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Preservation biases, rates of evolution and coherence of databases: Bivalvia as a study case

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Abstract. Several hypotheses about the influence of preservation on Bivalvia rates of evolution estimates (marine and freshwater families) were tested in a previous paper. However, the database used for those tests had a patchy quality and our results were provisional. Now an improved database dealing with only marine families has been used in order to test again those hypotheses. We removed freshwater families from the early database and we test the statistical hypotheses on these two data sources. Diversification patterns remain stable in general with these different databases; however, only the improved database shows the mass extinction at the end of the Triassic times. Statistical conclusions in the previous paper are generally confirmed in the present study. Since the presence of taxa having shell biominerals with different stability (aragonite or calcite) is not independent from geologic time (as expression of the fossil record rarefaction), the estimates of rates of evolution will be biased by these two factors. The influence of the mode of life, however, has been reinterpreted since it is mainly associated with mineralogical compositions. As a consequence, the mode of life does not influence preservation. In addition, age-sea character (aragonitic or calcitic seas) has significantly no influence on preferential preservation of the corresponding CO_3Ca polymorph. Some significant statistical results are better interpreted in evolutionary terms.

Resumen. SESGOS DE CONSERVACIÓN, TASAS EVOLUTIVAS Y COHERENCIA DE LAS BASES DE DATOS: LOS BIVALVOS COMO UN CASO DE ESTUDIO. En un trabajo previo, verificamos diferentes hipótesis acerca de la influencia de la conservación en las estimaciones de las tasas de evolución de los bivalvos (familias marinas y de agua dulce). Sin embargo, la base de datos utilizada era de calidad desigual. Por esta razón se indicaba que nuestros resultados eran provisionales. Ahora hemos usado una base de datos mejorada para volver a contrastar nuestras hipótesis, aunque sólo contiene familias marinas. Hemos eliminado las familias de agua dulce de la primera base de datos y hemos efectuado la contrastación de hipótesis para ambas. Las pautas de diversificación en las dos bases de datos permanecen estables en sus líneas generales; sin embargo, sólo la base de datos mejorada muestra bien la extinción en masa del final del Triásico. Las conclusiones estadísticas del trabajo previo se sostienen en general en este estudio. En tanto que la presencia de taxones poseyendo biominerales con distinta estabilidad (aragonito o calcita) no es independiente del tiempo geológico (como expresión de la rarefacción del registro fósil), las estimaciones de las tasas de evolución estarán sesgadas por estos dos factores. Sin embargo, la influencia del modo de vida ha sido reinterpretada en tanto que está principalmente asociado con las composiciones mineralógicas. En consecuencia, el modo de vida no influye en la conservación. Además, el carácter del mar ligado a la edad (mares aragoníticos o calcíticos) no influye en la conservación preferencial del correspondiente polimorfo del CO_3Ca. Algunos resultados estadísticos significativos se interpretan mejor en términos evolutivos.

Key words. Databases. Fossil record. Preservation biases. Bivalves. Rates of evolution.

Palabras clave. Bases de datos. Registro fósil. Sesgos de conservación. Bivalvos. Tasas de evolución.

Introduction

History of life is only partly reflected in the fossil record. In addition, the fossil record shows a structure and composition resulting from processes studied by taphonomy. At a given temporal interval, the taxonomic composition of the record will reflect the different biases produced by taphonomic processes. These biases would affect the taxonomic composition of the different clades; *e.g.* families or genera within classes; thus, according to De Renzi (1992), they affect our estimates of their rates of evolution. Bivalves supply an interesting example in this context.

Following De Renzi (1992), evolutionary rates of bivalves would be biased by (i) the easy solubility of calcium carbonate of their shells and (ii) rarefaction

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of the fossil record with age. Calcium carbonate has two different natural polymorphs: aragonite and calcite. The shell of the majority of bivalves consists exclusively of aragonite (the primitive condition); a small minority has shells containing low magnesian calcite (the derived condition). Since aragonite is more soluble than low magnesian calcite, a second bias is added: the more difficult preservation of the more common aragonitic bivalve shells. Calcite in bivalve shells may appear in two ways: (i) as bimineralic shells -calcite + aragonite-, in which calcite is always present as an outer layer; *e.g.* scallops, or (ii) consisting almost exclusively of calcite; *e.g.* oysters.

Rarefaction means decreasing area of sedimentary rocks outcrop with time (Raup, 1976a, 1976b); this produces an illusory impression of progressively decreasing diversity. Therefore, rarefaction would affect the oldest records (Cambrian) of Bivalvia. To the decreasing area of outcrop of the oldest records, we must add the increasing action through time of geologic processes involving destruction (weathering, erosion, diagenesis and metamorphism) followed -or not- by reduction of sedimentary volume.

Therefore, aragonitic taxa would be underrepresented in general. However, calcitic forms (shells having almost exclusively calcite and bimineralic shells) would have a more reliable palaeontological representation. Because of rarefaction, diversity would decrease with geologic age and this would affect more aragonitic than calcitic taxa. These hypotheses may be statistically tested (De Renzi and Ros, 2002).

We considered not only the possible influence of carbonate composition and rarefaction but the character of the sea and the mode of life as well. Specific intervals of geologic time would enhance the formation of aragonite or calcite in the seas; this is known as age-sea character (Carter *et al.*, 1998; Harper *et al.* 1997). This was thought to influence preservation of the corresponding mineralogical polymorph as well, with the consequent bias for that interval; *i.e.* aragonite would be more prone to be preserved in aragonitic seas whereas calcite would become better preserved in calcitic seas.

Finally, we considered the infaunal or epifaunal mode of life as a possible influence for preservation or destruction (see Palmqvist, 1991, 1993 for reviews and references). Although there are three modes of life (epifaunal, semiinfaunal and infaunal), semiinfaunal plus epifaunal were assembled as only one mode of life for taphonomic effects (De Renzi and Ros, 2002); semiinfaunal organisms are partly unprotected and aragonitic epifaunal and semiinfaunal families would be significantly more affected by biostratinomic processes. Taking into account this remark, we will call them in general "epifaunal". The infaunal animals live and usually die buried in the sediment and, in contrast to epifaunal organisms, they would be less subject to biostratinomic factors. Therefore, we expected a favourable bias for preservation of infaunal families throughout the Phanerozoic and a negative bias for the epifaunal families. In addition, there could be preferential preservation for infaunal aragonitic families and epifaunal calcitic families. However, members of epifaunal aragonitic families would be prone to the destruction since they are more subject to biostratinomic factors and aragonite is more soluble than calcite (there are no infaunal calcitic families).

