

PATTERNS OF ORIGINATION

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ABSTRACT: Like extinction rates, which they closely follow in magnitude and timing, origination rates for marine families decline exponentially through the Paleozoic, and are reset by the Permian extinction. Another exponential decline follows, but this one seems to last only until the late Cretaceous. Origination rates for individual higher taxa follow the overall pattern, unlike the case for extinction. So do those for Cenozoic mammals. The results imply, perhaps paradoxically, predominance of equilibrational and interactive effects during most of Phanerozoic community evolution.

Differential extinction, and therefore perhaps diffuse competition, not differential origination, causes the post-Paleozoic decline in brachiopod families relative to pelecypods. The sequential dominance of groups of taxa does not account for the high overall origination rates in the early Mesozoic. After a major extinction, origination rates are greater for those taxa affected by the extinction than for those unaffected.

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Origination is the obverse of extinction. If community evolution is largely random there will be little relation between the two, while if it is largely interactive we expect, in the simplest case, a close relationship.

To measure origination we should not use the total number of originations per million years, as this is strongly affected by the number of lineages available. Rather, we want the probability that one lineage, or taxon, gives rise to another in that million years. Most previous work on origination rates has used the former sort of measure, which is indeed partly appropriate if one is interested in change in overall diversity. It does not, however, lend itself to causal interpretation.

METHODS

We used an updated version of Sepkoski's (1982) compilation of the known stratigraphic ranges of marine families and a summary sheet kindly provided by Sepkoski. For ranges not given to stage we used a linear extrapolation; e.g., if a range began in the Silurian, which has 3 stages, the early Silurian was given 1/3 family, the middle Silurian 2/3, and the late Silurian 1. Our time scale is from Harland et al. (1982), modified to fit the stages Sepkoski used and in a few other ways on the basis of other work. For instance, Cambrian stage lengths are from Sepkoski (1979), modified to the Harland time scale, and the Miocene ages are from Kennett and Srinivasan (1983). Part of the Pliocene of older work (and therefore of older records) has been incorporated into the Miocene, so some bias here is expected although not as much as must occur earlier from artifacts of preservation and study. Appendix 1 includes the time scale we used. We ignored soft-bodied groups and, for analyses of specific taxa, those taxa with few families or represented in fewer than four geologic periods.

To calculate the origination rate for a particular stage, we first found the number of families initially present, N_0 , by subtracting the number of families

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going extinct in the previous stage from the number present in the previous stage. We then used a standard ecological equation,

$$\frac{N_t}{N_0} = e^{rt} ,$$

to estimate the origination rate r . t is the duration of the stage in millions of years and N_t is N_0 plus the number of families originating in the stage. Because of extinction, N_t is not necessarily the number of families at the end of the stage, but our analysis assumed that all extinctions occurred at the end of each stage. If there is a bias so introduced it is less than 10 percent, even on an arithmetic scale, usually much less, and it is not known to what extent extinctions really are concentrated at the ends of stages or are more uniformly dispersed. For intervals of more than one stage, used for individual taxa, we either combined estimates for the component stages or calculated the rate for the total interval directly. We combined intervals with no origination into adjacent intervals except for intervals before the extinction of the entire higher taxon, when the lack of origination is less likely to be due to sampling error. Some other intervals of ostensibly 0 origination may be real, but the data are not yet good enough to say which, and values of 0 are awkward in logarithmic transformations.

The rate r is the probability that one family gives rise to another family per million years. As such it can be compared directly with the corresponding probability of extinction as given by Van Valen (1984a, 1985a). The time scale used for the first paper differs a little but the information given there permits values to be interconverted if one wishes. More precisely, $r [= (1/N)(dN/dt)]$ is the expected number of families arising directly from one family per million years during exponential increase, assuming a continuous branching process. Thus r can be larger than 1, and we give examples of this at the species level elsewhere (Van Valen, 1985b).

The regressions of origination on time were estimated from logarithmically transformed data because the residuals are normally distributed only then, and only then are the regressions linear. For regressions of individual taxa, we weighted each logarithmically transformed datum by $t\sqrt{N_0}$. This weighting corrects for the large differences in lengths of intervals (t) often used for individual taxa. It also minimizes the effect of sampling error, as the second factor of the weight is proportional to the reciprocal of the sampling error. The only purpose of the weighting is to improve the accuracy of the regressions with respect to their intended biological meaning. Terminal intervals of 0 origination were ignored in one set of analyses and given values of 0.0001, lower than any observed value, in another set of analyses.

To investigate rebound effects after major extinctions we first separated those higher taxa which were appreciably affected by the extinction from those which were not. The criteria were that there be an appreciable extinction rate then, that this rate be arbitrarily at least twice that of the immediately earlier and later intervals, and (for the taxon to be used at all) that the number of families at risk be at least 3 (an arbitrary and perhaps too low value) and that there be a normal earlier interval to serve as control. For the Late Ordovician extinction, the only taxa appreciably affected were the Trilobita and Brachiopoda. For the Late Devonian they were the Porifera, Nautiloidea (only Famennian), Ammonoidea (only Famennian), Trilobita, Ostracoda, Malacostraca (only Famennian), and Conodonta. For the Late Permian they were all taxa except the Nautiloidea, Echinoidea, and Conodonta. For the Late Triassic they were the Porifera, Nautiloidea + Coleoidea, Ammonoidea, Malacostraca, and Brachiopoda. For the Maestrichtian they were the Foraminifera, Porifera, Gastropoda, Pelecypoda, Nautiloidea + Coleoidea, Ammonoidea, Bryozoa, and Echinoidea. As control intervals for origination rates we used the Middle and Late Ordovician, Early and Middle Devonian, Middle Carboniferous through Early Permian, Late Triassic, and all the Cretaceous. For each taxon we took the ratio of the origination rate in the stage of interest, to the rate in the control interval. We

then transformed each ratio to its arctangent (in radians) to normalize it, and found the mean of the resulting values.

For regressions, r^2 measures the proportion of the variance of \log_{10} origination rate that is explained by the regression, $s_{y \cdot x}$ measures the standard deviation of \log_{10} origination rate about the regression, and the tightness T (Van Valen, 1974b) measures the closeness of the joint distribution to its major axis, relative to the variance (eigenvalue) along that axis. T reduces to the correlation, r , when the slope is 1.

