

Continuous versus pulsed origination and extinction and biozones

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ABSTRACT:

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The count of biozones as an approximate measure of the origination and extinction rates of index taxa (mostly species) is proposed. The mean number of extinctions of these taxa per m.y. is 1.136 (Palaeozoic mean 0.902, Mesozoic mean 1.680, Cenozoic mean 0.789). In contrast with the majority of taxa, the originations and extinctions of index taxa, as well as of other taxa belonging to biostratigraphically important systematic groups, seems to be continuous.

Key words: Origination; Extinction; Rates; Biozones.

INTRODUCTION

An important question of evolutionary palaeobiology is whether originations and extinctions of species were concentrated during short periods within the time intervals (pulsed) or if they were distributed broadly throughout the intervals (continuous). To solve the problem, investigators have used the origination and extinction data of all known genera (e.g. Raup and Sepkoski 1984; Raup 1986; Foote 1994, 2005; Gradstein and Ogg 1996) as a proxy for species' speciation and extinction.

Essentially, the expectation of a continuous turnover of species within the time intervals is that longer intervals should have higher origination and extinction rates than shorter ones. This is, however, not the case (Raup and Sepkoski 1984; Raup 1986; Foote 1994; Gradstein and Ogg 1996; Alroy 2008, 2010), which is consistent with the idea of pulsed origination and extinction. Likewise, the scrupulous investigation of Foote (2005; see also Alroy 2008, 2010) clearly supports this model.

The idea and the aim of the present contribution is to use stratigraphic biozones to verify whether the turnover of biostratigraphically significant species is pulsed or continuous.

METHODS

There are many types of biozones (see e.g. MacLeod 2005) but almost every biozone records an origination and an extinction in its total range. For example, the lower boundary of a range zone denotes the origination of the index taxon and the upper limit of this zone identifies the extinction of the same taxon. Concurrent range zones and partial range zones record the origination of one taxon and the extinction of another taxon. As a result, the count of the number of biozones is also a rough proxy for the number of originations and extinctions of the index taxa on which the biozones are based.

Genus-level ranges define some biozones, for example the standard Devonian, Carboniferous and Per-

mian ammonite biostratigraphic schemes are based largely on genera (Ogg *et al.* 2008). But the majority of biozones are based on species ranges. Thus, the measure of the origination and extinction rates using biozones is usually the direct measure of the index species' rates.

The following operations were carried out during this study:

1. Examining whether the number of biozones correlates with the duration of intervals of geological time.

2. Verifying whether the origination and extinction rates within the taxonomic groups that supply index fossils for biostratigraphy are correlated with the durations of these intervals.

3. Checking whether the number of biozones is correlated with the origination and extinction rates of the groups on which the biozones are based.

Biozones that I have counted are the standard biozones ratified by the International Commission on Stratigraphy and the International Union of Geological Sciences (Ogg *et al.* 2008). For one geological period there is often more than one standard biostratigraphic zonation; for instance graptolite, conodont and chitinozoan biozones for the Ordovician or conodont, ammonite and ostracod zones for the Devonian and so on. Furthermore, there are also different zonations for different bioprovinces existing at the same time, for example Tethyan and Boreal ammonite zonations for the Jurassic. For the calculations herein I have consistently always chosen the zonal scheme with the largest number of biozones.

Thus, the chosen biozonal schemes (compare Ogg *et al.* 2008) are as follows: for the Cambrian – the Australian trilobite zonation with the exception of the Terreneuvian series (archaeocyathan and small shelly fossil zonation); for the Ordovician – the Australasian graptolite biozones; for the Silurian – the graptolite zonation; for the Devonian – the ammonite scheme with the exception of the Lochkovian and the Pragian stages (graptolite zonation); for the Carboniferous and the Permian – the conodont zones; for the Triassic – Tethyan ammonite zones with the exception of the Upper Ladinian (Boreal ammonite zonation); in the case of the Jurassic – the Tethyan and Boreal ammonite zones; for the Cretaceous – Tethyan ammonite zones for the Lower Cretaceous and the United States Western Interior ammonite zones for the Upper Cretaceous; and the planktonic foraminiferal biozones for the Paleogene and the Neogene.

