Vertebrate diversity reveals perturbations in faunal communities prior to the Hangenberg event in the Montagne Noire (France)

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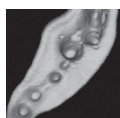
The Hangenberg crisis represents a mass extinction marked by a biodiversity turnover at the Devonian–Carboniferous boundary. However, the last million years before this dramatic event have been poorly investigated. Here we report new data on the size and abundances of vertebrate remains as well as carbon isotope data from the latest Famennian in the Montagne Noire (France). A significant decrease in fish abundance and a general reduction in the size of vertebrate remains are observed during a period of stable environment before the onset of the Hangenberg crisis. No perturbations are recorded by the carbon isotopes, supporting the stability of the environment. This significant change in the structuration of vertebrate communities prior to the Hangenberg crisis is not linked to any turnover in other faunal groups. That could be interpreted as changes in faunal repartition that predate mass extinctions. • Key words: Famennian, Hangenberg, vertebrate teeth, Montagne Noire, vertebrate diversity, carbon isotopes.

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From the first diversifications to modern times, life has been regularly subject to crises (Roberts & Mannion 2019). While some perturbations only poorly affected diversity, others had a deep impact and shaped the general organization of ecosystems (Sepkoski 1996). During the Phanerozoic, five mass extinction events have been recognized as the "Big Five" due to their impact on species communities, leading to extinction and later recovery (Walliser 1996, Bambach *et al.* 2004). The Late Devonian is known for one of the big five crises at the Frasnian–Famennian boundary (F–F) (Raup & Sepkoski 1982, McGhee 1996, Stigall 2012). 13 million years later, another major perturbation now recognized of the same "Big Five" magnitude occurred at the Devonian–Carboniferous (D–C) boundary (McGhee *et al.* 2013, Kaiser *et al.* 2015). This crisis affected faunal diversity on land and in the oceans and is known as the Hangenberg mass extinction event (Walliser 1984, Paproth *et al.* 1991, Feist *et al.* 2000). The Hangenberg crisis has been described as a multi-phased event that started at around 359.5 Ma (Becker *et al.* 2012), in the *Bispathodus ultimus* Zone (slightly below the former middle *praesulcata* Zone) and reached into the *Protognathodus kockeli* Zone (slightly above the former *praesulcata–sulcata* boundary) (Aretz 2020, Kaiser *et al.* 2020) (Fig. 1).

The 13 million years between the F–F and D–C crises seem to be punctuated by minor biological events and turnovers of various magnitude (Walliser 1996, Paschall *et al.* 2019, Girard *et al.* 2020), which may have been related to climate change (Kaiser *et al.* 2008, Isaacson *et al.* 2008), tectonic (Averbuch *et al.* 2005) and volcanic activities (Kravchinsky 2012) as well as the development of complex terrestrial plant ecosystems (Decombeix *et al.* 2011). At the same time eustatic sea level changes occurred as consequence of the onset of Gondwana glaciation (Isaacson *et al.* 2008).

Several bio-events are recognized before the last 1 my before the Hangenberg crisis. The last two bio-events of this interval are the Epinette (361.5 Ma) and Etroeungt (361 Ma) events (latest Famennian) which have been reported from different locations worldwide (Kaiser *et al.* 2008) (Fig. 1). These bio-events have been associated to positive carbon isotope excursions (Kaiser *et al.* 2008). Such positive carbon isotopes excursions are mostly correlated to eustatic sea level variations and for example weathering intensity and/or nutrient supply (Buggisch & Joachimski 2006).

The aim of the present contribution was to study changes in vertebrate biodiversity during the Hangenberg pre-crisis (360–359 Ma), in a time period between the
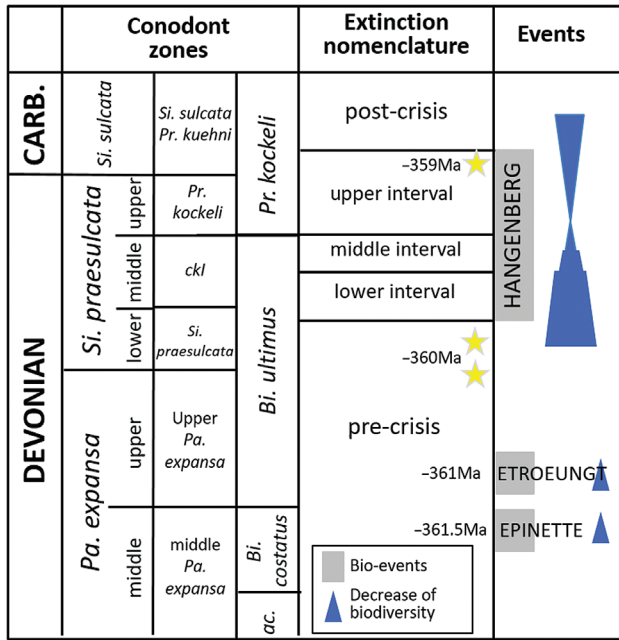
Figure 1. Temporal context of Late Famennian bio-events (after Aretz 2020). Conodont zones after Ziegler & Sandberg (1990) on the left, Kaiser *et al*. (2009) in the middle and Spalletta *et al*. (2017) on the right. Extinction nomenclature after Aretz (2020); location of the Epinette and Etroeungt events after Kaiser *et al*. (2008). Yellow stars: position of studied samples. Abbreviations: CARB. – Carboniferous; *Pa*. – *Palmatolepis*; *Si*. – *Siphonodella*; *Pr*. – *Protognathodus*; *Bi*. – *Bispathodus*; *ac*. – *aculeatus*; *ckl* – *costatus–kockeli* interregnum.

Etroeungt and Hangenberg events that corresponds to the Wocklum limestone (*sensu* Becker *et al*. 2016), which was previously interpreted as a relatively quiet interval (Aretz 2020) and to compare latest Famennian biodiversity with post Hangenberg biodiversity (359 Ma) (Fig. 1). While crises and post-crisis recovery periods have been widely studied, most investigations focused on the aspect of faunal renewal at the species level (Girard 1994, Ziegler & Lane 1987, Lelievre & Derycke 1998, Kulagina *et al*. 2021). This approach accentuates the catastrophic nature of the crises by highlighting extinctions followed by the appearance of new species in periods that are by definition exceptional.

