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CHAPTER 4

PUNCTUATED EQUILIBRIUM AND  
PHYLETIC GRADUALISM

Some Facts from the Quaternary  
Mammalian Record

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*Many breaks in the fossil record are real;  
they express the way in which evolution  
occurs, not the fragments of an imperfect  
record.*

Eldredge and Gould, 1972, p. 96

*Absence of evidence is absence of evidence,  
not evidence of absence . . . with respect to  
gaps in the evolutionary record.*  
Gingerich, 1984, p. 338

1. INTRODUCTION

Since Eldredge and Gould (1972) first wrote about "punctuated equilibrium" as a pattern for the history of life, three factions have appeared among evolutionary theorists. One faction favors the picture of punctuated equilibrium (Eldredge and Gould, 1972; Gould and Eldredge,

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1977; Gould, 1982, 1985; Stanley, 1975, 1979, 1982). Another favors the traditional alternative of phyletic gradualism or at least gradual change (Gingerich, 1976, 1984, 1985; Charlesworth et al., 1982; Rose and Bown, 1984; Malingren and Kennet, 1981, 1983; Ozawa, 1975). And the third faction suggests that the major differences between punctuated equilibrium and phyletic gradualism largely are semantic because evolution can and does produce both patterns, and moreover both were envisioned by the formulators of the modern evolutionary synthesis and even by Darwin (for example, Levinton and Simon, 1980; Stebbins and Ayala, 1981; Mayr, 1982; Hoffman, 1982; Johnson, 1982; Charlesworth and Lande, 1982; Ginzburg and Rost, 1982; Rhodes, 1983; Chaline, 1984; Newman et al., 1985). The differences in opinion persist largely because of a relative paucity of facts—facts about evolutionary relationships within lineages, about the rate of morphological change through time, about the distribution of the changes in space, and about the relationship between morphological change and speciation. The search for these facts has ranged with increasing success through several different geologic periods and kinds of organisms (for examples see recent summaries in Gingerich, 1985; Cope and Skelton, 1985, and Levinton, 1983), but only infrequently has it ventured into the realm of Quaternary mammals, that is, those that lived during the Pleistocene, which extends from about 1.8 million to 10,000 years ago, and the Holocene, which encompasses the last 10,000 years. In theory, however, Quaternary mammals should be able to provide information and precision about evolutionary tempos and modes that is not available from earlier parts of the geologic record. This is because the Quaternary is unique when compared to older time periods in at least five respects. It is a short period of geologic time, which provides the best glimpse of how evolution operates over a time scale of a few thousand up to 2 million years. Radiometric dating can be relatively precise, with uncertainties as little as  $10^2$ – $10^3$  years rather than  $10^4$ – $10^6$  years. Samples of fossil mammals commonly are larger and geographically more widespread than those from earlier times. Most of the genera and many of the species are still living or closely related to extant forms, so that we know more about their intraspecific morphological variation, their geographic distribution, their evolutionary relationships among species, and their habits and ecology. Finally, physical environmental changes are well enough documented for the Quaternary to aid us in assessing their impact on dispersal and evolution. What these special qualities of the Quaternary mammalian record add to the study of evolution is the subject of this chapter.

## 2. DEFINING THE MODELS

### 2.1. Punctuated Equilibrium

The picture of punctuated equilibrium clearly originated as an attempt to predict how allopatric speciation would appear in the fossil record. Eldredge (1971, p. 156) wrote, "I would suggest that the allopatric model (geographic speciation) be substituted in the minds of paleontologists for phyletic transformation as the dominant mechanism of the origin of new species in the fossil record." Eldredge and Gould (1972, p. 93) stated this theme more strongly: "We argue that . . . the theory of allopatric speciation . . . might reorient our picture for the origin of taxa." Eldredge and Gould (1972, p. 96) proposed that the fossil record could be used to test this assumption because in principle a certain pattern should result from the four "tenets and predictions" of allopatric speciation, namely:

*Tenet 1.* New species arise by the splitting of lineages;

*Tenet 2.* New species develop rapidly;

*Tenet 3.* A small sub-population of the ancestral form gives rise to new species; and

*Tenet 4.* The new species originates in a very small part of the ancestral species' geographic extent—in an isolated area at the periphery of the range.

From these tenets, Eldredge and Gould reasoned that we should not commonly see the transition of one species into another if we examine stratigraphically superposed fossils from a single geographic area, that is, in a local section. Rather, we should see a morphological break between ancestor and descendant. This is because the descendant evolved from a small, peripheral population that lived elsewhere and then migrated into the area of the local section. The four tenets do not mean that the descendant failed to change in sequential morphological steps from the ancestor in ecological time. They simply mean that we have a miniscule probability of finding the exact geographic region and slice of time where the change took place because that region is so small compared to the total range of the ancestral species, and because most morphological change is apt to be compressed into the short time when the ancestral population is still small and adapting to local conditions. Eldredge and Gould (1972, p. 96) clearly stated these points: "a sharp morphological break between the two forms . . . marks the migration of the descendant, from the peripherally isolated area in which it developed. . . . Since speciation occurs rapidly in small populations occupying small areas far from the center of ancestral abundance, we



will rarely discover the actual event in the fossil record" (*italics mine*). Punctuated equilibrium was the name they gave to the pattern that allopatric speciation should produce in the fossil record: relatively long stratigraphic intervals of morphological stasis punctuated by short stratigraphic intervals through which very different morphotypes appear. The new morphotypes appear suddenly because new species, evolved from peripheral populations, moved into the main part of the ancestral species' geographical range. Eldredge and Gould's null hypothesis became: The pattern of the fossil record frequently records stasis punctuated by rapid change. Reject the null hypothesis if gradual morphological change characterizes the fossils through most local sections. Do not reject it if punctuated equilibria prevail.

Eldredge and Gould (1972, pp. 108-110) then made a conceptual jump—they assumed punctuated equilibria was the dominant pattern in the history of life, which led to an important second-order hypothesis: Morphological trends in the fossil record result from selection at the species (or even higher) level, rather than at the level of organisms. The intent of their paper was to present the evidence and logic that led them to formulate the hypotheses, not the evidence to prove or disprove either one, although they openly admitted their bias to believe in punctuated equilibrium. Thus the stage was set for debate on two entirely different questions. Is punctuated equilibrium really the dominant pattern in the fossil record? And, assuming it is, what are the implications for macroevolution?

Gould and Eldredge (1977) more precisely drew the line between these questions. They devoted Section III of their paper to testing the hypothesis that punctuated equilibrium ruled in the fossil record, and with ten examples demonstrated that it did to their satisfaction (but certainly not to their opponents'). Section IV concentrated on the second question in framing "punctuated equilibria as the basis for a theory of macroevolution" (Gould and Eldredge, 1977, p. 139). Because they accepted that punctuated equilibrium via allopatric speciation was real, it became logically possible for them to assert that natural selection operates at "hierarchical levels higher than the local population," notably at the species level (Gould and Eldredge, 1977, p. 139). Stanley (1975) termed this concept "species selection," and Gould and Eldredge (1977, p. 139) regarded it as the most exciting outgrowth of their 1972 paper, because it was a new idea about how evolution works, that is, about modes. In particular, Gould and Eldredge (1977, p. 139) invoked species selection to explain evolutionary trends and thereby "challenged the central assumption that secured the admission of paleontology into the modern synthesis of evolutionary theory (Simpson, 1944

and 1953): change in gene frequency within populations is the building block of major evolutionary events."

Vrba (1980, p. 80) took the concept one step further when she proposed the effect hypothesis, which interpreted "trends as effects . . . of differential speciation rates, themselves effects of different degrees of environmental specialization between species, which in turn are effects of adaptation to local environments at the microevolutionary level." (She, later (Vrba, 1983, 1984a,b) was to point out that the effect hypothesis fundamentally differed from the concept of species selection, resembling it only in placing emphasis on selection at hierarchical levels higher than at the organismal level.) Whereas Gould and Eldredge (1977) restricted the term "punctuated equilibrium" to a model about tempos, and upon that model built species selection, the model about modes, Vrba (1980, p. 62) used "punctuated equilibrium" to encompass both tempo and mode.

Such a broad meaning became the common one when Gould (1982, p. 83) redefined punctuated equilibrium as

a theory . . . about the tempo and mode of evolution [*italics mine*]. It holds, speaking of mode, that significant evolutionary change arises in coincidence with events of branching speciation . . . speaking of tempo, that the proper geologic scaling of speciation renders branching events as geologically instantaneous and that, following this rapid origin, most species fluctuate only mildly in morphology during a period of stasis that usually lasts for several million years . . . 'geologically instantaneous' [is] . . . defined as 1 percent or less of later existence in stasis.

Furthermore, Gould retracted the earlier emphasis that punctuated equilibrium was intimately tied to allopatric speciation, because almost any model of speciation might produce a punctuated pattern over a geologic time scale. (He now cites peripatric speciation as being most consistent with punctuated equilibrium; Gould, 1985, p. 5.) Species selection became an operational part of the definition because

If the geometry of punctuated equilibrium prevails within the history of most clades . . . then traditional arguments for evolutionary trends (anagenetic trends within lineages) . . . must fail. . . . Trends must therefore be the product of a higher-order sorting that operates via the differential birth and death of species considered as entities . . . (Gould, 1982, p. 101)

Species selection was restricted to mean sorting of species through differential origination rates.

The concept of punctuated equilibrium thereby matured from a geologic projection of allopatric speciation into a theory of macroevolution in its own right, a theory which proclaims: (1) morphology of a species remains relatively stable through most of its geologic range; (2)

most morphological change occurs at or near a cladogenetic speciation event, that is, during splitting of lineages; and (3) as a consequence, evolutionary trends result from the propensity of some kinds of organisms to speciate more frequently than others, that is, species selection sensu Gould (1982, p. 104). Punctuated equilibrium is a name for a theory about how evolution operates only within the second of Gould's (1985) three tiers of time, the first tier being ecological moments, the second being geologic time (millions of years), and the third being times of mass extinction.

