The extinction of conodonts –in terms of discrete elements– at the Triassic-Jurassic boundary

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ABSTRACT

The extinction of conodonts at the end of Triassic times is studied. The possibility of random extinction is considered. Extinction and origination rate averages for lineages of the Phanerozoic marine invertebrates are not coherent with the dynamics of this group. Their extinction rate diminished since the Lower Triassic to the Upper Triassic, but the lineage origination rate diminished since the Ladinian as well, and the clade had negative growth rate, and the probability of extinction was high. Diffuse competition with better animal designs belonging to Paleozoic and Modern evolutionary faunas and, in a more secondary way, a decrease of available marine areas and spreading of environments with abnormal salinity in the Western Tethys are pointed out as possible causes of their extinction.

Key words: Conodonts, Triassic, Extinction, Internalism, Environmentalism.

RESUMEN

Se estudia la extinción de los conodontos al final del Triásico. Se investiga la posibilidad de extinción por simple azar. Las tasas medias de

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originación y extinción de linajes de invertebrados marinos fanerozoicos no son consistentes con la dinámica de este grupo. Su tasa de extinción disminuyó del Trias Inferior al Superior, pero la tasa de originación de linajes también lo hizo desde el Ladiniense, y el clado mantuvo tasa de crecimiento negativa, con la consiguiente alta probabilidad de extinción. Las posibles causas que se proponen para su extinciòn son la competencia difusa con mejores diseños animales pertenecientes a las faunas evolutivas paleozoica y moderna y, de una manera más secundaria, un decrecimiento de las áreas marinas aprovechables y la aparición de ambientes con salinidad anormal en el Thethys occidental.

Palabras clave: Conodontos, Triásico, Extinción, Internalismo, Ambientalismo.

INTRODUCTION

Extinctions have been told to be important events in the history of life. Their negative contribution is reflected in the elimination of many taxa and in evolution-they can undo large trends or other evolutionary issues (Gould, 1985). On the positive side, they prepare the global biota for new evolutionary experiments (cf. De Renzi, 1988).

Mass extinctions are generally thought as the result of external impacts against the biosphere (e.g. fall of large meteorites or internal activity of the Earth, such as vulcanism on a large scale). But the biosphere has a specifical dynamics involving several organic levels and their interactions. An example is the kinetic model for changing diversity across the Phanerozoic marine record (Sepkoski, 1978, 1979, 1984). Three evoutionary marine faunas (Sepkoski, 1981) are considered: The Cambrian fauna, the Paleozoic fauna and the Modern fauna. Their interplay causes the decadence of the Cambrian and Paleozoic faunas and the solitary expansion of the Modern fauna since the Permo-Triassic boundary. When new data have been available, macroevolutionary patterns seem to remain (Sepkoski, 1993).

Conodonts are components of both Cambrian and Paleozoic evolutionary faunas. They belong to a long-lived group, but their contribution to these faunas is not relevant (Sepkoski, 1981). The Permian extinction did not affect them (Clark, 1987a). A revival for the group took place at the Early Triassic, but they finish their geological existence in a piecemeal fashion during the Rhaetian after a declining situation. Only two

