasing PC scores was related to an increase in tooth size (vs. log transformed centroid size, PC1:  $N=480$ ,  $R^2=0.149$ ,  $P<0.001$ ; PC2:  $N=480$ ,  $R^2=0.079$ ,  $P<0.001$ ). This analysis was completed by a multivariate regression of Procrustes residuals vs. log-transformed centroid size, confirming a significant size-shape relationship corresponding to larger teeth being more elongated (Wilk's lambda: 0.675,  $P<0.001$ ). This size-shape relationship varies through time, however, as shown by a significant interaction term between size and stratigraphic zones in a MANCOVA ( $P<0.001$ ).

#### Variation in fish tooth height/width

The morphometric analysis suggested that the main temporal difference was related to a change in the elongation of the tooth. Subsequent analyses were therefore focused on width, height, and the height/width ratio (H/W).

Width varied slightly through time ( $P=0.016$ ) (Fig. 4a). Hints of multimodal distributions may indicate that a mixture of teeth of increasing size, corresponding either to different species, or ontogenetic series within a single species. Unfortunately, isolated teeth do not allow a decision between both hypotheses. In contrast, height varies highly significantly

across zones ( $P < 0.001$ ), with a shrinking of the distribution toward lower height value through time (Fig. 4b). Both combined led to marked variations in the height-width ratio H/W (Fig. 4c), with a significant decline over time ( $P < 0.001$ ). The shape change could not be attributed to changes along a single ontogenetic trajectory, since the height to width relationship changed over time (ANCOVA on height per zone, width as covariate: interaction term zone  $\times$  width  $P < 0.001$ ). A significant negative relationship between H/W and width ( $R^2 = 0.186$ ,  $P < 0.001$ ) further showed that although width variations through time were of minor importance compared to height variations, they also contributed to the overall tooth shape change. Teeth in the latest zones of the Devonian not only became less high, but also slightly wider.

High H/W values from *linguiformis* to *rhomboidea* corresponded to the occurrence of very elongated, needle-like teeth. This morphotype disappeared later on in the record, with only H/W corresponding to stocky teeth persisting throughout. The *rhomboidea* zone represents a transition, still with elongated teeth occurring, but with a beginning in the decrease of the mean value of H/W.

Further note that such variations in height and width distributions might be due to unbalanced and/or insufficient sample size. A random rarefaction procedure was thus applied ten times to each the shape variables in each zone, providing

estimates of height, width, and H/W (Fig. 4). The decrease of H/W through time appeared to be robust to sampling variations, and differences between the early and late parts of the record were significant in all ten replicates ( $P < 0.001$ ).

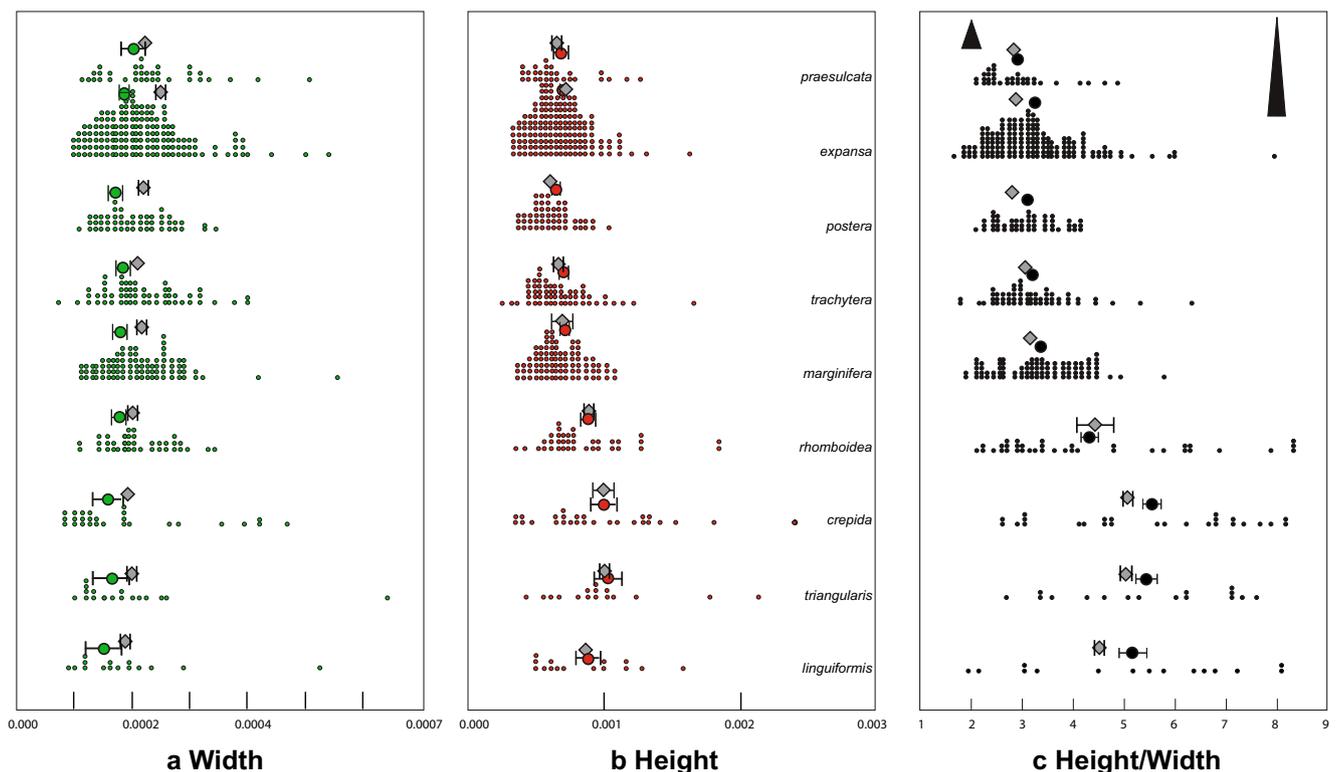
Although not an evidence of total absence, this shows that from rather balanced occurrence of elongated and stocky teeth in the early part of the record, the distribution switched to an overwhelming dominance of stocky teeth.

