same adaptive behavior" as do associative procedures, they say; in both cases "the propensity of the animal to adapt by rejecting a novel or distinctive fluid is revealed" (*18*, pp. 18–19). As to mechanisms of associative predisposition, speculation seems to me to be premature. It might be wiser to wait until we have evidence that there is such a thing—evidence which the literature of flavor aversion, however voluminous, fails to provide.

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References

1. M. E. Bitterman, *Science* **188**, 699 (1975).
2. J. Garcia, B. K. McGowan, F. R. Ervin, R. A. Koelling, *ibid.* **160**, 794 (1968).
3. J. Garcia, W. G. Hankins, K. W. Rusiniak, *ibid.* **192**, 265 (1976).
4. M. Domjan and N. E. Wilson, *Psychonomic Sci.* **26**, 143 (1972).
5. J. Garcia, R. Kovner, K. F. Green, *ibid.* **20**, 313 (1970).
6. J. Garcia and R. A. Koelling, *ibid.* **4**, 123 (1966).
7. J. Green, A. Bouzas, H. Rachlin, *Behav. Biol.* **7**, 513 (1972).
8. R. V. Krane and A. R. Wagner, *J. Comp. Physiol. Psychol.* **88**, 882 (1975).
9. M. Domjan and N. E. Wilson, *ibid.* **80**, 403 (1972).
10. D. F. Smith and S. Balagura, *ibid.* **69**, 308 (1969).
11. R. M. Bradley and C. M. Mistretta, *ibid.* **75**, 186 (1971).
12. P. Rozin, *ibid.* **67**, 421 (1969).
13. J. Garcia, W. G. Hankins, J. Robinson, J. Vogt, *Physiol. Behav.* **8**, 807 (1972).
14. J. Garcia, F. R. Ervin, C. H. Yorke, R. A. Koelling, *Science* **155**, 716 (1967).
15. H. C. Wilcoxon, W. B. Dragoin, P. A. Kral, *ibid.* **171**, 826 (1971). The authors assure us that sensitization was controlled in a subsequent experiment, but they present no supporting data.
16. A. Gelperin, *ibid.* **189**, 567 (1975).
17. R. E. Johnston and D. M. Zahorik, *ibid.* **189**, 893 (1975).
18. J. Garcia, B. K. McGowan, K. F. Green, in *Classical Conditioning II*, A. H. Black and W. F. Prokasy, Eds. (Appleton-Century-Crofts, New York, 1972).

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Stability of Species in Geologic Time

In assessing the distribution of evolutionary rates in phylogeny, Harper (*1*) has misconstrued my contribution (*2*). I did not feel compelled to choose between the two extreme alternatives: (i) that all evolutionary change is phyletic, or occurs as gradual transition within established species, and (ii) that nearly all evolution is associated with multiplication of species. In fact, I recognized that a spectrum of intermediate possibilities exists, but conducted four tests of the fossil record which showed that phyletic change is "generally slow and of minor consequence relative to changes that frequently occur in speciation events." No claim was made that phyletic change necessarily accounts for "considerably less than" 10 percent of all evolution.

Furthermore, Harper's inference that my tests can apply only to the extreme alternatives is incorrect. The fossil record offers crucial evidence for resolution of the question. Elaboration of the test of adaptive radiation (*2*) will make these points. This test begins with the observation that species durations within higher taxa are extremely long with respect to rates of large-scale evolution. For example, an average species of late Cenozoic mammals has survived 1 to 2 million years, and yet most orders of mammals arose from primitive ancestors during only about 12 million years of the early Cenozoic. Clearly, ten or so species-to-species phyletic transitions are insufficient to produce the enormous degree of change that occurred in the origin of such divergent taxa as bats or whales. It seems inconceivable that rates of phyletic evolution were somehow dramatically accelerated for an enormous variety of early Cenozoic mammalian taxa occupying unrelated niches in diverse habitats. On the other hand, we know that speciation was rampant, as a multitude of niches was invaded in the replacement of extinct reptiles. It is unlikely that this close association between speciation and rapid large-scale evolution was coincidental.