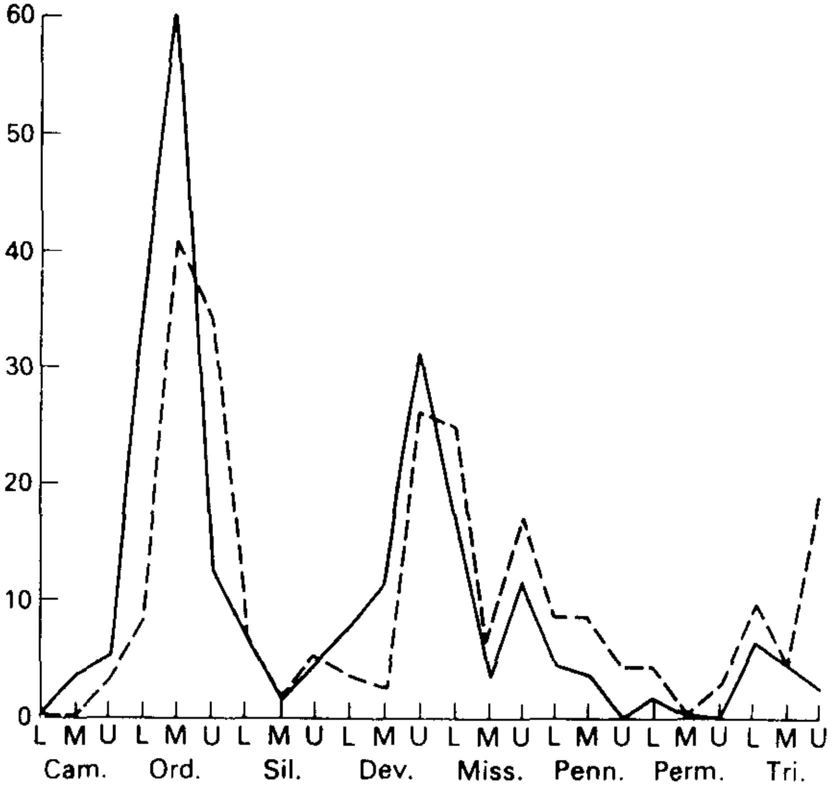

Fig. 1.–Riqueza de géneros (basados en elementos discretos) para los conodontos a través de su rango geológico completo (de Clark, 1987b). El número de géneros aparecidos en cada época (línea continua) se compara con el número total de géneros extinguidos durante el mismo período (línea de puntos).

Fig. 1.–Genera (based on discrete elements) richness for conodonts in their complete geological range (from Clark, 1987b). Number of genera appeared in each period (solid line) compared with total number extinct during the same period (dashed line).

species remained and they disappeared in two different moments of the Rhaetian times.

Their extinction poses several problems and some approaches to them are found in two seminal papers of Clark (1987a) and Aldridge (1988). Was it a Galtonian extinction with the normal extinction and speciation rates of marine Phanerozoic invertebrate species? Triassic conodonts form a small group of species, and origination and extinction patterns can be traced during the period. This can shed some light on these questions, but the nature of the Triassic fossil record must be taken into account as well. Since important punctual extinctions can be masked in a pattern of background extinction, polycohort analysis becomes a clue in evidencing these episodic situations. The extinction of the clade in the World at the end of the Triassic times will be considered under these premises in this paper.

SOME GENERAL REMARKS ON CONODONTA

Conodonts are animals of uncertain affinities represented by tiny skeletal elements preserved in the geological record since the Cambrian times until the end of the Triassic; conodont elements can be found in natural assemblages, clusters or reconstructed as apparatuses. These conodont elements are composed by francolite, a carbonate apatite (Clark, 1987b). Since they are originally phosphatic pieces, they can be preserved easier than other skeletal parts and therefore, conodont elements can «survive» to diagenesis and metamorphism whereas other common groups cannot. They appear in a variety of sedimentary materials deposited in a wide range of marine conditions. There is no general agreement about their taxonomical position. In order to avoid discussions, we refer to them as Clade Conodonta. They are classsified in terms of species grouped in higher taxonomic categories; these species are recognized on the morphological basis (morphospecies). On the other hand, by the reasons given by Raup (1985), we prefer to talk about lineages rather than species, and about lineage origination rate instead of speciation rate. When origination is used for other taxonomic categories, it will be indicated.

From a historical point of view, they show a cyclical declining pattern of generic diversity parallel to generic extinction with several decreasing peaks, as shown by Clark (1987b). A relative revival occurred during the Triassic times, but the generic richness did not reach the level of the Upper Mississipian maximum (Fig. 1).

PROBLEMS RELATED TO THIS STUDY

Analysis of patterns of extinction and origination requires previously the consideration of taphonomical biases which could hide paleobiological aspects. Differential preservation plays an important role in interpreting a historical record (De Renzi, 1992). Due to their mineralogy, the elements of the Clade Conodonta are exceptionally preserved in many fossilization conditions. Thus, its record is not biased by differential preservation (cf. Aldridge & Smith, 1993).

An important bias comes from the age of rocks (Raup, 1972; Raup & Stanley, 1978). Because rock outcrop area decreases with geological age, the fossil record becomes gradually rarefied and this character has to be considered when evolutionary rates in very old initial records of a clade are studied (De Renzi, 1992). Lineage numbers are very biased by this trait of the fossil record; but this trouble is not so much important when research is focused on numbers of supraspecific categories as genera, families or orders (Raup & Stanley, 1978; Sepkoski, 1978). Since conodonts are distributed between the Cambrian and the end of the Triassic, these remarks must be considered. Budurov and Sudar (here) have arranged the amount of conodont Triassic species –lineages– (107) in the World according to their stratigraphical distribution and their order of appearance; they are grouped in 26 genera (17 are based on platform elements and 9 are defined on blade-like elements) (Budurov & Stefanov, 1972; Budurov, 1980; Budurov & Sudar, 1990; Budurov & Trifonova, 1994, and Budurov & Sudar, in press). Although the lineage level is the most affected by rarefaction, lineage numbers for epochs of the same Period are affected by the same bias and it is valid to work with them.

