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New insights into the diversity dynamics of Triassic conodonts

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In this paper, we examine the diversity trends and the evolutionary patterns of Triassic conodonts through a newly powered large-scale data-set compiled directly from the primary literature. Paleodiversity dynamics analyses have been undertaken by working at the species level and using a system of time units based on biozone subdivisions for a fine temporal level resolution. The role of heterogeneous duration of taxa in diversity estimates has been evaluated through the probabilistic profiles. Results reveal three different stages in the diversity behaviour of Triassic conodonts from standing metrics delimited by two inflections at the mid-Anisian and mid-Carnian. Survivorship analysis supports this pattern. Origination–extinction metrics report a diversification pattern characterised by important fluctuations during the Lopingian–Induan (earliest Triassic), the early-middle Olenekian (Early Triassic) and the Anisian–Ladinian transitions (Middle Triassic), as well as in the early Late Triassic. In addition, two clear diversification peaks are observed in the late Carnian and in the end-Norian. Reported patterns are interpreted in the context of deep extinction and environmental instability by documenting the biological signal of the main diversification and turnover patterns observed from such records. This study emphasises the singularity behaviour of diversity trends derived from the conodont record.

Keywords: diversity estimates; conodonts; Triassic; extinction dynamics; paleontological data analysis; probability of surviving

Introduction

The study of taxonomic diversity through time has become a powerful tool to document macroevolutionary processes of the fossil record (Jablonski and Bottjer 1990; Erwin 2000; Jablonski 2000, 2005, 2007; Valentine and Jablonski 2003; Ausich and Peters 2005; Donoghue 2005; Eldredge and Vrba 2005; Fisher et al. 2010; Peters and Heim 2011; Cascales-Miñana 2012). Studies on loss of diversity, mass extinctions and radiation events have attracted extensive attention from paleontologists to provide new insights into the patterns of life evolution on Earth (Foote 1999, 2006; Hallam 2002; De Blasio and De Blasio 2005; Arens and West 2008; Clapham et al. 2009; Benson et al. 2010; Quental and Marshall 2010; Chen and Benton 2012). In fact, important studies have focused on Phanerozoic diversity changes by documenting the main extinction events throughout the marine and terrestrial fossil records at different hierarchical taxonomic levels (e.g. Benton 1985; Raup and Sepkoski 1986; Cleal et al. 2012). The conodont fossil record is especially relevant for such studies, mainly due to two reasons: an abundant and continuous fossil record in almost all marine environments and a wide geographical and stratigraphical distribution.

During recent years, the frequency of this kind of study has increased notably and an accurate attention of their

inherent biases has resurfaced in the same degree. Several authors have emphasised that the analysis of extinction and origination patterns requires the consideration of the different constraints that can hide important paleobiological aspects (Raup 1979; Norris 1991; Raymond and Metz 1995; Smith et al. 2001; Hunter and Donovan 2005; Ros and De Renzi 2005; Tarver et al. 2007; Uhen and Pyenson 2007; Lloyd et al. 2011, among others). In this regard, studying the diversity dynamics of conodonts affords a series of advantages, which make this group particularly attractive. Conodonts provide a rich fossil record from different marine environments throughout time. Indeed, this record probably represents the best fossil record among the clade of vertebrates (Foote and Sepkoski 1999; Purnell and Donoghue 2005), with clear utility across a range of geological and biological contexts (Purnell and Donoghue 2005). In addition, due to their mineralogical composition (conodont elements are composed of the calcium phosphate francolite; Pietzner et al. 1968), they are exceptionally well preserved in many fossilisation conditions, resisting diagenesis and metamorphism where other common groups cannot, being the only fossil found in many rocks (Aldridge and Smith 1993; De Renzi et al. 1996).

However, despite their excellent fossil record, problems arise from using different taxonomic concepts, as in any

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other group. This is an important handicap because their unique well-mineralised parts were a series of elements arranged in a complex apparatus in their oral region. These elements are the basis for the systematics of the group and normally became disarticulated after the death and decay of the animal; therefore, in order to establish species, or even genus with confidence, the apparatus composition must be known. After more than 150 years of intensive work, considerable progresses on the conodont taxonomy have been achieved. During the early Paleozoic, conodonts showed a large variety of apparatus styles, but most of them were poorly known. In contrast, the apparatus composition of the late Paleozoic and Mesozoic conodonts is better understood, due to the relatively abundant record of natural assemblages and fused clusters of different species (Rhodes 1953; Krivic and Stojanovic 1978; Ramovs 1978; Mietto 1982; Nicoll 1983, 1985; Mastandrea et al. 1999; Goudemand et al. 2011, 2012). These late Paleozoic and Mesozoic apparatus show a more stable architecture, with conservative ramiform elements (even at the family level) and distinctive pectiniform elements that evolved rapidly, becoming the base for the systematics of the group (Aldridge 1988).

