ISSN (print): 1698-6180. ISSN (online): 1886-7995
www.ucm.es/info/estratig/journal.htm

*Journal of Iberian Geology* 33 (2) 2007: 173-190

Journal of Iberian Geology
AN INTERNATIONAL PUBLICATION OF EARTH SCIENCES

# A contribution to knowledge of the development of marine life during the Permian and Triassic through the analysis of life histories of genera

## Contribución al conocimiento del desarrollo de la vida marina en el Pérmico y Triásico a través del análisis de la duración en el tiempo de los géneros

Salvador Reguant

*Catedrático Emérito de Estratigrafía, Facultad de Geologia, Universidad de Barcelona, 08028 Barcelona, Spain*
*sreguant@ub.edu*

Received: 12/01/06 / Accepted: 19/06/06

Abstract

Data recently published on the longevity of various marine animal genera permits in-depht study of the history of marine life. The Permo-Triassic boundary, as well as the Permian and Triassic periods themselves, constitute a particularly interesting point in the history of life in the Phanerozoic, in that they straddle the most extensive extinction ever recorded.The analysis of the development of abundant genera (using classes and orders) in 13 marine animal taxa reveals that, on the one hand, all the taxa studied suffered the biggest change in their generic composition during these two periods precisely at the Permo-Triassic boundary, and, on the other hand, that certain groups display patterns during these two periods that do not conform to the overall trend.

*Keywords*: Permian, Triassic, marine genera, life-history, diversity, extinctions

Resumen

El análisis de los datos que se conocen sobre la duración en el tiempo de todos los géneros marinos perminte profundizar en el conocimiento de la historia de la Vida. El límite Pérmico-Triásico y, en general, la historia de la Vida durante estos dos períodos presenta un particular interés debido a la existencia de la extinción más importante de seres vivos en el Fanerozoico. El análisis del comportamiento de los géneros en 13 grupos animales que presentan una particular abundancia ha permitido confirmar la situación en el tiempo del extraordinario cambio conocido como extinción permo-triásica y ver las diferencias en el comportamiento que cada grupo de los considerados presentan a lo largo del Pérmico y del Triásico.

*Palabras clave*: Conodontos, Permian, Triassic, marine genera, life-history, diversity, extinctions.

## 1. Introduction

According to Sepkoski's (1984) classification, the transition from Paleozoic to modern fauna occurs at the Permo-Triassic boundary, at the point of the largest mass extinction in the history of Phanerozoic.

Studies relating to this theme refer to both event and the probable causes of this crisis in the history of life.

Likewise, the appearances, extinctions and biodiversity of living beings throughout fossiliferous periods are constantly being analysed, as shown by the number of papers published in specialized journals. These papers approach the subject from highly varying perspectives (see, for example, Sepkoski, 1989; Erwin, 2000; Foote, 2003 and 2005; Bambach *et al*., 2004; Jablonski, 2005; Rohde and Muller, 2005). The papers of Foote are based on the Sepkoski compendium).

The publication of the compendium of fossil marine animal genera (Sepkoski, 2002), collated from the material published up to that point, has allowed us to review the history of marine life at the end of the Paleozoic and beginning of the Mesozoic, a period of particular interest due to the aforementioned extinction and the path to recovery that marine life took after the great catastrophe.

This paper describes this review and reveals some aspects of interest that may contribute to understanding the history of life in the Permian and Triassic periods.

## 2. The history of Life and of the Earth in the Permo-Triassic

Uncovering the history of the Permian, and in some aspects, the Triassic, has historically proven more challenging than of any of the other geological periods of the Phanerozoic.

The most important geologists of the nineeteenth century, for example, had obtain permission from the authorities to be able to visit Russia and study the stratigraphic void that existed in the succession above the well-known Carboniferous. On this return to Britain, one of these geologists, Roderick Impey Murchison, wrote to Tsar Nicholas I, informing him of the discoveries and that theyhad named the new system the Permian, based on sedimentary deposits with a large fossil record in the area they visited near the Urals (Baars, 1992)

Studying the Triassic has also been complex, since the original outcrops of three layers found in Germany, which give it its name – "trias" – do not provide much information on the history of life in this period. More complete information has been obtained in areas outside Germany, starting with the alpine area which, has given its name to some of the stages of the system.

Despite these difficulties, these periods have been the subject of numerous papers, thanks to interest in the Permo-Triassic mass extinction. These papers have either described the size of the extinction and diversity recovery process, or discussed possible causes of the catastrophe.

Two authors have made very complete descriptions of this extinction: P. Wignall and D. H. Erwin (Wignall, 1992; Erwin, 1994, 1996a, 1996b and 2006). They have been able to determine a single cause, as evidence that points towards various candidates has been found in the geological record.

These candidates include: a possible meteorite impact (Becker *et al*., 2004); the deterioration of atmospheric conditions leading to a drop in oxygen levels (Wignall and Hallam, 1992; Wignall and Twitchett, 1996; Weidlich *et al*., 2003; Foster and Afonin, 2005); a decrease in primary biological productivity (Twitchett, 2001); sea-level changes (Hallam and Wignall, 1999); and vulcanism (Wignall, 2001; Mundil *et al*., 2004).

In order to obtain a more complete view of how life evolved in this period and in response to a considerable interest surrounding the extinction, we posed the following question: what was the faunal composition of marine environments across the entire Permian and Triassic, not just at the time immediately preceding and following the extinction? The description that follow aims to make a contribution to this knowledge and may help to explain the complexity of this event.

## 3. The Sepkoski compendium and how it is used here

Jack John Sepkoski Jr's death in May 1999, meant that the compendium of fossil marine animal genera he had been collating had to be published by his two friends, David Jablonski and Michel Foote, of the University of Chicago.

This compendium is very important, including information that Spekoski basically obtained from the volumes of the *Treatise on invertebrate Paleontology* for invertebrates, from Romer (1966) for vertebrates and from Loeblich and Tappan (1998) for foraminifera.

On publishing the work, his colleagues checked the material, made some correction and explained how this compendium was produced.

Here, given that we only intend to analyse the history of marine animals in the Permian and Triassic, we have selected 13 varied taxa (mostly orders but also classes) that together represent a large proportion of the diversity of marine life existing during the time periods studied. Erwin (1993) also adopted this approach when studied teh Permian and part of the Triassic using data on the existence of particular families found in previously published catalogues.

The large number of studies, mentioned in the introduction, which were published before the compendium itself (though some of their authors had access to unpublished data that was later used in the compendium), has allowed us to analyse general aspects, not limited to the periods considered here, of the appearance and extinction of genera, and biodiversity throughout the fossiliferous periods. Our contribution aims to complete the vision of certain aspects of the history of marine life that have not been specifically dealt with previously.

| Epoch | Age | ***dt (in Ma)*** |
|---|---|---|
| LATE TRIASSIC | Norian<br>Carnian | 16.9<br>11.5 |
| MIDDLE TRIASSIC | Ladinian<br>Anisian | 9<br>8 |
| EARLY TRIASSIC | Olenekian<br>Induan | 4.7<br>1.3 |
| LATE PERMIAN | Tatarian<br>Guadalupian | 9.4<br>10.2 |
| EARLY PERMIAN | Leonardian<br>Sakmarian<br>Asselian | 9.4<br>14.6<br>4.4 |

Table 1.- Epochs, ages and time duration in the Permian and Triassic (see text for details)
Tabla 1.- Épocas, edades y lapsos temporales del Pérmico y el Triásico (ver texto para más detalle)

## 4. The data considered and its treatment

### *4.1. Chronostratigraphy*

Inconsistencies in the nomenclature used to refer to different chronostratigraphic units in the compendium, to the extent that some names were not taken from the International Stratigraphic Chart published by the "International Commission on Stratigraphy", required us to spend some time consulting chronostratigraphic scales and analysing equivalences. The epochs and ages we finally used, and their estimated duration (dt) can be seen in Table 1.

### *4.2. The taxa considered*

The names and categories of the taxa considered are as follows, taken from the compendium (for practical purposes we take Classes or Orders depending on the number of representatives of each kind of taxa)

Cl. **RADIOLARIA:**
- Ord. SPUMELLARIA
- Ord. NASSELLARIA

Ord. **FORAMINIFERIDA** (Cl. RHIZOPODEA)
Cl. **DEMOSPONGIA**
- Ord. POECILOSCLERIDA
- Ord. HAPLOSCLERIDA
- Ord. VERTICILLITIDA
- Ord. ASTROPHORIDA
- Ord. LITHISTIDA
- Ord. HADROMERIDA
- Ord. GUADALUPIIDA
- Ord. AXINELLIDA
- Ord. TABULOSPONGIDA
- Ord. (uncertain)

Cl. **CALCAREA** (Ph. PORIFERA)
- Ord. HETERACTINIDA
- Ord. PHARETRONIDA
- Ord. PERMOSPHINCTA
- Ord. SPHAEROCOELIDA
- Ord. (uncertain)

Ord. **ARCHAEOGASTROPODA** (Cl. GASTROPODA)
Ord. **NEOTAENIOGLOSSA** (Cl. GASTROPODA)
Ord. **NAUTILIDA** (Cl. CEPHALOPODA)
Ord. **PTERIOIDA** (Cl. BIVALVIA)
Ord. **PODOCOPIDA** (Cl. OSTRACODA)
Ord. **RHYNCHONELLIDA** (Cl. ARTICULATA)
Ord. **SPIRIFERIDA** (Cl. ARTICULATA)
Ord. **TEREBRATULIDA** (Cl. ARTICULATA)
Cl. **OSTEICHTHYES**
- Ord. COELOCANTHIFORMES
- Ord. PALAEONISCIFORMES
- Ord. PTYCHOLEPIFORMES
- Ord. BOBASATRANIFORMES
- Ord. SAURICHTHYFORMES
- Ord. PHOLIDOPLEURIFORMES
- Ord. PERLEIDIFORMES
- Ord. PELTOPLEURIFORMES
- Ord. SEMIONOTIFORMES
- Ord. PYCNODONTIFORMES
- Ord. AMIIFORMES
- Ord. MACROSEIMIIFORMES
- Ord. PACHYCORMIFORMES

### *4.3. Treatment applied*

For each of the taxa indicated, for each age, we calculated the number of first (FA) and last (LA) appearances, the number of existing genera (N) in that taxon in that age, and a quantification of the degree of change the genus composition (V) determined, based on the following formula:

$$V = 100C / N / dt$$

Where C is the sum of FA of the age under consideration plus the LA of the previous age in time, and dt is the duration of the age, values which are found in Table 1.

It should be noted that, in all these data and calculations we have ignored any genera that both appeared and disappeared within the age considered, as they most likely were restricted to only locality. This precaution has already taken by other authors, for example Erwin (1993, p. 86).

## 5. Results and interpretations: general treatment

The general treatment allows us, as it is apparent in the 4 figures, to know the diversity of behaviour in different data examined. The first (FA) and last (LA) appearances, and also biodiversity (N) follow a complex way through geologic time considered, being different in taxa considered. On the contrary the changes (V) are, in all taxa, describing the same pattern, one given the important mass extinction in Permo-Triassic boundary.

### *5.1. First appearances (FA) (Fig. 1)*

As can be seen in figure 1, the groups share little overall pattern and, in general, there are few common features. What is certain, however, is that in Tatarian, the last age of the Permian, there are few first appearances for any taxa. The Asselian witnessed a larger value of first appearances for Demospongia and Spiriferida. The other three ages of Permian, the Sakmarian, the Leonardian and the Guadalupian show variable results, with high values in some ages, while in others the values are low or even zero.

