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A NEW EVOLUTIONARY LAW

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ABSTRACT:

All groups for which data exist go extinct at a rate that is constant for a given group. When this is recast in ecological form (the effective environment of any homogeneous group of organisms deteriorates at a stochastically constant rate), no definite exceptions exist although a few are possible. Extinction rates are similar within some very broad categories and vary regularly with size of area inhabited. A new unit of rates for discrete phenomena, the macarthur, is introduced. Laws are appropriate in evolutionary biology. Truth needs more than correct predictions. The Law of Extinction is evidence for ecological significance and comparability of taxa. A non-Markovian hypothesis to explain the law invokes mutually incompatible optima within an adaptive zone. A self-perpetuating fluctuation results which can be stated in terms of an unstudied aspect of zero-sum game theory. The hypothesis can be derived from a view that momentary fitness is the amount of control of resources, which remain constant in total amount. The hypothesis implies that long-term fitness has only two components and that events of mutualism are rare. The hypothesis largely explains the observed pattern of molecular evolution.

*   *   *

Introduction

During a study (Van Valen, submitted) on the effects of extinction I wanted to show that a model I was using was oversimplified. It assumed no correlation of probability of extinction with age of the group, and I thought that generally more vulnerable groups should die out first. A test using data from Simpson (1953) showed to my astonishment that the assumption was reasonably correct in these cases. I did not believe it could be generally true and so tested these and other cases in more detail. The assumption proved to be consistent with all available data. Others (unpublished results) have now confirmed this finding for individual taxa. I will present a more extended treatment elsewhere; the present paper is condensed.

The Evidence

The method is an application of the survivorship curve of population ecology (including demography). It is a simple plot of the proportion of the original sample that survive for various intervals. In this case the sample is the set of all known subgroups of some larger group, no matter when in absolute time each subgroup originated. A logarithmic ordinate, standard in ecology, gives the property that the slope of the curve at any age is proportional to the probability of extinction at that age. Simpson (1944, 1953) compiled two well-known taxonomic survivorship curves but used an arithmetic ordinate (1-4).

The results (Figs. 1-5) for over 25,000 subtaxa show almost uniform linearity for extinct taxa except for effects attributable to sampling error (5,6). Sampling error is most noticeable at the bottom of the graphs, where
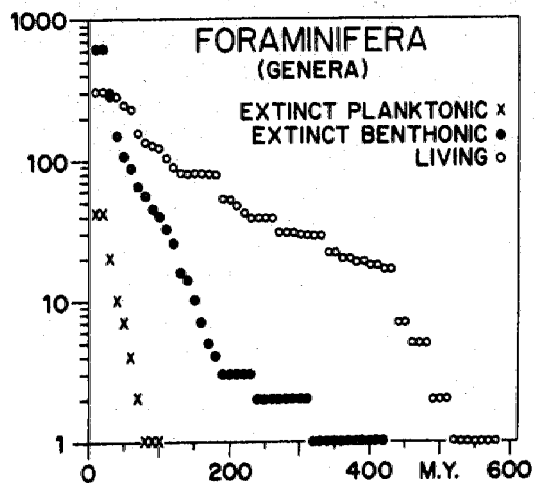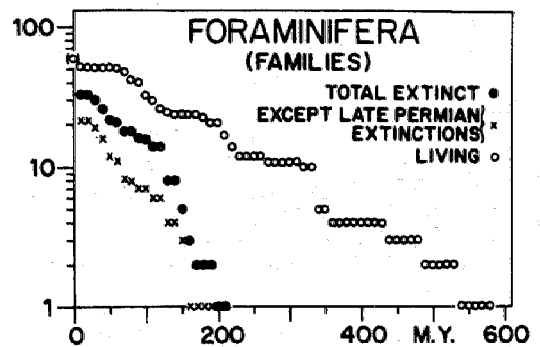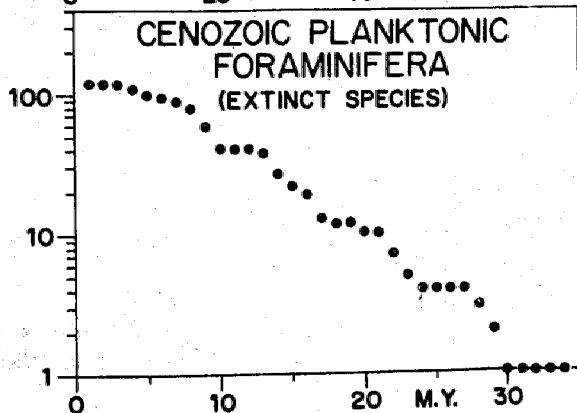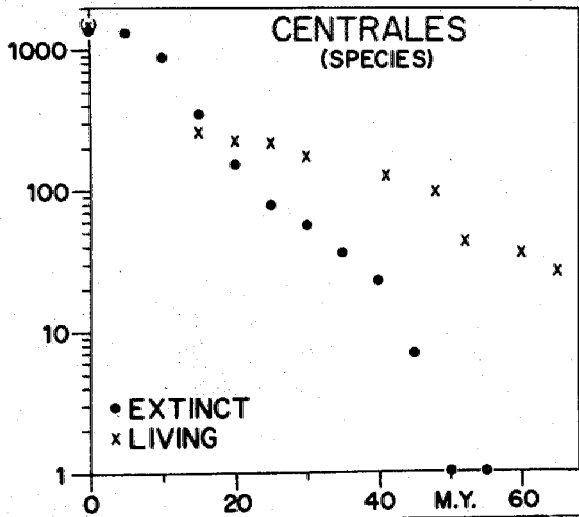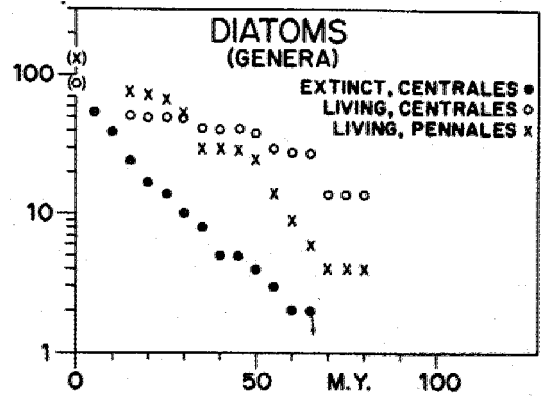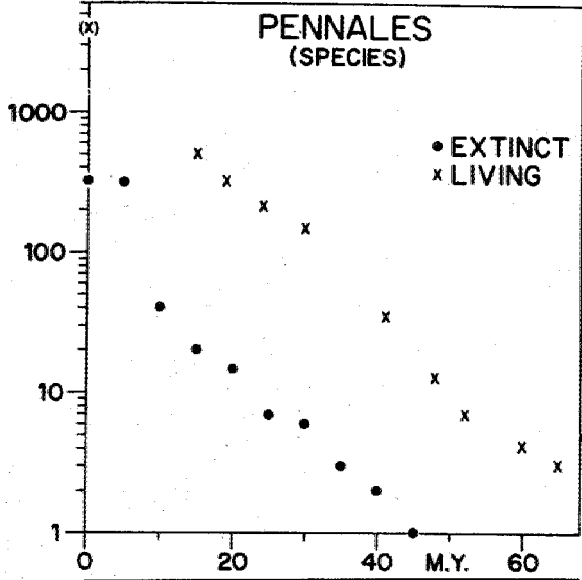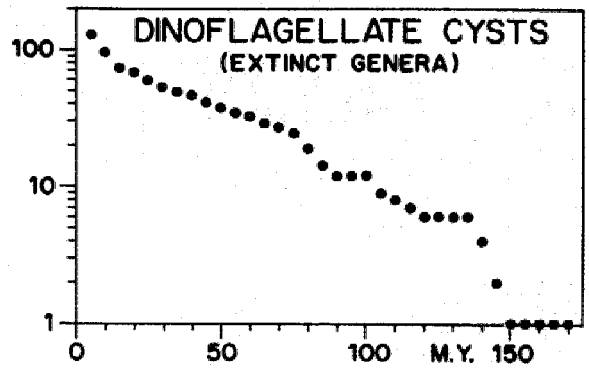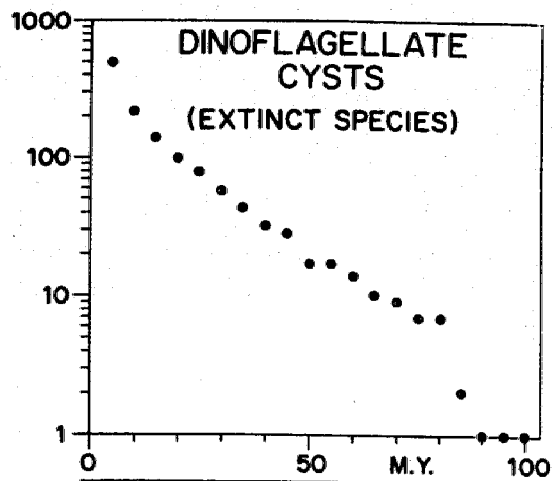
Fig. 1. Taxonomic survivorship curves for protists.
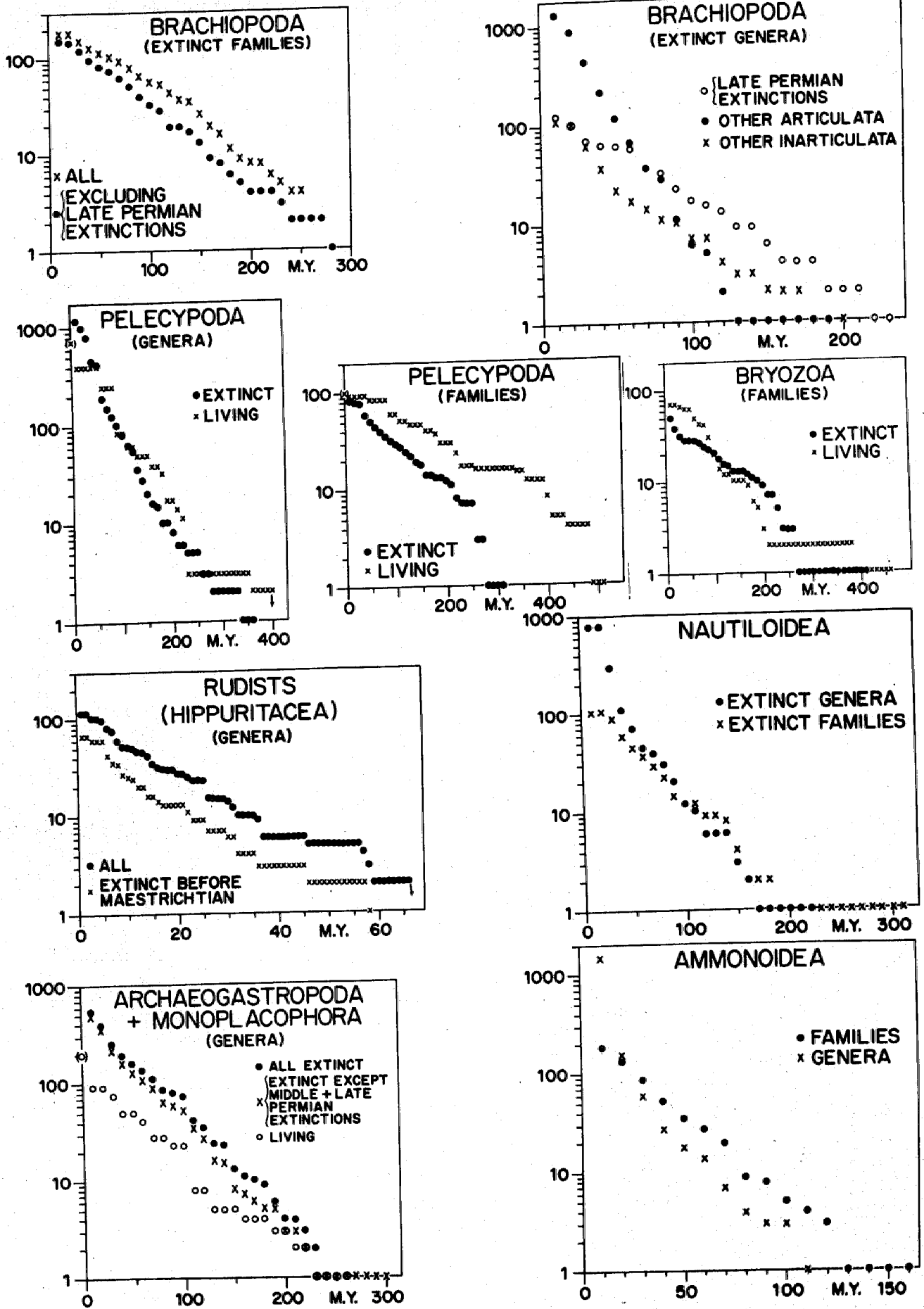
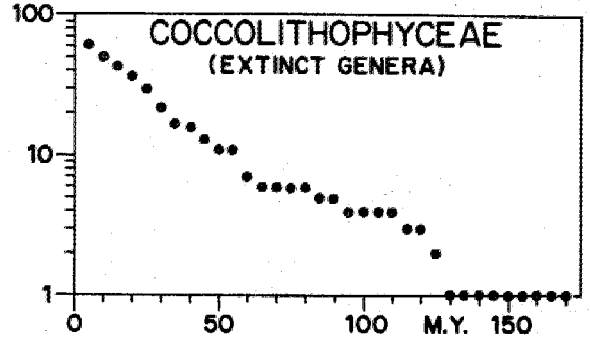Fig. 2. Taxonomic survivorship curves for Mollusca and Brachiopoda.