Several authors have focused their attention on the paleodiversity analysis of conodonts record, especially through the Triassic Times (Clark et al. 1981; Clark 1983, 1987; Aldridge 1988; Sweet 1988; De Renzi et al. 1996; Stanley 2009). Nevertheless, despite all of these works, additional efforts are still necessary to deepen the characterisation of dynamic aspects related to the ‘last evolutionary episode’ of the conodonts history. According to this background, we focused this work on this key period of the conodont fossil record, allowing us to develop an accurate database where most of the problems described above can be satisfactorily minimised. In this paper, we present a paleobiological data analysis from a new conodont data-set created for late Permian–Triassic species diversity under the general goal of improving our knowledge about their most recent fossil history and their last extinction dynamics. In order to reach this general aim we examine (1) the entire spectrum of their diversity dynamics for this time interval, (2) the extinction (descriptive and probabilistic) patterns and (3) the taxonomic turnover trends of this controversial group of early vertebrates.

Data

We analysed a new high-powered data-set given by Plasencia et al. (2013). Similar to Janevski and Baumiller (2009), the dataset is conducted at species level; cf., sp., aff. and other modifiers were excluded. Tentative taxonomic entities were also omitted. Only well-assigned species were considered for data compu-

tation. After filtering, we considered that our data-set avoids potential overestimation of apparent species diversity and allows us to obtain more realistic results. Our data-set embraces eminently the Triassic period, however, the lattermost Permian (Changhsingian) was also included. This addition was carried out for studying the Paleozoic–Mesozoic transition by providing a broad vision of the diversity dynamics during the earliest Triassic times.

Conodont data were codified with a high level of temporal resolution. In total, 327 taxa were considered through 48 time units, from the late Permian (Lopingian) to the end-Triassic (Rhaetian). To accommodate raw information from the primary literature, each time unit was built by subdividing the formalised sub-stages into a maximum of three time intervals, referred as Early, Middle and Late (see Table 1). These time units are equivalent to the ammonoid biozone subdivision for the Lopingian and Triassic periods (Tethyan Zones) (see Henderson et al. 2012; Ogg 2012, Table 25.3). The followed criteria to assign the interval lengths in each case are specified in Supplementary File 1. Diversity data can be consulted in Supplementary File 2.

Methods

Original data were treated following the four fundamental taxonomic categories in paleobiological analyses described by Foote (2000a). For a given time unit, we recovered information about the number of taxa confined to the interval (N_{FL} , singleton taxa); the number of taxa that cross only the bottom boundary (N_{bL} , last appearances); the number of taxa that cross only the top boundary (N_{Ft} , first appearances) and finally, the number of taxa that cross both boundaries (N_{bt} , range-through taxa). The original taxonomic counts per time unit appear in Table 1.

Four diversity metrics are used herein. First, we used two categories of diversity measures, which make reference to the minimum and maximum levels of registered diversity. Minimum sampled diversity was obtained by taking a single total of the species with first and/or last appearances in a given time unit (Peters and Foote 2001). Maximum sampled or total diversity correspond to the minimum sampled diversity plus the number of range-through taxa (Peters and Foote 2001). This approach was adopted to explore the effect of long-lived taxa on the diagnosis of diversity peaks. Second, we used two complementary measures to avoid the potential distorting effect associated with the singleton taxa (Foote 2000a, 2000b; Uhen and Pyenson 2007; Cascales-Miñana 2012). We plotted the total number of non-singleton taxa and the mean standing diversity per time unit. Standing diversity responds to the total number of species diversity

Table 1. Temporal framework, corresponding abbreviations and taxonomic parameters of the large-scale conodonts data-set explored in this work.

