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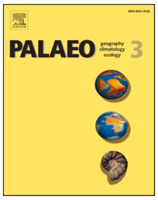

Eifelian (Middle Devonian) to Early Frasnian (Late Devonian) conodonts and strata in the Spanish Central Pyrenees: Global correlations and effects of climatic fluctuations in the biota☆

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ABSTRACT

The interval between the late Eifelian and early Frasnian was marked by significant paleoenvironmental instability, including major evolutionary, eustatic, and biotic events. This study analyzes conodont diversity and evolutionary dynamics in the Givetian of the Spanish Pyrenees, using integrated quantitative and qualitative methods, and focusing on responses to global Devonian paleoenvironmental events. Key global events are examined for their impact on conodont communities. Results show a steady rise in diversity peaking in the *ansatus* Zone, which saw the highest evolutionary turnover, followed by a decline into the *latifossatus* Zone. Origination generally outpaced extinction until this point. Major faunal changes correlate with the Taghanic and Geneseo events, while the Kačák and Lower *pumilio* events had limited regional effects. The Upper *pumilio* and Frasnes events influenced diversification. The findings underscore periodic biodiversity shifts, driven by both global events and regional factors, and in Devonian evolutionary and environmental patterns. These findings enhance understanding of regional and global conodont biodiversity dynamics, highlight regional differences, and underscore the complex biotic responses to Devonian climatic and sea-level changes.

1. Introduction

The interval between the late Eifelian and the early Frasnian is one of the most unstable in the Devonian. Brett et al. (2020) analyzed changes in the frequency of evolutionary, carbon cycle, eustatic, and biotic events and concluded that the late Eifelian-early Frasnian was the most environmental volatility period. Based on variations in $\delta^{18}O$ from conodont apatite, Joachimski et al. (2009), followed by Grossmann and Joachimski (2020), developed a general paleotemperature curve for the Devonian. Their findings indicate a cooling trend from the Lochkovian to the Emsian, followed by a brief warming period in the early Eifelian. Subsequently, another cooling phase reached its peak in the middle Givetian before transitioning into a warm period, the Givetian-Frasnian Warm Trend. Thereafter, an overall cooling trend persisted until the end of the Devonian, marked by a significant temperature drop discernible by two short $\delta^{18}O$ excursions at the Frasnian-Famennian transition.

Consequently, the beginning of the studied interval corresponds to the coolest paleoclimatic conditions, while the mid-Givetian to early Frasnian represents a transition from a general cooling trend to warming. During this time interval, a succession of Global Events has been recognized, primarily in pelagic facies (Walliser, 1996; House, 2002). The causes of these events remain poorly understood, but sea-level fluctuations and changes in paleoceonagraphic dynamics, driven by climate changes and plate tectonics, likely played a significant role. These Global Events disrupted the lithosphere and biosphere, inevitably affecting biotas, though the impact varied across marine and terrestrial environments. The different effects of these events led Becker et al. (2016) to classify them into five categories: First- to Fourth- order events and other minor events. Some of these events were long-lasting and multiphasic, warranting the term “Crisis”, such as the Taghanic Crisis (Aboussalam, 2003).

The impact of these Global Events on the conodont biota, particularly their evolutionary dynamics, remains insufficiently studied. The Givetian, a Period characterized by multiple environmental changes, likely influenced the conodont populations. However, only the pioneering work of Ziegler and Lane (1987) has examined conodont evolutionary

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cycles in Devonian and lower Pennsylvanian rocks. Our analysis partially includes two of their evolutionary cycles: the Pragian to early Givetian cycle and the mid-Givetian to Frasnian cycle.

Here, we investigate changes in the Pyrenean marine community, as reflected in the conodont record, around major Givetian Global Events, namely the Kačák, *pumilio* events, Taghanic, Geneseo, and Lower Frasnes. We measured diversity and origination and extinction rate changes over discrete stratigraphic intervals (Givetian zones) to assess the effects of these Global Events on conodont populations. Additionally, we compared these findings with data from selected sections in north and eastern Gondwana, Perigondwanan terrains, Central Asia, South China Block, and Euramerica to provide a comprehensive view of the global impact of these events on conodont evolution.

2. Material, methods, taxonomical approach and biostratigraphical framework

We conducted a detailed analysis bed-by-bed of conodont records from five selected Pyrenean sections (Fig. 1), whose detailed stratigraphy, depositional environments, and conodont distributions have been documented in previous studies (Liao, 2014; Liao and Valenzuela-Ríos, 2008, 2013, 2022; Liao et al., 2001, 2008; Gouwy et al., 2013, 2016) and summarized herein (Fig. 2). The presence of a given taxon in each of the Givetian zones follows the range-through approach. We have not observed evidence of diachroneity in the Pyrenean record relative to global occurrences, nor do we detect reversed stratigraphic orders that might suggest faunal migration. Thus, we can conclude that migration or environmental preference did not play a major role in shaping the observed species diversity.

Samples were collected independently, and the average volume or mass remains consistent across the studied interval, ensuring no deviation in the number of species per unit of sampling effort. The sample volume is adequate for the number of taxa recorded, ranging between 3 and 4 kg per sample.

Liao and Valenzuela-Ríos (2017) outlined the historical bio-and chronostratigraphic development of the Givetian conodont zonation. We follow their approach, subdividing the Givetian into three substages and ten global zones, supporting Bultynck's (2006) classification. Our zone-by-zone analysis adheres to the following global scheme: lower Givetian: *hemiansatus* and *timorensis* zones; middle Givetian: *rhenanus/varcus*, *ansatus* and *latifossatus* zones and upper Givetian: Lower and Upper *hermanni*, Lower and Upper *disparilis* and *norrisi* zones. The base of each zone is defined by the first appearance of the corresponding index taxon.

The base of the *hemiansatus* Zone, which marks the onset of the Givetian and lower Givetian, is defined by the entry of *Polygnathus hemiansatus* Bultynck, 1987. The base of the *timorensis* Zone corresponds to the entry of *P. timorensis* Klapper et al., 1970. The middle Givetian

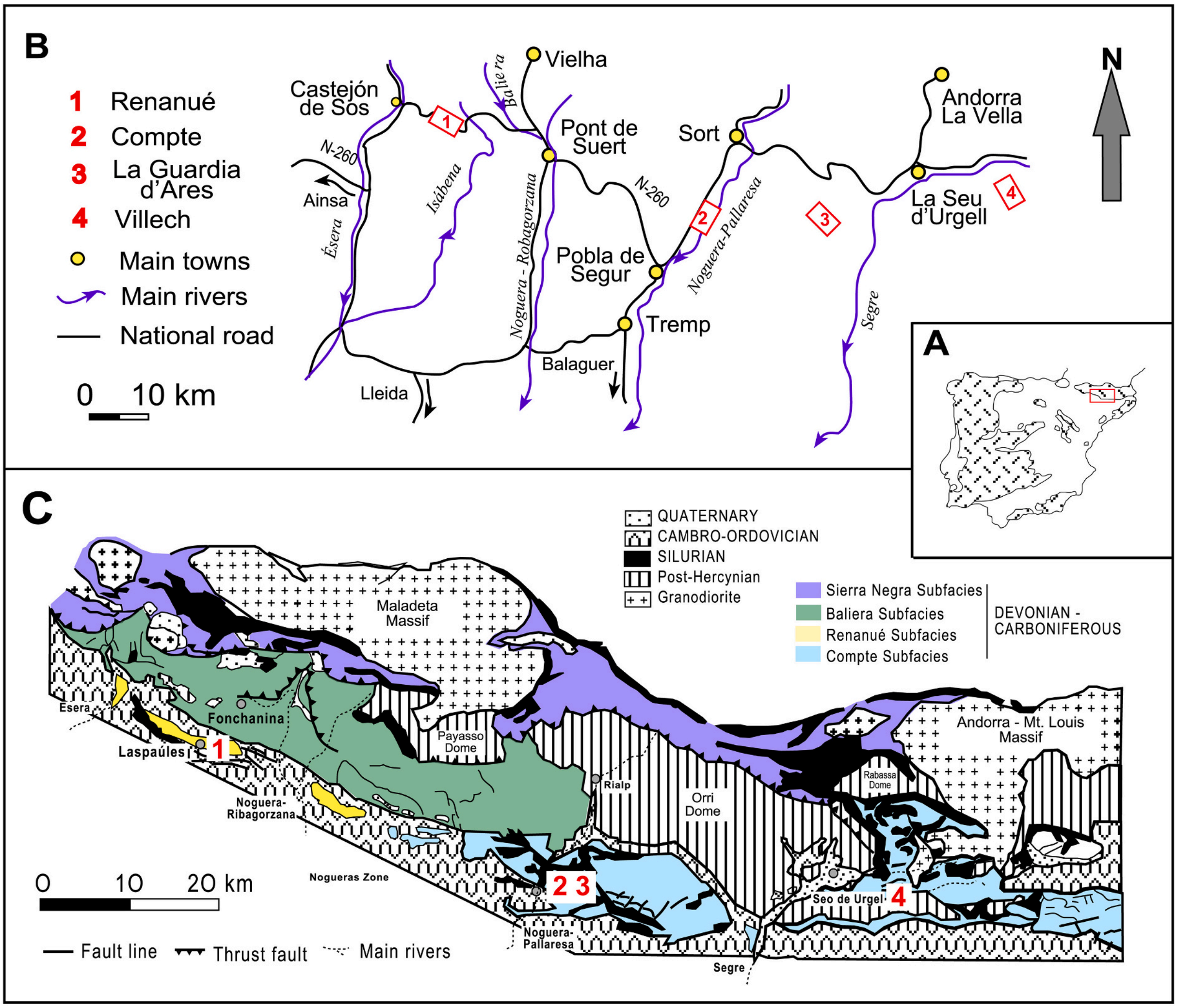

Fig. 1. A: Map showing the location of Pyrenean sections within the Iberian Peninsula, delineated by a rectangle to indicate the studied area. B: Situation of the studied sections. 1: Renanué section; 2: Compte section; 3: La Guàrdia d'Ares sections (La Guàrdia d'Ares and La Guàrdia d'Ares I); 4) Villech section. C: Geological map of the Axial Pyrenees, adapted from Valenzuela-Ríos et al. (2015), emphasizing the analyzed sections (1–4).

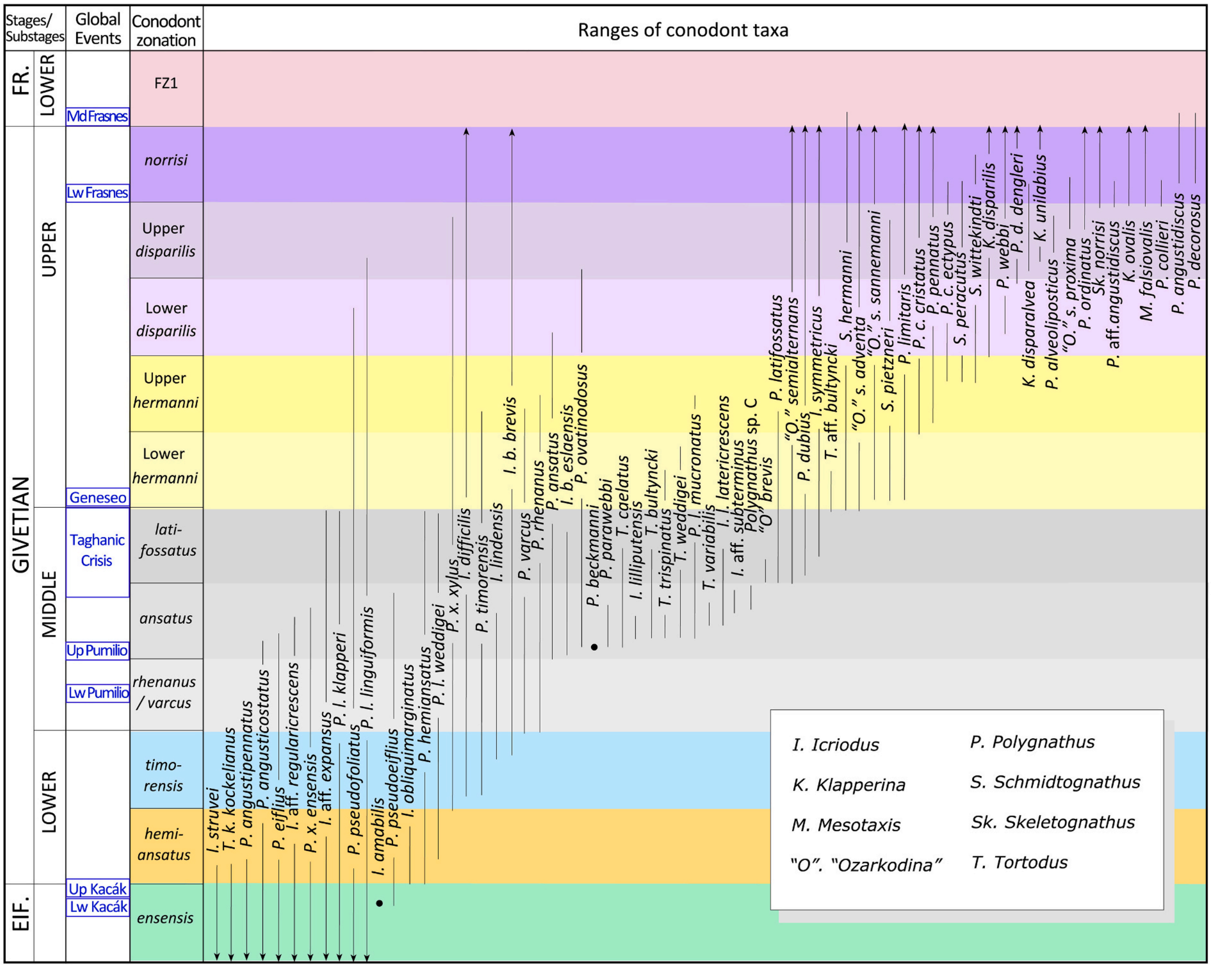

Fig. 2. Compiled stratigraphic ranges of the uppermost Eifelian to lowermost Frasnian conodont taxa in the Pyrenean sections based on Liao (2014) Liao et al. (2001, 2008), Liao and Valenzuela-Ríos (2008, 2013, 2022), and Gouwy et al. (2013, 2016). Position of Global Events according to Becker et al. (2016).

begins with the *rhenanus/varcus* Zone, defined by the first occurrence of either *P. rhenanus* Klapper et al., 1970 or *P. varcus* Stauffer, 1940. The base of the *ansatus* Zone is marked by *P. ansatus* Ziegler and Klapper, 1976 (in Ziegler et al., 1976). The lower boundary of the *latifossatus* Zone is defined by *P. latifossatus* Wirth, 1967. Some authors (e.g. Aboussalam, 2003; Aboussalam and Becker, 2007) argue that the species *latifossatus* belongs to *Schmidtognathus* rather than *Polygnathus*. However, this discussion is beyond the scope of this paper, and we adhere to the latter classification. The upper Givetian begins with the Lower *hermanni* Zone, defined by the entry of *Schmidtognathus hermanni* Ziegler, 1966. Subsequent zones are defined by the entry of *P. cristatus* Hinde, 1879 (Upper *hermanni* Zone), *Klapperina disparilis* (Ziegler and Klapper, 1976) (Lower *disparilis* Zone), *P. dengleri* Bischoff and Ziegler, 1957 (Upper *disparilis* Zone), and *Skeletognathus norrisi* (Uyeno, 1967) (*norrisi* Zone). The base of next Frasnian Zone, FZ1 (Klapper and Kirchgasser, 2016), corresponds with the Frasnian base and the Middle/Upper Devonian boundary, marked by the early form of *Ancyrodella rotundiloba* (Bryant, 1921).

