

Paleogeographic differences in temperature, water depth and conodont biofacies during the Late Devonian

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1	Paleogeographic differences in temperature, water depth and conodont biofacies
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21	
22	Abstract
23 24	The Famennian (Late Devonian) started after and ended with two of the seven largest
25	crises of the Phanerozoic, the Kellwasser and Hangenberg events, respectively. In
26	between, global environmental trends have been identified, involving cooling and
27	eustatic regression. Tropical and subtropical marine faunas were largely cosmopolitan.
28	Overall, this suggests that the Famennian was marked by long-term environmental
29	changes occurring in a relatively homogeneous manner despite being punctuated by
3U 21	several short-term events of limited faunal impact. How these trends were modulated
31 33	according to geographic location is investigated in this study by comparing two
32 22	Thuring in (Durght sich section, Commany). Both ware leasted in the subtranical and
33	I nuringia (Buschteich section, Germany). Both were located in the subtropical area
34 25	auring uns period and belonged to two former microcontinents bracketed between the
35	closing kneic Ocean and Gondwana. Sedimentary facies, oxygen isotopes, and the
36	generic conodont composition (biofacies) were studied in a high resolution and in the
37	same rock samples. Sedimentary facies provided an estimate of water depth and oxygen

38 isotopes were used as paleotemperature proxy. Conodont biofacies were analyzed using 39 a principal component analysis, allowing the expression of the variations in the two 40 outcrops on the same axes, and a quantitative comparison with the other proxies. Sea-41 level and temperature variations were different between the two areas. Saxo-Thuringia 42 displayed stable deep and warm conditions throughout. In contrast, the environment of 43 the Montagne Noire was shallower and cooler during the Late and latest Famennian 44 compared to the Early and Middle Famennian, congruent with the global change 45 evidenced elsewhere. The location of Saxo-Thuringia, close to the first point of closure of the Rheic Ocean, might have favored active tectonics, causing a local departure from the 46 47 eustatic trend. The stable temperatures at BU during the Late and latest Famennian may 48 be due to the position of Saxo-Thuringia in the remnant Rheic Ocean, limiting water 49 mass exchange with open seas, and favoring the persistence of warm conditions. 50 Offshore taxa persisted later at high abundance in the Saxo-Thuringian record. The two 51 conodont biofacies records were otherwise very comparable. This suggests that other 52 factors mitigated the water depth forcing on these conodont assemblages. 53 54 55 Keywords. Famennian; Montagne Noire; Saxo-Thuringia; Palmatolepis; oxygen 56 isotopes; sedimentary facies 57 58 59 **1. Introduction** 60 61 The Famennian is well known for being bracketed by two of the most important 62 biological crises in the Earth's history: the Upper Kellwasser Event just before the Frasnian-Famennian boundary (e.g. McGhee, 1996; Schindler, 1993; Walliser, 1996) and 63 64 the Hangenberg Crisis punctuating the Devonian-Carboniferous boundary (e.g. Becker et al. 2016; Kaiser et al. 2008, 2015; Walliser, 1996). Many studies were devoted to these 65 crises, allowing a fine-scale characterization of the biotic and abiotic variations during 66 67 the hundred thousand years involved in these worldwide perturbations (Becker et al., 68 2012; Corradini, 2003; Girard and Feist, 1997; Joachimski et al., 2009; McGhee, 1996; 69 Sandberg et al., 1988; Walliser, 1996). Environmental changes also occurred during the 70 time interval between the crises (ca. 13 Myr, Becker et al., 2012), but deserved much

71 less attention. Short-term events have nevertheless been described, with minor impact 72 on the faunas (e.g. Annulata Events by House, 1985; Korn, 2004; Hartenfels, 2011; 73 Hartenfels and Becker, 2017; Dasberg Crisis by Becker, 1993; Hartenfels and Becker, 74 2009; Hartenfels, 2011; Condroz Events by Becker, 1993; Becker and House, 1997). A 75 regressive trend punctuated by minor transgressive-regressive couplets has been 76 evidenced for the Famennian (Johnson et al., 1985, 1996). Global cooling inferred from 77 oxygen isotope data has been suggested for the same interval (Joachimski et al., 2004, 78 2009), an interpretation supported by independent evidence of Latest Famennian glacial deposits described from South America (Caputo et al., 2008; Isaacson et al., 79 80 2008). The congruence of climate cooling and a regressive trend is therefore coherent in 81 this eustatic context. Tropical and subtropical marine faunas were cosmopolitan at the 82 generic level (Feist and Becker, 1997; Korn and De Baets, 2015; Mottequin et al., 2013; 83 Spalletta et al., 2017) suggesting rather homogeneous environmental conditions and 84 efficient exchanges between the faunas. Conodonts, small, nektonic animals of chordate 85 affinities, were an abundant part of this marine fauna. Their taxonomic identification 86 provides a detailed stratigraphic framework for this period (Hartenfels, 2011; Spalletta 87 et al., 2017; Ziegler, 1962; Ziegler and Sandberg, 1984; 1990). Conodonts can also give 88 paleoenvironmental indications because conodont genera distribution was influenced 89 by several factors (Lüddecke et al., 2017), notably water depth (Sandberg, 1976; Seddon 90 and Sweet, 1971). The congruence of temporal variations in the conodont biofacies (i.e. 91 assemblage composition of the different genera) in different sections supported that the 92 Famennian was marked by long-term environmental changes that were not durably 93 perturbed by the short-term events punctuating it (Corradini, 2003; Girard et al., 2014; 94 2017).

95 This view, however, can also be the consequence of the paucity of detailed 96 records in different paleogeographic areas. Famennian paleogeography was 97 characterized by the closure of the Rheic Ocean bracketing microcontinents derived 98 from Gondwana (e.g. Franke et al., 2017; Stampfli et al., 2013) (Fig. 1). Discrepancies in 99 relative sea-level changes have been reported from these microcontinents (e.g. in the 100 Saxo-Thuringian area) and attributed to tectonic movements overprinting the global 101 eustatic trend (Girard et al., 2017). This raises the question whether the environmental 102 trends evidenced so far are of global significance, and/or whether local/regional factors related to tectonics and paleogeographic changes interfered with these (presumed)global trends.

