

## HOW CONSTANT IS EXTINCTION?

Leigh M. Van Valen  
 Department of Biology (Whitman)  
 The University of Chicago  
 915 E. 57th Street  
 Chicago, Illinois 60637, U.S.A.

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**ABSTRACT:** Extinction rates for families within single higher taxa are approximately constant over intervals of 50 million years or more. This stationarity supports an interactive and equilibrial view of large-scale community evolution. Cladistic classifications preclude any such analyses.

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That extinction rates may have an aspect of constancy is not apparent from a cursory examination of the fossil record. There are intervals (now believed to vary from geologically minuscule to several million years in length) of mass extinctions (Newell, 1967), and Simpson (1944, 1953) found appreciable variation in numbers of extinctions at other times in the higher taxa he examined. When looked at from the viewpoint of extinction intensity, i.e. the probability of extinction per unit time rather than the absolute numbers of extinctions, the variation over geologic time remained (Van Valen, 1973, pp. 10-11), despite statements to the contrary by McCune (1982) and others.

Constancy appears when extinction intensity is looked at from the viewpoint of the age (survivorship) of the taxa at risk. This result resembles the randomness of radioactive decay, but I gave evidence that there is instead a dynamic feedback effect of some sort (Van Valen, 1973, pp. 12-16) and proposed the Red Queen's Hypothesis to explain it.

Another sort of constancy is also possible, what mathematicians call a **stationary process** (Feller, 1971, p. 88). Here we again consider normal geologic time, rather than survivorship time, but the probability of extinction fluctuates about a constant value, so that over some period of time (called the characteristic interval) the probability averages out to a value like that of other, perhaps overlapping, equal intervals.

The possibility of a stationary process would seem to be ruled out by the discovery of an exponential decline in extinction rate (Van Valen, 1984). The probability of extinction of marine families declines exponentially during the Paleozoic, is reset by the great Permian extinction, and then again declines exponentially during the Mesozoic and Cenozoic. (Comparison of the results of Raup (1978) with my results for families suggest that genera may have a similar pattern of extinction, but this is not yet adequately shown.) In a curious piece of work Kitchell and Pena (1984) conspicuously claimed to disprove the results of Van Valen (1984), when in fact what they actually did do was to directly confirm its two main discoveries (exponential decline and the Permian resetting). What they did disprove, in agreement with that paper but contrary to their own statement, were most of the main interpretive conclusions of Raup and Sepkoski (1982).

However, there are two ways of getting the pattern found by Van Valen (1984). Each higher taxon, like the Foraminifera or Osteichthyes, may itself have the pattern. Alternatively, the pattern may come from different abundances of higher taxa at different geological times. Thus ammonites have a higher extinction rate than do pelecypods; the ratio of ammonites to pelecypods is greater in the Triassic than in the Cretaceous (not to mention the Cenozoic, when there are no ammonites at

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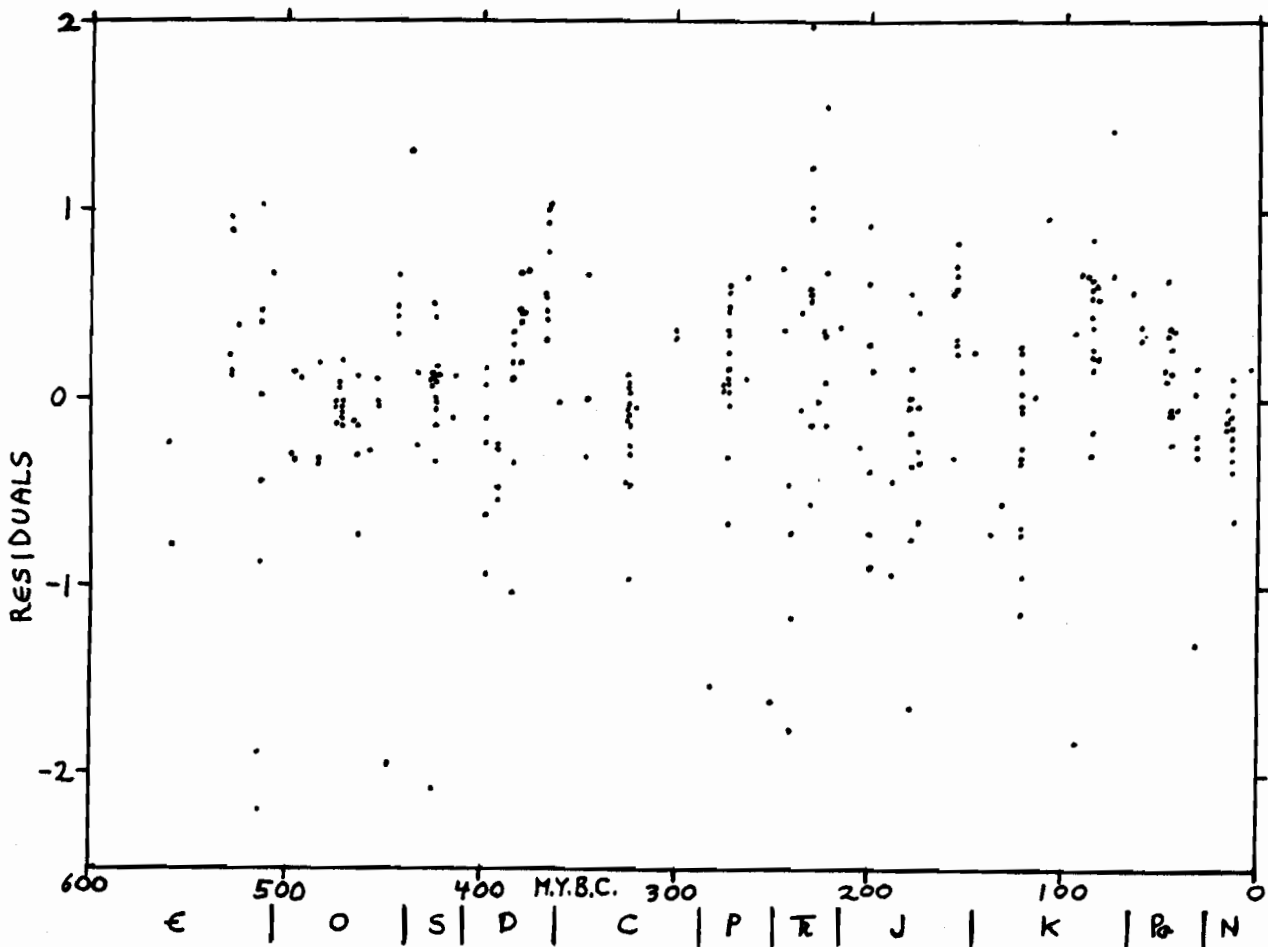