We tried at some length to quantify the diversity dependence of extinction and origination rates, but the complex and nonlinear interactions among diversities, rates, taxa, and time has precluded useful results. Diversity dependence is an obvious extension of the ecological phenomenon of density-dependent regulation of population density. Bartlett (1960), Mac Arthur and Wilson (1963), Valentine (1973), Rosenzweig (1975), Osman and Whitlatch (1978), Sepkoski (1979), Stenseth (1979), Carr and Kitchell (1980), and others have discussed the likelihood of diversity-dependence, and most of these authors have presented models of it. Carr and Kitchell even brought in a few actual paleontological data from around the Permian extinction, and Sepkoski's broader model provides a reasonable fit to more data. (The empirical relationship found in a local sequence by Bretsky and Bretsky, 1976, between number of species and extinction, may, however, be a sampling artifact at least in part: bedding planes with few specimens would also have few species and so an apparently high extinction during the preceding interval.) Our aim was broader, to see what degrees (if any) of diversity dependence in fact do characterize the variation in total familial diversity, that of specific taxa, and that of apparently more interacting sets of taxa (such as the shelf benthos) through the Phanerozoic. Our approach was via the causes of diversity change, as partitioned into origination and extinction probabilities. It may well be that more modest efforts would give clearer results by eliminating some of the (confounded!) confounding interactions.

RESULTS AND DISCUSSION

Just as for extinction rate, origination rate declines exponentially in the Paleozoic and is reset by the Permian extinction (Fig. 1). As for extinction, the time of demarcation is not arbitrary; none of the post-Paleozoic data are even close to an extension of the Paleozoic regression, let alone below it. And the time is the same for origination and extinction, which are not statistically interdependent in their rates even though there is a degree of biological relationship.

After the Paleozoic there is another exponential decline, steeper than the one earlier, but this continues only through the early Cretaceous. The picture thereafter is less clearcut, although an approximation to an exponential decline seems likely. The extent to which better knowledge of ranges after the early Cretaceous, and the inclusion of extant families, contribute to the apparent mid-Cretaceous rise in origination rate and to the greater scatter of the later data, is not known. The rate for the Cenomanian itself is rather high, so the late-Cenomanian extinction may not have had a large effect. None of the 18 data after the early Cretaceous fall below the Triassic/Early Cretaceous regression. 2 fall below the unweighted regression at 2 standard errors shallower and 3 fall below the corresponding weighted regression. The 2-tailed binomial probabilities of so few, if the distributions before and after the break follow the same real regression, are 0.00117 and 0.00622 respectively. Each shallower regression is at about the 0.06 significance level, which is independent of each other probability because the latter is in each case from a disjunct distribution. However, the position of the break between the two distributions itself depends on the shape of the distributions. There are 38 places to put a break between two regressions in a set of 41 data. This value, being a priori, is again independent of the other two probabilities. The final probability for the data after the early Cretaceous to follow the earlier regression is $0.06 \times 38 \times (0.00117 \text{ or } 0.00622)$, or 0.003 and