In order to test all these hypotheses, the statistical techniques used were the analysis of contingency tables of adjusted residuals (Everitt, 1977). These techniques corroborated our expectations with two exceptions: 1) the expected favourable bias for infaunal bivalves and preferable destruction of epifaunal families of this class during the Phanerozoic, and 2) the age-sea character enhancing preservation of the respective polymorphs.

The taxonomic level used for this statistical analysis was the family. However, our conclusions were provisional, since our data base (Skelton and Benton, 1993; from now on, we shall mention this paper as FR2; *i.e. Fossil Record* 2) was recognised by their authors as having patchy quality (Editor's note; p. 238). A more updated data base was necessary to strengthen these previous results and, above all, to see whether the general patterns remain stable in spite of differences among the sources of data. In this paper, we use the more recent Sepkoski (1992) database and carry out the same tests. From now, we shall mention it as CFMAF; *i.e. Compendium of Fossil Marine Families.* Moreover, FR2 included marine and freshwater families whereas CFMAF included exclusively marine families. Therefore, these two data bases were heterogeneous; in order to compare them correctly, we have removed freshwater families from FR2.

Hypotheses, material and methods

Four null hypotheses were statistically tested by De Renzi and Ros (2002). In order to attain the goal of the present study, these hypotheses will be simultaneously tested for the improved CFMAF data base and the FR2 marine data base. Data on marine families in FR2 come from different sources. One of them is Sepkoski's (1982) database. Sepkoski reviewed this early work and he published his CFMAF ten years later (see Sepkoski, 1993). This explains why we consider CFMAF as more updated, although it was published one year before FR2. Although the majority of families are common to both data bases, these differ on two items: 1) a small number of families are added or deleted in CFMAF, and 2) some families have different durations from one database to the other.

The four null hypotheses are 1) preservation of aragonite and calcite is independent of geologic age; 2) preservation of aragonite and calcite is independent of the aragonitic or calcitic character of the sea; 3) preservation of both polymorphs is independent of the mode of life of animals, and 4) preservation of every mode of life is independent of geologic age.

Mineralogy and mode of life of families have been mainly obtained from Amler *et al.* (2000). Other mineralogical data have been supplied by Hudson (1968), Stanley (1968, 1970, 1972), Moore (1969a, 1969b, 1971), Taylor *et al.* (1969, 1973), Garavelli *et al.* (1980), Carter (1980a, 1980b, 1980c; 1990a, 1990b, 1990c), Chinzei *et al.* (1982), Savazzi (1984), Newton *et al.* (1987), Harper and Skelton (1993), Heinberg (1999), Morris (1978), Kriz and Bogolepova (1995), Grimm (1998), Tunnicliff (1987), Pacaud (2001), Friebe (1995), Berkman *et al.* (1994), Pojeta and Zhang (1984) and Yancey (1985).

Analysis of contingency tables consists of building an arrangement, in which we observe simultaneously the presence of two kinds of attributes in every individual (families in this case) of our sample, whose size is *n*; *e.g.* in the first hypothesis (table 1), we observe the mineral composition and the geologic interval for each family and we count the number of families for every mineralogical composition for that interval. There are two compositions (aragonite or calcite) and four geologic time intervals (Cambrian-Devonian, Carboniferous-Permian, Mesozoic and Cenozoic). This gives a table with four rows and two columns and 4x2= 8 cells. In general, such tables have *r* rows, *c* columns and *r* x *c* cells; each cell is placed in an *i*-row and a *j*-column. Each *ij*-cell contains an observed frequency (n_{ij}) that must be tested against an expected frequency (E_{ij}) generated by the null hypothesis of independence. This is the typical structure of a chi-square test with (r-1) (c-1) degrees of freedom. When the null hypothesis is rejected, this does not happen for all the cells. In order to find those cells in which the null hypothesis fails, we use the adjusted residuals technique. An adjusted residual is a random variable with mean 0 and standard deviation 1 that has approximately normal distribution when the null hypothesis is not rejected. For the cells in which the null hypothesis fails, the absolute value of the adjusted residual is larger than the corresponding normal deviate for the specified significance level; its sign indicates if the expected value under the null hypothesis is smaller (positive sign) or larger (negative sign) than the observed value. In short, the following quantities are used: (i) the partial sum of cells in every row (for the i^{th} row, its value is $n_{i.}$); (ii) the partial sum of cells in every column (for the j^{th} column, its value is $n_{.j}$); (iii) the expected value for the *ij*-cell is $E_{ij} = n_{i.}\, n_{.j} / n$, and (iv) the adjusted residual for the *ij*-cell is defined as $d_{ij} = e_{ij} / \sqrt{v_{ij}}$, with $e_{ij} = (n_{ij} - E_{ij}) / \sqrt{E_{ij}}$ and $v_{ij} = (1 - n_{i.}/n)\,(1 - n_{.j}/n)$ (for a detailed description of these techniques, see Everitt, 1977).

These tables always show the two data sources; *i.e.* FR2 and CFMAF. Tables show the observed frequency in bold; the expected frequency is placed to its left as a subindex and the adjusted residual with its sign is placed to its right as a superindex. The significance of adjusted residuals is indicated by means of asterisks: * for $0.05 > p \geq 0.01$, ** for $0.01 > p \geq 0.00001$ and *** for $0.00001 > p$; *e.g.* $_{29.1}\,\mathbf{35}\,^{2.12*}$. The critical level of significance is $p = 0.05$. Since these tables always have two columns for the studied cases, adjusted residuals are always symmetric at every row, as an algebraic consequence; *i.e.*, they have the same absolute value, but with opposite signs.

