Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan

John C. Barry, Michèle E. Morgan, Lawrence J. Flynn, David Pilbeam, Anna K. Behrensmeyer, S. Mahmood Raza, Imran A. Khan, Catherine Badgley, Jason Hicks, and Jay Kelley

Abstract.—The Siwalik formations of northern Pakistan consist of deposits of ancient rivers that existed throughout the early Miocene through the late Pliocene. The formations are highly fossiliferous with a diverse array of terrestrial and freshwater vertebrates, which in combination with exceptional lateral exposure and good chronostratigraphic control allows a more detailed and temporally resolved study of the sediments and faunas than is typical in terrestrial deposits. Consequently the Siwaliks provide an opportunity to document temporal differences in species richness, turnover, and ecological structure in a terrestrial setting, and to investigate how such differences are related to changes in the fluvial system, vegetation, and climate. Here we focus on the interval between 10.7 and 5.7 Ma, a time of significant local tectonic and global climatic change. It is also the interval with the best temporal calibration of Siwalik faunas and most comprehensive data on species occurrences. A methodological focus of this paper is on controlling sampling biases that confound biological and ecological signals. Such biases include uneven sampling through time, differential preservation of larger animals and more durable skeletal elements, errors in age-dating imposed by uncertainties in correlation and paleomagnetic timescale calibrations, and uneven taxonomic treatment across groups. We attempt to control for them primarily by using a relative-abundance model to estimate limits for the first and last appearances from the occurrence data. This model also incorporates uncertainties in age estimates. Because of sampling limitations inherent in the terrestrial fossil record, our 100-Kyr temporal resolution may approach the finest possible level of resolution for studies of vertebrate faunal changes over periods of millions of years.

Approximately 40,000 specimens from surface and screenwash collections made at 555 localities form the basis of our study. Sixty percent of the localities have maximum and minimum age estimates differing by 100 Kyr or less, 82% by 200 Kyr or less. The fossils represent 115 mammalian species or lineages of ten orders: Insectivora, Scandentia, Primates, Tubulidentata, Proboscidea, Pholidota, Lagomorpha, Perissodactyla, Artiodactyla, and Rodentia. Important taxa omitted from this study include Carnivora, Elephantoidea, and Rhinocerotidae. Because different collecting methods were used for large and small species, they are treated separately in analyses. Small species include insectivores, tree shrews, rodents, lagomorphs, and small primates. They generally weigh less than 5 kg.

The sediments of the study interval were deposited by coexisting fluvial systems, with the larger emergent Nagri system being displaced between 10.1 and 9.0 Ma by an interfan Dhok Pathan system. In comparison to Nagri floodplains, Dhok Pathan floodplains were less well drained, with smaller rivers having more seasonally variable flow and more frequent avulsions. Paleosol sequences indicate reorganization of topography and drainage accompanying a transition to a more seasonal climate. A few paleosols may have formed under waterlogged, grassy woodlands, but most formed under drier conditions and more closed vegetation.

The oxygen isotopic record also indicates seasonal change in the patterns of precipitation beginning at 9.2 Ma, in what may have been a shift to a drier and more seasonal climate. The carbon isotope record demonstrates that after 8.1 Ma significant amounts of C_4 grasses began to appear and that by 6.8 Ma floodplain habitats included extensive C_4 grasslands. Plant communities with predominantly C_3 plants were greatly diminished after 7.0 Ma, and those with predominantly C_4 plants, which would have been open woodlands or grassy woodlands, appeared as early as 7.4 Ma.

Inferred first and last appearances show a constant, low level of faunal turnover throughout the interval 10.7–5.7-Ma, with three short periods of elevated turnover at 10.3, 7.8, and 7.3–7.0 Ma. The three pulses account for nearly 44% of all turnover. Throughout the late Miocene, species richness declined steadily, and diversity and richness indices together with data on body size imply that community ecological structure changed abruptly just after 10 Ma, and then again at 7.8 Ma. Between 10 and 7.8 Ma the large-mammal assemblages were strongly dominated by equids, with more balanced faunas before and after. The pattern of appearance and disappearance is selective with respect to inferred habits of the animals. Species appearing after 9.0 Ma are grazers or typical of more open habitats, whereas many species that disappear can be linked to more closed vegetation. We presume exceptions to this pattern were animals of the mixed C_3/C_4 communities or the wetter parts of the floodplain that did not persist into the latest Miocene. The pace of extinction accelerates once there is C_4 vegetation on the floodplain.

The 10.3 Ma event primarily comprises disappearance of taxa that were both common and of long duration. The event does not correlate to any obvious local environmental or climatic event,

and the pattern of species disappearance and appearance suggests that biotic interactions may have been more important than environmental change.

The 7.8 Ma event is characterized solely by appearances, and that at 7.3 Ma by a combination of appearances and disappearances. These two latest Miocene events include more taxa that were shorter ranging and less common, a difference of mode that developed between approximately 9.0 and 8.5 Ma when many short-ranging and rare species began to make appearances. Both events also show a close temporal correlation to changes in floodplain deposition and vegetation. The 7.8 Ma event follows the widespread appearance of C_4 vegetation and is coincident with the shift from equid-dominated to more evenly balanced large-mammal assemblages. The 7.3 to 7.0 Ma event starts with the first occurrence of C_4-dominated floras and ends with the last occurrence of C_3-dominated vegetation. Absence of a consistent relationship between depositional facies and the composition of faunal assemblages leads us to reject fluvial system dynamics as a major cause of faunal change. The close correlation of latest Miocene species turnover and ecological change to expansion of C_4 plants on the floodplain, in association with oxygen isotopic and sedimentological evidence for increasingly drier and more seasonal climates, causes us to favor explanations based on climatic change for both latest Miocene pulses.

The Siwalik record supports neither ''coordinated stasis'' nor ''turnover pulse'' evolutionary models. The brief, irregularly spaced pulses of high turnover are characteristic of both the stasis and pulse models, but the high level of background turnover that eliminates 65–70% of the initial species shows there is no stasis in the Siwalik record. In addition, the steadily declining species richness and abrupt, uncoordinated changes in diversity do not fit either model.

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Introduction

One research goal of paleobiology is investigation of how external environmental, and especially climatic, events shape species and ecosystems over geologic timescales (e.g., Vrba 1980). Such investigations seek to relate temporal patterns in species richness, composition, and ecological structure to concurrent environmental change. Previous investigations in both marine and nonmarine settings have found that a recurrent pattern in the preserved record is alternation between brief intervals of concentrated biotic change and much longer periods with little or no change, that is, ''coordinated stasis'' (Olson 1980; Webb 1984; Brett et al. 1996). Theoretical considerations suggest such patterns should be closely linked to environmental events and evolutionary responses to them (Vrba 1985, 1995). Authors have debated, however, the relative importance of environmental versus biotic factors, the causal relationships with environmental change, and even whether the terrestrial vertebrate record does document such patterns (e.g., Alroy 1996; McKinney et al. 1996; Behrensmeyer et al. 1997; Prothero 1998, 1999). In addition, the appropriate temporal and geographic scales for such investigations are uncertain, because significant climatic/environmental changes may be localized and can occur in just thousands of years, a level of resolution that is rarely found in fossil sequences of long duration.

The Siwalik formations of northern Pakistan consist of deposits of ancient rivers that accumulated throughout the early Miocene through the late Pliocene. The preserved sediments are highly fossiliferous and have been a focus of paleontological research for over 100 years (see summaries in Barry et al. 1985; Flynn et al. 1990; Badgley and Behrensmeyer 1995b). Since 1973, collaborative research between the Geological Survey of Pakistan (GSP) and several American universities has resulted in the compilation of a large body of new information on the age, sedimentology, and vertebrate paleontology of these sediments. Consequently the Siwaliks now comprise one

of the best-known Cenozoic nonmarine records of both environmental and biotic change, and they are an ideal site for exploring the problems and implications of temporal patterns of faunal change.

Previous analyses of Miocene Siwalik faunal change found evidence for short periods of high faunal turnover between longer periods with low turnover, as well as indications of a late Miocene decline in species richness. The strongest peaks of both appearances and disappearances were in the middle Miocene, with turnover in the late Miocene being more constant than in the middle Miocene, but there was no evidence that increased extinction coincided with increased first appearances (Barry et al. 1990, 1995; Barry 1995). Related studies of species longevity, trophic structure, and body size (Flynn et al. 1995; Gunnell et al. 1995; Morgan et al. 1995) have also documented differences between the middle and late Miocene. These earlier analyses all used 500-Kyr intervals as the temporal unit of analysis.

Considerable evidence for significant late Miocene Siwalik environmental change also exists. This evidence comes from both the sediments (Retallack 1991; Willis 1993a,b; Willis and Behrensmeyer 1994, 1995; Zaleha 1997a,b) and the stable isotopic content of paleosols and fossils (Quade et al. 1989, 1992; Morgan et al. 1994; Stern et al. 1994; Quade and Cerling 1995). Quade and others (1989, 1992, 1995) first reported changes in stable carbon and oxygen isotope ratios in both $\delta^{13}C$ and $\delta^{18}O$ values in the late Miocene, which they interpreted as resulting from long-term changes in climate and vegetation that led to drier, more seasonal climate and extensive grasslands. Both mammalian and avian isotopic values also show a transition from C_3-dominated diets to mixed and C_4-dominated diets (Morgan et al. 1994; Stern et al. 1994), but the dietary evidence implies an earlier change than that of the soil carbonates.

In the following, we summarize our work on faunal and environmental change in the Middle Siwaliks of northern Pakistan. In doing this we extend our earlier inquiries by including more species level taxa and improving the time resolution fivefold, while trying to present as much primary data as practicable. In contrast to our previous analyses using 500-Kyr intervals (Barry et al. 1990, 1991, 1995), in this paper we use a temporal resolution of 100 Kyr. The use of intervals of shorter duration is a compromise between analytic resolution and having adequate data in each unit. It may also be a lower limit imposed by the rock record. In addition, we restrict our analysis to the interval between 10.7 and 5.7 Ma (inclusive). This 5-Myr-long period approximates the late Miocene, a time of very significant global climatic change as well as more regional and local tectonic and habitat modifications. It is also the interval for which we currently have the best temporal calibration of Siwalik faunas and most comprehensive data on species occurrences. Equids first appear in the Siwaliks at 10.7 Ma as immigrants from North America, so this important faunal event marks an appropriate starting point. We occasionally include ''pre-hipparion'' intervals in our discussions to place trends into a larger context.

Our primary focus is on documenting patterns of faunal turnover and ecological change, and investigating the relationships between observed faunal patterns and changes in the fluvial system, climate, and local habitats. Methodological issues of dating and analysis are also significant concerns. We therefore attempt to incorporate uncertainties in the correlation and ages of localities in our analyses, and seek to control for the diverse sampling biases confounding the biological and ecological signals. We begin with discussion of the occurrence of the fossils and correlation of the fossil localities to the Geomagnetic Polarity Time Scale, and then assess the suitability and limitations of the vertebrate record for our analyses. We next describe the Siwalik fluvial system and the changes it underwent during the late Miocene, as well as the paleosol and stable isotope evidence for late Miocene environmental change. Finally, we analyze the faunal data and discuss the relationships between patterns of observed faunal change and indicators of environmental change. In doing this, we assume that if ecological and evolutionary change primarily results from environmental and especially climate change, then turnover events should temporally correlate to
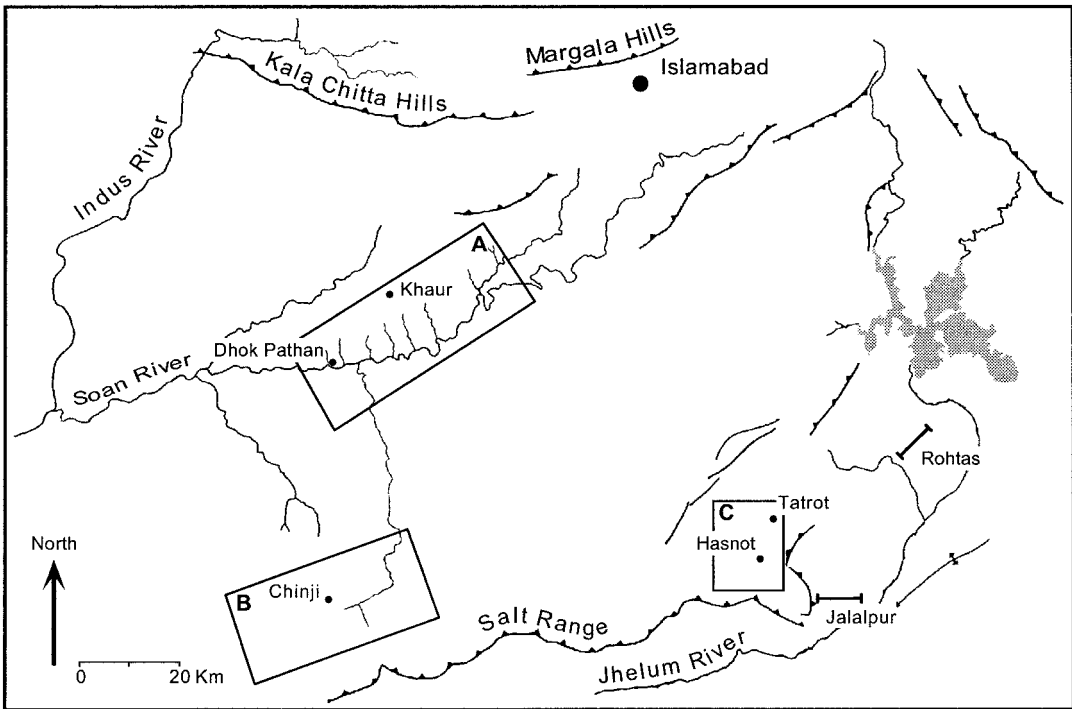
FIGURE 1.   Map of the Potwar Plateau in northern Pakistan, showing the locations of regional networks of strati-graphic sections along the Soan River (A), on the southern limb of the Soan Synclinorium near Chinji (B), and at the eastern end of the Potwar Plateau near Hasnot (C). The location of sections at Jalalpur and Rohtas are also shown. Barbed lines denote the boundaries of thrust sheets. Gray stippled area to east is a reservoir. Figure based in part on Burbank and Beck 1991: Figure 2b.

environmental events (Vrba 1985, 1995). Given a sufficiently well sampled, temporally resolved, unbiased record, we would expect turnover and other faunal events to (1) be concentrated in brief intervals separated by longer periods with little or no change and (2) show a close temporal correlation to environmental changes. Such correlations can be used to infer causal links between faunal and environmental change.

Stratigraphic and Fossil Data

Occurrence of the Fossils

The Siwalik formations comprise Neogene age fluvial deposits exposed widely throughout the Indian subcontinent along the northern and western mountains paralleling the collision zone between India and Asia. In Pakistan, Siwalik sediments are especially extensive on the Potwar Plateau, where they are exposed in a folded belt extending from the Salt Range in the south to the Margala Hills in the north, and from the Jhelum River in the east

to the Indus on the west (Fig. 1). The deposits fill basins with sediment eroded off adjacent uplifted areas, and in some places single sections exceed 3000 m in thickness and incorporate 10 Myr of time. Taken together, the sediments span the time interval from about 18 Ma to younger than 2 Ma. The sediments are well exposed throughout the Plateau along major streams and rivers, where the Pleistocene Potwar Loess has been removed by recent erosion. The combination of minimal deformation and faulting, great thickness, and lateral continuity of exposure allows a more detailed and temporally resolved study of the stratigraphic succession of lithologies and faunas than is usual in terrestrial deposits.

Siwalik lithologies include sandstones, siltstones, mudstones, and rare marls and clays. The Potwar sequence is frequently divided into six or more formations (Table 1) (Cheema et al. 1977). Primary importance in most classification schemes is given to the relative proportions of sandstones and fine-grained sed-

TABLE 1. Siwalik formations of the Potwar Plateau.

Formation	Age range (Ma)
Tatrot	3.5 to 3.3
Samwal	ca. 3.6 to ca. 1.5
Dhok Pathan	10.1 to ca. 3.5
Nagri	11.2 to 9.0
Chinji	14.2 to 11.2
Kamlial/Murree*	18.3 to 14.2
Murree	? to 18.3

* In the southern Potwar, the Kamlial and Murree Formations are not differentiated. In the north, the Murree is considerably older than 18 Ma.

iments, so that Siwalik formations are distinguished on the basis of the size and frequency of large sandstone bodies and the relative proportions of silt and mudstones. Correlations between outcrop exposures and sections throughout the Potwar Plateau and elsewhere are based on both magnetostratigraphy and the lateral tracing of distinctive isochronous lithological horizons (Behrensmeyer and Tauxe 1982; Johnson et al. 1988; Badgley and Tauxe 1990; McRae 1990; Kappelman et al. 1991; S. M. Raza unpublished data; K. A. Sheikh unpublished data). In Table 1 the overlap in ages between formations represents the approximate degree of known time transgression. All the formations are likely to be time transgressive to some degree, even if not shown.

Siwalik depositional environments include small to very large channels, levees, paleosols, and rare pond or swamp deposits. These depositional environments are present in all the Siwalik formations but differ in their frequency of occurrence. Vertebrate fossils are found in all lithologies, but are very rare in the thin marls deposited in shallow ponds. The fossils are thought to have accumulated as attritional assemblages derived from nearby surroundings, but habitat specific associations of fossils seem not to have been preserved (Badgley and Behrensmeyer 1980, 1995; Badgley et al. 1995). Fossil vertebrates are most common in the small floodplain channels, where they typically occur as concentrations of disarticulated, often fragmentary bones. In the small floodplain channels, a very few concentrations contain 1000 or more specimens, but the majority of concentrations have only 5–200 fossils. Because the large channel, levee, and paleosol facies contain only isolated specimens or small,

low-density scatters, our collections of fossils from the different facies are biased toward overrepresentation of small channel floodplain sites. This bias, in addition to those introduced by taphonomic processes common to the different facies, places strict limits on our ability to reconstruct the living communities from the fossil assemblages (Badgley 1986a,b), and draw meaningful conclusions from the occurrences of individual taxa. Some of these limitations are considered in subsequent sections, where we discuss uncertainties in our analyses. Specific concerns include uneven sampling through time, differential preservation of larger-bodied animals and durable parts such as teeth, errors in age-dating imposed by uncertainties in correlation and paleomagnetic timescale calibrations, and uneven taxonomic treatment across groups.

We use two terms to designate the provenience of our fossils; locality and survey block. A locality, as we use the term here, is limited temporally and spatially. Most localities encompass a few tens to several hundred square meters of outcrop and have a single sedimentary layer as the source of the fossil bone. The duration of accumulation of the fossil material in a given locality is thought to be brief, and generally between a few tens to, rarely, at most 50 Kyr (Behrensmeyer 1982; Badgley 1986b; Badgley et al. 1995; Behrensmeyer et al. 1995).

A survey block or collecting level is an alternative to designating and documenting individual localities for the many isolated fossils of biostratigraphic interest, such as single equid or bovid molars. Survey blocks differ from localities in that they are more extensive in area, span a greater stratigraphic thickness, and usually include fossils from multiple sedimentary layers. Survey blocks included in this paper span between 30 and 350 Kyr and extend laterally 1 to 2 km. Many of these survey blocks have been systematically searched, with all identifiable surface fossils recorded; others represent less-coordinated collecting of well-preserved material. Fossils collected from both survey blocks and localities are used in the analyses of this paper.

The Siwalik fossil collections have been made using a variety of techniques. Most of the larger specimens, and some of the smaller,

TABLE 2.   Biostratigraphic survey results.

Survey block	Age (Ma)	Duration (Myr)	Collecting effort (hours)	Scrap found	ID Fossils found	ID Mammals found	Equids	Bovids	Giraffes	Rhinos	Probosc.
KL07	7.289	0.324	10.3	100	42	32	1	4	0	2	1
KL09 + 10	7.561	0.292	7.8	94	28	24	2	4	0	1	3
KL08	7.719	0.125	13.3	181	95	63	5	14	0	3	3
KL11 + 21	7.949	0.344	18.3	—	164	148	22	24	6	12	0
KL12	8.485	0.149	10.4	210	139	98	10	15	4	6	14
ML04 + 05	8.658	0.123	10.6	206	148	107	8	7	0	0	14
KL16	8.733	0.137	10.5	154	104	78	15	4	4	8	8
ML06	8.787	0.246	8.3	76	46	39	8	5	0	0	4
KL02 + 14	8.840	0.126	10.7	179	123	81	14	8	3	5	15
DK01 + ML07 + KL13	9.001	0.155	15.1	176	108	80	14	6	4	5	9
KL01	9.184	0.043	9.5	180	130	102	24	4	3	4	12
KL03	9.270	0.062	13.8	125	100	78	15	4	6	7	2
KL05 + 06	9.543	0.126	12.8	169	140	108	14	5	3	8	13
KL04	9.703	0.109	12.7	154	147	129	17	14	4	11	2
KL20	9.784	0.139	11.3	—	42	39	7	2	3	1	0
RK01	10.307	0.114	9.5	148	80	66	5	6	3	6	5
RK02	10.385	0.124	6.5	48	37	29	0	6	5	1	1

were collected from the surface of naturally eroded outcrops. Quarrying is mostly unproductive, because even in the richest concentrations the density of fossils in the rock is low. Only four sites in the 5-Myr interval have been excavated to any extent (localities Y182, Y260, Y270, and Y311). On the other hand, screenwashing bulk samples has been successful in providing remains of very small species, such as rodents and insectivores. Over 60 sites have been screenwashed to date, and most of these localities also have remains of large species. We have also made controlled biostratigraphic surveys to document the relative number of fossils and the relative abundance of taxa at different levels (Table 2). These biostratigraphic surveys involved carefully searching and recording all occurrences of fossil bone along extensive, strike-parallel belts of outcrop within the well-defined stratigraphic intervals that comprise the survey blocks. During each survey we kept a record of the number of hours spent searching, and all finds were identified as closely as possible and tabulated, although most fossils were not collected. We believe the resulting data give less biased estimates of the abundance of fossils and the relative proportions of taxa than other collecting procedures.

Harvard-GSP localities and survey blocks are assigned unique letter prefixes and num-

bers, and their geographical positions are marked on topographic maps or overlays of aerial photographs. We also have a locality card file that includes a brief lithological description of each locality, sketch maps and cross-sections, Polaroid ground photographs, and other information (Behrensmeyer and Raza 1984). Collected fossils are cataloged with a field number, coded description of the specimen, taxonomic identification, notation of the locality or survey block, and a score for predepositional damage (Barry 1984). A very small number of fossils collected by Barnum Brown and G. Edward Lewis and now in the American Museum of Natural History and the Yale Peabody Museum are well enough documented as to provenience and stratigraphic horizon to include in our fossil and locality databases. Unfortunately the extensive collections made during the colonial era by the Geological Survey of India and its predecessors cannot be included, because the geographic and stratigraphic data are inadequate. This means that type specimens and other Siwalik fossils described by Falconer, Lydekker, and Pilgrim cannot be incorporated in our biostratigraphic analyses.

Both the GSP-Harvard Siwalik specimen and locality catalogs are configured as dBase files. In addition we have a species file, which contains information on each fossil species,

and related auxiliary files. The entire specimen database presently includes over 40,000 records of vertebrate and nonvertebrate fossils from 1291 localities and survey blocks, 86% of which are well-documented localities found since 1973. As noted, our project database also includes a few selected records for fossils in the American Museum of Natural History and Yale Peabody Museum collections that can be confidently placed in our stratigraphic framework. The data presented in this paper are derived from these databases.

Chronostratigraphic Framework

The drainage patterns of the Potwar Plateau are characterized by a latticelike arrangement of intermittent streams and smaller river tributaries (''kas'' or ''nala'' in local vernaculars), which have incised shallow ravines in the gently dipping Miocene-age strata. The major streams run perpendicular to strike, are typically spaced every 3–5 km, and are connected along strike by lateral valleys.

The chronostratigraphic framework of this paper is based on 20 measured sections that range between 250 and 3200 m thick, as well as 27 shorter sections. Of the 47 sections, 19 of the 20 long sections have determined magnetic-polarity stratigraphies, and 16 of the shorter have at least some magnetic determinations. Apart from the two sections at Rohtas and Jalalpur (Opdyke et al. 1979; Johnson et al. 1982), the included sections form three regional networks (Fig. 1): one on the northern limb of the Soan Synclinorium at Khaur, another on the southern limb near Chinji, and a third at the eastern end of the Potwar Plateau near Hasnot. Because exposures are continuous within each region, we are able to correlate sections in each regional network by means of lithological horizons, as well as by magnetic polarity. However, because of the distance and absence of continuous linking exposures between regions, chronostratigraphic correlations between the three areas depend on the magnetic-polarity stratigraphy. No sections were correlated on the basis of biostratigraphy.

In the Siwaliks individual stratigraphic sections of sufficient thickness to contain six or seven magnetic transitions (on the Potwar typically about 250 m) can usually be correlated to the Geomagnetic Polarity Time Scale (GPTS) (Johnson and McGee 1983). Although sections recording fewer transitions normally cannot be independently correlated to the GPTS, they can still be confidently placed in the chronostratigraphic framework by determining their stratigraphic relationships to the longer and better-constrained sections. This has been done by laterally tracing isochronous lithological horizons, such as sandstone bodies or paleosols (Behrensmeyer and Tauxe 1982; Johnson et al. 1988; Badgley and Tauxe 1990; McRae 1990; Kappelman et al. 1991; K. A. Sheikh unpublished data). In making correlations to the GPTS, it is not always possible to match every observed magnetic transition to a GPTS magnetic boundary, either because of sampling problems (Johnson and McGee 1983) or because of the presence of very short magnetic intervals not documented in the GPTS (Kappelman et al. 1991).

Appendix 1 lists the thicknesses and references for the sections used to construct the chronostratigraphic framework for the Potwar Siwaliks. In most cases we use the same polarity zonation and correlation to the GPTS as the references, or have made only trivial changes. In a few cases subsequent work has led us to make substantial reinterpretations of the polarity zonations or the correlations, and we comment on these in the remainder of this section. We also present results of new work done in the Hasnot area and provide more details for already published sections in the Khaur region.

Jarmaghal Kas.—Johnson et al. (1982) made no specific correlations for the middle third of this section. New details in the GPTS of Cande and Kent (1995) dictate different preferred correlations for the intervals between the base of 3An and the top of 4An. We now correlate the N^5 interval of Johnson et al. (1982) to 3An.1n, the N^4 interval to 3An.2n, N^3 to 3Bn, N^2 to 3Br.2n through 4N.2n, and N^1 to 4An.

Andar Kas.—Johnson et al. (1982) again made few specific correlations for this section, but we have correlated more of the observed transitions to the GPTS. Specifically we correlate the N^7 interval of Johnson et al. (1982) to 3An.1n, N^6 to 3An.2n, the top of N^4 to the

3Br.3r/4n.1n transition and its bottom to 4n.2n/4r.1r, the top of N_0 to the top of 5n.1n and the bottom to the base of 5n.2n, N_1 to 5r.2n, and the top of N_2 to 5r.3r/5An.1n and its bottom to the base of 5An.2n. We make no correlations between the top of zone R^4 and the base of R^1, nor below the base of N_2.

Dhok Saira.—This recently measured section parallels the upper part of the Dhala Nala section of Johnson et al. (1982). At its base the section is continuous with the lower Dhala Nala section, and its uppermost 20 m can be correlated by means of the Pillar Sand to the ''Tatrot'' and ''Pillar'' I–VI sections of McMurtry (1980). The stratigraphic and magnetic polarity data, together with our preferred correlation to the GPTS, are shown in Figure 2. The base of the uppermost N4 polarity zone is at the same stratigraphic level as a polarity transition in all of McMurtry's (1980) Pillar sections, and we follow his correlation of the transition to the 3An.2n/3Ar transition. The long reversed interval between 132 and 53 m is supported by only a few reversed sites, most of which are in the upper portion (R3). The lower part (R2) is in a single, thick sand in which our sampling efforts failed because the magnetics were unfavorable. If our correlation is correct, future sampling at this horizon should show normal polarity representing 4n.1n. A single low-quality site 92 m above the base suggests the presence of a short normal zone (N2). It could be the 3Br.2n zone. The upper Dhala Nala section of Johnson et al. (1982) also had a normal zone at this horizon. We have correlated the base of N1, which is sparsely sampled, to the base of 4r.1n, rather than the base of 4n.2n, because this correlation preserves the proportionality of the thickness of the zones.

Lower Dhala Nala.—Johnson et al. (1982) did not discuss this section in detail, but they did present lithologic and magnetic logs in their Figure 11. They correlated the section by means of marker beds to Kotal Kund, but they made no specific correlations to the GPTS other than to note it was very similar to their Kotal Kund section. Subsequently the section was extended downward an additional 329 m, and polarity determinations made for the upper 150 m (unpublished data from the late Noye Johnson personal communication 1981). Although the virtual geomagnetic pole latitudes and data quality are not available to us, we present the stratigraphic and polarity data in Figure 3. Our preferred correlation to the GPTS is the same as that of Johnson et al. (1982). In drafting Figure 3 we have assumed that the lowest normal sample at the base of the measured section is near the base of the 5n.2n interval. However, because that correlation is not confirmed by an underlying reversed site, we do not use it to determine the ages of any fossil sites in the section. The sparse sampling in the upper quarter of the N1 interval makes correlation of the N1/R1 transition particularly difficult. It is likely one or more reversed zones were missed in the interval between 300 and 400 m. The correlation of N4 is from the Dhok Saira section discussed above. New magnetic samples have recently been collected from the upper 200 m and from an additional 100 m below the base of this critical section, but the results are not yet available.

Dhok Pathan Rest House.—Polarities for this section were shown in Barry et al. (1980), but no details or correlations were given. The magnetic polarity and stratigraphic data are shown in Figure 4 (unpublished data from the late Noye Johnson personal communication 1980), together with a preferred correlation to the GPTS. Unfortunately, the position of the Soan River and structural complexities make it difficult to measure the complete section accurately. We think that the gap shown in Figure 4 below the 300-m level may be underestimated. The section includes the ''U'' Sandstone interval (Behrensmeyer and Tauxe 1982), which allows the base of the section to be placed in magnetozone 4Ar.1r. Nearby sections (Barry et al. 1980) indicate that the R1 interval should contain a substantial normal interval correlating to 4An. The N3 magnetozone is unbounded at its top, but rather than extrapolating locality ages from rates of the subjacent zones, we have used sediment accumulation rates from the same interval in the Kaulial Kas section. We do this because the two subjacent Dhok Pathan magnetozones are very short and their inconsistent rates give unrealistic estimates.
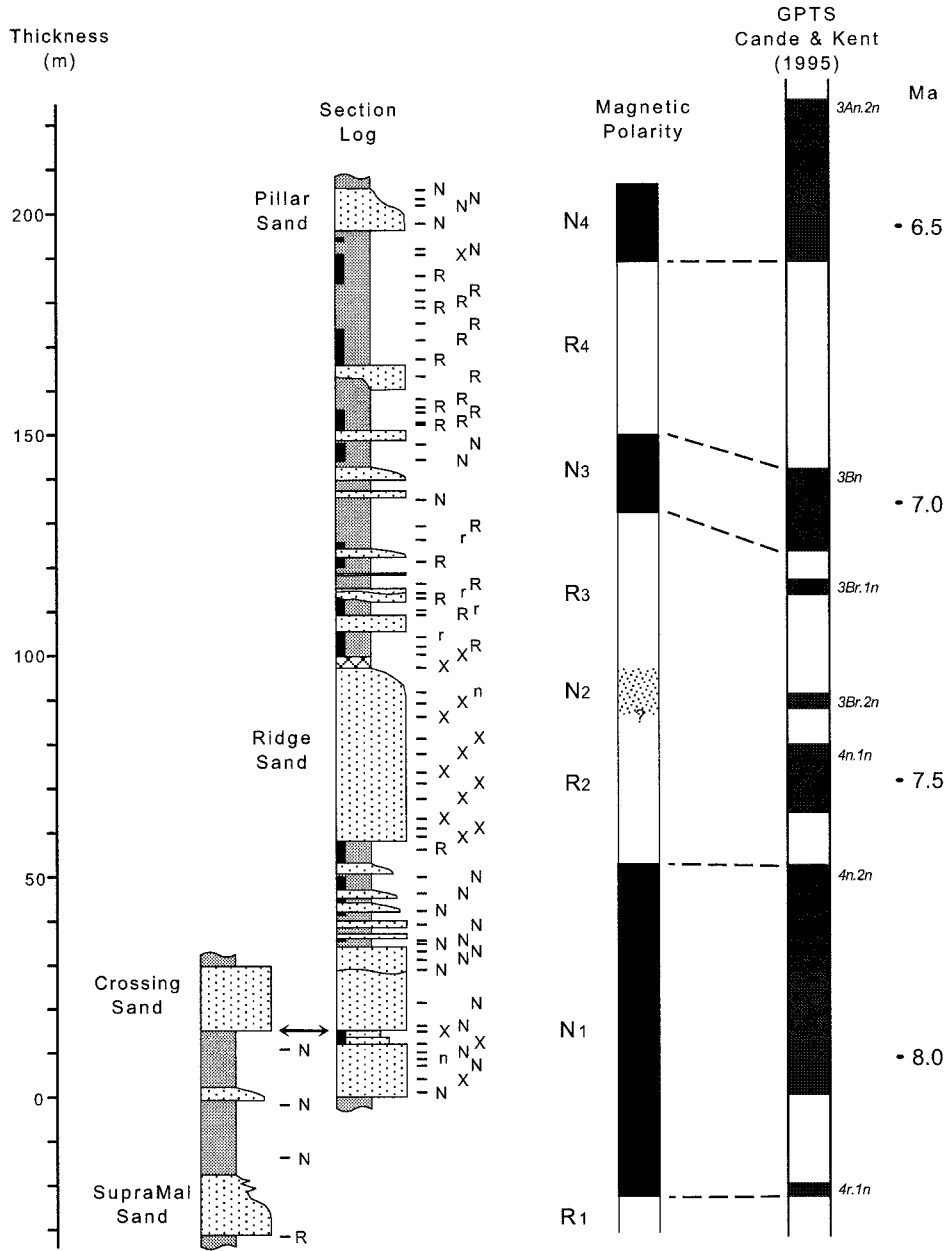
FIGURE 2. Dhok Saira lithologic log, magnetic polarity zonation, and correlation to geomagnetic polarity timescale of Cande and Kent (1995), with upper 70 m of Lower Dhala Nala section. Black shaded areas indicate paleosols; light-gray areas, fine-grained overbank; stippled areas, sandstone; cross-hatched areas, covered intervals; double-headed arrows, sandstones used to correlate lithologic sections; and dotted lines, correlations to geomagnetic polarity timescale. R, r = reversed site, N, n = normal site, X = indeterminate site. Uppercase letters indicate sites with samples having consistent polarity; lowercase letters indicate sites with questionable polarity.

