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# Preservational, paleoecological and evolutionary patterns in the Paleogene of Wyoming–Montana and the Neogene of Pakistan

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## Abstract

Contributions to this special issue have compared the tectonic settings, fluvial systems, paleoclimates, paleofloras and faunas, vertebrate taphonomy, and mammalian paleoecology and evolution from two long, continental records of Cenozoic ecosystems. In this concluding paper, we summarize highlights of earlier papers to provide an overview of similarities and differences between these Paleogene and Neogene records.

The relative influences of tectonic, climatic, and fluvial processes on lithofacies, environments of fossil preservation, and the productivity of the fossil record are compared for each sequence. Tectonism was the primary control on sediment accumulation rate and the distribution of major depositional environments in each basin. Fossil productivity, species richness, and the distribution of fossil localities among fluvial environments change across formation boundaries in each sequence. The taxonomic, temporal, and spatial resolution of vertebrate assemblages varies among fluvial environments and differs between the two sequences. As a result, the Paleogene record is better suited for detailed study of evolutionary change within local lineages and the Neogene record for detailed paleocommunity reconstruction.

Several aspects of biotic change are considered. (1) The timing and magnitude of mammalian faunal turnover in relation to climatic change are evaluated in terms of three models of evolutionary change within ecosystems: Van Valen's "Red Queen model," Stenseth and Maynard Smith's "stationary model," and Vrba's "turnover-pulse model." In both records, climatic change was accompanied by change in faunal composition and ecological structure, but both pulsed and diachronous biotic change, at a resolution of about 0.5 m.y., also occurred over periods when no significant climatic change was discernible. This pattern best matches the predictions of the Red Queen model. (2) In both records, the rate of mammalian faunal turnover (first and last appearances of taxa) is not highly correlated with standing richness, suggesting that paleocommunities were not at equilibrium richness on these time scales. (3) In the Paleogene record, plant species richness declined while mammalian species richness increased. (4) In each sequence, some episodes of mammalian faunal turnover were in step with changes in size or trophic structure, while other changes in faunal composition entailed no corresponding change in ecological structure.

While both records would benefit from improved paleoclimatic, temporal, species-level, and ecomorphological resolution, this initial synthesis suggests that both physical and biotic factors were important influences on faunal composition, the timing and rate of turnover, and ecological structure in these paleocommunities.

## 1. Introduction

In this final paper comparing two long continental sequences, our goals are to summarize highlights of this special issue and to evaluate three research questions that span two or more subjects addressed by the preceding papers. (1) How have tectonic, climatic, and sedimentologic factors affected the productivity and quality of the fossil record in each sequence? (2) How synchronous were physical change and biotic change in each record? (3) To what degree are change in ecological aspects (as represented by size and trophic structure) and evolutionary aspects (as represented by taxonomic composition) of mammalian faunas coupled in each sequence? For each question, the issue of relative timing is important for evaluating cause and effect. We approach these questions with information from earlier papers in this issue.

Although the Paleocene to early Eocene record of the Bighorn, Clarks Fork, and Crazy Mountains basins and the Neogene Siwalik record of northern Pakistan are well documented in the literature, the papers in this special issue are among the first attempts to examine geological and biotic change synthetically over each sequence. These syntheses represent interdisciplinary collaborations as well as preparation of great quantities of information, representing many years of field and laboratory work. Clearly, much work remains to be done, both in fieldwork and in analysis, and the comparisons presented in this issue help to focus future research goals. These studies illustrate the rewards as well as the limitations of intensive efforts to document the geological and paleontological record on land, or indeed in any rock sequences.

## 2. Highlights of earlier papers

The long sequences compared are similar in tectonic setting, in their predominantly alluvial deposits, in the rich vertebrate record dominated by mammals, and in a comparable breadth and duration of former and current study. The Paleogene sequences of Wyoming and Montana (USA) represent a window into early Cenozoic history during recovery from the mass extinction

at the end of the Cretaceous, when global climate was relatively warm and equable, whereas the Neogene Siwalik sequence of northern Pakistan is a window on late Cenozoic ecosystems during a period of global cooling and increasing seasonality. Climatic conditions, vegetation structure and composition, and ecological structure of mammalian faunas differed substantially between these sequences. Patterns of fossil preservation also differed, influencing the nature of paleoecological and evolutionary investigations in each area.

### 2.1. Physical substrate

The exposures of the three Paleogene basins encompass much of a foreland basin that developed east of part of the Cordilleran Overthrust during the Sevier and Laramide orogenies (Wiltschko and Dorr, 1983), whereas the area of Siwalik exposures is small relative to the size of the depositional basin of the Himalayan foredeep. The lateral distribution and frequency of fluvial environments changed over time in both sequences, reflecting primarily changes in basin subsidence rate and secondarily climatic change and the interactions of contemporaneous river systems (Willis and Behrensmeyer, this issue; see below).

Paleosols are important components of both records (Behrensmeyer et al., this issue). Pedogenic features overprinted a wide range of primary deposits, including near-channel, abandoned-channel, and floodplain sediments. Paleosol maturities vary in relation to paleotopography, distance from paleochannels, sediment accumulation rate, and other factors. Paleogene paleosols are major fossil-bearing deposits in the Wyoming–Montana sequence, whereas fossils are fairly rare in Siwalik paleosols. Differences in floodplain deposition and oxidation rates are proposed to explain the high frequency of vertebrate remains in Willwood paleosols and the low frequency in Siwalik paleosols.

### 2.2. Climate and flora

In both sequences, stable-isotope stratigraphy of carbon and oxygen isotopes provides information about climate and vegetation. Koch et al.

(this issue) evaluate the carbon- and oxygen-isotopic records from paleosol carbonates, bivalve molluscs, and mammalian enamel from the Bighorn and Clarks Fork basins. The carbon-isotopic record indicates a continuous  $C_3$  vegetation throughout the Paleogene sequence, as expected ( $C_4$  plants did not appear until later in the Cenozoic). A sharp decrease in  $\delta^{13}C$  around the Paleocene–Eocene boundary permits precise correlation to the marine isotopic record. At this time, changes in ocean circulation resulted in high-latitude warming and an extinction of benthic foraminifera; on land, intercontinental dispersal and local faunal turnover of mammals are documented. Koch et al. infer mean annual paleotemperatures local to the Bighorn and Clarks Fork basins from the difference in  $\delta^{18}O$  between biogenically precipitated  $CaCO_3$  (bivalves, mammals) and inorganically precipitated  $CaCO_3$  (paleosol carbonates). By this method, the late Paleocene Tiffanian was relatively warm ( $>20^\circ C$  mean annual temperature), the latest Clarkforkian to earliest Wasatchian, spanning the Paleocene–Eocene boundary, was cooler ( $10\text{--}20^\circ C$ ), and the late Wasatchian (late early Eocene) was warmer again. These inferences are quite preliminary and not in full agreement with those based on floral physiognomy (see below).

Two major events were noted in Siwalik stable-isotope stratigraphy (Quade and Cerling, this issue). The  $\delta^{13}C$  record, which indicates the metabolic pathway ( $C_3$  or  $C_4$ ) of the original vegetation, exhibited a substantial shift toward heavier values from 7.3–5.5 Ma. These changes signify a transition from vegetation dominated by  $C_3$  plants—including most trees, shrubs, and non-tropical grasses—to vegetation dominated by  $C_4$  plants—typically, tropical grasses. Enamel from herbivorous mammals indicates that  $C_4$  plants were present in Siwalik ecosystems almost 2 m.y. earlier than the isotopic shift recorded in paleosol carbonates (Morgan et al., 1994). The  $\delta^{18}O$  record shifted to markedly heavier values around 8.5 Ma. These isotopic shifts may reflect intensification of the Asian monsoon system or more global atmospheric changes.

The Paleogene sequences of Wyoming and Montana preserve a good floral record, while the

Neogene Siwalik record of Pakistan does not. Taxic richness, composition, and abundance of floral remains are correlated with the prevalence of particular depositional environments in the Paleogene Fort Union and Willwood formations (Wing et al., this issue). The latest Paleocene and earliest Eocene are poorly represented by floral remains. After correcting for sampling effects, the greatest floral turnover is noted between early and late Wasatchian (early and late early Eocene), well after the major turnover among mammals. Mean annual paleotemperatures, as inferred from the percentage of entire-margined leaves, rose almost steadily from the late Paleocene to the late early Eocene (fig. 6 in Wing et al., this issue). As currently understood, the oxygen-isotopic and paleofloral estimates of paleotemperature are not in agreement over all parts of this record. The relationship between floral and faunal change is considered further below.