Conodont fossils present a widespread distribution reflecting that of old species, and they range from pelagic to benthic organisms. Excluding some kinds of environments (extremely shallow waters, represented by stromatolitic facies; hypersaline conditions, brackish waters and very deep basinal bottoms as represented by their sediments), fossils of conodonts are very frequent in normal marine conditions (Clark, 1987b). After the Permian, the ratio continental/marine sediments was high. A more open marine character is only developed in certain areas of the world. Therefore, the observed strong decrease in invertebrate species richness during the Triassic could not only be produced by the Permo-Triassic extinction but by the dynamical evolution of the Earth crust as well (Marquez-Aliaga & De Renzi, 1990). Restricted conditions and deep-sea basins could affect conodont lineage richness in that time. Thus, the Triassic record of this group might partly be explained by environmental controls.

Another question to be considered is the character of the conodont skeletal parts. Discrete skeletal elements generate a taxonomy that has produced good results for stratigraphical purposes (Utilitarian classification; Aldridge & Smith, 1993). A more natural taxonomical approach can be obtained from reconstruction of apparatuses; multi-element assemblages have been found, but a conodont animal could have more than one apparatus (see also Clark, 1987b). However, our study is based on discrete elements only.

METHODS

Three approaches are developed here: 1) probabilistic analysis of extinction; 2) estimates of extinction and origination rates, and 3) polycohort analysis. All these procedures are applied to the stratigraphical distribution of the 107 lineages. Absolute ages for Triassic Stages have been taken from Harland et al. (1990). Minor divisions (ammonite or conodont zonations) are intercalated between well dated time points, but absolute ages for these intervals are unknown (see below).

The possibility for Galtonian extinction of a clade is analyzed according with the procedures described by Raup (1981, 1985). Cladal branching can be subjected to constant rates for origination and extinction (time-homogeneous model). Let be λ the origination rate and μ the extinction rate. When λ is different from μ, the formula applied is

$$P_0=\{\mu[\exp[(\lambda-\mu)t]-1]/[\lambda\exp[(\lambda-\mu)t]-\mu]\}^n \qquad (1)$$

(*t* is time and *n* is the number of lineages at the beginning of the interval).

Extinction and origination rates are really probabilities. Because of all the reasons given above about the Triassic record of conodonts, our estimates will be very crude images of the real situations. Both rates are measured in temporal intervals limited by two absolute ages; e.g. Griesbachian. According to population ecology, extinction and origination rates are analogous in structure to birth and mortality rates. For a given temporal interval Δt, birth (or origination) rate $\lambda=1/N\ (S/\Delta t)$; N is the number of individuals (lineages) at the beginning of the interval (those entering the interval and coming from the precedent one) and S is the number of births (origination events) produced during the interval. Death (extinction) rate has a similar definition: $\mu=1/N\ (E/\Delta t)$, where E is the number of individuals that died (extinct lineages) during the interval. The growth rate is defined as $R=\lambda-\mu$ (see Sepkoski, 1978).

Polycohort analysis was developed by Raup (1978), although there are other considerations on this procedure in Hoffman & Kitchell (1984)