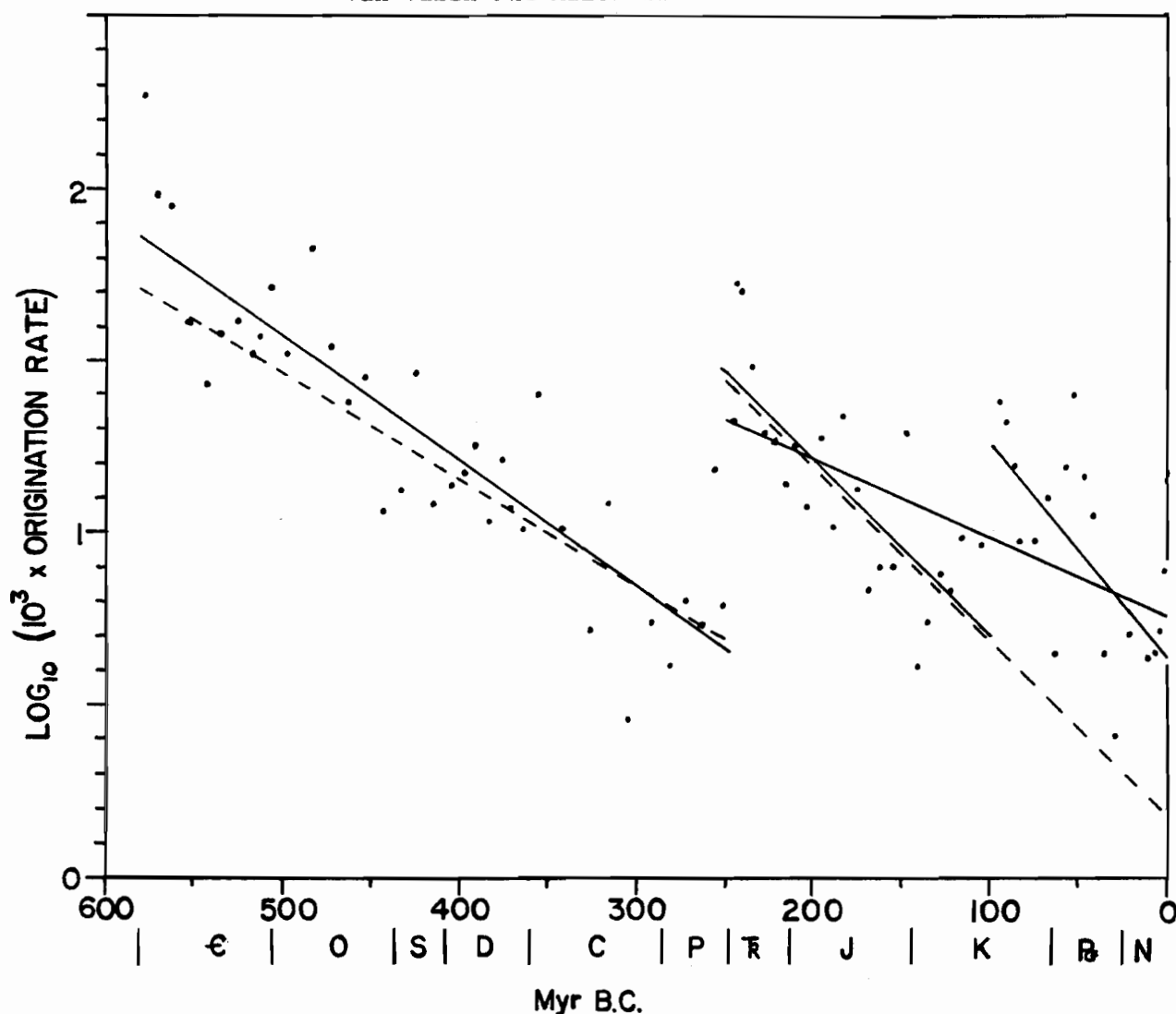


Fig. 1. Logarithmic unweighted regressions (solid lines) of origination rates on time, for all (combined) data. A joint regression for the entire post-Paleozoic is given in addition to those for its two components. The dashed lines represent the regressions for extinction rates, from Van Valen (1984a).

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Table 1. Regressions of \log_{10} origination rate on time, for combined data, unweighted and weighted by stage lengths.

	Slope	r^2	Tightness	$s_{y \cdot x}$
Paleozoic				
unweighted	-0.00362 ± 0.00034	0.77	0.99998	0.201
weighted	-0.00386 ± 0.00034	0.79	0.99998	0.195
post-Paleozoic				
unweighted	-0.00235 ± 0.00050	0.36	0.99996	0.242
weighted	-0.00232 ± 0.00050	0.35	0.99996	0.229
Triassic to Early Cretaceous				
unweighted	-0.00501 ± 0.00088	0.60	0.99993	0.185
weighted	-0.00430 ± 0.00086	0.54	0.99994	0.176
Late Cretaceous to Neogene				
unweighted	-0.00636 ± 0.00175	0.45	0.99980	0.226
weighted	-0.00699 ± 0.00192	0.45	0.99977	0.223

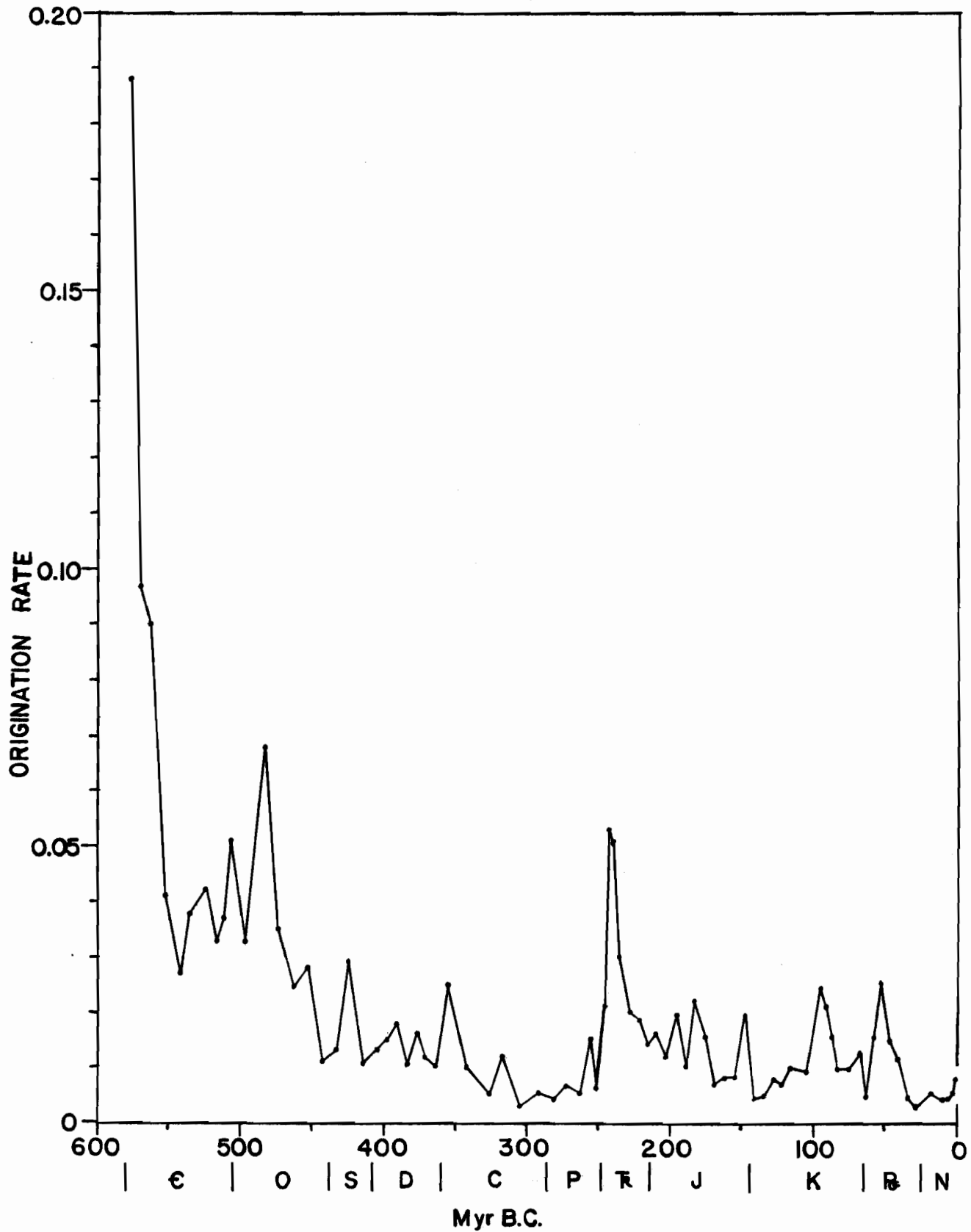


Fig. 2. Arithmetic plot of origination rates on time, for combined data. In Van Valen (1984a) the point for the Maestrichtian in Figure 2 is erroneously connected by lines so that it appears to be before the point for the Campanian.

0.014 respectively. Thus the change after the early Cretaceous indeed seems real, and the subsequent decline is again best represented by an overall exponential decline despite some undoubtedly real fluctuations. (For completeness, the four corresponding probabilities for the Permian break, for both extinction and origination, are all less than 10^{-3} .)