Our study was conducted to study the dynamic of vertebrate communities around a mass extinction, with no restriction to the taxonomic species level, and under assumed stable environmental conditions.

To address this question, we focused on the Col des Tribes section in the Montagne Noire, considered as a reference section for the Famennian (Girard *et al*.

2014). The uppermost part of the Famennian and the period following the Hangenberg event were sampled for geochemistry and faunal content. Carbon isotopes have been used as they are generally good proxies for locating environmental perturbations (Joachimski *et al*. 2002, Goddéris & Joachimski 2004). For the diversity study, vertebrate remains were chosen, due to their good preservation potential as consequence of their hydroxy-apatite mineralogy. Chondrichthyan, actinopterigyan and conodont teeth remains were studied in detail as they are common and well-preserved in this section (Gauchey *et al*. 2014). The taxonomic diversity, abundance and size of the teeth were considered. Combining these three aspects, and geochemical data allow a multi-proxy study of the vertebrate fauna in their environment.

While conodonts have been the subject of numerous studies in the Montagne Noire area (*e.g.* Feist & Flajs 1987, Girard & Albarède 1996, Girard *et al*. 2014, Girard *et al*. 2020), other coeval marine vertebrate remains have not received as much attention (Derycke *et al*. 1995, Ginter 2000, Gauchey *et al*. 2014) especially around the D–C boundary. Here we consider the diversity of the contemporaneous vertebrate groups in order to 1) analyse vertebrate diversity in a close time span that encompass the Hangenberg event and 2) perform a geochemical study of carbon isotopes across the Devonian–Carboniferous boundary.

Geological setting

The studied material has been collected in the carbonate succession of the Col des Tribes section, situated on the eastern slope of the Mont Peyroux in the Montagne Noire area (South France), with special focus to some levels around the Hangenberg crisis (Fig. 2).

Three levels that encompass the Hangenberg crisis have been considered. Two samples from the middle part of the CT69-7 and the base of the CT70-A level were taken before the onset of the Hangenberg crisis (Fig. 2). One sample was collected at the base of the recovery phase of the Hangenberg crisis at level CT70-5 (equivalent of the DC2 to DC4 levels of Feist *et al*. 2020) (Fig. 2).

Fossil separation

Four-kilogram carbonate rocks were dissolved for sample CT69-7, five-kilogram for CT70-A and CT70-5.

Figure 2. Col des Tribes (CT) section (Montagne Noire, France). • A – simplified geological map of the Montagne Noire (modified from Aretz *et al*. 2016) and position of the Col des Tribes section. • B – stratigraphical log. • C – facies. • D – carbon isotopes (in ‰V-PDB) and proportion of fossil remains in each sampled level. Diameter of the circular diagram is proportional to the number of specimens per kg. • E – column plot of the fossil remain abundance (log) in function of the different sieves used for the decalcification.
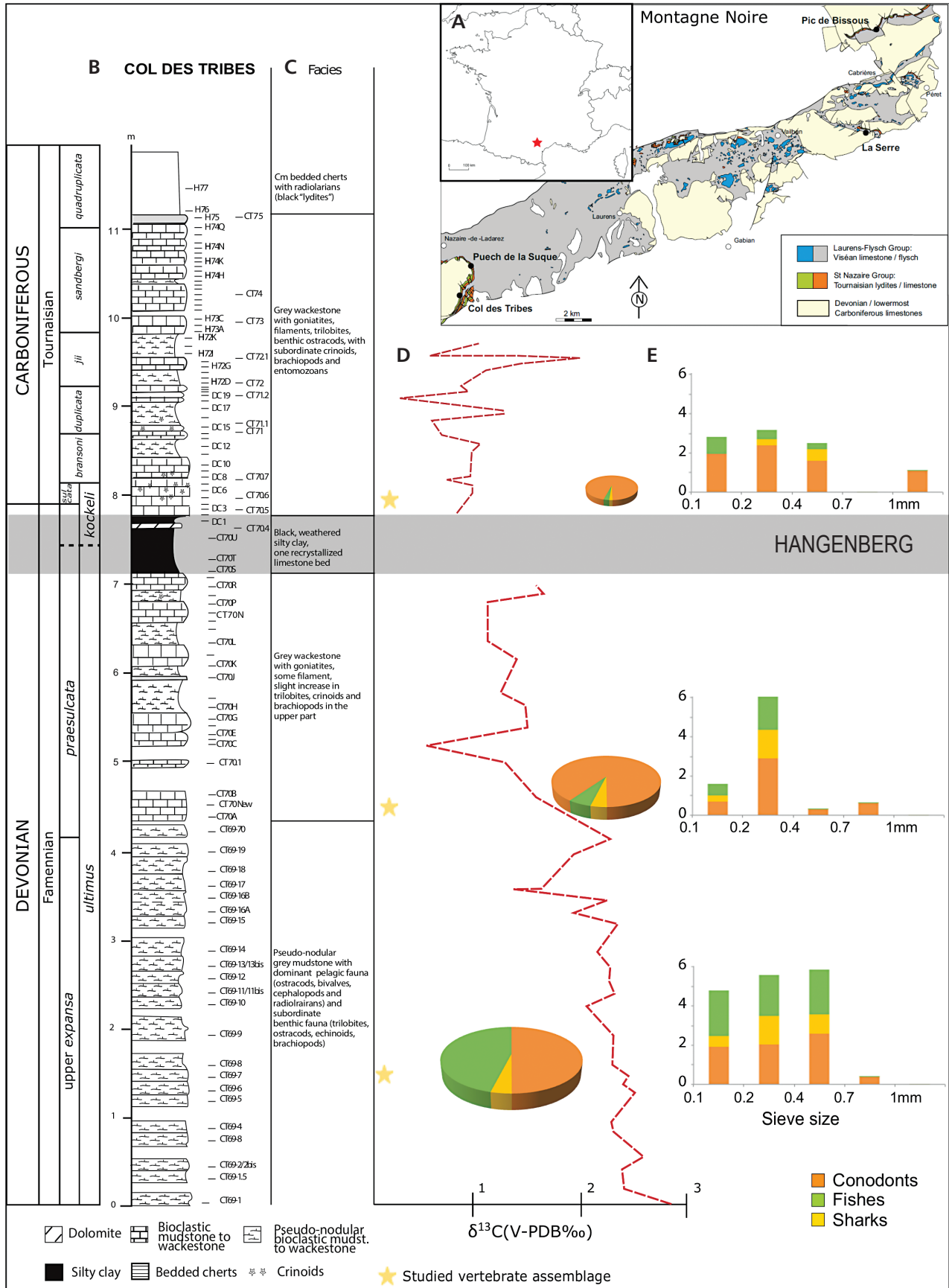
Table 1. Repartition of fossil remains per level regarding to their size (using sieves size as determination for size groups), sample numbers and fossil data for the Col des Tribes section (France). Weight: total dissolved samples in kilograms, abundance of the different groups per sieve size categories, total of the teeth remains per sample. Abbreviation: elem. – elements.

