Notice to Contributors

Efforts at *Science* to reduce a backlog of accepted reports in order to attain faster publication* have been successful. The acceptance rate for reports, which was reduced to about 10 percent over the summer, is now being increased. We are now able to publish reports within 2 months after acceptance on average.

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*See notice in *Science*, 15 July, p. 259.

Reports

Rates of Evolution: Effects of Time and Temporal Scaling

Abstract. *Rates of morphological evolution documented in laboratory selection experiments, historical colonization events, and the fossil record are inversely related to the interval of time over which they are measured. This inverse relationship is an artifact of comparing a narrow range of morphological variation over a wide range of time intervals, and it is also a product of time averaging. Rates measured over different intervals of time must be scaled against interval length before they can be compared.*

Evolutionary change is often studied by calculation and comparison of rates. Rates measured over different intervals of geological time have been used to argue in various ways that vertebrates (principally mammals) evolved more rapidly than mollusks and other invertebrates (*1–3*). Rates derived from the fossil record have also been used to argue that mammals evolved more rapidly during the Pleistocene than during preceding epochs (*4*), and that phyletic evolution (microevolution) is too slow to explain diversification during episodes of adaptive radiation (macroevolution) (*1, 5*). As I shall show, perceived evolutionary rates are a function of the time interval over which they are measured, and temporal scaling is required before rates measured over different intervals of geological time can be compared.

J. B. S. Haldane first proposed a standard unit, the darwin, widely used to measure rates of morphological evolution. A darwin (d) is defined as change by a factor of *e* per million years (my), where *e* is the base of natural logarithms (*6*). A logarithmic scale of measurement is appropriate because proportional rather than absolute change is of interest (*3, 7*). In an attempt to characterize distributions of empirically determined rates, I compiled 521 rates of morphological evolution calibrated in darwins and measured over intervals of time ranging from 1.5 years to 350 million years (Table 1). These include I, very high rates (averaging about 60,000 d) measured in laboratory selection experiments; II, high rates (about 400 d) associated with historical colonization events; III, moderate rates (about 4 d) associated with faunal change following Pleistocene glaciation; and IV, low rates (about 0.1 d) typical of change documented on a longer time scale in the fossil record.

Evolutionary rates are routinely calculated and compared on the assumption that dividing observed change by elapsed time removes the effect of time on the result, that is, that rates are independent of measurement interval. This assumption is unjustified. Rates of morphological evolution compiled here are plotted against the interval of time over which each rate was measured (Fig. 1A). The observed distribution approximates an inverse power function, which can most easily be studied in logarithmic form (Fig. 1B). Evolutionary rates are negatively correlated with measurement interval and, in logarithmic form, this correlation has a coefficient of −0.94.

The upper limit of ln rates observed over all ln time intervals (rates measured in darwins, time in million years) has a slope approximating −1.0 and an intercept of about 2.0 (dashed line in Fig. 1B).

Table 1. Relation of rates of morphological evolution (in darwins, d) to time intervals over which rates were calculated (in years, y, or million years, my) for each domain (Roman numerals) shown in Fig. 1. Rates are based on comparisons of linear measurements or counts (*11*). Average intervals and rates are calculated as geometric means (exponentiated means of ln values). Asterisks indicate correlations significant at $P < 0.001$ ($P \sim 0.10$ for others).

Domain	Sample size	Time interval		Evolutionary rate (d)		Regression of ln rate (d)/ln interval (my)	
		Range	Geometric mean	Range	Geometric mean	Slope	Correlation
I Selection experiments (*9*)	8	1.5–10 y	3.7 y	12,000–200,000	58,700	−0.90	0.60
II Colonization (*12*)	104	70–300 y	170 y	0–79,700	370	−2.08	−0.78*
III Post-Pleistocene Mammalia (*4, 13*)	46	1,000–10,000 y	8,200 y	0.11–32.0	3.7	−0.68	−0.22
IV Fossil Invertebrata and Vertebrata	363	8,000 y–350 my	2.8 my	0–26.2	0.08	−0.64	−0.70*
Fossil Invertebrata alone (*3, 14*)	135	0.3–350 my	7.9 my	0–3.7	0.07	−0.59	−0.52*
Fossil Vertebrata alone (*1, 4, 15*)	228	8,000 y–98 my	1.6 my	0–26.2	0.08	−0.82	−0.83*
I to IV combined	521	1.5 y–350 my	0.2 my	0–200,000	0.73	−0.85	−0.94*