### 2.3. Vertebrate taphonomy

Both sequences contain a range of fluvial environments and patterns of vertebrate preservation that changed in frequency upsection (Badgley et al., this issue). In the Paleogene record, vertebrate remains are concentrated primarily in (1) channel conglomerates in the lower Fort Union Formation, (2) channels, splays, swamps, and floodplain paleosols in the Upper Fort Union, and (3) floodplain paleosols in the Willwood Formation. In Siwalik deposits, fossil productivity is higher in the formations dominated by mudstone (Chinji and Dhok Pathan) than in the formations dominated by sandstone (Kamlial and Nagri). In mudstone-dominated formations, the predominant environment is floodplain, but more localities and specimens are preserved in floodplain channels than in any other environment. In both sequences, the abundance of certain aquatic and terrestrial vertebrates is correlated with particular depositional environments. Major changes in fluvial systems led to changes in the prevailing taphonomic processes—including mortality, dissociation of skeletal remains, fluvial transport and winnowing, and mechanisms of bone accumulation—from different depositional environments. Different

processes of mortality and accumulation resulted in different degrees of taxonomic, temporal, and spatial resolution of fossil assemblages (see below).

#### 2.4. Faunal turnover

Faunal turnover in these two records refers to change in faunal composition resulting from immigration, cladogenesis, local extinction, and anagenetic speciation or pseudoextinction. From the middle Paleocene to early Eocene, the highest generic diversity of mammals occurred during the earliest Eocene (early Wasatchian), with a peak of >60 genera (Maas et al., this issue). Tests for the effects of sampling—which could produce, for example, an apparent increase in diversity with a large increase in sample size—reveal two significant peaks in first appearances and two in last appearances. Neither peak of first appearances was synchronous with a peak of last appearances. Several higher taxa (mammalian orders and families) made first appearances in the middle to late Paleocene; few higher taxa disappeared over this period. The increase in generic diversity in the early Eocene resulted from immigration of new groups and from diversification within both established and new groups. This episode of first appearances coincided with global climatic changes that opened high-latitude corridors between continents. Decline in generic diversity during the late early Eocene affected mainly older groups, such as multituberculates and pliesiadapiforms; this decline coincided with major floral turnover.

In the Siwalik record, productive intervals typically contain  $\geq 50$  mammalian genera (Barry et al., this issue). Much of this diversity derives from three mammalian orders—rodents, artiodactyls, and perissodactyls. Species and generic richness increased between 15 and 13 Ma, then decreased gradually from 12 to 7 Ma. With consideration for sampling effects, Barry et al. (this issue) recognize major first-appearance peaks at 13.5 and 8.5 Ma and major last-appearance peaks at 12.5 and 8.0 Ma. Only the changes around 8 Ma were near-synchronous, coinciding with the shift in oxygen-isotopic ratios determined from soil carbonates. Smaller peaks of first and last appearances also occurred, and in two instances, a peak of first

appearances is matched by a peak of last appearances. The middle Miocene diversification in Siwalik faunas occurred at a time of global cooling that may have opened dispersal routes linking southern Asia with other parts of Eurasia (Barry et al., 1985). The late Miocene decline in genera preceded a period of intensified cooling and aridity.

#### 2.5. Mammalian species longevities, rates of change, and species origins

In this context, “species” refers to local species populations in an ecological community, or avatars, *sensu* Damuth (1985). Species longevities differed substantially between the Paleogene and Neogene sequences. For 125 Paleogene species, median duration, measured over an interval of 4.7 m.y., was 0.76 m.y. (Gingerich and Gunnell, this issue). For 57 species of Siwalik rodents, measured over an interval of 11 myr, median duration was 1.5 m.y. (Flynn et al., this issue). Middle Miocene rodent species were longer-lived than late Miocene species. The median duration for Siwalik artiodactyls and carnivores was 2.7 m.y. Thus, on average, species durations were greater in Neogene Siwalik faunas than in Paleogene faunas of the Clarks Fork Basin. We evaluate reasons, including methodological ones, for this difference below.

For well-sampled mammalian lineages, rates of morphological change were estimated from measurements of tooth size from superposed samples and quantified as proportional change in standard deviation units of morphological change versus time intervals in generations (Gingerich, 1993; Gingerich and Gunnell, this issue). For 18 Paleogene lineages analyzed in this manner, seven were stable over time, four cannot be distinguished from a random walk, five were stable with a random component, and two showed sustained directional change with a random component. For seven Siwalik lineages, two were stable over time, four showed random change, and one was stable with a component of random change.

The pattern of first appearances of species differs between the two records. Most first appearances of Paleogene mammals represent in-situ evolution within genera and families established in western North America; only about 20% of first appear-

ances represent immigration from other regions (P.D. Gingerich, pers. comm., 1994). Gingerich and Gunnell (this issue) report that, of species that evolved in situ, about 60% arose by anagenesis, 25% by cladogenesis, and 15% by cladogenesis accompanied by anagenetic change. First appearances of about half of the Siwalik species resulted from immigration into southern Asia (Barry et al., 1991). Among species that evolved in situ, cladogenesis was recognized for the origin of some and anagenetic speciation for others; in some instances, the mode of origin was indeterminate (Flynn et al., this issue).

## 2.6. Comparative paleoecology

The ecological structure of mammalian faunas is characterized in terms of trophic structure (distribution of genera among trophic categories) and size structure (rank-size distributions of species). (Trophic structure is evaluated over a greater number of biostratigraphic intervals than size structure. The generic level is used for trophic structure because species-level resolution is not consistently available over the entire record. Size structure is examined for selected biostratigraphic intervals and for selected higher taxa in which species-level resolution is available.) In Paleogene faunas, no single trophic category was significantly dominant in terms of frequency of genera (Gunnell et al., this issue). The dominant trophic category changed from herbivore to insectivore to carnivore to insectivore to herbivore over the late Paleocene to late early Eocene. Frugivores (adapid primates) appeared in the earliest Eocene. The taxonomic composition of trophic categories changed substantially from the late Paleocene to early Eocene. Siwalik trophic structure was dominated by one category (herbivores), and this pattern changed little from 17 to 7 Ma. Frugivores, omnivores, and insectivores each typically comprised less than 10% of generic diversity throughout the sequence. Carnivores increased in generic diversity from 5% in the middle Miocene to around 20% in the late Miocene. In terms of number of specimens (a rough indicator of relative abundance), herbivores were the most abundant throughout both records.

The typical early Paleogene mammal was much smaller than the typical Neogene mammal (Morgan et al., this issue). Few species of early

Paleogene mammals exceeded 100 kg, and the median size of species in Paleogene mammalian faunas was <1 kg. Siwalik faunas, on the other hand, had a dozen or more species >100 kg in body size, five or more species >1000 kg, and a median size of generally >10 kg. Cenograms, or rank-ordered size distributions of non-carnivorous species, were constructed for three time intervals in each sequence. Based on comparison to modern mammalian faunas of known vegetation and climate, the Paleogene cenograms suggest a shift from mesic forest in the Tiffanian (earliest late Paleocene) to humid forest in the early Wasatchian (early Eocene). Floral paleotemperature indicators suggest increases in mean annual temperature and in equability of temperature from the Tiffanian to the Wasatchian (Hickey, 1980; Wing and Greenwood, 1993; Wing et al., this issue). The paleofloral record neither falsifies nor confirms the inferences based upon cenograms, because different aspects of vegetation are reconstructed; also, the paleofloral and mammalian samples are not all from the same biostratigraphic intervals. The Neogene cenograms imply a shift from open woodland to savannah scrub from the middle to late Miocene. Inferences about vegetation from trophic structure are in agreement with those from cenograms for the Neogene record, but some inferences were not in agreement for the Paleogene record (Morgan et al., this issue).

Single-species and multi-species lineages from several families of mammals in each sequence were examined for major rapid changes in size. Size increases (>doubling) slightly outnumbered size decreases (<halving), but most lineages did not exhibit size changes of this magnitude between successive biostratigraphic intervals. Changes over time in the size distribution of families occurred mainly through first appearances (including immigrations) and last appearances, rather than by phyletic size increases or decreases. Cumulative size increases within lineages and families occurred more often than cumulative size decreases.

## 2.7. Nature of similarities and differences in the two records

In comparing the Paleocene to early Eocene record of Wyoming–Montana with the Neogene

Siwalik record of Pakistan, it is useful to identify the similarities that may characterize alluvial sequences in general and the differences that reflect the different historical periods of these records. Similarities that would plausibly be found in most fossiliferous, alluvial sequences are (1) changes over time in the distribution and frequency of fluvial facies, (2) the interaction of extrabasinal and intrinsic controls on fluvial systems, (3) the prevalence and diversity of paleosols, (4) the abundance of vertebrate remains and their distribution among fluvial facies, and (5) the influence of taphonomic processes on the quality of the record. Both sequences cover enough time (several million years) to reveal multiple faunal turnovers; changes in taxonomic richness, trophic structure, and size structure; and a variety of rates of change among mammalian lineages.

