

Longevity of orders is related to the longevity of their constituent genera rather than genus richness

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Abstract Longevity of a taxonomic group is an important issue in understanding the dynamics of evolution. In this respect a key observation is that genera, families or orders can each be assigned a characteristic average lifetime (Van Valen in *Evol Theory* 1:1–30, 1973). Using the fossil marine animal genera database (Sepkoski in *Bull Am Paleontol* 363, pp 563, 2002) we here examine the relationship between longevity of a higher taxonomic group (orders) and the longevity of its lower taxonomic groups (genera). We find insignificant correlation between the size of an order and its longevity, whereas we observe large correlation between the lifetime of an order and the lifetime of its constituent genera. These observations suggest that longevity of taxonomic groups is heritable intrinsically or on the grounds of environmental preferences.

Introduction

Extinction and existence times of taxonomic groups offer insights into the relationship between the longevity and diversity of an order by presenting a large sample of how

history at lower taxonomic levels influences higher levels. One interesting insight into this interplay is the observation of Van Valen (1973), stating numerous case studies where existence times of a family within a specified order was exponentially distributed. This relationship was interpreted to indicate randomness of extinctions, as well as distinct differences in lifetimes between the different orders. This widely recognized difference in characteristic extinction rates between higher-level taxa goes back to Simpson's "Tempo and Mode in Evolution" (Simpson 1944). Focusing on extinction events, Raup observed fractal patterns of extinctions and a possible periodicity in the large-scale pattern of extinction (Raup and Sepkoski 1984, 1986). Such periodicity has later been studied, e.g., by Kirchner (2002).

The pronounced taxonomic overturn in the fossil record of the Phanerozoic suggests that intrinsic differences exist between the taxonomic groups in their evolutionary properties (Holman 1989). Contrary, studies have been suggesting that evolution and extinction to some extent can be simulated as random branching processes, without differences between taxonomic groups (Gould et al. 1977; Pigolotti et al. 2005). This hypothesis has been criticized by others (Raup and Marshall 1980; Stanley et al. 1981; Crick 1981; Ward and Signor 1983; McKinney 1985, 1987), and we will here present further evidence against such a simplification.

We here will explore the presence or absence of correlation between longevity of a taxon, and the longevity of its constituting lower order taxa, a correlation that is characteristic for models based on branching processes (Raup 1985). Branching or logistic models for macroevolutionary processes have been explored, for example to model taxonomic diversity by Sepkoski (1979), and Miller and Sepkoski (1988), and for estimating background extinction

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rates by Gilinsky (1994) among others. In this paper, we will use the Sepkoski database of fossil marine animal genera (Sepkoski 2002), where origination times and extinction times of about 37,000 genera are recorded, to determine taxonomic order longevities as a function of constituent genera longevity. This complements recent studies of this database, focused on rates of originations and extinctions, and on the time pattern of activity in the fossil record (see e.g., Kirchner 2002; Plotnick and Sepkoski 2001). We present a detailed statistics of origination and extinction times, and their relationship with taxonomic levels. As we will see, it gives new hints at possible mechanisms for longevity of higher taxa, and allows for ruling out certain types of simple branching processes as models for inheriting longevity.

Results

When plotting the 36,506 marine genera extracted from Sepkoski's database as a "duration matrix" (Fig. 1), i.e. a compressed matrix format, each point denotes a time interval with a specific origination time and a specific subsequent extinction time. Each dot represents the lifetime interval of one or more genera that share the common fate of origination and extinction in the same respective stratigraphic intervals. Thus, the vertical distance from a point to the diagonal is the duration time, or lifetime, of the

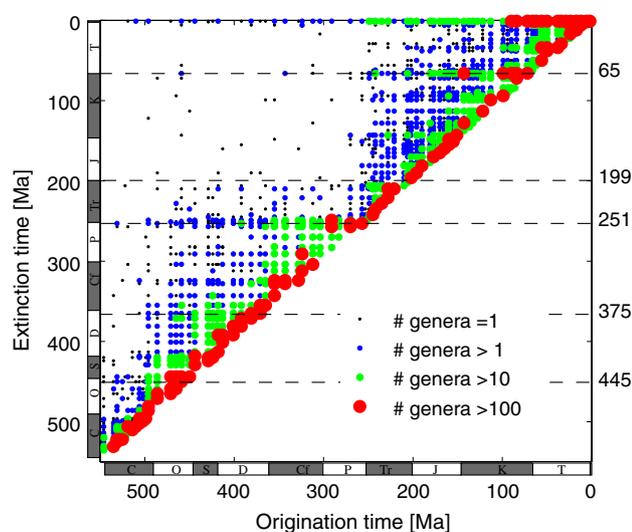


Fig. 1 Origination and extinction of 36,506 marine animal genera in the Phanerozoic. Points marking extinctions at $t = 0$ indicate genera living up to the recent. The vertical distance from a point to the diagonal measures the corresponding genus lifetime. Notice the collapse of many points close to the diagonal, reflecting the fact that most genera exist less than the overall genera average of about 27 Myr (million years)

