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PALEONTOLOGY AND PHYLOGENY: PATTERNS OF EVOLUTION AT THE SPECIES LEVEL IN EARLY TERTIARY MAMMALS

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ABSTRACT. The underlying tempo of the evolutionary process is determined by rates of evolution in single phyletic lineages and by rates of divergence in sister lineages following geographic speciation. These rates and hence the tempo of morphological evolution can be determined for natural populations only by detailed study of stratigraphic successions in areas where the fossil record is relatively complete. The stratigraphy of Middle Paleocene through Lower Eocene continental deposits in the Big Horn Basin of Wyoming is herein described, and fossils of the genera *Hyopsodus*, *Haplomylus*, *Pelycodus*, and *Plesiadapis* are placed in stratigraphic context. The resulting patterns of evolution at the species level illustrate the importance of gradual phyletic evolution in the origin of new species and the consistent presence of gradual morphological divergence following geographic speciation (geographic speciation seems best characterized as parapatric rather than allopatric in these examples).

Change in each phyletic lineage is nonrandom and apparently controlled by strong directional selection. Where two or more closely related species are present in the same time period, the species diverge gradually in size — presumably to minimize inter-specific competition. The gradual nature of this divergence may be explained by the high heritability of most morphological characters related to body size. Although gradual, the observed rates of divergence are sufficiently rapid that an appearance of abrupt change would be registered if (1) there were significant gaps in the fossil record, (2) stratigraphic sampling was not sufficiently refined, or (3) a typological species concept was applied. Examples of “quantum evolution” or “punctuated equilibrium” have not yet been substantiated adequately in terms of these three criteria, whereas an interpretation of gradual phyletic evolution and gradual divergence following cladogenic speciation appears fully justified in the evolutionary sequences of early terrestrial mammals described here.

INTRODUCTION

Speciation is the evolutionary process by which a new kind of animal or “species” which differs significantly from its parent species is formed. Traditionally, our concept of speciation has included two processes: one phyletic, the other geographic. Phyletic evolution or anagenesis involves the gradual transformation of one species into another, presumably as a result of strong directional selection; by this process each species simply replaces another in an evolutionary lineage, and the total number of species living at any one time remains constant (each of the successive species or kinds in this case are only arbitrarily separable). Geographic speciation or cladogenesis, on the other hand, proceeds by dividing a parent species into two or more populations (by separating them geographically), each of which may become genetically and phenotypically distinct and evolve independently; the result is an increase in the number of species living at one time; that is, a proliferation of evo-

lutionary lineages. The great increase in number of species through certain intervals of Earth history is one of the most striking features of the history of life, and it is thus natural that geographic speciation and cladogenesis have received the most attention from zoologists (see Mayr, 1970, for example). Gradual phyletic evolution appears to be a less challenging process theoretically, and it has consequently aroused less interest.

General agreement exists regarding the usual *modes* of animal speciation, both phyletic and geographic, based on over a century of research in systematics, genetics, and ecology. Mutation and recombination provide genetic variability in the reproductively separate gene pool of each species, population, or deme. Effects of the natural environment tend to eliminate selectively individuals of a species that are least fit in each generation, and, if this selection is directional, small but usually significant changes in the genetic and phenotypic constitution of the entire species will result. New lineages arise when viable populations are separated geographically, and each develops its own evolutionary identity.

The *tempo* of the speciation process in nature is less well documented, and it can, in fact, only be investigated by careful study of the fossil record. While rates of morphological evolution have been calculated for numerous actual or presumed individual phyletic lineages (see Simpson, 1953; Kurtén, 1955; Maglio, 1973; and others), rates of divergence associated with the establishment of new lineages have never been studied adequately. If rates of divergence are relatively slow; that is, as slow as documented rates of phyletic evolution, the diversification of life is properly viewed as a gradual process, species are dynamic links in a great chain, and the traditional branching tree is an adequate representation. If rates of divergence in cladogenic speciation are very rapid, that is instantaneous with respect to geological time, the diversification of life should be viewed more as a series of abrupt events, species are essentially static forms persisting through time, and the rectangular output of a computer-generated cluster analysis is an appropriate representation.

Paleontologists have, in the past, usually favored the gradual view, though Simpson's concept of "quantum evolution" at the species level is suggestive of abruptness (Simpson, 1944), and recently strong support for abrupt species transitions has been expressed in a "punctuated equilibrium" model by Eldredge and Gould (1972). Gradualistic and punctuated models of the origin of species have an important correlation with one's view of species (dynamic or static), and they imply different sequences of events in the speciation process itself. The distinctions are important, and the evidence for each view deserving of critical scrutiny.

In the first edition (1859) of *The Origin of Species*, Darwin included a hypothetical diagram (see fig. 1) showing species changing through time in the continuous gradual manner that has come to be associated with his name. He himself retreated from this dynamic view of species in the fourth edition (1866), adding a specific disclaimer of continuity to his original statement: "I do not suppose that the process ever goes on so regularly as is represented in the diagram, though in itself made some-

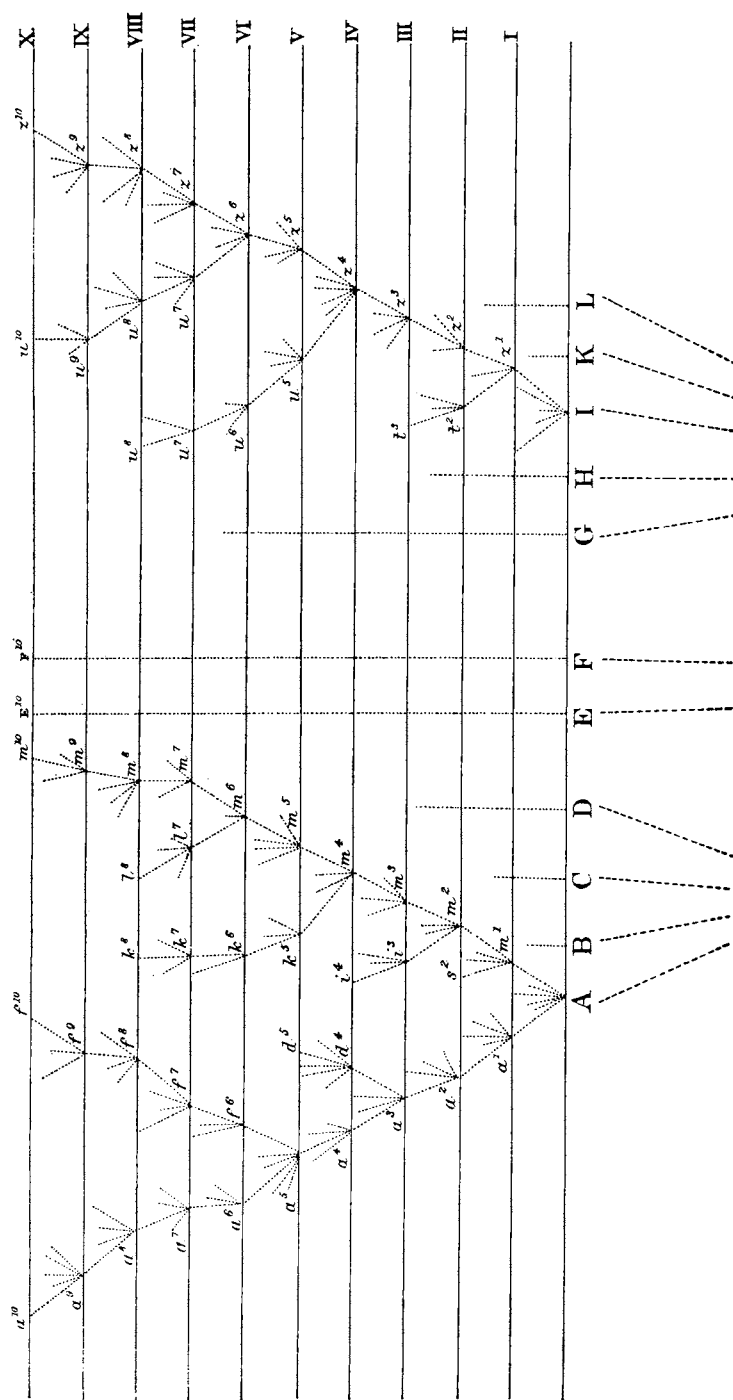


Fig. 1. Diagram from *The Origin of Species* illustrating Darwin's concept of evolutionary divergence of character and extinction in the descendants of a common ancestor. A through L are species of a genus "large in its own country". Each horizontal line (I-X) represents 1000 or more generations. The horizontal axis represents, in a general way, a line of morphology and inferred relationship among the species. Note that species A gives rise by time I to two "varieties" a^1 and a^2 , with the latter replacing species B (which became extinct). By time X, Darwin indicates that descendants of species A have replaced species B to D, that E and F have persisted little changed from the beginning, that G has become extinct, and that descendants of species I have replaced H, K, and L. While not denying that some species could persist little changed through long periods of time, Darwin indicated that gradual character divergence was of primary importance in the origin of new species. He retreated somewhat from this dynamic view of species in the later editions of the *Origin*, though the same diagram appears in all (see text; also Peckham, 1959, p. 210-220).

what irregular, nor that it goes on continuously; it is far more probable that each form remains for long periods unaltered, and then again undergoes modification" (Peckham, 1959, p. 213; my italics — italicized portion of quotation was first added in 1866 edition). Surprisingly, a century of subsequent paleontological research has contributed little to this fundamental question.

