

Why and how do mammals evolve unusually rapidly?

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

Received August 18, 1984; January 15, 1985

ABSTRACT: The maximum origination rates known for species and genera occur for protists just after the Cretaceous/Paleogene extinction. This and other evidence help in evaluating hypotheses for the observation that mammals evolve unusually rapidly in some but not all respects.

* * *

It has long been realized (Simpson, 1944) that the usual evolution of mammals is more rapid than that of most other groups of organisms. However, this difference in rate applies to only some aspects of evolution. Extending a distinction made by Wilson, Maxson, and Sarich (1974), I proposed that those aspects of evolution which are markedly faster in mammals evolve in an epistandard mode in mammals, while other aspects retain the standard mode (Van Valen, 1974). [The term "mode" here refers to kind of evolution, as in Tempo and Mode, not to a statistical parameter, and "mammals" refers only to those of the Cenozoic, as data for much earlier mammals are inadequate.]

Molecular evolution and linear ("size") measurements retain the standard mode in the Mammalia, whereas origination, extinction, community evolution, structural innovation and complexity ("shape"), chromosome number, and hybrid inviability seem to change to the epistandard mode there. In the present note I comment on more recent evidence bearing on some of these distinctions, and evaluate several competing hypotheses to explain the epistandard mode.

RECENT EVIDENCE

There have been at least four studies which have compared evolutionary rates of body size or structure size between mammals and other taxa. Two of these, Lerman (1965) and Bonner (1968), had too few data for any real conclusions, while the others (Van Valen, 1974, and Gingerich, 1983) used larger sets of data. All four studies found that invertebrates ostensibly evolve somewhat faster than mammals in linear measurements, although only Gingerich (1983) thought this difference probably either real or large. It has long been known (Kurtén, 1960) that shorter intervals of time for a rate measurement permit faster rates to be detected. (It is curious that Gingerich [1983], in claiming to discover this epistemic property, twice criticized Kurtén [1960] for not seeing it.) Gingerich's result is itself based on a methodological artifact (Gould, 1984), that both faster and slower rates than the band depicted will be undetectable, although I think Gingerich (1984) is correct that the pattern is not otherwise a result of plotting time against its reciprocal. (That would be the case if the numerator, the absolute amount of change, is about the same for all intervals, but this approximate equality is produced only by the veil lines just mentioned.) Therefore any appropriate comparison must probably use about the same time intervals, as was (deliberately) the case in my 1974 comparison. However, another artifact is incorporated into the data which I (and therefore Gingerich) used. I included only detectably evolving lineages, thereby excluding intervals of stasis. Weighting stasis properly, by a factor of perhaps 1 or 2 for the intervals used (cf. Stanley, 1979, on estimates of duration) relative to the

* * *

Evolutionary Theory 7: 127-132 (March, 1985)

The editors thank two referees for help in evaluating this paper.

© 1985, Biology Department, The University of Chicago

geometric average for my data, makes the invertebrates ostensibly but again nonsignificantly a bit slower.

Cherry et al. (1982) found that among taxa above the species level, "shape" variation for mammals is perhaps twice as large as for frogs and lizards. Because these taxa are several times younger for mammals than for the other groups, this study provides the first quantitative corroboration of the qualitatively apparent fact that "shape" is part of the epistandard mode in the mammalia.

In a potentially important paper, Prager, Fowler, and Wilson (1977) concluded that chromosomal evolution, and the evolution of new genera, in the Pinaceae has been about an order of magnitude slower, at least for the past 100 Myr or so, than is usual. Angiosperms are more normal here. They also concluded that protein evolution in the Pinaceae occurs at the standard rate, but this was based on immunological comparisons of gross seed extract. The possibility of appreciable variation in the amount of different proteins was therefore uncontrolled. Most living fossils (Eldredge and Stanley, 1984) are in low-diversity taxa and so cannot be easily tested for similar phenomena. It would, nowever, be more feasible to investigate evolutionary rates of "size" characters in lineages of some living fossils. Results here could be valuable.

