EVOLUTIONARY PATTERNS   ✻10137
IN EARLY CENOZOIC MAMMALS

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INTRODUCTION

Life in the past was different. This is one of the most important empirical generalizations we can draw from three centuries of inquiry into the nature of fossils. By 1859, when Charles Darwin published *The Origin of Species*, evolution itself was not in question. Darwin's contribution was in understanding the mechanism: natural selection. Earlier efforts of Lamarck, Smith, Cuvier, Lyell, and Darwin himself had already established beyond doubt that life changed through time. They had no *a priori* reason to expect this but all were at some time in their career paleontologists, and all had observed firsthand the petrified remains of forms now extinct. William Smith's principle of faunal succession and correlation lies at the heart of biostratigraphy—it is also at the core of empirical evidence for evolution.

The study of organic evolution is both a geological and a biological subject. Evolution means change, change implies time, and the great sweep of life history is recorded in sedimentary rocks and measured in geological time. There are two components of organic evolution: earth history records a general increase in both the *complexity* and the *diversity* of life. Each corresponds to a mode of speciation. The first can be explained by progressive change within a single lineage. The second requires a multiplication of lineages. We know that the study of genetics, ecology, behavior, biogeography, and morphology of living animals is all necessary for understanding the evolutionary process, but this is not sufficient. Fundamental questions persist about the origin and nature of species that can only be answered by more detailed study of the historical record.

In this paper I want to review the nature of the early Cenozoic record of mammalian evolution because it illustrates both the potential and limitation of the fossil record for contributing to a better under-

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standing of evolution at the species and faunal level. Since the most detailed record of Paleocene and Eocene mammalian evolution discovered to date is in the Clark's Fork Basin and the Big Horn Basin of Wyoming, most of the following discussion will be illustrated by examples documented there.

OUTLINE OF FAUNAL HISTORY

Dinosaurs became extinct at the end of the Cretaceous and their role in terrestrial ecosystems was rapidly filled by mammals as the Cenozoic "age of mammals" began. Paleocene mammalian faunas are dominated by archaic orders: Multituberculata, Proteutheria, Condylarthra, and plesiadapiform Primates. In contrast, Eocene mammalian faunas are dominated by modern orders: Insectivora, Chiroptera, Rodentia, Artiodactyla, Perissodactyla, Cetacea, and modern Primates. Oligocene faunas differ from those of the Eocene in being composed not only of modern orders but principally of modern families as well.

Paleogeography and Paleoclimates

Geographically, most of the major continents were approximately in their present positions by the beginning of the Cenozoic (Smith & Briden 1977). Exceptions with an important bearing on mammalian distributions were 1. a high latitude land connection between North America and Europe severed in the early Eocene by final opening of the North Atlantic, 2. partial or complete separation of eastern from western Asia by the epicontinental Obik Sea, with a high latitude land connection between eastern Asia and North America, 3. isolation of Indo-Pakistan in the present Indian Ocean, and 4. contiguity of Antarctica and Australia at high latitudes in the southern hemisphere.

Within the early Cenozoic, there were several major climatic fluctuations. The first half of the Cenozoic (Paleocene-Eocene) was characterized by an equable climate and mean annual temperatures some 10°C warmer than those of the less equable second half of the Cenozoic (Oligocene to Recent). The first half of the Paleocene was relatively warm, with climates in western North America being "subtropical." The second half of the Paleocene was cooler, with "warm temperate" climates in western North America. The lowest mean annual temperature appears to have been in the early or middle part of the late Paleocene. From this point through the early Eocene there was a general if variable increase in mean annual temperature, accompanied by a pronounced drying trend, restoring "subtropical" climates to western North America (Wolfe 1978). About 33 Ma before present (at the

end of the Eoccne or in the early Oligocene, depending on which boundary definition is followed) there was a major climatic change with a geologically sudden worldwide decrease in mean annual temperature and a major decrease in equability. (Ma refers to a specific date; m.y. to duration.) This event had a profound effect on marine (Savin et al 1975) and continental temperatures, and on floras (Wolfe & Hopkins 1967) and faunas (Lopez & Thaler 1975). In Europe the profound terminal Eocene or early Oligocene break in mammalian faunas is termed the *Grande Coupure* (Stehlin 1909). In North America this break corresponds to an apparently less dramatic change from forest to savanna faunas between the middle and upper parts of the Chadron Formation (Clark & Beerbower 1967).

Faunal History

The combined effect of changing paleogeography and changing climate on early Cenozoic mammalian faunas was complex. Late Mesozoic and early Cenozoic high latitude land connections such as those between North America and Asia, North America and Europe (McKenna 1975), or South America-Antarctica-Australia (Cox 1973, Tedford 1974) were easily crossed only during periods of warm climate and low sea level, and the latter two routes were subsequently broken by major tectonic rifting opening the northern part of the North Atlantic and the southern Indian Ocean, respectively. Retreat of the epicontinental Obik Sea connected eastern and western Asia. Finally, joining a land mass as large as the Indo-Pakistan subcontinent to the remainder of Asia must have had a profound effect on mammalian faunas either in releasing a mammalian fauna long evolving in isolation (if India was previously colonized by mammals) or by opening an enormous "empty" land mass for colonization by Asian mammals, with the rapid evolutionary radiations and specializations that probably accompany such an invasion.