corresponding genus or genera (whereby clearly an order cannot have a shorter lifetime than the longest-lived genus in that order). As seen from the high density of dots close to the diagonal, most genera have short lifetimes compared to the Phanerozoic. The figure also quantifies how large extinction events separate the matrix into a near block-diagonal form as, e.g., the Permian/Triassic extinction, that 251 million years before present (Ma) separated Paleozoic life from Mesozoic life. Although most genera have short lifetimes, the dots far above the diagonal in Fig. 1 show that outliers are also present. Finally, the modern elements of the Paleozoic, Mesozoic, and Cenozoic marine fauna line up at the top edge of the plot. The plot does not only illustrate the intensity, e.g., of the "Big Five" mass extinctions, it also shows the composition of the faunal elements going extinct with respect to origination time.

Figure 2 shows the lifetime data ordered by taxonomic groups, following the ordering given in the Sepkoski database that is taken as approximating taxonomic relationship. Here and in the following we consider the 31,071 genera of the dataset, which are extinct today, excluding all recent genera from the subsequent analyses. In Figure 2a, the time interval of each genus is represented by a vertical line starting at the geological stage of origination and ending at the end of the geological stage where it was last observed. This presentation reveals correlations between fates of genera listed close to each other. The more closely listed genera often tend to share both origination and extinction time. Also the data appear clustered in the sense that whole groups often are going extinct together. This implies that lifetimes between related genera are strongly correlated. This is also illustrated in Fig. 2b that gives the lifetimes of all the genera in the same ordering as Fig. 2a. This plot highlights a huge variability in lifetimes, with most genera existing for a shorter time interval than the overall genera mean lifetime of 27 Myr. The figure clearly pinpoints that closely related genera have closely related life spans, and implies that survivorship is heritable intrinsically or on the grounds of environmental preferences.

Figure 3 re-examines Fig. 2 in terms of ordinal lifetimes and average genus lifetimes within orders, subdividing the data into blocks consisting of orders, containing between one and more than 1,000 genera. Figure 4 shows the distribution of numbers of genera in the various orders, that display a very broad distribution that can be represented by a scale free distribution of the form $P(s) = 1/s^{1.5}$. Such power laws for taxonomic groups have been previously reported by Yule (1925) for genera size distribution in terms of number of extant species. In this regard, we obtain the $1/s^{1.5}$ scaling both for the accumulated number of genera within the total existence of the orders (shown in the figure), as well as for the number of genera in orders at any given time cohort (with upper cut of at about 100).

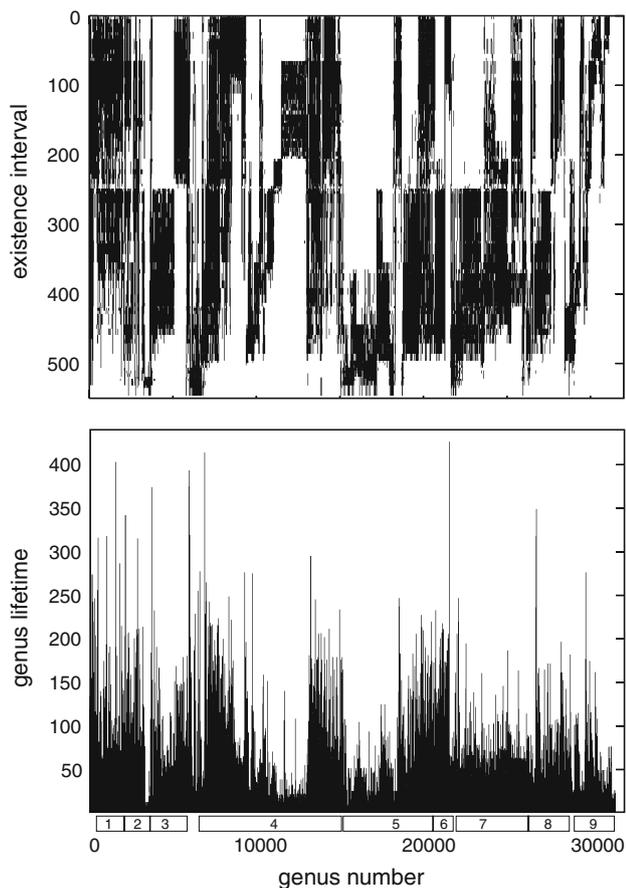


Fig. 2 Lifetime of 31,071 extinct genera represented by *vertical lines*, sorted by taxonomic groups as given by the ordering of the Sepkoski database. **a** Lifetime of each genus with respect to geological stages of origination and extinction. **b** Lifetime durations of genera in the same ordering as in (a) show that lifetimes between related genera are strongly correlated. Large phyla are marked in the plot by numbers on the *x* axis of (b). 1 Rhizopodea; 2 Porifera; 3 Cnidaria; 4 Mollusca; 5 Arthropoda; 6 Bryozoa; 7 Brachiopoda; 8 Echinodermata; 9 Chordata