Fig. 3. Taxonomic survivorship curves for plants and invertebrates.

Fig. 4. Taxonomic survivorship curves for vertebrates. "Major therian orders" are those with individual plots.

Fig. 5. Taxonomic survivorship curves for mammals. For Primates,
Madagascar genera are omitted because the island lacks pre-
Pleistocene fossils. Polyprotodonta includes Caenolestoidea.

a few taxa have disproportionate weight, and at the left side, where inaccuracies in dating are most important (7). Usually, the more taxa included the closer is the approach to linearity.
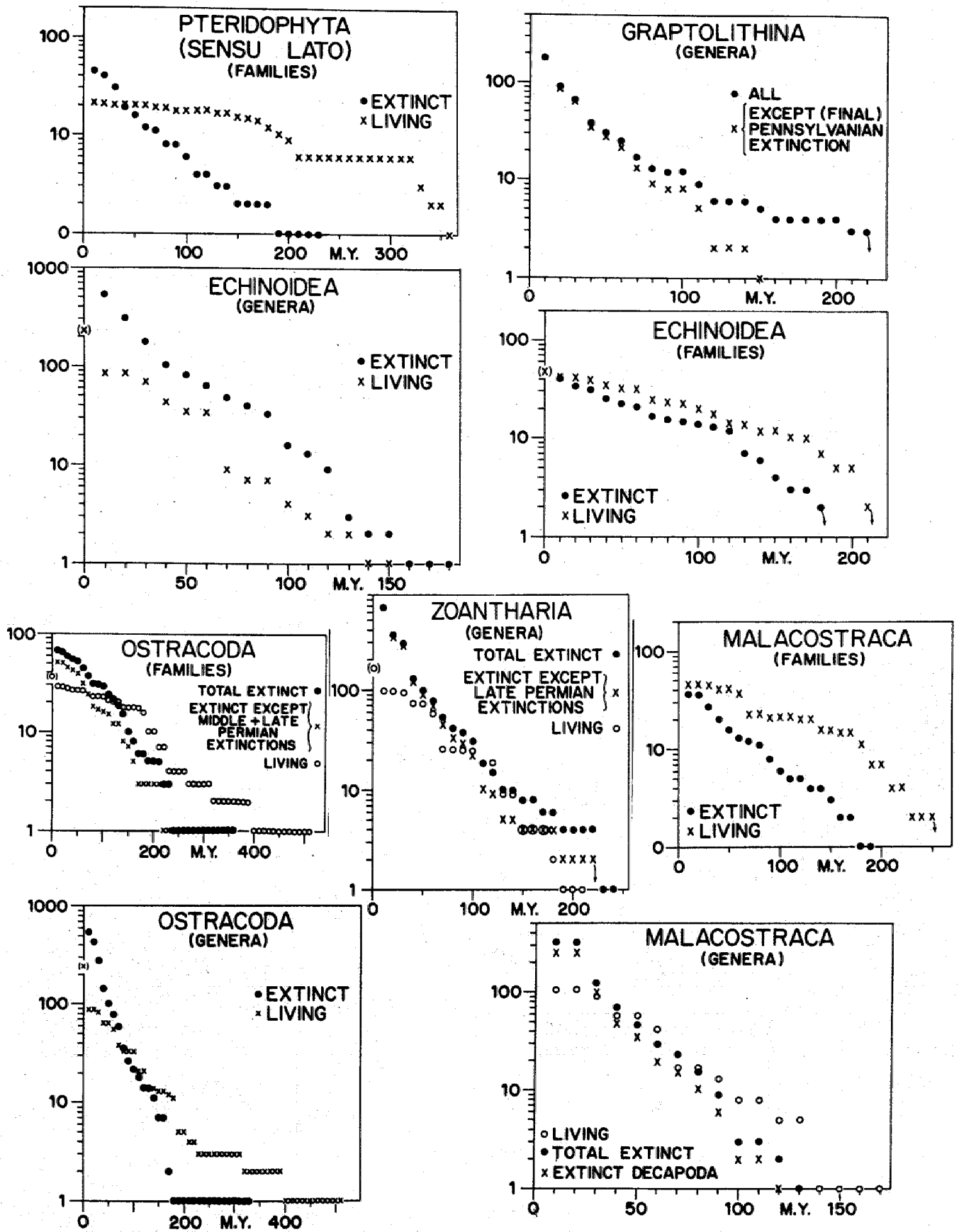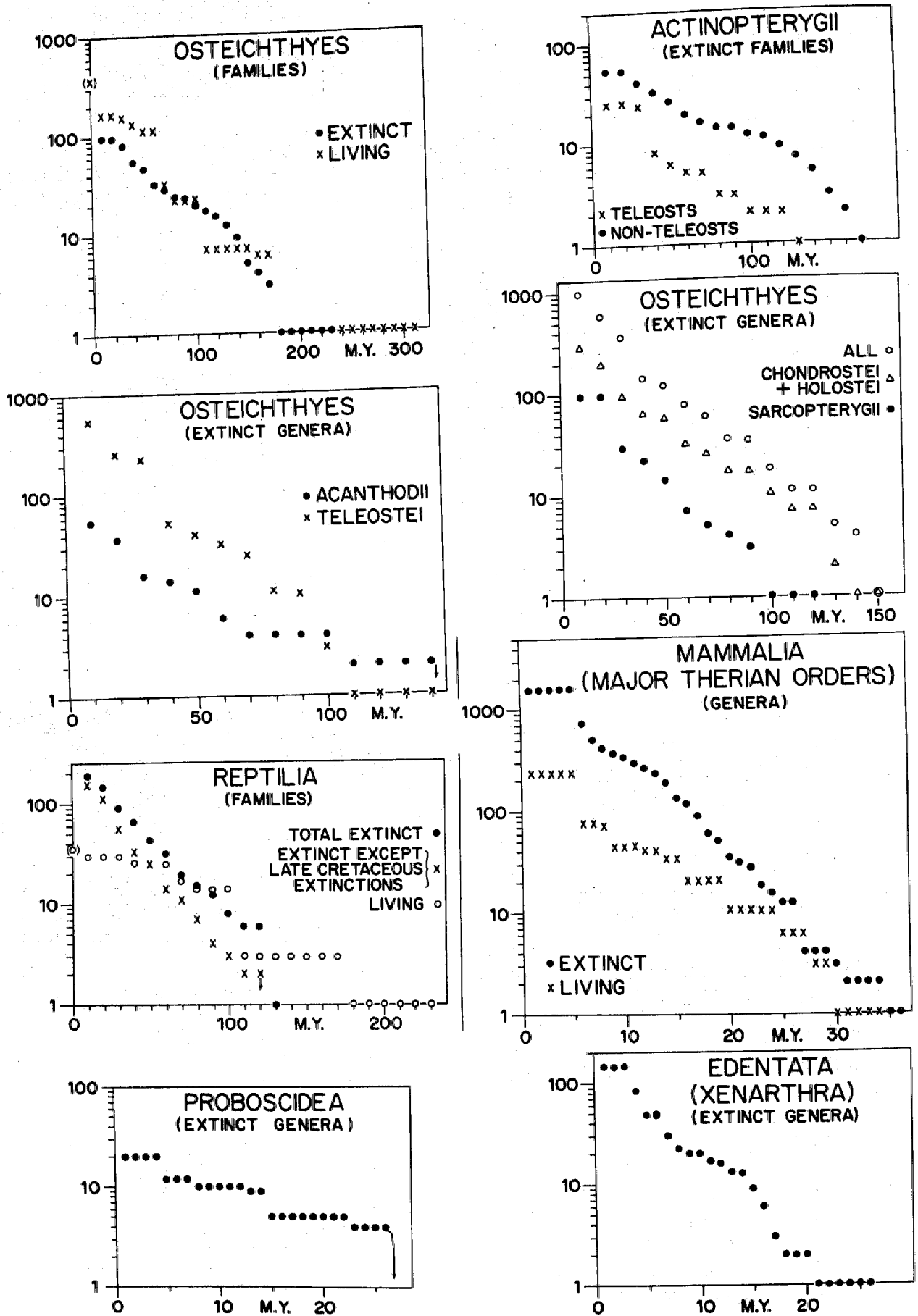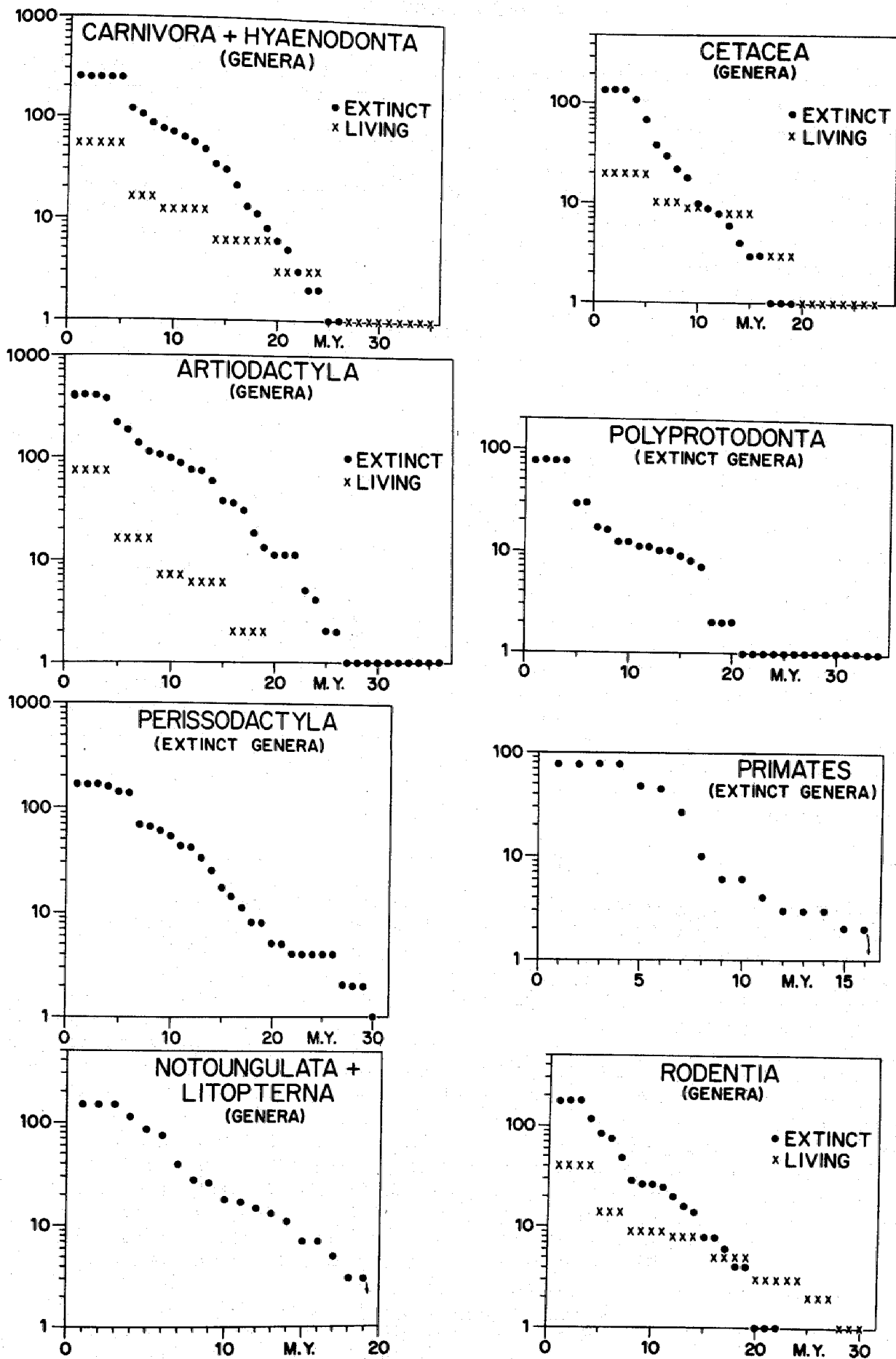
For living taxa linearity of the distribution requires both constant extinction and constant origination. It further requires that both be more nearly constant over absolute time than does a distribution for extinct taxa, which normally spans many overlapping half-lives of taxa, and that probability of discovery not decrease appreciably with age of strata. It is therefore surprising that many even of these distributions are linear (8).