105 To address these questions, we studied two recently described sections having a 106 detailed record from the Late Frasnian to the end-Famennian (Girard et al., 2014, 2017). 107 The Col des Tribes (CT) section in the Montagne Noire was part of the Armorica 108 microcontinent, whereas the Buschteich section (BU) was located on the Saxo-109 Thuringian microplate. Hence, both sections were located on former microcontinents 110 bracketed between the closing Rheic Ocean and Gondwana (Fig. 1). Water depth and 111 approximate position relative to the shore were assessed based on the macroscopic 112 description of the sediments as well as microfacies analysis (e.g. Flügel, 2004). Despite 113 limitations due to the scarcity of preserved bioclasts in the sediments (e.g. Brett and 114 Allison, 1998), this approach provided a paleoenvironmental estimate directly based on 115 the depositional environment. Water depths derived from sedimentological analysis 116 were compared with conodont biofacies, which have been proposed to react more 117 sensitive to water-depth changes than microfacies (Lüddecke et al., 2017). Nevertheless, 118 as for any biotic record, evolutionary changes through time (changes in water depth 119 preferences, decrease or increase in response to biotic factors such as predation or 120 competition) may interfere with the paleoenvironmental signature (Belka and Wendt, 121 1992). A multivariate approach was developed to quantitatively compare the conodont 122 assemblages in the studied sections. In addition, paleotemperatures were reconstructed 123 using oxygen isotopes measured on conodont apatite.

124 A strength of this study is that the three proxies are derived from the same rock 125 samples taken at a comparable temporal resolution, allowing for detailed and 126 quantitative comparisons. The following questions are addressed: (1) Did 127 environmental changes affect similarly and at the same pace both areas, and if not, how 128 to interpret any discrepancies? (2) Did water depth and temperature covary, as 129 expected for eustatic trends during a global cooling culminating with the Devonian-130 Carboniferous boundary glaciation (Buggisch et al. 2008; Caputo et al., 2008; Isaacson et 131 al., 2008)? (3) Was the forcing of water depth changes recorded as expected on 132 conodont biofacies? In that context, did conodont biofacies rather react to local 133 deviations from, or to globally recorded paleoenvironmental trends? 134

135 2. Geological setting

136 During the Late Devonian, the Col des Tribes (CT; Montagne Noire/France; Girard 137 et al., 2014) and Buschteich (BU; Thuringia/Germany; Girard et al., 2017) sections were 138 located in subtropical latitudes on different microcontinents (Fig. 1). These 139 microcontinents progressively migrated towards the equator and Laurussia during this 140 period due to the closure of the Rheic Ocean (Franke et al., 2017). The absence of 141 provincialism in benthic faunas compared to Laurussian faunas suggests that the Rheic 142 Ocean was, at that time, already reduced (Feist and Becker, 1997; Mottequin et al., 143 2013). It has been proposed that the Saxo-Thuringia microcontinent, on which BU was 144 located, was situated in the middle of the sea between the remnant Rheic Ocean and the 145 Paleotethys (Franke et al., 2017) during the Late Frasnian (375 Ma). By the latest 146 Famennian (~360 Ma), this seaway was almost or completely closed, locating BU at the 147 margin of the remnant Rheic Ocean (Fig. 1). The Montagne Noire, including CT, was 148 located on the Armorica microcontinent which was presumably positioned further 149 towards the Paleotethys Ocean. Nevertheless, the precise location of these 150 microcontinents relative to Laurussia as well as their position relative to each other is 151 debated (e.g. Eckelmann et al. 2014; Franke et al. 2017).

152 Both sections expose Late Frasnian to Late Famennian deposits, although with a 153 gap during the earliest Famennian in BU. Their stratigraphical context has been formerly 154 described (Girard et al., 2014, 2017) using the zonation of Ziegler and Sandberg (1990); 155 and has been updated applying the zonation of Spalletta et al. (2017) in this study (Fig. 156 2). The CT section (Girard et al., 2014) is ca. 80 m thick. It consists of fine-grained 157 bioclastic limestones from the *Palmatolepis rhenana* to the *Pa. glabra pectinata* 158 conodont Zone, followed by typical reddish griottes from the *Pa. rhomboida* to the *Pa.* 159 marginifera marginifera Zone. Lime mudstones were deposited from the *Pa. marginifera* 160 utahensis to the Pa. rugosa trachytera Zone and are overlain by wackestones with an age from the *Polygnathus styriacus* to the middle of the *Bispathodus ultimus* Zone. The 161 162 Famennian carbonate deposits are overlain by the Hangenberg shales. Depositional 163 environments ranged from mid to outer ramp. The BU section is ca. 35 m thick and 164 consists of lime mudstones and fine-grained turbiditic wackestones from the Pa. 165 *rhenana* to the *Scaphignathus velifer velifer* Zone, followed by nodular limestones of the 166 *Pa. rugosa trachytera* to the middle of the *Bispathodus ultimus* Zone and the Hangenberg 167 shales. Depositional environments ranged from distal slope to outer ramp (Girard et al., 168 2017).

169

170 3. Materials

171 Sixty-four and forty samples were collected from the CT and BU sections, 172 respectively (Supplementary Table). Thin sections were used for microfacies analysis. 173 Conodonts were extracted by dissolving a fraction of the samples using 10% formic acid. 174 All conodonts were manually picked from the insoluble residues and determined at the 175 generic and species level. The taxonomic identification allowed establishing a detailed 176 biostratigraphic scheme. The abundance of conodonts is high to exceptionally high, with 177 about 600 platform elements per kg at CT and about 7000 platform elements per kg at 178 BU. Entire and broken platform elements representing at least half of an element were 179 counted per genus to characterize conodont biofacies in each sample (Sandberg, 1976). 180 A fraction of these conodonts was thereafter used for oxygen isotope analyses. All 181 approaches (microfacies, conodont biofacies, and oxygen isotope geochemistry) were 182 performed on the same rock sample.

183

184 **4. Methods**

185 *4.1. Age model*

186 The stratigraphy of Late Devonian deposits is mostly based on conodont 187 biostratigraphy. A revised global standard of the Famennian (Late Devonian) conodont 188 zonation has been recently published (Spalletta et al., 2017). Zonal boundaries and 189 duration are essentially identical to those of Ziegler and Sandberg (1990), which was 190 used in the Global Time Scale 2012 (Becker et al., 2012) to date in absolute ages some 191 zonal boundaries. In this study, the zonal boundaries dated in the Global Time Scale 192 2012 were used as anchor points to establish local linear regressions between absolute 193 age and depth along the sections, thus providing age estimates for each sampled level. 194 Anchor points are the basis of the following zones: *Palmatolepis triangularis, Pa. crepida*, 195 Pa. rhomboidea, Pa. marginifera marginifera, Pa. rugosa trachytera, Polygnathus 196 styriacus, Palmatolepis gracilis expansa (adapted to the zonation of Spalletta et al. 2017), and the base of the Early praesulcata sensu Ziegler and Sandberg (1990). 197

198

199 4.2. Sedimentary facies description

The description of the sedimentary facies in the Col des Tribes and Buschteich
sections has been published by Girard et al. (2014) and Girard et al. (2017), respectively.