This discussion highlights the potential complexity of early Cenozoic mammalian evolution. At the same time, however complex, a better knowledge of the early Cenozoic is essential for understanding the radiation and diversification of mammals, our own order Primates included. Early Cenozoic mammalian faunas are still poorly known or entirely lacking for much of the world, exploration continues, and several important new faunas are discovered literally every year. It is also possible to study previously known areas more intensively to document patterns of faunal evolution in greater detail. The most complete record of mammalian evolution from the middle Paleocene through early Eocene is in the Clark's Fork Basin of Wyoming. This is a particularly interesting period in mammalian history because it spans the major late

Paleocene climatic cooling and subsequent warming, and it records the first appearance of most of the modern orders that dominate mammalian faunas today. Geologically this is an interesting period as well, because it coincides with the Laramide orogeny in western North America.

Figure 1 Biochronology of the Paleocene-Eocene transition in North America. Radiometric ages in million years before present (Ma) are from Berggren et al (1978). Tiffanian land mammal ages discussed in Gingerich (1976b), Clarkforkian extensively documented in Rose (1979), Wasatchian discussed by Savage (1977), Bridgerian reviewed by West (1976). Primate zones and biochrons documented in Figures 2 and 3. Subdivisions of land mammal ages corresponding to biochrons are listed in land mammal age column. Also shown are chronological ranges of sediments and faunas documented to date in the principal basins of the Western Interior. Right hand column shows approximate equivalence of Wasatchian subages based on first appearance of perissodactyl genera in the Clark's Fork, Big Horn, and Wind River basins.

Study of mammalian faunas in the Clark's Fork Basin is still in progress and the results presented here are incomplete, but they nevertheless serve to illustrate the potential contribution of detailed biostratigraphical studies for understanding evolution at the species level and at the faunal level.

Biostratigraphy

The Cenozoic time scale is subdivided into Epochs, and these are further divided into Ages. In North American continental sediments, land mammal "ages" have been defined based on faunas found primarily in the Western Interior (Wood et al 1941, Savage 1977). Each land mammal age has a duration of from 2 to 7 million years (Berggren et al 1978). Thus the land mammal ages themselves do not provide adequate resolution for detailed evolutionary study. In an attempt to provide a more detailed chronology for study of faunal evolution across the Paleocene-Eocene boundary, the Tiffanian, Clarkforkian, Wasatchian, and Bridgerian land mammal ages have been subdivided into biochrons based on successive species of rapidly evolving lineages of the primates *Plesiadapis*, *Pelycodus*, and *Notharctus* (Gingerich 1976b, 1979a, Gingerich & Simons 1977). These primate biochrons are listed in Figure 1. There is one gap between the ranges of *Plesiadapis* and *Pelycodus*, and the *Phenocodus-Ectocion* biochron is based on a zone of the same name in the upper Clarkforkian (Rose 1979).

The relationship of *Plesiadapis* biochrons to stratigraphy is illustrated in Figure 2. All of the *Plesiadapis* species shown, except *P. praecursor*, are now known from correlated measured sections in the Fort Union (Polecat Bench) and Willwood Formations on Polecat Bench and in the Clark's Fork Basin. *P. praecursor* is interpolated based on its occurrence between *Pronothodectes gidleyi* and *Plesiadapis anceps* in the Fort Union Formation of the Crazy Mountain Field of Montana, a northwesterly extension of the Clark's Fork Basin. Carpolestidae have also been used to refine the chronology of the middle and late Paleocene (Rose 1977), and an interpretation of carpolestid phylogeny is shown in Figure 2. In this case several of the species have been interpolated based on association with *Plesiadapis* in other basins (*Elphidotarsius shotgunensis* and *Carpodaptes hobackensis*, for example, have not been found in the Clark's Fork Basin or the Big Horn Basin).

The stratigraphic record of *Pelycodus* in the central Big Horn Basin and the sequence of *Notharctus* species in the Bridger Basin (Figure 3) provide the basis for the *Pelycodus-Notharctus* biochrons.