Linearity is not an artifact of the method. Most survivorship curves for individuals are either markedly concave or markedly convex (9). Most small passerine birds are exceptional in having linear survivorship curves. The very wide diversity (biologically and stratigraphically) of groups plotted here argues against any kind of special artifact.

The sources of data usually do not distinguish between real extinction of a lineage and pseudo-extinction by evolution of one taxon into a successor taxon (Simpson, 1953). The latter proves to be negligible. Most taxa which give rise to successor taxa continue in their original form for an appreciable period after the branching. For families of mammals, for which I am familiar with the phylogeny, a maximum (and surely inflated) estimate is 20 per cent pseudo-extinction; a more likely estimate is 5 per cent. Ammonites (1) give 6 per cent (12 of 188 taxonomic extinctions for families). All other available phylogenies give similar results. The pattern of constant extinction remains unchanged whether pseudo-extinctions are included or excluded. Additionally, it is plausible that even pseudo-extinction usually implies the end of an adaptive mode and so would fit into the hypothesis given below. Pseudo-extinctions are probably more common at lower taxonomic levels, despite the counter-claim made or implied by Ruzhentsov (1963), MacGillavry (1968), and Eldredge (1971; Eldredge and Gould, 1972) that they do not occur for species. Any example of an ancestral taxon co-existing with a descendant taxon violates a basic premise of cladistic systematics (Hennig, 1966). As noted, such examples not merely exist but greatly predominate.

Apparent Exceptions

There are some real and some spurious exceptions to constant extinction rates. As noted above, the ages of living taxa are not directly comparable to those of extinct taxa. Sampling error also causes deviations from linearity.

Some short intervals of geologic time have had massive extinctions of some kinds of organisms (Newell, 1963, 1967, 1971). All graptolites became extinct in the Pennsylvanian and almost all stony corals (Zoantharia) did so in the late Permian. This is clearly a different sort of event from the usual process of extinction and does not fit the general explanation given below. In the late Permian, almost everything in the adaptive zone of stony corals was eliminated (10). The adaptive zone itself was demolished for a while. If we eliminate such extinctions as being different from events within an adaptive zone (done supplementarily in parts of Figs. 1-4), linearity is never reduced and sometimes, as with corals, increased (11). When, as with brachiopod genera, extinctions at such a time are sufficiently numerous to be plotted separately, the slope is less than for others, as for the ages of genera living today and for the same trivial reason.

There is no accepted classification of corals at the family level. Two more or less orthogonal classifications are plotted in Figure 6. One is linear, the other convex. This gives some evidence that the Treatise
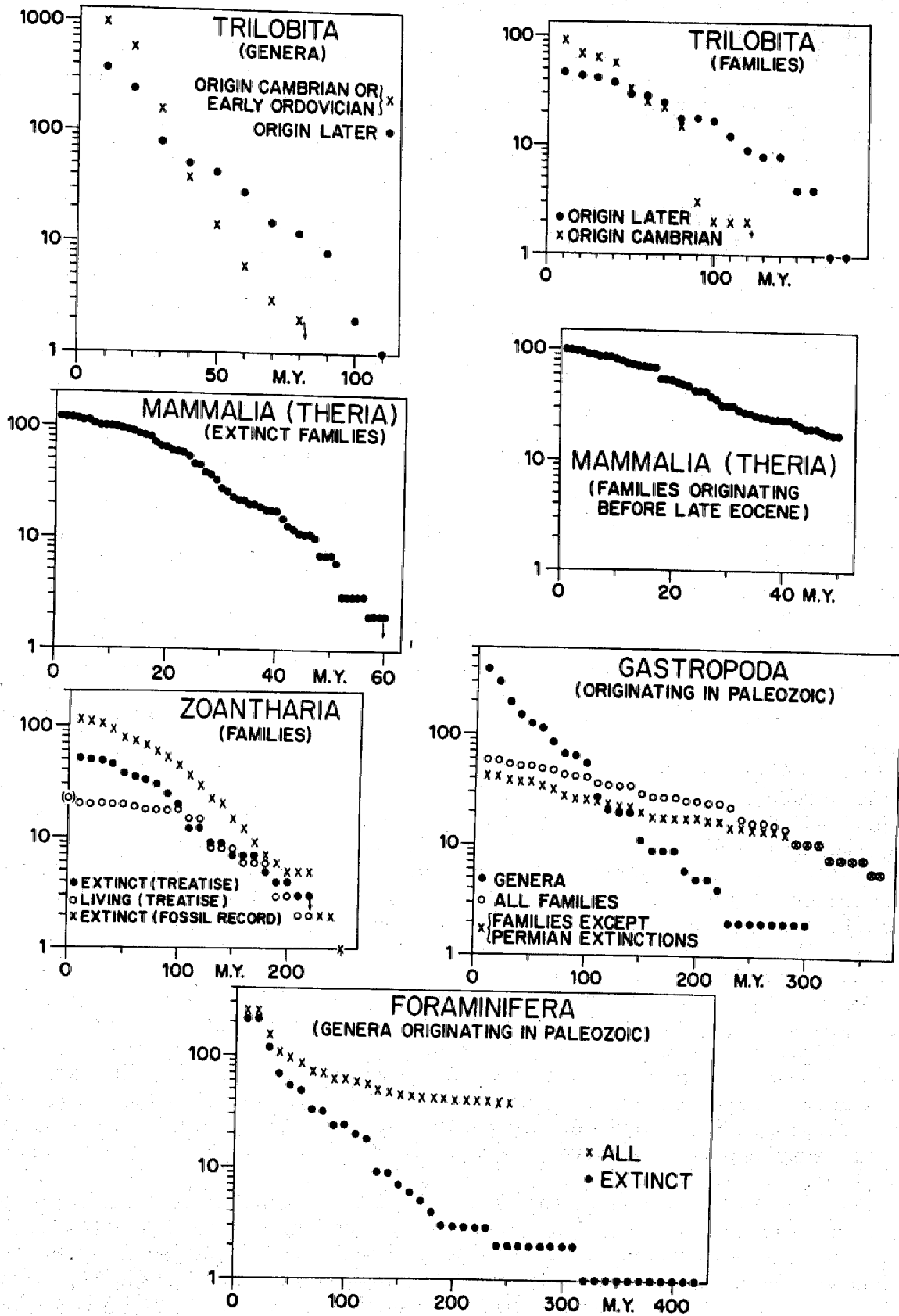
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Fig. 6. Taxonomic survivorship curves for apparent exceptions to linearity.
See text. Zoantharia families are from very different classifications.

classification is ecologically more realistic, but a decision must ultimately come from phylogeny.