The slopes of origination rates for the Paleozoic and early post-Paleozoic intervals (Table 1) are similar to those found earlier (Van Valen, 1984a) for extinction rates in the Paleozoic and entire post-Paleozoic. The values of the two kinds of rates are also about the same at any one time if one allows for scatter, with a little higher origination initially and in the recovery from the Permian crisis. Therefore origination and extinction kept pace with each other in a striking fashion; presumably they were causally interrelated. But in the last 100 million years originations seem to have greatly outstripped extinctions, producing the well-known rise in familial diversity (Sepkoski et al., 1981). This late-Mesozoic change from the approximate balance of the previous 400 million years or more, if real, as it seems to be, needs explanation. It is not restricted to the benthos; in fact the greatest single contributor is the predominantly pelagic group Osteichthyes. Thus benthic-specific explanations like those of Vermeij (1977) and Thayer (1979) are probably incomplete.

Unlike the situation for extinction (Van Valen, 1985a), the slopes for single taxa (Appendix 3) average even steeper than the joint slopes. This is ostensibly true for all four comparisons, but only for the Paleozoic is it significant ($P = 0.04$ whether or not terminal-0 intervals are included). For the Paleozoic there is no detectable heterogeneity among taxa in their slopes ($P > 0.1$, from a one-way analysis of variance); for the post-Paleozoic the data seem less suitable but again show no heterogeneity in any of the three tests. Of course there is large heterogeneity among taxa in the origination rates themselves.

For Cenozoic mammals, also, origination rates for families decline exponentially (Van Valen, 1973, pp. 10-11). The range is two orders of magnitude, greater than that for marine families for the entire Paleozoic, and the slope is correspondingly steeper (-0.023 ± 0.04 , when in probability measure). As for marine families, there is no overall trend in extinction rate. For community evolution, as in some other respects (cf. Van Valen, 1974a) mammals evolve unusually rapidly.

Sepkoski (1981) used factor analysis to separate three groups of marine higher taxa which have different patterns of change in familial diversity. His group 2 predominated in the Paleozoic, but was greatly reduced at its close; his group 3 predominated thereafter. We therefore thought it useful to see whether his grouping would account for the high overall origination rate in the early Mesozoic. The major constituents of group 2 are the Anthozoa, Cephalopoda, Ostracoda, Brachiopoda, Crinoidea, Graptolithina, and Conodonta, while the Foraminifera (not included in Sepkoski's analysis, but fitting here), Porifera, Gastropoda, Pelecypoda, Malacostraca, Echinoidea, Chondrichthyes, and Osteichthyes predominate in group 3. The Bryozoa are in both groups, so we ignored them. We compared origination rates for the two groups in the late Paleozoic, after recovery from the late Devonian extinction, using the interval from the Middle Carboniferous through the Late Permian. Group 3 actually seems to have had a lower origination rate in this interval: the mean values of \log_{10} (10 times origination rates) are 1.788 ± 0.099 and 1.477 ± 0.117 for groups 2 and 3 respectively. Therefore both groups participated in the low turnover of the late Paleozoic, and ecological rather than inherent causes must account for the high turnover in the early Mesozoic. The apparently greater susceptibility of members of group 2 to extinction may be the major, if not the only, difference between the groups.

It is not surprising that origination rates increase after a major extinction. In fact the rebound of planktonic foraminiferans and coccolithophores immediately after the Cretaceous-Paleogene extinction produces origination rates at the species and genus levels as high as the maximum known for mammals (Van Valen, 1984b, pp. 126-127; Van Valen, 1985b.)

It would, however, be surprising if origination rates sometimes remain low for

Table 2. Means of the arctan transformations of ratios of origination rates after a major extinction to rates before the extinction. A value of 0.785 indicates equal rates before and after.

Extinction (and) Interval after Extinction	Affected taxa		Unaffected taxa	
	Number	Mean rate	Number	Mean rate
Late Ordovician				
Early Silurian	2	0.80 ± 0.21	12	0.53 ± 0.14
Middle Silurian	2	1.00 ± 0.25	12	0.59 ± 0.16
Late Devonian				
Famennian	4	0.81 ± 0.42	11	0.66 ± 0.16
Tournaisian	7	1.07 ± 0.10	8	1.07 ± 0.13
Viséan	7	0.89 ± 0.12	8	0.51 ± 0.06
Late Permian				
Late Permian	12	0.96 ± 0.16	3	0.68 ± 0.36
Early Triassic	12	0.81 ± 0.21	3	0.26 ± 0.26
Middle Triassic	12	0.98 ± 0.18	3	0.74 ± 0.42
Late Triassic				
Hettangian	5	0.92 ± 0.24	10	0.75 ± 0.19
Sinemurian	5	0.63 ± 0.24	10	0.33 ± 0.17
Late Cretaceous				
Danian	7	0.42 ± 0.23	7	0.33 ± 0.17
Later Paleocene	7	0.84 ± 0.22	7	0.58 ± 0.21
Eocene	7	0.89 ± 0.15	7	0.93 ± 0.13
	*	*		*

millions of years after a major extinction, before increasing above their usual level. Boucot (1983) has implied that this occurred for the Frasnian (Late Devonian) and Late Permian extinctions, but the lower diversity of the Famennian and Early Triassic could alternatively be due merely to the fact that the same rate of increase produces less absolute increase when there are fewer families initially. The lag time of Carr and Kitchell (1980), e.g., is of the nature. Our data permit this hypothesis to be tested, as follows.

We see from Table 2 that 12 of the 13 comparisons are larger for the affected taxa (this includes the Tournaisian), for which the sign test gives a probability of < 0.02 , and 11 of the 13 are above the control level for the affected taxa. That only 2 of the 13 values for the unaffected taxa are above the control level ($P < 0.05$) suggests that a tendency for inhibition of adaptive radiation occurs after major extinctions, whether as a delayed effect of the cause of the extinction itself or as a byproduct of the adaptive radiation of the more affected groups even though overall diversity remains lower. Nevertheless, the familial origination rate after a major extinction is rarely much higher (even for affected taxa) than it was before, and for the Danian it is only about half the control value. The Danian gives the only suggestion of a general delay in response, and this may possibly be an artifact of relatively poorer knowledge of that stage. Delays may, however, occur for some individual taxa after some major extinctions, although the numbers involved are too small to say much at the level of family.