The different facies were characterized by the sedimentological and biological features
from outcrops as well as thin sections, allowing an interpretation of the different
depositional settings. For each section, this led to an ordering ('score') of the different
samples along a theoretical proximal-distal gradient. In order to compare BU and CT, the
scoring of the sedimentary facies (later on in the text: 'facies') in the two outcrops have
been compiled into a single scheme.

208

209 *4.3. Oxygen isotope analyses*

Oxygen isotope ratios of conodont apatite can be used as a paleotemperature 210 211 proxy (Joachimski and Buggisch, 2002; Joachimski et al., 2009; Luz et al., 1984). Twenty-212 seven conodont samples from the Buschteich section and 26 conodont samples from the Col des Tribes section have been studied for oxygen isotopes. Chemical conversion of 213 214 apatite bound phosphate into trisilverphosphate (Ag_3PO_4) was performed according the 215 method described in Joachimski et al. (2009). Oxygen isotope analyses were performed 216 using a TC-EA (high-temperature conversion-elemental analyzer) coupled online to a 217 ThermoFinnigan Delta V Plus mass spectrometer. 0.2 to 0.3 mg Ag₃PO₄ was weighed into silver foil and transferred to the sample carousel of the TC-EA. At 1450 °C, the silver 218 219 phosphate is reduced and CO forms as the analyte gas (Vennemann et al., 2002). CO was 220 transferred in a helium stream through a gas chromatograph via a Conflo III interface to 221 the mass spectrometer. All values are reported in ‰ relative to V-SMOW. Samples as 222 well as standards were generally measured in triplicate. The measurements were 223 calibrated by performing a two-point calibration (Paul et al., 2007) using NBS 120c 224 $(\delta^{18}O = 21.7\%)$ and a commercial Ag3PO4 (9.9‰). A laboratory standard was used as a 225 control standard and processed together with the samples. All standards were 226 calibrated to TU1 (δ^{18} O = +21.11‰) and TU2 (+5.45‰; Vennemann et al., 2002). The 227 average oxygen isotope composition of the internationally distributed standard NBS 228 120c was measured as +21.67 \pm 0.09 (1 σ ; n= 5).

229

230 4.4. Conodont biofacies

Late Devonian conodont taxa were supposed to have different water depth
preferences (Klapper and Barrick, 1978; Seddon and Sweet, 1971). Hence, the
proportion of the different genera within a given assemblage was interpreted as a proxy
of water depth (Sandberg, 1976; Seddon and Sweet, 1971). Refined biofacies

235 interpretations based on conodont subgenera or even species have been proposed (e.g. 236 Lüddecke et al., 2017) but due to species evolution and replacement through time, this 237 approach appeared difficult to apply to the relatively long record considered in the 238 present study. During the late Frasnian to late Famennian, at least seven genera are 239 present and can provide information about depositional environments (e.g. Corradini, 240 2003; Morrow, 2000; Sandberg, 1976; Seddon and Sweet, 1971). The genera that have 241 been most clearly associated to water depth preferences are the following. (1) For deep 242 waters, *Palmatolepis* and *Bispathodus/Branmehla/Mehlina*. It should be noted that 243 whereas *Palmatolepis* is considered to be a specialist of offshore environments, 244 *Bispathodus* presents wider tolerance to water depth and/or proximity to the shore 245 (Ziegler and Sandberg 1984). (2) Polygnathus for intermediate water depth. (3) Icriodus, 246 Scaphignathus, and Alternognathus for shallow waters. Due to their low abundance and 247 similar environmental preferences, the two latter genera have been grouped for 248 biofacies representation. Hence, in this study, the following biofacies were recognized: 249 the palmatolepid biofacies, the palmatolepid-polygnathid biofacies, and the bispathodid-250 polygnathid biofacies.

251

252 *4.5. Data analysis and statistics*

253 The proportion of each genus was estimated in each sampled level based on 254 counting (Girard et al., 2014, 2017). The description of these proportions corresponds to 255 the conodont biofacies analysis itself. A principal component analysis (PCA on the 256 variance-covariance matrix) was performed on these percentages to summarize the 257 variation of all genera on few main axes. This analysis also provided a representation of 258 the records of CT and BU on the same synthetic axes, allowing a direct comparison of the 259 biofacies variations in the two outcrops. The contribution of each genus percentage to 260 the axes allowed their interpretation in relation to the biofacies. The PCA was performed using the R package ade4 (Dray and Dufour, 2007). The different proxies (microfacies, 261 262 oxygen isotope ratios and the first axis of the PCA on the conodont percentages) were 263 compared using linear regression analysis in CT and BU separately, and in the combined 264 dataset (CT+BU). To test for a secular climate evolution, the relationship between 265 oxygen isotope values and time was tested using linear regressions in CT, BU and 266 CT+BU. In addition, this relationship was also investigated using a linear model 267 including as terms the age of the levels, the section and the interaction between the two

268 former terms. If the interaction between two terms, here age and section, is significant, this means that the relationship of the dependent variable (here, δ^{18} O values) to age 269 270 have a different slope in the two sections. To test if δ^{18} O values were different in two 271 phases of the record, t-tests were also used. All these tests were performed under R (R Core Team, 2017). An analysis of variance (ANOVA) on a linear model combining 272 273 microfacies and oxygen isotopes as explanatory variables was used to assess their 274 relative influence on conodont assemblages, estimated by the scores along the first axis 275 of the PCA on conodont percentages. A type II ANOVA was used, because this method is 276 invariant to ordering of the model terms and is powerful even with unbalanced datasets. 277 This test was done using the R package ffmanova (Langsrud and Mevik, 2012).

