Gingerich, P. D. 1984. Mammalian diversity and structure. In: *Mammals, Notes for a Short Course*, P. D. Gingerich and C. E. Badgley, eds., Paleontological Society Short Course, 1984: 1-16.

Mammalian Diversity and Structure

Philip D. Gingerich
Museum of Paleontology
The University of Michigan, Ann Arbor, Michigan 48109

INTRODUCTION

Mammalia constitute one of the five major classes of vertebrates (the others being Pisces, Amphibia, Reptilia, and Aves). There are, at latest count, some 4,170 species of mammals living today, classified in about 1010 genera, 130-140 families, and 18 orders (Corbet and Hill, 1980; Honacki et al., 1982). In addition, sixteen orders and uncounted genera and species of mammals are known to be extinct (see synoptic classification in Table 1). While most living mammals are terrestrial like their Mesozoic ancestors, one large progressive group has invaded the air (bats, represented by about 150 living genera and 920 species). Two other smaller groups are fully aquatic (whales, including some 40 genera and 80 species; and sirenians, 3 genera and 5 species). Mammals occupy all of the continents, and all of the larger oceanic islands. Faunal diversity is greatest in lowland tropical forests, woodlands, and savannas, decreasing rapidly at high elevations and latitudes.

Mammals differ from other Vertebrata in having hair and in having specialized mammary glands for suckling their young (hence the class name Mammalia). Different reproductive modes distinguish the major groups of living mammals. The duckbilled platypus (Ornithorynchus) and the spiny echidnas (Tachyglossus and Zaglossus) are egg-laying Ornithodelphia (literally, "bird-wombed"). The opossum (Didelphis) and its relatives are Marsupialia (having a marsupium, i.e., "pouched"), and most embryonic development takes place in this external pouch. The remaining groups of living mammals are all placentals -- development takes place in the uterus, and the embryo is nourished via intermediate tissues of a "placenta" (the tissues shed following a birth). Taxonomic nomenclature is rarely simple, complexity reflecting the tortuous progress of learning, and a parallel series of names, Prototheria, Metatheria, and Eutheria, used in classifying mammals reflects major grades of mammalian reproductive and structural organization.

Mammals are intelligent and, as a rule, they make a considerable investment in "educating" their young. Sight, hearing, olfaction, taste, and a sense of touch are unusually well developed and integrated in the behavior of mammals. Mammals are endothermic (warm-blooded), and usually have high metabolic rates, making it possible for them to sustain a high level of continuous activity between rest periods. Many of the distinctive osteological features of mammals can be related, in one way or another, to their active lifestyles and enhanced sensory

TABLE 1 -- Synoptic annotated classification of living and fossil mammals. This arrangement is traditional and conservative (cf. Simpson, 1945), grouping living mammals into 18 orders (numbered consecutively). An additional 16 orders are extinct (+). McKenna (1975a)provides an alternative cladistic arrangement.

MAMMALIA		
Subclass PROTOTHERIA		
Infraclass ORNITHODELPHIA		
(1)	Monotremata	- Egg-laying platypus and spiny echidna
Infraclass EOTHERIA		
(+)	Triconodonta	- Mesozoic, three cusps in a row
(+)	Docodonta	- Mesozoic offshoot of triconodonts
Subclass ALLOTHERIA		
(+)	Multituberculata	- Complex molars with many tubercles
Subclass THERIA		
Infraclass TRITUBERCULATA		
(+)	Symmetrodonta	- Mesozoic, three cusps in a V
(+)	Pantotheria	- Mesozoic, V plus talonid crest
Infraclass METATHERIA		
(2)	Marsupialia	- Diverse radiation of pouched mammals
Infraclass EUTHERIA		
(+)	Proteutheria	- Archaic insectivores (wastebasket)
(3)	Insectivora	- Shrews, hedgehogs, etc.
(4)	Dermoptera	- "Flying lemurs"
(5)	Chiroptera	- Bats
(6)	Primates	- Lemurs, monkeys, apes, and humans
(+)	Condylarthra	- Archaic ungulates (hoofed mammals)
(+)	Tillodontia	- Specialized archaic herbivores
(+)	Taeniodonta	- Specialized archaic herbivores
(+)	Notoungulata	- Archaic South American ungulates
(+)	Litopterna	- Archaic South American ungulates
(+)	Dinocerata	- Archaic amblypods, large herbivores
(+)	Pantodonta	- Archaic amblypods, large herbivores
(7)	Cetacea	- Whales, dolphins
(8)	Artiodactyla	- Even-toed ungulates
(9)	Perissodactyla	- Odd-toed ungulates
(10)	Xenarthra	- South American "edentates"
(11)	Pholidota	- Old World pangolins
(12)	Tubulidentata	- Old World aardvarks
(13)	Lagomorpha	- Hares, rabbits, pikas
(14)	Rodentia	- Enormous radiation of gnawing mammals
(15)	Carnivora	- Modern carnivores including pinnipeds
(+)	Creodonta	- Archaic carnivores
(16)	Hyracoidea	- Old World hyraxes
(+)	Embrithopoda	- Archaic Old World herbivores
(17)	Proboscidea	- Elephants, mastodons, deinotheres
(18)	Sirenia	- Sea cows, dugongs
(+)	Desmostylia	- Archaic marginal marine herbivores