Time units	Abbreviation	Mid-point	Δt	N_{bL}	N_{Ft}	N_{bt}	N_{FL}
Lopingian	L						
Late Wuchiapingian	LWu	254.85	1.30	0	14	0	4
Early Changhsingian	ECh	253.85	0.70	5	5	9	1
Middle Changhsingian	MCh	253.21	0.58	4	7	10	1
Late Changhsingian	LCh	252.54	0.76	13	13	4	7
Early Triassic	ETR						
Early Griesbachian	EGr	251.98	0.37	2	8	15	2
Middle Griesbachian	MGr	251.61	0.37	8	4	15	3
Late Griesbachian	LGr	251.04	0.77	15	5	4	1
Early Dienerian	EDi	250.44	0.42	4	3	5	1
Late Dienerian	LDi	250.12	0.22	1	10	7	4
Early Smithian	ESm	249.75	0.52	8	16	9	7
Middle Smithian	MSm	249.03	0.93	10	6	15	2
Late Smithian	LSm	248.51	0.10	19	1	2	1
Early Spathian	ESp	248.28	0.37	2	8	1	10
Middle Spathian	MSp	247.90	0.38	6	8	3	7
Late Spathian	LSp	247.39	0.65	7	3	4	4
Middle Triassic	MTR						
Early Aegean	E Ae	246.89	0.35	3	3	4	0
Late Aegean	LAe	246.54	0.35	0	1	7	0
Early Bythinian	EBy	246.01	0.71	0	1	8	0
Middle Bythinian	MBy	245.48	0.35	0	0	9	0
Late Bythinian	LBy	245.12	0.36	3	0	6	0
Early Pelsonian	EPe	244.71	0.47	3	5	3	0
Late Pelsonian	LPe	244.23	0.48	2	3	6	1
Early Illyrian	EIl	243.28	1.42	2	7	7	0
Middle Illyrian	MIl	242.34	0.47	3	9	11	0
Late Illyrian	LIl	241.80	0.60	4	7	16	1
Early Fassanian	EFa	240.90	1.20	13	5	10	3
Middle Fassanian	MFa	240.00	0.60	5	6	10	0
Late Fassanian	LFa	239.40	0.60	6	3	10	1
Early Longobardian	ELo	238.80	0.60	5	2	8	1
Middle Longobardian	MLo	238.20	0.60	3	5	7	0
Late Longobardian	LLo	237.45	0.90	1	5	11	3
Late Triassic	LTR						
Early Julian	EJu	236.60	0.81	13	5	3	4
Middle Julian	MJu	235.79	0.80	2	2	6	3
Late Julian	LJu	234.45	1.89	4	1	4	0
Early Tuvalian	ETu	233.10	0.81	2	2	3	2
Middle Tuvalian	MTu	231.89	1.61	1	6	4	0
Late Tuvalian	LTu	229.72	2.73	8	13	2	6
Early Lacian	ELa	226.44	3.82	9	4	6	4
Middle Lacian	MLa	221.35	6.37	2	2	8	0
Late Lacian	LLa	217.79	0.74	2	0	8	1
Early Alaunian	EAl	217.16	0.52	6	6	2	1
Middle Alaunian	MAl	216.07	1.67	3	4	5	3
Late Alaunian	LAl	214.60	1.26	6	5	3	0
Early Sevatian	ESe	212.71	2.52	4	0	4	2
Late Sevatian	LSe	210.46	1.99	0	7	4	0
Early Rhaetian	ERh	206.86	5.20	7	1	4	1
Middle Rhaetian	MRh	203.21	2.10	2	1	3	0
Late Rhaetian	LRh	201.83	0.66	4	0	0	3

Notes: The mid-point and time duration (Δt) of each time unit are shown in millions of years. N_{bL} , number of taxa that cross only the bottom boundary (last appearances); N_{Ft} , number of taxa that cross only the top boundary (first appearances); N_{bt} , number of taxa that cross both boundaries (range-through taxa); N_{FL} , number of taxa confined to the interval (singleton taxa). Absolute ages were extracted from Henderson et al. (2012) and Ogg (2012, Table 25.3). See Supplementary File 1 for details. Raw data can be found from Supplementary File 2.

per time unit by extracting half of the number of originations and extinctions (Harper 1975; Foote 2000a). Corresponding derived patterns were compared for interpretation.

However, we calculated the relative species origination and extinction rates (also called total per-taxon rates), Van Valen's evolutionary rates and Gilinsky metrics per time unit. The relative origination and extinction rates are the ratios of the total number of originated and extinguished species and the total observed diversity per time unit (Foote 2000a; Xiong and Wang 2011). All taxa were considered in this first approach. The rates of evolution throughout Van Valen's algorithms follow the identical structure of previous rates, but dividing the originated and extinguished taxa by the standing diversity for a given time unit (Van Valen 1984; Foote 1994, 2000a). In this case, singletons were not considered to obtain the relative weight of each event through time. Finally, standing origination and extinction rates are implemented according to Gilinsky rates. These metrics correspond to half of the ratio between the total number of originated and extinguished taxa minus singletons and the standing diversity, respectively (Gilinsky 1991; Xiong and Wang 2011). In this last context, singletons were completely avoided for calculation. In all cases, diversification rates were computed by calculating the rate of net increase from the differential value between the origination and extinction levels.