Mean longevity of mammal species was originally calculated by a technique that did not permit estimation of skewness or variance (*2*). Is the distribution of species durations strongly skewed, allowing for many short-lived species that might have undergone rapid phyletic transition? A new kind of analysis (Fig. 1) eliminates this possibility. The analysis is deceptively simple but should be highly accurate. Each point of Fig. 1A is derived from fossil data for a particular stage of the Plio-Pleistocene of Europe. It represents the percentage of all mammal species of the stage that survived into the Würm (last Pleistocene stage). Use of the Würm rather than the Recent as an end point in this particular example avoids the effects of the famous sub-Recent mass extinction. No bias is introduced because nearly every species of the preceding Eem stage is also recorded for the Würm. Even though the fossil data and absolute time scale come from different sources, the resulting curve is quite smooth. It can be transformed into a survivorship curve, depicting attrition from some imaginary time zero, as follows. Consider a single point of Fig. 1A representing a time α, approximately 1 million years before the Würm, when 30 percent of all existing species were to survive into the Würm. As will be justified below, it is assumed that an average species of the total fauna existing at any time, including α, was in mid-duration. The stratigraphic ranges of an idealized set of all species existing at time α are plotted in Fig. 1B. Figure 1B happens to display more species of medium duration than of long or short duration, but the shape of the distribution is immaterial to the analysis. An average species of each duration is placed in midrange. As required by Fig. 1A, 30 percent are extant at the start of the Würm. In plotting a survivorship curve, the time for decline to 30 percent will be longer than the interval from α to earliest Würm because survivorship represents decline starting with a "cohort" of brand new species. More precisely, realignment of the set of hypothetical species so that all originate simultaneously (Fig. 1C) doubles the decline time. This effect can also be seen by inspection of the symmetry of Fig. 1B. The 30 percent point is therefore plotted at 2 million years in Fig. 1D and, by extrapolation, a complete survivorship curve is produced by doubling the time scale of Fig. 1A. Finally, a histogram of species durations derived from Fig. 1D is plotted as Fig. 1E.

The assumption that at any time depicted in Fig. 1A an average species was in mid-duration amounts to the assumption that rates of speciation and extinction were constant, or that a stable age distribution of species was maintained (*3*). There is no theoretical reason to believe that these conditions should have been met. On the other hand, only major departures from the conditions would have caused significant deflection of the empirical curve. Sufficient adherence to them for the purpose of this analysis is indicated both by the smoothness of the empirical curve (Fig. 1A) and by the general similarity of age-frequency distributions for species entering the four final stages (Fig. 1F). These represent the critical portion of the curve because the "shoulder" adjacent to the ordinate attests to the presence of few short-lived species. The technique used to obtain the histogram avoids the sources of error attributed to similar curves plotted directly from recorded stratigraphic ranges (*4*). From the standpoint of preservation, it requires only that the fossil faunas analyzed be good statistical samples for the geologic intervals they represent, and the fossil record of Pleistocene mammals of Europe is exceptionally complete and well studied.

Figure 1E is skewed, with a mean of about 1.2 million years and a mode of about 0.7 million years, but displays very few species of short duration (< 0.3 to 0.4 million years) that could represent rapid phyletic turnover. Furthermore, much extinction was by termination of lineages rather than by phyletic transition. A histogram representing only ranges terminated by phyletic extinction would display even fewer short-lived species. Have the Mammalia somehow been afflicted by evolutionary stagnation in the late Cenozoic? Definitely not. Many groups, especially within the Artiodactyla, have been in the midst of adaptive radiation and wholesale change (*5*, *6*). Phyletic evolution has been too slow to account for this change.

The untreated data of Kurtén (*5*) provide supporting evidence. About 83 percent of living European mammal species are recognized in the excellent Pleistocene record, yet collection from dozens of sites has unearthed virtually no ephemeral species. Of about 190 species recorded for the Middle Pleistocene (Günz-Riss), only 3 are known from just one stage.

Analyses have not been completed for invertebrate taxa, but species of most of these last much longer than species of mammals. Doubling the age of the 50 percent point of Fig. 1A gives a good estimate of mean duration displayed in Fig. 1E. The 50 percent point for the mollusks, a typical group of marine invertebrates, falls in the middle Pliocene, indicating a mean duration of about 7 million years (*2*, *7*). An independent line of evidence corroborates these conclusions: phyletic evolution documented in the fossil record, including that cited by Harper (*1*), is invariably extremely slow (*8*).

