

## CHAPTER 15

### PATTERNS OF EVOLUTION IN THE MAMMALIAN FOSSIL RECORD

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#### Introduction

Mammals are the most successful and most intelligent of land vertebrates. While most mammals today remain terrestrial like the ancestral mammalian stock, one progressive group has invaded the air and others have invaded the sea. Living mammals differ rather sharply from other living vertebrates in bearing their young alive, in suckling their young (hence the class name Mammalia), and in sometimes "educating" their young. Mammals are warm-blooded, or endothermic, and their high metabolic rates make possible a sustained high level of continuous activity. Osteologically, living mammals also differ sharply from most other vertebrates in possessing a double occipital condyle on the skull, a single mandibular bone (the dentary) which articulates directly with the squamosal bone of the cranium, an eardrum supported by an ossified ectotympanic bone, three auditory ossicles, only two tooth generations — deciduous and permanent, cheek teeth of complicated morphology, a single bony nasal opening in the skull, and epiphyses on the long bones. While living mammals are well separated from other groups of vertebrates today, the fossil record shows clearly their origin from a reptilian stock and permits one to trace the origin and radiation of mammals in considerable detail.

If one could choose any one anatomical system of mammals for preservation in the fossil record, the system yielding the most information about the animals would undoubtedly be the dentition, and it is fortunate that this is the most commonly preserved element of fossil mammals. Dental enamel is the hardest mammalian tissue, and it thus has the best chance of being preserved in the fossil record. The teeth of different families and genera of mammals have a characteristic, genetically determined pattern which makes them ideal for systematic identifications. Teeth are involved in the mastication of food, and the pattern of cusps and crests characteristic of the teeth of different mammalian groups reflects the dietary preference of the group as well as its heritage, offering insight into the ecological adaptations of each group. Finally, the fact that there is a single definitive set of permanent teeth which form within the jaw before they erupt is of great importance for detailed evolutionary studies. Within related groups of mammals, body size is highly correlated with tooth size, which varies within recognized limits. Furthermore, this variance in tooth size has a demonstrated high additive genetic component (i.e., high heritability; see Bader, 1965, Alvesalo and Tigerstedt, 1974), meaning that tooth size does respond to natural selection. The fact that teeth do not continue to grow after they erupt greatly simplifies estimation and comparison of the definitive body size of individuals in different samples because it is not necessary to correct for

ontogenetic size increase in dental dimensions. This makes mammalian teeth ideal for microevolutionary studies, offering insight into the relative body size of related species, body size being one of the most important components of an animal's adaptation.

In the following pages I have outlined some of the major features of the radiation of mammals, including examples of major adaptive trends, rates of origination and extinction, and taxonomic longevity. Specific mammalian adaptations are also discussed, including some remarkable examples of convergence, mosaic evolution, and small-scale evolutionary reversals. This is followed by a consideration of speciation in mammals, including discussion of the origin of higher taxonomic groups of mammals.

### Mammalian Radiations

Mammals are first known from Upper Triassic (Rhaetic) strata in England, Wales, Switzerland, southern China, and South Africa. Most of these earliest mammals, including some known from skulls and skeletons, are prototherians of the family Morganucodontidae (e.g., *Eozostrodon*), with relatively simple triconodont molars (see below). Others, placed in the prototherian family Haramiyidae, have multicusped teeth and are possibly closely related to the origin of the Multituberculata, an important group of extinct rodent-like Mesozoic and Early Tertiary mammals. However, one Late Triassic mammal is also known, *Kuehneotherium*, which has the three major cusps on the upper and lower molars rotated to form interlocking triangles as in the more advanced "therian" mammals (see Fig. 1).

Morganucodontids, with their simple triconodont molars, are thought to represent an early prototypical stage in the evolution of the mammalian molar. *Kuehneotherium* from the Rhaetic represents an advance over the triconodont pattern in having the cusps rotated so that upper and lower cheek teeth form a row of interlocking triangles. The next stage, addition of a shearing heel onto the back of the lower molar triangles, is represented by the Early Cretaceous genus *Aegialodon*. By the mid-Cretaceous (Albian) two forms with fully developed tribosphenic dentitions characteristic of modern mammals are known, *Holoclemensia* and *Pappotherium*, which represent respectively the earliest marsupial and placental mammals. The mid-Cretaceous was the time of the initial major radiation of angiosperm plants, with a correlated radiation of insects and other terrestrial invertebrates, and it is not surprising that these changes in plant and insect communities were accompanied by a modest radiation of insectivorous mammals.

Near the end of the Cretaceous, placental mammals began the first of their major radiations, leading to a characteristic fauna in the Paleocene that was dominated by archaic primates, proteutherian insectivores, and a diverse assemblage of archaic ungulates, the Condylarthra. Multituberculates were also important elements of virtually all known Paleocene faunas. Other groups of placental mammals making their first appearance in the Paleocene were the

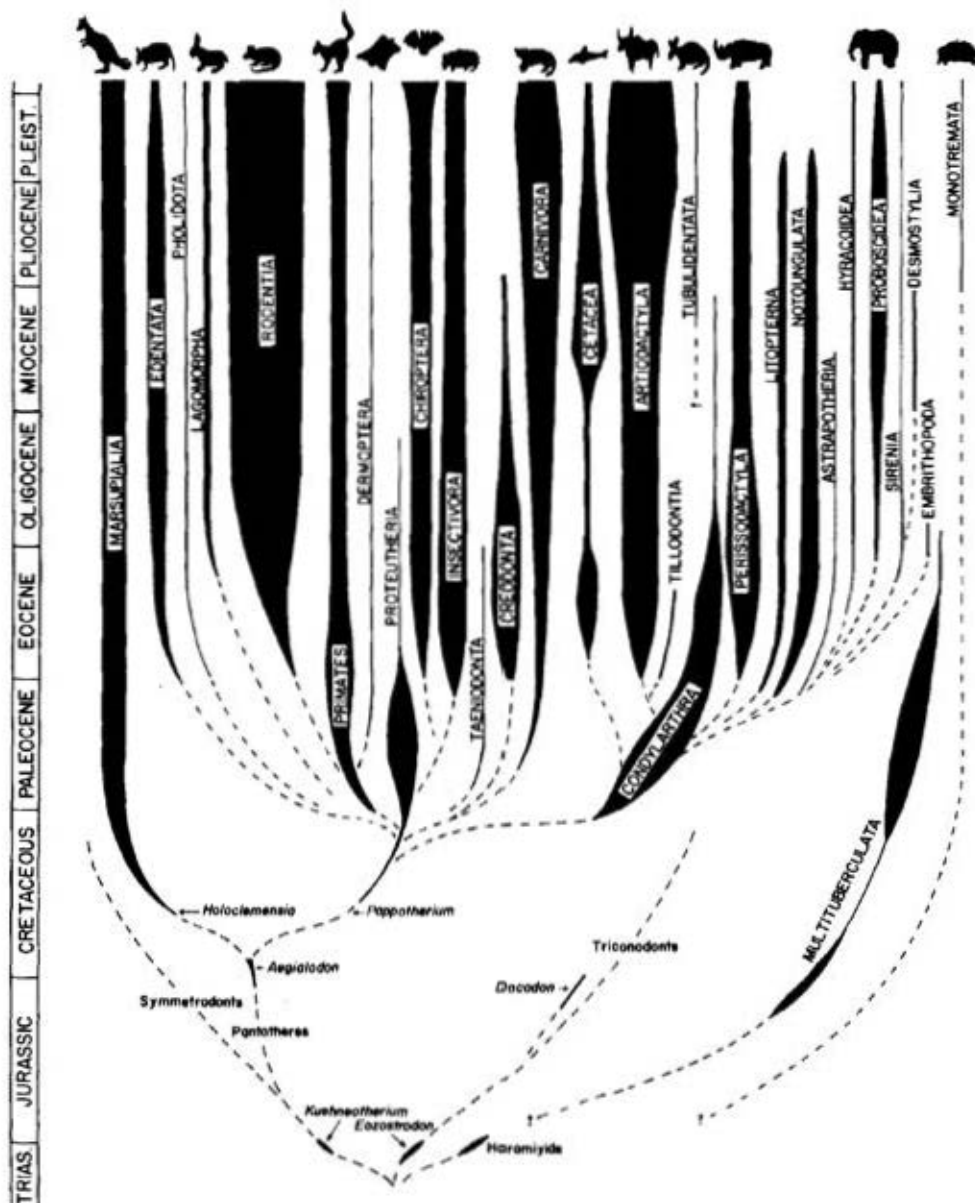


Fig. 1. Radiation of mammals during the Mesozoic and Cenozoic. Width of the shaded area gives a very general estimate of the relative number of genera in the fossil record for each order. See Figs. 2-5 for quantitative data on diversity.

Dermoptera, the Insectivora (sensu Lipotyphla), the Taeniodonta, archaic true Carnivora (Viverravinae), the Pantodonta, and several predominantly South American orders, the Litopterna, Notoungulata, and Astrapotheria. Most groups of archaic mammals typical of the Paleocene survived into the Eocene, but became extinct during or shortly after that epoch.

*Origin of modern orders of mammals*

The beginning of the Eocene is marked in the fossil mammal faunas of western North America and Europe by the sudden appearance of mammals belonging to modern orders. For example, Rodentia, Primates of modern aspect (Adapidae and Omomyidae), Chiroptera, primitive true Carnivora (Miacinae), Artiodactyla, and Perissodactyla all make their first appearance at the beginning of the Eocene. We do not have a fossil record actually documenting the origin of any of these major groups, but a consideration of the morphology of the most primitive forms together with the climatic history of the Paleocene and Eocene in Europe and western North America provides a possible clue to their origin.

The Late Paleocene was a time of climatic cooling, with the subtropical climate of the Middle Paleocene giving way to a warm temperature climate in the Late Paleocene, which was in turn followed by a return to a subtropical climate in the Early Eocene (Wolfe and Hopkins, 1967). Probable ancestors of several of the modern groups appearing in the Eocene are known from the Middle Paleocene of North America and possible ancestors are known for the others, but no connecting forms are yet known from the Late Paleocene (Gingerich, 1976b, table 13). This hiatus in an otherwise rich fossil record is correlated with Late Paleocene climatic deterioration, and was almost certainly a result of the temporary decline in average temperatures. During this climatic deterioration the geographic ranges of many mammals formerly inhabiting western North America (or Europe, or Asia) probably contracted, following the northern border of the subtropical climatic zone as it retreated southward. When the subtropical zone expanded again at the beginning of the Eocene, highly evolved descendants of the former North American Middle Paleocene fauna (which had remained in Central American refuges) reinvaded North America (Sloan, 1969). It is probable that a similar phenomenon occurred in Europe and in Asia.

The climatic warming in the Early Eocene not only brought new, highly evolved mammalian forms northward, but it made high-latitude land connections between the Holarctic continents accessible to many mammalian groups. The result was a high level of faunal interchange and rapid dispersal of modern mammals between North America, Europe, and Asia (McKenna, 1975). Thus the Early Eocene dispersal was perhaps as much a result of climatic change as it was of continental positions, although breaking up the land connection between Europe and North America and the final opening of the North Atlantic ocean created a permanent barrier to further mammalian migration between Europe and North America early in the Eocene.