Results

Our results are shown in tables 1, 2, 3 and 4. A simple glance at these tables shows some differences between the observed frequencies from FR2 (freshwater families have been removed from this database, as said before) and CFMAF. For tables including temporal intervals, we remark that the number of aragonitic families is always larger than the number of calcitic families throughout geologic time. Although it seems counterintuitive, the observed number of aragonitic families is significantly smaller than their expected number in specific intervals. Because of symmetry of the adjusted residuals, the number of the calcitic families is significantly larger than its expected number for the same intervals.

Table 1 tests the first null hypothesis; i.e. the independence of mineralogy (columns) and geologic time (rows). As in De Renzi and Ros (2002), we have subdivided geologic time in four intervals: (i) Cambrian-Devonian, with a small proliferation of calcitic families and a relatively high diversification of aragonitic families; (ii) Carboniferous-Permian, with an important expansion of calcitic families; (iii) Mesozoic and (iv) Caenozoic. For both data bases, the null hypothesis is fully rejected.

However, there are differences in the significance within cells. For FR2, the null hypothesis is rejected in all the cells, whereas it is rejected only for the Carboniferous-Permian and Caenozoic intervals for CFMAF. Looking at FR2, aragonite families are more represented than expected, whereas calcitic families represent the opposite situation for the Cambrian-Devonian interval. For the Carboniferous-Permian and

Table 1. Test of independence of mineralogical composition and geologic age (older and older rocks have more and more rarefied record / *Prueba de independencia de la composición mineralógica y la edad geológica (cuanto más antiguas son las rocas, más enrarecido es su registro).*

Mineralogy / Geologic Time	FR2		TOTAL FR2	CFMAF		TOTAL CFMAF
	Aragonite	Calcite		Aragonite	Calcite	
Cambrian-Devonian	$_{29.1}$ **35** $^{2.12*}$	$_{12.9}$ **7** $^{-2.12*}$	42	$_{33.9}$**37** $^{1.1}$	$_{13.1}$**10** $^{-1.1}$	47
Carboniferous-Permian	$_{36.0}$ **28** $^{-2.66**}$	$_{16.0}$ **24**$^{2.66**}$	52	$_{42.5}$**34** $^{-2.72**}$	$_{16.5}$**25** $^{2.72**}$	59
Mesozoic	$_{73.5}$ **64** $^{-2.47*}$	$_{32.5}$ **42** $^{2.47*}$	106	$_{90.1}$**83** $^{-1.77}$	$_{34.9}$**42** $^{1.77}$	125
Cenozoic	$_{71.4}$ **83** $^{3.05**}$	$_{31.6}$ **20** $^{-3.05**}$	103	$_{78.5}$**91**$^{3.23**}$	$_{30.5}$**18** $^{-3.23**}$	109
TOTAL	210	93	303	245	95	340
	χ^2_{FR2} = **19.86**; d.f.= 3; p<0.001			χ^2_{CFMAF} = **16.20**; d.f.= 3; p<0.005		

Table 2. Test of independence of mineralogical composition and age-sea character / *Prueba de independencia de la composición mineralógica y el carácter del mar con la edad.*

Mineralogy / Age-Sea Character	FR2		TOTAL FR2	CFMAF		TOTAL CFMAF
	Aragonite	Calcite		Aragonite	Calcite	
Ordovician-L. Carboniferous (C)	$_{36.2}$ **37** $^{0.28}$	$_{15.9}$ **15** $^{-0.28}$	52	$_{38.7}$**39** $^{0.09}$	$_{15.3}$**15** $^{-0.09}$	54
U. Carboniferous-Triassic (A)	$_{53.5}$ **43** $^{-2.97**}$	$_{23.5}$ **34** $^{2.97**}$	77	$_{62.4}$**53** $^{-2.56*}$	$_{24.6}$**34** $^{2.56*}$	87
Jurassic-Cretaceous (C)	$_{72.3}$ **70** $^{-0.59}$	$_{31.7}$ **34** $^{0.59}$	104	$_{81.7}$**78** $^{-0.94}$	$_{32.3}$**36** $^{0.94}$	114
Cenozoic (A)	$_{73.0}$ **85** $^{3.06**}$	$_{32.0}$ **20** $^{-3.06**}$	105	$_{78.2}$**91** $^{3.26**}$	$_{30.8}$**18** $^{-3.26**}$	109
TOTAL	235	103	338	261	103	364
	χ^2 FR2 = **13.58**; d.f.= 3; p<0.005			χ^2 CFMAF = **13.06**; d.f.= 3; p<0.005		

Table 3. Test of independence of mineralogical composition and mode of life / *Prueba de independencia de la composición mineralógica y el modo de vida.*

Mode of life/Mineralogy	FR2		TOTAL FR2	CFMAF		TOTAL CFMAF
	Infaunal	Epif +Semiinf		Infaunal	Epif +Semiinf	
Aragonite	$_{71.3}$ **99+1** $^{9.56***}$	$_{53.7}$ **24+1** $^{-9.56***}$	125	$_{88.8}$**117 + 1** $^{9.49***}$	$_{64.2}$**34 + 1** $^{-9.49***}$	153
Calcite	$_{29.7}$ **0+1** $^{-9.56***}$	$_{22.3}$ **50+1** $^{9.56***}$	52	$_{30.2}$**0 + 1** $^{-9.49***}$	$_{21.8}$**50 + 1** $^{9.49***}$	52
TOTAL	101	76	177	119	86	205
	χ^2_{FR2} = **91.37**; d.f.= 3; p<0.000005			χ^2_{CFMAF} = **90.13**; d.f.= 3; p<0.000005		

Table 4. Test of independence of mode of life and geologic age (rarefaction) / *Prueba de independencia del modo de vida y la edad geológica (rarefacción).*