The total number of biochrons listed in Figure 1 is 16, and the time represented is approximately 12.5 m.y. (60 Ma to 47.5 Ma). Thus the
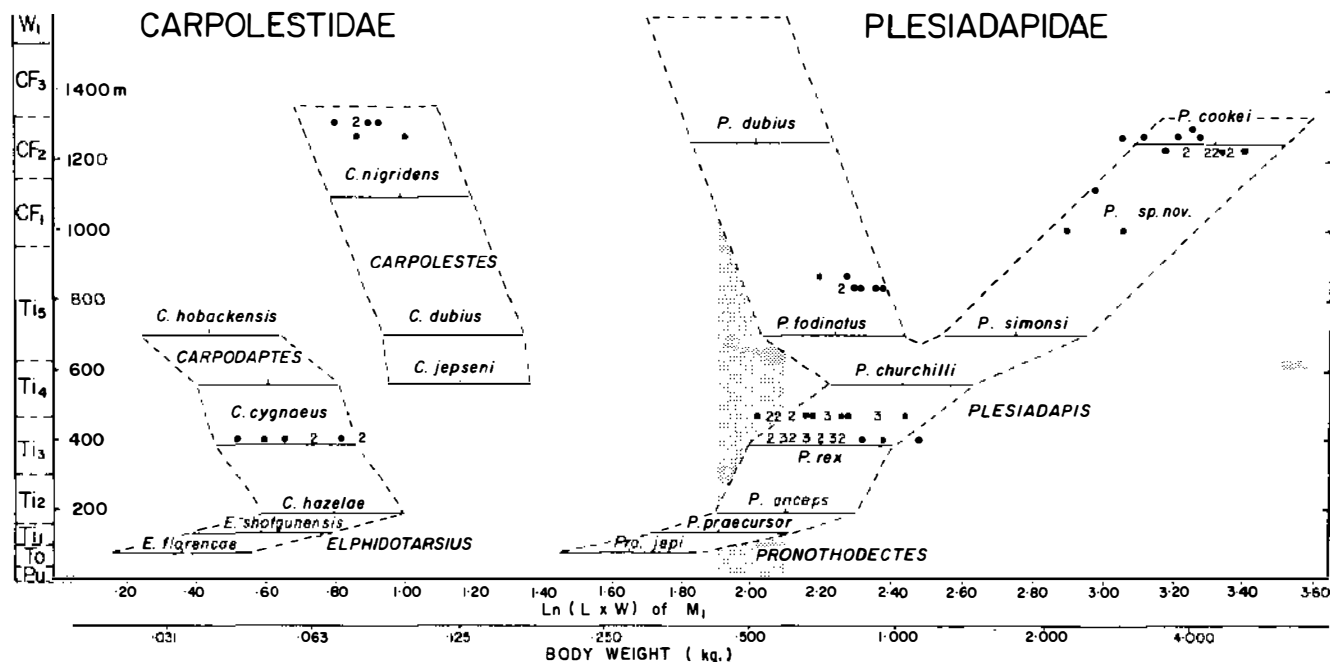
Figure 2 Stratigraphic distribution and interpreted phylogenetic relationships of North American Carpolestidae and Plesiadapidae. Ordinate is stratigraphic level (in meters) above Cretaceous-Tertiary boundary in Clark's Fork Basin, Wyoming, with appropriate *Plesiadapis* and *Pelycodus* biochrons indicated at left. Abscissa is standard measure of tooth size: Ln length multiplied by width of first lower molar (Gingerich 1976b). Solid lines with vertical slash are sample mean and expected ranges for largest sample of each species (carpolestid data from Rose 1975, Krause, 1978; plesiadapid data from Gingerich 1976b). *E. shotgunensis*, *C. hobackensis*, and *P. praecursor* interpolated: they are not yet known from the Clark's Fork Basin area. Dashed lines show phylogenetic hypotheses based on stratophenetic linking of published information. Both groups show progressive change in dental characters in addition to size changes shown here. New undescribed specimens collected recently are shown as solid circles, or small numerals in case of two or more specimens of same size. New specimens provide a test of the phylogeny and appear to corroborate it except for several minor adjustments in means and expected ranges. *Plesiadapis* sp. nov. links *P. simonsi* to *P. cookei*. Body weight estimated from tooth size using regression for living primates (Gingerich et al. in preparation). Vertical stippling shows Kay's threshold of body

average duration of each biochron is about 0.8 m.y. or 800,000 years. Although there was undoubtedly some variation in the length of time represented by different biochrons, there is close agreement of ages interpolated using biochrons with radiometric ages at the bases of Ti_4, CF_2, and B_1. As a result, it is possible to achieve much greater chronological resolution using *Plesiadapis-Pelycodus-Notharctus* biochrons than is possible using land mammal ages. Obviously mammalian biochrons are not a substitute for good radiometric ages, but they can be recognized in a suite of continental sediments not usually amenable to radiometric dating and the two approaches are complementary.