Differences that plausibly reflect the early Cenozoic aspect of one sequence and the late Cenozoic aspect of the other include (1) the different carbon-isotopic records and their corresponding implications for vegetation, (2) differences in taxonomic composition of Paleogene v. Neogene mammalian faunas, and (3) their respective differences in trophic and size structure. Other differences between the two sequences are not readily explained by the different historical periods. These additional differences include: (1) the highly fossiliferous Willwood paleosols in contrast to the poorly fossiliferous Siwalik paleosols, (2) the different patterns of species origins (i.e., in situ evolution v. immigration) in the two sequences, and (3) the contrast in preservation of floral remains.

Other similarities in patterns of change are noteworthy but are known from too few examples of densely sampled, fossiliferous sequences to determine whether or not they are a general feature of the history of terrestrial ecosystems. Included here are (1) the asynchronies between floral and faunal turnover noted in both records, (2) the individualistic aspect of taxonomic change (many diachronous first and last appearances) over much of each record, alternating with short episodes of high faunal turnover, and (3) the major changes over time in size structure happening mainly through first and last appearances, rather than by major

jumps in size within lineages. Below, we take up some of these issues in greater detail.

### 3. Facies, environments, and fossil preservation

Tectonic, climatic, and sedimentologic factors all potentially influence the productivity and quality of the fossil record. We present a general reconstruction of the scale and distribution of fluvial environments in each sequence and then assess the relative contribution of tectonic, climatic, and sedimentologic processes to each record.

#### 3.1. Reconstructed environments

The Paleogene alluvial environment was a gently sloping plain, approximately 100–200 km wide by 500 km long (from the Bighorn to Crazy Mountains area), ringed by low mountains to the west and larger mountain ranges to the northwest and east (Wing and Bown, 1985). A trunk river flowed from south to north along the western side of the basin and parallel to its axis. Tributary streams crossed the basin from east to west to join the main drainage. Along the tributaries and the trunk river were alluvial ridges that sloped gently to more distal areas of the floodplain, some of which were permanently wet or swampy. Relief on levees was probably on the order of a few meters above local swales and the lower parts of the floodbasin. Soils that formed on aggrading levees were weakly developed, whereas soils more distal to channels were more mature. Tributary channels were generally <10 m at bankfull depth. Increase in crevasse splays associated with channel avulsion resulted in rapid aggradation of low floodplain areas. The water table was moderately stable with some seasonal fluctuation. During periods of flooding, the alluvial ridges formed islands along the drainage channels. Temperatures were fairly equable, with warm summers and cool winters without frost. Rainfall was relatively equable, with no totally dry months.

In the Neogene system, large rivers, spaced at intervals of 100–200 km, crossed a plain >1000 km wide to join a major river, on the scale

of the modern Indus or Ganges, that probably flowed along the axis of the foreland basin (Willis, 1993). The proto-Himalayas bordered the plain to the north and northwest. Siwalik deposits of the Potwar Plateau were formed by the secondary rivers and their floodplain systems. These rivers were generally braided with channel belts up to a few kilometers across and individual channels up to 15–30 m at bankfull depth. Rivers were subject to frequent avulsions and did not form large alluvial ridges. Floodplains were crossed by subsidiary channels, and abandoned channels were common. Maximum bankfull depths of floodplain channels ranged from 1–10 m. Floodplains had a mosaic of higher and lower areas, resulting from variable sediment accumulation rates during flooding and scouring during avulsions. Maximum relief was probably about 10–12 m. Low areas often contained seasonal and some permanent lakes, which aggraded rapidly when crevasse-splay channels drained into them. Such processes transformed depressions into areas of higher elevation, and paleosols developed on surfaces of crevasse-splay lobes over periods of 20–40 ka. The water table fluctuated seasonally by up to several meters. The climate was warm and probably monsoonal, with a hot, rainy season alternating with a dry, cool, frost-free season.

### 3.2. Influences on lithofacies

The major vertical and lateral changes in lithofacies and sediment accumulation rate reflect a different hierarchy of influences in each stratigraphic sequence. The Paleogene sequence was an underfilled basin where rates of sediment input did not always keep pace with rates of basin subsidence (Willis and Behrensmeyer, this issue). The major vertical changes in facies and the spatial distribution of depositional environments—such as lacustrine, paludal, and fluvial—reflect changes in rates of basin subsidence relative to sediment supply. Some of the tectonic influences on uplift, subsidence, and sediment supply were localized within the basin, whereas others affected the entire basin (Bown, 1980). Gingerich (1983) interprets the transition from Fort Union to Willwood facies as the result of improved drainage resulting from a

decreased subsidence rate, whereas Wing and Bown (1985) emphasize regional climatic warming and drying as the main influence. Since the formation boundary is diachronous by ~1 m.y. over a distance of ~20 km (Wing and Bown, 1985), we would rank the tectonic influence as primary and the climatic influence as secondary. Kraus and Bown (1993) note that changes in sediment accumulation rate upsection in the Willwood Formation of the central Bighorn Basin reflect mainly change in the locus of sedimentation, as controlled by uplift on a basin-margin fault.

The Neogene sequence represents an overfilled basin in which vertical changes marked by formation boundaries were determined by tectonism and its effects on lateral displacement of contemporaneous river systems (Willis, 1993; Willis and Behrensmeyer, this issue). Increase in sediment accumulation rate in the upper Chinji Formation (Johnson et al., 1985) reflects mainly an increase in rate of subsidence; only a small fraction of sediment accumulation can be attributed to progradation of a fan wedge into the basin, and the Miocene shoreline was too far away (~900 km) for sea level to have had a substantial effect on observed sediment accumulation rates (Willis, 1993). The major discernible climatic shifts in the Siwalik record do not coincide with a formation boundary or other marked lithological change. Also, formation boundaries are time-transgressive by up to 1 m.y. over lateral distances of ~30 km. Thus, it appears that climatic effects had a subordinate influence on the main lithostratigraphic changes.

In summary, tectonism had a dominant role in each sequence, especially in determining formation-scale vertical and lateral variations in sediment accumulation rate. Climate had a strong secondary influence in the Paleogene sequence, while displacement of adjacent river systems was the major secondary influence in the Neogene sequence.

### 3.3. Fossil preservation and implications for paleobiological studies

In each sequence, major facies transitions at formation boundaries are correlated with striking

changes in fossil productivity, species richness, and the frequency of fossil localities among fluvial environments (Badgley et al., this issue). In the Paleogene record, the primary fossil-producing environment (channels) in the Fort Union Formation declines in productivity upsection, while a previously unproductive facies (floodplain paleosols) becomes the major source of fossils in the Willwood Formation. The Willwood Formation preserves a greater frequency of localities and fossils per unit thickness than the Fort Union Formation. In the Siwaliks, a variety of depositional environments produces fossils throughout the sequence, with channel lags and abandoned-channel fills preserving the greater part of the record. The frequency of localities and fossils among these and other depositional contexts changes across formations. In both sequences, the most prevalent facies is not always the main source of abundant fossil remains.

The number and sample size of localities per stratigraphic interval are correlated with species richness in both records. More productive formations are presumably better known faunally. More diverse faunas of course differ in taxonomic composition from less diverse ones, but the major episodes of mammalian immigration are not linked principally to increases in fossil productivity at formation boundaries. Moreover, time-transgressive formation boundaries are not paralleled by time-transgressive faunal changes in either the Paleogene (Wing and Bown, 1985) or Neogene (Barry et al., 1980) record.