The total number of the biozones counted equals 492.

I have calculated the origination and extinction rates for the groups, on which the biostratigraphies mentioned above are based, from the compendium of marine gen-

era (Sepkoski 2002) using Sepkoski's Online Genus Database constructed by Shanan Peters (www.strata-geology.wisc.edu/jack/), and from The Paleobiology Database (www.paleodatabase.org). The data from the compendium were used here for the percent and the per-capita (Foote 2000) metrics of the origination and extinction rates, while the data from The Paleobiology Database were used for the three-timer count (Alroy 2008) of the rates. The durations and the number of the geological periods and stages were taken from the International Chronostratigraphic Chart 2013 (www.stratigraphy.org).

RESULTS

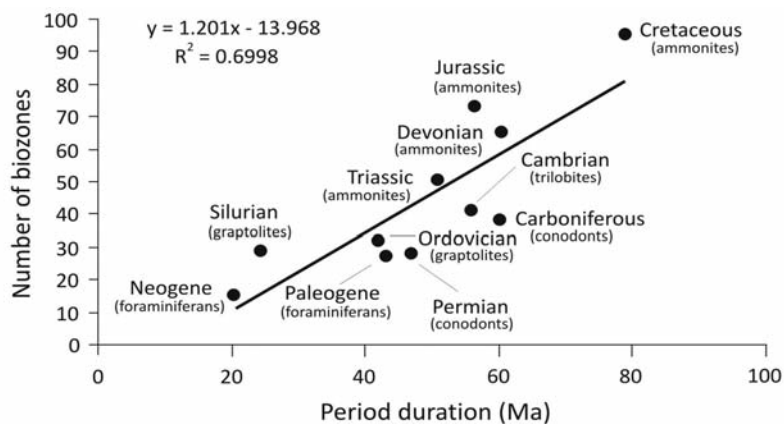
There is a strong correlative relationship ($r^2 = 0.6998$ at $p = 0.0013$) between the number of biozones and the duration of a geological period: a new biozone arrives nearly regularly every 1.2 m.y. of the Phanerozoic (Text-fig. 1). This suggests that the turnover of the index taxa defining biozones is continuous. There are 95 stages with durations from 0.97 to 18.5 m.y. (mean 5.67; standard deviation 3.47) and 492 biozones from 1 to 24 per stage (mean 5.22; standard deviation 3.61). Usually, there are several biozones per stage (Text-fig. 2) and, thus, several originations and extinctions of the index taxa within a stage, which also supports a continuous model for index taxa at a stage level of time resolution. If all extinctions and originations were restricted to a single episode per stage (compare Foote 2005), then constructing biozones shorter than a stage would be impossible.

Text-fig. 3 presents the durations of individual biozones within the stages of the Phanerozoic. I have obtained these figures by dividing the durations of the stages by the number of their biozones (Text-fig. 2). Actually, different biozones within the same stage may have various durations, therefore the durations shown in Text-fig. 3 are averaged and represent approximate per-stage estimates. The durations of biozones are from 0.14 to 6 m.y. (mean 1.46; standard deviation 1.15).

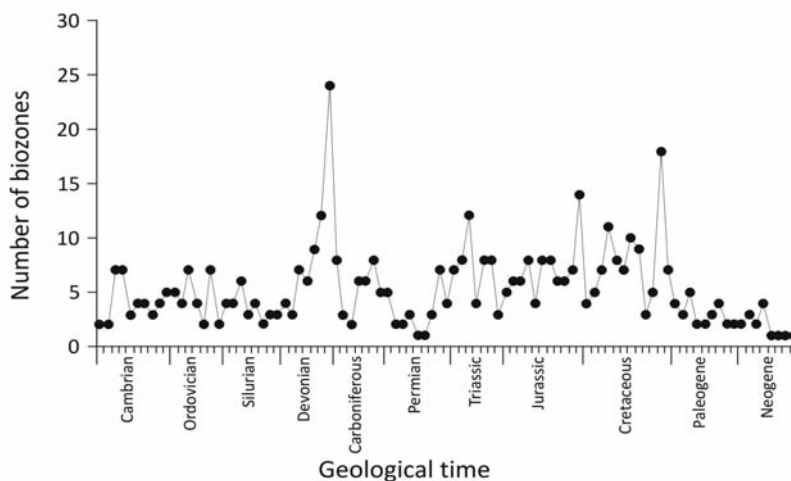
To calculate the number of extinctions per m.y. of the index taxa constituting the biozones of a stage, one needs to divide the number one by the mean duration of biozones that occur within the stage (compare Stanley 1975). The number of extinctions per m.y. equals from 0.166 to 7.14 (mean 1.136; Paleozoic mean 0.902; Mesozoic mean 1.680; Cenozoic mean 0.789). On the other hand, according to Raup (1991), the mean number of extinctions per m.y. for all Phanerozoic species equals 0.25.