## 2.2. Phyletic Gradualism

In contrast, the tiers of time are transcended by the most publicized alternative to punctuated equilibrium, phyletic gradualism. This is a theory rooted in the assumption that the morphological changes that evolve through geologic time—macroevolution—are the cumulative effects of the same processes that power evolution in ecological time—microevolution. Although the idea of such gradual, cumulative change stems from Darwin (1859) and permeates much of the literature about evolution, its implications for the fossil record were seldom articulated until 15 years ago. Eldredge and Gould (1972, p. 89) named their conception of gradual change "phyletic gradualism" and in emphasizing how it differed from punctuated equilibrium, defined its tenets as follows:

Tenet 1. New species arise by the transformation of an ancestral population into its modified descendants;

Tenet 2. Transformation is even and slow;

Tenet 3. The transformation involves large numbers, usually the entire ancestral population; and

Tenet 4. The transformation occurs over all or a large part of the species range.

Phyletic gradualism thus was cast as the opposite mode of speciation to allopatric as extended back in geologic time; it implied that "a long sequence of continuous, insensibly graded intermediate forms linking ancestor and descendent" should be found in most reasonably complete local sections (Eldredge and Gould, 1972, p. 89). Eldredge and Gould cited the frequent absence of such gradational links as evidence that phyletic gradualism did not occur often. But others envisioned that gradual change in the fossil record would result from less extreme modes of evolution than phyletic gradualism sensu Eldredge and Gould (1972), even from allopatric speciation, and that gradational links were found when data were examined properly. Gingerich (1976, p. 2), re-

porting on a stratigraphic sequence of Eocene mammals to make his case, summarized this view:

General agreement exists regarding the usual modes of animal speciation, both phyletic and geographic. . . . 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. . . . If rates of divergence [in allopatric speciation] 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.

In addition, Gingerich (1976, p. 25) suggested that character displacement was important in causing gradual morphological change, because when speciation was allopatric "differences in morphology postdate significantly the onset of genetic isolation, rather than pre-dating genetic isolation as postulated by Eldredge and Gould (1972)."

Three pictures of evolution therefore competed—punctuated equilibrium, phyletic gradualism sensu Eldredge and Gould (1972), and gradualism as explained by Gingerich (1976). Vrba (1980, p. 62) applied the Eldredge-Gould term "phyletic gradualism" to a concept similar to the gradual evolution that Gingerich (1976) had written about. What she considered the most extreme versions of phyletic gradualism and punctuated equilibrium contrasted in eight ways (Table 1).

With this contrast, the conception that both phyletic gradualism and punctuated equilibrium were names for models of macroevolution—not simply statements about tempo—became fixed. The points at which the models were not mutually exclusive—points 6–8 in Table 1—revealed the potential for argument at the purely semantic level. Later Levinton (1983, p. 115) and Gingerich (1984, p. 335; 1985) explained a confusion about point 3 in Table 1, concerning evolutionary rates. Although Vrba (1980, p. 62) said that under phyletic gradualism rates should be "uniformly low," the word "gradual" in fact connotes nothing about rates; the important concept is that change is continuous, advancing step by step in a single direction. Morphological change under phyletic gradualism therefore can be gradual over geologic time, yet still speed up and slow down. What point 3 does predict about phyletic gradualism is that, through time, within-species phenotypic



TABLE I  
Contrasts between Phyletic Gradualism and Punctuated Equilibrium\*

	Real differences between the models
1.	<i>Direction of phenotypic change within a species.</i> In phyletic gradualism change is unidirectional. In punctuated equilibrium change at most oscillates about a stable mean.
2.	<i>Importance of splitting events (cladogenesis).</i> In phyletic gradualism, both anagenesis (transformation of the ancestor species into the descendant by phyletic evolution) and cladogenesis (splitting of lineages) are important mechanisms of speciation. In punctuated equilibrium, cladogenesis dominates to the virtual exclusion of anagenesis. (Vrba stated this as: Species arise "by phyletic speciation in sympatry, and by allopatric speciation in large or small populations" in the model of phyletic gradualism, and "generally only by allopatric speciation in small, isolated populations" in punctuated equilibrium.)
3.	<i>Distribution of rate of phenotypic change.</i> In phyletic gradualism rates of phenotypic change do not increase significantly at the speciation event, be it cladogenetic or anagenetic. In punctuated equilibrium, most morphological changes takes place at or near the cladogenetic speciation event, and not much occurs between speciation events. (Vrba's extreme version of phyletic gradualism also cited "uniformly low" rates of evolution.)
4.	<i>Nature of species.</i> In phyletic gradualism anagenetic change can produce species that are arbitrary subdivisions of a lineage that continues through time. In punctuated equilibrium, species are real, discrete entities with beginnings and terminations.
5.	<i>Macroevolutionary trends.</i> In phyletic gradualism, trends arise from additive phyletic evolution. In punctuated equilibrium, trends arise from sorting among species. (Vrba said from "nonrandom survival of stochastic speciation events," but elsewhere in her paper, pp. 80-81, she, like Gould, 1982, p. 10, stressed that it is birth rate of species, not survival, that results in species sorting.)
Points on which the models are not mutually exclusive	
6.	<i>Population size required for adaptive change to occur.</i> Small or large populations, or even whole species, can transform through phyletic gradualism. In punctuated equilibrium changes are confined to small, isolated populations.
7.	<i>Dependence of rate of evolution on splitting events.</i> In phyletic gradualism, rates of evolution are independent of the number of splitting events (cladogenetic speciation events). In punctuated equilibrium, the number of lineage splitting events, and the amount of change that accompanies each one, control evolutionary rates.
8.	<i>The role of environmental change.</i> In phyletic gradualism, evolution is accelerated by environmental change, but does not require it. Punctuated equilibrium requires environmental change. (Vrba's view here is not necessarily shared by all proponents of either model.)

\*Modified from Vrba (1980, p. 62).

change should be nearly as pronounced as between-species change, and should proceed in the same direction.

It is only points 1-5 in Table I that define and contrast phyletic gradualism as presently understood. In those respects the differences between phyletic gradualism and punctuated equilibrium are very real—they cannot be dismissed as semantic.

### 2.3. Species Selection and the Effect Hypothesis

Although the importance of sorting among species is a principal difference between the two models, that concept itself is an ambiguous one. The concept commonly has been called "species selection," which means different things to different people. Vrba (1983, 1984a, p. 321, 1984b, p. 130) explained this in detail; the following discussion summarizes her review.

Prior to 1980, the term "species selection" referred to selection that operated by differential longevity, that is, survival or extinction, of species (Eldredge and Gould, 1972; Stanley, 1975, 1979; Gould and Eldredge, 1977; Eldredge and Cracraft, 1980). The process was conceived to be independent of selection that took place between organisms.

Vrba (1980) emphasized a different point of view, however, when she argued that birth rate of species—that is, speciation rate—also would tend to sort among species and might be more important than differential survival in causing macroevolutionary trends. Her view further differed in stating that the traits that caused sorting at the species level could result from traits that arose at the organismal or genomic level. Speciation rate, she posited, is the effect of microevolutionary processes, for example, adaptations that permit organisms to inhabit peripheral or restricted parts of a species range. Yet speciation rate per se is a trait that sorts among species over time, not among organisms. Kinds of species that speciate rapidly eventually will overwhelm the kinds that do not. Vrba (1980, p. 80) generalized that "Trends may be the effects of any factors which incidentally result in differential speciation rates" and called this idea the effect hypothesis.

Gould (1982) came to agree with Vrba's emphasis on speciation rate as an important cause of trends, but did not uphold the notion that speciation rate was linked to organism-level interactions. Accordingly, he retained the term species selection but recommended that it "be confined to . . . claims for selection among species based on species level properties." He envisaged "true species selection . . . is a dom-

inant process when trends are produced by differential origination rather than by differential extinction" (Gould, 1982, p. 94).

But Vrba (1984a, p. 323) pointed out that high speciation rate in itself does not imply species selection if species selection is defined to avoid a tautology: "Species selection is that interaction between heritable, emergent character variation and the environment which causes differences in speciation and/or extinction rates among variant species within a monophyletic group." This means that if species selection is to be analogous to natural selection among individuals, then species, like individuals, must have certain traits that natural selection can act upon in a specified environment. The trait must originate (become emergent) at the level of the species, not at the level of the organism or population. It must vary among species within any given higher monophyletic group. And it must be possible for the ancestor species to pass the trait on to the descendant species. Examples of such traits might be (1) the characteristic population size, (2) the spatial and genetic separation between populations, or (3) characteristic dispersal rates. In practice, of course, it is very hard to demonstrate, even for the examples above, that a species-level trait is not an outgrowth of an organism-level interaction. Nevertheless, this perception of species selection is a theoretically sound one.

Therefore, as now understood, the concept of "sorting among species" that is specified in the punctuated equilibrium model includes at least two distinct processes—species selection and the effect hypothesis. The processes are similar in that both recognize species as "higher-order individuals," which are capable of interacting at a hierarchical level above that of organisms (Gould, 1985, p. 6). The principal differences are, first, that species selection requires the unit of selection to be above the organismal level; the effect hypothesis does not. Second, species selection requires that the trait being selected for is independent of characters that arise at the organismal level; the effect hypothesis requires that traits at the organismal level combine to form a character that becomes an active sorter only at the species level. Third, natural selection itself is the sorting mechanism in species selection; differences in speciation rates and extinction rates are the cause of sorting in the effect hypothesis (Vrba, 1983a, pp. 323–325).

