Comparative paleoecology of Paleogene and Neogene mammalian faunas: body-size structure

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Abstract

Species size is correlated with many aspects of life history, ecology, and behavior, which means that size changes within species, lineages, and faunas represent an important component of evolutionary paleoecology. Comparison of Paleogene mammalian faunas from the Bighorn, Clarks Fork, and Crazy Mountains basins of Wyoming and Montana with Neogene mammalian faunas from the Siwalik Group of northern Pakistan reveals similarities and differences in patterns of size change through intervals of 10 m.y.

Two approaches to size change are presented. The first is to evaluate changes in the size distribution of faunas over three time intervals in each sequence. Rank-ordered size distributions, or cenograms, are used to depict faunal size structure for non-carnivorous species. The slopes and gaps in different regions of the size spectrum reflect conditions of vegetation and climate, by analogy with modern mammalian faunas (Legendre, 1986, 1989). For the Paleogene and Neogene faunas, subtle changes over time in size structure reflect changes in local vegetation and climate. The Paleogene cenograms suggest a habitat shift from mesic to humid forest, and the Neogene cenograms suggest a shift from open woodland to savannah scrub. These interpretations are supported by concurrent changes in trophic structure, faunal turnover, and in floral and geologic indicators.

The second approach focuses on size change within species and lineages in several families of predominantly herbivorous species. For 60 Paleogene species and 39 Neogene species, change in average species size over successive biostratigraphic intervals is assessed by a criterion of doubling or halving of body mass relative to the preceding interval. New occurrences are compared to established species of the same genus and of the same family. In both records, size increases occur slightly more often than size decreases. The size distribution of groups changes more often through appearances of species of more than double or less than half the size of established species of the same group or by disappearances, rather than through rapid change of size within species. The pattern of change in median size and size range of contemporaneous species varies among families in both records. Three causes of evolutionary size change—climatic change, competition, and predation—are evaluated. In both records, climatic change and interspecific competition are considered the principle mechanisms for the observed changes.

1. Introduction

Body size is a useful predictor of species adaptations, because it is correlated with many aspects of life history, ecology, and behavior. Trophic specialization, foraging habits, group size, and home-range area are all correlated with body size among terrestrial mammals in general, as well as within clades of mammals (e.g., Jarman, 1974; Pennycuick, 1979; Western, 1979; Eisenberg, 1981, 1990; Peters, 1983; Calder, 1984; Demment and Van Soest, 1985; Harvey et al., 1985; McNab, 1990). Within ecological guilds of mammals, species of different sizes concentrate on food resources of different sizes and are thereby inferred to reduce competition by minimizing the number of competing species of similar size (e.g., McNab, 1971; Emmons, 1980; Brown, 1987). For modern mammalian faunas, size structure varies along gradients of vegetation and climate (e.g., Fleming, 1973; Andrews et al., 1979; Legendre, 1986, 1989). Also, notable size changes in the Cenozoic history of mammalian clades and faunas have tracked environmental changes (e.g., Janis and Damuth, 1990; Stucky, 1990; Janis, 1993).

By analogy with living mammals, aspects of life history and behavioral ecology can be inferred for paleomammals by combining estimates of body size and functional morphology (e.g., Janis, 1982; Van Valkenburgh, 1988). Damuth and MacFadden (1990) have provided a useful survey of methods for estimating body weight from osteological remains and relating size to ecological and life-history properties. Although the skeletal element(s) best correlated with body weight vary among the major groups of mammals, most measures of element size are highly correlated with body weight for extant and, by inference, for extinct mammals.

The early Paleogene of Wyoming and Montana and the Siwalik Neogene of the Potwar Plateau, northern Pakistan, are distinctive among terrestrial sequences in that each is well sampled over an interval of about 10 m.y. In each record, trends in size change for species, higher taxa, and faunas can be examined over periods of environmental change and stability. In the Paleogene record, the terminal Paleocene was associated with a notable

shift in $\delta^{13}C$ values from both terrestrial and marine sediments (Koch et al., 1992; Koch et al., this issue). Intercontinental dispersal of mammals resulted in a distinctive set of immigrations at this time. Also, mean annual temperature increased slowly from the early to late Paleocene and more rapidly through Wasatchian time, according to floral indicators of paleotemperature (Wing et al., 1991, this issue). The mammalian response to this period of inferred global warming has been examined in terms of taxonomic richness and turnover (Maas et al., this issue), trophic structure (Gunnell et al., this issue) and body-size structure (this paper). In the Neogene record, notable shifts in mammalian faunal composition (Barry et al., this issue) and in $\delta^{18}O$ and $\delta^{13}C$ from Siwalik paleosol carbonates and from the marine record occurred during the latest Miocene (Woodruff et al., 1981; Quade et al., 1989; Quade and Cerling, this issue). These two periods, the Paleocene to early Eocene and the late Miocene, present opportunities to evaluate faunal response to environmental change. Also, episodes of immigration occurred in each sequence, and patterns of size change can be compared for immigrant and resident groups.

Here, we evaluate two aspects of size structure in Paleogene and Neogene mammalian faunas. The first approach is to examine the size distribution of most of the mammalian fauna at three time intervals in each sequence. We utilize cenograms — rank-ordered size distributions—of non-volant, non-carnivorous species to compare the size structure of paleofaunas through time and to evaluate the climate and vegetation of the fauna. Andrews et al. (1979), Emmons et al. (1983), Legendre (1986, 1989), and Legendre et al. (1991, in prep.) have demonstrated that size distributions of modern mammalian faunas—at the scale of ecological communities—vary in relation to vegetation and climate. These covariations suggest that the size distribution of an unbiased mammalian paleofauna can serve as a source of paleoclimatic information.

Second, patterns of size change over time are evaluated for species and lineages in selected mammalian groups that are well sampled, taxonomically well resolved, and predominantly herbivorous in trophic habits ("herbivorous" refers to reliance

mainly on green vegetation at ground level and excludes principal reliance on fruit; see also Gunnell et al., this issue). The size distribution and the number of modern herbivorous species change significantly along environmental gradients (Legendre, 1986), and the herbivore guild contains the broadest range of species size among guilds of terrestrial mammals (Maiorana, 1990). Thus, increase or decrease in species number, size range, and median size within the best-known clades of herbivorous mammals from the early Paleogene of Wyoming and the Siwalik Miocene of Pakistan should provide an indication of changes over time in resources, competitors, or other ecological factors. We document examples of size increase or decrease representing a doubling or halving, respectively, of body weight relative to an ancestral population in the same lineage or relative to other members of the same clade. This magnitude of size change has been suggested to reflect competitive size displacement (e.g., Hutchinson and MacArthur, 1959). Also, this magnitude just exceeds the typical intraspecific variation in size observed for many extant mammals (Maiorana, 1990). This criterion for size change focuses attention on the frequency of major jumps in size and away from the nearly continual smaller changes in size over time documented for many well-sampled mammalian lineages (e.g., Gingerich, 1991). Our goal here is not to analyze evolutionary rates of size change per se (for this subject, see Gingerich and Gunnell, this issue), but to assess whether median size and size range of species changed over several million years in phylogenetic subsets of the mammalian faunas.

Also, size change is evaluated for immigrant and resident species of the groups discussed in order to assess potential biotic interactions among guild members. In the Paleogene sequence, we examine size change in condylarths, rodents, tillodonts, pantodonts, artiodactyls, and perissodactyls. Notable faunal changes include the first occurrences of artiodactyls and perissodactyls. In the Neogene sequence, we examine size change for species of artiodactyls and rodents from the middle to late Miocene. Notable faunal changes include a middle Miocene diversification of artiodactyls and

rodents, followed by turnover among muroid rodents.

The paper is organized as follows. In the next section, we review causes of evolutionary size change that are potentially relevant to these two sequences. Then methods of inferring body size and criteria for recognizing size change are presented. Next, we document faunal size structure for three intervals from each sequence and examine (1) whether size structure of the faunas changes over time and (2) what size structure indicates about climate and vegetation. Then, on the subject of size change within selected lineages and higher taxa, we address four questions: (1) What is the overall pattern of size change over the duration of each group; e.g., are later species larger or smaller, or both, than earlier species? (2) Within and among the groups examined, is size change concentrated in a few time intervals or distributed over many? (3) Following significant immigrations, is size change noted in either the resident or immigrant groups of the same guild? (4) Is size change within lineages or faunas noted at times of significant climatic change? We present patterns of size change for Paleogene species in selected groups with a summary of general trends and plausible causes, followed by a parallel section for selected Neogene groups. Finally, we discuss the results of both approaches to size structure.

2. Causes of size change

In order to interpret patterns of size change, we review briefly the potentially relevant mechanisms of such change within mammalian lineages and faunas presented below. As paleontological examples rarely offer the ideal breadth of geographic and temporal information, we emphasize data that strongly rather than conclusively support a particular hypothesis of mechanism (Kitchell, 1985). Three hypotheses are considered—climatic change, competition, and predation. These hypotheses are not mutually exclusive, although there are circumstances under which the influence of one mechanism would outweigh that of the others.

(1) *Climatic change.* Climatic changes may have pervasive effects on the morphology, behavior, and

ecology of mammals via direct (such as climatic effect on physiology) and indirect effects (such as climatic effect on seasonal distribution of resources). The geographic trend within species known as Bergmann's rule, increasing size with decreasing mean annual temperature, probably reflects in part the relationship between heat loss and size (Searcy, 1980). Since vegetation structure is strongly influenced by climatic conditions, climate change typically promotes changes in the composition and structure of terrestrial vegetation and in the associated food web (e.g., Walter, 1979; Prentice et al., 1992). Mammalian size structure varies along gradients of vegetation and climate today. For example, species of large (8-250 kg) and very large (>250 kg) size are much more numerous in woodland and grassland than in forest habitats on several continents (Legendre, 1989). Larger herbivores can subsist on diets of relatively low-quality forage—which is available in grasses, shrubs, and leaves in the more open habitats. Forests generally offer a spectrum of fruits, leaves, gums, and nuts to primary consumers; frugivores, folivores, and granivores are small (generally <8 kg) due to the patchy distribution of these resources in time and space, due to lower absolute metabolic requirements at smaller size (Eisenberg, 1981), and due to constraints of size on effective arboreal locomotion (Fleagle, 1985).

The inference that climatic change is the cause of changes in mammalian size structure receives strong support when three conditions are met. First, clear evidence of climatic change from geological or floral data is necessary. Second, the observed changes in size structure of the mammalian fauna should be consistent with principles of physiology, energetics, and trophic preference. Third, changes in trophic structure should accompany changes in size structure, since substantial changes in vegetation alter the spatial and seasonal availability of food resources. Since climate influences the abundance and seasonal availability of resources, much of the fauna is likely to be affected at once by significant climatic change. Ideally, evidence for other causes of change should be minimal, but this may be an unrealistic expectation since change in climate and vegetation should change the nature of many biotic interactions.

(2) *Competition.* Competition for a limiting resource has been suggested from both the neontological and paleontological record as a mechanism for evolutionary character displacement (e.g., Dunham et al. 1979; Benton, 1983; Krause, 1986; Maas et al., 1988). The imputed character displacement often involves change in body size and correlated trophic apparatus. Among living mammals, a number of studies have demonstrated that species in the same guild partition resources by size (e.g., McNab, 1971, for bats; Emmons, 1980, for tropical forest squirrels; Brown, 1987, for desert rodents). For competition to be a plausible mechanism of body-size change, it is necessary initially that the taxa involved overlap enough in utilization of an essential resource that selection favors decreased overlap in resource use. In cases involving competition for the primary limiting resource, an increase in abundance of one taxon results in a decrease in abundance in the other and vice versa. But, in principle, competition for a shared but nonlimiting resource could also result in evolutionary character displacement. Following size displacement, the taxa may coexist with reduced resource overlap. Examples of competition may involve closely related species-which typically overlap in many resource uses (e.g., species of tree squirrels), distantly related species in the same larger clade (e.g., a squirrel and a primate), or distantly related and dissimilar species that overlap in use of a limited but critical set of resources (e.g., grasshoppers and ungulates).

The inference that competition is the cause of evolutionary size change receives strong support when several conditions are met. First, the hypothesized competitors must plausibly overlap in resource use; for paleospecies, this overlap can be assessed by a combination of size and functional (often trophic) morphology. Also, putative competitors should be found in the same fossil assemblages (evidence of sympatry). Second, the taxa must respond to each other in a consistent manner over time without a substantial time lag; for example, within a local section, differentiation in size/ morphology should occur when the competitors coexist and cease when one species becomes locally extinct. Ideally, a similar pattern would occur over space: in sympatry, the hypothesized competitors

would differ more than in allopatry. With a sufficient geographic dimension, the amount of size change attributed to the presence of putative competitors can be quantitatively compared to other causes of geographic variation (e.g., Dunham et al., 1979). In some cases, the effects of interspecific competition would be reflected also in the abundance of each species: each would exhibit a higher abundance in the absence (before, after, or in allopatry) of the other. Ideally, evidence for other causes of size change would be minimal, but realistically, environmental changes may influence competitive interactions through direct or indirect effects. A more useful distinction is that only the competing lineages should be affected, and changes across the whole fauna are not anticipated. Paleontological cases rarely meet all these idealized conditions.

(3) *Predation*. Predation (here, in the sense of carnivorous species preying upon other species of mammals) is a potential mechanism of adaptive evolutionary change, because selection of prey by predators may lead to differential mortality correlated with heritable traits, including body size, of prey species. Since size of predator is broadly correlated with size of prey species (Gittleman, 1985), evolutionary size change of prey species may result in avoidance of a particular kind of predator. Evolution toward smaller size may result in a greater range of opportunities for hiding or escape, whereas evolution toward larger size may effectively reduce or thwart predation if the predator of concern does not also change in size.