The Dhok Pathan Rest House section is particularly important because much of the Dhok Pathan fauna of Pilgrim, Brown, and Lewis apparently came from the vicinity of the Dhok Pathan Rest House. The most fossiliferous beds are above the Hilltop Sand in the N2, R3, and N3 magnetozones. It is from these levels that the older collections presumably came.

Hasal Kas.—Tauxe and Opdyke (1982) thermally demagnetized and reanalyzed the sam-

FIGURE 3.   Lower Dhala Nala lithologic log, magnetic polarity zonation, and correlation to geomagnetic polarity timescale of Cande and Kent (1995), with lower 70 m of Dhok Saira section. Symbols as in Figure 2.

ples of Barndt et al. (1978), and then related them to a remeasured lithological section. We follow Tauxe and Opdyke's (1982) polarity assignments and correlations to the GPTS, but we make four additional assignments by correlating their R[11] polarity zone to 4Ar.2r and the R[10] polarity zone to 4Ar.3r. Nevertheless

the polarity zonation of the upper third is not well defined, and many of the correlations of polarity reversals are based on lithological correlations to the nearby Mahluwala Kas and Ratha Kas sections.

Kaulial Kas.—Tauxe and Opdyke (1982) discussed this section, and we follow their cor-

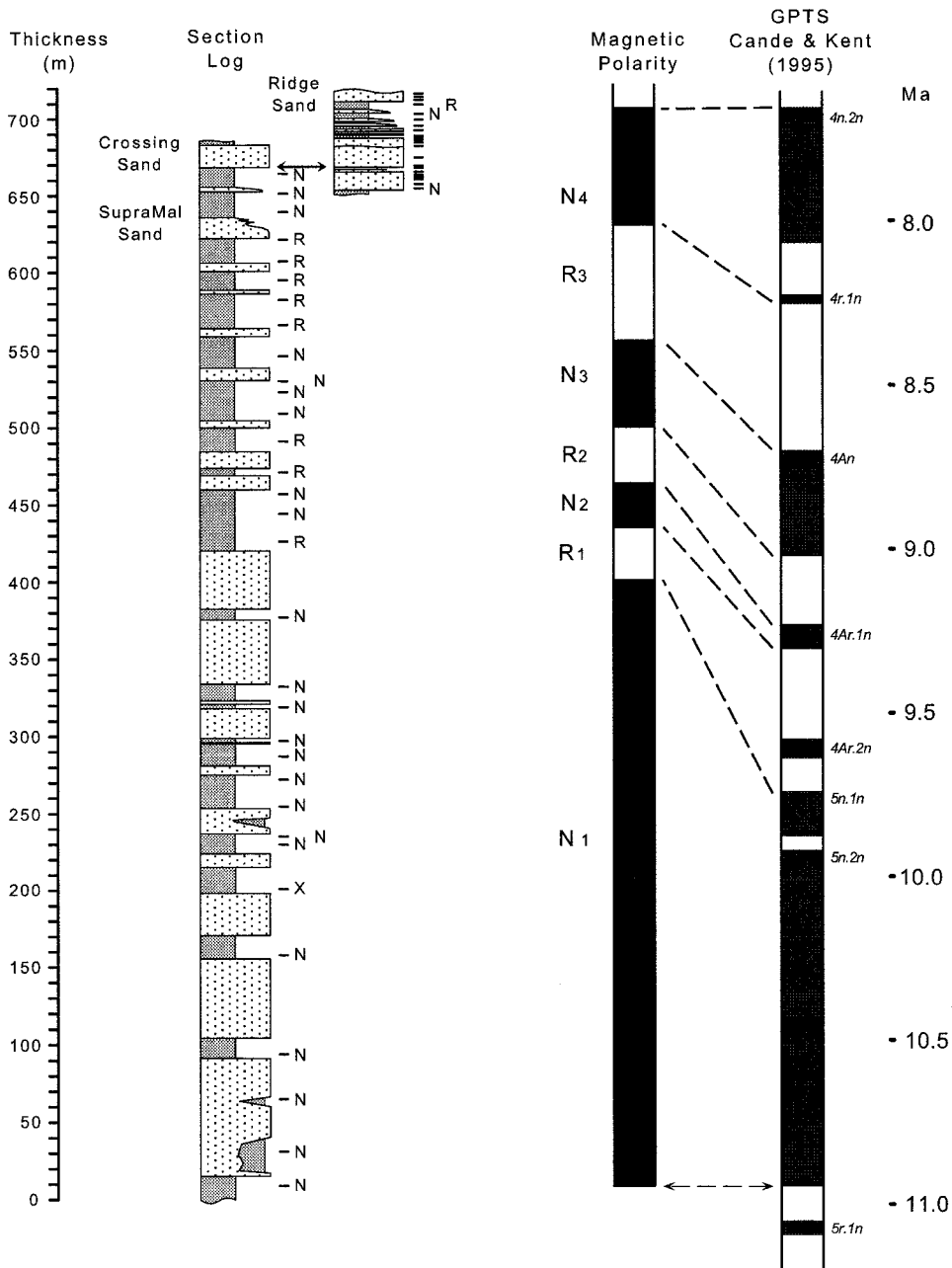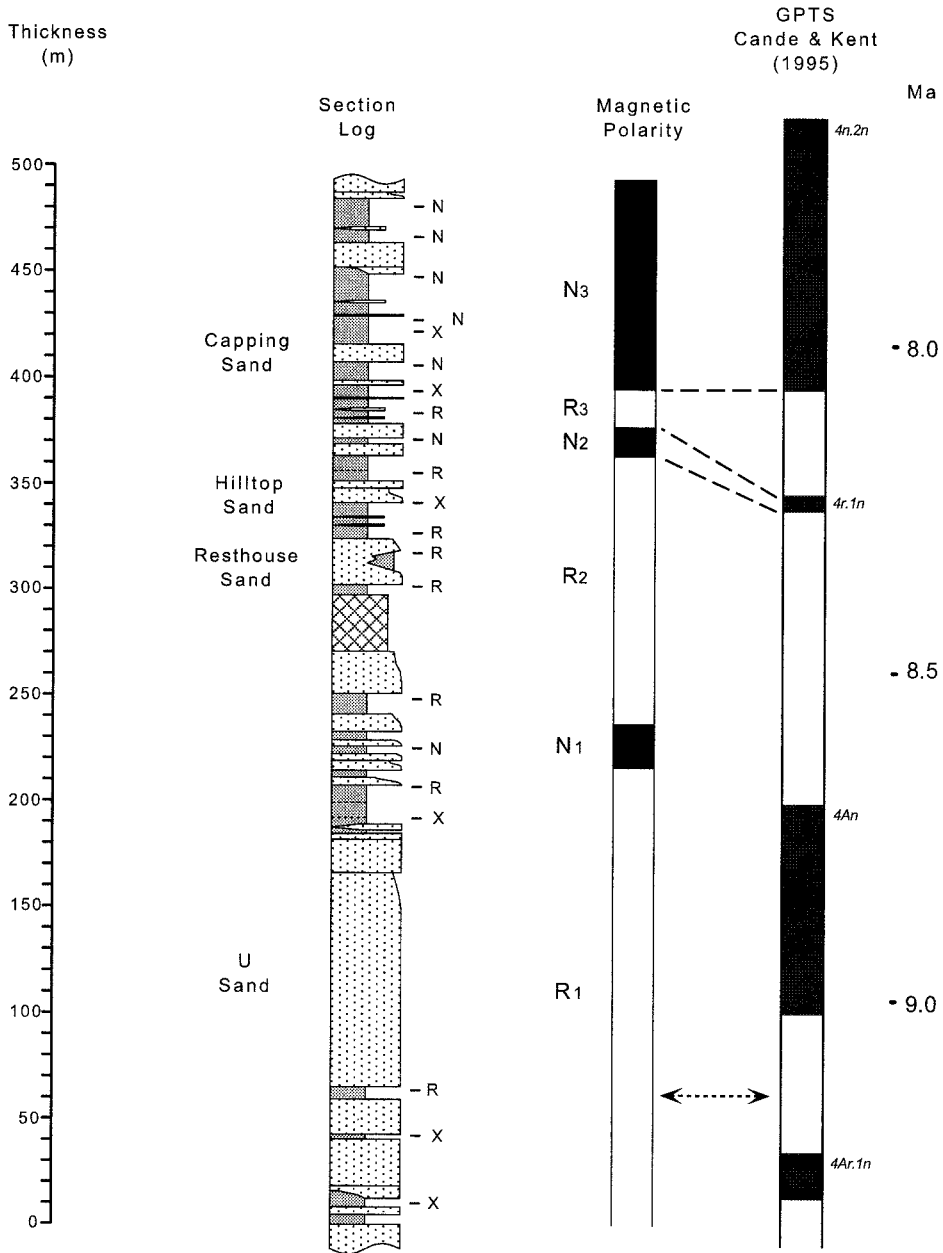FIGURE 4. Dhok Pathan Rest House lithologic log, magnetic polarity zonation, and correlation to geomagnetic polarity timescale of Cande and Kent (1995). Symbols as in Figure 2. The double-headed dotted arrow marks the correlation of the U-level to the GPTS as established by Behrensmeyer and Tauxe (1982).

relations with two minor differences. First, we correlate the uppermost N^7 zone to 3Br.1n, rather than 3Bn. This results from recognition of two new small polarity zones in the GPTS. Zone 3Br.2n is then missing, with zone N^6 correlated to 4N.1n, in agreement with Tauxe and Opdyke (1982). It follows then that zone N^5 is

a new normal zone in 4n.1r, not recorded in the standard GPTS. We note that it is based on a single sample of normal polarity and that it is the correlation implied by Tauxe and Opdyke (1982). Second, we treat the N^3 zone as a new normal interval, not as 4r.1n as implied by Tauxe and Opdyke (1982). It is noteworthy

that N^3 is based on a single sample having a VGP latitude near zero (Tauxe and Opdyke 1982: Fig. 4i). Zone 4r.1n is unrecorded in the Kaulial Kas section.

In the Chinji region there are many additional long and short sections, including those of Kappelman et al. (1991). The focus of this study, however, is limited to the interval between 10.7 and 5.7 Ma. We have therefore included only two sections (Gabhir and Chitaparwala) that extend down into the early and middle Miocene to provide a baseline for our study.

Ages of Localities and Assignment to Intervals

Most localities are in exposures near the streams along which we have measured local stratigraphic sections and are typically less than 1 km off the line of a section. To establish stratigraphic relationships for individual localities, we have then traced lithological markers back into the nearest section. These horizons are usually paleosols or small sandstone bodies, types of lithologies that have been demonstrated to be isochronous over the distances involved (Behrensmeyer and Tauxe 1982). Any such correlation has a degree of uncertainty. To preserve this uncertainty, we have recorded the stratigraphic positions of localities as being bracketed by uppermost and lowermost bounds in the sections. We are confident that localities are not above or below these bounds, but we assume that the locality could be at any level within the bracketed interval with equal likelihood.

To order faunal events in time, we had to assign each locality an absolute age, which can be interpolated from its stratigraphic position relative to known marker horizons or time lines. Ages can be estimated to varying degrees of accuracy. Estimates for the ages of 555 localities and survey blocks that lie between 10.7 and 5.7 Ma are presented in Appendix 2. The algorithm used to determine these ages is based on interpolation between two points of known age. In this paper all points of known age are magnetic polarity transitions, but in principle, radiometric dates and biostratigraphic or isotopic events of known age could

also be used. The formula for finding an age is

$$\text{Age} = \text{UAge} + ((\text{LAge} - \text{UAge})/T)\text{SD},$$

where UAge and LAge are, respectively, the ages of the top and bottom of the geomagnetic zone, T is the stratigraphic thickness of the magnetozone in the local section, and SD is the stratigraphic distance between the locality and top of the magnetozone. In this formulation the quantity $(\text{LAge} - \text{UAge})/T$ is the average rate of sediment accumulation in the section during the geomagnetic interval. Some localities lie in truncated topmost or bottommost magnetozones, and interpolation cannot be used to estimate their ages. In these cases ages are extrapolated, using the rate of sediment accumulation of the sub- or superjacent magnetic interval and the stratigraphic distance between the locality and the under- or overlying magnetic transition.

Input data used in the calculations include (1) the stratigraphic position of the locality in a local lithological section, (2) the stratigraphic positions of the magnetic transitions in the same section, and (3) the ages of the magnetic transitions, as derived from correlation of the section to the Geomagnetic Polarity Time Scale. From these input data, the quantities used in the above formula can be calculated. We have two further refinements in our current implementation. The first is to derive separate age estimates for the possible upper and lower limits of the stratigraphic positions for localities traced into sections. This allows our estimate to incorporate the uncertainty in the correlation of the locality to a stratigraphic section. When the stratigraphic position is precisely determined, these age estimates will be the same. The second refinement involves using the highest and lowest possible positions of the magnetic transitions in the lithological sections. Magnetic transitions are bracketed by sites of different polarity, and by convention the transition is placed at the midpoint between those sites. Noting the actual site horizons incorporates uncertainties in the stratigraphic positions of the magnetic transitions by generating two age estimates, one for the highest position and one for the lowest. When the magnetic transitions are strati-
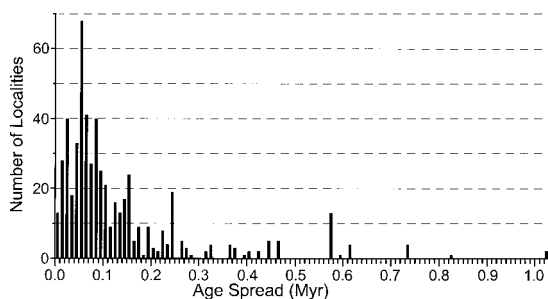
FIGURE 5. Differences between estimated maximum and minimum ages of 555 localities between 5.7 and 10.7 Ma (inclusive).

graphically constrained, these age estimates will converge. Taken together, these two refinements produce conservative estimates for a pair of maximum and minimum ages for each locality (i.e., the largest reasonable range of possible ages).

Five hundred fifty-five localities in our database are between 10.7 and 5.7 Ma and have both a minimum and a maximum age estimate (Appendix 2). The difference between the maximum and minimum estimates varies considerably among localities, with the largest being 1.025 Myr (Fig. 5). However, the ages of most localities are better delimited, as shown by the frequency distribution of the differences in Figure 5. Nearly 60% (*n* = 332) of the 555 dated localities have a temporal resolution equal to 100 Kyr or less, whereas 82% (*n* = 457) have a resolution of 200 Kyr or less.

For the purposes of our analyses, it is necessary to assign each locality to a single 100-Kyr interval and to identify localities too poorly dated to be assigned. If interval boundaries are drawn at ±0.05 (e.g., the 7.5-Ma interval has boundaries at 7.45 and 7.55 Ma), then 149 (27%) of the 555 localities included in Appendix 2 have both maximum and minimum age estimates in the same 100-Kyr interval. These localities can unambiguously be assigned to that interval. However, 183 (33%) of the localities straddle two intervals, even though the difference between their maximum and minimum ages is less than 100 Kyr duration. These localities cannot be so unambiguously assigned. In addition, a third group of 125 (23%) localities have differences that are greater than 100 Kyr and less than 200 Kyr, but they straddle two or three intervals. These

latter two classes of localities do, however, overlap one interval by at least 50% of their total duration. If the percent overlap with any interval is assumed equivalent to the probability that the true age lies within the interval, then these two groups of localities can be assigned to the interval with the greatest overlap. This will be the same interval containing the midpoint between the two age estimates. If a locality does not overlap with any interval by 50%, then it is left unassigned and excluded from our analyses. This is the case for the 98 (18%) localities with age spans greater than 200 Kyr.

The boundaries between intervals are arbitrary and it is possible that this arbitrary division might affect the patterns we wish to describe. The foregoing discussion used intervals centered at multiples of 0.1, with boundaries at ±0.05. To test the robustness of some our conclusions, we have redone some of our analyses using 100-Kyr intervals with boundaries at the multiples of 0.1 and centered at 0.05. (For instance, the 7.5-Ma interval has boundaries at 7.4 and 7.5 Ma, and is centered at 7.45 Ma.) These alternative analyses did not show significant differences.

Data Quality in the Siwalik Fossil Record

Comparisons of species richness and especially turnover depend on assumptions about the ages of the fossils and the preservational biases of the assemblages. If the patterns of species richness and faunal turnover are to be interpreted usefully, it is necessary first to consider the reliability and resolution of the dates, as well as the reliability of the fossil occurrence data.

Reliability of Age Estimates for Fossil Sites

The algorithm used to determine the ages of Siwalik localities makes several assumptions that affect the potential for errors in our estimates and the reliability of the ages. The most basic assumption is that the rate of sediment accumulation remains constant within each magnetic interval. Because sedimentation in fluvial systems is stochastically episodic, with many short hiatuses that collectively may represent more time than the accumulated sediment (Sadler 1981), the assumption is known

to be violated (Johnson et al. 1988). However, if no contained hiatus is large relative to an interval's duration and if the stratigraphic distribution of the many small contained hiatuses is random, then interpolation of ages can still be done (Badgley et al. 1986). This assumption of approximate sedimentological uniformity is consistent with correlations between our individual sections, which typically show the same magnetic intervals having the same relative stratigraphic thickness in separate sections.

Second, we assume that the probability of a locality lying somewhere between its upper and lower stratigraphic limits has a uniform distribution, with zero probability above and below the marked range. This is a conservative assumption, because it produces a wider spread between the maximum and minimum age estimates than if we assumed some other probability distribution, such as a normal distribution around the center of the interval.

A third assumption is that the age estimates of the magnetic transitions of the Geomagnetic Polarity Time Scale are correct. These ages are derived from interpolations between dated tie points in the marine record, and they assume constancy in oceanic ridge spreading rates. The age interpolations are vulnerable to errors in the ages of tie points, which in several cases are rather poorly constrained, and to error in identifying inflection points in the spreading-rate curves (Cande and Kent 1992, 1995). (See Pilbeam et al. 1996 for discussion of a particular case.) Numerous published geomagnetic polarity timescales are in use, reflecting different choices of tie points, spreading rates, and inflection points. Each variant timescale gives different estimates for the ages of Siwalik localities, with maximum differences close to 500 Kyr for the interval at 10.7–5.7 Ma. In previous publications we have used the timescales of Mankinen and Dalrymple (1979), Berggren et al. (1985), and Cande and Kent (1992). In this paper we use the now widely accepted timescale of Cande and Kent (1995).

Other potential sources of error in our age estimates are not included in the expressed uncertainties. Mistakes in field correlations between the localities and sections are impor-
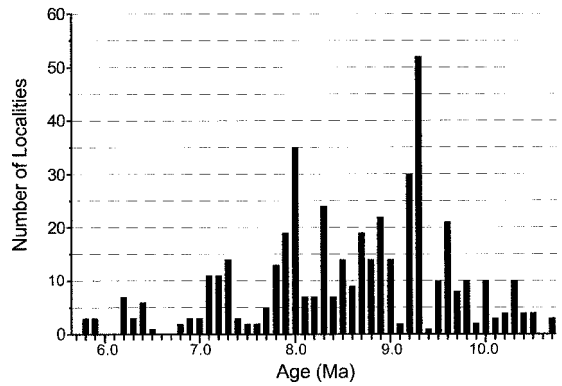
FIGURE 6.   Number of localities per interval. Data from Appendix 2, $n = 457$.

tant in this respect. In placing localities stratigraphically we have tried to express the uncertainties in our correlations and preserve them through the steps of our analysis. Nevertheless, the potential remains for undetected errors. Errors in placement of magnetic transitions are also possible, although to some extent alleviated by the refinement of using upper and lower positions of the transitions to calculate a pair of ages. This is again a conservative approach, and future paleomagnetic work refining the placement of transitions in our sections should improve the precision of our estimates. Finally, there may be a source of error in our correlations between the local magnetic sections and the geomagnetic timescale. These correlations are fundamentally interpretations of data, and we have undoubtedly misidentified some magnetic transitions. In this paper we present only a single favored correlation, although there may be plausible alternatives. In most cases additional fieldwork will resolve these problems.

Quality of Fossil Occurrence Data

Throughout the late Miocene nearly all Siwalik stratigraphic intervals have some fossils, and in many the record is really very good. Nevertheless, there are considerable differences in the number of fossils between intervals, as well as in the length of gaps between successive localities. This is illustrated in Figures 6 and 7A,B, which show, respectively, the number of localities and the number of cataloged large- and small-mammal specimens in each 100-Kyr interval between 10.7

A

B
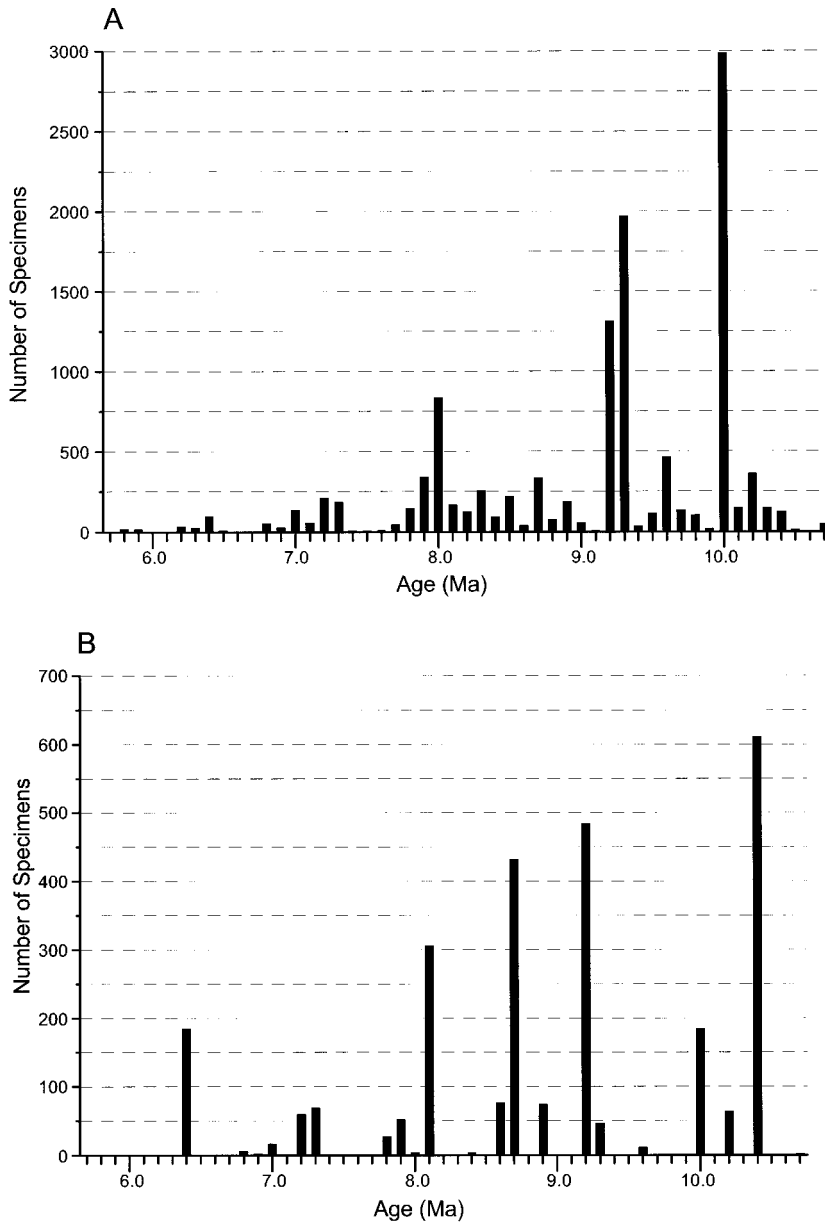
FIGURE 7. Number of catalogued fossils per interval. A, Large mammals (n = 11,779). B, Small mammals (n = 2730).

and 5.7 Ma. Figure 8 shows the distribution of gaps over the same interval.

The bias in fossil recovery results from a combination of factors that include (1) the area of outcrop and quality of exposure, (2) the types and mix of depositional environments, and (3) differences in the number of hours spent prospecting and collecting at individual levels. However, Figure 9, which shows the re-

lationship between the number of surveying hours and the number of fossils encountered during biostratigraphic surveys (data from Table 2), demonstrates that the greater abundance of fossils in some intervals is not due solely to collecting effort or outcrop area. Rather, greater abundance is also due to the intrinsic productivity of the lithologies.

Figures 6 and 7 show that the late Miocene
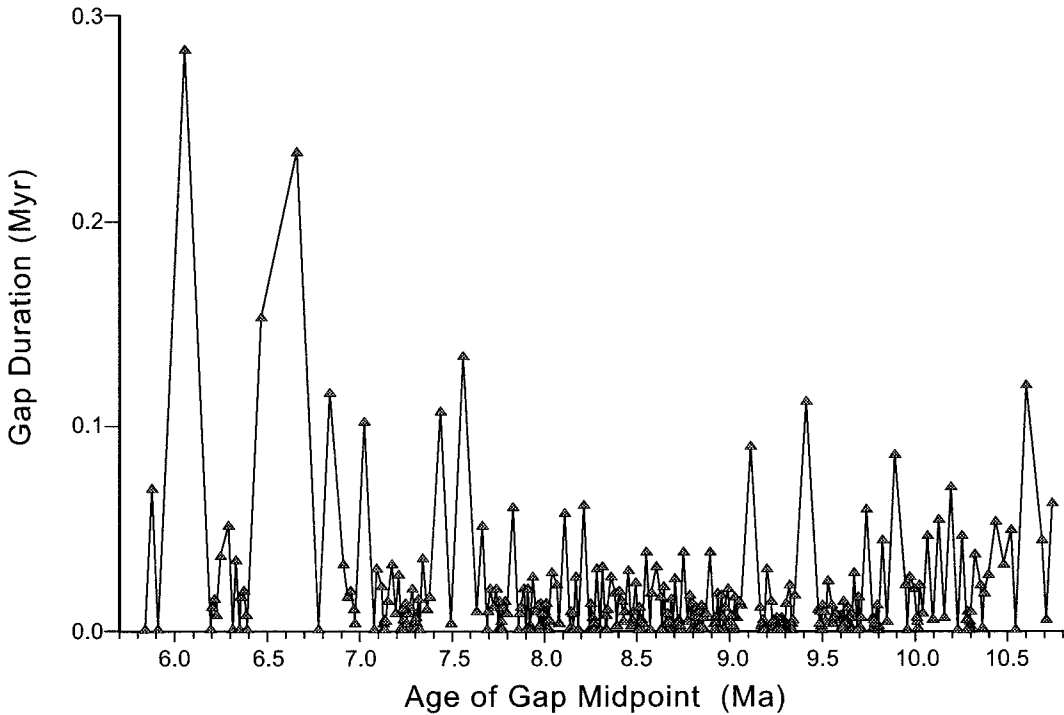
FIGURE 8. Gap age against duration. Gap age is the midpoint of the gap. Gap duration is calculated as the difference in age between chronologically successive localities. Data from Appendix 2; $n = 456$.

record on the Potwar Plateau is best over the approximately 2-Myr period between about 7.9 and 10 Ma, with all intervals having some fossils. In this same 2-Myr period, productivity is usually higher than that of the adjacent periods (Fig. 9), and the duration of gaps between localities is very much lower (Fig. 8). The details differ depending on whether gap lengths, number of localities, or fossil abundance is considered, but the record is noticeably poorer before 10 Ma and after 7.9 Ma; and it is especially so after 7.1 Ma.
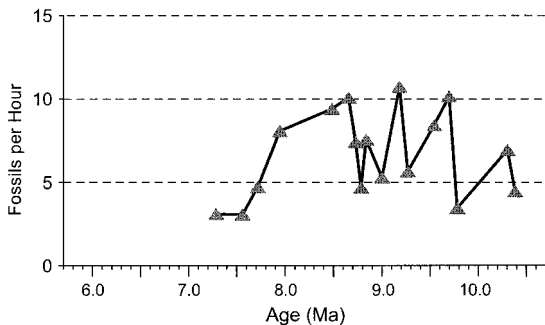
FIGURE 9. Number of mammalian fossils found in survey blocks per hour of searching.

This bias in the relative abundance of the fossils could in itself account for differences in the patterns of first and last occurrences, and thus in our assessments of the number of species in each stratigraphic interval (Badgley and Gingerich 1988; Badgley 1990). In previous papers we have therefore used two measures to determine whether data from different intervals could be compared and to estimate range extensions over intervals of poor record. These measures were interval-quality scores (Barry et al. 1990, 1995) and an index of completeness (Barry et al. 1995; Maas et al. 1995). The approach taken in this study, however, does not require either, because we now use a procedure (Shaw 1964; Koch 1987) to estimate range extensions directly from the occurrence data. This method uses counts of the number of fossils from each interval and the number of specimens in each taxon to assess the likelihood of discovering a fossil of a specified taxon at a specified level.

Other biases affecting the reliability of the fossil occurrence data result from diverse taphonomic processes and the methods used

to make the collections. The fragmentary nature of almost all Siwalik fossils also creates a bias that makes more-easily identified taxa, or those that can be identified from more skeletal elements, appear to be relatively more common. All these biases limit paleoecological inferences, such as assessing relative abundance of taxa or recognizing habitat specificity, but we presume they are the same for all intervals under study and do not affect comparisons between intervals.

Environmental Change

A fundamental question in paleobiology involves the relationship between environmental change and faunal evolution. In the Siwalik sequence, we have the opportunity to examine diversity fluctuations and other faunal patterns in relation to shifts in depositional environments and vegetation as well as to global and regional climate change. In this next section we review the evidence and interpretations for environmental change in the Potwar region during the late Miocene. In doing so we use several published sources, including studies of the sediments and paleosols, as well as data on stable isotopes from the paleosols and fossil mammals. Other than for very rare specimens, there is no plant record for the Potwar Siwaliks.

Because we focus foremost on the relationships between local environmental and faunal change, our discussion is limited to the Potwar Plateau (~30,000 km²). The small local geographic scale makes it possible to test whether changes in the fluvial system caused the faunal changes.

The present climate of the Potwar is warm and humid, with very marked monsoon seasonality. Spring months are dry and very hot, summer months bring the monsoon rains (with half the annual precipitation), and autumn and winter are cool and drier. Precipitation is highly variable throughout the Plateau and from year to year. Rainfall averages about 500–700 mm/yr over much of the Plateau, but can vary from 250 to 1300 mm/yr from one year to the next (Anonymous 1985; Shukla 1987). Much of the annual variation is due to differences in the intensity of monsoon rains, which are also highly irregular in time

of onset. As discussed below, climate apparently changed through the study interval, but it can be characterized during the middle and late Miocene as warm and humid with a strong monsoon circulation and marked seasonality.

Lithological Evidence

Detailed environmental reconstructions have been made for the Siwalik formations, reconstructions that, because of an inadequate plant record, draw heavily on sedimentological evidence and models based on the modern analogs provided by the Indus and Ganges Rivers. Although some work has been done on the Dhok Pathan Formation (Behrensmeyer and Tauxe 1982; Behrensmeyer 1987; Badgley and Tauxe 1990), most of the relevant field studies in the Potwar have focused on the middle Miocene Chinji Formation and the lower part of the middle-to-late Miocene Nagri Formation, with the transition between these two formations at ca. 12–10.5 Ma being of special interest (Retallack 1991; Willis 1993a,b; Willis and Behrensmeyer 1994, 1995; Badgley and Behrensmeyer 1995b; Behrensmeyer et al. 1995; Zaleha 1997a,b). Here we also use these studies to characterize the transition between the late Miocene Nagri and Dhok Pathan Formations. We believe this is justified because comparisons of the Chinji and Dhok Pathan Formations indicate similarities in their depositional environments and in their transitional stratigraphic relationships with the intervening Nagri Formation (Behrensmeyer and Tauxe 1982; Behrensmeyer 1987; Retallack 1991; Willis 1993b; Zaleha 1997a,b). Particularly noteworthy are the similarities between the Chinji/Nagri transition and the vertical and lateral changes documented between the Nagri and Dhok Pathan Formations. Ongoing research is documenting lateral and vertical change in lithofacies, paleosols, and isotopic composition within the Dhok Pathan Formation in the Khaur and Hasnot areas, with the continuing goal of integrating this information with the paleontological evidence we present below.