There are a number of important applications of improved chronological resolution using *Plesiadapis-Pelycodus-Notharctus* biochrons in
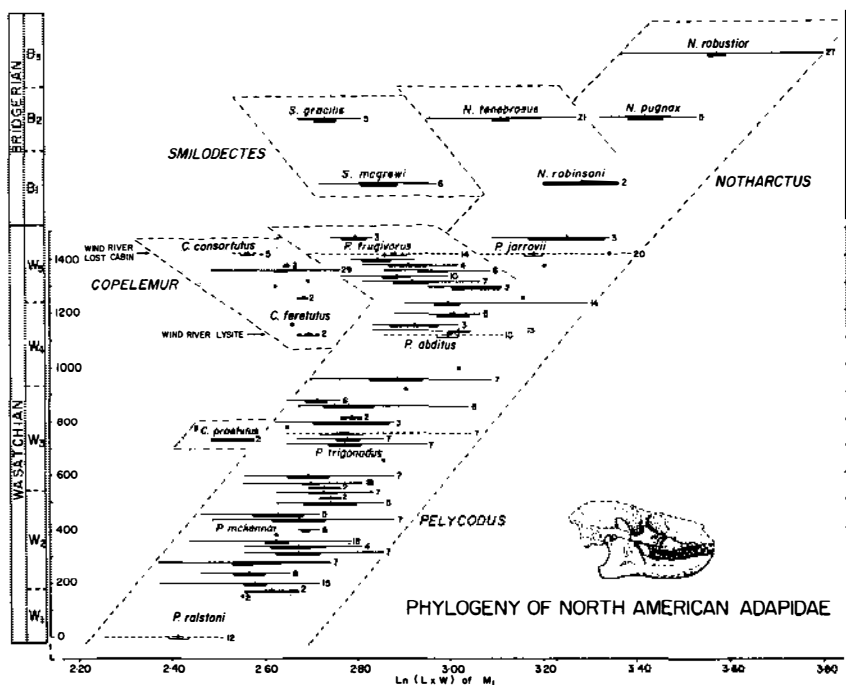

Figure 3 Stratigraphic distribution and interpreted phylogenetic relationships of North American Adapidae. Ordinate is stratigraphic level (in feet) above base of Willwood Formation in central Big Horn Basin (Gingerich 1976a), with superimposed Bridgerian faunal zones from the Bridger Basin. Abscissa is measure of tooth size. Horizontal line is observed range, vertical slash is mean, horizontal bar is standard error, and numeral at right of range is number of specimens in sample. Solid circles are individual specimens. Data from Gingerich & Simons (1977) and Gingerich (1979a). Dashed lines show pattern of stratophenetic linking and hypothesis of phylogenetic relationships.

the temporal interval spanning the Paleocene-Eocene boundary: 1. improved correlations between basins in the Western Interior (e.g. Gingerich 1976b, Figure 15; Krause 1978, Figure 11), 2. improved understanding of phylogenetic relationships in other less abundantly represented taxa, such as Carpolestidae (Figure 2) and Esthonychidae (Gingerich & Gunnell 1979), 3. dating of tectonic events, such as the movement of major thrust slices in the Wyoming thrust belt (Dorr & Gingerich 1979). Finally, as fossiliferous sections are studied in more detail it should be possible to compare types and rates of sedimentation within and between sedimentary basins of the Western Interior and thus gain a better understanding of the detailed chronology of many aspects of earth history as well as life history.

EVOLUTIONARY PATTERNS

The more detailed the stratigraphic sampling of a lineage or clade, the greater the power of resolution of events occurring in its evolution. Stratigraphic detail depends on several factors, especially on the thickness of section spanning a given temporal interval and the spacing of samples drawn from the section. In Figure 2, Plesiadapidae and Carpolestidae are known from approximately one sample per biochron, i.e. one sample every 0.8 m.y., which is sufficient to order the species in succession but not sufficient to document the transition from one species to another. The evolution of Wasatchian *Pelycodus* is known in much greater detail because there are an average of 10 successive samples per biochron, i.e. one every 80,000 years (Figure 3). In the central Big Horn Basin each foot of section represents about 2500 years on average, and each meter of section represents about 8000 years. The rate of sedimentation in the Clark's Fork Basin during the early Wasatchian was more rapid, and each meter of section represents about 3300 to 3400 years on average. The Clark's Fork Basin is not yet as thoroughly sampled as the central Big Horn Basin, but it potentially should yield a Wasatchian stratigraphic record more than twice as detailed as that in the central Big Horn Basin as a consequence of more rapid sedimentation.