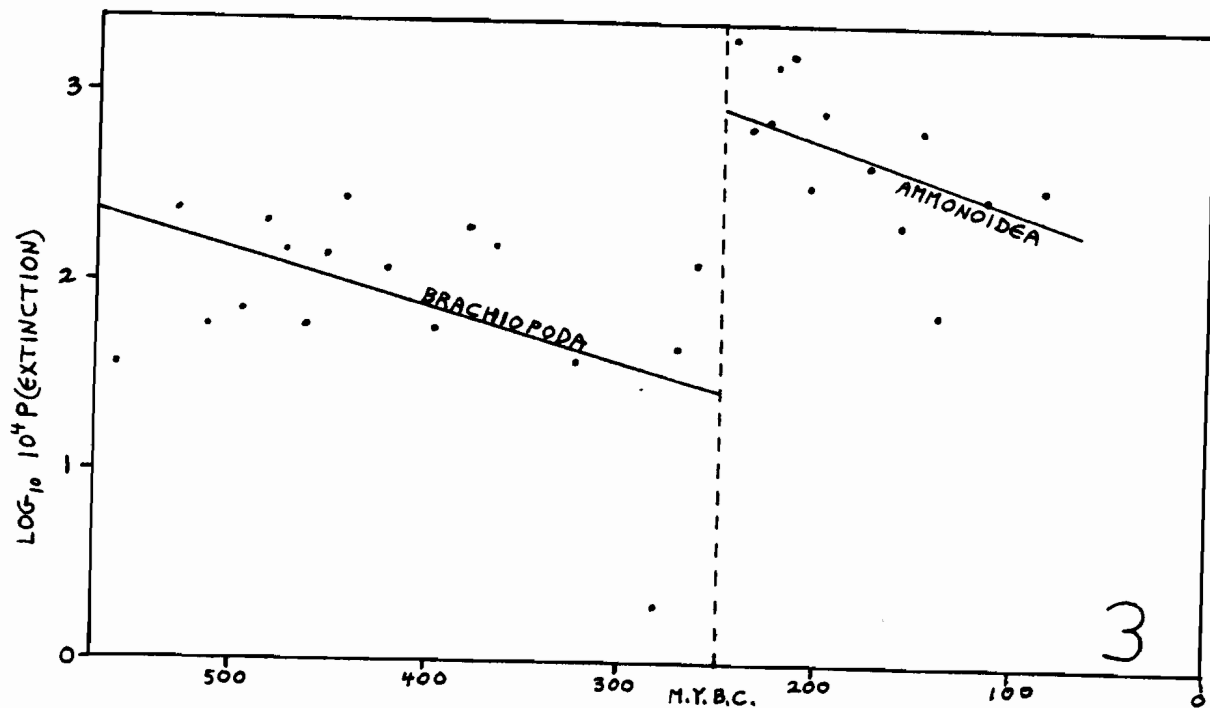
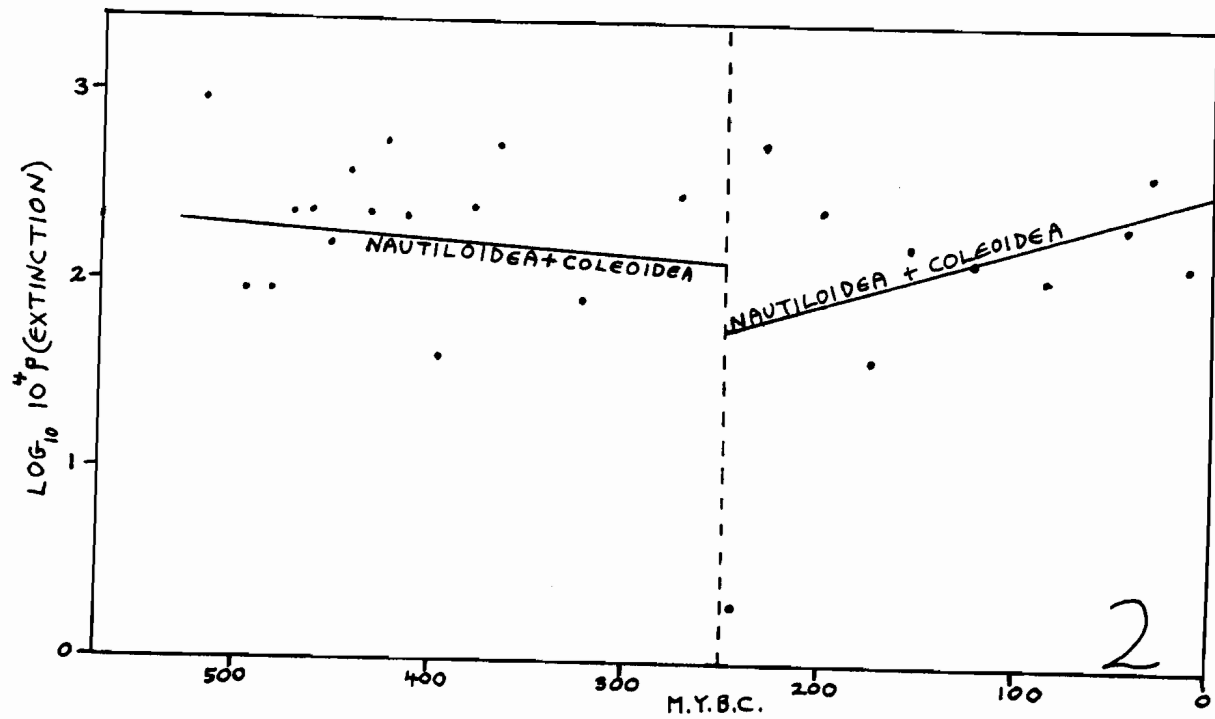
Figure 1. Residuals from the logarithmic regressions of extinction rate given in Table 1, plotted against geologic time. The points have very unequal precisions, in both directions.

