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Conodonts versus Triassic Climatic and Eustatic Changes

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Abstract

From astronomical, sedimentological, paleo-geographical and geochemical points of view, there is a general agreement that the Triassic period was exceptionally warm. The 51 MA long Triassic period started during the Siberian Traps and ended at the height of the Central Atlantic Magmatic Province activity. It is comprised between End Permian and End Triassic mass extinctions. Conodonts survived the former but got extinct by the end of the latter. Three major waves characterise the evolution of Triassic conodonts:

I. The 5 MA long Scythian recovery by intensive speciation (23 S/MA);
II. The 10 MA long Dinarian of intensive radiation (8.5 S/MA);
III. The 16 MA long Julian - Lacian survival (2S/MA) and 20 MA of Alaunian – Rhaetian decline until extinction.

The major causes of stress affecting the evolution of Triassic conodonts are environmental, such as marine regressions, anoxic episodes, and thermal or trophic (nutritional) stress. These stressful episodes caused dwarfing and extinction of larger forms (r-selection). Smaller forms with a short life span and rapid proliferation are the result of heterochrony such as proteromorphic retrogradation (Atavism).

The disappearance of the conodonts was not caused by a single mass extinction event, but the result of summing up stress factors from hostile environments over a long time.

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Keywords: Triassic conodonts; phylogeny; progenesis; proteromorphosis.

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1. Introduction

The Triassic conodont faunas have been analysed in relation to the impact of succeeding ecological crises of the marine ecosystems. Characteristic for the Triassic period are: (i) Start from Pangea; (ii) Aftermath of the P-T mass extinction; (iii) probable absence of an equatorial humid belt during most of the Triassic timespan (Truempy, 1982); (iv) low relative sea levels, although absolutely ice free; (v) Period among the hottest of Earth history (Shaviv and Veizer, 2003).

Triassic conodont databases (Plasencia, 2009; Plasencia et al., 2013) reveal approximately 60 genera and 400 species. These underwent periodic environmental stress, from the immediate aftermath of the end Permian mass extinction to subsequent sea level rises, cyclic changes, sudden regressions and the gradual sea level drop that lasted 27 MA until the end of the Triassic Period.

2. Developement

Three waves characterise the development of Triassic conodont lineages:

Wave I: From a dozen Permian-Induan survivors of the Families Spathognathodontidae, Ellisoniidae and Gondolellidae, only the latter's subfamily Neogondolellinae produced a wealth of genera that radiated until the end of the Spathian. Most lineages that appeared during the Scythian did not persist beyond the Olenekian and only one lineage of Neogondolellinae) persisted, thanks to repeated retrogradations, until the Rhaetian extinction of all conodonts. A great wealth of forms appeared and went during Olenekian times. The Spathian - Anisian transition was a first bottleneck through which a single lineage of Neogondolellinae could pass, together with the new family Gladigondolellidae that appeared in the latest Spathian and lasted until the Late Julian, as long as normal marine pelagic conditions persisted. Five MA had passed since recovery from the Permian - Triassic Boundary Mass Extinction.

Wave II: From the single survivor lineage of Neogondolellinae, several genera developed during the Dinarian (Anisian - Ladinian). Repeated punctuated atavistic iterations in Bithynian, Pelsonian, Illyrian and Fassanian times generated new genera, their lineages all ranging shortly into the Early Julian until the second bottleneck that 15 MA into the Triassic. Again, one lineage (Type P) of Neogondolellinae survived, as well as the single lineage of Gladigondolellidae.

Wave III: The 16 MA long Julian - Lacian timespan is one of intense diversification of at least seven generic lineages in which dominant evolutionary trends were increasing ornamentation and posterior widening and bifurcation of the unit. The Alaunian reversal of these trends, replaced by posterior acumination of the unit, initiated the last 20 MA of the Triassic, a period of few speciations and survival of two generic lineages. One that had survived the first bottleneck, the second being the product of atavistic retrogradation. At least seven such iterative retrogradations marked the Early Julian, Late Tuvalian, Alaunian, Sevatian and Rhaetian. Only atavistic genera are left during the Rhaetian and terminate the third wave with the final extinction of conodonts.