Mammalian families also give a convex curve (Fig. 6). As shown by plotting only families (extinct and living) originating before the late Eocene, however, this is an artifact of the short duration of the Cenozoic in relation to the durations of many families. Living families seem similar to extinct ones, because they jointly determine a single linear curve. This is also true for gastropods but not for foraminiferans.

This difference in foraminiferans of some living taxa from most extinct ones also occurs elsewhere, notably in the Pteridophyta. It is indeterminable from these data whether real exceptions are involved or whether the deviant taxa occupy sufficiently different adaptive zones as not to interact appreciably with the majority of related taxa. Simpson (1944) noted this phenomenon for pelecypods and made it the basis of his bradytelic evolution.

Deviant adaptive zones are obvious for genera of most of the different mammalian orders (Van Valen, 1971) and also for rudists, coral-like pelecypods which formed reefs in the late Cretaceous and seem to have caused the extinction of many corals while doing so (12). Their extinction rate is greater than that of normal pelecypods, although also greater than that of genera of corals, which may not be taxonomically similar (13).

Ammonite and nautiloid genera, but not families, give ostensibly concave curves. When grouped into more homogeneous classes (Fig. 7), approximate linearity results. This also applies to the lengths of the terminal branches (after each final branch-point) of the phylogeny of ammonite families (14). Removal of the late Devonian extinctions has a similar effect for genera as for terminal branches but is not plotted. I did not try to subdivide the nautiloids. I further suspect that pseudo-extinction is more common for ammonite and perhaps nautiloid genera than is true elsewhere, which would increase concavity by increasing short-lived taxa at the expense of longer-lived lineages.

The need to separate Paleozoic and Mesozoic ammonites shows that there is at least a descriptively real exception here. The extinction rate is definitely not constant throughout the existence of the group. The same is true for trilobites (Fig. 6), the separation here being in the Ordovician. Linearity again holds for each segment. I do not know what caused either change, but it may be relevant that effectively all Mesozoic ammonites descended from one Paleozoic lineage and that trilobites declined greatly in the Ordovician. In each case the division time found for extinction rates corresponds to the greatest separation in the group on other criteria (15).

Moreover, because of preservational bias and incomplete collecting and study, short-lived taxa will be found less often than long-lived taxa. However, for equally frequent groups the effect of this bias will be a reduction in observed longevity by a constant absolute amount. This will leave linearity and even the slope of the curve unchanged. Rarer groups will have a greater expected reduction in observed longevity than commoner groups. Any effect of this property depends on whether rarity is correlated with longevity, and I know of no relevant data.

Any combination of subgroups with unequal constant extinction rates produces a concave resultant curve. The amount of inequality can be estimated by this concavity, but unfortunately any concavity manifests itself most in the regions of greatest sampling error. Linearity is nevertheless sufficient that exceptions must be rare or slight. Abrupt ends to distributions, as with echinoid families, occur when (as we have seen with mammal families) the stratigraphic range of the group impinges on the possibility of long-lived taxa having already become extinct. Linearity is unaffected by multiplication or addition with a logarithmic (ordinate) or arithmetic (abscissa) constant.
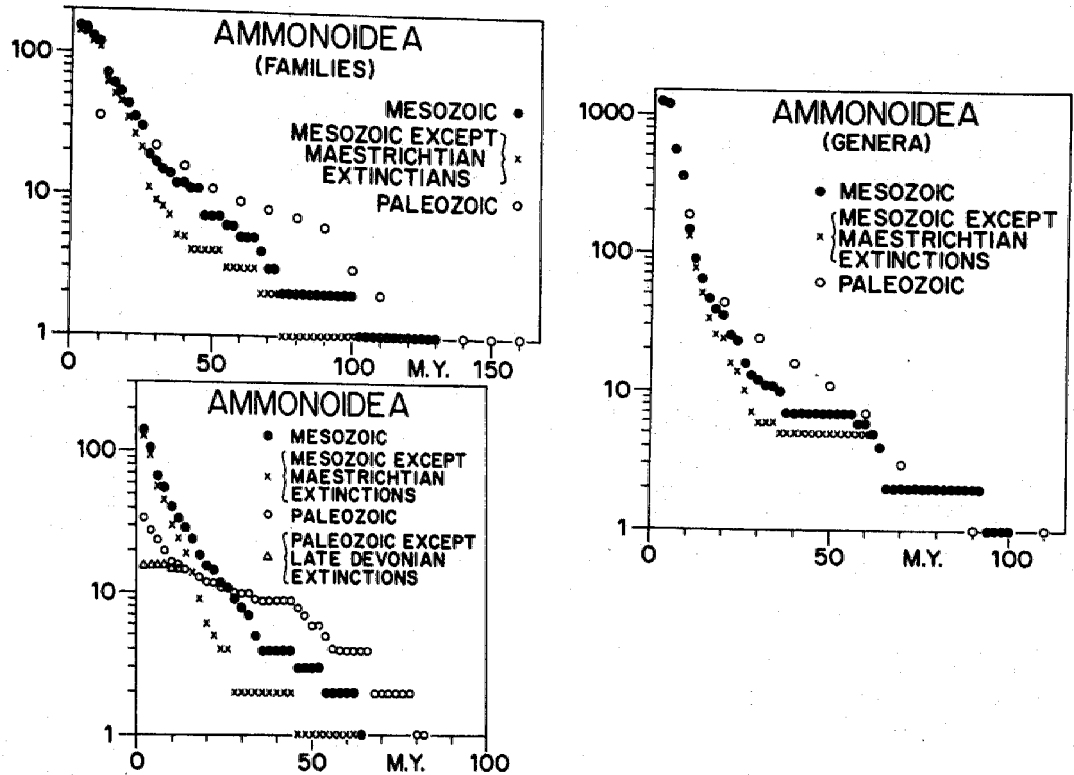
Fig. 7. Taxonomic survivorship curves for ammonites. See text. The graph on the lower left is for terminal twigs of a phylogeny of families.

*   *   *

We see that the exceptions are either spurious, rare, slight, doubtful, or exceptions only in part. The pattern is therefore sufficiently general that the minor exceptions are best explained by unusual circumstances peculiar to each case. There is a strong first-order effect of linearity, and it is this, rather than its perturbations by special and diverse circumstances, that deserves primary attention.

Related Phenomena

The constancy of extinction in terms of survivorship does not imply constancy over geological time, and vice versa. Any form of survivorship curve has a mean, as does any pattern of extinction rates over absolute time, and this is the only formal connection between the two phenomena. There may nevertheless be a deeper causal connection.

I give some extinction and origination curves over geological time to illustrate their variability in the measurement framework proposed here (Fig. 8). There is an extraordinary exponential decrease in origination rate of mammalian families, by two orders of magnitude, from the beginning of the Cenozoic. An inverse phenomenon occurs in diatoms, where the species of Pennales (a largely benthonic groups, unlike the Centrales) have increased exponentially, as in the log phase of bacterial culture, in the same interval (16; Fig. 1). We can look at Figure 8F inversely: there is a nearly linear increase in the proportion of families that had originated by a given time and that are now extinct.