all), and this could itself contribute to the pattern.

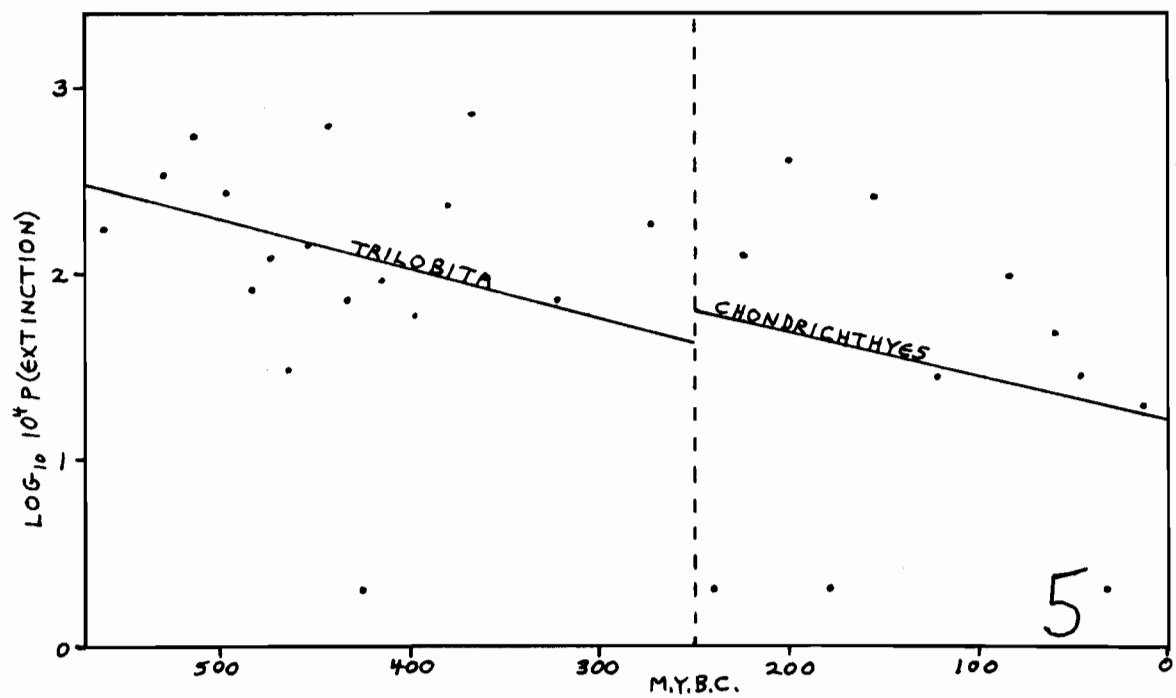
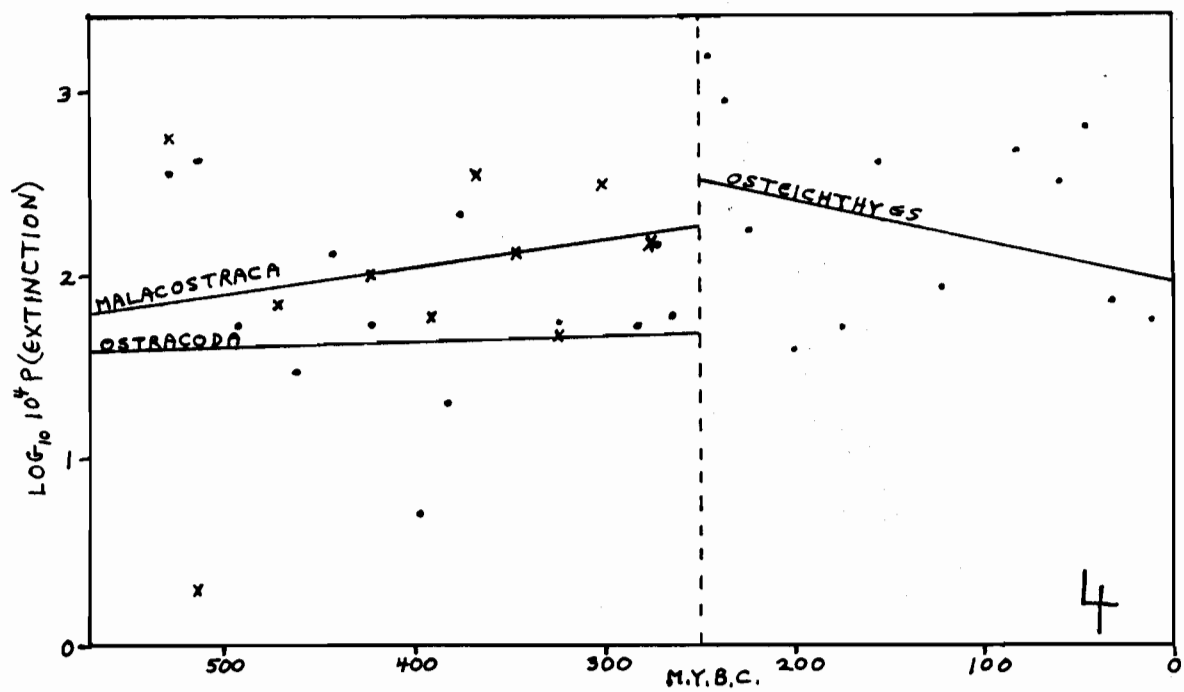
The second alternative turns out, surprisingly, to predominate. For single higher taxa, there is *no* overall trend in either the Paleozoic or post-Paleozoic: the average slope of extinction rate on time is not significantly different from 0, although there is some real heterogeneity among taxa in their slopes. This approximate stationarity (on this word see Feller, 1971) supports an equilibrial view of large-scale evolution.