As presented above, the turnover of the index taxa seems to be continuous. Do they constitute an exception in this respect? Or were the originations and extinctions

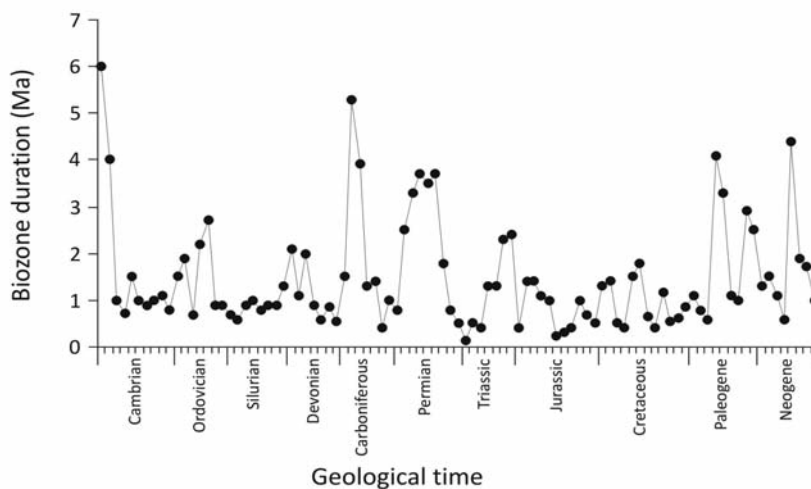
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Text-fig. 1. Relationship between the number of biozones and the duration of geological periods. Pearson's $r = 0.837$ at $p = 0.001$, $r^2 = 0.6998$; Spearman's $r_s = 0.845$ at $p = 0.001$; first differences - Pearson's $r = 0.831$ at $p = 0.003$, Spearman's $r_s = 0.809$ at $p = 0.005$. Names of animal groups like ammonites, conodonts, etc. refer to the group on which the biozones of a given period are based



Text-fig. 2. The number of biozones in the individual geological stages of the Phanerozoic. Intervals on the horizontal axis "Geological time" correspond to stages. The mean number of biozones per stage is 5.22; Palaeozoic mean = 4.83; Mesozoic mean = 7.4; and Cenozoic mean = 2.47. For animal groups on which the biozones are based see Text-fig. 1



Text-fig. 3. Durations of biozones in the individual geological stages of the Phanerozoic. Intervals on the horizontal axis "Geological time" correspond to stages. The mean duration of a biozone is 1.46 Ma; Palaeozoic mean = 1.65; Mesozoic mean = 0.93; and Cenozoic mean = 1.82. For animal groups on which biozones are based consult Text-fig. 1

of the taxa belonging to the biostratigraphically important groups but not used as index taxa likewise continuous?