Analysis of the empirical distribution of rates helps explain the correlation of rates with measurement interval. Assuming, for simplicity, that the slope of the whole distribution shown in Fig. 1B is −1.0 and taking the coordinates ln 0.2 my and ln 0.73 d as its midpoint (values from Table 1), the major axis of the distribution as a whole can be represented by the following equation:

$$\ln \text{rate (d)} = -1\,[\ln \text{interval (my)}] - 1.92 \qquad (1)$$

or, in exponential form:

$$\text{rate (d)} = 0.15\,[\text{interval (my)}]^{-1} = 0.15/\text{interval (my)} \qquad (2)$$

A rate in darwins is the absolute value of $(\ln x_2 - \ln x_1)/\text{interval (my)}$, where x_1 is an initial character state measured at time t_1, and x_2 is the final state at time t_2 (*6*). The interval of measurement is the difference between t_1 and t_2. Substituting and removing both denominators, Equation 2 simplifies to:

$$\ln x_2 - \ln x_1 = \ln (x_2/x_1) = 0.15 \qquad (3)$$

which is, in exponential form:

$$x_2/x_1 = 1.2 \qquad (4)$$

In other words, the average ratio of the initial and final states used to calculate the evolutionary rates shown in Fig. 1 appears to be about 1.2 regardless of time interval.

A similar calculation indicates that the upper limit observed in Fig. 1, with its intercept of 2.0, corresponds to a ratio of initial and final states x_2/x_1 of about 1600. The lower limit of evolutionary rates is 0 d (no change), but few rates are observed below the lower boundary of domains shown in Fig. 1B, corresponding to a ratio x_2/x_1 of about 1.0025. Difference by a factor of less than 1.0025 is generally not measurable, and it is reported as zero if recorded at all. Organisms differing by a factor of much more (or less) than 1.2 are so different (or so similar) that they are rarely compared in calculating rates, regardless of the time available for one to have changed into the other. The net effect of such a stable difference between initial and final states over all time intervals studied is to make interval length the principal determinant of rates. The greater the time separating similar initial and final states, the slower the inferred rate of change.

Interval length affects rates in another way. Rates are based on net change between initial and final states. A period of rapid change followed by a period of stasis will yield a rate of intermediate value for the entire interval. Similarly, a period of rapid change in one direction followed by a period of reversal will yield a low net rate. The shorter the interval of measurement, the more likely one is to observe high rates. The longer the interval, the more stasis and evolutionary reversal are likely to be averaged in the result. This effect, like that outlined above, systematically damps the values of rates calculated over longer and longer intervals (*8*).

Data summarized in Table 1 can be used to compare rates of morphological change in fossil vertebrates (principally mammals) with rates in fossil invertebrates. Direct comparison suggests that vertebrates evolved more rapidly than invertebrates (0.08 d compared to 0.07 d, respectively; see Table 1), and this is consistent with most comparisons of vertebrates and invertebrates in the literature (*1–3*). However, direct comparison ignores the fact that rates for vertebrates are calculated over an average interval of 1.6 my, while rates for invertebrates are calculated over an average interval of 7.9 my. Temporal scaling (that is, using regressions to predict rates for comparison at some appropriate standard interval length) indicates, on the contrary, that rates of morphological evolution of invertebrates as a whole exceed those of vertebrates over all intervals of geological time normally sampled. For a standard interval of 1 my, the average rate of evolution predicted for invertebrates is 0.21 d, while that for vertebrates is 0.12 d. For a standard interval of 10 my, the average rate of evolution predicted for invertebrates is 0.06 d while that for vertebrates is 0.02 d. Appropriately scaled, invertebrates appear to have evolved at least as fast as vertebrates,