The Triassic ages show great variety. Of most interest is the Induan, which witnessed very few first appearances. However, it should be noted that the number of first appearances for Osteichthyes is very high in this age, compared to other ages, both in Permian and the Triassic. Neotaenioglossa show high values in the Ladinian.

It can also be seen that some taxa experienced more first appearances during the Permian, while others experienced more during the Triassic.

### *5.2. Last appearances (LA) (Fig. 2)*

With regard to de last appearances (*i.e.* extinctions) we have also had to take into consideration those occurred at the end of the Carboniferous in order to be able to calculate the changes that occurred in the Asselian. These results confirm the pattern that largest LAs occurred at the end of each period, be it the Carboniferous, the Permian or the Triassic, and involved all studied taxa, except the Osteichthyes, which revealed a slightly more complex, erratic pattern.

For some taxa, mass extinctions began slightly earlier. Thus in many cases LAs are also important in the Guadalupian and in the Carnian. For some taxa they were even more numerous in the Guadalupian than in the Tatarian.

In the case of the Osteichthyes there are very few extinctions before the Tatarian and a greater number in some ages of Triassic.

### *5.3. Biodiversity*

Studying the number of genera per age and taxon (N) enables us to understand variations in biodiversity. Figure 3 shows these variations.

For almost all taxa, diversity is lowest at the beginning of the Triassic, in the Induan and Olenekian. In some cases there is a notable drop from the Tatarian to the Induan. In most cases this drop is followed by a recuperation of numbers, illustrated by the growth in the bars of the graphs.

A comparison between diversity in the Permian and in the Middle and Late Triassic shows that there are many taxa in which the number of genera in the Permian never fully recovers in Triassic, even though overall diversity is similar when considering all taxa together. However, the diversity of Radiolaria shows a different pattern, remaining low throughout the Permian and at the beginning of the Triassic, then increasing noticeably from the Ladinian.

One complexity distinct pattern is that of the taxon Osteichthyes, whose diversity in the Early Permian is at a minimum, only increasing sharply from the beginning of the Triassic. Such a pattern calls for an explanation specific to this group of vertebrates, rather than one related to end-Paleozoic extinction event.

### *5.4. Quantification of change*

The formula we have established to quantify change in the genus composition of a taxon is $V = 100C / N / dt$, in which, as described before, C is the total number of Fas for the age under consideration plus the LAs of the previous age, and dt is the duration of the age. This formula generates the results shown in figure 4.

The data clearly show the exceptional nature of the changes of genus composition at the Permo-Triassic boundary. To a lesser extent, there are also taxa that underwent notable change at the Carboniferous-Permian boundary.

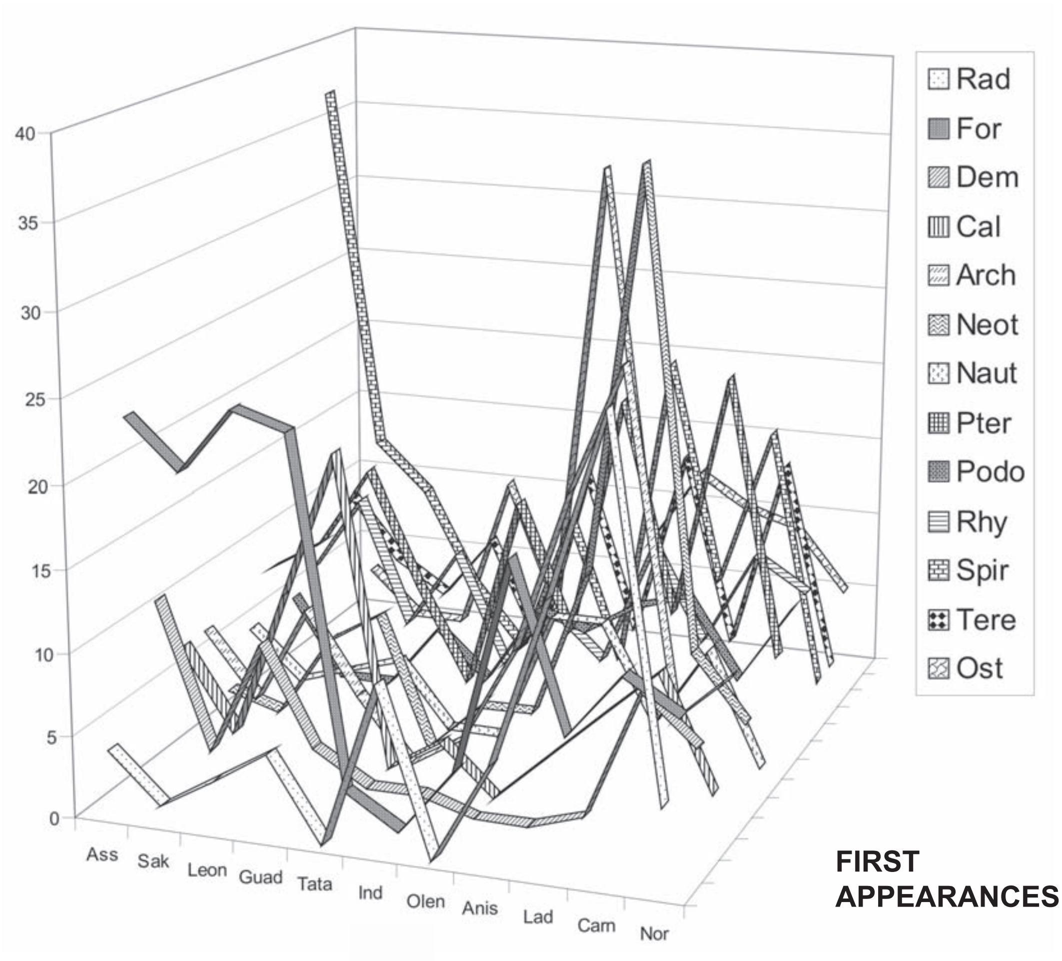
## 6. Results and interpretations: individualised treatment by taxa

It is also worth examining taxa separately, so as to understand differences in the pattern they follow. In this way some of the evolution variants of living beings, in these two periods of history that have particular characteristics throughout the Phanerozoic, can be made clear. The data are shown in the tables and graphs of the preceding section. The total number of genera present in the Permian and Triassic is indicated at the beginning of the description of each taxon. The comments always refer to genera that are present in more than one age.

Fig 1.- Number of first appearances (FA) by age and taxon

Fig. 1.- Número de Primeras apariciones (FA) en cada edad y taxón

| | Ass | Sak | Leon | Guad | Tata | Ind | Olen | Anis | Lad | Carn | Nor |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Rad** | 4 | 1 | 3 | 5 | 0 | 10 | 0 | 6 | 16 | 27 | 5 |
| **For** | 23 | 20 | 24 | 23 | 2 | 0 | 4 | 17 | 7 | 11 | 9 |
| **Dem** | 11 | 2 | 9 | 3 | 1 | 1 | 0 | 0 | 1 | 9 | 6 |
| **Calc** | 7 | 2 | 11 | 20 | 1 | 3 | 0 | 3 | 6 | 9 | 2 |
| **Arch** | 7 | 3 | 9 | 4 | 0 | 2 | 8 | 18 | 26 | 5 | 8 |
| **Neot** | 2 | 1 | 6 | 8 | 0 | 3 | 3 | 12 | 37 | 8 | 4 |
| **Naut** | 5 | 2 | 3 | 4 | 0 | 0 | 8 | 8 | 2 | 7 | 0 |
| **Pter** | 8 | 10 | 15 | 8 | 2 | 14 | 6 | 21 | 8 | 23 | 6 |
| **Podo** | 5 | 0 | 0 | 4 | 1 | 6 | 5 | 7 | 8 | 3 | 8 |
| **Rhyn** | 6 | 11 | 3 | 8 | 1 | 5 | 2 | 10 | 4 | 10 | 8 |
| **Spir** | 37 | 14 | 11 | 5 | 1 | 10 | 1 | 21 | 7 | 17 | 1 |
| **Tere** | 9 | 5 | 3 | 7 | 0 | 12 | 2 | 14 | 2 | 14 | 1 |
| **Oste** | 3 | 0 | 0 | 10 | 2 | 32 | 7 | 12 | 10 | 9 | 5 |




*6.1. Radiolaria: 144 genera (Fig. 5)*

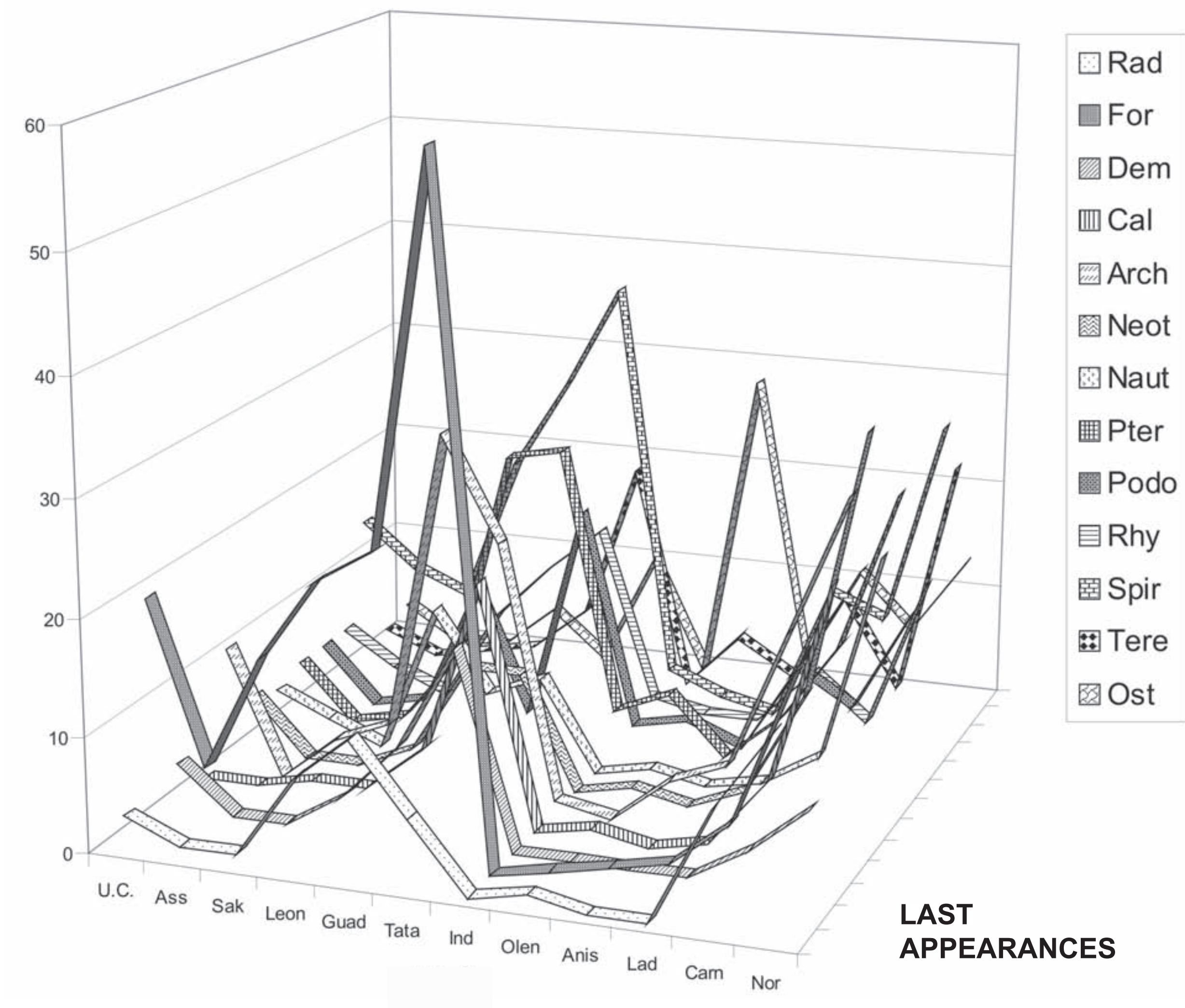
The number of genera across the ages show how diverse this class is. Few important variations occur until the Ladinian and, above all the Late Triassic when the numbefr of extant genera exceeds 67. In the Permian and until the Anisian it never exceeds 35. The minimum value recorded was in the Tatarian and there are slightly higher values at the beginning of the Triassic. In this respect, no important change can be deduced in the history of this taxon.