3. Causes and Effects

These waves seem to reflect a succession of environmental changes such as the opening of new niches (Induan, Late Olenekian, Ladinian, and Late Carnian) that were paced by the appearance and vanishing of generic lineages within the subfamily Neogondolellinae (Types N and P). In many cases stress conditions generated atavistic morphs (Type A). From these, new generic lineages radiated with no apparent phyletic link to the former, like the Smithian "restoration" of N types of earlier Late Permian tradition. The Late Spathian restoration of pelagic conditions brought the ascent of the family Gladigondolellidae (Type G). The Dienerian - Spathian type A lineage continued from the earliest Aegean into the more open marine type P lineage. Bithynian, Pelsonian, Illyrian and Fassanian retrogradations of Type A repeatedly radiated into type N "restorations" and unfolded the type S subfamily Sephardiellinae. Reduction of niches during the Late Ladinian - Early Carnian global regression and salinity crisis, caused the extinction of all N and S types, Neogondolellinae surviving only as a P type. The Early Julian type A iteration generated the poorly ornamented type M_1, while the Julian Pluvial Event may coincide with the ascent of an heavily ornamented type M_2. Successively, Tuvalian and Lacian oscillations of the sea level coincided with the ascent of increasingly ornamented types M_3, M_4 and M_5. The general reversal of the main evolutionary trend into the acuminate type E that characterises the dawn of the Alaunian, was preceded in the Late Tuvalian by an atavistic

retrogradation of type E that represents a premature first appearance of the trend, issued from type M_4. A meteorite impact at the dawn of the Sevatian may have precipitated the final extinction of conodonts by accelerating the simplification of the characters and the appearance of an ultimate Rhaetian type A. This hypothesis is substantiated by several craters approximately at the Alaunian - Sevatian boundary, such as Rochechouart (France), Manicouagan and Saint Martin (Canada), Obolon (Ukraine), Red Wing (USA) and Bristol (England). The comet or asteroid was synchronously fragmented during impact (Barash, 2006). The activity of the Central Atlantic Magmatic Province (CAMP) reached its apex at 201.58 MA (Schaltegger et al., 2008).