Table 1 summarizes the major associations between certain taxa and particular depositional environments and the different degrees of taxonomic resolution, temporal averaging, and spatial averaging of vertebrate assemblages in each record. The contrasting taphonomic patterns have implications for evolutionary and paleoecological studies

Table 1

Taphonomic comparison of Paleogene sequence of the Bighorn Basin (Wyoming, USA) and Neogene Siwalik sequence of Pakistan. Information from Badgley et al. (this issue) and Wing et al. (this issue)

	Paleogene	Neogene
<i>Fossil-bearing environments</i>		
Vertebrates	channels, abandoned channels, paleosols	channels, abandoned channels, crevasse splays, floodplains
Plant macrofossils	channels, levees, backswamps, ponds	none preserved
<i>Associations between biota and environments</i>		
	(1) Aquatic vertebrates more diverse in larger channels, floodplain lakes and swamps (2) Terrestrial vertebrates increase in floodplain paleosols (3) Angiosperm trees on alluvial ridges; conifers in backswamps	(1) Small mammals preserved mainly in abandoned-channel fills (2) Floodplain localities preserve more cursorial, hypsodont mammals (3) Bunodont, terrestrial and arboreal species more prevalent in channel-margin localities
<i>Vertebrate assemblages</i>		
Taxonomic resolution	High: most preserved material diagnostic to species level for mammals	Medium to high: most preserved material not diagnostic to species level for large mammals, but is diagnostic for small mammals
Temporal resolution	Medium: paleosol assemblages formed in $10^3$ – $10^4$ yr	Medium to high: $10^1$ yr for concentration by biological agent; $>10^4$ yr for reworked assemblages
Spatial resolution	Low to medium: ranges from $\sim 100$ m <sup>2</sup> to $\sim 10$ km <sup>2</sup>	Low, medium, high: ranges from $\sim 100$ m <sup>2</sup> to $>100$ km <sup>2</sup>



based on each record. Information needed for evaluating evolution within lineages and species-replacement patterns is provided by high taxonomic resolution, high temporal resolution, and consistent preservational context over a long record. These circumstances are best matched in the rich paleosol assemblages from the Willwood Formation and the small-mammal assemblages in abandoned-channel fills of the Siwalik record. The information needed for paleocommunity reconstruction is provided by high taxonomic resolution, large sample sizes, and varied, contemporaneous environments of preservation. These circumstances occur in limited portions of both records (Badgley et al., this issue).

#### 4. Timing of physical and biological changes

In addition to the issue of geologic and climatic effects on fossil preservation in each sequence, it is important to consider whether such physical processes exerted discernible influences on biotic change itself. Local geologic and climatic factors are the major physical agents for which we have evidence. But in both records, species immigrations were probably influenced strongly by distant changes in sea level, climate, or contacts between continents. The main biotic changes we evaluate are mammalian faunal turnover (change in taxonomic richness and composition) and the ecological structure of mammalian faunas, which consist of sets of avatars of more widely distributed species. We are attempting to distill the general patterns of change and influence in ecosystems, not in clades.

In the recent literature about causes of evolution, there is debate about whether evolution within lineages and clades, change in the taxonomic composition of local biotas, or change in the ecological structure of biotas are more strongly influenced by physical or by biotic processes (e.g., Van Valen, 1973; Stenseth and Maynard Smith, 1984; Ross and Allmon, 1990; Vrba, 1993). Critical tests are the timing of response to stimulus and the pattern of the response. Long fossil records can provide empirical tests of some of the predictions of models of evolutionary change within ecosystems.

For example, Van Valen's (1973) "Red Queen model" of evolution emphasizes biotic interactions among species (avatars) and predicts that changes in biotic composition of ecosystems should be rather evenly distributed over time. Physical perturbations also affect biotic interactions, so a major physical change should result in rapid faunal turnover diminishing to background levels of appearances and disappearances. The "stationary model" of Stenseth and Maynard Smith (1984) is based on biotic interactions within ecosystems; the evolutionary lag load of each avatar is a function of interactions with other avatars in the community. Their model predicts bursts of evolutionary change in lineages, accompanied by appearances and disappearances of avatars, initiated by discrete physical changes in the environment. Phyletic and faunal changes subside until another physical perturbation renews change. Phenotypic stasis prevails between the bursts of evolution. Vrba's "turnover-pulse hypothesis" assumes that physical changes, such as climatic change, force shifts in geographic ranges of species, resulting in speciation and extinction events and thereby changes in local ecosystem composition (Vrba, 1985, 1993). Predictions of Vrba's model about ecosystems are (1) that change in biotic composition (from immigration or splitting of lineages only) should occur at times of major climatic change (or other major perturbations in the physical environment), (2) if physical change is pulsed, then change in biotic composition should be concentrated in brief time periods, with little to no change in between these "pulses," and (3) if physical change is gradual, then change in biotic composition should also be gradual. These predictions are similar to those of Stenseth and Maynard Smith's stationary model, although the two models are based upon different assumptions (physical v. biotic interaction) about causes of biotic change. Table 2a summarizes predictions about faunal change for three circumstances of physical change for these models.

In the Paleogene and Neogene records presented here, we can examine the response of mammalian faunas to geologically short intervals of climatic change and to long periods of gradual or no discernible climatic change. Table 2b summarizes the major Paleogene episodes of faunal turnover

Table 2

Predictions of three models of evolutionary change within ecosystems and patterns of climatic and biotic change in the Paleogene and Neogene records

(a) Models			
Proponent	Van Valen	Stenseth & Maynard Smith	Vrba
Model	Red Queen	Stationary	Turnover-pulse
Major initiating cause	biotic interactions	biotic interactions	Physical change, especially climate
Predictions:			
(1) Following pulsed climatic change	rapid biotic turnover & phyletic evol.	rapid biotic turnover & phyletic evol.	rapid biotic turnover
(2) Following gradual climatic change	gradual turnover & phyletic evol.	gradual turnover & phyletic evol.	gradual turnover
(3) In absence of physical change	continued turnover & phyletic change	no turnover & phyletic stasis	no turnover & phyletic stasis

(b) Paleogene faunal and climatic change

Epoch	<i>late Paleocene</i>							<i>early Eocene</i>									
Interval	To3	To4	Ti1	Ti2	Ti3	Ti4	Ti5	Cf1	Cf2	Cf3	Wa0	Wa1	Wa2	Wa3	Wa4	Wa5	Wa6
Mammalian turnover	LA							FA			FA---						LA
Trophic structure					-----						-----						-----
Size structure											-----						-----
Paleotemperature:																	
Isotopes			cooling-								warm	Δ	cool	warming-			
Foliar physiognomy						warming-											cooling

(c) Neogene faunal and climatic change

Epoch	<i>middle Miocene</i>						<i>late Miocene</i>					
Interval (Ma)	17	16	15	14	13	12	11	10	9	8	7	
Mammalian turnover					FA	LA		fa---		FA	LA	fa
Trophic structure					-----					-----		
Size structure										-----		
Paleoclimate												
Isotopes											O	C

Abbreviations: To=Torrejonian, Ti=Tiffanian, Cf=Clarkforkian, Wa=Wasatchian  
 FA=first-appearance peak, LA=last-appearance peak; upper case = major peak, lower case=minor peak  
 O=Oxygen, C=Carbon, Δ=excursion, ----- = rapid change, - - - - = gradual change

(first and last appearances of genera, from Maas et al., this issue), change in trophic structure (from Gunnell et al., this issue), major rapid size change in herbivorous mammalian groups (from Morgan et al., this issue) and paleotemperature estimates based on oxygen isotopes (from Koch et al., this issue) and on foliar physiognomy (Wing et al., this issue). The stable-isotope record suggests grad-

ual shifts in paleotemperature over 10 m.y., with the exception of a short interval of pronounced warming at the Paleocene-Eocene boundary. Koch et al. stress that their estimates are quite tentative, since they vary greatly from level to level and from source to source within levels. Paleofloral temperature estimates depict sustained warming in the latest Paleocene to early Eocene. Climatic and

mammalian faunal changes coincide across the Paleocene–Eocene boundary, with a set of mammalian first appearances, including immigrations, and concurrent adjustments in size and trophic structure. More gradual, covarying climatic and biotic change occurs in the middle Wasatchian, with a decline in mammalian generic diversity and concurrent shifts in ecological structure. In contrast, changes in Tiffanian faunas are not correlated with any current evidence for climatic change. In part, this may reflect the more poorly resolved Tiffanian climatic record.

Faunal and climatic changes in the Siwalik record are summarized in Table 2c. Mammalian faunal turnover represents first and last appearances of species (avatars) of rodents and artiodactyls (from Barry et al., this issue). Change in trophic structure (from Gunnell et al., this issue) and major rapid size change in rodents and artiodactyls (from Morgan et al., this issue) depict shifts in ecological structure. Stable isotopes (from Quade and Cerling, this issue) are the only geologic indicators of climatic conditions in the Siwalik record. Prior to about 8 Ma, the isotopic record has a narrow range of values about a constant mean over an interval of >8 m.y. (Quade and Cerling, this issue). An oxygen-isotope shift at 8.0 Ma signifies an increase in temperature, a decrease in precipitation, a shift in the regional source of moisture, or a combination of these changes. The carbon-isotope shift at 7.3 Ma signifies replacement of woodland or savannah woodland with grassland. Mammalian faunal turnover and change in size structure slightly precede and then continue with the late Miocene climatic changes. (Both faunal and isotopic studies employ the same timescale, so these offsets in timing occur in a common system of measurement). The largest peak of first appearances (at 13.5 Ma) and of last appearances (at 12.5 Ma) occurred during the long interval from 17–9 Ma when no local climatic change is evident. Important oceanic cooling occurs in the deep-sea record from 15 to 13 Ma (Miller et al., 1987), and a deep-sea hiatus spans 13.0 to 12.5 Ma (Keller and Barron, 1983), but these events are not yet discernible in the Siwalik record. During this middle Miocene interval, Siwalik

mammalian avatars exhibited longer average durations than after 9 Ma (Flynn et al., this issue).