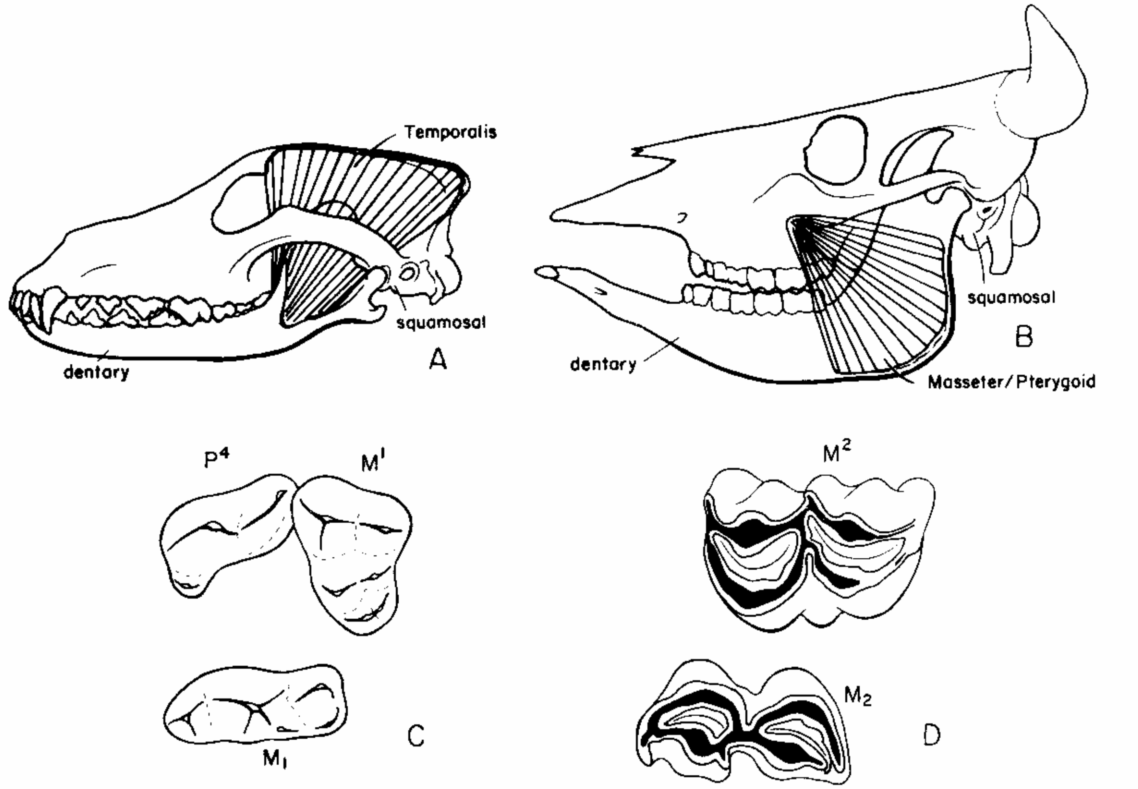

Figure 1-- Comparison of skulls and cheek teeth of the dog, a carnivore (A, C), and the ox, a specialized herbivore (B, D). Note the nearly straight dentary in the dog, where muscles of mastication are dominated by the temporalis (shaded in A), whereas the dentary is bent almost into a right angle in the ox, where the masseter (shaded in B) and underlying pterygoid dominate. Dogs bite by raising and retracting the lower jaw using both the temporalis and masseter-pterygoid, while an ox chews its food by raising and protruding the lower jaw with masseter and pterygoid alone. The ox has a very small temporalis muscle. Carnassial teeth of a dog (C) are enlarged to shear meat and bones efficiently, while the complex crown pattern on molars of an ox (D) is more useful in shearing leafy vegetation.

acuity. Mammals differ from other vertebrates in having a single bony nasal opening in the skull, paired occipital condyles, three auditory ossicles, an eardrum supported by an ossified ectotympanic bone, a single mandibular bone (the dentary) that articulates directly with the squamosal bone of the cranium, diphyodonty (two tooth generations--deciduous and permanent), molars with two or more roots and complex crown morphology, and epiphyses (separate ossifications at articular surfaces) on long bones. Mammals have determinate growth, that is, they grow rapidly early in life but achieve definitive body size as they mature. Once a mammal is fully grown, the epiphyses on long bones fuse with the shaft. The degree of fusion of epiphyses may, in some cases, be used to determine the ontogenetic age of a living individual or fossil specimen.

Modifications of the masticatory apparatus are particularly important in enabling mammals to chew food thoroughly, thus maximizing its nutritive and energetic value. Teeth do the work in chewing. They are composed of two highly mineralized tissues, enamel and dentine, of unusual hardness and density. Hardness and density make teeth resistant to wear during life, and these characteristics facilitate preservation of teeth as fossils. Generalized mammals are opportunistic feeders ("omnivores"), taking advantage of insects, mollusks, fishes, birds, nectar, tubers, fruits, seeds, and a wide variety of grasses and leafy vegetation as available in different seasons. Specialized mammals (i.e., "insectivores", "carnivores", "herbivores", etc.) tend to concentrate on one or more of these foods. The structure of mammalian teeth reflects both heritage and habitus features: different patterns characterize the arrangement of functional features on the molars of different orders, families, and genera of mammals, while the proportional representation of various functional features corresponds closely to diet. Generalists and specialists alike have teeth reflecting critical components of their respective diets. Mammalian teeth form within the jaws and, once erupted, do not continue to grow. The stage of eruption of teeth provides valuable information of ontogenetic age. Molar size is easily measured and highly correlated with the overall body mass of species, providing direct access to this exceedingly important parameter. Taken together, their hardness, density, complex structure, and correlation with body mass combine to make teeth particularly useful as fossils.

Bones too are highly mineralized and bones are commonly preserved as fossils, but mammalian bones surround or contain tissues of significant food value (brain, marrow, cartilage) that encourage destruction by predators. Bone lacks the density of enamel or dentine, and mammalian bones are thus more easily washed away before being buried and fossilized. Isolated bones are often difficult to identify taxonomically, which again decreases their general utility. Soft tissues are preserved and fossilized in a few special environmental circumstances where streams, scavengers, and oxidation fail in their customary role as agents of destruction. Mammalian fossils typically consist of isolated teeth or teeth associated in jaws, and much can be determined from such fragmentary material (which may explain why so many mammalian paleontologists are unabashedly preoccupied with teeth). Skulls, associated postcranial bones, articulated skeletons, and skeletons preserving soft tissues are rare, and they are thus unusually valuable in permitting more complete reconstruction of the biology of extinct mammals than would teeth alone.

Mammals are very useful for geochronology and correlation because of their mobility as living animals, and because of the complexity and consequent rapid evolution of their molar teeth. Biostratigraphically useful species typically have durations of about 0.5 - 1.0 m.y., meaning that they can be used to tell time on this scale when integrated with paleomagnetic profiles or radiometric ages. The Cenozoic record of mammalian evolution in North America is divided into eighteen biochronological land-mammal ages (following Wood et al., 1941; see

Table 2). Each land-mammal age is characterized by an association of genera, and each is bounded above and below by significant faunal turnover at the generic level. Land-mammal ages average about 3-4 m.y. in duration, and these can often be subdivided into 4-6 zones or biochrons based on characteristic assemblages of species. First appearance datums (FADs) are particularly important for broad continental and intercontinental correlation based on fossil mammals. The first appearance of advanced Proboscidea outside Africa (ca. 18 m.y.B.P.) and the first appearance of the three-toed horse Hipparion outside North America (ca. 12 m.y.B.P.) are two important examples. Last appearance datums (LADs) are of little value in correlation and biochronology for the same reason primitive characteristics of organisms have limited diagnostic value in taxonomy.

Mammalian remains are most often found in fluvial clastic sediments deposited on ancient flood plains during tectonic deformation of the continental crust, where they have great potential in dating tectonic events (Dorr and Gingerich, 1980; Gingerich, 1983b). Fossils typically occur as isolated finds eroding out at the surface; in concentrations of skeletons, skulls, jaws, and teeth worthy of quarrying; or as lesser concentrations of jaws and teeth requiring extensive screen washing (Hibbard, 1949; McKenna, 1962). Mammalian remains are also found in lacustrine deposits, where they are sometimes exceptionally well preserved, and in caves, springs, bogs, and other natural traps attracting animals. From the Eocene onward, mammalian remains are found in marine limestones and clastics as well.

The most important thing to do on finding bone in any sedimentary setting is to harden it with a thin, penetrating mixture of glue diluted with solvent (ordinary white glue diluted with water works well in many applications), and then look for more. Bones and teeth can be protected for transport by wrapping them tightly in tissue paper or plaster bandages. Isolated bones by themselves are much less useful than associations of bones and teeth. Where there is one bone or tooth, there are usually others. Samples of several individuals are required to identify most species with certainty, and consultation with a specialist invariably raises the question "Where's the rest of it?" The age of a fossil is ultimately, if not immediately, its most important attribute. Hence precise locality and stratigraphic records are very important. Most major universities and museums in the country employ at least one vertebrate paleontologist. Many important fossil mammal localities have been found by geologists and others whose primary interest was not paleontological, and it is important that any site found be sampled and reported to a professional vertebrate paleontologist. Fossil mammals are so useful chronologically that time spent collecting them will almost certainly be rewarded.