As noted above, evolutionary tempo in natural populations can only be studied in the fossil record. A number of apparent examples of Eldredge and Gould's "punctuated equilibrium" model exist in the literature on early mammals. To cite one, the phylogeny of the Early Eocene condylarth *Hyopsodus* envisioned by Matthew (1915) and outlined more explicitly by Guthrie (1967) and Gazin (1968) begins with a single Sand Coulee population of medium-sized individuals labeled *Hyopsodus miticulus*. In the overlying Gray Bull beds, *H. miticulus* persists unchanged, while a small species *H. wortmani* makes its first sudden appearance, as does a large species *H. powellianus*. All three species, large, medium, and small, are portrayed as continuing essentially unchanged through the overlying Lysite and Lost Cabin beds. From the data presented by Guthrie and Gazin, *Hyopsodus* seemed to show the abrupt appearance of species and the subsequent insignificant change characteristic of the punctuated equilibrium model. However, Simpson's original illustration of the chronocline concept (continuous gradual change through time in an evolving lineage) was based on the closely related condylarth *Ectocion* from the same stratigraphic horizons (Simpson, 1943). In an attempt to reconcile these very different pictures of phylogeny derived from the same order of mammals in the same stratigraphic framework, the large Yale collection of *Hyopsodus* (numbering close to 4000 jaw fragments) was restudied in a more detailed stratigraphic context than that of Guthrie or Gazin. The result (Gingerich, 1974a) indicated a gradualistic model of species transitions with new species originating by both anagenesis and cladogenesis, rather than the punctuated equilibrium model first suggested by the earlier, less detailed studies.

The data on *Hyopsodus* are further analyzed in this paper, and three additional examples of evolution at the species level are described in Paleocene and Eocene mammals, based on detailed stratigraphic studies in the Big Horn Basin of Wyoming. The general stratigraphy of Paleocene and Lower Eocene sediments in the Big Horn Basin is described first, followed by a description of evolutionary change in species of the genera *Hyopsodus*, *Haplomylus*, and *Pelycodus*, and in the family Plesiadapidae. Finally, the suitability of mammalian teeth for evolutionary analysis and the importance of sound systematic methods and detailed stratigraphy are discussed, together with some general implications for speciation theory.

THE GEOGRAPHIC AND STRATIGRAPHIC SETTING

The following biostratigraphic analyses are based on fossils taken from successive strata in a remarkably complete, highly fossiliferous se-

quence of sediments in the Big Horn Basin of northwestern Wyoming. Before describing the analyses, the geography and paleogeography of the area and the general stratigraphy of the deposits will be considered briefly.

The Big Horn Basin today is a great structural depression surrounded by ranges of the central Rocky Mountains. At least 6700 m of structural displacement are indicated between the Precambrian floor of the basin and the tops of the surrounding mountains, though most of this structural depression is filled with Paleozoic, Mesozoic, and Cenozoic sediments. The sea withdrew from the area sometime in the late Cretaceous, and, with the following intense Laramide orogeny, the bordering mountain structures were elevated, and the basin floor depressed. Today some 2500 m of topographic relief separate the surrounding mountains from the basin, though it appears that this topographic relief is a relatively recent feature. In the Paleocene and Eocene, erosion of the mountains and aggradation of the basins kept pace and maintained a mature topography (Van Houten, 1944). Thus, there is no reason to think that the Paleocene and Eocene faunas of the Big Horn Basin were geographically isolated from their counterparts preserved in other basins in the Rocky Mountains (though latitudinal and ecological gradients certainly had some effect).

The Tertiary sediments of the Big Horn Basin were first described as lake deposits, but it is now clear that most are fluvial in origin. Sediments of Paleocene age in the Big Horn Basin (Polecat Bench Formation) consist of an alternating series of sandstones and mudstones, with occasional beds of lignite and freshwater limestone. A cyclical pattern is evident: sandstones tend to be overlain by mudstones, these in turn by lignites, and the lignites are again overlain by sandstones (Gingerich, 1969). This sequence is what might be expected as meandering, aggrading streams carrying sand colonize low lying swampy environments. Later, as the stream is diverted, the sands are covered with overbank muds during times of flooding. Swamps develop in lowland areas of the flood plain, only to be invaded again by flooding, sand-carrying streams. The resulting sedimentary beds are discontinuous; while some can be traced for a kilometer or more, most probably cannot.

Lower Eocene rocks in the Big Horn Basin (Willwood Formation) are generally conformable with the underlying Paleocene deposits, and both represent an essentially continuous depositional sequence. Mudstones predominate in the Eocene, though the general stream channel and floodplain depositional setting was little changed. The most obvious difference is the introduction of bright red mudstones beginning at the base of the Eocene. Red or drab sediment color in the Willwood Formation appears to be dependent on oxidizing or reducing conditions, respectively, at the site of deposition (Neasham and Vondra, 1972), though the exact mechanism is less clear. In the Big Horn Basin the lowest appearance of redbeds is very closely correlated with the first introduction of characteristically Eocene mammals (such as *Hyracotherium*) in the

Clarkforkian, and it is likely that both events were related to similar environmental factors.

Deposition of the fluvial sediments of the Polecat Bench and Willwood formations was continuous but not in the sense that many marine or lacustrine deposits are continuous. Rather than an endless slow rain of sediment settling in still water, these fluvial sediments are a result of repeated cutting and filling. The rate of sediment accumulation was thus more dependent on the rate of basin subsidence than the rate of influx of sediment. All indications are that subsidence in the Big Horn Basin during the Early Tertiary was continuous, at least in the local areas of interest here, and sediments accumulated continuously (though not at an absolutely uniform rate). The low topographic relief within the basin at the time the sediments were deposited precludes mixing of faunas from significantly different ages or levels, though some insignificant mixing from adjacent levels possibly occurred. The principle of superposition, of course, applies equally to fluvial and lacustrine sediments.

EVOLUTION OF *Hyopsodus*, *Haplomylus*, AND *Pelycodus*

In 1962, Yale University field parties directed by E. L. Simons began an intensive program to collect fossil mammals in the Lower Eocene Willwood Formation in the Big Horn Basin of Wyoming. To date, over 400 localities have been found, concentrated in a band across an area of some 1000 square km south and west of the town of Basin, Wyo. The most common fossils found in these beds belong to species of the condylarths *Hyopsodus*, *Haplomylus*, *Ectocion*, and *Phenacodus*; the primate *Pelycodus*; the artiodactyl *Diacodexis*; and the early perissodactyls *Hyracotherium* and *Homogalax*. All have been or are in the process of being intensively studied in the context of their stratigraphic distribution.

The individual localities yielding the fossils discussed here range from a few square meters to as much as a square kilometer in area. Most localities sample a very restricted stratigraphic interval, though some may include fossils from a thickness of 5 m of strata, and, in a few cases, the collections might include specimens from as much as 15 m of stratigraphic section. The chief effect of lumping up to 15 m of strata at a single locality is to increase the range of variation in each sample of a species changing through time. The average value of each character in the species from such a locality should not be misrepresented, as long as the stratigraphic position to which the locality is assigned is a representative average for the locality. Most localities, like locality 429 illustrated in plate 1, represent essentially a single stratigraphic horizon. (All localities are plotted on detailed topographic maps filed in the Division of Vertebrate Paleontology, Yale Peabody Museum.)

In 1965, Grant E. Meyer and Leonard Radinsky measured a stratigraphic section across the Willwood Formation from its basal contact with the Polecat Bench Formation on Antelope Creek (southwest of the town of Basin) to its upper contact with the overlying Tatman Formation on the south side of Fifteenmile Creek in the general vicinity of

PLATE 1



Yale-Michigan locality 429 in the Big Horn Basin of Wyoming. Fossil specimens are locally abundant on flats such as those indicated here by arrows. Hill in background shows nearly horizontal bedding typical of study area, dark bands are red beds between gray mudstones, capping rock is a channel sandstone.

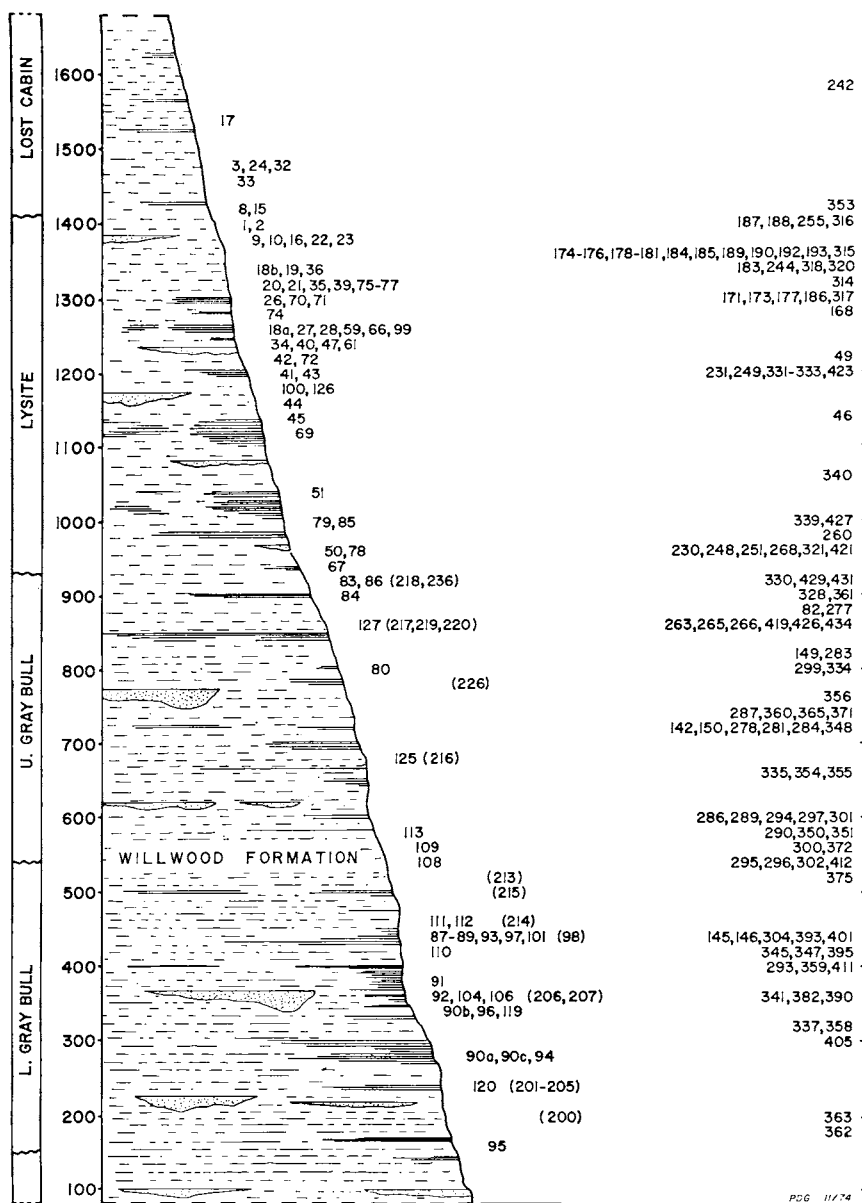


Fig. 2. Stratigraphic position of fossil localities in the Willwood Formation south and west of Basin, Wyoming; based on stratigraphic sections measured by G. E. Meyer, L. Radinsky, J. W. Neasham, and C. F. Vondra. Gray Bull, Lysite, and Lost Cabin are faunal and temporal subdivisions of the North American Wasatchian mammal Stage. As presently understood, the Wasatchian spans the time period from about 52.5 to 49 m.y. B.P. The underlying Clarkforkian Stage includes the period from about 54 to 52.5 m.y. (based on Berggren, 1972; and studies in progress on Late Paleocene and Early Eocene mammalian faunas).