Due to the diverse nomenclatural treatments of early *Ancyrodella* taxa near the Frasnian base—and although this interval is not the primary focus of this report—we include a brief comment on the issue. Klapper (1985) analyzed the sequence of early *Ancyrodella* forms in the Montagne Noire around the Givetian/Frasnian boundary and distinguished two successive, transitional forms (early and late) within the taxon *A. rotundiloba*. The early form was used to define the base of the Frasnian. Sandberg et al. (1989) erected a new species, *A. soluta* and recognized three morphotypes (1–3) for this species, as well as three morphotypes each for *A. pristina* Khalymbadzha and Chernysheva, 1970, and *A. rotundiloba.* Subsequently, Klapper (2000) examined in detail the taxonomic attributions and biostratigraphic positions of the early *Ancyrodella* taxa. He concluded that the specimens assigned by Sandberg et al. (1989) to *A. pristina*, actually correspond to his *A. rotundiloba* early form from the Montagne Noire sequences. Later, Klapper and Kirchgasser (2016) confirmed that the early form of *A. rotundiloba* corresponds to the types of *A. pristina*, whereas the late form corresponds to the types of *A. rotundiloba*. Because the differences between these taxa are minor and transitional forms exist, they treated both as subspecies: *A. rotundiloba pristina* for Klapper's (1985) early form and *A. rotundiloba rotundiloba* for his late form. Consequently, the former serves as the index taxon for the base of the Frasnian.

A parallel study on Lochkovian conodonts (Valenzuela-Ríos and Liao, 2024), discussed methodological aspects of diversity estimation and taxonomic rates, which we follow here, integrating qualitative and quantitative data. Quantitative analysis includes taxonomic diversity and rates, on a zonal basis, using Foote's method (Foote, 2000), and, briefly, Clark's conodont evolution index (Clark, 1972).

Foote (2000) categorized taxa as boundary crossers (bL, Ft, bt) or singletons (FL), quantified in various combinations (Table 1). We use three approaches to evaluate origination and extinction rates: per-taxon rate, Van Valen's metric, and Van Valen's metric excluding singletons (Foote, 2000; Van Valen, 1984; Harper Jr., 1996 respectively). These parameters, defined in Table 2, align with recommendations of Bambach (1999) and Foote (2000), emphasizing boundary crossers to mitigate underestimation of Mean Standing Diversity (MSD). (See Table 3.)

Table 1

This table displays the quantity of various taxa types per zone utilized in describing taxonomic diversity. It includes the following classification: Ntot: represents the total diversity, which is the total number of recorded taxa. Nb: number of taxa crossing the bottom boundary. Nt: number of taxa crossing the upper boundary. No: number of taxa appearing first in the interval. Ne: number of taxa becoming extinct within the interval. NFL: number of taxa confined to a single stratigraphic interval (singletons), with their first and last appearance happens during the interval. NbL: number of taxa crossing the bottom boundary and making their last appearance during the interval. NFt: number of taxa crossing the top boundary and making their first appearance within the interval. Nbt: number of taxa crossing both boundaries and ranging through the entire interval. N-St: represents the total diversity excluding singletons. MSD: represents the Mean Standing Diversity, calculated as the average of Nb and Nt. ICE: Index of conodont evolution after Clark (1972).

	Ntot	Nb	Nt	No	Ne	NFL	NbL	NFt	Nbt	N-St	MSD	ICE
norrisi	28	21	21	7	7	2	5	5	16	26	21	1
Upper disparilis	26	20	21	6	5	1	4	5	16	25	20.5	1.2
Lower disparilis	22	20	20	2	2	0	2	2	18	22	20	1
Upper hermanni	25	20	20	5	5	0	5	5	15	25	20	1
Lower hermanni	24	18	20	6	4	1	3	5	14	23	19	1.5
latifossatus	26	21	18	5	8	1	7	4	14	25	19.5	0.62
ansatus	34	19	21	15	13	6	7	9	12	28	20	1.15
rhenanus-varcus	19	17	19	2	0	0	0	2	17	19	18	∞
timorensis	17	12	17	5	0	0	0	5	12	17	14.5	∞
hemiansatus	15	12	12	3	3	0	3	3	9	15	12	1

Table 2

This table outlines regional Givetian origination and extinction rates according to different metrics. O and E: Origination and Extinction rates considering the total number of taxa per zone. VVO and VVE: Van Valen's metric utilizing the estimated Mean Standing Diversity to calculate the Origination (VVO) and Extinction (VVE) rates. VVO-St and VVE-St correspond to the Van Valen's metric after removing singletons as proposed by Harper Jr. (1996).

	O	E	VVO	VVE	VVO-St	VVE-St
norrisi	0.25	0.25	0.33	0.33	0.24	0.24
Upper disparilis	0.23	0.19	0.29	0.24	0.24	0.19
Lower disparilis	0.09	0.09	0.1	0.1	0.1	0.1
Upper hermanni	0.2	0.2	0.25	0.25	0.25	0.25
Lower hermanni	0.25	0.17	0.32	0.21	0.26	0.16
latifossatus	0.19	0.31	0.26	0.41	0.2	0.36
ansatus	0.44	0.38	0.75	0.65	0.45	0.35
rhenanus-varcus	0.1	0	0.11	0	0.11	0
timorensis	0.29	0	0.34	0	0.34	0
hemiansatus	0.2	0.2	0.25	0.25	0.25	0.25

3. Results and discussion

Our study focuses on identifying total diversity and the rates of evolution, origination, and extinction on a zonal scale, as well as comparing these metrics with the taxa involved.

3.1. Taxonomic diversity, variation in origination and extinction rates

A steady increase in diversity is observed from the beginning of the Givetian to the first middle Givetian Zone, with 15 taxa in the *hemiansatus* Zone, 17 in the *timorensis* Zone and 19 in the *rhenanus-varcus* Zone (Fig. 3A). A sharp increase in diversity occurs in the *ansatus* Zone, rising from 19 to 34 taxa, as reflected in a steep slope. This zone represents the peak of diversity during the Givetian. A subsequent decline follows in the last middle Givetian Zone (the *latifossatus* Zone), with 26 taxa. From there to the end of the Givetian, diversity fluctuates slightly, forming an almost symmetrical pattern. The total diversity of the upper Givetian reaches a minimum in the Lower *disparilis* Zone: Lower *hermanni* Zone (25 taxa), Upper *hermanni* (25), Lower *disparilis* (22), Upper *disparilis* (26) and *norrisi* (28).

Although these numbers suggest a degree of stability, qualitative analysis (discussed below) revealed significant changes in the composition of conodont faunas. This method of measuring diversity accounts for the total number of taxa at any point within the interval but does not reflect the specific taxa involved.

Foote (2000) following Bambach (1999) discussed the potential advantage of using the number of taxa that cross boundaries —Nb (bottom of the interval) and Nt (top of the interval)- along with their relationship, expressed through the estimated Mean Standing Diversity (MSD), as a measure of diversity (Fig. 3B). Both curves show a similar increase in slope up to their maximum point, followed by a comparable pattern of alternating decreases and increases from zone to zone. Although the two curves are broadly similar, they are offset by one zone.

The highest value for top crossers (Nt) occurs first in the *ansatus* Zone (21 taxa) and remains the same in the final two Givetian zones (Upper *disparilis* and *norrisi*). However, the highest value for bottom crossers (Nb) appears in the subsequent *latifossatus* Zone (21 taxa), corresponding to those that crossed the upper boundary of the previous zone. From this point to the end of the Givetian, the overall pattern remains comparable, with total number of taxa shifted by one zone, though slight differences exist in the exact totals for each. The Nt decreases to 18 taxa in the *latifossatus* Zone, rises slightly in the Lower *hermanni* Zone (20), remains stable in the Upper *hermanni* Zone and Lower *disparilis* zones, and then increases steadily in the Upper *disparilis* (21) and *norrisi* zones (21). Meanwhile, the Nb decreases to 18 taxa in the Lower *hermanni* Zone, rises slightly in the Upper *hermanni* Zone (20) –marking a trend

Table 3

This table presents the count of taxa attributed to each genus per zone and the total number of taxa per zone, constituting the overall diversity utilized in the corresponding figures.

	Icriodus	*Polygnathus*	*Tortodus*	*"Ozarkodina"*	*Schmidtognathus*	*Klapperina*	*Skeletognathus*	*Mesotaxis*	Total
norrisi	3	12	0	4	3	4	1	1	28
Upper disparilis	3	12	0	4	4	3	0	0	26
Lower disparilis	3	11	0	3	4	1	0	0	22
Upper hermanni	3	15	0	3	4	0	0	0	25
Lower hermanni	3	13	3	3	2	0	0	0	24
latifossatus	6	14	4	2	0	0	0	0	26
ansatus	10	19	5	0	0	0	0	0	34
rhenanus-varcus	6	13	0	0	0	0	0	0	19
timorensis	6	11	0	0	0	0	0	0	17
hemiansatus	4	10	1	0	0	0	0	0	15

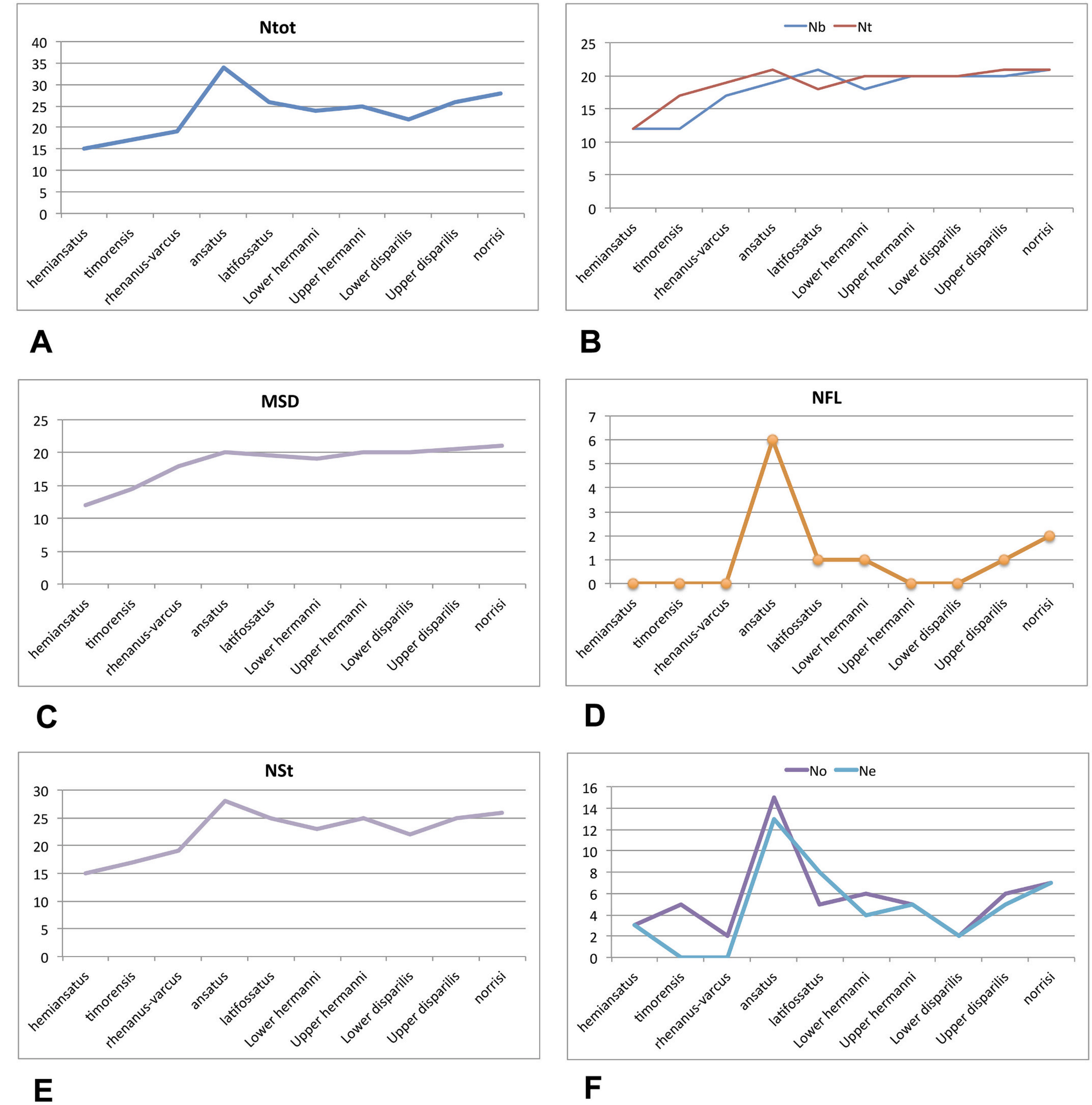

Fig. 3. Illustrative curves and plots representing Givetian conodont biodiversity on a zonal basis in the Pyrenees, using data from Table 1. A: Changes in total diversity (Ntot) zone by zone. B: Comparative changes in the number of taxa crossing boundaries; Nb: crossing the bottom of the interval; Nt: crossing the top of the interval. C: Comparison between boundary crossers and their zone-by-zone changes expressed through the estimated Mean Standing Diversity (MSD). MSD = (Nb + Nt)/2. D: Number of singletons (NFL) per zone. E: Total diversity curve excluding singletons (NSt). F: Diversity curves comparing the number of originations (No) and extinctions (Ne) based on zones.

reversal relative to Nt- remains stable in the Lower *disparilis* and Upper *disparilis* zones, and then rises again to 21 in the final Givetian *norrisi* Zone.