Sample	Fraction	>1 mm	1>>0.7 mm	0.7>>0.4 mm	0.4>>0.2 mm	0.2 >>0.1 mm	Total	Weight	W/kg
CT70-5	TOTAL	12	0	46	258	99	415	5	83
CT70-5	Conodonts P1 elem.	12	0	40	253	91	396		
CT70-5	Sharks	0	0	4	2	1	7		
CT70-5	Fishes	0	0	2	3	7	12		
CT70-A	TOTAL	0	5	3	770	11	789	5	158
CT70-A	Conodonts P1 elem.	0	4	2	692	5	703		
CT70-A	Sharks	0	1	1	31	2	35		
CT70-A	Fishes	0	0	0	47	4	51		
CT69-7	TOTAL	2	3	458	212	226	901	4	225
CT69-7	Conodonts P1 elem.	0	2	298	86	64	450		
CT69-7	Sharks	1	1	8	23	3	36		
CT69-7	Fishes	1	0	152	103	159	415		

Cycles of 24 hrs acid bath (10% formic acid or acetic acid) followed by 30 min washing of the residues were performed. The number of dissolution cycles varied for each sample due to varying clay contents stopping more or less the decalcification. We used 1, 0.7, 0.4, 0.2, and 0.1 mm sieves to separate the residues. Every fraction has been sorted separately in order to analyze more precisely the abundance of the teeth according to their size, and to estimate the proportion of respective size remains in each sample (Tab. 1).

As the quantity of dissolved sediments varied for each sample, we normalized the extracted tooth elements to 1 kg sediment in order to compare the abundance of specimens per sample. Following, we estimated the absolute abundance in percent among the different samples. All data are presented in the Table 2.

For illustration purposes, some specimens have been scanned using the SFR Biosciences (UMS3444/CNRS, US8/Inserm, ENS de Lyon, UCBL) AniRa-ImmOs facility. The surfaces were extracted slice-by-slice manually within AVIZO 9.0 (Visualization Sciences Group) and then oriented for illustration using the MorphoDig freeware (Lebrun 2018).

Specimens are hosted in the collections of the University of Montpellier (UM) France, and are listed in the caption of Figure 3.

Taxonomical determinations and occurrences are reported in Ginter (2000), Girard *et al.* (2014) and Feist *et al.* (2020).

Geochemical analyses

We performed carbon isotope analyses on the carbonates from the base of level CT69 (Late Famennian) to H73 (early Tournaisian, Fig. 2D) by sampling every carbonate

Table 2. Numerical data for the Col des Tribes section (Montagne Noire, France). Abundance of the different genera of chondrichthyes and conodonts P1 elements, and abundance of the bony fish teeth. Abbreviations: *Bi. – Bispathodus*; *Po. – Polygnathus*; *Pa. – Palmatolepis*; *Pr. – Protognathodus*; *Br. – Branmehla*; *Ja. – Jalodus*; *Ph. – Phoebodus*; *Si. – Siamodus*; *Th. – Thrinacodus*; *Pro. – Protacrodus*.

Level/Taxa	*Bi.*	*Po.*	*Pa.*	*Pr.*	*Br.*	*Ja.*	*Ph.*	*Si.*	*Th.*	*Pro.*	Sharks indet	Fishes	Total	Total/ kg
CT70-5	73	179	0	67	77	0	0	0	1	2	5	12	416	83
CT 70-A	355	197	120	0	31	23	3	3	0	0	6	51	789	158
CT69-7	183	125	60	0	82	21	0	6	0	0	9	415	901	225

Table 3. Stable isotope data (δ^{13}C) of the Col des Tribes section (France). Values in italics indicate that the samples were recrystallized and not included in the analysis due to their negative values.

