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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

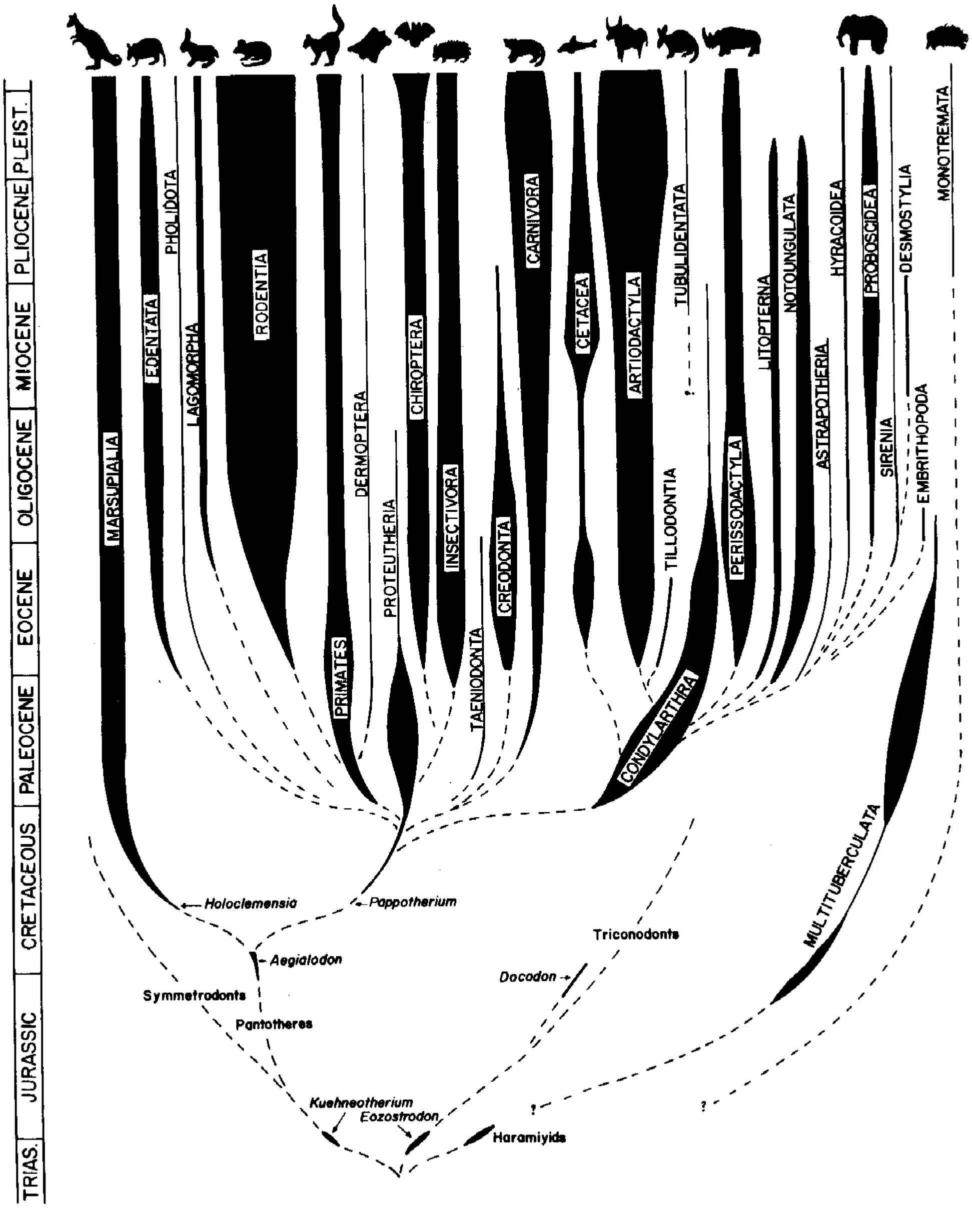

Fig. 1. Radiation of mammals during the Mesozoic and Cenozoic. Width of the shaded area gives a very general estimate of the relative number of genera in the fossil record for each order. See Figs. 2—5 for quantitative data on diversity.