The MSD values, which relate the two types of boundary crossers [MSD = (Nb + Nt)/2], clearly diverges from the one representing total diversity (Fig. 3C). Notable differences are evident in both the highest points of the curves and their respective trends. The MSD reaches its peak in the *norrisi* Zone, whereas Ntot displays a distinct peak in the *ansatus* Zone. In both curves, the lowest values occur in the lower Givetian *hemiansatus* and *timorensis* zones as well as in the lowest middle Givetian *rhenanus-varcus* Zone, followed by an upward trend from the *hemiansatus* Zone to the *ansatus* Zone. However, the MSD curve exhibits a gentler slope in this interval compared to Ntot (see Figs. 3A and C). Thereafter, the trends diverge, while Ntot fluctuates with a moderately pronounced low peak in the Lower *disparilis* Zone, the MSD curve remains nearly flat, showing only a subtle inflection in the Lower *hermanni* Zone, followed by a gradual and continuous increase in the Upper *disparilis* and *norrisi* zones.

Foote (2000) asserts that the interval length influences the number of singletons: "*As interval length increases, a progressively larger proportion of total diversity consists of singletons*". To examine this hypothesis, we have counted the singletons in our Givetian record (Fig. 3D) and compare diversity with and without singletons (Fig. 3A and E). The number of singletons is only relatively significant in the *ansatus* Zone, which contains six taxa. This zone spans a similar duration (approximately 1–1,1 Ma; compare Becker et al., 2020) to the three preceding zones (*hemiansatus*, *timorensis* and *rhenanus-varcus*); however none of these three zones contain singletons. The *norrisi* Zone has two singletons, while three other zones -*latifossatus*, Lower *hermanni*, and Upper *disparilis*- each contain a singleton. With the exception of the *latifossatus* Zone, which has a larger duration, approximately 0.7 Ma, the other zones have comparable time spans of 0.3–0.4 Ma. The remaining Givetian zones contain no singletons. These findings suggest that interval length does not influence the number of singletons at the zonal scales.

The singletons in the *ansatus* Zone belong to species of *Polygnathus* (3 taxa), *Icriodus* (2 taxa) and *Tortodus* (1 taxon). The two singletons in the *norrisi* Zone are species of *Polygnathus*, while the singletons in the *latifossatus*, Lower *hermanni*, and Upper *disparilis* zones correspond to species of "*Ozarkodina*", *Tortodus*, and *Polygnathus*, respectively. The total diversity excluding singletons (Fig. 3E) curve resembles the total diversity, which includes singletons (Fig. 3A), with identical patterns in several zones: *hemiansatus, timorensis*, *rhenanus-varcus*, and *ansatus* in the lower and middle Givetian, as well as Upper *hermanni*, Lower *disparilis*, Upper *disparilis*, and *norrisi* in the upper Givetian. The main differences appear in the lower peak of the *ansatus* Zone (28 vs 34 taxa), which remains the diversity peak, and in the smoother slope from this zone to the Upper *hermanni* Zone. However, overall, the diversity trend remains similar.

Two distinct diversity trends are observed in terms of origination (No) and extinctions (Ne) per zone for the Pyrenean records in the three oldest zones (*hemiansatus*, *timorensis*, and *rhenanus-varcus*), primarily due to the absence of extinctions in the latter two (Fig. 3F). In the remaining zones, both curves follow a similar pattern, with the highest peak in the *ansatus* Zone and the lowest in the Lower *disparilis* Zone. However, origination/extinction numbers vary across intervals. From the *hemiansatus* to the *ansatus* zones, originations consistently outnumber extinctions, except in the *hemiansatus* Zone where the numbers are equal (3 taxa each). The *latifossatus* Zone marks a shift in this pattern, with more extinctions (8 taxa) than originations (5 taxa). The Lower *hermanni* Zone returns to a slightly higher number of originations (6) than extinctions (4). The succeeding Upper *hermanni* and Lower *hermanni* zones, as well as the uppermost Givetian *norrisi* Zone, exhibit equal numbers of originations and extinctions. The Upper *disparilis* Zone deviates from this parity, with one more origination (6 taxa) than extinction (5 taxa).

In addition to evaluating diversity in terms of total origination and extinctions counts, we assessed their rates using different metrics (Table 2, Figs. 4A-C). In the *hemiansatus* Zone origination and extinction

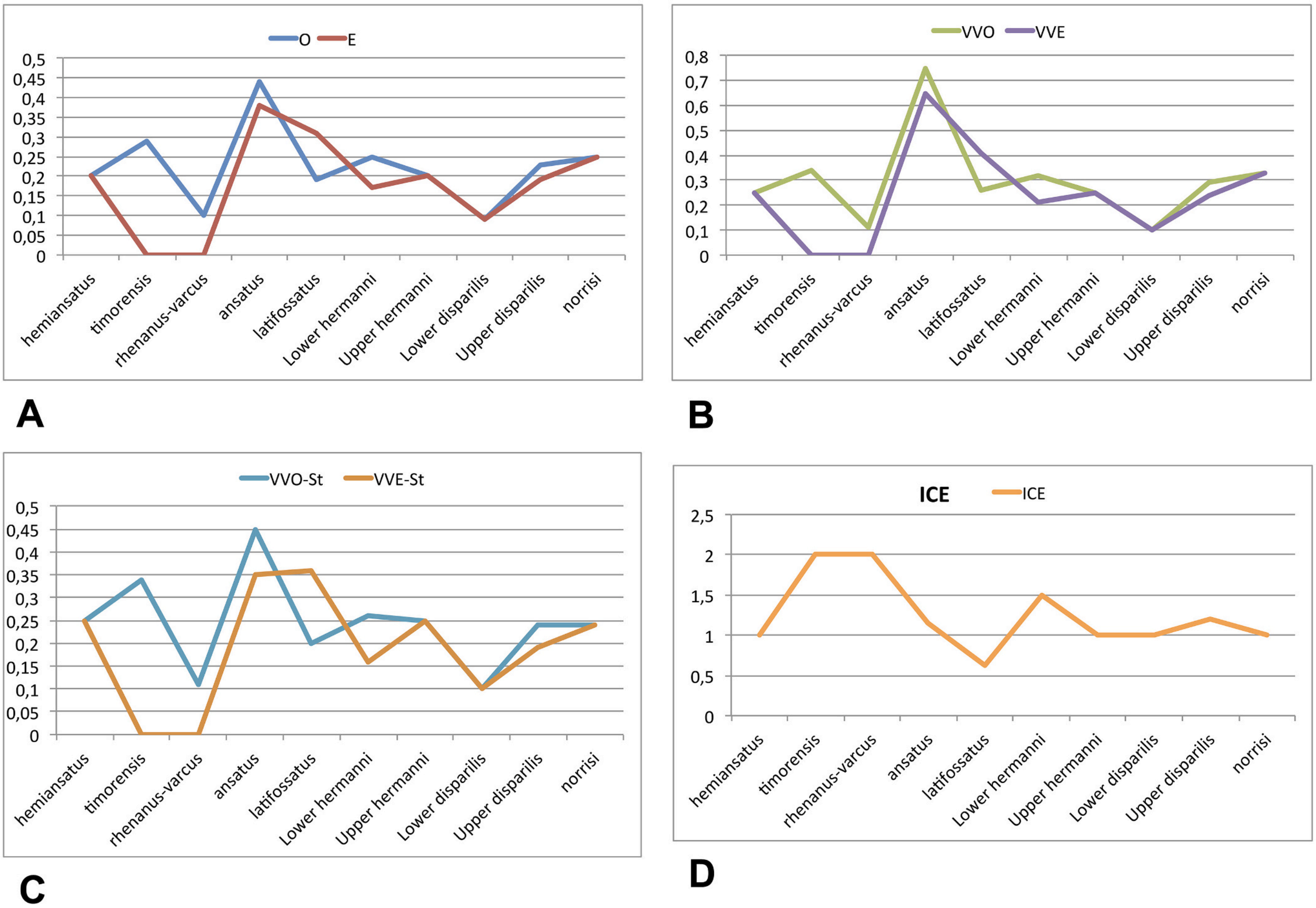

Fig. 4. A-C: Various plots displaying diverse taxonomic rate metrics to measure diversity based on data in Table 2. A: Evolution of diversity considering per-taxon rates of origination (O) and extinction (E). B: Diversity evolution considering the estimated Mean Standing Diversity. VVO: Van Valen's metrics for origination; VVE: Van Valen's metrics for extinction. C: Changes in diversity excluding singletons from Van Valen's metrics, VVO-St: origination; VVE-St: extinction. D: Changes in the Index of Conodont Evolution (ICE) according to Clark's metrics. Holding line = ICE 1, indicating equilibrium between evolution and extinction. Values above signify diversification and expansion, whereas values below indicate and extinction threshold.

rates are equal (0.2), resulting in identical starting point for both curves. The trend then differs in the following two zones: the origination rate fluctuates from a maximum of 0.29 in the *timorensis* Zone, the second highest after the peak in the *ansatus* Zone, to the lowest rates of the entire Givetian in the Lower *disparilis* (0.09) and *rhenanus-varcus* (0.1) zones forming a pronounced saw tooth for these intervals. The absence of extinctions in the *timorensis* and the *rhenanus-varcus* zones results in a flat extinction-rate line at 0.0.

Both rates increase sharply in the *ansatus* Zone, reaching their highest values: 0.44 for originations and 0.38 for extinctions. This results in a parallel slope for both curves, reflecting the high number of origination (15 taxa) and extinction (13 taxa) events in the *ansatus* Zone, significantly higher than in other Givetian zones (see Table 1). In the following *latifossatus* Zone, more species became extinct (8 taxa) than originated (5 taxa), leading to a higher extinction rate and the only interval where the extinction curve surpasses the origination curve.

The Lower *hermanni* Zone marks another shift: the origination rate increases to 0.25 and the extinction decreases to 0.17. In the Upper *hermanni* Zone, the extinction rate increases to 0.2, but the origination rate drops to 0.2 producing different curve profiles- origination trends downward, extinction trend upwards. Then, Lower *disparilis* Zone sees a sharp decline in origination (2 taxa) and extinction (2 taxa), resulting in both rates dropping to a low peak of 0.09. This represents the lowest origination rate of the entire Givetian. With the exception of the *timorensis* and *rhenanus-varcus* zones, which lack extinctions, the Lower *disparilis* Zone also records one of the lowest extinction peaks in the Givetian.

Both rates rise towards the end of the Givetian, but at different rates, producing distinct curve profiles. The origination rate increases sharply in the Upper *disparilis* Zone (from 0.09 to 0.23) and then rises gradually in the *norrisi* Zone to 0.25. In contrast, the extinction rate follows a steadier trajectory, increasing from 0.09 to 0.19 in the Upper *disparilis* Zone and reaching 0.25 in the *norrisi* Zone.

In analyzing evolutionary diversity, Van Valen (1984) used the estimated Mean Standard Diversity (MSD) to calculate origination and extinction metric rates (Fig. 4B). Following Harper Jr. (1975) and Van Valen (1984), the MSD value more accurately represents the number of taxa subject to origination and extinction within a given interval of time than the total diversity number used in the per-taxon rate measurement described above.

Origination and extinction rates in the *timorensis* Zone are identical (0.25). A "sawtooth" pattern is observed in the origination rate in the subsequent two zones (*timorensis* and *rhenanus-varcus*) with values of 0.34 and 0.11, respectively, while extinction rates remain absent (value = 0) in these two zones, depicting a flat line. The highest peak for both rates occurs in the *ansatus* Zone, with values of 0.75 and 0.65, respectively. In the *latifossatus* Zone, the extinction rate exceeds the origination rate (0.41 vs. 0.26). From this point onward, the origination rate remains higher (Lower *hermanni* and Upper *disparilis*) or equal to the extinction rate. The profile of both curves for this part of the interval is identical, with a minimum in the Lower *disparilis* Zone and a maximum in the *norrisi* Zone.

Harper Jr. (1996) identified potential challenges in using singletons and suggested their exclusion from Van Valen's metrics. In our Pyrenean records, singletons are significant only in the *ansatus* Zone (six taxa; Tb. 1, Fig. 3D). Most zones contain no singletons, except for the Lower *hermanni* and Upper *disparilis* zones, which each have one, and the *norrisi* Zone, which has two. The removal of singletons likely has minimal impact on taxonomic rate estimation, especially since the zone with a relatively high number of singletons (*ansatus* Zone) also has a considerably larger total number of taxa (34) (Tbs. 1 and 3). Nonetheless, we calculated these values without singletons (VVO-St and VVE-St for origination and extinction, respectively) and plotted the rates (Tb. 2, Fig. 4C). As expected, the resulting lines closely resemble the previous ones (Fig. 4A and B), with patterns that are nearly identical. The main differences appear in the profiles of the curves between the *ansatus* and the Upper *hermanni* zones. The origination rate profile is nearly flat in this metric rather than descending, as in Van Valen's metrics, between the Lower and Upper *hermanni* zones. This is due to the close index values for these two zones (0.26 and 0.25, respectively). Similarly, the profile from the Upper *disparilis* Zone to the *norrisi* Zone is flat rather than ascending, as in using Van Valen's metrics (Fig. 4B), because the index values in both zones are identical (0.24). Regarding extinction rates, the descending and ascending profiles between the *latifossatus* and Lower *disparilis* zones are more pronounced due to the greater differences in index values across these four consecutive zones. Likewise, the extinction's curve between the *ansatus* and *latifossatus* zones is nearly flat (gently ascending) rather than strongly descending, as in Fig. 4B, due to the smaller index difference, caused by the relatively high number of singletons in the *ansatus* Zone (6 taxa) and only one taxon in the *latifossatus* Zone (Fig. 3D).

3.2. Index of evolution, evolutionary, and diversity cycles

The index of conodont evolution (ICE) for each Givetian zone is shown in Table 1, while its evolution over time is illustrated in Fig. 4D. The values of this index should be interpreted with caution, as raw data sometimes produce anomalous results. For instance, the *timorensis* and *rhenanus-varcus*, two consecutives zones, show zero extinction, leading to an infinite index value. This would suggest a period of maximum evolutionary diversity, yet these zones exhibit some of the lowest total biodiversity levels (17 and 19 taxa, respectively) apart from the *hemiansatus* Zone.

According to the ICE, most zones maintain population stability (index of 1.0), aligning with zones where originations balance extinctions (*hemiansatus*, Upper *hermanni*, Lower *disparilis*, and *norrisi* zones). However, total biodiversity still fluctuates between consecutive zones, such as the Upper *hermanni* (25 taxa) and Lower *disparilis* (22 taxa). Only the *latifossatus* Zone has an index of 0.62, suggesting conodonts were at threshold of extinction. Nevertheless, this zone is bracketed by two zones with ICE values greater than 1 (*ansatus* Zone = 1.15 and Lower *hermanni* Zone = 1.5), indicating evolutionary expansion. The Upper *disparilis* Zone also shows an ICE value above 1.