The Miocene Siwaliks were deposited in a very large scale fluvial system, one comparable in size to the modern Indus or Ganges sys-

tems. These modern rivers occupy divergent basins paralleling the northern and western mountains and bounded by the Indian craton to the south and east. This arrangement of mountains, basins, and major drainages is a result of the tectonic movement of the subcontinent against Asia and existed throughout the Miocene. However, paleochannel directions and paleocurrents indicate that the paleo-Ganges system may have extended farther west and drained the Potwar region (Beck and Burbank 1990), which now is connected to the Indus drainage. The reconstructed Miocene Indo-Gangetic system extended over 2000 km to the east and 1000 km to the south, with floodplain widths on the order of 100 to 500 km. Thus, the Potwar Plateau encompassed only a small part of this ancient foreland basin and can give us only limited information on the whole system (Willis and Behrensmeyer 1995). In the Miocene, the Potwar study area was probably some 100–200 km to the southeast of the mountain front where its rivers originated (Zaleha 1997b). This distance is about the same as at present. At ca. 10 Ma, the Potwar region was at approximately 29°N latitude, that is 4° south of its current position (Tauxe and Opdyke 1982).

Reconstructions of the Siwalik rivers depict drainages coalescing into trunk rivers running to the Arabian Sea and Bay of Bengal along the axes of the two divergent basins. Large submarine sediment fans attest to the existence of these Indus-size trunk rivers in the Miocene (Rea 1992), but deposits of the axial system draining the late Miocene Potwar are not preserved, either because it flowed eastward to the Bay of Bengal or, if flowing south to the Arabian Sea, was confined by the slope of the floodplain to the margin of the depositional basin (Willis 1993a,b; Willis and Behrensmeyer 1995). Channel and floodplain deposits of large and small tributaries to the trunk river are preserved, however. These tributaries are interpreted to be of two subtypes. The first are deposits of large streams that emerged from the mountains at widely spaced intervals (100–200 km) and flowed several hundreds of kilometers southeast across the floodplain to join the trunk river (Fig. 10). These second-order streams, which we refer to

as ''emergent'' or ''upland-sourced'' streams, carried relatively unweathered sediment from the mountains and deposited it to form distally broadening, low-gradient megafans. Similar in size and morphology to modern Punjab rivers such as the Jhelum, the Miocene upland-sourced streams were braided and typically had channel belts more than 5 km wide with individual channel widths on the order of 200 to 400 m. They drained adjacent and distant mountain regions, flowed throughout the year, and were prone to avulsion during unusual flood events. Abandoned channels then became sites of short-lived lakes or swamps with more gradual sedimentation, while the active channels moved to lower and perhaps quite distant areas on the fan. Because of the instability of the channels, alluvial ridges along channels did not form, nor did channels migrate laterally to form extensive sheet bodies (Behrensmeyer et al. 1995).

In contrast, the second subtype are deposits of generally smaller, braided rivers having channel belts ~1–2 km wide and channels 70–200 m wide. Some of these third-order streams may also have had mountain sources, whereas others had sources in foothills or from groundwater on the floodplain (Fig. 10). Because they were confined to areas between the fans of the larger emergent rivers and carried finer, reworked material eroded from the floodplain, we refer to them as ''interfan'' or ''lowland-sourced'' streams. Their sources were closer to or even on the second-order floodplains, so their flow was probably influenced more by floodplain precipitation than by precipitation in distant, mountainous regions. Consequently, flow varied more throughout the year than in the larger, emergent streams. Channels of the third-order streams also seem to have been less prone to very large flood events but nevertheless had a more frequent rate of avulsion than the second-order, emergent streams (Willis 1993b; Zaleha 1997b).

As a result of the deposition on alluvial fans and interfan areas, the sloping floodplain was a mosaic of low and high areas, with local relief on the order of 10 m and at most a few hundred meters elevation difference across
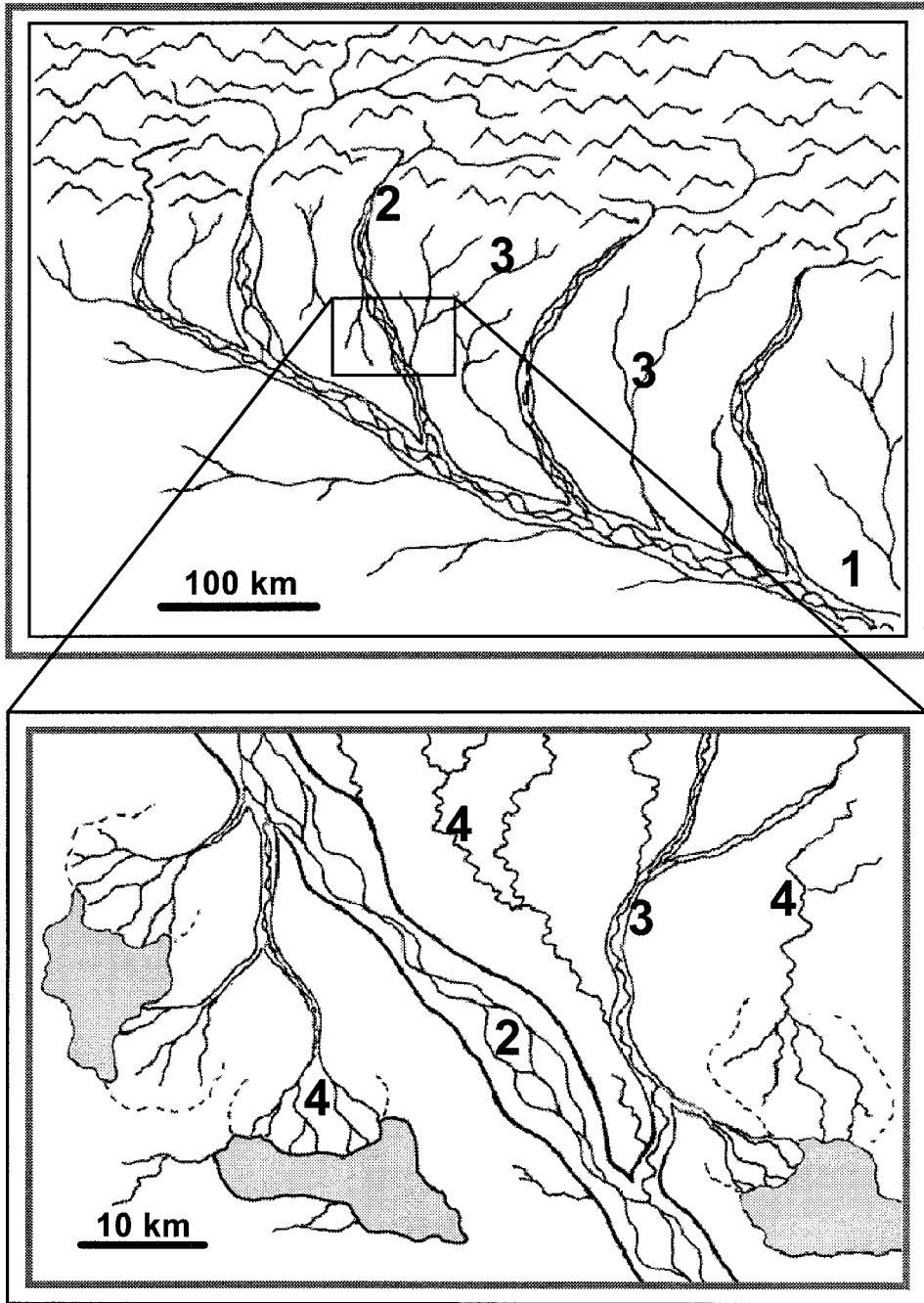
FIGURE 10. Reconstruction of late Miocene Siwalik fluvial system in plan view. Numbers refer to orders of streams as discussed in text. 1 = axial trunk river, shown flowing eastward to the Bay of Bengal. 2 = emergent or upland-sourced rivers, draining mountains and tributary to the axial trunk river. 3 = interfan or lowland-sourced streams, arising on the floodplain or near the mountain front and generally tributary to the axial or second-order rivers. 4 = small streams of the floodplain, often ephemeral. Note that the third- and fourth-order streams may also have drained into low areas on the floodplain, creating seasonal swamps or ponds as indicated by gray stippled areas. The boxed inset approximates the size of the modern Potwar Plateau.

TABLE 3. Types of Siwalik paleosols, their characteristics, and interpretations. (Data and interpretations taken from Retallack 1991. Study based on two sample sections at 9.4 and 8.6 Ma.)

Paleosol	Frequency[†]	Topographic setting	Parent material	Drainage	Maturity	Disturbance	Carbonate content	Inferred vegetation
Sarang	24/14 (χ^2 = 2.281, p = 0.131)	Pointbar, levee, and crevasse-splay	Stream and levee deposits of 2nd- and 3rd-order streams	Well drained	Very immature	Very frequent	Upper and lower horizons strongly calcareous; nodules not present	Early succession; streamside
Lal	13/0* (χ^2 = 5.706, p = 0.017)	Old, low-lying floodplain; distant from streams	Floodplain alluvium of 2nd- and 3rd-order streams	Well drained, with occasional flooding?	Mature to very mature	Infrequent	Matrix of upper horizons decalcified; lower horizons with scattered fine nodules	Old growth; deciduous woodland or dry forest
Naranji	0/2* (χ^2 = 5.256, p = 0.022)	Linear depressions on abandoned channels	Tops of coarse sands of 3rd- and 4th-order stream channels	Well drained, seasonally briefly waterlogged?	Mature to very mature	Infrequent?	Matrix of lower horizons moderately calcareous; nodules not present	Seasonally dry; tall riverine forest, with lush undergrowth
Bhura	19/2* (χ^2 = 4.358, p = 0.037)	Abandoned channels and levees, flanking Sarang soils	Channel and levee deposits of 2nd- and possibly 3rd-order streams	Well drained	Immature to mature	Frequent?	Upper and lower horizons moderately calcareous; with small scattered nodules	Streamside gallery forest
Sonita	12/13* (χ^2 = 9.289, p = 0.002)	Young floodplains near streams	Levee and floodplain deposits of 2nd- and possibly 3rd-order streams	Well drained and dry with only occasional flooding	Immature to mature	Infrequent? major floods	Upper horizons moderately decalcified; lower with scattered, small nodules	Mid-succession; dry woodland or forest
Pila	3/0 (χ^2 = 1.195, p = 0.274)	Low-lying abandoned channels and depressions; proximal crevasse-splays	Sandy alluvium of 3rd-order streams	Mildly waterlogged on seasonal basis	Mature	?	Upper and lower horizons moderately calcareous, scattered, small nodules	Moist, lowland; grassy woodland or wooded grassland
Khakistar	5/0 (χ^2 = 2.020, p = 0.154)	Abandoned channels, swales, and floodplain lakes; away from active channels	Calcareous and clayey alluvium of 2nd-order streams	Seasonally waterlogged and perhaps seasonally dry	Immature	Frequent, flood-prone	Upper horizons very weakly decalcified, very small or no nodules	Seasonally wet; lowland forest

TABLE 3. Continued.

Paleosol	Frequency[†]	Topographic setting	Parent material	Drainage	Maturity	Disturbance	Carbonate content	Inferred vegetation
Pandu	3/0 (χ^2 = 1.195, p = 0.274)	Elevated, distal parts of levee	Sandy and silty deposits of 2nd-order streams	Well drained most year; water-logged at times?	Very mature	Infrequent?	Upper horizons calcareous; lower with abundant, large nodules	Seasonally wet; forest or woodland
Kala	1/0 (χ^2 = 0.391, p = 0.532)	Small abandoned channel, flood-plain lake, or moist flood-plain	Silty deposits of 3rd order streams	Seasonally water-logged, also seasonally dry?	Mature to very ma-ture	Frequent, annually inundat-ed?	Upper horizons decalcified; lower with abundant nod-ules	Grasses or sedges with scattered trees; wet wooded grass-land

* Statistically significant difference in relative frequency between lower and upper sections.
[†] Number of occurrences in lower section/number of occurrences in upper section.

the floodplain (Willis 1993b). Low areas were sites of short-lived, perennial or seasonal ponds and swamps. Such low areas would have been rapidly filled by crevasse-splays and levees associated with the larger second- and third-order channels, and with sediment from even smaller fourth-order floodplain streams (Fig. 10) (Willis 1993a; Zaleha 1997a). Preserved floodplain deposits therefore consist predominantly of low-angle crevasse-splay lobes that built out into low areas, some of which contained wetlands or lakes, along with minor contributions from levees and small floodplain channels (Behrensmeyer et al. 1995; Willis and Behrensmeyer 1995). The preserved features of the fourth-order floodplain streams indicate that they typically cut into preexisting floodplain deposits, had single rather than braided channels, and were much smaller (10 to less than 100 m wide) than the individual channels of the third-order streams. The preserved deposits are mostly ribbon shaped, indicating that the channels did not migrate laterally, perhaps because they were stabilized by vegetation (Willis 1993a). Flow in these smaller channels was apparently slower and more episodic throughout the year than in the major channels and may have ceased at times as the smaller channels became sites of ponded water (Willis 1993a). In all three formations the smaller floodplain channels are exceptionally important as sites of vertebrate bone accumulation. Most of the larger fossil localities are from such depositional environments or from fine-grained fills associated with the tops of second- or third-order channels (Badgley and Behrensmeyer 1980, 1995; Behrensmeyer 1987; Badgley et al. 1995; Behrensmeyer et al. 1995; Willis and Behrensmeyer 1995).

Floodplain paleosols are well developed, common, and varied throughout the whole of the Siwalik sequence, although they have been studied in detail only very locally (Retallack 1991). The Chinji and Dhok Pathan Formations both have a larger number of well-differentiated paleosols than the Nagri, in keeping with overall differences in proportions of channel and overbank deposits. None of the formations have paleosols that are readily assigned to modern soil types, although they are

broadly similar to modern soils of the Indo-Gangetic plain (Retallack 1991; Behrensmeyer et al. 1995; Quade and Cerling 1995), especially those forming under 25°C mean annual temperature and 1400 mm/yr precipitation (Behrensmeyer et al. 1995). The nine paleosol series described by Retallack (1991) (Table 3) differed primarily in topographic setting, frequency of disturbance, degree of maturity, drainage, and parent material, as well as inferred vegetation and precipitation. At all stratigraphic levels, however, the paleosols give evidence of seasonal differences in the water table that produced waterlogging with formation of Fe-Mn nodules, followed by desiccation with leaching and precipitation of calcium carbonates. Leaching of matrix carbonate was essentially complete on coarse deposits and well-drained sites. There is also evidence for intense oxidation at the time of soil formation, which depleted organics and presumably helped destroy bone in mature paleosols as well (Willis 1993a; Behrensmeyer et al. 1995; Zaleha 1997b).

Temporal changes in the Siwalik fluvial system have been documented, but the degree to which they are related to climate or subsidence, or are due simply to autocyclic dynamics of the fluvial system, is not clear (Willis 1993b; Zaleha 1997b). The transition between the Chinji and Nagri Formations has been interpreted as due to the progradation of a second-order emergent system over a smaller, third-order interfan system (Willis 1993b; Zaleha 1997b). The Nagri and Dhok Pathan transition, on the other hand, seems a well documented case of the coexistence of two contemporaneous systems (Behrensmeyer and Tauxe 1982), the larger of which diverted from the study area between 10.1 and 9 Ma. Chinji floodplains were apparently more poorly drained than those of the Nagri Formation, with the abundance of lacustrine deposits and iron-concretion-rich paleosols indicating greater seasonal waterlogging (Willis 1993b; Behrensmeyer et al. 1995; Willis and Behrensmeyer 1995). Floodplain deposition in the Chinji, and perhaps Dhok Pathan, Formation was also more episodic than in the Nagri, with longer-lived small floodplain channels. Initially, flow in these small channels was continuous year-round, but in later stages it became more episodic with periods of subaerial exposure as the channels were abandoned and later infilled. By contrast, in the Nagri Formation even the initial stages of channel flow may have been more seasonal, with deposition of sediment occurring mostly during floods (Willis 1993a; Willis and Behrensmeyer 1995). Specific, important differences between the rivers of the Nagri and Dhok Pathan Formation include decreased channel size and discharge in the latter, as well as decreased avulsion period (Zaleha 1997b).

Our lateral facies studies in the Kaulial Kas section and nearby sections (Behrensmeyer 1987) provide a general reconstruction of the landscape in the Khaur region between 10.1 and about 7.0 Ma. Before ca. 9 Ma, in the upper part of the Nagri and lower part of the Dhok Pathan Formations, channels hundreds of meters wide were separated by fine-grained interfluves with modest topographic relief. The highest areas in these interfluve floodplains were associated with low-angle crevasse-splay fans, and the lowest areas with abandoned channels. Levees were generally poorly developed and channels show little evidence of lateral migration, indicating frequent avulsion. Floodplain soils are carbonate- and iron-rich and oxidized, suggesting seasonal alternation between waterlogged and moist-dry with intense bioturbation. The interfluves were crossed by small channels tens of meters wide that were tributaries or distributaries associated with the larger channels and probably active mainly during flood periods. The physical habitat between 10.1 and ca. 9 Ma varied on a scale of tens to hundreds of meters from floodplain silt-clay soils to sandy splay substrates to channel corridors with wet to dry beds depending on the season.

After ca. 9 Ma, in the upper part of the Dhok Pathan Formation, large scale, braided channels draining foothill source areas were more common in the Khaur region, expanding the area covered by sandy substrates (e.g., abandoned or seasonally dry channels) at the expense of silt/clay soils. Small-scale, erosional floodplain channels became much less frequent, reflecting a reduction in the role of such

channels in distributing floodwaters. This difference could reflect a shift in the rainfall regime and/or an increased role of the major rivers in controlling the topography and drainage of the alluvial plain. Low-angle crevasse-splay fans continued to create minor positive relief on this plain, but overall the interfluves were broader, flatter, and more homogenous than in the upper Nagri and lower Dhok Pathan Formations. Lateral variation in the physical habitat was on the order of hundreds to thousands of meters. Pedogenic carbonate is more poorly developed in the upper Dhok Pathan floodplain soils, which are leached of matrix $CaCO_3$, and this may reflect more effective soil drainage with less opportunity for vertical transpiration and evaporation of water-logged soils during the dry season.

This reconstruction of environmental change through time applies only to the Khaur region. It is likely that other parts of the Siwalik alluvial plain were changing at different rates and in different ways, providing varying ecological opportunities for the flora and fauna. Mountain-proximal regions, such as Khaur, were subject to the effects of encroaching lowland-sourced fluvial systems earlier than mountain-distal regions to the south. Nevertheless, the environmental developments seen in the north are indicative of what would be expected throughout the larger Siwalik system in the late Miocene, as lowland-sourced rivers became more dominant and the climate changed to greater seasonal aridity with more intense monsoons.

Retallack (1991) described and named nine paleosol series from two short sections in the lower Dhok Pathan Formation at ca. 9.4 and 8.6 Ma. In these two sections, which are within and just above the Nagri–Dhok Pathan transition, he documented differences in the frequencies of soil types (Table 3). He interpreted the dissimilarities as resulting primarily from differences in parent material, local topography, and drainage. Seasonality of rainfall and levels of disturbance may also have affected soil type (Retallack 1991). The Bhura Series and Sonita Series in particular are a couplet of frequently occurring, moderately developed paleosols that formed in similar settings on

similar parent material but differed in drainage and intensity of seasonal drying. The Lal Series and Naranji Series are another pair of mature paleosols that differed primarily in topographic setting, parent material, and distance from channels, and secondarily in drainage. Retallack's overall interpretation is that his sample of younger paleosols (at 8.6 Ma) formed closer to the channels and were better drained, with perhaps more marked seasonality. These observations on the paleosols can be related to the replacement of the emergent Nagri system by an interfan system, and they may also indicate a different climatic regime. However, although there are statistically significant contrasts between the older and younger sections in the frequencies of Lal, Bhura, Sonita, and Naranji soils (Table 3), subsequent work in the Kaulial area indicates that his conclusions should be viewed with caution. We find Retallack's sections were too short and too laterally restricted to include a representative sample of the soils of the two time intervals. Furthermore, both intervals have much more variation in soil features associated with lateral and vertical differences in the fluvial systems than can be accommodated by his system of soil classification.

Retallack (1991) found no evidence for extensive grasslands (e.g., ped structure, massive fine roots), although he suggested that the Pila Series and Kala Series paleosols formed under occasionally waterlogged, grassy woodlands. Paleosols belonging to either series are uncommon, occurring only four times among 111 recognized paleosols, and are found only in the older section. Nevertheless, yellow and light-colored soils become more common after 8 Ma. These could be examples of his Pila or Pandu soils, or they might be unrecognized soil types. Fewer paleosol types were reported by Retallack (1991) in the upper section (four versus eight in the lower), which he interpreted as evidence for a less varied landscape in the younger time interval. However, considering the much smaller number of recognized soil horizons in the upper section (31 versus 80), these proportions are not different. Nevertheless, our own observations suggest that the upper part of Dhok Pathan Formation (ca. 9.0–5.5 Ma) is less var-
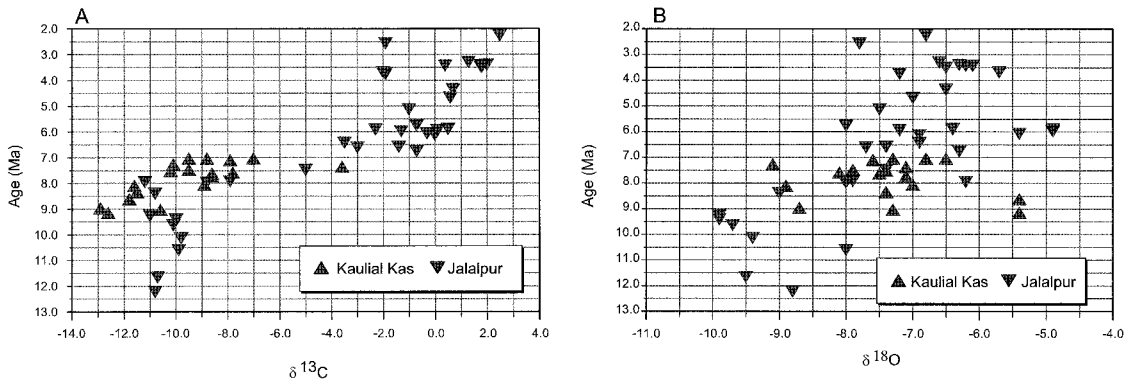
FIGURE 11.   Isotopic values of paleosol carbonates by age. A, δ^{13}Carbon. B, δ^{18}Oxygen. Ages from Appendix 3. All isotopic data are from Quade and Cerling 1995.

ied than the lower part (ca. 10.1–9.0 Ma) in types of paleosols; in the sizes, geometry, and frequency of channels; and in local topography. The difference between the older and younger parts of the Dhok Pathan Formation is also expressed in the decreased frequency of fossil-preserving environments in the upper Dhok Pathan (Fig. 6) (Behrensmeyer 1987).

It is noteworthy that at any stratigraphic level there is always considerable diversity in soil types, and by inference considerable diversity in vegetation. Low areas contained seasonal swamps or ephemeral ponds, whereas the paleosols suggest that other areas had extensive wet upland and lowland forests, dry old-growth deciduous woodlands, tall riverine or gallery forest with lush undergrowth, and wet grassy wooded meadows, as well as tracts of secondary growth and early succession (Retallack 1991). These vegetation types would have been common, coexisting elements of the landscape. It seems likely that organisms concentrated in some areas, and maybe especially in the lush vegetated corridors along the streams during the dry season. Animals may also have retreated to the higher crevasse-splay fans during flood periods or migrated off the floodplain altogether. After ca. 9 Ma, the decreased environmental variability, increased soil drainage, and particularly the diminished network of vegetated channel corridors on the alluvial plain would have reduced the diversity of habitats available to the Siwalik flora and fauna.

Isotopic Evidence

Temporal changes have also been found in the stable isotopic content of Siwalik paleosols and fossil material (Quade et al. 1989, 1992; Morgan et al. 1994; Stern et al. 1994; Quade and Cerling 1995). Quade and others (Quade et al. 1989, 1992; Quade and Cerling 1995) first reported differences in stable carbon and oxygen isotope ratios in soil carbonates in three Potwar sections, noting rapid shifts in both δ^{13}C and δ^{18}O values in the late Miocene. Quade and others initially reported the ages of their samples using the Berggren et al. (1985) timescale. We have now recalculated the ages of the Kaulial and Jalalpur samples using the Cande and Kent (1995) timescale (Appendix 3, Fig. 11A). (The upper, post-9-Ma part of the Gabhir section is not included because of uncertainties in correlation to the magnetic polarity timescale.) The new ages show that the beginning of the δ^{13}C shift is slightly younger than 8.1 Ma, when a value greater than -9.0‰ first appears in the Kaulial section. The shift is more or less completed by 5.9 Ma, after which values less than -2.0‰ no longer occur. (These beginning and end dates are respectively, approximately 800 Kyr and 400 Kyr older than previously reported.) However, as Quade and Cerling (1995) note, the shift is complex and certainly not monotonic. Samples that are strongly ^{13}C depleted occur even after 7.4 Ma, which is when the oldest sample with a value greater than -4.0‰ occurs. Values greater than -2.0‰ are present as early

as 6.8 Ma, suggesting that the more restricted interval between 8.1 and 6.8 Ma was the time of greatest change. There is no apparent difference in the timing of the carbon isotopic shift from the northwest at Kaulial to the southeast at Jalalpur (Fig. 1).

The $\delta^{18}O$ shift noted by Quade and others (Quade et al. 1989; Quade and Cerling 1995) is also conspicuous and appears to be as rapid as the carbon shift, although beginning earlier (Appendix 3, Fig. 11B). In the well-dated Kaulial section, the oldest available sample is greatly enriched relative to older samples from the Jalalpur section. It indicates that the shift in $\delta^{18}O$ values occurred as early as 9.15 Ma. Unfortunately, the ages of the Jalalpur samples older than 8 Ma are imprecise and do not establish the age of the transition's lower boundary. With the exception of one sample with an age between 10.7 and 10.5 Ma, all are less than $-8.0‰$, and the 9.15 Ma Kaulial sample might therefore be taken as marking a point of significant change. This date is at least 600 Kyr older than reported by Quade and Cerling (1995) and 1.1 Myr older than the beginning of the shift in carbon values. The $\delta^{18}O$ shift is also complex (Quade and Cerling 1995). The transition takes place in phases and lasts longer than the carbon transition. With the exception of a strongly depleted sample at 7.27 Ma, Ma $\delta^{18}O$ values after 8 are greatly enriched compared with older ones, whereas post-6-Ma values are even more enriched. The interval between 9.15 and 7.27 Ma may delineate a transitional period of unusually wide variation, with the most intense change coming before 8.0 Ma.

Paleosol $\delta^{13}C$ ratios reflect the isotopic composition of vegetation growing at the site of soil formation (Cerling et al. 1989). Quade and others consequently interpreted the reported differences in carbon isotope ratios as due to long-term changes in vegetation (Quade and Cerling 1995). They considered $\delta^{13}C$ values more positive than $-9‰$ to indicate the presence of at least a small number of plants using the C_4 photosynthetic pathway, while more negative values indicated the presence of only C_3 plants. Paleosol nodules with $\delta^{13}C$ values greater than $-2‰$ formed under pure C_4 grasslands, while those with values near $-5‰$ formed under mixed vegetation averaging about half C_3 and half C_4 during the period of soil formation (Quade et al. 1989; Quade and Cerling 1995). Accordingly, Quade and others (Quade et al. 1989; Quade and Cerling 1995) interpreted the carbon shift to be a change from C_3-dominated plant communities to C_4-dominated ones; that is, from closed-canopy forest and woodland communities to more open types of vegetation.

The transition between C_3- and C_4-dominated communities was rapid. Plant communities composed predominantly of C_4 species appear as early as 7.4 Ma, whereas pure C_4 grasslands were present at 6.9 Ma. Communities composed exclusively or predominantly of C_3 species apparently disappeared from the record after 7.0 Ma, when the last isotopic values less than $-9.0‰$ occur. Thus, although initially the transitional plant communities were spatial and temporal mosaics with forest, woodland, brush, and grassland, after 6.9 Ma apparently there were only grasslands and mixed C_3 and C_4 communities, with little or no pure C_3 vegetation. The available evidence also indicates that after 5.9 Ma C_4 grasslands were the dominant and maybe only vegetation on the Siwalik alluvial plain (Quade et al. 1989; Quade and Cerling 1995). It should be noted, however, that the inferred absence of C_3 communities is based on negative evidence, and there are numerous paleosols throughout this time interval that were not sampled because they lack carbonate and/or free carbon (see also Table 3). These soils may have continued to support C_3 vegetation.

Because environmental and climatic factors, such as CO_2 partial pressure, light intensity, rainfall, and temperature, govern growth and competition between C_4 and C_3 plants, the carbon shift implies climatic and environmental change. Most C_4 plants are grasses adapted for growth under higher temperature and lower rainfall regimes than C_3 grasses, trees, and shrubs. Increasing seasonality and reduced precipitation have therefore been cited to account for inferred temporal alteration in vegetation (Quade et al. 1989; Quade and Cerling 1995).

Carbon isotope ratios in mammalian tooth enamel and avian eggshells (Quade et al. 1992;

Morgan et al. 1994; Stern et al. 1994) have also been used to reconstruct ancient Siwalik vegetation. In this case the $\delta^{13}C$ values of enamel and eggshell reflect the isotopic composition of the animal's diet, but because animals can be highly selective feeders, such isotopic data cannot directly document relative composition of the vegetation. Rather, they only indicate plant availability. Enamel samples also represent very short intervals of time within the animal's life span (1–10 yr), whereas carbonate nodules form over longer periods (100–1000 yr). The time-averaging of an isotopic signal over longer periods in soil nodules could obscure any record of C_4 vegetation patches in a dominantly C_3 environment. Both mammal and avian isotopic data sets show a transition from C_3-dominated diets to mixed C_3/C_4- and C_4-dominated diets, with the transition being most striking after 8 Ma, as in the paleosol carbonate data. Nevertheless, both Morgan et al. (1994) and Stern et al. (1994) found some evidence for a C_4 dietary component before 8 Ma. Although the values are near the threshold for pure C_3 vegetation (Cerling et al. 1997), the animal data do suggest that C_4 vegetation was present earlier than the paleosol evidence shows. This conclusion gains support from occlusal microwear data on teeth, which also document herbivores with substantial amounts of grass in their diet, even in the middle Miocene (Morgan et al. 1994). Although seemingly in conflict with the soil carbonate data, it is likely that certain kinds of habitats, and especially disturbed habitats with vegetation in an early stage of succession, are not represented in the paleosol isotopic record. Many Siwalik paleosols lack pedogenic carbonate or have dispersed nodules too small to sample, because either they are immature or they formed on well-drained or permanently waterlogged sites where carbonate was not precipitated during pedogenesis (Quade and Cerling 1995). Because carbonate deficient soils are unrepresented in the isotopic samples, any vegetation restricted to them is consequently also unrepresented (or underrepresented) in the isotopically sampled record. Underrepresentation is especially likely for disturbed habitats with extensive open areas and grasses, because they are most likely

to have formed on immature or well-drained, nutrient-poor soils. Nevertheless, C_4 vegetation must have become more widespread on the floodplain after 8.1 Ma, because ^{13}C-enriched nodules begin to occur at that time in many different paleosols.

Paleosol $\delta^{18}O$ ratios are determined largely by temperature, evaporation, and the $\delta^{18}O$ values of precipitation at the site of soil formation (Quade and Cerling 1995), but interpretation of the shift in oxygen ratios reported in the Siwaliks is not straightforward. Quade and Cerling (1995) outlined several climatic factors that alone or together might have been responsible for the change, including an increase in mean temperature by about 5°C, a decrease in total amount or an increase in the seasonality of rainfall, a change in the sources of precipitation, or increased direct evaporation from the soil. Some of these same factors are also implicated in the carbon isotopic shift, but the connection between the carbon and oxygen isotopic shifts is not understood. Significantly, although the beginnings of the two events are separated by over one million years, the interval of most intense $\delta^{18}O$ change ends just when the carbon shift starts at 8.1 Ma. In addition, the most negative $\delta^{13}C$ values reported in the entire sequence are two samples from the Kaulial section at 9.15 and 8.97 Ma, which is when the $\delta^{18}O$ shift first starts. However, no simple relationship between carbon and oxygen values exists, as many of the ^{13}C-depleted samples from the upper part of the Kaulial section are ^{18}O-enriched, whereas others are ^{18}O-depleted (Quade and Cerling 1995).

