

Evolution and the fossil record: patterns, rates, and processes

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Mammals have an unusually good Cenozoic fossil record providing evidence of their evolutionary diversification. We view this record in hindsight, which biases our perception in many ways. Overall worldwide diversity appears to increase exponentially through time, while intensive sampling in local areas indicates that modern levels of diversity were achieved early in the Cenozoic. The evident significance of Pleistocene extinctions depends critically on how extinction rates are quantified. Our taxonomic hierarchy probably reflects the number of major faunal turnovers a group has survived rather than declining intensity of successive turnovers. Morphological innovation and taxonomic diversification appear following intervals of climatic cooling, suggesting that major features of evolution are extrinsically controlled. Favorable stratigraphic settings yield detailed records of gradual anagenesis and cladogenesis in mammals, with intermediates present as evidence of transition. The apparent dichotomy between high evolutionary rates measured by neontologists over short intervals of time and low evolutionary rates measured by paleontologists over long intervals of time disappears when rates are measured on intermediate scales of time. Microevolution and macroevolution are manifestations of common underlying processes expressed on different time scales.

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Les données remarquablement nombreuses sur les mammifères fossiles du Cénozoïque fournissent des preuves de leur diversification évolutive. En examinant ces données avec du recul, il faut admettre qu'elles faussent notre perception de bien des façons. La diversité des mammifères envisagée à l'échelle mondiale semble avoir augmenté de façon exponentielle au cours des âges, alors que des échantillonnages intenses en des localités précises indiquent que les degrés de diversité modernes ont été atteints au début du Cénozoïque. Les conclusions sur l'importance des extinctions au Pléistocène dépendent directement de la façon de quantifier les taux d'extinction. Notre hiérarchie taxonomique reflète probablement le nombre de remplacements faunistiques majeurs qu'a eu à subir un groupe plutôt que l'importance décroissante des remplacements successifs. Les phénomènes d'innovation morphologique et de diversification taxonomique apparaissent à la suite de refroidissements climatiques, ce qui permet de croire que l'évolution est surtout contrôlée par des facteurs externes. Des relevés stratigraphiques favorables ont mis en lumière l'anagénèse et la cladogénèse graduelles des mammifères et les intermédiaires servent d'indicateurs des situations de transition. La dichotomie apparente entre les taux rapides d'évolution mesurés par les néontologistes au cours d'intervalles courts et les taux évolutifs lents mesurés par les paléontologistes sur de longues périodes de temps disparaît lorsque ces taux sont mesurés sur des périodes de temps de longueur intermédiaire. La microévolution et la macroévolution sont les manifestations de processus sous-jacents communs exprimées sur des échelles de temps différentes.

[Traduit par la revue]

Introduction

The oldest tension in human perception is that between the world as we see it and the world as we think it should be. The former is the basis of science, the latter of politics and religion. Yet neither can be separated clearly from the other. This tension indicates, on one hand, that there is more to life than meets the eye and, on the other hand, that the mind is wonderfully creative, often even deceptive. A tension of perception exists within science too, where the world as we see it is expressed in our observations, our data, and the world as we think it should be is encompassed in theories and hypotheses. Theory, in a way, is the politics and religion of science.

It is often stated, downplaying the role of induction in science, that innocent unbiased observation is a myth: useful observations are always necessarily theory bound. Why then do we not recognize and require the converse, that theories be based on observations? The world of our scientific perception is but one of many worlds we might imagine. We do not have time, energy, nor funds to investigate all possible worlds: if creative induction yields many hypotheses, then emphasis in normal science is rightly placed on deduction, hypothesis testing, with rapid rejection of hypotheses lacking evidence or theories running counter to empirical observation.

Empirical observations combine to form *patterns*; patterns are what we have to work with. Evolution is the science of organic change, change over time, and the principal analytical approach in studying change requires quantification in terms of *rate*. Indeed all attempts to relate change on the scale of our lifetimes to change on the vast scale of our geological past require

comparison in terms of rate. The goal is to understand the history of life in terms of *processes* familiar today. When familiar processes fail, and only when they fail, new processes are required to explain patterns observed in the history of life.