Predation as a mechanism of evolutionary size change receives strong support when the following conditions are met. First, the hypothesized predator–prey relationship must be plausible in terms of substrate use, locomotor ability, and habitat. In the fossil record, size, functional morphology of limbs and trophic apparatus, and facies of preservation allow assessment of this relationship (e.g., Janis and Wilhelm, 1993; Van Valkenburgh and Hertel, 1993). Ideally, patterns of mortality, as sometimes indicated by characteristic patterns of bone damage (and in these cases, distinguishable from effects of scavenging), would also support the predator–prey relationship (e.g., Brain, 1981). Second, the prey lineage should not exhibit size

change before the putative predator appears. If the predator becomes locally extinct, the size change may reverse, if other factors, such as availability of food resources, exert selection for a different body size. If the predatory species is highly specialized, then a size change in the prey species may elicit a coevolutionary size change in the predator, but most predators on mammals exhibit prey switching when one prey species becomes rare or otherwise inaccessible. Third, evidence for other causes of size change should be minimal. While the interacting lineages are affected, changes across the whole fauna are not anticipated.

Finally, changes in size and morphology need not be driven at all. Change over time in size and other features may represent a random walk resulting from genetic drift over an adaptive landscape of low relief (Lande, 1976; Bookstein, 1988). Interpretation of a cause needs evidence of that cause and an appropriate relationship in time between "cause" and "effect."

3. Methods

3.1. Body-size estimates

Body-weight estimates for Paleogene and Neogene mammals are based mainly on dental measurements. Teeth were selected because of their numerical abundance in the fossil record, especially in the Paleogene sequences, and because they are more readily identified to species than postcranial elements. Problems of using tooth-based body weight estimates are discussed by Gould (1975), Smith (1984, 1990), Damuth (1990), Fortelius (1990), and Janis (1990). However, all agree that although fossil taxa without close living analogs are especially problematic, nevertheless, the major trends in body-size distributions based on dental measurements are generally robust.

The Paleogene specimens included in this study were collected in the Bighorn and Clarks Fork basins of Wyoming and the Crazy Mountains Basin of Montana and are in the collections of the University of Michigan Museum of Paleontology. The data presented span 17 biostratigraphic

zones—representing on average about 0.35 myr—from the middle Paleocene (Torrejonian) through much of the early Eocene (Wasatchian) (Fig. 1 from Maas et al., this issue).

The estimate of size is based on area of M_1, chosen because of the availability of specimens and the emphasis on this estimator in previous work. However, this measurement can overestimate body size of Paleogene ungulates by a factor of 1.7 (Damuth, 1990). Such an overestimate would not affect patterns of relative size change but could alter the cenograms. The extent to which similar size biases associated with M_1 area exist for other Paleogene taxa has not been examined in detail. For each species, the M_1 areas of all specimens within each faunal zone were averaged; from these averages, estimates of average body-weight were derived using taxon-specific regressions, based on extant species, from Legendre (1989). The choice of regression was based on phylogenetic considerations. For Paleogene taxa, several regressions were applied to examine differences. For example, application of Legendre's (1989) general herbivore regression to all Paleogene herbivores (except rodents) included in Fig. 2 yielded body-mass estimates generally within 4% of the estimates based on more taxon-specific (e.g., perissodactyl) regression equations, those actually used in Fig. 2. Sample sizes of M_1's ranged from 1 to >400 per species; the sample size used in the estimate for each taxon is given in the captions for Figs. 2 and 3. Data are presented on a logarithmic scale so that proportional change can be examined over a broad size range.

Body-weight estimates for specimens from the Neogene Siwalik sequence of the Potwar Plateau were generally determined in the manner described for Paleogene mammals, with some exceptions. Data were compiled for 0.5-myr intervals. Sample sizes were usually much smaller (1–49 specimens per species) than for Paleogene species, reflecting preservational differences between the two sequences (Badgley et al., this issue). Five muroid rodent groups were included: three cricetid subfamilies—megacricetodontines, dendromurines, and myocricetodontines, murids, and rhizomyids. A sixth Siwalik muroid group, the cricetid copemyines, is currently being revised and is not included

in this analysis. Due to small sample sizes for most muroid species, species body weights were estimated for all available specimens, and only differences among species were examined. For two murid lineages, intraspecific differences were examined. Siwalik megacricetodontine, dendromurine, myocricetodontine, and rhizomyid body weights were estimated from M_1 area (Flynn, 1982, unpublished data; Lindsay, 1988), using regressions from Legendre (1989). For murids, M^1's are the most diagnostic teeth, and only these data were available. Measurements on murid teeth were collected by Jacobs et al. (1990) and Jacobs (unpublished data). A comparison of the upper and lower molar areas for 13 species of Siwalik megacricetodontines, dendromurines and myocricetodontines (Lindsay, 1988) indicated that application of Legendre's regression for rodents using upper molars resulted in overestimates of body weight by 35–45% relative to estimates based on lower molars. A correction factor of 40% was therefore applied to all murid upper-molar data. This uniformly applied correction factor should not alter patterns of murid body-size change within lineages. Bovid and giraffid body weights were estimated from M_2 and M_3 occlusal lengths, using regressions of Janis (1990). For bovids, which could not generally be identified to species, size estimates of individual specimens are reported. Suid body weights were based on M_2 occlusal length only, using regressions from Janis (1990).

3.2. Estimating size increase and decrease

In order to evaluate whether size increase or decrease occurred within mammalian species and lineages, we used the criterion of doubling or halving in estimated body mass and a consistent protocol for comparing each taxon with others. For species with size estimates based on ln (area of M_1), the criterion for size change was a difference of ±0.4 ln unit from the mean being compared. The value of 0.4 ln unit corresponds to two standard deviations about the geometric mean of tooth area in logarithms (Gingerich and Smith, 1984), and in untransformed values corresponds to about a doubling or halving of body weight. Hence, size change within a species or lineage was

evaluated by whether time-successive values of mean size were 0.4 ln units greater or less than the value in the preceding interval (or the closest subjacent interval with a relevant sample). If this magnitude of size change *between intervals* was exceeded over any part of the lineage duration, then the lineage was considered to have undergone size increase or decrease. If significant increase and decrease were both noted by this metric, then both were counted (there is one Paleogene example). If this amount of size change occurred cumulatively via smaller steps over numerous intervals, it was not recorded as a major size change per se, although we noted long-term shifts in median size and size range of taxa. For certain Siwalik taxa with size estimates based on data other than ln (area of M_1), the metric for size change was a doubling or halving of the average estimated weight relative to the estimate from the preceding interval.

We made six sets of evaluations (Table 1). (1) Size change within species refers to change in mean size for samples attributed to the same species from different biostratigraphic intervals. For many Neogene species, the mean size of a species sample was evaluated over its entire range, and this form of size change could not be evaluated. (2) Size change within lineages refers to cases in which an unbranching lineage is interpreted to consist of two or more species. Some workers would consider such a lineage one species, while other workers would consider the same lineage to consist of multiple species. Here, change is evaluated only *between* species of such lineages. (3) For comparing multiple lineages, first congeneric species were compared. Size change of new species in relation to established species of the same genus refers to species in lineages not already present. The first occurrence of the earliest member of a genus was not evaluated, but in subsequent biostratigraphic intervals, newly appearing species were compared to the size(s) of already existing congeners–i.e., present in the preceding or closest subjacent interval. New species were recognized as larger or smaller if they satisfied the criterion of size change (± 0.4 ln unit or a doubling/halving of estimated weight). Size change of congeneric species in an anagenetic transformation was not counted here,

because this kind of change was evaluated in (2) above. (4) Size change of new species in relation to established species of the same family also refers to species in lineages not already present. Size decrease was noted if the newly appearing species was smaller by 0.4 ln unit (or its equivalent) than the smallest species of the same family in the preceding interval; size increase was evaluated in a parallel fashion. If a newly appearing species fell within the size range of already established species of the same family, then no size change was noted. The first occurrence of a species was counted if other members of the same family were already present; the first occurrence of the earliest species in the family was not counted. Size change of species in the same genus in an anagenetic series relative to established confamiliars was not counted. (5) Median size refers to change through the local biostratigraphic record in the median value for the size range of all species of a family. Size increase or decrease is recognized by a doubling or halving of the median value, a change corresponding to 0.7 ln unit. A family consisting of one lineage was not evaluated for median size change. (6) Size range of the family refers to the pattern of change in the difference between the largest and smallest contemporaneous species over the local biostratigraphic record of the family. If the size range at any time expanded or contracted by an amount representing a doubling or halving of species size (corresponding to 0.7 ln unit) relative to the range in an earlier interval, then we consider the range to have increased or decreased, respectively. In principle, the size range could increase and decrease over the duration of the group, and several such instances are noted in Table 1. For most groups, size range did not change between many adjacent intervals; we did not register such absence of change in Table 1, unless it characterized the entire local record. For these six evaluations, assessment of size change was limited to comparisons of closely related species, even though the details of their phylogenetic relationships are not fully studied for all groups evaluated. While this approach is sensitive to the interpretation of evolutionary relationships among species, such dependence affects most evaluations of size change.

Table 1

Size change for selected mammalian groups: within species (Column 1), within lineages (Column 2), for newly appearing species (not in lineages already present) relative to established members of the same genus (Column 3), for newly appearing species (not in lineages already present) relative to established species of the same family (Column 4), change in median size for species of the same family over their local biostratigraphic record (Column 5), and change in size range of species of the same family over their local biostratigraphic record (Column 6). In principle, the median size of size range could exhibit significant increase and decrease, if both occurred, a bold √ indicates the net change from beginning to end of local stratigraphic duration. S = number of species, L = number of lineages, I = increase, D = decrease, N = neither, – means data not available or not applicable. See text for explanation of how size change was determined. Entries given for change within lineages (Column 2) only when number of lineages differs from number of species

	(1) Within species				(2) Within lineage				(3) New sp. v. congeners			(4) New sp. v. confamiliars			(5) Median size, family			(6) Size range, family		
	S	I	D	N	L	I	D	N	I	D	N	I	D	N	I	D	N	I	D	N
PALEOGENE MAMMALS																				
PHENACODONTIDAE															√	√	√	√	√	
Ectocion	5	0	0	3	5				0	0	4	0	0	4						
Tetraclaenodon	1	–	–	–	1				–		–	–	–	–						
Copecion	2	0	0	1	2				–	1	–	0	0	1						
Phenacodus	6	0	0	4	6			··	1	1	3	4	0	2						
HYOPSODONTIDAE															√	√		√		
Litomylus	1	0	0	1	1				–	–	–	–	–	–						
Haplaletes	2	0	0	1	2				1	0	0	1	0	0						
Aletodon	2	0	0	1	1	0	0	1	–	–	–	1	0	0						
Haplomylus	3	0	0	3	3				0	1	1	0	2	1						
Hyopsodus	7	0	0	4	7				1	0	5	1	0	6						
PARAMYIDAE															√			√	√	
Microparamys	2	0	0	1	2				0	1	0	0	0	1						
Acritoparamys	2	0.5	0.5	1	2															
Paramys	1	0	0	1	1							0	0	1						
SCIURAVIDAE																				
Knightomys	1	0	0	1	1				–	–	–	–	–	–						
ESTHONYCHIDAE															√			√	√	
Azygonyx	3	0	0	1	3				–	–	1	–	–	–						
Esthonyx	2	0	1	1	2				0	0	1	0	0	2						
CORYPHODONTIDAE															√			√		
Coryphodon	6	0	0	6	3	0	0	3	0	0	3	0	0	2						
DICHOBUNIDAE															√			√		
Diacodexis	3	0	0	2	2	0	0	2	1	0	0	1	0	0						
EQUIDAE															√	√				
Hyracotherium	8	0	0	6	8				1	0	6	0	0	7						
ISECTOLOPHIDAE															√			√		
Cardiolophus	2	0	0	2	2				0	0	1	0	0	1						
Homogalax	1	0	0	1	1				–	–	–	0	0	1						
HELALETIDAE																				
Heptodon	1	–	–	–	1				–	–	–	0	0	1						
Paleogene total	61	0.5	1.5	41	56	0	0	6	5	4	24	8	2	30	3	3	6	4	3	5

Table 1 (continued)

	(1) Within species				(2) Within lineage				(3) New sp. v. congeners			(4) New sp. v. confamiliars			(5) Median size. family			(6) Size range. family		
	S	I	D	N	L	I	D	N	I	D	N	I	D	N	I	D	N	I	D	N
NEOGENE MAMMALS																				
CRICETIDAE (n=12)	12	–	–	–	?				–	–	–	0	0	8	√			√		
MURIDAE															√			√		
Antemus-																				
Progonomys-Mus	4	–	–	–	1	0	0	1	–	–	–	–	–	–						
Parapodemus	1	–	–	–	1				–	–	–	0	0	1						
Karnimata	4	–	–	–	2	0	0	2	1	0	1	1	0	2						
Parapelomys	2	–	–	–	1	0	0	1	–	–	–	0	0	1						
RHIZOMYIDAE												√			√			√		
Prokanisamys	2		–		1	0	0	1												
Kanisamys-																				
Protachyoryctes	4	–	–	–	1	1	0	0	–	–	–	0	0	2						
Eicooryctes	1	–	–	–	1				–	–	–	0	0	1						
Brachyrhizomys	2	–	–		2				0	0	1	1	0	1						
BOVIDAE												√			√					
Selenoportax	2	0	0	1	1	0	0	1	–	–	–	1	0	0						
GIRAFFIDAE																				
Giraffokeryx-																				
Bramatherium	2	0	0	1	1	1	0	0	–	–	–									
SUIDAE												√						√		
Listriodon	1	0	0	1	1															
Propotamochoerus	1	0	0	1	1															
Hippopotamodon	1	0	0	1	1							1	0	0						
Neogene total	39	0	0	5	15	2	0	6	1	0	2	4	0	16	3	0	2	3	0	3

3.3. Size structure of mammalian faunas

A cenogram portrays the pattern of rank-ordered body weight for members of a fauna. Following Legendre (1986, 1989), we omitted bats and carnivorous species (carnivores, creodonts, and carnivorous condylarths) from the cenograms. We constructed cenograms for faunas compiled from species lists for three intervals from both Paleogene and Neogene sequences (Table 2). Hence, these cenograms were analytically time-averaged. For the Paleogene faunas, body-weight estimates were all based on measurements of M_1 area as described above. For the Neogene faunas, most species' body weights were based on molar area or molar length, but for some species, body-

weight estimates were based on size comparisons with modern species. In comparing cenograms from different faunas, the important variables are the slope over certain portions of the size spectrum and breaks in the size distribution of species (see below).