Correlations to Oceanic and Himalayan Tectonic Events

Quade et al. (1995) have documented a similar carbon and oxygen isotopic shift beginning at ca. 7.0 Ma in terrestrial sediments in Nepal, whereas terrestrially derived sediments on the Bengal fan record a change in $\delta^{13}C$ values after ca. 7.8 Ma (France-Lanord and Derry 1994; date converted from Berggren et al. [1985] timescale). Mineral assemblages and rates of deposition on the Bengal and Indus fans also show marked contrasts between ca. 8 and 7 Ma (Amano and Taira

1992; Rea 1992; dates converted from Berggren et al. [1985] timescale), whereas foraminiferal evidence from the Arabian Sea suggests the beginning of strong summer upwelling at 9.4 Ma that continues to increase until about 8.2 Ma (Kroon et al. 1991, dates converted from Berggren et al. [1985] timescale). Although considerable uncertainty over the chronology of Himalayan and Tibetan Plateau uplift still exists, the consensus is that a phase of uplift and rapid erosion occurred from as early as 11 Ma to as late as 6 Ma (Amano and Taira 1992; Harrison et al. 1993; Turner et al. 1993; Meigs et al. 1995; but see also Copeland 1992; Burbank et al. 1993; Coleman and Hodges 1995). Although an elevated Tibetan Plateau and Himalayas may have existed long before 11 Ma, late Miocene uplift is seen as important in generating or intensifying the South Asian monsoon, as indicated by the onset of summer upwelling in the Arabian Sea (Prell and Kutzbach 1992; Rea 1992; but see also Ramstein et al. 1997). An intensified monsoon may then explain the observed $\delta^{18}O$ shift, through its effect on seasonality and precipitation in northern India and Pakistan in the interval between 9.4 and 8.2 Ma. Elevation of the Tibetan Plateau and Himalayas also may have been a critical factor in the evolution of late Miocene cooling on a global scale and consequent vegetation change, through its effects on chemical weathering rates, organic carbon burial, and atmospheric CO_2 content (Raymo and Ruddiman 1992; Molnar et al. 1993; Filippelli 1997). Atmospheric CO_2 content alone also has been seen as a cause of the isotopic shifts, through its direct effect on C_3/C_4 plant competitive relationships (Cerling et al. 1993, 1997). Pagani et al. (1999), however, found no evidence to support the claim.

Climate, Depositional System, and Vegetation

Although climate and interspecific competition are presumed to have been the primary agents acting on the plant communities, the depositional system also strongly affected the vegetation and landscapes of the 10.7–5.7-Ma interval. Preserved deposits include the sandy channels of large and small streams, their associated silty and sandy levees and crevasse splays, and the silt and clay fills of abandoned channels, ponds, and other depressions (Behrensmeyer et al. 1995; Willis and Behrensmeyer 1995). Position on the floodplain relative to the mountain front and axial trunk stream, as well as distance from the channel belts, were therefore important determinants of local topography, soil substrate, drainage, and frequency of disturbance. Because deposition was on both alluvial fans and interfans, areas of low and high elevation should have been irregularly distributed and patchwork-like, with low areas being both near to and distant from the channels (Behrensmeyer et al. 1995; Willis and Behrensmeyer 1995). Similarly, conditions affecting soil formation varied with proximity to the channels. Some areas would have been sites of continuing frequent deposition, whereas others would have had long periods for soil development between episodes of deposition. Presumably vegetation responded to specific local conditions. Consequently, plant communities formed mosaics that changed in an irregular manner over distances of hundreds of meters to a few kilometers, owing to edaphic factors such as topography, soil parent material, drainage, and height of the water table. The amount and seasonality of precipitation also would have been critical, although varying on a larger regional scale. Finally, high and unpredictable levels of disturbance due to flooding, stream avulsion, and fire would have left tracts of vegetation in different stages of succession, adding to the overall habitat mosaic. Forest glades, swamps, and meadows, as well as areas of secondary growth, should have been common features of the landscape, present within what were otherwise predominantly forests and woodlands. More speculatively, brushland and perhaps some grasslands also may have been present prior to the widespread expansion of C_4 vegetation. Presumably, this variety of vegetation created a complex of habitats favorable to different animals.

Climate change per se also may have been the primary agent affecting vegetation during the study interval. Increasing seasonality, reduced precipitation, and an increase in the incidence of fire have commonly been cited to

account for inferred differences in vegetation, as well as differences in the Siwalik sediments and faunas (e.g., Krynine 1937; Quade et al. 1989; Retallack 1991; Quade and Cerling 1995). These effects, however, are difficult to separate from those of the fluvial system's dynamics. The latter were especially likely to have been instrumental in transforming landforms and vegetation between 10.1 and 9 Ma, when a large emergent river system (Nagri Formation deposits) was replaced across the study area by a smaller interfan system (Dhok Pathan Formation deposits). The lower Dhok Pathan interfan system had smaller streams and narrower channel belts, with slower, more seasonally variable flow and more frequent avulsions than the emergent Nagri system (Willis 1993b; Willis and Behrensmeyer 1995; Zaleha 1997b). The lower Dhok Pathan system also had a more widely fluctuating water table, more frequent flood disturbances, and perhaps a more variable spatial mosaic of abandoned channels, soils, and topography. Small floodplain channels, which are important sites of vertebrate bone accumulation, were initially very common on the interfan Dhok Pathan system but became progressively less so after ca. 9 Ma (Behrensmeyer 1987), whereas the preserved soils seem to have formed nearer to the channels, where they were better drained and more susceptible to drying (Retallack 1991). After 9 Ma, the interfluves were broader with less topographic relief, and the physical environment appears to have been more homogenous than in the lower Dhok Pathan Formation.

Because small floodplain channels were so common, fossil productivity is much higher after 10 Ma in the interfan lower Dhok Pathan system then it is in the older emergent Nagri system. Differences in fossil productivity between the older and younger parts of the Dhok Pathan Formation are also expressed in decreased frequency of fossils in the upper Dhok Pathan Formation, especially after 7.1 Ma.

Biostratigraphic Record

In the following sections we examine aspects of faunal change in the late Miocene of the Siwaliks. To reconstruct a picture of such change, we ideally would like to know for each time interval the original relative species abundances within the community, as well as the patterns of species turnover. However, this is not possible with fossil taxa because of the taphonomic filters that modify death assemblages, fossil preservation, and recovery. As discussed below, our approach assumes that each species has a more or less constant abundance over its duration. At present we see no evidence for major fluctuations in abundance in more than a few species, and our record cannot detect and evaluate more subtle differences in abundance. At the family level, biostratigraphic surveys and skeletal-element analyses do show changing relative abundances. For example, the numbers of recovered astragali indicated that between 9.3 and 6.3 Ma tragulids decrease and bovids increase in relative abundance (Barry et al. 1991; M. E. Morgan unpublished data). We include some discussion of abundance patterns, but here we are more interested in the patterns of species presence or absence through time.

We begin by examining the patterns of *observed* first and last *occurrences,* that is, the distributions of empirically observed fossil data, and using them to *infer* the distributions of first and last *appearances.* We argue that these inferred first and last appearances better approximate the ''true'' appearances and disappearances of species in the Potwar. We then use several approaches—comparative anatomy, stable isotopes, occlusal microwear, body size—to infer diet and habitat preference in a number of these species in order to assess the extent to which community structure changes or remains stable over time. Finally, we examine the relationships between patterns of faunal change and indicators of environmental change.

Because the Potwar sequence is a local sequence, it is worth noting that first and last appearances are likely to be due to geographic range extensions and contractions, not to actual speciation or extinction events. This would be the case for any local sequence. A moment's reflection reveals the enormous amount and quality of data, in terms of geographical breadth and chronological control, necessary to document a sequence of actual

species originations, extinctions, and species-wide dispersal events for these taxa. In what follows ''extinction'' refers both to local extinctions resulting from range contractions and to global extinctions. ''Appearance'' refers to immigration as well as speciation.

Fossil Material

The Siwalik fossil material consists primarily of isolated dental, cranial, and postcranial elements of mammals, reptiles, and fish. Most of this material is fragmentary and difficult to assign to species; however, occasional more-complete specimens provide a comparative basis for assigning fragmentary fossils to species. We include in our analysis 115 mammalian taxa from eight orders: Insectivora, Scandentia, Primates, Tubulidentata, Lagomorpha, Perissodactyla, Artiodactyla, and Rodentia (Appendix 4). The major taxa omitted are the Carnivora, Elephantoidea, and Rhinocerotidae. These latter taxa contributed importantly to the Siwalik Neogene mammalian communities, but we have eliminated them from analysis primarily because comprehensive identifications of our material are still ongoing.

The stratigraphic occurrences reported here are based on collections in the American Museum of Natural History and the Yale Peabody Museum, as well as on collections made by the GSP-Harvard project. In some cases specimens that indicate significant range extensions are known from very poorly dated localities but are not included because of the inadequate dating. Such specimens include the types of *Tragoportax salmontanus* (ca. 7.9–8.1 Ma) and *Nycticeboides simpsoni* (ca. 8.8 Ma), and a skull of *Orycteropus browni* (ca. 7.9 Ma). In addition, the first occurrence of *Hexaprotodon sivalensis* might be as old as 6.1 Ma or even 7.2 Ma, the first occurrence of *Elephas planifrons* as old as 5.9 Ma, and the first occurrence of *Hippohyus lydekkeri* as old as 6.0 Ma.

With a few exceptions, the analyses of this paper are done with species or presumed species lineages that are treated as one taxon. The most important exception is the equids, which are represented by two or three species at all but the earliest horizons. Some recent progress has been made on the species-level systematics of the group, which indicates that

there were probably no more than six species in the Siwaliks during the late Miocene. The bulk of the available material consists of isolated teeth and skeletal elements that cannot easily be assigned to recognized species. We include the equids, however, because they are an important ecological component of latest Miocene fossil assemblages. Other exceptions include lorisids, tree shrews, and dormice, all of which are numerically insignificant. Where relative abundances are cited, the figures are based on counts of the number of cataloged specimens, corrected for multiple specimens thought to belong to one individual. Many species are new and not yet described, and others have not yet been confidently identified. In this paper we refer to such taxa by the number of a locality that has a typical specimen (e.g., *Dorcatherium* ''Y373 species'' or ''?Tragelaphini/D013 species''). Some taxa that we think may be new are referred to as ''unnamed.''

Stratigraphic Ranges and Pattern of First and Last Occurrences

Appendix 4 gives the age of first and last occurrence on the Potwar Plateau for the 115 taxa occurring in the interval from 10.7 to 5.7 Ma. For each species, we define as a first or last occurrence event (FO or LO) the locality on the Potwar Plateau that we infer to be stratigraphically the lowest or highest in the Potwar composite stratigraphic column, and therefore the oldest or youngest. Note that this is dependent both on the empirical observation that a fossil at a locality represents a particular species and on the inference that a locality is the lowest or highest in our composite section. As discussed earlier, such inferences are generally firm. The ages used are the locality age estimates discussed previously.

Figure 12 shows the observed stratigraphic ranges ordered from oldest to youngest (data from Appendix 4). Seventy-two species have observed ranges (i.e., both the first and the last occurrences) lying entirely within the 10.7–5.7-Ma interval, and another 43 have either a first or a last occurrence within the study interval, giving a total of 187 events. With three exceptions, there is a strong positive relationship between the number of events and the
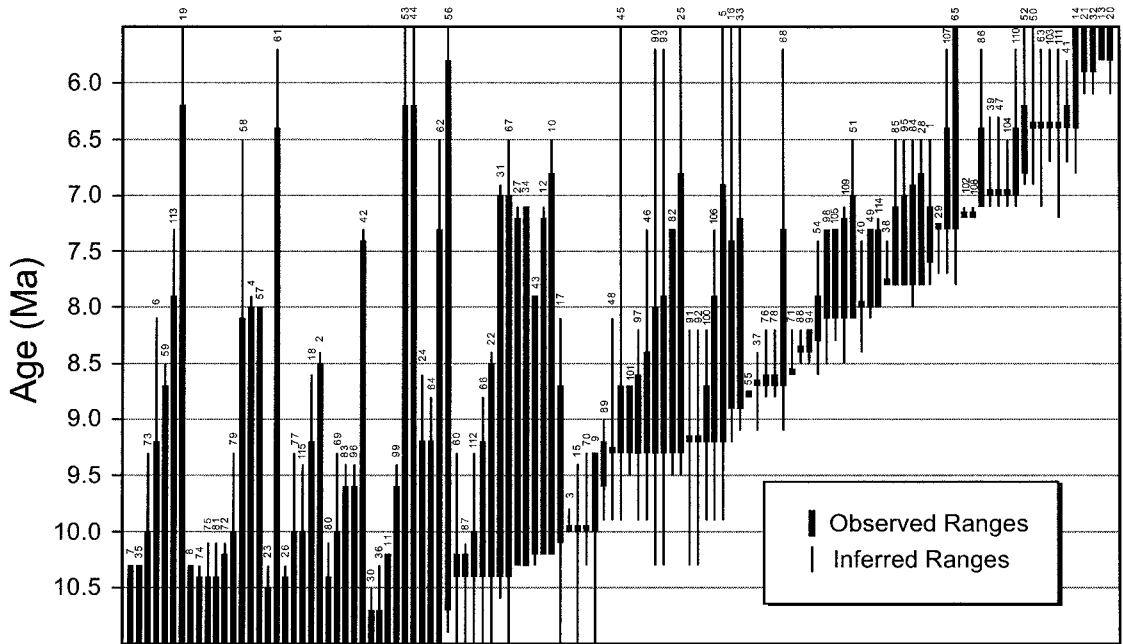
FIGURE 12.   Observed and inferred stratigraphic ranges of 115 taxa (data from Appendix 4). The numbers identify taxa in Appendix 4.

number of collected specimens within an interval, and this is especially so at 10.4 Ma, 10.0 Ma, 9.3–9.2 Ma, and 8.7 Ma (Fig. 13A,B). One exception to the concordance of well-sampled intervals and occurrence events is at 8.1–8.0 Ma, when there are many fossils of both large and small mammals, but only a slightly above average number of events. The other two exceptions are a broad interval of time between 7.0 and 7.3 Ma and the 6.4-Ma interval, during which unusually large numbers of events occur despite only average or below average fossil abundance.

The correlation between interval sample size and number of first/last occurrences (Fig. 13C) introduces a bias, making interpretation of the pattern of occurrences challenging (Badgley and Gingerich 1988). That is, episodes of low and high turnover may be ''real,'' or they may be artifacts of taphonomic factors that affected fossil productivity. Although sequences of first and last occurrences will rarely record the ''true'' pattern of first and last appearance, it is the ''true'' pattern we need to know to discuss faunal dynamics adequately. It is therefore necessary to take variation in the number of specimens (''data quality'') into ac-

count, and to eliminate or at least minimize its effects. Establishing confidence limits on species ranges is thus an important step toward understanding the dynamics of faunal change. In the following we refer to these ''true'' first and last appearances as ''inferred first/last appearances'' (IFA/ILA), or when we are referring to their confidence interval limits, ''inferred first/last appearance limits'' (IFAL/ILAL). Because we have a long, continuous, and relatively fossiliferous sequence in the Potwar Plateau, we are able to estimate such limits for a significant fraction of first and last occurrences.

Calculating Limits for Chronostratigraphic Ranges

In earlier papers (Barry et al. 1990, 1991, 1995) we analyzed the pattern of faunal turnover in the Potwar sequence by half-million-year intervals, and we judged its reliability using ''interval-quality scores'' and indices of completeness. Our goal was to assess the extent to which the actual fossil record reflected the original fauna in any particular interval. More recently (Pilbeam et al. 1996) we argued that, in addition to assessing data quality by
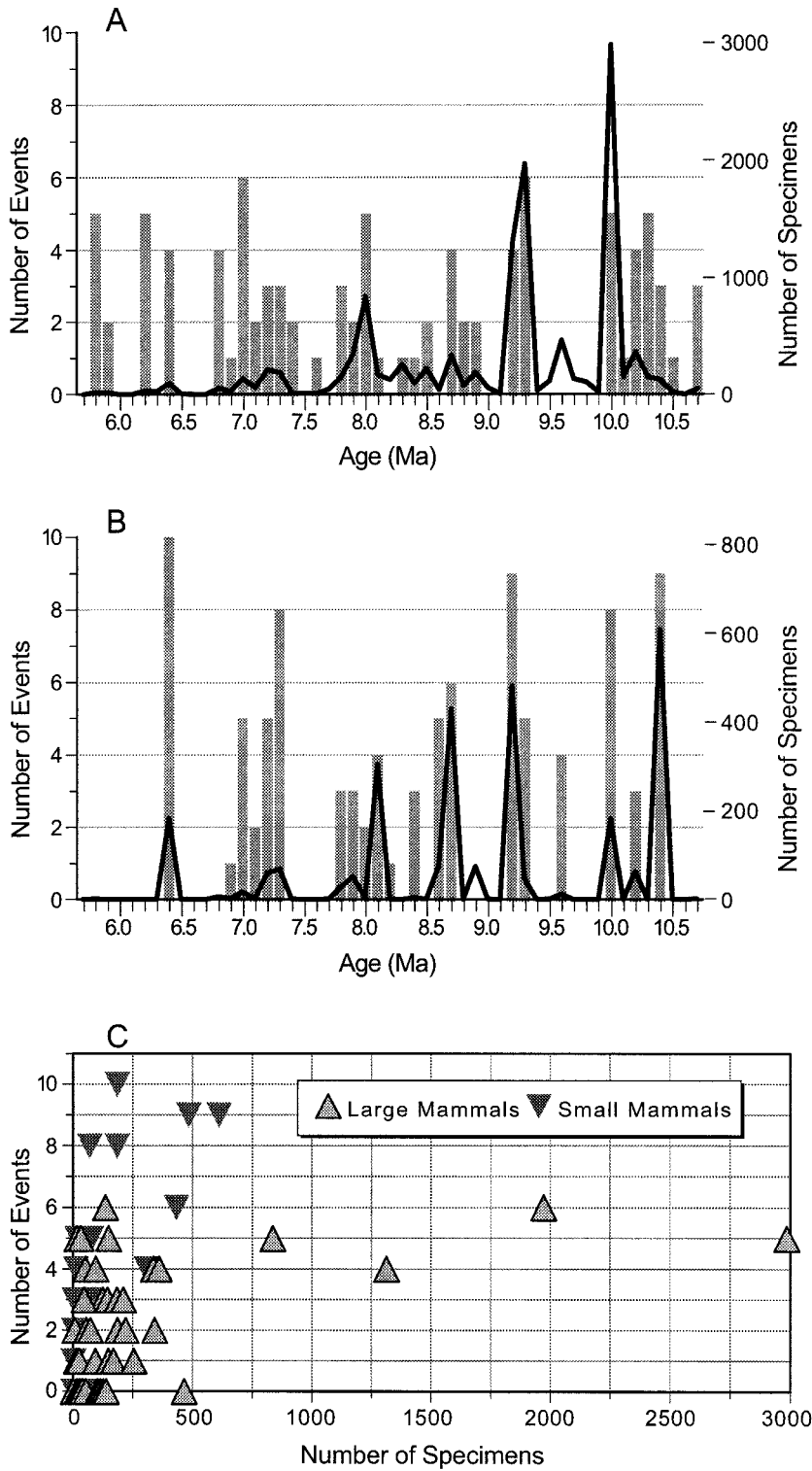
FIGURE 13. Relationships between number of specimens and number of events. A, Number of first and last occurrence events (gray bars) and number of specimens (black line) per interval for large mammals. B, Number of first and last occurrence events (gray bars) and number of specimens (black line) per interval for small mammals. C, Number of events against number of specimens for each interval (*n* = 102).

time intervals for the fauna as a whole, it is also necessary to do so for each individual taxon. For each species we should ask, How confident are we that the empirically observed first or last occurrence estimates the actual first or last appearance? And, if we lack confidence in the first or last occurrence, what is a reasonable limit to the species true stratigraphic range?

There are several possible approaches to the problem of inferring appearances from occurrences. Strauss and Sadler (1989), among others, used a method based on the distribution of the size of gaps between occurrences of a prescribed species to (1) set expectations about gap lengths and (2) estimate a confidence interval for the position of the endpoint of its stratigraphic range. We previously applied this approach to two genera, *Sivapithecus* and *Sayimys* (Flynn et al. 1990). Marshall expanded the Strauss and Sadler model in various ways, most interestingly by first using an approach that relaxed some assumptions about the distributions of gaps and allowed for the calculation of upper and lower bounds on the confidence interval (Marshall 1994), and subsequently using measures of fossil preservation and recovery bias to calculate confidence intervals (Marshall 1997). The distribution-free model (Marshall 1994), however, requires a rich fossil record, with at least seven fossil localities per taxon to calculate a 50% confidence interval with a confidence probability of 0.95. This is a condition not met for many Siwalik species. In addition, the stratigraphic distribution of gaps in the Siwaliks (Fig. 8) plainly violates a remaining critical assumption that there is no correlation between stratigraphic position and gap duration. To use gap-based approaches, therefore, it is first necessary to develop an independent preservation and collecting bias function (Marshall 1997). This we have not yet done.

Here we use instead an approach modified from ideas developed by Shaw (1964) and Koch (1987). This approach uses the abundance of a prescribed taxon relative to the overall abundance of the fossils within its observed range to determine an expectation for finding the taxon (its probability of occurrence). We then use the number of specimens in adjacent 100-Kyr intervals outside the observed range to place confidence limits on the taxon's range endpoints by determining at what point the expectation is not reasonably met. As with gap-based approaches, the resulting confidence limits identify only a stratigraphic interval over which the taxon appears or disappears. They do not specify a shorter interval in which the taxon is most likely to have appeared or disappeared. However, we subsequently cull the data, using in our analyses only species with short confidence intervals. We believe the confidence interval limits of the taxa that are not culled closely approximate the true first or last appearances.

For each taxon we estimate the IFA and ILA limits by first calculating the probability of collecting at least one specimen of the prescribed species as:

$$P_i = 1 - (1 - n/m)^r$$

where P_i = probability of finding taxon i; n = number of specimens attributed to taxon i over its total observed range; m = total number of specimens of either small or large mammals present during the observed range of the taxon; and r = number of small or large mammal specimens in the interval, or series of successive intervals, adjacent to the first or last occurrence of taxon i. (We evaluate small and large mammals separately because of the different recovery methods—screenwashing versus surface collection.)

Our formulation differs from that of Koch (1987) in two ways. First, he estimated the probability of occurrence for a taxon (n/m) as the number of times (n) it was present in a series of m samples or ''collections,'' whereas we estimate the probability as the number of specimens of the taxon relative to the total number of fossils in one collection spanning the whole observed range of the taxon. Second, Koch (1987) calculated the probability of the taxon occurring in a second series of r samples, whereas we calculate the probability of one occurrence in a single additional sample containing r specimens. In this way our approach is closer to that of Shaw (1964). We are, however, most interested in finding how large m has to be, that is how many adjacent

intervals have to be merged, before our expectation of finding one additional specimen becomes unlikely (given some critical value of P_i). We assume that the relative abundance of the specified taxon does not change throughout its stratigraphic range. That is, n/m as calculated over the taxon's whole range is a good estimator of the probability of occurrence at the ends of its range (Shaw 1964).

We have set the critical value for P_i to 0.8, for us a reasonable balance between having an adequate number of species for subsequent analyses and having a high level of confidence. The number of intervals required to obtain a probability equal to or greater than 0.8 below the FO and above the LO were then counted—these endpoints represent the limits to the IFA or ILA range extensions, respectively. As an example, the murid rodent cf. *Parapelomys robertsi* has a FO in 8.1 Ma and a LO in 7.2 Ma. Between 8.1 and 7.2 Ma, there are 521 small-mammal specimens (*m*) in our collections, 71 (*n*) of which are cf. *Parapelomys robertsi*. In the intervals at 8.2, 8.3, 8.4, 8.5, and 8.6 Ma, there are 1, 0, 4, 1, and 77 small-mammal specimens respectively. The cumulative sums of the values for P_i are then: 0.136, 0.136, 0.519, 0.585, and 1.00. Using a cutoff value of 0.8, we would place the limit of the IFA confidence interval in the 8.5-Ma interval, since the high P_i value for the 8.6-Ma interval indicates that it is unlikely that the species was present in that interval. The true appearance, however, could lie anywhere between 8.1 and 8.5 Ma. Similarly, there are 2, 17, and 2 small-mammal specimens in the intervals at 7.1, 7.0, and 6.9 Ma, giving successive probabilities of 0.254, 0.938, and 0.954, and a limit for the ILA confidence interval of 7.1 Ma.

Although the need to differentiate between observed and inferred appearances/disappearances is clear, not all of the range extensions are equally useful. For example, the limit to the ILA range extension for cf. *Parapelomys robertsi* falls within 100 Kyr of the observed LO, but the limit for the IFA range extension is 400 Kyr older than the FO. We believe that the shorter ILA range extension is a more informative, and therefore more useful, estimate than the longer IFA extension. This is because the closer the observed occurrence and inferred limit, the smaller the confidence interval and the more likely that the inferred appearances and disappearances, as equivalents of statistical sample estimates, represent population parameters (i.e., the ''true'' endpoints). Ideally we would prefer to use in our analyses only those species for which the difference between the observed occurrence and the inferred limit is less than 100 Kyr (the scale of resolution we seek to achieve). Because doing so would reduce our data set too much, we use a 200-Kyr cutoff, which increases sample size and remains justifiable on the grounds that confidence intervals only twice the length of the interval scale still provide sufficiently useful information. Accordingly, we have culled our data by eliminating all taxa with range extensions that differ from the corresponding FOs and LOs by more than 200 Kyr. The 78 first or last appearances meeting these limitations are marked in Appendix 4 with an asterisk, and the inferred limits are plotted in stratigraphic order in Figure 14A, with the number of points per interval in Figure 14B.

The Problem of Rare Species

Before discussing the patterns of Figure 14, it is important to recognize that they are derived from a highly reduced data set, and to proceed with our analyses we must assume that the culled data are representative of the whole. This culling is particularly worrisome if the reduced data set preferentially excludes classes of species, such as those that are rare or have short ranges (McKinney et al. 1996).

The data-culling procedure we use tends to exclude rare species. This is because rare taxa usually appear in only the most fossiliferous intervals, and the limits to their appearances and terminations in less fossiliferous adjacent intervals will be known with less precision. The problem is demonstrated in Figure 15, which compares the frequency distributions of abundances of species included to those of species excluded from analysis. (Abundance was determined as relative abundance over the species' observed stratigraphic range.) Although the figure has relatively more very rare species in the excluded set (32% versus 23%), and more common species in the included set (35% versus 23%), the effect is
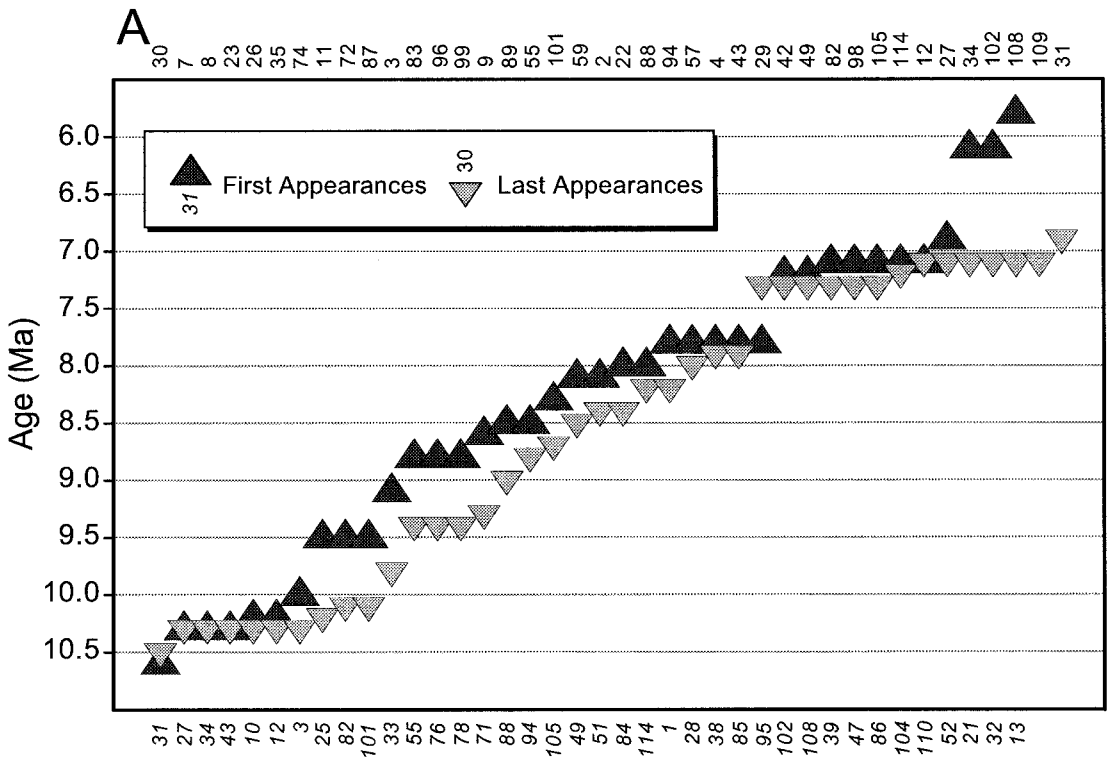
FIGURE 14A.   Seventy-eight culled first or last appearance events. Events in stratigraphic order. The numbers identify taxa in Appendix 4, with first appearances being on the lower border and last appearances on the upper.

weak. Importantly, some very rare species are included in the analysis.

Figure 16, which compares the observed durations of included and excluded taxa, shows that the two distributions are very similar, and that taxa with short durations, as well as those with moderate and long durations, are in both data sets. (The few taxa with very long durations are mostly undivided lineages of successive species. These lineages are under study and will be progressively resolved to the species level.) There are, however, interesting differences in the stratigraphic distributions of species when they are classified by duration. Species of short duration tend to appear after 9 Ma, whereas species with long durations are more likely to have appeared before 9 Ma. The pattern is apparent for both included (Fig. 17A) and excluded (Fig. 17B) taxa, whether observed or inferred ranges are considered. Flynn et al. (1995) previously reported the same changed pattern of species longevity.

Data Analysis

Patterns of Inferred First/Last Appearances.— The two issues that we want to evaluate are the following:

1. What is the pattern of appearances and disappearances? That is, are the IFALs and ILALs distributed fairly evenly, suggesting a relatively steady rate of faunal change; or are they clumped, suggesting a pulsed pattern of faunal change; or neither?

2. Is there detectable change in the ecology of the species over this 5-Myr period and, if so, what is the nature of the change?

When we remove the taxa that do not meet our criteria, we are left with less than one-half of our original data (Figs. 12, 14). As noted, we believe that significant new biases have not been introduced by our selective culling and that the remaining data should better represent the actual pattern of species first and last appearances in the Siwaliks than the complete data set. After culling, 78 faunal events remain, including 38 IFALs and 40 ILALs. The

B
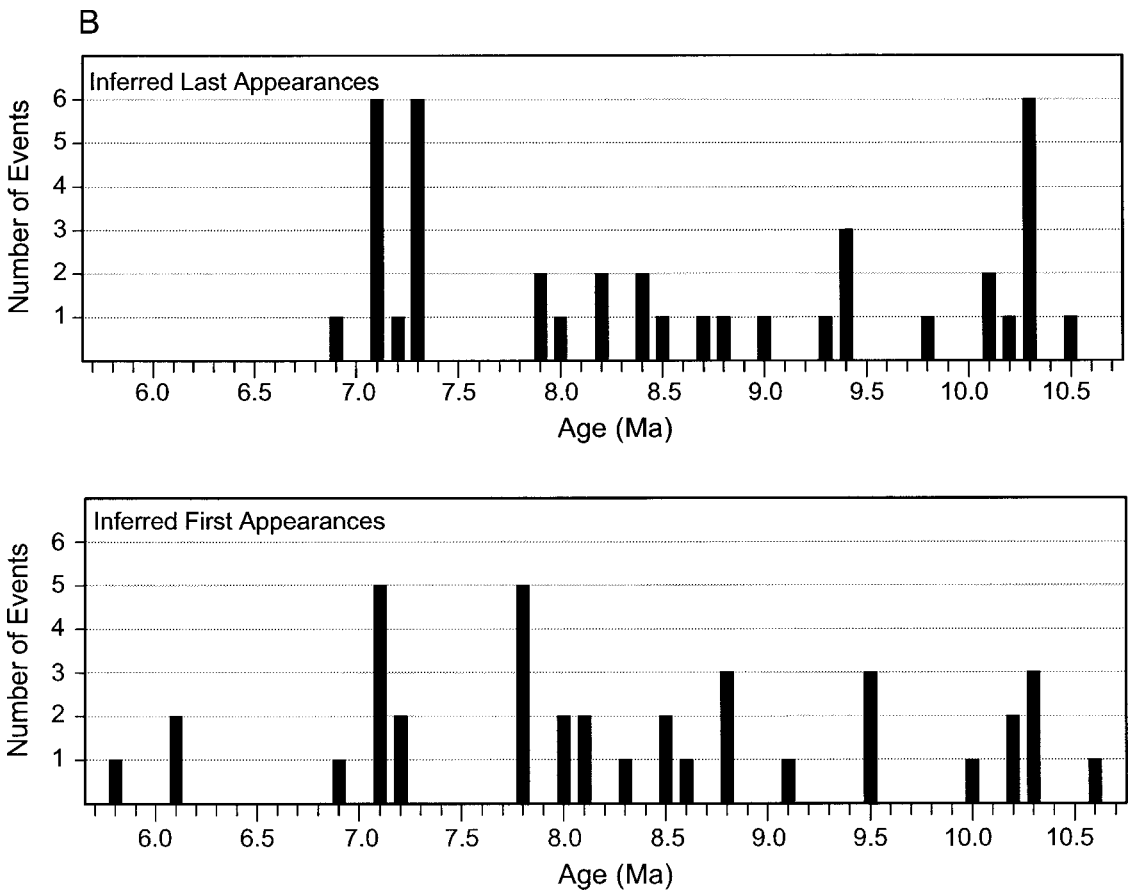
FIGURE 14B.   Seventy-eight culled first or last appearance events. Number of events per interval. There are 38 first appearances and 40 last appearances.

median number of events is 1 per 100-Kyr interval (mean: 1.5), with an observed range from 0 to 11 events per interval. Figure 14B shows that there are many intervals with no events and many intervals with one, two, or three events, and that such intervals are distributed throughout the sequence. This suggests that faunal change occurred at all times, with a background level of three or fewer events per 100 Kyr. However, a few intervals seem to incorporate times of more elevated faunal change and, although there is no sharp discontinuity from background, they are of special interest.