It is impossible to review all of the important characteristics of mammals in a brief survey like this. Many books have been devoted to living and fossil mammals. I have found Romer (1966) to give the most balanced introduction and overview. Other books and monographs surveying living and fossil mammals include Colbert (1969), Eisenberg

TABLE 2 -- Sequence of North American land-mammal ages employed in subdividing Cenozoic time. Radiometric ages are subject to almost constant revision, but this sequence of land-mammal ages has been reasonably stable for many years. Ages are given in million years (m.y.) before present, following Berggren (1972).

Radiometric age	Cenozoic epoch	Land-mammal age
present		
		Rancholabrean
	Pleistocene	Irvingtonian
1.8 m.y.		Blancan
	Pliocene	
5.0 m.y.		Hemphillian
		Clarendonian
	Miocene	Barstovian
		Hemingfordian
22.5 m.y.		Arikareean
	Oligocene	Orellan
		Chadronian
37.5 m.y.		Duchesnian
		Uintan
	Eocene	Bridgerian
		Wasatchian
53.5 m.y.		Clarkforkian
		Tiffanian
	Paleocene	Torrejonian
		Puercan
65 m.y.		

(1981), Hall (1981), Jerison (1973), Kurtén (1968, 1972), Kurtén and Anderson (1980), Lawlor (1979), Lillegraven et al. (1979), Nowak and Paradiso (1983), Paula Couto (1979), Piveteau (1957-1961), Savage and Russell (1983), Scott (1937), Simpson (1945), Thenius (1969), Vaughn (1978), and Young (1975). My purpose here is to outline three subjects fundamental for understanding mammalian history that are rarely treated in text or reference works: the biostratigraphic basis of mammalian phylogeny, the influence of geography and climate on mammalian diversification, and the form and function of mammalian teeth.

OUTLINE OF MAMMALIAN PHYLOGENY

The first bones of fossil mammals were described and illustrated in the seventeenth century (when they were sometimes mistaken for relics of giants!). Scientific study of fossil mammals progressed slowly. By the late eighteenth century, Georges Cuvier, widely acknowledged as the "father of comparative anatomy," was aware of several geological formations in the Paris Basin yielding skulls and skeletons of mammals. Studying these, he achieved a "most remarkable and most astounding result ... the older the strata in which these bones are found, the more they differ from those of animals living today." This was the time when William Smith in Britain, with Cuvier, Lamarck, and others in France, established the principal of faunal succession and correlation in the geological record, a principal that lies at the heart of empirical evidence for evolution.

The stratigraphic distribution of fossils is as important for understanding mammalian phylogeny today as it was in Cuvier's time. Fossils will never provide a complete evolutionary history for any group of organisms, but it is true too that little or nothing can be learned of evolutionary history without fossils. Comparative morphology, in the widest sense, depends on the sequence of appearance of new taxa, with associated morphological innovations, in the fossil record. The broad outline of phylogeny at any taxonomic level is determined by the pattern of phenetic linking of living and extinct taxa over time. The phylogeny of mammals shown diagrammatically in Figure 2 is an example. Here living orders are traced back in time by linking successive species, genera, and families that exhibit characteristic features of each order.

Some pairs of orders, like Lagomorpha and Rodentia, Dermoptera and Primates, Chiroptera and Insectivora, or Proboscidea and Sirenia appear to converge in the early Cenozoic, an indication of close phyletic relationship. Other orders, like Cetacea and Artiodactyla, converge with a common archaic order, here Condylarthra. On a broader scale, Metatheria (marsupials) and Eutheria (placentals) have a long history of independence since the mid or late Cretaceous. There is now some question that mid Cretaceous Holoclemensia and Pappotherium represent an early marsupial and an early placental, respectively (both are known from limited dental material of "metatherian-eutherian grade", Lillegraven et al., 1979), but the metatherian-eutherian divergence must have occurred in mid Cretaceous time or soon thereafter. Marsupials and placentals were clearly distinct in the late Cretaceous, by which time each group included some moderate diversity. Prototheria (monotremes) have a very limited fossil record. Comparing living monotremes to other taxa in the phylogeny outlined here, they appear likely to represent a very early divergence from other mammals. Multituberculata too represent a divergently specialized order of uncertain relationship to other mammals. The earliest mammals, of latest Triassic or early Jurassic age, include several distinct groups. The triconodont Eozostrodon represents the most primitive structural grade in terms of dental evolution. Kuehneotherium is a contemporary but more advanced symmetrodont. Haramiyids may be ancestral to multituberculates.

The advantage of organizing information about phylogeny in a traditional "stratophenetic" diagram like that in Figure 2 is threefold: (1) temporal relationships as well as morphological similarity of all taxa are shown simultaneously, (2) progressive divergence of form over time, direct evidence of descent with modification from a common ancestor of appropriate taxonomic rank, is easily shown diagrammatically, and (3) regions where historical evidence is lacking, gaps in the fossil record, are clearly identified. Current