278

279 **5. Results**

280 *5.1. Age model*

281 The absolute ages estimated in Becker et al. (2012) for some zonal boundaries 282 served us as anchor points. A correlation with sediment thickness allowed establishing an age model for each section (Fig. 2). The observed sediment thickness includes post-283 284 depositional processes such as compaction, erosion, and diagenesis, that may affect the 285 estimates of accumulation rates through time and between sections. With this limitation, 286 Famennian mean accumulation rates were low in CT (5 to 7 mm/kyr⁻¹) and extremely 287 low in BU (1 to 3 mm/kyr⁻¹). Two periods of more or less constant accumulation rates 288 can be identified in BU: one from the Pa. crepida Zone to the Sc. velifer velifer Zone, and a 289 second, with even lower rates, from the *Palmatolepis rugosa trachytera* Zone to the end 290 of the Famennian. In CT, these two intervals can also be recognized, with possibly a 291 temporary acceleration of deposition during the *Pa. marginifera marginifera* and 292 *marginifera utahensis* Zones. The ages estimated for each sample were thereafter used 293 to plot the variations of the conodont assemblages and of the environmental proxies. 294 This allowed a comparison of the timing of changes in both sections.

295

296 5.2. Sedimentary facies

The sedimentary facies of BU and CT have been compiled into a single scheme.
Five facies types have been distinguished based on microfacies and faunal content (Fig.
3). The interpolated scheme is summarized below and compared to the published facies
at CT (Girard et al., 2014) and BU (Girard et al., 2017). Details are provided in the Supp.

301 Table 1. Based on these facies characteristics, the temporal variation in the depositional 302 setting can be reconstructed. Note that all depositional environments are relatively 303 deep, and correspond to the deepest environments found on the shelf, and that the 304 terms 'shallow' and 'deep' are used in the context of relative shallowing or deepening. At 305 BU only minor variations can be observed (Fig. 4A). The depositional environment, 306 mostly corresponding to Facies 2, remained relatively deep throughout the record. 307 Intervals with the even deeper Facies 1 can be identified during the Late Frasnian, the 308 *Pa. crepida and termini* Zones, the *Pa. marginifera marginifera* Zone, the *Sc. velifer velifer* 309 Zone, and the top of *Bispathodus ultimus* Zone. The CT section shows evidence for more 310 important changes in water depth. A first shallowing episode occurred during the latest 311 Frasnian and earliest Famennian, followed by a second, shallower episode during the *Pa*. 312 gracilis gracilis and the Pa. marginifera marginifera Zones. From the top of the 313 *Pseudopolygnathus granulosus* Zone to the end of the Famennian, conditions were constantly shallower than during the two former episodes. These shallowing trends are 314 315 separated by two deepening episodes, from the Pa. minuta minuta to the Pa. rhomboidea 316 Zone and from the *Pa. marginifera marginifera* to the *Pseudopolygnathus granulosus* 317 Zone.

318

319 5.3. Oxygen isotopes

320 Oxygen isotope ratios measured on conodont apatite from CT are between +17.1 321 and +17.7‰ from the end Frasnian to the *Pa. crepida* zone (Fig. 4B). Values thereafter 322 more or less gradually increase to values around 18‰ in the Pa. marginifera utahensis 323 Zone. From the *Sc. velifer velifer* to the *Pa. gracilis expansa*, δ^{18} O increases to values 324 above +19‰. A slight decrease is observed to the end of the Famennian. Oxygen isotope 325 values of conodont apatite from BU are generally higher than values observed at CT. 326 δ^{18} O values range from +16.4 to +16.9 ‰ from the end Frasnian to the *Pa. crepida* zone. 327 From a minimum of +16.4 ‰ at the base of the *Pa. crepida* Zone, a trend to higher 328 values occurs up to the *Pa. marginifera marginifera* Zone, reaching δ^{18} O values of +17.8 329 $%_{0.0}$ A brief decrease marks the first part of the *Pa. marginifera utahensis* Zone, with δ^{18} O 330 values of around +16.7 %. Thereafter, up to the end of the Famennian, δ^{18} O values 331 remain close to +17.5 %.

- The offset in δ^{18} O between the two sections is relatively small (+0.5 to +1‰) from the *Pa. crepida* Zone to *Pa. marginifera utahensis* Zone, but increases after the *Sc. velifer velifer* Zone (+1 to +1.5 ‰). This difference in δ^{18} O translates into +6 to +6.5°C cooler temperatures in CT in case the offset is solely explained by temperature.
- 336

337 5.4. Conodont biofacies

338 The conodont biofacies follow overall comparable trends in both sections (Fig. 5; 339 Supp. Table 1), sharing a dominance of *Palmatolepis* for most of the time up to a 340 maximum at the base of the *Pa. marginifera marginifera* Zone (up to more than 95% of 341 the assemblage), followed by a progressive decrease towards the end Famennian. This 342 decrease of *Palmatolepis* was compensated almost exclusively by a rise of *Bispathodus* in 343 CT and by a rise of both *Polygnathus* and *Bispathodus* in BU. The Frasnian assemblages 344 were complemented by the occurrence of other genera such as *Polygnathus* and 345 Ancyrodella. The Pa. triangularis to Pa. minuta minuta Zones, which are missing in BU, 346 were marked by an increase in the abundance of *Icriodus* in CT. Another maximum in the 347 abundance of *Icriodus* in CT is recognized in the *Pa. glabra prima* Zone. Except for the *Pa.* 348 *crepida* Zone, *Icriodus* was rare in BU. In CT, a short-term rise of 349 Scaphignathus/Alternognathus occurred around the Ps. granulosus Zone. A similar but 350 more discrete rise is present at the base of the *Pa. rugosa trachytera* Zone in BU.

351

352 5.5. Multivariate analysis of the conodont taxa abundances

353 The principal component analysis performed on the proportions of the different 354 genera allowed summarizing the biofacies variations on one main axis (PC1) expressing 355 more than 75% of the total variance. The record of the two sections CT and BU can be 356 directly compared on these axes. The contribution of the variables (here, the 357 percentages of the different genera) to the axes (Fig. 6A) shows that positive values 358 along the first axis correspond to a high proportion of *Palmatolepis* whereas negative 359 values correspond to a high proportion of *Bispathodus*. Variations along the PC1 axis 360 thus correspond to the replacement of *Palmatolepis* by *Bispathodus*. The second axis represents only less than 20% of variance, and mostly corresponds to variations in the 361 362 proportion of *Polygnathus*. Other genera contribute very little to the two main axes, due 363 to their rare occurrence in the records.