Despite their usually much slower taxonomic turnover, protists have proven to have maximum origination rates at least as fast as those of mammals. (Their maximum "size" rates are also similar: Van Valen, 1974.) To be precise, the work of Perch-Nielsen (1981) on coccolithophores has shown that there are 4 species in 2 or 3 genera, in the first nannoplankton zone of the Paleocene (NP-1), which originated from a species of Biscutum, which itself lasts long enough to be included in the 4. (There are also other clades suitable for estimates in this explosive radiation.) Perch-Nielsen, McKenzie and He (1982) estimate the duration of NP-1 as 200,000 years. This gives values of r (Van Valen and Maiorana, 1985) of 6.9 for species and 4.6 for genera, if the number of genera is taken to be 2.5. r is the expected number of times one lineage branches per million years. Romein, Smit, and Hussain (1983) report an additional species and genus of this clade elsewhere from NP-1, by the criteria of Perch-Nielsen (1977) for this zone, but this record occurs after the appearance of the foraminiferan Globigerina pseudobulloides and so is probably really later than the end of NP-1 (cf. correlation by Perch-Nielsen, McKenzie, and He, 1982).

Smit (1982) finds 19 species and 8 genera (because another genus separates different species referred to Globigerina) of planktonic foraminiferans to have arisen from a single ancestral species (again included in the 19) in the first 33,000 years of the Paleocene, in the western Mediterranean alone. These data give extraordinary r values of 89 for species and 63 for genera. Planktonic foraminiferans are mutualistic units of algae and foraminiferans per se and thereby have generation lengths of perhaps as short as 2-4 weeks (Bé, 1982), which may make these rates somewhat less unbelievable, but the proper scale for comparison with other taxa and with foraminiferans at other times is that of absolute time.

The fastest known rates for mammals (cf. Van Valen, 1978, and Archibald, 1983, for earlier estimates from these data) come from condylarth evolution across the Cretaceous-Paleogene boundary, starting a few hundred thousand years before the boundary (Sloan and Van Valen, 1965; Van Valen and Sloan, 1977). I have listed and revised most of the species of the relevant faunas (Van Valen, 1978). 8 species and 7 genera at Mantua arose from 1 at Bug Creek Anthills, over an interval of about 0.5 Myr, and there are 29 species and 19 genera in the Puerco, about 1.0 Myr after Bug Creek Anthills. The resulting estimates of r are 4.3 and 3.4 respectively for species and 3.9 and 2.9 for genera. Shorter intervals give similar rates, based on fewer taxa. Like the estimates for plankton, these are based on single biotas; better geographic sampling, when suitable biotas are found elsewhere, will probably increase the mammalian rate somewhat more than that for the plankton because (recent) species of mammals have smaller average geographic ranges than do those of plankton. In all cases the time intervals could be in error by as much as a factor of 2; the rates are of course inversely proportional to the time

intervals used.

Fishes and mollusks, which also evolve in the standard mode, can nevertheless also have high origination rates when they have an evolutionary bloom by entering an empty part of the resource space. This is best shown for the occupation of new lakes. The classic radiations of cichlids in the great lakes of the African rift zone exemplify the phenomenon. In Lake Victoria about 170 species have come from one ancestral species in perhaps 750,000 years (Mayr, 1984). Although the time interval is, as usual, imprecise, it is more likely to be smaller than larger, and perhaps much smaller (Mayr, 1984). A value of $\bar{r}$ of 6.8 results for species. (A rate for genera is inappropriate because of what seems to have been an unusually large amount of generic lumping, before cladists destroyed the picture with their noncomparable taxa.) Stanley (1979) discussed the evolutionary bloom of the pelecypod family Limnocardiidæ during the Pliocene in the perhaps brackish Paratethys (or Pontian) Sea. More than 30 genera arose in less than 3 Myr., which gives a generic $\bar{r}$ of 1.1 (or quite possibly more, if the bloom decelerated.)

HYPOTHESES

About five hypotheses have been proposed to explain the epistandard mode. Some of the evidence discussed above is relevant to their evaluation.