Date	Strati	δ^{13}C ‰V-PDB	Date	Strati	δ^{13}C ‰V-PDB
03/23/17	CT68-8	2.89	06/16/14	CT 70j	1.38
06/23/20	CT 69-1	2.40	*06/18/14*	*CT 70K*	*−0.20*
06/23/20	CT 69-1.5	2.41	06/19/14	CT 70.2	1.08
06/23/20	CT 69-2	2.59	06/18/14	CT 70L	1.04
06/23/20	CT 69-2bis	2.62	06/19/14	CT 70L	1.14
06/23/20	CT 69-3	2.31	06/16/14	CT 70M	1.66
06/23/20	CT 69-4	2.29	06/19/14	CT 70N	1.54
06/23/20	CT 69-5	2.51	*06/18/14*	*CT 70P*	*−0.70*
06/23/20	CT 69-6	2.40	*06/19/14*	*CT 70Q*	*−0.82*
06/23/20	CT 69-7	2.45	*06/18/14*	*CT 70.R*	*−0.55*
06/23/20	CT 68-8	2.30	*06/18/14*	*DC 2*	*−2.17*
06/23/20	CT 69-9	2.34	06/19/14	DC 3	0.81
06/23/20	CT 69-10	2.05	*06/18/14*	*DC 4*	*−0.36*
06/23/20	CT 69-11	2.45	06/16/14	DC 6	0.96
06/23/20	CT 69-11bis	2.25	06/19/14	DC-7	0.95
06/23/20	CT 69-12	2.27	06/18/14	DC 8	0.69
06/23/20	CT 69-13	2.26	06/19/14	DC-9	0.92
06/23/20	CT 69-13bis	2.34	*06/18/14*	*DC 10*	*−0.07*
06/23/20	CT 69-14	2.13	*06/16/14*	*DC-11*	*−0.65*
06/23/20	CT 69-15	2.36	06/16/14	DC-13	0.95
06/23/20	CT 69-16a	1.91	06/19/14	DC-14	1.03
06/23/20	CT 69-16b	2.28	06/19/14	DC 15	0.66
06/23/20	CT 69-17	1.32	*06/16/14*	*DC-16*	*−1.12*
06/23/20	CT 69-18	1.73	06/16/14	DC 17	0.56
06/23/20	CT 69-19	1.89	06/19/14	DC-18	1.25
06/23/20	CT 69-70	2.27	06/18/14	DC-19	1.24
06/23/20	CT 70-1inf	1.90	06/19/14	H 72A	1.11
06/23/20	CT 70-1sup	1.41	06/16/14	H 72B	1.13
06/19/14	CT 70-1	1.26	06/19/14	H 72C	0.99
06/19/14	CT 70A	2.04	06/19/14	H 72D	0.75
06/16/14	CT 70b	2.12	06/16/14	H 72E	0.24
06/19/14	CT 70B	1.20	06/19/14	H 72F	0.68
06/18/14	CT 70-C	0.44	06/18/14	H 72G	0.91
06/19/14	CT 70D	0.86	06/19/14	H 72H	0.81
06/16/14	CT 70E	1.49	06/16/14	H 72K	1.10
06/16/14	*CT 70-F*	*−0.07*	06/19/14	H 73A	1.43
06/19/14	CT 70G	1.46	06/19/14	H 73B	2.01
06/19/14	CT 70H	1.22	06/16/14	H 73C	0.52

bed to obtain the finest possible resolution. Twenty-five samples were collected from CT69, while two samples were collected at the base of CT70. The new data are combined with unpublished analyses on samples from beds CT70 and CT71 performed in 2014. We collected carbonate powders using a microdrill.

Carbonate powders were reacted with 100% phosphoric acid at 70°C using a Gasbench II connected to a ThermoFisher Delta V Plus mass spectrometer at the University of Erlangen-Nuremberg/Germany. All values are reported in per mil relative to V-PDB. Reproducibility and accuracy were monitored by replicate analysis of laboratory standards calibrated by assigning $\delta^{13}C$ values of +1.95‰ to NBS19 and −46.6‰ to LSVEC. Reproducibility for $\delta^{13}C$ was ±0.05 (1 std. dev.). Carbon isotope values are presented in Table 3.

Results

In the three studied levels (CT69-7, CT70-A, CT70-5), hundreds of fossils remains mostly composed of conodonts P1 elements but also bony fish teeth (thereafter called fish) and less abundant shark teeth have been found. Representative specimens are shown in Figure 3. Some undissolved foraminifera, and rare crustaceans and scales have also been recovered from these levels.

The analysis of the conodont, fish and shark remains from the three levels permits to document heterogeneity between and among the levels concerning specimen size, abundance and diversity (Tabs 1, 2; Figs 2, 3).

Relative richness

In total 225 specimens (conodonts, fish and sharks) per kilogram were recovered from sample CT69-7, 158 specimens/kg in CT70-A, and 83 specimens/kg in CT70-5 (Fig. 2D, Tab. 2).

Pre-Hangenberg levels (CT69-7 versus CT70-A). – The CT69-7 level displays a comparable abundance of fish teeth and conodonts (46.1% fish teeth, 49.9% conodonts, 4% shark teeth) while CT70-A displays a drastic loss in fish teeth but higher relative abundance of conodonts (6.5% fish teeth, 89.1% conodonts, 4.4% shark teeth) (Tabs 1, 2; Fig. 3).

The difference is even more significant when richness is expressed in number of specimens per kg. The number of specimens per kg decrease from: fish = 104, conodont = 112 and shark = 9 in CT69-7 to fish = 12, conodont = 165, shark = 8 in CT70-A, highlighting ten times less fishes per kg in CT70-A than in CT69-7 and an increase in conodonts per kg.

Relative abundance of conodonts doubles between the CT69-7 sample and the CT70-A sample but the proportion of each genus remains the same in both levels (~15% of *Palmatolepis*, ~45% of *Bispathodus*, ~28% of *Polygnathus*, ~12% of *Branmehla* and *Mehlina*). Shark tooth relative abundance does not vary between CT69-7 and CT70-A, and remains low (~4 to 4.4%).

Post Hangenberg (CT70-5). – While the levels below the Hangenberg crises are fossil-rich, fossils in the post-Hangenberg deposits are very scarce and often damaged (Fig. 3). In the CT70-5 level, remains are 95% conodonts, 2% sharks and 3% fishes corresponding to 2.5 fish, 79 conodont and 1.5 shark remains per kg. This shows that despite the number of specimens decreased during the Hangenberg crisis, a similar distribution is observed compared to the pre-Hangenberg level CT70-A.

Vertebrate diversity

Even if they are the most abundant remains, conodonts appear to be represented by nearly as many genera as sharks. Seven conodont genera (*Bispathodus*, *Polygnathus*, *Palmatolepis*, *Protognathodus*, *Branmehla*, *Mehlina* and *Pseudopolygnathus*) and five genera of shark (*Siamodus*, *Jalodus*, *Protracrodus*, *Thrinacodus*, *Phoebodus)* are reported from the three levels. Fish teeth are represented by short to elongated cone-like remains (Fig. 3). Due to the poorly diagnosic features of these conic teeth, they can be determined neither at a species level nor at a generic level and remain in open nomenclature (Gauchey *et al.* 2014). Fishes are also represented by some scales, that likely belong to paleoniscoids and acanthods (according to Lelievre & Derycke 1998).