For the combined data (best seen from Fig. 1), there is a rather low origination rate just after the late Ordovician extinction, a high rate in the Tournaisian, high rates after the Late Permian extinction, a low rate in the Danian but high ones from the later Paleocene through the Eocene, and moderate rates in the other relevant stages.

The Brachiopoda and Pelecypoda provide a useful comparison. Gould and Calloway (1980) showed that their diversity changes give no indication of either group interfering with the other, although their data also do not at all exclude the

possibility. This is because competition can occur, e.g., between groups which both increase; at least one would have increased more rapidly without competition. Indeed, after the Permian extinction the brachiopods have largely been restricted to deeper water, a probable competitive effect (Steele-Petrović, 1979). During this time the origination rates for brachiopods (0.0097 if intervals are weighted by time only and 0.0096 if weighted also by number of families present) were similar to those of pelecypods (0.0070 and 0.0071 respectively) and were higher in 7 of the 12 post-Paleozoic intervals we used. The data do not take into account such things as the greater geographic restriction of many of the brachiopod families, but they do indicate that the lack of a major recovery by the brachiopods is not due to an inability to originate new families. The overall extinction rates for the post-Paleozoic are 0.0076 for brachiopods and only 0.0029 for pelecypods (from data of Van Valen, 1985a, with the double weightings); whether this difference, and the resulting preponderance of pelecypods, is due to diffuse competition between the groups will probably have to await better ecological and functional analyses. The functional analysis by Steele-Petrović (1979) does suggest that diffuse competition is at least plausible.

Other points of interest can be seen from close examination of Appendix 2, such as the relatively high origination rates in some intervals for otherwise rather sedate groups like the Bryozoa. For most taxa the initial rate of origination is highest, as expected; for the Ammonoidea the initial rate of 0 depends entirely on the Bactritidae, a family variously classified and omitted from our ammonoid results.

CONCLUSION

Extinction and origination rates have remarkably similar patterns in some ways but differ in others. The closeness of the two combined distributions to each other in both slope and position, until the late Cretaceous, implies that the two processes are closely interrelated. Origination can cause extinction and extinction can leave room for successful origination; the data do not distinguish between these effects, although the second of course causes rebounds.

The approximate balance between origination and extinction, despite large and concomitant variation in each, implies that there has been an approximate equilibrium, regulated as such, and other evidence (comparisons of Sepkoski's major groups and of species origination rates) indicates ecological rather than intrinsic causes.

An accompanying paper (Van Valen, 1985c) integrates the results into a more general theoretical framework.

Lower diversity does not itself require a smaller share of the total available free energy in the environment, for families or even species could average more. It does seem, though, that there has been a finer partitioning of available energy in the last 100 million years, if this is not somehow all an artifact of better knowledge of more recent faunas. The data do not tell us why this has occurred, but it is origination rather than extinction which has broken out of its previous pattern.

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REFERENCES

- Bartlett, M.S. 1960. Stochastic Population Models in Ecology and Epidemiology. London: Methuen. 90 pp.
- Boucot, A.J. 1983. Does evolution take place in an ecological vacuum? *Journal of Paleontology* 57: 1-30.

- Bretsky, P.W., and S. S. Bretsky. 1976. The maintenance of evolutionary equilibrium in Late Ordovician benthic marine invertebrate faunas. *Lethaia* 9: 223-233.
- Carr, T.R., and J. A. Kitchell. 1980. Dynamics of taxonomic diversity. *Paleobiology* 6: 427-443.
- Gould, S.J., and C.B. Calloway. 1980. Clams and brachiopods - ships that pass in the night. *Paleobiology* 6: 383-396.
- Harland, W.B., A.V. Cox, P.G. Llewelyn, C.A.G. Pickton, A.G. Smith, and R. Walters. 1982. A Geologic Time Scale. Cambridge: Cambridge Univ. Press. 131 pp.
- Kennett, J.P., and M.S. Srinivasan. 1983. Neogene Planktonic Foraminifera: A Phylogenetic Atlas. Stroudsburg, Pennsylvania: Hutchinson Ross. 265 pp.
- Mac Arthur, R.H., and E.O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17: 373-387.
- Osman, R.W., and R.B. Whitlatch. 1978. Patterns of species diversity: fact or artifact? *Paleobiology* 4: 41-54.
- Rosenzweig, M.L. 1975. On continental steady states of species diversity. In: *Ecology and Evolution of Communities* (M.L. Cody and J.M. Diamond, eds.), pp. 121-140. Cambridge, Massachusetts: Harvard Univ. Press.
- Sepkoski, J.J., Jr. 1979. A kinetic model of Phanerozoic taxonomic diversity. II. Early Phanerozoic families and multiple equilibria. *Paleobiology* 5: 222-251.
- _____. 1981. A factor-analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7: 36-53.
- _____. 1982. A compendium of fossil marine families. Milwaukee Public Museum, *Contributions to Biology and Geology*, 51: 1-125.
- _____, R.D. Bambach, D.M. Raup, and J. W. Valentine. 1981. Patterns of marine diversity and the fossil record. *Nature* 293: 435-437.
- Steel-Petrović, H.M. 1979. The physiological differences between articulate brachiopods and filter-feeding bivalves as a factor in the evolution of marine level-bottom communities. *Palaeontology* 22: 101-134.
- Stenseth, N.C. 1979. Where have all the species gone? On the nature of extinction and the Red Queen Hypothesis. *Oikos* 33: 196-227.
- Thayer, C.W. 1979. Biological bulldozers and the evolution of marine benthic communities. *Science* 203: 458-461.
- Valentine, J.W. 1973. *Evolutionary Paleoecology of the Marine Biosphere*. Englewood Cliffs, New Jersey: Prentice-Hall. 330 pp.
- Van Valen, L.M. 1973. A new evolutionary law. *Evolutionary Theory* 1: 1-30.
- _____. 1974a. Two modes of evolution. *Nature* 252: 298-300.
- _____. 1974b. Multivariate structural statistics in natural history. *Journal of Theoretical Biology* 45: 235-247.
- _____. 1984a. A resetting of Phanerozoic community evolution. *Nature* 307: 50-52, 660.
- _____. 1984b. Catastrophes, expectations, and the evidence. *Paleobiology* 10: 121-137.
- _____. 1985a. How constant is extinction? *Evolutionary Theory* 7: 93-106.
- _____. 1985b. Why and how do mammals evolve unusually rapidly? *Evolutionary Theory* 7: 127-132.
- _____. 1985c. A theory of origination and extinction. *Evolutionary Theory* 7: 133-142.
- Vermeij, G.J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* 3: 245-258.