One hypothesis (Schopf et al., 1975; Schopf, 1981) maintains that the epistandard mode is a methodological artifact of our way of looking at organisms. More complex organisms tend to have faster turnover rates, with a rather good correlation. Such organisms also have more characters for taxonomists to distinguish taxa with. Therefore the availability of more characters, rather than anything in the biology itself, may cause the appearance of faster turnover among more complex organisms. Williams and Hurst (1977) supported this hypothesis with data for different superfamilies of brachiopods. One could also argue for a non-artifactual version of this hypothesis by noting that the same rate of evolution per character, applied to more characters, will (*ceteris paribus*) give a higher overall rate.

This class of hypotheses is apparently refuted by the high origination rates for standard-mode organisms in bloom periods. That these rates are detectable shows that their normally slower rates are not a result of having fewer characters. Complexity must then correlate with something which is actually causal. Stanley (1979) gives other evidence against the complexity hypothesis, and Simpson (1944) had noted a very rapid family-level transition to the snail *Valenciennesia* as showing that slow rates were not inherent in the Gastropoda. The hypothesis can be further evaluated by estimating to what extent immediately related species or other taxa recognized in the modern biota can be distinguished by criteria used, or available, in paleontology. I know of no quantitative estimates, but for at least mammals, pelecypods, and planktonic foraminiferans I suspect the proportion is well over 90 percent.

A second class of hypotheses invokes real but internal causes, such as the greater social behavior of most mammals (Wilson et al. [1975 and later], Stanley [1979], and others) or presumptively greater habitat selection (Rosenzweig, 1978). It too would seem to be refuted by the bloom-phase rates of standard-mode taxa, but this may be premature. What is shown is that high origination rates need not occur with sociality. It may nevertheless be true that sociality can produce conditions which lead to the epistandard mode. A precise mechanism, however, is not clear, which makes evaluation difficult. For instance, Wilson et al. (1975) gave some evidence that dispersal is inversely related to rate of chromosomal evolution, yet later Wyles, Kunkel, and Wilson (1983) cited evidence for a direct relation. In each case the relation was supposed to support the hypothesis. (And it is clear that either low or high dispersal by itself is insufficient, by comparison with the diversity of standard-mode taxa with all degrees of dispersal.) Other mechanistic problems with the hypothesis have been noted by Gold et al. (1978), Bickham and Baker (1979), Schwartz and Armitage (1980), and Barrowclough (1980).

A third hypothesis (Novacek and Norell, 1983) is that the epistandard mode may not exist, that (at least for turnover rates) its estimation is incorrect or a stochastic fluctuation. For mammals, this suggestion was made because Mesozoic mammals were not included in earlier calculations. Unfortunately, the data still do not permit useful estimation of evolutionary rates of mammals more than 1 Myr or so before the Cenozoic; assuming a slow, steady increase in diversity from the middle of the Cretaceous, as Novacek and Norell did implicitly, is unwarranted even though perhaps correct. Even if correct, though, it would have no bearing on the various estimates from real Cenozoic data except to restrict the epistandard mode, among extant organisms, to Cenozoic placentals (and, possibly, birds [Wyles, Kunkel, and Wilson, 1983], a subject beyond the scope of this paper.)

The two final hypotheses involve differences in natural selection. Stanley (1974, 1979) has proposed that mammals undergo unusually large amounts of selection, while I proposed that mammals have more intense selection with a similar total amount (Van Valen, 1976), and a low threshold for extinction (Van Valen, 1974). As I can add nothing useful to my previous discussions of these hypotheses I will not repeat them, except to note that a normal amount of selection within species, and easy extinction, permit rapid turnover and its correlates while having "size" evolution at about the usual rate. If Carson's (1975) distinction between open (quasi-additive) and closed (coadapted) systems of genetic variability within single genomes really does have a basis in the genome, it is, however, presumably relevant to the problem, because Carson believed the latter system to evolve primarily during speciation. Carson's resolution would thus apply only in cases of punctuation.