In brief, the ICE suggests that most zones represent periods of diversification and evolutionary expansion (*timorensis*, *rhenanus-varcus*, *ansatus*, Lower *hermanni*, and Upper *disparilis*) or population stability (*hemiansatus*, Upper *hermanni*, Lower *disparilis*, and *norrisi*). Only the *latifossatus* Zone indicates a phase where more conodont taxa are became extinct than evolved, placing them at an extinction threshold. However, no zone exhibits an ICE value indicating a major crisis or extinction event.

Ziegler and Lane (1987) recognized seven conodont evolutionary cycles from the late Silurian to the lower Pensilvannian. Our study partially overlaps with two of these cycles: Pragian to mid-Givetian and mid-Givetian to Frasnian. In the former cycle, they identified a low-diversity episode during the Pragian, followed by a high-diversity episode spanning the late Pragian to the early Givetian, which concluded with an extinction event at the base of the then-defined *varcus* Zone (now *timorensis* Zone).

The mid-Givetian to Frasnian cycle, according to Ziegler and Lane (1987), starts in the *ansatus* Zone with a low-diversity episode ("*Mid-Givetian low-diversity episode*") lasting until the Lower *hermanni* Zone. They identified an Innovation Event at the transition between the middle and upper *varcus* zones, now corresponding to the *ansatus* and *latifossatus* zones. This episode was followed by a high-diversity phase that ended with an extinction event in the Frasnian uppermost *gigas* Zone (now FZ13c-*linguiformis* Zone).

Our results from the Pyrenees contrast with these general trends. The highest diversity occurs in the *ansatus* Zone (34 taxa), which also marks a major renewal of conodont faunas, featuring peak origination (15 taxa) and extinction (13 taxa) within the Givetian. Although diversity declines slightly from the *latifossatus* to the Lower *disparilis* zones, it remains higher rates than in the three lower Givetian zones preceding the *ansatus* Zone.

Key differences between our results and the general evolutionary cycles of Ziegler and Lane (1987) include: 1) the *hemiansatus* Zone does not correspond to a high-diversity Episode or an extinction Event; 2) the *ansatus* Zone does not belong to a low-diversity Episode; on the contrary, it represents the highest diversity interval of the entire Givetian; 3) the *latifossatus* Zone cannot be associated with a Givetian Innovation Event, as only three zones (*hemiansatus*, *rhenanus-varcus*, and Lower *disparilis*) show fewer originations. Furthermore, the preceding *ansatus* Zone exhibits three times more originations than the *latifossatus* Zone.

3.3. Qualitative analysis

Polygnathus is the dominant genus in all the conodont zones, representing between the 43–68 % of all genera. The percentage is highest in the lower three zones: *hemiansatus* (66.7 %), *timorensis* (64.7 %), and *rhenanus-varcus* (68.4 %). It then decreases in the *ansatus* (55.9 %) and *latifossatus* (53.8 %) zones before rising again in the Lower and Upper *disparilis* zones (54.2 % and 60 % respectively). From the Lower *disparilis* to the *norrisi* Zone, the percentage steadily declines (50 % to 42.9 %), with and intermediate value in the Upper *disparilis* Zone (46.1 %).

Beyond its total representation, the composition of *Polygnathus* taxa undergoes significant changes over time. In the *hemiansatus* Zone, the nominal taxon *P. hemiansatus* first appears, followed shortly by *P. linguiformis weddigei*, while *P. angustipennatus* becomes extinct. The *timorensis* Zone marks the entry of *P. timorensis* and *P. xylus xylus*. The base of the middle Givetian coincides with the base of the *rhenanus-varcus* Zone, defined by the simultaneous entry of *P. rhenanus* and *P. varcus*.

The *ansatus* Zone records the highest influx of new species, including the nominal *P. ansatus*, as well as *P. ovatinodosus*, *P. parawebbi*, *P. beckmanni*, and *P.* sp. C (the last three being singletons). Meanwhile, *P. angusticostatus*, *P. xylus ensensis*, and the three singletons disappear. In the *latifossatus* Zone, *P. latifossatus* develops, marking a morphological shift within the *Polygnathus*, followed slightly higher by *P. dubius*. *Polygnathus hemiansatus* and *P.* l. *weddigei* are the two species of this genus to become extinct in this zone.

The base of the upper Givetian is coincident with the base of the Lower *hermanni* Zone. Here only *P. limitaris* appears, while *P. ling. klapperi* disappears. The Upper *hermanni* Zone introduces *P. cristatus cristatus*, *P. cristatus ectypus*, and *P. pennatus*, which replace the higher occurrences of *P. timorensis*, *P. rhenanus*, *P. varcus*, *P. ling. mucronatus*, and *P. latifossatus*.

The Lower *disparilis* Zone records the entry, above the base of the zone, of *P. webbi*, while *P. pseudofoliatus* and *P. ansatus* became extinct. The Upper *disparilis* Zone documents the entry of *P. dengleri dengleri* and the disappearance of *P.* l. *linguiformis*, *P. xylus xylus*, and *P. ovatinodosus*. In the *norrisi* Zone, *P.* aff. *angustidiscus* and *P. collieri* (both singletons) appear, while *P. c. ectypus* records its last occurrence.

Icriodus is present in all zones and is a major component of all lower and middle Givetian assemblages, representing between 23.1 (*latifossatus* Zone) and 35.3 % (*timorensis* Zone) of taxa. In the *timorensis* and *rhenanus-varcus* zones, *Icriodus* occurs exclusive alongside *Polygnathus*. However, the onset of other genera and a reduction in *Icriodus* taxa-down to a minimum of three taxa per zone- results in a significant decline in its relative abundance in the upper Givetian zones (between 10.7 % in the *norrisi* Zone and 13.6 % in the Lower *disparilis* Zone).

Like *Polygnathus*, the composition of *Icriodus* changes over time. In the *hemiansatus* Zone, *I. struvei* becomes extinct, while *I. obliquimarginatus* appears. These species belong to distinct evolutionary branches; *I. struvei* to the *struvei*-branch and *I. obliquimarginatus* to the *regularicrescens*-branch (Weddige and Ziegler, 1979). The *timorensis* Zone marks the appearance of three new taxa: *I. difficilis*, *I. brevis*, and *I. lindensis*, representing both branches. The *rhenanus-varcus* Zone does not record any changes in *Icriodus* taxa.

The *ansatus* Zone represents a major renewal in *Icriodus* faunas. *Icriodus* aff. *regularicrescens*, *I. obliquimarginatus*, and *I. lindensis* species from the *regularicrescens*-branch disappear, replaced by *I. eslaensis*. The *werneri*-branch includes two singletons: *I. lilliputensis* and *I.* aff. *subterminus*, while *I. latericrescens*, which does not belong to any of the three main branches of Weddige and Ziegler (1979), also appears.

In the *latifossatus* Zone, *I. eslaensis* and *I. latericrescens* became extinct, alongside *I.* aff. *expansus*, a long-ranging taxon that originated in the Eifelian. The only renewal in this zone is the lowest occurrence of *I. symmetricus*, which has affinities with the *struvei*-branch. The upper Givetian zones show no further changes in *Icriodus*, with *I. brevis*, *I. difficilis*, and *I. symmetricus* persisting. *Icriodus brevis* represents the *regularicrescens*-branch, while the latter two the *struvei*-branch.

Tortodus occurs only in four zones (Fig. 5A, 5B), peaking in the *ansatus* and *latifossatus* zones. The *hemiansatus* Zone records the last occurrence of the Eifelian *T. kockelianus*. The genus then reappears in the *ansatus* Zone with five new taxa: *T. caelatus*, *T. bultyncki*, *T. trispinatus, T. weddigei*, and the singleton *T. variabilis*. The first two disappear in the following *latifossatus* Zone, while *T. trispinatus* and *T. weddigei* persist until the Lower *hermanni* Zone, where the genus becomes extinct. A singleton, *T.* aff. *bultyncki*, is also recorded in this zone.

The first Pyrenean records of "*Ozarkodina*" appear in the *latifossatus* Zone with the long-ranging "*O.*" *semialternans* and the singleton "*O.*" *brevis*, representing the 7.7 % of the total biodiversity. In the upper Givetian zones, this percentage increases to 12 % and 15.4 %. The Lower *hermanni* Zone marks the entry of "*O.*" *sannemanni adventa* and "*O.*" *s. sannemanni*, both of which, along with "*O.*" *semialternans*, persists through all upper Givetian zones. The record of "*Ozarkodina*" augments in the Upper *disparilis* and *norrisi* zones with the addition of "*O.*" *s. proxima*.

The upper Givetian records the radiation of the genus *Schmidtognathus*, whose first appearance occurs in the Lower *hermanni* Zone with the entry of the nominal taxon *S. hermanni* and *S. pietzneri*. The subsequent Upper *hermanni* Zone adds two more taxa, *S. wittekindti* and *S. peracutus*. These four taxa continue until the Upper *disparilis* Zone, where *S. pietzneri* becomes extinct. In the *norrisi* Zone, *S. wittekindti* and *S. peracutus* also disappear.

Klapperina makes its first appearance in the Pyrenean record in the Lower *disparilis* Zone with the entry of the nominal taxon *K. disparilis*, which ranges into the Frasnian. The *Klapperina* lineage expands its biodiversity in the Upper *disparilis* Zone with the entry of *K. disparalvea* and *K. unilabius*. The former last occurs in the *norrisi* Zone, while the latter continues into the Frasnian. The *norrisi* Zone also marks the entry of *K. ovalis*. *Skeletognathus norrisi* and *Mesotaxis falsiovalis* further contribute to biodiversity in the *norrisi* Zone; both taxa range into the Frasnian.

The origination peak in the *ansatus* Zone (15 new taxa, six of which are singletons) is driven by the radiation of the genus *Tortodus* (5 new species, including the singleton *T. variabilis* in the Pyrenean sequences) and the renewal of the genera *Polygnathus* (6 new species, three of which are singletons) and *Icriodus* (4 new species, two of which are singletons). The highest extinction peaks, occurring consecutively in the *ansatus* (13 taxa) and *latifossatus* (8 taxa) zones, are associated with the renewal of *Icriodus* and *Polygnathus* faunas and, to a lesser extent, to the partial extinction of *Tortodus*. In the *ansatus* Zone, five species of *Icriodus* (including the singletons *I. lilliputensis* and *I.* aff. *subterminus*), seven species of *Polygnathus* (including the singletons *P. beckmanni*, *P. parawebbi*, and *P.* sp. C), and *Tortodus variabilis* become extinct in the Pyrenean record. The *latifossatus* Zone contains only one singleton ("*O. brevis*") in the Pyrenees; three species of *Icriodus*, two of *Tortodus*, and two of *Polygnathus* disappear in this zone (Fig. 2). The rise in originations in the Upper *hermanni* and *norrisi* zones are linked to the radiation of *Klapperina*, the innovation of *Skeletognathus* and *Mesotaxis*, and, to a lesser extent, the modest increase of "*Ozarkodina*".

In brief, significant changes characterize the composition of Givetian biodiversity. *Polygnathus* and *Icriodus* dominate the *hemiansatus*,

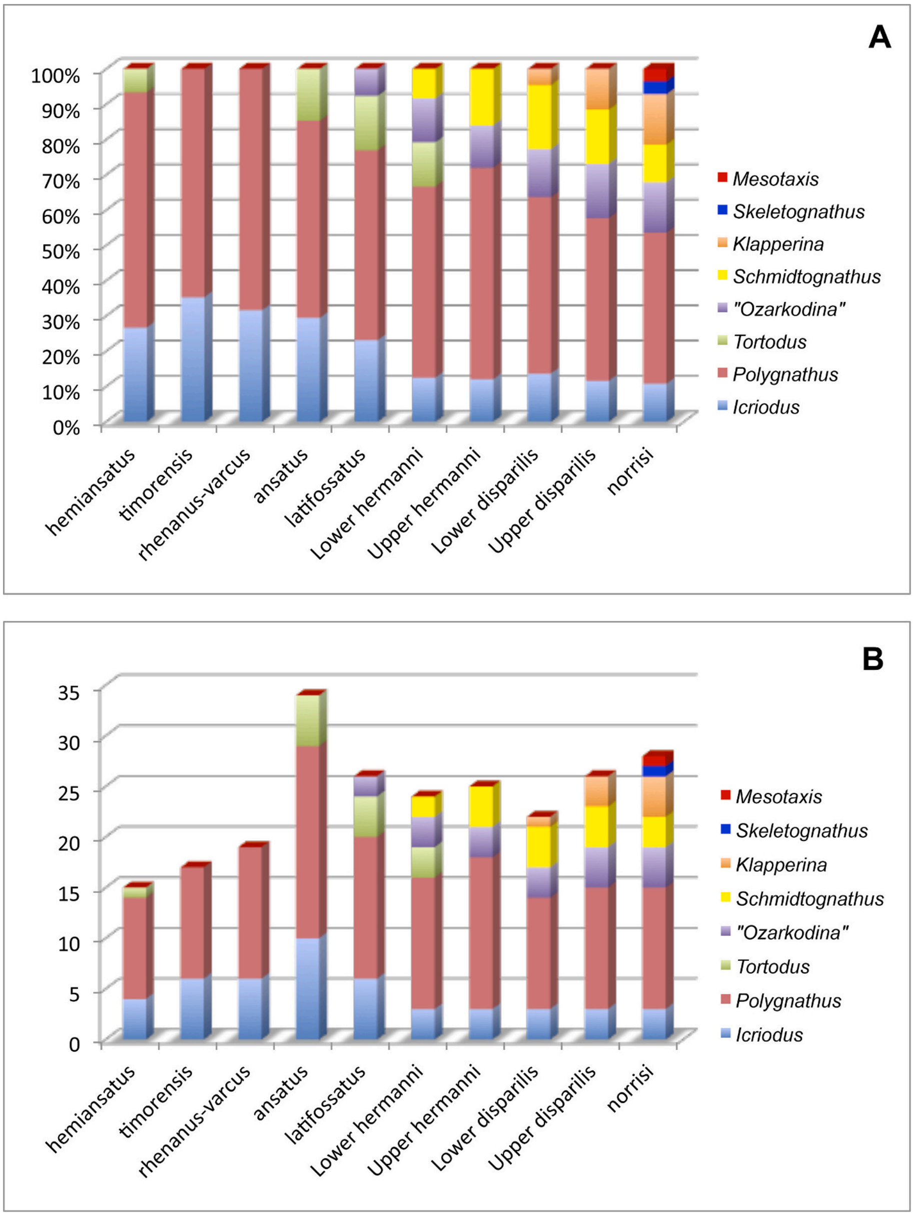

Fig. 5. Qualitative analysis, zone by zone, of diversity for Givetian genera in the Pyrenees. A: Proportional changes in diversity zone-by-zone for all recorded genera in the Givetian Pyrenean sequence. B: Absolute count of species for each genus in every Givetian zone.

timorensis, and *rhenanus-varcus* zones. The *ansatus* Zone represents a short, but important, radiation of *Tortodus*, lasting until the Lower *hermanni* Zone. From the *latifossatus* Zone upwards, species of "*Ozarkodina*" play a substantial role in conodont biodiversity. The onset of the upper Givetian (base of the Lower *hermanni* Zone) marks the radiation of *Schmidtognathus*, which becomes a key component of upper Givetian biodiversity. The innovation of *Klapperina* occurs in the Lower *disparilis* Zone, with its radiation continuing in the two following zones. The first occurrences of *Skeletognathus* and *Mesotaxis* in the *norrisi* Zone complete the transition in conodont faunal composition from the lower to the upper Givetian.