Harper (*1*) has pitted phyletic evolution against divergent allopatric speciation as a source of evolution. The latter mechanism has received emphasis following the classic contributions of Mayr (*9*), but other sources of rapid divergence must not be discounted. One is the appearance of polymorphism within species under conditions of relaxed selection pressure, through what has been termed a population flush (*10*). This may frequently occur after the invasion of ecologic "islands" lacking predators or competitors (*11*). It is immaterial exactly when the divergent morphs become reproductively incompatible, after perhaps some form of geographic or habitat isolation. Also we must recognize that certain kinds of selection, like sexual selection, which operates directly on the reproductive process, may account for more rapid phyletic evolution than is observed within most lineages.

As I have suggested elsewhere (*12*), it seems wise to define phyletic gradualism (*13*), or the gradualistic model, as the assertion that phyletic change is the clearly dominant mode of evolution. The rectangular (*2*) or punctuated equilibrium model (*13*) of phylogeny conversely should express the view that much more than 50 percent of evolution occurs through sudden events in which polymorphs and species are proliferated. Intermediate alternatives obviously exist, but fossil evidence discussed here and elsewhere (*2*) favors the rectangular model.

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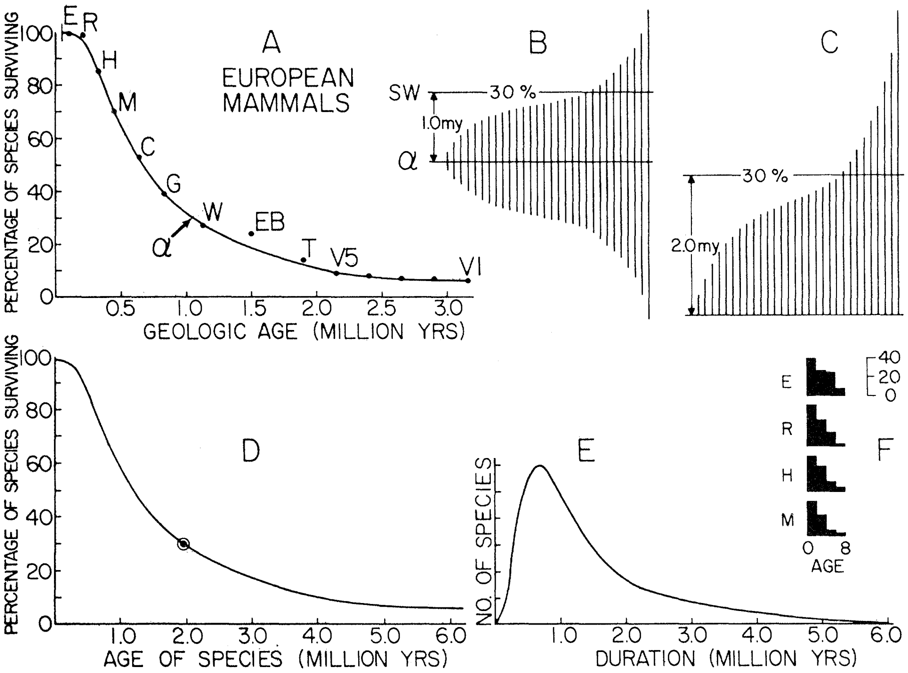

