

# Expansion of the generic diversity of bivalves during the Triassic (I): some comments on biases of their record

Sonia Ros\* and Miquel De Renzi\*

\*Instituto Cavanilles de Biodiversidad y Biología Evolutiva y  
Departamento de Geología, Universidad de Valencia

## INTRODUCTION

Since rates of origination and extinction are estimated as number of taxa by unit of time, this number can decrease by the effect of factors related with differential preservation in a broad sense and thus, this biases estimates (De Renzi, 1992). These factors are concerned with (i) more or less stable mineralogies; e.g., aragonite or calcite; (ii) differential representation of environments; e.g., marine or continental, and (iii) rarefaction of the fossil record with geologic age; e.g. Cambrian or Cretaceous. We tested the influence of these features on estimates of rates of evolution of bivalves based on the family level throughout the Phanerozoic (De Renzi & Ros, 2002; Ros & De Renzi, 2005). We conclude that rarefaction and mineralogy biased strongly the bivalve family record and thus, this would affect our estimates of their rates evolution.

The Triassic marine fossil record of the bivalve genera is analysed in these terms. In this period took place the recovery and later diversification after the Permian mass extinction. During this time, 169 marine genera (data from Sepkoski, 2002) had their origin and coexisted with older Palaeozoic genera. At the same time, many of these genera became extinct during the Triassic.

The Early Triassic, during which occurred an important part of the recovery of the biota, is mainly represented in the World by continental deposits. The same happens for an important part of the Upper Triassic (fig. 1). In addition to this, mineralogy (aragonite vs. calcite) and mode of life could bias the marine fossil record of Triassic generic richness (fig.2). We are going to cast some light on these questions.

## RESULTS

Hypothesis (i) is tested in table 1; hypothesis (ii) is tested in table 2 and hypothesis (iii) is tested in table 3. According to the results of these tests, tables 1 and 2 show dependence of attributes, whereas we have no reason to reject the null hypothesis of independence for table 3. In table 1, the Lower Triassic shows a significant excess (\*\*\*) of very long-life genera; the Middle Triassic has a bias for short-life genera (\*), but intermediate life genera have a significant positive representation(\*\*). However, the short-life genera have significant positive representation for the Upper Triassic (\*\*). Table 2 shows strong bias for infaunal mode of life during the Middle Triassic (\*\*); throughout this time, the epifaunal mode of life is significantly well represented (\*\*); this pattern is reversed for the Upper Triassic (\*). We have tested several hypothesis related with dependence of mineralogy and all these features, but the only relationship of dependence supported by the statistical analysis is that of mineralogy and mode of life. Infaunal bivalves have mainly aragonitic shells and epifaunal bivalves contain predominantly calcite in their shells.

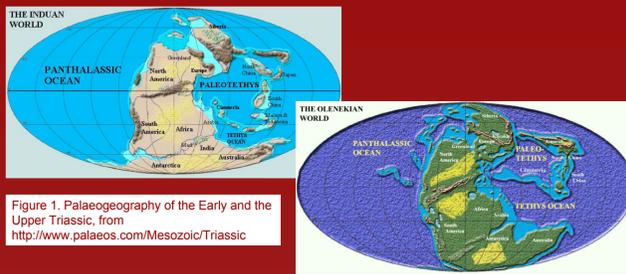
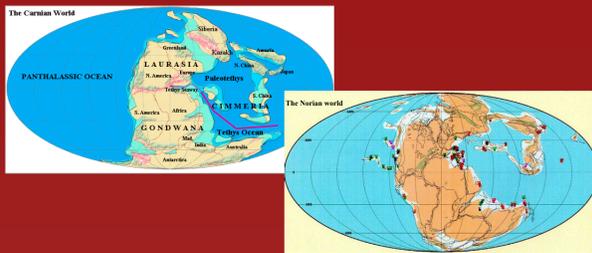


Figure 1. Palaeogeography of the Early and the Upper Triassic, from <http://www.palaeos.com/Mesozoic/Triassic>



Daonella, epifaunal bivalve  
Its shell contains calcite plus aragonite (from Márquez-Aliaga, 1985)

Figure 2. Examples of mode of life and mineralogy of Triassic bivalves

## HYPOTHESES AND THEIR TESTS

Decreasing outcrop area of marine deposits would reduce generic richness. Only those genera more eurytopic would have larger probability to be represented (as a proxy, duration would be an index of eurytopy—eurytopic taxa use to be evaders of local crises and thus, they have larger duration). We need to test (i) that the marine fossil record of bivalves is biased in the Early and Upper Triassic; (ii) mode of life could influence on preservation throughout the Triassic, because of infaunal organisms could be more easily preserved than infaunal ones, and (iii) eurytopy and infaunal mode of life ensure better preservation than stenotopy and epifaunal mode of life. We also test the association of mineralogy and other attributes.

