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1 **Conodont size in time and space: beyond the temperature-size rule**

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21

## 22 **Abstract**

23 The Temperature Size Rule (TSR) states that ectoderms display smaller adult body size in warmer  
24 conditions. Such a rule may have the potential to explain size response of fossil organisms to past  
25 temperature variations, but its validity in deep time has been seldom tested. The generality of this  
26 rule was investigated here by compiling data documenting conodont size of three genera  
27 (*Palmatolepis*, *Ancyrodella* and *Polygnathus*) at different spatial and temporal scales during the Late  
28 Frasnian and the Famennian, characterized by short- and long-term temperature variations.  
29 The expected TSR was validated in only one out of ten cases. Conodont size was occasionally related  
30 to temperature variations, especially during perturbed Late Frasnian time-interval, but the  
31 relationship was reverse to the expectations of the TSR. These deviations from the TSR might have  
32 several sources. First, size-frequency distributions in the fossil record not only growth patterns but  
33 also strategies of reproduction, that may not follow the TSR. Second, limitation in oxygen supply is  
34 supposed to be one of the primary drivers of the TSR, but anoxia may interfere with temperature in  
35 driving the response to oxygen concentration in the water column. Finally, complex eco-evolutionary  
36 dynamics, intermingling threshold response to temperature variation and temperature tolerance of  
37 each taxon, may control size evolution. Accordingly, modelling evolutionary modes suggested that  
38 size evolution towards new adaptive optima was a predominant pattern of conodont size evolution  
39 along the Famennian.

40

41 **Keywords:** Geometric morphometrics, *Palmatolepis*, *Polygnathus*, *Ancyrodella*, Upper Devonian,  
42 evolutionary models

43

## 44 **Highlights**

- 45 - Temperature-Size Rule fails to explain most conodont size variations
- 46 - A complex interplay of physical and biological factors affected conodont size
- 47 - Differential responses of conodont genera could be related to their temperature tolerance

48

49

## 50 1. Introduction

51  
52 Body size is a key feature of any organism, reflecting metabolism, physiology, life-history traits and  
53 evolutionary history, from unicellular organisms to metazoans (Schmidt et al. 2006). Being easily  
54 quantified, its variation in time and space deserved interest since a long time in biology and  
55 paleontology. The Bergmann's rule states that populations and species of larger size are found in  
56 colder environments (Bergmann 1847). The mechanism beyond being to minimize the surface to  
57 volume ratio of an organism in order to limit heat loss, the rule was initially proposed for endotherms  
58 (mammals and birds) (Ashton et al. 2000; Rodriguez et al. 2008; Olson et al. 2009; Sun et al. 2017).  
59 An extension has been proposed more recently as the "temperature-size rule" (TSR), postulating that  
60 ectotherms mature at smaller body sizes when reared in warmer conditions (Atkinson 1994). The  
61 response is one of the most taxonomically widespread patterns in biology (Forster et al. 2012), being  
62 observed in organisms from bacteria to vertebrates (Atkinson 1994). As a consequence, body-size  
63 reduction is considered as a general response to global warming (Sheridan & Bickford 2011).  
64 Oxygen supply has been proposed as a major process beyond the TSR (e.g. Atkinson et al. 2006;  
65 Forster et al. 2012; Walczyńska & Sobczyk 2017): cold water can hold more dissolved oxygen than  
66 warm water, and as a consequence the dissolved-oxygen concentration is often lower when the  
67 water temperature is high. Oxygen supply being more problematic in aquatic than aerial  
68 environment, this would explain why the TSR seems particularly well supported in aquatic organisms  
69 (Horne et al. 2015, 2017; Rollinson & Rowe 2018).  
70 The TSR acting through very basic metabolic and physiological pathways, it is supposed to be general,  
71 and to act across various levels of processes, from specific adaptations to plastic response. It should  
72 thus be expressed through space as geographic clines and through time as response to temperature  
73 variation (Forster et al. 2012; Salamon et al. 2021). Yet, other processes are susceptible to impact  
74 body size, such as food shortage related to primary productivity collapse or interspecific competition  
75 (He et al. 2010), possibly leading to deviation from the expected TSR pattern.  
76 Organisms delivering extensive fossil material through sequences documenting temperature changes  
77 offer ideal settings to test for the importance of the TSR in deep time (e.g. Schmidt et al. 2006).  
78 The Late Frasnian and the Famennian (Late Devonian, -381 to -360 Ma) are characterized by such  
79 changes in sea-water temperatures (Girard et al. 2020; Joachimski et al. 2009; Zhang et al. 2021). The  
80 Late Frasnian was characterized by a rapid succession of two anoxic events that were associated with  
81 rapid temperature variations (Girard et al. 2007; Joachimski & Buggisch 2002). The Lower Kellwasser  
82 event (LKW) was a bio-event of medium importance (Walliser 1996) while the Upper Kellwasser  
83 event (UKW), at the Frasnian/Famennian (F/F) boundary, caused a mass extinction among both  
84 benthic and pelagic organisms (McGhee 1996). The Famennian, in contrast, was rather characterized

85 by long term changes in temperature conditions (Joachimski et al. 2009; Zhang et al. 2021). The early  
86 Famennian experienced a long-term and stable greenhouse climate, while in the late Famennian, a  
87 transition towards an icehouse regime occurred, as premises of the Carboniferous glaciation  
88 (Buggisch et al. 2008).

89 During this period, conodonts delivered an abundant fossil record allowing for quantitative  
90 investigation of their size variation. They correspond to an extinct group of marine animals,  
91 presumably close to vertebrates (e.g. Aldridge et al. 1993; Janvier 1995). Because of the presence of  
92 developed eyes and fins, they have been interpreted as nektonic organisms with active swimming  
93 (Briggs et al. 1983; Purnell 1994). The most commonly preserved parts of these organisms are  
94 microscopic elements which composed a complex feeding apparatus (Purnell 1994; Donoghue &  
95 Purnell 1999) allowing them to exploit a trophic niche of first level consumers (Shirley et al. 2018;  
96 Balter et al. 2019).

97 Among the different types of elements composing the apparatus, the platform element (P1)  
98 displayed a rapid morphological evolution making it widely studied for biostratigraphic purposes (e.g.  
99 Spalletta et al. 2017; Ziegler & Sandberg 1990). These elements grew by addition of thin lamellae  
100 throughout the animal's life, and thus presumably constitute a proxy of body size (Purnell 1994).

101 While the species concept remains debated in this group of extinct organisms with extensive  
102 morphological variation (Scott & Collinson 1959; Koike 1988; Girard et al. 2004), genera can be easily  
103 recognized and may constitute a robust unit to assess size changes, including plastic response,  
104 evolution, and possibly cryptic species composition (Girard et al. 2004). Using such an approach at  
105 the generic level, it has been suggested that conodont size tracked temperature changes during the  
106 Frasnian, in areas corresponding nowadays to China (Zhang et al. 2020). The question rises whether  
107 this observation, congruent with the TSR, can be generalized to size variations in conodonts in other  
108 time intervals and in other areas.

109 The size-frequency distribution of the P1 elements of three genera was therefore quantified using  
110 geometric morphometrics methods (Renaud et al. 1999; Renaud et al. 2021). By comparing size  
111 values across time (along sections) and space (by comparing sections), the following hypotheses  
112 were investigated.

113 (1) TSR as general driver of conodont size variation should lead to congruent signatures among  
114 different genera, across time and space, and at various time scales.

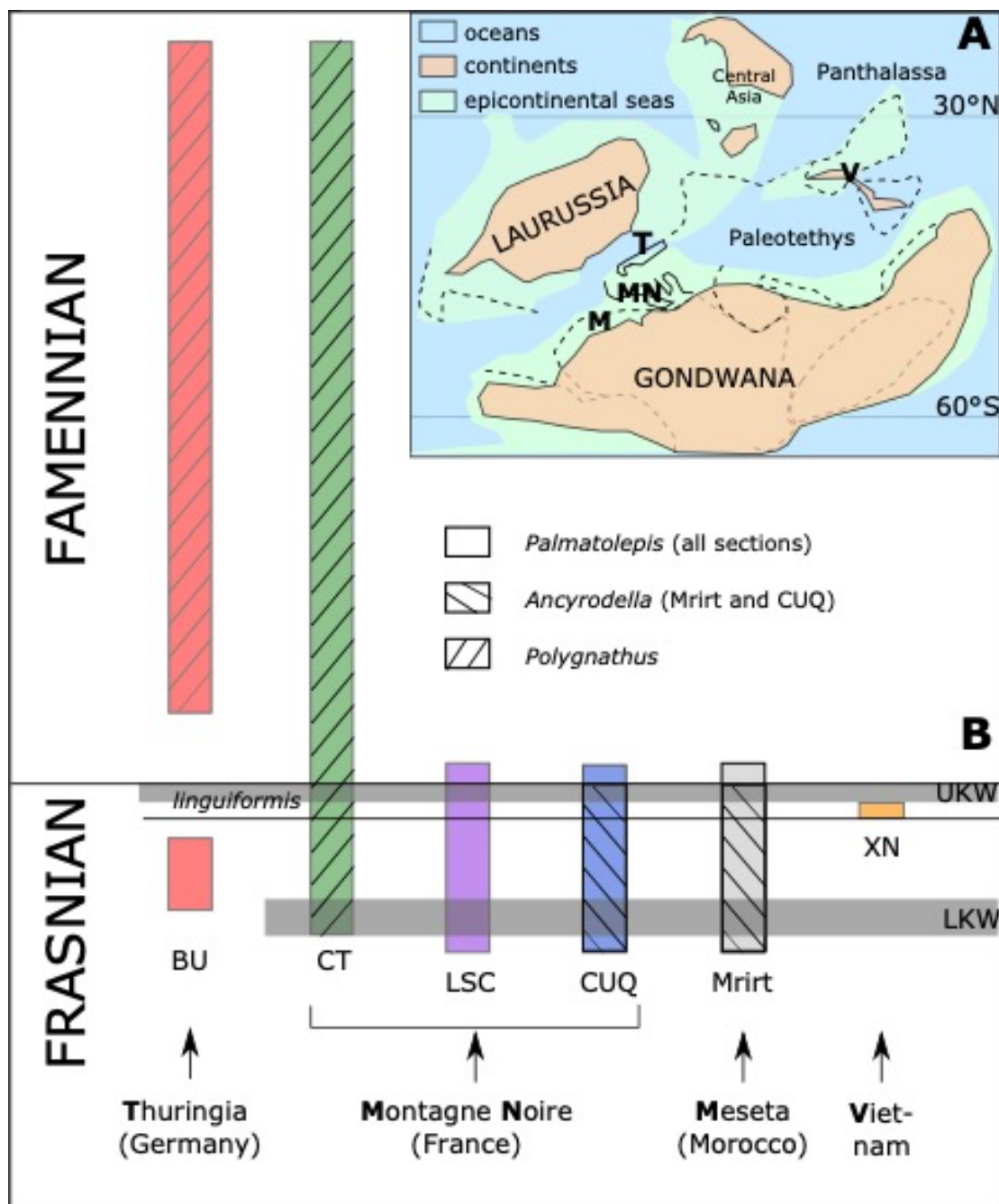
115 (2) Alternatively, crises as cause of size reduction (Twitchett 2006) should lead to deviation from  
116 the TSR. The response to the UKW event during the Late Frasnian might correspond to such a  
117 situation of interfering factors blurring the TSR response.