### 3. CASE STUDIES OF QUATERNARY MAMMALS

We know many of the skeletal traits that characterize species of modern mammals. These traits in living species, or in extinct species

that are closely related to living ones, can be traced through parts of the Quaternary record. In this respect Quaternary mammals are ideal for tracking evolutionary change within and between species, because we can analyze traits that are without doubt diagnostic of biological species.

In order to recognize evolutionary patterns, statistically large samples of fossils must be drawn from sequential small slices of time, and then the morphology at each slice of time compared. Such data are not commonly presented for Quaternary mammals. A computer search of the 1970–1984 BIOSIS and ZOOLOGICAL RECORD data bases found 732 articles that mention punctuated equilibria, or evolution and Pleistocene; approximately 30 more were found by sorting through a portion of the literature not included in the computerized files. Fewer than 25 (cited throughout the ensuing discussion) of these more than 760 articles gave the data necessary to support or reject conclusively some aspect of punctuated equilibrium or phyletic gradualism for Quaternary mammals.

#### 3.1. Direction of Phenotypic Change within Species

The model of punctuated equilibrium predicts that morphology should not vary much from a stable mean during most of a species' existence, whereas phyletic gradualism predicts that the mean of the trait should shift unidirectionally.

##### 3.1.1. Evidence for Stasis

3.1.1a. *Short-Tailed Shrews.* *Blarina brevicauda*, the short-tailed shrew, comprises two semispecies, *brevicauda* and *talpoides* (Jones et al., 1984). The semispecies are phena that have been distinct since at least 500,000 years ago (late Irvingtonian land-mammal age), but still hybridize where they are sympatric. *Blarina brevicauda brevicauda* is the only subspecies within the *brevicauda* semispecies. Eleven subspecies are included in the *talpoides* semispecies; one of these is *Blarina brevicauda kirtlandi*. A combination of 26 dental and dentary measurements subjected to canonical analysis reliably groups modern and fossil specimens of *B. brevicauda* into one or the other semispecies (Jones et al., 1984). Both semispecies are fairly common as Quaternary fossils.

At Baker Bluff Cave, Sullivan Co., Tennessee, specimens of *Blarina brevicauda* were recovered from seven superposed 1-ft thick stratigraphic levels (Guilday et al., 1978). Level A was 3–4 ft below the



surface, Level B was 4–5 ft below the surface, and so on to Level G, which was 9–10 ft down (Fig. 1). Radiocarbon dates show that the sequence spans at least 8600 years, from 19,100 years at the bottom to about 10,500 years two-thirds of the way up the sequence, at Level C. A member of the *Talpoides* semispecies, probably *B. brevicauda* kirtlandi, was present in all seven levels. The other semispecies, *B. brevicauda brevicauda*, appears only in the upper four levels (Guilday et al., 1978; Jones et al., 1984). The entrance of the *brevicauda* semispecies most likely was by immigration, because at the same level several boreal voles also make their first appearance.

Guilday et al. (1978) traced one taxonomically important character, length of the mandibular molar row (Jones et al., 1984; Graham and Semken, 1976), through all seven levels (Fig. 1). For the *talpoides* semi-

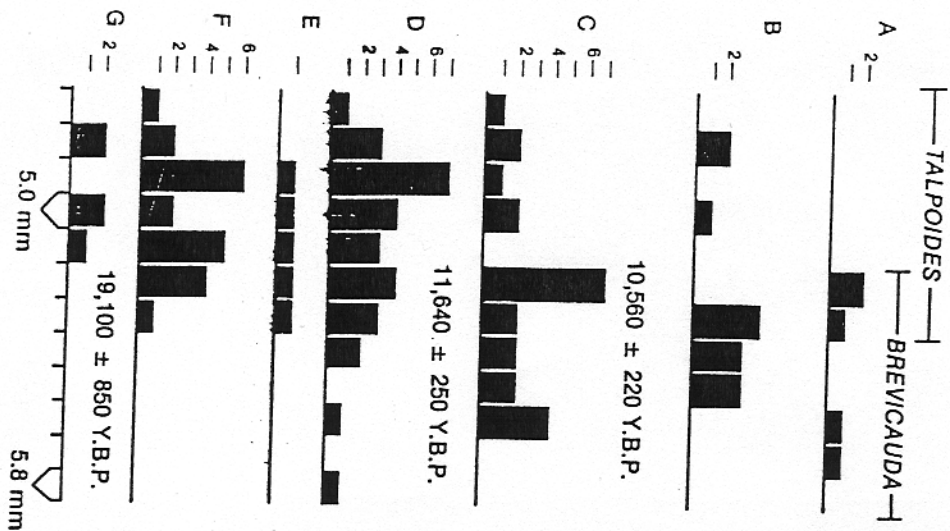


FIGURE 1. Length of  $M_1$  to  $M_2$  in the *talpoides* and *brevicauda* semispecies of the shrew *Blarina*. Specimens were excavated from Baker Bluff Cave, Tennessee. The histograms are arranged stratigraphically; each histogram plots specimens collected from a single 1-ft-thick stratigraphic level, with A being the youngest sample and G the oldest. Radiocarbon dates associated with the indicated levels provide the chronology. Y.B.P., Years before present. Tick marks at the left indicate the number of specimens in each frequency category. Data are from Guilday et al. (1978).

species, the character did not change much from Level G to Level B; the modal value remained near 4.9 mm. Likewise, molar-row length in the *brevicauda* semispecies remained relatively constant, near a mode of 5.4 mm through its stratigraphic range. This pattern indicates stasis through at least 8600 years, even through a time when the climate likely cooled coinciding with Level D (Guilday et al., 1978), and when an immigration brought the two closely related phenotypes into sympatry. The example clearly rejects the model of phyletic gradualism at the  $\pm 10,000$ -year time scale, but supports punctuated equilibrium.

3.1.1b. *Hamsters*. Size is one criterion that differentiates modern hamster species, particularly within *Cricetulus* (Corbet, 1978, p. 90). Color of the fur, which is unknown for fossils, is the other taxonomically important trait.

*Cricetulus bursae* and *Rhinocricetus ehiki* are two hamsters that differ primarily in size, as reflected by the length of the mandibular tooth row (Kurtén, 1968, pp. 211–212). The two species coexisted in central and eastern Europe from at least 1 million years ago (Waalian warm stage; late Villafrañan land-mammal age) to about 700,000 years ago (second cold phase of the Gunz Glaciation; Biharian land-mammal age). The sites at which they coexist are not demonstrably superposed, but five of the localities were arranged by relative age through biostratigraphic comparisons (Kurtén, 1968, pp. 25, 241), which in Figure 2 are matched with appropriate parts of the radiometric scale via correlation charts compiled by Van Eysinga (1978) and Repenning (1983). The “absolute” dates therefore are very approximate and must be regarded as order-of-magnitude estimates that suggest the sequence spans in the neighborhood of 300,000 years.

During this time, tooth-row length in *Cricetulus bursae* fluctuated from a modal value of about 4.8 mm to about 5.1 mm (Beremend and Villany samples), then down to 4.7 mm (Episcopia sample), then back up to about 5.1 mm (Sackdilling sample), then back down to about 4.7 mm (Brasso sample) (Fig. 2). The modal values for *Rhinocricetus ehiki* also fluctuate back and forth, from about 5.7 mm at Beremend and Villany, to 5.4 mm at Episcopia, to 5.9 mm at Brasso. Size does not change significantly or unidirectionally for either species; instead the rather minor fluctuations are just what the model of punctuated equilibrium predicts. The fact that the samples by Quaternary standards are sparsely distributed through time does not weaken the case for punctuated equilibrium; discontinuous, but strongly unidirectional change would be predicted by phyletic gradualism in this case.

3.1.1c. *Ground Squirrels*. *Spermophilus townsendii*, Townsend's ground squirrel, is present today in southeastern Washington state, where its fossil history extends back at least 40,000 years. *Spermophilus*

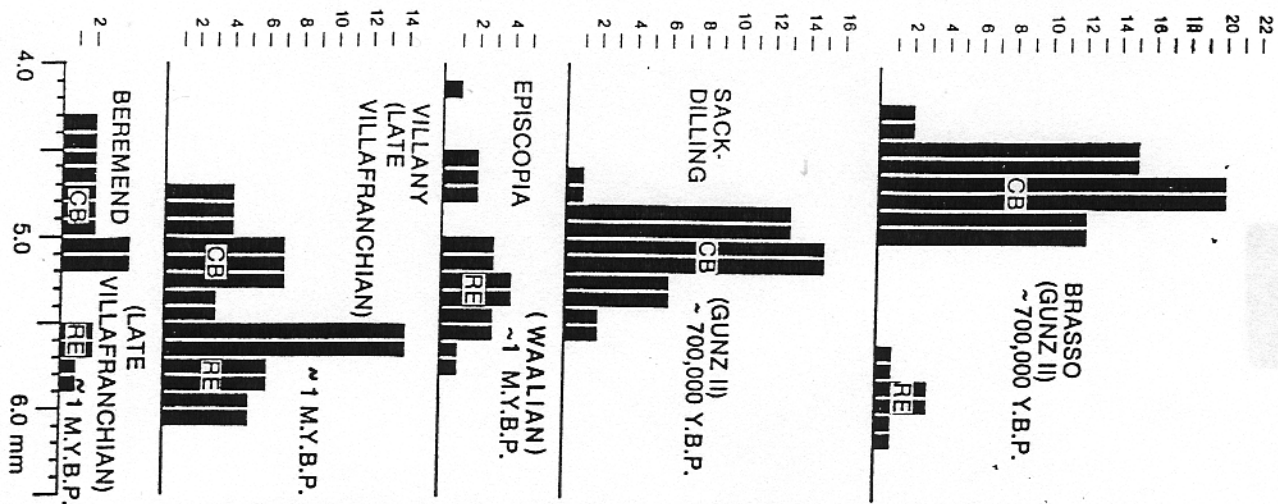


FIGURE 2. Length of mandibular tooth row in the hamsters *Cricetus bursae* (CB) and *Rhinocricetus ehiki* (RE) from various localities in central and eastern Europe. Beremend and Villany are near the Yugoslavian border in south-central Hungary; Episcopia is near the Hungarian border in Romania; Brasso is also in Romania, but farther east in the Transylvania region; and Sackdilling is in the Oberpfalz of Germany. The histograms are arranged in stratigraphic order, with the oldest locality at the bottom. Radiometric dates are at best order-of-magnitude approximations, which are estimated from stepwise correlations with biostratigraphic and paleomagnetic sequences. (M.)Y.B.P., (Million) years before present. Tick marks at the left indicate the number of specimens in each frequency category. Data are from Kurtén (1968, Fig. 101).