364 Representing the different levels in the first principal plane of this PCA allows for a comparison of BU and CT conodont biofacies variations (Fig. 6B-I). Most of the time, 365 366 the range of values covered by samples from the two sections largely overlaps. The 367 oldest samples (mostly Frasnian) are characterized by a peculiar diagonal distribution 368 (Fig. 6B). Their shift in the PCA space compared to Famennian samples is due to the 369 occurrence of genera such as Ancyrodella that went extinct during the Frasnian -370 Famennian crisis. Early Famennian levels of both sections are tightly clustered, sharing 371 extreme positive values along the first axis, due to the overwhelming dominance of 372 Palmatolepis.

373 In CT, a shift towards negative PC1 values is launched between the *Pa*. 374 marginifera marginifera and Pa. marginifera utahensis Zones (Fig. 4C, 6E), 375 corresponding to the onset of the decrease in the abundance of *Palmatolepis* (Fig. 5). 376 This shift went on to reach extreme negative PC1 values as early as the *Po. styriacus* 377 Zone (Fig. 6G, H). This change started more or less at the same time at BU, but it did not 378 occur in a consistent manner for a while. Only towards the end of the studied interval, 379 during the *Bispathodus ultimus* Zone, PC1 values in BU reach a range similar to the one 380 observed in CT (Fig. 6I). This corresponded to the final decrease of *Palmatolepis* at BU, 381 close before its extinction near the Devonian-Carboniferous boundary (Fig. 5). The 382 consequence of this delay in the decrease of *Palmatolepis* at BU was a temporary offset 383 between the two records of conodont genera proportions, starting during the Ps. 384 granulosus Zone and persisting until the base of the *Bi. ultimus* Zone (Fig. 4C).

385

386 5.6. Comparison of paleoenvironmental proxies and conodont biofacies

As a first step, we compared the different proxies (Table 2). Facies, oxygen isotope ratios, and the first axis of the principal component analysis on the conodont percentages (later on mentioned as conodont PC1) are all significantly correlated when considering the total dataset (CT+BU). In contrast, none of the correlations is significant when considering BU. At CT, conodont PC1 is significantly correlated to facies and δ^{18} O, but the two latter variables are not correlated.

The variation in the oxygen isotope ratios shows a significant secular trend, the relationship of δ^{18} O and age being significant in the CT, BU and CT+BU datasets. In the linear model investigating the variation of δ^{18} O depending on age in the two sections, the interaction term between δ^{18} O and age is not significant. This means that 397 the slope of the regression is the same in the two sections. While the two sections 398 display a similar increase in δ^{18} O when considering the whole record, from the end 399 Frasnian to the Late Famennian, the records of CT and BU do not follow a similar pattern 400 after the *Pa. marginifera utahensis* Zone (Fig. 4B). The oxygen isotope ratios increase in 401 CT but remain stable in BU. To test for such a discrepancy between the records of the 402 two sections, we performed t-tests between oxygen isotope values of the period 403 preceding and following the apparent shift in CT. The difference in δ^{18} O is indeed 404 statistically significant in CT (t-test [from *Pa. rhomboidea to Sc. velifer velifer*, n =8] vs. 405 [from *Pa. rugosa trachytera* to *Bi. ultimus*, n = 7], P = 0.0026). In contrast, the δ^{18} O values 406 of the same periods do not differ in BU (t-test [n = 6 and 11], P = 0.3443).

407 Finally, to investigate whether δ^{18} O or facies better explains the variation of the 408 conodont genera, linear models with conodont PC1 as dependent variable, and δ^{18} O and 409 facies as independent factors were considered (Table 3). The interaction term between 410 both factors (δ^{18} O and facies) is weak (p = 0.0311 for CT+BU) or not significant (for CT 411 and BU separately). This term was therefore discarded from the models. Facies and δ^{18} O 412 are significant explanatory variables of conodont biofacies when considering CT and BU 413 together, and CT alone. Facies explains more than three times more variance than δ^{18} O 414 in both cases. None has significant effect in BU.

415

416 6. Discussion

417 Our detailed oxygen isotope records generally show an increase in δ^{18} O in both 418 sections from the end Frasnian to end Famennian, coherent with described global 419 cooling during this time interval (Joachimski et al., 2009). However, in details, the two 420 records show different temperature variations from the *Pa. rugosa trachytera* Zone to 421 end Famennian. While temperature remained more or less stable throughout the 422 Famennian in the BU section (Saxo-Thuringia), it decreased in the CT section (Montagne 423 Noire) towards *Sc. velifer velifer* Zone. This difference in δ^{18} O between CT and BU is 424 mirrored by different sea-level variations in CT and BU, as pointed out by facies 425 description. Given these differences between the paleoenvironmental settings of the two 426 areas, conodont biofacies delivered remarkably similar records, questioning the role of 427 the paleoenvironmental forcing on conodont assemblages.

428

429 6.1. Paleotemperature variations: a global trend mitigated by paleogeography?

430 A global temperature trend has been sketched for the Late Devonian (McGhee, 2013), based on variations in δ^{18} O of conodont apatite (Joachimski et al., 2009). This 431 432 composite record showed a rapid succession of cooling and warming pulses around the 433 Frasnian-Famennian boundary (Balter et al., 2008; Joachimski and Buggisch, 2002; 434 Huang et al. 2018). After a warm period during the *triangularis* Zone, a progressive long-435 term cooling was proposed for the rest of the Famennian (Joachimski et al., 2009), 436 culminating into a period with stable ice caps during the early Carboniferous (Buggisch 437 et al. 2008). As for some other oxygen isotope studies in the Paleozoic, our isotope 438 records are based on conodont apatite, thus tracing the environment where the 439 conodont lived. Furthermore, all analyses were performed on the same genus, 440 Palmatolepis, avoiding the problem that different oxygen isotope values in the two 441 sections may be due to analyses on genera with different habitat preferences. Our 442 results support a long-term cooling, since the two sections displayed a parallel increase 443 in the oxygen isotope ratio from the end Frasnian to end Famennian, although more 444 pronounced in CT than in BU. An offset, however, exists between the records of the two 445 sections, with BU constantly showing lower δ^{18} O values than CT. Based on the 446 paleogeographic reconstruction (Fig. 1), BU and CT were both in the subtropical zone. 447 The constant offset between the two records can thus hardly be explained by a 448 latitudinal difference. Possibly, CT being positioned further towards the Paleotethys 449 (Franke et al., 2017), it might have been more exposed to the colder water masses of the 450 open Paleotethys Ocean and Paleo-Adria epicontinental sea.