4. Size structure of faunas

4.1. Comparison of Paleogene and Neogene mammalian faunas

The most obvious difference in size structure between early Paleogene and Neogene faunas is the prevalence of many more large species in the

Table 2
Species body-weight estimates included in Palaeogene and Neogene cenograms

Species	Average Cenograms Wt (in g)	(interval)
Palaeogene		
MULTITUBERCULATA		
Anconodon cochranensis	2.2	Til
Anconodon lewisi	3.8	Til
Anconodon russelli	4.3	Til
Mesodma pygmaea	2.3	Til
Neoplagiaulax hunteri	3.9	Til
Neoplagiaulax n. sp.	2.9	Til
Neoplagiaulax nelsoni	4.4	Til
Parectypodus cf. laytoni	2.3	CJ2
Mimetodon? sp.	4.0	Til
Ectypodus sp. C	4.1	Til
Ectypodus powelli	3.4	CJ2
Ectypodus tardus	3.8	Wa1
Microcosmodon woodi	4.1	Til
Microcosmodon rosei	3.4	CJ2
Microcosmodon conus	3.8	CJ2
Neoliotomus ultimus	5.0	Wa1
Ptilodus n. sp. 1	5.8	Til
Ptilodus n. sp. 2	6.2	Til
Ptilodus n. sp. 3	4.0	Til
MARSUPIALIA		
Peradectes cf. pauli	3.0	Til
Peradectes cf. cheseri	1.7	CJ2
Peradectes sp.	1.7	Wa1
PROTEUTHERIA		
Paravectes pattersoni	3.5	Til
Palaeoryctid sp. 1	4.4	Til
Palaeoryctid sp. 2	4.4	Til
Palaeoryctes sp.	2.5	Wa1
Aphronorus orieli	6.5	Til
Aphronorus n. sp.	8.2	Til
Bisondeus browni	4.8	Til
Palaeotomus senior	6.5	Til
Propalaeosinopa diluculi	4.7	Til
Palaeosinopa incerta	5.8	Wa1
Labidolemur kayi	2.9	CJ2, Wa1
Apatemys chardini	3.2	Wa1
LEPTICTIDA		
Prodiacodon concordiarcensis	3.9	Til
Prodiacodon furor	4.6	Til
Prodiacodon tauricinerei	4.1	Wa1
Diacodon minutus	2.9	CJ2
?Diacodon sp.	2.9	CJ2
Myrmecoboides montanensis	4.8	Til
Gen. et sp. indet.	6.7	Til

Table 2 (continued)

Species	Average Cenograms Wt (in g)	(interval)
INSECTIVORA		
Leptacodon munuscum	2.0	Til
Leptacodon cf. packi	2.7	Til
Leptacodon packi	2.1	CJ2
Leptacodon rosei	2.4	CJ2
Plagioctenodon krausae	1.1	CJ2, Wa1
Leipsanolestes siegfriedi	3.1	CJ2
Leipsanolestes sp.	3.1	Wa1
Tupaia? sp.	3.0	Wa1
?DERMOPTERA		
Elpidophorus elegans	6.2	Til
Worlandia inusitata	4.4	CJ2
Plagiomene accola	6.6	CJ2
PROPRIMATES		
Elphidotarsius russelli	3.9	Til
Carpolestes nigridens	4.4	CJ2
Ignacius fremontensis	3.9	Til
Ignacius sp.	4.1	Til
Ignacius graybullianus	5.8	CJ2, Wa1
Phenacolemur pagei	5.5	CJ2
Phenacolemur praecox	5.9	Wa1
cf. Palaechthon woodi	4.2	Til
Plesiolestes problematicus	5.3	Til
Pterodus silberlingi	4.8	Til
Nannodectes intermedius	5.5	Til
Plesiadapis praecursor	6.0	Til
Plesiadapis cookei	8.3	CJ2
Tinimomys graybullensis	1.9	CJ2, Wa1
Niptomomys doreenae	3.9	CJ2, Wa1
Arctodontomys wilsoni	5.8	Wa1
PRIMATES		
Cantius ralstoni	6.9	Wa1
Cantius mckennai	7.3	Wa1
Teilhardina tenicula	4.6	Wa1
"CONDYLARTHRA"		
New gen. et sp.	4.8	Til
Litomylus dissentaneus	5.5	Til
Haplomylus simpsoni	5.5	CJ2
Haplomylus speirianus	4.8	Wa1
Aphelsus n. sp.	3.8	Wa1
Hyopsodus loomisi	5.3	Wa1
Ectocion collinus	8.7	Til
Ectocion osbornianus	8.6	CJ2, Wa1
Phenacodus bisonensis	9.9	Til
Phenacodus intermedius	10.8	CJ2, Wa1
Phenacodus sp.	10.9	CJ2
Phenacodus vortmani	9.5	Wa1
"Tricentes" sp.	7.1	CJ2

Table 2 (continued)

Species	Average Wt (ln g)	Cenograms (interval)
Thryptacodon antiquus	7.5	Wa1
Chriacus gallinae	8.2	Wa1
PANTODONTA		
Titanoides sp.	11.7	Ti1
Coryphodon proterus	13.5	Cf2
Coryphodon eocaneus	12.9	Wa1
TILLODONTIA		
Azygonyx ancylion	9.8	Cf2
Azygonyx grangeri	10.3	Wa1
Esthonyx spatularius	8.8	Wa1
DINOCERATA		
Probathyopsis praecursor	10.0	Cf2
NOTOUNGULATA		
Arctostylops steini	8.1	Cf2
PERISSODACTYLA		
Hyracotherium grangeri	9.1	Wa1
Cardiolophus radinskyi	9.5	Wa1
ARTIODACTYLA		
Diacodexis metsiacus	7.5	Wa1
RODENTIA		
Microparamys cheradius	3.7	Cf2
Acritoparamys atavus	3.8	Cf2
Acritoparamys atwateri	5.0	Cf2
Acritoparamys francesi	5.1	Wa1
Acritoparamys pattersoni	6.1	Wa1
Paramys copei	6.5	Wa1
Paramys taurus	5.5	Wa1
Thisbemys sp.	6.2	Wa1
Knightomys cremneus	5.2	Wa1
Neogene		
INSECTIVORA		
Galerix rutlandae	5.3	13.5, 11.0
Galerix sp. B	5.3	11.0
Erinaceidae indet.	5.3	8.5
Crocidura sp. A.	2.3	11.0, 8.5
Crocidura sp. B	5.0	8.5
Amphechinus sp	5.2	13.5
SCANDENTIA		
Tupaiidae gen. et sp. indet.	4.6	13.5, 8.5
Dendrogale sp.	3.8	11.0
Tupaia sp.	5.0	11.0

Table 2 (continued)

Species	Average Wt (ln g)	Cenograms (interval)
PRIMATES		
Sivapithecus sivalensis	10.1	8.5
Sivapithecus indicus	9.9	11.0
Lorisidae indet. A	5.5	8.5
Lorisidae indet. B	5.3	13.5
Sivaladapidae sp.	6.2	13.5, 11.0
TUBULIDENTATA		
Orycteropus sp.	10.8	8.5
Orycteropus small sp.	10.7	13.5, 11.0
PROBOSCIDEA		
Zygolophodon metachinjiensis	14.9	13.5
Protanacus chinjiensis	14.9	13.5
Gomphotherium browni	14.9	13.5, 11.0
Gomphotherium sp.	14.9	8.5
cf. *Choerolophodon*	14.9	13.5, 11.0
Choerolophodon corrugatus	14.9	8.5
Deinotherium sp.	14.9	13.5, 11.0, 8.5
cf. *Stegalophodon*	14.9	11.0, 8.5
PERISSODACTYLA		
Chilotherium intermedium	13.6	13.5, 11.0, 8.5
Gaindatherium browni	13.6	13.5, 11.0, 8.5
Caementodon oettingenae	13.6	13.5, 11.0
Aprotodon fatehjanese	13.6	13.5
Brachypotherium perimense	14.5	13.5, 11.0, 8.5
Chalicotherium sp.	13.1	13.5, 11.0, 8.5
Sivalhippus sp.	12.4	8.5
Sivalhippus perimense	12.6	8.5
Hipparion sp.	12.4	8.5
ARTIODACTYLA		
Bramatherium megacephalum	13.5	8.5
Giraffokeryx punjabiensis	12.8	13.5, 11.0
Hippopotamodon sivalense	13.5	8.5
Listriodon pentapotamiae	11.6	13.5, 11.0
Propotamochoerus hysudricus	12.0	8.5
Hyotherium pilgrimi	11.3	13.5
Conohyus sindiense	10.5	13.5
Suid indet.	11.9	11.0
Tetraconodon magnus	13.1	8.5
Schizochoerus gandakasensis	10.3	8.5
Anthracotherium punjabiensis	10.3	13.5, 11.0, 8.5
Hemimeryx sp.	12.2	13.5, 11.0, 8.5
Selenoportax vexillarius	12.2	8.5
cf. *Gazella*	10.8	13.5, 11.0
Gazella lydekkeri	10.8	8.5
Sivoreas eremita	11.0	13.5, 11.0
Oiceros grangeri	10.3	13.5
Elaschistoceras khauristani	9.2	13.5, 11.0, 8.5

Table 2 (*continued*)

Species	Average Wt (ln g)	Cenograms (interval)
Protragocerus gluten	11.0	13.5, 11.0
Sivaceros gradiens	10.8	13.5, 11.0
cf. *Miotragocerus* sp.	11.0	13.5
Miotragocerus n. sp.	10.7	11.0
Helicoportax tragelaphoides	11.0	11.0
Tragocerides pilgrimi	11.0	8.5
Tragoportax salmontanus	11.5	8.5
Dorcabune anthracotheroides	10.8	13.5, 11.0
Dorcabune small sp.	7.6	13.5
Dorcabune nagrii	10.6	8.5
Dorcatherium majus	10.5	8.5
Dorcatherium minimus	8.8	13.5
Dorcatherium minus	9.2	13.5
Dorcatherium cf. *minus*	9.2	11.0
Dorcatherium small sp.	8.5	13.5, 11.0
Dorcatherium small sp. B	7.6	11.0
Dorcatherium cf. *nagrii*	8.5	8.5
Dorcatherium sp.	9.2	8.5

RODENTIA

Species	Average Wt (ln g)	Cenograms (interval)
Megacricetodon aguilari	2.8	13.5
Megacricetodon sivalensis	2.7	13.5
Megacricetodon daamsi	2.5	13.5, 11.0
Megacricetodon mythikos	3.3	13.5
Punjabemys leptos	3.2	13.5
Punjabemys downsi	3.7	13.5
Punjabemys mikros	2.8	13.5
Myocricetodon sp.	3.0	13.5
Myocricetodon sivalensis	2.7	13.5
Dakkamyoides perplexus	3.3	13.5
Dakkamyoides lavocati	3.3	13.5
Paradakkamys chinjiensis	3.1	13.5, 11.0
Dakkamys barryi	3.7	13.5
Dakkamys asiaticus	3.7	11.0
Antemus chinjiensis	3.0	13.5
Karnimata darwini	3.5	8.5
Karnimata large sp.	4.1	8.5
Muridae new gen. et sp.	3.0	11.0
Parapodemus sp.	3.6	8.5
Progonomys debruinji	2.8	8.5
Progonomys sp.	2.9	11.0
"*Brachyrhizomys*" *nagrii*	6.4	8.5
Kanisamys indicus	4.6	13.5, 11.0
Kanisamys sivalensis	5.3	8.5
Kanisamys nagrii	4.9	11.0
Kanisamys potwarienses	5.0	13.5
Prokanisamys benjavuni	4.1	13.5
Sciurid sp. B	4.8	13.5
Petauristine sp. B	3.4	13.5
cf. *Ratufa*	5.3	13.5, 8.5
Kochalia geespei	4.7	13.5

Table 2 (*continued*)

Species	Average Wt (ln g)	Cenograms (interval)
cf. *Hylopetes*	3.4	11.0, 8.5
Eutamias uriales	4.2	13.5, 11.0
Eutamias sp.	4.4	8.5
Gliridae indet.	3.7	13.5, 11.0, 8.5
Sayimys spp.	5.3	13.5, 11.0
Democricetodon kohatensis	4.1	13.5, 11.0
Democricetodon sp. A	4.1	13.5
Democricetodon sp. G	4.1	13.5, 11.0
Democricetodon sp. B+C	4.1	13.5, 11.0
Democricetodon sp. F	4.1	13.5, 11.0
Democricetodon sp. H	4.1	13.5, 11.0
Democricetodon sp. E	4.1	13.5, 11.0

Neogene than in the Paleogene. This difference characterizes all early Paleogene versus Neogene faunas, because substantial numbers of "large" species (>50 kg) do not appear until the middle Eocene. Most Paleocene and early Eocene mammals were smaller than a sheep (Archibald, 1983; Stucky, 1990). Larger early Paleogene species, such as those of the herbivorous pantodont *Coryphodon*, comprised a very small fraction of taxonomic richness. In contrast to Paleogene faunas, Neogene faunas include many species—especially from the orders Proboscidea, Perissodactyla, and Artiodactyla—that exceeded 100 kg in body weight. These species share an herbivorous diet comprised of large quantities of low-quality, fibrous foods. In modern faunas, these species are most numerous in woodland to grassland habitats, with an abundance of low-quality vegetation.