The appearance of modern orders was sudden in the fossil record, but it is probable that their evolutionary origin was gradual and continuous in areas (such as Central America) where we do not yet have an adequate Early Tertiary fossil record. It is also probable, in view of the structural changes involved in the origin of the characteristic ever-growing incisors present in the earliest known rodents, or the double pulley astragalus characteristic of artiodactyls,

that the evolution leading to differentiation of the modern orders was relatively rapid in the phyletic lineages involved. Rapid but continuous evolution of this sort can be traced in Early Tertiary primates in the transition from *Plesiadapis* to *Platychoerops*, where the incisors were considerably reorganized morphologically and functionally in the space of only 2–3 m.y. (Gingerich, 1976b).

These relatively rapid rates of change in phyletic lineages might be explained by either higher levels of selective pressure due to crowding stress and competition as diverse subtropical faunas that formerly inhabited the whole North American continent were crowded onto a narrow isthmus in Central America, by great reductions in population size in the subtropical forms, or both. There is no evidence to suggest that the origin of modern mammalian orders during the Late Paleocene was accompanied by higher than normal rates of cladogenetic speciation, and high rates of cladogenesis would be unlikely during a time of contraction in the geographic ranges of the subtropical species. A very similar abrupt appearance of many modern mammalian families occurred in the Early Oligocene (Stehlin's "*Grande Coupure*", see Stehlin, 1909) following a major climatic deterioration, and a similar explanation may be offered for the abrupt appearance of new forms at that time.

#### *Diversity through time*

During the first two-thirds of their 200 m.y. history, mammals constituted a very small part of the terrestrial vertebrate fauna. By the end of the Cretaceous many previously important reptile groups were extinct, and mammals became the dominant terrestrial vertebrates. Their diversity has increased almost continuously since that time (Fig. 2). The total number of genera of mammals present in each successive subdivision of the Tertiary epochs appears to have increased at a nearly constant rate, but when this total number is corrected for the duration of each subdivision (i.e., when genera per million years is calculated), the increase in diversity of mammals through geological time approximates an exponential curve. The shape of this curve (Fig. 2) is undoubtedly influenced by the increasing probability of finding fossils in more recent strata, i.e., the fact that more recent fossil mammal faunas are more adequately sampled than older ones, but at the same time there is no denying a great increase in the diversity of mammals through the course of geological time.

Mammals were well established in insectivorous, herbivorous, and carnivorous adaptive zones by the Early Paleocene, and these continued to be important throughout the Tertiary and up to the present day. Fig. 3 shows that the relative importance of each of these three basic adaptive zones has been nearly constant since the Paleocene. As one would expect, genera of herbivorous mammals outnumbered terrestrial carnivorous genera by a fairly constant factor of about 3 or 4 to 1.

Marine mammals (Sirenia and Cetacea — sea cows, whales and porpoises) and volant mammals (Chiroptera — bats) first appear in the Early Eocene fossil record, and represent important invasions of new adaptive zones for mammals. Each subsequently underwent a major adaptive radiation. It is not clear

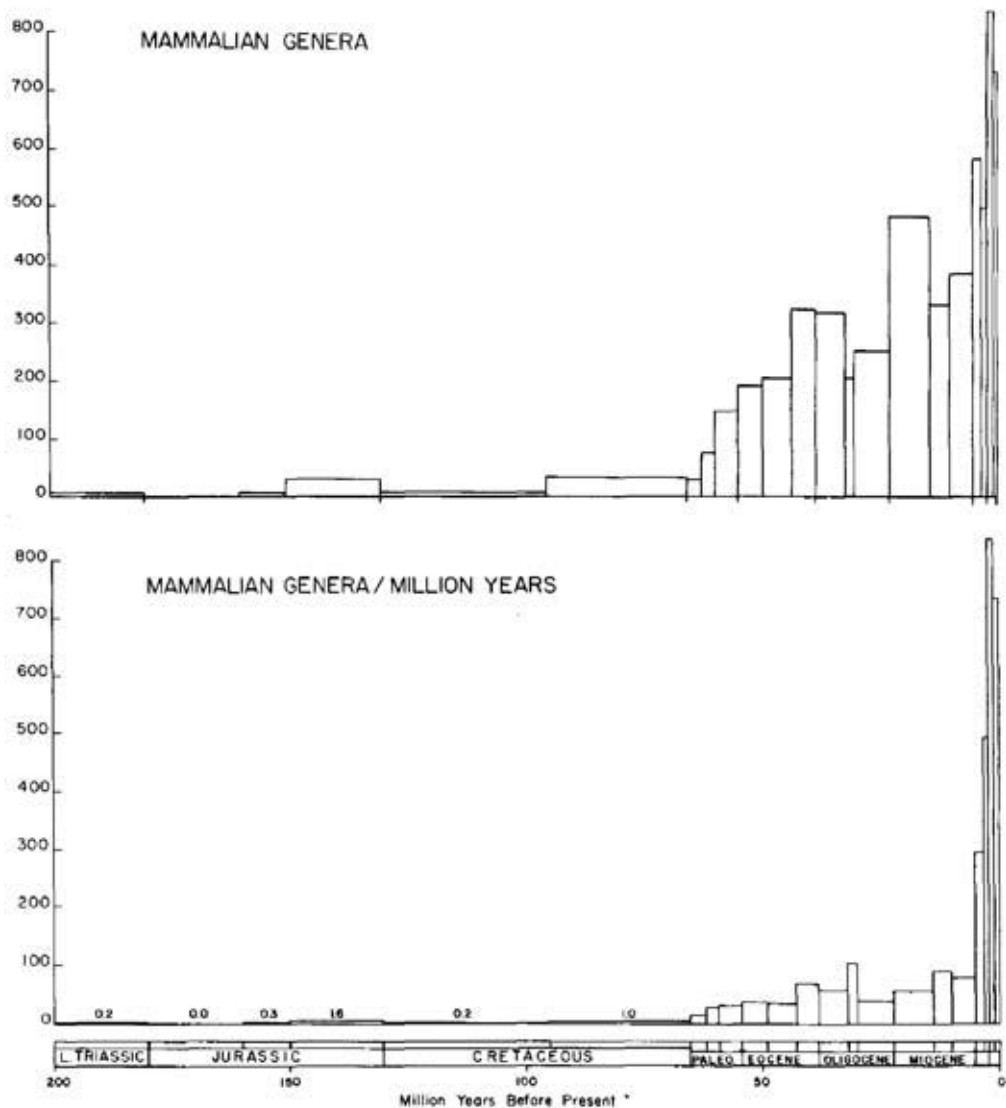


Fig. 2. Generic diversity in mammals through the Mesozoic and Cenozoic. Numbers of genera present in each subdivision of the geological time scale are shown in the upper figure. Numbers of genera per million years in each subdivision of the time scale are shown in the lower figure. Data from Romer (1966).

whether rodents, which also first appear in the Early Eocene, invaded a new adaptive zone, or one previously occupied by less efficient multituberculates and then archaic primates (Van Valen and Sloan, 1966; Hopson, 1967). With their wedge-shaped, self-sharpening, ever-growing incisors forming structural arches stressed by specialized and powerful masseteric musculature, rodents introduced a characteristic gnawing adaptation for ingesting food that has

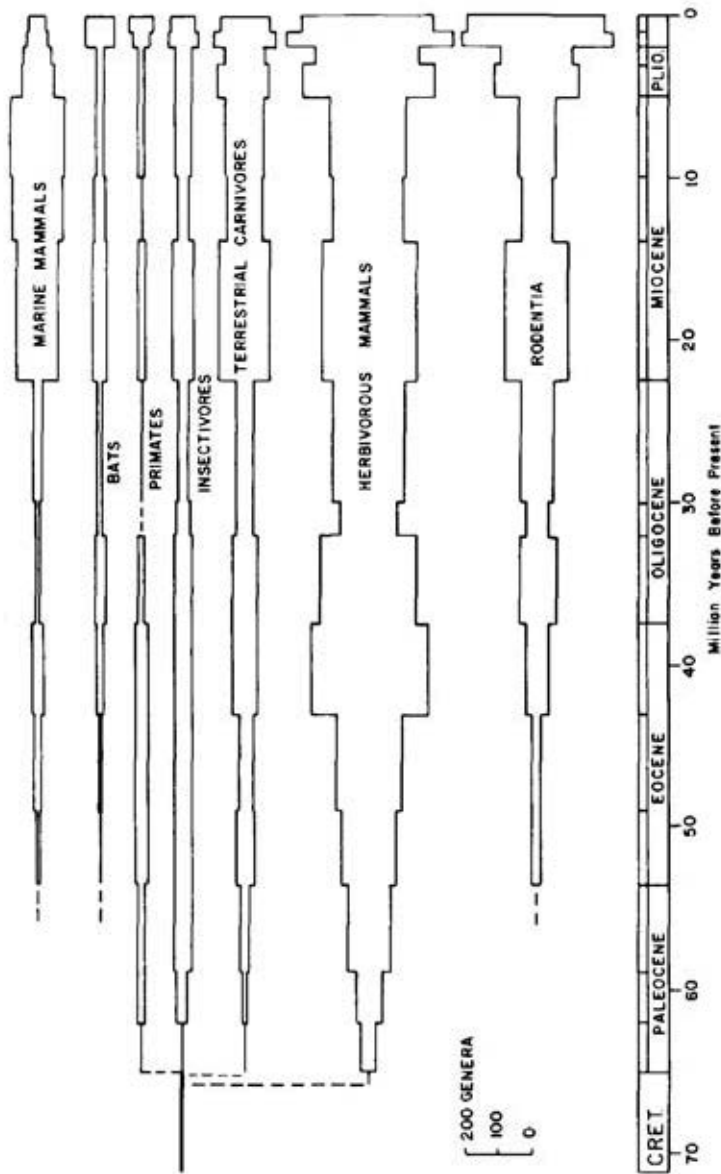


Fig. 3. Relative generic diversity within each major adaptive zone during the Cenozoic. Marine mammals include Sirenia, Desmostylia, Cetacea, and pinniped Carnivora. Terrestrial carnivores include Creodonta, fissiped Carnivora, and borhyaenid Marsupialia. Herbivorous mammals include Artiodactyla, Perissodactyla, Lagomorpha, Litopterna, Astrapotheria, Notoungulata, Embrithopoda, Hyracoidea, Proboscidea, Amblypoda, Condylarthra, Taeniodonta, and Tillodontia. Data from Romer (1966).

remained little modified during their 50 m.y. history. During this time rodents radiated rapidly to become very quickly the most important mammalian order in terms of generic diversity.

It has been mentioned that rodents may have replaced multituberculates and archaic primates in the small mammal herbivorous—omnivorous adaptive zone. Similarly, during the course of the Tertiary several specialized condylarth derivatives, the artiodactyls, perissodactyls, and others, replaced the remaining generalized ancestral condylarthran stock. Perissodactyls first underwent a broad radiation in the Eocene and Oligocene, only to be replaced in large part by a Miocene radiation of artiodactyls in the herbivorous adaptive zone. The carnivorous Creodonta were gradually replaced by true Carnivora during the course of the Tertiary. Thus, within each adaptive zone occurred important replacements of one taxonomic group by another group, the individual species of which were presumably better adapted in a variety of ways than the species they replaced.