Here I shall attempt to balance theory and observation in discussing recent developments in our understanding of evolution and the fossil record. I shall begin by outlining the evolutionary radiation of mammals as a whole. Next I shall illustrate patterns of evolution at the species level, including documented transitions between successive species. Finally I want to consider problems inherent in comparing evolutionary rates, showing how distributions of microevolutionary and macroevolutionary rates, long thought to be discrete and nonoverlapping, decoupled, grade continuously together when measured on intermediate time scales. Judging from this evidence, microevolution and macroevolution are manifestations, expressed on different time scales, of common underlying processes.

Cenozoic radiation of mammals

Paleontologists view the world a little differently than colleagues studying living plants and animals. Our charts and graphs reflect this in incorporating time as the principal axis and independent variable. The Cenozoic radiation of mammals is illustrated graphically in Fig. 1, based on Romer's (1966) compilation of generic ranges. Regrettably, this is the only comprehensive listing of generic ranges available at present. Many new genera of mammals have been described in the past 20 years, and the time scale too is now much better known. I

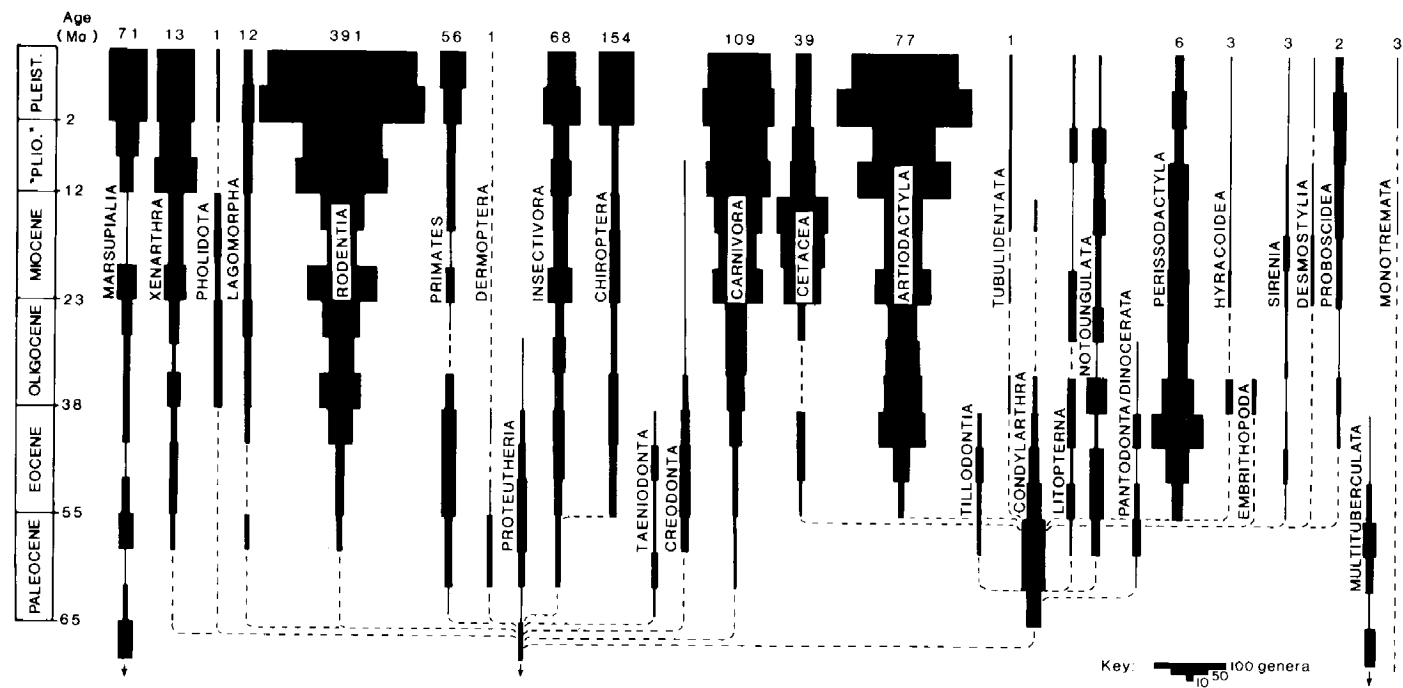


FIG. 1. Cenozoic history of diversification of mammals based on the fossil record. Width of each bar is proportional to the number of genera in each order known from the fossil record. Numerals above ordinal bars show number of living genera in each extant order. Vertical axis, time, is nonlinear. Note appearance of most modern orders of mammals at or near the Paleocene–Eocene boundary. Based on generic ranges in Romer (1966). Early Pliocene of Romer is here plotted as late Miocene in accordance with current subdivision of the geological time scale.

shall use Romer's data because they are readily available and because, based on experience working with early Cenozoic mammals and the origin of modern mammalian orders, broad patterns of mammalian diversification have changed little since publication of Romer's compilation. More narrowly focused questions require better data, and a modern compilation of mammalian temporal ranges is eagerly awaited.

Patterns

Figure 1 shows a number of interesting things about mammals and their evolutionary history. First, it appears that the 16 orders of placental mammals living today all originated during early Cenozoic time (Paleocene and Eocene). Marsupial Metatheria have a fossil record extending back through much of the late Cretaceous, making an early or mid Cretaceous divergence from placental Eutheria likely. Multituberculate Allotheria represent an extinct mammalian subclass that radiated during the middle part of the Mesozoic and again in the early Cenozoic. Monotreme Prototheria have only a limited late Cenozoic fossil record, but comparative evidence suggests that they diverged from metatherians and eutherians very early in mammalian history, probably in the late Triassic, some 200 million years before present.