In both sequences, some indicators of local evolutionary and ecological change occurred early in a period of climatic change, some aspects of faunal change slightly preceded major climatic change, and significant change in faunal composition occurred during periods when no local climatic change is discernible. The pattern of mammalian faunal change “anticipating” climatic change in both records indicates either that the onset of climatic change is not accurately documented in geologic and floral indicators or that some components of the mammalian faunas are affected by regional climatic change earlier than vegetation and soils of the floodbasin. The latter idea is plausible because the annual flood cycle should have forced many mammalian populations out of the floodbasin for part of each year, exposing them to different climatic conditions outside the floodbasin.

Another relevant point is how much faunal turnover occurred in pulses and how much in a gradual, sustained pattern of change. The stratigraphic ranges of mammals from well-sampled portions of the Paleogene and Neogene records provide a basis for estimating these two components of faunal change. For the Paleogene sequence, mammalian stratigraphic ranges at the species level are compiled for 20-m intervals, each representing about 40,000 years, in a well-sampled, 600-m section from the Clarks Fork Basin, Wyoming (Badgley and Gingerich, 1988). The number of species per interval ranges from 30 to 49, with most intervals recording  $\geq 36$  species. If we consider six or more first appearances per interval (17% for intervals with 36 species) as a pulse and anything less as background faunal change, then 19/37, or 51%, of first appearances occurred in pulses, while the remainder were gradual. Using the same approach to last appearances, 21/47 last appearances, or 45%, occurred in pulses, while the remainder were gradual. In addition, Badgley (1990) showed that a significant fraction of the major peaks of last appearances could be explained by a rapid drop in fossil productivity. Only first and last appearances of lineages (no pseudo-extinctions) were included in these counts.

For the Neogene record, faunal change is compiled over intervals of 0.5 m.y., based on stratigraphic ranges in Flynn et al. (this issue, Table 1). Well-sampled intervals often contain  $\geq 50$  mammalian species and poorly sampled intervals as few as 10 species (Barry et al., this issue). If 8 or more first appearances per interval (17%, as above, for intervals with 50 species) are counted as a pulse, then 35/88, or 40%, of first appearances occurred in pulses, while 60% did not. Thirty of 85 or 35% of last appearances occurred in such pulses, while 65% did not. A small portion of first and last appearances are pseudo-extinctions or pseudo-speciations in the Siwalik data set; these were not easily removed.

The measure of 6/36 or 8/50 events (17% of standing diversity for most intervals) as a pulse represents 2–3  $\times$  the “expected” values if first or last appearances were distributed evenly in proportion to taxic richness. A higher value for criterion of pulse would result in detection of fewer pulses and a greater amount of gradual change in both records. Overall, even this simple approach to evaluating the tempo of faunal change indicates that a substantial amount of change occurred both in pulses and in a gradual pattern. Neither fully gradual turnover nor turnover-pulse alternating with faunal stasis prevailed.

The patterns of faunal change documented in these two long sequences support the Red Queen model of faunal change better than the others, given the current understanding of faunal and climatic change. In each record, a substantial portion of faunal change occurred in pulses associated with major climatic change; this prediction (1) follows from all three models (Table 2a). In the Paleogene record (Table 2b), more gradual change in paleotemperatures is synchronous with one pulsed turnover and with gradual faunal change. The Neogene record (Table 2c) has no indicators of gradual climatic change. This pattern is approximately consistent with the prediction (2) that follows from all three models. The models differ principally over the prediction (3) of what happens in the absence of physical change. The Neogene record has a long interval in which no climatic change is discernible, yet the greatest faunal turnovers and the major shift in trophic

structure occur during this time; also, considerable gradual turnover occurs. This pattern matches the prediction of the Red Queen model but not the other two.

These two long mammalian records suggest that physical changes, such as regional climate change, are important initiating causes of rapid or gradual faunal change within ecosystems, but that change (both gradual and pulsed) in faunal composition and ecological structure continues in the absence of discernible physical changes, suggesting that biotic interactions also influence first and last appearances and changes in ecological structure of mammalian faunas. But these are preliminary rather than definitive tests of the models, because climatic inferences for each record are still relatively limited, turnover data include anagenetic speciation (or pseudoextinction), immigration, and splitting events, and the temporal resolution of change in both data sets is rather coarse. Also, key predictions of some models, particularly the turnover-pulse hypothesis, pertain to speciation and extinction within clades, and these records do not represent clade histories, so some aspects of these models are not tested.

## 5. Ecological and evolutionary changes

In this section, we consider additional aspects of ecological and evolutionary change in these ecosystem records. First, we describe each sequence as a reconstructed ecosystem. Next, we consider the extent of coupling of ecological and evolutionary change. We inquire whether episodes of first appearances were accompanied by episodes of last appearances and note the implications for saturation of communities with species. Also, the relationship of change in faunal composition to change in ecological structure of faunas is examined. Finally, we return to the difference in species durations between the Paleogene and Neogene records and evaluate evolutionary, ecological, and methodological influences.

### 5.1. Reconstructed ecosystems

The Paleogene ecosystem was a forested plain with gradients in topography, drainage, vegetation

composition, and faunal composition that extended from the channels and alluvial ridges to backswamps and floodplains. Gradients in soil maturity from channel to levee to floodplain suggest underlying gradients in drainage characteristics and disturbance rates. Abandoned channels and backswamps had ponded water with aquatic and emergent vegetation. The dominant forest trees were angiosperms along alluvial ridges and ponds, and conifers in swamps (Wing et al., this issue). Channels and ponded areas supported a high diversity of aquatic reptiles (Bartels, 1987) and probably more fish species than were actually preserved (Smith et al., 1988), as well as aquatic molluscs. The frequency of mammalian species <8 kg in body weight with insectivorous, carnivorous, frugivorous, or omnivorous feeding habits, and often clear arboreal adaptations (e.g., Gebo and Rose, 1993) indicates that the forest canopy was full of activity. Numerous slightly larger, more terrestrial mammalian herbivores indicate an abundance of browse or fallen fruit at ground level. At least some mammalian primary consumers exhibited preferences for alluvial-ridge versus floodplain habitats, since the frequency of certain species is correlated with pedofacies that reflect location on the alluvial plain (Bown and Beard, 1990). The modern analogues of size structure and trophic structure of the Paleogene mammalian faunas suggest that the vegetation was a mosaic of closed- and open-canopy areas.

The Neogene ecosystem was a huge alluvial plain crisscrossed with large and small rivers contributing to a huge trunk river not directly preserved. The high frequency of channel abandonment and crevasse-splays led to a mosaic of high, well-drained areas and low, wet areas, without simple proximal to distal gradients relative to channels. The rapid vertical and lateral alternation of facies suggests a diverse mixture of edaphic conditions at any one time. Channels and ponded areas supported a moderate diversity of aquatic reptiles (Pilbeam et al., 1979) and fishes (Roe, 1990), as well as molluscs. The absence of a floral record precludes direct evidence about composition of vegetation. The abundance of certain mammalian taxa is correlated with sedimentary environment: cursorial and hypsodont species are

more abundant in floodplain localities and bunodont species of diverse locomotor habits are more abundant in habitats associated with persistent water (Badgley, 1989). The low frequency of primary-consumer species with arboreal specializations suggests that the canopy was much less active than in the Paleogene ecosystem, but the high frequency of larger species with cursorial or ambulatory locomotion indicates that the terrestrial realm was much busier. The depth of oxidation and leaching in soil profiles and the ecological structure of mammalian faunas suggest that there was a pronounced dry season. The modern analogues for the ecological structure of mammalian faunas also suggest that much of the vegetation was at least as open as woodland, with large areas of little tree cover. Widespread grasslands per se are not indicated until the late Miocene, when paleosol carbon isotopes indicate a shift to C<sub>4</sub> vegetation.

The major differences between these Paleogene and Neogene ecosystems are representative of global differences in early versus late Cenozoic climates, vegetation, and mammalian faunas (Janis and Damuth, 1990; Stucky, 1990; Janis, 1993). The early Cenozoic up to the middle Eocene was warm with low climatic seasonality, whereas the late Cenozoic experienced sustained cooling and increasing seasonality of temperature and precipitation (Frakes et al., 1992). Forest and woodlands were prevalent in the early Cenozoic; these shrank as grasslands and savannah-woodlands spread in the late Cenozoic. Early Cenozoic mammalian faunas consisted mainly of species of relatively small size, of scansorial to arboreal locomotor habits, and of omnivorous, frugivorous, or insectivorous feeding habits—reflecting the structure and resources of forests. Late Cenozoic faunas had a high frequency of species of relatively large size, of obligate terrestrial or cursorial locomotor habits, and herbivorous or carnivorous feeding habits—reflecting the structure and resources of grasslands.