Overall, beyond possible variations of taxonomic composition that the present analysis failed to evidence based on tooth shape, and/or possibly ontogenetic variations, a temporal shift in disparity was evidenced, with a higher morphological disparity occurring early in the record (up to *rhomboidea* zone) and decreasing thereafter with the only occurrence of stocky teeth.

## Discussion

Shape variation of late Devonian fish teeth from the Col des Tribes

Only simple, coniform fish teeth are present in Col des Tribes record. In that respect, our results are in agreement with the low



**Fig. 4** Basic mensurations of fish teeth along time. **a** Width. **b** Height. **c** H/W. Each dot corresponds to a single tooth. Large symbols correspond to the mean value per zone  $\pm$  standard error. Gray diamonds correspond to

mean value of 10 random rarefactions to  $N=15$  for each zone,  $\pm$  standard error among repetitions. Triangles on the H/W plot represent schematic shape corresponding to ratios H/W=2 and H/W=8

disparity in jaw morphology for Devonian actinopterygian fishes (Anderson et al. 2011). Extensive shape variation was evidenced within these simple coniform teeth (Fig. 3). Interspecific differences (e.g., Wautier et al. 2002) could not be excluded even if they were not supported by the occurrence of clear morphological clusters. In modern fishes, sexual dimorphism, ontogenetic replacement, and position along the jaw are known to be related to differences in type, size, and/or shape of the teeth (e.g., Hatooka and Randall 1992; Streelman et al. 2003; Streelman and Albertson 2006; Grubich et al. 2008). All these factors might have contributed to the background variation in these Late Devonian teeth all along the record, but they are not likely to have driven the temporal shift in disparity.

Curvature is crucial in determining the functional properties of coniform teeth (Murdock et al. 2013). This feature was indeed variable in our record, corresponding to a diffuse variation within each zone and suggesting possible functional variation (e.g., Murdock et al. 2013) along the jaw of fishes of a same species or among separate species.

In contrast, a clear signal in tooth elongation emerges in our Late Devonian fish teeth (Fig. 3), with two end-member morphologies: elongated teeth vs. stocky teeth. This difference is mostly driven by variations in tooth height. The allometric relationship that was evidenced between tooth shape and centroid size was due to the fact that elongated teeth, being higher but not much narrower, were, by consequence, of larger global size than their stocky counterparts.

#### A functional significance for disparity in Devonian fish teeth?

Morphological disparity in fish tooth was overall low during the Famennian, with only coniform teeth. Their morphology corresponded to “caniniform” teeth, loosely arranged on jaws of modern and fossil fishes and interpreted as piercing graspers feeding on whole preys (Bellwood et al. 2014a). In agreement, the few Devonian entire specimens displaying teeth similar to those found in our record are arranged in a same, loose way (Choo et al. 2009). Devonian fishes were characterized by slender jaws with low closing mechanical advantages (Anderson et al. 2011). Overall, arguments converge to interpret Devonian coniform, stocky teeth as those of active predators feeding on the flesh of the preys they pierced.