118

119 **2. Material**

120

121 The conodont elements considered in this study come from sections located in different parts of the  
 122 world. Most of the sampling was located in Montagne Noire (France): Coumiac Upper Quarry (CUQ),  
 123 La Serre trench C (LSC) and Col des Tribes (CT). Samples from Buschteich (BU, Thuringia, Germany),  
 124 Mrirt (Moroccan Meseta, Morocco) and Xom Nha (XN, Central Vietnam) complemented this sampling  
 125 (Fig. 1).



126

127 Figure 1. A. Schematic paleogeographic map of the Late Devonian. T: Thuringia (Germany); MN: Montagne  
 128 Noire (France); M: Meseta (Morocco); V: Central Vietnam. B. Stratigraphic extension of the studied sections  
 129 (BU: Buschteich, CT: Col des Tribes, CUQ: Coumiac Upper Quarry, LSC: La Serre Trench C, XN: Xom Nha). In dark  
 130 grey, the Lower (LKW) and Upper (UKW) Kellwasser events.

131  
132 Three conodont genera occurring through all or part of the Upper Devonian were considered in the  
133 present study: *Ancyrodella*, *Palmatolepis*, and *Polygnathus* (Fig. 2). The stratigraphic extension of  
134 *Ancyrodella* was limited to the Frasnian, with its extinction coinciding with the F/F boundary.  
135 *Palmatolepis* stratigraphic extension covered the whole Upper Devonian, its extinction occurring at  
136 the end of the Famennian. *Polygnathus* was known during all the Devonian.

137 In order to study morphological variations on a broad geographical scale, the time-slice  
138 corresponding to the *linguiformis* Zone (last Zone of the Frasnian, Ziegler & Sandberg 1990) was  
139 selected. *Palmatolepis* size data were available from the literature (Girard et al. 2010), allowing for a  
140 comparison including samples located in the West (sections from Mrirt and from the Montagne  
141 Noire) and in the East (Vietnam) of the Paleotethys (Fig. 1). Three levels were included for Mrirt, two  
142 levels for CUQ, two levels for CT, and two levels for Xom Nha.

143 Short-term size variations of conodonts were documented in the period of the Late Frasnian and  
144 early Famennian, encompassing environmental perturbations around the Lower and Upper  
145 Kellwasser events. This period was thereafter designed as the “whole Kellwasser period”.

146 *Palmatolepis* size variations were considered in CUQ, LSC and Mrirt (Girard et al. 2007). *Ancyrodella*  
147 was further considered during the same period, with the difference that its extinction at the F/F  
148 boundary limited its sampling to the Late Frasnian. Size variations were documented in CUQ and  
149 Mrirt (Girard et al. 2008).

150 Long-term temporal variations were assessed along two Famennian sequences at the Col des Tribes  
151 (CT) and the Buschteich sections (BU) for *Palmatolepis* and *Polygnathus*. Few Frasnian levels were  
152 included in CT. Samples correspond to those considered in stratigraphic analyses (Girard et al. 2014,  
153 2017), in a study comparing temperature and water-depth variations in both sections (Girard et al.  
154 2020), and in a study devoted to *Polygnathus* morphological evolution over this time period (Renaud  
155 et al. 2021).

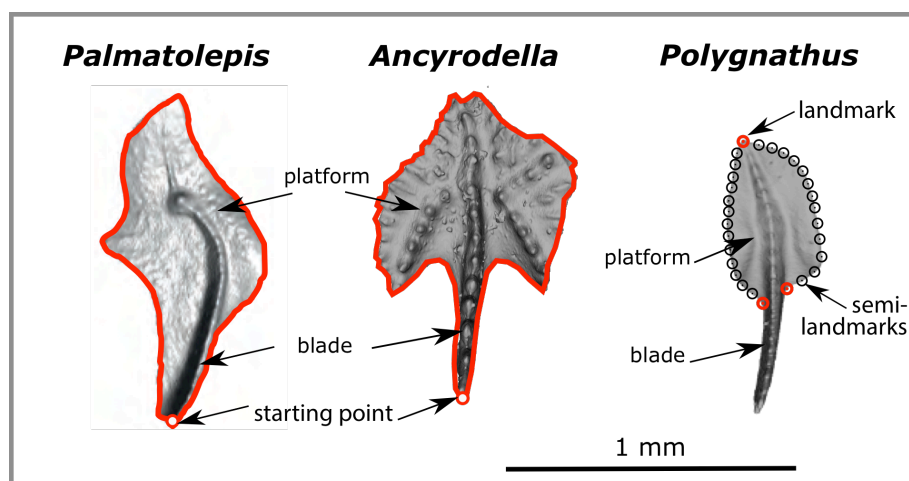
156 Oxygen isotope data, used as paleotemperature proxies, were available from previously published  
157 data (Balter et al. 2008; Le Houedec et al. 2013; Girard et al. 2020). Furthermore, ecological  
158 preferences of conodont genera are supposed to be dependent on water depth (Seddon & Sweet  
159 1971; Klapper & Barrick 1975) rather than on temperature. *Palmatolepis* being considered as off-  
160 shore dweller and then associated with deep waters, its percentage in the conodont assemblages  
161 was considered as a proxy of water-depth variations through the Famennian (Girard et al. 2020), in  
162 order to test an alternate candidate for external forcing on conodont size variation.

163

### 164 **3. Methods**

#### 165 *3.1. Size estimates*

166 3.1.1. *Outline analysis: Palmatolepis and Ancyrodella.* – A method based on Fourier outline analysis  
 167 was applied to quantify the form (size + shape) of the element platform (P1) for *Palmatolepis*  
 168 (Renaud & Girard 1999; Girard et al. 2010; Girard & Renaud 2012) and *Ancyrodella* (Girard & Renaud  
 169 2008) (Fig. 2). According to this method, the 2D platform outline was automatically digitized using an  
 170 image analyzer (Optimas v. 6.0) and 64 points were sampled at equally-spaced intervals along the  
 171 outline, the starting point being defined at the termination of the blade. From these coordinates, 64  
 172 radii were calculated, corresponding to the distance of each point to the center of gravity (centroid)  
 173 of the outline. A Fourier transform was then applied to this set of 64 radii expressed as a function of  
 174 the cumulated curvilinear abscissa along the outline, decomposing the empirical outline as a sum of  
 175 trigonometric functions of decreasing wavelength. Size was calculated as the zero harmonic (A0),  
 176 corresponding to the size of the best-fitting circle to the original outline. This procedure is  
 177 implemented as “sfourier” in Momocs (Bonhomme et al. 2014).  
 178



179 Figure 2. The P1 elements of the three genera considered in this study, with a schematic representation of the  
 180 method used for size quantification. *Palmatolepis*, *Ancyrodella*: in red, the outline sampled by 64 points.  
 181 *Polygnathus*: red dots: landmarks, open dots: sliding semi-landmarks.  
 182

183  
 184 3.1.2. Landmark-based estimate of *Polygnathus* size. – The description of *Polygnathus* 2D shape did  
 185 not include the blade, too frequently damaged on the collected specimens. Hence, the outline of the  
 186 (P1) platform was not closed, precluding the use of Fourier methods; landmark-based descriptors  
 187 were used instead (Fig. 2). Three landmarks and two series of 13 semi-landmarks were manually  
 188 digitized on the edges of the platform (Renaud et al. 2021). The size of the platform was estimated as  
 189 the centroid size (CS) of the configuration, defined as the square root of the sum of squared  
 190 distances of all landmarks to their centroid (Slice et al. 1996).



191 Since size distributions were skewed towards large size (Girard et al. 2004; Girard et al. 2010), size  
192 estimates were log-transformed for all analyses. Sample size and summary statistics are provided as  
193 Supplementary Tables 1 to 10.

194

### 195 3.1.3. Statistical analyses

196 Within each section, or within the *linguiformis* time-slice, size difference between levels were tested  
197 using Kruskal-Wallis tests, completed by pairwise Wilcoxon tests between applied to successive  
198 levels.

199 Mean size were calculated for each level. Within each section, or within the *linguiformis* time-slice,  
200 Pearson correlations were performed between these group means and the corresponding isotopic  
201 value ( $\delta^{18}\text{O}$ ).

202 Correlations between variables can however arise due to temporal autocorrelation. This possible  
203 effect was assessed using a first-order autoregressive (AR1) model using generalized least squares  
204 (gls) (Rita et al. 2019). This corresponds to using the order of the observations in the data as a  
205 covariate.

206 Such correlations on means per level however neglect the fact that sample size and variance are  
207 heterogeneous among levels. One way to circumvent this issue is to consider that all conodonts from  
208 a given level represent a random sample from the original population. They experienced similar  
209 growing conditions, that may have led to a pseudo-correlation between them, possibly blurring the  
210 correlation of interest with paleotemperature. Models with linear mixed effects (lme) were therefore  
211 constructed, considering size as a function of temperature, with levels as random effect. A last series  
212 of models further included first-order autocorrelation. These models were fitted using the package  
213 nlme (Pinheiro et al. 2018).

214

### 215 3.1.4. Evolutionary models

216 Using as entry data the size mean and variance per level as well as the estimated age, evolutionary  
217 models were fitted to the data using the paleoTS package (Hunt 2014). The models considered were  
218 the following.

- 219 - Stasis, with a constant mean and variance (Sheets & Mitchell 2001);
- 220 - General random walk (GRW), where each "step" is drawn from a distribution with a non-zero  
221 mean, corresponding to the directionality of the trend (Hunt 2006; Hunt & Carrano 2010);
- 222 - Unbiased random walk (URW), corresponding to non-directional random walk (steps drawn  
223 from a distribution with a zero mean) (Hunt 2006);
- 224 - Ornstein-Uhlenbeck (OU), corresponding to the evolution towards an adaptive peak (Hansen  
225 1997; Butler & King 2004; Beaulieu et al. 2012, Hunt et al. 2008);

- 226 - One punctuation along the sequence: all shift points are tested, with the constraint that the  
 227 number of steps in each segment is larger than a given threshold  $n$  (here, the value by  
 228 default  $n=7$  was retained) (Hunt 2016).
- 229 - Several models considered that the mode of trait evolution shifted once along the sequence.  
 230 The minimum number of steps in a segment was retained as  $n=7$ .
- 231 ○ URW-Stasis and Stasis-URW: first evolution according to an unbiased random walk  
 232 and then stasis (or the reverse);
  - 233 ○ GRW-Stasis and Stasis-GRW: first evolution according to an unbiased random walk  
 234 and then stasis (or the reverse).