### 5.2. Synchrony of ecological and evolutionary change

In each record, the major episodes of first appearances were not closely followed by major

episodes of last appearances. Rather, the new populations were incorporated into local communities, and total species richness increased. This pattern characterizes the episode of first appearances at the Paleocene–Eocene boundary, the largest faunal turnover in the Paleogene record. The peak of first appearances in the middle Miocene portion of the Siwalik record, the greatest episode of faunal change in that sequence, is accompanied by a small set of last appearances (but less than twice the expected number of last appearances for this interval; Barry et al., this issue). In both records, a major peak of last appearances did not occur until  $\geq 1$  m.y. later. The same pattern characterizes the other major first-appearance peaks in both records, with the possible exception in the Siwalik record around 8 Ma of a turnover among species of rodents. In this case, the pulse of first appearances was  $\sim 0.5$  m.y. earlier than the pulse of last appearances (Fig. 2a). Minor first- and last-appearance peaks did coincide in the Siwalik record. In both records, the rate of addition of mammalian species into or subtraction of species from the community was not highly correlated with the number of species present (see Fig. 8 in Barry et al., this issue). The major episodes of immigration per se may have been linked to the opening of dispersal routes in areas quite distant from each basin.

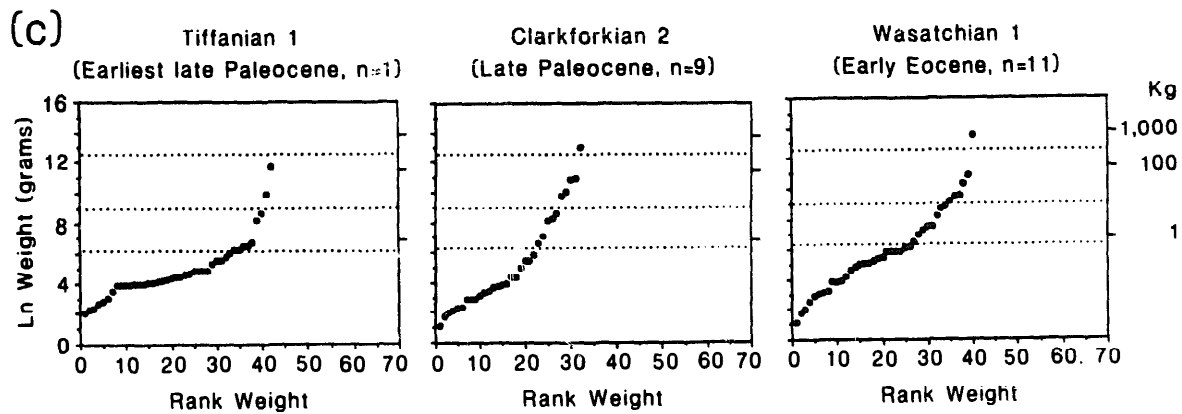
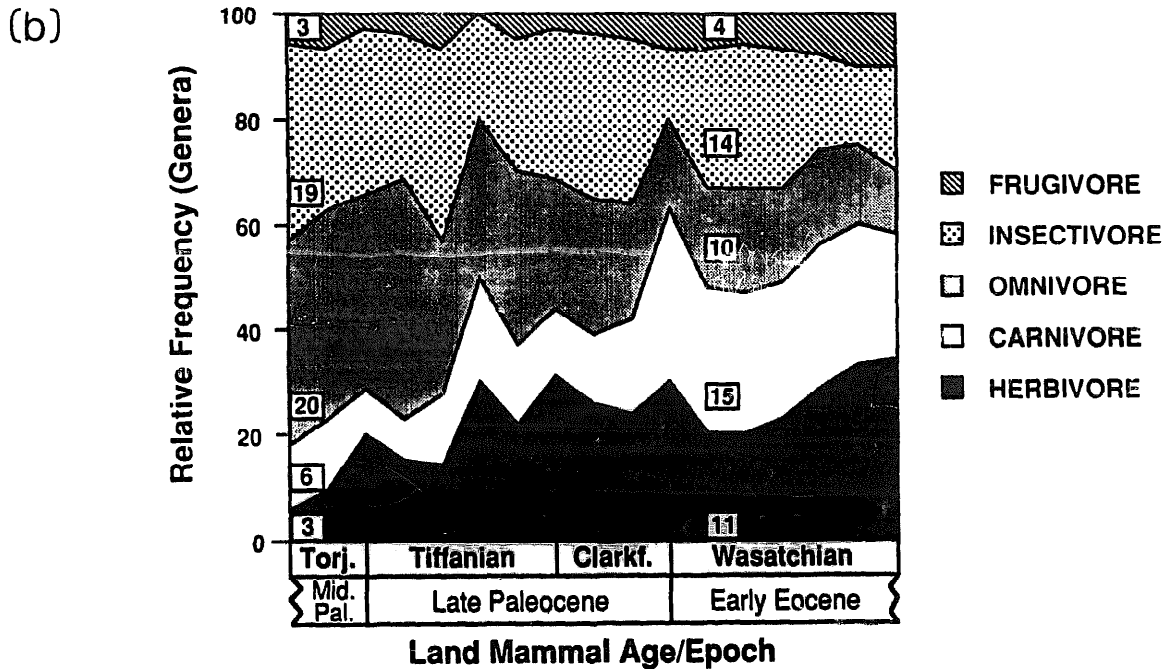
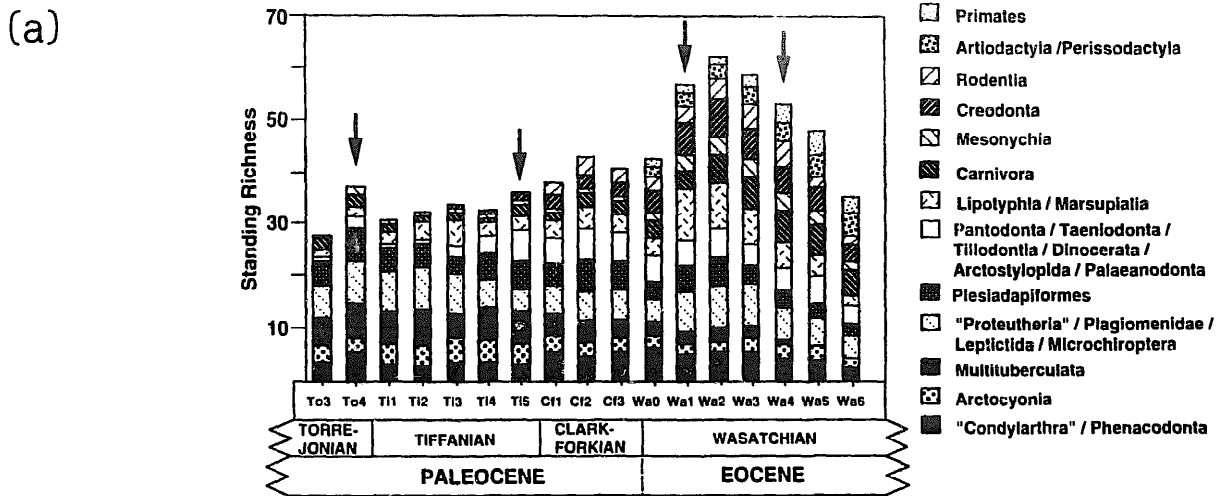
The lack of correspondence between episodes of first and last appearances and species richness suggests either that the ecological processes that regulated species richness in these paleocommunities were operating over very long time spans—in contrast to the stability of species richness over short time spans in many modern communities—or that these paleocommunities did not achieve equilibrium richness for much of their existence. Another possibility is that environmental changes caused equilibrium richness to shift substantially

over time. This hypothesis is especially plausible for the Wasatchian portion of the Paleogene record, because paleotemperature estimates indicate a sustained increase then brief decrease in mean annual temperatures, with concurrent floral changes. In the Siwalik record, increased aridity in the late Miocene was associated with decline in species richness and turnover in faunal composition. But substantial changes in species richness also occurred over a long period during which no local climatic change is evident. Still another possibility is that few intervals contain samples that estimate original species richness well, so that we are not documenting accurately the rate of turnover in relation to species richness. Clearly, the issue of equilibrium richness has unanswered questions for these paleocommunity records and in general.