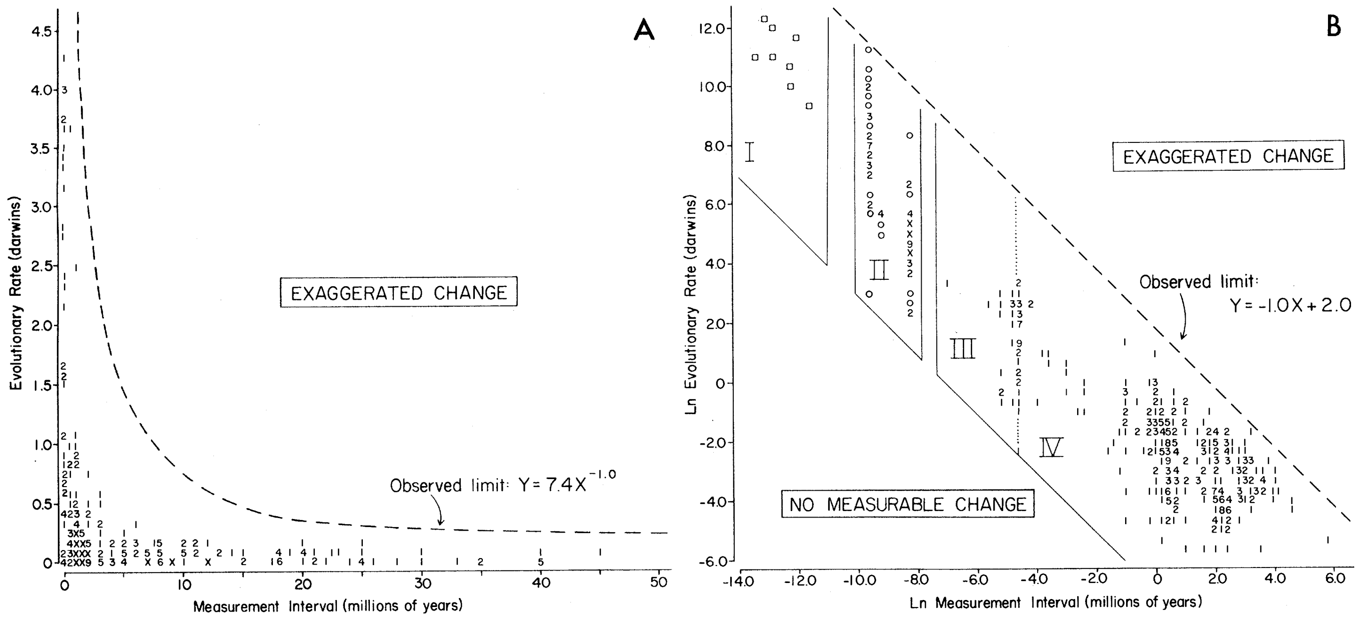

Fig. 1. Inverse relationship of evolutionary rates and interval of time over which rates were measured. (A) Central portion of distribution of 521 morphological rates measured in darwins over intervals ranging from 1.5 years to 350 million years (data from Table 1). Observed limit (dashed line) is derived from that in (B). (B) Logarithmic transformation of entire distribution shown in (A). The observed limit and the distribution as a whole have a slope approximating −1.0. Low rates of evolution over short intervals of time yield no measurable change, whereas high rates over long intervals yield exaggerated change making animals so rapidly different that they are no longer compared. Domains I to IV correspond to rates from laboratory selection experiments (open squares), historical colonization events (open circles), post-Pleistocene faunal recovery from glaciation, and fossil invertebrates and vertebrates, respectively. Unitary digits in domains III and IV are individual cases; higher digits in all domains represent multiple cases falling at the same point (*x* denotes numbers greater than 9).

and they may have evolved, on average, two to three times as rapidly. Analysis of the possible significance of this difference is a complex problem. Different long-term rates for invertebrates and vertebrates may reflect differences in intrinsic evolutinary potential (as a function of population structure, generation length, and so forth) or extrinsic environmental factors.