Appendix 1. Origination rates per million years for families of all taxa jointly.

Stage	Beginning of Stage (million years B.C.)	Initial Number of Families	Number of Originations	Origination Rate
Cambrian (C)				
Early Tommotian	580	11	23	0.188
Late Tommotian	574	32	31	0.079
Atdabanian	567	59	74	0.090
Botomian	558	112	79	0.041
Lenian	548	98	20	0.027
Early Middle Cambrian	538	82	25	0.038
Late Middle Cambrian	531	81	48	0.042
Early Late Cambrian	520	99	22	0.033
Middle Late Cambrian	514	99	20	0.037
Late Late Cambrian	509	102	23	0.051
Ordovician (O)				
Tremadocian	505	102	76	0.033
Arenigian	488	138	134	0.068
Llanvirnian	478	242	100	0.035
Llandeilan	468	293	79	0.024
Caradocian	458	335	109	0.028
Ashgillian	448	395	48	0.0115
Silurian (S)				
Llandoveryian	438	344	49	0.0133
Wenlockian	428	360	81	0.0290
Ludlovian	421	391	58	0.0106
Devonian (D)				
Gedinnian	408	386	38	0.0134
Siegenian	401	401	44	0.0149
Emsian	394	418	55	0.0177
Eifelian	387	449	35	0.0107
Givetian	380	431	44	0.0162
Frasnian	374	411	35	0.0117
Famennian	367	387	29	0.0103
Carboniferous (C)				
Tournaisian	360	332	72	0.0248
Viséan	352	364	79	0.0103
Namourian	333	401	28	0.0052
Bashkirian	320	391	24	0.0119
Moscovian	315	407	23	0.0039
Stephanian	296	408	23	0.0055
Permian (P)				
Asselian	286	397	15	0.0041
Sakmarian	277	397	23	0.0063
Leonardian	268	396	22	0.0054
Guadelupian	258	368	29	0.0152
Dzhulfian	253	257	8	0.0061
Triassic (T)				
Induan	248	184	12	0.0210
Olenekian	245	180	31	0.0531
Anisian	242	193	43	0.0502
Ladinian	238	223	52	0.0300
Carnian	231	255	32	0.0197
Norian	225	250	29	0.0183
Rhaetian	219	230	20	0.0139

Appendix 1. (cont.) Origination rates for all taxa jointly.

Stage	Beginning of Stage (million years B.C.)	Initial Number of Families	Number of Originations	Origination Rate
Jurassic (J)				
Hettangian	213	232	27	0.0157
Sinemurian	206	256	23	0.0118
Pliensbachian	199	267	27	0.0185
Toarcian	192	285	18	0.0102
Bajocian	186	297	49	0.0220
Bathonian	179	333	32	0.0131
Callovian	172	356	17	0.0067
Oxfordian	165	363	21	0.0080
Kimmeridgian	158	371	22	0.0079
Tithonian	151	378	55	0.0194
Cretaceous (K)				
Berriasian	144	401	10	0.0041
Valanginian	138	403	13	0.0045
Hauterivian	131	409	19	0.0076
Barremian	125	415	17	0.0067
Aptian	119	421	25	0.0096
Albian	113	432	63	0.0091
Cenomanian	98	477	74	0.0241
Turonian	92	512	33	0.0210
Coniacian	89	528	25	0.0154
Santonian	86	539	31	0.0093
Campanian	80	551	48	0.0093
Maestrichtian	71	573	45	0.0126
Paleogene (P _e)				
Danian	65	530	12	0.0045
Middle + Late Paleocene	60	524	42	0.0154
Early Eocene	55	557	75	0.0252
Middle Eocene	50.5	624	62	0.0146
Late Eocene	44	673	47	0.0113
Early + Middle Oligocene	38	707	16	0.0045
Late Oligocene	33	716	15	0.0026
Neogene (N)				
Early Miocene	24.5	721	32	0.0051
Middle Miocene	16	743	20	0.0044
Late Miocene	10	754	17	0.0045
Pliocene	5	761	12	0.0052
Pleistocene	2	763	12	0.0078

Appendix 2. Origination rates per million years for families of specific taxa.

	Early Cambrian	Middle Cambrian	Late Cambrian	Early Ordovician
Foraminifera	---	---	---	0.047 ²
Porifera	---	---	0.024	0.016
Anthozoa	---	---	---	---
Gastropoda	---	---	0.299	0.039
Pelecypoda	---	---	---	0.062
Nautiloidea + Coleoidea	---	---	0.486	0.084
Ammonoidea	---	---	---	---
All Cephalopoda	---	---	0.486	0.085
Trilobita	0.109	0.067	0.040	0.028
Ostracoda	0.052	0.054	0	0.085
Malacostraca	---	0.021 ²	---	0.026
Bryozoa	---	---	---	---
Brachiopoda	0.071	0.023	0.012	0.049
Crinoidea	---	---	---	0.150
Echinoidea	---	---	---	---
Conodonta	---	0.039	0.084	0.058
Graptolithina	---	0.268	0.051	0.058
Chondrichthyes	---	---	---	---
Osteichthyes	---	---	---	---

¹Including Pleistocene

²Including Late Cambrian

³Including Ordovician

⁴Including Carboniferous

⁵Including Late Devonian

Appendix 2. (cont.) Origination rates per million years for specific taxa.