However, as for all the studied taxa, the quantified change (V) was extraordinarily high at the beginning of the Triassic, a fact that is significant in confirming the exceptional change in faunal composition due to the end-Permian extinction event.

Fig. 2.- Number of last appearances (LA) by age and taxon.

Fig. 2.- Número de últimas apariciones (LA) en cada edad y taxón.

| | U.C. | Ass | Sak | Leon | Guad | Tata | Ind | Olen | Anis | Lad | Carn | Nor |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Rad** | 3 | 1 | 1 | 8 | 12 | 6 | 0 | 1 | 0 | 0 | 10 | 17 |
| **For** | 20 | 6 | 16 | 23 | 26 | 59 | 0 | 1 | 2 | 3 | 7 | 20 |
| **Dem** | 4 | 0 | 0 | 3 | 8 | 17 | 0 | 0 | 0 | 0 | 3 | 7 |
| **Calc** | 1 | 1 | 2 | 2 | 6 | 21 | 0 | 1 | 0 | 1 | 7 | 24 |
| **Arch** | 11 | 0 | 4 | 6 | 32 | 23 | 1 | 0 | 4 | 6 | 18 | 30 |
| **Neot** | 5 | 0 | 0 | 2 | 10 | 10 | 0 | 1 | 0 | 2 | 11 | 34 |
| **Naut** | 4 | 2 | 0 | 13 | 6 | 8 | 0 | 1 | 0 | 1 | 4 | 22 |
| **Pter** | 5 | 0 | 1 | 7 | 26 | 27 | 4 | 6 | 1 | 5 | 12 | 26 |
| **Podo** | 5 | 0 | 1 | 12 | 1 | 20 | 1 | 2 | 0 | 8 | 5 | 14 |
| **Rhyn** | 5 | 2 | 0 | 8 | 13 | 17 | 2 | 1 | 1 | 6 | 2 | 15 |
| **Spir** | 14 | 10 | 8 | 21 | 29 | 38 | 3 | 1 | 0 | 12 | 10 | 28 |
| **Tere** | 2 | 0 | 1 | 2 | 6 | 20 | 0 | 5 | 2 | 10 | 2 | 23 |
| **Oste** | 3 | 0 | 0 | 4 | 0 | 10 | 0 | 28 | 2 | 11 | 6 | 13 |



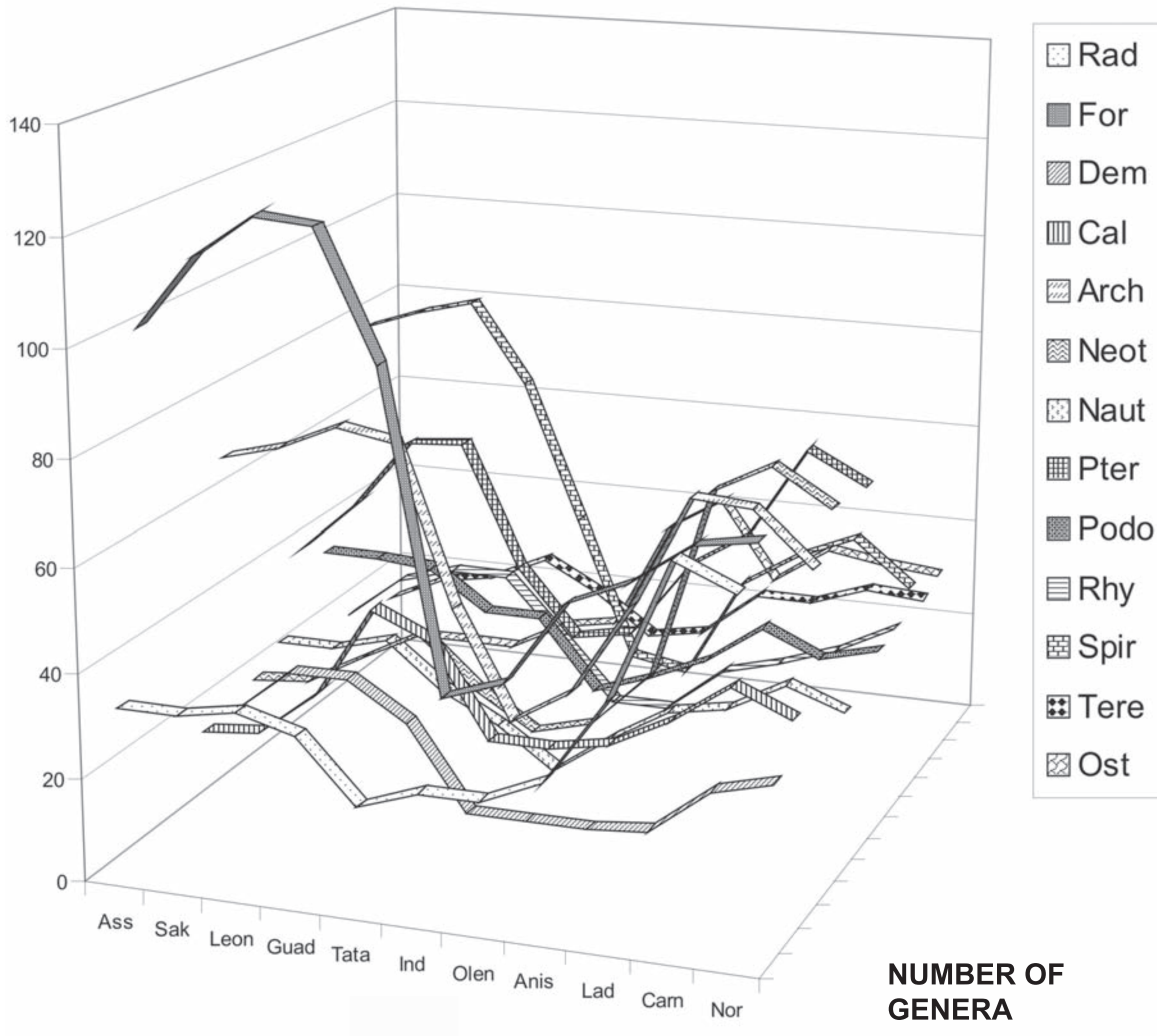

An analysis of the figures counting appearances and extinctions can help us understand the changes that occurred in genus diversity for Radiolaria in this time interval.

As was to be expected, given the number of genera, there is an antagonistic relationship between appearances and extinctions. Extinctions are important in the Late Permian and also in the Late Triassic. Appearances are notable in the Induan, a fact which suggests a rapid recovery of diversity after the Permo-Triassic extinction event. There are also large numbers of appearances in the Ladinian and Carnian, obviously corroborating the aforementioned increase in the number of genera in these ages.

| | Ass | Sak | Leon | Guad | Tata | Ind | Olen | Anis | Lad | Carn | Nor |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Rad** | 33 | 33 | 35 | 32 | 20 | 24 | 24 | 29 | 45 | 72 | 67 |
| **For** | 101 | 115 | 123 | 122 | 98 | 38 | 42 | 58 | 63 | 71 | 73 |
| **Dem** | 24 | 26 | 35 | 35 | 28 | 12 | 12 | 12 | 13 | 22 | 25 |
| **Calc** | 17 | 18 | 27 | 45 | 40 | 22 | 22 | 24 | 30 | 38 | 33 |
| **Arch** | 68 | 71 | 76 | 74 | 43 | 22 | 29 | 47 | 69 | 68 | 58 |
| **Neot** | 20 | 21 | 27 | 33 | 23 | 16 | 19 | 30 | 67 | 73 | 66 |
| **Naut** | 24 | 24 | 27 | 18 | 12 | 4 | 12 | 19 | 21 | 27 | 23 |
| **Pter** | 40 | 50 | 64 | 65 | 41 | 28 | 30 | 45 | 52 | 70 | 64 |
| **Podo** | 36 | 36 | 35 | 27 | 27 | 13 | 17 | 22 | 30 | 25 | 28 |
| **Rhyn** | 19 | 28 | 31 | 31 | 19 | 7 | 7 | 16 | 19 | 23 | 29 |
| **Spir** | 78 | 82 | 85 | 69 | 41 | 13 | 11 | 31 | 38 | 43 | 34 |
| **Tere** | 16 | 21 | 23 | 28 | 22 | 14 | 16 | 25 | 25 | 29 | 28 |
| **Oste** | 4 | 4 | 4 | 10 | 12 | 34 | 41 | 25 | 33 | 31 | 31 |

Fig.3.- Number of genera present (N) in each age and taxon.

Fig.3.- Número de géneros (N) presentes en cada edad y taxón.