We also calculated the corresponding turnover rates. These rates represent an estimation of the change in taxonomic composition from past biota (Shen et al. 2004). In agreement with Xiong and Wang (2011), relative and Van Valen turnover rates were calculated by adding the corresponding origination and extinction rates and discounting the proportion of singleton taxa. The singletons component was obtained from the ratio between the total number of singletons and the total or standing diversity per unit time, respectively. For the last case, by following Fröbisch (2008), and as the singletons were directly not considered by the raw algorithms, turnover rates were obtained directly by addition of the corresponding values of origination and extinction rates taken as a single total.

Finally, following De Renzi et al. (1996), we used the original formulations of Raup (1985) to calculate the probability of a conodont species surviving or being extinguished for each time unit (see Foote 1988, p. 260, Equations (1) and (2)). Similarly, this analysis was also complemented with taxonomic survivorship curves (Raup 1975, 1978; Hoffmann and Kitchell 1984; Foote 1988; Raup and Boyajian 1988; De Renzi et al. 1996; see Cascales-Miñana and Cleal 2012 and references therein for further explanations).

Results

Diversity dynamics

Figure 1 contains the diversity trends of the fossil history of conodonts between the Changhsingian (late Lopingian, end-Permian) and the Rhaetian (end-Triassic) interval. Figure 1(A) shows a first peak of diversity in the late Changhsingian followed by a quick fall in the Early Triassic. Figure 1(A) shows that the maximum level of species diversity during the Triassic was registered at early Smithian (Olenekian). A major negative trend was observed between this time unit and the earliest Middle Triassic. Figure 1(A) also shows that the species diversity reached a new maximum in the early Fassanian (Anisian–Ladinian transition). After a diversity peak at early Julian (earliest Late Triassic), our results highlighted three consecutive diversity peaks of decreasing intensity at late Tuvalian (end-Carnian), the time interval compressed between the early-middle Alaunian (mid-Norian) and the early Rhaetian.

The profile of the parameter of minimum sampled diversity reflected the general trends previously exposed but emphasised the fall of diversity at the Spathian–Aegean transition (Early–Middle Triassic boundary) (Figure 1(B)). This suggests that both the heterogeneous longevity of taxa originated from previous intervals and the taxa of wide record do not distort our vision of general diversity trends of Triassic conodonts. In addition, Figure 1(C) shows the effect of discounting singletons in data computation. This analysis revealed that singletons seem to be not a major source of distortion in data analysis. Figure 1(C) follows identical trend of total diversity. Likewise, a genuine pattern is observed from Figure 1(D). From the diagram of standing diversity, three different stages can be inferred. First, we detected a zone of instability with two peaks at mid-Griesbachian (early Induan) and mid-Smithian (early Olenekian) followed by an abrupt disruption at the Smithian–Spathian transition (mid-Olenekian). Only slight fluctuations were subsequently registered at this stage. A second phase appeared, which was dominated by two maximums at late Illyrian (end-Anisian) and late Longobardian (end-Ladinian), ending with the lowest diversity value at early Tuvalian (mid-Carnian). Finally, a negative trend was observed from the late Tuvalian until the total extinction of conodonts with two minor increments of diversity levels during the mid-late Alaunian interval and the early Rhaetian.

Evolutionary patterns

Figure 2 documents the main evolutionary events (origination, extinction, net increase and turnover) of Triassic conodonts. The relative origination rate revealed its main stages in the early Spathian, early Pelsonian, late Tuvalian, early Alaunian and late Sevatian (Figure 2(A)).