Returning to Fig. 3, the plot shows a box-like distribution, each box representing an order with a width equal to the number of constituent genera, and with a height given by the average lifetimes of the genera in the order. Figure 3 thus demonstrates that even large orders might have very different average genus lifetimes. Figure 3 also shows the total lifetimes of the orders. The heights of black and white boxes in the figure are correlated, whereas there is no systematic tendency that big orders, represented by broad boxes, are longer lived than smaller orders (narrow boxes).

To elucidate the overall statistical properties of genus lifetimes, seen over the whole taxonomic record, we in Fig. 5 investigate genus lifetime distributions in the subset of genera that went extinct (there are no extant genera in this analysis). Figure 5a demonstrates that genus lifetimes are broadly distributed, consistent with a log-normal distribution, as illustrated by the slightly bent dashed line in

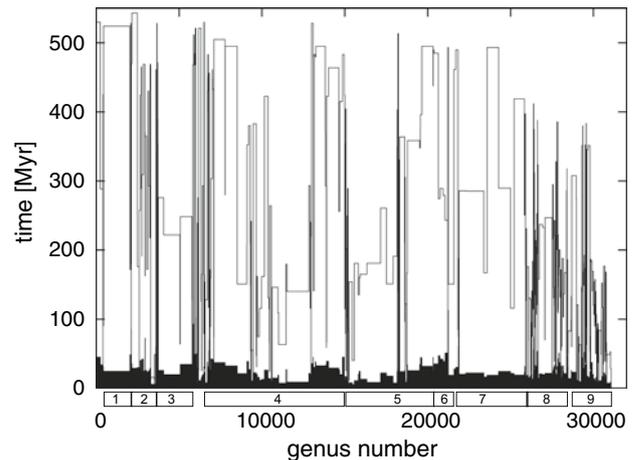


Fig. 3 Lifetime of orders (*histogram with thin lines*) and average genus lifetimes within orders (*black shaded histogram*). Orders with numerous genera are represented by wide blocks in the histogram. Ordering of genera as in Fig. 2; phyla are marked as in Fig. 2. As these two plots do not resolve the full dataset, an electronic plot of the data is available at <http://cmol.nbi.dk/models/fossil/fossil.html>, where one can zoom into them and resolve all details

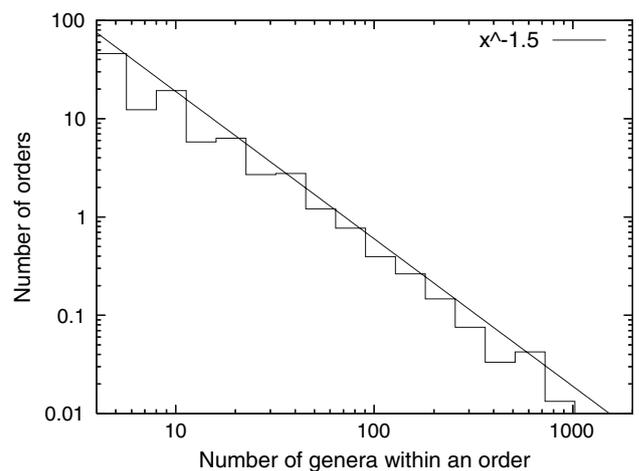


Fig. 4 Distribution of order size as quantified by the total number of genera during the lifetime of the respective order. The *histogram* shows the average number of orders (*y* axis) with a given number of genera (*x* axis). Note that the *y* value may drop below one, because the histogram bins become wider to the right, and the number of orders in each bin has been divided by the width of the bin to yield the corresponding *y* value. One observes a near-perfect power law; $1/\text{size}^{1.5}$

the figure, fitting well the overall distribution with mean lifetime of 27 Myr and with a standard variation of 36.1 Myr. For historical reasons let us note that lifetimes are indeed so broadly distributed, that they can be fitted by a $1/t^{2.4}$ power law from 20 to 200 Ma. At larger time intervals finite size effects due to the limited length of the fossil record occur, whereas genera with shorter lifetimes are also not counted correctly in the range where the finite duration of stratigraphic intervals is of comparable size.