The stratigraphic record of the lemur-like primate *Pelycodus* in the Clark's Fork Basin is shown in Figure 4. The pattern is exactly the same as that shown in Figure 3, with gradual increase in size in a single lineage. Measured in darwins [defined by Haldane (1949) as change by a factor of *e* per m.y.], the rate of increase in size in *Pelycodus* was approximately 0.20. At the same time, in the same stratigraphic section and localities, tarsier-like *Tetonoides* and *Tetonius* show a very different evolutionary pattern. *Tetonoides* is present through biochron W_1 and the
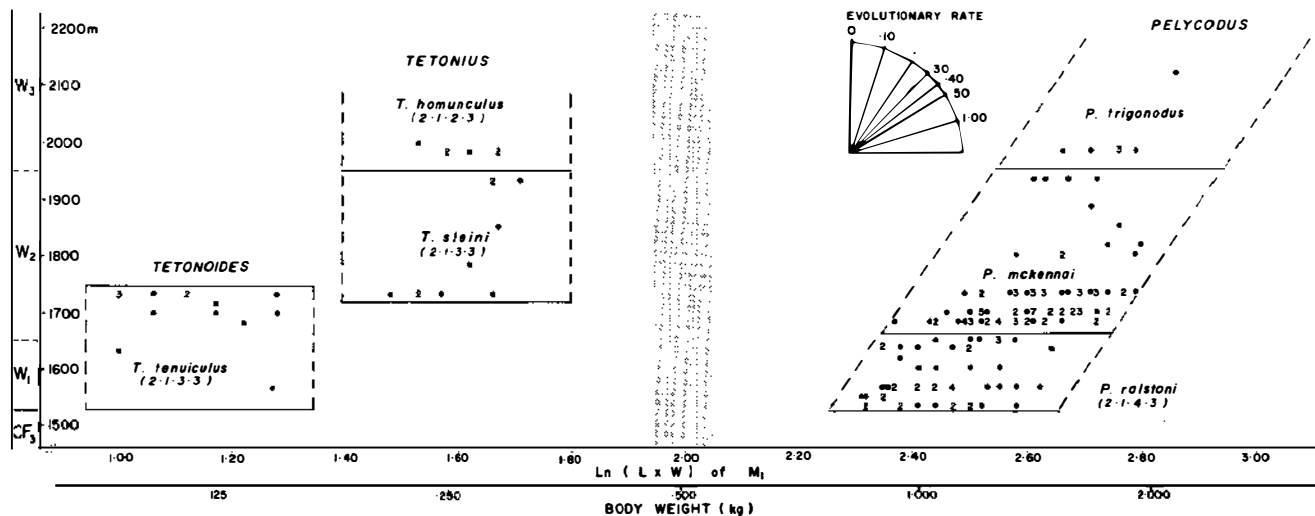
Figure 4 Evolutionary patterns in early Eocene Primates. Abscissa, ordinate, and stippling as in Figure 2. Individual and multiple specimens shown with solid circles and numerals, respectively. Note replacement of *Tetonoides* by a larger *Tetonius* with the same dental formula (2.1.3.3). Evolution of *Pelycodus* in the Clark's Fork Basin is identical to that in the Big Horn Basin (Figure 3). *Tetonoides* and *Tetonius* show little change in size within species lineages, whereas tooth size in *Pelycodus* increased at a rate of about 0.20 darwins.

lower part of W_2. It exhibits no change through time, and apparently disappeared at about level 1750 m. Just before *Tetonoides* disappeared, the closely related larger genus *Tetonius* appeared abruptly as an immigrant. *Tetonius* exhibits little or no change in tooth size through time (although the loss of one tooth, P_2, and enlargement of the central incisor distinguish *T. homunculus* from *T. steini*).

The stratigraphic record of the Clarkforkian and Wasatchian tillodont *Esthonyx* is shown in Figure 5. *Esthonyx* is a tillodont the size of a small pig and it was also probably pig-like in dental adaptation. One lineage of *Esthonyx* appears at or near the beginning of the Clarkforkian and it became larger through time, evolving at a rate of 0.50 darwins. At the beginning of the Wasatchian a second lineage of *Esthonyx* appeared and it also became larger through biochron W_1 and part of W_2. Initially the
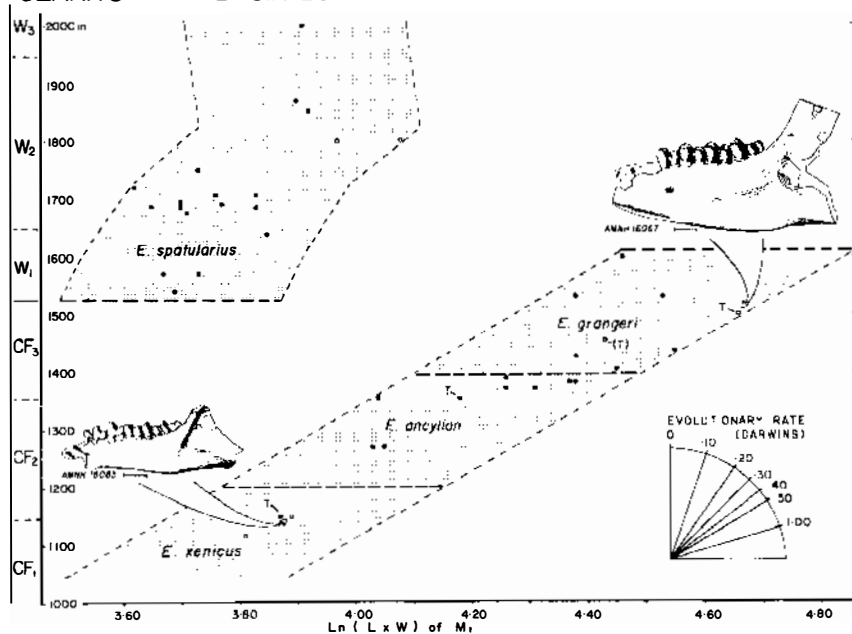
CLARK'S FORK BASIN *ESTHONYX*

Figure 5 Evolutionary patterns in early Eocene Tillodontia. Abscissa and ordinate same as Figure 2. One lineage of *Esthonyx* appeared in the early Clarkforkian (CF_1) and evolved rapidly toward larger size (tooth size increased at about 0.50 darwins). This lineage was replaced in the early Wasatchian by another lineage that initially became larger and then stabilized. It is possible that the transition from *E. spatularius* in lower W_2 to the species present in upper W_2 and W_3 was discontinuous but critical evidence is lacking. Figure from Gingerich & Gunnell (1979).

rate of size evolution in *E. spatularius* was about 0.20 darwins, and then it stabilized and changed little through the last half of biochron W_2 and W_3. Both lineages are found in the same fossil localities in biochron W_1. The transition from one lineage to the other, like that from *Tetonoides* to *Tetonius*, is not preserved in the Clark's Fork Basin.