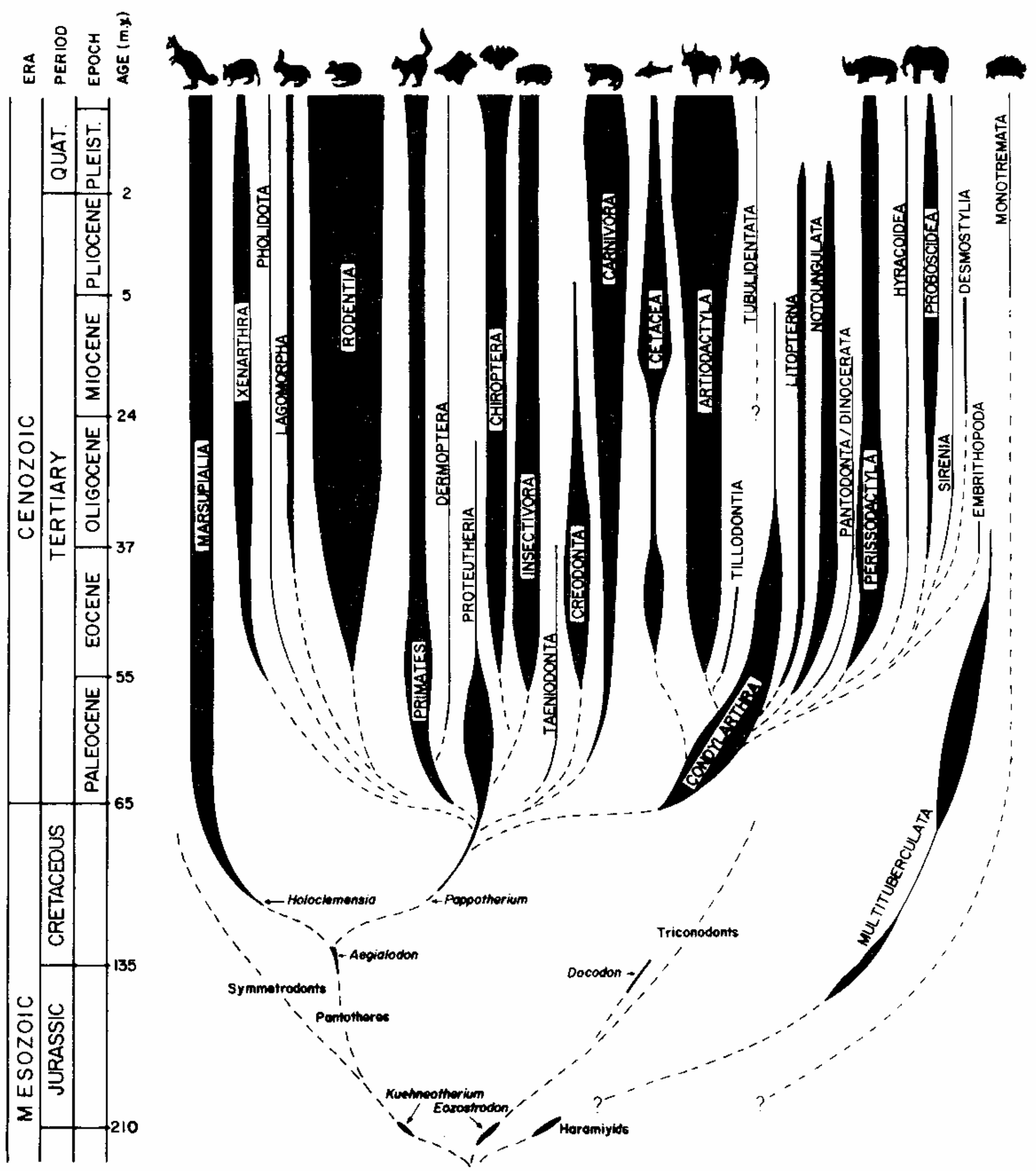

Figure 2-- Outline of mammalian phylogeny based on fossil record. Width of bars approximates number of genera in the fossil record for each order. Vertical axis, time, is nonlinear. Note appearance of most modern orders of mammals at or near the Paleocene-Eocene boundary. Reproduced with modification from Gingerich (1977), based on information in Romer (1966).

understanding of hypothesized relationships, and the evidence on which such hypotheses are based, are evident at a glance. Problematical relationships can be tested cladistically within the context of the whole outline. The morphology of soft tissues known only in living

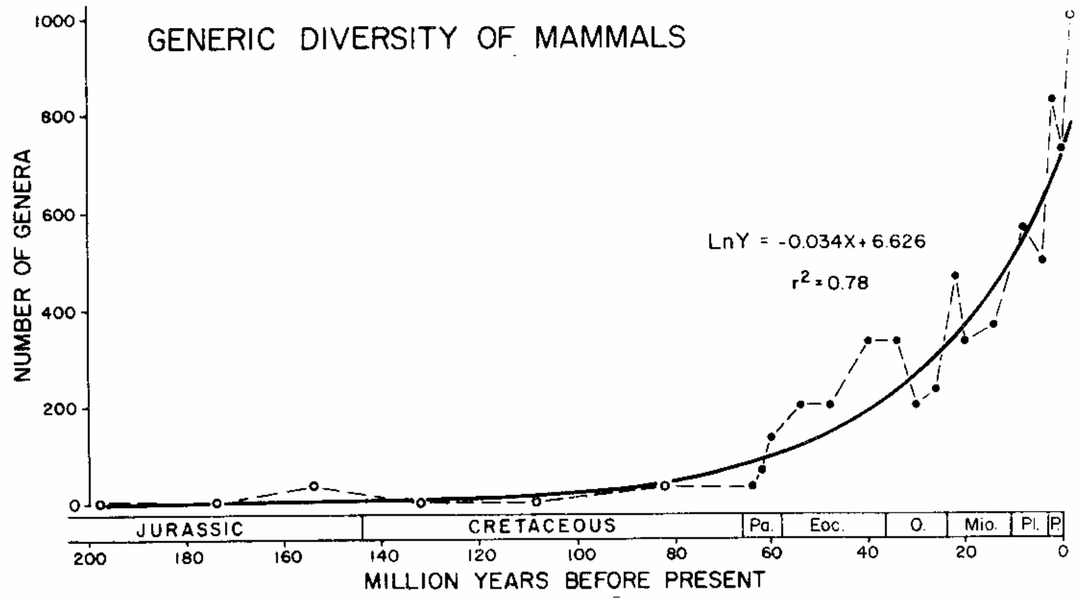

Figure 3-- Apparent history of diversification of mammals, based on worldwide generic diversity in the Cenozoic (data from Romer, 1966). Cenozoic record predicts about 750 genera should be living today, compared with 1010 extant genera known (Honacki et al., 1982). Cenozoic record accurately predicts low diversity observed in Mesozoic. Geological age is a better predictor of generic diversity than any other factor, and the observed pattern reflects the strong bias inherent in viewing change from modern perspective (as well as any actual increase in diversity).

animals becomes truly comparative when interpreted in light of an independent phylogeny based on historical information. Such an outline provides an independent historical basis for testing ideas about molecular evolution as well -- and evidence now accumulating suggests that linear molecular clocks are too simplistic to represent branching times in mammalian phylogeny with acceptable accuracy (Radinsky, 1978).

The representation of diversity shown in Figure 2 is partially quantitative in the sense that the width of each bar is roughly proportional to the relative abundance of genera inferred for each order at any given time. However, plotting generic diversity for each of the Cenozoic subepochs reveals a surprising pattern (Figure 3). Well collected and studied latest Cretaceous faunas from Wyoming and Montana typically contain only 20-30 mammalian species (Archibald, 1982), while those of the middle Paleocene contain 50-60 mammalian species (Rose, 1981a), an essentially modern level of diversity. This marked increase in diversity, known to have occurred at the beginning of the Cenozoic, is not reflected at all in worldwide generic levels plotted in Figure 3. Judging from Figure 3, there was a slow, steady exponential increase in worldwide generic diversity throughout the Cenozoic, a trend that accurately predicts observed diversity during the Jurassic and Cretaceous, and comes close to predicting modern generic diversity.

This pattern exhibits what Raup (1978) has called the "pull of the Recent": it is impossible to separate a true pattern of increasing generic diversity from the bias imposed by studying such a pattern entirely in hindsight. The older a mammalian fauna is geologically, the less adequately it is likely to be known because of increasingly limited worldwide exposure of sediments containing the fauna and a host of other prejudicial factors. Hence quantitative patterns involving changing diversity must always be viewed with some skepticism.

CLIMATE AND GEOGRAPHY

There is no comprehensive theory, as yet, relating mammalian diversification to climate and geography. However, it is becoming increasingly clear that climate and geography have played a major role in producing the diversity we see today. Mean annual temperature and the seasonality of climate changed markedly during the Cenozoic, and continental positions shifted significantly as well. The effect was kaleidoscopic: ranges shifted constantly, and genera and species were combined and recombined successively in changing associations. The extrinsic environment governing rates and patterns of mammalian evolution was rarely stable.