Among the inferred first appearances, only two intervals (7.8 and 7.1 Ma) have more than three events. At 7.8 Ma, two of the five inferred appearances are small mammals, the murid *Progonomys* ''new sp. at Y581'' and the rhizomyid *Eicooryctes kaulialensis*, and three

are large mammals, the tragulid *Dorcatherium* ''Y373 species,'' the bovid ''Bovidae/Y905 unnamed species,'' and the colobine cf. *Presbytis sivalensis*. The first four of these also have their first occurrences at 7.8, whereas the colobine is first known from the 7.6-Ma interval. In this case, the four coincident first appearances and first occurrences give us confidence in the timing of this event. At 7.1 Ma, three of the inferred events are rodents, the murids *Parapelomys robertsi* and *Karnimata* cf. *huxleyi*, and the rhizomyid *Rhizomyides sivalensis*. The other two are as yet undescribed bovids, known only from a single interval. In this case, the precise timing of the appearances is less certain, as four of the five taxa have their actual first occurrences in the 7.0-Ma interval.

The inferred last appearances also show intervals of marked faunal change, with one at 10.3 Ma and two others at 7.3 and 7.1 Ma. Five
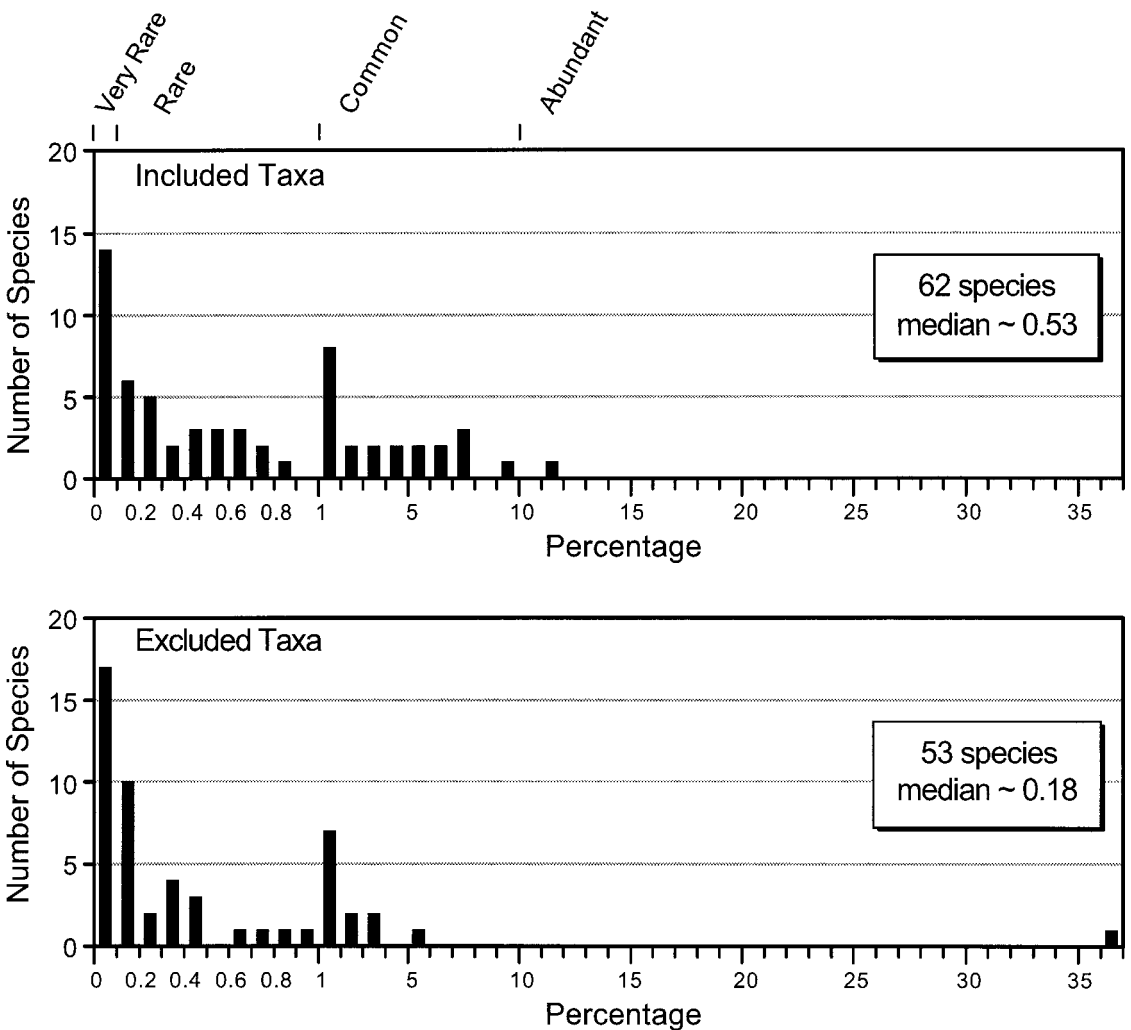
FIGURE 15. Frequency distribution of relative abundances of included taxa compared with that of excluded taxa. (Relative abundance was determined over the species' observed stratigraphic range as n/m, where n is the number of specimens of the taxon and m is the total number of either small or large mammal specimens over the observed range of the taxon.) Abundance classes at top; very rare: less than 0.1%; rare: 0.1%–1%; common: 1%–10%; abundant: greater than 10%.

of the six events at 10.3 Ma involve large mammals, including two suids, *Conohyus sindiense* and *Listriodon pentapotamiae*, two tragulids, *Dorcatherium* cf. *majus* and *Dorcabune anthracotherioides*, and the giraffe *Giraffokeryx punjabiensis*. The sole small mammal is an undescribed species of cricetid rodent. Three of these six taxa also have last occurrences at 10.3 Ma and two others at 10.4 Ma, and the timing of the event seems reasonably placed at 10.3 Ma. Disappearing taxa at 7.3 Ma include the murids *Karnimata* ''Y024 unnamed species'' and *Progonomys* nr. *debruijni*, the rhizomyid

Kanisamys sivalensis, the large tragulid *Dorcatherium* ''Y457 species,'' the large bovid ''Large Boselaphini/Y927 species,'' and the very small bovid *Elachistoceras khauristanensis*. The first five taxa have their last occurrences in the same 7.3-Ma interval. At 7.1 Ma there are three large mammals, the suid *Hippopotamodon sivalense*, the tragulid *Dorcatherium* ''Y311 species,'' and the giraffe *Bramatherium megacephalum*, as well as the murid rodents we refer to as cf. *Parapelomys robertsi*, cf. *Mus* ''Y931 species,'' and *Karnimata* cf. *darwini*. Only one of these six has a last occurrence in
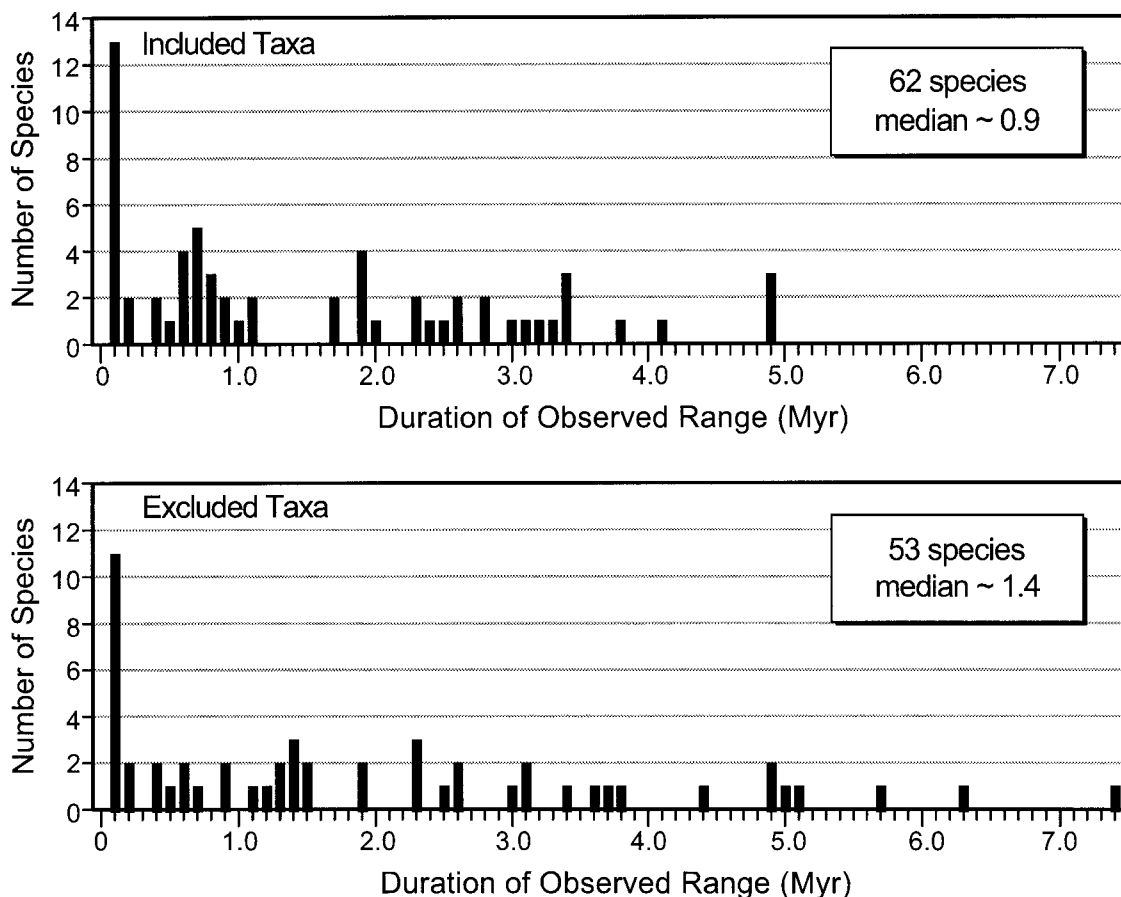
FIGURE 16. Frequency distribution of observed durations of included taxa compared with that of excluded taxa. Median duration of 62 included taxa was approximately 0.9 Myr. Median duration of 53 excluded taxa was approximately 1.4 Myr.

the 7.1-Ma interval; the other five are last found at 7.2 Ma.

For each taxon, we place the events on Figure 14 at the limit of the potential range extension, without attempting to consider where within the extension the event might actually have been. An alternative procedure is to assume that the probability of finding the "true" first/last appearance is the same for each successive interval, and then to divide the event equally among all the intervals in which it might lie (Barry et al. 1990). For our purposes this procedure is conservative, because it results in the distribution of events over time that most underestimates the magnitude of turnover maxima and minima, and best visually expresses the uncertainty of their ages. Figure 18 is the resulting plot of the inferred first and last appearances for the 78 events in

Figure 14, but with each event now partitioned as described above. Inspection of this figure leads us to the same conclusions. That is, many intervals have little or no faunal change, and a very few have apparently elevated change that could be interpreted as pulses. Among the latter is a period centered on 10.3 Ma, which is best characterized by disappearances, another at 7.8 Ma with the largest number of first appearances, and a much broader period from ca. 7.3 to 7.0 Ma, which encompasses both appearances and disappearances. It is important to note that the three pulses cannot be attributed to changing levels of fossil abundance because they occur within intervals with consistently low numbers of specimens (Fig. 7A,B).

With 40 last and 38 first appearances, if turnover were constant we would expect 1.5 events
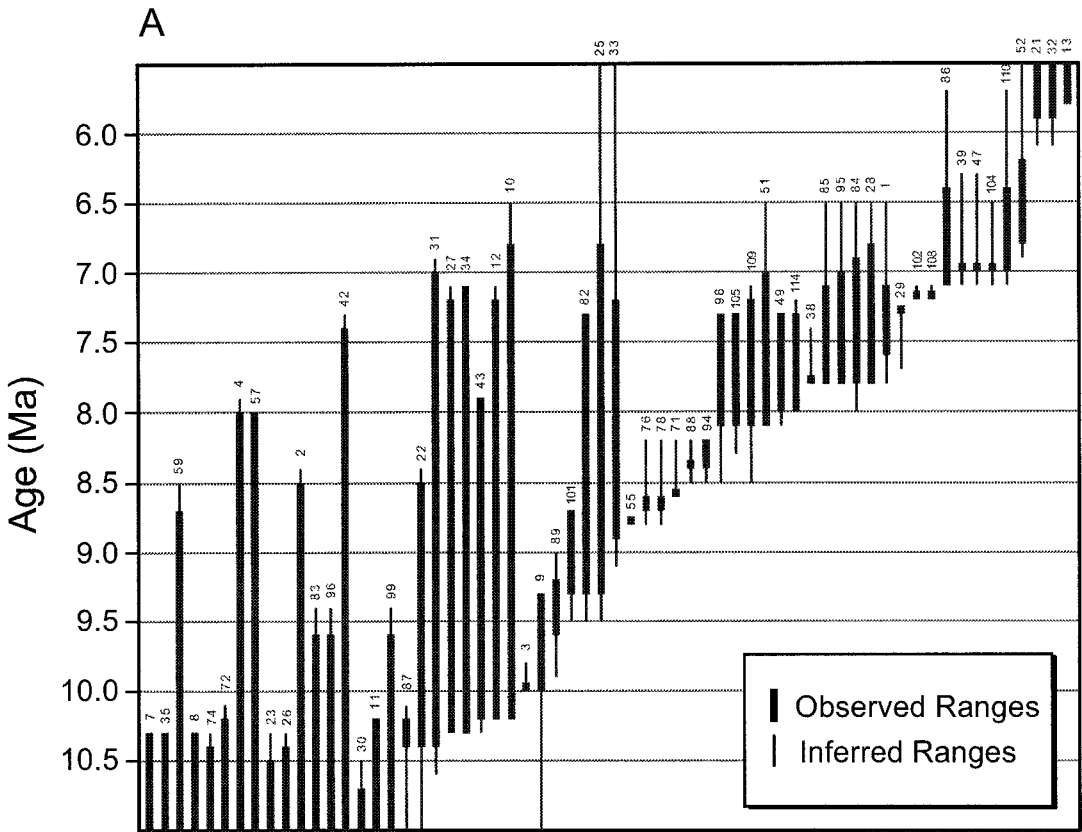
FIGURE 17A. Observed and inferred stratigraphic ranges of 115 taxa (data from Appendix 4). Taxa included in analyses ($n = 62$).

to occur in each 100-Kyr interval. That is, each interval would have slightly less than 2% of the total turnover. At 10.3 Ma there are 9 events, at 7.8 Ma 5 events, and between 7.3 and 7.1 Ma 20 events (Fig. 14A,B). These three periods constitute 11.5%, 6.4%, and 25.6% respectively of the observed turnover (or summed 43.6%), against expectations of 1.9%, 1.9%, and 5.7% (total 9.6%). A comparison to a uniform distribution with 1.53 events per interval shows that this is a highly significant difference (Kolmagorov-Smirnov $D_{0.5} = 0.22333$, $p \ll 0.01$). We conclude that turnover is not constant between 10.7 and 5.7 Ma.

We estimate that 43 species were present in the 10.3-Ma interval because (1) they have been found in the interval, (2) their inferred range extension overlaps with the interval, or (3) they are documented in both an older and a younger interval. Of these 43 species, 6 disappear in the interval and only 11 (30%) of the remaining 37 survived to the 7.3-Ma interval. (The discrepancy between this number and Figure 14B is due to the inclusion of 14 species in the 10.3-Ma fauna that were excluded from the preceding analysis because their terminations are too poorly known, e.g., *Orycteropus* spp. Two of the 14 might range into the 7.3-Ma interval.) Similarly, of 31 species in the 7.3-Ma interval, only 11 (35%) persisted from the 10.3-Ma interval. Thus, when looked at from either perspective, about two-thirds of the species change between the two bounding events, and turnover seems to be relatively rapid. With the exception of the secondary-appearance event at 7.8 Ma, turnover during the period from 10.3 to 7.3 Ma also seems rather steady (Figs. 14A,B, 18). Of the 11 species persisting between 10.3 and 7.3 Ma, there is no significant difference in the number of large species (8) versus small species (3), compared with those that disappear (14 and 18) ($\chi^2 =$
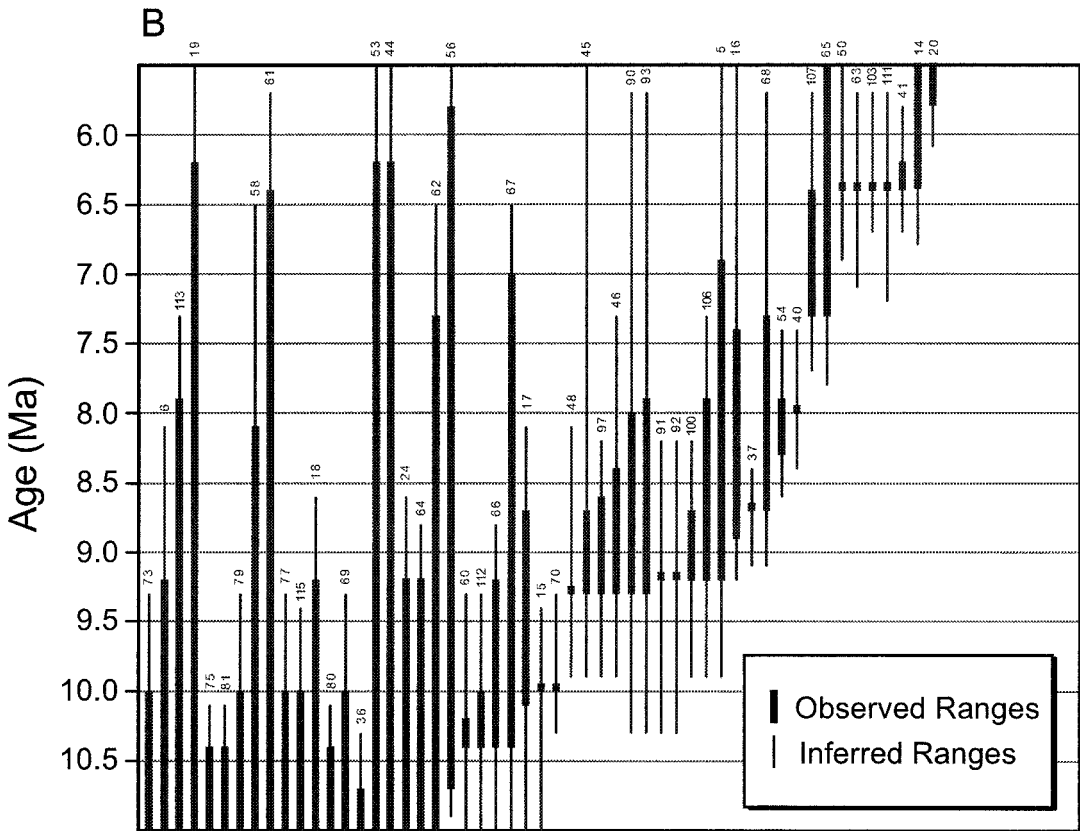
FIGURE 17B. Observed and inferred stratigraphic ranges of 115 taxa (data from Appendix 4). Taxa excluded from analyses (*n* = 53). The numbers identify taxa in Appendix 4.

2.751, *p* = 0.097). We conclude that Siwalik mammal assemblages do not exhibit stasis between 10.7 and 5.7 Ma.

The peaks reported here are not the same as the late Miocene turnover peaks reported by Quade and Cerling (1995) and Cerling et al. (1998). Those authors calculated faunal change indices by weighing the number of first/last occurrences by the estimated number of species reported or inferred for each interval, and consequently they reported high levels of turnover at 9.3 Ma and between 8.3 and 7.8 Ma (dates converted to the Cande and Kent [1995] timescale). Apart from theoretical uncertainty about the expected relationship between species richness and the number of appearances on one hand and extinctions on the other (Van Valen 1973; Webb 1984), there are methodological problems with Quade and Cerling's indices. Quade and Cerling (1995) and Cerling et al. (1998) used observed occur-

rences instead of inferred appearances, as well as a measure of species richness ("standing richness") that is, as discussed in the next section, at best poorly estimated and always unreliable. As a result, the reported index values are very sensitive to the declining quality of the latest Miocene Siwalik record. Similarly, the turnover peaks reported by Köhler et al. (1998) are also largely artifacts of the changing quality of the Siwalik record.

Number of Species per Interval.—Species richness, the number of species found or inferred to be present, is notoriously dependent on the number of specimens collected. It is, nevertheless, of interest. In Table 4 and Figure 19A,B we present data on species richness for the Potwar Siwaliks between 10.7 and 5.7 Ma. So they would be comparable to other published studies, these data are based on the observed occurrences, not the inferred extensions, and are calculated as "standing richness." (Stand-
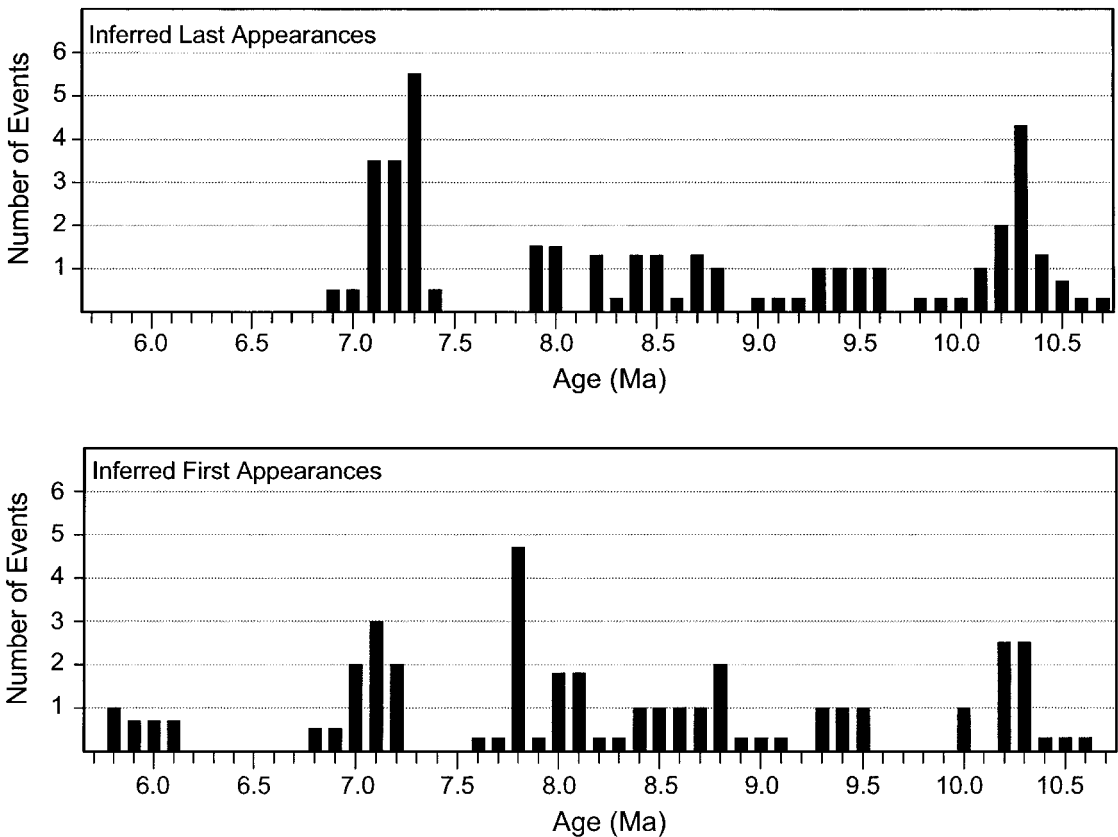
FIGURE 18.   Seventy-eight culled first or last appearance events, partitioned equally among all the intervals included in the species' range expansion. Top, Number of inferred last appearances per interval ($n = 40$). Bottom, Number of inferred first appearances per interval ($n = 38$).

ing richness is the number of taxa known before and after the interval, plus the sum of first occurrences, last occurrences, and only occurrences, divided by two. See Maas et al. [1995] for elaboration and justification of this method.) The calculation assumes that an unrecorded taxon is present in an interval if it is known from both older and younger intervals (the so-called range-through assumption).

As expected, Figure 19A,B shows strong effects of specimen number, with intervals having few specimens registering few taxa. In a previous study we concluded that intervals with more than about 400 specimens of large mammals or more than 150 small mammals were roughly comparable in data quality across intervals (Barry et al. 1995). If these same criteria are used, few of our much shorter intervals can be compared with each other because few have that many specimens, and there is consequently considerable uncertain-

ty about any trend in species richness over time. Clearly the large decline in both data sets after 7.5 Ma is an effect of declining record quality, as is the modest decline in small mammals between 10.3 and 9.2 Ma. These results are inconclusive as to whether the number of species remains stable or changes in either direction between 9.2 and 7.4 Ma, although a separate analysis of small-mammal richness recorded from single sites reinforces the perception of declining numbers of species (Flynn et al. 1998).

Other measures of species richness have been proposed that are less sensitive to sample size (Magurran 1988). Among these is Fisher's α diversity index, which relates the number of species (S) to the number of specimens (N) using a log series model of species abundances. (The value of α approximates the number of species in the sample that should be represented by a single individual. Note

TABLE 4.   Standing species richness by interval.

Interval (Ma)	Large mammals	Small mammals
5.7	5.0	1.0
5.8	4.5	1.0
5.9	3.0	1.0
6.0	2.0	1.0
6.1	2.0	1.0
6.2	4.5	1.0
6.3	7.0	1.0
6.4	6.5	4.5
6.5	5.0	5.0
6.6	5.0	5.0
6.7	5.0	5.0
6.8	6.0	5.0
6.9	7.5	5.5
7.0	10.0	7.0
7.1	11.0	7.0
7.2	13.5	8.5
7.3	16.0	10.0
7.4	17.0	12.0
7.5	18.0	12.0
7.6	17.5	12.0
7.7	17.0	12.0
7.8	17.0	10.5
7.9	17.0	10.5
8.0	19.0	12.0
8.1	18.5	11.0
8.2	18.0	10.5
8.3	17.5	11.0
8.4	17.5	11.0
8.5	19.0	10.0
8.6	20.0	12.0
8.7	21.5	13.0
8.8	22.5	13.0
8.9	21.0	13.0
9.0	20.0	13.0
9.1	20.0	13.0
9.2	21.0	14.5
9.3	21.5	11.5
9.4	20.0	9.0
9.5	20.0	9.0
9.6	20.0	10.0
9.7	20.0	11.0
9.8	20.0	11.0
9.9	20.0	11.0
10.0	20.5	14.5
10.1	18.5	17.0
10.2	17.0	18.5
10.3	16.5	20.0
10.4	16.5	19.5
10.5	16.5	19.0
10.6	17.0	19.0
10.7	17.5	19.0

also that here S is the number of species actually recorded in the interval, not ''standing richness,'' which includes ''range through'' taxa.) Although the assumption that the abundance data should fit a log series is restrictive, the index is known to be robust, and inspection of our raw data from each interval sug-

gests that the species abundance patterns approximately fit log series. Figure 20A,B shows the α values calculated for intervals with adequate samples for large and small mammals plotted against time, with 95% confidence limits. (In the case of the small mammals, minimum sample size was 25 specimens, but intervals with a high proportion of unidentified material also were excluded even if sample size was large. Material from these excluded intervals had been selectively culled for identification, and the subsample of identified fossils is therefore not representative of the whole assemblage in relative proportions. In the case of the large mammals, minimum sample size was 50, except for four intervals at the top and bottom of the section. These were the intervals at 6.4, 6.8, 10.4, and 10.7 Ma.)

Although there is a wide range of values in both data sets, there is a trend toward decreasing α in the younger intervals, most noticeably in the small mammals. In both large and small mammals, the magnitude of the decrease indicates a substantial reduction in the number of species, although certainly not as large as suggested by Figure 19A,B. The trend of decreasing species richness is most apparent if only the largest values are taken from the whole series, but the wide total range in both cases makes interpretation difficult—especially because adjacent intervals may have significantly different values. Inspection of the abundance data suggests that before 7.5 Ma, intervals with low α values either are dominated by a single site (particularly so for the small mammals) or have large numbers of fragmentary equid teeth cataloged as separate specimens. (The latter effect would include the intervals at 7.9, 8.3, and possibly 8.5 Ma.) Thus, we think that the very low values before 7.5 Ma are artifacts of taphonomy, or in a few instances overzealous cataloging practices that led to overrepresentation of equids. Nevertheless, the low values after 7.5 Ma are likely to reflect a real change in the number of species.

A second richness measure is the Margalef diversity index (Magurran 1988), which makes use of the same information on the number of species and number of specimens, but as $D = (S - 1)/\ln N$. In both our large- and
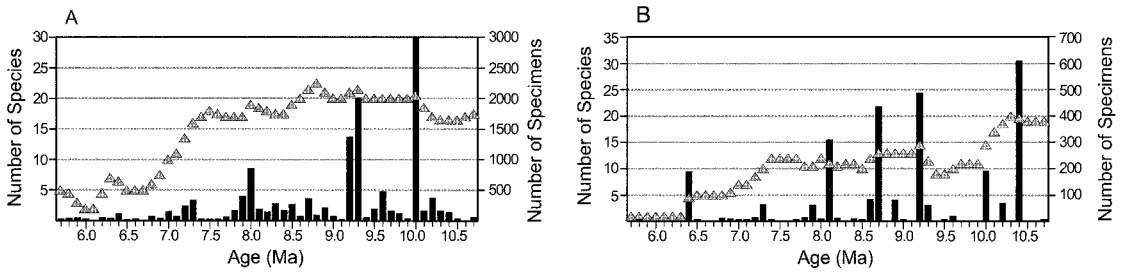
FIGURE 19. Number of species (triangles) and number of specimens (bars) per interval. A, Large mammals. B, Small mammals.

small-mammal data sets the Margalef index closely tracks Fisher's α index (Fig. 20A,B), reinforcing the impression of overall declining species richness in both large and small mammals.

Relative Abundances within Fossil Assemblages.—Other diversity indices emphasize differences in the relative abundance of taxa, as opposed to the number of species. Among these are the Berger-Parker, Simpson, and Shannon Evenness indices, the first two of which measure the dominance of common species relative to the others, whereas the third measures the evenness of the species abundances (Magurran 1988). The Berger-Parker index is usually represented as the inverse of the proportion of the most common taxon relative to the total sample, but here (Fig. 21A,B) we show it as the basic proportion with 95% confidence limits. (Confidence limits were calculated using the formulas of Ehrenfeld and Littauer [1964].) The Simpson and Shannon Evenness indices (Fig. 22A,B) both use the proportional abundances of all species. The Simpson index disproportionally weighs the most abundant species, whereas the logarithmic transforma-

tion in the Shannon Evenness index weighs species of intermediate abundance most heavily. In using these indices we assume that, although the relative abundances of the fossil assemblages within a given interval do not closely approximate those of the original living communities (Badgley 1986b), the underlying taphonomic biases are constant between intervals (i.e., isotaphonomic). Thus, the comparison of diversity indices between intervals should reveal something about contrasts between the living communities, not just variation in taphonomic conditions. Our assumption rests on the similarity through time of the fluvial environments that preserved the fossils.