The fossil record of the horse has been an evolutionary classic for over a century (Drake 1978). The earliest well-dated record of horses in North America is in the Clark's Fork Basin, where *Hyracotherium* first ·appeared at the beginning of the Wasatchian [intensive collecting in the vicinity of Princeton Quarry has failed to corroborate Jepsen & Woodburne's (1969) record of a late Tiffanian *Hyracotherium* in the Clark's Fork Basin]. *Hyracotherium* first became larger, then smaller, and then larger again, with *H. grangeri* giving rise to *H. aemulor* (Figure 6). The maximum rate of evolution in this lineage was about 0.50 darwins. Near the beginning of biochron W_3 a second lineage represented by *H. pernix* appeared abruptly and both lineages subsequently evolved with little change. The tapiroid *Homogalax* is represented in the Clark's Fork Basin by two species, the earlier of which appeared near the base of the Wasatchian and became smaller at a rate of about -0.30 darwins. It was replaced by E. D. Cope's Big Horn Basin "*Systemodon*," or
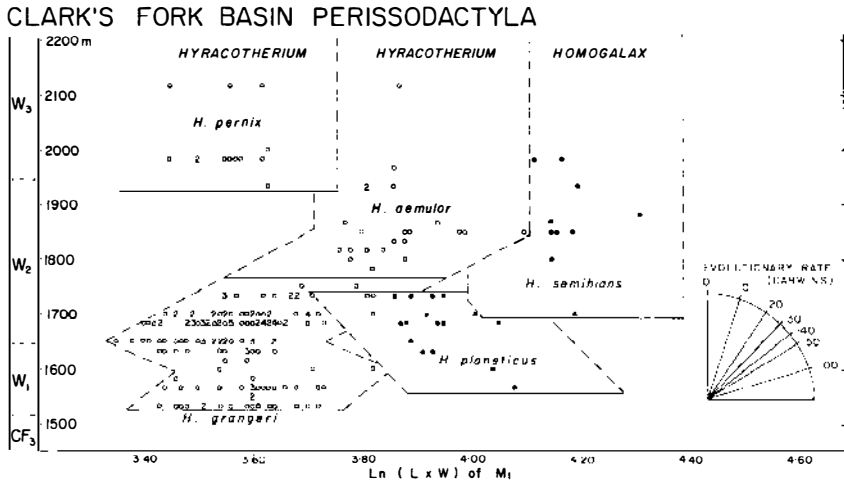
CLARK'S FORK BASIN PERISSODACTYLA

Figure 6 Evolutionary patterns in early Eocene Perissodactyla. Abscissa and ordinate same as Figure 2. Note zigzag pattern of gradual evolution in *Hyracotherium grangeri* leading to the large *H. aemulor*. Maximum rate of change in tooth size in this transition was about 0.50 darwins. *Homogalax semihians* immigrated into the Clark's Fork Basin, replacing *H. planeticus*. *Hyracotherium pernix* also appears to be an immigrant. Figure from Gingerich (1979b).

Homogalax semihians. The two species are both found together in the interval from 1700 to 1750 m. Following its abrupt appearance, *H. semihians* apparently changed very little during subsequent evolution.

Species Level Evolution

The detailed species level evolutionary patterns discussed here represent only six genera in an early Wasatchian fauna containing approximately 50 or more mammalian genera, most of which remain to be analyzed. These examples clearly do not adequately represent all possible patterns, but they do document a spectrum of evolutionary rates and two distinct modes of appearance of new species.

Cope's Rule is an evolutionary generalization sometimes cited as law: animals tend to evolve toward larger body size (Stanley 1973). Considering the direction of evolution in the lineage patterns shown in Figures 2–6, a total of ten lineage segments (45%) evolved toward larger tooth and body size, eight (36%) evolved toward smaller size, and four (18%) remained unchanged. Thus there is a slight tendency in these examples for evolution in the direction of larger body size to predominate over evolution toward smaller size, but since it occurs in less than 50% of the examples this is hardly a general rule. The simple historical fact that mammals originated at relatively small body size is probably sufficient to explain the slight tendency for increases in size to predominate.

Evolutionary rates of change in tooth size in these examples range from 0 to a maximum rate of about 0.50 darwins. A rate of 0.50 darwins is an order of magnitude greater than the average rate for mammals, but it is well within the range of rates previously documented (Kurten 1960, Van Valen 1974).