Pre-Hangenberg assemblages (CT69-7 and CT70-A). – The conodont assemblages from the pre-Hangenberg levels are dominated by the abundance of *Polygnathus* (some scarce representatives of *Pseudopolygnathus* are also reported) and the complex of genera without platform composed by *Bispathodus, Branmehla* and *Mehlina*. Regarding the sharks, Famennian chondrichthyes remains in CT69-7 and CT70-A are dominated by the assemblage of *Jalodus* and *Siamodus* but also present are some representatives of the genus *Phoebodus*. No changes are reported in fish morphologies between these two levels.

Post-Hangenberg assemblages (CT70-5). – The conodont assemblage in sample CT70-5 is marked by the disappearance of *Palmatolepis* and its replacement by *Protognathodus*, which has a relative abundance at this level close to the one previously observed for the *Palmato-*
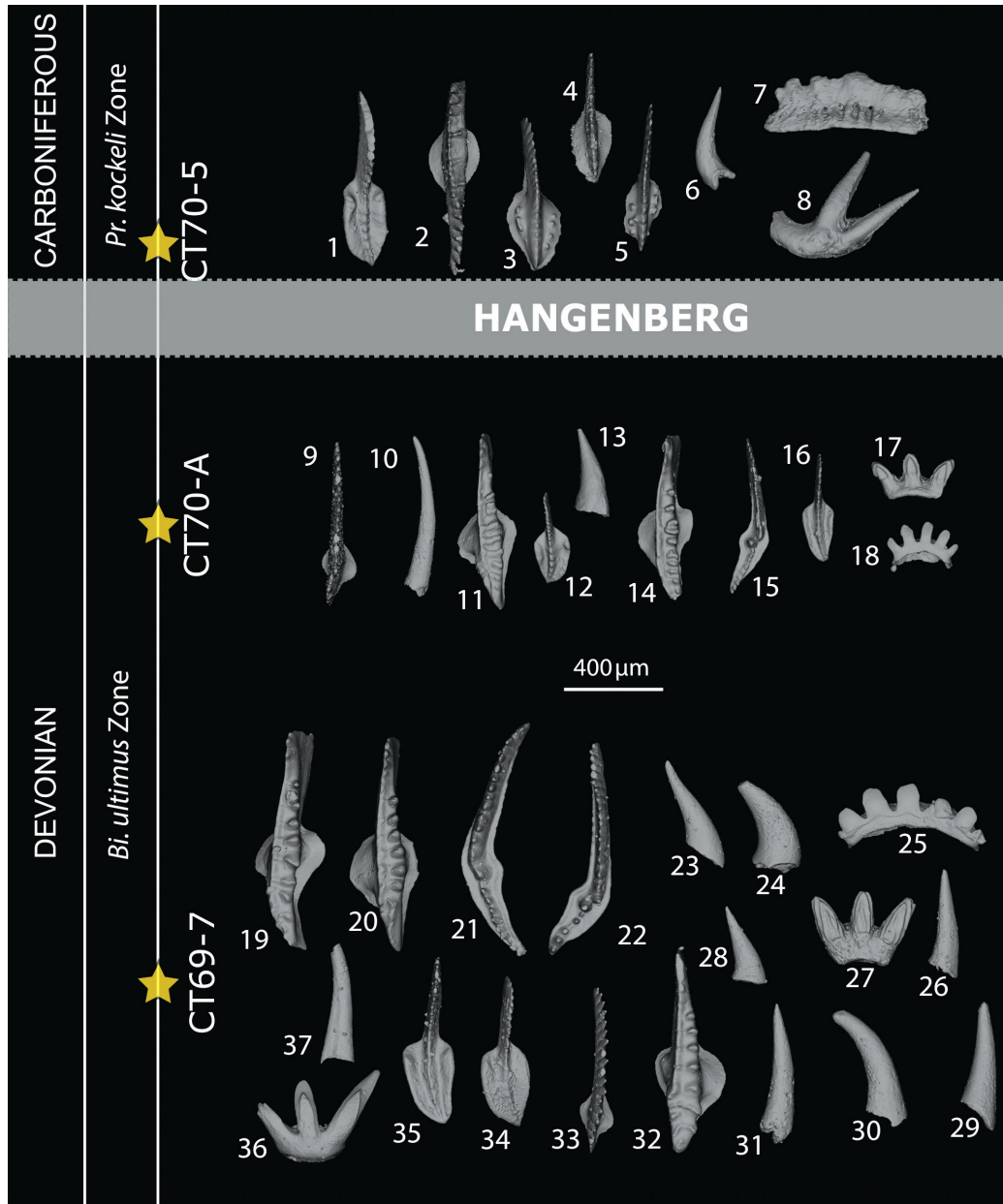
Figure 3. Some representative teeth remains of conodonts, chondrichthyes and actinopterygian fishes illustrating their abundance and diversity in the three studied samples of the Col des Tribes section (France). • 1–8 – sample CT70-5; 1 – *Polygnathus communis dentatus* Druce 1969 (UM CTB 041); 2 – *Bispathodus aculeatus aculeatus* (Branson & Mehl 1934a) (UM CTB 042); 3 – *Protognathodus kockeli* (Bischoff 1957) (UM CTB 043); 4 – *Bispathodus stabilis* (Branson & Mehl 1934a) (UM CTB 044); 5 – *Protognathodus kockeli* (Bischoff 1957) (UM CTB 045); 6 – Actinopterygii gen. et sp. indet. (UM CTB 046); 7 – Protacrodonte indet. (UM CTB 047); 8 – *Thrinacodus ferox* (Turner 1982) (UM CTB 048). • 9–18 – sample CT70-A; 9 – *Branmehla inornata* (Branson & Mehl 1934a) (UM CTB 049); 10 – Actinopterygii gen. et sp. indet. (UM CTB 050); 11 – *Bispathodus ultimus* (Bischoff 1957) (UM CTB 051); 12 – *Polygnathus communis dentatus* Druce 1969 (UM CTB 052); 13 – Actinopterygii gen. et sp. indet. (UM CTB 053); 14 – *Bispathodus spinulicostatus* (Branson 1934) (UM CTB 054); 15 – *Palmatolepis gracilis gracilis* Branson & Mehl 1934a (UM CTB 055); 16 – *Polygnathus communis communis* Branson & Mehl 1934b (UM CTB 056); 17 – *Jalodus australiensis* Long (1990) (UM CTB 057); 18 – *Siamodus janvieri* Long (1990) (UM CTB 058). • 19–37 – sample CT69-7; 19 – *Bispathodus costatus* (Branson 1934) (UM CTB 059); 20 – *Bispathodus costatus* (Branson 1934) (UM CTB 060); 21 – *Palmatolepis gracilis gracilis* Branson & Mehl 1934a (UM CTB 061); 22 – *Palmatolepis gracilis gracilis* Branson & Mehl 1934a (UM CTB 062); 23 – Actinopterygii gen. et sp. indet. (UM CTB 063); 24 – Actinopterygii gen. et sp. indet. (UM CTB 064); 25 – *Siamodus janvieri* Long (1990) (UM CTB 065); 26 – Actinopterygii gen. et sp. indet. (UM CTB 066); 27 – *Jalodus australiensis* Long (1990) (UM CTB 067); 28 – Actinopterygii gen. et sp. indet. (UM CTB 068); 29 – Actinopterygii gen. et sp. indet. (UM CTB 069); 30 – Actinopterygii gen. et sp. indet. (UM CTB 070); 31 – Actinopterygii gen. et sp. indet. (UM CTB 071); 32 – *Branmehla inornata* (Branson & Mehl 1934a) (UM CTB 072); 33 – *Bispathodus costatus* (Branson 1934) (UM CTB 073); 34 – *Polygnathus communis communis* Branson & Mehl 1934b (UM CTB 074); 35 – *Polygnathus communis communis* Branson & Mehl 1934b (UM CTB 075); 36 – *Jalodus australiensis* Long (1990) (UM CTB 076); 37 – Actinopterygii gen. et sp. indet. (UM CTB 077).