#### *Rates of origination and extinction*

There are as yet very few groups of mammals in the fossil record that are sufficiently well known stratigraphically to permit tracing individual species lineages through time. The lineages of *Plesiadapis*, *Hyopsodus*, and *Pelycodus* discussed later in this chapter (Figs. 11–13) all show species durations of something on the order of one million years. In these examples, rate of origination and extinction of species in the fossil record is about one per million years in each lineage. Cladogenic branching tends to happen less frequently, varying from a rate of nearly one per million years in *Hyopsodus*, to one per three or four million years in the Plesiadapidae and in *Pelycodus*. Kurtén (1959) has calculated mean "species longevities" varying from 0.3 to 7.5 m.y. for various orders of Cenozoic mammals, and more recently Stanley (1976) has calculated mean species durations of 1.2 m.y. for Plio-Pleistocene mammals of Europe.

Since there are so few good examples of evolution at the species level in fossil mammals, considerations of rates of origination and extinction are generally based on analyses of the geological ranges of higher taxa. Simpson (1953, p. 38) has discussed the advantages and the limitations of such analyses, and his comments apply equally to the analysis presented here. The genus is the smallest taxonomic unit for which geological range data are readily available, and the genus is probably the unit most consistently defined by mammalian palaeontologists. Rates of origination and extinction have been calculated here for rodents, artiodactyls, terrestrial carnivores, and primates, and these rates are plotted in Fig. 4. Each point on the charts in Fig. 4 represents the number of genera making their first (or last, in the case of extinctions) appearance in each subdivision of the geological time scale, divided by the duration of that subdivision.

In Fig. 4, a general overall trend toward increasing rates of both origination and extinction is apparent since the Cretaceous, correlated with the general increase in generic diversity illustrated in Fig. 2. As noted above, this trend is



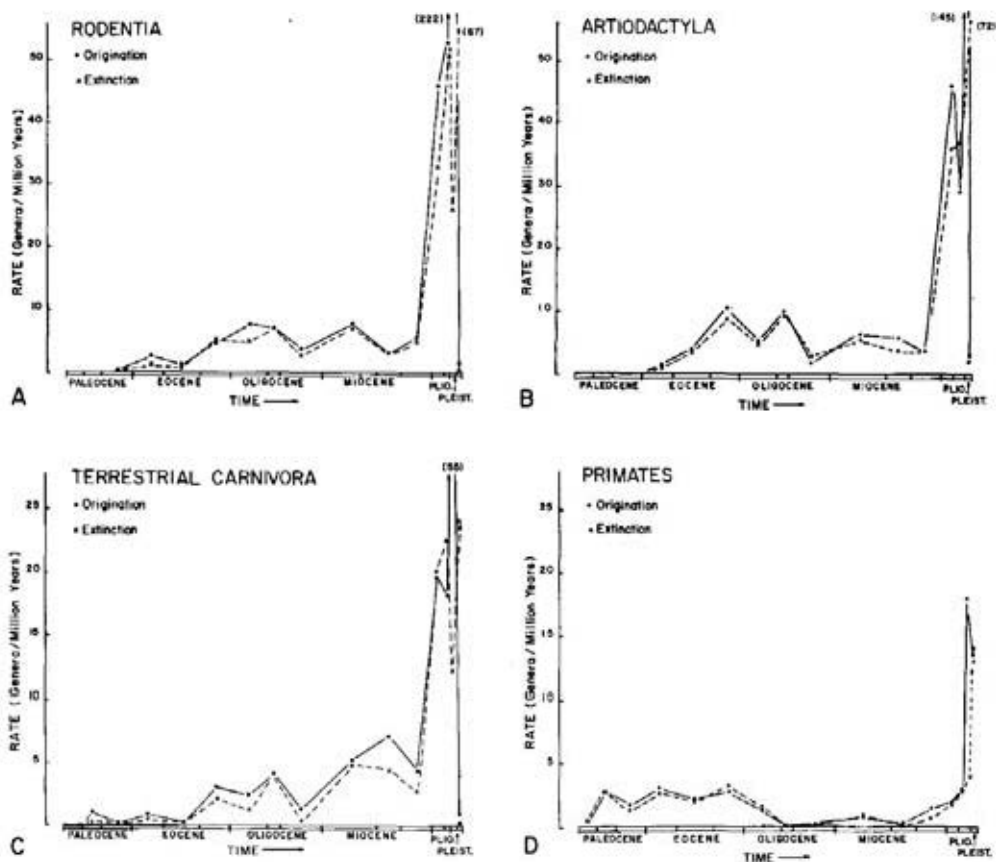


Fig. 4. Rates of origination and extinction at the generic level in Cenozoic mammals. Originations (solid circles) and extinctions (marked by x's) follow a similar pattern in small herbivores (Rodentia), large herbivores (Artiodactyla), carnivores (fissiped Carnivora), and Primates, with relatively high levels of faunal turnover in the Early Eocene, Early Oligocene, Early Miocene, and Plio-Pleistocene. Modern Primates, being largely confined to the tropics, are underrepresented in Neogene sediments. Note the close correlation of origination and extinction throughout the Cenozoic, and the very high rates of origination in the Early Pleistocene preceding high rates of extinction in the Late Pleistocene. Pseudo-originations and pseudo-extinctions (where one known genus evolved directly into another) may account for as much as 20% of rates shown here, although Van Valen (1973) has estimated that 5% is a more likely figure. Data from Romer (1966).

probably in part due to better sampling in the later epochs. Extinction follows origination very closely in each chart of Fig. 4, as one would expect from equilibrium theory and from the relative stability of generic diversity within each major adaptive group of mammals through the course of the Tertiary (Fig. 3). Thus the charts in Fig. 4 give a measure of faunal turnover during the Tertiary. Interestingly, the relatively high levels of generic turnover in the Early Eocene, Early to mid-Oligocene, and Early Miocene correspond to periods of major climatic change (cf. Wolfe and Hopkins, 1967). As was discussed above, a major

influx of new genera into western North America and Europe occurred with expansion of the subtropical climatic belt at the beginning of the Eocene. The major faunal turnover of the Early Oligocene ("*Grande Coupure*") was correlated with a major climatic warming (see Crochet et al., 1975). Similarly, the high rate of faunal turnover in the Early Miocene coincided with a third major period of climatic warming. Lillegraven (1972) has documented a similar correlation of high rates of faunal turnover at the ordinal and familial level in Cenozoic mammals during major periods of climatic warming.

The major extinction of mammals during the Pleistocene has justly received much attention in the literature on extinction (Axelrod, 1967; Martin and Wright, 1967; Webb, 1969; Van Valen, 1969). As Fig. 4 shows, rates of extinction at the generic level were very high in all groups (67 genera/m.y. in Rodentia, 72 genera/m.y. in Artiodactyla, 23 genera/m.y. in terrestrial Carnivora, and 13 genera/m.y. in Primates). In each example, the Late Pleistocene rate of extinction exceeded that of any other subdivision of the Cenozoic. Van Valen (1969) has tabulated possible causes proposed to account for the high rate of extinction in the Late Pleistocene. Most important among these are severe climatic deterioration and/or human intervention.

While the rates of extinction of mammalian genera were at their highest in the Late Pleistocene, these rates were far below the rates of origination of new genera in the Early Pleistocene. Considering the close correlation and general equilibrium of rates of origination and extinction shown in Fig. 4 (see also Webb, 1969), it is only to be expected that high extinction rates would follow the incredible rates of origination seen in the Early Pleistocene. *What requires explanation is not so much the high rate of Late Pleistocene extinctions, but rather the extraordinarily high rate of Early Pleistocene originations.* Late Pleistocene mammal extinctions can be explained as a simple return to faunal equilibrium following an extraordinary over-diversification in the Early Pleistocene. Early Pleistocene over-diversification of mammals was probably a result of abnormal spatial and temporal fragmentation of habitats due to Pleistocene climatic fluctuations and continental glaciations.

The Pleistocene extinction of mammals on many continents has sometimes been attributed to human interference (Martin, 1967). If Late Pleistocene extinctions were due to natural diversity equilibration, then the human contribution to Pleistocene extinctions was probably insignificant. As during the course of the Tertiary, climate more than anything else controlled the level of faunal diversity and the equilibrium level of rates of origination and extinction during the Pleistocene. Humans, rather than controlling mammal diversity in the Late Pleistocene, were apparently subjected to the same pattern of Plio-Pleistocene diversification as other mammals; there is good evidence of two distinct hominid lineages in the Early Pleistocene, but only one thereafter.

### *Survivorship*

Having described the pattern of extinction through the course of the Cenozoic, we can now consider a related pattern — survivorship. In the previous sec-

tion, the longevity of a mammalian species was given as something on the order of a million years (in the few cases where data are available). For genera and higher taxa there is information available for many more examples, and the following discussion will concentrate on generic-level longevity and survivorship.

Fig. 5 shows the distribution of generic longevity in rodents. When all rodent genera with a fossil record are considered, whether now living or extinct, the average length of life of a rodent genus is 5.85 m.y. As the figure clearly shows, 2 m.y. is the dominant modal longevity. The longevity distribution of rodent genera can be converted into survivorship by considering the total number of genera that survive for various intervals of time. All 558 genera survived at least 1 m.y., the minimum time interval considered. Of these, 521 survived for at least 2 m.y., 286 survived for at least 3 m.y., etc.

Plotting the number of genera surviving each interval of time (on the ordinate) versus the duration of that interval (on the abscissa) gives a survivorship curve. If a logarithmic scale is used on the ordinate, the resulting curve has the property that the probability of extinction at any given age is given by the slope of the curve at that age. Van Valen (1973) was the first to apply this property of survivorship curves in analyzing probabilities of extinction in mammals (and other groups of animals as well). He discovered that the survivorship curves of mammals are very nearly linear with constant slope, i.e., the probability of extinction of a genus is independent of the age of the genus. Raup (1975) has suggested pooling data on living and extinct taxa into a single survivorship curve, and such a curve is given in Fig. 5 for the genera of rodents. The survivorship curve given for rodent genera in Fig. 5, calculated independently

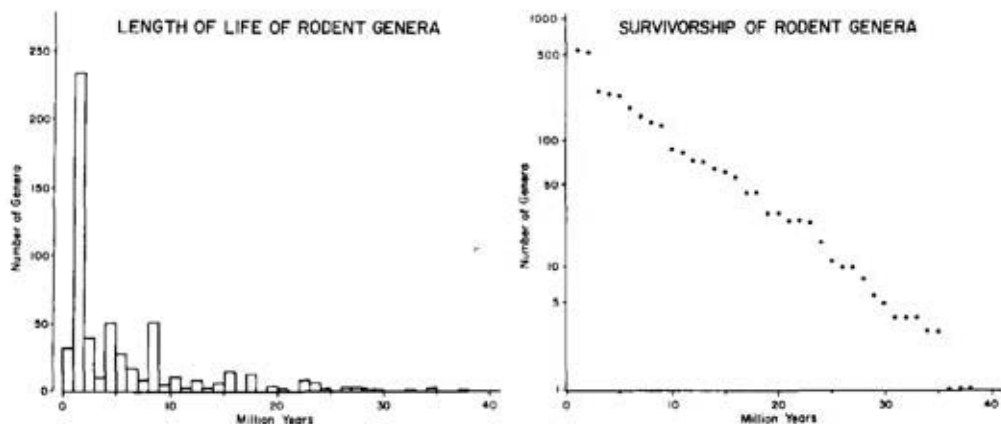


Fig. 5. Survivorship in Rodentia. Histogram (left) shows number of living and extinct genera with a fossil record known from various intervals of geological time. One genus lived for 38 m.y., and the average length of life of a genus is 5.85 m.y. Almost half of the genera known survived for only 2 m.y. Survivorship curve (at right) shows a cumulative plot of the same data, with number of genera on a logarithmic scale. This very nearly straight survivorship curve indicates that the probability of extinction of a rodent genus is nearly constant, regardless of its age (see Van Valen, 1973; Raup, 1975). Data from Romer (1966).

of that given by Van Valen (1973), demonstrates even more closely than his figures the linearity of the curve, and adds additional weight to Van Valen's law of the constancy of extinction. The fact that the probability of extinction of a genus is independent of its age means that extrinsic factors control the survival of the genus. Van Valen emphasizes stochastic deterioration of an animal's effective environment as a critical extrinsic factor.