#### METHODS AND RESULTS

I used Sepkoski's (1982) compilation of known stratigraphic ranges of marine families, the ranges being given to the stage level whenever possible, and an updated erratum sheet. I ignored soft-bodied groups, taxa with fewer than 25 families, taxa represented in fewer than 4 geologic periods, and (except for taxa abundant then) intervals before the late Cambrian. The arbitrary cut-off points were chosen before compilation of data and merely exclude groups with inadequate data. I calculated probabilities of extinction per million years in the way I did before (Van Valen, 1984), for each stage or (when very few families were present) set of several stages, of each of the 18 higher taxa listed in Appendix 1. Too few families ordinarily go extinct to make stage-level comparisons meaningful, so I



Figures 2-5. Scatter-plots and regressions for all regressions of Table 1 which are based on 10 or more groups of data. The points have very unequal precisions; in particular, the most deviant points are mostly of low precision. The vertical lines separate Paleozoic and post-Paleozoic regressions. In Figure 4, Malacostraca are represented by X.



combined the probabilities into, approximately, geologic periods or series by weighting the probability for each stage by the product of the estimated length of the stage and the number of families at risk. The number of stages combined depended on the number of extinctions occurring, so that error of estimation would not overwhelm any results. The result of this weighting approximates the average probability of extinction per family per million years over the combined interval. There is no reason to use equal intervals in this analysis, and use of unequal intervals permits identification and removal of effects of mass extinctions.

Among the higher taxa there is obvious heterogeneity in their probabilities of extinction, as is known; within taxa, there is some degree of homogeneity, except for mass extinctions. A hierarchical analysis of variance among periods, even excluding the late Ordovician, late Devonian, late Permian, and Maestrichtian mass extinctions and weighting each higher taxon equally, does show temporal heterogeneity in extinction rate within taxa, however ( $P < 0.01$ ). This heterogeneity remains when the Paleozoic and post-Paleozoic intervals are used for separate analyses of variance. Figure 1 shows the residuals from the regressions (discussed below) of  $\log_{10}$  extinction rate on time, plotted against time. The points have very unequal precision both vertically and horizontally, but nevertheless some regularities appear. Residuals for the early and middle Ordovician, early Devonian, Carboniferous, and Neogene are mostly below their regressions, while they are mostly above their regressions in the middle and late Devonian, early Permian, middle and late Triassic, late Jurassic, and pre-Maestrichtian late Cretaceous. Some other intervals are also probably deviant overall, but these are the clearest. In this respect the single taxa resemble, more than not, the pattern for the combined data of Van Valen (1984). Some intervals are relatively safe, for most taxa and overall, while others are more dangerous.

Appendix 2 shows how the specific taxa differ in their mean extinction probabilities. The range is more than an order of magnitude, and most taxa are similar before and after the late-Permian crisis. The Anthozoa, Ostracoda, Malacostraca, and probably the Bryozoa and Ammonoidea, do differ between the two intervals. In each case but the Ammonoidea the change is a decrease, and in each case there is a more or less severe bottleneck in diversity caused by the Permian crisis. Later ostracodes came from 6 families, malacostracans and bryozoans from only 3 each, and ammonites and anthozoans from 1 each. Thus the difference may reflect either temporal differences in their adaptive zones or differences in the organism's ability to respond adaptively to the perennial sea of troubles.

On the whole, taxa of more mobile individuals (including macroplankton) have a higher extinction rate, as found earlier (Van Valen, 1973) for genera and other taxa. Brachiopoda, post-Paleozoic Malacostraca, Paleozoic Anthozoa, Archaeocyatha (see below), and perhaps Crinoidea are exceptions. It is also possible to compare the groupings of Sepkoski (1981). By factor analysis of familial diversity patterns over time he separated three main groups of taxa, which succeeded each other in dominance through the Phanerozoic. The earliest large taxon, which he did not consider, would be the Archaeocyatha, which is almost confined to the early Cambrian. Its weighted extinction probability for families is  $0.0357 \pm 0.0115$ . Next, for Sepkoski's group 1, there is only the Trilobita among analyzable groups, with a probability of  $0.0247 \pm 0.0047$ . In both groups 1 and 2 are found the Brachiopoda, Graptolithina, and Conodonta, with a mean of  $0.0170 \pm 0.0039$ . Group 2 contains the Anthozoa, Cephalopoda, Ostracoda, and Crinoidea, with a mean of  $0.0142 \pm 0.0056$ . In both groups 2 and 3 are the Bryozoa,  $0.0040 \pm 0.0010$ . Group 3 contains the Foraminifera (or it would if Sepkoski had used them in his analysis), Porifera, Gastropoda, Pelecypoda, Malacostraca, Echinoidea, Chondrichthyes, and Osteichthyes, with a mean of  $0.0066 \pm 0.0022$ . Thus there is indeed an overall decline in extinction probabilities among groups which predominate later in time. This analysis, though, does not demonstrate that intergroup replacement is involved in the post-Paleozoic exponential decline, because group 3 predominates throughout this interval. The analysis also sheds no light on whether the differences among groups of higher taxa, or among the higher taxa themselves, are due to differences