Kurtén's (*4*) conclusion that rates of morphological evolution in Quaternary (Pleistocene and post-Pleistocene) mammals exceeded those in Tertiary mammals is also based on comparison of rates measured over different intervals of time. Kurtén's mean value for Tertiary rates is predicted almost exactly by a regression of his Quaternary rates on temporal interval, indicating that Quaternary and Tertiary rates are not significantly different.

Finally, we can address the question of how rates of phyletic evolution measured over long intervals of geological time relate to rates characteristic of speciation and adaptive radiation on shorter time scales, a point crucial in the argument that ordinary microevolutionary processes cannot explain macroevolutionary events observed in the fossil record (*5*). Rates on the order of 60,000 d in laboratory selection experiments (Table 1 and domain I in Fig. 1) were sustained for only a few years; they exceed homeostatic limits (*9*) and exceed rates to be expected in nature. Rates observed during colonization of new or empty adaptive zones average about 400 d (domain II); all populations studied were viable, and rates on the order of 400 d probably characterize speciation and radiation in new adaptive zones. Post-Pleistocene rates (domain III) average about 4 d in integrated coevolved faunas, while rates measured over longer intervals in the fossil record (domain IV) average less than 1 d. These low rates are measured over such long temporal intervals that differences in morphology are swamped by interval length, and net change greatly underestimates total change. Microevolutionary rates measured on a scale of tens or hundreds of years are much higher than phyletic rates derived from fossils. A microevolutionary rate of 400 d is sufficient to change a mouse into an elephant in 10,000 years. However, the stratigraphic record is rarely complete enough on a scale of hundreds or even thousands of years to preserve such a rapid transition (*10*). Evolution on a microevolutionary scale is invisible in the fossil record, but this does not preclude microevolutionary processes operating over geological time from producing macroevolutionary change on the longer time scale. Microevolution and macroevolution are different manifestations of a common underlying process.

Rates of evolution measured over different intervals of time cannot be compared without appropriate temporal scaling. This conclusion is based on comparative study of morphological rates, but it holds in principle for rates of taxonomic and molecular evolution as well.

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Solar System Ice: Amorphous or Crystalline?

Abstract. *The role of meteoritic bombardment on icy surfaces in the solar system is investigated. Using recent theoretical results concerning the nature of ejecta from impact craters in ice, the author concludes that the ratio of amorphous to crystalline ice surfaces should be lower than 1.0.*

The discovery of many partially or totally ice-covered satellites of the giant planets and the well-known presence of ice on the rings of Saturn and in cometary nuclei have prompted questions about the structure of this ice. It is assumed here that water ice, which is presumably the main constituent, is not much influenced by the addition of other types of ice. Exceptions are ice-ammonia solutions which have a significantly lower melting temperature and the clathrates. Golitsyn (*1*) drew attention to the process of slow deformation of ice in the crust of satellites, which may lead to tectonic phenomena resembling those on the earth. Reynolds and Cassen (*2*) concluded that radioactive heating may permit convective motions of ice corresponding to Rayleigh numbers between 10^3 and 10^6 and that the ice should be crystalline because the temperature in the interior would be higher than 150 K, which is the upper limit for the existence of amorphous water ice. On the other hand, Klinger (*3*) suggested that ice in the interior of some satellites could be amorphous and that its slightly exothermic behavior during heating below 150 K by radioactive and tidal effects may produce sufficient heat to melt and resurface satellites such as Enceladus. This mechanism may be valid if the ice contains enough NH_3 to lower its melting temperature considerably. This report focuses on the meteoritic bombardment of icy surfaces and, in particular, on the formation of amorphous ice with its significantly different thermal, mechanical, and optical properties. These differences may be observable.

Cratering impacts in ice. Impacts that lead to plastic deformation and fragmentation both of the projectiles and of the target materials are difficult to treat theoretically because the fracture mechanism and fracture resistance are not bulk properties but structure-sensitive properties of solids. These properties depend on the microscopic perfection of the solids, and thus their evaluation requires making drastic approximations on the basis of experimental data. Inasmuch as ice has seldom been studied both as a target and as a projectile, not many facts are available with which to make suitable generalizations. The main questions concern the size of the craters, the amount