### *Size increase — Cope's Rule*

The earliest mammals were very small shrew-sized forms, with cheek teeth only 1–2 mm in length. By the Early Eocene, mammals of the size of hippopotami (*Coryphodon*, etc.) were present. The largest land mammal known, the rhinocerotid *Baluchitherium*, comes from Oligocene and Early Miocene deposits in Asia. *Baluchitherium* stood nearly 5.5 m tall, and had a skull almost 1.2 m in length (Granger and Gregory, 1936).

In many groups of Cenozoic mammals, lineages can be traced in which there was a progressive trend toward larger size through time. The reasons for this general tendency toward larger body size ("Cope's Rule") have recently been discussed by Stanley (1973). Stanley presents data showing the number of North American rodent species with molars of a given size in the Eocene, Miocene, and Pliocene. These plots become progressively more right-skewed toward larger size through time, while the modal size category remains approximately constant near the small end of the range observed. This indicates that rodents began as small animals, and most remained small while some became larger and invaded niches requiring larger body sizes than those for which the group as a whole was adapted.

Thus, Cope's Rule as a generalization is not to be explained by the intrinsic advantages of large size. It is rather the tendency for new groups to arise at small size that accounts for the observed pattern of net size increase. Stanley (1973) has proposed that the specialized nature of large species, required by problems of similitude, renders these forms unlikely potential ancestors for major new descendant taxa, but it must be remembered that the simple fact that most mammals are small introduces a bias favouring origins from small size by chance alone. It has not yet been shown that more mammalian orders, for example, originated at small size than would be expected given the fact that the great majority of mammalian species at any given time were small. Van Valen (1975) has cited the repeated radiations of large mammals from smaller ones as an example of group selection favouring small mammals, but here again the tendency for small mammals to give rise to successive radiations of large mammals may be due simply to the fact that small mammal species have always been much more abundant than large ones.

### *Morphological diversity — dental complication and simplification*

The broad radiation and diversification of different dental types in Cenozoic mammals has long been known, and as a result of recent work the outline of

dental evolution in the Mesozoic is becoming clearer (see Kermack, 1967; Crompton, 1971, 1974; Clemens, 1968, 1970; Parrington, 1971; among others). Early work by Butler and by Mills on the significance of wear patterns on teeth has recently been considerably expanded by cineradiographic (Crompton and Hiiemae, 1970) and electromyographic (Kallen and Gans, 1972) studies of chewing in living mammals. The result is a fairly clear pattern of functional diversification including a general tendency toward the acquisition of progressively more complicated teeth, which was followed in some groups by specialization and secondary simplification of molar morphology.

The most generalized Late Triassic mammals have cheek teeth similar to those of *Eozostrodon*, illustrated in Fig. 6. A large apical cusp and a secondary smaller cusp behind it dominate the crown. Reptiles as a rule have simple pointed teeth that oppose each other in a point-to-point manner, but little precise occlusion is possible. The pointed teeth may function as the mandible is

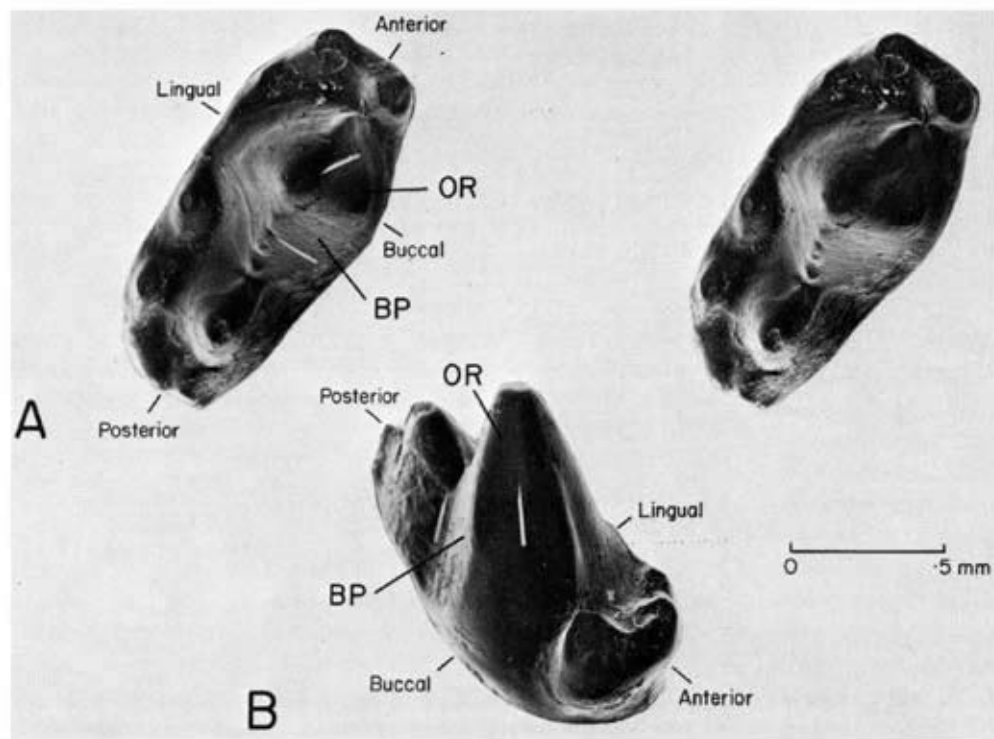


Fig. 6. Crown morphology of a lower molar of the Late Triassic mammal *Eozostrodon*. Scanning electron micrographs in stereocclusal (A) and oblique (B) anterior views to show the pattern of wear facets. White arrows on facets indicate inferred directions of mandibular movement during function. OR facets with upward and backwardly oriented striations are associated with the apex of the major cusp. BP facets with upward and forwardly oriented striations are associated with the linear crest connecting the major and secondary cusps. Specimen is in the University of California Museum of Paleontology, Berkeley (UCMP 82771).

drawn up and backward by the adductor musculature, or up and forward by the pterygoid muscles. Points may function to hold or puncture food, but they cannot cut food into finer pieces. *Eozostrodon* has rather reptile-like molars with large puncturing cusps, but it also shows a clear advance over most reptiles in that the major cusps were connected by precisely occluding linear shearing edges, permitting food to be cut as well as punctured (see Fig. 6). Interestingly, these two functions appear (from study of minute occlusal wear facets on the teeth) to have been associated with different directions of mandibular motion during chewing; the puncturing cusps functioned as the mandible was drawn up and backward, whereas the shearing crests functioned as the mandible was drawn up and forward.

Several different molar types were derived from the primitive pattern seen in *Eozostrodon* (see Fig. 7). Multituberculates may have split off from the remain-

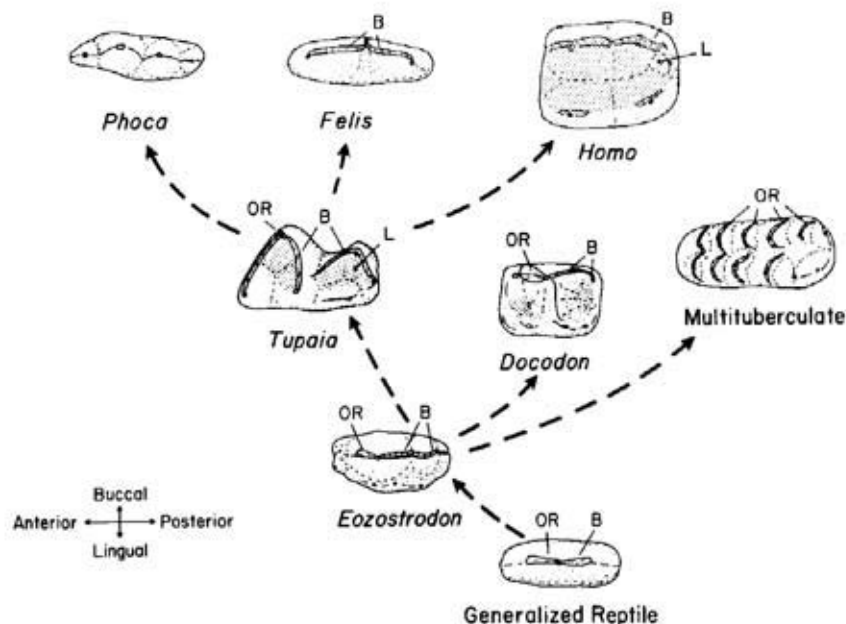


Fig. 7. Adaptive radiation of molar types in mammals. At the hypothetical generalized reptile stage, the teeth had a single puncturing cusp. This cusp functioned to puncture food with either an upward and backward (OR) movement or an upward and forward movement (B). In the Late Triassic mammal *Eozostrodon*, OR wear facets are associated with puncturing cusps, while B facets are associated with linear shearing crests (see also Fig. 6). *Docodon* and multituberculates (see Fig. 9) represent two evolutionary experiments in molar design. In therian mammals, representing a third experiment, the principal molar cusps became rotated to form interlocking triangles. Eventually, a heel or talonid was added to the back of the lower molar, as in *Tupaia*, providing a large planar grinding surface (L) for the upper molar protocone. Later mammals derived from a *Tupaia*-like ancestor specialized for puncturing only (*Phoca*), shearing only (*Felis*), for grinding (*Homo*), or for some combination of these three possibilities.

ing mammalian stock before upward and forwardly directed shearing like that present in *Eozostrodon* evolved. Instead multiple cusps were added to the upper and lower molar teeth and precise shearing occlusion evolved that was designed to function as the mandible was drawn upward and backward. As will be discussed below, this experiment represented a basically different evolutionary pathway to a microshearing dentition from that taken by most other mammals. The genus *Docodon*, like *Eozostrodon*, had both puncturing and shearing features well developed on its molars (Gingerich, 1973), and it is possible that *Docodon* represents an early experiment in the development of a crushing dentition as well.

Zero-dimensional points (cusps) and one-dimensional lines (crests) were well developed in *Eozostrodon*. Of particular interest and importance for the later evolution of mammals was the addition of two-dimensional planar areas (basins) in the therian mammals. These planar areas added a grinding capability to mammalian mastication. By the mid-Cretaceous both *Holoclemensia* and *Pappotherium* show the combination of geometrical points, lines, and planes correlated with puncturing, shearing, and grinding that is found in generalized living mammals such as the tree shrew *Tupaia*. The three functional features found in various combinations on the teeth of therian mammals are analogous to the corners, edges, and surfaces of a solid cube, and the therian molar pattern presumably represents the most efficient way of packing these features onto occluding tooth crowns. With the augmentation of shearing and the addition of grinding, generalized therians like *Tupaia* are able to triturate their food much more completely than their primitive precursors like *Eozostrodon*. The evolution of the mammalian molar from *Eozostrodon* to *Tupaia* provides a nice example of increasing geometrical complexity in the course of mammal evolution.