The function of the elongated needle-like coniform teeth is more problematic. Their long and fine shape should have made them efficient for piercing, but less resistant to bending and torsion that prey items may have exerted during feeding (Murdock et al. 2013). Very long and thin teeth have been described to constitute a recent adaptation to feeding on small and soft items as do detritivores (Bellwood et al. 2014a). These long teeth are flexible, being larger at the summit than at the basis, and densely packed, serving as brush to remove fine detrital particles. There is no evidence of such geometry

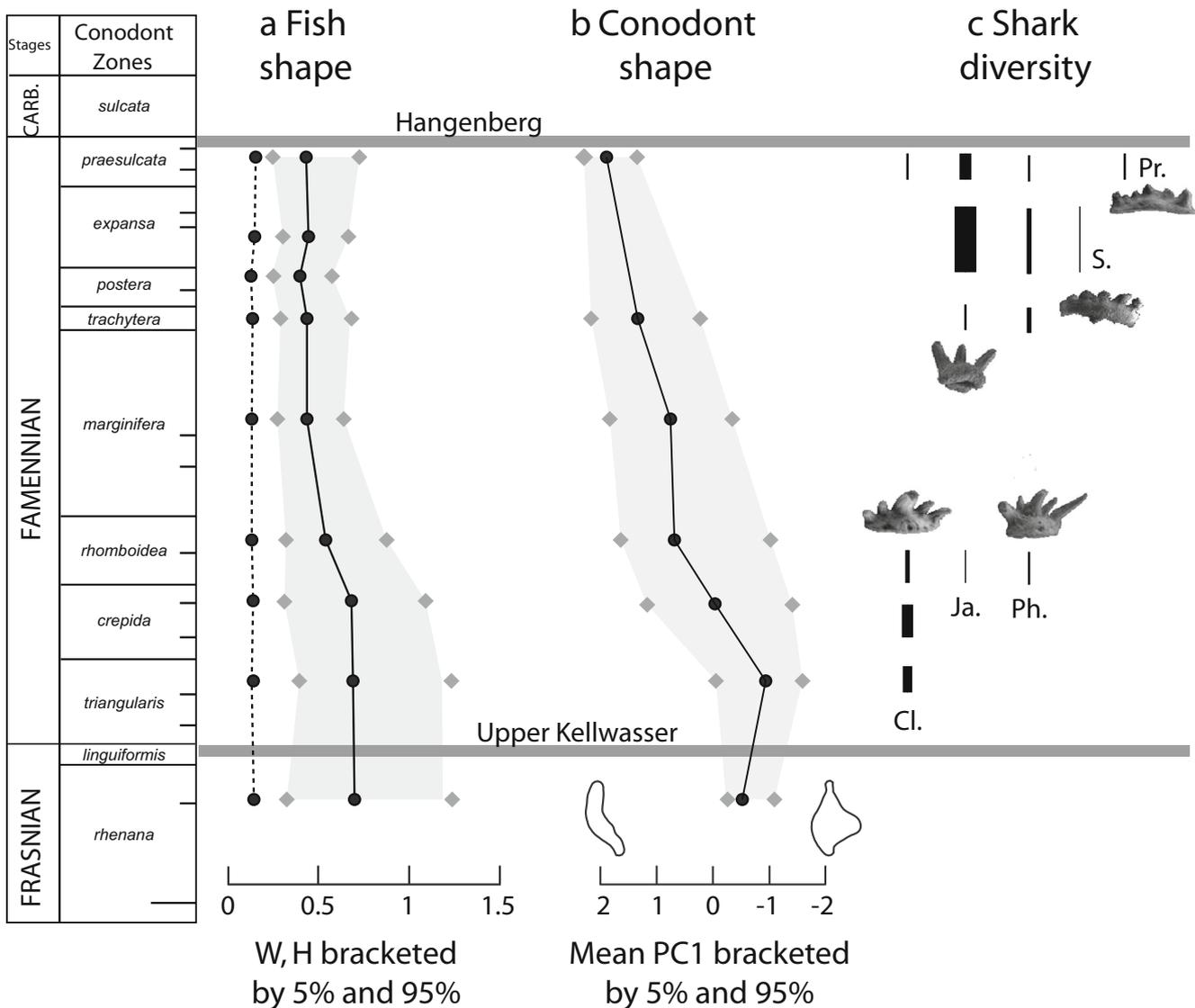
and arrangement in Late Devonian fishes (Choo et al. 2009). Late Devonian needle-like teeth might thus have served for feeding on fine particles, or on very soft preys. Whatever their interpretation, their mere occurrence in the Famennian points to a first trial for dental specialization. This evidences an uncoupling between evolution of teeth and jaws (Anderson et al. 2011).