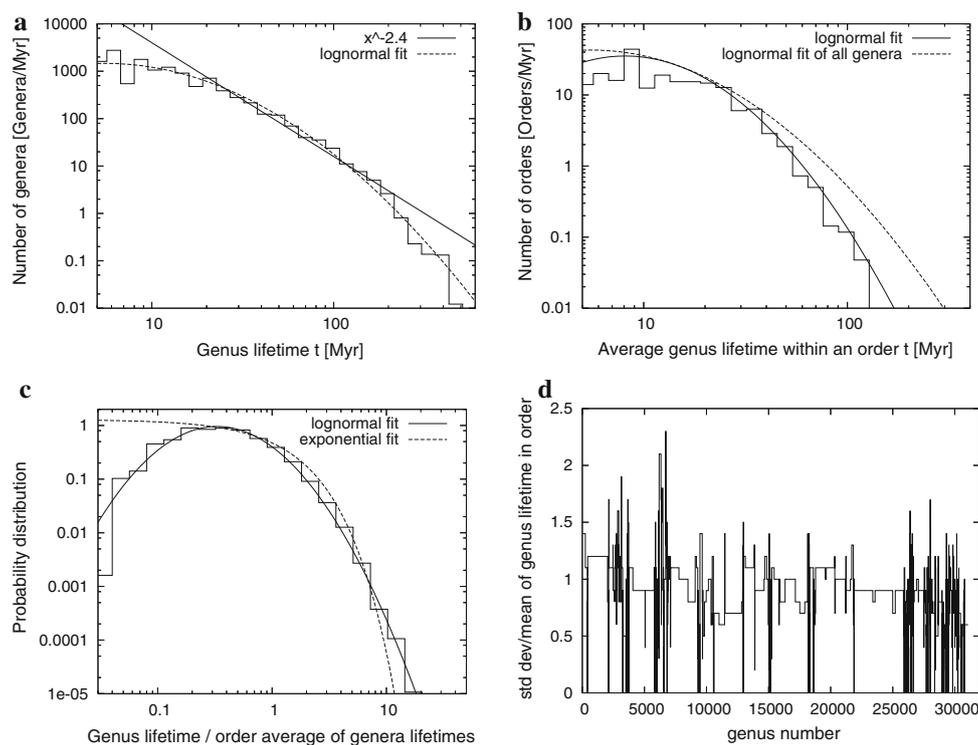


Fig. 5 **a** Distribution of lifetimes of extinct genera throughout the Phanerozoic. The data present the lifetimes of 31,071 genera in a *log-binned histogram*, where the histogram bins become broader at larger times. The height of bins is normalized to number of genera per Myr. **b** Distribution of average genus lifetimes within orders for the 522 extinct orders in the dataset. **c** Collapsed plot of the probability distribution of genus lifetimes inside orders, renormalized by their respective average lifetime within the order $\sigma(t)/\langle t \rangle$. Note that this distribution and its lognormal fit are much narrower than the unrenormalized distribution given in **(b)**. It is thus nearly as steep as an exponential curve (*right part of the dashed line*). The deviation from

an exponential decay reflects that some orders have very diverse lifetimes, as also seen in **(d)**. **d** The ratio of spread to mean of genera existence times within respective orders. For comparison, this ratio equals 1.34 when considering the full dataset. Assuming an exponential distribution, the expected “standard deviation/mean” stays close to 1, depending on sample size N . For $N = 100$, we find that $\sigma/\text{mean} < 1.12$ for 95% of the samples, whereas samples with larger N have even smaller deviations (see Fig. 7 for the full relationship between sample size and confidence interval). A σ/mean value well outside this range marks orders with a high degree of diversity in genus lifetimes

Power laws have one free parameter less than a lognormal distribution and are therefore interesting from a theoretical point of view as they may point to specific underlying mechanisms (Bornholdt and Sneppen 1998, 2000; Sneppen et al. 1995). Figure 5b shows the distribution of average genera times within orders from Fig. 3. In accordance with the observation of the different heights of the boxes in Fig. 3, one observes a quite broad distribution of these average genus lifetimes, ranging from a characteristic scale of a few Myr to 100 Myr: In fact, these averages can also be fitted by a log-normal distribution. This distribution is narrower than the overall distribution of genus lifetimes in Fig. 5a, the difference reflecting the scatter of individual events within each order. Figure 5c finally shows the genus lifetime distribution where one rescales all genus lifetimes to the expected mean for their respective orders. The resulting distribution is so narrow that it matches a log-normal distribution that is only slightly wider than the exponential distribution Van Valen (1973) found in his