Five major cooling events dominate climatic history on a worldwide scale during the past 100 m.y. These occurred (1) near the end of the Cretaceous period, (2) near the end of the Paleocene, (3) at the Eocene-Oligocene boundary or early in the Oligocene (lasting through much of this epoch), (4) near the end of the Miocene, and (5) repeatedly during the Pleistocene (Buchardt, 1978; Frakes, 1979; Hickey, 1981; Savin, 1977; Wolfe, 1978). These events serve to define, generally if not exactly, the boundaries of Cenozoic epochs. Predictably, cooling events on this scale all had a significant effect on mammalian faunal evolution. The major radiation of placental mammals at the beginning of the Paleocene coincides with climatic warming following the first major cooling event. Modern orders of mammals appear during climatic warming following the second cooling event, when Eocene faunas replaced archaic Paleocene faunas. Many modern families of mammals appeared during climatic warming following the third cooling event, the <u>Grande Coupure</u> of Stehlin (1909), at or near the Eocene-Oligocene boundary. Climates became more seasonal, artiodactyls replaced perissodactyls as dominant herbivores on the northern continents, and modern whales replaced archaeocetes in world oceans. The fourth cooling event, widely known as the Messinian crisis, witnessed emergence of Bovidae among artiodactyls, and Cercopithecidae and Hominidae among primates as dominant savanna herbivores in the Old World. Apes, widely distributed throughout the Old World during the Miocene, disappeared or became much more restricted in distribution. The "Great American Interchange" of North American and South American faunas (Webb, 1976) occurred during climatic warming following the Messinian crisis. Successive Pleistocene glaciations were accompanied by rapid diversification, with unusually high rates of origination and extinction of mammalian taxa.

South America and Australia each separated from Antarctica during the late Cretaceous or early Cenozoic, and the Indian subcontinent came into contact with Eurasia sometime in the early Cenozoic. North America, Europe, and Asia were all in contact at high latitudes through the Paleocene and earliest Eocene. The configuration of continents was one of north-south pairs spanning the tropics (North America-South America, Asia-India, Europe-Africa) interconnected by land bridges only at high latitudes. High latitude land bridges are more accessible to mammals during intervals of warmer climate. Thus climatic fluctuations would serve to expand or restrict ranges of taxa within each north-south pair of continents, and to open and close connections between continental pairs. The effect may have been somewhat like that postulated by Moore (1955) and Valentine (1968) for evolution in the marine realm. Times of climatic cooling, with associated restriction and latitudinal stratification of geographic ranges, should be times of enhanced competition, leading to morphological divergence and major innovation. The predicted result would be evolution of highly endemic mammalian faunas in the tropical belts on each pair of continents, with further endemic differentiation at higher northern and southern latitudes. Times of climatic warming, with associated expansion of all geographic ranges, should be times of reduced competition, with little morphological divergence or innovation. The principal feature associated with climatic warming should be development of a cosmopolitan mammalian fauna in the northern hemisphere, where intermixing of faunas between continents was possible, and continued endemism in the southern hemisphere, where oceanic barriers prevented mixing. Climatic fluctuations continually pump diversity into the system as a whole, the process being more effective in northern faunas where intercontinental mixing provides additional morphological and taxonomic raw material for evolution.

FORM AND FUNCTION OF MAMMALIAN TEETH

As noted above, the hardness, density, and morphological complexity of mammalian teeth, and the close correlation of tooth size with body size, make teeth extraordinarily valuable in paleomammalogy. One must know something of the form and function of mammalian teeth to understand much of the evidence on which mammalian history is based. Living monotremes lack functional teeth as adults, they have little in the way of a fossil record, and consequently nothing is known of their dental history. Other mammals generally have four classes of teeth in each jaw. The most anterior teeth, usually simple in form, are called incisors. Upper incisors always develop and erupt in a bone called the premaxilla. Lower incisors develop in the dentary and occlude with the upper incisors. Generalized mammals have a single large tooth with a simple conical crown following the upper and lower incisors. The upper canine is the most anterior tooth to develop and erupt in the maxilla. The lower canine develops in the dentary behind the lower incisors and occludes just in front of the upper canine. Teeth immediately behind the upper and lower canines are called premolars. These usually become increasingly molariform in structure posteriorly along the tooth row.

Premolars and molars function as an integrated unit, and they are often collectively labelled "cheek teeth." As a rule, incisors, canines, and premolars (at least the most posterior premolars) have deciduous precursors ("baby teeth"), that are shed early in life. Molars have no deciduous precursors, and they do not erupt until an animal begins to reach its definitive body size. As a rule of thumb, upper molars usually have square crowns with three roots, while lower molars have narrower rectangular crowns with only two roots. The number of teeth in each class (incisors, canines, premolars, molars) is summarized in a dental formula, written I5/4, C1/1, P3/3, M4/4 in the common opossum Didelphis, a generalized marsupial. Upper teeth are counted above the diagonal, and lower teeth below. By comparison, generalized placentals have a dental formula of I3/3, C1/1, P4/4, M3/3. Counting left and right sides, the total number of teeth is 50 in Didelphis, and 44 in a generalized placental. An individual tooth may be referred to by position within its class, e.g., P3/ would be an upper third premolar, M/1 would be a lower first molar, etc.

Marsupials and placentals are both derived from Cretaceous therian mammals with tritubercular or tribosphenic cheek teeth, that is, both upper and lower molars have three prominent tubercles or cusps. On upper molars these form what is called a trigon, consisting of a medial protocone, anterior paracone, and posterior metacone. On lower molars these form what is called a trigonid, consisting of a lateral protoconid, anterior paraconid, and posterior metaconid. The fourth cusp, if present, is almost always directly behind the protocone or protoconid, and it is called a hypocone or hypoconid, depending on whether one is dealing with an upper or lower molar. A fifth cusp, the entoconid is often present on lower molars. The entoconid and hypoconid together enclose a heel or talonid posterior to the trigonid (see diagram in Figure 4). The trigons and hypocones on successive upper molars form a series of triangles that interlock in occlusion with a reversed series of triangles formed by the trigonid, hypoconid, and entoconid on lower molars. Upper and lower cheek teeth occlude in a number of different ways, corresponding to one of three specialized functions discussed below. The fossil record demonstrates beyond question that the enormous diversity of molar types characteristic of different living mammals is derived from a simple tritubercular plan common to marsupials and placentals. The better one understands this basic plan and possible modifications of it, the easier it is to recognize different functional and taxonomic groups of mammals.