451 Beyond the cooling trend registered in both sections from the *Pa. crepida* to *Pa.* 452 marg. marginifera Zone, the oxygen isotope records from BU and CT show differing 453 trends after the *Pa. marginifera utahensis* Zone. This pattern is also seen in other 454 sections studied by Joachimski et al. (2009). For example, in the La Serre section 455 (Montagne Noire) an increase in δ^{18} O is reported between the *marginifera marginifera* 456 and Sc. velifer velifer Zones, similar and synchronous to the one documented in CT. In 457 contrast in the Kahlleite section (Saxo-Thuringian area) δ^{18} O is relatively stable as in BU (Fig. 4). The difference in the δ^{18} O records of the BU and CT sections after the *Pa*. 458 459 marginifera utahensis Zone is thus confirmed at the regional scale, suggesting that the 460 paleogeographic position of the two microcontinents may have controlled the 461 temperature changes.

462 Paleogeographic reconstructions suggest that Saxo-Thuringia was located close 463 to the first zone of closure of the Rheic Ocean (Franke et al., 2017). As the closure of the 464 Rheic Ocean progressed during the Famennian, the area might have been influenced by 465 a relative restriction of the water masses exchanges between the Rheic Ocean and the 466 Paleotethys Ocean. The upper water column temperatures might have been warmer 467 than in the open sea, as e.g. nowadays in the Caribbean Sea, the Persian Gulf, or the 468 eastern Mediterranean (see for instance Schlitzer, 2006; Schmidt et al., 2016), 469 dampening the effects of the global cooling, especially in a subtropical area. In contrast, 470 the CT section and more generally the Armorica area, being opened towards the 471 Paleotethys Ocean, would have been exposed to the Paleotethys water circulation and 472 global temperature trends, as established by Joachimski et al. (2009). This 473 interpretation is corroborated by the fact that Late Famennian δ^{18} O values recorded in 474 the Carnic Alps (Paleo-Adria, Fig. 1; Pa. gracilis expansa and Bi. ultimus Zones: ~18,3 ‰; 475 Kaiser et al., 2006, 2008), and hence also in an environment open towards the 476 Paleotethys (Paleo-Adria on Fig. 1), were closer to those recorded at CT than at BU. 477

478 6.2. Water depth variations, combination of eustatic trends and local tectonics

479 Sea-level variations correspond to a high-stand during the end of the Frasnian, 480 followed by a progressive sea-level fall during the Famennian (Haq and Schutter, 2008; 481 Johnson et al., 1985, 1996; Sandberg et al., 2002). These variations appear to have 482 occurred world-wide, thus pointing to eustatic trends (Johnson et al., 1985, 1996). In 483 this context, a decrease in water depth should coincide with increasing ice volume, a 484 glacio-eustatic sea-level fall and a temperature decrease. In the CT section, a regressive 485 trend and a cooling are indeed registered, but they do not occur in parallel with the 486 shallowing clearly postponing the shift towards colder temperature. Another 487 discrepancy with the expectation is that both the temperature and water depth decrease 488 do not seem to have occurred in a progressive manner, but rather abruptly. Possibly, 489 paleogeographic and/or tectonic events might have temporarily mitigated the 490 expression of the long-term trend in CT. Water depth variations in BU do not follow this 491 global trend. In BU, the depositional environment remained deep throughout the 492 Famennian, and tectonic activity has been invoked to explain this discrepancy (Girard et 493 al., 2017). The paleogeographic position of Saxo-Thuringia, close to Baltica and hence

- 494 one of the first microcontinent to collide with it, matches well with active tectonics495 causing a local departure from the eustatic trend.
- 496

497 6.3. Congruent variations of the conodont assemblages despite discrepant

498 paleoenvironmental settings

499 In contrast to the different patterns of temperature variation after the *Pa*. 500 *marginifera utahensis* Zone, and differences in water depth records in CT and BU, trends 501 in conodont biofacies are quite comparable. Both sections reflect a dominance of 502 *Palmatolepis* for most of the Famennian with a decline starting in the *Pa. marginifera* 503 *marginifera* Zone. If the difference between the environments at CT and BU had any 504 impact on the conodont assemblages, it was only minor and corresponded to a transient 505 offset between the two conodont records. However, conodont biofacies are advocated to 506 be mostly driven by water depth variations, due to the habitat preferences of the 507 different conodont genera (Sandberg, 1976; Seddon and Sweet, 1971). Initially, two 508 ecological models, i.e. depth stratification vs. lateral segregation, were proposed 509 (Klapper and Barrick, 1978; Seddon and Sweet, 1971). The depth-stratification model 510 implies that specific conodont taxa inhabited different depth zones within the water 511 column, whilst the lateral segregation model proposes that bottom-dwelling taxa were 512 dominantly controlled by habitat properties near the sediment-water interface. The 513 abundant occurrence of conodonts during anoxic events precludes a benthic or 514 nektobenthic lifestyle. During the Frasnian and the Famennian, genera supposed to have 515 "shallow preferences "(e.g. *Icriodus*) and "preferences for deep environments" (e.g. 516 *Palmatolepis*) have been shown to share similar oxygen isotope signatures, suggesting 517 that they were living in the same water-mass (Joachimski et al., 2009). This supports the 518 interpretation that all genera were at that time living close to the surface, but occupying 519 proximal or distal locations. The higher proportion of the offshore surface dweller genus 520 Palmatolepis in the sediments from BU than from CT is coherent with the more off-shore 521 depositional setting in BU. The decrease of the genus *Palmatolepis* after the *Pa*. 522 *marginifera marginifera* Zone is also coherent with the regressive trend characterizing 523 the Famennian. Possibly, before the *Sc. velifer velifer* Zone, water depth was constantly 524 deep enough to favor the dominance of this offshore surface dweller genus. However, if 525 a direct forcing of water depth on conodont distribution is assumed, conodont biofacies 526 at BU should have been relatively stable through time, and depart more clearly from the

527 trend observed at CT. This suggests that the response of conodont assemblages to water 528 depth was mitigated by other factors. Possibly, the eustatic regressive trend was 529 disadvantageous to the offshore surface dweller genus *Palmatolepis* at a worldwide 530 scale, triggering its global decline. Ultimately, it would have even declined in constantly 531 deep environments such as BU, although with a time lag suggesting that it temporarily 532 found there a refuge of favorable environments.