among the organisms themselves or among the adaptive zones they occupy.

Examination of the data themselves shows various points of interest. For instance, all but one of the Triassic extinctions of gastropods are in the Archaeogastropoda, which was being replaced then; and for the Ostracoda, Bryozoa, and Brachiopoda the first stage of the Triassic seems to continue the late Permian extinction.

Nevertheless, there is no significant trend in familial extinctions within higher taxa. Appendix 3 shows the slopes of regressions of  $\log_{10}$  of the probability of extinction on time. (This procedure linearizes exponential decline such as found for the whole data set, and the residuals are distributed normally on a logarithmic scale, not on an arithmetic one.) The late Permian and Maestrichtian were excluded, as my earlier analysis (Van Valen, 1984) showed these extinctions to deviate far from their respective regressions and thus to represent unique events. The other major extinctions are part of the normally distributed residuals about the regressions, so I include them in the analyses as I did before. Excluding them makes both the Paleozoic and the post-Paleozoic slopes of Table 1 average slightly and nonsignificantly greater in the positive direction, and thus even closer to stationarity. In this analysis I weighted the intervals as before.

In Figures 2-5 the data are plotted for all regressions which used 10 or more groupings of data. The degree of linearity can be seen, despite the inclusion of some data of low precision.

The mean slopes are  $+0.00059 \pm 0.00083$  for the Paleozoic and  $-0.00144 \pm 0.00133$  for the post-Paleozoic, not significantly different from 0 or from each other, although a difference may well exist. The corresponding slopes for all families considered jointly (Van Valen, 1984) are  $-0.00313 \pm 0.00044$  and  $-0.00453 \pm 0.00060$ . Both mean slopes are larger in the positive direction, and are closer to 0, than are the respective joint slopes ( $P = 0.0002$  and  $0.04$  for the Paleozoic and post-Paleozoic, respectively). These results mean that any average within-group decline in the probability of extinction is less than the overall decline and may be 0 or even an increase. Nevertheless, there is significant heterogeneity among the slopes of different taxa in each of the two time intervals ( $P < 0.02$ ).

The null result is not an artifact of the method. It is well known (Kurtén, 1960) that longer intervals do not permit detection of as high evolutionary rates as do shorter intervals. However, although the intervals covered by the regressions are long, the standard errors are small enough to allow detection of trends appreciably less pronounced than those found earlier (Van Valen, 1984) for the combined data. If the data were measured in units of, say, 10 Myr rather than of 1 Myr, the slopes would be ten times as steep but the standard errors would also be ten times as great. The inclusion of extant taxa in the post-Paleozoic data does create some bias (Raup, 1979; Van Valen, 1979) toward a decreasing regression. This obviously does not account for the ostensibly opposite average trend in the Paleozoic, which moreover is in ostensibly the opposite direction from the trend for the combined Paleozoic data.

## DISCUSSION

Within higher taxa in more or less normal times there is little or no overall trend in the probability of extinction of their constituent families. Therefore a rough approximation to a stationary process exists, i.e. a situation where the probability over some characteristic interval (here about 50 million years) does not change over time. It does change in some taxa, but in the opposite direction in others, and in 28 of the 31 cases the ostensible change has a less negative slope than that of the overall trend, or even an ostensibly positive slope ( $P < 0.01$  by the sign test). Individual higher taxa contain too few families to permit taxon-specific idiosyncrasies to be identified to specific taxa with any confidence. It is interesting that the extinction rate of Cenozoic mammalian families also approximates a stationary process (Van Valen, 1973, Fig. 8D.)

The combination of approximate stationarity in extinction within higher taxa,

with the exponential decline in the combined data, is discussed in a broader context in an accompanying paper (Van Valen, 1985). It is not, however, an automatic result of there being some taxa with high extinction rates for families and others with low rates. One might think that groups with high extinction would die out and leave a low-extinction residue. Indeed, the Archaeocyatha have a high rate and do die out very soon, in fact too soon to make a regression useful for them. However, the Cephalopoda also have a high rate and have persisted since the Cambrian. The overall effect comes both from early extinction or great decline of some such groups and a larger increase in number of families within groups having low extinction rates.

Families now alive have more species, on the average, than families did in the Triassic, and families with more species are normally more resistant to extinction than are those with fewer. Flessa and Jablonski (1985) have proposed that the conjunction of these facts may explain the decrease in probability of familial extinction since the end of the Paleozoic. Probably this mechanism does have some effect, but it should operate at least as strongly within single higher taxa as for the combined data. We see that there is no detectable decline at all within higher taxa. The Echinoidea, for which the evidence on increase in species per family is best (Raup, 1975), have a nonsignificant **increase** in extinction rate. Therefore the two overall declines, which are of surprisingly large magnitude, must be predominantly explained otherwise.