Some modern orders of placental mammals made their first appearance in the early or middle Paleocene (Xenarthra, Lagomorpha, Rodentia, Primates, Dermoptera, Insectivora, Carnivora), while others did not appear until the early Eocene (Chiroptera, Cetacea, Artiodactyla, Perissodactyla, Sirenia). The first appearance of Pholidota, Tubulidentata, Hyracoidea, and Proboscidea is problematical because of the limited nature of the African Eocene record. Similar diagrams constructed at the familial and generic level would show times of first appearances of modern families to be concentrated at the Eocene–Oligocene transition (Lillegraven 1972), and first

appearances of modern genera to be concentrated at the Oligocene–Miocene and Miocene–Pliocene transitions. I am not concerned here with the precise time of origin of any particular order (or other taxon), but rather in noting that the first appearances of modern groups are clustered in geological time.

There was a major pulse of mammalian origination in the early Paleocene, following terminal Cretaceous extinctions; this resulted in significant diversification expressed at an ordinal level. There was a second major pulse of mammalian origination associated with the Paleocene–Eocene transition that resulted, again, in significant diversification expressed at an ordinal level. Not shown is a third pulse of diversification at the familial level at or near the Eocene–Oligocene boundary, and fourth and fifth pulses of diversification at the generic and specific levels at or near the Oligocene–Miocene and Miocene–Pliocene boundaries, respectively. There is a clear association of taxonomic level (ordinal, familial, generic, and specific) with decreasing geological age of appearance (Cretaceous–Paleocene and Paleocene–Eocene, Eocene–Oligocene, Oligocene–Miocene, and Miocene–Pliocene transitions, respectively). We impose taxonomic levels in hindsight and what began as generic differentiation at the Cretaceous–Paleocene or Paleocene–Eocene transition was elevated to familial distinction during the Eocene–Oligocene transition. Iteratively, familial differences were elevated to ordinal distinction, and generic differences were elevated to familial distinction during the Oligocene–Miocene and Miocene–Pliocene transitions, respectively. The important point here is that later pulses of diversification are expressed at lower taxonomic levels because they were later, not because they were any less profound. Consequently, our taxonomic hierarchy probably reflects the number of major faunal turnovers a group has survived rather than declining intensity of successive turnovers.