In order to test these hypotheses, we have used contingency tables with adjusted residuals; the null hypotheses are always independence of the considered attributes (see De Renzi & Ros, 2002). Our contingency tables show three numbers within each cell: the central is the actual frequency; the left number (subindex) is the expected frequency and the right number (superindex) is the adjusted residual. If statistically significant, positive adjusted residuals mean that our actual frequency is larger than the expected one, whereas negative adjusted residuals indicate that the actual frequency is smaller than the expected one. This last one is the most interesting case, because it shows a bias against preservation. Signification levels are shown as asterisks in the following way: 0.02 < p < 0.05\*, 0.002 < p < 0.01\*\* and p < 0.002\*\*\*.

Pleuromya, infaunal bivalve  
Aragonitic shell (from Márquez-Aliaga, 1985)

Table 1: GENERIC DURATION vs. EPOCH

Duration	Triassic			TOTAL
	Lower	Middle	Upper	
0 – 15 my	8.83 7 -0.86	21.67 15 -2.29 *	32.5 41 2.77 **	63
15 – 100 my	8.69 5 -1.73	21.32 30 2.98 **	31.99 27 -1.63	62
> 100 my	4.48 10 3.15 ***	11.01 9 -0.84	16.51 13 -1.39	32
TOTAL	22	54	81	157

$\chi^2 = 18.42$  p < 0,005

Table 2: MODE OF LIFE vs. EPOCH

Mode of life	Triassic			TOTAL
	Lower	Middle	Upper	
Epifaunal	13.45 13 -0.21	33.02 40 2.41 **	49.53 43 -2.14 *	96
Infaunal	8.55 9 0.21	20.98 14 -2.41 **	31.47 38 2.14 *	61
TOTAL	22	54	81	157

$\chi^2 = 6.05$  p ~ 0,05

Table 3: GENERIC DURATION vs. MODE OF LIFE

Duration Intervals	Mode of life		TOTAL
	Epifaunal	Infaunal	
0 – 15 my	42	21	63
15 – 40 my	23	14	37
40 – 100my	13	12	25
> 100 my	18	14	32
TOTAL	96	61	157

$\chi^2 = 2.03$  Non significant

## DISCUSSION AND CONCLUSIONS

Since duration is a proxy for area of geographic distribution, hypothesis (i) (table 1) is certain for the Early Triassic (only the most eurytopic genera; i.e., >100 my, show positive departure) and the Middle Triassic (bias against stenotopic genera; i.e., 0 – 15 my, but significant excess of eurytopic genera; i.e., 15-100 my). However, the Upper Triassic shows excess of stenotopic genera (0 – 15 my). This last conclusion could be explained because there were possibly an enormous diversification at this time and thus, with a large impact on the fossil record. We are prone to interpret results for the Early and Middle Triassic as reflecting a smaller area of marine deposits, as we postulated at the beginning. Hypothesis (ii) does not seem well supported by the statistical analysis (table 2). The hypothesis is seemingly accomplished for the Upper Triassic, but it is rejected for the Middle Triassic. Since the Middle Triassic has the broadest marine area, it is difficult to explain the bias against the infaunal bivalves and the significant excess for the epifaunal ones. At the same time, infaunal bivalves have always smaller numbers. Since infaunal bivalves have always the very soluble aragonite as the only component of their shell and the majority of epifaunal and semiinfaunal bivalves have the more stable calcite, we confirm our assertion that mode of life has smaller influence on preservation than mineralogy (Ros & De Renzi, 2005). In addition, we have not recognised any increase of preservation when infaunal mode of life is combined with eurytopy, as we predict with hypothesis (iii) (table 3). This independence has to do possibly with mineralogy as a prevalent trait influencing preservation.

## LITERATURE

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## ACNOWLEDGMENTS

We thank Ana Márquez-Aliaga, Dave Bottjer and Susana Damborenea  
This research has been supported by project CGL2005-08238-02-02/BTE