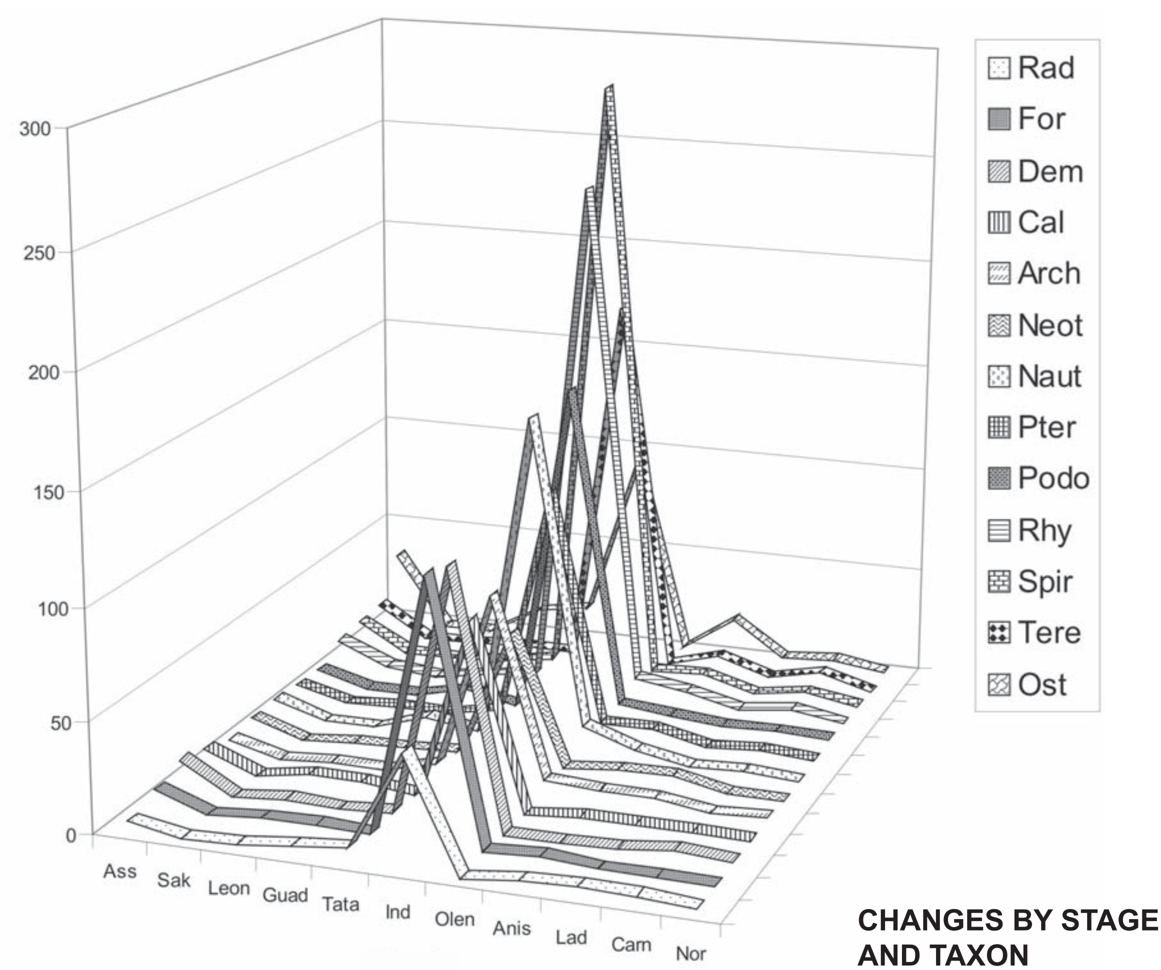

*6.2. Foraminiferida: 324 genera (Fig. 6)*

Diversity in this order is notably higher in the Permian than in the Triassic. In the latter period it begins at a lower value, growing steadily through the ages. In the Permian the lowest value corresponds to the last age. Diversity, therefore, begins to decrease very gently in the Tatarian, but experiences a sharp drop coinciding with the Permo-Triassic extinction event, which is confirmed by the exceptionally high value of change at the beginning of the Triassic.

There are a remarkable number of appearances in the Permian, with the exception of the Tatarian age. In the Triassic such appearances are generally rarer (in the In-

Fig. 4.- Número de cambios (V) para cada edad y taxón.
Fig. 4.- Number of changes (V) by age and taxon.

| | Ass | Sak | Leon | Guad | Tata | Ind | Olen | Anis | Lad | Carn | Nor |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Rad** | 4.8 | 0,4 | 1.2 | 4 | 6.4 | 51.3 | 0 | 3 | 4 | 3.3 | 1.3 |
| **For** | 9.7 | 1.5 | 3.5 | 3.7 | 3 | 119.4 | 2 | 3.9 | 1.6 | 1.7 | 1.3 |
| **Dem** | 14.2 | 0.5 | 2.7 | 1.7 | 3.4 | 115.4 | 0 | 0 | 0.8 | 3.6 | 2.1 |
| **Calc** | 10.7 | 1.1 | 5.1 | 4.8 | 1.9 | 83.9 | 0 | 2.1 | 2.2 | 2.3 | 1.6 |
| **Arch** | 6 | 0.3 | 1.8 | 1.3 | 7.9 | 87.4 | 6.6 | 4.8 | 4.8 | 1.4 | 2.7 |
| **Neot** | 8 | 0.3 | 2.4 | 3 | 4.6 | 62.5 | 3.4 | 5.4 | 6.1 | 1.2 | 1.2 |
| **Naut** | 8.5 | 1.1 | 1.2 | 9.3 | 5.3 | 153.8 | 14.2 | 5.9 | 1.1 | 2.6 | 1 |
| **Pter** | 7.4 | 1.4 | 2.7 | 2.3 | 7.3 | 112.6 | 7.1 | 7.5 | 1.9 | 3.5 | 1.7 |
| **Podo** | 6.3 | 0 | 0.3 | 5.8 | 0.8 | 153.8 | 7.5 | 5.1 | 3 | 3.8 | 2.7 |
| **Rhyn** | 13.2 | 3.2 | 1 | 5.1 | 7.8 | 241.8 | 12.2 | 8.6 | 2.9 | 6 | 2 |
| **Spir** | 14.9 | 2 | 2.4 | 3.7 | 7.8 | 284 | 7.7 | 8.9 | 2 | 5.9 | 1.9 |
| **Tere** | 15.6 | 1.6 | 1.9 | 3.2 | 2.9 | 175.8 | 2.7 | 9.5 | 1.8 | 7.2 | 0.6 |
| **Oste** | 34.1 | 0 | 0 | 13.7 | 18 | 95 | 3.6 | 20 | 4 | 5.6 | 2.2 |




duan there are none). Only in the Anisian is there a number of appearances comparable to those of Permian. Extinctions become progressively more important during the Permian, while they are practically non-existent in the Triassic, growing slowly from 0 in the Induan to 20 in the Norian.

*6.3. Demospongia: 92 genera (Fig. 7)*

Diversity is notably higher in the Permian, there are being roughly twice the number of genera in existence per age. Only in the Late Triassic does diversity begin to ressemble that seen at the beginning of the Permian.

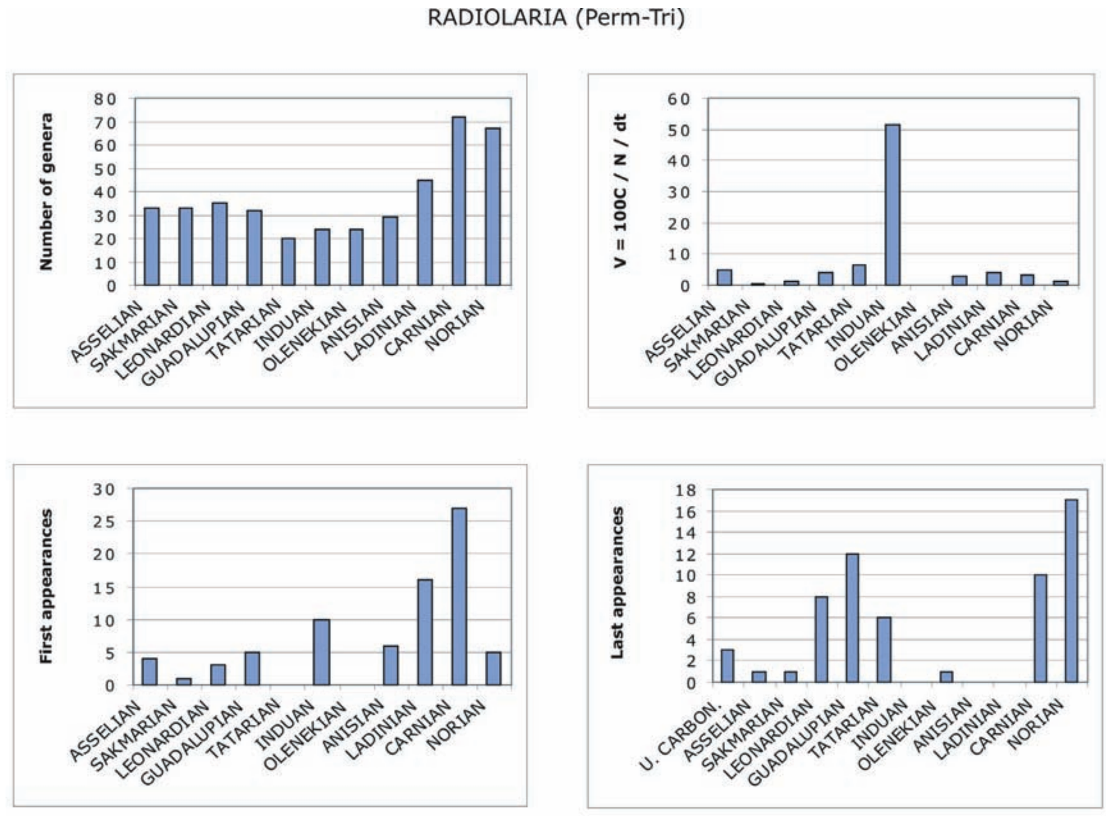



Fig. 5.- N, V, FA and LA in Radiolaria.
Fig. 5.- N, V, FA and LA en los Radiolarios.

No important drop in values is recorded in the Tatarian, although, as in all the examined taxa change in biodiversity is very dramatic at the beginning of the Triassic, in the Induan. No or little change occurs in all post-Induan and it is also low in the Permian, with the exception of the Asselian, though even here, V is some eight times lower than in the Induan. Once again this highlights the importance of the Carboniferous-Permian extinction event.

Most ages witnessed few appearances and in some there are none, with the exception of de Asselian and the Leonardian (Permian), and the Carnian and the Norian (Late Triassic). No extinctions occur in six ages and, as was to be expected, it is in the Tatarian where the highest value is found, with recovery developing gradually from the Leonardian onwards. There are, once again, fewer first appearances in the Late Triassic than in the Late Permian.

### *6.4. Porifera Calcarea: 120 genera (Fig. 8)*

Diversity over time is shown in the shape of two waves corresponding to the Permian and the Triassic, respectively. In the Permian it begins with lower values and reaches a maximum in the Guadalupian, to drop very slightly in the Tatarian. The Triassic begins with slightly greater diversity than the Permian, but the maximum values are lower than those recorded in the Guadalupian and in the Tatarian. Mirroring the pattern seen in the Permian the Carnian enjoyed greater diversity in this taxon than the Norian. The change in biodiversity follows the pattern seen in all the other taxa.

The maximum number of appearances occur in the Guadalupian with a considerably lower number in the Leonardian. Following these, we find the Asselian, the Ladinian and the Carnian. The Olenekian age failed to produce any appearances in this taxon. There are an increasing number of extinctions, both in the Permian and in the Triassic, from the base of the last stage.

### *6.5. Archaeogastropoda: 224 genera (Fig. 9)*

The number of genera is considerable in the Permian until the Tatarian which shows the beginning of a decrease that continues to the Induan. From this point there is an increase in the diversity through to the Late Triassic, which goes beyond that found during the Permian. The change in biodiversity in the Induan is clearly the highest, as is expected.

