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

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Abstract

Data recently published on the longevity of various marine animal genera permits in-depth 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

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 nineteenth 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 Impy Murchison, wrote to Tsar Nicholas I, informing him of the discoveries and that they had 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 foraminifers.

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 the 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.
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)

<table>
<thead>
<tr>
<th>Epoch</th>
<th>Age</th>
<th>dt (in Ma)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LATE TRIASSIC</td>
<td>Norian</td>
<td>16.9</td>
</tr>
<tr>
<td></td>
<td>Carnian</td>
<td>11.5</td>
</tr>
<tr>
<td>MIDDLE TRIASSIC</td>
<td>Ladinian</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Anisian</td>
<td>8</td>
</tr>
<tr>
<td>EARLY TRIASSIC</td>
<td>Olenekian</td>
<td>4.7</td>
</tr>
<tr>
<td></td>
<td>Induan</td>
<td>1.3</td>
</tr>
<tr>
<td>LATE PERMIAN</td>
<td>Tatarian</td>
<td>9.4</td>
</tr>
<tr>
<td></td>
<td>Guadalupian</td>
<td>10.2</td>
</tr>
<tr>
<td>EARLY PERMIAN</td>
<td>Leonardian</td>
<td>9.4</td>
</tr>
<tr>
<td></td>
<td>Sakmarian</td>
<td>14.6</td>
</tr>
<tr>
<td></td>
<td>Asselian</td>
<td>4.4</td>
</tr>
</tbody>
</table>

Table 1.- Epochs, ages and time duration in the Permian and Triassic (see text for details)

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:

\[ V = \frac{100C}{N / dt} \]

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 consid-
ered. On the contrary the changes (V) are, in all taxa, de-
scribing 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 Guada-
lupian 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 appear-
ances. 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 expe-
rienced 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 calcu-
late the changes that occurred in the Asselian. These re-
sults 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 Guada-
lupian 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 ex-
tinctions 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 In-
duan. In most cases this drop is followed by a recupera-
tion 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, remain-
ning low throughout the Permian and at the beginning of
the Triassic, then increasing noticeably from the Ladin-
ian.
One complexity distinct pattern is that of the taxon Os-
teichthyes, 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 spe-
cific 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 previ-
ous 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 un-
derwent 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 un-
derstand 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 sec-
tion. The total number of genera present in the Permian
and Triassic is indicated at the beginning of the descrip-
tion of each taxon. The comments always refer to genera
that are present in more than one age.
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 number 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.
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.
6.2. Foraminifera: 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-
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 being roughly twice the number of genera in existence per age. Only in the Late Triassic does diversity begin to resemble that seen at the beginning of the Permian.
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
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.
Tatarian) and, as in some other taxa, are important in the Norian.

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

Diversity is particularly 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.

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

Fig. 16. - N, V, FA and LA in Terebratulida.
Fig. 16. - N, V, FA y LA en Terebratulida.
The first evidence is the complexity of the evolution of each taxon through 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 behavior 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 we 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.

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References