*townsendii* is closely related to *S. washingtoni*; the two species are known to be separated chromosomally by only one pericentric inversion (Nadler et al., 1984). *Spermophilus townsendii* and *S. washingtoni* can be differentiated reliably by an osteological character, namely the length of the third upper molar relative to its width; the molars are relatively shorter in *S. townsendii* (J. E. Martin et al., 1983, p. 16; Rensberger et al., 1984, p. 30).

From data listed in Rensberger et al. (1984, pp. 5, 12-13, 17, 30), the ratio of width to length of *S. townsendii* third upper molars can be traced through 12 samples that are stratigraphically superposed in loess near Kennewick, Benton Co., Washington (Fig. 3). The oldest sample is between 40,000 and 320,000 years old, as estimated from the amount of time it must have taken for eight overlying calcretes (accumulations of calcium carbonate in fossil soils) to form (Gile et al., 1965, 1966; Warren, 1983; Pye, 1983; Wajtanowicz and Buraczynski, 1978; Turcholka, 1977). The youngest sample occurs above a tephra identified as the Mazama volcanic ash (Rensberger et al., 1984, p. 15), which is between 6600 and 7000 years old (Sarna-Wojcicki et al., 1983).

The width to length ratios fluctuate very slightly around a mean of about 1.00, never exceeding 0.98 or 1.15 as extremes (Fig. 3). The slight changes that do take place are not unidirectional. Therefore, proportions of the upper third molars in *S. townsendii* have remained static for at least 33,000 years, and possibly for as long as 320,000 years, depending on the age of the lowest sample.

### 3.1.2. Evidence for Unidirectional Change

3.1.2a. Sagebrush Voles. Complexity of the upper third molar is a diagnostic feature of species within *Lagurus*, the steppe and sagebrush voles. Triangles and reentrants are developed to varying degrees on the  $M^3$ , so that *Lagurus curtatus* and *Lagurus luteus* have only three labial and two lingual vertical ridges, whereas *Lagurus lagurus* has four labial and three lingual ridges.

*Lagurus curtatus*, the sagebrush vole, is found in the same eastern Washington loess deposits that are described above for *Spermophilus townsendii*. The fossils are grouped into seven stratigraphically superposed samples,  $\Delta$  at the bottom through I at the top (Fig. 4) (Rensberger et al., 1984, p. 59). In the lowest two samples, all of the third upper molars are morphologically similar; they have a very shallow anterolabial reentrant. As a consequence, the labial margin of these  $M^3$ 's is characterized by one poorly developed vertical ridge (the anterior one) and two prominent vertical ridges (the middle one and the posterior



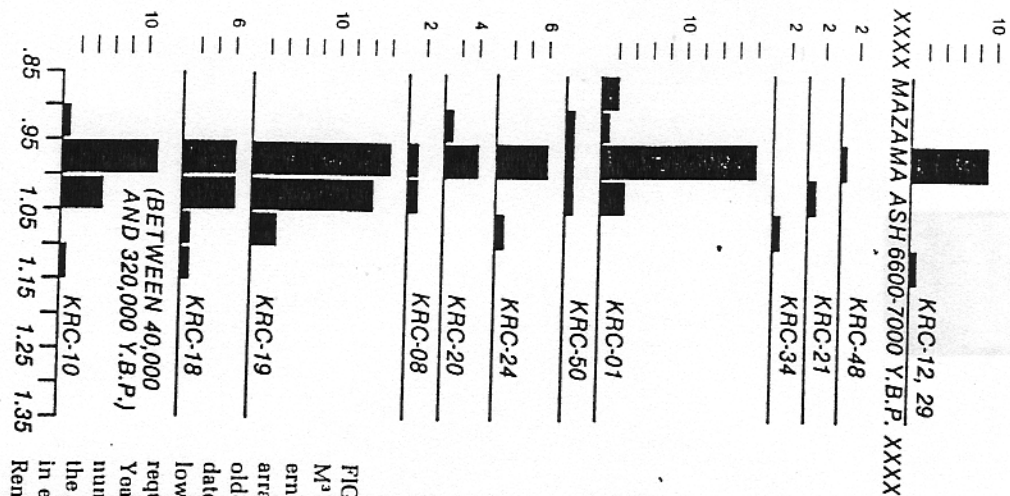


FIGURE 3. Ratio of the width to length of  $M^2$  in *Spermophilus townsendii* from eastern Washington state. The histograms are arranged in stratigraphic order, with the oldest locally on the bottom. The upper date is based on the Mazama Ash, and the lower age range is estimated from the time required for eight calcretes to form. Y.B.P., Years before present. KRC followed by a number is the locality name. Tick marks at the left indicate the number of specimens in each frequency category. Data are from Rensberger et al. (1984).

one). In Level C a new morphotype of  $M^2$  appears, in which the anterolabial reentrant is very deep. This makes the anterior and middle vertical ridges more prominent than the posterior one. The deep-reentrant morphotype becomes more abundant through time, comprising 25, 80, and finally 100% of the sample in Levels C and D, Level E, and Levels F and I, respectively (Fig. 4). Therefore, individuals with a deep reentrant composed increasingly more of the population, and at last completely replaced the shallow-reentrant forms over a time span of between 33,000 and 320,000 years (the dates explained above for *Spermophilus townsendii* also apply here). The same kind of unidirectional

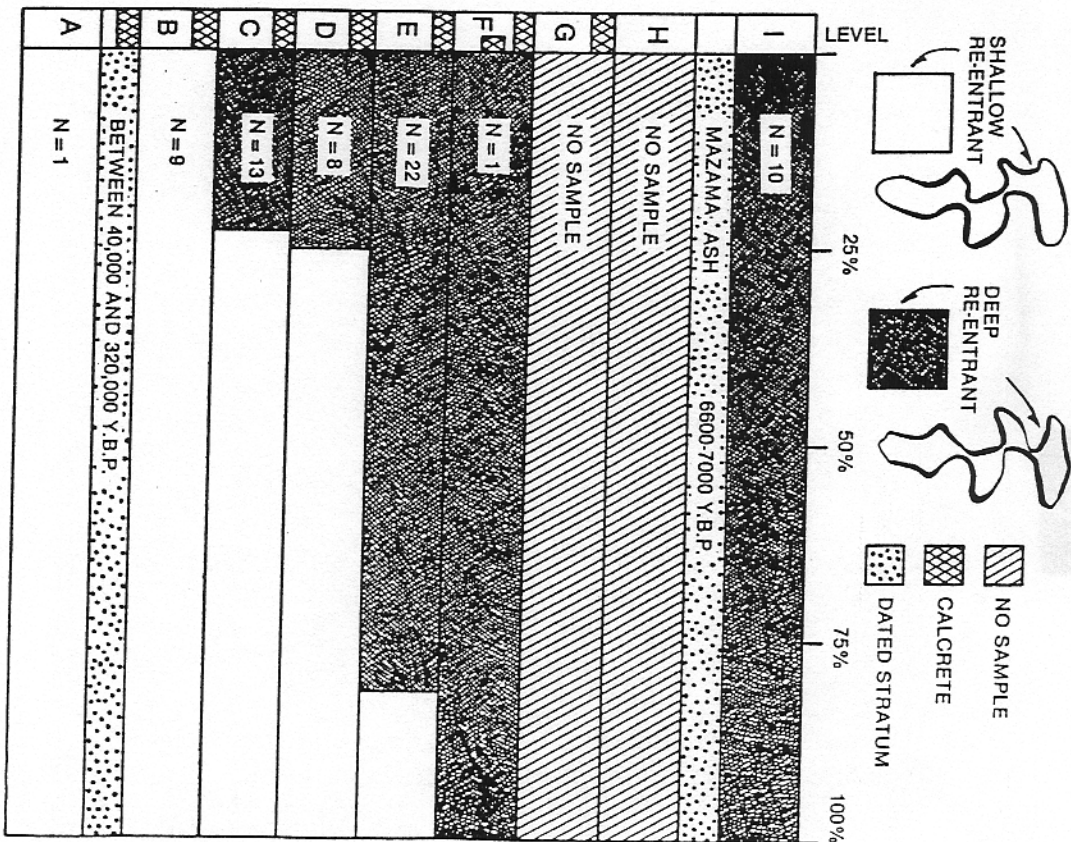


FIGURE 4. Bar diagram showing the sequentially changing percentages of  $M^2$  morphotypes in *Lagurus curtatus* from eastern Washington state. Localities are arranged in stratigraphic order, with A the oldest and I the youngest. White bars illustrate the percentage of  $M^2$ 's with a shallow anterolabial reentrant; black bars depict the percentage with a deep reentrant. The upper date is determined from the Mazama Ash; the lower age range is estimated from the time required for the eight calcretes to form. Y.B.P., Years before present. Data are from Rensberger et al. (1984).

increase takes place in the first lower molar, in which five-triangle forms replace four-triangle forms through the section (Rensberger et al., 1984, p. 59). The most parsimonious explanation is that the alleles that cause deep reentrants on  $M_1$  and five triangles on  $M_1$  spread through more and more of the eastern Washington population over time, until the traits finally became fixed. The other alternative—that a separate population with complex teeth gradually encroached into eastern Washington as the physical environment correspondingly altered—seems much less likely. Eight calcrites in the section argue for several dry–moist cycles that do not correlate well with the unidirectional changes in *Lagurus*.