Large foraminiferans (17) have originated about 41 times independently from smaller foraminiferans, almost always from much smaller ones. About 33 of these clades have existed since the end of the early Cretaceous, when an approximate equilibrium was established. Figure 9 shows that the numbers of clades and genera present simultaneously have followed more or less log-normal
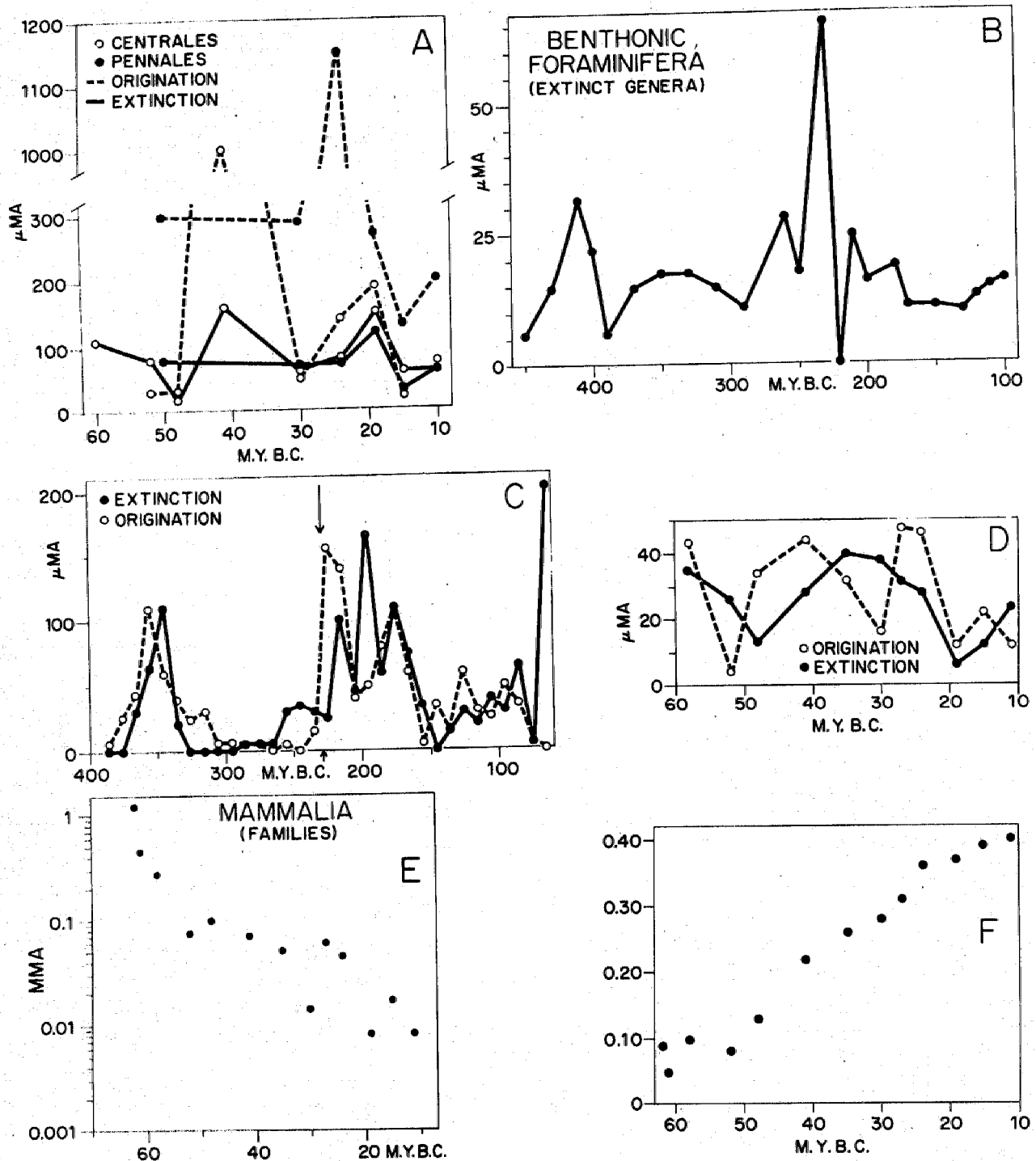
Fig. 8.   A: Origination and extinction rates for species of diatoms.
          B: Extinction rates for genera of benthonic foraminiferans.
          C: Origination and extinction rates for families of ammonites.
          High origination rates precede high extinction rates except for
          the Permian and latest Cretaceous.   D: Extinction rates of
          mammalian family lineages, and origination rates for mammalian
          families now surviving.   E: Origination rates for all mammalian
          families (new families per family in previous age per unit time).
          F: For mammalian families, (cumulative recent families originated)/
          (cumulative total families originated).
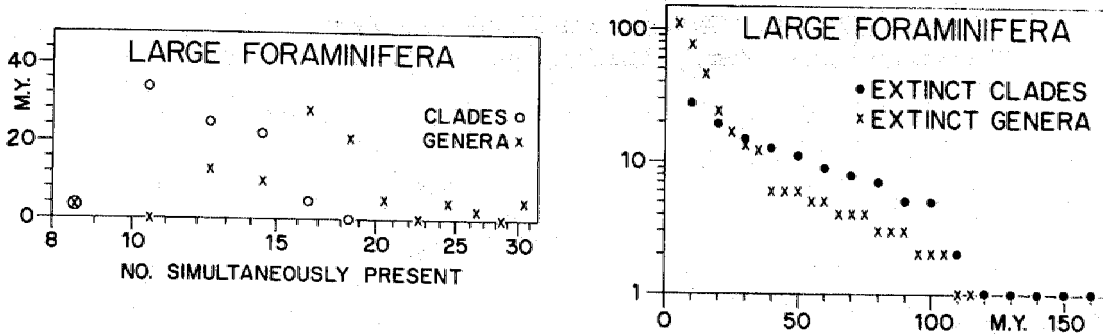
Fig. 9. Survivorship curves for genera and clades of large foraminiferans, and distribution of number of genera and clades simultaneously present after the early Cretaceous (Albian).

*   *   *

distributions since that time. Survivorship curves for clades and genera of this taxonomically very heterogeneous, but ecologically rather homogeneous, group are linear within sampling error and differ from the curve for genera of all benthonic foraminiferans.

It would be useful to know whether the extinction of entire lineages also occurs at a constant rate, or if some taxa can avoid it by evolving successor taxa. This appears to represent an unsolved problem in graph theory (18).

Measurement of Rates

I propose a general unit of rates for phenomena which can be treated as discrete.

A macarthur (ma) is the rate at which the probability of an event per 500 years is 0.5. Robert H. MacArthur showed the importance of extinction in ecology (19).

Let $\underline{P}$ be the probability per $\underline{t}$ thousand years.

$$ma = -\log_2(1-\underline{P}^{\frac{2t}{}})$$

(1)

With respect to extinction, one macarthur is the rate of extinction (Ω) giving a half-life of 500 years. With respect to origination, one macarthur is the occurrence of one origin per thousand years per potential ancestor. With respect to molecular evolution, one millimacarthur (mma) is the rate giving one substitution per million years (20).

Apparent equilibrium extinction rates of bird species on islands that have been studied (21) are 0.5 to 10 ma. Mammal species in the late Pleistocene of Florida (Martin and Webb, in press) had a rate of regional turnover (time from immigration to local extinction) of about 7 mma (Fig. 10).

Table 1 gives estimated extinction rates for the taxa studied. The sedentary marine benthos is remarkably homogeneous, and motile marine organisms have somewhat higher rates less similar among themselves. Mammalian genera (and Mesozoic ammonites) have the highest rates, but rates for reptilian families are as high as those for mammalian families. For everything except mammals the extinction rate for families is about half that for genera. Groups in relatively new adaptive zones (at least to them) usually have higher rates than long-established groups. Not surprisingly, ecology is a better predictor of evolutionary rate than is amount of information-bearing DNA (22).

If genera of a family go extinct independently, the extinction rate of families will depend directly on the number of contemporaneous genera per family

TABLE 1: Extinction Rates (in μma).
Abbreviations: fam., family; gen., genus; sp., species

| GROUP	RATE		
	fam.	gen.	sp.
Pteridophyta	20		
diatoms		50	90
Coccolithophyceae		25	
Dinoflagellata		20	55
Foraminifera	10		
benthonic		20	
planktonic		30	100
large		50	
Ostracoda	10	25	
Graptolithina		30	
Bryozoa	7		
Brachiopoda	15		
Articulata		45	
Inarticulata		25	
Malacostraca	12	30	
Trilobita			
early	20	80	
late	10	35	
Echinoidea	10	25	
Zoantharia	10	25	
Ammonoidea			
Paleozoic	20	35	
Mesozoic	75	150	
Nautiloidea	15	30	
Archaeogastropoda + Monoplacophora		20	
Gastropoda			
Paleozoic	4	20	
Pelecypoda	8	20	
rudists		50	
Osteichthyes	15	30	
Teleostei	20	35	
Holostei + Chondrostei	12	25	
Sarcopterygii		30	
Acanthodii		30	
Reptilia	30		
Mammalia (Theria)	30	150	
Polyprotodonta		150	
Primates		220	
Rodentia		160	
Carnivora + Hyaenodonta		120	
Edentata		180	
Proboscidea		60	
Notoungulata + Litopterna		170	
Perissodactyla		120	
Artiodactyla		120	
Cetacea		200	
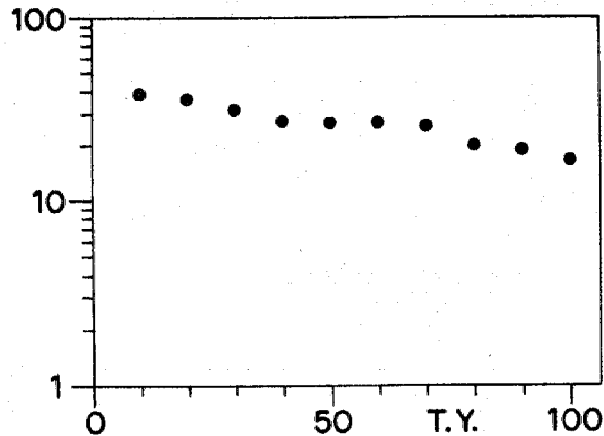
Fig. 10. Regional survivorship curve for mammalian species in Florida during the late Pleistocene.

<center>*   *   *</center>

if there is no origination of new genera in the family. Rough estimates, weighted by the number of taxa in each interval, give 2.9 contemporaneous genera per family of Ostracoda, 2.8 for Echinoidea, and 5.1 and 5.8 species per genus respectively for pennate and centric diatoms. With 2.9 genera per family, independent extinction will give an extinction rate per genus 2.6 times that per family. This ratio would be 2.5 for echinoids and 3.5 for average diatom species. I take the expected time of family extinction to be when the expected number of genera per family reaches 0.5. With branching (origination of new genera), the families will of course have longer expected longevity and so the expected ratio will increase. If the rate of branching equals that of extinction, simulation in the above range indicates roughly a doubling of the expected ratio, although a high variance among families in genera per family probably increases it more.

Table 1 shows that genera of echinoids and ostracodes have about 2.5 times the extinction rate of families, a result indistinguishable from that on the assumptions of independence and no branching. Because branching exists, some degree of correlated extinction of genera within families seems probable. The observed rate for species of diatoms is only twice that for genera, much less than the expected value of 3.5, so there is a strong correlation in extinction here even without considering branching.

<center>Contemporaneous Subgroups</center>

Extinction rate obviously depends on the area considered as well as on the inhabitants. Fig. 11 gives a relation between area and extinction rate, using all available data (21). Approximate linearity holds over 11 orders of magnitude on a log scale. With   the extinction rate in $\log_{10}$ macarthurs and $\underline{A}$ the area in $\log_{10}$ sq. km, the regression is $\Omega = -0.66\underline{A} + 1.53$ when calculated from the birds and mammals and excluding the world fauna. A regression from complete data would presumably differ somewhat. As expected, the arthropods on Simberloffia seem to require less area for the same extinction rate than do vertebrates (23). A continent seems to be the largest area in which organisms can interact more or less as they do in any smaller area that is large enough for a population.

Therefore species and higher taxa occupying smaller areas, as will often be the case when they originate, have an expected rate of extinction greater than that of more widespread taxa. Similarly, as Small (1946, 1948b) noted in
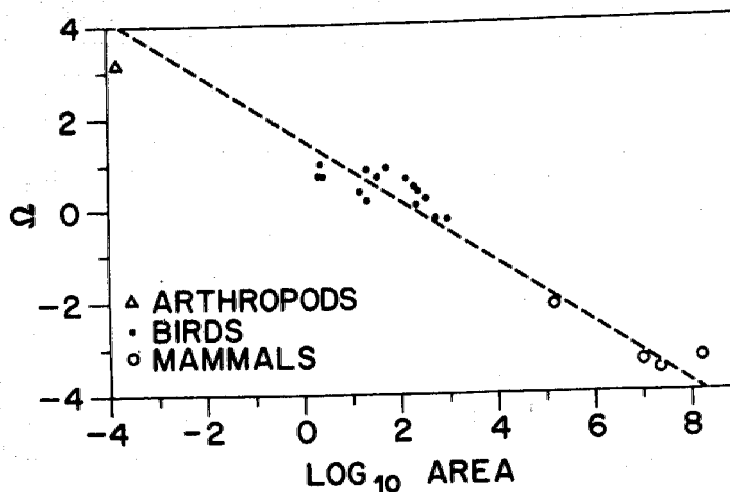
Fig. 11. Extinction rate (Ω, in $\log_{10}$ ma) of species as a function of area (sq. km.).