Most Late Cretaceous insectivores had molars functionally similar to those of *Tupaia*, and molar evolution in the Cenozoic can be seen as a series of trends towards specialization for one or a combination of the functional components present in *Tupaia* molars: puncturing, shearing, or grinding. Phocid seals provide an example of a group specialized for puncturing only, and felid carnivores illustrate molar specialization for shearing only. Human molars are specialized for grinding. These specializations provide examples of decreasing geometrical complexity in the course of mammal evolution.

### Mammalian Adaptations

Adaptations of three general types are the ones most often studied in the fossil record: those having to do with the dentition, with the brain, or with locomotion. Evolution of adaptations can either be studied directly by determining morphological trends in established phylogenetic lineages, or indirectly by noting the independent acquisition of particular morphological features in closely related (acquisition via parallelism) or distantly related (acquisition via convergence) groups of animals. Where changes in several morphological fea-

tures are studied simultaneously, it is often the case that different features change independently, providing examples of mosaic evolution.

### Convergent evolution

Locomotor evolution provides a spectacular case of convergence in the independent elongation and reduction in number of the toes in North American horses and in South American litopterns during the Tertiary. Equally dramatic examples are seen in the dental adaptations of diverse mammals known from the fossil record (Fig. 8). The well-known Pleistocene sabre-toothed cat *Smilodon* was probably a scavenger, using its enlarged canine teeth to open and

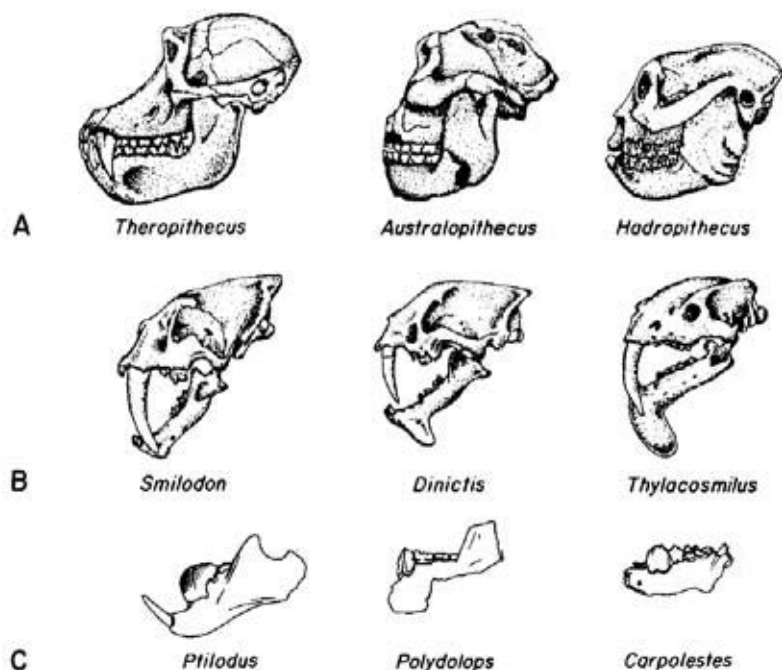


Fig. 8. Examples of convergence in the dental adaptations of mammals. A. *Theropithecus*-complex: the extant baboon *Theropithecus*, the Pleistocene hominid *Australopithecus*, and the subfossil lemur *Hadropithecus* all show a similar shortening of the facial region of the skull with a short, deep mandible in correlation with a diet of seeds, rhizomes, and other small tough objects (inferred in *Australopithecus* and *Hadropithecus*: see Jolly, 1970a,b). B. Sabre-toothed carnivores: the Pleistocene true sabre-toothed cat *Smilodon*, the Oligocene false sabre-toothed cat *Dinictis*, and the Pliocene borhyaenid marsupial *Thylacosmilus* all evolved enlarged shearing upper canine teeth independently (see Riggs, 1934; Miller, 1969). C. Plagiaulacoid herbivores of the Paleocene: the multituberculate *Ptilodus*, the marsupial *Polydolops*, and the primate *Carpolestes* all independently evolved an enlarged ribbed, blade-like tooth in the center of the lower dental series (see Simpson, 1933; Rose, 1975). Drawings are not to the same scale — primates and carnivores in A and B have skulls approximately the size of a human skull or slightly smaller, whereas the plagiaulacoids in C are much smaller and would have a skull approximately the size of a squirrel.



divide carcasses. An independent line of distantly related "false" sabre-toothed felids (including the Oligocene *Dinictis*) acquired a similar morphological adaptation, as did a very distantly related Pliocene South American borhyaenid marsupial *Thylacosmilus*. These forms too were presumably scavengers like *Smilodon*.

In the Paleocene of Europe and North America, the small herbivore niche was dominated by multituberculates, which were characterized by an enlarged, blade-like tooth in the center of the tooth row. The evolution of North American carpolestid primates can be traced in detail through the Middle and Late Paleocene, during which time they developed an enlarged blade-like tooth in the middle of the tooth row similar to that seen in multituberculates (Rose, 1975). Also, completely independently, a group of South American polydolopid marsupials acquired the same blade-like tooth in the center of the tooth row. This convergence of "plagiaulacoid" dental types has been described in greater detail by Simpson (1933).

More recently a very interesting "seed eating" model has been proposed by Jolly (1970a,b) to explain the origin of human dental and cranial morphology. Jolly's model is based on a baboon analogy: he noted that the morphological series from long-snouted mandrills to intermediate *Papio* baboons to short-snouted geladas is similar to the series from the great apes to humans. *Theropithecus* geladas have their mandibles tucked underneath the cranium like the condition in hominid primates. Geladas differ from other baboons in feeding on a greater proportion of small, tough seeds and rhizomes in more open savanna. Jolly proposed that a progressive ecological shift to open country seed eating might explain the morphological shift from long-jawed, forest living apes to short-jawed humans. Skulls of *Theropithecus* and the archaic hominid *Australopithecus* are illustrated in Fig. 8A, along with another remarkable primate showing a similar morphological pattern, *Hadropithecus*, a subfossil lemur from Madagascar that convergently evolved very hominid-like skull proportions.

### *Multiple evolutionary pathways*

The examples of convergence discussed above all show similar morphological adaptations. Another example is known from the mammalian fossil record that shows a very similar functional adaptation acquired by very distantly related mammals: multituberculates and rats — animals whose last common ancestor lived some 200 m.y. ago. Both acquired a cheek tooth complex adapted for microshearing, but they acquired this from such different morphological backgrounds that the whole functional complex is oriented in opposite directions in the two (see Fig. 9).

The functional evolution of mammalian molars summarized in Fig. 7 shows that primitively upward and backward jaw movements powered by the mandibular adductor musculature were the most important. During the course of mammal evolution in the Mesozoic, upward and forward jaw movements became progressively more important for shearing and grinding. Correlated

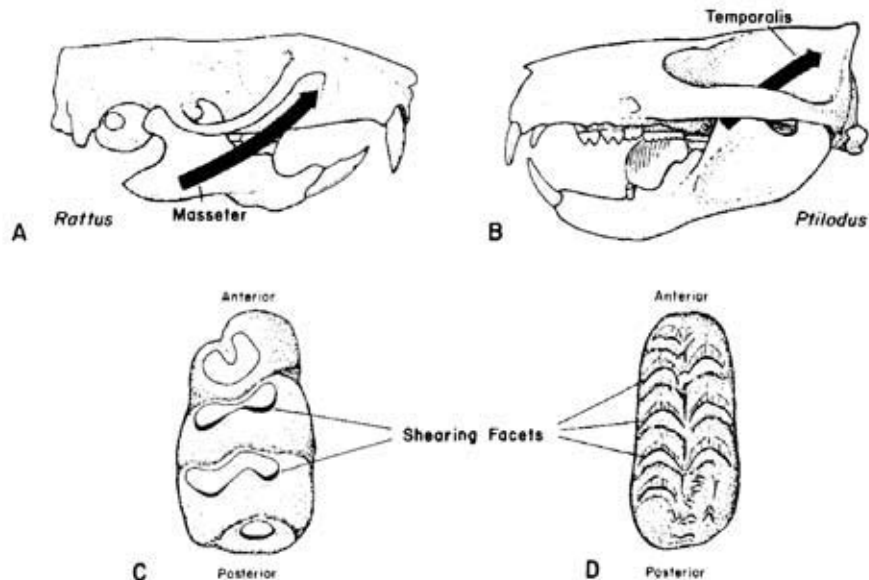


Fig. 9. Multiple evolutionary pathways to a microshearing dentition. The living rat *Rattus* (A) and the Paleocene multituberculate *Ptilodus* (B) were approximately the same size and had skulls that were fundamentally similar in having enlarged central incisors, a diastema, and a battery of multicusped cheek teeth, however the jaw musculature of *Rattus* is dominated by the masseter muscles, whereas multituberculates were temporalis dominated. Concave microshearing crests on *Rattus* molars (C) show that the molars functioned as the mandible was drawn upward and forward, whereas the concave microshearing crests are oriented to function as the mandible was drawn upward and backward in multituberculates (D). See also Fig. 7.

with this was progressive enlargement of the masseter musculature pulling the mandible upward and forward. Multituberculates developed a microshearing dentition by multiplying the number of cusps on upper and lower molars, and by pulling the lower jaw backwards during the power stroke of chewing with their enlarged adductor or temporalis musculature. The orientation of concave shearing facets on the upper and lower molars of multituberculates shows clearly that they functioned during the upward and backward power stroke. The mandibular mechanics of the earliest rodents, on the other hand, were already dominated by the masseter pulling the lower jaw upward and forward (an adaptation perhaps acquired in correlation with the gnawing incisors present in the earliest rodents). Thus, when rodents specialized for a microshearing cheek dentition, they did it by developing small concave shearing blades functioning when the jaw was drawn forward. Functionally the result was the same as in multituberculates but the two systems were oriented in opposite directions — an example of multiple evolutionary pathways to the same morphological adaptation.

### Parallel evolution

Many examples of parallel evolution have been documented in the fossil record. The archaic family Plesiadapidae shows development of crenulated enamel, molarization and reduction in number of premolar teeth, increase in overall size, etc. in parallel but independent lineages during the Paleocene (Gingerich, 1976b). Numerous lineages of primates and other mammals independently evolved larger brain size through the course of the Tertiary (Jerison, 1973).