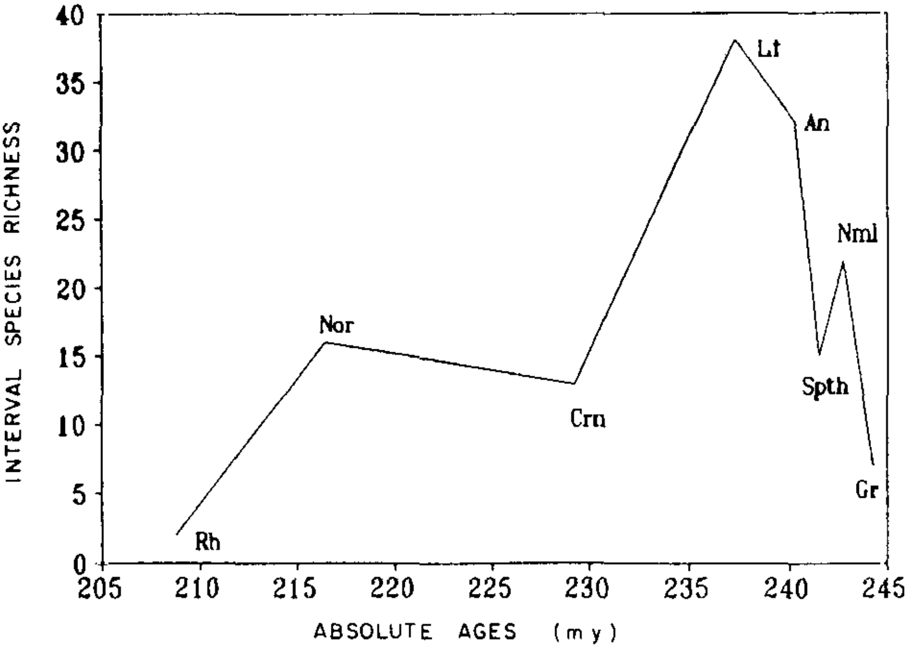

Fig. 2.–Riqueza en linajes de conodontos durante el Triásico. La riqueza se da en el punto medio de cada piso como su número total de linajes. **Gr**, Griesbaquiense. **Nml**, Nammaliense. **Spth**, Spathiense. **An**, Anisiense. **Ld**, Ladiniense. **Crn**, Carniense. **Nor**, Noriense. **Rh**, Retiense.
Fig. 2.–Conodont lineage richness during the Triassic. Richness is given at the middle point of each stage as its total number of lineages. **Gr**, Griesbachian. **Nml**, Nammalian. **Spth**, Spathian. **An**, Anisian. **Ld**, Ladinian. **Crn**, Carnian. **Nor**, Norian. **Rh**, Rhaetian.

and Raup (1987). In our paper, we use the pseudo-polycohort approach (Hoffman & Kitchell, 1984), by using all taxa in each time interval. Raup (1978) outlines the essential technique as follows: members of each cohort became extinct or survive in consecutive time intervals; thus, a taxonomic survivorship curve can be traced from these data. This curve may be drawn by regression analysis or it may be approached by connecting the points for survivorship by straight-line segments. A linear regression can result in illusive examples of Van Valen's law; i.e. the extinction rate is constant during time (see Raup, 1987). The second procedure proposed by Raup shows inflections in the slope of segments. They reflect change in the extinction probability as caused by environmental change or something related to the internal aspects of the pattern mortality. When successive cohorts exhibit inflections that coincide at the same time point, this indicates that an external event has troubled all the cohorts crossing that point.

In our case, absolute time markers are not evenly distributed along the Triassic duration and narrower subdivisions (biozones) are not dated. However, these subdivisions are not evenly distributed in the whole duration of each stage. Then, absolute time for them may be considered approximately proportional to the extension of each subdivision in the whole stage. By this reason, a qualitative approach may only be carried out.

λ	μ	R	P_0
0.09	0.095	-0.005	0.008
0.09	0.1	-0.01	0.014
0.09	0.15	-0.06	0.29
0.09	0.2	-0.11	0.73
0.09	0.25	-0.16	0.93
0.09	0.3	-0.21	0.98

Tabla 1.- Probabilidades de extinción galtoniana 1) con los promedios de λ y μ propios de los invertebrados marinos fanerozoicos (primera fila), y 2) para valores de μ creciendo con pequeños incrementos (filas 2 a 6): Los valores altos de probabilidad están subrayados.
Table 1.- Probabilities for Galtonian extinction 1) with averages for λ and μ of the marine Phanerozoic invertebrates (first row), and 2) for values of μ increasing by small steps (row 2 to row 6): High probability values are underlined.

RESULTS

General considerations.—A glance at the raw data shows a climax of lineage (specific) richness in the Anisian and the Ladinian followed by an irregular decrease until final extinction in the Rhaetian (Fig. 2). From the end of Permian until the Ladinian, the lineage richness was growing with a small decrease in the Spathian. Let verify wheter the Rhaetian end of the clade was a Galtonian extinction when the starting point is the early Ladinian richness (the largest richness associated to a well dated point; 18 lineages). Using 0.09 for lineage origination rate average in marine Phanerozoic invertebrates, and 0.095 as mean extinction rate (Raup, 1981), the probability for Galtonian extinction given by formula (1) is

0.008, a relatively low value. By increasing in small steps the extinction rate, the event is possible with a moderate to high probability (see table 1).

However, taking into account the consideration about the absolute duration of the Triassic biozones made above, a *grosso modo* assessment for mean duration of conodont lineages may be carried out during the Lower, Middle and Upper Triassic. These values differ very much because the three epochs are very different in duration and hence, their biozones as well. For the Lower Trias, the biozone duration average is smaller than 1 My, and about 1 My for the Middle Triassic. However, for the Upper Triassic, biozones perhaps range between 1 and 2 My. Therefore, since many conodont lineages embrace more than two biozones, differences in mean lineage duration are expected according to their stratigraphical position. Then, lineage mean duration for conodonts increases from the Lower to the Upper Triassic.