235 Finally, a model where evolution tracks a covariate was considered (Hunt et al. 2010). This allowed to  
 236 test for size covarying with the paleotemperature proxy  $\delta^{18}\text{O}$ . To test an alternate model of  
 237 environmental forcing, the percentage of *Palmatolepis* in the assemblage was considered (Girard et  
 238 al. 2020), supposedly tracing water depth variations. These models were only considered for the  
 239 evolution along the Famennian.

240 The constraint on the minimum number of steps in a segment precluded to estimate two-segments  
 241 models for several sequences that were documented by too few levels.

242 All models were estimated using a full likelihood approach (“Joint”). The Akaike information criterion  
 243 (AIC) estimated the quality of each model; based on the number of parameters and the Log-  
 244 likelihood of the model. The corrected criterion (AICc) was calculated from the AIC test by correcting  
 245 for small sample sizes. The preferred model is the one with the minimum AICc value. While  
 246 comparing several models, two other parameters were provided to help identifying the preferred  
 247 one:  $d\text{AICc}$ , corresponding to the difference in AICc score between the best model and the model  
 248 being compared, and Akaike weight (Akaike.wt), corresponding to the proportion of the total amount  
 249 of predictive power provided by the full set of models, contained in the model being assessed.

250 All analyses were performed under R (R-Core-Team 2018).

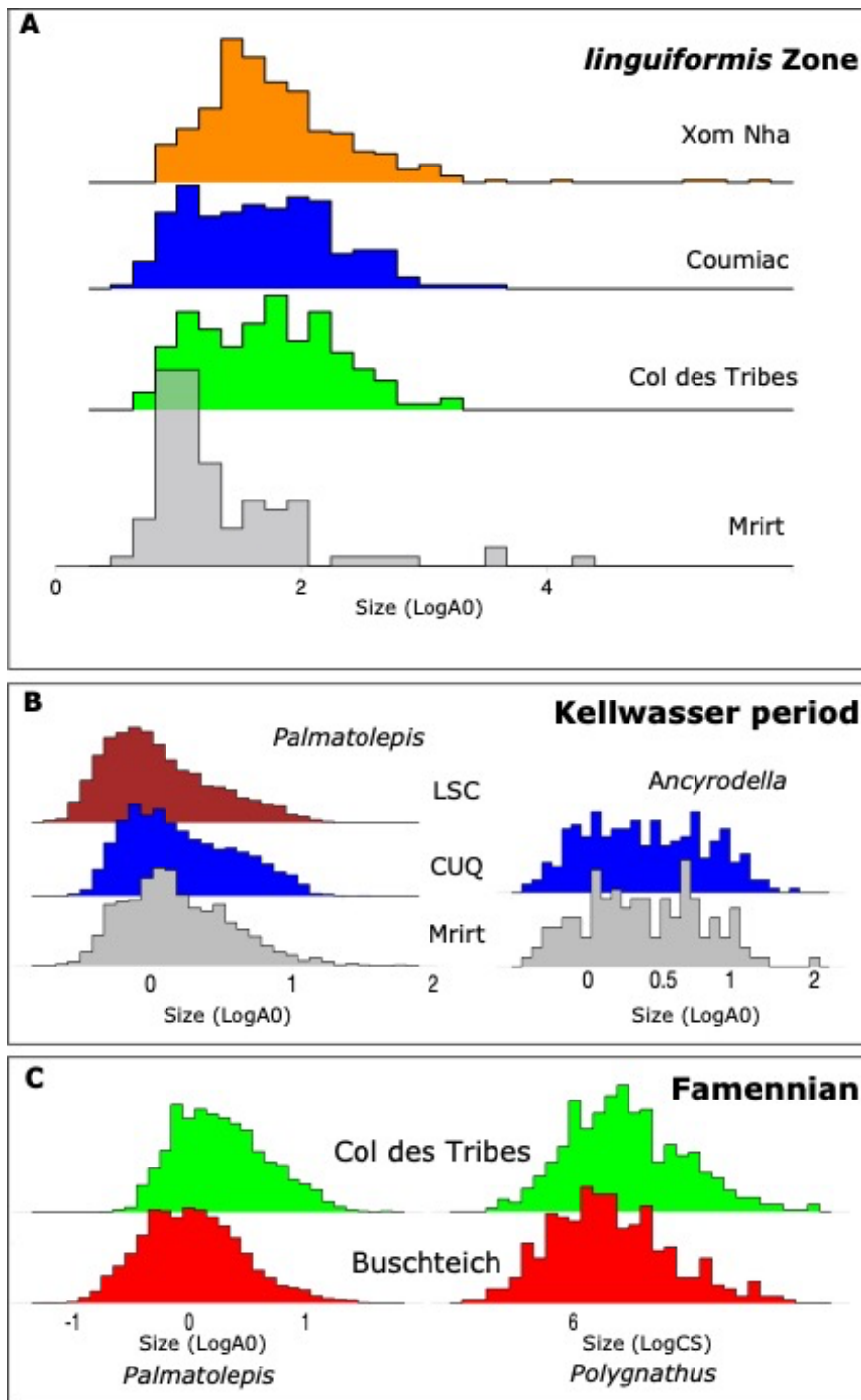
251

## 252 4. Results

253

### 254 4.1. Size distribution in the different genera and sections

255 Conodont size distributions differed in the four sections considered for the *linguiformis* zone ( $P <$   
 256  $0.0001$ ). Mrirt displayed more abundant small-sized *Palmatolepis* specimens than the other outcrops  
 257 (Fig. 3A). When considering the “whole Kellwasser period”, size differed as well between the three  
 258 outcrops considered ( $P < 0.0001$ ) but the most abundant small sized *Palmatolepis* elements were  
 259 found in LSC. Regarding *Ancyrodella*, no size difference was observed between the two sections  
 260 involved ( $P = 0.8055$ ) (Fig. 3B).



261  
 262 Figure 3. Size frequency-distribution of the conodont P1 elements for the three periods considered. (A)  
 263 Distribution of *Palmatolepis* size per section in the « *linguiformis* » time-slice. (B) Distribution per section for  
 264 *Palmatolepis* and *Ancyrodella* over the « whole Kellwasser period ». (C) Distribution per section over the  
 265 Famennian for *Palmatolepis* and *Polygnathus*. *Palmatolepis* and *Ancyrodella* size is estimated as the zero  
 266 harmonic (A0) of a Fourier analysis of the platform outline. *Polygnathus* size is estimated as the Centroid Size  
 267 (CS) of landmark configurations. All data were log-transformed. CUQ: Coumiac Quarry, LSC: La Serre Trench C.  
 268

269 Considering the Famennian record, *Palmatolepis* elements were smaller in BU than in CT ( $P <$   
 270 0.0001). The difference was also significant when considering *Polygnathus* ( $P = 0.0002$ ) and the  
 271 pattern was similar, with elements tending to be smaller in BU than in CT (Fig.3C).

272

#### 273 4.2. Differences between levels along sections

274 Significant size differences among levels were found in the *linguiformis* data set (Table 1) and along  
 275 all sections and genera, except for *Ancyrodella* at Mrirt (Table 2, Supplementary Tables).

276 In the *linguiformis* time slice, the difference was mostly driven by Mrirt levels being different from  
 277 most other samples. Pairwise Wilcoxon tests among successive levels along sections showed that  
 278 significant differences were scattered all over the record for *Palmatolepis* in CUQ, Mrirt and LSC  
 279 during the Kellwasser period, and all along the Famennian in CT and BU. Only few differences were  
 280 significant between the two Kellwasser events for *Ancyrodella* in CUQ, and few differences towards  
 281 the end of the Famennian were significant for *Polygnathus* in CT (Supp. Tables 1 to 10).

282

283 Table 1. Differences between levels in the *linguiformis* time-slice. Non-adjusted probabilities of pairwise  
 284 Wilcoxon tests are provided. In bold,  $P < 0.01$ , in italics  $P < 0.05$ . CT: Col des Tribes; CUQ: Coumiac Upper  
 285 Quarry; M: Mrirt; XN: Xom Nha.

	CT22	CT23	CUQ31f	CUQ31g1	CUQ31g2	M09	M11a	M11b	XN52-1
CT23	0.3493								
CUQ31f	0.1220	0.9620							
CUQ31g1	0.5458	0.7090	0.5180						
CUQ31g2	0.7678	0.4717	0.1939	0.5423					
M09	<b>0.0000</b>	<b>0.0009</b>	<b>0.0000</b>	<b>0.0000</b>	<b>0.0001</b>				
M11a	<i>0.0173</i>	0.1020	0.0664	<i>0.0497</i>	0.0580	0.9673			
M11b	<b>0.0058</b>	0.0950	0.0523	<i>0.0306</i>	<i>0.0358</i>	0.2466	0.4653		
XN52-1	0.3395	0.6519	0.2978	0.9071	0.3192	<b>0.0000</b>	<i>0.0204</i>	<b>0.0098</b>	
XN53-1	0.3649	0.0688	<b>0.0033</b>	0.1317	0.7107	<b>0.0000</b>	<b>0.0042</b>	<b>0.0004</b>	<i>0.0198</i>

286

287 Table 2. Differences in size between levels, and summary of Pearson correlations between mean size and  $\delta^{18}\text{O}$   
 288 in the different cases considered. N tot: total number of specimens; P KW: probabilities of size differences  
 289 between levels, based on Kruskal Wallis tests; N mean: number of levels; P: probabilities of correlation  
 290 between mean size and  $\delta^{18}\text{O}$  per level; R: Pearson coefficient of correlation; range Size: range between  
 291 minimum and maximum mean size values; range  $\delta^{18}\text{O}$ : range between minimum and maximum  $\delta^{18}\text{O}$  values.  
 292 Kellwasser: "whole Kellwasser period". In bold,  $P < 0.01$ , in italics  $P < 0.05$ .