3.1.2b. *Water Voles*. *Arvicola cantiana* lived in the British Isles from <350,000 years ago (Gromerian Interglacial) to between 70,000 and 50,000 years ago (early Devensian Glacial Stage, Chalford Interstadial). *Arvicola cantiana* was replaced stratigraphically by *Arvicola terrestris*, which first appeared between 50,000 and 30,000 years ago (Middle Devensian, Upton Warren Interstadial) and is still extant (Stuart, 1982, p. 168). Differences between these two species are evident in at least three characteristics of their molars—size, the ontogenetic age at which roots grow, and thickness of enamel (Stuart, 1982, p. 38). Molar size also distinguishes *A. terrestris* from the other living species, *A. sapidus* (Corbet, 1978, p. 105).

Stuart's (1982, p. 186) compilation of data shows that the length of  $M_1$  in *A. cantiana* changes unidirectionally through seven stratigraphic intervals encompassing roughly 290,000 years. From the stratigraphically lowest to the highest sample, the mean lengths are 3.2, 3.3, 3.6, 3.7, 3.75, and 3.95 mm (Fig. 5).

The general trend for the ensuing species, *Arvicola terrestris*, likewise is toward increased size. Late Flandrian (<6000 years) and modern specimens are larger than late Devensian ones (10,000–26,000 years old), which in turn are larger than middle Devensian ones (26,000–50,000 years old) (Fig. 5). However, *A. terrestris* does not provide as conclusive evidence for unidirectional change as does *A. cantianus*, because the general size increase is interrupted by an apparent reversal or immigration at the Devensian/Flandrian boundary, and details are obscured partially by the uncertain stratigraphic position of the late Devensian samples (Stuart, 1982, p. 186).

3.1.2c. *Elephants*. The living species of elephants, *Loxodonta africana* and *Elephas maximus*, can be diagnosed by traits of their molars—the number of enamel plates, the frequency of plates per 10 cm of tooth (= lamellar frequency), thickness of plates, and crown height, among other traits. These characters change unidirectionally through

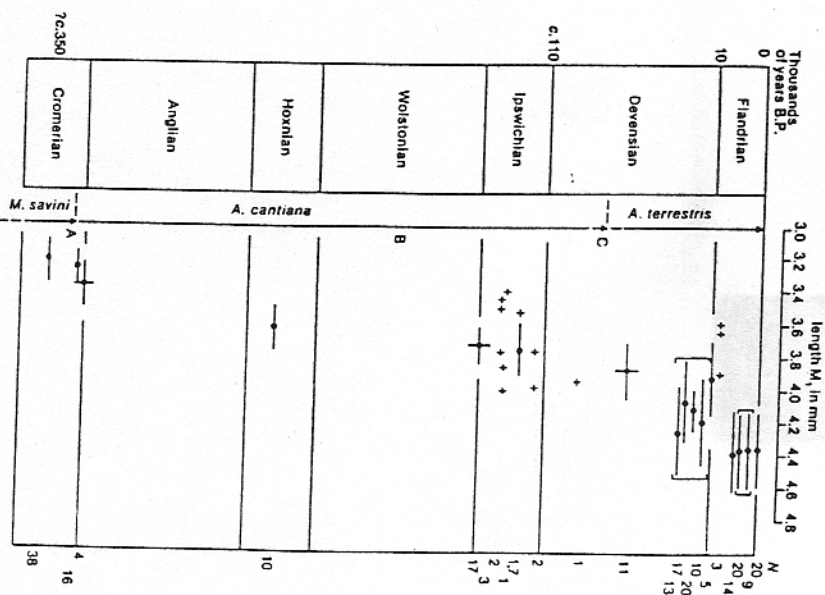


FIGURE 5. Preliminary diagram of size changes in the *Mimomys savini* to *Arvicola terrestris* lineage, relative timing of morphological changes, and suggested taxonomic divisions. Means of samples are indicated by dots, standard deviations by horizontal bars. Single measurements are indicated by crosses. Vertical bars denote some uncertainty in stratigraphic position. (A) Loss of roots and achievement of permanently growing molars; (B) last occurrence of "Mimomys fold"; (C) last occurrence of convex-thickened enamel. Note that the relative time scale is schematic only. (Reprinted from Stuart, 1982.)

time within some fossil species. A good example is *Elephas recki*, which lived in Africa from the late Pliocene to the middle Pleistocene, about 3.5 million to 500,000 years ago. Maglio (1973, p. 35) recognized "four evolutionary stages [within *E. recki*] based on morphological changes and stratigraphic succession (Maglio, 1970), but these grade into each other making the taxonomic designation impossible." From the earliest (Stage 1) to the latest (Stage 4) representatives, morphology of *E. recki* changed in the following ways: (1) increase in enamel plates, (2) in-



crease in lamellar frequency, for example, in  $M_3$ , from 4.7–5.0 in Stage 1 up to 5.0–6.2 in Stage 4, (3) increase in enamel folding, (4) increase in crown height, for example, in  $M_3$ , from a hypsodonty index of 126.6–133.0 in Stage 1 up to 144.0–186.4 in Stage 4, and (5) decrease in enamel thickness, for example, an average thickness in  $M_3$  from 3.0–3.1 mm in Stage 1 down to 2.5–3.6 mm in Stage 4 (Maglio, 1973, p. 36) (Fig. 6). Maglio (1973, p. 56) documented that molars of *Mammuthus meridionalis* underwent similar unidirectional modifications from about 3 million to 1 million years ago.

3.1.2d. Pigs. The third molars of living pigs are distinctive taxonomically (Harris and White, 1979, p. 7). *Mesochoenrus limnetes* is a pig that frequently is represented by third molars in successive stratigraphic intervals of the Shungura Formation, Ono Basin, Ethiopia (Harris and White, 1979). The stratigraphic levels are identified from bottom to top as B, C, D, E, F, G, H, J, K, and L. Level B is thought to be between 2.6 and 3 million years old, Level G about 1.8–2 million years old, and the bottom of Level L about 1 million years old (Cooke, 1978, Fig. 2). The following aspects of *Mesochoenrus limnetes* change gradually: (1) length of  $M^3$  increasing through Levels B, C, E, F, G, H, and lumped K and L; (2) length of  $M_3$  increasing through Levels B, C, D, G, H, J, K, and L; (3) ratio of  $M^3$  length:trigon length increasing through Levels B, C, D, G, H, K, or L; (4) ratio of  $M^3$  length:breadth increasing through Levels B, C, D, E, F, G, H, K, and L; and (5) ratio of  $M_3$  length:breadth increasing through Levels B, C, D, G, H, J, K, and L.

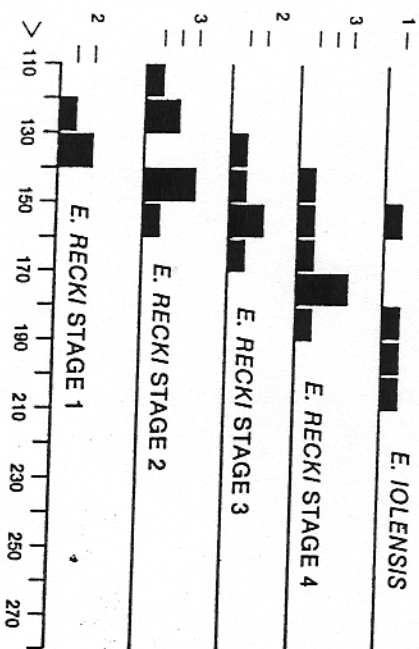


FIGURE 6. Successive stages of hypsodonty within the species *Elephas recki*, and the transition into *E. iolensis*. Histograms are arranged in stratigraphic order. Tick marks at the left indicate the number of specimens in each frequency category. Data are from Maglio (1973, Tables 13, 15).

J, and K (Harris and White, 1979, Figs. 80, 81, and 126–131). Morphology essentially remained static or fluctuated slightly between Levels C and F for  $M^3$  length and the ratio  $M_3$  length:trigon(id) length. The time spanned by this "stasis" was relatively short, perhaps 500,000 years, in comparison to the  $\pm 1.5$  million years over which unidirectional changes took place. The suite of characters for *Mesochoenrus limnetes* therefore exemplifies unidirectional change in general, but at varying rates through time.

The same holds true for *Metridiochoerus andrewsi*, another pig from the Shungura Formation. The  $M^3$  increases in length through levels B, C, and E, then remains static in Levels F, G, and H. The  $M_3$  increases in length rather uniformly through Levels B, C, D, E, F, G, and H (Harris and White, 1979, Figs. 121 and 122). These characters and others led Harris and White (1979, p. 49) to recognize two distinct evolutionary stages within *Metridiochoerus andrewsi* in the Shungura Formation, and a third stage in the lower part of the upper member of the Koobi Fora Formation.

3.1.2e. Hominids. Wolpoff (1984) used 13 measurements to compare samples of *Homo erectus* from three stratigraphic intervals—the lower Pleistocene, the early-middle Pleistocene, and the later-middle Pleistocene, which total 1 million years. The measurements reflect cranial and mandibular size, both of which are used to distinguish various hominid species. Wolpoff's histograms conclusively show that seven of the nine cranial measurements increase unidirectionally through the three temporal levels, and three of the four mandibular measurements decrease (Fig. 7). Other studies, which claim stasis as the pattern for *Homo erectus*, do not present such conclusive data (Rightmire, 1981; see also Cronin et al., 1981).