lepis. Nevertheless, the *Bispathodus*/*Branmehla*/*Mehlina* complex shows a minor relative abundance compensated by an increase in *Polygnathus* remains. Protacrodont sharks and the only specimen of *Thrinacodus* only occur in the post Hangenberg CT70-5 level replacing the previously dominant assemblage of *Jalodus* and *Siamodus*. Fish remains stay in open nomenclature because isolated teeth are poorly diagnostic and could neither be used to determine specimens at genus level nor to estimate changes in fish communities through time.

Specimen size

Pre-Hangenberg levels (CT69-7 and CT70-A). – For all three groups, a general decrease in specimen size is observed between CT69-7 and CT70-A (Fig. 4). At the CT69-7 level, most of the shark material has been sorted from the 0.2 mm sieve while conodonts are most commonly found in the 0.4 mm sieve. Fishes are well represented in all fractions. Concerning level CT70-A, nearly all shark and fish teeth as well as conodonts P1 have been collected in the 0.2 mm sieve. For both levels, few elements have been found in the largest fractions (>0.7 mm) (Tab. 1, Fig. 2E). As the size of teeth seems to decrease in each group with no change in taxonomic diversity and as specimens do not present morphological characteristic of juveniles, we suggest that the decrease of teeth size testifies a decrease in body size.

Post-Hangenberg (CT70-5). – At the CT70-5 level, all specimens have been found in fractions <0.7 mm. Conodonts are almost equally represented in the 0.4, 0.2 and 0.1 mm fractions. Shark and fish teeth are very scarce at this level. However, sharks seem to be more present in the 0.4 mm fraction, with some representatives in the 0.2 and 0.1 mm fractions. For fishes, most of the fish teeth have been found in the smallest fraction (0.1 mm).

Carbon isotope analyses

Twenty seven samples from the base of CT69 to the top of the CT70 level have been analyzed for carbon isotopes. The first carbonate beds of CT70 have been sampled twice with $\delta^{13}C$ showing consistent values. Some low $\delta^{13}C$ values measured in 2014 (in italics, Tab. 3) have not been considered for reconstructing the general curve as these values are interpreted as diagenetically altered. The values from the former *expansa* to *praesulcata* conodont zones (*ultimus* Zone) show general decrease in $\delta^{13}C$ from values between 2 to 3‰ in the *Bi. ultimus* (upper *expansa)* Zone to values around 1‰ above the Hangenberg crisis.

Discussion

What conodonts, sharks and fishes can tell us when considered together?

The Hangenberg crisis is defined by a global faunal turnover in vertebrate communities, exhibiting more extinctions than diversification of several taxa sometimes coupled with a strong Lilliput effect (Sallan & Galimberti 2015). Studies on diversity in response to biological events are generally focusing on the event interval and concentrating on one taxonomic group, which does not allow to identify possible ecosystem reorganization. Our results cover the last million year preceding the Hangenberg crisis with the fauna already experiencing perturbations that induced restructuration at different levels of abundance and size (Fig. 2).

Hangenberg pre-crisis (CT69-7 to CT70-A)

The Devonian was a period of diversification including the rise of numerous vertebrates as bony fishes, cartilaginous fishes (sharks), conodonts and tetrapods (Sallan & Coates 2010). At the end of the Devonian, the time interval after the Epinette/Etroeungt to Hangenberg event has mostly been considered as a relatively quiet period (Fig. 1). Studies by Girard *et al.* (2014) and Aretz (2020) indicated relative stability in extinction rates of marine organisms, and carbon isotope curves published by Buggisch & Joachimski (2006) and Matyja *et al.* (2021) indicate no major perturbations in the global carbon cycle.

In the Col des Tribes section, the gradual and small decrease in $\delta^{13}C$ seems not to be related to any environmental perturbations contrary to the former Etroeungt/ Epinette event (Kaiser *et al.* 2008),which is supported by the carbonate facies of the three studied levels that seem not to vary representing of a stable outer ramp environment (Feist *et al.* 2020).