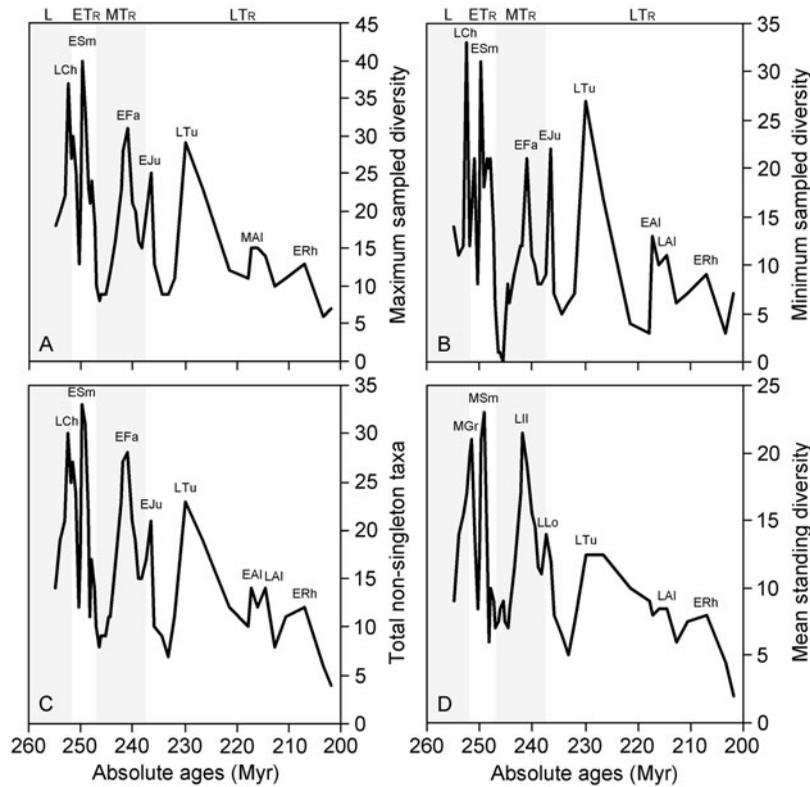


Figure 1. Taxonomic species diversity curves through time. Diversity profiles of Triassic conodonts are traced through (A) maximum sampled diversity, (B) minimum sampled diversity, (C) non-singleton taxa and (D) the mean standing diversity. See ‘Methods’ section for details and Table 1 for abbreviations.

We observed similar peaks from the Van Valen origination rate but with a peak during early Julian (Figure 2(B)). No major differences were observed from the Gilinsky origination rate (Figure 2(C)). The main moments of extinction were placed by the relative extinction metric in the late Smithian, early Fassanian, early Julian, early Lacinian, early Sevatian and early Rhaetian (Figure 2(D)). This general pattern of extinction peaks is maintained independently of the metric used (Figure 2(E),(F)). Only minor differences were detected from the Van Valen and Gilinsky extinction metrics. Van Valen extinction metrics point out the late Tuvalian (Figure 2(E)), whereas Gilinsky metrics focus attention on the early Alaunian (Figure 2(F)) time units.

However, the relative diversification rate indicates the highest negative value in the late Smithian (Figure 2(G)). This fact can also be described through the Van Valen and Gilinsky metrics (Figure 2(H),(I)). Nevertheless, the context is not similar for the positive net increase of diversity between rates. Relative metrics do not show a clear positive peak in the early Spathian, despite the fact that this metric reports a clear origination peak in this time unit. The other diversification metrics illustrate the highest values for this time unit, by suggesting a singleton effect for this reading through relative metrics (Figure 2(H),(I)).

Negative diversification values were documented in the early Fassanian, early Julian, early Sevatian and during the Rhaetian (Figure 2(G)–(I)). Conversely, the main positive diversification values were observed in the mid-Tuvalian and the end-Sevatian (Figure 2(G)–(I)).

The turnover patterns highlighted especially in the early Spathian, early Fassanian, early Julian, late Tuvalian and early Alaunian (Figure 2(J)–(L)). On this general pattern, as a function of the metric used, a clear peak was observed in the late Alaunian, being especially clear through Gilinsky metrics (Figure 2(L)). Also, we detected two main deflections in turnover patterns. The first of these occurs during the Early–Middle Triassic transition, whereas the other one is documented during mid-Late Triassic. Both decreases of turnover rates were observed independent of the metric (Figure 2(J)–(L)).

Probability of surviving and taxonomic survivorship curves

Figure 3(A) illustrates the survivorship profile of Triassic conodonts. The probability of surviving shows two clear peaks before the total extinction of the group. These deflections appear marked in the late Smithian (late Early Triassic) and early Julian (earliest Late Triassic). The

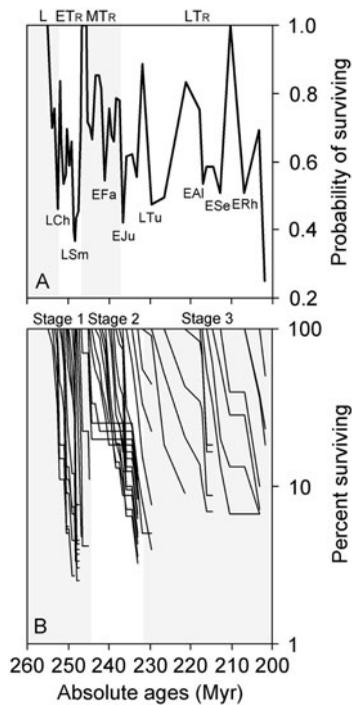


Figure 3. Probabilistic profiles of species survivorship for Triassic conodonts (A) and taxonomic survivorship curves (B). See 'Methods' section for details and Table 1 for abbreviations.