AGE	MEAN *DURATION* (MY)	EXTINCT. *RATE* (MY^{-1})	ORIG. RATE (MY^{-1})
Lower Trias	~0.5	~2	~1.9
Middle Trias	~1	~1	~1.4
Upper Trias	~5.5	~0.2	~0.1

Tabla 2.- Valores aproximados de duración media de las especies de conodontos para las tres épocas de los tiempos triásicos; las tasas de extinción están calculadas como inversas de las duraciones medias (ver el texto). Las tasas de especiación están calculadas según el procedimiento de Stanley (1975, 1979) (ver el texto).

Table 2.- Approximate values of mean duration of conodont species for the three Epochs of the Triassic times; extinction rates are calculated as the inverse of mean durations (see text): Speciation rates are calculated according to Stanley (1975, 1979) (see text).

From the study of the extinction rate μ, which can be estimated from the mean duration D as 1/D (Stanley, 1975, 1979), results that the extinction rate decreases from the Lower to the Upper Triassic (table 2). Origination rates are calculated by assuming constant growth rate (Stanley, 1975, 1979), although this approach is considered very crude (see below -a detailed analysis of origination and extinction rates, and table 3- and Discussion). Therefore, $R=1/T \ln(N_T/N_0)$; N_T and N_0 are the number of lineages at the beginning and at the end of the interval T. Since $\lambda=R+\mu$, calculation is possible. From this viewpoint, origination rates show a progressive decline, from relatively high values (Lower and Middle Triassic) to a low value (Upper Triassic) (table 2).

This shows variable rates for diversification of the Clade Conodonta in time (time-inhomogeneous model). There are 8 lineages at the beginning of the Carnian, and the Early Carnian-Late Rhaetian interval duration equals 27 My. Consequently, the extinction and origination rates for the Upper Triassic predict that Galtonian extinction would be a very probably event at that time ($P_0=0.75$).

Detailed analysis of origination and extinction of Conodonta during the Triassic.- This analysis is carried out for each Stage whose absolute duration is well known; results are presented in table 3. High values (>1) of origination (λ) and extinction (μ) rates are observed from the Nammalian to the Anisian. Since the origination rate is usually larger than the extinction rate for this interval, the growth rate is positive, except during the Spathian Stage, with lower values for both rates and negative growth rate. The largest values for both origination rate and growth rate are reached in the Anisian, in which the richness is extremely large and prepares the largest richness for the Ladinian. From the Ladinian to the end of the

STAGE	N	S	E	Δt	λ	μ	R
Gr	5	2	6	1.6	0.25	0.75	-0.5
Nml	1	21	17	1.5	14	11.33	2.67
Spth	5	10	14	0.8	2.5	3.5	-1.0
An	1	31	14	1.6	19.38	8.75	10.63
Ld	18	20	32	4.5	0.25	0.4	-0.15
Crn	6	7	8	11.6	0.10	0.11	-0.01
Nor	6	11	14	13.9	0.13	0.17	-0.04
Rh	2	0	2	1.5	0	0.67	-0.67

Tabla 3.- Valores de las tasas de especiación, extinción y crecimiento para cada piso del Triásico. Los símbolos, como en el texto. Gr = Griesbaquiense; Nm = Nammaliense; Spth = Spathiense; An = Anisiense; Ld = Ladiniense; Crn = Carniense; Nor = Noriense; Rh = Retiense.
Table 3.- Values of speciation, extinction and growth rate for each Triassic stage. Symbols as in text. Gr = Griesbachian; Nm = Nammalian; Spth = Spathian; An = Anisian; Ld = Ladinian; Crn = Carnian; Nor = Norian; Rh = Rhaetian.