*   *   *

a different context for diatoms, genera with fewer species have a higher probability of extinction than do genera with more species. This is of course because branching at the specific level increases the probability of survival of the entire sub-tree, since the species will usually have different ecologies.

For these and other, less well-documented, reasons, there are definable and large subgroups that have a higher extinction rate than others, and moreover these subgroups should be relatively most frequent among younger taxa. Therefore a concave survivorship curve should result. How can it be that the curves are nevertheless linear?

There are two possibilities: incorrect assumptions and compensatory feedback. It may be that, by the time taxa have an appreciable probability of appearing in the fossil record, they have the same mean area occupied as older taxa. This sort of rapid increase may also be true, although it doesn't seem as likely, for number of species in a genus. Enough data are probably available to resolve the latter point. Compilations by Sloss (1950) and Simpson (1953), Small's studies (e.g. 1946) on diatoms, and data by Berggren (1969) and others on planktonic foraminiferans, suggest that there is indeed usually an appreciable lag before the number of subordinate taxa approaches its maximum value. The kinds of evidence in these papers are by no means conclusive on the present point, however. Furthermore, there may well be a threshold (like those found by MacArthur [1972] and others for population size in simplified models of colonization) above which survival is virtually assured and below which rapid extinction is likely. Other possible inadequacies of the assumptions, that the effects are too small to be detected or that they affect only a small proportion of taxa, are clearly unrealistic.

Even if an initial concavity in survivorship curves is avoided by the rapid changes invoked above, there still remains a major heterogeneity among the surviving taxa with respect to area, number of species or genera, and other factors relevant to survival. There must then be some kind of compensatory feedback to give the observed degree of linearity. Two kinds of feedback seem possible. There might be an interaction between age and area (or number of species) such that older and younger taxa have different effects of area on probability of extinction. No simple model fits this biologically implausible alternative. However, if for new taxa small area and low number of species were not harmful, or as harmful as later, the expected initial concavity would be reduced or eliminated.

The other kind of feedback is by the continual appearance at all ages of taxa of low area and other characters giving greater susceptibility to extinction. In fact this could be regarded as an aspect of the extinction process: taxa would become more susceptible at a constant average rate per taxon per time. This transformation need not be by feedback per se, but it does require that the production of greater susceptibility be part of the same process as the extinction. There is no requirement that each subordinate taxon be equally likely at any given time to become more susceptible, but the overall control must compensate for survival by greater susceptibility at some other time or for some other species. This second alternative is plausible (given linear survivorship) but largely untested. It predicts that, at least after a short initial period, criteria of susceptibility will have a steady-state distribution in survivorship time independent of the age of the taxon. Small (1946, 1947, 1948a,c) found such a steady-state distribution in real time for generic sizes of diatoms through the Cenozoic.

An Evolutionary Law

The effective environment (24) of the members of any homogeneous group of organisms deteriorates at a stochastically constant rate.

This law goes a bit beyond the observations in postulating the cause to be extrinsic rather than intrinsic, like nuclear decay. There is of course much other evidence (Simpson, 1953) for such a step. The law is also stated in terms of real time rather than survivorship time, although it applies to both and ties them together. A more neutral statement is that extinction in any adaptive zone occurs at a stochastically constant rate.

"Homogeneous" is a necessarily ambiguous word, and its meaning in a particular case must depend on the particular circumstances and on the degree of precision desired. Paleozoic and Mesozoic ammonites may differ sufficiently to be nonhomogeneous, but the entire marine benthos could be treated together almost as well as subdividing it. This does not lead to circularity; no subdivision of a group with racial senescence (25) would give a set of linear survivorship curves. The homogeneity required (and so its verification) is entirely ecological and is in terms of ultimate regulatory factors (Van Valen, 1973) of population density. Mice and fruit-eating flies might be homogeneous with each other but not with blood-sucking flies, although a scaling problem would remain. We could say that there always exists a degree of homogeneity at which the law is true, and try to measure it independently. Homogeneity does not imply equality of ability to respond to the deterioration; but counterexamples to a constant distribution of such abilities would disprove the law in its first form as a universal phenomenon (26).

Like any law (27), the effects of the law of extinction are observable only under appropriate conditions (here, persistence of the width of the adaptive zone). Unlike many laws (28), it may not be universal. If it is not universal, it should be possible to limit its domain in an objective manner. Such limitation should derive from an understanding of the causal basis for the law.

It is not fashionable to speak of laws in evolutionary biology or for historical processes generally. I think this is based on both a misunderstanding of the regularity of actual processes (29) and on an over-reaction to poorly formulated laws of earlier workers (30). Laws are propositions that specify sufficient conditions for a result; given the conditions, the result will occur, although some of the conditions (the bounds of the domain) may be implicit. The degree of confirmation of a law is of course a different matter from whether a proposition is (or represents) a law in this sense. Any general statement of the nature of a causal process states a law (31).

The Red Queen's Hypothesis (32)

The probability of extinction of a taxon is then effectively independent of its age. This suggests a randomly acting process. But the probability is strongly related to adaptive zones. This shows that a randomly acting process cannot be operating uniformly. How can it be that extinction occurs randomly with respect to age but nonrandomly with respect to ecology?

We can consider the situation in terms of an ensemble of mutually incompatible optima. It is selectively advantageous for a prey or host (including plants) to decrease its probability of being eaten or parasitized. It is often selectively advantageous for a predator or parasite species, and much more often for a predator or parasite individual, to increase its expected rate of capture of food. It is selectively advantageous for a competitor for resources in short supply (food and space in the broadest senses, and sometimes also externally supplied adjuncts to reproduction or dispersal) both to increase its own effect on its competitors and to decrease the effect of its competitors on itself (33).

Every species does the best it can in the face of these pressures. Probably all species are affected importantly by them at least over intervals of a few generations. Response to one kind of pressure may well decrease resistance to some other, at that time weaker, kind.

The various species in an adaptive zone (Van Valen, 1971), whether or not this zone is sharply delimited from others, can be considered together. We can assume as an approximation that a proportional amount w of successful response by one species produces a total negative effect of $v = w$ on other species jointly, usually less than v for any one of these species. For n species, the mean decrement of fitness per species is v/n. For m successful responses simultaneously (in an interval τ), the mean total decrement per species is mv/n. Over some interval t (in units of τ), the decrement is then mvt/n. To maintain itself as before, the species must increase its fitness by an amount mwt/n. Since each decrement generates a response, $m = n$. Most species will be able to recoup their loss, more or less while it occurs, but in doing so they jointly produce another disadvantage of v for the average species. This process of successive overlapping decrements of v may continue indefinitely. Species at least locally new may replace those for which the rate of environmental deterioration has been too great.

For the momentary fitness F of a random species,

$$\phi \equiv \frac{dF}{dt} = \frac{m(w-v)}{n} \; . \tag{2}$$

For a given species, ϕ will of course vary from time to time as its specific decrements and possible responses covary. However, since $w = v$ on the average, $E(\phi) = 0$, i.e. the mean fitness in the adaptive zone is constant in the long run. If we take a standard average fitness F_1, the real average fitness will be $F_0 = F_1 - v$, because any response of one species above F_0 will bring a corresponding decrement from the counter-response of other species. v is the environmental load. Thus, even for a single species, the total selection pressure is constant over intervals that are long enough to average out irregularities.

ϕ is of course itself a variable among the species at any time, and its variation (or that of F) will determine the extinction rate in the adaptive zone. Species may (and do, but to an unknown extent) differ in the spectral

threshold $\underline{T}$ (Reyment and Van Valen, 1969) of ϕ or its components to which they can no longer respond successfully and at which they therefore become extinct. Which species have which values of ϕ and $\underline{T}$ will change markedly with the nature of the stresses at a given time. The observed pattern of extinction seems to imply that the stresses are sufficiently diverse that they affect most species similarly over a very long interval. Assume, as justified in part by the Central Limit Theorem, that both ϕ and $\underline{T}$ are normally distributed, with means μ_1 and μ_2 respectively. Then, since both distributions range over the same set of species and so have the same area, the rate of extinction is the overlap of the distributions. In the case of equal variances for ϕ and $\underline{T}$,

$$\Omega \equiv \frac{dE}{dt} = \frac{1}{\sqrt{2\pi}} e^{-\frac{(\mu_1 - \mu_2)^2}{8}} . \tag{3}$$

Uncompensated departures from normality and from equal variances in the distribution will of course affect the accuracy of this expression but not the dependence of Ω on the real area of overlap.

On this self-contained system we must now impose the physical environment and irregular biotic perturbations. Almost all changes in the physical environment of an adaptive zone will be deleterious to its inhabitants, either directly or by permitting the establishment of other species which can then survive there. Therefore regular changes in the physical environment can be treated as constant factors of ϕ. The observed constancy of Ω is evidence that such a treatment is permissible.

Important perturbations do, however, occur, from both biotic and physical causes. They can be treated together. The probability of extinction is not constant over geological time, as Fig. 8 and the extinctions at the end of the Cretaceous suffice to remind us. When major perturbations occur well within the geological range of a group, as for brachiopods in the late Permian, Paleozoic ammonites at the end of the Devonian, or coccoliths at the end of the Cretaceous, it happens that if we ignore the subgroups that became extinct then, the remainder show a constant rate of extinction (34). There is no important lasting effect of the unique event, unless total extinction occurred, nor do its effects extend detectably beyond the subgroups prematurely eliminated. Newly appearing subgroups after the event continue in the same way as those that lived through it. Smaller perturbations occur much more frequently, however (Fig. 8), and it is the very resultant of these perturbations that determines the long-term constancy.

Therefore the effects of these minor perturbations are not independent of each other over time. If they were, they should not be distributed about a constant mean. The rate of deterioration of the effective environment has what we can descriptively call the property of homeostasis. A large change in one interval is compensated for by a small one later, on the average, and vice versa; the mean itself does not undergo a random walk. It is the organisms in the adaptive zone that can link the perturbations across time in that the effects of one perturbation may depend on the effects of those before it. Species easily removed by one kind of perturbation are not there if it comes again soon, and may accumulate if it does not come for a long time. Meanwhile other kinds of perturbations are taking their own toll, more or less independently of the first kind (35).

We see here a major difference from the usual theory of genic selection. The latter depends only on the current distribution of frequencies of alleles and their interactions with each other and the environment. It does not depend

at all on the process by which the current distribution was obtained. In formal language, it is a Markov process. But any process can be made Markovian by choice of a suitable level of analysis. With extinction we can see that a non-Markovian analysis of selection is appropriate. This is probably true for the general case also (36).