One of the most interesting cases of parallel evolution yet documented in the fossil record was described by Radinsky (1971). Radinsky's example shows the independent evolution of a cruciate sulcus at least four times in different families of modern Carnivora. Radinsky's data are presented in Fig. 10. Practically all modern carnivores have a cruciate sulcus dividing the frontal lobe of the brain. The earliest representatives of the Ursidae (bears), Procyonidae (racoons), and Mustelidae (weasels), known from the Late Eocene and Oligocene, all have a well-developed cruciate sulcus. However, the Felidae (cats), Viverridae (civets), and Canidae (dogs) can be traced back to distinctive Late Eocene and Oligocene genera that do not have a cruciate sulcus. Thus, this important morphological feature of the brain evolved at least four times: in Felidae, in Viverridae, in Canidae, and in the common ancestor of Ursidae, Procyonidae, and Mustelidae. Radinsky attributes the multiple independent

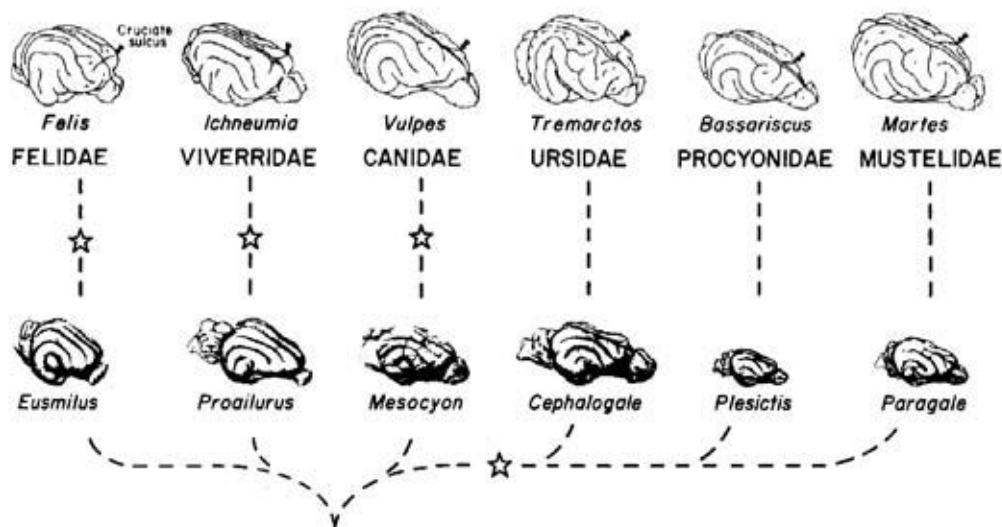


Fig. 10. Parallel evolution of the cruciate sulcus in fissioned Carnivora. Representatives of six modern carnivore families are shown at the top. Eocene or Oligocene ancestral forms of each of these families are shown at the bottom. Position of the cruciate sulcus is indicated by an arrow in the living genera. Stars show the independent evolution of a cruciate sulcus at least four times in Felidae, Viverridae, Canidae, and the common ancestor of Ursidae, Procyonidae, and Mustelidae. Data and inset figures from Radinsky (1971).

origins of a cruciate sulcus in carnivores to the functional requirements of folding the neocortex in association with expansion of the motor cortex. Since these advances were presumably adaptive in all of the different families of carnivores, it is not surprising that all eventually acquired a similar cruciate sulcus.

The independent evolution of a mammal-like dentary-squamosal jaw articulation in different groups of advanced cynodont reptiles (Crompton and Jenkins, 1973), and the independent origin of the mammalian middle-ear mechanism in monotremes and therian mammals (Hopson, 1966) provide additional examples of parallel evolution in complex anatomical systems.

### *Mosaic evolution*

When intermediate stages connecting a primitive mammal with a more modern one are known, it is usually found that the characters by which the modern form differs were not all acquired at the same time in its evolutionary history. The appearance of different characteristics at different times is termed mosaic evolution.

One of the most interesting examples of mosaic evolution in mammals has been documented in the evolution of humans from more primitive ape-like ancestors (as yet inadequately known). Humans differ from apes in two obvious ways — humans walk bipedally and have much larger brains. Lamarck, Haeckel, and Darwin all postulated that human bipedality preceded the evolution of a large brain, but only over the past fifty years has evidence been collected and analyzed that demonstrates this to be so. The pelvis of *Australopithecus* is intermediate between modern apes and modern humans when its total morphological pattern is analyzed. However, when the morphological features associated only with locomotion are studied, they show that the gait of *Australopithecus* was that of a fully modern human biped (Lovejoy et al., 1973). The features of the pelvis of *Australopithecus* which make it resemble the pelvis of apes are all related to the small size of the birth canal, which is in turn related to the relatively slight degree of encephalization of *Australopithecus* when compared to modern humans. The fossil record shows that human bipedalism clearly preceded human encephalization, which illustrates the mosaic nature of human evolution (McHenry, 1975).

### *Evolutionary reversals*

Evolution, like history, is irreversible for the simple reason that time is unidirectional. Few would deny the progressive nature of evolution when organisms are considered in all their complexity. As a consequence we might expect that individual parts of organisms evolve progressively and irreversibly as well. However, this is not always the case. The occurrence of minor evolutionary reversals in no way diminishes the irreversibility of evolution as a whole, but it does again emphasize both the mosaic nature of the process and the importance of adaptation.

Kurtén (1963) has described a most interesting case of minor evolutionary

reversal in the reappearance in some specimens of *Felis lynx* of the lower second molar  $M_2$  — a tooth unknown in the Felidae since the Miocene. A similar minor morphological reversal can be seen in the phylogenetic history of the primate family Plesiadapidae (Fig. 11), where a minute central cusp first appeared in the upper incisors in the species *Plesiadapis rex*. In one subsequent branch leading to *P. fodinatus* and *P. dubius* this cusp was reduced and lost, while in another derived branch leading to *P. tricuspis* it was retained in well-developed form before being lost in the genus *Platychoerops*. After becoming fully developed, the cusp was reduced and lost in two independent lineages. To take another example, in the lineage from *Plesiadapis* to *Platychoerops* the paraconule cusp on the premolars was lost and then regained (Gingerich, 1976b). Thus it is not possible to infer from the general pattern of progressive evolution in Felidae or Plesiadapidae that individual characters will behave in the same progressive way.

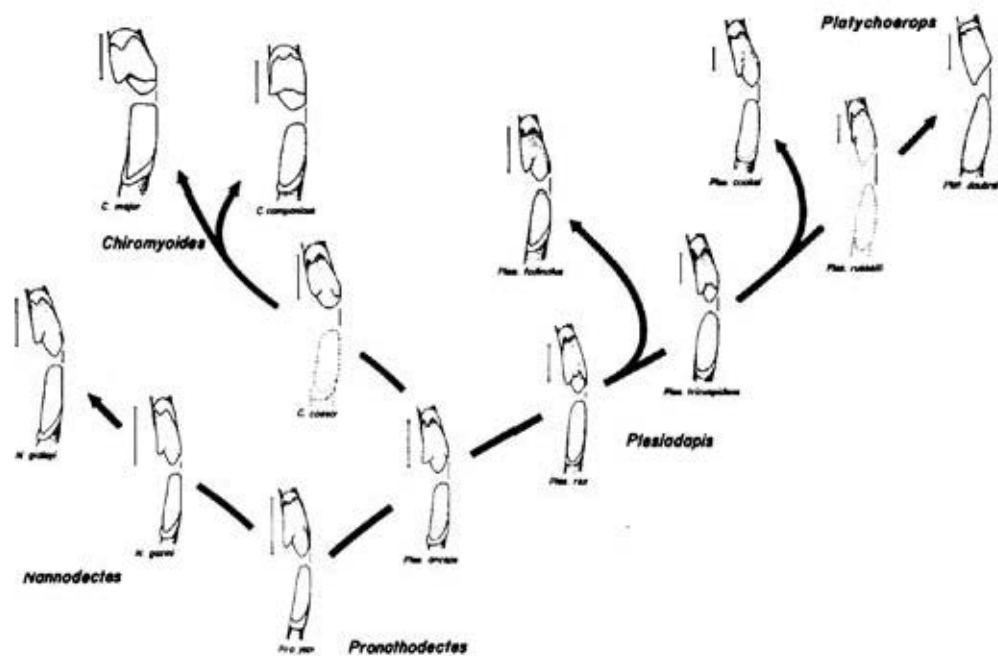


Fig. 11. Minor reversal in the evolution of a distinctive centroconule on the upper incisors of *Plesiadapis*. The primitive species of *Pronothodectes*, *Nannodectes*, *Chiromyoides*, and *Plesiadapis* all had a simple tricuspid apex on the upper incisors. In *Plesiadapis rex* a distinctive fourth cusp, the centroconule, was added in the center of the apex. In one derived North American lineage, leading to *Plesiadapis fodinatus*, this cusp was reduced. In another lineage derived from *Plesiadapis rex*, leading to the North American *Plesiadapis cookei*, the centroconule was lost completely. The centroconule may have been lost independently in Europe in the lineage leading from *Plesiadapis tricuspis* to *Platychoerops daubrei*. Note also the gradual simplification of upper and lower incisors in the line leading to *Platychoerops*. Figures show left upper and lower incisors in posterior view. Scale bar = 5 mm. From Gingerich (1976b).

Oscillations in dental size and shape have been very nicely demonstrated and correlated with Pleistocene climatic fluctuations in European hamsters (*Cricetus*, see Kurtén, 1960) and in North American muskrats (*Ondatra*, see Nelson and Semken, 1970), and many other examples of this kind of reversal could probably be given. Another interesting example of evolutionary reversal in size occurred when large mammals became isolated on islands. Elephants, hippos, and deer, whose general evolutionary history was one of increasing size, are known from the fossil record to have become smaller when they were isolated on islands (Thaler, 1973). Finally, a third case of evolutionary reversal in size, due to character divergence, will be discussed and illustrated in the following section.

### Origin of Species and Higher Taxa

As described in the introduction to this chapter, mammals are ideal for evolutionary studies at the species level. It is thus surprising that more detailed study has not been devoted to those mammals that have a good fossil record. In the remaining pages stratigraphically documented patterns of evolution at the species level, evolution at higher levels, and hominid evolution are discussed.

#### *Evolution at the species level*

For the past century, since 1876 when Marsh demonstrated his fossil collection to Huxley, the evolution of the horse has been the standard textbook example of mammalian evolution in the fossil record. Unfortunately, much of this remarkable sequence is still only understood at the level of the genus. For an understanding of evolution at the species level one must turn to smaller forms: condylarths, lagomorphs, rodents, and primates.

Simpson (1943) originally illustrated his "chronocline" concept with an example from the Early Eocene condylarths. The genus *Ectocion* shows continuous, gradual increase in size in a single evolving lineage as one goes from Clark Fork beds through Sand Coulee beds and into the overlying Gray Bull beds in Wyoming. Simpson's example is especially important because in presenting it he revised the diagnoses of the successive species to reflect the fact that they are stages in a single lineage. Previously, he and others had diagnosed the species strictly on morphology, which had resulted in an overlapping pattern of species ranges suggesting that multiple lineages were present and that the origin of one from another was an abrupt saltation. A similar example of the importance of using time planes to separate adjacent species in a single lineage is illustrated by Simpson's (1953, p. 387) modification of Trevisan's (1949) typological diagnosis of *Elephas meridionalis* from its ancestor *E. planifrons*.

Other chronoclines have been very nicely documented in the evolution of the mid-Tertiary lagomorph *Prolagus* (Hürzeler, 1962, see also Kurtén, 1965) and in the Middle Oligocene rodent *Theridomys* (Vianey-Liaud, 1972). In

*Prolagus* a very complete fossil record shows a remarkable but continuous and gradual reorganization of the premolar crown morphology in a single lineage. In two independent lineages of *Theridomys*, Vianey-Liaud has shown that "synclinide I" was present in an increasing percentage of specimens, and the molars became gradually more hypsodont in successive species. As more lineages are studied in detail it is virtually certain that many of the species already known will be found to intergrade continuously. Wood's statement (1954) that "whenever we do have positive palaeontological evidence, the picture is of the most extreme gradualism" was based on his stratigraphic studies of fossil rhinoceroses, and should probably not be lightly dismissed.