During the middle Eocene, species of substantially larger size evolved in many clades, and trophic structure changed via decrease in species of arboreal frugivores and omnivores and increase in species of terrestrial herbivores and obligate carnivores (Stucky, 1990; Wing and Sues, 1992) (nonetheless, taxa of smaller size persisted and remain the most numerous as well as the most speciose components of modern mammalian faunas). These faunal changes occurred after the early Eocene thermal maximum, when global temperatures renewed their long decline into the cool-climate mode (Frakes et al., 1992). From the

Paleogene to the Neogene, the trend of increasing size among ungulate and subungulate herbivores reflects the changing temporal and spatial distribution of plant resources resulting from increased climatic seasonality, increase in open habitats (woodland, shrubland, grassland), and increase in heterogeneity of vegetation (Wolfe, 1978, 1985; Janis and Damuth, 1990; Janis, 1993). The changes in size structure and trophic structure of mammalian faunas in relation to climate change over the Cenozoic broadly parallel changes in size structure and trophic structure along gradients of climate and vegetation today (Legendre et al., in prep.).

4.2. Cenograms

The distribution of species by size in a fauna is an important aspect of ecological diversity along with trophic structure, taxonomic composition, and locomotor diversity (Fleming, 1973; Andrews et al., 1979; Van Valkenburgh, 1988; Damuth et al., 1992). Size distribution is sensitive to three-dimensional habitat structure and the abundance, quality, and seasonal availability of food resources. Here, we depict the size structure of Paleogene and Neogene mammalian faunas through cenograms, or rank-size distributions (Legendre, 1986, 1989). By comparison with modern faunas, vegetation and some aspects of climate are inferred for the paleofaunas. In addition, the influence of local climatic change on mammalian size structure is evaluated.

Interpretation of cenograms has focused on the *slope*—a function of species number and sizes—for portions of the overall distribution and on the magnitude of *gaps* or *offsets*—indicating absence of species from a portion of the size range (Legendre, 1986, 1989). Legendre's survey of cenograms of modern mammalian faunas reveals three salient features of cenograms for ecological reconstruction. (1) An offset (absence of species) in the domain of medium-sized species occurs in faunas from habitats with more open vegetation, while a more continuous distribution occurs in faunas inhabiting more closed vegetation. (2) The slope for large mammals (>8 kg) changes with moisture availability, with steeper slopes characterizing faunas in drier conditions. (3) The slope for small

species (<0.5 kg) varies with mean annual temperature, with a steeper slope for faunas in regions with lower mean annual temperatures.

Three potential problems arise in constructing cenograms (or any other kind of size distribution) from fossil-assemblage data. First, taphonomic biases in either the preservation or collection of fossils (Badgley, 1986; Behrensmeyer, 1988; Badgley et al., this issue) could result in the underrepresentation of species from a portion of the size spectrum. Typically, species of small size are most vulnerable to such biases. In these Paleogene and Neogene records, screen-washing has supplemented other forms of collecting fossil localities, so that the bias in collection has been minimized. Also, the abundance of small mammals in all the cenograms presented strongly suggests that preservational biases against small species were not severe. Second, some ancient biotas have no valid modern analogs because of differences in climate, physiography, and historical contingency in evolution. In the present context, the best gauge of this problem is the opportunity to compare environmental inferences based on cenograms with inferences based on other kinds of data (see below). Third, analytical time-averaging that results from constructing faunal lists from localities spanning intervals of 0.5 m.y. may associate species that were not originally coeval (Legendre, 1989). This concern applies more to the Paleogene than to the Neogene dataset, as species ranges are on average significantly shorter in the Paleogene record than in the Neogene record (Gingerich and Gunnell, this issue). There, a finer temporal resolution could slightly steepen some of the cenogram slopes, by removing short-lived species.

Cenograms for three intervals from the Paleogene record of Wyoming/Montana and three intervals from the Neogene Siwalik record are shown in Fig. 1. The smallest mammals were of similar size—between 10 and 30 g—in all six faunas. The largest Paleogene species were those of *Coryphodon*, weighing from 250 to 750 kg (Gingerich, 1989, 1990; Uhen and Gingerich, in prep.). The Miocene faunas contained many more large taxa, including several species weighing several thousand kilograms, in the megaherbivore size range (Owen-Smith, 1988). This substantial
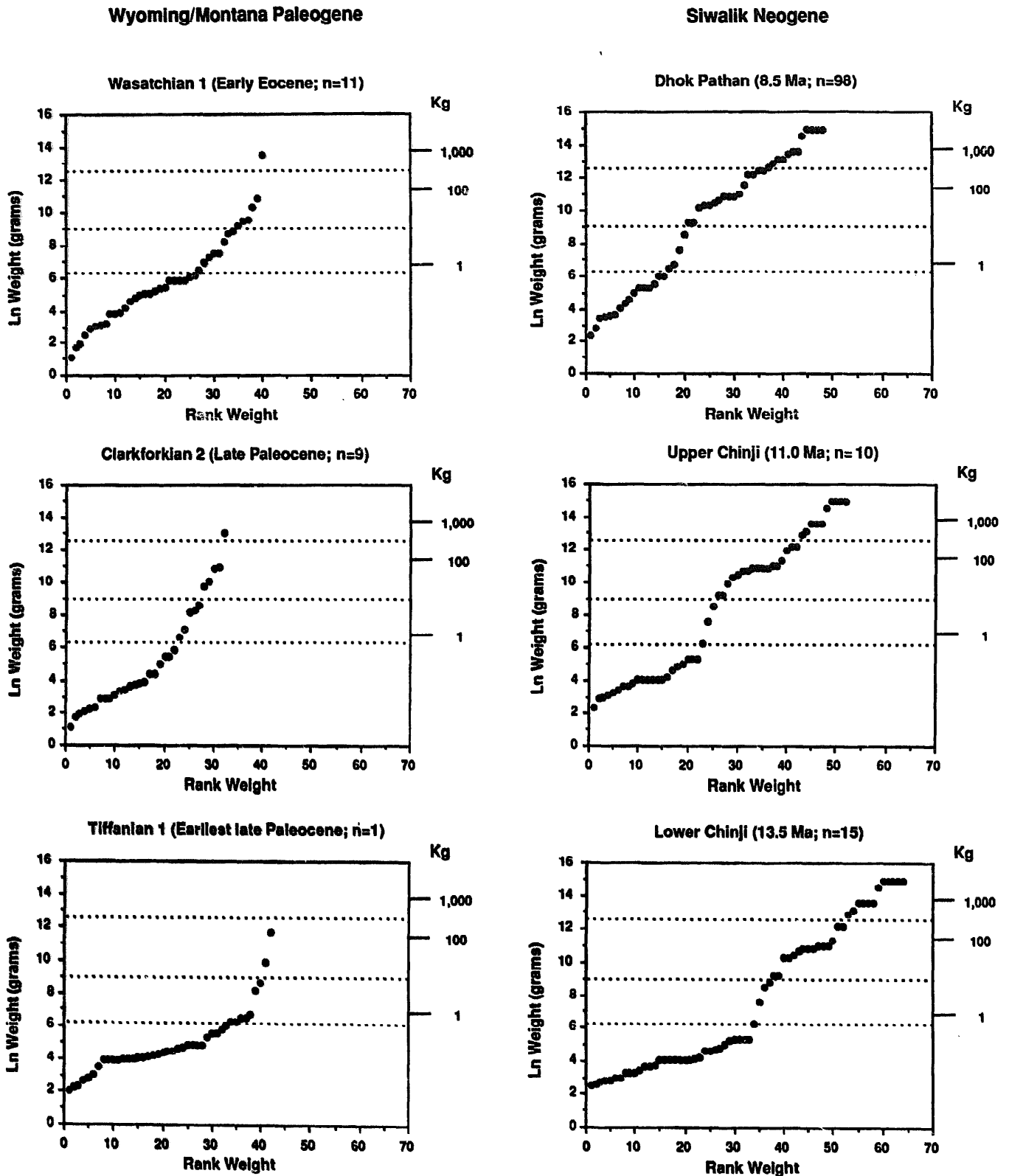
Wyoming/Montana Paleogene

Siwalik Neogene

Fig. 1. Cenograms (rank-size distributions) of three Paleogene and three Neogene faunas from different time intervals. Faunas are based on multiple localities from stratigraphic intervals of about 0.35–0.5 m.y., except for the fauna from Ti1, which is based on Douglass Quarry. Horizontal dotted lines separate small (<0.5 kg), medium (0.5–8 kg), large (8–250 kg), and very large (>250 kg) species. Body-weight estimates (Table 2) are derived from dental measurements and other data described in text. Paleoenvironmental interpretations are based on the slopes and gaps over different portions of the size spectrum (see text for explanation).

difference in maximum size between the early Paleogene and the Neogene faunas represents a general pattern arising from the evolution of large size in many mammalian lineages, beginning in the later Paleogene and persisting through the Cenozoic.

For the Paleogene cenograms of Fig. 1, the changes from Tiffanian to Wasatchian faunas include a slight decrease in the number of small species, an increase in the number of species of medium and large size, and the addition of very large species of *Coryphodon* in late Paleocene and early Eocene faunas. The gaps in the medium-size range suggest more open-forest conditions in the latest Paleocene and more closed-forest habitats in the early Eocene. The slopes for large mammals are high in all three Paleogene cenograms, with a slight decrease from the Tiffanian to the Clarkforkian and Wasatchian, suggesting a shift from mesic to more humid conditions. The paucity of larger mammals in the early Tiffanian cenogram is likely a preservational feature of this fauna, based on a single locality, Douglass Quarry (Maas and Krause, in press). The low slopes for the small species in all three Paleogene cenograms suggest tropical to subtropical annual temperatures and winters without frost, with somewhat cooler temperatures for the Clarkforkian (latest Paleocene). Extant faunas that exhibit cenograms similar to those of these Paleogene faunas include southeast Asian tropical forest sites for the Tiffanian assemblage; Colima, Mexico, with tropical seasonal forest for the Clarkforkian assemblage; and a Vietnamese tropical forest for the early Wasatchian assemblage (Legendre et al., in prep.).

Other sources of paleoenvironmental information from the same Paleogene record include mammalian trophic structure and paleofloral data. Gunnell et al. (this issue) compared the trophic structure of Paleogene mammalian faunas from the same record to that of several modern mammalian faunas to infer habitats. For Tiffanian assemblages, forested, humid conditions were inferred; for the Clarkforkian, a drier climate with woodland instead of forest; and for the early Wasatchian, woodland to thornwood. These inferences based on trophic structure are broadly similar to those based on size structure except for the

Wasatchian: the small gap within the medium-size mammal species suggests forest rather than woodland. Estimates of mean annual temperature from paleofloras of the Bighorn Basin range from 10°C in the late Tiffanian to 13°C in the Clarkforkian, then from 14 to >18°C through the Wasatchian (Wing et al., 1991; Wing et al., this issue). Isotopic evidence from the Bighorn Basin and the marine record also indicate global warming in the early Eocene (Koch et al., this issue). The Tiffanian cenogram suggests a warmer temperature than the estimate based on floras; oxygen-isotopic data from Tiffanian mammals also suggest warmer temperatures (Koch et al., this issue). These conflicts in interpretation may arise from a discrepancy in time between the cenogram (early Tiffanian) and the floral sample (late Tiffanian), the Tiffanian cenogram depicting just one quarry, or poor matches in modern analogs for the faunas or floras. Earlier interpretations of late Paleocene to early Eocene floras and herbivorous mammals (e.g., sexual dimorphism in species of *Hyracotherium*) suggested that late Paleocene habitats were dominated by closed forest and early Eocene habitats were more open with a mixture of forest, woodland, and more open areas (Gingerich, 1981). The cenograms presented here suggest a different history of vegetation.

For the Neogene record, the overall trends over a 5-m.y. period are a decrease in the number of small species and a slight increase in the number of medium species between the lower Chinji and the Dhok Pathan faunas. The increase in slope for small species suggests a slight decrease in mean annual temperature, but not freezing winters. In the lower and upper Chinji faunas, the sparsely occupied interval of medium mammals represents the low frequency of animals weighing between 500 g and 2 kg. This region is better filled in the Dhok Pathan fauna. Although pre-burial taphonomic processes, such as carnivory and scavenging, as well as collecting methods may have contributed to these gaps, it is unlikely that taphonomic processes created the gaps in their entirety, since the three intervals depicted include very rich localities and smaller species are well represented. Rather, the persistent low frequency of non-carnivorous species in this size range in Siwalik assemblages is

likely to reflect original faunal composition. If so, then Siwalik vegetation was likely as open as modern seasonal woodland. Yet the slopes for large mammals are fairly low, suggesting that the environment was humid rather than arid. This apparent paradox may reflect the effects of a fluvial system in an area with highly seasonal rainfall. Extant mammalian faunas that resemble these Siwalik faunas in size distribution all occur in African savannah woodlands and savannah scrub (Legendre et al., in prep.). The modern faunas that most closely resemble the lower and upper Chinji faunas have mean annual rainfall ranging from 800–1350 mm/yr, while the modern faunas that most closely resemble the Dhok Pathan cenogram have mean annual rainfall of <700 mm/yr.