The Red Queen does not need changes in the physical environment, although she can accommodate them. Biotic forces provide the basis for a self-driving (at this level) perpetual motion of the effective environment and so of the evolution of the species affected by it (37).

The Red Queen's Hypothesis is a sufficient explanation of the law of extinction but not one that is yet derivable with confidence from lower-level knowledge of the causes of individual extinctions and the nature of species interactions. There may be other sufficient explanations that I have not been imaginative enough to see, and predictions by the Red Queen may be duplicated by such undiscovered explanations. Disproof of the Red Queen's Hypothesis is possible in several ways, but fully adequate confirmation must await derivation of it from what we can reasonably regard as facts.

We can go a step further by thinking of an adaptive landscape in a resource space (Van Valen, 1971). The amount of resources is fixed and can be thought of as an incompressible gel neutrally stable in configuration, supporting the peaks and ridges. If one peak is diminished there must be an equal total increase elsewhere, in one related peak or more uniformly. Similarly, increase in a peak results in an equal decrease elsewhere.

Species occupy this landscape and can be thought of as trying to maximize their share of whatever resource is scarcest relative to its use and availability. This resource will take the role of the gel, and the _momentary fitness_ of a species will be proportional to the amount of gel under its area (the amount of the limiting resource it controls). To a sufficiently close approximation this momentary fitness seems to be what natural selection maximizes.

The landscape is changing continuously, at three levels. Species displace each other from areas of the adaptive surface. This can be by resistance to predation as well as other means, and some parts of the landscape may in this way or others (e.g. severe weather) be under-occupied. Incompatible optima maintain diversity. Secondly, the distribution of gel within the landscape changes, as with climatic change or (for herbivores) when the flora changes. Finally, the total amount of gel (or the amount in fact used) can change. This can occur by another necessary resource becoming limiting, by constraints on occupation of the adaptive zone, or by a change in the amount of the same limiting resource. The entire landscape can in this way disappear.

The first two kinds of change in the landscape lead to the the Red Queen's Hypothesis, while the third is, without compensatory changes, inconsistent with it. Empirically extinction is less independent of age when extinctions caused by major constrictions of adaptive zones are included. The observed degree of independence suggests that the third kind of change is relatively unimportant on the evolutionary time scale. We can hardly regard such a conclusion as established, but it does show that the question of variation in the size of major adaptive zones is fundamental.

Molecular Evolution

The Red Queen's Hypothesis provides reason to expect a long-term approximate constancy in the rate of evolution of individual proteins within any single adaptive zone (38). It does so without ad hoc assumptions, although

such assumptions could be invoked to explain away exceptions just as they have
been invoked (Clarke, 1970) to explain away constancy by the usual selective
framework. Constancy of the rates of protein evolution is often regarded as
the most important evidence for what King and Jukes (1969) called non-Darwinian
evolution, despite serious misinterpretations (39).

A further prediction is that rates of protein evolution will be related
monotonically to rates of taxonomic evolution, to the extent that the subtaxa
in different groups are comparable (13,40). Some evidence (41) is available
that rates are not always constant, and preliminary results I obtained long
before discovering constant extinction suggest that the mean rate of protein
evolution during the relatively short time while the orders of placental
mammals diverged from each other was greater than that later (42). Lingula,
a brachiopod genus present since the Ordovician or Silurian, and Triops
cancriformis, a branchiopod (not brachiopod) species not detectably changed since
at least the early Triassic (1), would be expected to have proteins more similar
to those of the common ancestor than would their more divergent relatives. The
evidence for approximately constant evolutionary rates of proteins comes from
organisms (mainly vertebrates) which have all evolved appreciably since their
separation from each other.

The Red Queen in her simplest gown also predicts a perhaps real pheno-
menon, which Ohta and Kimura (1971) noted as mysterious: that irregularities
in the rate of molecular evolution seem to be more or less cancelled out over
long intervals by a seemingly negative autocorrelation.

Implications of the Red Queen

Thoday (1953) proposed a concept of fitness as the probability of survival
of a lineage to some very distant time in the future. More generally, we can
take

$$F_t = \int_0^\infty w(t)P(t)dt \tag{4}$$

where $P(t)$ is the probability (43) at time 0 of survival to time t, and $w(t)$
is a weighting function (the same for all lineages and perhaps integrating to
1 for scale) for which I would choose exponential decay at a low rate (44).
Time 0 is the variable present.

The Red Queen proposes that this fitness has only two components for
almost any real lineage: which adaptive zone is occupied and what the probability
distribution is of new sublineages occurring by branching. Artiodactyls have
largely replaced perissodactyls in the same adaptive zone, yet their extinction
rates are identical (Tables 1,2). It is the rates of branching that are
decisive. Monotremes still linger on in two isolated subzones, one of which
has already been invaded by marsupials. The gradual extinction of multi-
tuberculates (Van Valen and Sloan, 1966) occurred by herbivorous placentals
diversifying into parts of the joint adaptive zone formerly held by multi-
tuberculates. One multituberculate survived 15 or 20 million years after the
rest of the extinction was completed (45); the latter had taken only about
10 million years. The Red Queen's proposal implies that extinction of
lineages (subtrees) will prove not to be constant when it can be measured.

For the Red Queen, curiously, does not deny progress in evolution. By
group selection such as this, as well as by individual selection, properties of
communities can change in a directional manner. It may well be that the
average Cenozoic species could outcompete the average Cambrian one; some
information on this can probably be derived from functional analysis. It is

TABLE 2: Extinction and origination rates (in ma) for genera of two competing
          orders of mammals.
                          E: early; M: middle; L: late

| | EXTINCTION | | ORIGINATION | |
Epoch	Perissodactyla	Artiodactyla	Perissodactyla	Artiodactyla
E. Eocene	120	160	1300	500
M. Eocene	80	90	340	920
L. Eocene	120	90	290	260
E. Oligocene	120	100	80	150
M. Oligocene	100	160	40	130
L. Oligocene	170	130	130	80
E. Miocene	90	130	130	260
M. Miocene	30	90	90	90
L. Miocene	40	60	60	100
E. Pliocene	90	130	90	320
L. Pliocene	90	80	20	70
	*	*	*	

well known (cf. Romer [1966]) that such functional progress has occurred in
vertebrate evolution. The Red Queen measures environmental deterioration on
a scale that is determined by the resistance of contempory species to it, so
the scale and real deterioration themselves may well change without a change
in the measured deterioration. Darwin's example of wolf and deer exemplifies
this.

     The Red Queen proposes that events of mutualism, at least on the same
trophic level, are of little importance in evolution in comparison to negative
interactions, although she does not consider other cases where mutualism is so
great that the mutualists function as an evolutionary unit, as with lichens and
perhaps chloroplasts. She considers the usual contrary view to be a result
of wishful thinking, the imposition of human values on nonhuman processes.

     The existence of the law of extinction is evidence for ecological signi-
ficance and ecological comparability of taxa from species to family, within
any adaptive zone.

     We can think of the Red Queen's Hypothesis in terms of an unorthodox
game theory (46). To a good approximation, each species is part of a zero-sum
game against other species. Which adversary is most important for a species
may vary from time to time, and for some or even most species no one adversary
may ever be paramount. Furthermore, no species can ever win, and new adversaries
grinningly replace the losers. This is a direction of generalization of game
theory which I think has not been explored.

     From this overlook we see dynamic equilibria on an immense scale, deter-
mining much of the course of evolution by their self-perpetuating fluctuations.
This is a novel way of looking at the world, one with which I am not yet com-
fortable. But I have not yet found evidence against it, and it does make
visible new paths and it may even approach reality.

Notes

(1). The taxonomic data I used are from the following sources: For vertebrates, Romer (1966), with a few modifications from various later work. For invertebrates and genera and families of Foraminifera, R.C. Moore (ed.), Treatise on Invertebrate Paleontology (Boulder, Colorado: Geological Society of America and Univ. Kansas Press), 1953-present, including revisions (C. Teichert, ed.), with supplementation or (for Bryozoa) substitution from The Fossil Record (W. B. Harland et al., eds.; London: Geological Society of London [1967]). I deliberately ignored later pertinent work (e.g. Yochelson [1969]) on invertebrates. Pteridophytes and coccoliths are also from The Fossil Record. For species of Foraminifera, Berggren (1969). For Dinoflagellata, Sarjeant (1967). For diatoms, Small (1945,1946).

(2). The time scale I used is from the following sources: Berggren (1972); Anonymous (1964); Everndon, Savage, Curtis, and James (1964); Everndon and Curtis (1965); Kauffman (1970); and Van Valen and Sloan (1966). Experiments show that the results are robust to reasonable changes in the time scale.

(3). Various conventions are necessary in any such compilation. Some general ones I used are the following: I took the duration of a taxon as from the middle of the epoch (or other shortest interval) before the first record, to the middle of the epoch of the last record. I ignored questioned records and unrecognizable taxa. For data accurate only to period I plotted the range as ending in the middle unit of the period. I used all data regardless of degree of precision (unless imprecise beyond a period) but used them to the precision allowable. Also, summaries of ranges (even of individual taxa) are too often inaccurate, as shown by unquestioned records of subordinate taxa beyond the stated limits, so whenever possible I compiled data at the level of genus.

(4). I knew of this deficiency for many years but saw no reason to pursue it, as I expected the shape of the curves to remain concave. In hindsight one could also expect that the group as such might have a progressively higher probability of extinction as the biota around it evolves while it does not. This would give convex survivorship curves.

(5). In addition to the data plotted, I made several dozen plots of subsets of the same data, using such criteria as exclusion of a major extinction or subtaxon, or restriction of the time interval used. All important deviations from the total distribution are included in the figures given here. There is a bias in using all extinct subtaxa of a living group in that the longer-lived of subtaxa originating recently are still alive. Tests show that this effect is negligible for long-ranging groups (not, e.g., for families of mammals or echinoids) and obviously all living and extinct subtaxa cannot be combined into one useful curve (Simpson, 1953).

(6). I used all groups for which adequate data were available. Omissions are due to poverty of the fossil record or its study (e.g. Insectivora), small number of extinct taxa, error of dating being a substantial part of estimated durations (e.g. Archaeocyatha), or lack of adequate compilation (e.g. Gymnospermae).

(7). This is the reason for the apparently flat tops of some distributions.

(8). The initial figure in parentheses in distributions of most living taxa represents the total now alive, including those not known as fossils. Many living taxa in some groups are not easily fossilizable, and our knowledge of the present fauna is better than that at any other time even aside from this.

(9). Examples can be found in the following: Pearl (1928); Allee, Emerson, Park, Park, and Schmidt (1949); Kurten (1953); Odum (1971).