The above studies document the gradual evolution of one species into another within single lineages. In a series of more recent studies an attempt has been made to document the division and separation of lineages as well as evolutionary change within them. *Hyopsodus* is the most common fossil mammal in collections from Lower Eocene strata in North America. Several distinct biological species are present in single locality samples, as indicated by discrete gaps in the size variation of individual teeth (each species within the sample having the variation typical of a modern mammalian population). When all of the samples of *Hyopsodus* that can be placed in stratigraphic position are so ordered, the pattern of change in tooth size that emerges is one of continuous gradual change within lineages, with gradual divergence following the separation of new sister lineages (Gingerich, 1974). A more complete picture of *Hyopsodus* evolution based on additional collecting is presented in Fig. 12 (see Gingerich, 1976a, for discussion).

Other Early Eocene mammals can be studied in the same stratigraphic context, and Fig. 13 shows the pattern of change in dental size in the early primate *Pelycodus*. As in Simpson's *Ectocion* example, there is no evidence for more than a single evolving lineage of *Pelycodus* in Sand Coulee through Gray Bull strata. However, in the upper levels, during Lysite and Lost Cabin time, there is clear evidence that species of two lineages of *Pelycodus* were present. Tracing these two distinct species, *Pelycodus frugivorus* and *P. jarrovi* back in time, they converge with *Pelycodus abditus* in size, mesostyle development, and every other character available for study, and there can be little doubt that each was derived from that species. A similar pattern is seen in the North American Paleocene Plesiadapidae, stratigraphically the best known family of primates. *Nannodectes*, *Chiromyoides*, and two lineages of *Plesiadapis* can be traced back in the fossil record until each converges with a known species of known geological age (Gingerich, 1976b).

These examples are important for several reasons. First, they demonstrate that in some cases phylogenetic patterns, including branching sequences, can be determined empirically from the fossil record. Second, these examples illustrate again the importance of gradual phyletic evolution within single lineages and the importance of this mechanism (anagenesis) in the origin of new species. Finally, they provide the first palaeontological evidence on the geometry of cladogenic branching patterns in mammalian speciation.

Patterns such as these have sometimes been used to support the idea of sym-

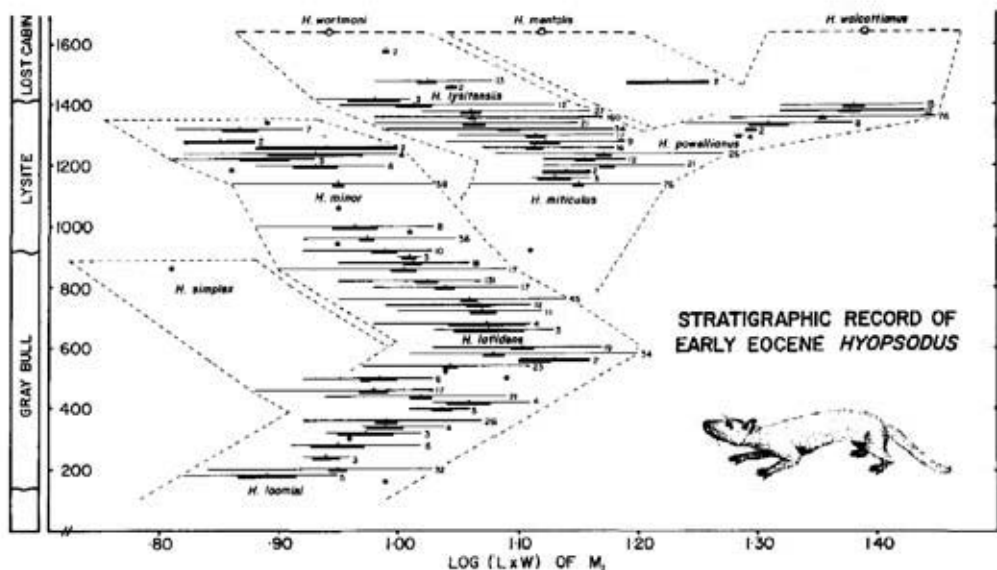


Fig. 12. Stratigraphic record of Early Eocene *Hyopsodus* in northwestern Wyoming. Figure shows variation and distribution of tooth size in samples from many levels spanning most of Early Eocene time (conventionally divided into Gray Bull, Lysite, and Lost Cabin intervals). Specimens come from localities at approximately 6-m intervals in or near a measured stratigraphic section totalling about 500 m in thickness. The small species *Hyopsodus loomisi* became larger gradually through time, until it differed sufficiently to be recognized as a different species *H. latidens*. *H. "simplex"* was another early species derived from *H. loomisi*. *H. latidens* apparently gave rise to both *H. minor* and *H. miticulus*, which in turn gave rise to *H. lysitensis* and *H. powellianus*. Note the regular pattern of divergence in tooth size (and by inference body size) in pairs of sympatric sister lineages. Vertical slash is sample mean, solid bar is standard error of mean, horizontal line is total range, and small number is sample size. From Gingerich (1976a).

patric speciation, but they do not, in fact, support a totally sympatric origin of new clades. Geographic disruption is probably essential in subdividing populations, some of which are or become genetically isolated from each other. However, the fact that size divergence in recently separated sister lineages is so pronounced suggests that character displacement is an important mechanism acting to make genetically separated populations into morphologically different species. The morphological features that distinguish two descendant species from each other and from their common ancestor are acquired gradually (albeit probably as rapidly as possible given the genetic basis underlying most morphological characteristics) only after the two descendants have become sympatric. Since in the above examples it is the close sympatric interaction of two sister species (which became genetically different allopatrically) that makes them different morphologically, I previously characterized speciation in these cases as "parapatric" to indicate that it was a form of speciation intermediate between strictly allopatric or sympatric speciation (Gingerich, 1976a). It now seems better just to recognize that in these examples the genetic separation stage of spe-



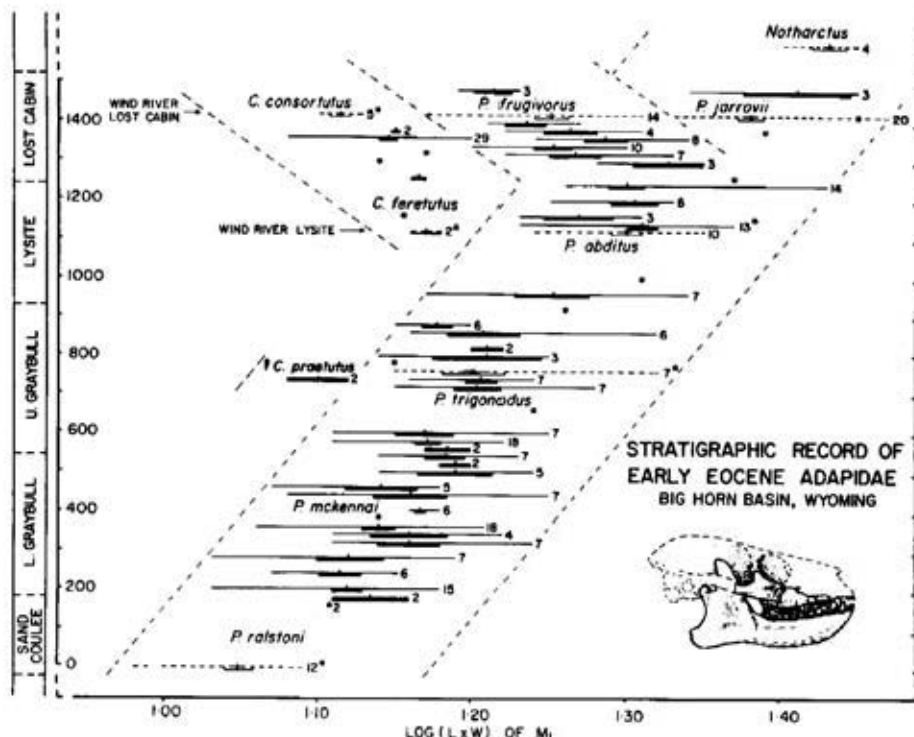


Fig. 13. Stratigraphic record of Early Eocene *Pelycodus* in northwestern Wyoming. Samples from same localities and stratigraphic section as Fig. 12, and the symbols are the same. Note again the continuous, gradual connection between successive species, and the reversed trend toward smaller tooth size in *Pelycodus frugivorus* with the appearance of *P. jarrovi*. Other characters available for study in this sequence, such as mesostyle development, show the same pattern of gradual evolutionary change, but mesostyle development continues progressively through the whole sequence and does not show the character divergence seen in tooth size. From Gingerich and Simons (1977). *C. praetulus*, *C. feretulus* and *C. consortulus* belong to a new genus related to *Pelycodus*.

ciation probably occurred allopatrically, while the subsequent stage of morphological differentiation occurred in large part sympatrically.

The examples discussed here certainly do not rule out the possibility that both genetic separation and morphological differentiation occur allopatrically in some cases, but they do suggest that the strictly allopatric view of speciation, such as that advanced by Eldredge and Gould (1972), may not be as important as it has been thought to be. Three common flaws in the fossil record and in palaeontological methodology would give a "punctuated" picture of phylogeny even where the actual case was one of gradual phyletic change. These potential sources of bias toward a pattern of "punctuated equilibria" (see Eldredge and Gould, 1972) have been discussed in detail elsewhere (Gingerich, 1976a,b) but are listed here as well: Gaps in the fossil record, coarse stratigraphic sampling of

a continuous record, or typological analysis of fossils collected could all yield a pattern of "punctuated equilibria" as an artifact of methodology.

### *Evolution above the species level*

Migration is another potentially important source of abrupt change in fossil sequences. At the beginning of this chapter the importance of climate was discussed in connection with the abrupt origin of many modern mammalian orders at the beginning of the Eocene. The first rodents appeared then, with their diagnostic gnawing incisors. Similarly, the first artiodactyls appeared abruptly at the beginning of the Eocene with their distinctive double pulley astragalus already fully developed (see Schaeffer, 1948). The earliest known bats appeared early in the Eocene with their wings fully adapted for flight (Jepsen, 1966). Saltational, or quantum, or punctuated evolution has been invoked to explain the sudden appearance of modern groups of mammals at different times in the fossil record. However, we do not yet know the fossil ancestors of these groups and, from the gradual generic level transitions seen, for example, in going from *Plesiadapis* to *Platychoerops* (Gingerich, 1976b), we might do well to wait until there is more evidence before hypothesizing special evolutionary mechanisms to explain sudden appearances in the fossil record.

One problem in understanding the origin of higher categories of mammals arises when authors assume that since the incisors, or wings, or astragali characteristic of a modern order of mammals were present in the Eocene, the mammals with such diagnostic characters differed at an "ordinal" level from other Eocene mammals. This is rarely true. Apart from the relatively minor specializations distinctive of each order, most "modern" Eocene mammals were as yet very little differentiated. The origin of higher categories of mammals may have involved higher than average rates of evolution, but there is as yet no reason to suppose that the basic mechanism was any different from that operating in normal speciation. To propose that natural selection operates too slowly to account for the major features of evolution (Stanley, 1975) probably underestimates potential rates of gradual evolutionary change within lineages, underestimates the control of natural selection on cladogenic speciation, and overestimates rates of morphological change during cladogenic speciation events. If nothing else, the patterns of phylogeny in *Hyopsodus* and *Pelycodus* presented in Figs. 12 and 13 indicate that new evidence on the origin of species and higher categories should be forthcoming from careful studies of fossil mammals with good stratigraphic records.