DISCUSSION

The detection of maximum rates of origination obviously requires special circumstances for the data. A real bloom phase may last only a geological instant before diversity-dependent effects begin to intervene, and geological instants are often not preserved at all (Schindel, 1983). Therefore estimation of bloom-phase parameters over intervals of tens of millions of years (e.g. Stanley, 1979; Novacek and Norell, 1983; Walker and Valentine, 1984) must be questioned, as such estimates are likely to be low by one or two orders of magnitude. There may nevertheless occasionally be an approximation to exponential diversification on such time-scales (Sepkoski, 1979). Because the origination rates then are much lower than the maximum, and many extinctions occur (even though at a lower than expected rate), such intervals do not seem to represent unimpeded filling of empty resource space, but rather bloom-like periods of comparatively little inhibiting pressure from the biotic environment.

The epistandard mode may have occurred in rapidly evolving extinct groups such as ammonites, and there is no reason to believe that it is sharply distinct from the standard mode. Thus there may be no mode in the statistical sense. Such questions as these require more comparisons between, at least, rates of single measurements ("size") and of character complexes ("shape") or taxonomic turnover.

ACKNOWLEDGMENTS

I thank J.S. Levinton, V.C. Maiorana, R.M. May, and the referees for comments on the topics in this paper.

LITERATURE CITED

- Archibald, J.D. 1983. Structure of the K-T mammal radiation in North America: speculations on turnover rates and trophic structure. *Acta Palaeontologica Polonica* 28: 7-17.
- Barrowclough, G.F. 1980. Patterns in the genetic and social structuring of vertebrates. Second International Congress of Systematic and Evolutionary Biology, Abstracts, p. 140.

- Bé, A.W.H. 1982. Biology of planktonic foraminifera. *In: Foraminifera, Notes for a Short Course* (M.A. Buzas and B.K. Sen Gupta, eds.), pp. 51-89. Univ. Tennessee, Dept. Geological Sciences, Studies in Geology no. 6.
- Bickham, J.W., and R.J. Baker. 1979. Canalization model of chromosomal evolution. *Bulletin of Carnegie Museum of Natural History* 13: 70-84.
- Bonner, J.T. 1968. Size change in development and evolution. *Paleontological Society Memoir* 2 (*Journal of Paleontology*, 42, part 2): 1-15.
- Carson, H.L. 1975. The genetics of speciation at the diploid level. *American Naturalist* 109: 83-92.
- Cherry, L.M., S.M. Case, J.G. Kunkel, J.S. Wyles, and A.C. Wilson. 1982. Body-shape metrics and organismal evolution. *Evolution* 36: 914-933.
- Eldredge, N., and S. Stanley. (eds). 1984. *Living Fossils*. New York: Springer-Verlag. 291 pp.
- Gingerich, P. 1983. Rates of evolution: effects of time and temporal scaling. *Science* 222: 159-161.
- _____. 1984. (Reply to Gould, 1984.) *Science* 226: 995.
- Gold, J.R., W.D. Womac, F.H. Deal, and J.A. Barlow, Jr. 1978. Gross karyotypic change and evolution in North American cyprinid fishes. *Genetical Research* 32: 37-46.
- Gould, S.J. 1984. Smooth curve of evolution rate: a psychological and mathematical artifact. *Science* 226: 994-995.
- Kurtén, B. 1960. Rates of evolution in fossil mammals. *Cold Spring Harbor Symposia on Quantitative Biology* 24 (for 1959): 205-215.
- Lerman, A. 1965. On rates of evolution of unit characters and character complexes. *Evolution* 19: 16-25.
- Mayr, E. 1984. Evolution of fish species flocks: a commentary. *In: Evolution of Fish Species Flocks* (A.A. Echell and I. Kornfield, eds.), pp. 3-11. Orono, Maine: Univ. Maine at Orono Press.
- Novacek, M.J., and M.A. Norell. 1983. Fossils, phylogeny, and taxonomic rates of evolution. *Systematic Zoology* 31 (for 1982): 366-375.
- Perch-Nielsen, K. 1977. Albian to Pleistocene calcareous nannofossils from the western South Atlantic, DSDP Leg 39. *Initial Reports of the Deep-Sea Drilling Project, Leg 39*: 699-823.
- _____. 1981. Les coccolithes du Paléocène près de El Kef, Tunisie, et leurs ancêtres. *Cahiers de Micropaléontologie* 3: 7-23.
- _____, J. McKenzie, and Q. He. 1982. Biostratigraphy and isotope stratigraphy and the 'catastrophic' extinction of calcareous nannoplankton at the Cretaceous/Tertiary boundary. *Geological Society of America, Special Paper* 190: 353-371.
- Prager, E.M., D.P. Fowler, and A.C. Wilson. 1977. Rates of evolution in conifers (Pinaceae). *Evolution* 30 (for 1976): 637-649.
- Romein, A.J.T., J. Smit, and S.T. Hussain. 1983. Calcareous nannoplankton from the Cretaceous/Tertiary boundary interval in the western Gaj River section (Pakistan). *Koninklijke Nederlandse Akademie van Wetenschappen, Proceedings (B)* 86: 393-400.
- Rosenzweig, M.L. 1978. Competitive speciation. *Biological Journal of the Linnean Society*, 10: 275-289.
- Schindel, D.E. 1983. Resolution analysis: a new approach to gaps in the fossil record. *Paleobiology* 8 (for 1982): 340-353.
- Schopf, T.J.M.S. 1981. Punctuated equilibrium and evolutionary stasis. *Paleobiology* 7: 156-166.
- _____, D.M. Raup, S.J. Gould, and D.S. Simberloff. 1975. Genomic versus morphologic rates of evolution: influences of morphologic complexity. *Paleobiology* 1: 63-70.
- Schwartz, O.A., and K.B. Armitage. 1980. Genetic variation in social mammals: the marmot model. *Science* 207: 665-667.
- Sepkoski, J.J., Jr. 1979. A kinetic model of Phanerozoic taxonomic diversity. II. Early Phanerozoic families and multiple equilibria. *Paleobiology* 5: 222-251.