Period	Genus	Section	N tot	P KW	N mean	Pcor.test	R	Range Size	Range $\delta^{18}\text{O}$
<i>linguiformis</i>	<i>Palmatolepis</i>		830	<b>&lt;0.00001</b>	10	<b>0.0031</b>	0.8277	0.3816	4
Kellwasser	<i>Palmatolepis</i>	CUQ	2625	<b>&lt;0.00001</b>	19	<i>0.0109</i>	-0.5696	0.4557	1.66
		M	1295	<b>0.00005</b>	13	0.2069	0.3749	0.3220	1.3
		LSC	3178	<b>&lt;0.00001</b>	21	0.8040	0.0576	0.5836	1.78

	<i>Ancyrodella</i>	CUQ	283	<b>0.00493</b>	17	0.1797	-0.3415	0.8667	1.66
		M	124	0.15770	8	0.3452	-0.3858	0.3985	1.3
Famennian	<i>Palmatolepis</i>	CT	2229	<b>&lt;0.00001</b>	26	0.0374	-0.4102	0.5812	2.1
		BU	4370	<b>&lt;0.00001</b>	26	0.1628	-0.2820	0.5823	1.5
	<i>Polygnathus</i>	CT	745	<b>&lt;0.00001</b>	21	0.9858	0.0041	0.7155	2.1
		BU	347	<b>0.00001</b>	17	0.7692	0.0726	1.0850	1.2

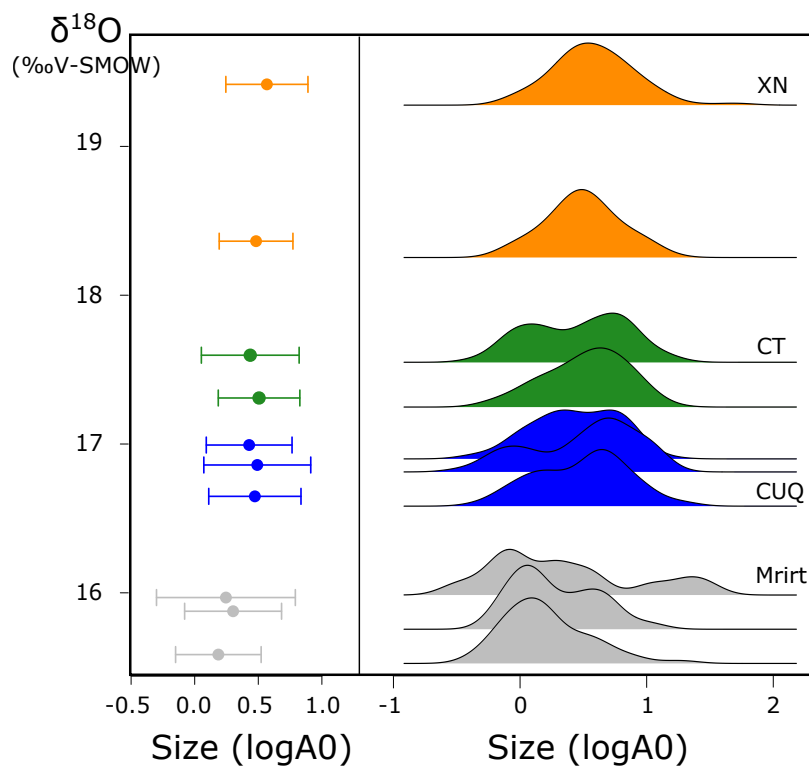
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294 

### 4.3. Correlations between mean size and $\delta^{18}\text{O}$

295 Among the ten datasets considered, the expected relationship according to the TSR (positive  
 296 correlation between size and  $\delta^{18}\text{O}$ ) was only supported in the case of the geographic variation in the  
 297 *linguiformis* time slice (Fig. 4; Table 2).

298

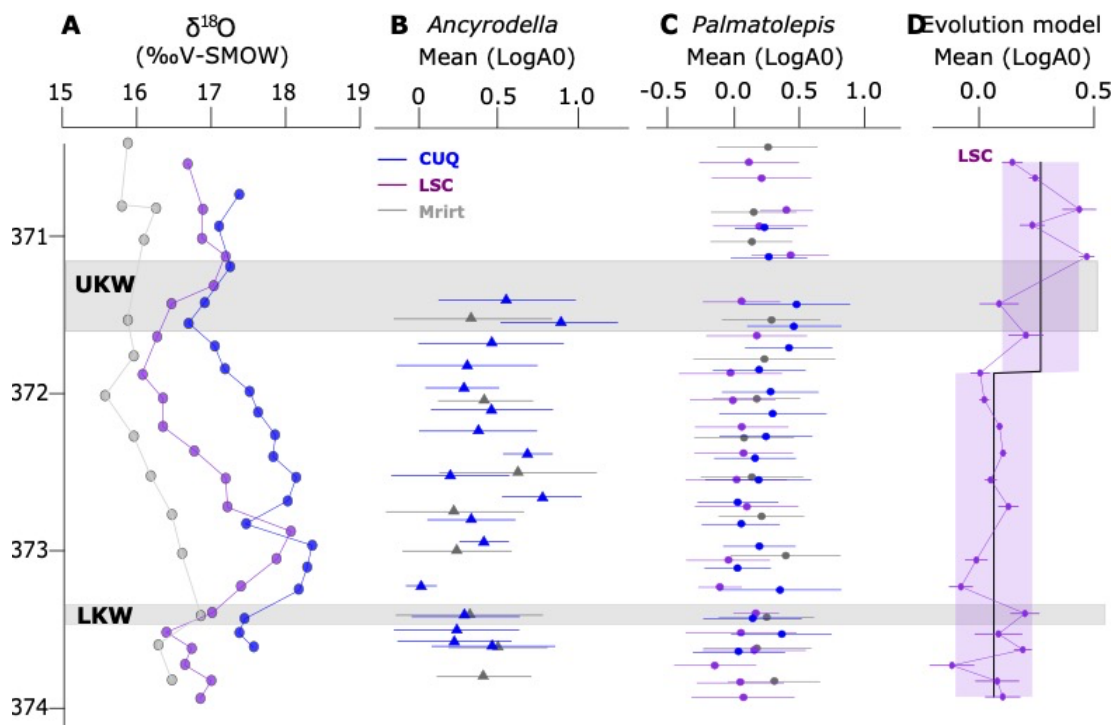


299

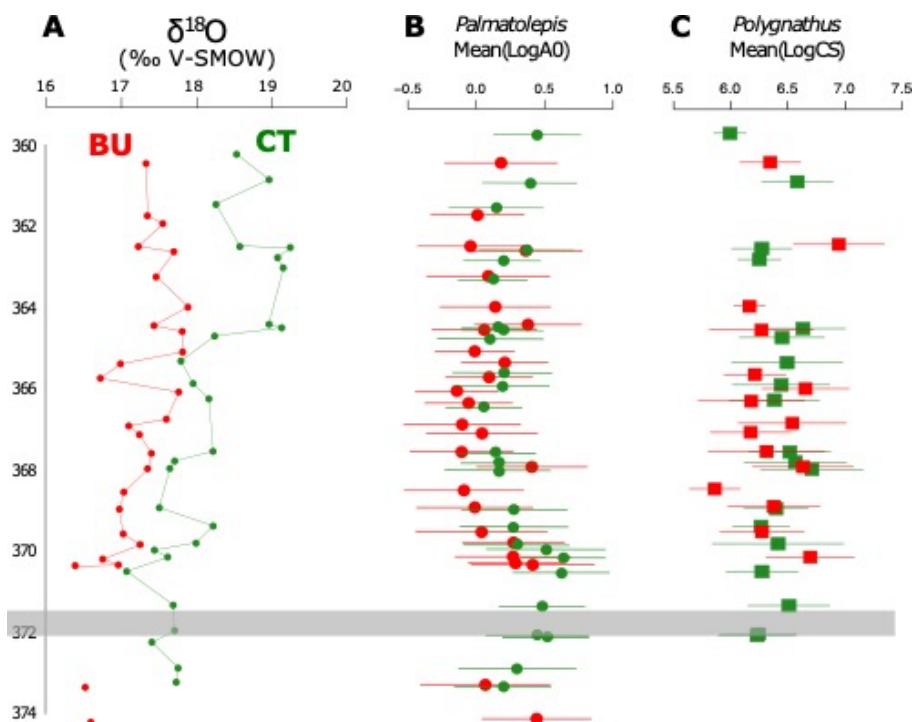
300 Figure 4. *Palmatolepis* size as a function of  $\delta^{18}\text{O}$  in the “*linguiformis*” time-slice. A. Mean size per level  $\pm$   
 301 standard deviation (SD). B. Size frequency distribution of *Palmatolepis* size (LogA0) as a function of  $\delta^{18}\text{O}$ . CUQ:  
 302 Coumiac Upper Quarry, CT: Col des Tribes, XN: Xom Nha.

303

304 Only two other correlations were significant, but with a negative relationship between mean size and  
 305  $\delta^{18}\text{O}$ . They involved *Palmatolepis* during the Kellwasser period at CUQ (Fig. 5C), and along the  
 306 Famennian at CT (Fig. 6B).



307  
 308 Figure 5. Paleotemperature proxy and conodont size variation during the “whole Kellwasser period”. A.  $\delta^{18}\text{O}$   
 309 variations. B. *Ancyrodella* mean size  $\pm$  SD. C. *Palmatolepis* mean size  $\pm$  SD. D. One punctuation as best-fitting  
 310 model for size evolution of *Palmatolepis* at LSC. Mirt in grey, LSC in violet, CUQ in blue. Dots: circles,  
 311 *Palmatolepis*; triangles, *Ancyrodella*. Grey boxes: Lower and Upper Kellwasser events.  
 312



313  
 314 Figure 6. Paleotemperature proxy and conodont size variation during the “Famennian period”. A.  $\delta^{18}\text{O}$   
 315 variations. B. *Palmatolepis* mean size (logA0) per level  $\pm$  SD. C. *Polygnathus* mean centroid size (logCS) per level

316 ± SD. Circles: *Palmatolepis*, squares: *Polygnathus*. CT in green, BU in red. The grey box represents the Upper  
317 Kellwasser event.

318

#### 319 4.4. Investigating temporal autocorrelation and levels as random effects

320 The different models considered as alternate to the basic Pearson correlation (Table 2) provided  
321 overall congruent results (Table 3). Variation between size and temperature was supported during  
322 the “*linguiformis*” time-slice, and in most of the case for *Palmatolepis* during the Kellwasser period at  
323 CUQ. This correlation was only marginally significant, however, when considering the linear mixed  
324 effects model with temporal auto-correlation. The same was true for *Palmatolepis* in the CT  
325 Famennian record, where the size –  $\delta^{18}\text{O}$  relationship was consistently significant except when  
326 considering the gls model on mean values corrected for auto-correlation. The size- $\delta^{18}\text{O}$  relationship  
327 emerged as significant for *Ancyrodella* at CUQ only when considering the lme model.