Discussion

Diversity fluctuations in the Triassic conodont record

Results have reported a broad vision of the conodont history in a biological context flanked by the end-Permian and end-Triassic extinction events, two of the 'Big Five' extinctions registered in the Phanerozoic diversity (Raup 1979; Raup and Sepkoski 1982; Erwin 1993). Our paleodiversity analysis provides a high-resolution perspective of this time interval for the conodont record. Previous works have shown general patterns for the Triassic conodonts with two maximum species diversity peaks during the Induan and Ladinian times (Clark 1987; Aldridge 1988; Renzi et al. 1996). Several extinction moments during the Early Triassic and the mid-Late Triassic transition have also been documented (Aldridge 1988; De Renzi et al. 1996; Stanley 2009). However, our data show that the diversity behaviour of Triassic conodonts is more complex. For instance, the rates of evolution show an unstable extinction–origination pattern (Figure 2). We have found six negative diversification peaks especially significant in the late Griesbachian, late Smithian, early Fasnian, early Julian, early Lacinian and early Sevatian (Figures 2(G)–(I)). Also, early Fasnian and early Julian peaks can be recognised as important turnover moments (Figure 2(J)–(L)).

We have documented an initial instability of diversity profiles during the Permian–Triassic transition that it is extended until the beginning of the Middle Triassic

(Figures 1, 2). During Changhsingian, conodonts seem not to be particularly affected by the extinction events at the Permian–Triassic transition. Late Changhsingian represents one of the most intense diversification peaks (Figure 1(A)). An important part of the total species registered during the latest Lopingian corresponds to single appearances (Table 1). This fact could be conditioning by an effect of worker effort on this interval (e.g. Bernard et al. 2010). Moreover, we have found important differences in intensity terms regarding the probability of surviving for this transition. End-Permian diversity peaks appear registered together with deflections of probability of surviving. We consider that this trend is a consequence of the expansion of the family Anchnognathodontidae, whereas other families (Sweetognathidae, Gondolellidae) are strongly affected in accordance with the context of the end-Permian extinction event.

We have detected a genuine pattern in which standing diversity increases respecting Permian intervals (Figure 1). From Figure 3(A), we infer a favourable survival context for the earliest Induan. In fact, the family Anchnognathodontidae had a brief heyday. Following the analysis, the end-Griesbachian represents a significant period of diversification for Gondolellidae. This family is the most representative of Triassic times and is responsible for the diversity peak during Dienerian–Smithian transition (mid-Early Triassic) (Figure 1).

The maximum level of species diversity appears during Smithian times (early Olenekian) (Figure 1). The diversity curves record a sudden fall after the Smithian–Spathian transition in which the standing diversity levels are halved (Figure 1(D)). Figure 2 also shows the main deflection of diversification patterns at this transition (end-Smithian, mid-Olenekian). Raw data reflect the loss of diversity of the family Ellisonellidae at this point. Our profiles suggest that the end-Smithian extinction probably represents the most significant event for conodonts diversity before their final extinction (Figure 2(D)–(F)).

Rates of evolution have revealed the highest pulse of origination towards the end-Early Triassic (Figure 2(A)–(C)). Likewise, we have also registered an important level of extinction rates in this age. Consequently, diversification rates reflect negative increments during the end-Spathian (Figure 2(G)–(I)). Taxonomic survivorship curves only reflect vertical lines of the corresponding polycohorts (Figure 3(A)). Therefore, the early Anisian times is characterised by an episode of low diversity. All analyses reflect this context (Figures 1–3). Figure 3(A) again shows that a down peak is observed in the early Julian. This framework is in concordance with the limit observed around the earliest Late Triassic by the polycohorts analysis. This context suggests a change of diversity behaviour at this point. This observation can also be interpreted by following the diversity trends from standing

metrics (Figure 1(D)) and turnover rate measures (Figure 2(J)–(L)).