	Middle & Late Ordovician	Silurian	Early & Middle Devonian	Late Devonian
Foraminifera	0.004	0.016	0.012	0.030
Porifera	0.033	0.013	0.002	0.004
Anthozoa	0.094	0.030	0.014	0.022
Gastropoda	0.009	0.010	0.012	0.002
Pelecypoda	0.019	0.005	0.013	0.013
Nautiloidea + Coleoidea	0.020	0.031	0.019	0.007
Ammonoidea	—	0 ³	0.079	0.170
All Cephalopoda	0.020	0.030	0.028	0.063
Trilobita	0.008	0.011	0	0.016
Ostracoda	0.021	0.015	0.014	0.002
Malacostraca	0.027	0.010	0.020	0.036
Bryozoa	0.028	0.006	0.010	0.016
Brachiopoda	0.026	0.016	0.016	0.013
Crinoidea	0.070	0.038	0.018	0.005
Echinoidea	—	0.042 ³	0.005 ⁵	—
Conodonta	0.012	0.012	0.005	0.048
Graptolithina	0.011	0.010	0 ^{4,5}	—
Chondrichthyes	—	—	0.183	0.101
Osteichthyes	—	—	0.075	0.010

Appendix 2. (cont.) Origination rates per million years for specific taxa.

	Early Carboniferous	Middle Carboniferous	Late Carboniferous	Early Permian
Foraminifera	0.030	0.009	0.004	0.001
Porifera	0.014	0.002	0.006	0.010
Anthozoa	0.015	0.005	0.003	0.001
Gastropoda	0.004	0.001	0	0.001
Pelecypoda	0.010	0.006	0.001	0.007
Nautiloidea + Coleoidea	0.027	0.006	0.002	0.011
Ammonoidea	0.094	0.046	0.023	0.021
All Cephalopoda	0.051	0.028	0.014	0.017
Trilobita	—	—	—	0 ⁴
Ostracoda	0.008	0.002	0	0
Malacostraca	0.039	0.010	0.005	0.016
Bryozoa	0.010	0	0.001	0.002
Brachiopoda	0.007	0.003	0.005	0.007
Crinoidea	0.029	0.022	0.004	0.003
Echinoidea	0.013	0	0	0
Conodonta	0.012	0.019	0.006	0.007
Graptolithina	—	—	—	
Chondrichthyes	0.014	0.021	0.013	0
Osteichthyes	0.026	—	—	0 ⁴

Appendix 2. (cont.) Origination Rates per million years for specific taxa.

	Late Permian	Early Triassic	Middle Triassic	Late Triassic
Foraminifera	0.004	0	0.018	0.014
Porifera	0.007	0	0.018	0.002
Anthozoa	0.035	0.041	0.162	0.003
Gastropoda	0.008	0.005	0.051	0.011
Pelecypoda	0.008	0.009	0.017	0.015
Nautiloidea + Coleoidea	0.018	0	0.046	0.018
Ammonoidea	0.036	0.425	0.154	0.060
All Cephalopoda	0.029	0.228	0.132	0.047
Trilobita	—	—	—	—
Ostracoda	0.022	0.026	0	0
Malacostraca	0.081	0.026	0.013	0.032
Bryozoa	0	0	0	0.028
Brachiopoda	0.005	0.034	0.016	0.021
Crinoidea	0.021	0	0.167	0.023
Echinoidea	0	0	0	0.116
Conodonta	0	0	0	0
Graptolithina	—	—	—	—
Chondrichthyes	0	0	0	0.012
Osteichthyes	0.041	0.155	0.086	0.020

Appendix 2. (cont.) Origination rates per million years for specific taxa.

	Early Jurassic	Middle Jurassic	Late Jurassic	Early Cretaceous
Foraminifera	0.005	0.007	0	0.007
Porifera	0.007	0.012	0.022	0.003
Anthozoa	0.021	0.010	0.011	0.011
Gastropoda	0.008	0.006	0.009	0.006
Pelecypoda	0.006	0.006	0.003	0.005
Nautiloidea + Coleoidea	0.077	0.021	0.020	0.003
Ammonoidea	0.122	0.088	0.046	0.049
All Cephalopoda	0.094	0.051	0.031	0.029
Trilobita	---	---	---	---
Ostracoda	0.015	0.017	0.005	0.002
Malacostraca	0.023	0.019	0.020	0.009
Bryozoa	0.017	0.036	0.008	0.006
Brachiopoda	0.014	0.021	0	0.002
Crinoidea	0.036	0.029	0.017	0.005
Echinoidea	0.039	0.014	0.004	0.007
Conodonta	---	---	---	---
Graptolithina	---	---	---	---
Chondrichthyes	0.040	0	0.025	0.003
Osteichthyes	0.004	0.005	0.040	0.008

Appendix 2. (cont.) Origination rates per million years for specific taxa.

	Late Cretaceous	Paleocene	Eocene	Oligocene	Neogene ¹
Foraminifera	0.008	0.017	0.003	0.001	0.001
Porifera	0.008	0	0.003	0.002	0.005
Anthozoa	0.007	0.003	0.008	0	0.001
Gastropoda	0.013	0.016	0.006	0.002	0.002
Pelecypoda	0.005	0.006	0.014	0.004	0.005
Nautiloidea + Coleoidea	0.010	0.051	0.057	0.011	0.035
Ammonoidea	0.013	---	---	---	---
All Cephalopoda	0.011	0.051	0.057	0.011	0.035
Trilobita	---	---	---	---	---
Ostracoda	0.007	0.004	0.002	0	0
Malacostraca	0.005	0.003	0.021	0.005	0.005
Bryozoa	0.035	0.002	0.019	0.002	0.003
Brachiopoda	0.007	0	0.020	0	0.007
Crinoidea	0.017	0.011	0.012	0	0.008
Echinoidea	0.015	0.004	0.024	0.012	0.007
Conodonta	---	---	---	---	---
Graptolithina	---	---	---	---	---
Chondrichthyes	0.009	0.005	0.003	0	0.002
Osteichthyes	0.045	0.031	0.061	0.007	0.006

Appendix 3. Weighted regressions of \log_{10} origination rate on time, for families of single taxa.