3.4. Global Events and their Effects on Pyrenean Conodont Shifts

3.4.1. Kačák Event

The Kačák Event (Walliser, 1984, 1996; House, 1985, 1996, 2002) is a multiphase, third-order Event (Becker et al., 2016) that happened in the late Eifelian, near the Eifelian-Givetian boundary. The lithologic expression of this Event is associated with an episode of black shales, initially identified as the Kačák Member of the Srbsko Formation in the Prague Synform (House, 1985). Subsequently, Walliser (1996) distinguished two separate events within this interval: the Lower Kačák Event at the base of the shale sequence, and the Upper Kačák Event, at its top. The Lower Kačák Event is positioned near the boundary between the Eifelian *kockelianus* and *ensensis* conodont zones, while the Upper Kačák Event coincides with the Eifelian-Givetian boundary (Walliser, 1996).

Walliser and Bultynck (2011) analyzed conodont sequences across the Kačák Event in the Jebel Mech Irdane section, where the GSSP for the base of the Givetian is defined, as well as in the Bou Tchrafine and Jebel Ou Driss sections. They extended the Kačák Episode from the uppermost part of the Eifelian *kockelianus* Zone to the lower part of the *hemiansatus* Zone, just above the base of the Givetian, and identified two distinct phases within this interval: the Late Eifelian 1 Event and the Late Eifelian 2 Event. In terms of conodonts, they observed extinction events restricted to five taxa of the *Polygnathus angusticostatus* group. However, innovation and survival were more significant. They highlighted the innovation of *P. hemiansatus* (the index taxon of the base of the Givetian) within the *P. pseudofoliatus* group, marking the beginning of this lineage.

In the Pyrenean section of Renanué (Liao et al., 2001, 2008; Liao, 2014; Liao and Valenzuela-Ríos, 2022), basal dark shales underlying grey limestones may represent the local expression of the Kačák Event. However, the boundary between these two units is tectonised, making it difficult to determine the precise age of the shaly interval. Two other Pyrenean sections spanning the Eifelian-Givetian boundary- La Guàrdia d'Ares (Liao and Valenzuela-Ríos, 2013) and Villech (Gouwy et al., 2013)- do not show any shale intervals, and no lithological evidence of the Event has been recognized. The La Guàrdia d'Ares section exhibits a continuous limestone succession in the interval where the Kačák Event is expected (from the *kockelianus* to the *hemiansatus* zones). The Villech section, on the other hand, has a covered interval between the *eiflius* and the *timorensis* zones.

The Pyrenean conodont record in the *hemiansatus* Zone, particularly its lower part-, which correlates with the Late Eifelian 2 Event of Walliser and Bultynck, or, with the end of the Kačák Event-, contains the lowest taxonomic diversity (15 taxa) among all Givetian zones. The Index of Conodont Evolution (ICE) is 1, indicating a stable phase with neither significant extinction nor diversification. Most of these 15 taxa are Eifelian survivors, crossing the boundary into the Givetian. *Icriodus struvei*, *Polygnathus angustipennatus*, and *Tortodus kockelianus* disappear in this zone, mirroring extinctions observed in Morocco, although their timing differs. In Morocco, *P. angustipennatus* disappears within the Late Eifelian Event 1 in the Bou Tchrafine and Jebel Ou Driss sections and within the Late Eifelian Event 2 in the Jebel Mech Irdane section, whereas in the Pyrenees, it survives into the Givetian before going extinct shortly after. Similarly, *I. struvei* disappears during the Late Eifelian Event 1 in the Bou Tchrafine and Jebel Ou Driss sections. *Tortodus kockelianus* disappears even earlier, before the base of Late Eifelian Event 1 in the Jebel Mech Irdane section and within this Event in the Bou Tchrafine section. Thus, while these taxa became extinct in Morocco during the late Eifelian, they survived into the Givetian in the Spanish Pyrenees before disappearing shortly thereafter.

The three Pyrenean conodont innovations of *Polygnathus hemiansatus*, *Icriodus obliquimarginatus*, and *Polygnathus linguiformis weddigei* are consistent with Moroccan records. *Polygnathus hemiansatus* represents the evolutionary innovation of the *P. pseudofoliatus* group during the Late Eifelian Event 2. *Icriodus obliquimarginatus* represents diversification within the *I. regularicrescens* lineage, and *P. linguiformis weddigei* symbolizes an innovation within the *P. linguiformis* group.

In brief, the Kačák Event had a relatively minor impact on Pyrenean conodont faunas, affecting only three species. However, these taxa disappeared shortly after the Event, suggesting that its effects in the Pyrenees may have lasted slightly longer than in other regions. Additionally, three major conodont lineages emerged at the end of the Event or shortly thereafter.

3.4.2. Pumilio Events

The Lower and Upper *pumilio* events are characterized by dark-black lumaquelles of micromorphic brachiopods. These events represent a faunal bloom rather than an extinction and are linked to a transgressive pulse, which has been interpreted as a widespread tsunami event (Lottmann, 1990; House, 2002). Becker et al. (2016) placed the Lower *pumilio* within the *rhenanus-varcus* Zone and the Upper *pumilio* in the lower part of the *ansatus* Zone.

In two Pyrenean sections, we have identified comparable lumaquelles of micromorphic brachiopods. One of these levels is located in Bed 44 of section Renanué (Liao et al., 2001, 2008; Liao, 2014). This bed is an oncoid rudstone, with oncoid cores predominantly composed of brachiopods (Liao et al., 2008). The conodont record places this bed within the upper half of the *ansatus* Zone (Liao, 2014; Liao and Valenzuela-Ríos, 2022), making it younger than the Upper *pumilio* and therefore not correlatable with this Event. Instead, if related to any event, it would more likely correspond to Phase 1 of the Taghanic Crisis (Aboussalam, 2003; Aboussalam and Becker, 2011; see below).

The second level is found in Bed 29 of the Villech section (Gouwy et al., 2013) and consists of a thin black limestone layer with a lumaquelle of micromorphic shells of either brachiopods or ostracods, interbedded between two thin black shale layers. The lithological characteristics suggest this level represents a *pumilio* Event. However, the conodont record situates it within the *latifossatus* Zone, precluding its correlation with any *pumilio* Event.

The effects of the Upper *pumilio* Event on Pyrenean conodont faunas are evident in the *ansatus* Zone, which exhibits the highest taxonomic diversity of the entire Givetian (34 taxa), along with a significant income of 15 new taxa- the highest origination rate observed in all metrics: 0.44 in per-taxon rate, 0.75 in Van Valen, and 0.45 in Van Valen excluding singletons (Tb. 2). This diversification is charazterized by the radiation of *Tortodus* (five species: *T. caelatus*, *T. bultyncki*, *T. trispinatus*, *T. weddigei*, and *T. variabilis*), *Polygnathus* (six new taxa: *P. ansatus*, *P. ovatinodosus*, *P. beckmanni*, *P. parawebbi*, *P. linguiformis mucronatus*, and *P.* sp. C) and *Icriodus* (four taxa: *I. brevis eslaensis*, *I. lilliputensis*, *I.* l. *latericrescens*, and *I.* aff. *subterminus*). Most of these originate in the lower part of the zone, aligning with the timing of the Upper *pumilio* Event.

In contrast, the Lower *pumilio* Event appears to have had no effect on conodont diversity. The *rhenanus-varcus* Zone shows no significant change in conodont diversity compared to the preceding *timorensis* Zone (19 and 17 taxa respectively). Moreover, origination is limited to only the two index taxa, *P. varcus* and *P. rhenanus*, resulting in the second lowest origination rate of the entire Givetian (Tb. 2).

3.4.3. Taghanic Crisis

The Taghanic Event (House, 1985; Walliser, 1996) is a prolonged multiphased event associated with multiple major extinctions (House, 2002; Aboussalam, 2003). Due to its significant biotic impact, Aboussalam (2003) and Aboussalam and Becker (2011) elevated it to the status of a second-order global Crisis. Walliser (1996, p. 232) placed the beginning of this Event at the base of the *hermanni* conodont Zone and noted that "*the maxima of extinctions did not occur simultaneously in the different groups*", indirectly supporting its polyphasic nature. He documented peak extinction rates in the *latifossatus* Zone and between the Lower and Upper *hermanni* zones.

Aboussalam (2003), in her comprehensive monograph on the Taghanic Event, focusing primarily on Moroccan sections, with additional data from France and Germany, identified three phases spanning 400–800 ka, from the upper part of the *ansatus* Zone to the base of the Lower *hermanni* Zone. This interval corresponds to the period between the Taghanic Onlap (Johnson, 1970) and the Geneseo Transgression in New York, during which the Tully Limestone was deposited.

Aboussalam (2003) and Aboussalam and Becker (2011) considered the *semialternans* Zone to be positioned between the *ansatus* and Lower *hermanni* zones. However, Liao and Valenzuela-Ríos (2017) reassessed the Givetian zonation and incorporate most of what these authors classified as *semialternans* Zone into the *latifossatus* Zone. In many sections studied in Aboussalam (2003), the entry of *P. latifossatus* seems to be delayed, as it first occurs in the Lower *hermanni* Zone (e.g. Bou Tchrafine, Seheb el Rhassal 2, Pic de Bissous, Côl de Puèche de la Suque –data from this section are not from her samples). Other sections lack identification of either taxon, making biostratigraphical interpretations uncertain (e.g. Jebel Amelame, El Atrous Nord, Tiguisselt, Oufrane West, Oufrane Ost, Oued Mzerreb West). In yet other sections, "*Ozarkodina*" *semialternans* or both taxa enter at the same level in the succeeding Lower *hermanni* Zone, and consequently, the position of the *semialternans* Zone is arbitrary (e.g. Ouidane Chebbi, Hassi Nebech 2, Burgberg). In our analysis, we considered the *latifossatus* Zone as the set of strata characterized by the entry of *Polygnathus latifossatus*, positioned between the top of the *ansatus* Zone and the base of the Lower *hermanni* Zone. Furthermore, Aboussalam and Becker, 2011, Fig. 2) plotted the lowest occurrences of "*O.*" *semialternans* and *P. latifossatus* at the same stratigraphic level.

Above, we identified two potential lithologic expressions of these events in the Pyrenees: Bed 44 of the Renanué section and Bed 29 of the Villech. The conodont record places these two levels in the upper part of the *ansatus* Zone and amid the *latifossatus* Zone, respectively. Liao et al. (2008) previously noted an abrupt lithologic break between Beds 42 and 47 in the Renanué section, suggesting the onset of a transgressive phase, with Bed 44 marking the main transgressive level. Consequently, these levels could represent the basal transgression at the beginning of the Taghanic Crisis.

Bed 29 in the Villech section, characterized by a thin black limestone with small-shell lumaquelles bracketed by black shales, may signify a brief deepening pulse within the mid-*latifossatus* Zone. Although it resembles typical *pumilio* Beds sedimentologically, it likely corresponds to the highest Event interval of the Taghanic Crisis (Aboussalam, 2003).

The Pyrenean conodont record exhibits a decline in diversity from the *ansatus* Zone (34 taxa) to the *latifossatus* Zone (26 taxa). Origination rates in the *latifossatus* Zone are among the lowest recorded (0.19) and third lowest in Van Valen metrics excluding singletons (0.2). Meanwhile, the *ansatus* Zone experiences the highest extinction rate of the entire Givetian (13 taxa), with the largest loss percentages in per-taxon rate and Van Valen metrics (Tb. 2).

The following *Icriodus* become extinct in the *ansatus* Zone: *I.* aff. *Regularicrescens*, *I. obliquimarginatus*, and *I. lindensis*; these three taxa belong to the *regularicrescens*-branch, which is severely affected. Furthermore, *I.* aff. *Subterminus* and *I. lilliputensis* as a singleton of the *werneri*-branch also disappear. Among the *Polygnathus*, *P. eiflius*, *P. x. ensensis*, *P. angusticostatus*, *P. parawebbi*, *P. pseudoeiflius*, and the singletons *P. beckmanni* and *P.* sp. C are the losses. *Tortodus variabilis* is a singleton of this zone. Most of these extinctions could be related to the lower phase of the Taghanic Crisis. The subsequent *latifossatus* Zone shows the second highest number of extinction and the unique interval where the Index of Conodont Evolution is below 1, and therefore, conodonts are at extinction threshold. *Polygnathus linguiformis weddigei*, *P. ansatus, I.* aff. *expansus*, *I. b. eslaensis*, *I.* l. *latericrescens*, *T. caelatus*, *T. bultyncki*, and the singleton"*O." brevis* are the taxa that go extinct in the *latifossatus* Zone. They can be related to either the high or the highest Event interval of the Taghanic Crisis; even some of them can be affected by the interval in the lower part of the *latifossatus* Zone and others by the one in the upper part of the zone.

3.4.4. *Geneseo Event*

The Geneseo Event represents the final transgressive phase of the Taghanic Crisis and corresponds to the transgression of the Geneseo shales over the Upper Tully Limestone in New York (García-Alcalde et al., 2012). It is placed at the base of the Lower *hermanni* Zone, coinciding with the middle-to-upper Givetian boundary.

Pyrenean conodont biodiversity in the Lower *hermanni* Zone remains similar to that of the underlying *latifossatus* Zone, with a low extinction count (four taxa). However, significant faunal turnover occurs. Three of the extinct taxa include *Tortodus trispinatus*, *T. weddigei*, and *T.* aff. *bultyncki* –a singleton, leading to the disappearance of the genus from the Pyrenees. The fourth extinct taxon is *Polygnathus linguiformis klapperi*.