Other sources of paleoenvironmental information yielded similar reconstructions. Gunnell et al. (this issue) evaluated trophic structure of Siwalik mammalian faunas and found the closest modern analogs in African savannah-woodlands. Quade and Cerling (this issue) inferred that annual rainfall was <1000 mm/yr throughout the Siwalik record, from leaching depths in paleosols. Prior interpretation of the habitats of Siwalik mammalian faunas was a mosaic of diverse vegetation types, including forest, woodland, and grassland, to accommodate the diversity of inferred mammalian diets (Badgley and Behrensmeyer, 1980). The habitat inferences based on the cenograms in Fig. 1 point toward a semi-arid version of this vegetational mosaic.

5. Size change within selected groups

5.1. Paleogene mammals

We examined patterns of size change for 61 species from six orders of Paleogene mammals that occurred between the late middle Paleocene (late Torrejonian Land Mammal Age) and the early Eocene (early Wasatchian Land Mammal Age) in the Bighorn-Crazy Mountains system. Fig. 2 and Table 1a document these Paleogene groups. Figs. 2a,d depict condylarths in the Hyopsodontidae (15 species) and Phenacodontidae (14 species). Figs. 2b,e depict Rodentia (eight species), Tillodontia (five species), and Pantodonta

(six species). Figs. 2c,f depict the Artiodactyla (three species) and Perissodactyla (12 species). In each biostratigraphic interval, each species is represented by the natural logarithm of estimated mean size. The data for each group are plotted on two scales of estimated body mass. The scales in Figs. 2a–c differ and serve to facilitate comparison of size change within groups. In Figs. 2d–f, the data are plotted on a common size axis for comparison across groups.

5.2. Condylarths

The most common and diverse mammals during the Paleogene were species from the order Condylarthra. Two well-represented condylarth families were the Phenacodontidae and the Hyopsodontidae (Fig. 2a,d). All documented species of phenacodontids and hyopsodontids in the local biostratigraphic record are included.

Phenacodontids spanned the entire interval under consideration. The earliest species depicted, *Tetraclaenodon puercensis*, from biozone To-3 (Torrejonian-3), had an estimated weight of about 7 kg, and the latest species depicted, *Phenacodus vortmani*, from Wa-6 (Wasatchian-6), had an estimated weight of about 10 kg. The range of body sizes expanded between To-3 and Wa-6, with species of *Ectocion* and *Copecion* generally weighing 5 kg or less and species of *Phenacodus* generally weighing from 8 to >40 kg (*P. robustus*). At this scale and resolution, none of the phenacodontids exhibited rapid increase or decrease in size by our criterion (Table 1a). At its first occurrence in the middle Tiffanian, *P. grangeri* was more than double the size of established congeners, and *P. matthewi(?)*, which appeared in the early Clarkforkian, was less than half the size of established congeners. Other species of *Phenacodus* did not appear at sizes corresponding to doubling or halving relative to established congeners. At first occurrence in Wa-0, *Copecion davisi* was less than half the size of established *Copecion brachypternus*. Because of local extinction of phenacodontids in Paleogene intervals, several newly appearing phenacodontids were larger than established species in the same family. Most phenacodontids were locally extinct by Wa-4. The median size

of contemporaneous Paleocene phenacodontids increased and decreased several times over the local record, but the net result was no significant change by our criterion. The size range increased from Ti-1 (Tiffanian-1) through Ti-4, decreased in Ti-5 and Cf-1, and increased again in Cf-2.

The hyopsodontids were smaller at all times than contemporaneous phenacodontids. Estimated hyopsodontid weights spanned from 150 g to just over 1 kg (Fig. 2a,d). The earliest species were among the smaller hyopsodontids, and notably larger species arose twice–with the middle Tiffanian to late Clarkforkian *Aletodon* lineage and with *Hyopsodus powellianus* in Wa-6. At this scale and resolution, no major jumps in size occurred in hyopsodontid species or lineages (Table 1a). At first occurrence, *Haplaletes serior* was more than double the size of the earlier congener; *Haplomylus speirianus* was less than half as large as earlier *H. simpsoni*; and *Hyopsodus powellianus* was more than twice as large as established species of *Hyopsodus*. Comparing first occurrences to other species of the same family, there were more instances of newly occurring species that met the doubling/halving criterion than for comparisons within genera (Table 1a). For hyopsodontids as a whole, the median size of contemporaneous species in each biostratigraphic interval increased from the late Torrejonian to the late Clarkforkian, decreased at Wa-0 and Wa-1, then increased over the local Wasatchian record. The size range increased from the Tiffanian to Clarkforkian and Wasatchian species. The hyopsodontids maintained smaller sizes than contemporaneous species of early artiodactyls.

5.3. Rodentia

At the beginning of the Clarkforkian, the order Rodentia, represented by the family Paramyidae, appeared in the North American record (Rose, 1981; Ivy, 1990). Korth (1984) proposed that North American rodents were derived from Asian ctenodactyloids; subsequent hypotheses have consistently suggested that early North American rodents were immigrants. Rodent species ranged between 15 and 250 g (Fig. 2b). The earliest species were *Microparamys cheradius*—estimated at about

40 g. *Acritoparamys atavus*—estimated at about 50 g, and *A. atwateri*—estimated at about 150 g. In the Wasatchian, species of *Acritoparamys* and *Paramys* exceeded 200 g. *Knightomys*, an early representative of the family Sciuravidae, appeared later in the Wasatchian at a size of about 25 g. One rodent species exhibited change in size over time by our criterion (Table 1a): *Acritoparamys atwateri* from Wa-3 was less than half the size of samples from the preceding and succeeding intervals; small sample sizes may have contributed to this unusual pattern of size change. *Microparamys hunteri*, known only from Wa-1, was less than half the size of its established congener (Ivy, 1990). Overall, rodents expanded toward smaller size more than toward larger size in the Wasatchian of the Clarks Fork Basin. By our criterion, the median size of paramyids increased from Cf-2 to Cf-3 and did not substantially decrease through Wa-4. The size range of paramyids increased significantly in Wa-1, decreased in Wa-2, and decreased further from Wa-3 to Wa-4. The size range of rodents (paramyids and sciuravids) in the early Eocene is comparable to that of most extant rodents.

5.4. Tillodontia

The Tillodontia (family Esthonychidae) were represented by five species in two genera from Clarkforkian and Wasatchian biozones (Fig. 2). Their ancestors dispersed to North America probably from Asia at the end of the Paleocene (Krause and Maas, 1990). Esthonychids first occurred in Cf-1, but samples of M_1's are not present until Cf-2. The three species of *Azygonyx* in the mid-Clarkforkian ranged in estimated size from 9–22 kg. *Azygonyx grangeri* nearly doubled in size in the latest Clarkforkian, then decreased in size in the early Wasatchian. While the latest Clarkforkian specimens represented the largest tillodonts in the local record, the increase did not meet our criterion of doubling. The earliest known *Esthonyx, E. spatularius*, was from Wa-0. This species experienced size decrease between Wa-0 and Wa-1. The latest tillodont, *E. bisulcatus*, was at the small end of the size range of the earliest tillodonts, with larger species having become
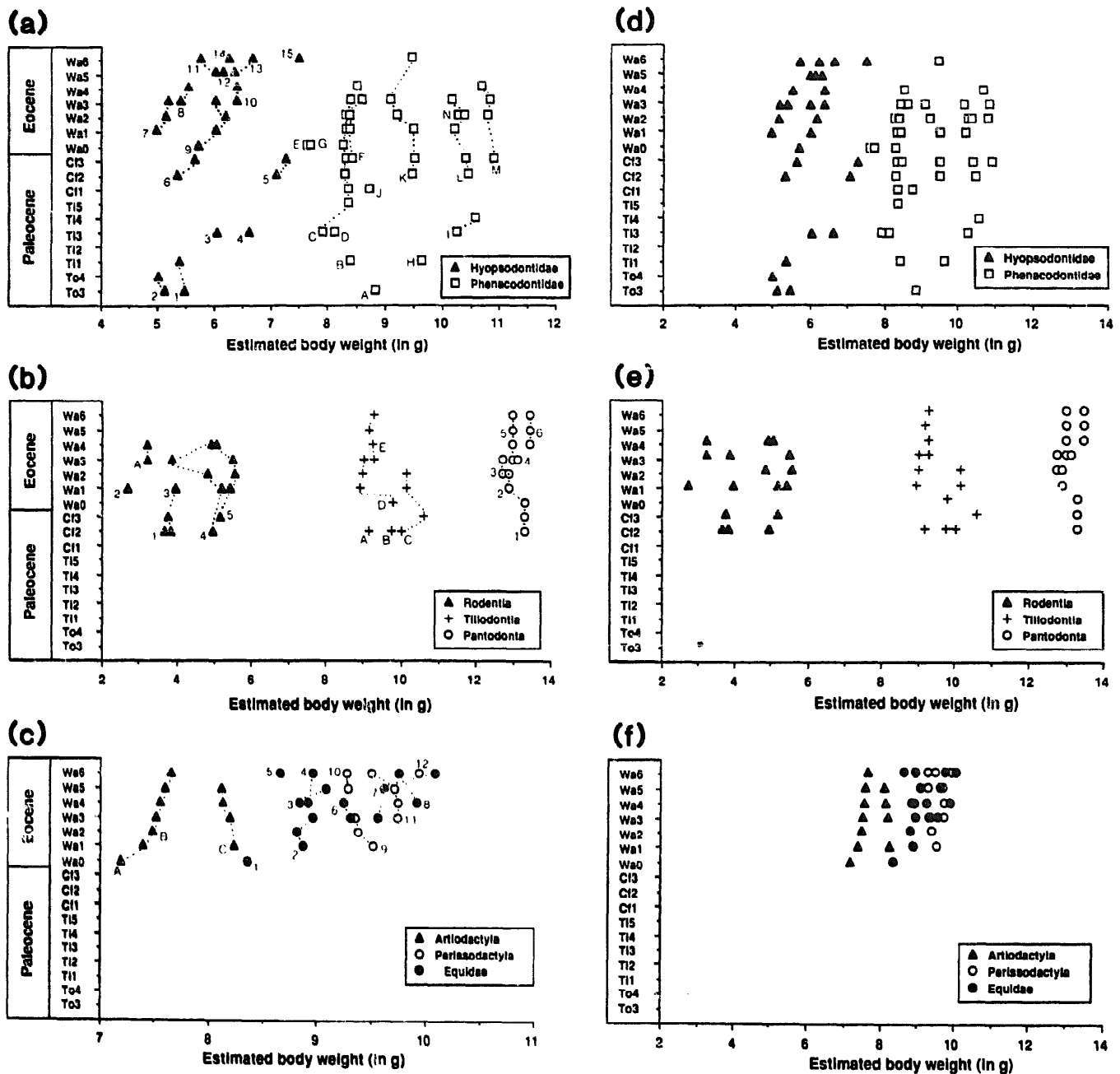
Fig. 2. Size change of Paleogene species in selected mammalian families, from the Bighorn, Clarks Fork, and Crazy Mountains basins of Wyoming and Montana. Each datum represents mean size for all relevant specimens in a biostratigraphic zone. The sample size for each species is given in parentheses following species name. (a) Condylarthra: Phenacodontidae and Hyopsodontidae. Estimation of body weight (y) from Legendre's (1989) regression formula for mammals: $\ln(y) = 1.7054 \ln(x) + 2.247$, with ($x$) = area of M_1. Key to species: for Hyopsodontidae, $1 = Litomylus\ dissentaneus$ (<10), $2 = Haplaletes\ disceptrix$ (<10), $3 = Haplaletes\ serior$ (<10), $4 = Aletodon\ quadravus$ (1), $5 = Aletodon\ gunnelli$ (9), $6 = Haplomylus\ simpsoni$ (18), $7 = Haplomylus\ speirianus$ (563), $8 = Haplomylus\ scottianus$ (156), $9 = Hyopsodus\ loomisi$ (851), $10 = Hyopsodus\ latidens$ (337), $11 = Hyopsodus\ minor$ (43), $12 = Hyopsodus\ simplex$ (9), $13 = Hyopsodus\ miticulus$ (95), $14 = Hyopsodus\ lysitensis$ (1), $15 = Hyopsodus\ powellianus$ (7); for Phenacodontidae, $A = Tetraclaenodon\ puercensis$ (<10), $B = Ectocion\ collinus$ (19), $C = Ectocion\ osbornianus$ (449), $D = Ectocion\ cedrus$ (<10), $E = Ectocion\ parvus$ (14), $F = Copecion\ brachypternus$ (20), $G = Copecion\ davisi$ (14), $H = Phenacodus\ bisonensis$ (<10), $I = Phenacodus\ grangeri$ (<10), $J = Phenacodus\ matthewi$ (1), $K = Phenacodus\ vortmani$ (27), $L = Phenacodus\ intermedius$ (49), $M = Phenacodus\ robustus$ (8), $N = Phenacodus\ primaevus$ (2). (b) Rodentia: Paramyidae and Sciuravidae, Tillodontia: Esthonychidae, and Pantodonta: Coryphodontidae. Estimated body weights from taxon-specific regression formulas in Legendre (1989). For paramyids and

extinct or decreasing in size. For the group as a whole, the median size did not change by our criterion. The size range (when two or more species were present) decreased between Wa-2 and Wa-3, but the overall change from Cf-2 to Wa-3 was not significant.