A second interesting observation on the evolutionary radia-

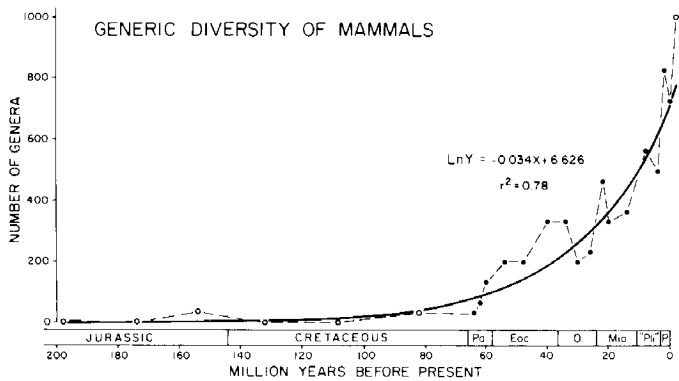


FIG. 2. Apparent history of diversification of mammals, based on worldwide generic diversity in the Cenozoic (solid circles, data from Romer 1966). Cenozoic record accurately predicts low diversity observed in the Mesozoic. Cenozoic record predicts about 750 genera should be living today, compared with 1010 extant genera known (Honacki et al. 1982). Geological age appears to be a better predictor of overall worldwide generic diversity than any other factor, and the observed pattern reflects the strong bias inherent in viewing change from a modern perspective (as well as any actual increase in diversity; the two factors are very difficult to separate). Early Pliocene of Romer is now regarded as late Miocene. Figure from Gingerich (1984b).

tion of mammals is its apparent stochasticity; the orders shown in Fig. 1 appear to wax and wane at random. There is little uniformity within orders in level of diversity or in changing diversity plotted over time. Gaps in the fossil record on some continents contribute to this randomness, but some of it is likely to be real, reflecting the kaleidoscopic nature of biotic interactions and environmental change over geological time. Apparent randomness in levels of diversity within orders (or families or genera) through Cenozoic time does not, of course, imply that structure and function are unrelated nor does it preclude continuing local adaptation at the level of individuals and breeding populations.

A third pattern emerging from Fig. 1 is a progressive (if fluctuating) increase in generic diversity through the Cenozoic history of mammals. This trend, shown graphically in Fig. 2, is exponential. Extrapolation accurately predicts low mammalian diversity observed in the Mesozoic and it comes close to predicting the number of mammalian genera living today (750 predicted compared with 1010 extant). The marked increase in diversity known to have occurred at the beginning of the Cenozoic is hardly reflected at all in worldwide generic levels plotted in Fig. 2. However, well-studied latest Cretaceous faunas from Wyoming and Montana typically contain only 20–30 mammalian species (Archibald 1982), while those of the middle Paleocene contain 50–60 mammalian species (Rose 1981), an essentially modern level of diversity.

The pattern of increasing overall worldwide diversity seen in Fig. 2 parallels what Raup (1978) has called the “pull of the Recent.” Geological age appears to be a better predictor of overall generic diversity recorded in mammals than any other factor. It is difficult to separate a true pattern of increasing generic diversity, which is necessarily some function of geological age, from the bias imposed by studying such a pattern entirely in hindsight. The older a mammalian fauna is geologically, the less adequately it is likely to be known because of increasingly limited worldwide exposure of sediments containing the fauna and a host of other prejudicial factors. It may be that we do not yet know the generic diversity of epochs

and subepochs in the past in sufficient detail to reveal patterns of diversity change. Hence quantitative patterns involving changing diversity must always be viewed critically to ensure that they are based on sufficient evidence collected in comparable ways for each successive interval of time.