328

329 Table 3. Summary of the models exploring the correlation between Log size and  $\delta^{18}\text{O}$  in the different cases  
330 considered. First line indicates if models were performed on the means or on all specimens. Probabilities are  
331 provided for the following models: Pearson correlation on the means per level; gls on the means per level,  
332 including first-order autocorrelation; lme on all specimens including levels as a random effect; the same models  
333 including first-order autocorrelation. Models including first-order autocorrelation are not provided for the  
334 *linguiformis* time-slice, since time is not involved. Palm: *Palmatolepis*; Ancyro: *Ancyrodella*, Poly: *Polygnathus*;  
335 KW: whole Kellwasser period; CUQ: Coumiac; M: Mrirt; LSC: La Serre, CT: Col des Tribes; BU: Buschteich. In  
336 bold,  $P < 0.01$ , in italics  $P < 0.05$ .

	means		all specimens	
	cor.test	gls - corAR1	lme   Level	lme   Level - corAR1
<i>linguiformis</i>	<b>0.0031</b>		<b>0.0001</b>	
Palm_KW_CUQ	<i>0.0109</i>	<b>0.0004</b>	<b>0.0074</b>	0.0967
Palm_KW_M	0.2069	0.2935	0.2070	0.5872
Palm_KW_LSC	0.8040	0.4887	0.6584	0.1699
Ancyro_CUQ	0.1797	0.1822	<i>0.0319</i>	0.1745
Ancyro_M	<u>0.3452</u>	0.3680	0.3693	0.8439
Palm_Fam_CT	<i>0.0374</i>	0.8715	<i>0.0252</i>	<i>0.0357</i>
Palm_Fam_BU	0.1628	0.1938	0.1663	0.2406
Poly_Fam_CT	0.9858	0.9339	0.9562	0.9441
Poly_Fam_BU	0.7626	0.7421	0.9404	0.9495

337

#### 338 4.5. Testing evolutionary modes

339 Given the constraints of minimum seven steps per segment, two-segments models were only tested  
340 when 19 or more levels were available along a section (*Palmatolepis* CUQ and LSC during the  
341 Kellwasser, CT and BU along the Famennian; *Polygnathus* at CT).

342 4.5.1. *Whole Kellwasser period, Palmatolepis*. – In CUQ, the best model by far pointed to size  
 343 evolution tracking  $\delta^{18}\text{O}$  variations along the section (Table 4). In Mrirt, the best model among the few  
 344 tested emerged as the stasis (Table 5). In LSC (Table 6), the best model involved one punctuation  
 345 located at step 14 (LSC14b). Accordingly, *Palmatolepis* elements tended to reach larger size towards  
 346 the end of the record (Fig. 5D).

347  
 348 Table 4. Comparison of support for each model of *Palmatolepis* evolution in CUQ (comparing 10 models [n =  
 349 19, method = joint]. LogL = model log likelihood, K = number of model parameters, AICc = Akaike's Information  
 350 Criterion corrected for small sample size, dAICc = difference in AICc score between the best model and the  
 351 model being compared, Akaike.wt: Akaike weights (proportion of the total amount of predictive power).

	LogL	K	AICc	dAICc	Akaike.wt
GRW	12.65087	3	-17.701743	5.0689095	0.032
URW	12.56427	2	-20.378539	2.3921128	0.122
Punc-1	16.35977	4	-21.862401	0.9082516	0.257
OU	15.03664	4	-19.216147	3.5545050	0.068
Stasis	10.75232	2	-16.754644	6.0160081	0.020
URW-Stasis	13.66500	5	-12.714623	10.0560287	0.003
Stasis-URW	15.19252	4	-19.527894	3.2427580	0.080
GRW-Stasis	13.79502	6	-8.590034	14.1806180	0.000
Stasis-GRW	13.79502	5	-15.882376	6.8882759	0.013
$\delta^{18}\text{O}$	<b>15.18533</b>	3	<b>-22.770652</b>	<b>0.0000000</b>	<b>0.405</b>

352  
 353 Table 5. Comparison of support for each model of *Palmatolepis* evolution in Mrirt (comparing 5 models [n = 13,  
 354 method = joint]. LogL = model log likelihood, K = number of model parameters, AICc = Akaike's Information  
 355 Criterion corrected for small sample size, dAICc = difference in AICc score between the best model and the  
 356 model being compared, Akaike.wt: Akaike weights (proportion of the total amount of predictive power).

	logL	K	AICc	dAICc	Akaike.wt
GRW	11.67972	3	-14.69278	6.818228	0.018
URW	11.67321	2	-18.14642	3.364583	0.103
OU	14.78178	4	-16.56356	4.947449	0.047
<b>Stasis</b>	<b>13.3555</b>	<b>2</b>	<b>-21.511</b>	<b>0.000000</b>	<b>0.556</b>
$\delta^{18}\text{O}$	14.38439	3	-20.10211	1.408892	0.275

357  
 358  
 359 Table 6. Comparison of support for each model of *Palmatolepis* evolution in LSC (comparing 10 models [n = 21,  
 360 method = joint]. LogL = model log likelihood, K = number of model parameters, AICc = Akaike's Information  
 361 Criterion corrected for small sample size, dAICc = difference in AICc score between the best model and the  
 362 model being compared and Akaike.wt: Akaike weights (proportion of the total amount of predictive power).

	logL	K	AICc	dAICc	Akaike.wt
--	------	---	------	-------	-----------



GRW	11.56475	3	-15.71773	10.020576	0.005
URW	11.55291	2	-18.43916	7.299153	0.020
<b>Punc-1</b>	<b>18.11915</b>	<b>4</b>	<b>-25.73831</b>	<b>0.000000</b>	<b>0.757</b>
OU	13.82143	4	-17.14286	8.595449	0.010
Stasis	11.52432	2	-18.38198	7.356329	0.019
URW-Stasis	16.07685	5	-18.1537	7.584605	0.017
Stasis-URW	16.43132	4	-22.36264	3.375668	0.140
GRW-Stasis	16.17297	6	-14.34594	11.392364	0.003
Stasis-GRW	16.40713	5	-18.81425	6.924054	0.024
$\delta^{18}\text{O}$	11.56613	3	-15.7205	10.017807	0.005

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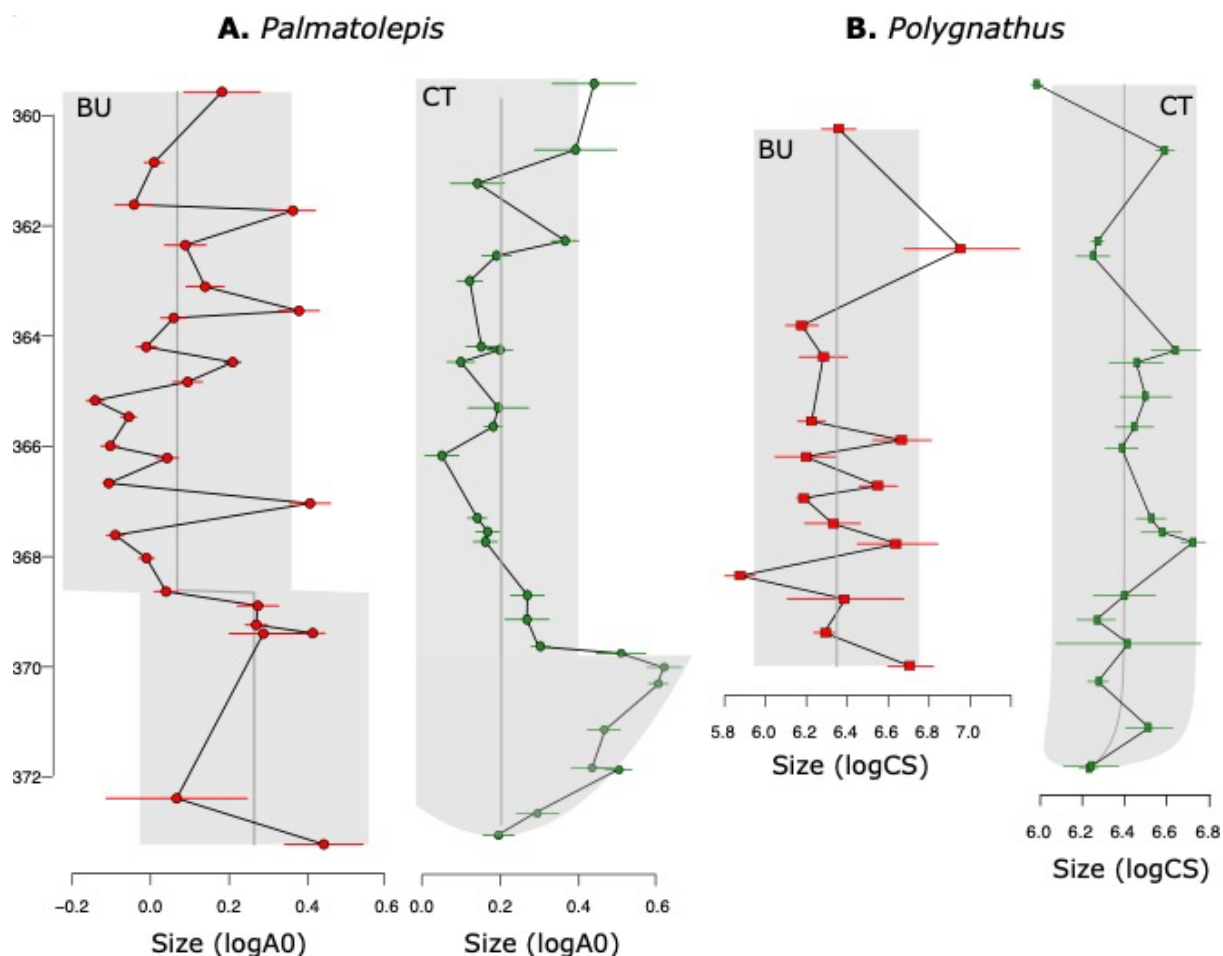
365 4.5.2. *Whole Kellwasser period, Ancyrodella*. – Two models were almost equally performant for this  
366 record, suggesting either a stasis, or an evolution of size coupled to the paleotemperature proxy  
367 (Table 7).

368 Table 7. Comparison of support for each model of *Ancyrodella* evolution in CUQ (comparing 5 models [n = 17,  
369 method = joint]. LogL = model log likelihood, K = number of model parameters, AICc = Akaike's Information  
370 Criterion corrected for small sample size, dAICc = difference in AICc score between the best model and the  
371 model being compared and Akaike.wt: Akaike weights (proportion of the total amount of predictive power).  
372

	logL	K	AICc	dAICc	Akaike.wt
GRW	-0.4723795	3	8.7909128	7.875884	0.010
URW	-0.5474194	2	5.9519817	5.036953	0.040
OU	2.7027708	4	5.9277918	5.012763	0.041
<b>Stasis</b>	<b>1.9710571</b>	<b>2</b>	<b>0.9150286</b>	<b>0.000000</b>	<b>0.499</b>
<b><math>\delta^{18}\text{O}</math></b>	<b>3.2678661</b>	<b>3</b>	<b>1.3104216</b>	<b>0.395393</b>	<b>0.410</b>

373  
374 4.5.3. *Famennian record, Palmatolepis*. – Along the Famennian record in CT, the best model fitting  
375 *Palmatolepis* evolution corresponded to a shift from an unbiased random walk to stasis (Table 8),  
376 occurring at step 8 (CT34, 369.7 Ma). In BU, one model also emerged clearly, corresponding to one  
377 punctuation (Table 9) occurring at step 7 (BU21, 369.3 Ma). Both shifts appear thus to be almost  
378 perfectly congruent, despite being estimated independently in the two sections. In both cases, the  
379 shift corresponded to smaller *Palmatolepis* size in the second part of the record (Figure 7A).