study of a sample of taxonomic groups (see dashed line for comparison). This is in spite of the fact that the numbers of genera within different orders vary over a large range (from one to 1,000 genera per order, in fact, as also seen later). Such an exponential distribution is consistent with a model where genera have characteristic lifetimes set by their heritable properties, and go extinct solely due to an external random event that comes from outside, such as climate change or co-evolutionary changes in the environment. Figure 5d finally decomposes Fig. 5c into the normalized spread over mean of lifetimes for each order, $\sigma(t)/\langle t \rangle$. For an exponential distribution, this number equals 1, whereas a larger $\sigma(t)/\langle t \rangle$ pinpoints a distribution of lifetimes which is broader than exponential. In particular, considering lifetimes of all genera we have $\sigma(t)/\langle t \rangle = 1.34$. Figure 5d shows that for most orders, $\sigma(t)/\langle t \rangle$ stays close to one, which means they have well defined lifetimes, as given by a single exponential. The significance level of a deviation depends on the order size and is further

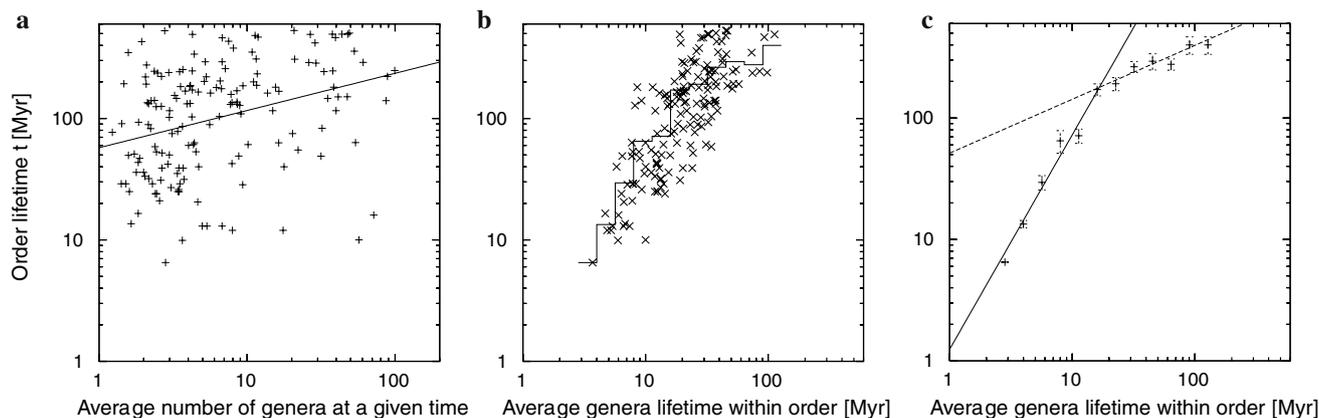


Fig. 6 **a** Existence time of orders versus average number of genera at a given time during the respective order history. Note that there is only a weak dependence, as exemplified by the regression line ($y = 57x^{0.3}$, $R^2 = 0.10$). We only examine orders that have more than four genera, have a continuous record, and which are extinct now. **b** Existence times for same sample of orders as in **(a)** are shown here as function of the average existence times for genera composing the respective order. The steps denote the average order lifetime for all average constituent genus lifetimes in the width of each step. We observe that the order lifetime grows more than proportionally with

the characteristic time of the genera composing the order for typical genus lifetimes up to about 20 Myr, whereas turning into a plateau of near-vanishing correlation for genus lifetimes larger than this threshold. This is further quantified in **(c)**, where the order lifetime has been averaged over bins of ranges in average genus lifetime, as indicated by the steps in **(b)**. We observe a steep dependence of order lifetime on the lifetime of constituent genera for small genus lifetimes, and only a weak dependence once typical genus lifetimes exceed about 20 Myr

quantified in the caption of Figs. 5d and 7. An example for a significant exception is the Foraminiferida (from genus number 1,000 to genus number 3,000) with apparently widely varying genus lifetimes.

We now return to our prime observation of Fig. 3, namely that lifetimes of orders do not correlate with their size but rather correlate with the average lifetime of genera within them. To substantiate this observation we confine our study to orders that (1) do not exist any more, (2) contain more than four genera, and (3) have a continuous record (i.e. at least one genus exists at any time during the lifetime of the order). This reduced sample of 159 orders (out of a total of 522 extinct orders in the database) with in total 18,534 genera is subsequently examined in Fig. 6. Of these 159 orders, only about 29 terminate at one of the Big Five mass extinctions, we therefore expect to also obtain information about background extinction. Figure 6a shows a scatter plot of the lifetimes of orders and the average number of constituent genera of these orders during their duration; i.e. averaged over all time slices of the order lifetime. This plot shows how well one could predict the future fate of an order based on how numerous the constituent genera of that order are at a given time. The figure, however, reveals that there is weak or no correlation between order lifetime and the average number of its constituent genera, while average genus lifetimes vary over nearly two orders of magnitude, the corresponding average order lifetime only varies by a factor of 4. On the other hand, order lifetime is correlated with the average lifetime of its constituent genera as can be seen in Fig. 6b. The