There is a considerable rise in the number of appearances in the Triassic from the Induan with a sharp decrease

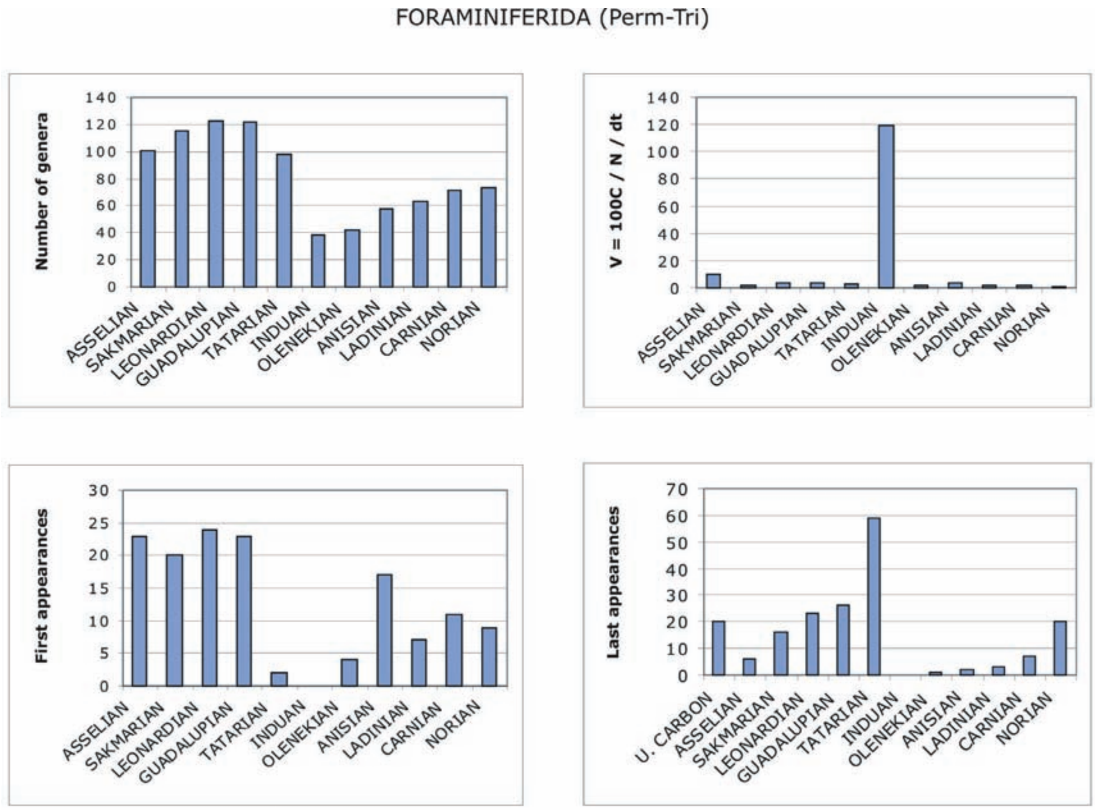



Fig. 6.- N, V, FA and LA in Foraminiferida.
Fig. 6.- N, V, FA y La en los Foraminíferos.

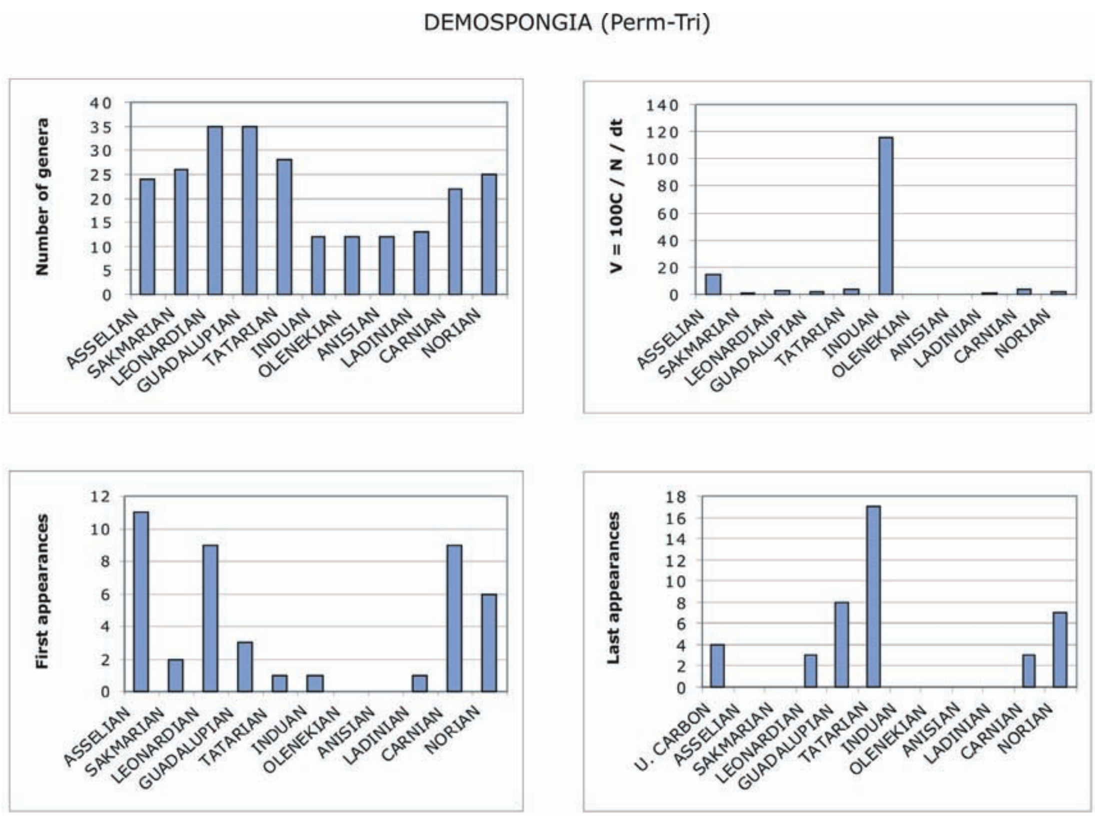



Fig. 7.- N, V, FA and LA in Demospongia.
Fig. 7.- N, V, FA y La en las Demospongias

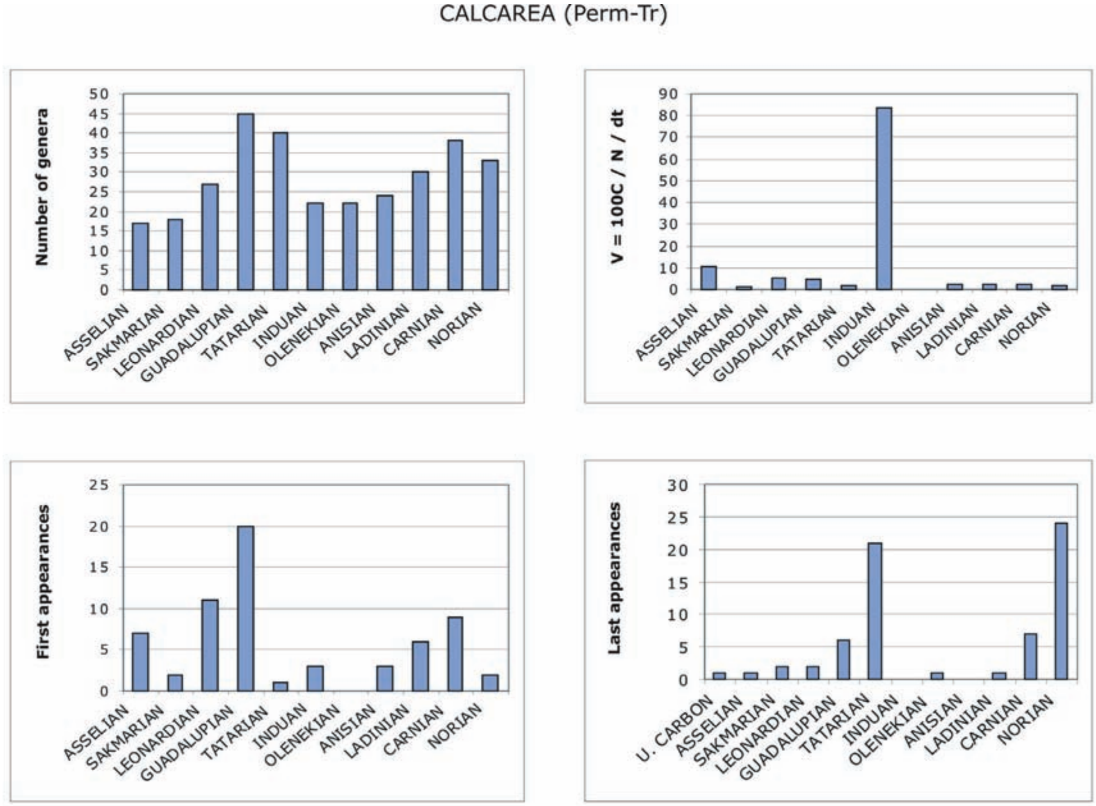



Fig. 8.- V,. FA and LA in Porifera Calcarea.
Fig. 8.- V, FA y LA en Poríferas calcáreas.

in the Late Triassic. The pattern seen during the Permian ages is comparable, with the exception of the Tatarian during which no new genus appears. There are several mass extinctions in the Late Permian and slightly fewer in the Late Triassic. The biodiversity curve increases and falls in the Permian whereas it only increases in the Triassic.

### *6.6. Neotaenioglossa: 141 genera (Fig. 10)*

Diversity shows no variability throughout the Permian and until the Anisian, before growing considerably during the Middle and Late Triassic. The most significant change in biodiversity occurs, as always, in the Induan.

Most ages record few first appearances with none whatsoever in the Tatarian. The exception is the Ladinian where the number of appearances increases threefold from that in the Anisian, which in turn is slightly higher than in other ages. Extinctions have not been recorded in many ages either, with the notable exception being the Norian. Once again, this leads us to believe that there was a possible extinction event at the Triassic-Jurassic boundary.

### *6.7. Nautilida: 88 genera (Fig. 11)*

The number of genera existing in the Early Permian is notable. This is also the case in the Late Triassic. Between them there is a biodiversity curve where the lowest value is in the Induan: it is higher before and after. An exceptional high change in biodiversity is also recorded in the Induan, as in all the other taxa.

There are no new appearances at the end of the Permian nor at the beginning of the Triassic, indeed there are few in general, with the greatest numbers witnessed during the Olenekian, Anisian and Norian. Appearances are rarest during the Permian, the highest number being in the Asselian. Extinctions are concentrated in the Middle and Late Permian and are particularly notable in the Norian, suggesting, as in case of the Neotaenioglossa, an extinction event at the Triassic-Jurassic boundary.

### *6.8. Pterioida: 214 genera (Fig. 12)*

The biodiversity curve is similar to that of other taxa with peaks in the middle of both periods; the lowest diversity occurs at the end of the Permian and in particular at the beginning of the Triassic. The Permo-Triassic extinction event also becomes evident when analysing the change in biodiversity.

New appearances take place in all ages, the Tatarian sees the fewest, whilst the greatest number took place in the Leonardian, Induan, Anisian and Carnian. Mass extinctions occur in the Late Permian (Guadalupian and

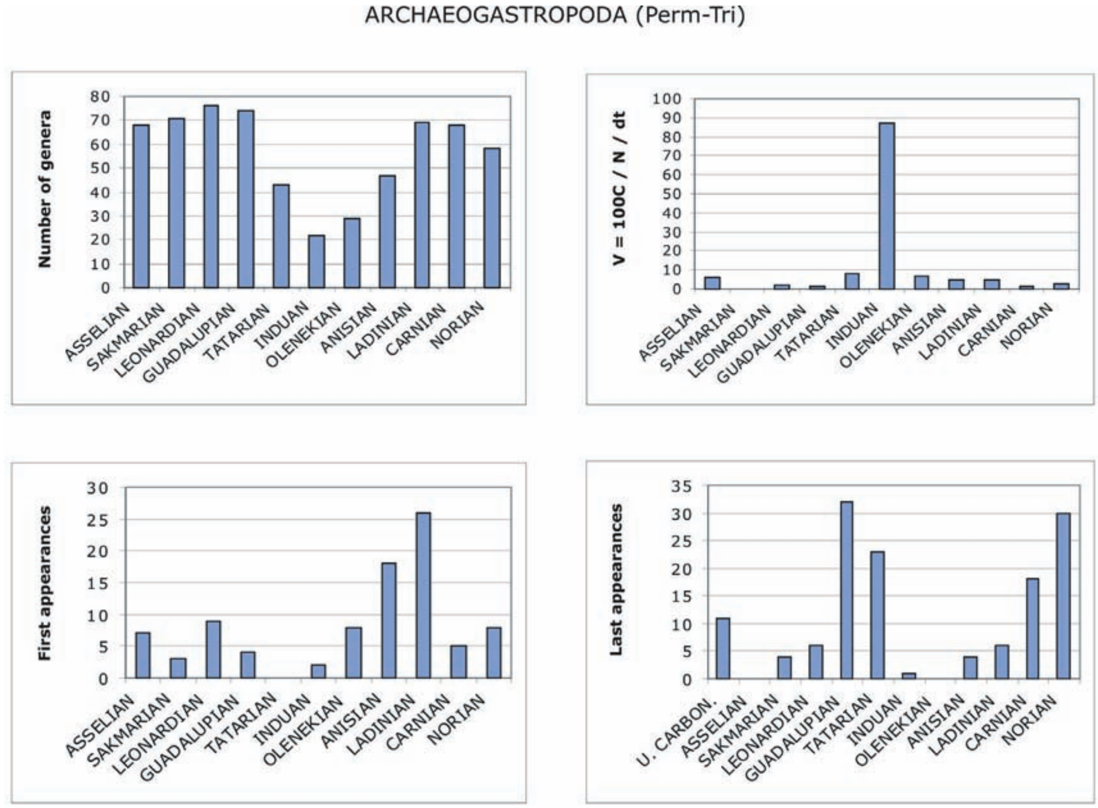



Fig. 9.- N, V, FA and LA in Archaeogastropoda.
Fig. 9.- N, V, FA y LA en Archeogasteropoda.