Conversely, "*Ozarkodina*", which first appears in the *latifossatus* Zone, begins its radiation with the income of "*O.*" *s. sannemanni* and "*O.*" *s. adventa* in the "*O.*" *sannemanni* lineage. Simultaneously, the genus *Schmidtognathus* undergoes its initial radiation with the appearance of *S. hermanni* and *S. pietzneri*.

Additionally, *Icriodus* biodiversity declines significantly, with only the three long-ranging taxa *I. difficilis*, *I. b. brevis*, and *I. symmetricus* persisting. This turnover marks the culmination of the Taghanic Crisis and the transgressive phase of the Geneseo Event.

3.4.5. *Frasnes Event*

The Frasnes Event (House, 1985; Walliser, 1996) was initially characterized by the extinction of most pharciceratids and the onset of a major global transgression. It has been classified as a second-order Global Event, consisting of three major transgressive pulses: the lower one at the base of the *norrisi* Zone, the middle one at the base of the Frasnian, and the upper one in FZ2 (Becker et al., 2016, 2020).

Neither the lower nor middle phases of the Frasnes Event appear to have significantly impacted the overall biodiversity of Pyrenean conodont faunas. In fact, the number of taxa increased slightly from 26 taxa in the underlying Upper *disparilis* Zone to 28 in the *norrisi* Zone. However, extinction rates during this interval were among the highest of the entire Givetian, with seven 7 taxa disappearing. The relative extinction rates (per-taxon rate and Van Valen) were the third highest after those of the *ansatus* and *latifossatus* zones. This elevated extinction rate was counterbalanced by an equivalent number of new originations, resulting in a compositional shift within the conodont faunas.

During this period, *Klapperina* reached its acme with four taxa: *K. disparilis*, *K. disparalvea*, *K. unilabius*, and *K. ovalis*. Additionally, two new genera appeared in the *norrisi* Zone: *Skeletognathus*, represented by *Sk. norrisi*, and *Mesotaxis*, with *M. falsiovalis*.

The Givetian-Frasnian transition, corresponding to the second (middle) phase of the Frasnes Event, had little impact on Pyrenean conodont faunas. Many taxa successfully crossed the boundary, and only *P. angustidiscus* and *P. decorosus* disappeared slightly above it. At the same time, several new taxa emerged at the base of and within FZ1, above the middle Frasnes Event. Notable among these were *Ancyrodella rotundiloba pristina, A. rotundiloba rotundiloba*, *A. binodosa, A. soluta, P. rugosa, M. asymmetricus*, and *P. tafilensis*, the latter of which first appeared earlier in Morocco.

Thus, in the Pyrenees, both the lower and middle phases of the Frasnes Event represented periods of conodont faunal innovation and radiation rather than extinction.

3.5. *Comparison with selected relevant areas (Tables 4A-C; Figs. 6A-C)*

The comparison of conodont evolution and biodiversity across different regions during the Givetian posses difficulties due to inconsistencies in taxonomic studies, the lack of illustrated taxa, and differing biostratigraphical schemes. Furthermore, relatively few studies cover the entire Givetian in a single section or region. While certain intervals have been thoroughly studied (e.g. the Taghanic Crisis in Morocco, Aboussalam, 2003; Aboussalam and Becker, 2011), other zones remain insufficiently explored, complicating comprehensive evolutionary comparisons for the entire Givetian. A detailed discussion of taxonomical and biostratigraphical approaches falls beyond the scope of this report; thus, we rely on published studies from various sections within the Central Asian Orogenic Belt, South China Block, eastern Gondwana (Australia), the perigondwanan outcrops in the Carnic Alps, the North Africa segment of Gondwana, and the Euramerican outcrops in Canada.

3.5.1. *Central Asian orogenic belt*

3.5.1.1. Zeravshan Range. Bardashev and Ziegler (1985) documented the conodont fauna from the Shishkat section in the Zeravshan Mountains (Tajikistan). This section spans from the *serotinus* Zone (Emsian) through the Lower *asymmetricus* Zone in the lower Frasnian. The presence of *Ancyrodella alata* without major precision suggests a correlation with zones FZ2 or FZ3. The lower Givetian zones were not identified. The middle Givetian zones are distinguished by the entry of index taxa. The authors grouped all records under the *varcus* Zone but identified the bases of the lower, middle, and upper *varcus* zones based on the entry of *Polygnathus varcus*, *P. ansatus*, and *P. latifossatus*, respectively. We utilize these data for correlation with our records. The successive entries of *Schmidtognathus hermanni* and *P. cristatus* allow for the subdivision of their *hermanni-cristatus* Zone into Lower and Upper *hermanni* zones. Their *disparilis* Zone was identified by the entry of *Palmatolepis* (now *Klapperina*) *disparilis.* While the authors did not subdivide this zone, they

Table 4

Comparison of Pyrenean data with other selected sections. For full references to these sections see descriptions in the text, chapter 3.5. Table 4A: Total number of taxa per zone. Table 4B: Number of originations per zone. Table 4C: Number of extinctions per zone. As described above, some intervals lack data; these are left blank in the tables.

Table 4A

N total	Pyrenees	Shishkat	Tien-Shan+Pamir	Sihongshan	Broken River	Zuc di Malaseit	Oberbuchach II	Morocco	Canada
norrisi	28	15	25	9				44	6
Upper disparilis	26	13	24	11				36	5
Lower disparilis	22	15	27					41	
Upper hermanni	25	11	21	4				49	
Lower hermanni	24	12	21				9	61	
latifossatus	26	12	18		15		7	54	22
ansatus	34	8	14	5	19	18	6	51	16
rhenanus-varcus	19	7	13	5	18	18	7		
timorensis	17					14	11	15	9
hemiansatus	15				16	13	10	21	9

Table 4B

Originations	Pyrenees	Shishkat	Tien-Shan+Pamir	Sihongshan	Broken River	Zuc di Malaseit	Oberbuchach II	Morocco	Canada
norrisi	7	7	1	3				10	1
Upper disparilis	6	2	2	7				5	0
Lower disparilis	2	6	9					10	
Upper hermanni	5	1	3	4				4	
Lower hermanni	6	3	10				5	18	
latifossatus	5	4	6		1		1	6	7
ansatus	15	2	5	2	3	2	1	16	3
rhenanus-varcus	2	5	4	3	4	4	2		
timorensis	5					2	5	3	2
hemiansatus	3				2	2	2	8	2

Table 4C

Extinctions	Pyrenees	Shishkat	Tien-Shan+Pamir	Sihongshan	Broken River	Zuc di Malaseit	Oberbuchach II	Morocco	Canada
norrisi	7	9	3	6				20	0
Upper disparilis	5	3	1	5				3	0
Lower disparilis	2	5	4					9	
Upper hermanni	5	3	3	0				5	
Lower hermanni	4	1	3				9	14	
latifossatus	8	3	6		5		3	13	8
ansatus	13	2	1	5	5		0	9	1
rhenanus-varcus	0	1	4	2	2	3	2		
timorensis	0					1	4	1	1
hemiansatus	3				2	2	4	6	1

noted the presence of *Polygnathus dengleri* at higher stratigraphic levels within it, allowing differentiation between Lower and Upper *disparilis* zones. Finally, they recognized the *asymmetricus* Zone, which currently comprises several Givetian and Lower Frasnian zones. The presence of *Polygnathus* (now *Skeletognathus*) *norrisi* identifies the *norrisi* Zone, with the lower Frasnian positioned above by the entry of *Ancyrodella r. rotundiloba*.

In our comparison, we reinterpret their zonation as described above and apply the range-through approach to count total diversity within recognized intervals. The diversity in the Shishkat section is significantly lower. The number of taxa in the middle Givetian *rhenanus/varcus*, *ansatus*, and *latifossatus* zones is 7, 8 and 12 respectively, compared to 19, 34 and 26 in the corresponding Pyrenean zones. Notably, in the Zeravshan section, the highest middle Givetian diversity occurs in the *latifossatus* Zone rather than in the *ansatus* Zone, as seen in the Pyrenean sections. Furthermore, the number of originations in the *ansatus* Zone (2) is considerable lower than in the *latifossatus* Zone (4), in stark contrast to the Pyrenean *ansatus* Zone (15 new taxa), and its similar with respect to the *latifossatus* Zone (5). Another striking difference is that the Asian section records an upper Givetian minimum of diversity in the Upper *hermanni* Zone (11 taxa). In contrast, the Pyrenean Lower *disparilis* Zone represents the minimum value of the upper Givetian (22 taxa).

3.5.1.2. Middle and Southern Tien-Shan and the central Pamirs. Bardashev (1992) conducted a comprehensive study of the Middle Devonian of Central Asia, analyzing 20 sections and recognizing eight conodont zones from the Eifelian *partitus* Zone to the Givetian *disparilis* Zone. For the Givetian, he recognized the *varcus*, *hermanni-cristatus*, and *disparilis* zones. He identified subdivisions of the *varcus* Zone in the section Shiskat section based on the successive entries of *Polygnathus timorensis*, *P. ansatus*, and *P. latifossatus* (Ziegler et al., 1976). However, *P. timorensis* appears in the Shishkat section after *P. varcus*, indicating that this interval corresponds to the middle Givetian *rhenanus-varcus* Zone rather than the lower Givetian *timorensis* Zone. Furthermore, Bardashev (1992) reported *P. timorensis* and *P. varcus* from the same sample, aligning this level with the Lower *varcus* Subzone (fig. 14). This interpretation aligns with Bultynck (1987), who subdivided the Lower *varcus* Subzone into the *timorensis* and *rhenanus/varcus* zones, with the latter marking the base of the middle Givetian (Liao and Valenzuela-Ríos, 2017). In our comparison, we consider Bardashev's Lower *varcus* Subzone equivalent of the *rhenanus/varcus* Zone.

The entry of *Polygnathus cristatus* in the upper part of the *hermanni-cristatus* Zone allows for it subdivision into Lower and Upper subzones, currently aligning with the Lower and Upper *hermanni* Zones. For the *disparilis* Zone, Bardashev (1992) recognized three subzones, with the middle and upper subzones based on the occurrence of early and late forms of *P. dengleri*, respectively. The entry of *Ancyrodella rotundiloba* marks the beginning of the Frasnian. We correlate his middle *disparilis* Zone, marked by the entry of *P. dengleri*, with the Upper *disparilis* Zone.

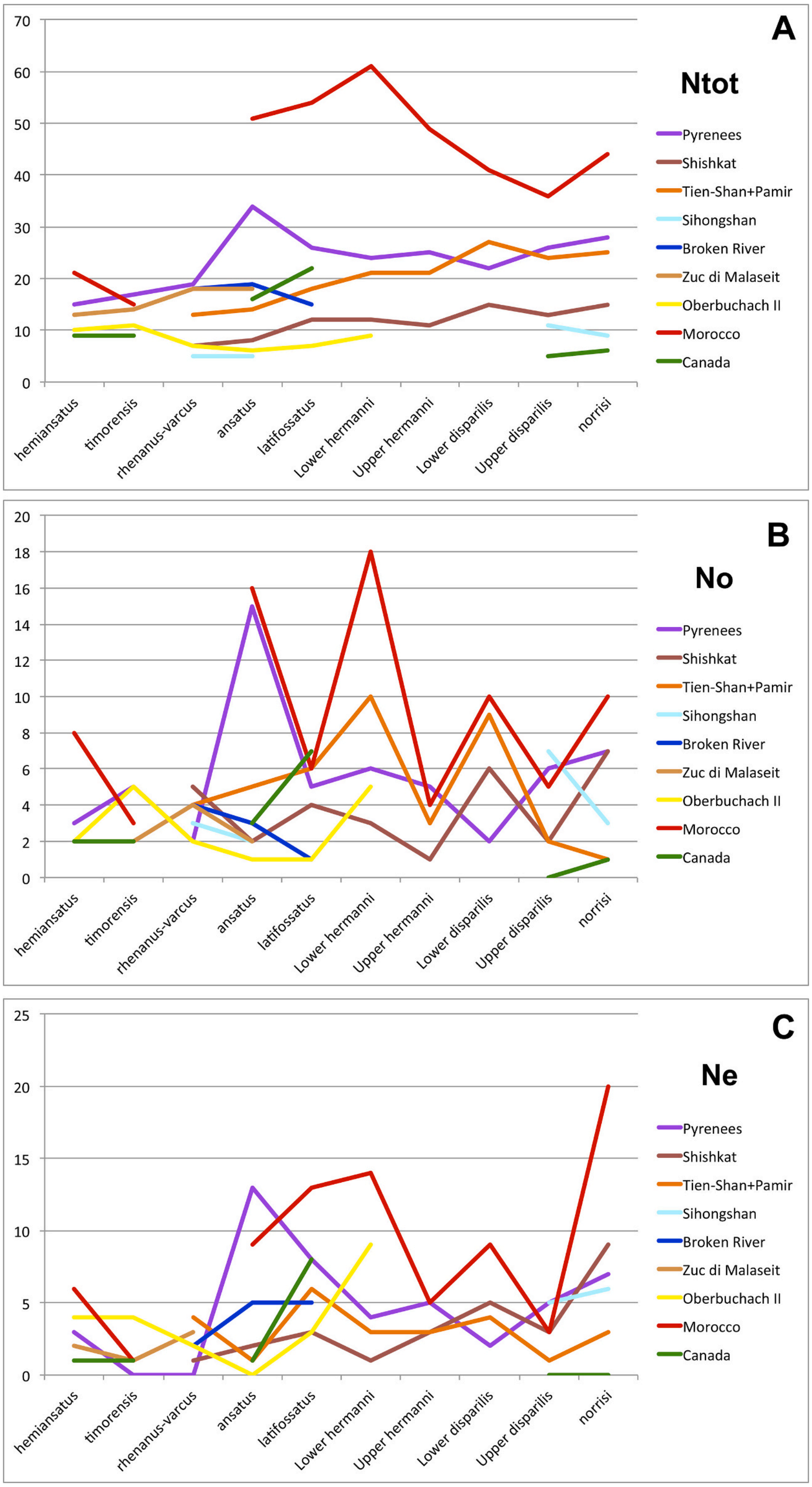

Fig. 6. Various plots showing the total number of taxa (Ntot, 6 A), originations (No, 6B), and extinctions (Ne, 6C), based on data in Tables 4A-C respectively. Discontinuous or partial lines represent incomplete data for the different sections, as previously mentioned.

Surprisingly, Bardashev (1992) did not document the presence of *Skeletognathus norrisi* in the Shishkat section, despite previous reports of its entry within sample 8B-45 (Bardashev and Ziegler, 1985). This discrepancy highlights the challenges in correlating conodont faunas globally. Our comparison is based on figs. 14 and 15 of Bardashev (1992) and our interpretation of biozones according to his data.