Rates

Information in Fig. 1 can be quantified to yield rates bearing on dynamics of mammalian evolution studied at the generic level. Of greatest interest are patterns of origination and extinction during Cenozoic time. How common is extinction? How is extinction related to origination? Are there clearly defined peak rates rising above normal background extinction?

The standard method of calculating rates requires that the number of genera originating or becoming extinct in any geological interval be divided by the estimated length of the interval in millions of years (cf. Simpson 1953). Rates of origination and extinction for Cenozoic Rodentia, Artiodactyla, and fissiped Carnivora are shown graphically in Fig. 3A. Analyzed in this way, late Pleistocene extinctions appear as a peak rising high above background extinction (early Pleistocene originations appear as an even higher peak). However, a simple calculation of extinction rate in terms of genera per million years overlooks the progressively increasing diversity shown in Fig. 2; more genera are known in the Pleistocene than in previous epochs. Rates are ratios, and Pleistocene rates calculated as a ratio of genera per million years are necessarily higher because they have a larger numerator. Pleistocene rates are also higher because they have a smaller denominator. Previous epochs are subdivided into intervals ranging from 2 to 8 Ma in duration, while the Pleistocene is subdivided into two approximately 1-Ma intervals. Consequently, Pleistocene rates are artificially inflated by comparison with rates for previous epochs.

Pleistocene rates of origination and extinction can be made comparable to rates of origination and extinction during other Cenozoic epochs by dividing originations and extinctions by the total number of genera in each subepoch being analyzed, yielding a rate in generic originations or extinctions per total known genera, or, in other words, percentage of total fauna. To the extent that longer intervals should contain more genera for their age than shorter intervals, calculating rates as percentages of total fauna corrects for differing interval lengths as well. Rates of origination and extinction calculated as genera per total genera are illustrated graphically in Fig. 3B. Late Pleistocene extinctions in this example no longer exceed background and, for Rodentia, most Artiodactyla, and fissiped Carnivora at least, explanations involving climate and (or) human overkill no longer seem to be required. The important point here is to contrast the evident significance of late Pleistocene extinctions as they appear in Figs. 3A and 3B. Careful quantification of changing patterns in terms of appropriate rates sometimes removes the need for special explanation in terms of process. (The complex subject of Pleistocene extinctions is reviewed by Webb (1984) and other authors in Martin and Klein (1984).)

Processes

Patterns of evolution in mammalian families, orders, and the class as a whole are known only in outline, and rates of change based on such limited evidence are difficult to evaluate and compare. We surely exceed present evidence to speak of evolutionary processes operating at generic and higher levels. There is, however, one observation that bears on our general understanding of processes.