- 533
- 534 *6.4. Relationship between the different paleoenvironmental proxies*

535 The three paleoenvironmental proxies considered here (sedimentary facies, 536 oxygen isotopes, and conodont biofacies) are potentially interrelated: oxygen isotopes 537 are temperature proxies; facies traces water depth and distance to the shore, related to 538 temperature trends through eustatic variations; and conodont biofacies are interpreted 539 as related to water depth due to habitat preferences of the different conodont genera 540 along a proximal-distal gradient in the surface waters. No relationship between these 541 proxies is evident in BU, but this absence of a significant correlation is probably due to 542 the reduced range of variation in the oxygen isotope ratios and facies observed in this 543 section. Oxygen isotopes and facies are correlated when considering the total data set. 544 However, conodont PC1 displays a stronger relationship with oxygen isotopes on the 545 one hand, and with facies on the other hand, than oxygen isotopes with facies: the 546 percentage of variance explained is larger, leading to significant relationships in CT as 547 well (Table 2). Considering the percentage of variance explained, facies furthermore 548 appears as a better explanatory variable for conodont variations than δ^{18} O. The 549 sedimentary facies trace directly the depth of the depositional environment but the 550 relevance of this approach has been discussed due to the paucity of preserved biotas in 551 old sediments (e.g. see Flügel, 2004; Lüddecke et al., 2017). The correlation evidenced 552 between facies and conodont biofacies is nevertheless coherent with the interpretation 553 of conodont genera distribution being controlled by water depth, along a proximal-distal 554 gradient (Klapper and Barrick, 1978). The fact that conodont biofacies respond earlier 555 and more progressively to the global regressive trend may be due to the fact that CT and 556 BU being located in outer shelf environments, the decrease in water depth should be 557 important enough to cause a change in the facies.

558

559 6.5. Paleogeography and paleoenvironment: a complex interplay

560 Many studies focused on global environmental trends in the Devonian (e.g. Goddéris and Joachimski, 2004; Haq and Schutter, 2008; Miller et al., 2005; Sandberg et 561 562 al., 1988; Wilson and Norris, 2001), especially during the Late Devonian for which 563 environmental conditions have been suggested to be homogeneous within the 564 subtropical zone, and the marine faunas to be cosmopolitan. However, our results, based 565 on two detailed 13 My long records, indicated different paleoenvironmental changes in 566 BU and CT. After the end of the *Pa. marginifera utahensis* Zone, the cooling and the 567 regressive trend found little expression in BU compared to CT, but these differences are only weakly mirrored in the conodont assemblages. The differences in the temperature 568 569 records of CT and BU are not only observed in the two studied sections, but registered 570 as well in two other sections (Kahlleite and La Serre) from the Saxo-Thuringian and 571 Montagne Noire areas (Joachimski et al., 2009), respectively. We propose that the 572 deviation of the BU record from what we interpret as the global trend may be attributed to the paleogeography of the Saxo-Thuringian area, where a progressive restriction of 573 574 water-mass exchange possibly accompanied the closing of the seaway between the 575 remnant Rheic and Paleotethys oceans. This restricted paleogeography together with a 576 subtropical location might have favored the persistence of warm conditions in the sea-577 waters where conodonts lived despite the onset of global cooling. Such setting should 578 also have been prone to active tectonics overprinting the eustatic trend. Not mutually 579 exclusive, the closure of the Rheic Ocean itself might have contributed to the global 580 climate change, by interrupting the circum-equatorial circulation (see for instance for 581 the closure of the Panama Isthmus: Bartoli et al., 2005 and Haug and Tiedemann, 1998), 582 but this remains speculative and challenges further studies.

Increasing the geographic coverage of a multi-proxy approach, such as the one
outlined here, may thus provide relevant information to better constrain
paleogeographic reconstructions characterized by a complex distribution of land and
water masses, as e.g. in the Late Devonian. This key step will contribute to a better
understanding of the complex interplay between paleogeography, climate, and biotic
response and go beyond the tempting, but misleading, view of global trends affecting the
different regions in a relatively homogeneous manner.

590

591 **7. Conclusions**

592 This study presents a detailed comparison of two Famennian successions in the 593 Montagne Noire (France) and Saxo-Thuringia (Germany). During the Famennian, both 594 areas were located in the subtropical realm and were part of two microcontinents 595 bracketed between the remnant Rheic Ocean and Gondwana. Based on the same rock 596 samples, paleotemperatures were estimated using oxygen isotopes of conodont apatite, 597 depositional environments were assessed based on sedimentary facies, and the 598 response of conodont assemblages was evaluated using conodont biofacies. Applying a 599 principal component analysis to biofacies data provided a synthetic axis summarizing 600 the biofacies variations along the two sections. This allowed for a quantitative 601 comparison of the biofacies records with paleoenvironmental proxies.

602 During the Famennian, both the Montagne Noire and Saxo-Thuringia display a 603 parallel increase in the oxygen isotope ratios translating into long-term cooling. 604 However, during the Late Famennian, temperatures remained stable in Saxo-Thuringia, 605 leading to a temperature offset compared to the Montagne Noire record. The Late and 606 latest Famennian are also characterized by a regressive trend which was found to be 607 well expressed in the sedimentary facies in the Montagne Noire, but not in Saxo-608 Thuringia, where the depositional environment remained deep throughout. Despite 609 these environmental differences, conodont biofacies were rather comparable in the 610 Montagne Noire and Saxo-Thuringia. A temporary offset however suggested that 611 *Palmatolepis*, the typical off-shore surface dwelling taxon, was abundant for a longer 612 time period in the deep Saxo-Thuringian environment. The environmental differences 613 between the two areas are tentatively explained by their paleogeographic location. The 614 Saxo-Thuringian microplate is interpreted as located close to the point of first closure of 615 the Rheic Ocean and thus might have been influenced by active tectonism and a 616 restricted water mass exchange, blurring the impact of the long-term trends in this 617 setting.

618

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Figure captions

Figure 1. Paleogeographic reconstruction during the latest Famennian (simplified after Franke et al. 2017). BU: Buschteich; CT: Col des Tribes. Rectangles: investigated areas.

Figure 2. Age model allowing comparison of carbonate production rates between Buschteich (BU; red circles) and Col des Tribes (CT; green diamonds). Depth is given in meters. Conodont zonations according Ziegler and Sandberg (1990) on the right and Spalletta et al. (2017) on the left, absolute ages based on Becker et al. (2012). Each symbol corresponds to a sampled level. FRS: Frasnian. *Pa.*: *Palmatolepis*; *del.*: *delicatula*; *gl.*: *glabra*; *marg.*: *marginifera*; *gr.*: *gracilis*; *Sc.*: *Scaphignathus*; *v.*: *velifer*; *r.*: *rugosa*; *Ps.*: *Pseudopolygnathus*; *Bi.*: *Bispathodus*, *ac.*: *aculeatus.* In grey, zones which were not recognized in both sections.