However, our results indicate some unexpected changes in the structure of vertebrate communities between two successive latest Famennian vertebrate assemblages, 1 my before the Hangenberg event. These differences are marked both by changes in assemblage composition (diversity and abundance) and size of the teeth remains (Figs 3, 4). Furthermore, considering that depositional environments were below or close to storm wave base throughout the studied time interval (Girard *et al.* 2014), fluctuations in sea level and depositional environment could contribute to the observed changes in the vertebrate community (Fig. 2). However, neither changes in sea level (Girard *et al.* 2014) nor major sedimentological changes (Feist *et al.* 2020) were recorded in the Col des Tribes section. The changes in the assemblage composition and the size of the remains that characterize the uppermost
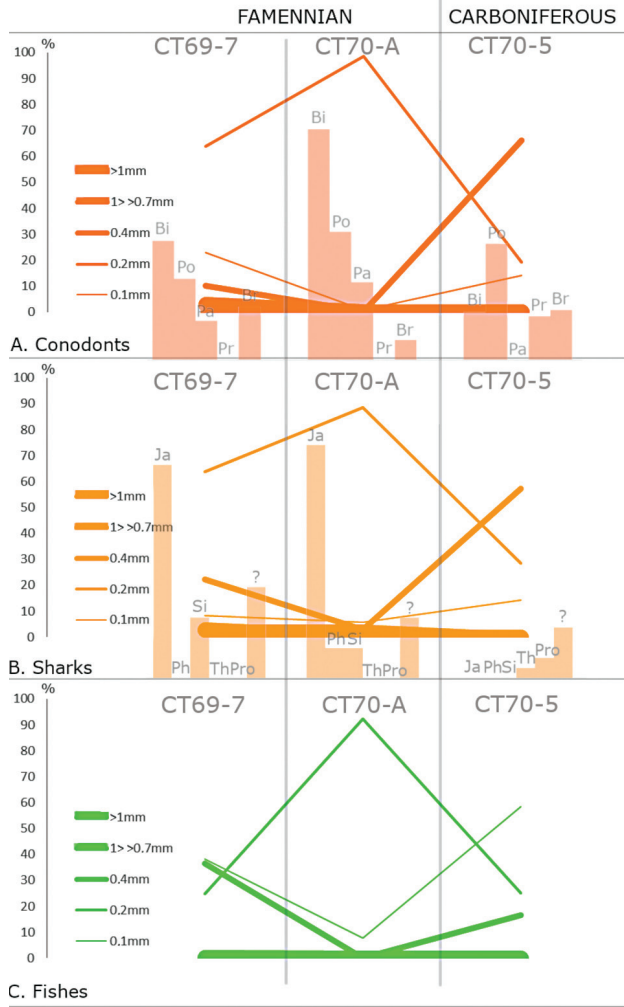
Figure 4. Abundance of fossils remains in our three temporal levels regarding to their size. • A – conodonts. Abbreviations: Bi – *Bispathodus*; Po – *Polygnathus*; Pa – *Palmatolepis*; Br – *Branmehla/Mehlina*; Pr – *Protognathodus*. • B – sharks. Abbreviations: Ja – *Jalodus*; Si – *Siamodus*; ? – sharks indet; Ph – *Phoebodus*; Th – *Thrinacodus*; Pro – Protacrodont indet. • C – fishes. In transparency in A and B, abundancies of fossil genera in the three levels (Tabs 1, 2).

and sharks from around the Hangenberg levels (Gauchey *et al.* 2014) reveal comparable abundances. Moreover, Gauchey *et al.* (2014) as well as this study document an obvious decrease in fish abundance remains through the *Bi. ultimus* Zone (between the former *expansa* and *praesulcata* zones) (Fig. 5). This suggests that marine ecosystems were affected differently during this so-called "relatively quiet period" compared to the terminal Hangenberg extinction, inducing changes in repartition of vertebrate groups in the ecosystem rather than a faunal turnover, since these time levels are not marked by any extinction of conodonts (Spalletta *et al.* 2017) and sharks (Ginter 2000). Just before the Hangenberg crisis (between CT69-7 and CT70-A), changes in size of teeth between CT69-7 and CT70-A (Fig. 2), considered here as change in body size of the teeth bearers (Luer *et al.* 1990, Purnell 1994, Gabbott *et al.* 1995, Chavez *et al.* 2012), coupled with
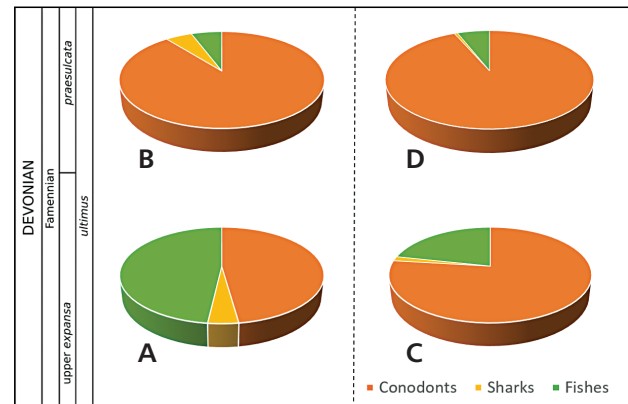

Figure 5. Comparison of the abundance of marine vertebrate remains in the Col des Tribes section. A, B – this paper; C, D – data from the literature from Gauchey *et al.* (2014) and Girard *et al.* (2014).