Vertical scale at left is thickness of measured section in feet (1600 ft = 490 m). Small numbers near idealized section are localities actually in Meyer-Radinsky section, those in parentheses were added from Neasham-Vondra section. Small numbers at right are localities interpolated into measured sections on basis of geographic proximity to a locality in the measured sections and/or the morphology of the *Hyopsodus* from that locality.

Squaw Buttes. The total thickness of the Willwood Formation along this traverse was found to be nearly 550 m (1800 ft), and 83 localities known at that time were included in this original measured section. The numbers of these localities are listed in relative stratigraphic position in figure 2.

Subsequently, Neasham and Vondra (1972) measured two stratigraphic sections across the Willwood Formation in the general area of this study: the first, from near the town of Meeteetse to Tatman Mountain, measured a total thickness of 400 m (1320 ft); and the second, from Antelope Creek to Tatman Mountain, included a total thickness of 700 m (2300 ft) of Willwood Formation. The three measured sections agree in showing an east-to-west decrease in thickness of the Willwood Formation in this area. On faunal evidence, it appears that the lower 300 m (1000 ft) are missing on the western flank (where contact with the underlying Polecat Bench Formation is an angular unconformity). The Neasham-Vondra section included 37 Yale fossil localities known at that time, 18 of which were previously included in the Meyer-Radinsky section. The 19 additional localities are listed in parentheses in figure 2.

In figure 2, and throughout the following discussion, the stratigraphic position of a locality has been rounded to the nearest 6.1 m (20 ft). This is done to retain as much resolution as possible, yet not overestimate the precision of the methods of stratigraphic measurement or fossil collecting. This study is based on real rather than hypothetical computer-generated data, and some imprecision is inevitable. Even so, the stratigraphic position of each locality is unlikely to be in error by more than 15 m (50 ft), due to depositional, measuring, or collecting imprecision, which would not affect the general results appreciably.

An example of the data available from individual localities is illustrated in figure 3, which shows the size distribution of the entire collection of *Hyopsodus* from locality 45. The product of length and width of the first molar is, in general, the best measurement to characterize the

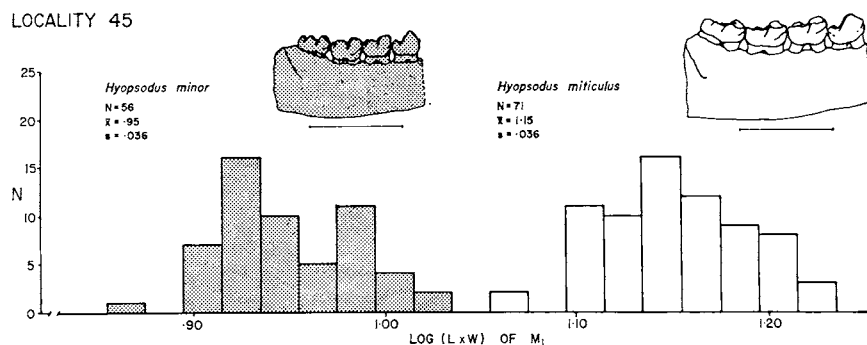


Fig. 3. *Hyopsodus* from locality 45 (level 1140, see fig. 2). Histograms show size distribution of specimens of *Hyopsodus minor* (shaded) and *H. miticulus* (plain) on a log scale. Inset figures show a jaw fragment of each species drawn to the same scale (bar = 1 cm) for comparison. Use of log scale and area of M_1 on abscissa are discussed in Gingerich (1974b).

size of closely related fossil mammals (Gingerich, 1974b), and this quantity is plotted on a logarithmic scale to make the variability of the sample of large specimens comparable to that of small specimens. Two species, the small *Hyopsodus minor* and the larger *H. miticulus*, are clearly present at locality 45. The coefficient of variation of the length of M_1 in this sample of *H. minor* is 4.65, and that of M_1 length in this sample of *H. miticulus* is 4.61. These coefficients are clearly comparable in the two species samples, and each is well within the range of variation expected of a single mammalian species, based on a consideration of variation in living species (Gingerich, 1974b), whereas the coefficient of variation of 11.93 for the entire pooled sample of 127 specimens from locality 45 is clearly too large to represent a single species. The examples of figure 3 also give a measure of the maximum range of variation to be expected in a species of *Hyopsodus*: both species have a maximum range of 0.17 for the log (L x W) of M_1 .

Considering all the information available, the two species of *Hyopsodus* present at locality 45 can still only be distinguished on the basis of size — *H. minor* includes small individuals, and *H. miticulus* includes large individuals, but the two species are otherwise morphologically identical. Although some progressive change in form can be seen when a lineage is traced upward through the stratigraphic column (for example, paraconids on M_1 are reduced in *Hyopsodus*, mesostyles are added in *Pelycodus*, and enamel is crenulated in *Plesiadapis*), progressive change in the size of individual specimens is the most obvious and most easily quantified change through the stratigraphic record. Other morphological characteristics (paraconid development, mesostyle development, et cetera) and other measurements of individual size (for example, measurements taken on different teeth) are usually highly correlated with the measure of individual size used in the following analysis, and, if sufficient data could be collected, study of other size and form characteristics in stratigraphic context would almost certainly yield precisely the same pattern of phylogeny for each of the genera reported here.

In the previous treatment of the evolution of *Hyopsodus* (Gingerich, 1974a), 928 jaws and jaw fragments having the first lower molar were available from 45 localities actually in the Meyer-Radinsky measured section and from an additional 90 localities in or near their traverse. The 90 additional localities were all interpolated into the measured section on the basis of their geographic location vis-à-vis localities already in the section. This was done *before* any specimens were measured to ensure that the morphology of the specimens could not influence where any locality was placed in the stratigraphic section, which was necessary to avoid any circularity of reasoning when evolutionary patterns were subsequently inferred from morphological changes seen in the stratigraphic distribution. The previously published figure is an unrefined initial picture of *Hyopsodus* evolution. Such a procedure is necessary if sequences of fossils are used to test the evolutionary hypothesis itself: the stratigraphic framework must be set up completely independently of the fossils

of interest in each particular instance. Because the figure of *Hyopsodus* phylogeny presented previously has here been refined to make as simple a picture as possible, given the available stratigraphic information, the new figure cannot be cited as evidence for gradual phyletic evolution (however, the phylogeny of *Hyopsodus* presented previously and those of *Haplomylus*, *Pelycodus*, and *Plesiadapis* presented here do qualify in this regard). In this study a different approach was taken to the study of *Hyopsodus* itself, though the general results of the previous study are very little changed.

Phylogeny of Hyopsodus.—As a result of additional collecting, 1078 jaws and jaw fragments of *Hyopsodus* are now known from the localities listed in figure 2 which preserve the first lower molar (isolated teeth of *Hyopsodus* have never been included because of the possibility of confusing M_1 and M_2). These specimens come from 212 localities in the study area. In the present study, 420 specimens from 60 localities actually in either the Meyer-Radinsky or the Neasham-Vondra section were plotted initially. This plot (fig. 4) shows the major features of the phylogeny proposed in the previous study (Gingerich, 1974a), as it should since much of the information is the same. The remaining specimens (658) from the remaining localities (152) were then interpolated into figure 4, locality by locality, based *both* on the geographic relationship of the locality in question to those already in the section and on the average size of each species sample from the locality. The stratigraphic positions of the localities added to the section by this interpolation are listed at the right in figure 2, and the final *Hyopsodus* plot is illustrated in figure 5.

The refined phylogeny of *Hyopsodus* presented here (fig. 5) differs in some details from the initial picture presented previously (Gingerich, 1974a), but the major features of the two plots are the same: both exhibit gradual phyletic evolution, overall size increase, iterative evolution of small species, and character divergence following the origin of each new lineage. Worthy of note in the new plot (fig. 5) is the abrupt reversal in the evolutionary trend toward larger size seen in *H. latidens*, a reversal apparently not associated with any recorded cladogenic bifurcation.