### 3.2. Anagenesis and Cladogenesis

Phyletic gradualism recognizes both cladogenesis and anagenesis as important. Consequently, phyletic gradualism never can be rejected simply by presenting examples of cladogenesis, even though such examples abound in the fossil record—for instance, the Quaternary clades of African bovids discussed by Vrba (1984c), at least nine species of elephants (Maglio, 1973), and the three species within *Blarina* (Jones et al., 1984). However, the model of punctuated equilibrium denies that species arise by anagenesis. Therefore one can reject the model of punctuated equilibrium for a given lineage if anagenesis can be demonstrated.

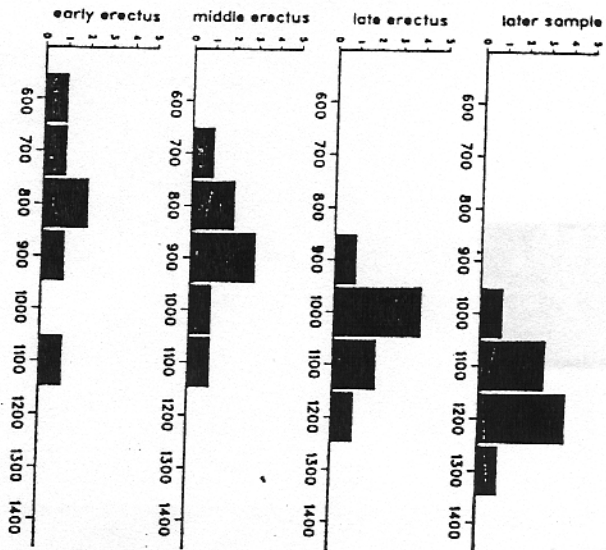


FIGURE 7. Distribution of cranial capacity in cubic centimeters for three *Homo erectus* samples and a sample of later hominids. Histograms are arranged in stratigraphic order. The tick marks at the left indicate the number of specimens in each frequency category. See Wolpoff (1984, Table 2) for means and other statistics. (Reprinted from Wolpoff, 1984.)

### 3.2.1. Examples of Anagenetic Change

To demonstrate anagenesis, one must show that the morphology of the ancestral species grades continuously into that of the descendant, until the descendant morphology completely replaces the ancestral morphology. By definition the ancestor and descendant cannot live in the same place at the same time—if they do, the lineage has split, not transformed. The following examples are consistent with the postulate of anagenetic transformation, but would be hard to reconcile with cladogenesis.

**3.2.1a. Water Voles in the British Isles.** *Mimomys savini* last appears in Cromerian Pollen Zone Cr11b. In the overlying Pollen Zone Cr1V, *Arvicola cantiana* replaces *M. savini*. The replacement spanned at most a few thousand years approximately 350,000 years ago. The generic distinction belies the extremely similar morphology of the two species where they are stratigraphically close. In *Mimomys savini*, roots appeared on the cheek teeth only in old animals. Stuart (1982, p. 185) noted that "the formation of roots was retarded until progressively later in life [throughout the history of *Mimomys*], until a point was reached where the cheek teeth ceased to root altogether, and had become permanently growing. This step is generally accepted as marking the boundary between the genera *Mimomys* and *Arvicola*." The other differences between *Mimomys savini* and *Arvicola cantiana* are in size, in the

frequency of specimens with a crenulation on the anterior loop of  $M_1$  (the "*Mimomys* fold"), and in enamel thickness. None of these differences are pronounced in stratigraphically adjacent samples of the two species. The mean size of  $M_1$  is 3.25 mm in the highest sample of *M. savini*, and 3.3 mm in the lowest of *A. cantiana*. Later *A. cantiana* increase in size so that by the Hoxnian Interglacial they overlap little if any with *M. savini* (Fig. 5). The *Mimomys* fold is present in most of the unrooted teeth of *M. savini* (that is, teeth from young animals); the frequency of this character decreases to 30% in Cromerian *A. cantiana*, then becomes rarer yet in later samples, until it becomes "virtually absent" in the specimens from the Ipswichian Interglacial (somewhat earlier than 110,000 years ago) (Stuart, 1982, p. 185). Enamel in *M. savini* is thick on the convex angles of the cheekteeth; it is also thick in Cromerian and Hoxnian samples of *A. cantiana*. This trait becomes less frequent in Ipswichian and early Devensian *A. cantiana*.

By 50,000 years ago, *A. cantiana* was replaced by the modern *A. terrestris*. The morphological transformation was a smooth one. The species boundary between the two is drawn "for convenience" at the last appearance of thick enamel on the  $M_1$  (Stuart, 1982, p. 185). Subsequent samples on each side of this species boundary are otherwise nearly identical; subsequently *A. terrestris* became significantly larger than *A. cantiana* (Fig. 5).

**3.2.1b. Elephants.** Maglio (1973) provided convincing evidence that seven of the 17 Quaternary elephant species arose through anagenesis, and he suspected that at least one more did. Most of the morphological transformations are documented by stratigraphically sequential changes in the characters of the molars, such as those discussed above for *Elephas recki*. None of the descendant species coexist with their respective ancestors in time or space; rather, they replace them. The anagenetic species transitions are as follows:

*Elephas ekorensis* → *E. recki* → *E. iolensis*. There is progressive increase in the number of molar plates, in their relative height and spacing, and in folding of enamel, and progressive reduction in enamel thickness and in the median enamel loop. Maglio (1973) stated, "At present, a direct phyletic relationship between *E. ekorensis* and *E. recki* seems certain" (p. 81), and "*E. iolensis* appears to have been the direct descendant of *E. recki* and for this reason transitional specimens may be impossible to assign to one species unit or the other" (p. 38).

*Elephas hysudricus* → *E. maximus*. *Elephas maximus* continues the dental trends exhibited in *E. hysudricus*. Maglio (1973, p. 85) felt that retardation of ontogenetic development in *E. hysudricus* produced *E. maximus*.



*Mammuthus meridionalis*→*M. armeniacus*→*M. primigenius*. The progressive changes that merge one species into the next include increase in the number of molar enamel plates and in lamellar frequency and decrease in the median enamel loop and in enamel thickness. Maglio concluded (1973, p. 87) that *Mammuthus meridionalis* "passes both morphologically and stratigraphically into *M. armeniacus* and this into *M. primigenius*. The last two 'species' certainly represent arbitrary segments of a continuous lineage along which progressive molar and cranial changes occur through the middle and late Pleistocene."

*Mammuthus imperator*→*M. columbi*. Changes in this lineage parallel those described for the *M. primigenius* lineage (Maglio, 1973, p. 87).

*Elephas planifrons*→*E. platycephalus*. This is a lineage that Maglio (1973) speculates is an anagenetic one, but only a single specimen of *E. platycephalus* is known.

### 3.3. Distribution of Rate of Phenotypic Change

Under the model of punctuated equilibrium, most morphological change should take place at or near the speciation event. Speciation and the accompanying phenotypic changes should be accomplished within 1% of the time the species later exists in stasis (Gould, 1982, p. 83). Phyletic gradualism predicts that change throughout the life of the species should exceed the amount of change that takes place across a species boundary.

#### 3.3.1. Morphological Change Confined to Speciation Events

3.3.1a. *Short-Tailed Shrews*. *Blarina brevicauda brevicauda* and *B. carolinensis* split off from the *B. brevicauda talpoides* semispecies in the late Irvingtonian. No transitional morphologies can be detected; the first representatives of the *B. carolinensis* and the *brevicauda* semispecies show all of the taxonomically important dental characters of modern representatives (Jones et al., 1984). Stasis prevailed for about 500,000 years. It is impossible to resolve for certain whether the new species actually originated within 5000 years—that is, 1% of the time that they later have existed in stasis—but they certainly must have undergone much more morphological change near the speciation event than they have subsequently. Speciation within short-tailed shrews undoubtedly has taken place in much less than 10,000 years, as shown

by splitting of *B. hylophaga* from the *B. carolinensis* line between 9000 and 11,000 years ago, and the subsequent morphological stasis of *B. hylophaga* to the present (Jones et al., 1984, p. 135).

3.3.1b. *African Bovids*. Vrba (1984c) suggested that aspects of facial structure, particularly horn morphology, are important for specific-mate recognition for bovids. Therefore horn cores and cranial and mandibular characters are reliable for distinguishing between species. She subjected 58 mandibular and cranial characters to cladistic analysis to define fossil and recent species and recognize relationships among them. Within the tribe Alcelaphini, which includes the blarbucks, hartebeests, and wildebeests, 25 species lived during the Quaternary. The origin of all of these was apparently sudden, by cladogenesis in a minimum of 18 cases (Vrba, 1984c, pp. 65, 68). Ancestors with transitional morphologies are not known. The species-specific characters persisted approximately 250,000 years or somewhat less in seven species, 500,000 years in nine species, 1 million years in five species, 1.5 million years in two species, and 2 million years or more in two species. Through these times, none of the species underwent significant morphological changes; the changes that did occur were either oscillatory, or "gradual average modifications" that were minor compared to the morphological change that took place between species (Vrba, 1984c, p. 68). This pattern accords most closely with punctuated equilibrium, although data are not available to calculate whether most of the change indeed took place within the first 1% of the time the species existed.

3.3.1c. *Elephants*. Three species of elephants show very little change in their molar structure through stratigraphic ranges in excess of 750,000 years (Maglio, 1973). These include *Loxodonta adaurora* (ca. 2–4.5 million years ago), *L. africana* (ca. 750,000 years ago to present), and *Elaphus namadicus* (ca. 1 million years ago to late Pleistocene).