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383 Figure 7. A. Models of evolution for *Palmatolepis* size along the Famennian. BU: the best-fitting model  
384 corresponded to one punctuation. CT: the best-fitting model corresponded to a shift from URW to stasis; the  
385 one-punctuation model provides a visualization of the shift in evolutionary mode. B. Models of evolution for  
386 *Polygnathus* size along the Famennian. BU: The best-fitting model corresponded to a stasis. CT: The best-fitting  
387 model corresponded to a Ohrstein-Uhlenbeck model, corresponding to an initial evolution towards an adaptive  
388 peak, followed by stability around this peak.

389

390 Table 8. Comparison of support for each model of *Palmatolepis* evolution in CT (comparing 11 models [n = 26,  
391 method = joint]. LogL= model log likelihood, K = number of model parameters, AICc = Akaike's Information  
392 Criterion corrected for small sample size, dAICc = difference in AICc score between the best model and the  
393 model being compared and Akaike.wt: Akaike weights (proportion of the total amount of predictive power).

	logL	K	AICc	dAICc	Akaike.wt
GRW	18.10755	3	-29.1242	7.9418906	0.010
URW	18.0473	2	-31.57285	5.4932343	0.034
Punc-1	19.88463	4	-29.86451	7.20158	0.015
OU	20.05839	4	-30.21203	6.8540608	0.017
Stasis	10.21039	2	-15.89905	21.1670384	0.000
<b>URW-Stasis</b>	<b>25.03304</b>	<b>5</b>	<b>-37.06609</b>	<b>0.000000</b>	<b>0.533</b>

Stasis-URW	18.83415	4	-27.76354	9.3025436	0.005
GRW-Stasis	26.41616	6	-36.41127	0.6548168	0.384
Stasis-GRW	18.84199	5	-24.68398	12.3821035	0.001
$\delta^{18}\text{O}$	12.93283	3	-18.77475	18.2913371	0.000
p[?][?][?]	10.22268	3	-13.35444	23.7116426	0.000

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395

396 Table 9. Comparison of support for each model of *Palmatolepis* evolution in BU (comparing 11 models [n = 26,  
397 method = joint]. LogL= model log likelihood, K = number of model parameters, AICc = Akaike's Information  
398 Criterion corrected for small sample size, dAICc = difference in AICc score between the best model and the  
399 model being compared, Akaike.wt: Akaike weights (proportion of the total amount of predictive power).

	logL	K	AICc	dAICc	Akaike.wt
GRW	-1.258698	3	9.608306	21.960669	0.000
URW	-1.273532	2	7.068803	19.421166	0.000
<b>Punc-1</b>	<b>11.128563</b>	<b>4</b>	<b>-12.352363</b>	<b>0.000000</b>	<b>0.295</b>
OU	10.68761	4	-11.470458	0.881905	0.190
Stasis	7.894902	2	-11.268065	1.084298	0.171
URW-Stasis	10.366653	5	-7.733307	4.619056	0.029
Stasis-URW	2.279478	4	5.345807	17.69817	0.000
GRW-Stasis	10.884588	6	-5.348124	7.00424	0.009
Stasis-GRW	2.281291	5	8.437418	20.789781	0.000
$\delta^{18}\text{O}$	9.015465	3	-10.940022	1.412342	0.145
pcPa	9.114587	3	-11.138266	1.214098	0.161

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402 4.5.4. *Famennian record*, *Polygnathus*. – Two models were very close in fitting *Polygnathus* size  
403 evolution at CT, corresponding either to an unbiased random walk or evolution towards an adaptive  
404 peak (Ohrstein-Uhlenbeck) (Table 10). In BU, the best model was by far the stasis (Table 11). In both  
405 cases, this suggested an overall stability of size throughout the record, with possibly a phase of initial  
406 evolution towards this adaptive peak that could be documented in CT due to the more extensive  
407 record in the early Famennian compared to BU where this period is missing (Fig. 7B).

408 Table 10. Comparison of support for each model of *Polygnathus* evolution in CT (comparing 11 models [n = 21,  
409 method = joint]. LogL= model log likelihood, K = number of model parameters, AICc = Akaike's Information  
410 Criterion corrected for small sample size, dAICc = difference in AICc score between the best model and the  
411 model being compared, Akaike.wt: Akaike weights (proportion of the total amount of predictive power).  
412

	logL	K	AICc	dAICc	Akaike.wt
GRW	7.300514	3	-7.189263	3.406202	0.049
URW	7.244408	2	-9.822149	0.7733159	0.182
Punc-1	7.719622	4	-4.939243	5.6562214	0.016
<b>OU</b>	<b>10.547732</b>	<b>4</b>	<b>-10.595465</b>	<b>0.000000</b>	<b>0.268</b>

Stasis	6.643551	2	-8.620435	1.9750297	0.100
URW-Stasis	11.053871	5	-8.107743	2.4877218	0.077
Stasis-URW	9.91964	4	-9.33928	1.2561847	0.143
GRW-Stasis	11.100333	6	-4.200666	6.3947989	0.011
Stasis-GRW	9.954323	5	-5.908646	4.6868189	0.026
$\delta^{18}\text{O}$	6.645781	3	-5.879798	4.715667	0.025
pcPa	8.047335	3	-8.682905	1.9125599	0.103

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415 Table 11. Comparison of support for each model of *Polygnathus* evolution in BU (comparing 6 models [n = 17,  
416 method = joint]. LogL= model log likelihood, K = number of model parameters, AICc = Akaike's Information  
417 Criterion corrected for small sample size, dAICc = difference in AICc score between the best model and the  
418 model being compared, Akaike.wt: Akaike weights (proportion of the total amount of predictive power).

	logL	K	AICc	dAICc	Akaike.wt
GRW	-4.89080337	3	17.627761	12.212885	0.001
URW	-4.92236396	2	14.701871	9.286995	0.005
OU	2.13569649	4	7.06194	1.647064	0.225
<b>Stasis</b>	<b>-0.27886661</b>	<b>2</b>	<b>5.414876</b>	<b>0.000000</b>	<b>0.512</b>
$\delta^{18}\text{O}$	-0.27475861	3	8.395671	2.980795	0.115
pcPa	-0.07352906	3	7.993212	2.578336	0.141

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## 5. Discussion

### 424 5.1. "Temperature – Size Relationship" – A rule valid at a larger geographic scale ?

425 In this review of ten datasets documenting paleotemperature vs conodont size variation, the  
426 temperature-size rule (TSR) was supported in one case only, corresponding to the geographic  
427 variation during the *linguiformis* time slice. This case by far involved the largest range of  
428 paleotemperature variation ( $\delta^{18}\text{O}$  range ~ 4‰), twice as large as the largest range of temporal  
429 variation among the records involved here ( $\delta^{18}\text{O}$  range ~ 2‰ along the Famennian record at CT).  
430 Further in line with the TSR hypothesis, conodonts (both *Palmatolepis* and *Polygnathus*) tended to be  
431 larger during the Famennian in CT than in BU, characterized by warmer environment.  
432 Possibly, consistent shifts in life history traits, leading to the TSR signature, may only arise as large-  
433 scale patterns. In agreement, during the *linguiformis* zone, different kinds of size-frequency  
434 distributions were found for *Palmatolepis* between the Western Paleotethys, characterized by highly  
435 skewed distributions, and the Eastern Paleotethys, with flatter distributions characterized by a more  
436 balanced contribution of small and large specimens, and the occurrence of largest specimens (Girard  
437 et al. 2007). These environments, located on the eastern shelves of Paleotethys (Northern Australia)  
438 were offshore of stromatoporoid reefs. In modern oceans, the presence of symbiont-bearing reefs

439 usually indicates conditions with low levels of nutrient content and primary productivity, associated  
440 with clear waters favoring the development of photosymbionts (Wood 1993; Humphreys et al. 2018).  
441 Such conditions might have reinforced the TSR, with warm oligotrophic waters offering less resources  
442 for growth, and hence leading to smaller conodonts (Girard et al. 2007).

443

#### 444 *5.2. Size distribution in conodonts – what biological processes beyond?*

445 The concept of TSR has been developed for describing animal's growth at different temperatures  
446 (Atkinson 1994). By transferring the TSR to conodonts, one tacitly assumes that the size of the  
447 elements found in the fossil record approximate body size (Purnell 1993). This hypothesis may be  
448 valid given the continuous growth of the conodont elements, through addition of thin lamellae along  
449 the life of the former animal. It remains that the frequency of accretion of new lamellae is unknown,  
450 and might have varied with the age of the animal, and the environmental conditions.

451 According to the TSR, the animal's growth is accelerated in warm waters, leading to younger animals  
452 reaching maturity at a smaller size. In cold waters, animals would grow slower and but ultimately  
453 reach larger size. As a consequence, size-frequency distribution for cold water animals should be  
454 flatter and reach larger maximal size. Assuming that in conodonts, element size approximates body  
455 size, the size-frequency distribution in an assemblage records another parameter, namely the  
456 pattern of reproduction: abundant production of small-sized juveniles should heavily contribute to  
457 skewed distributions, with a peak of small-sized elements (Fig. 8). Such differences in life-history  
458 traits have been evoked to explain differences in the shape of the size-frequency distribution  
459 between *Palmatolepis* and *Ancyrodella* in the Late Frasnian (Girard & Renaud 2008) as it has been  
460 observed on two branchiopod (crustaceans) species (Huang & Chou 2017). Such dynamics might  
461 interfere with the TSR sensu stricto, and even if biologically valid, make it difficult to be detected in  
462 the fossil record.

463

#### 464 *5.3. Local conditions interfering with global trends*

465 If a TSR-like pattern was found across the Paleotethys, the trend was not validated at a smaller  
466 geographic scale among the sections from the Western Paleotethys. The sections LSC and CUQ were  
467 relatively close to each other, and both characterized by colder waters than the Moroccan Mrirt  
468 section. Yet, LSC is characterized by the smallest-sized distribution. This section is characterized  
469 throughout by poorly oxygenated conditions (Girard & Renaud 2007). Oxygen supply is an important  
470 factor controlling body size of marine organisms. The challenge of oxygen supply being more acute at  
471 high temperature, and for large body size, this may explain why animals grow to smaller size in warm  
472 waters, oxygen supply has been invoked as the main driver of the TSR itself (Forster et al. 2012).  
473 Anoxic environments may represent cases where limitation in oxygen supply is not driven primarily

474 by water temperature, leading to deviation from the TSR. Further arguing in this direction, the level  
475 experiencing a punctuation towards smaller *Palmatolepis* size in LSC corresponds to the onset of  
476 anoxic facies in the section. However, the paucity of anoxic levels in most of the sections considered  
477 in the present study precluded to further disentangle the importance of decreased oxygen supply  
478 due to increasing water temperature or local anoxic conditions on conodont size. An alternate  
479 explanation would be the ability of organisms to adjust their physiology to such oxygen limitation at  
480 high temperature, at least within the range of tolerance of the concerned group (Einum et al. 2021).