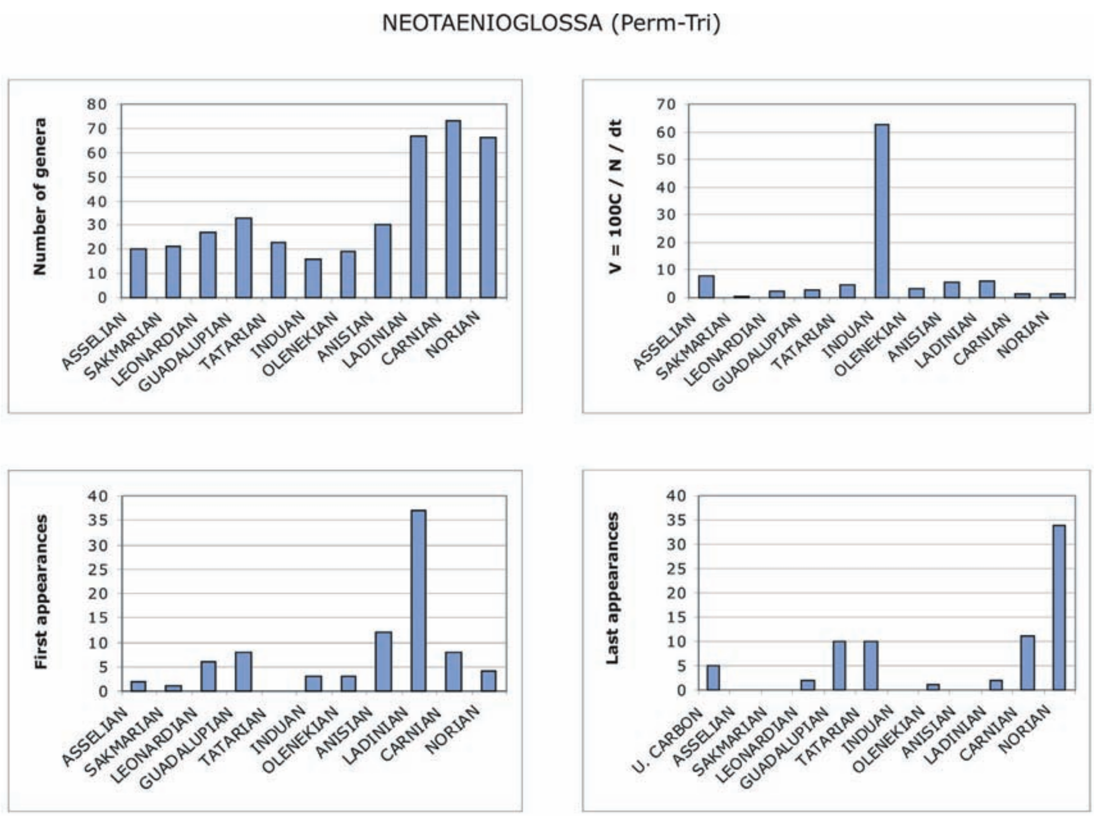



Fig. 10.- N, V, FA and La in Neotaenioglossa.
Fig. 10.- N, V, FA y La en Neotaenioglossa.

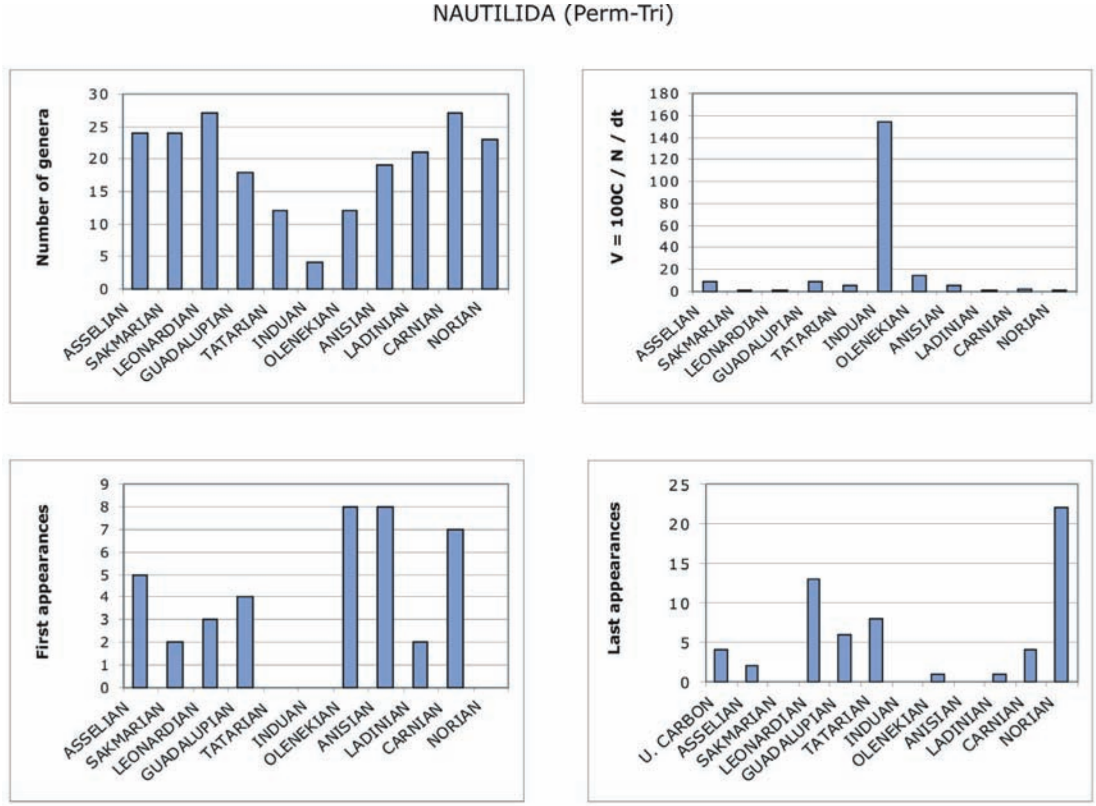



Fig. 11.- N, V, FA and LA in Nautilida.
Fig. 11.- N, V, FA y LA en Nautilidos.

Tatarian) and, as in some other taxa, are important in the Norian.

*6.9. Podocopida: 118 genera (Fig. 13)*

Diversity is paticularly high in the Permian and to a lesser degree from the Ladinian onwards. The Induan has a slightly lower value, though not exaggeratedly so. Change in biodiversity, however, is particularly high in this age.

No new appearances occur in the Sakmarian and Leonardian and they are practically non-existent in the Tatarian. In general, there are very few appearances, but there are more in the Triassic than in the Permian. There are a considerable number of extinctions in the Leonardian, the Norian and, above all, in the Tatarian. In some ages there are none whatsoever.

*6.10. Rhynchonellidae: 143 genera (Fig. 14)*

What can be seen in the corresponding table and graph is a wave in the Permian and a continued rise in the Middle and Late Triassic. Values are considerably lower in the Early Triassic. The change in biodiversity is, as always, very high in the Induan.

New appearances oscillate constantly. The highest values correspond to the Sakmarian, the Guadalupian, the Anisian and the Carnian; with moderate values during the Asselian, Induan and Norian. Extinctions are concentrated in the Leonardian, the Late Permian and the end of the Triassic. However, they are rare throughout, and there is no extinction in the Sakmarian.

*6.11. Spiriferida: 250 genera (Fig. 15)*

Diversity is much greater in the Permian than in the Triassic. Despite this, there is a drop that begins in the Guadalupian and continues in the Tatarian. As regards the Triassic, the number of genera is very low at the beginning (Induan and Olenekian) and a little higher in the Middle and Late Triassic. Change in biodiversity in the Induan is exceptionally high.

The Asselian is characterised by a number of quite important new appearances; appearance rates drop considerably in the subsequent ages, reaching minimum values in the Tatarian, Olenekian and Norian. Extinctions occur almost progressively in the Permian, especially from the Leonardian to the Tatarian. There are hardly any in the Early Triassic and none in the Anisian. A slight increase later leads to quite a high value in the Norian.

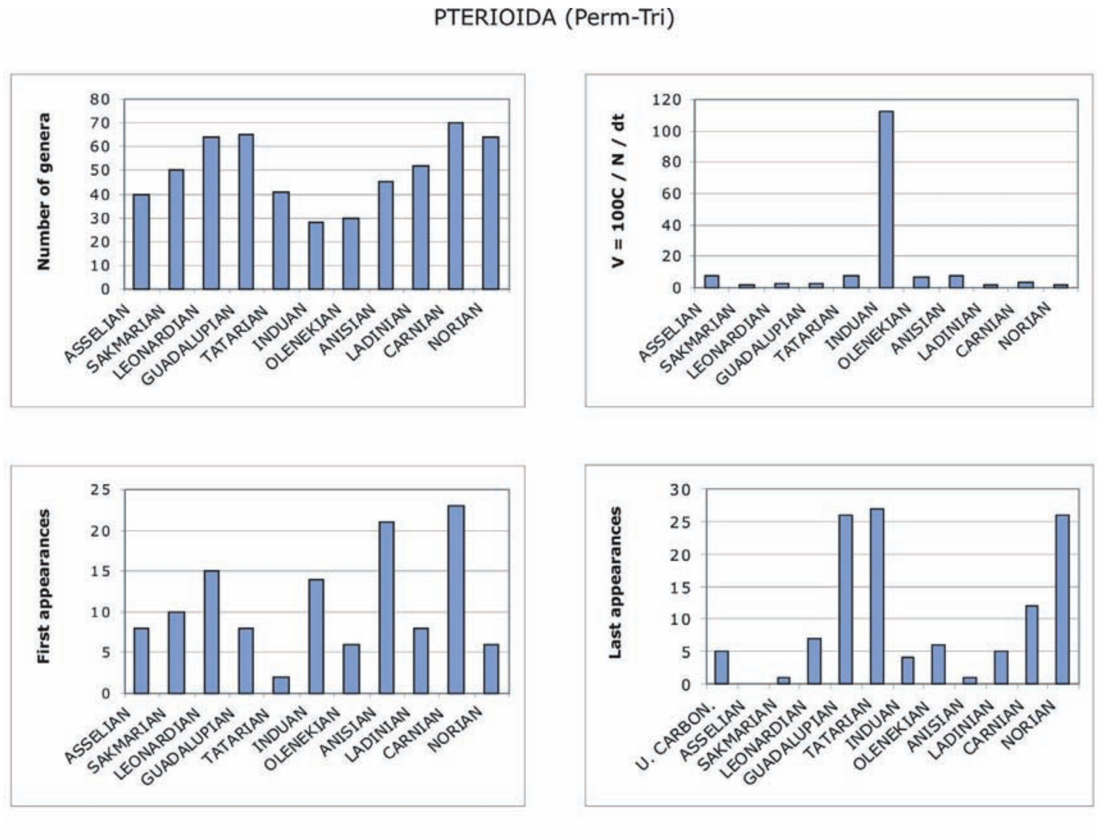



Fig. 12.- N, V, FA and LA in Pterioida.
Fig. 12.- N, V, FA y LA en Pterioida.