Much of the current disagreement about species and speciation is semantic. It is possible to define species in a given place at a given time as clusters of morphologically similar animals separated by real discontinuities from other such clusters (morphological, or "skin and skull" species). It is also possible to define species based on patterns of reproduction and gene flow (genetical species). If patterns of gene flow were congruent with gross morphology there would be no problem, but the two are not always congruent (Endler 1973). Some morphological species consist of many genetical species and the converse is possible. The fact that both concepts are included under the term "species" is confusing. *Deme* is a term meaning an "interbreeding community" and it is an appropriate name for the "genetical species." Normally many demes make up a morphological species, and restriction of the term *species* to the larger "skin and skull" concept would be consistent with historical precedent going back to Linnaeus. Natural selection probably operates

at many levels in evolution, selectively favoring individuals, demes, and even species (Stanley 1975). Knowledge of evolution at each level is important for understanding the general process. Patterns of evolution at the individual and deme level are beyond the power of resolution of virtually all paleontological sampling, and the patterns described here illustrate evolution at the level of the Linnaean species.

There are three principal components of evolutionary space: morphology, time, and geography. These components are all portrayed in Figures 2–6. Morphology is on the horizontal x-axis, time is on the vertical y-axis, and geography is (theoretically) on the z-axis going into the page. In a sense, the different figures each represent different positions of the morphological component as well, since each includes only genera that are closely similar. All of the figures illustrate evolution in one geographical area, and consequently values on the z-axis are constant and all changes can be shown in the morphology-time plane. This is not to say that geography is unimportant in evolution or that it should purposely be ignored. Geography is another important component necessary for a full understanding of species and speciation, but the level of our knowledge of the geographical distribution of Paleocene and Eocene taxa is not yet sufficient to adequately characterize geographical distributions.

Some Wasatchian species are found from Wyoming to New Mexico, while others appear to be confined to one region or the other. Before a real geographical component can be added to Figures 2–6, vertical successions in other sedimentary basins will have to be studied in the detail shown here. Detailed study of any one basin is a large undertaking, and we are not likely to have sufficient knowledge to discuss geographical distributions of species in the near future. On a related problem, the "subspecies" is a geographical concept clearly violated by use in a temporal sense, with the unnecessary burden of writing a trinomial when a binomial conveys exactly the same information. Taking the evolution of *Esthonyx* shown in Figure 5 as an example, reference of *Esthonyx ancylion* and *E. xenicus* to the previously named *E. grangeri* as subspecies (*E. grangeri ancylion, E. grangeri xenicus,* with *E. grangeri grangeri*) conveys no additional information over writing *E. grangeri, E. ancylion,* and *E. xenicus.* In either case, relationships must be shown in a diagram.

Species, as portrayed in Figures 2–6, are groups of similar individuals. They are segments of evolving lineages bounded by morphological and temporal (and potentially geographical) discontinuities from other such lineages. Apparent branching points like the one shown in *Plesiadapis* (Figure 2) or in *Pelycodus* (Figure 3) also bound species lineages

temporally at the point where one lineage becomes two. Within some lineages there is sufficient change in size or other characteristics to require subdivision of the lineage into two or more successive species. In practice, the amount of size change separating successive easily recognizable species is a shift in mean size of one-half of the expected range of size variation, or a shift of 0.2 units on the scale of tooth size used in Figures 2–6. Species are naturally bounded in most dimensions, but this is the one case where an arbitrary boundary must be drawn between species, similar to the arbitrary boundary that separates successive hours in our daily lives. Successive hours are different and worthy of delimitation, and successive species in a single lineage are also worthy of delimitation if the lineage is changing significantly.

Two modes of species appearance are evident in Figures 2–6. Some new species arise by gradual evolution within lineages (anagenesis). Appearance of most of the successive species of *Carpodaptes, Plesiadapsis*, or *Pelycodus* are examples of speciation by gradual evolution. Other species appear abruptly in the record as immigrants from elsewhere. *Pelycodus ralstoni, Esthonyx spatularius*, and *Hyracotherium grangeri* are three examples of species that first appear by immigration at the beginning of the Wasatchian. In several cases an immigrant replaces a closely related species previously present, for example *Tetonius steini* (Figure 4), *Esthonyx spatularius* (Figure 5), or *Homogalax semihians* (Figure 6). This pattern conforms closely to a prediction of the "punctuated equilibria" model of speciation (Gould & Eldredge 1977), although the geographical perspective necessary to confirm rapid speciation in a small peripheral isolate is still lacking. Leaving out ambiguous cases, there are 24 examples of species appearing by gradual evolution and 14 examples of species appearing by immigration shown in Figures 2–6. The relative frequencies of the two modes may change as additional components of Paleocene and Eocene faunas are studied, but this evidence is sufficient to establish that both modes are present. It is, of course, possible that species first appearing as immigrants in the Clark's Fork Basin evolved gradually elsewhere.

Faunal Evolution

Definitive study of evolution at a faunal level will not be possible until the systematics of all of the component species are well understood. This is not yet the case. Nevertheless, it is possible to make some preliminary observations on patterns of faunal evolution across the Paleocene-Eocene boundary. Some species evolved rapidly while others evolved more slowly. Some appeared abruptly by immigration and disappeared by emigration or extinction. Our work to date has shown that

the net result is relatively slow gradual evolution of the mammalian fauna as a whole, interrupted by several episodes of major faunal turnover.