481

#### 482 5.4. Reverse TSR during stressful periods – nanism counterbalancing TSR?

483 A significant relationship between conodont size and paleotemperature proxy was found in few  
484 other cases: *Palmatolepis* during the Late Frasnian at CUQ and along the Famennian at CT; and  
485 possibly in *Ancyrodella* at CUQ. Results derived from linear models and the comparison of  
486 evolutionary modes were on this respect very congruent. The linear mixed effect model including all  
487 specimens in the analysis, but integrating the level as random factor appeared as especially efficient  
488 in retrieving the correlation in *Ancyrodella* at CUQ, that also emerge as highly probable using the  
489 comparison of evolutionary modes. Using the correction for temporal auto-correlation failed to  
490 identify some otherwise consistent size – paleotemperature relationships (*Palmatolepis* during the  
491 Kellwasser period at CUQ, *Palmatolepis* during the Famennian at CT). Possibly, by correcting for  
492 temporal autocorrelation, the effect of congruent trends is discarded, that however correspond to  
493 biologically relevant covariation between variables.

494 However, in all these cases where the size – paleotemperature relationship emerged as consistently  
495 supported, the direction of the relationship was reverse to the expectations of the TSR: size  
496 decreased with increasing  $\delta^{18}\text{O}$  and hence with decreasing temperature.

497 The Late Frasnian was punctuated by two major anoxic events, the Lower and Upper Kellwasser  
498 events, the later culminating in the mass extinction punctuating the Frasnian / Famennian boundary.  
499 The events LKW and UKW were associated with cooling phases (Joachimski & Buggisch 2002), leading  
500 to a morphological response of *Palmatolepis* (Balter et al. 2008). The trends reported here suggest  
501 that *Palmatolepis* and possibly *Ancyrodella* responded to these short-term cooling phases by a  
502 decrease in size, and not an increase as expected by the TSR. The Kellwasser events, especially the  
503 UKW, were associated with extinctions pointing to momentary destabilization of the marine faunas  
504 (Racki 1998; Barash 2016). Disruption of food chains are prone to drive size reduction in various  
505 organisms (Rita et al. 2019; He et al. 2010). In this case, external driver related to available resources  
506 would override the effects related water temperature in determining size evolution.

507

#### 508 5.5. A threshold response to temperature?

509 The reverse TSR during the Late Frasnian at CUQ was however not supported in the two other  
510 sections documented, LSC and Mrirt, where little size variation was observed. A possible explanation  
511 would be that conodont size responded to temperature decrease only below a certain threshold. The  
512 range of paleotemperature variations was not more important at CUQ as at Mrirt and LSC, but it was  
513 shifted towards colder temperatures. A threshold of temperature tolerance might thus have been  
514 crossed in CUQ during cold phases but not in the warmer conditions of LSC and Mrirt, explaining why  
515 conodont size responded to temperature variation in CUQ only. A similar process might be  
516 responsible for the patterns observed during the Famennian, with a significant size-temperature  
517 relationship observed at CT but not at BU. The threshold for the temperature response ( $\sim 18\text{‰ } \delta^{18}\text{O}$ )  
518 might have been passed in the colder CT but not in the warmer BU, where the range of  
519 paleotemperature variation was anyway reduced (Girard et al. 2020).

520 The differential response of genera like *Palmatolepis* and *Polygnathus* might be due to different  
521 temperature tolerance, although they are mostly known for preference regarding water depth /  
522 distance to the shore (Seddon & Sweet 1971; Klapper & Barrick 1975; Sandberg 1976). During the  
523 Famennian, *Polygnathus* might have displayed a wider tolerance to temperature than *Palmatolepis*,  
524 explaining the different patterns for the two coexisting genera. This hypothesis is supported by the  
525 fact that *Polygnathus* flourished in the icehouse Carboniferous context, while *Palmatolepis* went  
526 extinct during the crisis punctuating the Devonian/Carboniferous boundary.

527

#### 528 5.6. An unknown forcing to *Palmatolepis* size evolution in the Famennian

529 Two alternate strategies were explored to test for the TSR hypothesis: exploring the correlation  
530 between size and paleotemperature records, or modelling modes of size evolution, among which  
531 tracking an environmental variable. Both approaches agreed when a temperature-size relationship  
532 was strongly supported (Late Frasnian *Palmatolepis* at CUQ). However, evolutionary models further  
533 allowed to explicitly test for alternate scenarios, such as punctuation or stasis. Comparing such  
534 models is only relevant for sequences with a sufficient number of levels, allowing to integrate modes  
535 of evolution involving switch from one mode to another.

536 This was the case for the Famennian sequence (more than 10 My), and the separate analysis of the  
537 CT and BU record of *Palmatolepis* size delivered amazingly congruent results, suggesting a sudden  
538 decrease in size at  $\sim 369.7$  Ma. The congruence in both outcrops suggests a common environmental  
539 forcing.

540 It antedates a shift in detrital supply observed in several outcrops from the NW Paleotethys during  
541 the early *marginifera* Zone, dated earlier as 368 Ma (Girard et al. 2021). This abrupt shift in detrital  
542 supply is interpreted as due to a remnant oceanic barrier vanishing during the early middle  
543 Famennian due to sea-level changes and/or tectonic events. Response of marine fauna to such

544 modifications in water masses exchanges can antedate the final closure or opening, as exemplified by  
 545 deep-water foraminifera being affected earlier by the closure of the Panama Isthmus compared to  
 546 shallow-water species (Schmidt et al 2016). Such a dynamic regarding *Palmatolepis* response remains  
 547 highly speculative given the poor knowledge of the timing of the different processes involved.  
 548 More simply, the shifts in the size record of *Palmatolepis* could match the onset of the temperature  
 549 decrease that will characterize the second part of the Famennian. It may have triggered an evolution  
 550 towards a new adaptive optimum after an initial phase of random walk following the  
 551 Frasnian/Famennian crisis; the paucity of the record during the early Famennian in BU probably  
 552 limited the assessment of the evolutionary mode during the initial phase.  
 553 The critical time of ~369.5 Ma also corresponds to a pivotal point after which the relative abundance  
 554 of *Palmatolepis* decreases (Girard et al. 2020). With a wider tolerance to temperature, *Polygnathus*  
 555 would have been little affected, explaining its stable size through the record. The case of these two  
 556 contrasted responses to the Famennian environmental changes highlight that the TSR hypothesis, for  
 557 being seducing, constitutes an oversimplification of complex eco-evolutionary processes.

558

#### 559 **Declaration of competing interest**

560 The authors declare that they have no conflict of interest.

561

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- 730

731  
 732 **Supplementary Tables:** data per section and per genus. P Wilcox: probabilities of pairwise size  
 733 differences between successive levels along a section (pairwise Wilcoxon tests). In bold,  $P < 0.01$ , in  
 734 italics  $P < 0.05$ .

735  
 736 **Whole Kellwasser Period - CUQ**

<i>Palmatolepis</i>	Age	$\delta^{18}\text{O}$	N	LogA0	SD	P Wilcox
CUQ23d	373.6	17.6	121	0.044	0.355	
CUQ23e	373.5	17.4	18	0.377	0.388	<b>0.0008</b>
CUQ24a	373.4	17.5	37	0.153	0.383	<i>0.0410</i>
CUQ24bc	373.2	18.2	15	0.362	0.472	0.1984
CUQ24d	373.1	18.3	19	0.036	0.257	0.0709
CUQ24e	372.9	18.4	34	0.203	0.279	<i>0.0232</i>
CUQ25b	372.8	17.5	48	0.062	0.301	<i>0.0461</i>
CUQ25cd	372.7	18.1	49	0.039	0.312	0.3942
CUQ26b	372.5	18.2	235	0.199	0.413	<i>0.0110</i>
CUQ27	372.4	17.9	170	0.173	0.319	0.8133
CUQ28c	372.2	17.9	263	0.256	0.362	<i>0.0231</i>
CUQ29b	372.1	17.6	350	0.307	0.416	0.2739
CUQ30a	372.0	17.5	469	0.290	0.376	0.8425
CUQ31c	371.8	17.2	481	0.204	0.359	<b>0.0005</b>
CUQ31f	371.7	17.1	94	0.428	0.337	<b>0.0000</b>
CUQ31g1	371.5	16.7	68	0.473	0.363	0.5180
CUQ31g2	371.4	16.9	58	0.492	0.420	0.5423
CUQ32a	371.1	17.4	51	0.280	0.296	<b>0.0019</b>
CUQ32b	370.9	17.3	45	0.240	0.229	0.5471

737  
 738 **Whole Kellwasser Period - Mrirt**

<i>Palmatolepis</i>	Age	$\delta^{18}\text{O}$	N	LogA0	SD	P Wilcox
M01	373.8	16.5	63	0.323	0.354	
M02	373.6	16.3	200	0.190	0.421	<b>0.0043</b>
M03	373.4	16.9	71	0.264	0.370	0.1423
M05	373.0	16.6	59	0.413	0.424	<i>0.0283</i>
M06	372.8	16.5	420	0.224	0.332	<b>0.0010</b>
M07	372.5	16.2	81	0.151	0.395	<i>0.0197</i>
M08	372.3	16.0	74	0.091	0.383	0.2931
M09	372.0	15.6	52	0.186	0.336	0.0717
M11a	371.8	16.0	13	0.246	0.546	0.9673
M11b	371.5	15.9	25	0.302	0.381	0.4653
M12	371.0	16.1	6	0.150	0.314	0.5095
M13	370.8	16.3	133	0.164	0.333	0.9876
M15a	370.4	15.9	98	0.273	0.389	<i>0.0499</i>

739  
 740 **Whole Kellwasser Period - LSC**

<i>Palmatolepis</i>	Age	$\delta^{18}\text{O}$	N	LogA0	SD	P Wilcox
LSC03A	373.9	16.9	28	0.081	0.397	
LSC04D	373.8	17.0	13	0.058	0.339	0.8574
LSC05A	373.7	16.7	11	-0.138	0.316	0.1863
LSC06A	373.6	16.8	115	0.168	0.399	<i>0.0171</i>