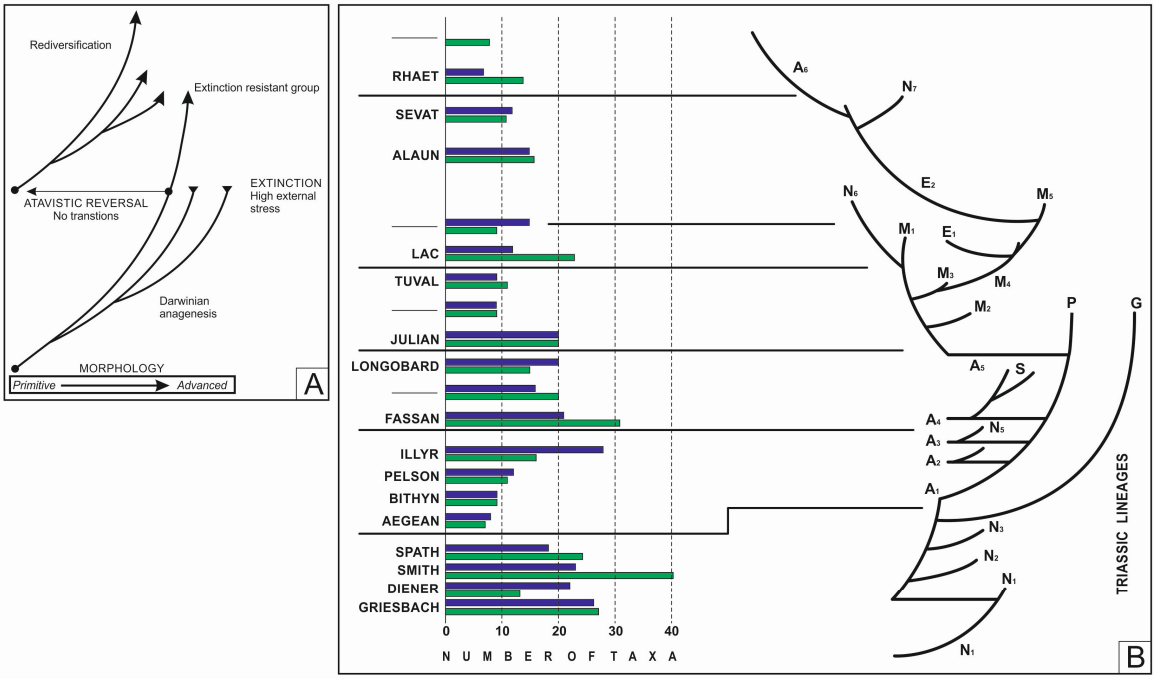

Fig. 1. Distribution of Triassic conodont lineages and number of taxa through time. Key (**A**) after Guex (2001); Scheme (**B**) Taxa numbers, compiled from Martinez-Perez et al. (2013).
Legend: N: Neogondolellinae; A: *Neospathodus*; A_1:*Chiosella*; A_{2-3}: *Nicoraella*; A_4: *Pseudofurnishius*; A_5: *Mosherella*; A_6: *Misikella*; N_1: *Clarkina*; N_2: *Scythogondolella*; N_3: *Borinella*; N_4: *Pridaella*; N_5: *Neogondolella*; N_6: *Norigondolella*; N_7: *Parvigondolella*; P: *Paragondolella*; M_1:*Metapolygnathus*; M_2: *Mazzaella*; M_3: *Hayashiella*; M_4: *Carnepigondolella*; M: *Ancyrogondolella*; S: Sephardiellinae; E: Epigondolellinae: E_1: *Acuminatella;* E_2: *Mockin.*

External causes, such as paleo-climatic changes, abnormal temperature or chemical stress, could uncover morphological variants for selection to act upon (Rutherford and Lindquist, 1998). These may allow some of the rapid morphological radiations observed in the fossil record (Guex, 2001). In this context, strong activity of the Siberian Trap lasted until the end of the Griesbachian (Korte and Kozur, 2010). Also recurrent environmental changes, triggering Early Triassic ecosystem instabilities, such as the Middle Smithian spore spike concurring with a negative $\delta^{13}C$ anomaly, preceded a Late Smithian marine extinction event (Hermann et al. (2011)). The major phylogenetic developments in Triassic conodonts seem to coincide with severe sea level changes that possibly related to anoxic events. Correspondingly, chemical stress and high temperatures may cause inheritable resurgences of atavistic structures. Discrete, short anoxic episodes, such as an Early Dienerian shelf event on the northern Gondwanian margin that correlates in time with similar paleooceanographic changes on the equatorial North American margin and southern Tethys, were part of the Early Triassic biotic recovery (Ware et al., 2011).

The accumulation of geologic and biological circumstances may have stressed the extinction of conodonts. Faunal competition (fide F. D. Por, pers. comm. 1990) and the difficulties, since Julian times, for conodont taxa to adapt to both stressful environmental conditions and competition from new Mesozoic biota (Martinez et al., 2013).

Iteration of Paleozoic morphologies are interpreted as the result of retrogradation and atavistic homeomorph forms appearing during sublethal stress events, often separated by several millions of years (Guex (2001). This is the

case of the proteromorphic retrogradation in type N, shortly after the P/Tr boundary, the sudden appearance of a simple and economic architecture as a potential source for renewed phylogenetic development (Guex et al., 2014).

4. Conclusion

The disappearance of conodonts was not caused by a single mass extinction event, but the result of summing up stress factors from hostile environments over a long time. Environmental stress, such as marine regressions, anoxic episodes, and thermal or trophic (Hallam, 1978; Mancini, 1978; Valentine et al., 1994; Hirsch, 1994) may, in comparison with Cope's rule, cause decreasing sizes and morphological complexity, sometimes explained by elimination of the more complex forms during extinction events (Saunders et al., 1999). The larger forms being more vulnerable to extinction (r-selection), more and more decreasing small forms with short life span and rapid proliferation through proteromorphic retrogradations of type A appear during stressful episodes.

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