Most data on taxa below family are not yet adequate to test stationarity of extinction rates in a general way. For instance, the variation in extinction rate of planktonic foraminiferal species, erroneously claimed by Wei and Kennett (1983) to oppose my earlier work (Van Valen, 1973), is as consistent with a stationary process with a characteristic interval of perhaps 5 Myr as it is with nonstationarity. Nevertheless, data for species of both centric and pennate diatoms, and for genera of benthic foraminiferans, support stationarity (Van Valen, 1973, figs. 8A and 8B), with characteristic intervals of perhaps 8 Myr and 20 Myr respectively. As can be seen from Figure 1 of Van Valen (1975), clades of large mammals also have stationary extinction except for the magafaunal extinction of the late Pleistocene. (What is there called early Pliocene is now called late Miocene, by recent definitional fiat.)

I find it surprising that there is even such a rough approximation to stationarity as occurs with families. It has long been known that extinction rates vary appreciably over time. However, the stationarity shows that much or probably most of this variation is over relatively short intervals and that something (presumably ecological) constrains the probability to fluctuate about a more or less characteristic value. This then is, in one sense, how different taxa like ammonites and pelecypods come to have different probabilities of extinction which are rather characteristic for the group.

It should be obvious that a cladistic classification would completely preclude any analysis of this sort: ranks of such taxa depend on time, indirectly if not directly, and so such taxa cannot be compared over time. For instance, the Ordovician nautiloid family Ellesmeroceratidae, if recognized as a taxon at all (it may be paraphyletic), would be placed either in a different rank from the extant Nautilidae (itself paraphyletic with respect to some extinct families) or in a "plesion" which is given no rank at all. The same conclusion holds for each holophyletic subset of these families. But the families are comparable to each other adaptively and are parts of phylogenies delimited adaptively, as inferred from changes in morphology. They are thus natural taxa (Van Valen, 1978) and are suitable for use in comparative analysis.

Invariants are rare in the complex ebb and flow of evolutionary processes. That extinction rates can approximate such invariants makes them unexpectedly valuable in the prospective development of evolutionary theory.



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## Appendix 1. Probabilities of familial extinction per million years.

	Late Cambrian	Early & Middle Ordovician	Late Ordovician	Silurian	Early & Middle Devonian	Late Devonian
Foraminifera	---	0	0	0	0	0.005
Porifera	0.014	0.002	0.006	0.010	0.002	0.034
Anthozoa	---	0.005	0.020	0.013	0.024	0.021
Gastropoda	0	0.001	0	0.001	0.005	0.002
Pelecypoda	---	0.004	0.010	0.005	0.006	0.009
Nautiloidea & Belemnoida	0.091	0.016	0.039	0.030	0.012	0.054
Ammonoidea	---	0	0	0	0.037	0.094
all Cephalopoda	0.091	0.016	0.039	0.029	0.017	0.073
Trilobita	0.029 <sup>2</sup>	0.015	0.061	0.006	0.013	0.071
Ostracoda	0.043	0.004	0.013	0.005	0.005	0.028
Malacostraca	---	0.007 <sup>3</sup>	0	0.010	0.006	0.035
Bryozoa	---	0.003	0.011	0.007	0.009	0.006
Brachiopoda	0.016 <sup>4</sup>	0.011	0.028	0.012	0.012	0.016
Crinoidea	---	0.019	0.033	0.016	0.020	0.016
Echinoidea	---	0 <sup>5</sup>	0.050	---	0	0
Conodonta	0	0.022	0.046	0.020	0.005	0.032
Graptolithina	0.016	0.015	0.036	0.030	0.033 <sup>6</sup>	---
Chondrichthyes	---	---	---	---	0	0.016
Osteichthyes	---	---	---	---	0.018	0.059

<sup>1</sup>Including Pleistocene.<sup>2</sup>Including early and middle Cambrian.<sup>3</sup>Including late Cambrian.<sup>4</sup>Including middle Cambrian.<sup>5</sup>Including Silurian.<sup>6</sup>Including Carboniferous.

## Appendix 1. Probabilities of familial extinction per million years (cont.)

Early	Early		Late		Jurassic	Cretaceous
	Carboniferous	Permian	Permian	Triassic		
Foraminifera	0.002	0.001	0.054	0.002	0	0
Porifera	0.001	0.008	0.025	0.007	0.001	0.0003
Anthozoa	0.007	0.008	0.135	0	0.002	0
Gastropoda	0.002	0.005	0.029	0.010	0.004	0
Pelecypoda	0.001	0.003	0.013	0.004	0.003	0.001
Nautiloidea & Belemnoides	0.008	0.030	0	0.029	0.016	0.013
Ammonoidea	0.022	0.015	0.128	0.123	0.047	0.024
all Cephalopoda	0.016	0.019	0.089	0.085	0.031	0.020
Trilobita	0.007	0.018	0.200	---	---	---
Ostracoda	0.006	0.008	0.061	0.015	0.001	0.001
Malacostraca	0.018	0.015	0.040	0.019	0.005	0.002
Bryozoa	0.003	0.005	0.100	0.030	0	0.001
Brachiopoda	0.004	0.006	0.105	0.022	0.010	0.005
Crinoidea	0.010	0.010	0.190	0.037	0.006	0.014
Echinoidea	0.005	0.036	0.067	0.009	0.003	0.002
Conodonta	0.013	0.020	0	0.029	---	---
Graptolithina	---	---	---	---	---	---
Chondrichthyes	0.012	0	0.086	0.007	0.005	0
Osteichthyes	0.007	0	0.044	0.022	0.007	0.004