part of the pre-Hangenberg Famennian cannot be related to a faunal turnover, because no major species replacement was observed, neither for conodonts (Girard *et al.* 2014) nor for sharks (Gauchey *et al.* 2014; this study). Conodonts and shark assemblages from the pre-Hangenberg levels (CT69-7 and CT70-A) are composed of the same genera which seem not to present variations in terms of relative proportions. The decrease in the abundance of fish remains between CT69-7 and CT70-A is compensated by an increase in conodont abundance (Fig. 4). These observations are supported by the analysis of raw data extracted from the literature for conodonts (Girard *et al.* 2014) and fishes and sharks (Gauchey *et al.* 2014) (Fig. 5). In addition to results from this study, fishes

changes in the repartition of the vertebrate assemblages are probably underlining the relationship between these marine groups. The evolution of the abundance and size of these groups could be explained by natural competition among them, all living in the same ecological niche (Bengtsson 1989). A strong pressure on feeding resources could have favored opportunistic feeders. In the CT69-7 level, where conodonts and fishes are equally represented, we observe a wide size range for fish teeth that could allow predate a wide range of prey. In the CT70-A level, only small sized fish and conodont remains are observed, the latter dominating in terms of abundance. Coupled with a loss in abundance of fishes, this could be interpreted as a change in the ecological/trophic niche occupied by fishes. At the same time, conodonts also show a decrease in size but this decrease is correlated with an increase in abundance. Both phenomena could be explained by competition between these two groups.

Numerous studies present fishes as conodont predators (*e.g.* Choo *et al*. 2009, Zaton *et al*. 2017). Considering changes in resource availability, we suggest a nonlinear trophic chain where conodonts could be as well prey and competitor for fish communities. The notable loss of fishes could be explained by the fact that they did not succeed to predate conodonts in the studied levels. This could suggest that conodont animals were highly competitive marine organisms and should be considered as an opportunistic group, *i.e.* a group specialized in invading newly vacated habitats where there was little competition from other groups or where other groups were unable to establish (Rodland & Bottjer 2001).

This could explain the success of conodonts in invading all epicontinental Devonian seas (Klapper & Johnson 1980). On the other hand, fishes could have been more impacted by changes in the available prey, indicating that they were more specialized feeders. Independently, fluctuations in vertebrate size have been tentatively correlated to changes in temperature (Ray 1960, Pincheira-Donoso *et al*. 2008), the decrease in the size of vertebrates with increasing temperature described by Bergmann's rule. However, palaeoclimatological studies of the Late Devonian suggested global cooling just before the Hangenberg crisis (Buggisch *et al*. 2008, Issacson *et al*. 2008, Kaiser *et al*. 2008, Joachimski *et al*. 2009, Zhang *et al*. 2021). As studied levels cover a short period (hundreds of thousands of years), we cannot exclude a local increase in temperature, as suggested by the data published by Girard *et al*. (2020) for the Col des Tribes section, but without detailed temperature analyses in this area, further interpretations of the relationship between size and temperature variations are not possible.

The Lilliput effect has also been described, introducing the fact of a strong decrease in size after a crisis period (Harries & Knorr 2009, Song *et al*. 2011). We observe that when conodonts became the dominant group of the marine vertebrates, the teeth of all groups (conodonts, bony fishes and sharks) were of similar small size. We suppose that the Lilliput effect could have affected shark, fish and conodont communities before the Hangenberg crisis and acted as an answer to resource competition linked to perturbations at the base of the trophic chain (Twitchett 2006, Brom *et al*. 2016, Rita *et al*. 2019) that occurred between CT69-7 and CT70-A during the last million year before the Hangenberg crisis (Fig. 4). Studies have described a Lilliput effect with numerous fishes and foraminifers of small size occurring after the Hangenberg event (Aretz *et al*. 2014, Sallan & Galimberti 2015). However, regarding the relative abundances and sizes of conodonts, sharks and fishes, it could be considered that the Lilliput effect happened prior to the Hangenberg and that the impact of this Lilliput effect differs regarding each group (Schaal *et al*. 2015). As conodonts seems to

benefit from the crisis in terms of abundance, it might be suggested that their shift in size involved that feeding resources became scarcer, but without a major change in their preys across time. This scenario could have favored small individuals and allow them to subsist as they present lower metabolic requirement (Calder 1984, Harries *et al*. 1996, Chen *et al*. 2019). The strong decrease in fish communities could be explained by a different scenario, considering that their preys were more drastically impacted by the global perturbations preceding the Hangenberg event and drove fishes to feed on other organisms, less represented and that did not allow to maintain large fishes communities. Sharks were very scarce in these levels but specimens that have been uncovered seem not to present changes in size supposing that they were less affected during the transition from CT69-7 and CT70-A.

Post-Hangenberg crisis (CT70-A to CT70-5)

In contrast to the relative stability of taxonomic diversity between the pre-Hangenberg levels CT69-7 and CT70-A, the Hangenberg crisis, which is recognized as a major extinction event, has induced a significant turnover in marine groups as for example conodonts and sharks (*e.g.* Walliser 1996, Ginter 2000, Kaiser *et al*. 2008). This is characterized in the Col des Tribes section by a strong decrease in the amount of specimens (nearly three times lower than before the crisis). However, relative abundances of sharks, conodonts and fishes did not change across the crisis, supposing that the ecosystem reached a trophic balance with a probable lack of ecological niche turnover inducing that the replacement of pre-Hangenberg taxa has not lead to a trophic restructuration.

Regarding the pre- and post-Hangenberg impacts on biodiversity, we argue that the crises that affected the uppermost Famennian faunas and led to the the Hangenberg extinction have acted in different ways. First, a pre-Hangenberg restructuration of faunas with no faunal turnover and on the other hand the post-Hangenberg turnover that did not affect the repartition of the main marine vertebrate groups. The perturbations registered around the Hangenberg crisis in the Montagne Noire should be investigated in other localities to understand whether the observed faunal restructuration depends on local or more global perturbations.

Conclusions

Crises selectivity can be expressed in different ways. Here we demonstrate that the study of faunal turnover through time is not sufficient to understand the whole perturbations around crises. It appears that changes in community sizes and abundances prefigure the Hangenberg event even if

faunal composition remains unchanged. In the Col des Tribes section, the three levels from the last million years before the Hangenberg event document changes that were not previously highlighted and give more clues about the timing and shaping of marine vertebrate communities at the edge of the Hangenberg crisis. The changes are not linked to major environmental perturbations as evidenced by facies and the carbon isotope record but indicate that community restructuration occurred even in relatively stable environments.

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