The differences that do appear between figure 5 and the phylogeny published previously have resulted from the addition of new specimens and slight revision of the stratigraphic position of localities in two specific areas: (1) The beds on the south fork of Elk Creek (especially loc 363) appear to be lower in the section than was previously recognized, altering the evidence for two sympatric species of *Hyopsodus* at level 440. While it still appears that two species very close in size were probably present at level 440, one leading to *H. "simplex"*, the other to *H. latidens*, the two species were less clearly differentiated at this level than was previously indicated. (2) The beds in the vicinity of Red Butte are higher stratigraphically than previously recognized, and the isolated specimen of early *H. miticulus* (loc. 331) from level 980 in the previous plot now falls within the more abundantly represented population of this species at level 1200. In addition, localities near the major creeks in the region are

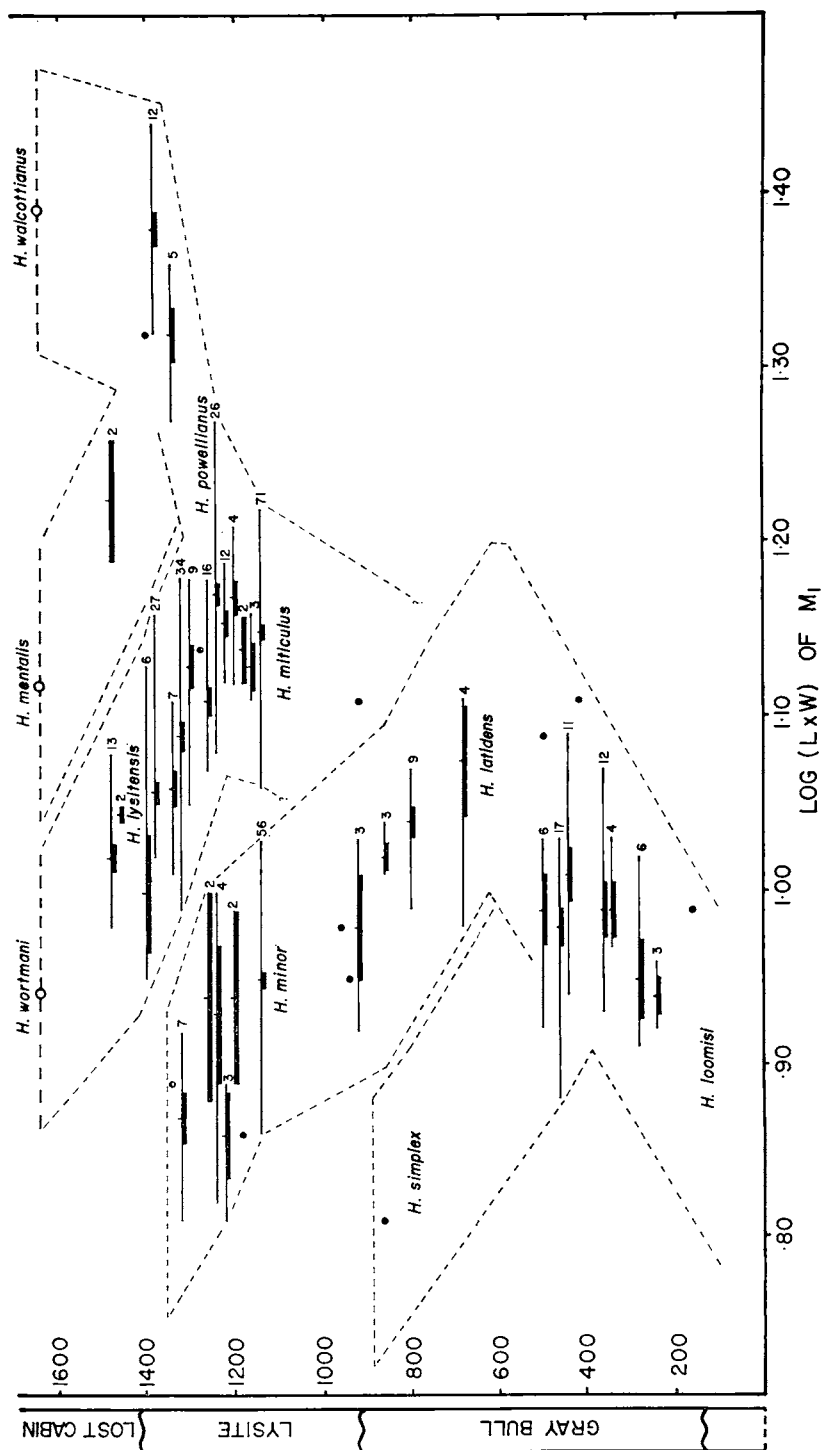


Fig. 4. Stratigraphic distribution of *Hyopsodus* specimens actually in measured sections (loc. listed at left in fig. 2), with dashed lines added from fig. 5. Vertical slash indicates mean, horizontal bar is standard error, and horizontal line is range of variation for the sample of each species from a given level (compare level 1140 here with fig. 3). Small numerals indicate sample size. Open circles are means of Lost Cabin samples measured by Guthrie (1971). (It is now clear that *Hyopsodus simplex* is an indeterminate synonym of *H. loomisi*, *H. latidens*, or *H. minor*, and the specimen here labeled as *H. simplex* belongs to a new species. The name *H. simplex* is retained for it provisionally, pending publication of the new species.)

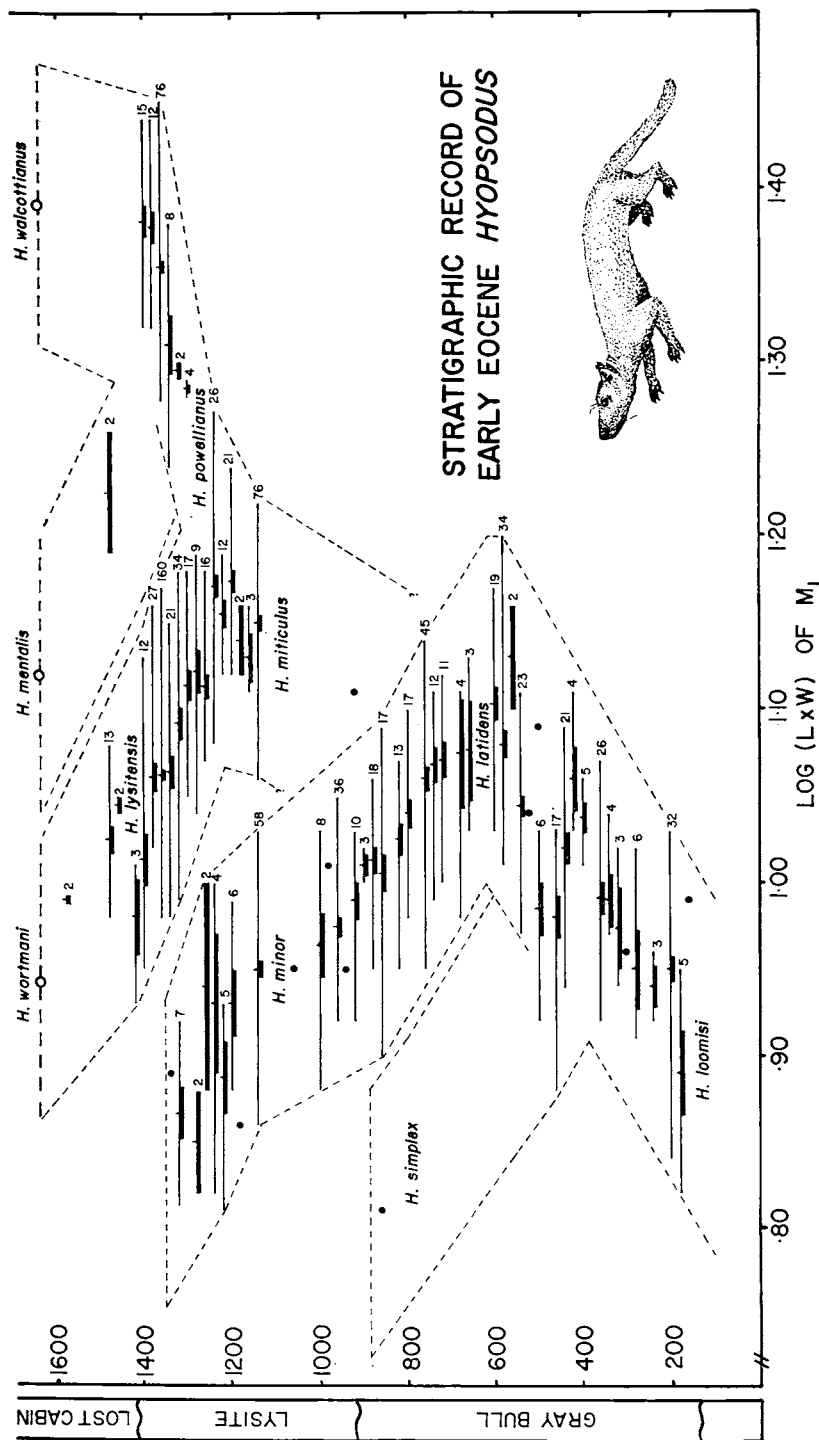


Fig. 5. Evolution of the Early Eocene condylar length *Hyopsodus* in northern Wyoming. Same as figure 4, with the addition of specimens from interpolated localities (listed at right in fig. 2). This figure differs slightly from figure in Gingerich (1947a) due to collection of additional specimens and altered positions of some interpolated localities (see text). Specimens in collections of Yale Peabody Museum and University of Michigan Museum of Paleontology.

significantly lower than adjacent localities farther away from the drainage. In other words, topography plays a greater role in the correlation than it was previously assigned. This possibility was observed during the field work of 1974, and subsequent analysis of specimens in the laboratory (as outlined above) has confirmed its importance. An isopach map of the study area prepared from the data of figure 2 shows the importance of topographic relief quite clearly.

The phylogeny of *Hyopsodus* was reanalyzed and refined, integrating the Meyer-Radinsky and Neasham-Vondra stratigraphic sections with data on *Hyopsodus* in an isopach map showing the stratigraphic positions of all localities in the region, to build up as comprehensive a stratigraphic framework as possible using all available evidence. Thus, as many localities as possible were correlated and added to the stratigraphic column derived from the measured sections. The results of this effort are summarized graphically in figure 2. The purpose of building this detailed stratigraphic framework based on measured sections and correlations using both *Hyopsodus* and geographic proximity was to test further models of phylogeny by studying the evolution of *other* Early Eocene mammals (that is, not *Hyopsodus* itself). Results of a study of *Haplomylus* and of *Pelycodus* in this stratigraphic context are summarized below.