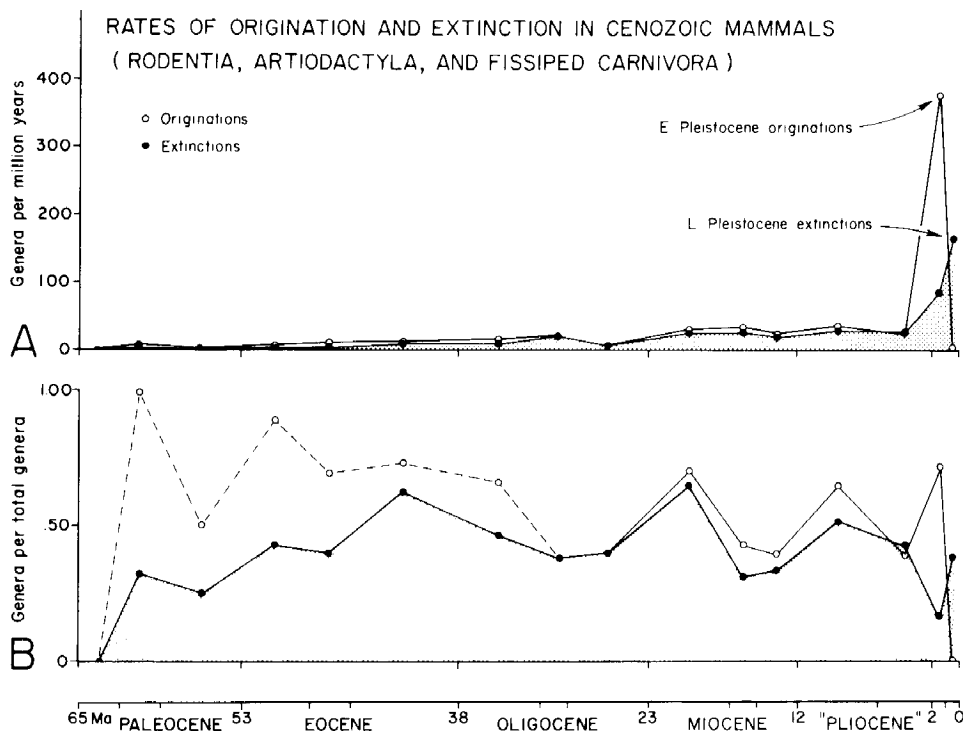


FIG. 3. Patterns of change in the origination and extinction of genera of Rodentia, Artiodactyla, and fissiped Carnivora, expressed in terms of (A) genera per million years, and (B) genera per total genera for each subdivision of the Cenozoic time scale. Note the close correlation of origination and extinction throughout most of the Cenozoic. Note also the unusually high rate of early Pleistocene originations preceding late Pleistocene extinctions, regardless of whether this is expressed in terms of rate per million years or percentage of the total fauna. Based on data from Romer (1966; early Pliocene of Romer is now regarded as late Miocene by most authors, i.e., the Miocene–Pliocene boundary is now placed at 5 Ma before present). Modified from Gingerich (1984a).

Association of times of appearance of modern mammalian groups (orders, families, and genera) with transitions between discrete epochs suggests that evolutionary diversification is neither evenly nor randomly distributed in geological time. There are intervals of diversification and longer intervening periods of relative stability. Cenozoic epoch boundaries coincide with (or immediately postdate) times of worldwide climatic cooling (Wolfe 1978). Morphological innovation and new diversity appear following such episodes of cooling, which suggests that cooling itself and (or) associated equatorward contraction of geographic ranges are important factors forcing innovation and diversification at high rates over relatively short intervals of time. Intrinsic mechanisms involving random mutation, recombination, and fortuitous development must play some role in evolution, but patterns of diversification coinciding with episodes of climatic cooling suggest that extrinsic environmental change controls most morphological innovation in mammals.

Evolution at the species level

My interest in the fossil record as a source of information about evolution dates to a 1971 graduate course in evolutionary biology, a course devoted almost entirely to "adaptation" and "speciation." Fossils were hardly mentioned. The textbook we used (Grant 1963) included a long section on trends in the evolutionary radiation of horses taken from Simpson (1951, 1953), but all of the examples involved *genera* not *species*. I began to see that patterns of change at the level of genera were of limited relevance in discussing adaptation and diversification at the level of species. If the best examples of evolution in the fossil record, indeed the basic data of paleontology, are all

compiled at the generic or even familial level, what relevance do paleontological patterns have for understanding species-level processes?

Can evolution in the fossil record be studied at the species level? The aim of my dissertation research, initiated in the autumn of 1971, was to see whether one could understand anything of species-level evolution from fossils. The group I chose to study in detail, squirrel-like *Plesiadapis* and its archaic primate relatives from the Paleocene and early Eocene of North America and Europe, is one of the most common groups of fossil mammals preserved in sediments deposited during uplift of the Rocky Mountains some 65 to 55 Ma ago. When I began my dissertation work, *Plesiadapis* was known from large samples that I and other students had collected in northwestern Wyoming while employed by a former professor, the late Glenn Jepsen of Princeton. Professor Jepsen generously (if reluctantly, given his lifetime investment in the material) made this collection available for study.