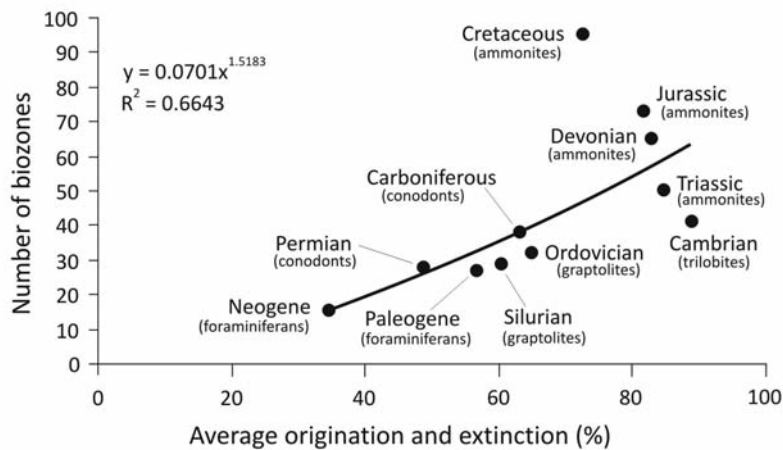
To check this I have correlated the number of biozones with the average percent origination and extinction of all genera reported in the compendium of Sepkoski (2002) belonging to the groups on which the biozones are based: Cambrian trilobites, Ordovician and Silurian graptolites, Devonian, Triassic, Jurassic and Cretaceous ammonites, Carboniferous and Permian conodonts, and Paleogene and Neogene foraminifera.

For an individual period, I have first calculated jointly the percent origination and extinction in every stage of a period:

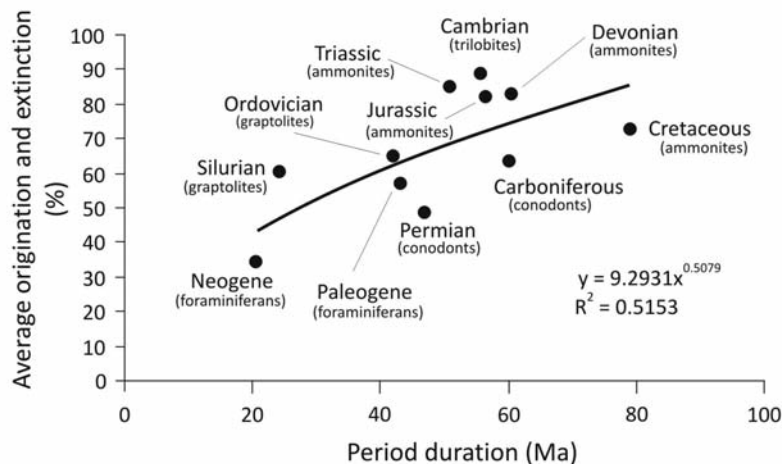
$$\left[\frac{\text{number of extinctions} + \text{number of originations}}{\text{number of recorded taxa}} \right] \times 100,$$

obtaining the “integrated” origination and extinction for the stages. Then I have added the results for particular stages and divided the obtained sum by the number of stages in a period, thus achieving the average percent origination and extinction in a given period.

I have found (Text-fig. 4) that there is a correlation between the number of biozones in a period and the average genus-level percent origination and extinction per stage in that period ($r^2 = 0.6643$, $p = 0.0022$), and that there is also a correlation (Text-fig. 5) between the average genus-level percent origination and extinction



Text-fig. 4. Relationship between the number of biozones within an individual period and the average origination and extinction of all genera belonging to the animal groups on which the biozones are based. Pearson's $r = 0.815$ at $p = 0.002$, $r^2 = 0.6643$; Spearman's $r_s = 0.8$ at $p = 0.003$; first differences – Pearson's $r = 0.766$ at $p = 0.01$, Spearman's $r_s = 0.818$ at $p = 0.004$. Further explanation in the text



Text-fig. 5. Relationship between the average origination and extinction of all genera belonging to the animal groups on which the biozones are based and the duration of a period. Pearson's $r = 0.718$ at $p = 0.013$, $r^2 = 0.5153$; Spearman's $r_s = 0.6$ at $p = 0.051$; first differences – Pearson's $r = 0.653$ at $p = 0.041$, Spearman's $r_s = 0.648$ at $p = 0.043$. Further explanations in the text

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and the durations of individual periods ($r^2 = 0.5153$, $p = 0.013$). Thus, it is likely that the turnover of most taxa belonging to the biostratigraphically important groups may also be continuous. Moreover, the results shown in Text-figs 4 and 5 suggest that not only is the turnover of the index species defining the biozones continuous but that the turnover of the genera belonging to the biostratigraphically important groups may be continuous as well.