Inspection of Figure 21A indicates that the Berger-Parker index values for the large-mammal assemblages delineate three distinct phases. One phase encompasses intervals 10.0 Ma and older, which have faunas with low dominance; a second phase includes intervals from 9.8 to 7.9 Ma, which have faunas with consistently higher (and sometimes markedly higher) dominance; and a third consists of intervals 7.8 Ma and younger, which again have
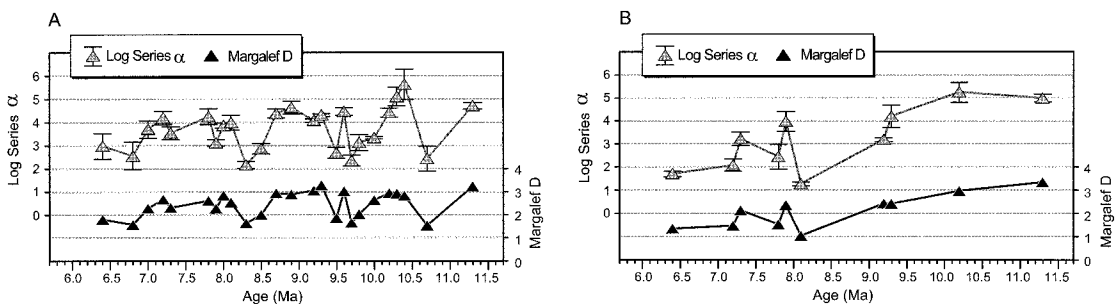
FIGURE 20. Species richness indices over time. Bars on "log series α" points are upper and lower 95% confidence limits. A, Large mammals. B, Small mammals.
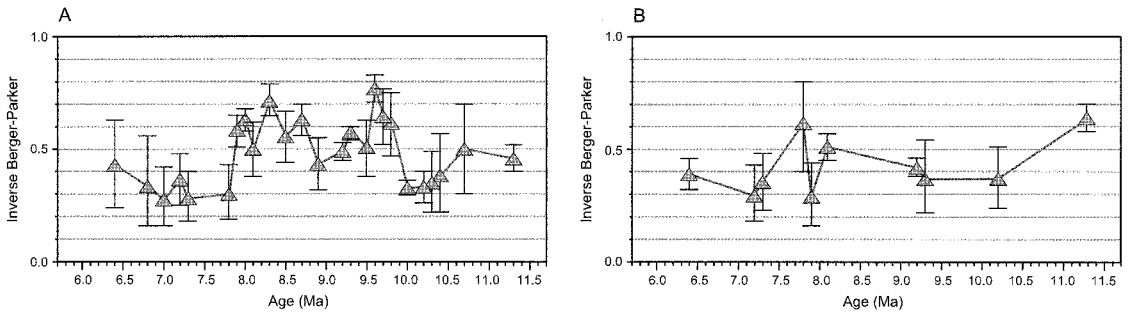
FIGURE 21. Relative abundance (species diversity) over time. Triangles represent value of inverse of Berger-Parker index; bars indicate upper and lower 95% confidence limits. A, Large mammals. B, Small mammals.

more evenly balanced faunas displaying low dominance. Although there is considerable heterogeneity within each phase, χ^2 tests (with a sequential Bonferroni correction) comparing the relative abundances of the taxa in the intervals at 10.0 and 7.8 Ma with those in the intervals between 9.8 and 7.9 Ma confirm the significance of the differences; the only non-significant pairs are the comparisons with the 8.9-Ma interval (Table 5). In the same manner, the Simpson and Shannon Evenness indices (Fig. 22A) track the Berger-Parker index closely, also forming three more or less distinct phases. Notably, both indices show the same changes in faunal dominance from evenly balanced to one-taxon-dominated and back to more evenly balanced. As with the Berger-Parker index, the Simpson and Shannon Evenness indices show the anomalous 8.9-Ma interval to have a more balanced fauna than in either the immediately preceding or the following intervals. The 9.6-Ma interval is also an outlier, registering on both indices as extremely uneven. However, the exceptional index values are probably artifacts of mistakenly

counting equid postcranials from one site as separate individuals, with a resulting over-representation.

With very few exceptions, after 10.7 Ma equids are the most common fossils. They often attain very high relative frequency in our collections (Fig. 23), and their changing relative abundance controls the various dominance-evenness indices. In our preceding discussion of species richness, we noted that high equid relative abundance in the intervals at 7.9, 8.3, and 8.5 Ma might be in part an artifact arising from overemphasis on collecting and cataloging equid teeth. However, such an artifact cannot explain all of the high values from 9.8 to 7.9 Ma (Fig. 23), and there are plainly intervals in which equids strongly dominate the faunas and intervals in which they do not. The observed change in dominance is supported by our biostratigraphic survey data (Table 2, Fig. 24), which shows the proportion of equids relative to that of bovids rising at 9.8 Ma and then falling at ca. 8.5–8.0 Ma. We think it is likely that the shift after 10 Ma from balanced to unbalanced equid-dom-
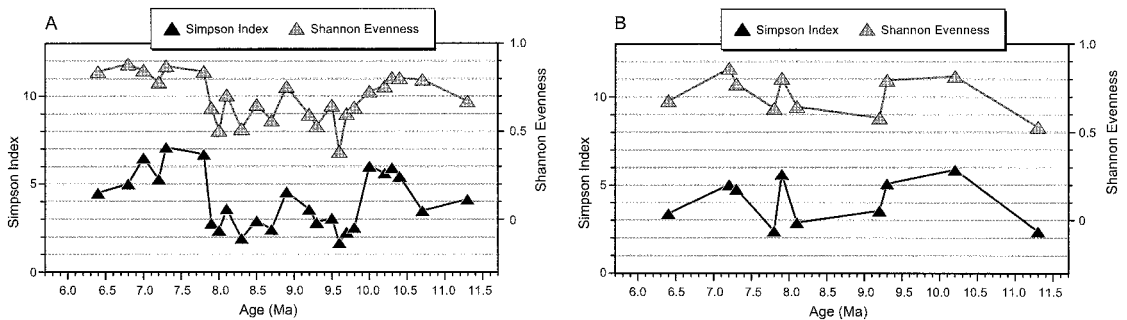
FIGURE 22. Relative abundance (species diversity) over time. The Simpson index is a dominance measure; the Shannon index is an evenness measure. A, Large mammals. B, Small mammals.

TABLE 5. Comparisons of relative abundances of large mammals at 7.8 and 10.0 Ma with relative abundances in intervening intervals.

Interval (Ma)	Most common taxon	All other taxa	χ^2 (7.8 Ma)	p (7.8 Ma)	χ^2 (10.0 Ma)	p (10.0 Ma)
7.8	**20**	**47**			0.230	0.631
7.9	114	81	16.336	0.000*	48.954	0.000*
8.0	251	146	26.282	0.000*	118.530	0.000*
8.1	38	38	5.996	0.014*	9.666	0.002*
8.3	95	38	31.518	0.000*	78.438	0.000*
8.5	50	40	10.271	0.001*	19.610	0.000*
8.7	103	60	21.214	0.000*	58.526	0.000*
8.9	39	51	2.976	0.084	4.308	0.038
9.2	336	348	9.090	0.003*	51.352	0.000*
9.3	633	469	19.499	0.000*	148.591	0.000*
9.5	37	36	6.282	0.012*	10.054	0.002*
9.6	150	45	48.496	0.000*	140.365	0.000*
9.7	44	24	16.444	0.000*	29.453	0.000*
9.8	32	20	11.949	0.001*	18.633	0.000*
10.0	**425**	**876**	0.230	0.631		

* Significant at 0.05 (with a sequential Bonferroni correction).

FIGURE 24. Relative abundance of equids and bovids over time, calculated as percentage of total number of large mammals.

inated faunas is the result of an increase in the number of equid species, which are treated as one taxon in our current analysis. We also speculate that the shift back to more balanced faunas at 7.8 Ma may reflect a reduction in the number of equid species. Finally, on Figures 20, 21, and 22 we have included some ''pre-hipparion'' intervals to place trends in species richness and abundance into a larger context. The large mammals of the 11.3-Ma interval show intermediate dominance, although the giraffe *Giraffokeryx punjabiensis* is by far the most abundant taxon. This species persists into the 10.3-Ma interval, but at much reduced abundance.

None of the dominance/evenness diversity indices show a trend for the small mammals,
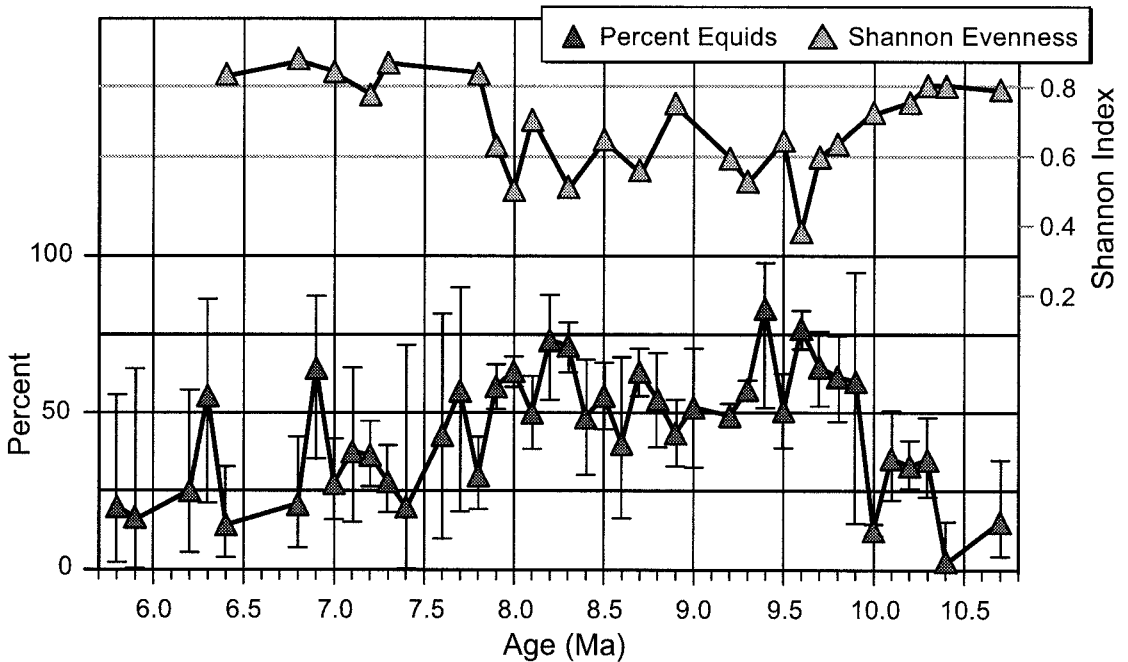
FIGURE 23. Relative abundance of equids over time contrasted with the Shannon Evenness index. Percent equids calculated as the number of equid specimens over the total number of large mammal specimens in each interval. Bars on ''percent equid'' points are upper and lower 95% confidence limits. Intervals with very small samples excluded.

TABLE 6. Comparisons of relative abundances of small mammals at 7.8 and 8.1 Ma with relative abundances in intervening intervals.

Interval	Most common taxon	All other taxa	χ^2 (7.8 Ma)	p (7.8 Ma)	χ^2 (8.1 Ma)	p (8.1 Ma)
6.4	70	110	4.792	0.029	6.652	0.010
7.2	17	41	7.817	0.005*	9.177	0.002*
7.3	24	44	5.299	0.021	5.482	0.019
7.8	**16**	**10**			1.068	0.301
7.9	13	32	7.270	0.007*	7.667	0.006*
8.1	**155**	**149**	1.068	0.301		
9.2	197	276	3.985	0.046	6.512	0.011
9.3	15	26	3.985	0.046	2.998	0.083
10.2	21	36	4.408	0.036	3.844	0.050

* Significant at 0.05 (with a sequential Bonferroni correction).

although the three indices closely track each other. The assemblages at 7.8 and 8.1 Ma are separated from the others on the Berger-Parker and Simpson indices, but χ^2 comparisons (with a sequential Bonferroni correction) of the relative abundances of taxa between these and the other intervals indicate few comparisons are significant at a 0.05 level (Table 6). As noted, small-mammal assemblages tend to be dominated by single localities and could retain a strong taphonomic imprint of predation or hydraulic sorting.

Body Size.—The overall pattern of size structure within a group of related taxa can provide additional information about guild responses to change induced by abiotic and/or biotic events. Within the two most abundant and well-studied groups, muroid rodents and artiodactyls, there is significant change in body size structure between 10 and 9 Ma (Morgan et al. 1995 with revised age estimates; M. E. Morgan unpublished data). Among the rodents, notably larger species of both the Muridae and Rhizomyidae appear. Size estimates are derived from M1 area (see Morgan et al. 1995 for data and methods). Murids first appear at 13.7 Ma and do not change notably in size until the appearance of *Karnimata* ''Y388 unnamed species,'' estimated at about 60 g and first occurring at 9.2 Ma (IFAL 9.9). This species is more than twice the size of its presumed ancestor, *Karnimata* ''Y450 unnamed species,'' estimated at about 25 g and last occurring at 9.6 Ma (ILAL 9.4). The two later species, cf. *Parapelomys robertsi* at 8.1 Ma

(IFAL 8.6) and *Parapelomys robertsi* at 7.0 Ma (IFAL 7.2), continue this increase. Among the rhizomyids, there is size increase within the long-lived *Kanisamys* lineage with the first occurrence of *K. sivalensis* at 9.3 Ma (IFAL 9.5). In addition, several large species of the genus *Brachyrhizomys* (rhizomyids that were comparable in size and habits to living, fossorial bamboo rats) also appear between 10 and 9 Ma, and even larger species such as *Brachyrhizomys choristos* appear at 8.4 Ma (IFAL 8.5). Other notable large rodent species appearing later are the rhizomyid *Protachyoryctes tatroti*, thought to be a large derivative of *Kanisamys sivalensis* (Flynn 1982), at 7.8 Ma (IFAL 8.0), *Rhizomyides sivalensis* at 7.1 Ma (IFAL 7.1), and the porcupine *Hystrix sivalense* at 8.0 Ma (IFAL 8.0). Leporids, which typically weigh more than 1 kg, have an IFAL of 7.8 Ma.

Body weight can be estimated for the five dominant Siwalik artiodactyl families (anthracotheres, suids, giraffes, tragulids, and bovids) from dimensions of the astragalus (Morgan et al. 1995.) Taken as a group, the five taxa occupy a nearly continuous range of sizes that expands markedly just before 10 Ma. In the giraffes, the observed size change at 10.3 Ma occurs at a species boundary, when *Giraffokeryx punjabiensis*, estimated at 233 ± 8 kg (n = 51), is replaced by *Bramatherium megacephalum*, estimated at 840 ± 32 kg (n = 27) (Fig. 25). Although most astragali cannot be attributed to species, a marked size increase also occurs between 11 and 10.3 Ma with the first appearances of the *Selenoportax* and *Tragoceridus* lineages (early populations estimated at 114 ± 4.5 kg, n = 26, and 53 ± 1.3 kg, n = 70 respectively) (Fig. 25). Both giraffes and bovids exhibit continuing size increases after 10 Ma, but trends are difficult to quantify in the absence of associated cranial and postcranial remains that could be used both to recognize species and to estimate size. Nevertheless, horn cores of cf. *Protragelaphus skouzesi* at 8.8 Ma (IFAL 8.8) and ''Large Boselaphini/Y927 species'' at 8.0 Ma (IFAL 8.1) record the appearance of very large bovids and postcranial remains indicate the presence of species weighing nearly 250 kg. In addition, late occurring individuals of *Bramatherium megacephalum* and the *Tragoceridus* lineage all tend to
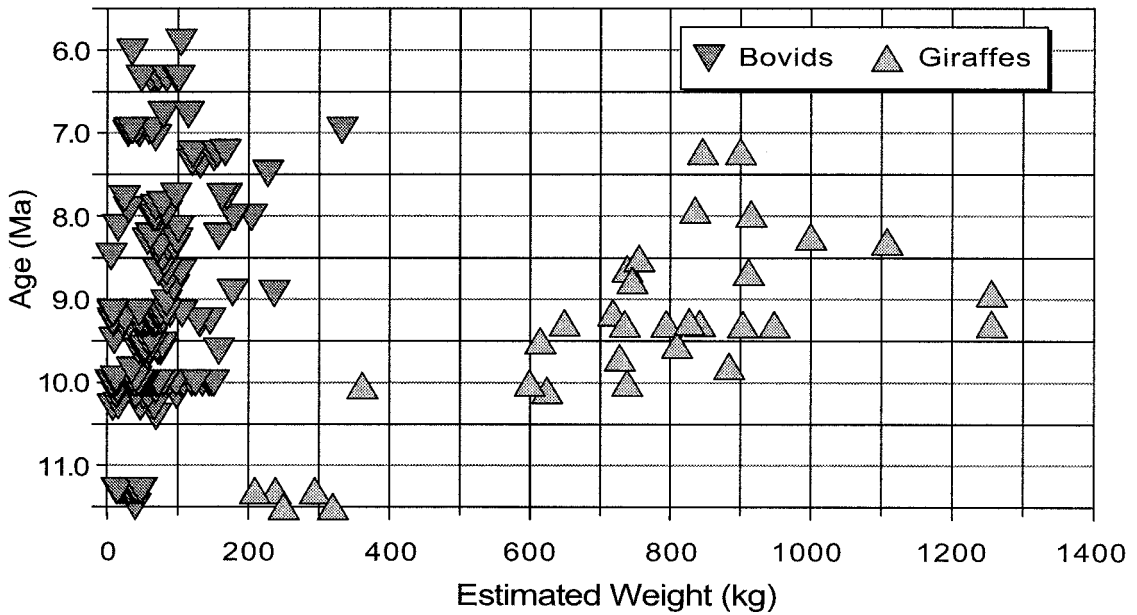
FIGURE 25. Weight estimates for bovids and giraffes, based on distal width of astragalus (DWA). Bovid regression: $2.894 * \log_{10}(DWA) + 0718$. Giraffe regression: $2.725 * \log_{10}(DWA) + 0.776$.

be noticeably larger than older conspecifics. Large suids of the genus *Hippopotamodon* also appear at 10.2 Ma (IFAL 10.2), and in the anthracothere *Hemimeryx* lineage there is a size increase at about 10 Ma.

Ecomorphological Analyses.—Ecomorphological studies provide a means of assessing the ecological requirements of species, which then allow evaluation of differences in community composition. Our objective is to determine to what extent ecologically related groups of taxa behave similarly in their patterns of first and last appearances, or how their patterns might be related to other documented differences. That is, can we detect critical environmental thresholds for species occupying similar niches or sharing key limiting resources such as certain types of vegetation and water availability? Ecomorphological approaches used here include a variety of dietary studies, such as qualitative morphological studies of the dentition, occlusal microwear studies, and isotopic analyses of enamel apatite, as well as body size estimates from dental and postcranial remains (Gunnell et al. 1995; Morgan et al. 1994, 1995; M. E. Morgan unpublished data). We also use information from comparative and functional studies of closely related

extant taxa (Flynn 1982). We identified taxa likely to have arboreal and/or closed habitat requirements and those with grazing and/or open habitat requirements.

Thirty-eight taxa have IFALs between 10.7 and 5.7 Ma. With the possible exception of the large hominoid *Sivapithecus parvada*, known only from one locality at 10.0 Ma, none of the remaining 37 IFALs can be characterized ecologically either as restricted to forested environments or as completely arboreal. However, several newly appearing taxa might be indicative of more-open conditions, including a species of *Giraffa* (IFAL 9.1 Ma), the large antilopine cf. *Protragelaphus skouzesi* (IFAL 8.8 Ma), the gerbil *Abudhabia pakistanensis* (IFAL 8.6 Ma), a second very large bovid with high-crowned teeth that we refer to as ''Large Boselaphini/Y927 species'' (IFAL 8.1), and an indeterminate species of Hippotragini (IFAL 6.9 Ma). Other appearing taxa not meeting the criteria for inclusion in the turnover analysis that have strong ecological signals include the leporids at 7.8 Ma—interpreted as able to utilize relatively open environments—and the hippopotamid *Hexaprotodon*, a likely grazer probably present by 6.1 Ma and possibly as early as 7.2 Ma. Rhizomyid rodents, which are

present throughout the middle and late Miocene in the Siwaliks, show an increase in hypsodonty at 9.5 Ma with the IFAL of *Kanisamys sivalensis*, and marked hypsodonty at 7.8 Ma with the IFAL of *Eicooryctes kaulialensis* (Flynn 1982). Finally, although we cannot directly ascertain the individual diets of any of the bovid species because of difficulties in associating teeth with horn cores (the basis of species identifications), we can say that, overall, bovids show an increased reliance on C_4 grasses, judging from stable carbon isotope analysis of bovid teeth (Morgan et al. 1994).

Forty taxa have ILALs during this 5-Myr interval, including several with arboreal, closed, or moist habitat requirements. These include species of the *Sivapithecus* clade (ILAL 8.4 Ma), deinotheres and chalicotheres (both ILAL 8.0), and seven species of tragulids. The latter were dominant or equal in abundance to bovids until 10 Ma, but in the late Miocene they became much rarer as well as less diverse (Barry et al. 1991; M. E. Morgan unpublished data). Other locally disappearing taxa, which were culled from our turnover analysis but are still relevant, include the ctenodactylid rodent *Sayimys chinjiensis* (ILAL 9.4 Ma), the tree squirrel *Ratufa* (ILAL 8.8 Ma), lorisids (ILAL 8.8 Ma), cricetids (ILAL 8.2 Ma), and dormice (ILAL 7.3).

The concordant ILALs of three very large bodied mammals at 10.3 Ma (*Giraffokeryx punjabiensis*, *Conohyus sindiense*, and *Listriodon pentapotamiae*) is interesting considering their high relative abundances and long species durations. These three taxa coexisted in the Siwaliks for at least 4 million years, including 0.4 Myr after the first appearance of equids. At the same time, two new large herbivores appear in the Potwar record, the giraffid *Bramatherium megacephalum* and the suid *Hippopotamodon sivalense*. Both may have evolved in situ. These two new species are much larger than any earlier artiodactyl species. This observed size shift within the artiodactyls suggests restructuring of at least a segment of the herbivore guild. However, molar microwear patterns of *Bramatherium megacephalum* and its possible ancestor *Giraffokeryx punjabiensis* are similar (both are browsers), as are the microwear patterns of *H. sivalense* and the disappearing suids *C. sindiense* and *L. pentapota-*

miae (M. E. Morgan unpublished data). Stable carbon isotope analysis of *Hippopotamodon* suggests that it included C_4 grasses in its diet (Morgan et al. 1994).

The rodent faunas between 10.7 and 5.7 Ma were dominated by rhizomyids and murids. Cricetids are last recorded at 8.6 Ma with an ILAL of 8.2 Ma. Among the murids, species turned over completely between 9.6 and 9.3 Ma, and between 8.4 and 7.8 Ma. Most of this turnover is attributed to congeneric replacements of species with short durations. In contrast, the youngest cricetids are all long-ranging species that first appear in the middle Miocene. It is presently difficult to assess the ecological significance of the observed Siwalik murid and cricetid species differences.

Discussion and Conclusions

Previous analyses of Siwalik mammal assemblages used coarser levels of time resolution and concentrated on species composition, with only passing discussion of body size and species richness (Barry et al. 1991, 1995; Barry 1995). In this paper we have used 100-Kyr intervals in place of 500-Kyr intervals and developed additional measures of ecological diversity and structure. One hundred thousand years may be the finest level of resolution possible for studies of terrestrial vertebrate faunas over periods of millions of years because of sampling limitations inherent in the fossil record. In other published analyses of terrestrial assemblages, observed first and last occurrences, instead of inferred appearances, have been used to estimate species ranges and turnover. Thus the changing quality of the various fossil records is not usually considered to be important in shaping the patterns under analysis. We believe this failure potentially compromises the results and conclusions of any study, and a crucial part of our present effort has been to allow for the incompleteness of the fossil record and the biases it introduces. To do this we have used observations of first and last occurrences to infer local first and last appearances, which are then used as the estimators of the endpoints of species ranges. We have also weighed the basic observations by how well constrained the ages of localities are, rejecting those that are too impre-
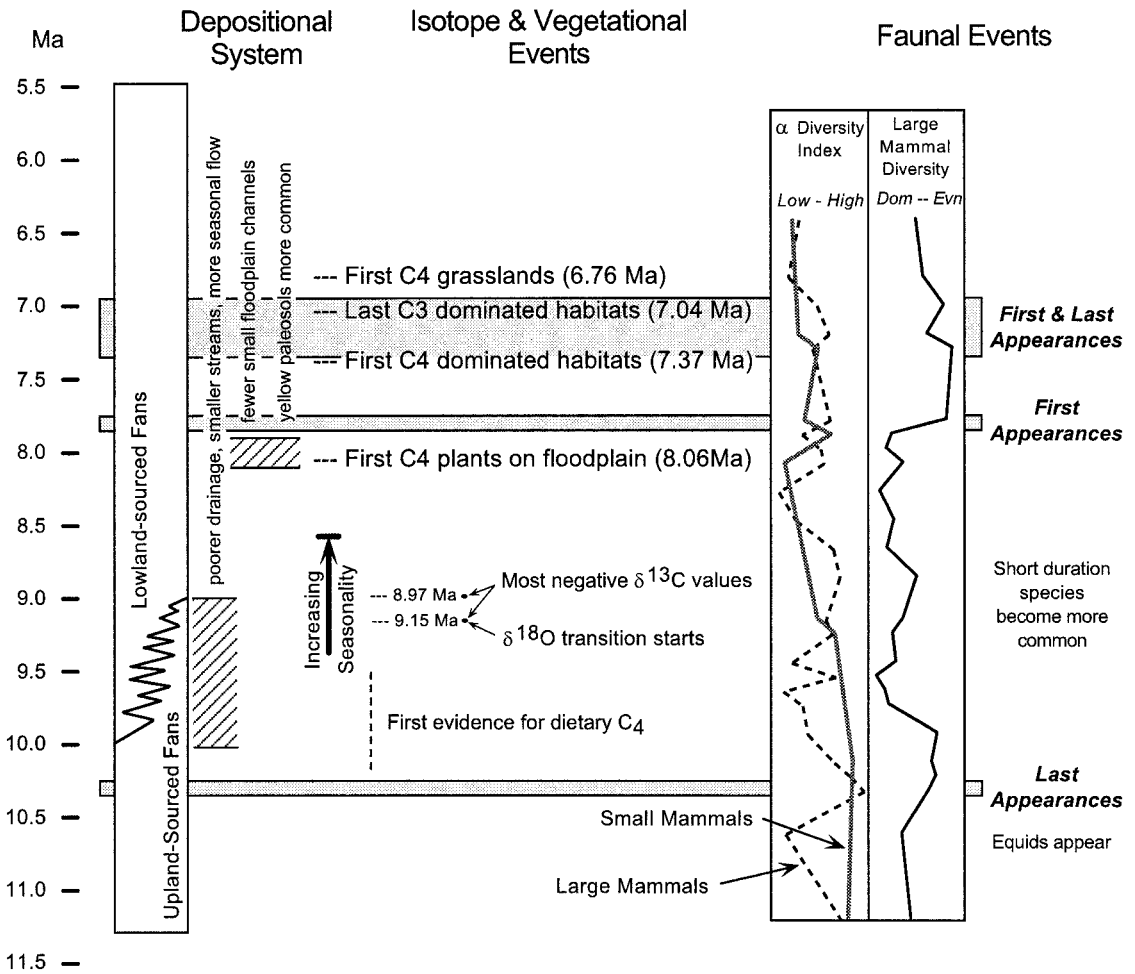
FIGURE 26. Summary diagram, showing temporal relationships of changes in the depositional system, isotopes, vegetation, and fauna. Horizontal bands delineate periods with greater faunal turnover. Hatched regions denote approximate time periods during which a feature of the depositional system changes. The arrow labeled ''increasing seasonality'' marks the interval between Retallack's (1991) two paleosol sections.

cise. In the following we relate the biotic differences derived from our analyses to the indicators of environmental change.

Environmental and Faunal Change

Our previous analyses of Siwalik mammal assemblages documented brief periods of high turnover between longer periods of low-level turnover, a pattern that could be interpreted as demonstrating coordinated stasis, although the evidence for pulses in the late Miocene was weak at best (Barry 1995; Barry et al. 1995). Our more resolved data set now shows stronger evidence for three very brief periods of high turnover in the late Miocene, and as we show in the following there is con-

cordance between faunal turnover and some Siwalik environmental events. In Figure 26 we graphically summarize these relationships.

The depositional systems of the Potwar underwent substantial changes during the late Miocene. The Nagri and Dhok Pathan Formations are interpreted as having been deposited by coexisting emergent and interfan river systems, with the larger emergent Nagri system being displaced from the study area beginning at ca. 10.1 Ma (Willis and Behrensmeyer 1995). After 9 Ma, the floodplains of the interfan Dhok Pathan deposits were less well drained, with smaller rivers having more seasonal flow than previously (Zaleha 1997b). Comparison of two paleosol sequences, at 9.4

and 8.6 Ma (Retallack 1991), also suggests re-organization of topography and drainage accompanying a transition to a more seasonal climate. A very few paleosols may have formed under waterlogged, grassy woodlands, but more extensive grasslands were not present in either of Retallack's sample sections. Similar sedimentological differences have been observed in younger parts of the sequence. Most striking, after ca. 8 Ma small floodplain channels become less common, while lighter colored and carbonate-depleted paleosols are more common (Behrensmeyer 1987).

The stable carbon and oxygen isotopic evidence also indicates significant, accelerating environmental change. The period of transition begins at 9.2 Ma with a shift in $\delta^{18}O$ values and continues to nearly the end of the Miocene for both the $\delta^{18}O$ and $\delta^{13}C$ records. The carbon isotope record demonstrates that after 8.1 Ma significant amounts of C_4 grasses began to appear on the floodplains of the Potwar Miocene rivers, and very open woodlands with predominantly C_4 plants were present by 7.4 Ma. Communities composed exclusively or predominantly of C_3 plants disappeared after 7.0 Ma, and by 6.8 Ma floodplain habitats included extensive C_4 grasslands. The two most negative paleosol carbonate $\delta^{13}C$ values reported for the Potwar Siwaliks occur at approximately 9.2 and 9.0 Ma (Quade and Cerling 1995). Among other possibilities, the $\delta^{18}O$ record suggests changes in precipitation leading to a drier and more seasonal climate. After 7.3 Ma, $\delta^{18}O$ values typical of middle Miocene Siwalik rocks are absent (Quade and Cerling 1995).

Inferred first and last appearances are the most sensitive indicators of faunal change. They show a constant, low level of faunal turnover throughout the interval at 10.7–5.7 Ma, with three short periods of elevated turnover at 10.3, 7.8, and 7.3–7.0 Ma (Fig. 26). The oldest period is characterized primarily by extinction, the second by a large number of first appearances, and the youngest by a combination of extinction and first appearances. The three periods combined account for nearly 44% of all turnover between 10.7 and 5.7 Ma, compared with the ~10% expected if turnover were constant. Indices of species richness and ecological diversity are much less sensitive indicators, but still of interest (Fig. 26). The number of species, as gauged by Fisher's α diversity index, exhibits a decline for both large and small species throughout the late Miocene. In the case of the large mammals, α diversity declines by about one-third from the earlier values, whereas small-mammal α diversity falls by more than one-half. In both cases the decrease indicates a substantial reduction in the number of species, although probably not as drastic as suggested by the species richness values themselves. Relative abundances of species also change abruptly between 10 and 9.8 Ma (Fig. 26), at which time the large-mammal assemblages come to be dominated by equids, and then again between 7.9 and 7.8 Ma, when equids cease to be so overwhelmingly abundant. Body sizes of rodents and artiodactyls generally increase during the same period, with notable steps among the rodents between 10.3 and 9.2 Ma, and for artiodactyls at 10.3–10.2 Ma (Morgan et al. 1995). The diversity and richness indices together with the data on body size strongly imply that the ecological structure of the mammal communities changed substantially shortly after 10 Ma, and then again at 7.8 Ma. The brief reappearance of more-balanced large-mammal assemblages in the 8.9 interval is also noteworthy.

The taxa that undergo the changes noted above are difficult to characterize ecologically, but the pattern of appearance and disappearance is highly selective with respect to presumed habits. Some of the newly appearing rodents or other small species are hypsodont, or are likely to have fed on underground plant organs or have been fossorial (*Kanisamys sivalensis*, *Eicooryctes kaulialensis*, species of *Brachyrhizomys*, and *Hystrix sivalensis*), all characteristics that suggest open habitats. Other species that appear belong to extant higher-level taxa usually found in open habitats (gerbils, rabbits). Similarly, among the larger taxa the tragulid *Dorcatherium* Y373 species is high crowned, and its successor ''Tragulidae/L101 unnamed species'' is even more so, implying dependence on grass. Extant species of *Manis*, *Sus*, and *Giraffa* are commonly found in open

woodlands, whereas *Hexaprotodon sivalensis* is presumed to have been a grazer. Extant reduncines are grazers associated with wet meadows, floodplains, or permanent drainages, whereas hippotragines and antilopines are grazers and mixed feeders of open terrain, or brush and scrub. Tragelaphines are browsers or mixed feeders and inhabitants of forest to lightly wooded areas near water. The majority of these taxa have inferred appearances younger than 9.0 Ma.