Mode of life/Geologic Time	FR2		TOTAL FR2	CFMAF		TOTAL CFMAF
	Infaunal	Epif +Semiinf		Infaunal	Epif +Semiinf	
Cambrian-Devonian	$_{18.3}$ **21** $^{1.02}$	$_{14.7}$**12** $^{-1.02}$	33	$_{21.0}$ **23** $^{0.7}$	$_{15.0}$ **13** $^{-0.7}$	36
Carboniferous-Permian	$_{24.9}$ **19** $^{-1.92}$	$_{20.1}$ **26** $^{1.92}$	45	$_{32.1}$ **28** $^{-1.24}$	$_{22.9}$ **27** $^{1.24}$	55
Mesozoic	$_{59.8}$ **54** $^{-1.4}$	$_{48.3}$ **54** $^{1.4}$	108	$_{70.1}$ **65** $^{-1.2}$	$_{49.9}$**55** $^{-1.2}$	120
Cenozoic	$_{58.1}$ **67** $^{2.19*}$	$_{46.9}$ **38** $^{-2.19*}$	105	$_{63.7}$ **71** $^{1.75}$	$_{45.3}$ 38 $^{-1.75}$	109
TOTAL	161	130	291	187	133	320
	χ^2_{FR2} = **8.35**; d.f.= 3; p<0.05			χ^2_{CFMAF} = **4.64**; d.f.= 3; 0.21>p>0.05		

On significance levels: / *Sobre los niveles de significación*:

* 0.05 > p ≥ 0.01 Residuals have values between 1.96 and 2.576 / *Los residuales han de estar comprendidos entre 1,96-2,576*
** 0.01 > p ≥ 0.00001 Residuals have values between 2.576 and 4.417 / *Los residuales han de estar comprendidos entre 2,576-4,417*
*** 0.00001 > p Residuals have to be larger than 4.417 / *Los residuales han de ser mayores que 4,417*

Mesozoic, the reverse situation is observed. Throughout Caenozoic times, aragonitic families are overrepresented and calcitic families are underrepresented. For CFMAF, statistical significance only takes place for the Carboniferous-Permian and Caenozoic times, with the same distribution of adjusted residuals as in FR2.

The second hypothesis is tested in table 2. As in De Renzi and Ros (2002), we search for the possible dependence of preservation of specific mineralogies (columns) and the sea character (rows); *i.e.* aragonitic sea (A) or calcitic sea (C), linked to a specific geologic time interval (Carter *et al.*, 1998; Harper *et al.*, 1997). Mineralogy is represented by columns (c=2) and the time intervals for sea character, by rows (r=4). The null hypothesis is rejected for both databases.

The failure of the null hypothesis follows the same pattern for the cells of both FR2 and CFMAF. The hypothesis fails only for the Upper Carboniferous-Triassic interval (aragonitic sea) and for the Caenozoic interval (aragonitic sea). For the former, we observe fewer aragonitic families than expected and more calcitic families than expected. For the latter, the reverse takes place.

The third hypothesis, about the independence of mineralogy (rows) and mode of life (columns) is also rejected for both data bases (table 3). Moreover, we observe that calcitic families have no representation in an infaunal style of life and this will be discussed later. Since Everitt (1977) advises that a small quantity be added to all the cells when a zero appears in one of them, we did this for table 3.

We find the same pattern for these two data bases: significant overrepresentation for epifaunal calcitic families and aragonite infaunal families; epifaunal aragonitic families are underrepresented.

Last, the fourth hypothesis (table 4) refers to the independence of mode of life (columns) and geologic age (rows). Geologic time intervals are the same as those in table 1. For FR2, the null hypothesis is rejected with the lowest significance level admitted. However, it is not rejected for the CFMAF data base. We include their adjusted residuals.

For the FR2 database, the null hypothesis fails only for the Caenozoic times; there is underrepresentation for epi- plus semiinfaunal families, whereas infaunal families are overrepresented.

Discussion

The subdivision of the clade Bivalvia into aragonitic and calcitic families as well as epifaunal (including epifaunal plus semiinfaunal forms) and infaunal families has no general phylogenetic or taxonomic meaning; *e.g.* the subclass Heteroconchia contains aragonitic and calcitic groups as well as epifaunal or infaunal forms. Therefore, we shall call them collectives; *i.e.* the aragonite collective, the calcite collective, the epifaunal collective and the infaunal collective. The clade Bivalvia consists of families of all these collectives at every instant of geologic time; thus biases affecting some of these collectives will affect the total diversity of the clade. Figure 1 shows the diversification of the mineralogical collectives of Bivalvia throughout the Phanerozoic and the diversification of Bivalvia as the sum of these two collectives at every instant of the geologic time for the two databases.

Another point to take into account is that rates of evolution are the ratio of the number of taxa to the unit of time; e.g. number of families/my. We use time intervals for such estimations. Thus, rates of evolution may be biased: 1) the first appearance of a family may not be recorded and it does not appear during the actual interval but during the next one; a similar reasoning may be followed for extinction. 2) Since some collectives are significantly more prone to destruction by taphonomic processes than others, their number of taxa is lowered within a given interval. Because of these two arguments, the number of taxa does not reflect the actual number during a specific interval and hence the value of the ratio is generally diminished.

Our results show a general congruence for both data bases. Figure 1 is similar to figure 1 in De Renzi and Ros (2002), which contains marine and freshwater records, whereas figure 1 here only refers to the record of marine bivalves. General patterns of bivalve diversification do not seem substantially altered in their major traits (total diversification, aragonite collective and calcite collective). Although the general pattern is preserved in figure 1, we can observe minor differences between FR2 and CFMAF. Curves (for total and mineralogical collectives) show good coincidence throughout the Early and the Middle Palaeozoic. Mesozoic times show the largest divergences; they are concentrated in the aragonite collective and this is reflected in the total diversification curves. The calcite collective shows almost no differences between the two databases. A second point of interest: CFMAF shows well the extinction at the end of the Triassic, a very important event that is nearly not apparent for FR2 (with or without freshwater families). The abundance of the aragonite collective is always seen as increasing in FR2 throughout the Triassic-Jurassic boundary; only the calcitic collective declines sharply at the end of the Triassic according this data source.