#### Tooth disparity: fishes among other groups in the Devonian

During the Famennian, placoderms, sarcopterygians, and chondrichthyans were more diverse components of the jawed vertebrate fauna than were actinopterygians (Sallan and Coates 2010). In the Col des Tribes, conodont and actinopterygian remains were overwhelmingly dominant, with only rare sarcopterygian teeth and no placoderm remains. This points to a discrepancy between global diversity vs. local abundance in the fossil record, dependent on density of the former animals, paleoenvironment, and preservation potential of the remains.

Conodonts were eel-like animals with a complex oropharyngeal feeding apparatus (e.g., Jones et al. 2012). In *Palmatolepis*, the most abundant conodont representative during the Famennian, the apparatus was composed of series of denticulated elements that might have been used for piercing or grasping food (Goudemand et al. 2011) and elements with a blade that might have served for draw cut (Jones et al. 2012) or in slicing scissor-like function (Donoghue 2001). Disparity trends have been evidenced in this genus during the Famennian (Girard and Renaud 2012; Fig. 5b) for such a blade-bearing element (P1). The shape of the blade was not quantified, however, but the shape of the platform bearing it. The platform may have contributed to food processing, for instance for stabilizing food items (Donoghue 2001), or it might have served for anchorage into tissues, one of the major limitations for efficient food processing in this jawless animal. The trend of decreasing platform surface across the Famennian would suggest anyway a progressive specialization for processing very easy-to-process food only. A relay might thus have occurred between actinopterygian fishes and *Palmatolepis* conodonts in the specialization on very soft food items. Note that late Famennian *Palmatolepis* with very narrow platforms were themselves outcompeted by other conodont genera displaying more robust platforms (e.g., *Bispathodus*, Ziegler et al. 1974).

Chondrichthyans (sharks) were the other abundant group to co-occur with actinopterygian fishes in the Col des Tribes. They evidenced an increasing morphological diversity from the early to the late Famennian (Fig. 5c), in agreement with more extensive sampling along Famennian sections (Ginter 2000). All these teeth corresponded to morphologies with relatively sharp cusps, interpreted as those of generalist predators, in agreement with slender, generalist jaw morphology,



**Fig. 5** Dental variations across co-occurring marine groups during the Late Devonian. **a** Actinopterygian fish tooth height/width bracketed by 5 and 95 % percentiles. **b** Conodont shape variations (genus *Palmatolepis*; Girard and Renaud 2012). A synthetic shape axis (PC1) is represented (mean per sample bracketed by 95 and 5 % percentiles; note that the direction of a PC axis is arbitrary and has been reversed for the representation). The *postera* and *expansa* zones have not been sampled. **c**

Stratigraphical distribution of the different types of shark teeth. Bars are proportional to the estimation of number of teeth per kg. *Cl.* Cladodont, *Ph.* Phoeodont, *Ja.* Jalodont, *S.* *Siamodus*, *Pr.* Protacrodont. Photographs are not to scale. Note that only three shark teeth were found in between. Upper Kellwasser (Frasnian/Famennian boundary) and Hangenberg (Uppermost Famennian) anoxic events are shown as *dark gray boxes*

functionally comparable to the ones of the actinopterygians (Anderson et al. 2011). Once again, tooth morphology would suggest a higher functional diversity than jaws, with the possible bias that jaw remains for that ancient time are much rarer than isolated teeth. These first hints of dental specialization might have been made possible because of the ongoing “nekton revolution” (Klug et al. 2010) increasing food resource in the water column.

All teeth found at the Col des Tribes, being of actinopterygians, chondrichthyans, sarcopterygians, or conodonts, were of very similar size (Fig. 1). Possibly, teeth of larger size being much less abundant, they had

less chance to be found on a sampling mostly devoted to microfossils. Conodont elements have been argued to face peculiar functional constraints due to their small size (Jones et al. 2012), but obviously, these constraints were also shared by many fishes and sharks. Altogether, our results challenge further researches and especially a more comprehensive picture of the morpho-functional space of teeth in this pivotal period of the Paleozoic. Initial feeding specializations might have been overlooked based on jaw morphology. Assessing dental disparity might thus complement our understanding of initial radiation of crucial groups such as actinopterygian fishes.

**Acknowledgments** Henri Cappelletta and Sébastien Enault are thanked for discussions and Michal Ginter for helping in determination of shark remains. This study was supported by the ANR project Ecodev (ANR-13-BSV7-0005). Three referees are greatly acknowledged for their constructive comments and stimulating remarks. This is publication ISE-M 2014–085.

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