*6.12. Terebratulida: 126 genera (Fig. 16)*

Diversity is not very variable during these two periods. The graph shows two waves with an unpronounced minimum at the beginning of the Triassic and some high persistent values from the Anisian. As always, change in biodiversity is very high in the Induan.

The number of first appearances is not very high in most stages. In Tatarian is none. In the Triassic the highest values occur adjacent to the lowest ones.

There are no or few extinctions in the Early Permian. The rate rises from the Guadalupian, on achieving a very high value in the Tatarian. In Triassic there are few or none, except in the Ladinian and Norian.

*6.13. Osteichthyes: 165 genera (Fig. 17)*

Diversity is very low in the Early Permian, increases slightly in the Late Permian and is high, with certain important variations, throughout the Triassic. Whilst, as with other taxa, the Induan age sees the greatest change in biodiversity. There are other ages with a value that could be considered significant, for example, the Asselian at the Carboniferous-Permian boundary. What these data show is that this taxon of well-developed vertebrates does not follow the pattern of the other taxa we have considered.

Few first appearances are found in many of the ages and are non-existent in some of the Permian. The maximum value is found in the Induan with the Anisian a distant second, followed by some ages of the Triassic.

The highest extinction value occurs in the Olenekian and, with this exception, extinctions have considerably low values in other ages of the Triassic. There are none in many ages of the Permian and in other ages are generally very rare.

## 7. Final considerations

The elementary exercise we have carried out using data on marine animal genera taken from Sepkoski (2002) has allowed us to see that the history of faunal composition has been more complex than general statements made on the basis of less precise data might lead us to believe. This is because more and more information on the existence of living beings known to be present in certain time periods of the geological scale has become available. The first general catalogues referred to families (Sepkoski 1982 and 1992) and now, thanks to the same author, we can work with lower order taxons.

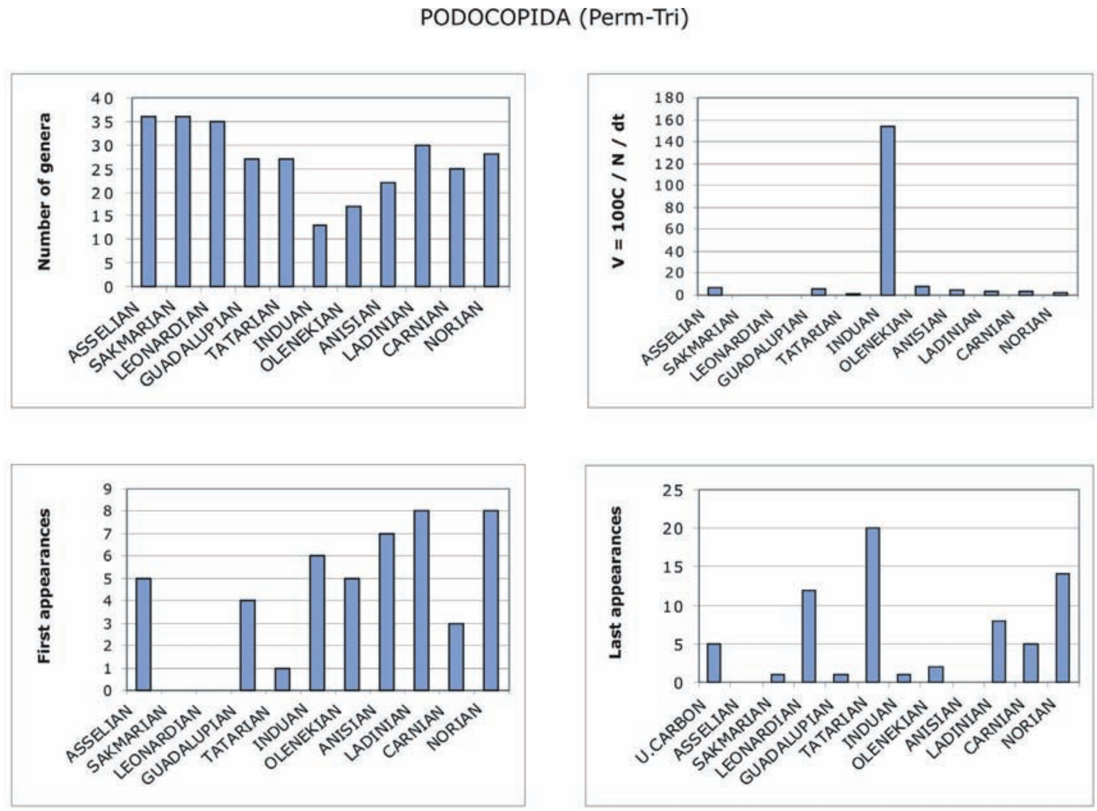



Fig. 13, N, V, FA and LA in Podocopida.
Fig. 13, N, V, FA y LA en Podocopida.

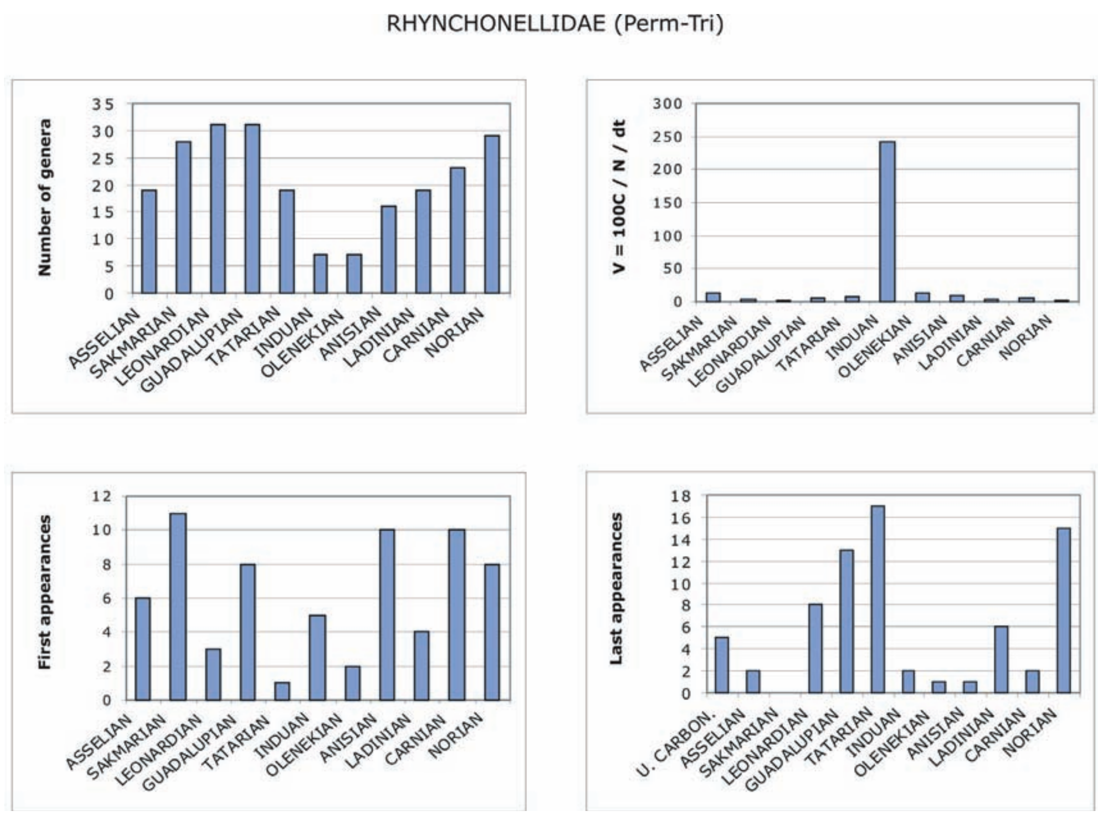



Fig. 14. N, V, FA and LA in Rhynchonellidae.
Fig. 14. N, V, FA y LA en Rhynchonellidae.

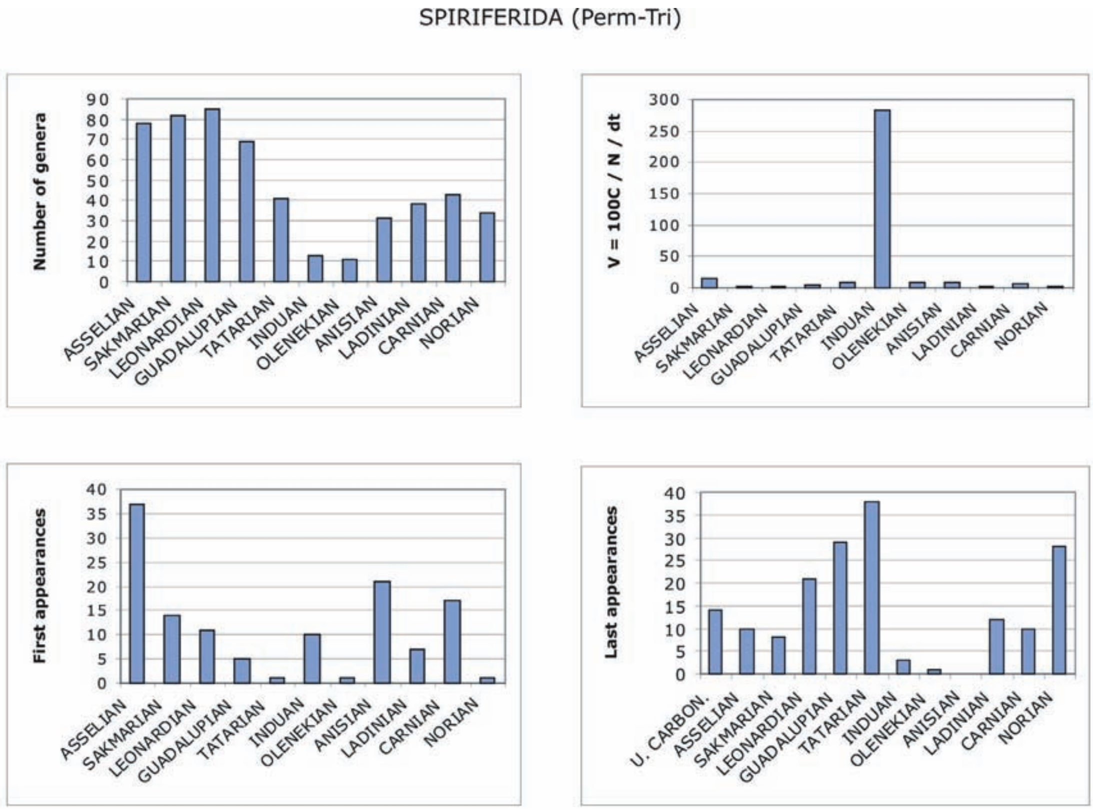



Fig. 15.- N, V, FA and LA in Spiriferida.
Fig. 15.- N, V, FA y LA in Spiriferida.