Phylogeny of Haplomylus.—*Haplomylus speirianus* is a small condylarth originally described by Cope (1880) as a species of *Hyopsodus* but now known to differ significantly from the latter genus, particularly in the structure of its premolar teeth. Various authors have discussed the different forms of *Haplomylus*. Among these, Simpson (1937b) described the Sand Coulee or earliest Eocene specimens of *Haplomylus* as significantly smaller than those from the Gray Bull interval. The situation was confused in that several "Clark Fork" specimens thought to be the earliest representatives of *Haplomylus* were among the largest specimens known. More recently, Delson (1971) concluded, from an analysis of the American Museum collections, that *Haplomylus* shows no significant change in size as one looks at successive Early Eocene horizons. The same could be said for many samples of fossil mammals in collections made by early workers. However, as these early collections were not clearly restricted to small localities within limited stratigraphic intervals, they do not give a fair test of the presence or absence of significant size or other change as one looks at successive intervals. There is little question that collections from widely separated horizons were often mixed either in the field or during subsequent cataloging, and, as Wood (1967) has discussed at length, some of the early collections from the Clark Fork and Gray Bull beds of Wyoming are unfortunate examples of this.

Analyzing the recent Yale and Michigan collections from the Gray Bull beds in the stratigraphic context of figure 2, an unmistakable trend toward larger size is indicated as one goes up the section. This trend is illustrated in figure 6. In addition to the Graybull specimens, two from Clark Fork beds (one from the Bear Creek mine, the other from the Hoback Formation) are clearly significantly smaller than those of the

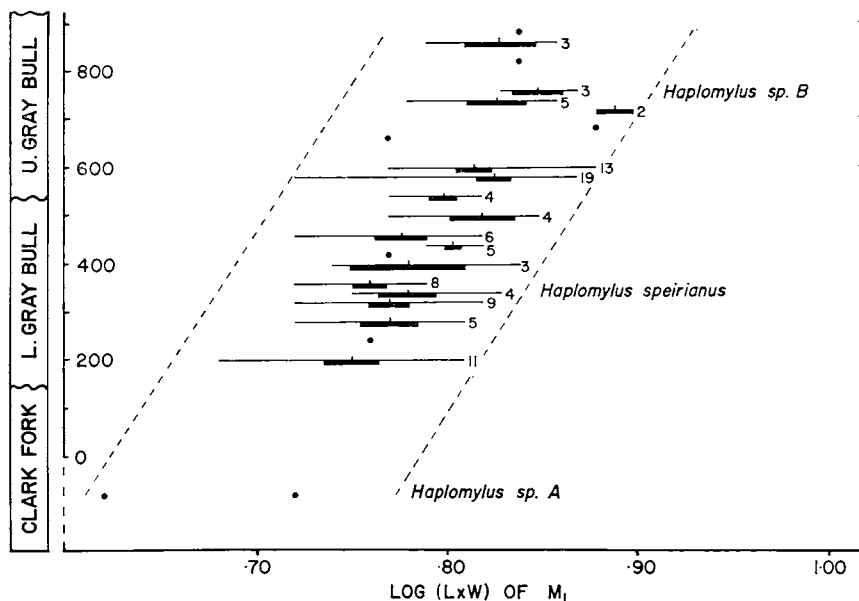


Fig. 6. Evolution of the early Eocene condylarth *Haplomylus* based on specimens from Graybullian localities listed in figure 2 and two additional Clarkforkian specimens. Note that each sample has the variability characteristic of a single species, and that size increased significantly going up the stratigraphic column. Compare this gradual evolutionary interpretation with the typological punctuated interpretation of *Haplomylus* phylogeny in table 1. Specimens in collections of Yale Peabody Museum, University of Michigan Museum of Paleontology, and Princeton University.

lower Gray Bull. Comparison of Simpson's "Clark Fork" specimens with those from the upper Gray Bull leaves little question that they were actually obtained from upper Graybull beds.

The available samples of *Haplomylus* from restricted localities of known stratigraphic level thus point to a single lineage of *Haplomylus* evolving in the Early Eocene, a lineage that gradually became larger with time. Three stages of *Haplomylus* evolution are recognized: "*H. sp. A*", *H. speirianus*, and "*H. sp. B*." Whether these are recognized as different species or subspecies or merely as informal stages of evolution, the essential fact is that they all form a connected series of successive populations changing gradually but significantly through time.

A note might be added here concerning the interaction of *Haplomylus* and *Hyopsodus* in the Early Eocene. If the plot of *Haplomylus* evolution illustrated in figure 6 were replotted on the scale of figure 5, *Haplomylus* would fit nicely into the latter figure as a lineage evolving in parallel with *Hyopsodus loomisi*. The very small species *Hyopsodus* "*simplex*" appeared only as *Haplomylus* became relatively rare and neared extinction (or at least was about to leave the region and ecology being sampled). The absence of a connection between the isolated specimen of *H. "simplex"* at level 860 and the suggested origin of this species at

about level 440 might reasonably be ascribed to the presence of *Haplomylus*. It is, of course, not possible at this stage to determine whether *H. "simplex"* appears because *Haplomylus* was disappearing or *vice versa*, but there appears to have been an exclusive interaction between the two.

Phylogeny of Pelycodus.—Species of *Pelycodus* are the most common primate fossils found in the Early Eocene beds of the Big Horn Basin. *Pelycodus*, like *Hyopsodus*, occurs through the complete sequence of Early Eocene sediments. Some 255 specimens are plotted in stratigraphic context in figure 7, the stratigraphic position of samples being derived from figure 2.

Five valid species names have been applied to stages of the evolution of *Pelycodus*. As is illustrated in figure 7, *Pelycodus ralstoni* gave rise to *P. trigonodus*, which was in turn ancestral to *P. jarrovi*. *P. jarrovi* apparently gave rise to both "*N.*" *nunienus* and "*N.*" *venticolis* (these two species are presently placed in *Notharctus*, an implied diphyletic origin of that genus that will be revised in a subsequent study).

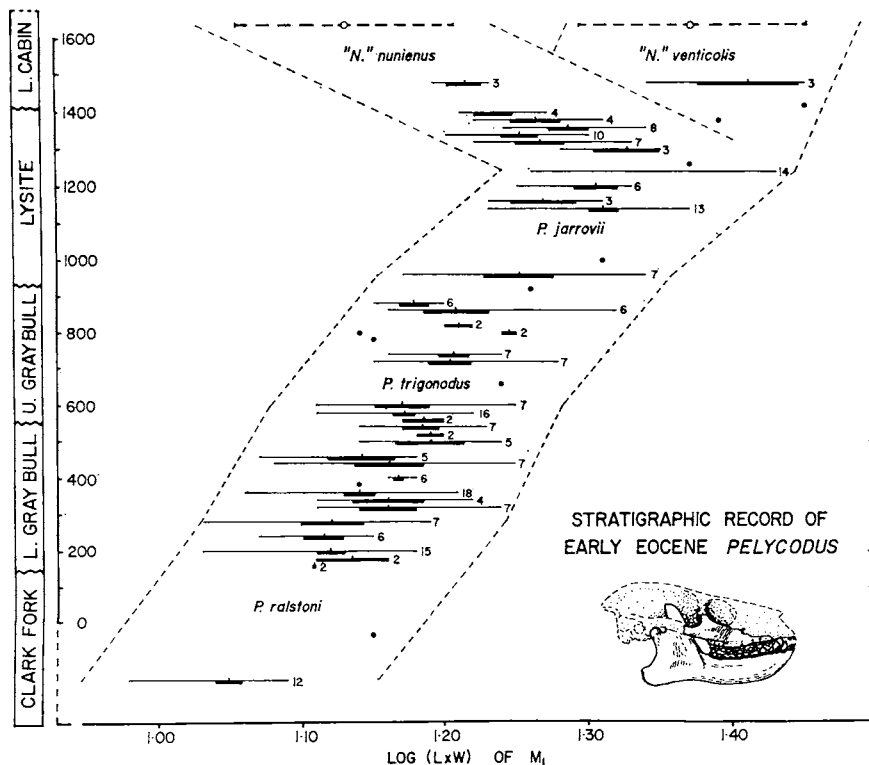


Fig. 7. Evolution of the Early Eocene primate *Pelycodus*. Specimens from localities listed in figure 2, with the addition of two Clarkforkian samples. Open circles are means of Lost Cabin samples measured by Guthrie (1971). Based on specimens in the collections of Yale Peabody Museum, American Museum of Natural History, and Princeton University.

As was the case with *Haplomylus*, the genus *Pelycodus* exhibits a relatively long period of continuous gradual phyletic change (anagenesis) leading from *P. ralstoni* to *P. jarrovi*. The type specimens of these three species in this sequence represent populations that are significantly different in size (and in other morphological characters as well), but of primary importance is the fact that these distinct species populations are connected by a continuous, gradually evolving chain of related populations. Recognition of the separate species is based on an arbitrary division of the lineage into suitable evolutionary units.

As was mentioned in the introduction, cladogenesis is a more challenging process conceptually than anagenesis and the record of lineage branching, where *P. jarrovi* gives rise to "*N.*" *nunienus* and "*N.*" *venticolis*, is of particular interest. The two derived species appear, as in *Hyopsodus*, to diverge gradually from a common ancestral population (though this is better illustrated by *N. nunienus* than by *N. venticolis*). The last common ancestral population of the two derived species may have been that represented by the sample of 14 specimens from level 1240 illustrated in figure 7, a sample of which appears slightly too variable to represent a single species, but is not yet sufficiently bimodal to give clear evidence for two.

One curious feature of the lineage bifurcation in *Pelycodus* that also appears in the division of lineages in *Hyopsodus* is the tendency for the smaller of the two new species to be the one best represented in the fossil record. If the fossil record gives an adequate indication of local population size, it appears that the morphologically larger species resulting from a bifurcation generally exists initially with a smaller population size than the morphologically smaller species does (this is also true in the Plesiadapidae, see fig. 8).

Some competitive exclusion was suggested by the distributions of the condylarths *Hyopsodus* and *Haplomylus*, but the same cannot be said of *Hyopsodus* and the primate *Pelycodus*. *Hyopsodus* and *Pelycodus* overlap considerably in size and are found commonly in the same sedimentary beds, indicating significantly different adaptations and microhabitats in the two, as is common in mammals placed in distinct Orders.