In addition, the statistical analysis in De Renzi and Ros (2002) is coherent with the present analysis. We remark a notable coincidence for the hypothesis of independence of mineralogy and age-sea character: in the early analysis (De Renzi and Ros, 2002), the full record of Bivalvia (marine and freshwater taxa) was analysed. We considered the number of freshwater families at each interval negligible; now we have removed them. However, the statistical conclusions are the same for both the earlier paper (the full record) and the present study (only the marine record) (see table 2). The hypothesis of independence

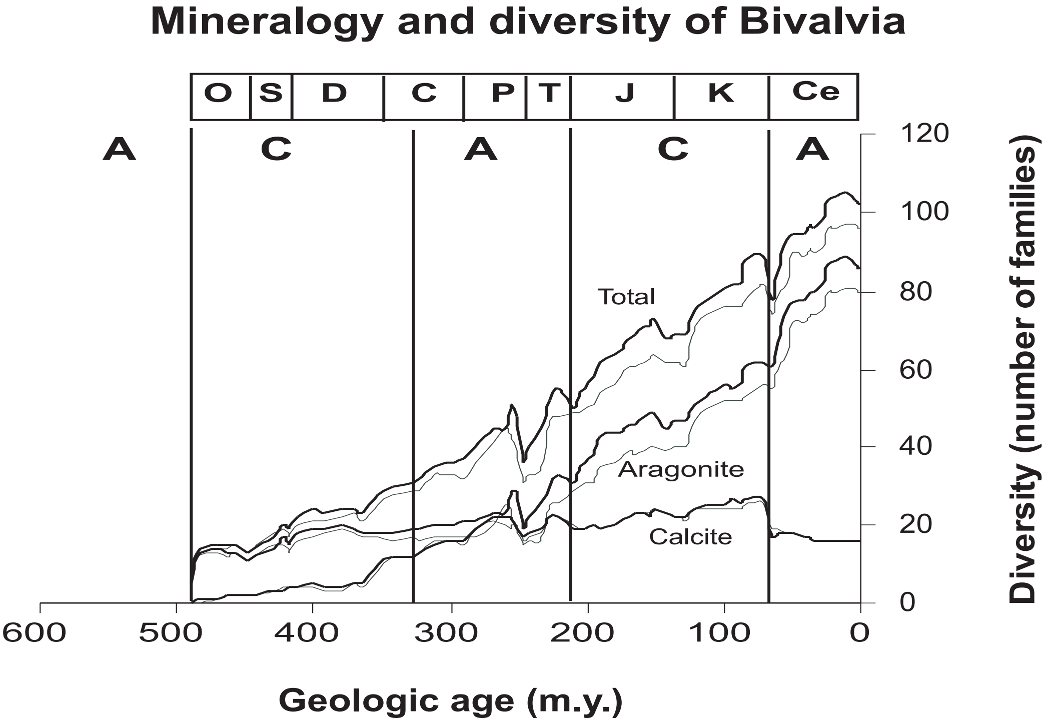

Figure 1. Diversification of the class Bivalvia (total) and the two collectives (aragonite, calcite). Thick line: data from CFMAF. Thin line: data from FR2. Vertical divisions limit the time intervals of aragonite seas (A) or calcite seas (C). O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; Ce, Caenozoic / *Diversificación de la clase Bivalvia (total) y los dos colectivos (aragonito, calcita). Línea gruesa: datos del CFMAF. Línea fina: datos del FR2. Las líneas verticales limitan los intervalos temporales de los mares de aragonito (A) o de calcita (C). O, Ordovícico; S, Silúrico; D, Devónico; C, Carbonífero; P, Pérmico; T, Triásico; J, Jurásico; K, Cretácico; Ce, Cenozoico.*

is rejected; adjusted residuals are allocated in the same way and the significance has increased. However, the rejection of the null hypothesis does not mean accepting a differential preservation according to the calcitic or aragonitic character of the sea. As concluded in De Renzi and Ros (2002), this is in contradiction for the Upper Carboniferous-Triassic interval that has aragonitic character; during which, however, aragonitic families are significantly underrepresented and calcitic families are overrepresented.

Another point of full coincidence is referred to mode of life and mineralogy. A previous remark must be done: the mode of life of some extinct bivalves is unknown. Therefore, table 3 is based on a sample from the pool of Phanerozoic marine families of Bivalvia. However, this sample is large (n=177 for FR2 from a whole amount of 209 families, about 85%; and n=205 for CFMAF from a pool of 212 families, about 97%). There is a statistically significant overrepresentation for the aragonite infaunal collective and the same may be said for the calcite epifaunal collective. The aragonite epifaunal collective is underrepresented. However, we mentioned two calcitic infaunal families (De Renzi and Ros, 2002). A more refined analysis of modes of life shows no infaunal calcitic bivalves. This was probably the result of an evolutionary constraint rather than a feature of evolutionary contingency. These results can be explained by two rival hypotheses: the first one is concerned with the action of taphonomic processes, as we supposed above. We must note that infaunal bivalves climb out on to the sediment surface when they are sick or stressed. In addition, shells of dead infaunal bivalves living in shallow bottoms use to become exposed after storms. The consequence of these two situations is that many shells of infaunal bivalves are exposed to the biostratinomic agents. Although all this is true, bivalves inhabit all ocean depths and high levels of energy do not usually reach protected or moderately deep bottoms. The second hypothesis pays attention to evolutionary processes since the aragonite epifaunal collective has a very poor Recent diversity. Therefore, a competing and better explanation would be the poor evolutionary success of these epifaunal taxa with aragonitic shell, a much reduced subset within the whole epifaunal collective. In addition, this would be in accordance with the general decline of the epifaunal mode of life of bivalves during the Caenozoic rather than with shell mineralogy. This new interpretation contradicts our early conclusion.

We are now going to discuss the points of no coincidence of the statistical analysis. The acceptance of

CFMAF as an improved data base with respect to FR2 involves taking the results based on the former as the most valid conclusions. Let us examine these divergences. In De Renzi and Ros (2002), and for the present analysis of FR2 without the freshwater families, the aragonite collective is underrepresented for both Carboniferous-Permian and Mesozoic intervals. This does not happen for CFMAF, in which the aragonite collective is only underrepresented throughout the Carboniferous-Permian interval, although we could accept the significance for Mesozoic times with a lower level of significance ($0.05<p<0.1$). In addition, the aragonite collective in FR2 has a number significantly larger than expected during the Cambrian-Devonian times (the reverse is certain for the calcite collective). This last issue is neither the case for De Renzi and Ros (2002) nor for CFMAF. For Caenozoic times, significant results are coincident for all these statistical analyses.