3.3.1d. *Suggestive Data*. In Europe, at least 111 modern species first appeared during the Pleistocene. A maximum of 25 of these can be linked to an ancestor by transitional morphologies (Kurtén, 1968, pp. 255, 258). That may suggest that the morphologies that characterize the other 86 modern species appeared relatively suddenly in the fossil record, and were followed by periods of stasis that range from 10,000 to 2 million years. Stanley (1978, p. 26) elaborated on these data by converting them to species-survivorship curves, which led him to conclude that "most net evolutionary change must have been associated with saltational speciation." Arguing for the validity of this approach is the fact that if the Pleistocene specimens were not morphologically identical to modern specimens, paleontologists probably would not

refer them to the modern species. Arguing against it is that the morphology of stratigraphically superposed samples has not been compared adequately for the vast majority of the species in question.

### 3.3.2. Morphological Change Distributed through Stratigraphic Range

The examples discussed under Sections 3.1.2 and 3.2.1 illustrate cases in which less morphological change took place across species boundaries than in the succeeding life span of the species. Particularly convincing examples are the *Mimomys savini*→*Arvicola cantiana*→*A. terrestris* sequence (Fig. 5), the *Elephas recki*→*E. iolensis* sequence (Fig. 6), the *Mammuthus meridionalis*→*M. primigenius* line, and the transition through *Homo erectus* to post-*H. erectus* samples (Fig. 7) (Wolpoff, 1984).

### 3.4. Nature of Species

The previous examples also serve to illustrate that the following species emphatically are arbitrary subdivisions of a morphological continuum: *Mimomys savini*, *Arvicola cantiana*, *A. terrestris*; *Elephas ekmeridionalis*, *M. armeniacus*; *Mammuthus primigenius*, *M. imperator*, and *M. columbi*. Kurtén (1968, p. 256) adds 22 more species for which transitions between pairs are "actually recorded": *Maccaca florentina*→*M. sylvana*, *Felis issiodorensis*→*F. cf. pardina*, *Gulo schlosseri*→*G. gulo*, *Cuon majori*→*C. alpinus*, *Ursus minimus*→*U. etruscus*, *Ursus deningeri*→*U. spelaeus*, *Ursus etruscus*→*U. thibetanus*, *Dicerorhinus*→*D. etruscus*, *Dama clactonia*→*D. dama*, and *Lagurus panonicus*→*L. lagurus*. Vrba (1984c, p. 65) suggests that the transformation of *Aepyceros* species no. 34 to *Aepyceros* species no. 35 was similarly continuous.

Other examples just as emphatically argue for species being discrete in space and time. Those discussed in previous parts of this paper include the short-tailed shrews *Blarina brevicauda*, *B. carolinensis*, and *B. hylophagus*, the hamsters *Cricetulus bursae* and *Rhinocricetus ehiki*, the squirrel *Spermophilus townsendii*, the elephants *Loxodonta adaurora*, *L. africana*, and *Elephas namadicus*, and the 25 species of alcelaphine bovids.

### 3.5. Macroevolutionary Trends

Some of the evolutionary trends exemplified by Quaternary mammals include the following:

1. Progressive development of dentine tracts, hypsodonty, and complexity in the anterior loop of  $M_1$ , along with increasing size in muskrats from the Pliocene through the Quaternary (Nelson and Semken, 1970; Zakrzewski, 1974; L. D. Martin, 1979, 1984).

2. Increasing crown height and dentine tracts in numerous arvicoline rodents, such as *Mimomys*, *Arvicola*, *Pliophenacomys*, and *Ophiomys*, through the Quaternary (Hibbard and Zakrzewski, 1967, 1972; Stuart, 1982; Barnosky, 1985).

3. Increasing crown height and addition of molar enamel plates in elephants from the Pliocene through the Quaternary (Maglio, 1973).

4. Increasing height and length of third molars in the *Nyctanachoerus*-*Notochoerus* and *Metridiochoerus* lineages of pigs from the late Pliocene through the middle Pleistocene (Harris and White, 1979).

5. An increase in size, enlargement of the carnassial tooth, reduction of the third premolar, development of an area of overlap between  $P_4$  and  $M_1$ , lowering of the coronoid process, reduction of the anterior flange on the mandible, and increasingly inclined occiput region in dirk-toothed cats (*Smilodontini*) from the Pliocene through the late Pleistocene (L. D. Martin, 1984).

6. Increasing size in *Sigmodon* (colton rats), complemented by increasing hypsodonty and increase in the roots of  $M_1$  from two to four, from the latest Pliocene through the Pleistocene (R. A. Martin, 1979, 1984).

7. Increased complexity of horn-core and frontlet morphology, general increase in size, and reduction in premolar-molar ratio in alcelaphine bovids (the blesbucks, hartebeests, and wildebeests) through the Pliocene and particularly in the Quaternary (Vrba, 1984c, p. 64).

#### 3.5.1. Additive Microevolution

The model of phyletic gradualism regards trends as the sum of many microevolutionary changes, initiated mainly by natural selection among phenotypes, that were produced through geologic time. To support this idea, the data used to recognize trends in the fossil record must have two qualities—successive (stratigraphically higher) populations or species should change only in the direction of the trend, and the evolving traits should be related clearly to some important function of the organism.

Trends 1–6 all fulfill the criterion of unidirectional change through successive stratigraphic intervals. These trends further are consistent with the model of phyletic gradualism because all can be adequately explained by the differential survival of organisms with functionally



advantageous traits. In this sense, they parallel a very clear example of Vrba's (1984a, p. 324):

If all organisms in a species are black, black colour is a species character. If black organisms are subsequently removed by selection, but those of different colour in a related species survive, this is differential species extinction. Selection of organisms is enough to account for events, and there is no need for concepts of species adaptation and selection.

In trends 1–4, which involve increasing crown height and related traits, low-crowned animals are analogous to the black ones in Vrba's example. Animals that eat abrasive foods, such as grass, wear down their teeth quickly. The more hypsodont and lophodont the tooth, the better an animal can cope with abrasive diets, as Rensberger (1973) and Maglio (1973) demonstrated by biomechanical analyses of mastication in rodents and elephants, respectively. Thus, natural selection among organisms would produce a trend by the following mechanism. In a given population of abrasive-food eaters, individuals with high-crowned teeth survive longer and produce more progeny than their low-crowned competitors. Generation by generation the average crown height thereby increases for the population as a whole. The process continues until teeth are so hypsodont that their abrasion no longer affects reproductive success. New, more hypsodont species originate either through anagenesis as the optimal crown height for a given food resource is approached, or through cladogenesis when a single population begins to utilize a new, more abrasive food.

Similar logic can be extended to the trends in the dirk-toothed cats (trend 5), because all of the modifications result in a more efficient predator (L. D. Martin, 1980; Emerson and Radinsky, 1980). Likewise, the trends for cotton rats (trend 6) are "directly coupled with the evolution of hypsodonty and the successful transition from browsing to grazing" (R. A. Martin, 1979, p. 1).

### 3.5.2. Sorting among Species

The model of punctuated equilibrium attributes trends to sorting among species, by the mechanisms of species selection or the effect hypothesis. Trends produced by these mechanisms should be apparent in the fossil record of a clade by, first, the presence of large numbers of relatively short-lived species, which would be necessary to supply a sufficient pool of variability, and second, by the random directions that speciation proceeded in with respect to the overall trend (analogous to the randomness of genetic mutations with respect to phenotypic trends at the organismal level) (Gould and Eldredge, 1977, p. 148).

The general trends in alcelaphine bovids—increasing complexity in horn morphology, increasing size, reduction of premolars—may provide an example. Twenty-five species comprising nine genera originate and/or become extinct at various times through the Quaternary (Vrba, 1984c, p. 65). In contrast, the trends cited above as fitting the model of phyletic gradualism spanned fewer species in the same amount of time—seven species in two genera of muskrats (trend 1), at most 12 known species of *Minomys* and *Arvicola*, three species of *Pliophloeomys*, five species of *Ophiomys*, at most 15 species of *Sigmodon*, four species in two genera of dirk-tooth cats, and 17 species in three genera of elephants. Speciation of Quaternary alcelaphines was random with respect to the overall trends, because not all species evolve in the same morphological direction. For example, at least seven species proceed toward the overall trend for large individuals, but at least two other speciation events are toward smaller size (Vrba, 1984c, p. 66). Horn complexity increases in a minimum of eight species, but remains relatively simple in three others (see Fig. 2 in Vrba, 1984c). For most species the molar-premolar ratio decreases through time, but one of the latest appearing species, *Damaliscus dorcas*, has relatively long premolars (Vrba, 1980, p. 69).

## 4. DISCUSSION

Examples given in the last section comprise 98 species with well-documented data. The evidence one needs to test for phyletic gradualism or punctuated equilibrium falls into five data categories, which correspond to the five points of difference between the two models as explained in Table I. How the evidence distributes among the 98 Quaternary-mammal species and the five data categories is shown in Table II, where an E indicates that convincing data support punctuated equilibrium, and a G that convincing data support phyletic gradualism. These distributions can be examined both by taxon and by category to gain some idea of whether phyletic gradualism or punctuated equilibrium is supported more frequently.