Additional well-represented Early Eocene taxa are presently being studied in the stratigraphic framework outlined here.

EVOLUTION OF PLESIADAPIDAE

A comprehensive study of the European and North American Plesiadapidae (the most common primates in Paleocene collections) has recently been completed (Gingerich, ms), and it will eventually be published in full. Certain aspects of that study, which pertain to the subject of the present investigation, are summarized here. Complete documentation will be available when the longer manuscript is published.

Paleocene mammals in North America are generally preserved in a setting rather different from that described above for the Early Eocene faunas of the Big Horn Basin, although some of the richest Paleocene

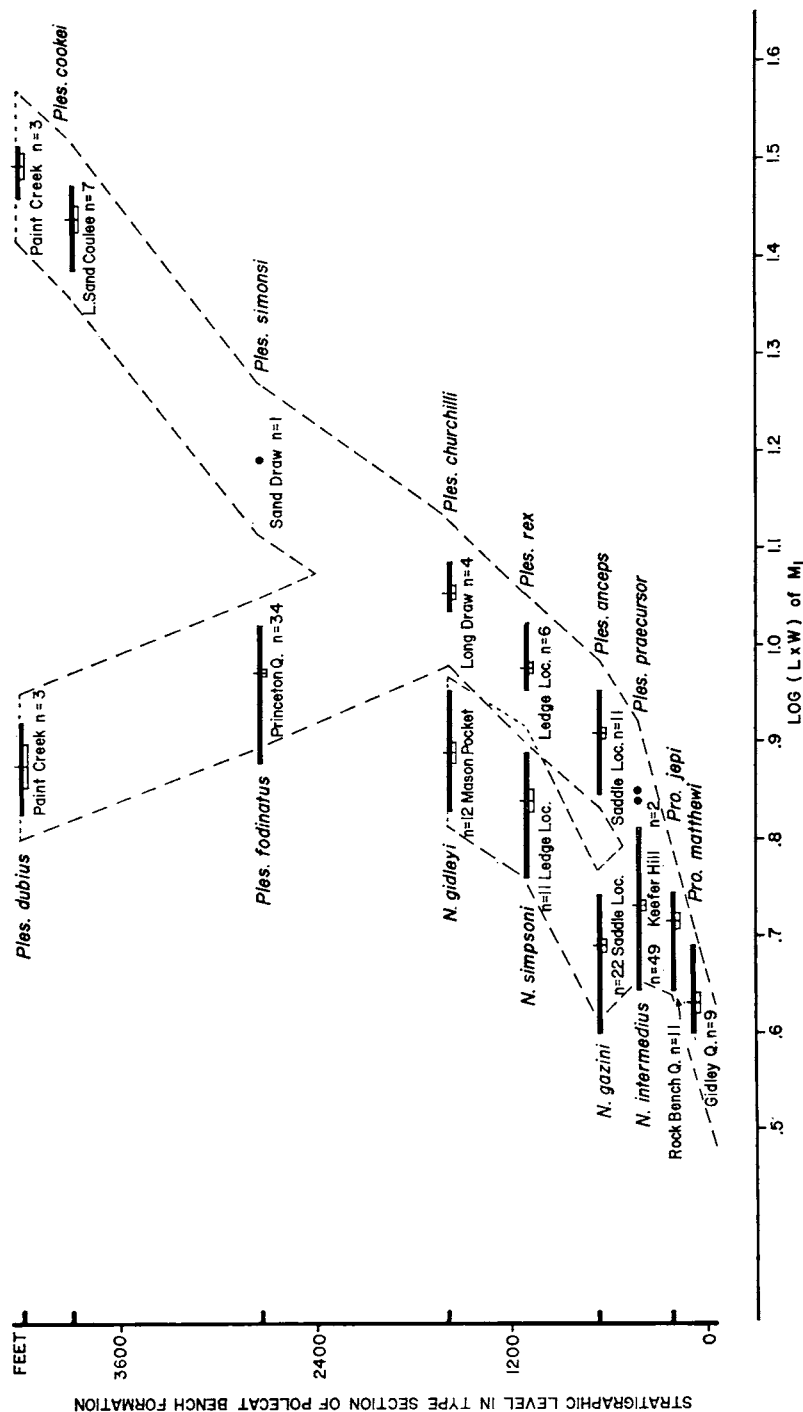


Fig. 8. Evolution of the Early Tertiary Plesiadapidae in North America, based on specimens from eight successive stratigraphic zones. Vertical scale from measured type section of Poolecat Bench Formation near Powell, Wyo., which includes specimens from five zones, the remaining zones are interpolated from other stratigraphic sections. Upper part of diagram exaggerated by more rapid sediment accumulation than in lower part. Total time represented is about 62 to 53 m.y. B.P. Symbols show mean, standard error and range as in previous figures. Data from Gingerich (ms, 1975), based on specimens in many museums.

faunas are also found in the Big Horn Basin. Localities yielding Paleocene mammals are relatively rare but, once found, often yield large collections. The most important of these collections are quarry samples from single very thin stratigraphic layers. Sedimentary evidence of deposition in such quarries often suggests a single catastrophic mortality (such as a drought followed by a flood), in which case the sample probably represents animals living in a single ecological and temporal community.

A major drawback to evolutionary studies of Paleocene mammals has been the absence of documented stratigraphic relationships between excellent quarry samples of Paleocene mammals. Fortunately, Simpson (1937a) published a detailed stratigraphic ordering of four Paleocene quarries in Montana which yielded plesiadapids. Similarly, six quarries and surface localities yielding plesiadapids, discovered by the late G. L. Jepsen of Princeton University, can be dated relative to each other by superposition in the type section of the Polecat Bench Formation of the Big Horn Basin in Wyoming. By studying additional local sections with two or more plesiadapid species in stratigraphic sequence, then correlating the levels that contain identical species, a sequence of eight distinct zones has been built up spanning the Middle and Late Paleocene.

The logic and the procedures of this method are essentially those embodied in William Smith's principle of faunal succession. While some morphological change is necessary before Smith's principle can be applied, no particular tempo or direction need be assumed for this change. It is thus possible to place the species of Plesiadapidae in their zones, then ask what the direction and rate of change has been. Assuming an evolutionary change from small to larger sized individuals, placing the given species at their appropriate grade in this sequence, then concluding that the species showed gradual evolution from small to larger size would obviously be an essay in circularity. On the other hand, arranging the species in a sequence of superposed zones based on their demonstrated stratigraphic positions and correlations shares none of this circularity. The latter is the methodology adopted here.

For comparison with the previous plots of *Hyopsodus*, *Haplomylus*, and *Pelycodus*, the evolutionary change in size of the North American Plesiadapidae is plotted in figure 8, where the vertical scale is based on the measured type section of the Polecat Bench Formation. This entire sequence was not deposited at a uniform rate, and there is considerable evidence to suggest that the rate of deposition in the lower part of the section was much slower than in the upper part, leading to an apparent stretching out of the upper part of the phylogeny.

The Plesiadapidae, like *Hyopsodus*, *Haplomylus*, and *Pelycodus*, exhibit gradual phyletic evolution, overall size increase, iterative evolution of small species, and character divergence following the origin of each new lineage. Interestingly, the *Nannodectes* lineage became smaller than its sister *Plesiadapis* lineage until the ranges of their variation no longer overlapped, then it evolved larger size in parallel with *Plesiadapis*.

In addition to tooth size, all the other characters of *Plesiadapis* studied exhibited continuous gradual change: incisor morphology and occlusion, premolar morphology and occlusion, the pattern of crenulations and shape of M_3 , and reduction of the dental formula. The latter is perhaps the most interesting since the number of teeth in a mammalian jaw is a discrete or meristic character and cannot show the minute continuous variations possible in such characteristics as size or shape. Loss of a tooth, a discrete jump from one state to another, in several instances proceeded continuously by continuous changes in the frequencies of dimorphism—the percentage of specimens retaining the tooth gradually being reduced until it was lost entirely from the population.

DISCUSSION

The classic examples of mammalian evolution taken from the fossil record are by and large arrangements of genera in time (the evolution of the horse from *Hyracotherium* to *Equus* is the one most often cited). That our heralded examples should be generic in level, when we have long known that the most significant evolutionary change occurs at the level of the species, seemed a curious failure of the fossil record. Thus study of the Plesiadapidae was begun several years ago to see whether the fossil record might be sufficiently complete to record evolutionary changes at the level of the species.

When the paper on "Punctuated Equilibria" was published by Eldredge and Gould (1972), new impetus was given for detailed studies of the fossil record. Eldredge and Gould (1972, p. 94) outline in an apparently logical series of steps a concept of geographic speciation (cladogenesis) current among modern biologists, concluding that equilibrium or a lack of significant change should characterize the evolution of lineages through time, and that when new lineages arise they should do so instantaneously with respect to geological time. The result is a "punctuated equilibrium" model of phylogeny standing in direct contrast to the model of gradual phyletic change accepted for most of the past century. Few problems are of more fundamental importance to our understanding of evolution than an exhaustive testing of these two models, models that can only be tested by detailed studies of the fossil record utilizing sound methods of stratigraphical paleontology.

The studies reported here appear in all respects to support the traditional model of phyletic gradualism *in the limited geographic, stratigraphic, and systematic portion of evolutionary history that they test*, but much of the evolutionary biosphere remains to be tested. That the results reported here differ significantly from those of Eldredge and Gould may be due to a number of factors. First, it is possible that the tempo of evolution in the marine setting differs from that of the continental setting. Second, the early Tertiary is a time of explosive initial radiation in the history of many groups of mammals. Studies of more mature animal radiations might be expected to be more stable than the early condylarths and primates analyzed here (the radiation of trilobites,

for example, would presumably be a relatively mature one by the Devonian). Finally, trilobites and pulmonate gastropods (the examples of Eldredge and Gould) are far removed from mammals, and widely differing tempos and modes of speciation might characterize such different groups of animals.

Three further points need to be discussed in evaluating the examples presented here: (1) the importance of heritability in evolution by natural selection, (2) the reason why few previous studies of fossil mammalian species exhibit phyletic gradualism, and (3) the implications of these examples for evolutionary theory.