For the aragonite collective, these expected values significantly smaller than the observed frequencies for a specified temporal interval are related to evolutionary events rather than taphonomic processes. Because of aragonite instability, the aragonite collective would have to be underrepresented or in accordance with the independence hypothesis. This significant overrepresentation of aragonite families may have two meanings in an evolutionary context: (i) higher diversification of taxa containing aragonitic families than those containing calcitic families or (ii) decline in diversity for taxa containing calcitic families together with -or not- expansion of taxa with aragonitic families.

An example of (i) is, for table 1 and FR2, the interval Cambrian-Devonian. In this interval, the aragonite collective is significantly overrepresented whereas the calcite collective shows the reverse situation. Figure 1 shows the aragonite collective with a strong expansion throughout this temporal interval in contrast to the calcite collective. However, this significant issue was attained neither in De Renzi and Ros (2002) nor in the analysis of CFMAF. In spite of the large observed number for the aragonite collective as compared to the calcite one, this does not mean a departure from the null hypothesis of independence in accepting CFMAF as the improved data base. This absence of significance could be due to the small numbers observed for both collectives as compared with the larger numbers observed for other intervals. The small whole sample size, moreover, is also a cause for this lack of significance. These small oscillations from one database to another could mask a significantly higher diversity for the aragonite collective. Therefore, FR2 has significance for all the intervals and CFMAF has only significance above the critical level ($p=0.05$) for two intervals. Observe, however, that the signs of residuals are distributed in the same way in the cells, independently of the considered database, and also in De Renzi and Ros (2002). Low numbers throughout the Early Palaeozoic could be the effect of diagenesis plus metamorphism combined with rarefaction. Although the calcite collective was affected by the same kind of agents, its diversification could better reflect a part of the evolutionary processes displayed at the origin of the Class Bivalvia, since the more stable calcite is less affected than the instable and easily soluble aragonite; *i.e.* it would be more frequently and easily preserved (see also De Renzi, 1992). However, the larger amount of aragonitic taxa would have an enormous impact on the record in spite of the taphonomic destruction of many of them.

The Caenozoic interval in table 1 (FR2 and CFMAF) and in De Renzi and Ros (2002) is a case of (ii). Calcitic families have a higher probability of becoming preserved than aragonitic families. Thus, the significant low observed number in the calcite collective has an evolutionary meaning as does the significantly high observed number for the aragonite collective. Figure 1 exhibits an expanding diversity for the aragonite collective and a declining diversity for the calcite collective during this interval. The diversity decreases for the calcite collective would be due again to the general decline of the epifaunal style of life throughout Caenozoic times (see above) since calcitic forms are exclusively linked to this mode of life. In this case, there is no remarkable action of diagenetic processes (shells with their original aragonite are very frequent during Caenozoic times; remember the rocks of the Palaeogene Anglo-Parisian basin -the oldest Caenozoic deposits- containing large amounts of aragonitic molluscan shells, or the Neogene deposits of the Mediterranean area). In addition, rarefaction is comparatively absent. Therefore, this is not related with the aragonitic character of the Caenozoic seas.

According to De Renzi and Ros (2002) and results shown in table 4 for CFMAF, mode of life does not seem to bias the record of bivalves related to rarefaction as represented by geologic age. The null hypothesis of independence is only rejected for FR2, but this happens only for Caenozoic times. Paying attention to the significant adjusted residuals for this interval, the epifaunal collective is underrepresented whereas the infaunal collective is overrepresented. Although the null hypothesis is not rejected for CFMAF, the adjusted residuals for Caenozoic (-1.75 for the epifaunal collective; 1.75 for the infaunal collective) are close to the significant critical values. Even accepting the significance of this result, this has not the meaning of a taphonomic bias as we expected initially (see also De Renzi and Ros, 2002) but it is the consequence of the declining character of the calcite collective, that supplies the main bulk of this joint kind of life styles (semiinfaunal bivalves is a small collective). For FR2, moreover, the Carboniferous-Permian interval shows adjusted residuals very close to the critical value 1.96 ($p = 0.05$). The adjusted residual corresponding to the infaunal collective is -1.92 (by symmetry, the adjusted residual of the epifaunal collective is 1.92). According to our hypothesis of preservation, we would have expected a positive residual for the infaunal collective and now we observe the reverse situation. Since the infaunal collective consists exclusively of aragonitic taxa and the epifaunal collective consists mainly of calcitic taxa, we may conclude that mineralogy is more important than mode of life for preservation. This is confirmed by the distribution of residual signs, which is the same as in table 1. Although the CFMAF has no statistical significance, the signs of residuals are distributed in the same way. Adjusted residuals were not shown in De Renzi and Ros (2002), due to lack of significance of the test at the critical level, namely $p=0.05$; however, we could accept the significance at $0.05<p<0.15$. Now we have computed them for this discussion. The distribution of their signs remains and absolute values of residuals are relatively high for the Carboniferous-Permian and the Caenozoic. We expected a relationship between biomineralization and life habits and the present discussion seems to strengthen our argument.

This discussion sheds light on the main problem set by this paper: how do taphonomic features affect our estimates of rates of evolution? For bivalves, mode of life was expected to be a relevant factor for differential preservation, but evolutionary hypotheses rather than taphonomic arguments explain better our statistical results. However, presence of shells of the different calcium carbonate polymorphs as dependent on geologic age (an indirect measurement of rarefaction of the fossil record) may be partly a good proof of how taphonomic factors affect our estimates of rates of evolution. Statistical significance associated with two intervals (Cambrian-Devonian and Caenozoic) has an evolutionary explanation. However, the underrepresentation of the aragonite collective (and the overrepresentation of the calcite collective) during the Carboniferous-Permian interval has reasonably a taphonomic explanation. The sample of aragonite collective families is lower because many of them are not preserved, although the calcite collective approaches the actual value. This influences the full diversity throughout the interval (this is the sum of families from the aragonite and calcite collectives). Thus, origination rates would be lowered (there are less families present than expected because aragonite families are more prone to be not preserved throughout this interval) and the same may be said for extinction rates. The aragonite collective displays an almost null diversification during this interval, especially between the end of Devonian and the Asselian; the CFMAF suggests a very slow growth of the collective (see figure 1). This may be in accordance with our taphonomic assumptions. As a consequence, the real diversity curve for this interval should have a more abrupt slope.