An intriguing puzzle is the poor correlation between plant species richness and mammalian species richness in the Bighorn Basin record (Wing et al., this issue). Especially in the late Paleocene to early Eocene part of the record, plant species richness declined substantially while mammalian species richness increased substantially; concurrently, mean annual temperature increased. These different trends could be partly the consequence of changes in environments of preservation, since the decline in plant species richness occurs near the boundary between the Fort Union and Willwood formations, where fluvial environments changed substantially. But Wing et al. (this issue) suggest that the floral trend is part of a broader continental pattern. A more detailed examination of floral and mammalian species in relation to facies and areal extent of facies in the Bighorn Basin could illuminate this discrepancy.

Another aspect of the synchrony of ecological and evolutionary change is the relationship between change in the richness and composition

Fig. 1. Change in mammalian faunal composition, trophic structure, and size structure over much of the Paleogene record from the Bighorn and Crazy Mountains basins. (a) Standing richness of mammalian genera among major groups. Arrows indicate four major faunal turnovers in terms of first and last appearances of genera. From Maas et al. (this issue). (b) Trophic structure of mammalian faunas, expressed as relative frequency of genera among trophic categories and compiled over early Paleogene biostratigraphic zones. Numbers enclosed in boxes are counts of genera for selected intervals. From Gunnell et al. (this issue). (c) Cistograms, or rank-size distributions, of non-carnivorous species from three biostratigraphic intervals. Dotted horizontal lines mark boundaries between small, medium, large, and very large species. Modified from Morgan et al. (this issue).



of mammalian faunas and change in their ecological structure. If the environment of a species consists predominantly of other species (an assumption of the Red Queen and stationary models of evolution), then change in the number or identity of populations in an ecological community should initiate evolutionary or ecological adjustments. Also, climatic change could cause shifts in species ranges that would result in concurrent change in faunal composition and ecological structure, a prediction of the turnover-pulse hypothesis. We examine this relationship here only at a very general level.

Changes in taxonomic composition and ecological structure of Paleogene faunas are summarized in Table 2b and Fig. 1. Three of the four most significant episodes of faunal turnover (Fig. 1a) resulted in significant changes in standing generic richness. Only one of the four turnovers (at Torrejonian 4) coincided with the first or last appearance of genera in major groups (Mesonychia in this case). However, some of the major changes in trophic structure (Fig. 1b) did coincide with the first or last representatives of major groups. Notable changes in trophic structure include the relative increase in insectivores at Ti-3 (an increase in genera within established orders) and the relative increase of herbivores at Ti-4 (an increase in genera within established orders, but also a poorly sampled interval), Cf-1 (when rodents and tillodonts first appeared), Wa-0 (when artiodactyl and perissodactyl herbivores first appeared), and from Wa-5 to Wa-6 (an increase in genera of artiodactyls and perissodactyls). In the three cenograms (Fig. 1c), the increasing number of medium and large species from the late Paleocene to early Eocene reflects the increasing frequency of larger, herbivorous species. Among

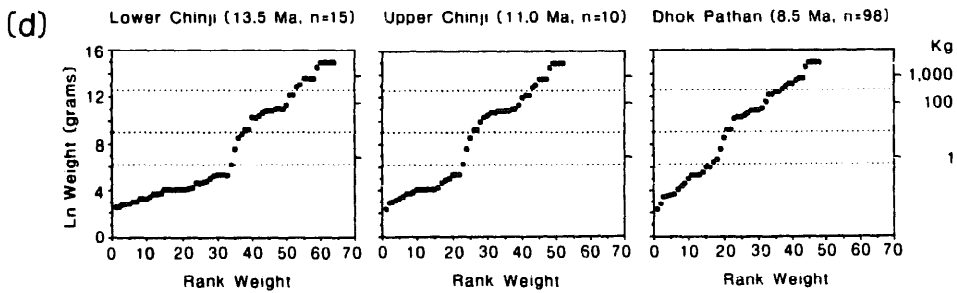
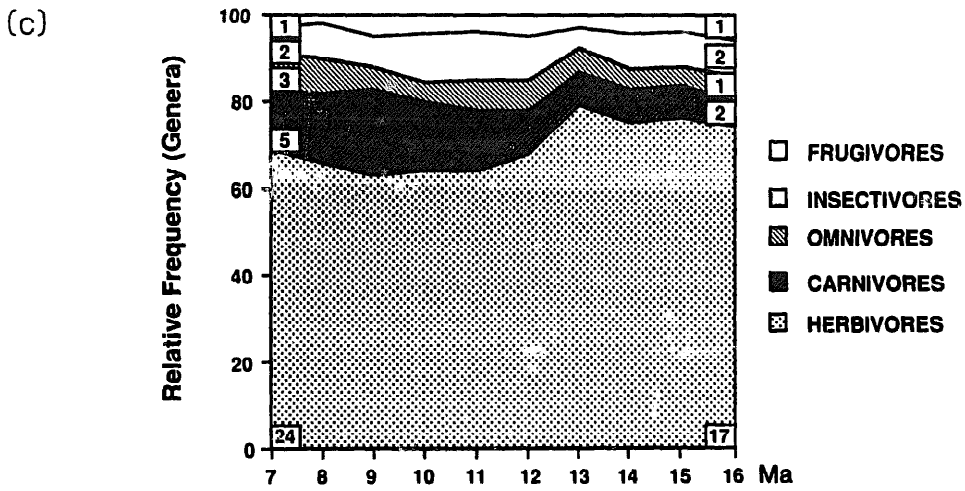
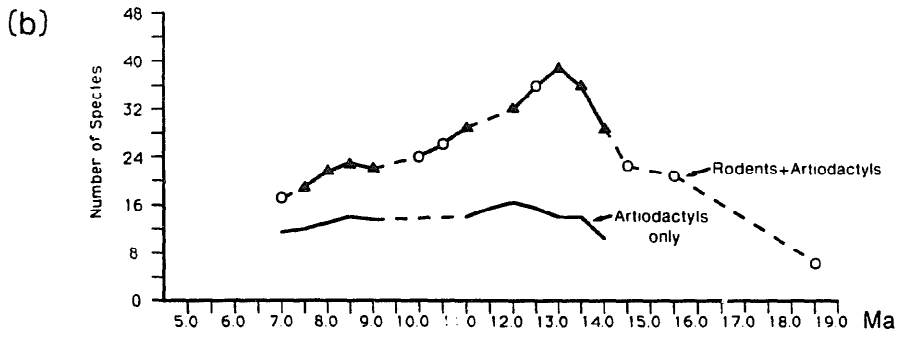
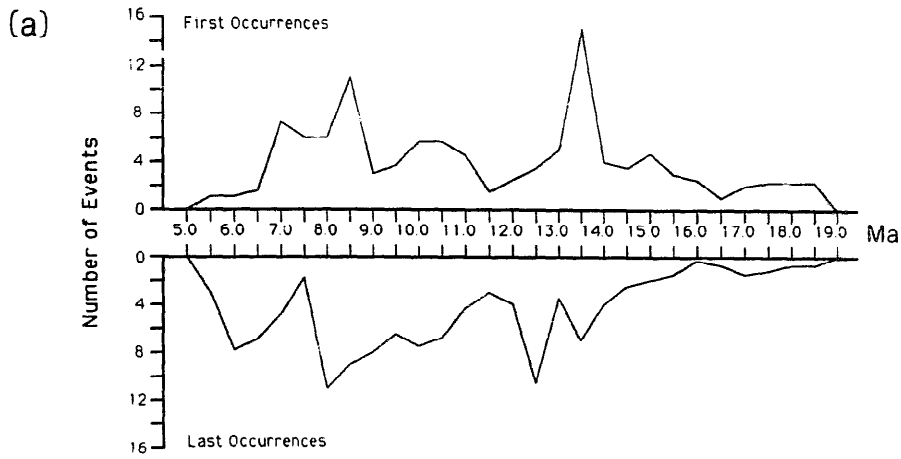
species in several major groups of herbivorous mammals, most major rapid jumps in size occurred in the Wasatchian, especially during the transitions from Wa-0 to Wa-1 and from Wa-3 and Wa-4 (Table 2b, Morgan et al., this issue). In some intervals, faunal composition changed without leading to significant changes in trophic structure or size structure. For example, a substantial turnover (> 10 first appearances and > 10 last appearances) of genera occurred in Ti-5 without a change of similar magnitude in trophic structure.

The patterns of taxonomic composition and ecological structure of Neogene mammalian faunas are summarized in Table 2c and Fig. 2. The major episodes of faunal turnover (Fig. 2a) include two major peaks (> 10 species) of first appearances and two major peaks (> 10 species) of last appearances. Much of the change in these peaks consists of turnover among rodents (Fig. 2b). Trophic structure (Fig. 2c) did not change substantially over this record. The major turnovers at 13.5 and 12.5 Ma each had a corresponding minor change in trophic structure, but the turnovers at 8.5 to 8.0 Ma did not. The major change in the three cenograms (Fig. 2d) is the decline in small-mammals, mainly rodents. Within rodent and artiodactyl families, most of the major rapid jumps in size occurred between 9.0 and 8.5 Ma (Table 2c, Morgan et al., this issue). This interval coincides with a modest increase in species richness (Fig. 2a) but not with a notable change in trophic structure.