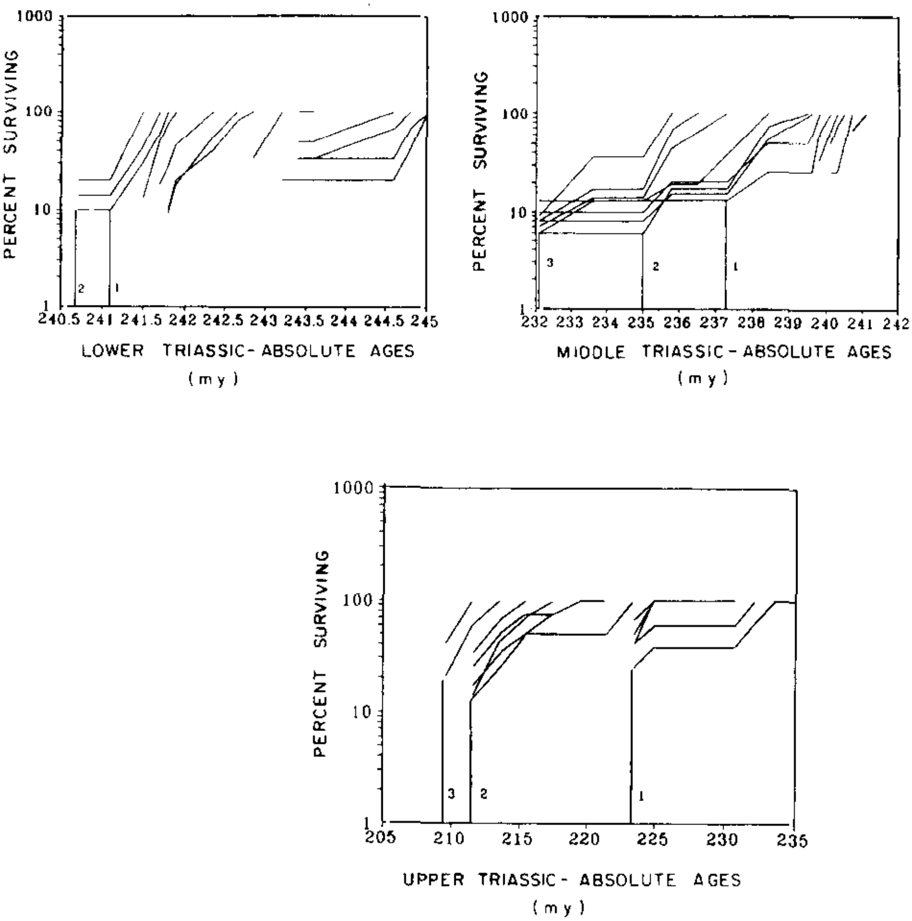

Fig. 3.—Análisis de la policohorte incluyendo todas las cohortes de conodontos del Triásico. Para una mejor representación, la policohorte ha sido subdividida en tres policohortes parciales, correspondientes a las tres principales épocas triásicas. Los puntos críticos (terminación o declive simultáneos de varias cohortes) están indicados por líneas verticales con un número. Los límites zonales (en edad absoluta) son solamente aproximados. Policohorte del Triásico Inferior: **1**. Límite Spathiense-Anisiense; **2**. Base de la zona de *Paragondolella regale*. Policohorte del Triásico Medio: **1**. Base de la zona de *poseidon*; **2**. Límite Ladiniense-Carniense; **3**. Base de la zona de *Trachyceras aonoides*. Policohorte del Triásico Superior: **1**. Límite Carniense-Noriense; **2**. Base de la zona de *Cochloceras suessi*; **3**. Base de la zona de *Choristoceras marshi*.

Fig. 3.—Polycohort analysis including all the conodont cohorts of the Triassic. For a better representation, the polycohort has been subdivided into three partial polycohorts corresponding to the main Triassic Epochs. Critical points (simultaneous end or decline of several cohorts) are indicated by vertical lines with a number. Zonal boundaries (in absolute age) are only approximate. Lower Triassic polycohort: **1**. Spathian-Anisian boundary; **2**. Base of *Paragondolella regale* zone. Middle Triassic polycohort: **1**. Base of *poseidon* zone; **2**. Ladinian-Carnian boundary; **3**. Base of *Trachyceras aonoides* zone. Upper Triassic polycohort: **1**. Carnian-Norian boundary; **2**. Base of *Cochloceras suessi* zone; **3**. Base of *Choristoceras marshi* zone.

Rhaetian, origination and extinction rates decrease strongly (<1), being extinction always larger; thus, the growth rate is negative. These data make up a more refined approach to the inhomogeneous character of conodont diversification.

Polycohort analysis.–Limits of biozones are starting points for cohorts. Ammonoids and conodonts establish 41 limits from the Permo-Triassic boundary to the Rhaetian base. There are, therefore, 41 cohorts for conodonts. This analysis shows some principal moments for important amounts in extinction (Fig. 3). Many cohorts diminish the percentage of survivors at the Ladinian-Carnian limit (base of *Frankites sutherlandi* zone; this has a precedent with a critical point in the *poseidon* zone) and many others became extinct during the *Trachyceras aonoides* zone. The *Mojsisovicsites kerri* zone (its base is the Carnian-Norian limit) and the *Cochloceras suessi* zone are also terminal points for several cohorts. Only two cohorts reach the Rhaetian and the practical extinction of the clade could be placed at the *Cochloceras suessi* zone. Cohorts during the Lower Triassic have short live compared with those of Middle and Upper Triassic.