LSC07C	373.5	16.4	18	0.063	0.432	0.2102
LSC08C	373.4	17.0	8	0.178	0.175	0.1147
LSC09B	373.2	17.4	11	-0.100	0.167	<b>0.0068</b>
LSC10A	373.0	17.9	47	-0.033	0.327	0.9377
LSC11B	372.7	17.2	89	0.106	0.401	0.0104
LSC12	372.5	17.2	251	0.029	0.394	0.0510
LSC13A	372.4	16.8	799	0.083	0.383	0.0211
LSC13B	372.2	16.4	934	0.067	0.361	0.7505
LSC13C	372.0	16.4	264	0.001	0.331	0.0189
LSC14B	371.8	16.1	95	-0.017	0.398	0.2478
LSC14C2	371.6	16.3	27	0.182	0.388	0.0127
LSC14D	371.4	16.5	13	0.066	0.300	0.3602
LSC14F1	371.1	17.2	94	0.445	0.304	<b>0.0002</b>
LSC14F2	370.9	17.1	48	0.209	0.365	<b>0.0000</b>
LSC14G	370.8	16.9	8	0.413	0.204	0.0302
LSC14H	370.6	16.9	226	0.221	0.383	0.0755
LSC15A	370.5	16.7	79	0.123	0.382	0.0458

741

742

**Whole Kellwasser Period - CUQ**

<i>Ancyrodella</i>	Age	$\delta^{18}\text{O}$	N	LogA0	SD	P Wilcox
CUQ23D	373.6	17.6	4	0.466	0.390	
CUQ23D2	373.6	17.6	7	0.224	0.360	0.3152
CUQ23e	373.5	17.4	11	0.237	0.392	1.0000
CUQ24a	373.4	17.5	39	0.292	0.342	0.5024
CUQ24BC	373.2	18.2	4	0.013	0.096	0.1305
CUQ24E	372.9	18.4	3	0.408	0.154	0.0571
CUQ25b	372.8	17.5	7	0.327	0.276	0.5167
CUQ25C	372.7	18.1	3	0.772	0.252	0.1167
CUQ26b	372.5	18.2	14	0.199	0.368	0.0324
CUQ27	372.4	17.9	5	0.680	0.151	0.0143
CUQ28c	372.2	17.9	16	0.375	0.369	0.0401
CUQ29b	372.1	17.6	16	0.457	0.383	0.5147
CUQ30	372.0	17.5	3	0.280	0.234	0.7121
CUQ31C	371.8	17.2	8	0.301	0.440	0.6303
CUQ31f	371.7	17.1	118	0.453	0.453	0.3496
CUQ31g1	371.5	16.7	10	0.880	0.369	<b>0.0062</b>
CUQ31g2	371.4	16.9	15	0.550	0.429	0.0709

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**Whole Kellwasser Period - Mrirt**

<i>Ancyrodella</i>	Age	$\delta^{18}\text{O}$	N	LogA0	SD	P Wilcox
M01an	373.8	16.5	7	0.408	0.298	
M02an	373.6	16.3	18	0.493	0.310	0.5339
M03an	373.4	16.9	27	0.316	0.462	0.1425
M05an	373.0	16.6	6	0.237	0.341	0.7329
M06an	372.8	16.5	15	0.218	0.441	0.8500
M07an	372.5	16.2	20	0.616	0.494	0.0116
M09an	372.0	15.6	25	0.415	0.297	0.1616
M11an	371.8	16.0	6	0.336	0.496	0.7515

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746 Famennian - *Palmatolepis* CT

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	Age	$\delta^{18}\text{O}$	pcPa	N	LogA0	SD_LogA0	pWilcox
CT07	373.1	17.7	32.8	83	0.184	0.356	
CT11c	372.6	17.7	45.8	56	0.288	0.437	0.2186
CT22	371.8	17.4	62.9	95	0.506	0.321	<b>0.0001</b>
CT23	371.8	17.7	76.5	51	0.437	0.384	0.3493
CT24	371.1	17.7	67.4	53	0.471	0.315	0.7061
CT30	370.3	17.1	79.5	195	0.611	0.360	0.0123
CT32	369.9	17.6	94.4	52	0.626	0.318	0.9156
CT34	369.7	17.4	96.8	48	0.499	0.441	0.0650
CT35	369.6	18.0	97.3	235	0.289	0.405	<b>0.0025</b>
CT36	369.1	18.2	70.5	50	0.263	0.401	0.7132
CT37	368.7	17.5	98.4	88	0.265	0.404	0.9558
CT39	367.7	17.6	67.6	174	0.157	0.406	0.0302
CT41	367.6	17.7	89.2	89	0.163	0.292	0.3698
CT42	367.3	18.2	77.6	148	0.136	0.298	0.2218
CT48	366.2	18.2	97.5	42	0.045	0.282	<b>0.0090</b>
CT51	365.6	17.9	80.2	217	0.177	0.345	<b>0.0076</b>
CT52	365.3	17.8	62.3	23	0.190	0.373	0.8820
CT56	364.5	18.2	81.4	119	0.094	0.386	0.2190
CT59	364.3	19.1	75.0	92	0.194	0.313	0.0111
CT59-1	364.2	19.0	85.1	45	0.146	0.263	0.4292
CT61-1	363.0	19.2	51.9	64	0.116	0.259	0.3805
CT62	362.5	19.1	22.5	60	0.185	0.291	0.1069
CT63	362.3	19.2	29.1	106	0.362	0.354	<b>0.0039</b>
CT66	361.2	18.3	23.4	24	0.136	0.340	<b>0.0051</b>
CT69-1	360.6	19.0	8.8	11	0.389	0.351	0.0345
CT70-2	359.4	18.5	14.2	9	0.436	0.323	0.6027

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749 Famennian - *Palmatolepis* BU

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	Age	$\delta^{18}\text{O}$	pcPa	N	LogA0	SD_LogA0	Pwilcox
BU007	374.0	16.6	61.8	16	0.441	0.398	
BU010	373.1	16.5	67.9	7	0.066	0.474	0.0469
BU010G1	370.1	16.4	82.5	16	0.287	0.345	0.4515
BU011	370.1	16.9	76.9	209	0.413	0.450	0.2937
BU012	370.0	16.7	70.2	236	0.269	0.424	<b>0.0006</b>
BU018	369.6	17.2	96.7	50	0.273	0.372	0.5884
BU021	369.3	17.0	79.5	255	0.039	0.480	<b>0.0005</b>
BU025	368.7	17.0	97.8	442	-0.010	0.425	0.3421
BU029	368.3	17.0	94.1	391	-0.090	0.435	<b>0.0032</b>
BU035	367.7	17.3	86.9	60	0.406	0.404	<b>0.0000</b>
BU038	367.4	17.4	98.0	615	-0.106	0.377	<b>0.0000</b>
BU040	366.9	17.2	92.1	202	0.042	0.406	<b>0.0000</b>
BU044	366.7	17.1	92.2	340	-0.103	0.427	<b>0.0002</b>
BU051	366.2	17.6	96.5	254	-0.056	0.320	0.0770

BU055	365.9	17.8	95.3	177	-0.141	0.302	<b>0.0009</b>
BU060	365.5	16.7	89.9	71	0.094	0.317	<b>0.0000</b>
BU065	365.2	17.0	86.3	243	0.209	0.318	0.0049
BU069	364.9	17.8	81.2	125	-0.011	0.289	<b>0.0000</b>
BU076	364.3	17.8	62.6	137	0.059	0.382	0.1829
BU078	364.2	17.4	83.1	57	0.378	0.391	<b>0.0000</b>
BU082	363.8	17.9	51.8	70	0.139	0.404	0.0013
BU087	363.0	17.5	60.5	73	0.088	0.449	0.5221
BU093	362.4	17.7	58.5	53	0.363	0.413	<b>0.0020</b>
BU094	362.3	17.2	48.3	62	-0.042	0.385	<b>0.0000</b>
BU095	361.5	17.3	75.9	191	0.009	0.341	0.4926
BU103	360.2	17.3	37.4	18	0.182	0.411	0.1087

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Famennian – *Polygnathus* CT

	Age	$\delta^{18}\text{O}$	pcPa	N	LogCS	SD_LogCS	Pwilcox
CT_007	373.1	17.7	32.8	180	6.259	0.375	
CT_011c	372.6	17.7	45.8	57	6.382	0.389	<b>0.0037</b>
CT_022	371.8	17.4	62.9	64	6.225	0.337	<b>0.0091</b>
CT_023	371.8	17.7	76.5	7	6.237	0.335	0.6365
CT_024	371.1	17.7	67.4	11	6.503	0.357	0.1042
CT_030	370.3	17.1	79.5	44	6.268	0.316	0.0434
CT_035	369.6	18.0	97.3	3	6.408	0.574	0.6352
CT_036	369.1	18.2	70.5	8	6.260	0.249	0.9212
CT_037	368.7	17.5	98.4	4	6.391	0.283	0.2828
CT_039	367.7	17.6	67.6	65	6.705	0.449	0.1695
CT_041	367.6	17.7	89.2	23	6.561	0.448	0.1745
CT_042	367.3	18.2	77.6	28	6.511	0.358	0.6728
CT_049	366.0	18.2	92.9	27	6.377	0.394	0.2510
CT_051	365.6	17.9	80.2	24	6.436	0.426	0.8151
CT_053	365.1	17.8	82.5	17	6.488	0.485	0.7436
CT_056	364.5	18.2	81.4	9	6.444	0.371	0.9579
CT_059	364.3	19.1	75.0	11	6.626	0.372	0.2947
CT_062	362.5	19.1	22.5	6	6.245	0.188	0.0365
CT_063	362.3	19.2	29.1	79	6.266	0.265	0.8570
CT_069-1	360.6	19.0	8.8	53	6.577	0.311	<b>0.0000</b>
CT_070-2	359.4	18.5	14.2	25	5.989	0.140	<b>0.0000</b>

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Famennian - *Polygnathus* BU

	Age	$\delta^{18}\text{O}$	pcPa	N	LogCS	LogCS	P Wilcox
BU_012	370.0	16.7	70.2	12	6.697	0.386	
BU_021	369.3	17.0	79.5	53	6.275	0.367	<b>0.0019</b>
BU_025	368.7	17.0	97.8	2	6.379	0.402	0.6693
BU_029	368.3	17.0	94.1	9	5.863	0.222	0.1455
BU_035	367.7	17.3	86.9	5	6.634	0.441	<b>0.0010</b>
BU_038	367.4	17.4	98.0	14	6.315	0.511	0.2566
BU_040	366.9	17.2	92.1	98	6.176	0.352	0.3054
BU_044	366.7	17.1	92.2	26	6.540	0.473	<b>0.0005</b>
BU_051	366.2	17.6	96.5	10	6.181	0.465	0.0255

BU_055	365.9	17.8	95.3	7	6.656	0.381	0.0330
BU_060	365.5	16.7	89.9	16	6.214	0.270	<b>0.0046</b>
BU_065	365.2	17.0	86.3	45	6.135	0.322	0.4595
BU_069	364.9	17.8	81.2	20	6.088	0.554	0.2858
BU_076	364.3	17.8	62.6	15	6.271	0.455	0.1585
BU_082	363.8	17.9	51.8	3	6.166	0.138	0.6544
BU_093	362.4	17.7	58.5	2	6.948	0.398	0.2000
BU_103	360.2	17.3	37.4	10	6.347	0.265	0.1212

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