The diversity trends in these sections are similar to those observed in the Shishkat section but with increased biodiversity. During the middle Givetian, the *rhenanus/varcus* and *ansatus* zones exhibit comparable diversity values (13 and 14 taxa respectively), with the *latifossatus* Zone reaching a maximum of 18 taxa. These values highly contrast with the Pyrenean record, where diversity is markedly higher, and the diversity peak occurs in the *ansatus* Zone. Similarly, the number of new taxa differs: in the Pyrenees, the *ansatus* Zone exhibits the highest number of originations (15 new taxa), whereas in the Asian sections, this zone yields only five new taxa, with the subsequent *latifossatus* Zone showing a slightly higher number of new taxa (6).

The upper Givetian zones exhibit diversity levels comparable to those in the Pyrenees, but regional trends differ. The Asian sections reach maximum diversity in the Lower *disparilis* Zone (27 taxa), whereas in the Pyrenees, this zone marks the low diversity peak (22 taxa). Similarly, the Lower and Upper *hermanni* zones have lower diversity in Asia (21 taxa each) than in the Pyrenees (24 and 25 taxa respectively).

The Central Asian sections, including the Zeravshan Range and the Middle and Southern Tien-Shan, exhibit lower overall diversity compared to the Pyrenean sections, with notable differences in diversity peaks and origination rates. The placement of maximum diversity in the Lower *disparilis* Zone in Central Asia, as opposed to the *ansatus* Zone in the Pyrenees, underscores the complexity of global conodont distribution patterns. Additionally, discrepancies in reported taxa, such as the absence of *Skeletognathus norrisi* in later studies despite previous documentation, highlight the limitations of existing datasets and the difficulties in worldwide correlation. These findings emphasize the need for more comprehensive, high-resolution taxonomic and biostratigraphic studies to refine global correlations and better understand conodont evolution during the Givetian.

3.5.2. South China Block: Sihongshan section (SW Guangxi)

The Sihongshang section is one of the most continuous known Devonian sections in the South China Block, comprising strata from the Pragian to the Famennian (Ziegler and Wang, 1985). Regarding the Givetian, the following zones have been identified: Lower, Middle and Upper *varcus* zones; Lower and Upper *hermanni-cristatus* Zone; *disparilis* Zone; and the Lowermost *asymmetricus* Zone.

The base of the Lower *varcus* Zone is marked by the first occurrence of *Polygnathus varcus* in Bed 30 (conodont samples 385–389), which corresponds to the first middle Givetian *rhenanus/varcus* Zone. The base of the Middle *varcus* Zone is defined by the entry of *P. ansatus* in Bed 31 (samples 381–384), correlating with the *ansatus* Zone. However, the bases of the Upper *varcus* Zone (= *latifossatus* Zone) and the Lower *hermanni-cristatus* Zone (=Lower *hermanni* Zone) were arbitrarily placed in Bed 33 (sample 375–8 for the former and sample 375–7 for the latter). Notably neither of these two samples yielded any conodonts (Ziegler and Wang, 1985, tb. 1), resulting in an interval of uncertainty between the *ansatus* and the Upper *hermanni* Zone. The base of the latter zone (termed the Upper *hermanni-cristatus* Zone by Ziegler and Wang) is defined by the occurrence of *P. cristatus* at the base of Bed 34 (sample 375-6a).

The position of the base of the overlying *disparilis* Zone is also uncertain. Ziegler and Wang (1985) placed its beginning with the entry of *Palmatolepis disparilis* (= *Klapperina disparilis*) in the lower part of Bed 34 (sample 375-6c), above the lowest record of *Polygnathus dengleri* (sample 375-6b). The former *Pa. disparilis* Zone has been subdivided into the Lower and Upper *disparilis* zones, with the base of the former defined by the entry of *K. disparilis* and the base of the latter by the entry of *P. dengleri*. Consequently, the entry of *K. disparilis* in the Sihongshan section is delayed and cannot be used to trace the base of the zone. In contrast, the entry of *P. dengleri* allows the identification of the Upper *disparilis* Zone. The Lower *disparilis* Zone in this section is confined to a strongly condensed interval of less than 10 cm, between the entries of *P. cristatus* and *P. dengleri*. Finally, the lowermost *asymmetricus* Zone (now *norrisi* Zone) is recognized by the first occurrence of *P. asymmetricus* (now *Mesotaxis asymmetricus*) in sample 375-6e. Consequently, only the *rhenanus/varcus*, *ansatus*, Upper *hermanni*, Upper *disparilis*, and *norrisi* zones can be reliably identified in the Sihongshan section.

A comparison of the conodont records between this Chinese section and the Pyrenean record reveals strong discrepancies. Firstly, biodiversity in the Sihongshan section is significantly lower. Both identified middle Givetian zones (*rhenanus/varcus* and *ansatus*) contain only five conodont taxa each, compared to 19 and 34 taxa, respectively, in the Pyrenees. Moreover, all conodonts of the *ansatus* Zone disappear in the Sihongshan section. While extinction is also high in the Pyrenees (13 taxa), more than half of the taxa persist into the *latifossatus* Zone or higher. The Upper *hermanni* Zone represents a limited renewal of conodont fauna, with only four taxa identified, whereas the Pyrenean record contains 25 taxa. The Upper *disparilis* Zone shows a relative increase in diversity, with up to 11 taxa, which slightly decreases to nine in the *norrisi* Zone. This trend contrasts with the Pyrenean record, where 26 taxa are recorded in the Upper *disparilis* Zone and 28 in the *norrisi* Zone. Additionally, in the Sihogshan Upper *disparilis* Zone, five of these 11 taxa become extinct, whereas in the Pyrenees, five taxa disappear out of 26. Extinction rates are even higher in the *norrisi* Zone of the Sihongshan section, where six of the nine taxa disappear, compared to seven of 28 taxa in the Pyrenees. Consequently, the extinction rate in the Chinese section is much higher than in the Pyrenean sections for the upper part of the Givetian.

The Sihongshan section presents a highly condensed Devonian sequence with significant gaps in conodont records, leading to uncertainties in zonal boundaries. Compared to the Pyrenean sections, biodiversity is markedly lower, with fewer taxa identified in each zone. This reduced diversity, coupled with higher extinction rates, suggests a more environmentally stressed or taphonomically biased setting. Despite these limitations, the section provides critical insights into middle and upper Givetian conodont distributions in South China, with identifiable zones including *rhenanus/varcus*, *ansatus*, Upper *hermanni*, Upper *disparilis*, and *norrisi*.

3.5.3. Eastern Gondwana: Broken River, Australia

Mawson and Talent (1989) compiled data from 23 sections in the Broken River area of northern Queensland, Australia, spanning from the Lower Devonian *inversus* Zone (Emsian) to the Middle Devonian *hermanni-cristatus* Zone (Givetian). They documented the range of all pectiniforms up to the upper *varcus* Zone, beyond which they denote "*Younger Zones*" (Mawson and Talent, 1989, fig. 9). Mawson and Talent (1989) maintained the subdivision of the *varcus* Zone into Lower, Middle and Upper subzones, with the successive entries of the respective key indexes allowing precise correlation with current zonal nomenclature. They recognized *Polygnathus hemiansatus*, within the upper parts of their *ensensis* Zone; thus identifying the *hemiansatus* Zone and the Eifelian/Givetian boundary in the Broken River sequences. Slightly above this, *Icriodus obliquimarginatus* appears. The next *timorensis* Zone is not well defined in the Australian sequences, *P. timorensis* and *P. varcus* appear together in the Lower *varcus* Zone; this level correlates with the base of the first middle Givetian *rhenanus/varcus* Zone. The sequential entries of *P. ansatus* and *P. latifossatus* establish the bases of the *ansatus* and *latifossatus* zones, respectively. However, the dearth of records higher than these levels makes precise zonal assignment difficult. In four sections in the Dosey Creek-Storm Dam-Page Creek area (SD15 north, SD164, SD210, and SD216) the recovery of five specimens of *Schmidtognathus* n. sp. A suggests that these levels are not older than the upper Givetian, but their exact zonal placement remains uncertain. Additionally, a broken specimen from Bed 192 (section SD15) comparable to *S. peracutus* suggests an age of the Upper *hermanni* Zone or higher. An isolated record of *I. symmetricus* in the highest limestone strata (spot sample) of section SD205 is also inconclusive. Consequently, only lower and middle Givetian data can be reliably compared with the Pyrenean record.

Biodiversity in the *hemiansatus* Zone is comparable between the Australian (16 taxa) and Pyrenean (15 taxa) sections, with similar low numbers of originations and extinctions (two taxa in Australian and three in Spain). However, taxonomic composition is slightly different, as Australian faunas include two subspecies of *Eognathodus bipennatus* and the species *Prioniodina sardinia*, which are absent from the Pyrenees. Biodiversity in the *rhenanus/varcus* Zone is also similar, with 18 taxa in Australia and 19 in the Pyrenees, although two taxa become extinct in Australia while none disappear in the Pyrenees. The originations in

Australia (4 taxa) are double than in the Pyrenees (2 taxa).

However, the *ansatus* and *latifossatus* zones exhibit significant differences. The Australian *ansatus* Zone contains only 19 taxa, whereas the Pyrenean record shows 34. Furthermore, origination and extinction rates are much lower in Australia (three and five taxa, respectively) than in the Pyrenees (15 and 13 taxa, respectively). The Australian *latifossatus* Zone has 15 taxa, with five extinctions and only one origination (the index taxon), whereas the Pyrenean record contains 26 taxa, with five originations and eight extinctions.

The Broken River sections offer a relatively detailed conodont succession up to the middle Givetian but become less well-resolved beyond the *latifossatus* Zone. Compared to the Pyrenean sections, biodiversity is similar from the *hemiansatus* to the *rhenanus/varcus* zones, but declines significantly in the middle Givetian *ansatus* and *latifossatus* zones. This suggests a lower degree of faunal turnover and a more stable paleoenvironment in Australia. However, the scarcity of upper Givetian records limits direct correlations beyond the *latifossatus* Zone. Despite these challenges, the Broken River sequences remain an important reference for Devonian biostratigraphy in eastern Gondwana.

3.5.4. *Perigondwanan outcrops: Carnic Alps*

One of the most comprehensive Devonian conodont sequences in the Carnic Alps is found in the section Oberbuchah II (Schönlaub, 1980, 1985). The latter paper remains a key reference for conodont biostratigraphy in the Carnic Alps, covering records from the Lochkovian through the Givetian. Schönlaub et al. (2017) later re-examined the section identifying the *hemiansatus*, *timorensis*, *rhenanus*, *ansatus, latifossatus*, and *hermanni* Givetian conodont zones. However, assigning records to the *hermanni* Zone is problematic since *K. disparalvea* appears in the lowermost bed attributed to this zone, whereas its global range does not start until the *disparilis* Zone. Consequently, in our comparisons, we only consider records up to the *latifossatus* Zone. Additionally, we include the Zuc di Malaseit Basso (ZMB) section (Suttner et al., 2017), which provides records from the *hemiansatus* to the lower part of the *ansatus* zones within a broader study of the Kacák Event in the Carnic Alps, supplementing our comparison with the Pyrenean sequences.

The Oberbuchah II section exhibits lower diversity in pectiniform elements compared to the Pyrenees across all zones. In contrast to the Pyrenees, where diversity is lowest in the lower Givetian *hemiansatus* and *timorensis* zones with 15 and 17 taxa, respectively, these zones have the highest biodiversity in the Carnic Alps, with 10 and 11 taxa, respectively. Middle Givetian zones in the Oberbuchah II section show exceptionally low diversity, with 7 taxa in the *rhenanus/varcus* and *hermanni* zones and 6 in the *ansatus*. This sharply contrast with the Pyrenean *ansatus* Zone, which records peak diversity of 34 taxa. The *rhenanus/varcus* and *latifossatus* zones in the Pyrenees also have higher diversity than their Carnic Alps counterparts (19 and 26 taxa, respectively). Another major difference is the low number of originations in the *ansatus* Zone in the Alpine section, where only the index taxon appears, compared to 15 origination events in the Pyrenees.

The ZMB section exhibits slightly higher biodiversity than Oberbuchah II, aligning more closely with the Pyrenees. The *hemiansatus* Zone records 13 pectiniform conodonts, the *timorensis* Zone 14, and the *rhenanus* Zone 18, slightly fewer than in the Pyrenean sections (15, 17, and 19, respectively), but following a similar slow increasing trend. Extinctions rates remain low in both records, though with differing trends. The ZMB section records two extinctions in the *hemiansatus* Zone, one in the *timorensis* Zone, and three in the *rhenanus* Zone. In contrast, the Pyrenean sections, document three extinctions in the *hemiansatus* Zone and none in the following two zones. The peak origination rate occurs in the *rhenanus* Zone in the ZMB section (4 taxa), whereas in the Pyrenees, the peak is in the *timorensis* Zone (5 taxa).

The conodont biodiversity trends in the Carnic Alps reveal distinct differences from those observed in the Pyrenees. The Oberbuchach II section is characterized by low diversity and minimal origination events, particularly in the middle Givetian zones, suggesting different paleoenvironmental or ecological constraints. In contrast, the ZMB section shows a biodiversity trend more similar to the Pyrenean sequence, albeit with lower overall taxonomic richness.

These disparities suggest regional differences in conodont community dynamics, potentially influenced by variations in depositional environments, water chemistry, or ecological pressures. The lower origination rates in the *ansatus* Zone of the Carnic Alps, compared to the Pyrenees, may indicate more stable conditions with fewer ecological opportunities for diversification. Further studies integrating geochemical and sedimentological data could help clarify the underlying causes of these biodiversity discrepancies between the two perigondwanan regions.

3.5.5. *North Africa segment of Gondwana: Morocco*

The data from Morocco are compiled from multiple sections: Walliser and Bultynck (2011) for the *hemiansatus* and the lower part of the *timorensis* zones; Aboussalam (2003) and Aboussalam and Becker (2011) for the *ansatus* to Upper *hermanni* zones; Aboussalam and Becker (2007) for the Lower *disparilis* to *norrisi* zones. Liao and Valenzuela-Ríos (2017) discussed the position of the *sagitta* Zone in a global context and concluded that the base of the *sagitta* Zone nearly coincides with that of the Lower *disparilis* Zone. Consequently, they did not include the *sagitta* Zone in the Givetian zonation, an approach we follow herein.

The *hemiansatus* and *timorensis* zones exhibit a reverse conodont biodiversity pattern compared to the Pyrenean sections. The former zone contains 21 taxa and the latter 15 in the Moroccan sections, whereas the Pyrenean sections record 15 and 17 taxa, respectively. Furthermore, the origination and extinction record is significantly higher in the Moroccan sections. In Morocco, eight taxa originated in the *hemiansatus* Zone and three in the *timorensis* Zone, while In the Pyrenean sections, the number of originations and extinctions in the *hemiansatus* Zone is equal (3 each) and originations in the *timorensis* Zone rises to five taxa, with no extinctions.