5.5. Pantodonta

Species of *Coryphodon* were the largest members of their faunas. Their estimated body weights ranged from 250–750 kg (M. Uhen, pers. comm., 1993); hence, they were about an order of magnitude larger than contemporaneous herbivores (Fig. 2b). Uhen and Gingerich (in prep.) recognized six species of *Coryphodon* in the Bighorn Basin. The earliest, Clarkforkian *C. proterus*, had an estimated body weight of about 700 kg. Higher in the section, two species continuing the same lineage (*C. eocaenus* and *C. ryani*) were smaller than *C. proterus*. At the resolution of Fig. 2, none of the six species exhibited a doubling or halving of size from biozone to biozone, and none of the first occurrences were either double or half the size of congeners already present. By our criterion, neither the median nor size range of coryphodontids changed over the local record.

5.6. Artiodactyla and Perissodactyla

Artiodactyls and perissodactyls have radiated considerably since the Paleogene to become diverse

or dominant members of many modern ecosystems. They appeared during the earliest Eocene, probably as immigrants from other Holarctic continents (Krause and Maas, 1990). In the Clarks Fork Basin, artiodactyls were represented by three species in two lineages of the Dichobunidae (Fig. 2c,f). The earliest dichobunid lineage, *Diacodexis ilicis-metsiacus*, appeared at Wa-0. In Wa-1, *D. robustus* appeared at more than double the size of the established species. All species weighed less than 4 kg and were similar in size to the modern Asian *Tragulus* and the smallest neotragines. Neither lineage exhibited major rapid jumps in size by our criterion (Table 1a) within the local record. Species of *Diacodexis* were always larger than contemporaneous hyopsodontids and overlapped in size with the smallest, contemporaneous phenacodontids (*Ectocion osbornianus*). Median size did not change substantially and the size range decreased by our criterion.

Perissodactyls consisted of eight species in one genus of Equidae, three species among two genera of Isectolophidae, and one species of Helaletidae. The equids increased in size range and species richness through the Wasatchian (Fig. 2c,f), from the single species *Hyracotherium sandrae*, estimated at 5 kg, during the earliest Eocene, to *H. crasspedotum*, estimated at around 25 kg, one of four species present in Wa-6. Although no later species in the local record were as small as *H. sandrae*, species of about 8 kg or less (*H. grangeri*, *H. etsagicum*, *H. pernix*, and *H. borealis*) persisted through the

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sciuravids, Legendre's regression for rodents was used: ln(y) = 1.6375 ln(x) + 2.2446. For esthonychids, Legendre's herbivore regression was used: ln(y) = 1.7894 ln(x) + 2.2224. For coryphodontids, Legendre's ungulate regression was used: ln(y) = 1.5147 ln(x) + 3.6049. x and y as above. Key to species: for Paramyidae, *1 = Microparamys cheradius* (1), *2 = Microparamys hunteri* (1), *3 = Acritoparamys atavus* (5), *4 = Acritoparamys atwateri* (15), *5 = Paramys taurus* (24); for Sciuravidae, *A = Knightomys cremneus* (2); for Tillodontia, *A = Azygonyx xenicus* (2), *B = Azygonyx ancylion* (9), *C = Azygonyx grangeri* (12), *D = Esthonyx spatularius* (38), *E = Esthonyx bisulcatus* (38); for Pantodonta, *1 = Coryphodon proterus* (8), *2 = Coryphodon eocaenus* (18), *3 = Coryphodon ryani* (9), *4 = Coryphodon radians* (8), *5 = Coryphodon armatus* (19), *6 = Coryphodon lobatus* (8). (c) Artiodactyla: Dichobunidae, and Perissodactyla: Equidae, Isectolophidae, Helaletidae. Estimated body weights from taxon-specific regression formulas in Legendre (1989). For dichobunids, Legendre's artiodactyl regression was used: ln(y) = 1.528 ln(x) + 3.5503. For equids, isectolophids, and helaletids, Legendre's perissodactyl regression was used: ln (y) = 1.5594 ln(x) + 3.2818. x and y as above. Key to species: for Artiodactyla, *A = Diacodexis ilicis* (2), *B = Diacodexis metsiacus* (333), *C = Diacodexis robustus* (9); for Perissodactyla, *1 = Hyracotherium sandrae* (5), *2 = Hyracotherium grangeri* (401), *3 = Hyracotherium etsagicum* (3), *4 = Hyracotherium pernix* (32), *5 = Hyracotherium borealis* (3), *6 = Hyracotherium aemulor* (76), *7 = Hyracotherium crasspedotum* (6), *8 = Hyracotherium cristatum* (3), *9 = Cardiolophus radinskyi* (42), *10 = Cardiolophus semihians* (10), *11 = Homogalax protapirinus* (37), *12 = Heptodon calciculus* (2). (d) Same data as in (a), plotted at the same scale as in (e) and (f). (e) Same data as in (b), plotted at the same scale as in (d) and (f). (f) Same data as in (c), plotted at the same scale as in (d) and (e).

sequence. One species, *H. crasspedotum*, was at first occurrence more than double the size of established congeners (Table 1a). For equids as a whole, the median size increased significantly from Wa-0 to Wa-3, but via small steps. By Wa-6, the size range had increased but the median size for contemporaneous species of *Hyracotherium* was about the same as in Wa-3.

The Isectolophidae were represented by two species of *Cardiolophus* and one species of *Homogalax*. *Cardiolophus radinskyi* appeared in Wa-1 and *C. semihians* in Wa-5. The two species were similar in size and weighed between 10 and 20 kg. Neither species exhibited major jumps in size by our criterion. *Homogalax protapirinus* appeared in Wa-3 and persisted through the local sequence without major rapid changes in size. For isectolophids, median size did not increase but size range did, by our criterion. The helaletid, *Heptodon calciculus*, appeared in Wa-6; its range is too short to evaluate size change by our method.

5.7. Patterns of size change for Paleogene mammals

No single pattern of size change characterizes the six orders of late Paleocene and early Eocene mammals considered. By our criteria, the hyopsodontids and phenacodontids experienced increase and decrease in median size over the duration of each group (Table 1a). A net increase in median size occurred for hyopsodontids and paramyids, while the median size of phenacodontids was similar at the end of their local record to the median at the beginning. The remaining families—esthonychids, coryphodontids, dichobunids, equids, and isectolophids—exhibited no significant change in median size over their duration. Of 61 species examined, only two (3%), *Acritoparamys atwateri* (a rodent) and *Esthonyx spatularius* (a tillodont), exhibited size change that exceeded a doubling or halving of body weight relative to an earlier pop·ulation, at this scale of study. No additional size change of this kind occurred for species within lineages. Among newly occurring species, 5/33 (15%) were more than double the size of established congeners, 4/33 (12%) were less than half the size of established congeners, and 24/33 (73%) did not differ significantly by our criterion. Among

newly occurring species relative to established species of the same family, 8/40 (20%) were more than twice as large, 2/40 (5%) were less than half as small, and 30/40 (75%) did not differ in size. By our criterion, size change more often involved new occurrences than major jumps in size within species or lineages, based on the current interpretation of evolutionary relationships. By our criterion, the size range increased for phenacodontids, hyopsodontids, and equids over the local biostratigraphic record. Paramyids showed a net decrease in size range, with significant increase in the early Wasatchian. Esthonychids, coryphodontids, dichobunids, and isectolophids exhibited no significant net change in size range, although the size range of esthonychids did change significantly over portions of their stratigraphic range.

The instances of major jumps in size fell in several time intervals (Fig. 2), with most occurring in the Wasatchian. Tiffanian examples involved species of *Haplaletes* (Ti-3) and *Phenacodus* (Ti-1, Ti-3). Clarkforkian examples involved species of *Haplomylus* (Cf-2) and *Phenacodus* (Cf-1, Cf-2). At Wa-0, size decrease relative to an established congener occurred in a species of *Copecion*. During the transition from Wa-0 to Wa-1, size decrease occurred in *Esthonyx spatularius*. In Wa-1, first occurrences involving a doubling of size relative to established congeners occurred in species of *Diacodexis*, *Microparamys*, and *Haplomylus*. Additional size changes occurred in Wa-3 (*Hyracotherium crasspedotum*) and in Wa-6 (*Hyopsodus powellianus*).

Two major intervals of immigration occurred for the mammals presented here: the early Clarkforkian appearance of rodents and tillodonts and the earliest Wasatchian appearance of artiodactyls and perissodactyls. Species in all four groups are considered herbivores, according to Gunnell et al. (this issue). Regarding the Clarkforkian immigrants, size change by our criterion occurred within both rodent and tillodont lineages, but not until the Wasatchian. Among resident groups, some phenacodontids were close in size to the esthonychids but did not exhibit major jumps in size following appearance of the latter. After the Wasatchian immigration of artiodactyls and perissodactyls, there were major

jumps in size within species of the immigrant groups as well as within species of the resident groups (Table 1a). Among congeners, size increase occurred for species of *Diacodexis* and *Hyracotherium* (immigrants), while size decrease occurred within a lineage of *Esthonyx* and for new species of *Microparamys* and *Haplomylus* (resident groups). Size increase also occurred for a species of *Hyopsodus* (resident). The most notable change involving herbivorous taxa in the same size range was the decline in the number of species of *Phenacodus* from Wa-3 to Wa-4 and the simultaneous increase in the number of species of *Hyracotherium* and other perissodactyls.

For these patterns of Paleogene size change, the principal causes were probably climate and competition. Climate change elsewhere indirectly facilitated immigration of new groups, including rodents, tillodonts, artiodactyls, and perissodactyls, through the opening of high-latitude, intercontinental dispersal routes (Gingerich, 1980; Krause and Maas. 1990; Koch et al., 1992). A short, intense interval of global warming occurred at the Paleocene–Eocene boundary (Koch et al., this issue), and the earliest Wasatchian fauna (from Wa-0) exhibited distinctive size changes in a number of mammalian lineages (Gingerich, 1989). Among the groups presented here, almost half of the instances of doubling or halving in size occurred in the transition from Wa-0 to Wa-1; these instances involved one immigrant species and three resident species and included both increase and decrease in size. The species involved did not overlap in size. Relative to Clarkforkian faunas, overall trophic structure changed toward an increase in the frequency of carnivorous and frugivorous species and a decrease in the frequency of omnivorous, insectivorous, and herbivorous species (Gunnell et al., this issue). Altogether, these data suggest climatic change as a primary cause better than the alternative mechanisms considered, although climatic change may have important consequences for competitors and predator–prey relations.

There is little evidence for competition through size change within species or lineages, but some evidence involving first occurrences in relation to local extinctions. Only two species exhibited major jumps in size by our criterion. *Esthonyx spatularius*

decreased in size from Wa-0 to Wa-1 and then remained stable through Wa-3 (Fig. 2b). Although we presented evidence for climatic change over this interval, it is also plausible that size decrease in this tillodont lineage was a response to competition from perissodactyls or phenacodontids in the same size range (Figs. 2d,f). *Acritoparamys atwateri* decreased in size in Wa-3 and then increased to its former size. The only other lineages presented here in the same general size range are *Paramys taurus* and *Haplomylus speirianus*. The former is considered an herbivore and the latter an insectivore by Gunnell et al. (this issue), so that competition for trophic resources would more likely have involved the two rodent lineages. But by Wa-5, the two rodent lineages were almost identical in size, diminishing the plausibility of competition between these two rodent species as a mechanism of change. Diffuse competition with contemporaneous herbivores of larger size (hyopsodontids and dichobunids) may have limited the expansion of rodent species to larger size. Although species of phenacodontids did not undergo major jumps in size in the Wasatchian, it is noteworthy that three phenacodontid lineages and one tillodont lineage became locally extinct in Wa-3, as perissodactyls (equids and isectolophids)—herbivores in the same size range—diversified. For these larger Paleogene herbivores, some of the criteria for competition are met; observed criteria include sympatry, overlap in resource use, and overlap in size.

There is less evidence to invoke predation than competition or climate change. In these Paleogene faunas, predatory mammals were in the size range of modern weasel to large wolf. Only species of *Coryphodon* had possibly reduced vulnerability to predation through large size; the first species to appear in the local sequence was already quite large, and this group did not exhibit change in median size or size range. Possibly, the instances of size decrease in two lineages of paramyid rodents represent evolutionary responses to predation, resulting in a wider range of refuges at smaller size.

5.8. Neogene mammals

Body-size structure was examined over a period of 10 myr for 39 species from the two most diverse

orders of Siwalik herbivorous mammals, rodents and artiodactyls. Fig. 3 and Table 1b document the taxa included in this analysis. Figs. 3a,c depict patterns of size change within muroid rodents, which include 12 species of cricetids, 11 species of murids, and nine species of rhizomyids. Figs. 3b,d document the artiodactyls, which include bovids (two of the species are indicated), three suid species, and two giraffid species. Fig. 3 depicts average body mass plotted on two scales of size: one scale chosen for ease of comparing changes in species' sizes within groups, the other scale chosen for comparison of changes across groups.