Fig. 1. Construction of a histogram for species durations of late Cenozoic mammals. (A) Extinction curve for Plio-Pleistocene mammal species of Europe. Geologic time extends backward toward the right. On the left, the curve terminates at the beginning of the Würm. Each point represents the percentage of all species occurring in a given stage that survived into the Würm. Points are placed at the midpoints of stages. An average stage contains more than 90 species. Percentages are derived from Kurtén (*5*). Dates for stages are from Berggren and van Couvering (*14*). Points within the Villafranchian are equally spaced, in the absence of an established chronology. Stage abbreviations: *E*, Eem; *R*, Riss; *H*, Holstein; *M*, Mindel; *C*, Cromerian; *G*, Günz; *W*, Waalian; *EB*, Eburonian; *T*, Tegelen (Tiglian); and *V5* and *V1*, last and first phases of the Villafranchian. (B) Hypothetical set of average ranges (vertical bars) of species existing at time α, approximately 1 million years (*my*) before the start of the Würm (*SW*). (C) Realignment of the ranges of (B) so that all species originate simultaneously. Twice as long is required for decline to 30 percent. (D) Survivorship curve for species constructed by doubling the time scale of (A). Circle indicates the point derived from point α of (A), as illustrated in (B) and (C). (E) Histogram of species durations derived from (D). The vertical scale is arbitrary. (F) Age-frequency distributions for species entering the four final stages of (A). Ages are measured by number of stages of existence. Species older than eight stages are not plotted.

References and Notes

1. C. W. Harper, *Science* **190**, 47 (1975).
2. S. M. Stanley, *Proc. Natl. Acad. Sci. U.S.A.* **72**, 646 (1975).
3. The analogous stable age distribution for individuals in populations was elucidated by A. J. Lotka [*Science* **26**, 21 (1907)].
4. D. M. Raup, *Paleobiology* **1**, 82 (19 J. J. Sepkoski, *ibid.*, p. 343.
5. B. Kurtén, *Pleistocene Mammals of Europe* (Aldine, Chicago, 1968).
6. A. S. Romer, *Vertebrate Paleontology* (Univ. of Chicago Press, Chicago, 1966).
7. An extinction curve for mollusks published elsewhere [D. M. Raup and S. M. Stanley, *Principles of Paleontology* (Freeman, San Francisco, 1971)] is not accurate. It is an assumed curve by which faunas were crudely dated.
8. Well-documented invertebrate lineages display chronospecies that last several million years unless extinguished by termination of linea [D. Nichols, *Philos. Trans. R. Soc. London Ser. B* **242**, 347 (1959); W. L. Fisher, P. U. Rodda, J. W. Dietrich, *Univ. Texas Publ. No. 6413* (1964), p. 117; A. M. Ziegler, *Palaeontology* **9**, 542 (1966); T. R. Waller, *Paleontol. Soc. Mem. 3* (1969); A. Lenz, *Lethaia* **7**, 265 (1974); I. Hayami and T. Ozawa, *ibid.* **8**, 1 (1975); D. E. Kellogg and J. D. Hayes, *Paleobiology* **1**, 150 (19 A. Hallam and S. J. Gould, *Proc. R. Soc. London Ser. B* **189**, 511 (1975)]. Well-documented vertebrate lineages display species longevities consonant with Fig. 1E [V. J. Maglio, *Trans. Am. Philos. Soc.* **63**, 149 (1973); P. D. Gingerich, *Nature (London)* **248**, 107 (1974)].
9. E. Mayr, in *Evolution as a Process*, J. Huxley, A. C. Hardy, E. B. Ford, Eds. (Allen & Unwin, London, 1954), p. 156; *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, Mass., 1963).

10. H. L. Carson, in *Population Biology and Evolution,* R. C. Lewontin, Ed. (Syracuse Univ. Press, Syracuse, N.Y., 1968), p. 123.
11. B. W. Walker, *Calif. Fish Game Fish Bull.* **113**, 105 (1961).
12. S. M. Stanley, *Science* **190**, 382 (1975).
13. N. Eldredge and S. J. Gould, in *Models in Paleobiology*, T. J. M. Schopf, Ed. (Freeman, Cooper, San Francisco, 1972), p. 82.
14. W. A. Berggren and J. A. van Couvering, *The Late Neogene* (Elsevier, Amsterdam, 1974).
15. I thank S. A. Woodin for evaluating this comment.

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The beginning of Stanley's comment is misleading in that item (ii) should read "multiplication of species in small peripheral isolates."