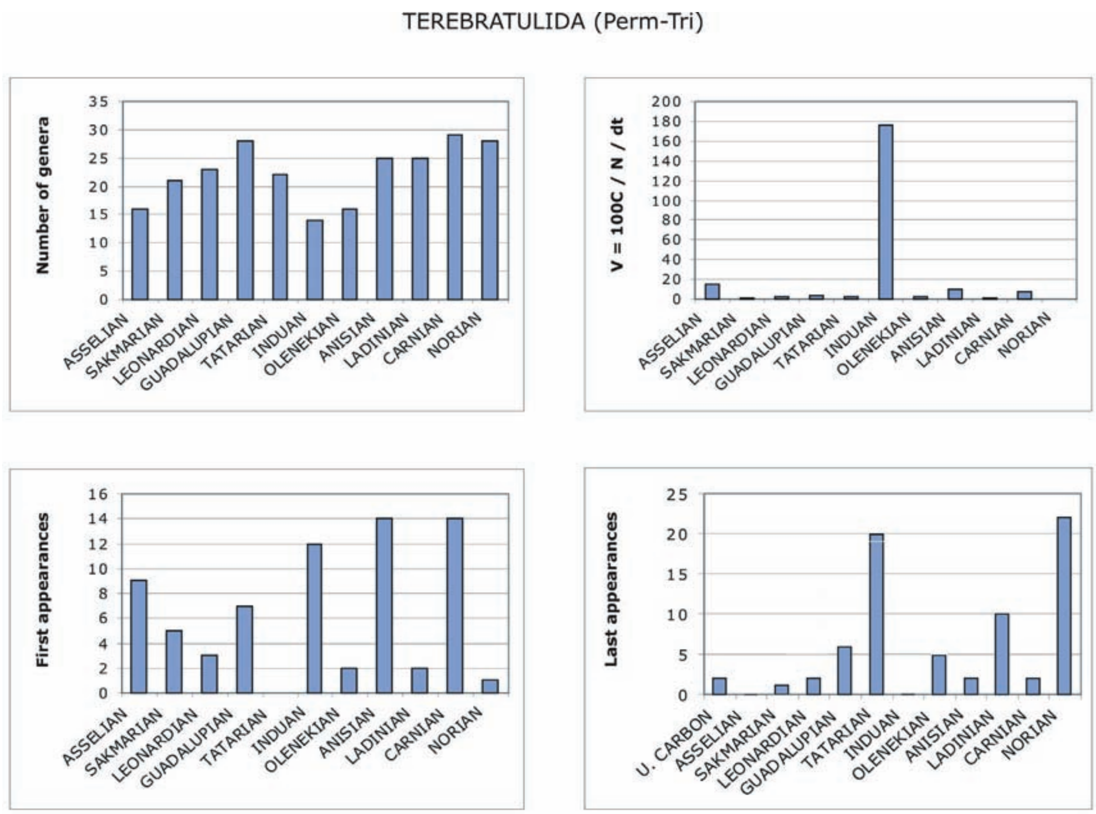



Fig. 16.- N, V, FA and LA in Terebratulida.
Fig. 16.- N, V, FA y LA en Terebratulida.

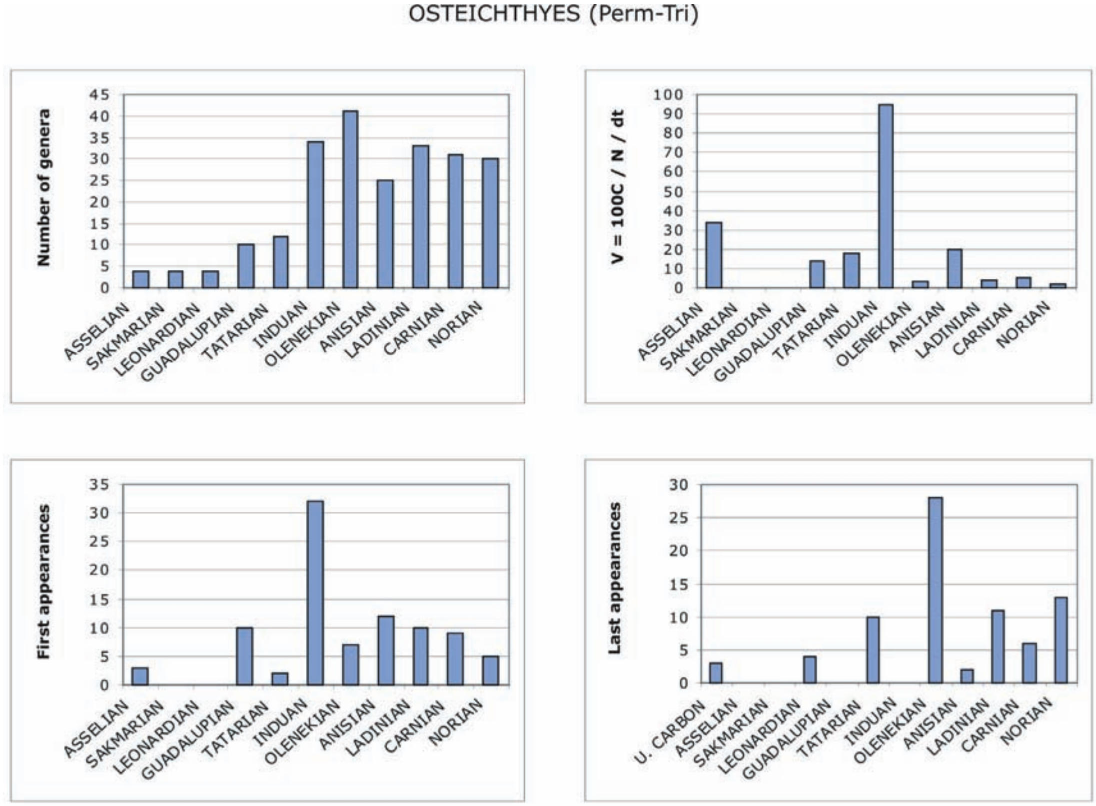



Fig. 17.- N, V, FA and La in Osteichthyes.
Fig. 17.- N, V, FA y La en Osteichthyes.

The first evidence is the complexity of the evolution of each taxon trough geologic time considered: Permian and Triassic. There are many differences between them considering the first appearances (FA), the last (LA) and also the biodiversity calculated through describing the number of genera present by successive ages. The changes, at the opposite, present a behaviour according to the known fact of the Permo-Triassic extinction.

All these observations lead us to believe that we can develop a greater understanding of the evolution of living beings, if you can get more and more knowledge of the presence of lower taxa by age. It allows us to describe more precisely their biodiversity, their appearances and extinctions, and so their particular history.

## Acknowledgements

The author is grateful to Mr. E. Blasco for help in delineating the figures, and to Mr. R. Rycroft for the translation and revision of the English text. Also, and very specially, to the two reviewers, Dr. Diego Garcia-Bellido Capdevila and Dr.Spencer G. Lucas that have allowed to improve the text.

## References

Baars, D. L. (1992): International Congress on the Permian System of the World. *Episodes*, 15 (2): 128.

Bambach, R. K., Knoll, A. H., Wang, S. C. (2004): Origination, extinction and mass depletions of marine diversity. *Paleobiology*, 30 (4): 522-542.

Becker, L., Poreda, R. J., Basu, A. R., Pope, K. O., Harrison, T. M., Nicholson, C., Iaski, R. (2004): Bedout: A possible End-Permian Impact Crater offshore of Northwestern Australia. *Science*, 304: 1469-1476.

Erwin, D. H. (1993): *The great Paleozoic crisis. Life and death in the Permian*. Columbia University Press, New York, 327 p.

Erwin, D. H. (1994): The Permo-Triassic extinction. *Nature*, 367: 231-236.

Erwin, D. H. (1996a): Understanding biotic recoveries: extinction, survival, and preservation during the end-Permian mass extinction. In: D. H. Erwin, J. H. Lipps (eds.): *Evolutionary Paleobiology*, The University of Chicago Press, 398-418.

Erwin, D. H. (1996b): La mayor extinción biológica conocida. *Investigación y Ciencia*. Septiembre: 62-69.

Erwin, D. H. (2000): Life's downs and ups. *Nature*, 404: 129-130.

Erwin,D. H. (2006): *Extinctions: How life on Earth nearly enden 250 millions years ago*. Princeton University Press, Princeton, 306 p.

Foote, M. (2003): Origination and extinction through the Phanerozoic: a new approach. *The Journal of Geology*, 111: 125-148.

Foote, M. (2005): Pulsed origination and extinction in the marine realm. *Paleobiology*, 31 (1): 6-20.

Foster, C.B., Afonin, S. A. (2005): Abnormal pollen grains: an outcome of deteriorating atmospheric conditions around the Permian-Triassic boundary. *Journal of the Geological Society, London*, 162: 653-659.

Hallam, A., Wignall, P. B. (1999): Mass extinctions and sea-level changes. *Earth-Science Reviews*, 48: 217-250.

Jablonski, D. (2005). Mass extinctions and macroevolution. *Paleobiology*, 31 (Suppl. To nº 2), 192-210.

Loeblich, A., Tappan, H. (1988). *Foraminiferal genera and their classification*. 2 volumes: Van Nostrand Reinhold, New York, 970 and 847 p.

Mundil, R., Ludwig, K. R., Metcalfe, I., Renne, P. R.(2004): Age and timing of the Permian mass extinctions: U/Pb dating of closed-system zircons. *Science*, 305: 1760-1763.

Rohde, R. A., Muller, R. A. (2005): Cycles in fossil diversity. *Nature*, 434: 208-210.

Romer, A. S. (1966). *Vertebrate Paleontology*. 3rd edition, University of Chicago Press, Chicago, 468 p.

Sepkoski Jr. J. J. (1982): A Compendium of fossil marine animal families. *Milwaukee Public Museum Contributions in Biology and Geology*, 51: 1-125.

Sepkoski Jr. J. J. (1984): A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology*, 10 (2): 246-267.

Sepkoski Jr. J. J. (1989): Periodicity in extinction and the problem of catastrophism in the history of life. *Journal of the Geological Society, London*, 146: 7-19.

Sepkoski Jr. J. J. (1992). A Compendium of fossil marine animal families. 2nd edition. *Milwaukee Public Museum Contributions in Biology and Geology*, 83: 1-156.

Sepkoski Jr. J. J. (2002): A Compendium of fossil marine animal genera. D. Jablonski, M. Foote (eds.). *Bulletin of American Paleontology*, 363: 1-560.

Twitchett, R. J. (2001): Incompleteness of the Permian-Triassic fossil record: a consequence of productivity decline? *Geological Journal*, 36: 341-353.

Weidlich, O., Kiessling, W., Flügel, E. (2003): Permian-Triassic boundary interval as a model for forcing marine ecosystem collapse by long-term atmospheric oxygen drop. *Geology*, 31 (11): 961-964.

Wignall, P. B. (1992): The day the world nearly died. *New Scientist*, 25: January: 51-55.

Wignall, P. B. (2001): Large igneous provinces and mass extinctions. *Earth-Science Reviews*, 53: 1-33.

Wignall, P. B., Hallam, A. (1992). Anoxia as a cause of the Permian-Triassic mass extinction: facie evidence from northern Italy and the western United States. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 93: 21-46.

Wignall, P. B., Twitchett, R. J. (1996): Oceanic anoxia and the end Permian mass extinction. *Science*, 272: 1155-1158.