Dental form and function can be approached by comparing teeth of different taxonomic and dietary groups. It can also be approached through detailed examination of polished and striated wear facets formed by occlusion of dental elements during function. These are visible to the naked eye on the teeth of large mammals, and they can be studied using a binocular microscope or scanning electron microscope on smaller mammals. A striated wear surface results when teeth occlude repeatedly in a regular pattern, and striations indicate the direction of jaw motion producing wear. Two or three different sets of wear facets can usually be distinguished on the molars of generalized mammals,

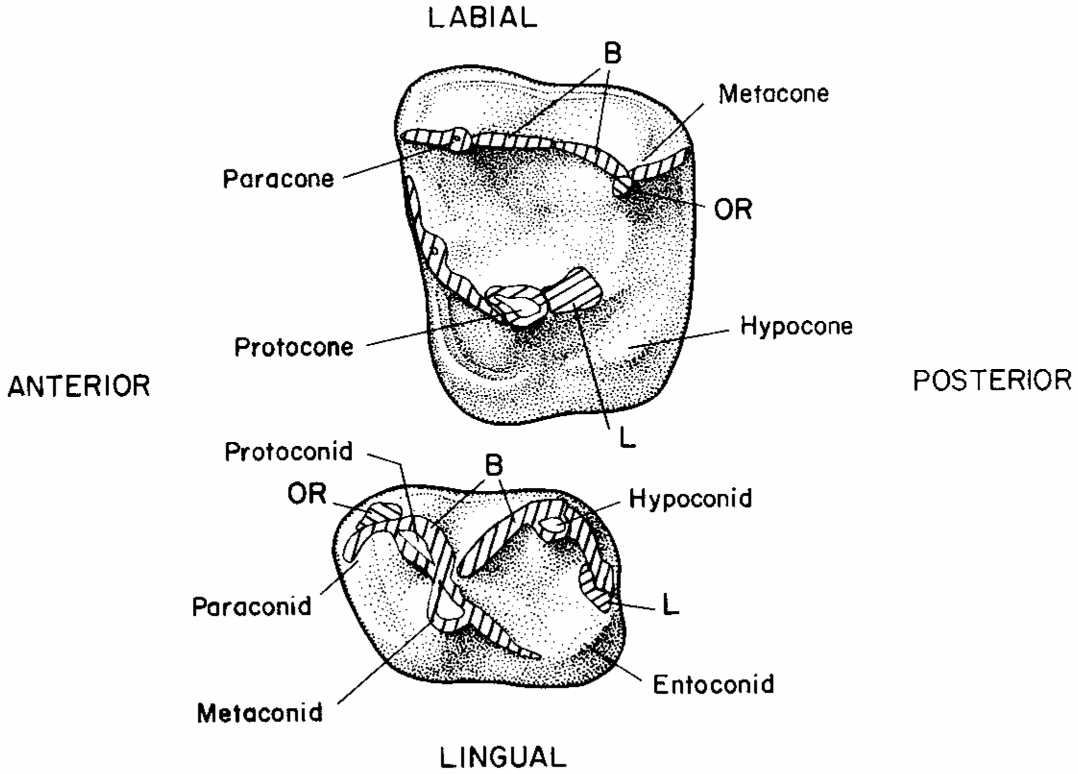

Figure 4-- Upper and lower molars (left M1/ and right M/1) of Eocene primate Adapis parisiensis showing the principal cusps, crests, basined areas, and wear pattern of a generalized marsupial or placental. Orthal retraction wear facets (OR) are associated with sharp cusps, buccal phase facets (B) are present on shearing crests, and lingual phase facets (L) are found where planar surfaces contact during crushing and grinding. After Gingerich (1972).

indicating two or three different modes of occlusion requiring different directions of jaw movement. Three modes of occlusion may occur in species exhibiting only two sets of wear facets if one of the modes requires no tooth-on-tooth occlusion. Experimental studies of living opossums, insectivores, bats, primates, and rodents (e.g., Crompton and Hiiemae, 1970; Kallen and Gans, 1972; Kay and Hiiemae, 1974; Weijs, 1975; Crompton and Parker, 1978) have largely confirmed this pattern.

Mammals with a generalized dentition have molars with three principal features arranged in such a way that they can function independently in occlusion: (1) cusps or points, connected by (2) crests or lines, enclosing (3) broad basined areas or planes. The geometric progression from points to lines to planes is as simple as it could possibly be. A pair of cubes can be used to illustrate all of these features and how they function in occlusion (point to point, edge to edge, and surface to surface). Points puncture, crests shear, and planar surfaces crush and grind. Occlusion of upper and lower molars against each other during mastication produces three distinct sets of wear facets, each set being associated with cusps, crests, or basins, respectively. Fine striations

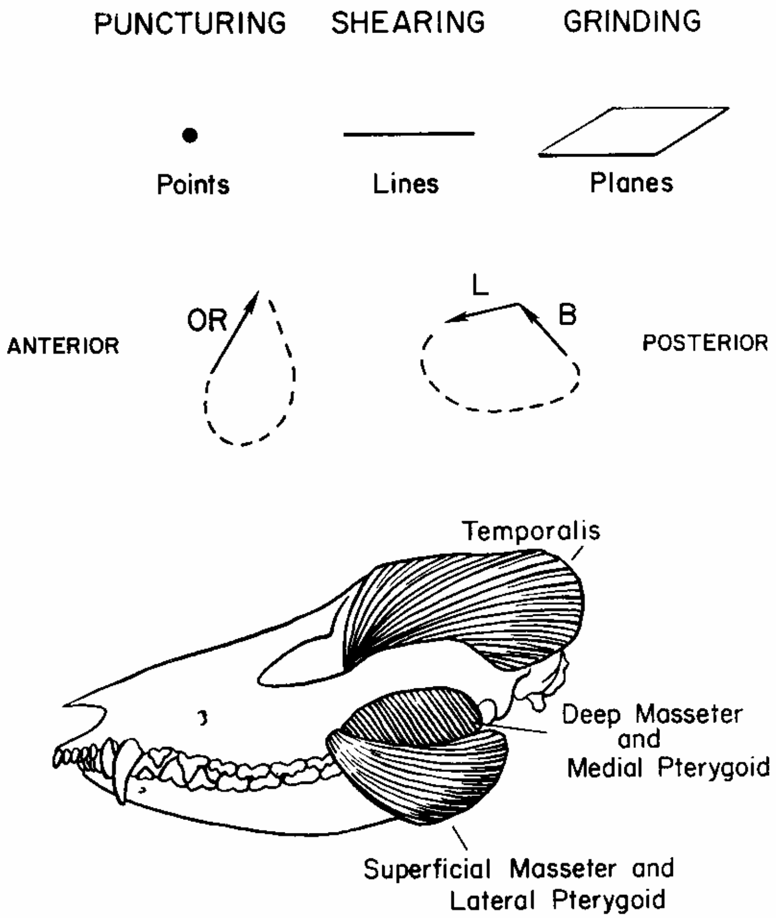

Figure 5-- Relationship of morphological features on the molars of mammals to their function in mastication and to the muscles producing coordinated jaw movements. Initially, puncturing is performed by pointed cusps during orthal retraction (OR), when the dentary is pulled upward and backward by the temporalis and other muscles. Subsequently, shearing is performed by linear crests during the buccal phase (B, phase 1), when the dentary moves upward and forward. Grinding takes place between planar surfaces during the lingual phase (L, phase 2), a continuation of the buccal phase cycle, when the dentary moves forward and downward out of occlusion. The buccal and lingual phases of occlusion are powered largely by deep masseter and medial pterygoid, and superficial masseter and lateral pterygoid muscles, respectively, pulling in the direction of jaw movement.

on the facets indicate that each set is produced by movement in a different direction during function: orthal retraction (OR) facets are produced by moving projecting cusps on lower teeth up and back against corresponding features on upper teeth, buccal phase (B, phase 1) facets are produced by moving crests on lower teeth up and forward against corresponding features on upper teeth, and lingual phase (L, phase 2) facets are produced by moving planar areas on lower teeth forward and down against corresponding features on upper teeth. A characteristic pattern of distribution of wear facets is illustrated in Figure 4.