Plesiadapis and other mammals have several attributes making them ideal for evolutionary study. (i) Mammalian teeth are highly mineralized, with the hardness and density of enveloping sedimentary rocks, meaning that they preserve well in the fossil record. Mammals have an extraordinarily rich fossil record, and I do not exaggerate in claiming that important new paleontological evidence bearing on mammalian history is discovered daily. (ii) Mammalian teeth are complex in form, making it possible to identify and distinguish most mammals in a fauna based on their teeth alone. (iii) Mammalian teeth vary in size and form, making them amenable to natural selection, but variation within species is small compared with variation between species, permitting most species, even those closely

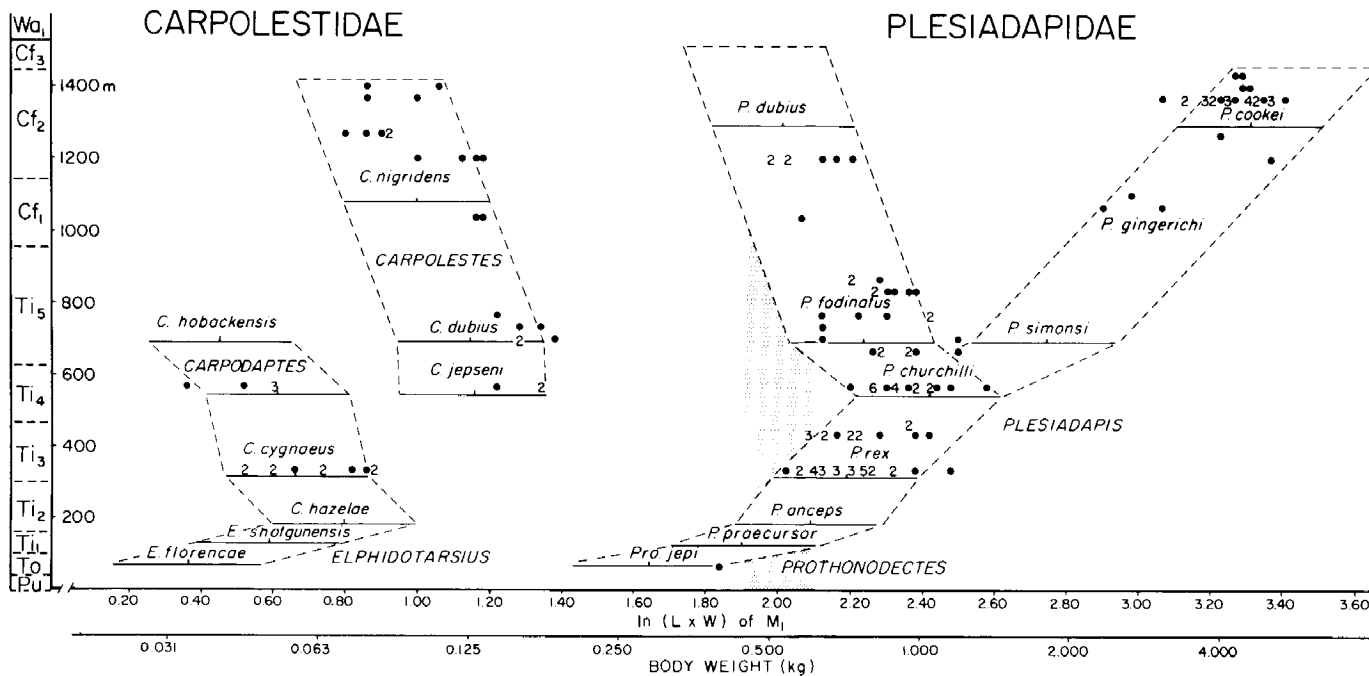


FIG. 4. Patterns of evolution in two families of North American Paleocene primates, Carpolestidae and Plesiadapidae, respectively, through 8 Ma of geological time (ca. 61–53 Ma before present), based on fossils and stratigraphic sections from the Clark's Fork and Bighorn basins of northwestern Wyoming. Abrupt first appearances of *Elphidotarsius florenceae*, *Carpolestes jepseni*, and *Pronothodectes jepi* are all correlated with episodes of faunal turnover and these animals can plausibly be explained as immigrants from some as yet unknown faunal province. Gradual divergence of the *Plesiadapis dubius* and *Plesiadapis cookei* lineages from a *Plesiadapis churchilli*-like ancestor is corroborated by discovery of new specimens intermediate between *P. fodinatus* and *P. dubius* and between *P. simonsi* and *P. cookei*. This cladogenic event is recorded in detail only in the Clark's Fork Basin, Wyoming, but it presumably reflects allopatric speciation in populations covering a much larger geographic area. Abscissa is tooth size and, by inference, body size. Stippled vertical bar is Kay's 500-g threshold separating insectivorous from folivorous primates. Solid circles show how new specimens collected through 1985 (numerals represent multiple specimens of same size) conform to pattern of phylogeny (solid bars and broken lines) hypothesized by Rose (1975) and Gingerich (1976).

related, to be distinguished. (iv) With few exceptions, mammalian teeth are formed before they emerge from the jaws and they cannot grow after eruption, giving teeth a definitive size and form and eliminating ontogenetic variation as a complicating factor. (v) Mammalian teeth have demonstrated high heritability and observed phenotypic variation has a high additive genetic component, meaning that the phenotype has little independent plasticity. (vi) Definitive tooth size in mammals reflects definitive body size, providing entrée to all of the many life-history and adaptational parameters associated with body size. (vii) Finally, teeth interact directly with ingested food, providing a reliable indication of diet in many instances. For all these reasons, mammals are more suitable as a group for detailed evolutionary analysis than are invertebrates or most other groups of vertebrates.