Conclusions

Sepkoski (1993) said that "analysis of transitory data can be robust, so long as a large component of the biosphere is being considered". This is corroborated in the present paper, because its main conclusion refers to the robustness of our initial statistical analyses (De Renzi and Ros, 2002). We have restricted the present study to the marine families from both the FR2 and the CFMAF, and we accept the CFMAF as the best provisional data base for the bivalve families; thus, we also prefer the conclusions drawn from CFMAF. A first conclusion concerns the diversification pattern of Bivalvia during the Phanerozoic, which is very consistent in its general outline for the databases considered, although there are some divergences for Mesozoic times. However, only the CFMAF reflects well the mass extinction at the end of the Triassic times. In order to explain the cases in which the pertinent null hypotheses of independence are rejected, we have used two kinds of explanations: evolutionary and taphonomic; however, they were used jointly for certain cases.

The hypothesis by which the aragonite collective would be negatively biased by both the instability of the polymorph and rarefaction has been corroborated for the broad Carboniferous to Permian interval. An earlier conclusion reached by us (De Renzi and Ros, 2002) about the whole Mesozoic is not sustained by our present analysis at the critical level; however, we can say that it is supported at a slightly lower level. In addition, it seems that the initial radiation of bivalves during the Cambrian-Devonian interval could be partly biased by these factors and we only observe a small part of the diversification of both the aragonite collective and the calcite collective, with the former as the dominant one.

The sea character (aragonite or calcite sea) does not seem to have any effect on preservation of the respective polymorphs as could be reasonably thought. Age-sea character and mineralogy of shells are not apparently independent. However, one of the significant results (for the Upper Carboniferous-Triassic interval, corresponding to an aragonitic sea) shows reverse preservation; *i.e.* the aragonite collective is worse preserved than the calcite collective. This conclusion is fully coincident with De Renzi and Ros (2002), but it would be related rather to the conclusion about negative bias for the Carboniferous-Permian interval in table 1. In addition, the apparent aragonitic character of the Caenozoic sea may be the result of the evolutionary success of the infaunal bivalves (only aragonitic) *versus* the epifaunal collective.

Contingency tables relating mineralogy\mode of life and geologic age\mode of life supply the same statistical conclusions as in De Renzi and Ros (2002). However, all concerning those mode of life as influencing preservation have been reinterpreted. Our new interpretation is in evolutionary rather than taphonomic terms. The epifaunal collective is a reduced group throughout the Phanerozoic. It consists largely of animals having calcitic shells; a smaller fraction of them has aragonitic shells. Infaunal bivalves, however, are always dominant and they have exclusively aragonitic shells. Therefore, the significantly exceeding proportion of aragonite infaunal bivalves reflects their evolutionary success, but this does not tell us anything about a preservational bias. This is supported by the analyses concerning mode of life and geologic age. It reflects the mineralogical biases rather than those due to the modes of life.

All these preservational features have an effect on our estimates of rates of evolution, since they bias negatively the aragonitic skeletal remains, the most unstable kinds of skeletons that could fossilize. These diminished numbers will lower the values of rates.

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References

Amler, M., Fischer, R. and Rogalla, N. 2000. Systematische Einheiten. In: H.K. Erben, G. Hillmer and H. Ristedt (eds.), *Muscheln*, Haeckel-Bücherei, Band 5. Enke, pp. 70-133.

Berkman, P.A., Garton, D.W. and Van Bloem, S.L. 1994. *Zebra mussel* habitat expansion by soft substrate modification. *American Zoologist* 34: 60A.

Carter, J.G. 1980a. Environmental and biological controls of bivalve shell mineralogy and microstructure. In: D.C. Rhoads and R.A. Lutz (eds.), *Skeletal Growth of Aquatic Organisms. Biological Records of Environmental Change.* Plenum Press, New York, pp. 69-113.

Carter, J.G. 1980b. Selected mineralogical data for the bivalvia. Appendix 2: bivalve shell mineralogy and microstructure, Part A. In: D.C. Rhoads and R.A. Lutz (eds.), *Skeletal Growth of Aquatic Organisms. Biological Records of Environmental Change.* Plenum Press, New York. pp. 627-643.

Carter, J.G. 1980c. Guide to bivalve shell microstructures. Appendix 2: bivalve shell mineralogy and microstructure, Part B. In: D.C. Rhoads and R.A. Lutz (eds.), *Skeletal Growth of Aquatic Organisms. Biological Records of Environmental Change.* Plenum Press, New York, pp. 645-673.

Carter, J.G. 1990a. Evolutionary significance of shell microstructure in the Palaeotaxodonta, Pteriomorphia and Isofilibranchia (Bivalvia: Mollusca). In: J.G. Carter (ed.), *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends.* Van Nostrand Reinhold, New York, pp. 136-296.

Carter, J.G. 1990b. Shell microstructural data for the Bivalvia. In: J.G. Carter (ed.), *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends.* I. Van Nostrand Reinhold, New York, pp. 297-411.

Carter, J.G. (editor) 1990c. *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends.* II. Atlas and index. Van Nostrand Reinhold, New York, 101 pp.

Carter, J.G., Barrera, E. and Tevesz, M.J.S. 1998. Thermal potentiation and mineralogical evolution in the Bivalvia (Mollusca). *Journal of Paleontology* 72: 991-1010.

Chinzei, K., Savazzi, E. and Seilacher, A. 1982. Adaptational strategies of bivalves living as infaunal secondary soft bottom dwellers. *Neues Jahrbuch für Geologie und Paläontologie* 164: 229-244.

De Renzi, M. 1992. Evolución tafonómica: sobre la posibilidad de lectura de la evolución orgánica a través del registro fósil. In: *Conferencias de la Reunión de Tafonomía y Fosilización* (S. Fernández López, coord.). Editorial Complutense, Madrid, pp. 63-85.