5.9. Neogene Muroidea

Middle Miocene rodent assemblages were dominated taxonomically and numerically by several subfamilies of cricetids (Lindsay, 1988; Barry et al., 1991), including the megacricetodontines, dendromurines, and myocricetodontines presented here, that ranged in body weight from approximately 10-45 g (Fig. 3a). For the duration of the cricetid record, median size remained fairly stable, and size range did not change by our criterion. Following the occurrence at 13.7 Ma of the first murid species, *Antemus chinjiensis*, possibly a descendant of the cricetid *Potwarmus primitivus* (Lindsay, 1988; Jacobs et al., 1990), cricetids, as defined here, became less numerous. With the advent of *Progonomys*, a descendant of *Antemus*, at 12 Ma, cricetid diversity and abundance declined markedly.

By 9 Ma, murid species comprised over 90% of recovered muroid specimens (Barry et al., 1991) despite low taxonomic diversity. Successive anagenetic change within the *Antemus-Progonomys-Mus* lineage showed minor size decrease between *Antemus chinjiensis* (estimated at 20 g) and *Mus* (estimated at 16 g) over 8 m.y. The size range of murids did not change markedly until 8.5 Ma, when *Karnimata* large sp. (murid species 8 in Fig. 3a) arose at more than double the size (about 60 g) of its ancestor, *Karnimata* sp. (murid species 5), estimated at about 25 g. From *Karnimata* large sp., there arose slightly larger species in the lineage *Parapelomys*. No other newly occurring murid lineages exceeded a doubling or halving of size

relative to established species (Table 1b). By our criterion, median size did not change and size range of murids increased in the Siwalik record. The size range of murids at 8.5 Ma—from 15 to 60 g—was comparable to that of their modern representatives in the Indian subcontinent (Jacobs et al., 1990).

The Rhizomyidae, although not diverse until the late Miocene, were present throughout the Siwalik sequence. Two long-lived, coeval species, *Prokanisamys benjavuni* and *Kanisamys indicus*, had estimated body weights of 60 and 100 g, respectively. Successive, derived species of *Kanisamys*, *K. nagrii* and *K. sivalensis*, were each approximately 50% larger than their ancestral species (rhizomyid species 3-5 in Fig. 3a); the mean size of the lineage increased in small steps by our criterion. *Protachyoryctes* (species 6 in Fig. 3a) was a large derivative of *Kanisamys* (Flynn, 1982); at first occurrence around 7 Ma, *Protachyoryctes* was more than double the size of ancestral *K. sivalensis*. The other rhizomyid lineage that exhibited size increase relative to established confamiliars was *"Brachyrhizomys"* (rhizomyid species 8 and 9 in Fig. 3a) which appeared in the Siwaliks around 9 Ma. These species were large rhizomyids with fossorial adaptations and were comparable in size with living, fossorial bamboo rats (Flynn, 1985). The appearance of *"B." nagrii* at 8.7 Ma significantly expanded the size range of the family, by our criterion; but the net change in size range was not significant. Flynn (1982) thought that *"B." nagrii* showed anagenetic size increase over an interval of 0.5 myr, but the increase was substantially less than a doubling in size.

Overall, rhizomyids were the largest muroids present at any time. By our criteria, both the median size and the size range of coeval rhizomyids and murids increased between 9 and 8.5 Ma, with the appearance of two species—*Karnimata* large sp. and *"Brachyrhizomys" nagrii*. One rhizomyid lineage, *Kanisamys-Protachyoryctes*, exhibited a major jump in size at 7 Ma. By our criterion, no major size change was observed for the additional muroid lineages that could be evaluated and no muroids showed major, rapid size decrease over 10 m.y.
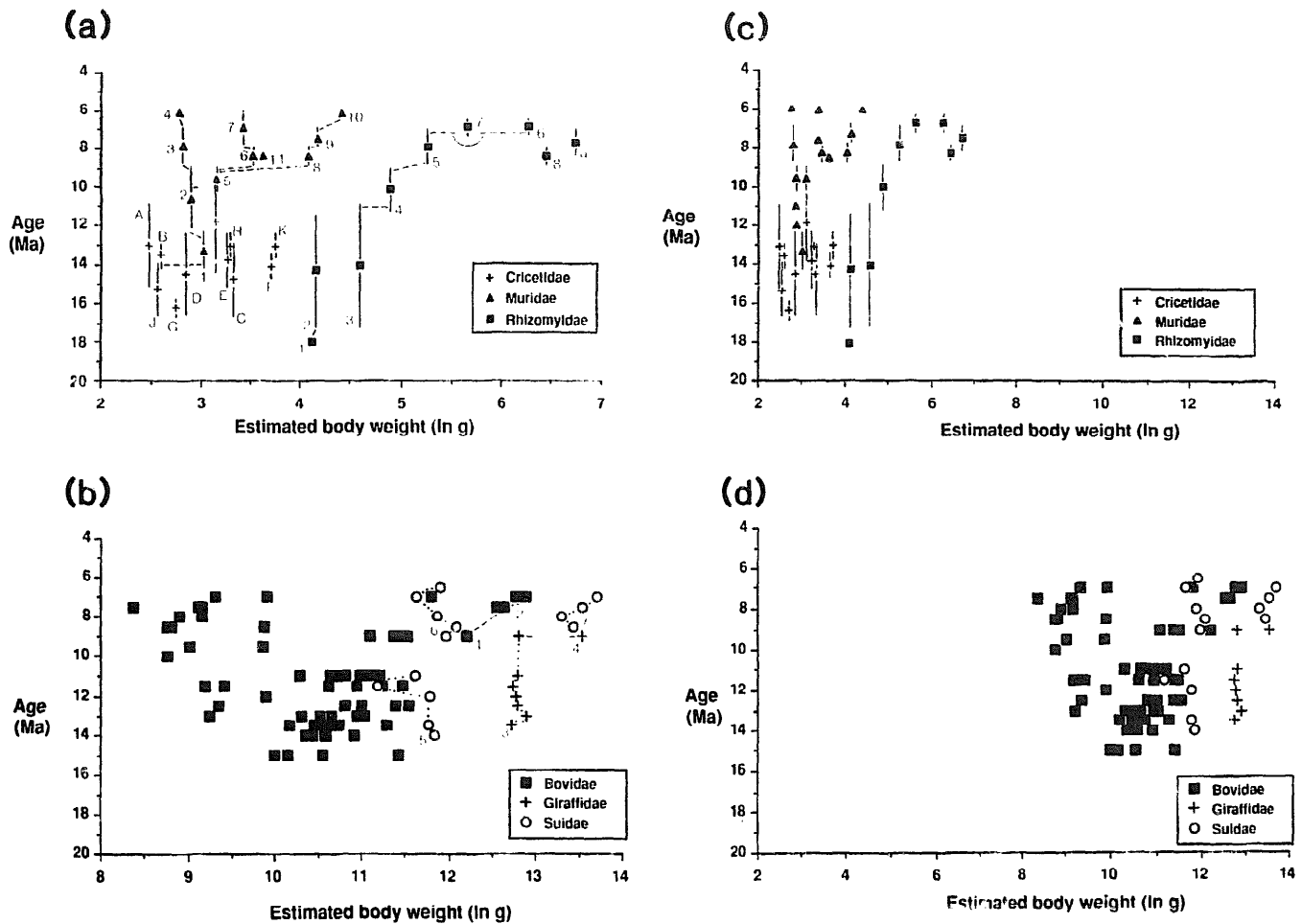
(a)

(c)

(b)

(d)

Fig. 3. Size change of Neogene species from selected mammalian families from Siwalik rocks of northern Pakistan. The sample size for determining size estimate(s) of each species is given in parentheses following species name. (a) Muroid rodents: Cricetidae, Muridae, Rhizomyidae. Estimated body weights from taxon-specific regression, formulas in Legendre (1989). For muroids, Legendre's rodent regression was used: $\ln(y) = 1.6375 \ln(x) + 2.2446$, where ($y$) is body weight and ($x$) is area of M_1. Murid estimates are based on M^1 and decreased by 40% (see text for details). For muroid species, each datum is the mean size of all specimens, with biostratigraphic range indicated by vertical line. Key to species: for Cricetidae, $A = Megacricetodon$ $daamsi$ (6), $B = Megacricetodon$ $sivalensis$ (15), $C = Megacricetodon$ $mythikos$ (1), D (16.5–13.5 Ma) = $Megacricetodon$ $aguilari$ (3), D (16.5–12.5 Ma) = $Punjabemys$ $mikros$ (1), $E = Punjabemys$ $leptos$ (4), $F = Punjabemys$ $downsi$ (9), $G = Myocricetodon$ $sivalensis$ (8), $H = Dakkamyoides$ $perplexus$ (1), $I = Paradakkamys$ $chinjiensis$ (3), $J = Potwarmus$ $primitivus$ (4), $K = Dakkamys$ $barryi$ (2); for Muridae, $1 = Antemus$ $chinjiensis$ (20), $2 = Progonomys$ sp. (47), $3 = Progonomys$ $debruinji$ (49), $4 = Mus$ $auctor$ (22), $5 = Karnimata$ sp. (22), $6 = Karnimata$ $darwini$ (45), $7 = Karnimata$ $huxleyi$ (18), $8 = Karnimata$ large sp. (11), $9 = Parapelomys$ sp. (3), $10 = Parapelomys$ $robertsi$ (11), $11 = Parapodemus$ sp. (4); for Rhizomyidae, $1 = Prokanisamys$ sp. (1), $2 = Prokanisamys$ $benjavuni$ (7), $3 = Kanisamys$ $indicus$ (16), $4 = Kanisamys$ $nagrii$ (6), $5 = Kanisamys$ $sivalensis$ (37), $6 = Protachyoryctes$ $tatroti$ (3), $7 = Eicooryctes$ $kauliensis$ (1), $8 = "Brachyrhizomys"$ $nagrii$ (1), $9 = "Brachyrhizomys"$ $tetracharax$ (1). (b) Artiodactyla: Bovidae, Suidae, Giraffidae. Estimated body weights from regressions in Janis (1990), converted to ln logarithmic scale for figures. For Bovidae and Giraffidae, Janis's regression for ruminants was used: $\log(y) = 3.337 \log(x) + 1.118$, when x = length of M_2, and $\log(y) = 3.264 \log(x) + 0.749$, when x = length of M_3. For Suidae, Janis's regression for ungulates was used: $\log(y) = 3.201 \log(x) + 1.13$, with x = length of M_2. For Bovidae, data points represent individual specimens; most teeth are not identified to species, except for $1 = Selenoportax$ $vexillarius$ (1), $2 = Selenoportax$ $lydekkeri$ (4). For Giraffidae and Suidae, each datum represents mean size of species for intervals of 0.5 m.y. Key to species: for Giraffidae, $3 = Giraffokeryx$ $punjabiensis$ (15), $4 = Bramatherium$ $megacephalum$ (2); for Suidae, $5 = Listriodon$ $pentapotamiae$ (7), $6 = Propotamochoerus$ $hysudricus$ (10), $7 = Hippopotamodon$ $sivalense$ (7). (c) Same data as in (a), plotted at same scale as in (d). (d) Same data as in (b), plotted at same scale as in (c).

5.10. Neogene Artiodactyla

Artiodactyls increased substantially in both body size and taxonomic diversity between the Eocene and the Miocene. In the Siwalik record, all three groups examined—Bovidae, Suidae, and Giraffidae—exhibited a doubling of maximum body size of species from 15 to 7 Ma (Fig. 3b,d). The earliest Siwalik bovids ranged in size from 20 to 100 kg. Bovids initially showed a marked increase in size around 9 Ma, with the first occurrence of Selenoportax vexillarius, estimated at 200 to 300 kg. This species may have evolved in situ from Helicoportax (Thomas, 1984). S. lydekkeri, a larger bovid, which appeared around 7.4 Ma, is a likely descendant of S. vexillarius; the size increase is not significant by our criterion. In Figs. 3b,d, the apparent reduction in body size between 11 and 9 Ma results from a paucity of well-preserved teeth from this interval. Examination of bovid astragali throughout the sequence indicates that the range of bovid body sizes was fairly stable between 15 and 9.5 Ma (Barry et al., 1991; Morgan, 1994). Small bovids of < 10 kg appeared at 13 Ma and persisted throughout the sequence depicted. Siwalik bovids increased in median size and size range.

Suids were present throughout the Siwalik sequence. Three well-represented species—Listriodon pentapotamiae, Propotamochoerus hysudricus, and Hippopotamodon sivalense, were included in this analysis. L. pentapotamiae, present from 16.9 to 9.6 Ma, and P. hysudricus, present from 9.3 to 5.9 Ma, ranged between 80 and 150 kg. These two species showed no major jumps in size by our criterion; size variation between age intervals is likely due in part to small sample sizes. Two other middle Miocene suids, Hyotherium pilgrimi and Conohyus sindiensis, were not included in this analysis due to a lack of well-provenienced mandibular dentitions, but overlapped in size with Listriodon and Propotamochoerus (Morgan, 1994). In addition, the rare species Tetraconodon magnus (not depicted in Fig. 3), which probably weighed nearly 1000 kg, existed between 9.2 and 8.5 Ma. Suids increased markedly in size range around 9.2 Ma with the first occurrence of Hippopotamodon sivalense, estimated at around 750 kg. (The oldest

M_3's that could be measured occurred during the interval centered on 8.5 Ma.) H. sivalense showed no marked size change over a 2-m.y. period. As noted earlier, dental measurements generally overestimate body weight for suids, because they are relatively megadont (Janis, 1990). Postcranial estimates for suid body weights were considerably smaller than these molar-based estimates (Morgan, 1994). But although dental and postcranial size estimates for suids differ, both support the overall pattern of size change. Median size increased with the introduction of Hippopotamodon sivalense at 9.2 Ma, but the size range did not change by our criterion.