Figure 3. Depositional model for the Col des Tribes (CT) and Buschteich (BU) sections during the Famennian.

Figure 4. Famennian environmental changes and conodont assemblage variations in the Buschteich section (BU; Saxo-Thuringia) and Col des Tribes section (CT; Montagne Noire). A: Facies distribution for CT and BU from the deepest (1) to the shallowest (5). B: δ^{18} O in CT and BU samples, compared with data of Joachimski et al. (2009) from Thuringia (Kahlleite, blue circles) and the Montagne Noire (La Serre; grey diamonds). C. Variations of conodont assemblage through time depicted as variations along the first axis of the PCA on conodont genera percentages. Green diamonds: CT; red circles: BU. Abbreviations: see Figure 2.

Figure 5. Conodont biofacies in CT and BU (after Girard et al. 2014; 2017). The proportions have been plotted again the age model. Note the absence of data (Gap) for the *Pa. linguiformis* to *Pa. crepida* zones at BU (white rectangle). *Scaphignathus and Alternognathus: Sc., Siphonodella: Si.* on the figure.

Figure 6. Principal component analysis of the variations in the percentages of the conodont genera in BU and CT. The first two axes of the PCA are represented (PC1 = 77.5%; PC2 = 18.3%). Upper left panel: contribution of the percentages of the different genera to the first two PC axes. Next panels: distribution of the different levels in the plane defined by the first two PC axes (PC1 = 77.5%; PC2 = 18.3%). The representation has been split by temporal zones (because of their limited sampling, *Pa. triangularis* to *Pa. gl. pectinata* Zones have been grouped). Each dot represents the assemblage in a level. CT: green diamonds, green diamonds with black outlines: levels from the *triangularis* and *minuta minuta* Zones; BU: red circles. *Pa.: Palmatolepis; gl.: glabra; gr.: gracilis; marg.: marginifera; Sc.: Scaphignathus; v.: velifer; r.: rugosa; Ps.: Pseudopolygnathus; Po.: Polygnathus; Bi.: Bispathodus.*













Table 1. Facies and environmental settings for the Col des Tribes and the Buschteich sections

FACIES	DIAGNOSTIC FEATURES	SEDIMENTARY FEATURES	STRATAL PATTERN	BIOCLASTS	DEPOSITIONAL SETTING	Girard et al. *2014 (CT) **2017 (BU)
Facies 1 : pelagic mudstone	Structureless lime mudstone with few bioclasts (2 – 10%)		Well stratified, dms thick	Pelagic ostracods and bivalves, goniatites, radiolarians, rare benthic ostracods, trilobites and crinoids	Outer ramp	Facies 1 at CT and BU
Facies 2: fine-grained turbidites	Laminated wackestone with pelagic fauna and scarce hardparts of benthic organisms	Mm to cm scale thick graded bedding, erosional surfaces at bottom	dm thick beds	Pelagic ostracods and bivalves, radiolarians, some transported benthic ostracods, blind trilobites brachiopods and crinoids	Distal turbidites in outer ramp interbedded within F1	Facies 2 and 3 at BU
Facies 3: pelagic wackestone	Structureless wackestone dominated by pelagic fauna and with 5 % benthic organisms	Pseunodular structure	cm to dm thick beds	Pelagic bivalves and ostracods, diversified cephalopods, radiolarians, crinoids, benthic ostracods and trilobites	Outer ramp, shallower than F1 and F2	Facies 2 at CT
Facies 4: cephalopod wackestone to floatstone (griottes)	Reddish nodular to wavy laminated wackestone to floatstone with abundant goniatites	cm sized lime nodules coated by argillaceous and iron hydroxydes, intraformational breccias, rotated geopetal structures	Cm to dm thick beds	Goniatites, pelagic ostracods and bivalves, trilobites, brachiopods, crinoids and foraminifers	Slope in the upper outer ramp	Facies 3 at CT
Facies 5: wackestone with diversified fauna	Structureless to pseudonodular well stratified wackestone with pelagic and benthic organisms	Pseudonodular structure with cm to dm thick beds	cm to dm thick beds	Pelagic ostracods and abundant goniatites, trilobites, crinoids, brachiopods, gastropods, bivalves, foraminifers	Mid ramp	Facies 4 at CT

			CT+BU			СТ			BU	
		n	R	р	n	R	р	n	R	р
δ180	Facies	41	0.5023	0.0008	22	0.4107	0.0576	19	0.3149	0.1891
Conodont PC1	$\delta^{18}0$	51	-0.5304	6.2e-5	25	-0.5665	0.0031	26	-0.3039	0.1312
Conodont PC1	Facies	78	-0.6576	6.1e-11	52	-0.7058	5.1e-09	26	0.1799	0.3791
$\delta^{18}0$	Age	51	-0.5150	0.0001	25	-0.7532	1.388e-05	26	-0.7018	6.455e-05

Table 2. Relationship between oxygen isotopes, microfacies, and conodont assemblages.

Correlations between two variables using the Pearson's product-moment correlation, coefficient of correlation (R) and probability (p) are given. Analyses were performed for CT and BU combined, and CT and BU alone. Significant correlations marked in bold (p < 0.05). Age is estimated based on the age model.

			CT+ BU			СТ			BU		
	Dependent variable	Independent variable	n	Pve	р	n	Pve	р	n	Pve	р
(1)	$\delta^{18}0$	Age	51	30.5%	1.83E-09						
		Section		47.0%	4.06E-12						
		Age * Section		0.4%	0.375						
(2)	Conodont	$\delta^{18}0$	41	6.1%	0.0311	22	9.0%	0.0316	19	11.2%	0.175
	PCI	Facies		22.3%	0.0001		33.6%	0.0003		0.5%	0.769

Table 3. Analyses of variance on oxygen isotopes and conodont proportions.

Two models were considered. (1) A model considered δ^{18} O as dependent variable, and age, section, and interaction (age * section) as effects. (2) A model considered PC1 based on conodont proportions in the assemblages as the dependent variable. The effects tested were δ^{18} O and facies score. Percentage of variance explained (pve) and probability (p) are given. Significant correlations marked in bold (p < 0.05).