Taxa that become locally extinct and about which we can make habitat inferences include species with extant relatives that are characteristic of closed vegetation (tree shrews, lorisids, hominoids, dormice, some tree squirrels, dendromurines, and several species of tragulids). Many other species disappear during the time interval, but with few exceptions none give indications that they were bound to more-open habitats. The exceptions include cf. *Presbytis sivalensis* and one tragelaphine, one reduncine, and two antilopine bovids. The colobine monkey, the tragelaphine, and the reduncine are taxa that first appeared after the carbon isotopic transition started and subsequently disappeared at a later stage. We assume they were inhabitants of the mixed C_3/C_4 communities or the wetter parts of the floodplain that did not persist in the increasingly open conditions in the latest Miocene. Both of the antilopines, on the other hand, entered the Siwalik record before the beginning of the carbon transition and may have had narrow habitat tolerances. Almost three-fourths of the disappearances in Figure 14 are younger than 9.4 Ma, with the pace of extinction accelerating after the appearance of C_4 vegetation on the floodplain.

Turnover during the 10.3 Ma event differs greatly from that of the two latest Miocene events with respect to the duration of the species involved. The event at 10.3 Ma comprises taxa that were both common and of long duration, whereas the latest Miocene events include more taxa that were shorter ranging and less common (Fig. 17A). This is true of both the taxa that appear and those that disappear. That is, long enduring taxa both appear and go extinct at 10.3 Ma, whereas in the latest Miocene taxa of brief duration appear and dis-

appear. This difference of mode develops between approximately 9.0 and 8.5 Ma, at which time many short ranging and very rare species begin to make appearances. It is therefore a general feature of latest Miocene faunal change that contrasts to older periods, not just a peculiarity of the phase of more intense turnover.

Correlations Between Environmental and Faunal Events

The 5-Myr period between 10.7 and 5.7 Ma witnessed a qualitative change in the mammalian fauna of the Potwar Plateau. Some of the differences seem to reflect responses to changing environmental conditions, but others are not easily correlated to recognized local environmental events.

The 10.3 Ma turnover event does not correlate to any obvious local environmental or climate event. It is about 200 Kyr older than the onset of replacement of the emergent Nagri system by the Dhok Pathan interfan system, and although approximately contemporary with the earliest isotopic dietary evidence for C_4 vegetation, it is more than 2 Myr older than paleosol evidence for extensive C_4 vegetation on the floodplain. It is also much older than the oxygen isotope shift marking a transition to drier and more seasonal climates. The 10.3 Ma event marks the extinction of the *Giraffokeryx-Listriodon* fauna, which historically has been linked to the first appearance of equids in the Siwaliks. Nonetheless, the turnover and extinction actually follow the first appearance of equids by 400 Kyr and are at least 300 Kyr older than the transition to hipparionine-dominated faunas. The pattern of species disappearance and appearance described above suggests that biotic interactions may have been more important than environmental change in creating a pulse of faunal change around 10.3 Ma.

In contrast, the two latest Miocene turnover events show a close temporal correlation to changes in floodplain deposition and vegetation. The event at 7.8 Ma follows by 250 Kyr the first paleosol evidence for widespread C_4 vegetation on the floodplain and is approximately contemporary with other changes in floodplain deposition (Behrensmeyer 1987).

The 7.8 Ma turnover is also coincident with the shift from equid-dominated to more evenly balanced large-mammal assemblages. Appearing taxa include a hypsodont rodent and a high-crowned tragulid, implying a grass and possibly C_4 diet. The carbon isotope event indicates that habitats with C_4 plants became more common on the floodplain. This is strong evidence of changing habitat availability and is concordant with the appearance of grazing or mixed-feeding taxa. At the same time, the paleosol carbon record indicates that C_3-dominated habitats still persisted and were even common, thus explaining the absence of elevated extinction.

The younger turnover event between 7.3 and 7.0 Ma is composed of both appearances and disappearances. It begins very shortly after the first occurrence of C_4-dominated floras at 7.37 Ma and ends with the last occurrence of C_3-dominated vegetation at 7.04 Ma. These two isotopic thresholds are critical to understanding the impact of this vegetation change on the mammals, in that they record the appearance and disappearance of end-members from the vegetation spectrum. They thus indicate both the gain and the loss of types of extreme open and closed habitats, and are likely related directly to the appearance and disappearance of individual species. This same broad interval also gives evidence of increasingly seasonal stream flow and perhaps higher levels of habitat disturbance.

The change in large-mammal diversity between 10 and 9.8 Ma potentially could be related to fluvial system dynamics, as it closely follows the initial appearance at 10.1 Ma of the interfan Dhok Pathan system (Fig. 26). However, although there are very few large localities associated with the emergent Nagri system on which to base a comparison, there does not seem to be a relationship between position on the floodplain and composition of the faunal assemblages. Two large sites (Y258, Y251), both associated with the interfan Dhok Pathan system and dated at 10.1 and 10.0 Ma respectively, have low numbers of equids (31% and 28%) when compared with younger sites in the same interfan setting. In contrast, two sites (Y309, Y317), closely associated with the emergent Nagri system and dated at 9.3 and 9.2 Ma, have numbers of equids (52% and 50% respectively) comparable to contemporary sites of the interfan system. This suggests that before 9.8 Ma the habitats situated on the Dhok Pathan interfan system were similar to those of the Nagri emergent system. Furthermore, the transitory reappearance of a more balanced large-mammal assemblage in the 8.9-Ma interval, which comes after the displacement of the emergent Nagri system, suggests there is no direct connection between depositional system and faunal structure. This transitory reappearance of more balanced assemblages closely follows the two most negative carbon isotope values in the sequence and the beginning of the oxygen isotope transition.

General Patterns

Biotic change in the late Miocene Siwaliks is a combination of steady, low-intensity change in species composition and ecological structure, punctured by brief, irregularly spaced intervals with accelerated species turnover and ecological change. Episodes of accelerated species turnover amidst longer quiescent periods are characteristic of both the ''coordinated stasis'' (Brett et al. 1996) and the ''turnover pulse'' (Vrba 1985, 1995) models of evolutionary change. The presence, however, of a steady background species turnover leading to the loss of 65–70% of the members of the initial fauna, coupled with steadily declining diversity and abrupt, unrelated changes in relative abundance, does not fit the observed or predicted patterns of either model. Although there seem to be pulses of change, there is no attending stasis in this Siwalik record. This difference in pattern compared with previous results is due in large part to the inclusion of rare and low-abundance species in our analysis (McKinney et al. 1996).

Although interpretation of the events at 10.3 Ma is uncertain, species turnover and ecological changes in the latest Miocene are closely tied to change in the vegetation, and, we believe, through the vegetation change to climatic change. Evolution of the fluvial system could have played some minor role, but we favor explanations based on climatic change for both latest Miocene pulses. The strongest ev-

idence for this is the association of the most significant faunal changes and expansion of C_4 plants on the floodplain with oxygen isotopic and sedimentological evidence for increasingly drier and more seasonal climates. Displacement of the emergent Nagri system by the interfan Dhok Pathan system seems not to be related to significant faunal differences, but climate change as well as tectonics may have affected evolution of the fluvial system. This makes the precise chain of causality difficult to trace. Because high levels of background turnover also occur within the period of progressive climate change, the background turnover may also be a result of climate change. Our earlier analyses did not detect these coincidences of faunal, floral, and climatic change because those analyses used a resolution of only 500 Kyr. The climatic and environmental changes considered here take place on timescales of a few hundreds of thousands of years or less, and testing the relationships needs faunal data with the same resolution. A further testing of these ideas will now also require data gathered on a larger geographic scale—one large enough to include coexisting megafan systems, each with a rich and long fossil record. Such tests are achievable in the Miocene of Pakistan and adjacent regions. It is, however, always necessary to recognize the limits of paleontological data and its adequacy for resolving our questions.

Acknowledgments

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Appendix 1

Stratigraphic sections.

Region/Section	Thickness (m)	Pmag	References*	Comments
Rohtas				
Sanghoi/Basawa	1850	Yes	1	
Jalalpur				
Jarmaghal Kas	2100	Yes	1, 2	Same as Chambal Kas in Ref. 1
Hasnot Area				
Andar Kas	1300	Yes	2	
Kotal Kund	1800	Yes	2	
Lower Dhala Nala	862	Yes	2, this paper (Fig. 3)	Includes two lower extensions totaling 313 m that are not included in Ref. 2. Lower 100 m without paleomag
Dhok Saira	250	Yes	This paper (Fig. 2)	Remeasured section for upper part of Ref. 2
Padhri	180	No	This paper	
Y910 Section	68	No	This paper	
Hasnot	180	No	This paper	
East of Bhandar	100	No	This paper	
Pillar I	64	Yes	3	
Pillar II	71	Yes	3	
Pillar III	66	Yes	3	
Pillar IV	55	Yes	3	
Pillar V	80	Yes	3	
Pillar VI	90	Yes	3	
Tatrot-Bhandar	52	Yes	2, 3	''Tatrot'' in Ref. 3
Tatrot	60	Yes	1	
Khaur Area				
Kundval Kas	500	Yes	4	
Dhok Pathan Rest House	497	Yes	5, this paper (Fig. 4)	
Bhianwala Kas	1692	No	5	Shown as lower part of Dhok Pathan Section in Ref. 5
Utran	1300	Yes	4, 6	
Utran (UN)	70	No	7	
Kot Maliaran	600	Yes	4, 5, 6	
Kot Maliaran (KM)	60	No	7	Remeasured segment
Choutriwali Kas	1708	No	5	Remeasured segment
Choutriwali Kas (CH)	100	Yes	7	Remeasured and resampled upper segment
Dhok Mila	1000	Yes	4, 6	
Khaur Kas (KK)	270	Yes	5, 7	Paleomag sampling in lower 75 m
Hasal Kas (HL)	2425	Yes	4, 6, 7, 8	Main section measured by G. D. Johnson. ''Bora Kas'' in Ref. 8
Hasal Kas	2850	No	5	Section of Ref. 4 remeasured by Raza and Meyer
Y227 Section	75	No	7	
Dinga Kas (DK)	120	Yes	5, 7, 8	
Malhuwala Kas	1200	Yes	4, 6	

Appendix 1. Continued.

Region/Section	Thickness (m)	Pmag	References*	Comments
Malhuwala Kas (MKM)	2230	Yes	5, 7, 8	Upper 838 m of paleomag sampling of Ref. 8 transferred to measured section of Ref. 5
Jabbi	203	Yes	5, 8	Upper part of section in Refs. 5 and 8 has a duplicated segment
Gandakas Road (GKR)	70	No	7	
Gandakas (GK)	160	Yes	5, 6, 7, 8	
Bhagwa Kas South (BWS)	75	Yes	7, 9	Is "Section 5" in Ref. 9
Bhagwa Kas (BW)	110	Yes	5, 7, 8, 9	Is "Section 6" in Ref. 9
Y269 Section	75	No	7	
Silt Bridge (SB)	30	No	7	
Ratha Kas South (RKS)	35	No	7	
Ratha Kas (RK)	1006	Yes	5, 7, 8	
Thagenwali Dhok (TWD)	170	Yes	7, 8	
Y260 Section (KAK)	75	Yes	7	
Kaulial Kas (KUL)	3231	Yes	5, 8	Is "KUL" and "LK" of Ref. 8 combined
Kaulial Kas (KUL)	70	Yes	7	Additional paleomag added to Ref. 8
Chinji Area				
Gabhir	2100	Yes	2, 10, 11	Paleomag sites of Refs. 2 and 10 placed onto section of Ref. 11
Chitaparwala	745	Yes	10, 12	

* References
1. Opdyke et al. 1979.
2. Johnson et al. 1982.
3. McMurtry 1980.
4. Barndt 1977.
5. Barry et al. 1980.
6. Barndt et al. 1978.
7. Behrensmeyer and Tauxe 1982.
8. Tauxe and Opdyke 1982.
9. Tauxe and Badgley 1988.
10. Johnson et al. 1985.
11. Willis 1993a.
12. Stix 1982.

Appendix 2

Locality data.

Locality	Midpoint	Upper age	Lower age	Age spread	No. of intervals	Assigned interval
Y551	5.843	5.838	5.847	0.009	1	5.8
Y567	5.843	5.838	5.847	0.009	1	5.8
Y820	5.843	5.838	5.847	0.009	1	5.8
Y552	5.912	5.906	5.917	0.011	1	5.9
Y568	5.912	5.906	5.917	0.011	1	5.9
Y569	5.912	5.906	5.917	0.011	1	5.9
B109	6.196	6.122	6.269	0.147	3	6.2
D006	6.196	6.122	6.269	0.147	3	6.2
D011	6.196	6.122	6.269	0.147	3	6.2
Y930	6.196	6.122	6.269	0.147	3	6.2
Y913	6.207	6.191	6.222	0.031	1	6.2
Y914	6.222	6.191	6.253	0.062	2	6.2
D066	6.229	6.193	6.264	0.071	2	6.2
Y903	6.265	6.242	6.288	0.046	2	6.3
Y911	6.316	6.257	6.374	0.117	2	6.3
Y912	6.316	6.257	6.374	0.117	2	6.3
Y453	6.341	6.216	6.465	0.249	4	6.3
D012	6.350	6.292	6.408	0.116	2	6.4
D013	6.350	6.292	6.408	0.116	2	6.4
Y915	6.366	6.289	6.442	0.153	2	6.4
B118	6.385	6.290	6.480	0.190	3	6.4
B110	6.392	6.303	6.480	0.177	3	6.4
B112	6.392	6.303	6.480	0.177	3	6.4
Y556	6.401	6.295	6.507	0.212	3	6.4
Y560	6.401	6.295	6.507	0.212	3	6.4
B008	6.488	6.306	6.670	0.364	5	6.5
B024	6.488	6.306	6.670	0.364	5	6.5
B135	6.488	6.306	6.670	0.364	5	6.5
L097	6.488	6.306	6.670	0.364	5	6.5
Y919	6.545	6.504	6.585	0.081	2	6.5
D010	6.558	6.438	6.677	0.239	4	6.6
B006	6.566	6.448	6.684	0.236	4	6.6
B007	6.566	6.448	6.684	0.236	4	6.6
D028	6.566	6.448	6.684	0.236	4	6.6
Y908	6.779	6.748	6.810	0.062	2	6.8
Y920	6.779	6.748	6.810	0.062	2	6.8
Y928	6.784	6.670	6.898	0.228	3	6.8
Y909	6.895	6.863	6.927	0.064	1	6.9
Y925	6.927	6.864	6.990	0.126	2	6.9
Y929	6.943	6.912	6.974	0.062	2	6.9
Y916	6.962	6.931	6.993	0.062	2	7.0
Y581	6.972	6.934	7.009	0.075	2	7.0
Y910	6.975	6.940	7.009	0.069	2	7.0
Y373	7.007	6.902	7.112	0.210	3	7.0
Y456	7.061	6.847	7.275	0.428	6	7.1
Y922	7.077	7.041	7.112	0.071	2	7.1
Y923	7.077	7.041	7.112	0.071	2	7.1
Y939	7.107	7.066	7.148	0.082	1	7.1
Y370	7.128	7.118	7.138	0.020	1	7.1
Y386	7.128	7.118	7.138	0.020	1	7.1
KL15	7.131	7.105	7.156	0.051	2	7.1
Y372	7.136	7.105	7.166	0.061	2	7.1
Y374	7.136	7.105	7.166	0.061	2	7.1
Y377	7.136	7.105	7.166	0.061	2	7.1
Y438	7.140	7.126	7.153	0.027	2	7.1
Y933	7.144	7.119	7.169	0.050	2	7.1

Appendix 2. Continued.

Locality	Midpoint	Upper age	Lower age	Age spread	No. of intervals	Assigned interval
Y458	7.158	7.139	7.177	0.038	2	7.2
L082	7.190	7.119	7.261	0.142	3	7.2
Y936	7.198	7.155	7.240	0.085	1	7.2
B117	7.222	7.083	7.360	0.277	4	7.2
L072	7.222	7.083	7.360	0.277	4	7.2
L079	7.222	7.083	7.360	0.277	4	7.2
Y937	7.225	7.199	7.250	0.051	2	7.2
D029	7.226	7.176	7.275	0.099	2	7.2
Y452	7.226	7.176	7.275	0.099	2	7.2
Y437	7.236	7.161	7.311	0.150	2	7.2
Y921	7.236	7.210	7.261	0.051	2	7.2
Y931	7.236	7.211	7.261	0.050	2	7.2
Y932	7.236	7.211	7.261	0.050	2	7.2
Y924	7.241	7.206	7.276	0.070	2	7.2
Y927	7.254	7.225	7.282	0.057	2	7.3
Y940	7.254	7.228	7.279	0.051	2	7.3
Y907	7.257	7.232	7.282	0.050	2	7.3
Y419	7.265	7.190	7.339	0.149	2	7.3
Y459	7.276	7.225	7.327	0.102	2	7.3
KL07	7.289	7.127	7.451	0.324	5	7.3
Y376	7.291	7.133	7.449	0.316	4	7.3
Y382	7.291	7.133	7.449	0.316	4	7.3
Y941	7.296	7.260	7.332	0.072	1	7.3
Y934	7.300	7.275	7.325	0.050	1	7.3
Y457	7.301	7.260	7.342	0.082	1	7.3
Y938	7.307	7.275	7.339	0.064	1	7.3
Y375	7.310	7.272	7.348	0.076	1	7.3
Y926	7.325	7.303	7.346	0.043	1	7.3
Y935	7.325	7.303	7.346	0.043	1	7.3
Y943	7.325	7.303	7.346	0.043	1	7.3
Y944	7.325	7.303	7.346	0.043	1	7.3
Y876	7.330	7.209	7.451	0.242	4	7.3
Y369	7.360	7.319	7.400	0.081	2	7.4
Y378	7.370	7.329	7.410	0.081	2	7.4
Y440	7.386	7.327	7.444	0.117	2	7.4
Y873	7.493	7.411	7.575	0.164	3	7.5
KL10	7.496	7.415	7.577	0.162	3	7.5
KL09	7.630	7.553	7.707	0.154	2	7.6
Y872	7.639	7.613	7.664	0.051	2	7.6
Y435	7.690	7.663	7.716	0.053	1	7.7
Y900	7.690	7.646	7.733	0.087	2	7.7
Y436	7.699	7.673	7.725	0.052	1	7.7
L076	7.717	7.592	7.842	0.250	3	7.7
KL08	7.719	7.656	7.781	0.125	2	7.7
Y945	7.730	7.688	7.771	0.083	2	7.7
Y400	7.750	7.726	7.774	0.048	2	7.8
Y434	7.750	7.726	7.774	0.048	2	7.8
Y946	7.764	7.723	7.805	0.082	2	7.8
Y950	7.764	7.723	7.805	0.082	2	7.8
Y947	7.765	7.688	7.842	0.154	2	7.8
Y948	7.769	7.729	7.809	0.080	2	7.8
Y898	7.770	7.715	7.825	0.110	2	7.8
Y905	7.770	7.715	7.825	0.110	2	7.8
Y917	7.770	7.715	7.825	0.110	2	7.8
Y918	7.770	7.715	7.825	0.110	2	7.8
Y951	7.781	7.715	7.846	0.131	2	7.8
Y906	7.795	7.752	7.838	0.086	1	7.8

Appendix 2. Continued.

Locality	Midpoint	Upper age	Lower age	Age spread	No. of intervals	Assigned interval
Y949	7.803	7.760	7.846	0.086	1	7.8
B104	7.863	7.802	7.924	0.122	2	7.9
Y009	7.863	7.802	7.924	0.122	2	7.9
Y011	7.863	7.802	7.924	0.122	2	7.9
Y015	7.863	7.802	7.924	0.122	2	7.9
Y021	7.863	7.802	7.924	0.122	2	7.9
Y029	7.863	7.802	7.924	0.122	2	7.9
Y109	7.863	7.802	7.924	0.122	2	7.9
Y112	7.863	7.802	7.924	0.122	2	7.9
Y886	7.871	7.831	7.910	0.079	2	7.9
Y016	7.882	7.802	7.962	0.160	3	7.9
Y097	7.902	7.802	8.001	0.199	3	7.9
Y098	7.902	7.802	8.001	0.199	3	7.9
Y099	7.902	7.802	8.001	0.199	3	7.9
Y953	7.902	7.802	8.001	0.199	3	7.9
Y954	7.902	7.802	8.001	0.199	3	7.9
KL11	7.922	7.777	8.066	0.289	4	7.9
Y472	7.922	7.889	7.955	0.066	2	7.9
Y399	7.924	7.902	7.945	0.043	1	7.9
L011	7.926	7.802	8.049	0.247	3	7.9
L012	7.926	7.802	8.049	0.247	3	7.9
L013	7.926	7.802	8.049	0.247	3	7.9
L014	7.926	7.802	8.049	0.247	3	7.9
L015	7.926	7.802	8.049	0.247	3	7.9
L016	7.926	7.802	8.049	0.247	3	7.9
L019	7.926	7.802	8.049	0.247	3	7.9
L056	7.926	7.802	8.049	0.247	3	7.9
Y027	7.926	7.802	8.049	0.247	3	7.9
Y031	7.926	7.802	8.049	0.247	3	7.9
Y116	7.926	7.802	8.049	0.247	3	7.9
Y129	7.926	7.802	8.049	0.247	3	7.9
Y130	7.926	7.802	8.049	0.247	3	7.9
Y131	7.926	7.802	8.049	0.247	3	7.9
Y133	7.926	7.802	8.049	0.247	3	7.9
Y541	7.926	7.902	7.950	0.048	2	7.9
Y547	7.926	7.902	7.950	0.048	2	7.9
Y393	7.952	7.944	7.960	0.016	2	8.0
B114	7.960	7.592	8.327	0.735	8	8.0
L075	7.960	7.592	8.327	0.735	8	8.0
L096	7.960	7.592	8.327	0.735	8	8.0
Y371	7.960	7.592	8.327	0.735	8	8.0
Y887	7.961	7.935	7.987	0.052	2	8.0
B043	7.973	7.896	8.049	0.153	2	8.0
Y013	7.973	7.896	8.049	0.153	2	8.0
Y017	7.973	7.944	8.002	0.058	2	8.0
Y022	7.973	7.896	8.049	0.153	2	8.0
Y023	7.973	7.896	8.049	0.153	2	8.0
Y025	7.973	7.896	8.049	0.153	2	8.0
Y090	7.973	7.896	8.049	0.153	2	8.0
Y092	7.973	7.896	8.049	0.153	2	8.0
Y093	7.973	7.896	8.049	0.153	2	8.0
Y108	7.973	7.896	8.049	0.153	2	8.0
Y110	7.973	7.896	8.049	0.153	2	8.0
Y111	7.973	7.896	8.049	0.153	2	8.0
Y118	7.973	7.896	8.049	0.153	2	8.0
Y132	7.973	7.896	8.049	0.153	2	8.0
Y889	7.975	7.953	7.996	0.043	1	8.0

Appendix 2. Continued.

Locality	Midpoint	Upper age	Lower age	Age spread	No. of intervals	Assigned interval
Y540	7.988	7.972	8.004	0.032	1	8.0
Y890	7.988	7.972	8.004	0.032	1	8.0
Y019	7.996	7.943	8.049	0.106	2	8.0
Y020	7.996	7.943	8.049	0.106	2	8.0
B046	8.005	7.961	8.049	0.088	1	8.0
Y033	8.005	7.961	8.049	0.088	1	8.0
L071	8.018	7.708	8.327	0.619	7	8.0
L073	8.018	7.708	8.327	0.619	7	8.0
L074	8.018	7.708	8.327	0.619	7	8.0
L080	8.018	7.708	8.327	0.619	7	8.0
Y107	8.018	7.989	8.047	0.058	1	8.0
Y539	8.019	7.992	8.045	0.053	1	8.0
Y542	8.019	7.992	8.045	0.053	1	8.0
Y545	8.019	7.992	8.045	0.053	1	8.0
Y546	8.019	7.992	8.045	0.053	1	8.0
Y599	8.019	7.992	8.045	0.053	1	8.0
Y600	8.019	7.992	8.045	0.053	1	8.0
Y606	8.019	7.992	8.045	0.053	1	8.0
Y888	8.019	7.992	8.045	0.053	1	8.0
Y171	8.023	7.984	8.062	0.078	2	8.0
Y392	8.023	7.984	8.062	0.078	2	8.0
Y538	8.028	8.013	8.043	0.030	1	8.0
Y548	8.056	8.042	8.070	0.028	2	8.1
Y605	8.078	8.059	8.097	0.038	1	8.1
KL21	8.081	8.040	8.121	0.081	2	8.1
Y018	8.084	8.012	8.155	0.143	3	8.1
B025	8.088	7.802	8.374	0.572	7	8.1
B026	8.088	7.802	8.374	0.572	7	8.1
B027	8.088	7.802	8.374	0.572	7	8.1
B028	8.088	7.802	8.374	0.572	7	8.1
B029	8.088	7.802	8.374	0.572	7	8.1
B030	8.088	7.802	8.374	0.572	7	8.1
B031	8.088	7.802	8.374	0.572	7	8.1
B032	8.088	7.802	8.374	0.572	7	8.1
B033	8.088	7.802	8.374	0.572	7	8.1
B034	8.088	7.802	8.374	0.572	7	8.1
B035	8.088	7.802	8.374	0.572	7	8.1
B036	8.088	7.802	8.374	0.572	7	8.1
B037	8.088	7.802	8.374	0.572	7	8.1
D063	8.112	7.999	8.225	0.226	3	8.1
Y565	8.112	7.999	8.225	0.226	3	8.1
Y577	8.112	7.999	8.225	0.226	3	8.1
B103	8.125	8.012	8.238	0.226	3	8.1
B106	8.125	8.012	8.238	0.226	3	8.1
L009	8.125	8.012	8.238	0.226	3	8.1
Y117	8.125	8.012	8.238	0.226	3	8.1
Y006	8.141	8.045	8.237	0.192	3	8.1
Y012	8.141	8.045	8.237	0.192	3	8.1
Y024	8.142	8.062	8.221	0.159	2	8.1
Y034	8.143	7.912	8.374	0.462	6	8.1
Y035	8.143	7.912	8.374	0.462	6	8.1
Y036	8.143	7.912	8.374	0.462	6	8.1
Y114	8.143	7.912	8.374	0.462	6	8.1
Y115	8.143	7.912	8.374	0.462	6	8.1
B040	8.151	8.065	8.237	0.172	2	8.2
Y176	8.159	8.082	8.235	0.153	2	8.2
Y214	8.159	8.082	8.235	0.153	2	8.2

Appendix 2. Continued.

Locality	Midpoint	Upper age	Lower age	Age spread	No. of intervals	Assigned interval
Y014	8.170	8.068	8.271	0.203	3	8.2
Y899	8.185	8.086	8.284	0.198	3	8.2
Y901	8.185	8.086	8.284	0.198	3	8.2
Y172	8.246	8.226	8.266	0.040	2	8.2
Y173	8.246	8.226	8.266	0.040	2	8.2
Y168	8.259	8.229	8.288	0.059	2	8.3
L006	8.265	8.235	8.295	0.060	2	8.3
Y002	8.265	8.235	8.295	0.060	2	8.3
Y007	8.265	8.235	8.295	0.060	2	8.3
Y390	8.267	8.229	8.305	0.076	2	8.3
Y391	8.267	8.229	8.305	0.076	2	8.3
B038	8.270	8.226	8.313	0.087	2	8.3
B044	8.270	8.226	8.313	0.087	2	8.3
B105	8.270	8.226	8.313	0.087	2	8.3
L004	8.270	8.226	8.313	0.087	2	8.3
Y005	8.270	8.226	8.313	0.087	2	8.3
B042	8.300	8.226	8.374	0.148	3	8.3
Y028	8.300	8.226	8.374	0.148	3	8.3
Y032	8.300	8.226	8.374	0.148	3	8.3
Y113	8.300	8.226	8.374	0.148	3	8.3
Y119	8.300	8.226	8.374	0.148	3	8.3
B041	8.331	8.287	8.374	0.087	2	8.3
B045	8.331	8.287	8.374	0.087	2	8.3
L008	8.331	8.287	8.374	0.087	2	8.3
Y004	8.331	8.287	8.374	0.087	2	8.3
Y030	8.331	8.287	8.374	0.087	2	8.3
Y100	8.338	8.313	8.362	0.049	2	8.3
Y106	8.338	8.313	8.362	0.049	2	8.3
Y174	8.348	8.299	8.396	0.097	2	8.3
Y535	8.374	8.286	8.462	0.176	3	8.4
Y155	8.392	8.343	8.441	0.098	2	8.4
Y473	8.394	8.354	8.433	0.079	1	8.4
ML03	8.413	8.366	8.460	0.094	2	8.4
Y394	8.427	8.388	8.465	0.077	2	8.4
Y543	8.431	8.386	8.475	0.089	2	8.4
Y443	8.440	8.413	8.467	0.054	2	8.4
Y897	8.469	8.441	8.497	0.056	2	8.5
Y603	8.471	8.405	8.536	0.131	2	8.5
Y442	8.476	8.447	8.504	0.057	2	8.5
Y199	8.480	8.257	8.702	0.445	5	8.5
Y200	8.480	8.257	8.702	0.445	5	8.5
Y201	8.480	8.257	8.702	0.445	5	8.5
Y203	8.480	8.257	8.702	0.445	5	8.5
Y204	8.480	8.257	8.702	0.445	5	8.5
KL12	8.485	8.410	8.559	0.149	3	8.5
Y602	8.508	8.457	8.558	0.101	2	8.5
Y604	8.508	8.457	8.558	0.101	2	8.5
Y608	8.508	8.457	8.558	0.101	2	8.5
Y167	8.510	8.420	8.599	0.179	3	8.5
Y192	8.510	8.420	8.599	0.179	3	8.5
Y441	8.521	8.491	8.551	0.060	2	8.5
Y460	8.524	8.494	8.554	0.060	2	8.5
Y461	8.524	8.494	8.554	0.060	2	8.5
Y444	8.529	8.498	8.559	0.061	2	8.5
Y467	8.532	8.502	8.562	0.060	2	8.5
ML02	8.570	8.535	8.605	0.070	2	8.6
Y156	8.570	8.535	8.605	0.070	2	8.6

Appendix 2. Continued.

Locality	Midpoint	Upper age	Lower age	Age spread	No. of intervals	Assigned interval
Y389	8.570	8.535	8.605	0.070	2	8.6
Y477	8.588	8.556	8.620	0.064	1	8.6
Y408	8.619	8.573	8.664	0.091	2	8.6
Y387	8.635	8.598	8.672	0.074	2	8.6
Y407	8.635	8.598	8.672	0.074	2	8.6
Y445	8.635	8.598	8.672	0.074	2	8.6
ML01	8.636	8.600	8.671	0.071	2	8.6
Y169	8.657	8.625	8.689	0.064	2	8.7
ML05	8.658	8.596	8.719	0.123	2	8.7
Y544	8.661	8.626	8.696	0.070	2	8.7
Y158	8.669	8.628	8.710	0.082	2	8.7
ML04	8.673	8.628	8.717	0.089	2	8.7
Y360	8.676	8.645	8.707	0.062	2	8.7
Y891	8.677	8.645	8.708	0.063	2	8.7
Y388	8.679	8.648	8.710	0.062	2	8.7
Y146	8.694	8.664	8.724	0.060	1	8.7
Y421	8.694	8.664	8.724	0.060	1	8.7
Y178	8.719	8.675	8.763	0.088	2	8.7
Y164	8.722	8.694	8.749	0.055	1	8.7
Y165	8.722	8.694	8.749	0.055	1	8.7
Y166	8.722	8.694	8.749	0.055	1	8.7
RK03	8.725	8.560	8.890	0.330	4	8.7
Y748	8.727	8.707	8.747	0.040	1	8.7
Y468	8.731	8.711	8.751	0.040	2	8.7
Y469	8.731	8.711	8.751	0.040	2	8.7
Y470	8.731	8.711	8.751	0.040	2	8.7
KL16	8.733	8.664	8.801	0.137	2	8.7
B111	8.760	8.247	9.272	1.025	12	8.8
B115	8.760	8.247	9.272	1.025	12	8.8
Y609	8.771	8.704	8.837	0.133	2	8.8
Y398	8.775	8.750	8.799	0.049	1	8.8
ML06	8.787	8.664	8.910	0.246	3	8.8
Y142	8.792	8.724	8.859	0.135	3	8.8
Y143	8.792	8.724	8.859	0.135	3	8.8
Y153	8.792	8.724	8.859	0.135	3	8.8
Y415	8.805	8.778	8.831	0.053	1	8.8
Y396	8.812	8.785	8.838	0.053	1	8.8
Y404	8.812	8.785	8.838	0.053	1	8.8
Y355	8.823	8.794	8.851	0.057	2	8.8
Y141	8.829	8.802	8.855	0.053	2	8.8
Y352	8.829	8.802	8.855	0.053	2	8.8
DM03	8.831	8.788	8.873	0.085	2	8.8
KL14	8.840	8.777	8.903	0.126	2	8.8
Y148	8.842	8.809	8.874	0.065	2	8.8
Y325	8.854	8.643	9.064	0.421	6	8.9
Y449	8.854	8.837	8.870	0.033	2	8.9
Y476	8.855	8.828	8.881	0.053	2	8.9
Y406	8.861	8.835	8.886	0.051	2	8.9
Y322	8.869	8.834	8.903	0.069	2	8.9
KL02	8.877	8.851	8.903	0.052	1	8.9
Y149	8.915	8.880	8.949	0.069	1	8.9
Y193	8.918	8.892	8.944	0.052	1	8.9
Y194	8.918	8.892	8.944	0.052	1	8.9
Y196	8.918	8.892	8.944	0.052	1	8.9
Y197	8.918	8.892	8.944	0.052	1	8.9
Y474	8.918	8.892	8.944	0.052	1	8.9
Y480	8.918	8.892	8.944	0.052	1	8.9

Appendix 2. Continued.