## Appendix 1. Probabilities of familial extinction per million years (cont.)

	Late Cretaceous except Maestrichtian	Maestrichtian	Paleogene	Neogene <sup>1</sup>
Foraminifera	0.002	0.012	0.003	0.002
Porifera	0.010	0.036	0.006	0.005
Anthozoa	0.005	0	0.003	0.001
Gastropoda	0.002	0.015	0.002	0.0004
Pelecypoda	0.004	0.024	0.0009	0.002
Nautiloidea & Belemnoidea	0.011	0.106	0.027	0.013
Ammonoidea	0.034	0.167	---	---
all Cephalopoda	0.026	0.142	0.027	0.013
Trilobita	---	---	---	---
Ostracoda	0	0.007	0	0
Malacostraca	0.005	0.007	0	0
Bryozoa	0.007	0.020	0.002	0.003
Brachiopoda	0.003	0.013	0.002	0
Crinoidea	0.019	0	0.005	0.004
Echinoidea	0.007	0.037	0.007	0.004
Conodonta	---	---	---	---
Graptolithina	---	---	---	---
Chondrichthyes	0.002	0.001	0.004	0.002
Osteichthyes	0.024	0.024	0.003	0.006

Appendix 2. Weighted means and coefficients of variation for extinction probabilities (of families, per million years), on an arithmetic scale. Values are given  $\times 10^4$ .

	Excluding Late Permian and Maestrichtian		Including Late Permian and Maestrichtian	
	Mean	C.V.	Mean	C.V.
Foraminifera				
all	15.1 $\pm$ 3.3	91	28.4 $\pm$ 17.6	271
Paleozoic	16.7 $\pm$ 5.2	88	53.0 $\pm$ 44.8	253
post-Paleozoic	14.4 $\pm$ 4.4	93	18.1 $\pm$ 7.2	130
Porifera				
all	49.5 $\pm$ 14.5	117	59.2 $\pm$ 18.0	129
Paleozoic	60.7 $\pm$ 29.7	130	68.9 $\pm$ 30.3	125
post-Paleozoic	42.9 $\pm$ 13.3	93	53.5 $\pm$ 21.9	130
Anthozoa				
all	83.2 $\pm$ 21.6	90	102.5 $\pm$ 47.1	172
Paleozoic	127.3 $\pm$ 27.7	53	161.0 $\pm$ 79.7	131
post-Paleozoic	20.3 $\pm$ 6.6	80	19.7 $\pm$ 6.2	83
Gastropoda				
all	25.6 $\pm$ 6.8	100	31.8 $\pm$ 10.7	135
Paleozoic	24.9 $\pm$ 5.8	57	35.2 $\pm$ 20.0	150
post-Paleozoic	25.9 $\pm$ 10.5	114	30.2 $\pm$ 12.3	122
Pelecypoda				
all	26.5 $\pm$ 5.6	85	32.4 $\pm$ 9.2	120
Paleozoic	34.6 $\pm$ 9.6	74	40.2 $\pm$ 11.6	82
post-Paleozoic	23.5 $\pm$ 6.8	87	29.4 $\pm$ 12.8	138
Nautiloidea + Coleoidea				
all	206.2 $\pm$ 30.3	73	210.2 $\pm$ 32.0	79
Paleozoic	219.0 $\pm$ 40.2	71	216.5 $\pm$ 39.1	72
post-Paleozoic	176.2 $\pm$ 43.4	78	195.4 $\pm$ 56.4	96
Ammonoidea				
all	437.2 $\pm$ 88.1	86	479.5 $\pm$ 93.3	87
Paleozoic	307.3 $\pm$ 111.5	81	298.6 $\pm$ 99.2	81
post-Paleozoic	536.9 $\pm$ 116.6	78	565.3 $\pm$ 120.6	80
all Cephalopoda				
all	301.5 $\pm$ 42.0	80	321.5 $\pm$ 45.9	84
Paleozoic	242.8 $\pm$ 50.4	86	260.8 $\pm$ 54.4	88
post-Paleozoic	386.1 $\pm$ 65.2	68	409.5 $\pm$ 72.9	73
Trilobita				
all = Paleozoic	246.6 $\pm$ 45.8	77	246.5 $\pm$ 44.5	77
Ostracoda				
all	48.7 $\pm$ 15.7	144	57.3 $\pm$ 20.7	170
Paleozoic	69.3 $\pm$ 21.4	111	82.5 $\pm$ 30.2	137
post-Paleozoic	15.8 $\pm$ 15.0	252	17.5 $\pm$ 14.2	230
post-Early-Triassic	4.9 $\pm$ 4.1	206	7.1 $\pm$ 5.8	218
Malacostraca				
all	50.6 $\pm$ 20.5	176	54.1 $\pm$ 20.4	173
Paleozoic	171.5 $\pm$ 41.3	76	182.2 $\pm$ 41.1	75
post-Paleozoic	23.4 $\pm$ 14.5	186	24.8 $\pm$ 13.8	176