The mid-Triassic conodont record reflects a maximum peak of diversity during the end-Anisian (Figures 1(D)). After registering this maximum, an important loss of diversity was observed during the Ladinian (Figure 2(D)–(F)). High activity is registered on the earliest Late Triassic regarding the first and last appearance patterns (Figure 2(A)–(F)). Despite the fact that during the Julian high levels of standing diversity are not recovered (Figure 1(D)), we have registered comprehensible peaks of diversity from several diversity estimates during the early Carnian (Figure 1(A)–(C)). This time interval also represents a high moment of biological turnover (Figure 2(J)–(L)). Two extinction events affecting the conodont diversity during this interval have been recognised. First, Hornung et al. (2007) documented a salinity crisis during the early Julian. The second crisis is more intense and has been documented at the Julian–Tuvallian boundary, when a humid climate pulse called ‘Carnian Pluvial Event’ occurred in all of the Triassic Oceans, affecting the productivity of the carbonate platforms and the life of many marine organisms, including conodonts (Rigo et al. 2007; Mazza et al. 2012a, b). This extinction during the Carnian appears comparable to the previous loss of diversity observed during the mid-Olenekian (Figure 1(D)). Taxonomic survivorship curves show that the Julian–Tuvallian time interval was a key moment for understanding the last extinction dynamics of conodonts (Figure 3). We interpret these curves together with the standing metrics to mark other inflection points in their diversity fluctuations. Notwithstanding, diversity profiles provide the last clear diversity peaks (end-Carnian) (Figure 1(D)). After that, Figure 1 indicates the last events of reduction of diversity. Finally, along the Rhaetian, the diversity loss is steady, and only a few species arrive at the end-Triassic until their final extinction at the Triassic–Jurassic boundary.

Interpreting paleodiversity curves

The description of the diversity and extinction dynamics of conodont species during the Triassic has allowed us to stress the singularity of the diversity behaviour of this clade in a context of deep extinction and environmental instability. Primarily, the observed patterns draw a series of extinctions preceded and/or followed by increments of total diversity (Figure 1(A)) through subsequent origination peaks and minor diversity fluctuations (Figure 2(A)–(C)). Some of the exposed origination–extinction events have been identified by previous works (Clark 1987; Aldridge 1988; Sweet 1988; Stanley 2009). However, our reading of such patterns differs from previous interpretations. Clark (1987), by reviewing an extensive database

for the same time interval studied herein, concluded that this group shows rapid diversification processes terminated by extinction periods in a framework characterised by apparent very compressed cycles during the Triassic. Sweet (1988) also emphasised the perspective of Permian and Triassic cycles of conodont diversity. Our results also show explosive diversification processes and turnover events in short intervals during the Triassic (Figure 2(G)–(L)). However, we believe that these results could be probably more in agreement with an erratic pattern of observed diversity than with some type of cyclicity on these processes.

A continuous decline of conodont diversity levels is observed towards the end-Triassic (Figure 1(D)). The same tendency can be traced for the probability of surviving species (Figure 3(A)). This behaviour seems not to be concordant with the perspective supplied by other marine fossil records (Sepkoski 1978, 1979, 1984; Stanley 2009; Ros et al. 2011; Chen and Benton 2012; Ros and Echevarría 2012). Sepkoski (1984) described the main diversity trends of marine invertebrates through a logistic model that came back to the exponential behaviour (growth phase) after a strong perturbation by entering into a recovery period. For example, for bivalves trajectories, Ros et al. (2011, Figure 2), using standing diversity, document a characteristic pattern that could be associated with an exponential phase of diversification during the Early–Middle Triassic. After the end-Permian crises, the standing diversity of conodonts also shows a recovery pattern, which could be accommodated in a fast process of diversification (Figure 1(D)). This aspect would be in agreement with the Sepkoski’s model. The dynamics proposed by Chen and Benton (2012) would also support this view. We believe that conodonts represent a particular case study taking into account its Triassic trajectory, where any stabilisation is achieved. In fact, the total extinction of conodonts at the end-Triassic can be interpreted as the accumulative result of several factors (geologic and biological aspects), and not just a single and punctual intense perturbation that terminated the clade.