	Slope	r^2	Tightness	$s_{y \cdot x}$
Foraminifera				
Paleozoic	-0.00377 \pm 0.00182	0.35	0.99989	0.380
post-Paleozoic	-0.00364 \pm 0.00166	0.38	0.99991	0.362
Triassic/Early Cretaceous	-0.00181 \pm 0.00259	0.14	0.99992	0.221
Late Cretaceous/Neogene	-0.01650 \pm 0.00182	0.85	0.99980	0.234
Porifera				
Paleozoic	-0.00193 \pm 0.00177	0.12	0.99989	0.421
post-Paleozoic	-0.00181 \pm 0.00153	0.15	0.99992	0.330
Triassic/Early Cretaceous	-0.00198 \pm 0.00399	0.06	0.99975	0.396
Late Cretaceous/Neogene	-0.00475 \pm 0.00617	0.23	0.99970	0.294
Anthozoa				
Paleozoic	-0.00611 \pm 0.00224	0.52	0.99986	0.389
post-Paleozoic	-0.00484 \pm 0.00132	0.60	0.99994	0.288
Triassic/Early Cretaceous	-0.00235 \pm 0.00379	0.07	0.99971	0.377
Late Cretaceous/Neogene	-0.00974 \pm 0.00338	0.81	0.99991	0.161
Gastropoda				
Paleozoic	-0.00641 \pm 0.00211	0.54	0.99986	0.453
post-Paleozoic	-0.00247 \pm 0.00122	0.29	0.99994	0.300
Triassic/Early Cretaceous	-0.00299 \pm 0.00213	0.28	0.99991	0.225
Late Cretaceous/Neogene	-0.01332 \pm 0.00268	0.89	0.99991	0.148
Pelecypoda				
Paleozoic	-0.00268 \pm 0.00140	0.31	0.99994	0.285
post-Paleozoic	-0.00090 \pm 0.00079	0.12	0.99998	0.195
Triassic/Early Cretaceous	-0.00399 \pm 0.00148	0.59	0.99996	0.157
Late Cretaceous/Neogene	-0.00029 \pm 0.00334	0.00	0.99987	0.188
Nautiloidea + Coleoidea				
Paleozoic	-0.00367 \pm 0.00146	0.41	0.99992	0.317
post-Paleozoic	-0.00079 \pm 0.00195	0.02	0.99986	0.446
Triassic/Early Cretaceous	-0.00877 \pm 0.00310	0.67	0.99985	0.305
Late Cretaceous/Neogene	+0.00679 \pm 0.00539	0.35	0.99965	0.305
Ammonoidea				
Paleozoic	-0.00506 \pm 0.00166	0.65	0.99994	0.193
post-Paleozoic	-0.00626 \pm 0.00133	0.79	0.99996	0.187
Triassic/Early Cretaceous	-0.00415 \pm 0.00172	0.54	0.99994	0.198
All Cephalopoda				
Paleozoic	-0.00101 \pm 0.00100	0.10	0.99996	0.227
post-Paleozoic	-0.00343 \pm 0.00118	0.46	0.99994	0.271
Triassic/Early Cretaceous	-0.00527 \pm 0.00146	0.72	0.99996	0.157
late Cretaceous/Neogene	+0.00655 \pm 0.00474	0.39	0.99973	0.266
Trilobita				
all = Paleozoic	-0.01088 \pm 0.00139	0.91	0.99995	0.279
Ostracoda				
Paleozoic	-0.00552 \pm 0.00171	0.57	0.99991	0.392
post-Paleozoic	-0.00381 \pm 0.00144	0.54	0.99995	0.259
Triassic/Early Cretaceous	-0.00558 \pm 0.00262	0.60	0.99992	0.225
Late Cretaceous/Neogene	-0.01446 \pm 0.00112	0.99	0.99999	0.036
Malacostraca				
Paleozoic	+0.00064 \pm 0.00111	0.04	0.99996	0.263
post-Paleozoic	-0.00310 \pm 0.00097	0.50	0.99996	0.228
Triassic/Early Cretaceous	-0.00389 \pm 0.00134	0.63	0.99996	0.142
Late Cretaceous/Neogene	-0.00010 \pm 0.00516	0.00	0.99968	0.286

Appendix 3., cont.

	Slope	r^2	Tightness	$s_{y \cdot x}$
Bryozoa				
Paleozoic	-0.00604+0.00146	0.77	0.99996	0.231
post-Paleozoic	-0.00335+0.00221	0.22	0.99984	0.438
Triassic/Early Cretaceous	-0.00445+0.00292	0.44	0.99990	0.238
Late Cretaceous/Neogene	-0.01448+0.00745	0.56	0.99933	0.411
Brachiopoda				
Paleozoic	-0.00323+0.00060	0.73	0.99998	0.177
Post-Paleozoic	-0.00241+0.00139	0.30	0.99995	0.298
Triassic/Early Cretaceous	-0.00896+0.00171	0.87	0.99995	0.166
Late Cretaceous/Neogene	-0.00418+0.00542	0.37	0.99988	0.202
Crinoidea				
Paleozoic	-0.00545+0.00177	0.54	0.99990	0.342
post-Paleozoic	-0.00375+0.00136	0.49	0.99994	0.271
Triassic/Early Cretaceous	-0.01006+0.00199	0.86	0.99994	0.175
Late Cretaceous/Neogene	-0.00813+0.00141	0.94	0.99998	0.065
Echinoidea				
Paleozoic	-0.00663+0.00357	0.77	0.99995	0.273
post-Paleozoic	-0.00201+0.00160	0.17	0.99992	0.316
Triassic/Early Cretaceous	-0.00935+0.00296	0.77	0.99990	0.226
Late Cretaceous/Neogene	-0.00368+0.00467	0.17	0.99974	0.262
Conodonta				
Paleozoic	-0.00480+0.00170	0.44	0.99988	0.460
all	-0.00665+0.00172	0.60	0.99988	0.525
Graptolithina				
all = Paleozoic	-0.02003+0.00339	0.90	0.99982	0.377
Chondrichthyes				
Paleozoic	-0.01161+0.00288	0.84	0.99990	0.200
post-Paleozoic	-0.00514+0.00189	0.55	0.99992	0.354
Triassic/Early Cretaceous	-0.00469+0.00616	0.22	0.99970	0.422
Late Cretaceous/Neogene	-0.01654+0.00031	1.00	1.00000	0.014
Osteichthyes				
Paleozoic	-0.00471+0.00430	0.38	0.99985	0.344
post-Paleozoic	-0.00146+0.00205	0.05	0.99983	0.477
Triassic/Early Cretaceous	-0.00440+0.00439	0.17	0.99962	0.467
Late Cretaceous/Neogene	-0.01518+0.00518	0.74	0.99968	0.272