DISCUSSION

A conodont taxonomy can be based on discrete elements or/and apparatuses. In this paper, we are constrained to work with discrete elements because apparatuses of Triassic conodonts are not available at this stage of research, although this would be a more natural approach. However, some possible causes for extinction can be supplied.

First, we are going to discuss our results with reference to those reached by Clark (1987a). Absolute ages surveyed by Harland et al. (1990) are more refined than the previous ones. Clark could only calculate rates for the whole Scythian but not for its substages (Griesbachian, Nammalian and Spathian). On the other hand, the old estimate for the Middle Triassic was 10 My, whereas the new estimate is 6.1 My. Diversity reductions and expansions during the Lower Triassic are explained in function of negative and positive growth rates and large oscillations of both origination and extinction rates (see table 3). The Nammalian was the interval of maximum diversification (2.67), although the extinction rate reached the highest value of the whole Period (11.33). On the other hand, the Middle Triassic has a very expansive phase during the Anisian (the highest origination rate, 19.38, and the highest growth rate, 10.63).

However, the decline of the group begins in the Ladinian (negative growth rate) and not in the Upper Triassic, which follows the same pattern of the Ladinian, with smaller and smaller origination rates.

A discussion about the deviations of estimates according to Stanley (1975, 1979) procedures is needed. Lineages are evenly distributed during the Upper Triassic. On the other hand, growth rates are relatively similar during the Upper Triassic because λ and μ vary very slightly (table 3) and this is the condition for a time homogeneous model. Therefore, the extinction and origination rates inferred from mean duration are fairly close to the average of that obtained with the formulae given by Sepkoski (1978) and used above. Differences are striking for the two kinds of estimates in the Lower and Middle Trias, due to the inhomogeneous character of both Epochs (see table 3).

Polycohort analysis shows that crisis during the Lower Triassic are minimal. During the Lower Triassic, survivorship lines do not seem to exhibit simultaneous inflections reflecting external deletereous factors, and they show a more constant extinction probability pattern (van Valen model) than an episodic one for this epoch. Only at the end of the Spathian is possible to see the sharp declining of three cohorts (Fig. 3). Thus, high extinction rates are perhaps not related to critical events during this time. Clark (1987a) asked about a possible conodont extinction concentrated in a specific moment of the Scythian times, that the crudeness of the temporal scale did not make possible to infer. Polycohort analysis does not seem to show any special time for extinction during the Scythian. The raw data distribution exhibits a piece-meal extinction for this interval. However, episodic alternation between no extinction and more or less pronounced extinction characterizes the Middle Triassic, and also the Upper Triassic, but in a minor degree. Several critical moments have been detected for these two Epochs (see fig. 3).

Explanations for conodont extinction can be internalist or environmentalist. An internalist explanation could be as follows: They declined through the Upper Triassic after a climax in the Ladinian; a possible causal factor could be that they competed disadvantageously with other better fitted animal designs. Their Triassic revival could be related to the Permo-Triassic extinction affecting more stenotopic Permian competitors versus the better capability of the remaining conodonts to evade extinction, because of their more eurytopic character and widespread distribution. This could be supported by the assertion that conodonts were very little affected by the Permo-Triassic extinction related to other groups (Sweet in Clark, 1987a). However, a problem arises when the lineage duration is considered. The mean lineage duration increases considerably in the Upper Triassic. Large duration of lineages is not the best condition for a gradually decrease of diversity leading towards extinction. But origination rates diminish as well, and they are lower than extinction rates. Extinction becomes possible because growth rate is negative since the Ladinian times. This is neatly an internalist cause for extinction.

Let analyze the problem from an environmental point of view. The paleogeography of Triassic times is changing from the Permo-Triassic limit until the end of the Period in the Mediterranean region. Lower Triassic sediments were deposited in non-marine conditions for large extensions in this area, due to an inherited Upper Permian paleogeography of the Tethys; in the Middle Triassic, this region was invaded by the sea, and a regression took place on broad extensions in the same zone during the Upper Triassic (Middle Carnian; see Hirsch, 1986).