### *Hominid evolution*

One of the most interesting patterns of evolution in the mammalian fossil record is that now emerging in the history of the human family Hominidae. The study of hominid evolution has suffered from the same methodological problems that have plagued study of the rest of primate and mammalian evolution. In the absence of a good fossil record, the study of comparative anatomy

alone has often been used to "reconstruct" human evolution (in the manner that best suited each individual scholar). Typology and inadequate studies of variation have led to overly complex or overly simple patterns of human descent. Lack of fossil dating has led some workers to postulate that the human line has been distinct from other primates for many millions of years, while other workers have advocated a much shorter time. Fortunately, in the past few years concentrated efforts in the field have been rewarded by an abundance of new fossil hominid specimens, many of which can now be dated either absolutely or stratigraphically relative to other hominid fossils.

It is curious how little the dynamic nature of evolution is recognized in discussions of human evolution. Kortlandt (1974, p. 444) for example, is unable to understand how the profound changes making a hominid (*Ramapithecus*, dated at 10–14 m.y.) out of an ape (*Dryopithecus*, 18 m.y.) could have taken place in the space of a few million years, and he proposes that on the contrary, *Ramapithecus* must have diverged from apes several million years earlier, at about 20–25 m.y., if it was to be distinct by 14 m.y. ago. In reply to this one might note that first of all, *Ramapithecus* can hardly be distinguished from *Dryopithecus* morphologically. The differences which separate the two are barely sufficient to justify placing them in two genera, but they indicate that *Ramapithecus* was more like a hominid than *Dryopithecus* was. Since *Ramapithecus* is the only fossil form known before *Australopithecus* to show certain hominid dental features, it is grouped with *Australopithecus* and *Homo* in the family Hominidae, even though it differed only slightly from species of the ape *Dryopithecus*. This procedure is perfectly normal in mammalian palaeontology, and again illustrates the point made above about the earliest representatives of mammalian orders: the early representatives of new higher taxa usually differ only very slightly from each other.

The second point that should be noted in reply to Kortlandt is that species are dynamic — the time period from 18 m.y. to 14 m.y. is sufficient for a considerable amount of change to occur in a lineage of *Dryopithecus*, the amount necessary for it to become *Ramapithecus* being well within that occurring in 4 m.y. in other generic level transitions known in the fossil record. There is a strong predilection to regard species as fixed in time, with all change being concentrated in unknown transitions between fixed types (a predilection given some theoretical justification by Eldredge and Gould, 1972), but in practically all of the cases where samples are known from successive stratigraphic intervals, species are seen to be changing continuously.

Surprisingly little attempt has been made to look at patterns of variation in an explicitly stratigraphic or temporal context in the hominid fossil record. When Pilbeam and Zwell (1972) attempted this using dental measurements of all Plio-Pleistocene hominids, grouping them into 0.5-m.y. bands, they were able to show a fairly clear pattern of divergence of two hominid lineages at about 2–2.5 m.y. ago. To avoid problems of correlation between distant sites, Schoeninger (in Gingerich and Schoeninger, 1976) made a similar analysis of fossil hominids recently collected and described by R.E.F. Leakey from a restricted geographic area east of Lake Turkana in northern Kenya. The results

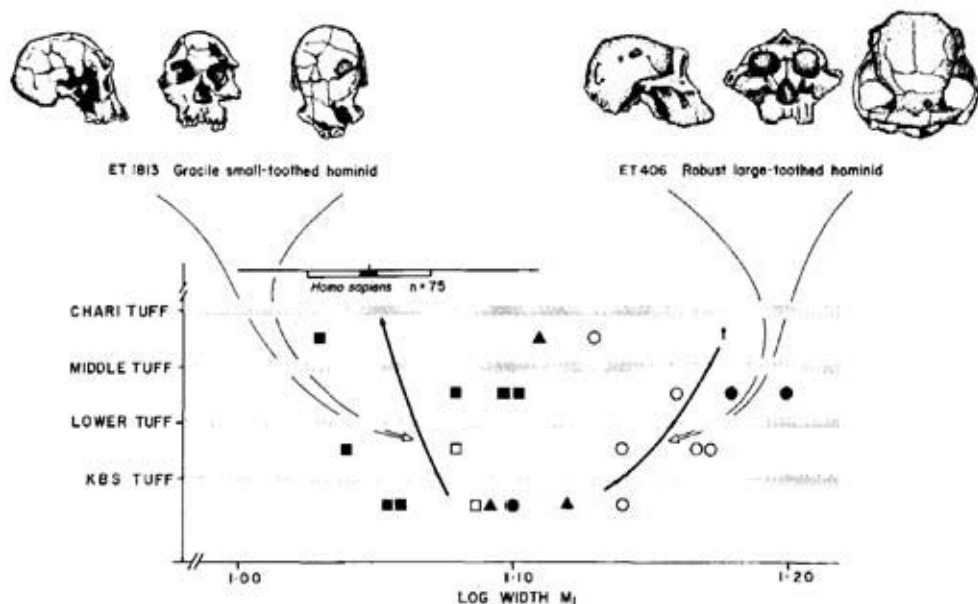


Fig. 14. Stratigraphic distribution of fossil hominids east of Lake Turkana in northern Kenya. Tooth size is plotted for four successive stratigraphic intervals separated by tuffs. The sample of a single population of modern *Homo sapiens* at the top gives a scale for interpreting the east Turkana fossil hominids at each level (horizontal line is range, vertical slash is mean, solid bar is standard error of the mean, open bar encloses one standard deviation from the mean, and the distribution is unimodal). In the east Turkana samples, squares represent *Homo* sp. of authors, circles represent *Australopithecus* sp., and triangles represent undetermined specimens. Open symbols are all estimated from other tooth dimensions for those specimens using regressions, and thus they are less reliable than the solid symbols. Note particularly the well-separated modes in the two middle intervals, suggesting the presence of two hominid lineages. Gracile, small-toothed skulls, some with relatively large endocranial volumes, are thought to be ancestral to modern *Homo sapiens*, while the robust, large-toothed skulls are a divergent extinct lineage. The KBS Tuff is dated at about 2.4 m.y., while the Middle Tuff is dated at about 1.5 m.y. Redrawn from Gingerich and Schoeninger (1976), with inset figures of skulls from Leakey (1976).

of her analysis are presented here in Fig. 14. Specimens discovered from below the KBS tuff (dated at about 2.4 m.y.) have teeth which do not differ greatly in range of distribution of variation from modern comparative populations, although two distinct hominoid lineages may already have been present. The stratigraphic intervals between the KBS and Middle tuffs (the latter dated at about 1.5 m.y.) have yielded samples which exceed the range of variation typical of modern human populations. More importantly, they show a bimodality in the distribution of size of the first molar that would be extremely unlikely in a single species, whether hominids, forest living gorillas, or savanna living baboons (with their extreme sexual dimorphism) were being sampled. Furthermore, these differences correlate with other cranial differences separating "gracile" and "robust" hominids. As variation in morphological characteristics such as endocranial volume, external cranial anatomy, and postcranial anatomy

becomes better known it is to be hoped that these too will be studied in an explicitly stratigraphic context. The studies by Pilbeam and Zwell, and Schoeninger show clear evidence of two lineages of Plio-Pleistocene hominids, based on the available tooth measurements. The smaller toothed lineage appears to be the one leading to modern humans, and unless evidence to the contrary is forthcoming, it seems more reasonable to associate large endocranial volumes and human-like tali and ulnae with this dental lineage rather than postulating extension of a third dentally unknown "*Homo erectus*-like" lineage back to 5 m.y. as Oxnard (1975) has recently advocated. Whatever the true pattern of hominid evolution eventually found, it is now clear that hominid phylogeny was sufficiently complicated that only the discovery of well-dated fossil specimens will ever reveal its true course.

## Conclusions

Several general trends are apparent in the evolutionary history of mammals. For the first two-thirds of their history, mammals were little diversified, of small body size, and basically insectivorous (multituberculates excluded). During the final one-third of mammalian history, spanning the past 65 m.y., mammalian diversity increased rapidly, mammals of large body size first appeared, and mammals invaded new herbivorous and carnivorous adaptive zones. Relative diversity within each major terrestrial adaptive zone has been fairly stable since the Paleocene. Flying mammals and swimming marine mammals are first known from the Early Eocene, and each underwent a separate major radiation during the Tertiary.

Rates of origination and extinction have remained in close equilibrium through the course of the Cenozoic, with major periods of faunal turnover in the Early Eocene, Early Oligocene, Early Miocene, and Early Pliocene. These periods of high faunal turnover correlate with major periods of climatic warming. The high rate of extinction of mammalian genera in the Late Pleistocene is seen to be less remarkable than the incredibly high rate of origination of mammalian genera in the Early Pleistocene. This high rate of origination requires explanation, whereas a high rate of extinction following such a high rate of origination is a predictable result, given the close equilibration of extinction with origination.

There has been a general trend toward increasing size and complexity during mammalian evolution, when the order Mammalia is considered as a whole, but many lineages became smaller, and many anatomical complexes became simpler through time. These facts, plus the great amount of parallelism, convergence, and minor evolutionary reversal all point to functional adaptation as the goal of morphological evolution. Species are dynamic, and natural selection acts continuously to maintain adaptations. Patterns of phylogenetic change are sometimes complex, and a detailed, dense, and continuous fossil record is usually required to decipher the course of evolution at the species level and within higher taxa.

Study of stratigraphically documented transitions from one species to another reveals that both anagenesis and cladogenesis are important in the origin of new species. Patterns of cladogenic speciation indicate that new lineages diverge morphologically when they occur sympatrically *after* genetic barriers have formed between populations during geographic separation. The genetic basis of cladogenic speciation is thus allopatric, but morphological divergence is probably due, in some cases at least, to character divergence during subsequent sympatry. Thus, it appears that cladogenic speciation normally involves both allopatric and sympatric phases associated with genetic and morphological differentiation, respectively.

New taxa of higher than species level sometimes appear abruptly in the fossil record. In one of the most important instances, the sudden appearance of many modern mammalian orders in the Early Eocene, the new ordinal level taxa appeared abruptly as immigrants (in the areas where fossil deposits are known) due to major climatic warming and expansion of their geographic ranges northward. The diagnostic differences between members of different orders sometimes receive disproportionate attention — Eocene mammals placed in different orders were not nearly as different as their modern counterparts are today. Generic level transitions documented in the fossil record of archaic plesiadapid primates show that higher categories may arise by gradual phyletic change in single lineages without any distinguishable periods of abrupt morphological reorganization. In other words, there is as yet no evidence that the origin of higher taxa involves any mode or process different from the origin of species.

Phylogenetic patterns documented in *Plesiadapis*, *Pelycodus*, and *Hyopsodus* give the impression that populations within a species are constantly being shuffled by vagaries of climate and geography, producing a constant supply of genetically separated populations partially isolated by reproductive barriers from sister populations. Sometimes, when a sufficient width of ecological niche is available, two genetically separated incipient sister species survive sympatrically, diverging in character to minimize competition. In other cases the two incipient species might recombine into one, or one might replace the other. Geographic shuffling produces a constant source of slightly different populations of a species, which is analogous to the production of slightly different individuals within a population by recombination and mutation. Natural selection limits this variability in populations through ecological competition between them, which is analogous to the way natural selection channels variation in individuals through differential survival within populations. In mammals like *Hyopsodus*, lineages of species which apparently differed only in body size were closely packed in narrow adjoining adaptive zones. Interestingly, the width of hominid niche available during the Late Pliocene and Early Pleistocene was sufficient to permit the coexistence of two lineages of early bipedal humans, but by the Late Pleistocene only one lineage remained — the gracile form *Homo* survived, while the robust one became extinct.

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