Heritability.—Mammalian teeth have two properties that make them especially attractive for evolutionary studies. The first of these concerns the ontogeny of teeth in mammals. The crowns of mammalian teeth are mineralized within the upper and lower jaw before they erupt—once formed and erupted the teeth of most mammals can no longer grow, and ontogenetic changes in the size of teeth are thus impossible. Most other skeletal characters in vertebrate and invertebrate animals undergo significant changes in ontogeny, making many of these characters unsuitable for detailed analysis in the fossil record (where age changes can rarely be controlled or taken into account).

Mammalian teeth have an additional important property. Natural selection acts in response to the additive component of genetic variance of any given trait. The fraction of phenotypic variance resulting from additive genetic factors is designated the heritability of a trait, and heritability is thus the proportion of total variability on which selection can act (Falconer, 1960). Measures of general body size, of which the tooth measurements plotted in figures 5 to 8 are an example, usually have high components of additive genetic variance. Actual measurement of the heritability of tooth size in mammals has rarely been attempted. In one such study, Bader (1965) obtained the high heritability value of 0.67 for the width of the central cheek tooth in the house mouse *Mus musculus* (a central tooth is the one plotted here in figs. 5–8). While additional study of the heritability of teeth in other animals is obviously needed, it is clear that tooth size is a trait susceptible to evolution by natural selection. (This raises an obvious question as to how *natural selection* could produce a *Phacops* trilobite with 17 dorsoventral files of eye lenses from an ancestral stock uniformly possessing 18 files, if the files evolve as described by Eldredge and Gould, 1972). In addition, it seems likely that the high heritability of characters related to body size imposes a finite limit on rates of morphological change resulting from natural selection, such as the relatively slow rates of character divergence following cladogenesis outlined here in figures 5 to 8.

It has been suggested in discussion that the patterns of phylogeny illustrated here might simply be the result of environmental influences. The demonstrated high heritability of tooth measures argues against this, and the presence of diverging lineages would seem to defy purely external environmental influences.

Previous studies of fossil mammals.—W. D. Matthew, who was a leading mammalian paleontologist, a man of considerable field experience, and one of the first to appreciate the importance of keeping precise stratigraphic records with specimens, published an important observation on field work a few years before his death. Writing of his field experience, he noted that “one could actually trace in the succession of strata the progressive evolution of the different races, verifying in specimen after specimen the primitive characters of those from the lower layers, the progressive characters of those from the upper layers, and the intermediate conditions in specimens from the middle beds” (Matthew, 1926, p. 454). Why this conviction of continuous gradual change in the more complete stratigraphic columns has not been documented by many more detailed publications on the fossil record is a mystery. Perhaps all those with experience similar to Matthew’s learned in the field to share the conviction and never realized the need for published documentation. As the proportion of paleontologists making their own collections has decreased in recent years, the conviction has eroded.

Comparing the results illustrated here in figures 5 to 8 with the results of previous studies published on the same species, and in some cases on the very same collections, two methodological problems appear in the previous studies which made a punctuated picture of phylogeny inevitable, if indeed a coherent picture emerged at all. The first of these problems stems from typology, the second from pooling samples collected from broad stratigraphic intervals.

The earliest study of *Hyopsodus* evolution was published by Matthew himself in 1915. Matthew had available almost a thousand specimens from the Early Eocene of New Mexico and Wyoming. Furthermore, the specimens came from four distinct zones known to be positioned one above the other. The essential character of Matthew’s key to the species of *Hyopsodus* was the length of the molar series, each species being identified by the length of its molars in millimeters. The result, if one examines Matthew’s tables, was a curiously punctuated concept of phylogeny. Simpson (1943, p. 174) has illustrated this problem nicely for the case of *Ectocion*, contrasting the typological with the evolutionary concept of the species. A similar, but rather more simple hypothetical example is illustrated in table 1, which is derived from figure 6.

The typological interpretation of *Haplomylus* evolution in table 1 shows clearly the attributes of a punctuated equilibrium model of phylogeny. The equilibrium of each lineage and the abrupt transitions from one species lineage to another were, however, dictated by the typological methodology, not by any lack of continuous variation in the specimens themselves. Figure 6 shows clearly for this same example that when the first question asked of the sample from each stratigraphic level is “how many biological species are represented at this level?” (and this is the first question to ask of any sample)—the answer is one. This one lineage changes significantly through time, and, by dividing the stratigraphic

TABLE 1

Typological "punctuated equilibrium" interpretation of the fossil record of *Haplomylus* in the Big Horn Basin, based on data of figure 6. Though hypothetical, this example illustrates the typological approach taken in some earlier studies of *Hyopsodus*, *Pelycodus*, *Plesiadapis*, and *Ectocion* (see Simpson, 1943, p. 174, for a similar example). Typology has here led to recognition of small specimens as one species, medium-sized specimens as a second species, and large specimens as a third species. Numbers in the table indicate the number of specimens of each typological "species" found in each stratigraphic unit. Given that the ancestral form was small, the phylogeny shown here by arrows would be favored. Solid arrows show lines of descent, dashed lines suggest the origin of new species as peripheral isolates and/or migration into the area of study. Whereas application of a biological species concept shows that only a single gradually evolving population is represented in the collections of Early Eocene *Haplomylus* (fig. 6), application of a typological concept leads one to postulate up to three lineages, each persisting unchanged through time, with new lineages (such as species "B") appearing abruptly in the geological record.

Species:	<i>H. sp. A</i> "Small species" size $M_1 < 0.70$	<i>H. speirianus</i> "Medium species" $0.70 < \text{size } M_1 < .80$	<i>H. sp. B</i> "Large species" $0.80 < \text{size } M_1$
Stratigraphic level:			
Upper Graybullian		16	41
Lower Graybullian	1	38	15
Clarkforkian	1	1	

units finely enough, it is clear that the transition from species "A" to *H. speirianus* to species "B" is both continuous and gradual.

The second methodological problem leading to the appearance of punctuated equilibrium, when in fact transitions are now known to have been gradual, is due to pooling samples from broad stratigraphic intervals. This problem, too, is illustrated by previous interpretations of the phylogeny of *Hyopsodus*. Guthrie (1967) and Gazin (1968) made major advances over Matthew's study of *Hyopsodus* by abandoning his typological species concept. Both Guthrie and Gazin plotted histograms showing the variation of molar size in each successive level of the Early Eocene. Through no fault of theirs, the best information available with

each specimen identified it to one of the four major stratigraphic divisions shown in figure 2 (Lower Gray Bull, Upper Gray Bull, Lysite, or Lost Cabin), each of which represents approximately a million years of geological time. Taking a conservative view, Guthrie and Gazin connected the central peaks of histograms from the four stratigraphic levels, then connected the lateral peaks. The result once again was an appearance of punctuated equilibrium, but here as in the typological example discussed above, both the punctuations and the equilibrium were imposed on the data by interpretation, an interpretation the data presented were not adequate to test. With much finer division of the stratigraphic column, the same specimens studied by Guthrie and Gazin yield a pattern of gradual phyletic change (fig. 5).

From the more detailed stratigraphic study, it is clear that a major cladogenic speciation event occurred on the order of once every million years. Similarly, gradual change in simple phyletic lineages is sufficient in a million years time to lead to recognition of distinctive species originating through anagenesis. The point of this discussion is that if new species are arising on the average of every million years, a stratigraphic system that divides the fossil record into units as coarse as a million years in duration will not be sufficient to resolve the evolutionary changes occurring in the origin of these species.

Detailed stratigraphy is more important than even Matthew realized. Any study adopting a typological methodology, or failing to provide stratigraphic evidence several times finer in scale than the events it is being called on to clarify, is almost certain to yield a "punctuated equilibrium" picture of phylogeny simply because the methods are not sufficiently precise to resolve gradual change if it is present. The examples presented by Eldredge and Gould (1972) to illustrate the punctuated equilibrium model appear to fall in the latter category: only with finer stratigraphic study will *Phacops* or *Poecilozonites* provide evidence for or against the punctuated equilibrium model—as presently understood they are not an adequate test of the model.

Speciation models.—A final subject growing out of the detailed studies of evolution presented here relates to the implication of gradual phyletic patterns for our understanding of the geographic speciation mechanism itself. The "instantaneous" splitting of fossil lineages has sometimes been cited as evidence for sympatric speciation, but the previous examples have now all been ascribed to migration or colonization (Mayr, 1970). The evolution of *Hyopsodus lysitensis* and *H. powellianus* from *H. miticulus* and the evolution of "*Notharctus*" *nunienus* and "*N.*" *venticulis* from *Pelycodus jarrovi* are new examples of lineage splitting, where the initial changes in the descendants are so minor that they are unlikely to be the result of migrations from some isolated peripheral population.

According to the orthodox allopatric speciation model "the morphological features that distinguish a descendant species from its ancestor are present close after, if not actually prior to, the onset of genetic isola-

tion" (Eldredge and Gould, 1972, p. 94-95). If, in fact, the morphological features distinguishing a descendant species do appear prior to the onset of genetic isolation, disruption of gene flow between populations of the ancestral and new species should result in two distinct morphotypes showing little or no overlap in morphology. However, the paired descendant species appearing after speciation events in *Hyopsodus*, *Pelycodus*, and *Plesiadapis* were not initially distinctive, but only became so after a significant period of time. The remaining discussion will center on the phylogeny of *Pelycodus*, although the points raised are illustrated by *Hyopsodus* and *Plesiadapis* as well.

Comparing the early members of the species "*N.*" *nunienus* and "*N.*" *venticolis* with each other (fig. 7), the two are virtually identical in size as well as every other morphological characteristic of the upper and lower dentition available for comparison (one can of course postulate that the two differed significantly in coat color, tail length, or some other character that will never be available for study, but the evidence that is available for analysis indicates that the two were very similar). The fact that the two species, once established sympatrically, diverge in a regular way from each other in size suggests that size was indeed an important property of their general adaptation, further supporting the thesis that the two species did not differ in an important way when founded (this is also true of the bifurcations in the phylogenies of *Hyopsodus* and *Plesiadapis*).