The conodont evolution depended on the ecological requirements of this group. The range of favorable environments for conodonts was enlarged when new areas were invaded by the sea. This took place since the Middle Triassic, when the sea entered the Mediterranean region and the World underwent a major provincialization (Yin, 1991). This is according with Clark (1987a), who considered the Permian as an anomalously low interval of diversification. Therefore, the progressive transgression was the cause of the rising of origination rates. When the regression took place in broad zones in the region during the Upper Triassic, the distribution of available biotopes for conodonts was reduced again. There is no indication of provincialism in this time. The climax in the Middle Triassic and the declining during the Upper Triassic seem coherent with the changing paleogeography. Furthermore, conodonts are related to fossils of stenohaline organisms (see above). Hallam & El Shaarawy (1982) remarked a salinity reduction of the end-Triassic sea caused by a transgression of a shallow epicontinental sea from the Alpine region into northwestern Europe during the Rhaetian. Diminution in lineage richness for bivalves, foraminifers and ostracodes, and disappearance of stenohaline elements, such as ammonoids are the evidences for this inference. A recent review by Fürsich (1993) remarks that the same groups of organisms can live associated to abnormal salinity (from hypersaline to brackish waters) because they have physiological adaptations for both regimes, and their populational answers are similar. Under this light, and since speciation depends on a geographical ground, the reduction in conodont lineage richness since the early Upper Triassic could be related to two main factors affecting to Western Tethys as an important region: 1) a general reduction of marine areas during the Upper Triassic; 2) an abnormal salinity during the Rhaetian. However, the relative importance of paleogeographical changes during the Upper Triassic of the World cannot be assessed in the actual state of knowledge.

Let return to the internalist viewpoint: Conodonta cannot be considered a successful clade during the Paleozoic. Family richness of this group is lower than the richness of other typical Paleozoic clades like Articulata or Crinoidea; but they are similar in family richness to other clades not so relevant; e.g. Stelleroidea or Blastoidea (cf. Sepkoski, 1981). Although Aldridge & Smith (1993) use a multi-element classification, their data on the family record may supply a good information. *Grosso modo*, the number of conodont families suffered a continuous reduction since the Ordovician climax and only four families arrived to the Lower Triassic, according to the data of these authors. Two of these disappeared in the Griesbachian and the Dienerian (Lower Nammalian) whereas the other two became extinct in the Carnian and the Rhaetian. This family richness dynamics is coherent with the observed pattern for lineages. The use of the family level is advantageous because it removes rarefaction effects when Paleozoic and Mesozoic records are compared.

Several questions arise. Gould (1989) concluded that many evolutionary experiments carried out in Cambrian times (Baupläne preserved in the Burgess Shale) were not successful. According to Gould, the reason of their rapid extinction was bad luck, not a lack of fitness. Bad luck may be interpreted in terms of critical cladal size, in a parallel comparison with the critical population size. What happened with conodonts? Their large time span (around 300 My) is not coherent with extinction by chance. In fact, our calculations show that a relatively high extinction rate and negative growth rate during the Upper Triassic made the removal of the group a very probable event (tables 2 and 3). A possible scenario could be as follows: conodonts proliferated during the Earliest Paleozoic times, once they overcome the critical cladal size. Their design was comparable in fitness with that of other groups. When better adapted animals emerged, disadvantageous competition with them began (diffuse competition with increased species packing –cf. Sepkoski, 1978– could be a credible mechanism). This occurred probably since the Silurian; in this time, the Ordovician family richness (35) is cut by more than half (14). The Permo-Triassic mass extinction could remove many competitors as pointed out above (mass extinctions are decoupled from fitness established during «normal» times; see Gould, 1985); hence the fact that their last Triassic flourishment occurred (Figs. 1 and 2), although spreading provinciality during the Early and Middle Triassic could play a role as well. The last Upper Triassic lineages could probably be successful as generalist animals –their long durations seems to suggest their generalist character–; but reduction of marine areas and diversification of competitors could prevent any attempt of origination of new lineages in more specialized ways (on the other hand, generalist lineages have a very small origination capability.) Small crisis gradually diminished the impoverished richness (see polycohort analysis). Thus, this meant the extinction of the group.

CONCLUSIONS

Conodonts made up a minor group during the Paleozoic and the Early Mesozoic. Their cladal ramification fit a time-inhomogeneous model and they became extinct within the Rhaetian times. The impoverishment of the group -at the family level- is gradual since the Silurian, after the Ordovician acme. Diffuse competition with better animal designs could diminish their origination rate to be lower than extinction rate in the Ladinian and the Upper Triassic (probably, the last lineages were generalist). Environmental causes were not probably the principal agents for this extinction, but they could play a role as well. Pseudo-polycohort analysis evidences some intra-Triassic extinction episodes possibly caused by small crisis. Since the conodont diversification seems partly related to the available marine areas and provincialization, the decrease of these areas in some regions of the world would be a new challenge for the group; an abnormal salinity could be another important factor in regions initially occupied by them, because these organisms were mainly stenohaline. These environmental factors also contributed to the extinction of the group.

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