## Appendix 2, cont.

	Excluding Late Permian and Maestrichtian		Including Late Permian and Maestrichtian	
	Mean	C.V.	Mean	C.V.
Bryozoa				
all	40.0 $\pm$ 10.3	86	58.5 $\pm$ 34.2	211
Paleozoic	50.0 $\pm$ 8.4	38	82.2 $\pm$ 70.6	210
post-Paleozoic	32.0 $\pm$ 16.8	128	39.9 $\pm$ 20.3	134
post-Early-Triassic	27.3 $\pm$ 9.1	74	35.6 $\pm$ 17.1	118
Brachiopoda				
all	91.5 $\pm$ 14.7	77	118.7 $\pm$ 34.7	146
Paleozoic	95.6 $\pm$ 17.1	74	129.2 $\pm$ 44.6	147
post-Paleozoic	75.2 $\pm$ 28.1	92	76.4 $\pm$ 25.9	90
Crinioidea				
all	133.4 $\pm$ 16.7	47	165.5 $\pm$ 61.6	149
Paleozoic	141.6 $\pm$ 23.2	37	183.3 $\pm$ 111.2	149
post-Paleozoic	104.0 $\pm$ 28.1	81	101.7 $\pm$ 26.8	83
Echinoidea				
all	49.7 $\pm$ 13.2	84	61.2 $\pm$ 21.6	123
Paleozoic	68.8 $\pm$ 49.3	143	78.9 $\pm$ 55.7	158
post-Paleozoic	46.8 $\pm$ 8.7	45	58.5 $\pm$ 24.2	109
Conodonta				
all	200.2 $\pm$ 25.7	38	197.7 $\pm$ 25.2	40.3
Paleozoic	197.4 $\pm$ 27.1	39	194.9 $\pm$ 26.4	40.7
post-Paleozoic	290	—	—	—
Graptolithina				
all = Paleozoic	216.5 $\pm$ 27.5	28	—	—
Chondrichthyes				
all	103.3 $\pm$ 45.9	178	111.5 $\pm$ 47.5	181
Paleozoic	188.8 $\pm$ 134.3	159	224.3 $\pm$ 134.2	146
post-Paleozoic	72.8 $\pm$ 30.2	137	70.5 $\pm$ 28.6	140
Osteichthyes				
all	209.3 $\pm$ 58.2	108	210.5 $\pm$ 54.1	106
Paleozoic	190.2 $\pm$ 78.8	72	203.0 $\pm$ 72.0	71
post-Paleozoic	210.1 $\pm$ 66.0	109	210.9 $\pm$ 62.6	107

Appendix 3. Regressions of  $\log_{10}$  probability of familial extinction on time.

	slope	$r^2$	T	$s_{y \cdot x}$
Foraminifera				
Paleozoic	0.00632 $\pm$ 0.00399	0.29	0.99962	0.606
post-Paleozoic	0.00622 $\pm$ 0.00288	0.40	0.99977	0.547
Porifera				
Paleozoic	-0.00113 $\pm$ 0.00302	0.03	0.99982	0.499
post-Paleozoic	0.00603 $\pm$ 0.00362	0.28	0.99963	0.659
Anthozoa				
Paleozoic	-0.00164 $\pm$ 0.00198	0.15	0.99994	0.234
post-Paleozoic	0.00333 $\pm$ 0.00479	0.11	0.99963	0.664
Gastropoda				
Paleozoic	0.00297 $\pm$ 0.00151	0.49	0.99996	0.222
post-Paleozoic	-0.00314 $\pm$ 0.00338	0.13	0.99973	0.626
Pelecypoda				
Paleozoic	-0.00306 $\pm$ 0.00199	0.32	0.99992	0.318
post-Paleozoic	-0.00000 $\pm$ 0.00232	0.00	0.99985	0.463
Nautiloidea + Coleoidea				
Paleozoic	-0.00070 $\pm$ 0.00142	0.02	0.99990	0.338
post-Paleozoic	0.00369 $\pm$ 0.00294	0.17	0.99972	0.564
Ammonoidea				
Paleozoic	0.00301 $\pm$ 0.00627	0.05	0.99937	0.550
post-Paleozoic	-0.00354 $\pm$ 0.00129	0.41	0.99993	0.240
Trilobita				
Paleozoic	-0.00273 $\pm$ 0.00192	0.12	0.99978	0.468
Ostracoda				
Paleozoic	0.00027 $\pm$ 0.00200	0.00	0.99982	0.462
post-Paleozoic	-0.00605 $\pm$ 0.00406	0.31	0.99967	0.666
Malacostraca				
Paleozoic	0.00141 $\pm$ 0.00202	0.06	0.99987	0.395
post-Paleozoic	-0.01303 $\pm$ 0.00368	0.64	0.99962	0.501
Bryozoa				
Paleozoic	-0.00085 $\pm$ 0.00140	0.11	0.99998	0.175
post-Paleozoic	0.00492 $\pm$ 0.00395	0.28	0.99975	0.496
Brachiopoda				
Paleozoic	-0.00293 $\pm$ 0.00146	0.21	0.99987	0.434
post-Paleozoic	-0.00843 $\pm$ 0.00206	0.81	0.99993	0.337
Crinoidea				
Paleozoic	-0.00226 $\pm$ 0.00061	0.82	0.99999	0.076
post-Paleozoic	-0.00158 $\pm$ 0.00280	0.04	0.99978	0.486
Echinoidea				
Paleozoic	0.00844 $\pm$ 0.01120	0.22	0.99900	0.935
post-Paleozoic	0.00164 $\pm$ 0.00152	0.23	0.99996	0.210
Conodonta				
Paleozoic	-0.00002 $\pm$ 0.00249	0.00	0.99985	0.474
Graptolithina				
Paleozoic	0.00230 $\pm$ 0.00110	0.59	0.99999	0.082
Chondrichthyes				
post-Paleozoic	-0.00231 $\pm$ 0.00386	0.04	0.99946	0.754
Osteichthyes				
post-Paleozoic	-0.00218 $\pm$ 0.00240	0.09	0.99977	0.443

The tightness, T, measures how close the data are to colinearity relative to the variance (eigenvalue) along the major axis of the distribution; at a slope of 1, T reduces to the correlation, r (Van Valen, 1974). Estimated probabilities of 0 were taken to be 0.00002, a value lower than any non-0 value found. Most of the regressions were calculated using shorter intervals than those of Appendix 1.