I stand corrected if I too narrowly construed the range of alternative hypotheses that Stanley intended to evaluate with his critical tests. Although Stanley states that he did not intend to limit his tests to the evaluation of two extreme alternatives, his initial paper (*1*) gives the opposite impression. For example, referring to his critical tests in (*1*) he refers only to the rectangular model [of evolution], the gradualistic model, and "both models" (*2*). So I assumed that he was following the characterization of two alternative models explicitly stated by Eldredge and Gould (*3*), and that his tests were designed to evaluate one model against the other. At no place in this paper does Stanley refer to a spectrum of intermediate possibilities. Further, Stanley states above that his four tests showed that phyletic change is generally slow and of minor consequence relative to changes that frequently occur in speciation events—that is, that his rectangular model is correct. Yet, the only way he could show this using the method of critical tests (*4*) would be to proceed by systematically rejecting competing hypotheses. In fact, the only competing hypothesis referred to in his original paper (*1*) is his gradualistic model.

Stanley's critical tests are interesting and thought-provoking, but, apart from his citation of counterexamples such as the Pontian Cockles (*1*, p. 647), I am not convinced that they even serve to rule out the hypothesis $P(S,S_i) = 0$ (*5*), let alone less extreme alternatives. His test of adaptive radiation is relevant here only if we associate each phyletic evolution of a new species with a phyletic extinction on a one-to-one basis. Yet, gradual phyletic change could occur in large established populations undergoing speciation where all daughter populations are large and widespread, even continent-wide, in distribution, and none of which are small peripheral isolates [species originating in this way are not counted in S_i in (*5*)]; S. Bretsky (*6*, pp. 114–116) nicely illustrates this point. Phyletic extinction need not be involved in this process (the ancestral species may persist); also one ancestral species could yield very many daughter species. Adaptive radiation, by definition, involves much speciation and is obviously an important process of evolution. Yet, it need not necessarily involve speciation in small peripheral isolates. Further, gradual phyletic change during adaptive radiation can occur without attendant phyletic extinction, and one ancestral species can yield very many daughter species. Thus, Stanley's conclusion that most species are long-ranging does not preclude the possibility of rapid phyletic change.

The observation above that all seemingly valid documentations of phyletic evolution reveal extremely slow rates can be explained by appealing to the inadequacy of the fossil record: these are the only ones that are likely to be represented in the record. With regard to Stanley's test of the living fossils (*1*, pp. 647–648), let A represent groups of taxa that have survived at consistently low diversities over long periods of time and B represent those that have survived over long periods of time and exhibited very little evolutionary change. Stanley reasons that if the rectangular model is true, then all (at least most) A should be B; he then points out that some A are B. The latter is not an impressive confirmation of the former. Regarding lack of correlation between rate of evolution and generation time (*1*, p. 648) it should be noted that many variables other than generation time are involved in determining rate of evolution.

These shortcomings of the critical tests are no reflection on Stanley; they are due to the magnitude of his undertaking—to test fundamental biologic generalizations by studying the fossil record (analogous to testing sociological generalizations by examining the data of archeology).

One criticism of my treatment of Stanley's paper is that I did not mention his major contribution: he shows that if the Eldredge-Gould model is true, then evolution above the species level is determined by a process of species selection, "which is analogous to natural selection but acts upon species within higher taxa rather than upon individuals within populations" (*1*, p. 646). Also, his method of estimating the average geologic duration of species, elaborated above, stands on its own as contribution of note.

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References

1. S. M. Stanley, *Proc. Natl. Acad. Sci. U.S.A.* **72**, 646 (1975).
2. Some clarification of Stanley's terminology may be useful. The latter is his term for phyletic gradualism, a model explicitly defined by Eldredge and Gould (*3*, p. 89). In (*1*, p. 646), he equates the former with the "*allopatric model* of evolution [which] represents the geographic concept of speciation . . . in which small peripheral populations of established species are seen as occasionally becoming separated . . . to form new species," adding that "sympatric speciation, whatever its incidence, can also produce a rectangular pattern of phylogeny" [a minor point which I failed to acknowledge in (*5*)].
3. N. Eldredge and S. J. Gould, in *Models in Paleobiology*, T. J. M. Schopf, Ed. (Freeman, Cooper, San Francisco, 1972), p. 82.
4. J. R. Platt, *Science* **146**, 347 (1964).

C. W. Harper, Jr., *ibid.* **190**, 47 (1975).
S. S. Bretsky, *Syst. Zool.* **24**, 113 (1975).

22 December 1975