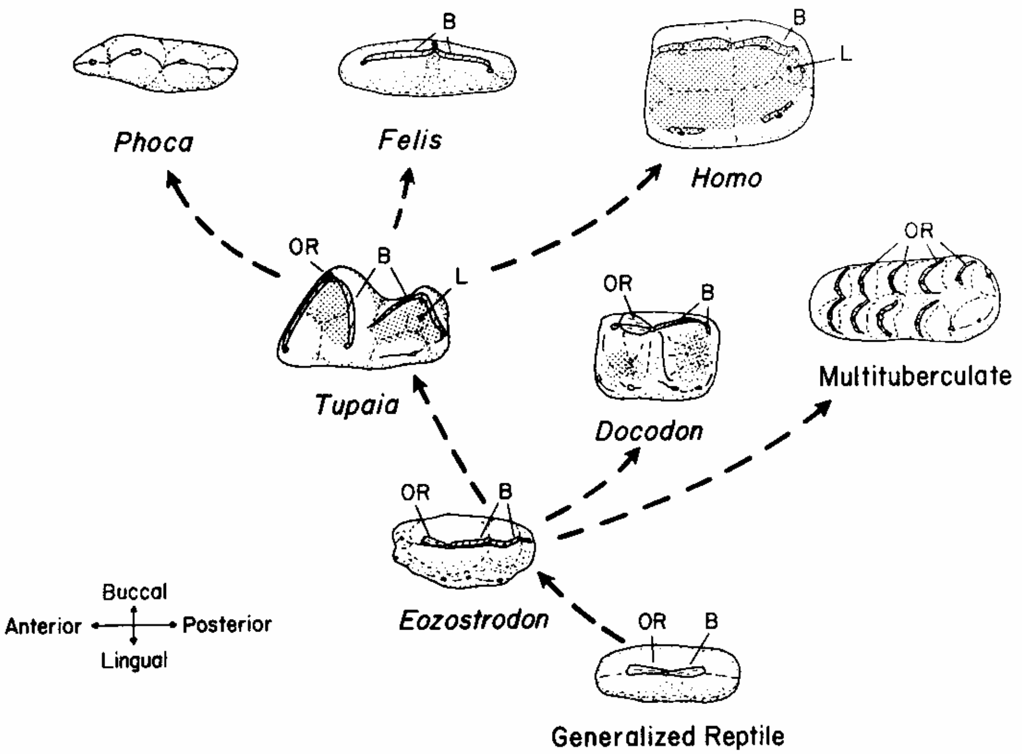

Figure 6-- Outline of the adaptive radiation of molar form and function in mammals, interpreting functional patterns observed in Figures 4 and 5 in light of the phylogeny of mammals outlined in Figure 2. Note addition of lingual phase (L) of grinding occlusion in generalized therians, here represented by Tupaia. Reproduced from Gingerich (1977c).

Incisors and canines serve principally in the acquisition of food, biting off large pieces or gathering small pieces for ingestion. Premolars and molars may be considered as a single functional unit for processing food. As a rule, anterior premolars are simple pointed puncturing teeth, intermediate premolars and molars combine puncturing, shearing, and grinding features, while posterior molars specialized for crushing and grinding often have flat surfaces. Food ingested at the front of the mouth is punctured, then punctured and sheared, then sheared, crushed, and ground before being swallowed at the back of the mouth. A typical masticatory sequence can be illustrated by chewing a carrot or other resistant food. A bite acquired with the incisors is first reduced by puncturing and splitting it with the premolars, splitting and shearing it with the premolars and molars, and then crushing it and grinding it with the molars. Two distinct masticatory stages are involved. During the first, the puncturing stage, the lower jaw is drawn upward and backward (OR mentioned above) through as many cycles as necessary to reduce the food for shearing and grinding. During the second, the shearing and grinding stage, the lower jaw is drawn upward and forward (B mentioned above) then forward and slightly downward (L mentioned above) through a number of cycles before the food, now finely divided for digestion, is swallowed. The entire process is summarized in Figure 5.

The functional progression generalized mammals use in puncturing, shearing, and grinding food to prepare it for digestion can also be seen in the order functional features are added to mammalian teeth during their evolution (Figure 6). Most reptiles have simple conical teeth capable of holding or sometimes puncturing vegetation and animal prey as the lower jaw is moved up and forward or up and backward, but reptiles, as a rule, lack precise functional occlusion of upper and lower cheek teeth. Triconodont mammals, like Eozostrodon, show clear evidence of two distinct modes of occlusion: puncturing associated with upward and backward movement of the lower jaw (OR), and shearing associated with upward and forward movement of the lower jaw (B). These two modes are elaborated in docodonts. A third occlusal mode involving grinding (L) is first added in therians, with addition of a hypoconulid cusp on the talonid of lower molars. All three modes are present in generalized therians like the tree shrew Tupaia. Mammals today exhibit a wide range of dental morphology involving specialization for puncturing (e.g., simple pointed molars of the seal Phoca), shearing (e.g., linear carnassials of the cat Felis), and grinding (e.g., flat molars with large planar occlusal surfaces of humans). Shearing in modern mammals, whether rodents, artiodactyls like the ox (Figure 1), or elephants, invariably takes place during an upward and forward movement of the lower jaw, powered largely by the masseter and pterygoid muscles. Modern herbivores are masseter-pterygoid dominated.

Multituberculates, an important but divergent group already distinct from other mammals in the Jurassic, evidently separated from modern mammals before the masseter-pterygoid complex of jaw muscles became associated with shearing occlusion. Multituberculates chewed backwards by comparison with modern counterparts. Mastication in multituberculates involved moving the lower jaw upward and backward rather than upward and forward (Krause, 1982a), a motion powered largely by the temporalis complex of jaw muscles rather than the masseter-pterygoid complex. Multituberculates are exceptional, however, and virtually all therian mammals conform to a highly stereotyped pattern of occlusion and mastication. Some are divergently specialized to be sure, but even the specialized forms can be explained in terms of a common underlying pattern of form and function.

Acknowledgments-- I thank Dr. B. H. Smith for reading the text. Figures 1, 3, 4, and 5 were prepared by Karen Klitz with support from National Science Foundation grant DEB 82-06242.

REFERENCES

ARCHIBALD, J. D. 1982. A study of Mammalia and geology across the Cretaceous - Tertiary boundary in Garfield County, Montana. University of California Publications in Geological Sciences, 122:

BERGGREN, W. A. 1972. A Cenozoic time-scale -- some implications for regional geology and paleobiology. Lethaia, Oslo, 5: 195-215.

BUCHARDT, B. 1978. Oxygen isotope palaeotemperatures from the Tertiary period in the North Sea area. Nature, London, 275: 121-123.