The implication of this for speciation is that, for the examples studied here, differences in morphology postdate significantly the onset of genetic isolation, rather than predating genetic isolation as postulated by Eldredge and Gould (1972) and others. These data thus lend considerable support to the model of speciation outlined by Remington (1968, p. 374, in discussing suture-zones of hybridization among North American animals today) and by Bock (1972). Furthermore, they are consistent with the pluralistic view of speciation endorsed by Gould and Johnson (1972, p. 489).

If one looks at the distribution of a typical mammalian species today (the mountain gorilla furnishes a good example, Emlen and Schaller, 1960), the species is distributed in relatively small populations isolated by regions unsuitable for habitation (rivers, mountains, et cetera), and it is likely that these small populations are shuffled stochastically by the vagaries of climate. It is not unreasonable to postulate a network of rivers and highlands dividing *Pelycodus*, *Hyopsodus*, and *Plesiadapis* in western North America each into subpopulations merging and dividing through the course of the Early Tertiary. These subpopulations were presumably virtually identical phenotypically and genotypically and, when merged, usually hybridized freely. Occasionally however a subpopulation might differ sufficiently genetically from an adjacent population to cause a significant barrier to hybridization. Such a barrier almost certainly developed in an "allopatric" geographically distinct subpopulation, but the term parapatric is preferable to describe this situation since the subpopulation

or deme in question was probably never really isolated by any great distance from surrounding subpopulations. A deme barred from free hybridization with surrounding subpopulations probably often became extinct, swamped by the competition of its neighbors. Under certain conditions (an available niche of sufficient width to accommodate two closely related species being most important) both the differing deme and its homogeneous neighbors might survive, each creating a strong directional field of selection operating on the other, leading to the character divergence seen in figures 5, 7, and 8. While most such stochastic experiments in cladogenesis were probably doomed to fail, the remarkable radiation of Early Tertiary mammals stands as clear evidence of considerable success as well.

The model of speciation outlined here is basically geographic in separating a species' gene pool into smaller units, each with a separate geographic range, but the interactions that cause species derived from cladogenesis to differ from each other and from their ancestors are a result of at least parapatric processes. This is not to deny that a species originating as an isolated peripheral population could ever become superior to and replace its parent species in a wave of migration, but the examples of cladogenesis illustrated here in *Hyopsodus*, *Pelycodus*, and *Plesiadapis* suggest that a parent species divided into two new sister species which subsequently diverged to minimize competition with each other.

SUMMARY

Large collections of the three early Eocene mammals *Hyopsodus*, *Pelycodus*, and *Haplomylus* from over 50 successive stratigraphic levels and an additional large collection of *Plesiadapis* specimens from eight successive Paleocene zones exhibit gradual phyletic evolution, overall size increase, iterative evolution of small species, and character divergence following the origin of each new lineage.

Earlier studies of these same animals indicated abrupt transitions from one species to another followed by long periods of time during which each species persisted relatively unchanged. This "punctuated equilibrium" picture of phylogeny suggested by the previous studies is now seen to be an artifact of methodology: the previous studies adopted (1) an essentially typological species concept or (2) an insufficiently divided stratigraphic context, or both. Either of these methodological approaches, or (3) study of stratigraphic sections that include significant gaps in sedimentation, will invariably lead to a "punctuated equilibrium" model of phylogeny, if indeed any coherent picture of phylogeny emerges at all.

Studies aimed at testing models and patterns of phylogeny must meet three criteria: (1) the stratigraphic sections being studied must be complete, or sufficiently overlapping that a relatively complete composite section can be constructed; (2) the stratigraphic sections must be subdivided into units representing significantly less time than that separating

the evolutionary events being studied, the more finely divided the better; and (3) the samples from each level must be treated as "biological" species, that is, the number of species present at each level must be based on the number of reproductively isolated evolutionary lineages indicated for that level rather than on the total number of morphotypes present. The four genera of early Tertiary mammals discussed in this paper meet each of the three criteria. While these examples consistently show gradual evolutionary change, this tempo may not be characteristic of all animal speciation, and much additional study of other animals in other environments and geological periods is needed.

To the extent that the origin of new lineages in *Hyopsodus*, *Pelycodus*, and *Plesiadapis* is representative of this process in terrestrial mammals in general, cladogenic speciation appears to be geographically a parapatric rather than strictly allopatric phenomenon. Morphological differences appear following the contact of two new species rather than before contact, and the differences appear to be due to character divergence to minimize competition between recently sympatric, closely related, morphologically similar, but reproductively distinctive populations. In conclusion, the sequence of events outlined here for cladogenic speciation appears to accord better with the pluralistic sympatric or parapatric view of speciation of Gould and Johnson (1972) than with the allopatric orthodoxy of Eldredge and Gould (1972).

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REFERENCES

- Bader, R. S., 1965, Heritability of dental characters in the house mouse: *Evolution*, v. 19, p. 378-384.
Berggren, W. A., 1972, A Cenozoic time-scale—some implications for regional geology and paleobiogeography: *Lethaia*, v. 5, p. 195-215.

- Bock, W. J., 1972, Species interaction and macroevolution: *Evolutionary Biology*, v. 5, p. 1-24.
- Cope, E. D., 1880, The northern Wasatch fauna: *Am. Naturalist*, v. 14, p. 908-909.
- Darwin, C., 1859, The origin of species: London, John Murray, 502 p.
- Delson, E., 1971, Fossil mammals of the early Wasatchian Powder River local fauna, Eocene of northeast Wyoming: *Am. Mus. Nat. History Bull.*, v. 146, p. 305-364.
- Eldredge, N., and Gould, S. J., 1972, Punctuated equilibria: an alternative to phyletic gradualism, in Schopf, T. J. M., ed., *Models in Paleobiology*: San Francisco, Calif., Freeman, Cooper and Co., p. 82-115.
- Emlen, J. T., and Schaller, G. B., 1960, Distribution and status of the mountain gorilla: *Zoologica*, v. 45, p. 41-52.
- Falconer, D. S., 1960, Introduction to quantitative genetics: Edinburgh, Oliver and Boyd, 365 p.
- Gazin, C. L., 1968, A study of the Eocene condylarthran mammal *Hyopsodus*: *Smithsonian Misc. Colln.*, v. 153, no. 4, p. 1-90.
- Gingerich, P. D., 1969, Markov analysis of cyclic alluvial sediments: *Jour. Sed. Petrology*, v. 39, p. 330-332.
- 1974a, Stratigraphic record of Early Eocene *Hyopsodus* and the geometry of mammalian phylogeny: *Nature*, v. 248, p. 107-109.
- 1974b, Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species. *Jour. Paleontology*, v. 48, p. 895-903.
- ms, 1974, Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates): Ph.D. thesis, Yale Univ., New Haven, 370 p.
- 1975, New North American Plesiadapidae (Mammalia, Primates) and a biostratigraphic zonation of the Middle and Upper Paleocene: *Univ. Mich. Mus. Paleontology Contr.*, v. 24, no. 13, p. 135-148.
- Gould, S. J., and Johnson, R. F., 1972, Geographic variation: *Ann. Rev. Ecology and Systematics*, v. 3, p. 457-498.
- Guthrie, D. A., 1967, The mammalian fauna of the Lysite member, Wind River Formation (Early Eocene) of Wyoming: *Southern California Acad. Sci. Mem.*, v. 5, p. 1-53.
- 1971, The mammalian fauna of the Lost Cabin Member, Wind River Formation (Lower Eocene) of Wyoming: *Carnegie Mus. Annals*, v. 43, p. 47-113.
- Kurtén, B., 1955, Sex dimorphism and size trends in the cave bear, *Ursus spelaeus* Rosenmüller and Heinroth: *Acta Zool. Fennica*, v. 90, p. 1-48.
- Maglio, V. J., 1973, Origin and evolution of the Elephantidae. *Am. Philos. Soc. Trans.*, v. 63, no. 3, p. 1-149.
- Matthew, W. D., 1915, A revision of the Lower Eocene Wasatch and Wind River faunas. Part II. Order Condylarthra, family Hyopsodontidae: *Am. Mus. Nat. History Bull.*, v. 34, p. 311-328.
- 1926, Early days of fossil hunting in the high plains: *Natural History*, v. 26, p. 449-454.
- Mayr, E., 1970, Populations, species, and evolution: Cambridge, Mass., Harvard Univ. Press, 453 p.
- Neasham, J. W., and Vondra, C. F., 1972, Stratigraphy and petrology of the lower Eocene Willwood Formation, Bighorn Basin, Wyoming: *Geol. Soc. America Bull.*, v. 83, p. 2167-2180.
- Peckham, M., ed., 1959, The origin of species by Charles Darwin, a variorum text: Philadelphia, Univ. Pennsylvania Press, 816 p.
- Remington, C. L., 1968, Suture-zones of hybrid interaction between recently joined biotas: *Evolutionary Biology*, v. 2, p. 321-428.
- Simpson, G. G., 1937a, The Fort Union of the Crazy Mountain field, Montana and its mammalian faunas: *Smithsonian Inst., U.S. Natl. Mus. Bull.*, v. 169, p. 1-277.
- 1937b, Notes on the Clark Fork, upper Paleocene, fauna: *Am. Mus. Novitates*, no. 954, p. 1-24.
- 1943, Criteria for genera, species, and subspecies in zoology and paleozoology: *New York Acad. Sci. Annals*, v. 44, p. 145-178.
- 1944, Tempo and Mode in Evolution: New York, Columbia Univ. Press, 237 p.
- 1953, The major features of evolution: New York, Columbia Univ. Press, 434 p.
- Van Houten, F. B., 1944, Stratigraphy of the Willwood and Tatman Formations in northwestern Wyoming: *Geol. Soc. America Bull.*, v. 55, p. 165-210.
- Wood, R. C., 1967, A review of the Clark Fork vertebrate fauna: *Harvard Mus. Comp. Zoology Breviora*, no. 257, p. 1-30.