Aboussalam (2003) and Aboussalam and Becker (2011) identified the *semialternans* Zone at the top of the *ansatus* Zone, and just below the Lower *hermanni* Zone. In our study, we place the *latifossatus* Zone between the *ansatus* and Lower *hermanni* zones. Consequently, we reassign the records attributed to the *semialternans* Zone in Morocco to the *latifossatus* Zone. Additionally, most of Aboussalam's (2003) attributions to the *semialternans* Zone were based on their position below the Lower *hermanni* Zone rather than on conodont evidence, except in the Bou Tchrafine section, where "*O.*" *semialternans* occurs one bed (B1b) below the entry of *S. hermanni* (B2), the index taxon of the Lower *hermanni* Zone. In fact, in their range compilation for the Tafilalt area, Aboussalam and Becker, 2011, Fig. 2) placed the entry of "*O.*" *semialternans* and *P. latifossatus* at the same level.

The interval between the *ansatus* and Upper *hermanni* zones exhibits greater diversity in the Moroccan sequences, peaking in the Lower *hermanni* Zone with 61 taxa, in contrast to 24 taxa in the Pyrenees. In the Pyrenees, the peak of diversity occurs in the *ansatus* Zone with 34 taxa, whereas this zone in Morocco contains 51 pectiniform taxa. The *latifossatus* Zone also hosts a significantly higher number of taxa in Morocco (54) than in the Pyrenees (26). In general, the biodiversity trends differ: in Moroccan sections, diversity rises from the *ansatus* to the Lower *hermanni* Zone before declining in the Upper *hermanni* Zone, whereas In the Pyrenees, biodiversity peaks in the *ansatus* Zone and then declines into the Lower *hermanni* Zone.

The total number of originations in the *ansatus* Zone is similar in both regions (at least 16 in Morocco and 15 in the Pyrenees). However, since the total number of taxa is considerable higher in the Moroccan sequences, the Pyrenees sections exhibit a higher rate of origination. The number of originations in the Lower *hermanni* Zone (18) is much higher than the one in the Pyrenean sequences (6); however, due to the large difference in total taxa, origination rates are comparable: 0.29 in Moroccan sections and 0.25 in Pyrenean sections.

The last three Givetian zones also exhibit greater biodiversity in

Moroccan sequences than in the Pyrenean ones: Lower *disparilis* Zone (41 vs. 22 taxa) Upper *disparilis* Zone (36 vs. 26 taxa), and *norrisi* Zone (44 vs. 28 taxa). In both regions, diversity peaks in the *norrisi* Zone, however, the lowest biodiversity is observed in the Upper *disparilis* Zone in Morocco and in the Lower *disparilis* Zone in the Pyrenees. In both regions the highest number of originations and extinctions occurs in the *norrisi* Zone. Origination ratios are similar in both areas (0.23, 10/44 in Morocco and 0.25, 7/28 in Spain), but the extinction ratio is significantly higher in Morocco (0.45, 20/44) than in Spain (0.25, 7/28). Conversely, the lowest number of originations and extinctions occurs in the Moroccan Upper *disparilis* Zone (5 originations and 3 extinctions) and in the Pyrenean Lower *disparilis* (2 originations and 2 extinctions).

The analysis of Moroccan conodont assemblages reveals significant differences in biodiversity trends, origination, and extinction patterns when compared to the Pyrenean sections. Moroccan sequences generally exhibit higher taxonomic richness across all zones, with the most notable differences occurring in the *hemiansatus*, *latifossatus*, and Lower *hermanni* zones.

Biodiversity trends in Morocco show a progressive increase from the *ansatus* Zone to the Lower *hermanni* Zone, followed by a decline towards the Upper *hermanni* Zone. This contrast with the Pyrenean sequences, where the peak in biodiversity occurs in the *ansatus* Zone, followed by a steady decline. Despite these differences, both sequences indicate that the Taghanic Crisis had minimal impact on conodont diversity, instead, a gradual turnover in conodont taxa occurred post-crisis marked by the disappearance of the genus of *Tortodus*, the replacement of *Icriodus* and *Polygnathus*, and innovation and/or radiation of *"Ozarkodina"*, *Schmidtognathus*. Subsequent, during the lower Frasnes Event, the radiation of *Klapperina*, and the innovation of *Skeletognathus*, and *Mesotaxis* are observed.

Origination and extinction rates also differ between the two regions. Although origination rates in some zones are comparable, Moroccan sections generally show higher absolute numbers of newly appearing taxa. The *norrisi* Zone represents the peak of both origination and extinction events in both regions, but extinction rates in Morocco are significantly higher than in the Pyrenees. Additionally, the lowest origination and extinction events occur in different zones for each region, further highlighting their distinct evolutionary dynamics.

These findings emphasize that regional environmental and ecological factors likely played a crucial role in shaping conodont biodiversity patterns during the Givetian.

3.5.6. *Euroamerica: Canada*

From the numerous Canadian Devonian sections and samples analyzed by Uyeno, this study considers those from the Northwest Territories (Uyeno, 1998) and a well in Alberta (Uyeno and Wendte, 2005).

The first set of samples comes from the Pine Point area, on the southern shore of Great Slave Lake in the District of Mackenzie, yielding conodonts from the *kockelianus-ensensis* to the Middle *varcus* zones (Uyeno, 1998). However, the precise positioning of the bases of the identified zones remains uncertain. The first Givetian Bed is identified in sample 56NBa (GSC locality C-94569) with the lowest occurrence of *Tortodus* cf. *T. variabilis*. Uyeno (1998) noted that this taxon "*is not known to occur below the Givetian*". The base of the Lower *varcus* Zone was identified in sample 16NBc (GSC locality C-94445) by the lowest occurrence of *P. x. xylus*. Approximately four meters higher (sample 90NBa, GSC locality C-94791), *P. timorensis* first appears, alongside a delayed lowest record of *P. hemiansatus*. For comparative purposes with Spanish biodiversity, we tentatively consider the beginning of the *timorensis* Zone at this locality and attribute the strata between this sample and the first appearance of *P. x. xylus* to the *hemiansatus* Zone. The first occurrence of *P. ansatus* (sample 87NBa, locality C-94692), recorded less than two meters above the entry of *P. timorensis*, defines the base of the *ansatus* Zone. The base of the *latifossatus* Zone is identified by the first occurrence of *P.* cf. *P. latifossatus* (sample 63 NBc, locality C-94586), approximately 13.5 m above the base of the previous zone. No further zones could be recognized beyond this level.

Uyeno and Wendte (2005), in an integrated study of the subsurface carbonates of the Beaverhill Lake Group in Alberta, examined conodont biostratigraphy in two cores. The Archie well yielded conodonts from the Upper *disparilis* Zone to FZ4, while the Imperial Forestry well contained only Frasnian conodonts (FZ2 to FZ4 zones). The Archie well, thus, provides relevant data for upper Givetian comparison.

Canadian conodont biodiversity is considerable lower than that of the Pyrenees, except in the *latifossatus* Zone. In the lower Givetian *hemiansatus* and *timorensis* zones, each Canadian zone contains nine conodonts taxa, significantly fewer than in the Pyrenean sequences (15 and 17 taxa, respectively). The number of originations and extinctions is the same in both Canadian zones (two originations and one extinction), differing from the trends observed in the Pyrenees. Three taxa first appear in the *hemiansatus* Zone and five in the *timorensis* Zone. However, given the lower overall taxon count, the per-taxon origination and extinction rates remain comparable between the two regions: 0.22 for the Canadian section and 0.2 for the Pyrenean sections.

The *ansatus* Zone in Canada contains 16 taxa, contrasting sharply with the 34 taxa recorded in the Pyrenees. Originations are significantly lower in the Canadian sections, with only three new taxa appearing, compared to 15 in the Pyrenees. Extinction patterns also differ: only one taxon disappears in Canada, whereas 13 taxa go extinct in the Pyrenees.

The *latifossatus* Zone represents the peak of biodiversity in Canada, with 22 recorded taxa, approaching the 26 taxa observed in the Pyrenees. Notably, origination and extinctions rates are higher in Canada for this interval. Seven new taxa appear in the *latifossatus* Zone, while eight become extinct. In contrast, the Pyrenees record five new taxa and eight extinctions.

These findings suggest distinct biodiversity trends in the lower and middle Givetian. In Canada, diversity remains relatively stable in the lower Givetian before progressively increasing to a peak in the *latifossatus* Zone. In contrast, the Pyrenean biodiversity curve peaks in the *ansatus* Zone.

The Upper *disparilis* and *norrisi* zones exhibit pronounced differences in biodiversity, origination and extinction rates. The Upper *disparilis* Zone in Canada contains only five taxa, with no apparent originations or extinctions. The *norrisi* Zone contains six taxa, including one new appearance, with no recorded extinctions. In contrast, the Pyrenean Upper *disparilis* and *norrisi* zones, show much greater diversity, with 26 and 28 taxa, respectively, with six originations and five extinctions in the Upper *disparilis* Zone, and seven originations and seven extinctions in the *norrisi* Zone.

Besides these quantitative differences, the faunal composition is also different. *Icriodus orri*, *I. arkonensis, I. subterminus*, "*O.*" *raaschi*, *P. alatus*, and *Pandorinellina insita* are recorded only in the Canadian samples.

These findings highlight notable differences in conodont biodiversity between Canada and the Pyrenees during the Givetian. The lower diversity in Canadian sections suggests regional environmental constraints or differing evolutionary dynamics. The disparity in biodiversity peaks between the two regions emphasizes the importance of local paleoenvironmental conditions in shaping evolutionary trends. Such regional variability underscores the need for caution when extrapolating global evolutionary models from geographically limited datasets.

4. Conclusions

Our results, based on data from the Pyrenees, challenge the evolutionary cycles proposed by Ziegler and Lane (1987), demonstrating that the *ansatus* Zone, contrary to prior interpretations, represents the peak of conodont diversity. The findings suggest that conodont evolution during the Givetian was more dynamic and regionally variable than traditionally recognized, with local trends deviating from global evolutionary models. Moreover, our results enhance the understanding of conodont evolution during the Givetian and provide insights into broader patterns of biodiversity change in Devonian marine ecosystems. We highlight the following conclusions.

1. Diversity Trends: Conodont taxonomic diversity in the Spanish Pyrenees increased steadily from the *hemiansatus* to the *rhenanus-varcus* zones, peaking in the *ansatus* Zone before declining and stabilizing. Mean Standing Diversity (MSD) trends diverge from total diversity, emphasizing the importance of boundary crossers in evolutionary studies.

2. Origination and Extinction Rates: Origination rates consistently exceeded extinction rates until the *latifossatus* Zone, where extinctions briefly surpassed originations. The *ansatus* Zone exhibited the highest origination and extinction rates, driven by significant radiations and faunal turnover within key genera.

3. Singleton Influence: Singletons were largely restricted to the *ansatus* Zone and had minimal impact on diversity trends. Their exclusion did not significantly alter evolutionary rate patterns, reaffirming the robustness of the observed trends.

4. Evolutionary Implications: Periodic fluctuations in diversity, origination, and extinction suggest that conodont communities experienced episodic environmental and ecological pressures. Renewals of *Polygnathus*, *Icriodus*, and *Tortodus* in the *ansatus* Zone and later radiations of *Klapperina*, *Skeletognathus*, and *Mesotaxis* in the Upper *hermanni* and *norrisi* zones highlight key evolutionary events in the Givetian.

5. Methodological Contributions: By integrating multiple diversity metrics and rate calculations, this study provides a comprehensive approach to taxonomic turnover and evolutionary processes. Our results underscore the necessity of combining traditional diversity measures with boundary-crossing metrics for a more nuanced interpretation of paleoecological dynamics.

6. Index of Conodont Evolution (ICE): Analysis of ICE across Givetian biozones reveals that most zones reflect periods of radiation or stability, with only the *latifossatus* Zone suggesting a potential extinction threshold. However, no major extinction events were detected.

7. Comparison with Ziegler and Lane's (1987): Significant regional deviations from the proposed conodont evolutionary cycles were observed, particularly in the *ansatus* and *latifossatus* zones. The *ansatus* Zone emerges as a key interval of conodont renewal, showing the highest diversity and origination rates, challenging its previous classification as a low-diversity episode. These findings highlight the importance of regional studies in refining broader evolutionary models and caution against extrapolating global trends from localized data.

8. Impact of Global Events:

The Kačák Event had a minor but possibly prolonged effect on the Pyrenean conodont faunas, particularly in comparison to Morocco.

The Lower *pumilio* Event had no apparent impact on conodont diversity, while the Upper *pumilio* Event significantly affected the lower half of the *ansatus* Zone.

The multiphase Taghanic Crisis coincided with the highest conodont extinction rates in the *ansatus* and *latifossatus* Zones. The marked turnover in the Lower *hermanni* Zone represents the final transgressive phase of the Taghanic Crisis, corresponding to the Geneseo Event.

The Frasnes Event in the *norrisi* Zone aligned with a period of conodont innovation and radiation.

9. Regional Comparisons

Central Asia: Lower diversity compared to the Pyrenees, with key differences in diversity peaks and origination rates. Maximum diversity occurred in the *latifossatus* Zone, unlike the *ansatus* Zone in the Pyrenees.

China (Sihongshan Section): Markedly lower biodiversity than the Pyrenean sections, with a higher extinction in the upper Givetian.

Australia: Comparable biodiversity to the Pyrenees from the *hemiansatus* to the *rhenanus/varcus* zones, but a significant decline in the middle Givetian *ansatus* and *latifossatus* zones, suggesting lower faunal turnover and a more stable paleoenvironment.

Carnic Alps: The Oberbuchach II section consistently exhibits lower diversity than the Pyrenees, with fewer originations and different trends. The Zuc di Malaseit Basso section, though taxonomically less rich, displayed similar biodiversity trends to the Pyrenees.

Morocco: Generally higher taxonomic richness across most zones compared to the Pyrenees. Diversity increases from the *ansatus* to the Lower *hermanni* Zone, whereas in the Pyrenees, the peak occurred in the *ansatus* Zone. Origination and extinction rates were higher in Morocco, with the lowest rates occurring in different zones, indicating different evolutionary dynamics.

Canada: Lower biodiversity trends and origination/extinction rates than in the Pyrenees, with differences in faunal composition.

10. The observed regional differences in conodont biodiversity trends underscore the influence of paleoenvironmental factors and regional evolutionary pressures on Devonian conodont communities. These findings contribute to a broader understanding of Devonian biogeography and the drivers of marine diversity during the Givetian.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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