- Simpson, G.G. 1944. *Tempo and Mode in Evolution*. New York: Columbia University Press. 237 pp.
- Sloan, R.E., and L.M. Van Valen. 1965. Cretaceous mammals from Montana. *Science* 148: 220-227.
- Smit, J. 1982. Extinction and evolution of planktonic foraminifera at the Cretaceous/Tertiary boundary after a major impact. *Geological Society of America Special Paper* 190: 329-352.
- Stanley, S.M. 1974. Effects of competition on rates of evolution, with special reference to bivalve mollusks and mammals. *Systematic Zoology* 22 (for 1973): 486-506.
- _____. 1979. *Macroevolution*. San Francisco: Freeman. 332 pp.
- Van Valen, L.M. 1974. Two modes of evolution. *Nature* 252: 298-300.
- _____. 1976. Energy and evolution. *Evolutionary Theory* 1: 179-229.
- _____. 1978. The beginning of the Age of Mammals. *Evolutionary Theory* 4: 45-80.
- _____, and V.C. Maiorana. 1985. Patterns of origination. *Evolutionary Theory* 7: 107-125.
- _____, and R. E. Sloan. 1977. Ecology and the extinction of the dinosaurs. *Evolutionary Theory* 2: 37-64.
- Walker, T.D., and J.W. Valentine. 1984. Equilibrium models of evolutionary species diversity and the number of empty niches. *American Naturalist* 124: 887-899.
- Williams, A., and J. Hurst. 1977. Brachiopod evolution. In: *Patterns of Evolution* (A. Hallam, ed.), pp. 79-121. Amsterdam: Elsevier Scientific.
- Wilson, A.C., G.L. Bush, S.M. Case, and M.-C King. 1975. Social structuring of mammalian populations and rate of chromosomal evolution. *Proceedings of the National Academy of Sciences, U.S.A.*, 72: 5061-5065.
- _____, L.R. Maxson, and V.M. Sarich. 1974. Two types of molecular evolution: evidence from studies of interspecific hybridization. *Proceedings of the National Academy of Sciences, U.S.A.*, 71: 2843-2847.
- Wyles, J.S., J.G. Kunkel, and A.C. Wilson. 1983. Birds, behavior, and anatomical evolution. *Proceedings of the National Academy of Sciences, U.S.A.*, 80: 4394-4397.