### 4.1. Examination by Data Category

#### 4.1.1. Category 1: Direction of Phenotypic Change within a Species

Only 14 of the 98 species provide convincing data about how phenotypic changes through the life span of a species. Six of the species

TABLE II  
Summary of Evidence Indicating Punctuated Equilibrium or Phyletic Gradualism for Species of Quaternary Mammals Discussed in the Text<sup>a</sup>

	1 Direction of phenotypic change within species	2 Anagenesis or cladogenesis	3 Morphological change at speciation	4 Nature of species	5 Cause of trends
<b>Shrews</b>					
<i>Blarina brevicauda</i>	E		E	E	
<i>Blarina carolinensis</i>	E		E	E	
<i>Blarina hylophaga</i>	E		E	E	
<b>Hamsters</b>					
<i>Cricetulus bursae</i>	E			E	
<i>Rhinocricetus ehiki</i>	E			E	
<b>Cotton rats</b>					
<i>Sigmodon</i> (15 species)					G × 15
<b>Squirrels</b>					
<i>Spermophilus townsendii</i>	E			E	
<b>Voles</b>					
<i>Lagurus curtatus</i>	G				
<i>Mimomys savini</i>		G	G	G	G
<i>Arvicola cantiana</i>	G	G	G	G	G
<i>Arvicola terrestris</i>	G	G	G	G	G
<i>Ophiomys</i> (five species)			G	G	G × 5
<i>Pliophenacomys</i> (three species)					G × 3
<b>Muskrats</b>					
<i>Pliopotamys</i> and <i>Ondatra</i> (seven species)					G × 7
<b>Elephants</b>					
<i>Elephas ekorensis</i>		G	G	G	G
<i>Elephas recki</i>	G	G	G	G	G
<i>Elephas iolensis</i>		G	G	G	G
<i>Elephas hysudricus</i>		G		G	G
<i>Elephas maximus</i>		G		G	G
<i>Elephas namadicus</i>			E	E	G
<i>Mammuthus meridionalis</i>	G	G	G	G	G
<i>Mammuthus armeniacus</i>		G	G	G	G
<i>Mammuthus primigenius</i>		G	G	G	G
<i>Mammuthus imperator</i>		G		G	G
<i>Mammuthus columbi</i>		G		G	G
<i>Elephas planifrons</i>					G
<i>Elephas platycephalus</i>					G
<i>Loxodonta adaurora</i>			E	E	G
<i>Loxodonta africana</i>			E	E	G
<b>Pigs</b>					
<i>Nyanazachoerus tulotos</i>					G
<i>Nyanazachoerus kanamensis</i>					G
<i>Nyanazachoerus jaegeri</i>					G

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(Continued)



TABLE II (Continued)

	1 Direction of phenotypic change within species	2 Anagenesis or cladogenesis	3 Morphological change at speciation	4 Nature of species	5 Cause of trends
Pigs					
<i>Notochoerus euilus</i>					G
<i>Notochoerus scotti</i>					G
<i>Mesochoerus limnetes</i>	G				G
<i>Metridiochoerus andrewsi</i>	G				G
<i>Metridiochoerus modestus</i>					G
<i>Metridiochoerus hopwoodi</i>					G
<i>Metridiochoerus compactus</i>					G
Bovids					
Alcelaphini (25 species)			E × 25	E × 25	E × 25
Aepycerotini (three species)		G × 2	G × 2, E × 1	G × 2, E × 1	
Hominids					
<i>Homo erectus</i>	G		G	G	
Dirk-toothed cats					
<i>Smilodon</i> and <i>Meganteron</i> (four species)					G × 4
Modern European species known as fossils <sup>b</sup>		G 25	G 25, E 86	G 25, E 86	
Total species 98					
Punctuated equilibrium	6		32	35	25
Phyletic gradualism	8	15	12	16	61
Cannot distinguish with available data	84	83	54	47	12

<sup>a</sup>E. Data provide convincing support for punctuated equilibrium; G, data provide convincing support for phyletic gradualism.

<sup>b</sup>Only suggestive (not firm) data are available: therefore these are not counted in the totals.

support punctuated equilibrium, and eight support phyletic gradualism. The relevant data are unknown for the remaining 84 species.

#### 4.1.2. Category 2: Does Anagenesis Occur Frequently?

Anagenesis apparently took place in at least 15 species, which rejects punctuated equilibrium in those cases. The frequency of cladogenesis was not tallied, because it can occur in both punctuated equilibrium and phyletic gradualism. It is, however, common among the other 83 species. Data from this category only provide a minimum frequency for phyletic gradualism, because some of the cladogenetic events could also be encompassed in the model.

#### 4.1.3. Category 3: Does Most Phenotypic Change Occur at Speciation?

Phenotypic change evidently was concentrated near the speciation event for 32 species and distributed throughout the stratigraphic range for 12 species. The prediction of punctuated equilibrium is fulfilled more frequently.

#### 4.1.4. Category 4: Are Species Discrete Entities?

Species can be demarcated as discrete entities in 35 cases, as stipulated by punctuated equilibrium, but appear transitional in only 16 instances.

#### 4.1.5. Category 5: Trends from Additive Microevolution or Species Sorting?

Most of the evolutionary trends are consistent with the model of phyletic gradualism. These include six different trends, which cumulatively involve 61 species. The fossil evidence suggests that only one trend, which involved 25 species, is consistent with what punctuated equilibrium predicts.

#### 4.1.6. Quantitative versus Qualitative Morphological Traits

Mensural data support punctuated equilibrium in shrews and squirrels, but phyletic gradualism in voles, elephants, pigs, and *Homo erectus*. Qualitative characters, for example, the complexity of horn morphology and the presence or absence of a molar reentrant, suggest punctuated equilibrium in alcelaphine bovids, but phyletic gradualism

in voles. Therefore, the correlation is at most weak between the kind of trait analyzed—qualitative or quantitative—and a particular model of evolution—punctuated equilibrium or phyletic gradualism. Nevertheless, it is important to recognize that qualitative traits are inherently more likely to show punctuated rather than gradual change, especially if only their presence or absence is the subject of analysis. One way to compensate for this bias is by tracing the frequency of a presence-absence trait among individuals of stratigraphically successive samples.

#### 4.2. Examination by Taxon

##### 4.2.1. Numbers of Species Supporting Each Model

Data in all five categories exist for only four species, all of which support phyletic gradualism. Data in three or four categories exists for 43 species; 31 of these argue for punctuated equilibrium. Therefore, of species that can provide data in at least three of the five data categories, 16 support phyletic gradualism, whereas 31 support punctuated equilibrium.

##### 4.2.2. Correlation between Higher Taxon and Mode of Evolution.

The distribution of species that support a given model is not random with respect to higher taxonomic group. Of the taxa for which evidence was available in at least three data categories, the shrews (soricids) and alcelephines (bovids) showed evolutionary patterns consistent with punctuated equilibrium. The voles (arvicolines), elephants (elephantids), and *Homo erectus* (hominid) strongly support phyletic gradualism; impalas (aepycerotines) also fit this model best. In taxa for which more limited data were available, two hamsters (cricetines) and a single squirrel (sciurid) suggest punctuated equilibrium, but muskrats (arvicolines), cotton rats (cricetines), pigs (suids), and dirt-tooth cats (felids) imply phyletic gradualism. Thus, evolution in three groups—soricids, alcelephine bovids, and sciurids—seems inclined to punctuated equilibrium. In six others—arvicolines, elephants, pigs, impalas, *Homo erectus* and probably dirt-tooth cats—evolution tends toward phyletic gradualism. The cricetines may exhibit both patterns.

## 5. CONCLUSIONS

The Quaternary time scale comes into focus between the ecological moment and the usual conception of geologic time. That is, one can

observe events that take place over thousands of years, rather than over the tens or hundreds that ecologists deal with, or the millions that studies of the pre-Quaternary encompass. The data presented here leave little doubt that, for Quaternary mammals, evolution proceeded within this intermediate time scale in ways consistent with the models of both phyletic gradualism and punctuated equilibrium. There is still considerable doubt, however, as to which mode of evolution was more frequent. An accurate assessment of this requires data from all five of the categories listed in Table II for more than just four species. Nevertheless, the patches of data that are available lead to some preliminary notions.

One or the other model seems to dominate within certain taxa. Punctuated equilibrium is evident for shrews, alcelephine bovids, and probably squirrels and hamsters. It is worth noting that shrews and squirrels are morphologically conservative for most of their fossil history—stasis for such groups may go back a long way. Phyletic gradualism is apparently the norm for voles and muskrats, elephants, pigs, impalas, *Homo erectus*, and probably cotton rats and dirt-tooth cats. Therefore, if one considers only the higher taxa analyzed here, phyletic gradualism appears as the more frequent mode of evolution.

But if one considers instead only the total numbers of species consistent with a given model, punctuated equilibrium is supported twice as often as phyletic gradualism. The evidence leading to that conclusion is weighted heavily by a single taxonomic group of 25 alcelephine species, and is found mainly in two of the five data categories (3 and 4, Table II)—the majority of species considered exhibit most of their morphological change near a speciation event, and most species seem to be discrete entities.

Punctuated equilibrium does not fare as well in the other two data categories that are able to test for it (1 and 5, Table II). It presently is impossible to tell if this is an artifact of the limited facts at hand or a real discrepancy. For example, if most of the alcelephine bovids show stasis (which they may well, although I have not seen the data that would allow me to say for sure), category 1 undoubtedly would support the thesis of punctuated equilibrium. Category 5, on the other hand, presents a serious challenge to the model of punctuated equilibrium as now formulated—most of the evolutionary trends we have recognized in Quaternary mammals are not easily attributed to sorting among species.

Definitive resolution of such conflicting conclusions must of course await additional studies of how morphology changes within and among related species through well-dated stratigraphic intervals. Such paleontological studies are the best and most applicable tools we have to sculpt the models of phyletic gradualism and punctuated equilibrium



into their finished form, or, if empiricism demands it, to disassemble them. The Quaternary mammalian record abounds in the information we need for refining and testing these two conceptions of evolution. Its relatively minor utilization already has shown that both punctuated equilibrium and phyletic gradualism can be corroborated over spans of time that are short in the geologic sense, but long in ecological terms—that is, through as little as 10,000–30,000 years, up to 2 million years. This portends an exciting possibility—bridging the temporal gap between studies of evolution at the ecological time scale and those at the geologic scale. We should not ignore the opportunity.

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