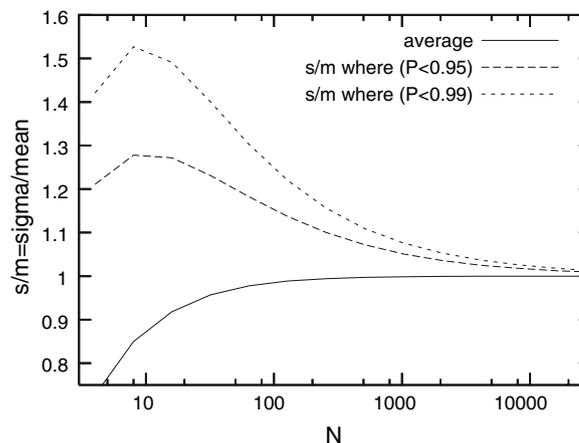


Fig. 7 The “standard deviation/mean” is equal to 1 for an exponential distribution. For a random sample of N data points drawn from an exponential distribution, σ/mean may deviate from 1. The plot shows the average value for different sample size N , as well as the 95 and 99 percentiles, i.e., with 95 (99) percent probability the σ/mean of a given random sample lies below the *dashed (dotted) line*. This plot helps judging the statistical significance of deviations from exponentially distributed genus lifetimes within orders (see Fig. 5d)

steps denote the average order lifetime when genus lifetimes lie in the step interval. For genus lifetimes below about 20 Myr, order lifetime tends to scale with about the square of the average genus lifetime as can be seen in Fig. 6c. This scaling for example means that with genera, which are twice as long lived, the order tends to be four times longer lived. For average genera lifetimes larger than about 20 Myr, this correlation flattens out to a plateau:

order lifetimes do not benefit from much longer average genus lifetime in that range.

Discussion

Species richness as well as geographic range, local abundance, reproductive mode, body size and inferred generation time, trophic strategy, and life habit have been put forward as significant factors for survivorship during “background extinction” times (Jablonski 1986, 2005; Flessa and Jablonski 1985). Such an intuitively appealing notion is the mathematical consequence of any model where extinctions of individual genera are random and independent from each other. Our findings emphasize, however, that models with this feature do not match observational evidence and, consequently, that parameters as the ones above may not be decisive after all.

Many simple growth models, as well as recent models as the one suggested by Pigolotti et al. (2005) where genera replicate or go extinct with equal probability and thereby generate an overall power law distribution of lifetimes of higher taxa, also predict at least a proportional growth of order lifetime with the number of its constituent genera per time cohort. Thus, the lack of correlations between order longevity and size in the data (Fig 6a) pinpoints some coordination of extinctions at least between closely related genera. In this regard, we have also found no correlation between size of an order at the last stage before its extinction, and how long the order existed. Even very large orders at the peak of their existence can undergo sudden extinction. In fact, 10% of the orders had a larger genera count than their average at their last stage.

The fact that no significant correlation exists between order size and longevity thus in itself implies that similar genera share similar longevity as confirmed by the strong correlation between neighboring genera (Fig. 2a). Another unexpected observation is the fact that the lifetime of an order increases more than linearly with the lifetime of its constituent genera, at least if genera are not too long lived. This contradicts what one would trivially expect, namely that the lifetime of an order increases proportionally to the lifetimes of its constituting lower taxa, i.e. if every constituent exists twice as long, the lifetime of the whole group would be doubled.

A secondary finding in accordance with Van Valen’s observation of exponentially decaying lifetime distributions (Van Valen 1973) is the near-exponential distribution of genus lifetimes within a given order (Fig. 5c). As also noticed by Van Valen, an exponential distribution of lifetimes implies that the extinction of a genus is a random event, happening with a rate given by some properties that are similar for all genera within an order. In contrast, a

broader than exponential distribution obtained for the full dataset of lifetimes shows that genera from different orders have different intrinsic stabilities to whatever could cause their extinction (Fig. 5a). From this we conclude that all genera within an order have closely related (although not necessarily identical) longevity, whereas genera in total have a much broader distribution of intrinsic longevity. Note that whereas the intrinsic longevity is already defined at origination, the actual extinction event exhibits the statistics of a random event that only depends on external factors, including competition with other species. Observable intrinsic longevities may result, e.g., from heritability of geographic range (Jablonski 1987) that in turn affects survival during the major mass extinctions in the geologic past (Jablonski 1995); and a general negative relationship between geographical range and extinction rate on species level as has been demonstrated for different taxonomic groups (Jablonski 1986, 1987, 1995; Jackson 1974; Brown 1995; Jablonski et al. 2003).