It is documented that the Lopingian (end-Permian)–Early Triassic time interval represents a long period of instability that extended until the beginning of the Middle Triassic (Erwin 1993, 1998, 2006; Rodland and Bottjer 2001; Benton 2003; Pruss and Bottjer 2004; Payne et al. 2006). It has also been stated that the Early Triassic was a period of slow recovery and following diversification of the biota, reaching the complete recovery of the ecosystems during the Middle Triassic times (Rodland and Bottjer 2001; Benton 2003; Pruss and Bottjer 2004; Payne et al. 2006; Chen and Benton 2012). The Permian–Triassic boundary mass extinction was the most extreme of the mass extinctions documented, with a low percentage of species surviving (~10%) in a devastated planet with poor-quality environmental conditions affecting all of the

trophic levels (Sepkoski 1978, 1984; Raup and Sepkoski 1982; Raup 1994; McKinney 1995; Benton and Twitchett 2003; Clapham et al. 2009). This unstable condition is clearly shown by the conodont diversity curves (Figure 1). This fast-evolving group apparently recovered quickly after the end-Permian extinction event. Nevertheless, due to this environmental instability, they suffered several extinctions throughout the Early Triassic (see Figures 1, 2; Erwin 1998, 2006; Orchard 2007; Stanley 2009). It is known that marine ecosystems were not completely recovered until the early to mid-Anisian (8–9 Myr after the crisis) at mid-Triassic (Chen and Benton 2012). However, conodont data continue to show small peaks of extinction in the Middle Triassic (Figure 2(D)–(F)).

Finally, during the Middle–Late Triassic boundary, the group starts a constant decay, with several fluctuations once the ecosystems were presumably recovered. For the end-Triassic biological crisis, several environmental causes have been proposed, highlighting sea-level changes or long-term climate changes among others (e.g. Tanner et al. 2004, and references therein). Although all of these situations could be significant causes for the extinction of conodonts, the beginning of these events seems to be before the crisis. This fact would support the idea that although the combination of several factors (extrinsic/geological or intrinsic/biological) could cause their extinction, we believe that the biological factors were probably decisive. This assumption, although speculative, is worthy of consideration because this could explain the observed diversity dynamics, with taxa being unable to adapt to both stressful environmental conditions and to the competition from the new Mesozoic biota.

Final remarks and forthcoming goals

New diversity curves for Triassic conodonts have been presented. This study is placed in the conceptual framework of Raup et al.'s (1973) nomothetic vision of paleontology.

Three different stages of diversification were detected. Robust probabilistic measures were included to complement the interpretation obtained from descriptive indicators of extinction. However, we must not exclude the possibility that several biases can be acting on the observed diversity, either by distorting stratigraphic ranges or by sampling resolution. It is therefore necessary to include a note of caution in this regard.

It is generally assumed that taxonomic databases provide a consistent tool for documenting an overview of diversity fluctuations through the fossil record. Nevertheless, the reading of diversity data from the fossil record is constrained by the inherent nature of the record, and by human and sampling factors. Recent studies on these matters have targeted attention on the taxonomic and/or

stratigraphical errors, especially when a taxonomic data-set is computed without a sampling control on diversity estimates. These aspects are being corrected each time regarding current tendencies on taxonomic estimates. Notwithstanding, since Raup (1972) seriously considered the role of sampling biases in the fossil record and the associated sedimentary constraints, several workers have further investigated this question (Crampton et al. 2003; Fröbisch 2008; McGowan and Smith 2008; Butler et al. 2009; Mannion et al. 2010; Wall et al. 2011; Holland 2012). Ruban and van Loon (2008) provide a good summary of biases related to diversity curves. An excellent discussion can also be found from Smith's works (Smith 2001, 2003, 2007; Smith et al. 2001; Smith and McGowan 2007, 2011). Special relevance acquires the recent Benton and Dunhill's studies on these limitations for interpreting paleodiversity curves (Benton et al. 2011, 2013; Dunhill 2011, 2012; Dunhill et al. 2012).

Taking into account these considerations, we have just explored herein the biological dimension of the Triassic conodonts by describing their diversity curves. This is in spite of the lack of quantitative assessment of the corresponding sampling biases being attempted herein. We consider, however, that a reasonable reliable 'dynamic picture' of the main diversity trends registered from the conodonts record can be interpreted. Our analysis represents then the first approach in this regard.

We are conscious that further work will be focused on evaluating the depth of the sampling effect on such patterns. Then again, due to the continuous improvements in the conodont research, we assume that the raw data can always be subject to modification both as new data and when different taxonomic appointments are considered. The conclusions derived from such modifications could provide alternative visions.

Supplementary online material

Supplementary File 1. Table S1. Timescale, time units and ammonoid biozones used for subdivisions. Data were extracted from Henderson et al. (2012) and Ogg (2012). See 'Methods' section for details.

Supplementary File 2. Binary (presence–absence) matrix used in this study. Species diversity of conodonts appears in the rows. The temporal distribution of the considered taxonomic entities is codified in the columns. See 'Methods' section for details.

Supplementary File 3. References list cited in Supplementary File 2.

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