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 Palaeocene 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

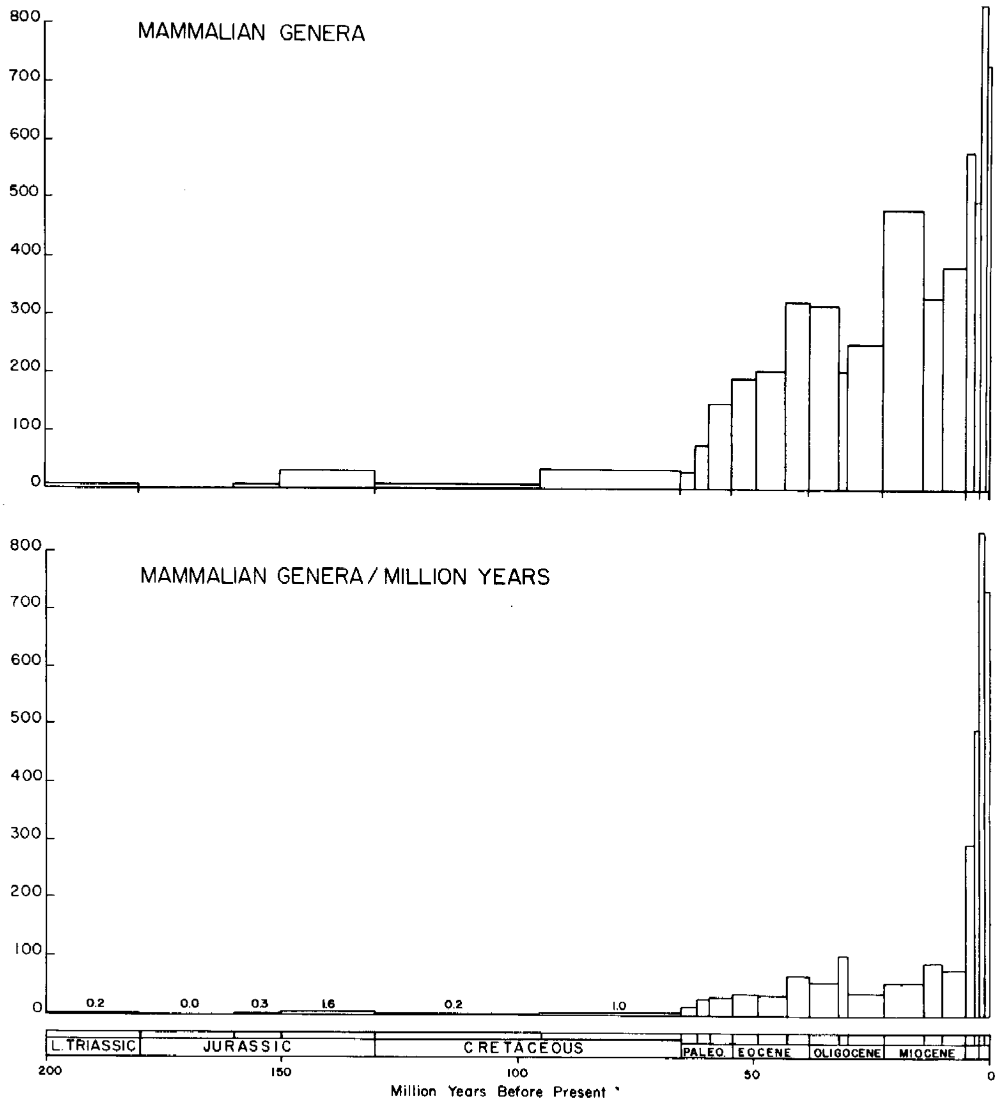

Fig. 2. Generic diversity in mammals through the Mesozoic and Cenozoic. Numbers of genera present in each subdivision of the geological time scale are shown in the upper figure. Numbers of genera per million years in each subdivision of the time scale are shown in the lower figure. Data from Romer (1966).