Our good fits of genus lifetimes at different taxonomic levels with log-normal distributions suggest a heritable longevity, which could be represented by products of random numbers, the more similar the genera the more similar their respective numbers in the product. Such models for the emergence of log-normal distributions are well known from physics of complex systems, including fragmentation phenomena and turbulence heuristically modeled already by Kolmogorov (1941a, b) and Filippov (1961).

Evolution of life has involved strongly varying rates of origination and extinction with a general tendency of decreasing turnover over the Phanerozoic (Raup and Sepkoski 1982; Van Valen 1984; Sepkoski 1998). The effect of the overall decline in turnover rates over the Phanerozoic as described, e.g. by Flessa and Jablonski (1985) is not reflected in our analyses of ordinal longevity. To see this, we divided the 159 orders that fulfilled the criteria for being in Fig. 6 into subsets of 77 orders that existed only during the Paleozoic (before the Permian–Triassic extinction), (77 out of 242 orders that existed in the Paleozoic only fulfilled the criteria of Fig. 6), and 43 orders that existed only during the Mesozoic to Cenozoic (43 out of 137 orders that existed in the Mesozoic to Cenozoic only fulfilled the Fig 6 criteria). In both cases we again observe no significant increase in order lifetimes when comparing orders with less than three genera in average, to orders with more than 30 genera in average during their existence, matching the observation for the full Phanerozoic shown in Fig. 6a. Similarly, we reanalyzed the correlation with average genus lifetimes, and at least the Paleozoic orders confirmed our faster than linear scaling from Fig. 6b. The statistics of the Mesozoic (42 orders total, 14 fulfilling the criteria of Fig. 6) vs. Cenozoic (14 orders total, 5 matching criteria) orders were too weak to be conclusive. Thus,

overall the Paleozoic taxa compared to the Mesozoic plus Cenozoic taxa do not show any significantly different behavior. This means that there is no dependency in behavior on the geological time when the order existed.

To summarize from our study we conclude that:

1. There is substantial variation among higher taxa (orders) in characteristic genus durations.
2. Longevity of higher taxa is predicted by longevity of lower taxa. Put another way, orders that are longer lived tend to consist of genera that are longer lived.
3. Longevity of orders is not well predicted by the number of constituent genera.

Data and methods

We use the last version of Sepkoski's database of fossil marine animal genera as published in Sepkoski (2002). The effect of the incompleteness and bias of the fossil record (Sepkoski and Koch 1996; Kidwell and Holland 2002; Foote 2003) is minimized by studying this large database.

Genera originations (approximated by first appearances) and extinctions (approximated by last appearances) are translated to absolute ages using 98 distinct time intervals (on stage level where practicable; and otherwise merging stages) derived from the current IUGS Geochronology (Renne et al. 2001) and the Harland stratigraphic time scale (Harland et al. 1989), leaving us with 36,506 genera in 561 orders, of which 31,071 genera in 522 orders are extinct today. To check sensitivity of our analysis to the exact choice of stratigraphic timescale, we crosschecked

with a second implementation of time intervals based entirely on the Harland stratigraphic time scale (Harland et al. 1989) and found comparable results. For our analyses, we define the origination time of a genus as the beginning of the stratigraphic interval where this genus first occurred, and the extinction time point as the end of the stratigraphic interval where it last occurred. The results of our study do not depend sensitively on this convention.

To avoid bias due to the pull of the recent, we base our analysis on the subset of extinct genera only (except for Fig. 1 where the complete dataset is shown, with all recent genera located on the upper boundary).

We are aware of the incompleteness of Sepkoski's database, which in the past has caused considerable artifacts (Foote 2003; Lu et al. 2006). In our analysis, we focus on statistical measures based on averages that are insensitive to this property of the database (contrary to, e.g., time covariances of momentary rates or taxon numbers, or similar quantities that tend to amplify statistical fluctuations).

For practical reasons, Sepkoski's orders are taken as the biological units in the analysis, although some of them are paraphyletic. A purely monophyletic dataset would be ideal when analyzing, e.g., characteristic lifetimes and their possible correlation with environmental or intrinsic factors. As a paraphyletic order simply lacks a branch of its lineage that evolved a different phenotype, lifetime correlations among its members may be underestimated if intrinsic factors are the cause, and overestimated if environmental factors dominate. In any case, correlations are at most weakened, not counteracted, by missing parts of the lineage.