Locality	Midpoint	Upper age	Lower age	Age spread	No. of intervals	Assigned interval
Y205	8.924	8.836	9.012	0.176	3	8.9
Y320	8.924	8.836	9.012	0.176	3	8.9
GK01	8.927	8.880	8.973	0.093	2	8.9
Y147	8.927	8.880	8.973	0.093	2	8.9
Y323	8.927	8.896	8.958	0.062	2	8.9
Y366	8.945	8.919	8.970	0.051	2	8.9
Y367	8.945	8.919	8.970	0.051	2	8.9
Y397	8.945	8.919	8.970	0.051	2	8.9
Y402	8.945	8.919	8.970	0.051	2	8.9
Y484	8.945	8.919	8.970	0.051	2	8.9
Y420	8.962	8.936	8.988	0.052	2	9.0
Y181	8.968	8.931	9.004	0.073	2	9.0
Y198	8.968	8.931	9.004	0.073	2	9.0
DM02	8.969	8.920	9.017	0.097	2	9.0
Y401	8.980	8.954	9.005	0.051	1	9.0
Y321	8.984	8.798	9.170	0.372	5	9.0
Y324	8.984	8.798	9.170	0.372	5	9.0
Y326	8.984	8.798	9.170	0.372	5	9.0
DK01	9.000	8.923	9.076	0.153	3	9.0
Y241	9.004	8.961	9.047	0.086	1	9.0
Y446	9.011	8.998	9.023	0.025	1	9.0
ML07	9.018	8.977	9.058	0.081	2	9.0
ML08	9.018	8.977	9.058	0.081	2	9.0
Y447	9.020	9.006	9.033	0.027	1	9.0
Y210	9.021	8.981	9.060	0.079	2	9.0
Y152	9.025	8.862	9.187	0.325	4	9.0
Y208	9.025	8.862	9.187	0.325	4	9.0
KL13	9.037	8.995	9.078	0.083	2	9.0
Y448	9.043	9.027	9.058	0.031	2	9.0
DM01	9.057	9.014	9.100	0.086	2	9.1
Y361	9.069	9.023	9.115	0.092	2	9.1
D065	9.134	8.934	9.333	0.399	5	9.1
Y182	9.159	9.148	9.170	0.022	2	9.2
Y243	9.170	9.163	9.176	0.013	1	9.2
Y137	9.172	9.157	9.186	0.029	1	9.2
Y317	9.175	9.152	9.197	0.045	1	9.2
Y327	9.177	9.145	9.208	0.063	2	9.2
Y409	9.177	9.155	9.198	0.043	1	9.2
Y418	9.177	9.145	9.208	0.063	2	9.2
Y463	9.177	9.155	9.198	0.043	1	9.2
Y464	9.177	9.155	9.198	0.043	1	9.2
Y358	9.179	9.173	9.185	0.012	1	9.2
KL01	9.184	9.162	9.205	0.043	1	9.2
Y466	9.187	9.173	9.200	0.027	1	9.2
Y260	9.188	9.176	9.200	0.024	1	9.2
Y412	9.188	9.176	9.200	0.024	1	9.2
Y414	9.188	9.176	9.200	0.024	1	9.2
Y465	9.188	9.176	9.200	0.024	1	9.2
Y471	9.188	9.176	9.200	0.024	1	9.2
Y485	9.188	9.176	9.200	0.024	1	9.2
Y235	9.201	9.100	9.302	0.202	3	9.2
Y238	9.218	9.163	9.272	0.109	2	9.2
Y190	9.232	9.156	9.308	0.152	2	9.2
Y191	9.232	9.156	9.308	0.152	2	9.2
Y239	9.232	9.231	9.232	0.001	1	9.2
Y439	9.236	9.219	9.253	0.034	2	9.2
Y631	9.241	9.235	9.246	0.011	1	9.2

Appendix 2. Continued.

Locality	Midpoint	Upper age	Lower age	Age spread	No. of intervals	Assigned interval
Y211	9.242	9.234	9.250	0.016	2	9.2
Y240	9.243	9.237	9.248	0.011	1	9.2
Y385	9.243	9.241	9.245	0.004	1	9.2
Y314	9.244	9.235	9.253	0.018	2	9.2
Y229	9.247	9.233	9.260	0.027	2	9.2
Y231	9.247	9.233	9.260	0.027	2	9.2
Y403	9.250	9.240	9.260	0.020	2	9.3
Y351	9.252	9.247	9.256	0.009	2	9.3
Y255	9.258	9.251	9.265	0.014	1	9.3
Y223	9.259	9.211	9.306	0.095	2	9.3
Y232	9.259	9.211	9.306	0.095	2	9.3
Y242	9.259	9.211	9.306	0.095	2	9.3
Y313	9.259	9.211	9.306	0.095	2	9.3
Y316	9.259	9.211	9.306	0.095	2	9.3
Y318	9.259	9.211	9.306	0.095	2	9.3
Y244	9.260	9.247	9.272	0.025	2	9.3
Y416	9.260	9.253	9.267	0.014	1	9.3
Y310	9.261	9.248	9.274	0.026	2	9.3
Y207	9.266	9.256	9.276	0.020	1	9.3
Y212	9.266	9.248	9.283	0.035	2	9.3
Y154	9.268	9.256	9.279	0.023	1	9.3
Y221	9.268	9.254	9.281	0.027	1	9.3
Y226	9.268	9.257	9.279	0.022	1	9.3
Y315	9.268	9.256	9.280	0.024	1	9.3
Y359	9.268	9.257	9.279	0.022	1	9.3
Y633	9.269	9.257	9.281	0.024	1	9.3
KL03	9.270	9.239	9.301	0.062	2	9.3
Y880	9.270	9.239	9.301	0.062	2	9.3
Y356	9.275	9.263	9.287	0.024	1	9.3
Y601	9.275	9.265	9.285	0.020	1	9.3
Y952	9.275	9.266	9.283	0.017	1	9.3
Y245	9.276	9.243	9.308	0.065	2	9.3
Y150	9.278	9.247	9.308	0.061	2	9.3
Y151	9.278	9.247	9.308	0.061	2	9.3
Y195	9.278	9.247	9.308	0.061	2	9.3
Y328	9.284	9.271	9.297	0.026	1	9.3
Y209	9.286	9.269	9.302	0.033	1	9.3
Y230	9.286	9.264	9.308	0.044	1	9.3
Y159	9.288	9.279	9.297	0.018	1	9.3
Y163	9.290	9.278	9.301	0.023	1	9.3
Y312	9.290	9.274	9.305	0.031	1	9.3
Y213	9.291	9.276	9.306	0.030	1	9.3
Y224	9.291	9.277	9.305	0.028	1	9.3
Y225	9.291	9.277	9.305	0.028	1	9.3
Y227	9.291	9.277	9.305	0.028	1	9.3
Y309	9.291	9.277	9.305	0.028	1	9.3
Y410	9.291	9.281	9.300	0.019	1	9.3
Y161	9.293	9.281	9.305	0.024	1	9.3
Y160	9.296	9.287	9.305	0.018	1	9.3
Y269	9.300	9.292	9.308	0.016	1	9.3
Y350	9.300	9.292	9.308	0.016	1	9.3
Y365	9.300	9.292	9.308	0.016	1	9.3
Y237	9.303	9.100	9.506	0.406	5	9.3
Y341	9.303	9.100	9.506	0.406	5	9.3
Y413	9.313	9.301	9.324	0.023	1	9.3
Y270	9.335	9.304	9.366	0.062	2	9.3
Y482	9.335	9.304	9.366	0.062	2	9.3

Appendix 2. Continued.

Locality	Midpoint	Upper age	Lower age	Age spread	No. of intervals	Assigned interval
Y307	9.338	9.266	9.409	0.143	2	9.3
Y308	9.338	9.266	9.409	0.143	2	9.3
Y549	9.343	9.277	9.409	0.132	2	9.3
Y140	9.360	9.300	9.419	0.119	2	9.4
Y273	9.472	9.386	9.557	0.171	3	9.5
Y217	9.482	9.430	9.534	0.104	2	9.5
Y219	9.485	9.438	9.532	0.094	2	9.5
Y262	9.494	9.483	9.505	0.022	1	9.5
Y481	9.494	9.483	9.505	0.022	1	9.5
KL05	9.496	9.480	9.512	0.032	1	9.5
Y216	9.508	9.426	9.590	0.164	3	9.5
Y895	9.517	9.512	9.521	0.009	1	9.5
Y218	9.521	9.461	9.581	0.120	2	9.5
Y228	9.545	9.495	9.594	0.099	2	9.5
Y236	9.557	9.509	9.604	0.095	2	9.6
Y894	9.560	9.555	9.565	0.010	1	9.6
Y896	9.566	9.563	9.569	0.006	1	9.6
Y426	9.574	9.572	9.576	0.004	1	9.6
KL06	9.581	9.555	9.606	0.051	1	9.6
Y607	9.586	9.572	9.600	0.028	1	9.6
Y261	9.593	9.590	9.595	0.005	1	9.6
Y428	9.598	9.594	9.601	0.007	1	9.6
Y893	9.605	9.599	9.610	0.011	1	9.6
Y462	9.606	9.598	9.613	0.015	1	9.6
Y276	9.607	9.602	9.612	0.010	1	9.6
Y424	9.609	9.600	9.618	0.018	1	9.6
Y329	9.623	9.571	9.675	0.104	2	9.6
Y330	9.623	9.571	9.675	0.104	2	9.6
Y362	9.623	9.571	9.675	0.104	2	9.6
Y869	9.626	9.614	9.637	0.023	1	9.6
Y578	9.630	9.217	10.043	0.826	9	9.6
Y892	9.630	9.617	9.642	0.025	1	9.6
Y425	9.632	9.623	9.641	0.018	1	9.6
Y427	9.643	9.629	9.657	0.028	2	9.6
Y340	9.644	9.609	9.679	0.070	2	9.6
Y250	9.650	9.620	9.679	0.059	2	9.6
Y268	9.658	9.610	9.705	0.095	2	9.7
Y338	9.658	9.610	9.705	0.095	2	9.7
Y337	9.659	9.629	9.688	0.059	2	9.7
Y579	9.687	9.632	9.741	0.109	2	9.7
Y580	9.687	9.632	9.741	0.109	2	9.7
KL04	9.703	9.648	9.757	0.109	3	9.7
Y875	9.704	9.668	9.739	0.071	1	9.7
Y411	9.710	9.680	9.739	0.059	1	9.7
Y287	9.769	9.746	9.791	0.045	2	9.8
Y286	9.775	9.752	9.798	0.046	1	9.8
Y284	9.776	9.748	9.804	0.056	2	9.8
Y285	9.781	9.758	9.804	0.046	1	9.8
KL20	9.784	9.714	9.853	0.139	3	9.8
Y874	9.788	9.763	9.813	0.050	1	9.8
Y246	9.800	9.777	9.823	0.046	1	9.8
Y249	9.800	9.777	9.823	0.046	1	9.8
Y288	9.802	9.778	9.826	0.048	1	9.8
Y573	9.846	9.767	9.925	0.158	2	9.8
Y870	9.850	9.827	9.873	0.046	2	9.9
Y222	9.865	9.566	10.163	0.597	7	9.9
Y289	9.936	9.898	9.974	0.076	2	9.9

Appendix 2. Continued.

Locality	Midpoint	Upper age	Lower age	Age spread	No. of intervals	Assigned interval
Y248	9.958	9.932	9.983	0.051	2	10.0
Y251	9.958	9.932	9.983	0.051	2	10.0
Y493	9.958	9.932	9.983	0.051	2	10.0
Y357	9.984	9.954	10.014	0.060	1	10.0
Y311	10.004	9.969	10.039	0.070	1	10.0
Y597	10.010	9.984	10.035	0.051	1	10.0
Y598	10.014	9.988	10.039	0.051	1	10.0
D062	10.015	9.940	10.090	0.150	3	10.0
Y252	10.037	9.991	10.082	0.091	2	10.0
Y596	10.045	10.002	10.087	0.085	2	10.0
Y423	10.091	10.037	10.145	0.108	2	10.1
Y258	10.096	10.061	10.130	0.069	1	10.1
Y368	10.101	10.049	10.153	0.104	3	10.1
Y450	10.155	10.095	10.215	0.120	2	10.2
L094	10.161	10.080	10.242	0.162	2	10.2
D064	10.231	10.162	10.300	0.138	2	10.2
Y554	10.231	10.162	10.300	0.138	2	10.2
Y871	10.277	10.236	10.317	0.081	2	10.3
Y729	10.282	10.242	10.322	0.080	2	10.3
Y789	10.282	10.242	10.322	0.080	2	10.3
Y728	10.291	10.252	10.330	0.078	1	10.3
Y571	10.292	10.224	10.359	0.135	3	10.3
Y572	10.292	10.224	10.359	0.135	3	10.3
Y536	10.296	10.260	10.332	0.072	1	10.3
Y395	10.298	10.257	10.339	0.082	1	10.3
RK01	10.307	10.250	10.364	0.114	2	10.3
Y254	10.344	10.297	10.391	0.094	2	10.3
Y537	10.366	10.332	10.400	0.068	2	10.4
Y550	10.367	10.323	10.410	0.087	2	10.4
RK02	10.385	10.323	10.447	0.124	2	10.4
D025	10.406	10.275	10.537	0.262	3	10.4
D027	10.406	10.275	10.537	0.262	3	10.4
Y454	10.406	10.275	10.537	0.262	3	10.4
Y902	10.406	10.275	10.537	0.262	3	10.4
Y904	10.406	10.275	10.537	0.262	3	10.4
Y259	10.412	10.367	10.457	0.090	2	10.4
Y555	10.465	10.402	10.528	0.126	2	10.5
KL17	10.497	10.416	10.577	0.161	3	10.5
Y334	10.546	10.482	10.609	0.127	2	10.5
Y364	10.546	10.482	10.609	0.127	2	10.5
Y779	10.666	10.618	10.714	0.096	2	10.7
Y635	10.710	10.655	10.765	0.110	2	10.7
Y799	10.715	10.665	10.765	0.100	2	10.7

Appendix 3

Recalculated ages for isotopic samples.

Sample number	Section	Fraction	δ¹³C*	δ¹⁸O*	Age (Ma)	Minimum age (Ma)	Maximum age (Ma)
9733	Jalalpur	Carbonate	2.5	−6.8	2.270	2.203	2.337
9730	Jalalpur	Carbonate	−1.9	−7.8	2.575	2.517	2.633
9729	Jalalpur	Organic	−14.5	—	2.575	2.517	2.633
9701	Jalalpur	Carbonate	1.3	−6.6	3.303	3.188	3.418
9702	Jalalpur	Organic	−14.3	—	3.303	3.188	3.418
9684	Jalalpur	Organic	−16.5	—	3.394	3.370	3.418
9698	Jalalpur	Carbonate	2.0	−6.3	3.394	3.370	3.418
9694	Jalalpur	Carbonate	1.8	−6.2	3.425	3.396	3.453
9693	Jalalpur	Carbonate	0.4	−6.1	3.441	3.410	3.471
9689	Jalalpur	Carbonate	1.8	−6.5	3.502	3.463	3.541
9683	Jalalpur	Carbonate	−2.0	−5.7	3.690	3.463	3.917
9669	Jalalpur	Carbonate	−1.9	−7.2	3.743	3.569	3.917
9676	Jalalpur	Carbonate	0.7	−6.5	4.360	4.221	4.499
9672	Jalalpur	Organic	−14.6	—	4.680	4.570	4.789
9671	Jalalpur	Carbonate	0.6	−7.0	4.680	4.570	4.789
9665	Jalalpur	Carbonate	−1.0	−7.5	5.127	5.058	5.196
9663	Jalalpur	Carbonate	−0.7	−8.0	5.767	5.755	5.778
9657	Jalalpur	Carbonate	0.5	−6.4	5.894	5.894	5.894
9656	Jalalpur	Organic	−14.7	—	5.906	5.894	5.917
9655	Jalalpur	Carbonate	−2.3	−4.9	5.912	5.906	5.917
9654	Jalalpur	Carbonate	0.1	−7.2	5.938	5.924	5.952
9652	Jalalpur	Carbonate	−1.3	−4.9	5.982	5.953	6.010
9648	Jalalpur	Carbonate	−0.3	−5.4	6.069	6.013	6.125
9646	Jalalpur	Carbonate	0.0	−6.9	6.125	6.072	6.178
9643	Jalalpur	Carbonate	−3.5	−6.9	6.429	6.255	6.603
9640	Jalalpur	Carbonate	−1.4	−7.4	6.594	6.567	6.621
9639	Jalalpur	Carbonate	−3.0	−7.7	6.612	6.586	6.638
9637	Jalalpur	Carbonate	−0.7	−6.3	6.761	6.740	6.781
9187	Kaulial Kas	Carbonate	−7.0	−6.8	7.042	7.040	7.045
9186a	Kaulial Kas	Carbonate	−9.5	−7.3	7.042	7.040	7.045
9186b	Kaulial Kas	Carbonate	−8.8	−6.5	7.042	7.040	7.045
9185	Kaulial Kas	Carbonate	−7.9	−7.6	7.102	7.096	7.107
9184	Kaulial Kas	Carbonate	−10.1	−9.1	7.267	7.232	7.302
9183	Kaulial Kas	Carbonate	−3.6	−7.1	7.366	7.335	7.397
9182	Kaulial Kas	Carbonate	−9.5	−7.9	7.475	7.456	7.493
9630	Jalalpur	Carbonate	−5.0	−7.4	7.477	7.190	7.763
9181	Kaulial Kas	Carbonate	−10.2	−7.4	7.523	7.505	7.540
9180	Kaulial Kas	Carbonate	−7.8	−8.1	7.586	7.570	7.601
9178	Kaulial Kas	Carbonate	−8.6	−7.5	7.627	7.607	7.646
9179	Kaulial Kas	Organic	−24.2	—	7.627	7.607	7.646
9179	Kaulial Kas	Humate	−24.3	—	7.627	7.607	7.646
9177	Kaulial Kas	Carbonate	−8.6	−7.1	7.736	7.707	7.764
9625	Jalalpur	Carbonate	−7.9	−7.9	7.922	7.859	7.984
9624	Jalalpur	Carbonate	−11.2	−6.2	7.952	7.889	8.015
9622	Jalalpur	Carbonate	−8.8	−8.0	7.984	7.920	8.047
9174	Kaulial Kas	Carbonate	−8.9	−7.0	8.058	8.040	8.076
9175	Kaulial Kas	Carbonate	−11.6	−8.9	8.109	8.089	8.129
9173	Kaulial Kas	Carbonate	−11.5	−7.4	8.341	8.317	8.364
9619	Jalalpur	Carbonate	−10.8	−9.0	8.401	8.072	8.729
9168	Kaulial Kas	Carbonate	−11.8	−5.4	8.625	8.587	8.663
9162	Kaulial Kas	Carbonate	−12.9	−8.7	8.969	8.955	8.982
9160	Kaulial Kas	Carbonate	−10.6	−7.3	9.038	9.022	9.053
9161	Kaulial Kas	Organic	−24.0	—	9.038	9.022	9.053
9161	Kaulial Kas	Humate	−24.0	—	9.038	9.022	9.053
9158	Kaulial Kas	Carbonate	−12.6	−5.4	9.154	9.141	9.167
9613	Jalalpur	Carbonate	−11.0	−9.9	9.270	9.008	9.532
9607	Jalalpur	Carbonate	−10.0	−9.9	9.411	9.153	9.668
9611	Jalalpur	Carbonate	−10.1	−9.7	9.642	9.472	9.812
9764	Jalalpur	Carbonate	−9.8	−9.4	10.139	9.940	10.338
9762	Jalalpur	Carbonate	−9.9	−8.0	10.601	10.505	10.696
9758	Jalalpur	Carbonate	−10.7	−9.5	11.673	11.593	11.752
9757	Jalalpur	Carbonate	−10.8	−8.8	12.229	12.146	12.311

* Isotopic values from Quade and Cerling 1995.

Appendix 4

Stratigraphic ranges.

	Species	Inferred last appearance (Ma)	Last occurrence (Ma)	First occurrence (Ma)	Inferred first appearance* (Ma)	No. of intervals in which observed
	Large mammals					
1 Colobinae	cf. *Presbytis sivalensis*	6.5	7.1	7.6	7.8[†]	3
2 Hominoidea	*Sivapithecus* spp.	8.4[†]	8.5	12.3	14.0	11
3 Hominoidea	*Sivapithecus parvada*	9.8[†]	10.0	10.0	10.0[†]	1
4 Deinotheriidae	*Deinotherium* spp.	7.9[†]	8.0	12.9	14.0	16
5 Manidae	*Manis* ''Y260 species''	2.2	6.9	9.2	9.9	2
6 Orycteropodidae	*Orycteropus* spp.	8.1	9.2	13.6	14.0	8
7 Listriodontinae	*Listriodon pentapotamiae*	10.3[†]	10.3	13.7	14.0	13
8 Tetraconodontinae	*Conohyus sindiensis*	10.3[†]	10.3	13.1	14.0	10
9 Tetraconodontinae	*Tetraconodon magnus*	9.3[†]	9.3	10.0	11.2	3
10 Suinae	*Propotomochoerus hysudricus*	6.5	6.8	10.2	10.2[†]	29
11 Suinae	?*Hippopotamodon* ''Y450 unnamed species''	10.2[†]	10.2	11.3	11.4	5
12 Suinae	*Hippopotamodon sivalense*	7.1[†]	7.2	10.2	10.2[†]	21
13 Suinae	*Potamochoerus* ''Y553 species''	2.2	5.4	5.8	5.8[†]	2
14 Suinae	?*Sus* ''D013 species''	2.2	3.3	6.4	6.8	3
15 Suinae	''Small Suinae/Y311 species''	9.4	10.0	10.0	11.4	1
16 Suinae	''Small Suinae/Y406 species''	2.2	7.4	8.9	9.2	3
17 Doliochoerinae	*Schizochoerus gandakasensis*	8.1	8.7	10.1	11.2	6
18 Anthracotheriidae	*Microbunodon punjabiense*	8.6	9.2	12.3	14.0	8
19 Anthracotheriidae	*Hemimeryx* spp.	3.6	6.2	13.6	14.0	40
20 Anthracotheriidae	?*Merycopotamus dissimilus*	2.2	3.3	5.8	6.1	2
21 Hippopotamidae	*Hexaprotodon sivalensis*	2.2	3.5	5.9	6.1[†]	4
22 Tragulidae	*Dorcabune nagrii*	8.4[†]	8.5	10.4	11.2	10
23 Tragulidae	*Dorcabune anthracotherioides*	10.3[†]	10.5	12.8	14.0	9
24 Tragulidae	*Dorcatherium* ''Y270 species''	8.6	9.2	11.1	11.2	6
25 Tragulidae	*Dorcatherium nagrii*	2.2	6.8	9.3	9.5[†]	12
26 Tragulidae	*Dorcatherium* ''Y259 species''	10.3[†]	10.4	12.3	14.0	3
27 Tragulidae	*Dorcatherium* ''Y311 species''	7.1[†]	7.2	10.3	10.3[†]	21
28 Tragulidae	*Dorcatherium* ''Y373 species''	6.5	6.8	7.8	7.8[†]	5
29 Tragulidae	*Dorcatherium* ''Y457 species''	7.3[†]	7.3	7.3	7.7	1
30 Tragulidae	*Dorcatherium* cf. *majus*	10.5[†]	10.7	11.3	11.4	3
31 Tragulidae	*Dorcatherium majus*	6.9[†]	7.0	10.4	10.6[†]	19
32 Tragulidae	''Tragulidae/L101 unnamed species''	2.2	3.3	5.9	6.1[†]	4
33 Giraffinae	*Giraffa punjabiensis*	2.2	7.2	8.9	9.1[†]	3
34 Sivatheriinae	*Bramatherium megacephalum*	7.1[†]	7.1	10.3	10.3[†]	26
35 Sivatheriinae	*Giraffokeryx punjabiensis*	10.3[†]	10.3	13.6	14.0	20
36 Bovidae	*Sivoreas eremita*	10.3	10.7	11.3	14.0	2
37 Bovidae	''Bovidae/Y166 unnamed species''	8.4	8.7	8.7	9.1	1
38 Bovidae	''Bovidae/Y905 unnamed species''	7.4	7.8	7.8	7.8[†]	1
39 Bovidae	''Small Bovidae/Y581 unnamed species''	6.3	7.0	7.0	7.1[†]	1
40 Bovidae	''Bovidae/Y545 unnamed species''	7.4	8.0	8.0	8.4	1
41 Tragelaphini	''?Tragelaphini/D013 species''	5.8	6.2	6.4	6.7	3
42 Boselaphini	*Elachistoceras khauristanensis*	7.3[†]	7.4	11.5	14.0	16
43 Boselaphini	*Selenoportax* spp.	7.9[†]	7.9	10.2	10.3[†]	12
44 Boselaphini	*Tragoceridus* spp.	2.2	6.2	11.2	11.2	22
45 Boselaphini	cf. *Eotragus* ''Y166 unnamed species''	3.6	8.7	9.3	9.9	2
46 Boselaphini	*Tragoportax salmontanus*	7.3	8.4	9.3	9.9	3
47 Boselaphini	''Medium Boselaphini/Y581 unnamed species''	6.3	7.0	7.0	7.1[†]	1
48 Boselaphini	''Medium Boselaphini/Y195 unnamed species''	8.1	9.3	9.3	9.9	1
49 Boselaphini	''Large Boselaphini/Y927 species''	7.3[†]	7.3	8.0	8.1[†]	2
50 Reduncini	''?Reduncini/D013 species''	2.2	6.4	6.4	6.9	1
51 Reduncini	*Dorcadoxa porrecticornis*	6.5	7.0	8.1	8.1[†]	8
52 Hippotragini	''?Hippotragini/Y453 species''	2.2	6.2	6.8	6.9[†]	3
53 Antilopini	*Gazella* spp.	2.2	6.2	11.3	14.0	23
54 Antilopini	cf. *Prostrepsiceros vinayaki*	7.4	7.9	8.3	8.6	4

Appendix 4. Continued.

Species	Inferred last appearance (Ma)	Last occurrence (Ma)	First occurrence (Ma)	Inferred first appearance* (Ma)	No. of intervals in which observed
55 Antilopini cf. *Protragelaphus skouzesi*	8.8[†]	8.8	8.8	8.8[†]	1
56 Hipparionini ''*Hipparion s.l.*'' spp.	3.7	5.8	10.7	10.9	43
57 Chalicotherini *Chalicotherium salinum*	8.0[†]	8.0	12.9	14.0	13
Small mammals					
58 Tupaiidae Tupaiidae, spp.	6.5	8.1	13.0	13.6	10
59 Galericinae *Galerix rutlandae*	8.5[†]	8.7	13.6	13.6	7
60 Galericinae *Schizogalerix* ''Y259 species''	9.3	10.2	10.4	11.0	2
61 Crocidurinae cf. *Crocidura* ''Y367 species''	5.7	6.4	12.7	13.6	12
62 Crocidurinae cf. *Crocidura* ''Y311 species''	6.5	7.3	11.1	11.2	11
63 Crocidurinae cf. *Crocidura* ''D013 species''	5.7	6.4	6.4	7.1	1
64 Lorisidae Lorisidae, spp.	8.8	9.2	11.1	12.2	4
65 Leporidae ''Leporidae/D013 species''	3.6	3.6	7.3	7.8	6
66 Ratufini *Ratufa* ''Y259 species''	8.8	9.2	10.4	11.0	4
67 Tamiini *Eutamias* ''259 species''	6.5	7.0	10.4	11.0	7
68 Petauristinae *Hylopetes* ''Y388 species''	5.7	7.3	8.7	9.1	3
69 Petauristinae cf. *Hylopetes* ''Y259 species''	9.3	10.0	11.5	13.6	5
70 Petauristinae ''Petauristinae/Y311 species''	9.3	10.0	10.0	10.3	1
71 Gerbillinae *Abudhabia pakistanensis*	8.2	8.6	8.6	8.6[†]	1
72 Copemyinae *Democricetodon* ''species D''	10.1[†]	10.2	13.0	13.6	10
73 Copemyinae *Democricetodon* ''species B''	9.3	10.0	13.6	13.6	10
74 Copemyinae *Democricetodon* ''species E''	10.3[†]	10.4	13.0	13.6	9
75 Copemyinae *Democricetodon* ''species H''	10.1	10.4	13.0	13.6	9
76 Copemyinae *Democricetodon* ''species F'' (young)	8.2	8.6	8.7	8.8[†]	2
77 Copemyinae *Democricetodon* ''species F'' (old)	9.3	10.0	12.3	13.6	6
78 Copemyinae *Democricetodon* ''species G'' (young)	8.2	8.6	8.7	8.8[†]	2
79 Copemyinae *Democricetodon* ''species G'' (old)	9.3	10.0	13.0	13.6	8
80 Dendromurinae *Dakkamys asiaticus*	10.1	10.4	11.5	13.6	4
81 Dendromurinae *Paradakkamys chinjiensis*	10.1	10.4	13.0	13.6	6
82 Tachyoryctinae *Kanisamys sivalensis*	7.3[†]	7.3	9.3	9.5[†]	10
83 Tachyoryctinae *Kanisamys nagrii*	9.4[†]	9.6	11.5	13.6	7
84 Tachyoryctinae *Protachyoryctes tatroti*	6.5	6.9	7.8	8.0[†]	3
85 Tachyoryctinae *Eicooryctes kaulialensis*	6.5	7.1	7.8	7.8[†]	3
86 Tachyoryctinae *Rhizomyides sivalensis*	5.7	6.4	7.1	7.1[†]	3
87 Tachyoryctinae *Rhizomyides punjabiensis*	10.1[†]	10.2	10.4	11.0	2
88 Rhizomyinae *Brachyrhizomys* ''Y535 species''	8.2[†]	8.4	8.4	8.5[†]	1
89 Rhizomyinae *Brachyrhizomys nagrii*	9.0[†]	9.2	9.6	9.9	4
90 Rhizomyinae *Brachyrhizomys pilgrimi*	5.7	8.0	9.3	10.3	2
91 Rhizomyinae *Brachyrhizomys micrus*	8.2	9.2	9.2	10.3	1
92 Rhizomyinae *Brachyrhizomys blacki*	8.2	9.2	9.2	10.3	1
93 Rhizomyinae *Brachyrhizomys tetracharax*	5.7	7.9	9.3	10.3	4
94 Rhizomyinae *Brachyrhizomys choristos*	8.2[†]	8.2	8.4	8.5[†]	2
95 Murinae *Progonomys* ''Y581 unnamed species''	6.5	7.0	7.8	7.8[†]	4
96 Murinae *Progonomys* ''Y259 unnamed species''	9.4[†]	9.6	11.5	13.6	7
97 Murinae *Progonomys debruijni*	8.2	8.6	9.3	9.9	5
98 Murinae *Progonomys* nr. *debruijni*	7.3[†]	7.3	8.1	8.5	3
99 Murinae *Karnimata* ''Y450 unnamed species''	9.4[†]	9.6	11.3	11.4	6
100 Murinae *Karnimata* ''Y388 unnamed species''	8.2	8.7	9.2	9.9	3
101 Murinae *Karnimata darwini*	8.7[†]	8.7	9.3	9.5[†]	4
102 Murinae *Karnimata* cf. *darwini*	7.1[†]	7.2	7.2	7.2[†]	1
103 Murinae *Karnimata huxleyi*	5.7	6.4	6.4	6.7	1
104 Murinae *Karnimata* cf. *huxleyi*	6.5	7.0	7.0	7.1[†]	1
105 Murinae *Karnimata* ''Y024 unnamed species''	7.3[†]	7.3	8.1	8.3[†]	3
106 Murinae *Parapodemus* ''Y182 species''	7.3	7.9	9.2	9.9	2
107 Murinae *Mus auctor*	5.7	6.4	7.3	7.7	3
108 Murinae cf. *Mus* ''Y931 species''	7.1[†]	7.2	7.2	7.2[†]	1
109 Murinae cf. *Parapelomys robertsi*	7.1[†]	7.2	8.1	8.5	5
110 Murinae *Parapelomys robertsi*	5.7	6.4	7.0	7.1[†]	3
111 Murinae ''Murinae/D013 species''	5.7	6.4	6.4	7.2	1

Appendix 4.   Continued.

Species	Inferred last appear-ance (Ma)	Last occur-rence (Ma)	First occur-rence (Ma)	Inferred first appear-ance* (Ma)	No. of intervals in which observed
112 Murinae ''Murinae/Y311 unnamed species''	9.3	10.0	10.4	11.0	2
113 Gliridae Gliridae, spp.	7.3	7.9	13.6	13.6	13
114 Hystricinae *Hystrix sivalensis*	7.2[†]	7.3	8.0	8.0[†]	4
115 Ctenodactylidae *Sayimys chinjiensis*	9.4	10.0	12.3	13.6	8

* Inferred ages of appearance for those taxa appearing before 10.7 Ma are only approximately determined.
† Events included in analysis of first and last appearances. See text for details.