COLBERT, E. H. 1969. Evolution of the Vertebrates, 2nd Edition. John Wiley and Sons, New York, 479 pp.

CORBET, G. B. and J. E. HILL. 1980. A World List of Mammalian Species. British Museum (Natural History), London, 226 pp.

CROMPTON, A. W. and K. M. HIIEMAE. 1970. Molar occlusion and mandibular movements during occlusion in the American opossum, *Didelphis marsupialis* L. Zoological Journal of the Linnean Society, 49: 21-47.

CROMPTON, A. W. and P. PARKER. 1978. Evolution of the mammalian masticatory apparatus. American Scientist, 66: 192-201.

DORR, J. A. and P. D. GINGERICH. 1980. Early Cenozoic mammalian paleontology, geologic structure, and tectonic history in the overthrust belt near LaBarge, western. Contributions to Geology, University of Wyoming, 18: 101-115.

EISENBERG, J. F. 1981. The Mammalian Radiations: an Analysis of Trends in Evolution, Adaptation, and Behavior. University of Chicago Press, Chicago, 610 pp.

FLOWER, W. H. and R. LYDEKKER. 1891. An Introduction to the Study of Mammals Living and Extinct. Adam and Charles Black, London, 763 pp.

FRAKES, L. A. 1979. Climates Throughout Geologic Time. Elsevier Scientific Publishing Co., Amsterdam, 310 pp.

GINGERICH, P. D. 1972. Molar occlusion and jaw mechanics of the Eocene primate *Adapis*. American Journal of Physical Anthropology, 36: 359-368.

GINGERICH, P. D. 1977. Patterns of evolution in the mammalian fossil record. In A. Hallam (ed.), Patterns of Evolution as Illustrated by the Fossil Record, Elsevier Scientific, Amsterdam, pp. 469-500.

GINGERICH, P. D. 1983. Paleocene-Eocene faunal zones and a preliminary analysis of Laramide structural deformation in the Clarks Fork Basin, Wyoming. Wyoming Geological Association Guidebook, 34: 185-195.

HALL, E. R. 1981. The Mammals of North America, 2nd Edition. John Wiley and Sons, New York, 1181 pp.

HIBBARD, C. W. 1949. Techniques of collecting microvertebrate fossils. Contributions from the Museum of Paleontology, University of Michigan, 8: 7-19.

HICKEY, L. J. 1981. Land plant evidence compatable with gradual, not catastrophic change at the end of the Cretaceous. Nature, London, 292: 529-531.

HONACKI, J. H., K. E. KINMAN, and J. W. KOEPPL. 1982. Mammal Species of the World: A Taxonomic and Geographic Reference. Association of Systematics Collections and Allen Press, Lawrence, Kansas, 694 pp.

KALLEN, F. C. and C. GANS. 1972. Mastication in the little brown bat, *Myotis lucifugus*. Journal of Morphology, 136: 385-420.

KAY, R. F. and K. M. HIIEMAE. 1974. Jaw movement and tooth use in recent and fossil primates. American Journal of Physical Anthropology, 40: 227-256.

KRAUSE, D. W. 1982. Jaw movement, dental function and diet in the Paleocene multituberculate *Ptilodus*. Paleobiology, 8: 265-281.

KURTÉN, B. 1968. Pleistocene Mammals of Europe. Weidenfeld and Nicolson 317, London,

KURTÉN, B. 1971. The Age of Mammals. Columbia University Press 250, New York,

KURTÉN, B. and E. ANDERSON. 1980. Pleistocene Mammals of North America. Columbia University Press, New York, 442 pp.

LAWLOR, T. E. 1979. Handbook to the Orders and Families of Living Mammals. Mad River Press, Eureka, California, 327 pp.

LILLEGRAVEN, J. A., Z. KIELAN-JAWOROWSKA, and W. A. CLEMENS (eds.). 1979. Mesozoic mammals: the first two-thirds of mammalian history, University of California Press, Berkeley, 311 pp.

MCKENNA, M. C. 1962. Collecting small fossils by washing and screening. Curator, 3: 221-235.

MCKENNA, M. C. 1975. Toward a phylogenetic classification of the Mammalia. In W. P. Luckett and F. S. Szalay (eds.), Phylogeny of the Primates, Plenum Publishing Corporation, New York, pp. 21-46.

MOORE, R. C. 1955. Expansion and contraction of shallow seas as a causal factor in evolution. Evolution, 9: 482-483.

NOWAK, R. M. and J. L. PARADISO. 1983. Walker's Mammals of the World, 4th Edition. Johns Hopkins University Press, Baltimore, 1362 pp.

PAULA COUTO, C. D. 1979. Tratado De Paleomastozoologia. Academia Brasileira de Ciencias, Rio de Janeiro, 590 pp.

PIVETEAU, J. (ed.). 1957-1961. Mammifères, Primates, Homme. Traité de Paléontologie 6(1), 6(2), 7, Masson, Paris, 1138, 962, 675 pp.

RADINSKY, L. B. 1978. Do albumin clocks run on time? Science, 200: 1182-1183.

RAUP, D. M. 1978. Cohort analysis of generic survivorship. Paleobiology, 4: 1-15.

ROMER, A. S. 1966. Vertebrate Paleontology. Third Edition. University of Chicago Press 468, Chicago,

ROSE, K. D. 1981. The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene-Eocene boundary. University of Michigan Papers on Paleontology, 26: 1-197.

SAVAGE, D. E. and D. E. RUSSELL. 1983. Mammalian Paleofaunas of the World. Addison-Wesley 432, London,

SAVIN, S. M. 1977. The history of the earth's surface temperature during the past 100 million years. Annual Review of Earth and Planetary Sciences, 5: 319-355.

SCOTT, W. B. 1937. A History of Land Mammals in the Western Hemisphere, 2nd Edition. Macmillan, New York, 786 pp.

SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History, 85: 1-350.

STEHLIN, H. G. 1909. Remarques sur les faunules de mammifères des couches Éocènes et Oligocènes du Bassin de Paris. Bulletin de la Société Géologique de France, Série 4, 9: 488-520.

THENIUS, E. 1969. Stammesgeschichte Der Säugetiere, Handbuch Der Zoologie 8 (47-48). 722 pp.

VALENTINE, J. W. 1968. Climatic regulation of species diversification and extinction. Geological Society of America Bulletin, 79: 273-276.

VAUGHAN, T. A. 1978. Mammalogy, 2nd Edition. Saunders, Philadelphia, 522 pp.

WEBB, S. D. 1976. Mammalian faunal dynamics of the great American interchange. Paleobiology, 2: 220-234.

WEIJS, W. A. 1975. Manibular movements of the albino rat during feeding. Journal of Morphology, 145: 107-124.

WOLFE, J. A. 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. American Scientist, 66: 694-703.

WOOD, H. E., R. W. CHANEY, J. CLARK, E. H. COLBERT, G. L. JEPSEN, J. B. REESIDE, and C. STOCK. 1941. Nomenclature and correlation of the North American continental Tertiary. Bulletin of the Geological Society of America, 52: 1-48.

YOUNG, J. Z. 1975. The Life of Mammals. Their Anatomy and Physiology. Second Edition. Clarendon Press, Oxford, 820 pp.