Patterns

Paleocene *Plesiadapis* proved interesting in showing relationships of successive species through 8 Ma of geological time (Fig. 4). Judging from available evidence, anagenesis appears to have been the dominant speciation mode. The earliest plesiadapid species known from northwestern Wyoming, *Pronothodectes jepi*, is connected to the latest, *Plesiadapis dubius* and *Plesiadapis cookei*, by a continuous series of intermediates (Gingerich 1976). *Plesiadapis* exhibits a pattern of gradual divergence during cladogenesis that contrasts with the sudden appearance of *Carpolestes* in contemporary, closely related Carpolestidae (Rose 1975). The *Elphidotarsius*–*Carpodaptus* and *Carpolestes* lineages, and the *Pronothodectes*–*Plesiadapis*

clade appear abruptly in the fossil record of northwestern Wyoming, with no evidence of ancestors in underlying strata. *Elphidotarsius* and *Pronothodectes* appear together, making their first appearance in concert with numerous other middle Paleocene taxa. *Carpolestes* makes its first appearance in concert with numerous other late Paleocene taxa. These first appearances are plausibly explained by dispersal of coevolved faunal groups of highly mobile mammals from environments and regions not sampled in the fossil record. Temporal resolution in the middle and late Paleocene is still poor, on the order of 500 000 years, which tends to sharpen the evident abruptness of first appearance of groups of immigrant taxa. Temporal resolution in the fossil record rarely exceeds 50 000 years, meaning that evolution on finer temporal scales is usually invisible to paleontologists.

The fossil record is full of gaps because of poor geographic sampling at any given time in the past and poor temporal resolution in the stratigraphic record. Gaps in the fossil record are gaps, missing evidence. Consequently, the abrupt appearance of new lineages and clades in any local stratigraphic section cannot be considered evidence of saltation, macromutation, or discontinuous speciation of any kind.

Plesiadapis, for all its interest as an evolutionary radiation, contributes little to understanding the problem I originally set out to study: transitions between successive species. More detailed biostratigraphic sampling was required. This could not be accomplished in reasonable time working in the Paleocene (Fig. 4 shows the limited results of 10 summers' collecting, superimposed on our 1975 and 1976 understanding of car-