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

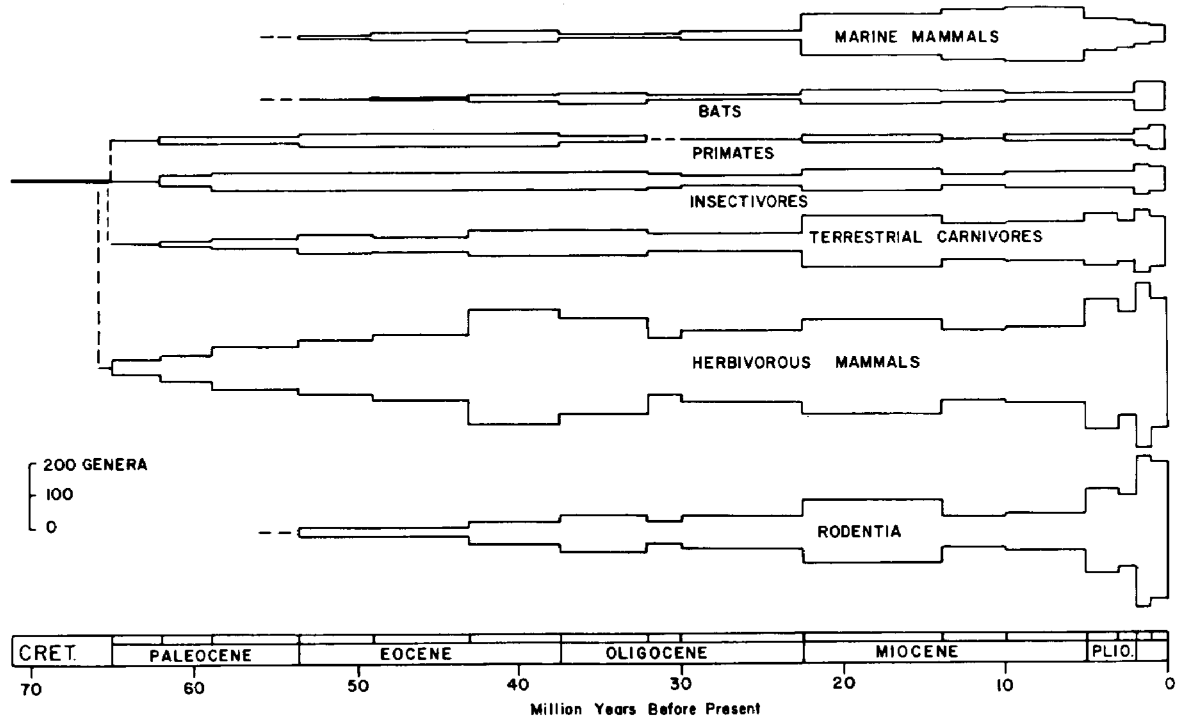

Fig. 3. Relative generic diversity within each major adaptive zone during the Cenozoic. Marine mammals include Sirenia, Desmostylia, Cetacea, and pinniped Carnivora. Terrestrial carnivores include Creodonta, fissiped Carnivora, and borhyaenid Marsupialia. Herbivorous mammals include Artiodactyla, Perissodactyla, 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

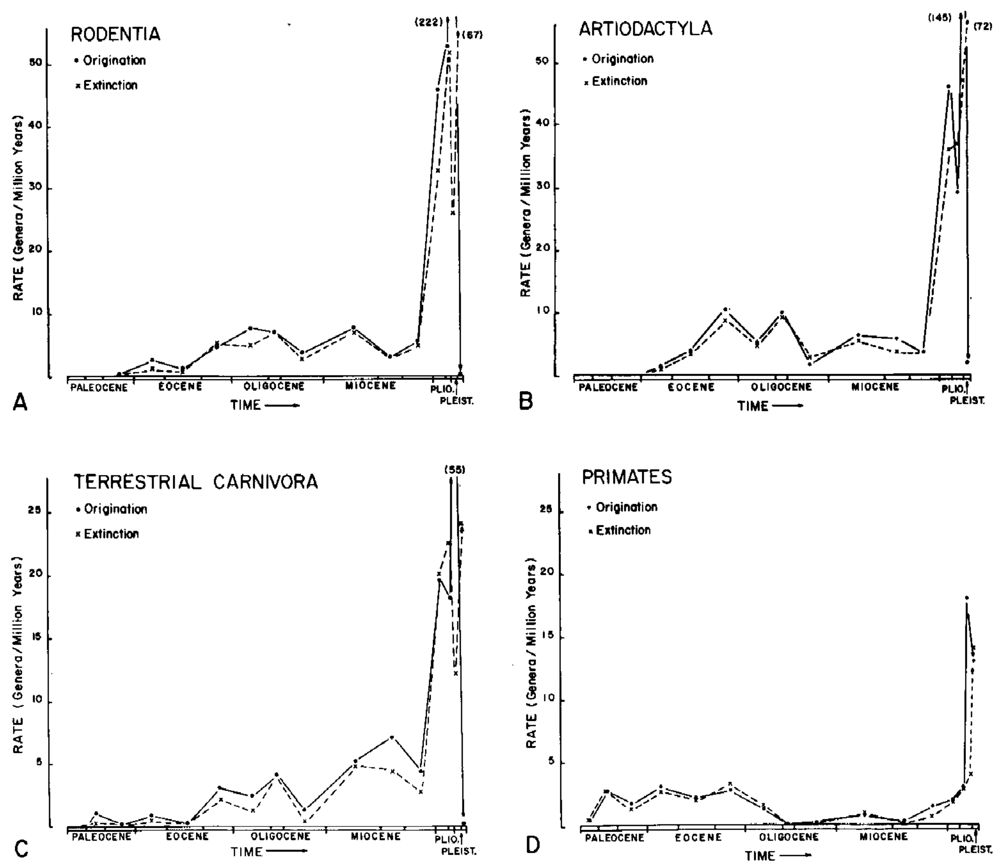

Fig. 4. Rates of origination and extinction at the generic level in Cenozoic mammals. Originations (solid circles) and extinctions (marked by x's) follow a similar pattern in small herbivores (Rodentia), large herbivores (Artiodactyla), carnivores (fissiped Carnivora), and Primates, with relatively high 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-