In both records, some changes in faunal composition coincided with changes in ecological structure, while others did not. In the Paleogene record, changes in trophic structure were always accompanied by changes in faunal composition; the former involve increases or decreases in the number of mammalian genera among trophic categories and

Fig. 2. Change in mammalian faunal turnover and richness, trophic structure, and size structure over much of the Neogene record from Siwalik deposits of northern Pakistan. (a) First and last appearances of rodent and artiodactyl species, compiled over 0.5-m.y. intervals. Modified from Barry et al. (this issue). (b) Standing richness of rodents and artiodactyls which together comprise more than half the species in Siwalik mammalian faunas. Closed triangles denote well-sampled stratigraphic intervals and open circles indicate moderately well-sampled intervals. Modified from Barry et al. (this issue). (c) Trophic structure of mammalian faunas, expressed as relative frequency of genera and compiled at 0.5-m.y. intervals. Numbers in boxes are counts of genera for selected intervals. From Gunnell et al. (this issue). (d) Cenograms, or rank-ordered size distributions, of non-carnivorous species from three 0.5-m.y. intervals. Dotted horizontal lines separate regions of small, medium, large, and very large species. Modified from Morgan et al. (this issue).





not phyletic evolution from one trophic category to another. On the other hand, some changes in size structure involve significant phyletic size change; these cases do not all involve changes in taxonomic composition. The major changes in faunal composition and ecological structure occurred over the period of greatest climatic change (Wasatchian). Changing faunal composition was more in step with change in trophic structure than change in size structure but did not always affect either. In the Neogene record, the major changes in trophic structure and size structure preceded the major episodes of discernible climate change. Late Miocene changes in faunal composition were more consistently in step with changes in size structure than with changes in trophic structure. Some changes in faunal composition and species richness were not accompanied by significant changes in either trophic or size structure.

### 5.3. Species durations

The species durations discussed here refer to local biostratigraphic ranges. Mean and median durations were more than twice as long for Neogene species as for Paleogene species (Flynn et al., this issue; Gingerich and Gunnell, this issue). Evolutionary, ecological, and methodological factors probably contribute to this difference. The evolutionary consideration is the potential influence of body size on longevity. At the generic level, large mammals survive longer than small ones (Van Valen, 1975). In the Siwalik record, large mammals (carnivores and artiodactyls) have longer durations than do rodents over the same span of geologic time (Flynn et al., this issue). Fig. 3 depicts the distribution of species durations by size class. There is a weak negative correlation

(Spearman rank correlation,  $r = -0.2$ ) for 124 Paleogene species (Figs. 3a–b) and a weak positive correlation (Spearman,  $r = 0.2$ ) for 108 Neogene species; both values of  $r$  are statistically significant at  $p < 0.05$  (Siegel and Castellan, 1988). Thus, the presence of numerous species in size classes 5 and greater in Siwalik faunas has a small but significant effect on mean longevity. But 57 Siwalik rodents (size classes 1–3) have a median duration of 1.5 m.y., whereas the median duration of all 124 Paleogene mammals is 0.75 m.y. Thus, body-size differences alone are not a sufficient explanation.

The ecological consideration that may relate to species duration is environmental stability. For Siwalik rodents, durations are significantly longer before 9 Ma than after (Flynn et al., this issue), when climatic indicators suggest increased seasonality and aridity in the latest Miocene. The interval from 16 to 9 Ma was apparently more climatically stable. In the Paleogene record, the interval over which durations were measured (Clarkforkian to middle Wasatchian) experienced sustained warming and changes in the composition and ecological structure of mammalian faunas. Thus, in both records, periods of greater change in climate and vegetation could be associated with shorter mean durations and more rapid faunal turnover.

There are two methodological considerations, however. The first is that the time interval over which species durations are measured is more than twice as long (11 m.y.) in the Neogene record as in the Paleogene record (~5 m.y.). There is no possibility of recording durations  $\geq 5$  m.y. for Clarks Fork Basin mammals. However, it is clear from comparison of Figs. 3b–c that the distributions of durations  $< 5$  m.y. in length still differ. The second issue is how species are recognized. Over half the species in the Paleogene data set terminated by anagenesis, according to Gingerich

Fig. 3. Distribution of species durations in millions of years versus body-size class. Size class 1:  $< 100$  g, size class 2: 101–500 g, size class 3: 501–8000 g, size class 4: 9–50 kg, size class 5: 51–250 kg, size class 6: 251–1000 kg, size class 7:  $> 1000$  kg. (a) Distribution for 124 species of Paleogene mammals from the Clarks Fork Basin, Wyoming, measured over an interval of 4.7 m.y. Data from Gingerich and Gunnell (this issue); we omitted the longest duration from their data set because it is determined in part from information outside the Clarks Fork Basin. Mean and median durations were recalculated for the modified data set. (b) Data of (a) plotted to the same scale as the graph in (c) for ease of comparison. (c) Distribution for 108 species of Siwalik mammals, measured over an interval of 11 m.y. Data from Flynn et al. (this issue). Mean and median durations are greater for Neogene than for Paleogene mammals.



and Gunnell (this issue). For these cases, the lineage continued with a change of name, and the duration of the unbranching, multi-species lineage was longer. Such cases of pseudo-extinction are also present in the Neogene data but comprise a smaller fraction (perhaps 25%) of species. A related influence is the working style of the individual taxonomist. A large fraction of species in each record was named by a small group of collaborating taxonomists; their collective impact on approaches to species recognition is substantial.

Overall, the difference in mean durations from these two records is probably partly an artefact of these methodological differences and partly a real difference, reflecting the contrast in environmental history and size distributions of Paleogene versus Neogene mammalian faunas.

## 6. Conclusion

The earlier papers in this special issue and the research questions discussed here demonstrate the influence of tectonism, climate, and preservation on paleoecological and turnover patterns in these two Cenozoic records. The original paleoenvironments established the array of biotic habitats and circumstances of fossil preservation. In turn, the patterns of preservation limit the taxonomic, temporal, and spatial resolution of fossil assemblages and thereby constrain the data for paleoecological and evolutionary studies.

Comparison of the early Paleogene record of Wyoming and Montana with the Neogene Siwalik record of Pakistan has revealed as many differences as similarities in controls on fluvial systems, environments of fossil preservation, and taphonomic attributes of fossil assemblages. The two sequences differ in their suitability for certain kinds of paleoecological and evolutionary studies. On the whole, the Paleogene record can better address issues of evolutionary change within lineages and species-replacement patterns among faunas because of greater taxonomic resolution (more specimens identifiable to genus or species level) in most fossil assemblages. The Neogene record can better address issues of paleocommunity structure and change because, for at least 11 m.y., fossils are

preserved from a greater variety of contemporaneous fluvial environments, in both autochthonous and allochthonous assemblages. But individual localities have poorer species-level resolution than in the Paleogene record.

Both records show a similar relationship between physical change and biotic change. Change in fluvial systems at the scale of formation boundaries coincided with changes in fossil productivity and species richness but not the major turnovers in taxonomic composition of mammalian faunas. Episodes of pulsed climatic change were accompanied by changes in faunal composition and ecological structure of mammalian faunas. Biotic changes of a similar magnitude occurred during periods of gradual to no discernible climatic change, based on current understanding of stable isotopes and foliar physiognomy. For the Siwalik record, either our knowledge of paleoclimate is misleading, or substantial faunal changes occurred with and without climatic change as an initiating cause. Faunal turnover occurred both in brief pulses and in a diachronous, gradual manner in each record. Some evolutionary changes in mammalian faunas (resulting from first and last appearances) were in step with changes in ecological structure (trophic structure and size structure), while other turnovers did not affect these aspects of ecological structure. These dual patterns of biotic in relation to physical change and of ecological change in relation to turnover suggest that physical and biotic factors were both important influences on faunal composition, the timing and rate of turnover, and ecological structure in these communities.

Detailed records such as the two presented here are not abundant, and a relatively small number of case histories provides tests of the predictions of models of evolutionary and ecological change in ecosystems and clades. Future work in these two sequences should enhance the paleoclimatic information, the temporal resolution of biotic and physical change, the species-level resolution of mammalian faunas, and the ecomorphological resolution of floras and faunas, so that these long records become more definitive histories of ecosystems and evolution.

## Acknowledgments

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