Giraffids appeared in the Siwaliks at 14 Ma. The single lineage was represented by two species. The younger species, Bramatherium megacephalum, here represented only at 9 Ma (although present in the sequence until after 7 Ma), probably evolved in situ from Giraffokeryx punjabiensis between 9.5 and 9.0 Ma. The two Siwalik giraffids did not overlap in body size. G. punjabiensis, present between 14 and 9.5 Ma, weighed around 350 kg and B. megacephalum weighed around 750 kg. Neither species alone exhibited marked size change (Fig. 3b and Gingerich and Gunnell, this issue); however, the younger species was more than double the size of the older. At 750 kg, Bramatherium was only slightly smaller than the modern giraffe (Kingdon, 1982; Owen-Smith, 1988).

The pattern of size increase within the artiodactyl taxa examined here shows an increase in the maximum body size from approximately 400 kg to nearly 800 kg at around 9 Ma. The largest bovid, Selenoportax lydekkeri, present at 7.4 Ma, was similar in size to the older giraffid species, Giraffokeryx punjabiensis, last recorded in the sequence two million years earlier. The smaller suid species were generally slightly larger than the largest bovids, with the exception of Selenoportax. As with muroid rodents, no major size decrease was observed among the artiodactyl taxa. Size increase occurred within each of the three artiodactyl families examined.

5.11. Patterns of size change for Neogene mammals

Among the taxa presented, all but one family exhibited significant increase in size range or in

median size over the period examined (Table 1b). Only the cricetids (including megacricetodontines, dendromurines, and myocricetodontines) did not increase in median size or size range, but their murid descendants did. No taxa met our criterion for size decrease. It was possible to evaluate intraspecific size change for only five species; none exhibited a doubling or halving in size between adjacent intervals. For eight unbranching lineages or unbranching portions of lineages consisting of > 1 species, 2/8 or 25% showed size increase (>doubling) at the transition from one species to the next, and 6/8 or 75% showed no change by our criterion. For new species versus established congeners, we could evaluate three examples. The branching of *Karnimata* sp. into two lineages, each containing additional species of *Karnimata*, showed one instance of significant increase (*K. large* sp.) and one instance of no change (*K. darwini*) by our criterion. The third example involves the first occurrence of "*Brachyrhizomys*" *tetracharax* relative to "*B.*" *nagrii*; the size increase of "*B.*" *tetracharax* represented less than a doubling. For the 20 examples of new species relative to established confamiliars, 4/20 or 20% first occurred at greater than double the size of established confamiliars, while 16/20 or 80% were not significantly larger or smaller.

All but one of the size-increase events clustered between 9 and 8.5 Ma. The significant size expansion between 9 and 8.5 Ma occurred in body-size distributions of artiodactyls and muroid rodents–large and small herbivores, respectively. Together these two taxa were the most abundant components of Siwalik faunas, both taxonomically and numerically (Barry et al., 1990). Among artiodactyls, size increase at 9 Ma occurred with the appearances of the giraffid, *Bramatherium megacephalum*, the bovid, *Selenoportax vexillarius*, and the suid *Hippopotamodon sivalense*. Within muroid rodents, the size-increase events occurred around 8.5 Ma and included first occurrences of the murid *Karnimata* large sp. (Jacobs, pers. comm., 1993) and the rhizomyid, "*Brachyrhizomys*" *nagrii*. Other groups not included here, such as carnivores, also showed increased body size in the late Miocene (J. Barry, pers. comm., 1993). The only other size-

increase noted was at 7.0 Ma, with the first occurrence of the rhizomyid *Protachyoryctes*.

The observed changes in taxonomic composition and body-size distributions of Siwalik artiodactyls and muroid rodents between 9 and 8.5 Ma reflect altered faunal composition and structure and suggest that habitat structure had also changed. A noteworthy addition to the large-mammal herbivore guild as 10.1 Ma was the appearance of hipparionine equids. Isotopic evidence for changing vegetational composition associated with the introduction of C_4 grasses has been found in mammalian herbivore enamel at 9.4 Ma (Morgan et al., 1994), with a more pronounced shift to C_4-dominated vegetation occurring between 7 and 5 Ma (Quade et al., 1989; Quade and Cerling, this issue). The dominance of the late Miocene rodent fauna by murids and hypsodont rhizomyids was interpreted to indicate increasing aridification of environments, by analogy with the adaptations and habitats of extant rodents (Flynn and Jacobs, 1982). Siwalik herbivore trophic structure also suggests that a change in habitat structure occurred in the late Miocene (Gunnell et al., this issue). The increase in large-bodied, non-rodent herbivores relative to small-bodied, rodent herbivores between 9 and 8 Ma suggests development of more open habitats based on comparison with modern African faunas. Thus, climate change favoring open habitats can be invoked as a cause of the late Miocene size increases among Siwalik herbivores.

Competition may have played a complementary role to climate change. At the time of the size increases noted above, there were numerous herbivorous species present in the subjacent portion of the size spectrum for both muroids and artiodactyls. The prevalence of smaller species may have limited the opportunity for appearances of new species in the densely occupied portion of the size spectrum. Also, the replacement of megacricetodontine, dendromurine, and myocricetodontine rodents by murids may have involved some interspecific competition, but we do not have sufficient data to evaluate this hypothesis nor rule out alternatives at present.

Predation may have been a cause of size change among large artiodactyl herbivores, especially

bovids, as there is some evidence for increased size among Siwalik carnivores in the late Miocene. However, at present the data are too limited to evaluate this hypothesis.

6. Conclusion

6.1. Did size structure change when climate changed?

In both the Paleogene and Neogene records, mammalian size structure as depicted by cenograms (Fig. 1) changed in subtle but important ways. These changes occurred across much of the size spectrum and reflected in part the patterns of size change documented above for selected mammalian groups. In both records, the changes in cenograms appear to accompany changes in the nature of local vegetation and climate. This interpretation is consistent with the interpretation of climate as the primary cause of size change, based on the timing of change, the concurrent changes in trophic structure, and the breadth of size change among different groups and sizes of mammals.

In the Paleogene record, the major changes in size structure from the Tiffanian to the Wasatchian cenograms were a slight decrease in the frequency of small species and an increase in the number of species of medium and large size. This increase consisted mainly of immigrant artiodactyl and perissodactyl species, as well as increase in the number and size of hyopsodontids, an endemic group. Local and global evidence for paleoclimatic change indicates a general Paleogene warming trend up to the early Eocene thermal maximum, with a brief interval of intensive warming at the Paleocene-Eocene boundary. Although there are conflicting interpretations of Tiffanian (early late Paleocene) paleotemperatures, by either interpretation there is a greater difference between the Tiffanian and the succeeding Clarkforkian (latest Paleocene) than there is between the Clarkforkian and the Wasatchian (early Eocene). In Fig. 1, the cenogram for Ti-1 differs more from the cenogram for the middle Clarkforkian fauna than the latter differs from the cenogram for the early Wasatchian. This pattern of change is consistent

with the hypothesis that size structure of these Paleogene faunas tracked changes in vegetation and climate, although clearly more detailed work is needed to document this relationship.

In the Neogene record, the major changes in size structure involved a decrease in the number of small species and a slight increase in the number of medium-size species. The marked decrease in numbers of small species between 13.5 and 8.5 Ma was largely due to a decline in rodent diversity, particularly cricetid rodents. Differences between the upper Chinji and Dhok Pathan cenograms were more pronounced than changes between the lower and upper Chinji. Isotopic data from mammalian enamel (Morgan et al., 1994) and paleosol carbonates (Quade et al., 1989; Quade and Cerling, this issue) indicate fairly stable circumstances of climate and vegetation from 18 to around 9.5 Ma, the introduction of C_4 grasses at 9.4 Ma, and a major shift in the vegetation from C_3-dominated plants to C_4-dominated plants between 7 and 5 Ma. These changes imply increasing seasonality of rainfall in the late Miocene of the northwestern Indian subcontinent. The Siwalik cenograms (Fig. 1) indicate a greater change in mammalian size structure between the Upper Chinji (11.0 Ma) and the lower Dhok Pathan (8.5 Ma) than between the Lower Chinji (13.5 Ma) and Upper Chinji. The major difference between the two Chinji Formation cenograms is the lower frequency of small species (<500 g) in the Upper Chinji Formation. This lower frequency possibly reflects differences in sampling: the Lower Chinji and Dhok Pathan intervals depicted have more localities and larger sample sizes for small mammals than the Upper Chinji interval (Badgley et al., this issue). Hence, the pattern of change for these Neogene faunas supports the interpretation that size structure changed in response to climatic change; but clearly the latest Miocene portion of the Siwalik record will better address this issue.

6.2. Size change within groups

The survey of size change within species and lineages of selected mammalian groups in each record revealed relatively few size changes by our criterion of doubling or halving. In both records,

there were few instances of major jumps in size for species or lineages from one 0.5-m.y. interval to the next (Table 1). Data at finer time scales present a noisier record of size change within species, as exemplified in the evaluation of evolutionary rates by Gingerich and Gunnell (this issue). A few more instances of size change were noted in comparing newly appearing species (that arose by immigration or branching of lineages) with established species of the same genus and with established species of the same family; in these contexts, the number of size increases (>double) was slightly greater than the number of size decreases (<half). Small sample sizes may have exaggerated the actual pattern of size change for some taxa. For most species or lineages that could be evaluated for size change, body size fluctuated within fairly narrow limits over time or changed more slowly than our criterion would recognize. Changes over time in mammalian size structure, as depicted in the cenograms (Fig. 1), happened mainly by originations and extinctions rather than by major jumps in size within species or unbranching lineages.

Patterns of change in median size and size range of species within families (the local, potentially interacting members of mammalian clades) differed between the Bighorn–Crazy Mountains record as compared to the Siwalik record. In the Paleogene record, the median size of contemporaneous species within families changed significantly for three of eight families (Table 1). Two of these families, Phenacodontidae and Hyopsodontidae, had the longest stratigraphic durations of any of the Paleogene families examined in this study. By our criterion, the net change in size range of contemporaneous species increased for three families, decreased for one, and did not change for five. Two families exhibited both increase and decrease in size range. For the Phenacodontidae and Equidae, in which the size range increased but the median size did not, species of both smaller and larger size were added over time. For the Paramyidae, in which median size increased and size range decreased, single-species lineages converged in size through anagenetic change. Among the Neogene groups examined, the median size of contemporaneous species increased for three fami-

lies and did not change for two, and the giraffid lineage increased significantly in size (Table 1). By our criterion, the net change in size range increased for two families and did not change for three families. The size range of murids increased significantly following the branching of a lineage at larger size. The size range of rhizomyids increased both by addition of new species of larger size and by significant size increase within one lineage. The size range of bovids expanded by addition of larger and smaller taxa. Overall, change in size range at the family level did not fit any single pattern in either record.

6.3. Summary

The major difference between the Paleogene and Neogene faunas is the increased maximum body size of the younger faunas, as indicated by the presence of many Neogene species greater than 100 kg in body mass, compared with only one to two such species in the Paleogene faunas. But within each sequence, the range of body sizes was relatively stable over millions of years and change occurred by increase or decrease of species within certain regions of the size spectrum. The cenograms of Paleogene faunas from three time intervals suggest habitats with low seasonality of temperature and precipitation, and a shift from mesic to more humid forests from the Tiffanian to early Wasatchian. The cenograms of Neogene faunas from three time intervals suggest low seasonality of temperature and high seasonality of precipitation with decrease in annual precipitation from the Chinji levels to Dhok Pathan levels.

For selected families, several patterns of size change occurred in both sequences. In some groups, maximum body size increased while species of smaller size persisted, as seen among the Paleogene hyopsodontids and equids and the Neogene bovids and murids. Siwalik giraffids and rhizomyids, however, showed a directional increase toward larger body size. No groups exhibited net decrease in median size or size range, although episodes of size decrease occurred for some groups, including paramyids and esthonychids. Change in the size distribution of groups occurred mainly through appearances of new species of significantly

larger or smaller size or by disappearances rather than through major jumps in size within species. Our results are consistent with the distribution of evolutionary rates of size change documented by Gingerich and Gunnell (this issue) for many of the same Paleogene and Neogene taxa.

In the Paleogene record, most size change within lineages occurred in the early Wasatchian (early Eocene) via appearances of species significantly larger or smaller than established members of the same genus or family. These changes involved both increases and decreases in size and occurred in lineages of both immigrant and resident groups. Change in the size distribution of mammalian faunas accompanied climatic change independently inferred. Interspecific competition was a plausible mechanism for species replacement of phenaco-dontids by equids—herbivores of similar size—in the early Wasatchian.

In the Neogene record, the greatest increase in body size within rodents and artiodactyls occurred between 9 and 8.5 Ma. Murid and rhizomyid rodents and bovid, suid, and giraffid artiodactyls substantially increased in maximum size; also, from 9–8 Ma, bovids, suids, and murids increased markedly in frequency of specimens (Barry et al., 1991). Although these changes in size structure began almost two million years prior to pervasive habitat change associated with the dominance of tropical C_4 grasses (Quade et al., 1989; Quade and Cerling, this issue), isotopic analysis of herbivore tooth enamel indicates consumption of C_4 grasses by some members of the Siwalik fauna as early as 9.4 Ma (Morgan et al., 1994). This isotopic evidence suggests that around 9 Ma, environmental changes associated with the development of increasingly open habitats influenced faunal composition and size structure. In addition, analysis of trophic structure (Gunnell et al., this issue) and turnover among rodents (Flynn and Jacobs, 1982) suggest increased seasonality and aridity by 8.5 to 8.0 Ma.

Acknowledgments

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