De Renzi, M. and Ros, S. 2002. How do factors affecting preservation influence our perception of rates of evolution and extinction? The case of bivalve diversity during the Phanerozoic. In: M. De Renzi, M.V. Pardo and M. Belinchón (eds.), *Current topics on Taphonomy and Fossilization,* Ayuntamiento de Valencia , pp. 77-88.

Everitt, B.S. 1977. *The Analysis of Contingency Tables*. Monographs on Applied Probability and Statistics, Chapman and Hall, London, 128 pp.

Friebe, A. 1995. Die Schwammfazies im Mitteljura des nordöstlichen Keltiberikums (Spanien). *Profil* 8: 239-279.

Garavelli, C.L., Melone, N. and Vurro, F. 1980. Composizione mineralogica e contenuti di elementi minori ed in traccia entro conchiglie di Gasteropodi e Bivalvi viventi. *Mineralogica et Petrographica Acta* 24: 161-180.

Grimm, M.C. 1998. Systematik und Paläoökologie der Buchiolinae nov. subfam., Cardiolidae, Arcoida, Lamellibranchiata, Devon. *Schweizerische Palaeontologische Abhandlungen* 118: 1-173.

Harper, E.M. and Skelton, P.W. 1993. The Mesozoic Marine Revolution and epifaunal bivalves. *Scripta Geologica, Special Issue* 2: 128-153.

Harper, E.M., Palmer, T.J. and Alphey, J.R. 1997. Evolutionary response by bivalves to changing Phanerozoic sea-water chemistry. *Geological Magazine* 134: 403-407.

Heinberg, C. 1999. Lower Danian bivalves, Stevns Klint, Denmark: continuity across the K/T boundary. *Palaeogeogaphy, Palaeoclimatology, Palaeoecology* 154: 87-106.

Hudson, J.D. 1968. The microstructure and mineralogy of the shell of a Jurassic Mytilid (Bivalvia). *Palaeontology* 11: 163-182.

Kriz, J. and Bogolepova, O.K. 1995. *Cardiola signata* community (Bivalvia) in cephalopod limestones from Tajmyr (Gorstian, Silurian, Russia). *Geobios* 28: 573-583.

Moore, R.C. (editor) 1969a. *Treatise on Invertebrate Paleontology. Mollusca 6, Bivalvia.* Geological Society of America and University of Kansa Press. Part 1: 1-489.

Moore, R.C. (editor) 1969b. *Treatise on Invertebrate Paleontology. Mollusca 6, Bivalvia.* Geological Society of America and University of Kansa Press. Part 2: 490-952.

Moore, R.C. (editor) 1971. *Treatise on Invertebrate Paleontology. Mollusca 6, Bivalvia.* Geological Society of America and University of Kansa Press. Part 3: 953-1224.

Morris, N.J. 1978. The infaunal descendants of the Cycloconchidae: an outline of the evolutionary history and taxonomy of the Heteroconchia, superfamilies Cycloconchacea to Chamacea. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 284: 259-275.

Newton, C.R., Whalen, M.T., Thompson, J.B., Prins, N. and Delalla, D. 1987. Systematics and paleoecology of Norian (Late Triassic) bivalves from a tropical island arc: Wallowa terrane, Oregon. *Journal of Paleontology* 61, *Memoir* 22: 1-83.

Pacaud, J. 2001. Première observation du genre *Pulvinites* (Mollusca, Bivalvia) dans le Danien (Paléocène inférieur) de Vigny (Val-d'Oise, France). *Geodiversitas* 23: 5-16.

Palmqvist, P. 1991. Differences in the fossilization potential of bivalve and gastropod species related to their life sites and trophic resources. *Lethaia* 24: 287-288.

Palmqvist, P. 1993. Trophic levels and the observational completeness of the fossil record. *Revista Española de Paleontología* 8: 33-36.

Pojeta, J. Jr. and Zhang, R. 1984. *Sinodora* n. gen.-A chinese Devonian homeomorph of Cenozoic Pandoracean Pelecypods. *Journal of Paleontology* 58: 110-1025.

Raup, D.M. 1976a. Species diversity in the Phanerozoic: a tabulation. *Paleobiology* 2: 279-288.

Raup, D.M. 1976 b. Species diversity in the Phanerozoic: an interpretation. *Paleobiology* 2: 289-297.

Savazzi, E. 1984. Functional morphology and autecology of *Pseudoptera* (Bakevelliid bivalves), Upper Cretaceous of Portugal. *Palaeogeogaphy, Palaeoclimatology, Palaeoecology* 46: 313-324.

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

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

Sepkoski, J.J. Jr. 1993. Ten years in the library: new data confirm paleontological patterns. *Paleobiology* 19: 43-51.

Skelton, P.W. and Benton, M.J. 1993. Mollusca: Rostroconchia, Scaphopoda and Bivalvia. In: M.J. Benton (ed.), *The Fossil Record 2*. Chapman and Hall, London, pp. 237-263.

Stanley, S.M. 1968. Post-Paleozoic adaptive radiation of infaunal bivalve mollusks - a consequence of mantle fusion and siphon formation. *Journal of Paleontology* 42: 214-229.

Stanley, S.M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). *The Geological Society of America, Memoir* 125, 296 pp.

Stanley, S.M. 1972. Functional morphology and evolution of byssally attached bivalve mollusks. *Journal of Paleontology* 46: 165-212.

Taylor, J.D., Kennedy, W.J. and Hall, A. 1969. The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea-Trigonacea. *Bulletin of the British Museum (Natural History) Zoology Supplement* 3: 125 pp.

Taylor, J.D., Kennedy, W.J. and Hall, A. 1973. The shell structure and mineralogy of the Bivalvia. II. Lucinacea-Clavagellacea. Conclusions. *Bulletin of the British Museum (Natural History) Zoology* 22: 253-294.

Tunnicliff, S.P. 1987. Caradocian bivalve molluscs from Wales. *Palaeontology* 30: 677-690.

Yancey, T.E. 1985. Bivalvia of the H.S. Lee Formation (Permian) of Malaysia. *Journal of Paleontology* 59: 1286-1297.

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