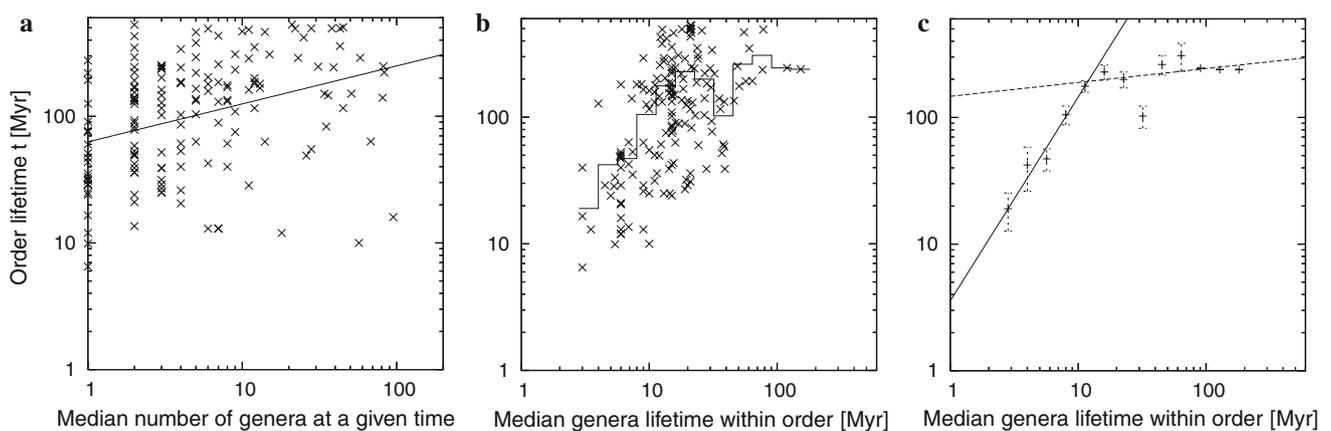


Fig. 8 **a** Existence time of orders versus median number of genera at a given time during the respective order history. Note that using the median instead of the mean does not change the general picture of Fig. 6a; **b** existence times for same sample of orders as in (a) are here shown as function of the median (instead of mean) existence times for genera composing the respective order (compare plot using mean existence times in Fig. 6b); **c** here, the order lifetime has been

averaged over bins of ranges in average genus lifetime, as indicated by the steps in (b). We observe a steep dependence of order lifetime on the lifetime of constituent genera for small genus lifetimes and only a weak dependence once typical genus lifetimes exceed about 20 Myr. Thus, we observe a similar pattern as in Fig. 6a–c, supporting the conclusions made in that context

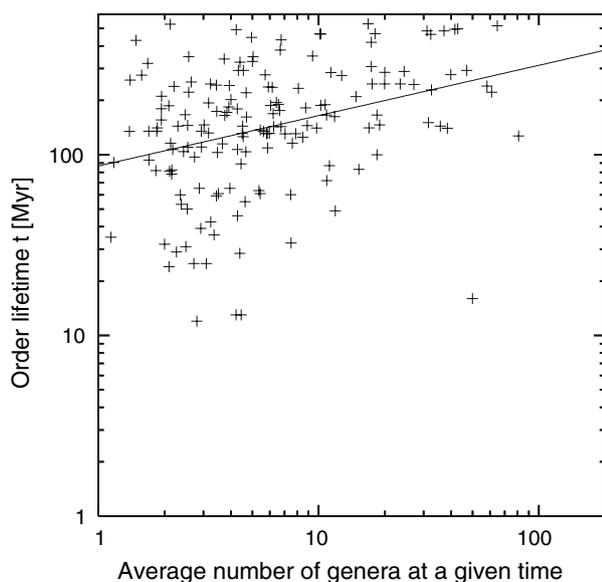


Fig. 9 Same as Fig. 6a, based on the subset of Sepkoski's data where only genera are included that cross at least one stratigraphic boundary (singletons removed). This has no significant effect

As outliers may dominate averages of broadly distributed quantities as longevities or order sizes, we checked that our main results are robust by alternatively using the median instead of mean. This version of Fig. 6a–c is shown in Fig. 8a–c.

Average numbers of genera within orders at a given time are determined by bin counting within time bins. As each genus is assumed to have existed throughout the stratigraphic intervals where it has been observed, this method is equivalent to bin counting within the stratigraphic intervals themselves, except for normalization w.r.t. the length of each stage when determining the average over all bins. These methods tend to overestimate diversity. The overall effect, however, is only a small one, as a comparison with the reduced dataset shows where only taxa are counted that cross a stratigraphic boundary (see Fig. 9).

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