The best documented episode of turnover is at the beginning of the Wasatchian (W_1), when Artiodactyla, Perissodactyla, modern Primates, and hyaenodontid Creodonta first appeared. Another faunal turnover occurred at the beginning of the Clarkforkian (CF_1), when Rodentia, Tillodontia, miacine Carnivora, and coryphodontid Pantodonta first appeared (Rose 1979). A possible episode of faunal turnover occurred in the Tiffanian near the end of the *Plesiadapis rex* biochron or beginning of the *P. churchilli* biochron (Ti_3 or Ti_4), when a number of archaic primate and other genera first appeared. This turnover may have been more gradual than the others, and it is not yet well documented. Several elements with possible South American affinities (an edentate, a notoungulate, and *Probathyopsis*) first appeared in the late Tiffanian (Ti_4 or Ti_5), possibly as part of this turnover. Finally, as Figures 4–6 suggest, there may have been another distinct episode of faunal turnover in the early Wasatchian (W_2) between levels 1650 and 1750 m in the Clark's Fork Basin: *Tetonius* replaced *Tetonoides*, *Esthonyx grangeri* disappeared, and *Homogalax semihians* replaced *H. planeticus*. Evolution at a faunal level across the Paleocene-Eocene boundary included periods of episodic turnover as well as gradual evolution.

Rose (1979) has made an extensive study of faunal composition and diversity in mammalian faunas spanning the Torrejonian, Tiffanian, Clarkforkian, and early Wasatchian, and he shows a clear relationship of mammalian faunal diversity with changing climate. Diversity was high in the Torrejonian. It was relatively low in the middle Tiffanian (Ti_2 and Ti_3), corresponding to the low in mean annual temperature discussed above. Diversity then increased gradually though the early Wasatchian as mean annual temperature increased.

Climate and high latitude ·land connections between the northern continents can be combined in a tentative hypothesis to explain the episodes of faunal turnover across the Paleocene-Eocene ,boundary. A warming climate would expand the potential geographic range of subtropically and tropically adapted animals. In the late Tiffanian this may explain the first appearance of mammals with Central American or South American affinities in northwestern Wyoming (Sloan 1969, Gingerich 1976b). The initial Clarkforkian episode of faunal turnover includes immigrants with Asian affinities, suggesting that climates had warmed sufficiently for these mammals to cross into North America from Asia. The immigration at the beginning of the Wasatchian includes no taxa clearly indicating area of origin, but there is suggestion of European (*Hyracotherium*) ·or African (adapid primates, hyaenodontid

creodonts) affinities. It is probable that this immigration was the only major one to cross the high latitude route between Europe and North America after late Paleocenc climatic cooling. The route was closed permanently by further rifting of the North Atlantic in the early Wasatchian. Considering present knowledge, every detail of this hypothesis is tentative and subject to change with future discoveries. One critical gap, the nature of eastern Asian mammalian faunas, is rapidly being filled by colleagues in China, Mongolia, and the U.S.S.R. Other major gaps remain, but the hypothesis gives some structure for further inquiry and it is one possible explanation for documented episodes of faunal turnover.

SUMMARY AND CONCLUSIONS

Historical records are essential for deciphering past events. Geology, stratigraphy, and paleontology contribute uniquely to understanding evolution in its temporal dimension. The stratigraphic record of early Cenozoic mammals is remarkably complete in some areas, although we certainly still lack an adequate geographical perspective. Faunal changes across the Paleocene-Eocene boundary are documented in a 2000 m stratigraphic section spanning the Tiffanian, Clarkforkian, and early Wasatchian land mammal ages in the Clark's Fork Basin of Wyoming. Here it is possible to trace individual mammalian lineages through time. In the illustrated examples ten species lineages become larger, eight become smaller, and four exhibited little or no change. The maximum rate of change in tooth size is about 0.50 darwins. In the examples where mode of appearance of new species is clearly shown, 24 originated by gradual evolution and 14 show a "punctuated" pattern of first appearance by immigration into the Clark's Fork Basin from elsewhere.

At a faunal level, the net result of dynamic change in individual lineages is slow gradual evolution of the mammalian fauna as a whole, interrupted by several episodes of faunal turnover. Interpreted in light of early Cenozoic paleoclimates, mammalian faunal diversity appears to be closely related to climate, and episodes of faunal turnover may coincide with the successive introduction of South American, Asian, and European-African elements, respectively, into North America. The latter two introductions possibly appear episodic rather than gradual because they resulted from a threshold effect of immigration across high latitude land bridges opened by progressively warming climates.

Mammalian paleontology has reached a stage where progress in understanding early Cenozoic faunal evolution, including the origin and diversification of Primates and other modern orders of mammals, depends

on detailed biostratigraphic documentation. Fortunately there are many sedimentary basins in the Western Interior where mammalian remains are abundantly preserved in stratigraphic context, and in future these promise to yield a better perspective on evolution at the species level as well.

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