(10). Coral-like brachiopods of the Permian also became extinct, as did many other organisms superficially less similar to corals.

(11). Tests are necessarily weak, but data from several groups give no indication that a major extinction affects taxa of different ages to a different extent.

(12). A third (17 of 51) of the families of stony corals present in the late Cretaceous became extinct then, but only one of these did so at the major crisis at the end of the Cretaceous. The Fossil Record families are the only ones with adequate data on this point. Rudists diversified throughout the late Cretaceous and abruptly disappeared at its close.

(13). I give several ways of evaluating comparability of taxa elsewhere (Van Valen, in press).

(14). The phylogeny is from the Treatise (1) and excludes 5 families of unknown ancestry. Schindewolf (1961-1968) has given a rather different phylogeny, but parts of it are not detailed enough for this application.

(15). A brief discussion of possible factors in the crisis for trilobites can be found in The Fossil Record (1), p. 54. Some other curves also probably exhibit real deviations from linearity, but the ones discussed are the largest.

(16). Small (1946,1952) noticed this exponential increase for some individual genera, as Small (1950) and Tappan and Loeblich (1971) did for the entire group.

(17). I arbitrarily define these as having a maximum diameter of at least 5 mm. Most are highly complex internally, and most are discoidal, fusiform, or low conical.

(18). What is necessary is the expected distribution of the durations of all sub-trees, including parts of larger sub-trees, given a constant extinction rate and a branching rate that varies from time to time. Harris (1963, p. 32) considered the problem for a constant branching rate and found it intractable. It would further be useful if some sub-trees could be ignored as effectively infinite (extending an unknown amount beyond some absolute date such as the present). The point is directly resolvable by simulation, but this requires more money for computer use than I have.

(19). MacArthur died (at the age of 42) two weeks after the discovery of constant extinction.

(20). 1 ma is the reciprocal of a half-life of 500 years; in general, ma = (half-life in units of 500 years)$^{-1}$. Macarthurs apply also to phenomena (such as origination rates) for which half-lives are inappropriate. Applications in the text are to phenomena variously with and without replacement of the item sampled; the derivations therefore differ in detail. Some computational aids: ma = $(\log_{10}2)^{-1}(-\log_{10}(1 - p^{2t}))$; $P_{0.5}(1 \text{ day})$ = 183 kilomacarthurs (kma); $P_{0.5}(1 \text{ minute})$ = 263 megamacarthurs (Mma). Given $P(t)$ of an event per interval t, $P(kt) = [P(t)]^k$. The rate for interval kt is ma$(kt) = k^{-1}$ma(t), given the same probability for both intervals. Haldane (1949) proposed an analogous measure for rates of continuous phenomena: a darwin is the rate giving a change by a

factor of _e_ per million years. Kimura (1969) defined a unit of rates for
molecular evolution: a _pauling_ is, in this context, the same as a
millimacarthur.

(21). For birds, the data are for islands and of variable quality: MacArthur
and Wilson (1967); Lack (1942); Diamond, (1969,1971). The islands are,
in order of size, Los Coronados, Santa Barbara, Anacapa, St. Kilda, the
Scillies, Krakatoa, San Miguel, San Nicolas, San Clemente, Santa Catalina,
Santa Rosa, Santa Cruz, Karkar, Man, and the Orkneys. For arthropods,
Simberloff and Wilson (1969) have approximate data from mangrove islets.
The inaccuracy of the estimated extinction rates for birds and arthropods,
in the present context, is about an order of magnitude. Estimates for
both groups are probably too high, but I use available values. Mammal
data are from Kurten (1968) for Europe, Martin and Webb (in press) for
Florida, Webb (1969) for North America, and the data of Table 1 for the
world. There are now about 4 species per genus of mammals in both North
America and the world; if they go extinct independently, the extinction
rate of species is three times that of genera. This inaccurate assump-
tion, which ignores the correlation between number of species present
and number of new species produced, is reasonable at the scale used. The
grouping of birds and mammals into one equation is less defensible but
is supported by the Florida data. The same is true for grouping data
from islands, a peninsula, and two partly isolated continents.

(22). Treatments of evolutionary rates in paleontology not in other notes can
be found in, e.g., the books by Schindewolf (1950), Zeuner (1958), and
Kurten (1968); a symposium (J. _Paleont_. 26: 297-394 [1952]); and papers
by Williams (1957), Kurten (1960), Bone (1963), Lerman (1965), House
(1967), Newell (1967), Valentine (1969), Lipps (1970), Kurten (1971),
Olsson (1972), and Cooke and Maglio (1972). DNA estimates are readily
accessible in the _Atlas_ (Dayhoff, 1972); various guesses exist on the
proportions that are informational.

(23). A more extreme divergence from the regression would be expected for smaller
organisms. Cairns, Dahlberg, Dickson, Smith, and Waller (1969) in fact
give data for protozoans on blocks of an artificial substrate in a lake.
An extinction rate of about 12 kma [P(extinction) = 0.043 per species
per day] can be derived from their data. However, the substrate was a
foam and so the effective area is unknown; the area of the top was 5 x 10^{-9}
sq. km. Furthermore, the extinction rate may be higher than that in
naturally occurring isolated substrates of the same effective area, and
the experiment lasted only about 40 days. The glass slides that Patrick
(1967) used as islands for diatoms would seem an excellent model system
for such estimations, especially because the effect of area itself can
be isolated from that of spatial heterogeneity and both studied together.
The estimated extinction rate on Simberloffia may also be higher than a
rate comparable to that for vertebrates; Simberloff and Wilson (1969)
say that most "extinctions" seem to have been of species that couldn't
colonize the islets under any circumstances, so no real populations of
them existed to become extinct. This is a serious bias even if one
difficult to overcome, and illustrates the danger of letting what we
can easily measure determine what we think we want to measure, the
tyranny of epistemology on ontology.

(24). The _effective_ _environment_ of any organism is its adaptive zone (Van Valen,
1971) plus the effects of any other organisms within that adaptive zone.

(25). A hypothesis recently revived in terms of DNA by Bachmann, Goin and
Goin (1972).

(26). If we look at too narrow a part of the zone, with only a few taxa, discrete

single events will be individually noticeable, as with any random process in the real world. In a causal universe a claim of randomness is a badge of ignorance. With evolutionary diversification the causes of seemingly random patterns may well be important and discoverable (Van Valen and Sloan [1972] give an example). The law of extinction is on the next level of abstraction from such causes.

(27). Gravitation does not cause an object resting on the floor to fall. Lakatos' critique (1963-1964) of mathematical proof is based on the difficulty of delimiting domains objectively.

(28). But like, e.g., Mendel's Laws or the gas laws.

(29). I have treated this subject elsewhere (Van Valen, 1972).

(30). For instance, E.D. Cope proposed a famous law in the nineteenth century that primitive taxa have a greater expected longevity than their descendants. This has never been adequately tested and should be re-formulated in terms of degree of primitiveness (assuming a threshold is absent) and a definition of primitiveness by entrance to an adaptive zone.

(31). A law need not be quantitative (although the law of extinction is). The contrary tradition is a myth derived, as Egbert Leigh has said, from physics envy.

(32). "Now here, you see, it takes all the running you can do, to keep in the same place." (L. Carroll, Through the Looking Glass.)

(33). Fisher (1930) and others, including Darwin and especially Lyell (1832), foreshadowed the Red Queen's Hypothesis but had no reason to impose the crucial constraint of constancy, and did not do so. I regard interference competition as causally a mechanism of resource competition, a proximal rather than ultimate regulator.

(34). Whether the total group does also depends on the distribution of longevities of the subgroups omitted.

(35). On one level, the probability of extinction of a group is related to its own properties because different groups go extinct for different reasons and so at different times. But on the next level, the Red Queen says that having one set of properties is not appreciably better than having another because the expected time to extinction is the same.

(36). Levine and Van Valen (1964) showed experimentally for Drosophila that natural selection has rather non-Markovian aspects. Lewontin (1966) later elaborated the point theoretically but without specific results.

(37). Origination-extinction equilibria are implicit in Simpson's work (1944,1953), and in Lyell's (1832). I realize that the Red Queen's Hypothesis is at least a simplification of reality. It is directly analogous to Newton's third law of motion.

(38). That the Red Queen in her simplest gown implies long-term constancy in total evolutionary rate is obvious. For any single protein we must invoke an analogue of the Central Limit Theorem: pervasive pleiotropy makes the rate for one protein roughly proportional to that for all, or linkage effects have a similar result. For instance, many proteins are to some extent attached, and the other components of the attachment may change for extraneous reasons, making the previous structure nonoptimal. Dickerson (1971) and others have made a similar point from the other end of the microscope.

(39). Stebbins and Lewontin (1972) actually think that "the entire argument is based upon a confusion between an average and a constant." What is remarkable is, however, precisely that the average rate (over shorter segments of a phylogeny) is so nearly constant (among these segments) for a given protein, rather than reflecting a branching random walk or some other process.

(40). More precisely, the prediction is of a monotone relationship of the average rate of protein evolution with the average rate of change among phenotypic characters (including the origin of new characters).

(41). Horne (1967), Kohne (1970), Ohta and Kimura (1971), Uzzell and Pilbeam, (1971), Jukes and Holmquist (1972). Also, constancy predicts the same expected number of changes in each lineage after the latest common ancestor. The data for hemoglobins in the Atlas (Dayhoff, 1972) seem inconsistent with this expectation. The assumption of total constancy leads to the expectation, presented seriously by D. Boulter (1972) and Ramshaw et al. (1972) that angiosperms originated in the early or middle Paleozoic.

(42). The approach used the protein sequence data of the Atlas,1969 edition, and probability estimates of various alternative placental phylogenies as determined by myself.

(43). Probability in the sense of a propensity, a property of any single lineage.

(44). The rank-order of different groups with respect to F_t can depend on the choice of $w(t)$. It is an almost universal mistake to think that evolution locally maximizes fitness. Evolutionary fitness is F_t except to some population geneticists, but evolution doesn't maximize it. Selection at any level locally maximizes momentary fitness for that level, but the optima of different levels need not coincide. This is obvious between prezygotic and individual selection but is equally true for higher levels. Individual selection, the most important evolutionary force, can decrease F_t until extinction by, e.g., forcing the occupation of only a temporary niche.

(45). The latest record has now been found by J.F. Sutton, University of Kansas (talks at 1971 and 1972 meetings of the Society of Vertebrate Paleontology).

(46). Lewontin (1961), Warburton (1967), and Maynard Smith (1972) have made applications of game theory to evolution within the usual *evolutionary* framework.

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