On the other hand, there is no correlation (Text-fig. 6) between the average percent origination and extinction of all genera presented in the compendium of Sepkoski (2002) and the durations of the geological periods ($r^2 = 0.014$, $p = 0.726$). This suggests that most turnover is pulsed in accordance with Raup (1991) and Foote (2005) and that when all genera are counted together, then the majority of taxa having a pulsed turnover shadows the existence of less numerous taxa with continuous turnover.

I have examined the relationship between the number of biozones and the genus-level origination and extinction rates of the biostratigraphically important groups, and between the origination and extinction rates and the period duration, using not only the percent counts of rates (Text-figs 4 and 5) but also other measures of origination and extinction rates: the per-capita method of Foote (2000) and the three-timer method of Alroy (2008). In this case, I have correlated the number of biozones and the duration of a period not with the integrated origination and extinction rate but separately with the extinction rate and separately with the origination rate. To obtain the mean rate of the origination or of the extinction in a given period I averaged results for particular stages in a period in the case of the per-capita metrics, and averaged results for 11 m.y. bins in the case of the three-timer count.

In the case of the rates of Foote (2000), there is a cor-

relation between the number of biozones and the origination rate ($r^2 = 0.4695$, $p = 0.02$; Spearman's $r_s = 0.755$, $p = 0.007$), and between the number of biozones and the extinction rate ($r^2 = 0.4936$, $p = 0.016$; Spearman's $r_s = 0.8$, $p = 0.003$). There was, however, no statistically significant correlations between the origination rate and the period duration and between the extinction rate and the period duration. Similarly, when using the rates of Alroy (2008), then only the correlations between the number of biozones and the extinction rate ($r^2 = 0.3383$, $p = 0.06$; Spearman's $r_s = 0.682$, $p = 0.021$) and between the number of biozones and the origination rate ($r^2 = 0.213$, $p = 0.153$; Spearman's $r_s = 0.661$, $p = 0.027$) turned out to be nearly significant.

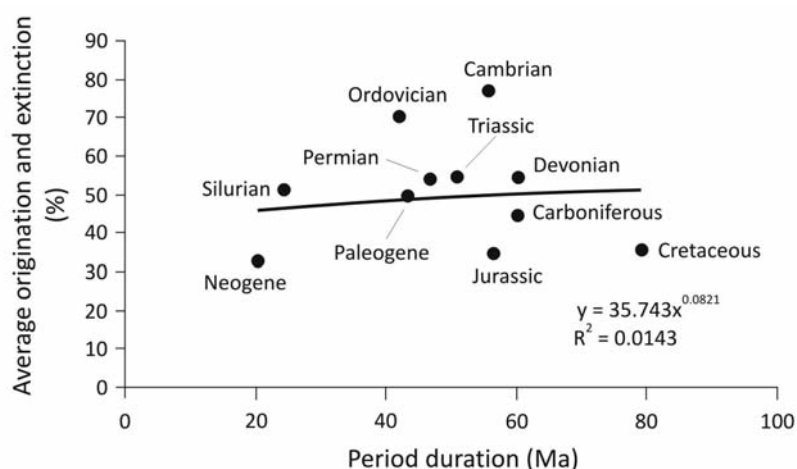
The lack of correlation between the origination rate and the period duration and between the extinction rate and the period duration, is not surprising, however, because the method of Foote (2000) does not take into consideration the single-interval taxa (so called singletons), whereas that of Alroy (2008) does not take into account both singletons and the continuous turnover within the time intervals.

CONCLUSIONS

Biozones record originations and extinctions. Therefore the number of biozones may be used as an approximate measure of the origination and extinction rates of the index taxa on which the zones are based.

The number of extinctions of the index taxa per m.y. equals approximately from 0.166 to 7.14 (mean 1.136; Palaeozoic mean 0.902; Mesozoic mean 1.680; Cenozoic mean 0.789).

The origination and extinction of the index taxa as well as of other taxa belonging to biostratigraphically important animal groups seems to be continuous.



Text-fig. 6. Lack of correlation between the average origination and extinction of all known marine genera and the duration of a period

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