FOSSIL MAMMALS OF ASIA

NEOGENE BIOSTRATIGRAPHY AND CHRONOLOGY

Edited by Xiao-ming Wang, Lawrence J. Flynn, and Mikael Fortelius

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Chapter 15

The Neogene Siwaliks of the Potwar Plateau, Pakistan

JOHN C. BARRY, ANNA K. BEHRENSMEYER, CATHERINE E. BADGLEY, LAWRENCE J. FLYNN, HANNELE PELTONEN, I. U. CHEEMA, DAVID PILBEAM, EVERETT H. LINDSAY, S. MAHMOOD RAZA, ABDUL RAHIM RAJPAR, AND MICHELE E. MORGAN

The Siwalik formations of the Indian Subcontinent comprise fluvial sediments of Miocene through Pleistocene age deposited in a series of basins along the southern margin of the collision zone between peninsular India and Asia. The deposits are thick and fossiliferous, with a diverse fauna of terrestrial and freshwater vertebrates and for well over 170 yr have been the subject of considerable scientific interest.

Research on Siwalik fossils and sediments has touched on diverse subjects, but a recent focus has been on a fundamental problem in paleobiology, the relationship between biotic evolution and environmental change. This is a line of inquiry we have been involved with for over 30 yr, and one that has had a major influence on our collective research agenda. Our primary focus has been on documenting patterns of faunal turnover and ecological change, as well as on investigating the relationships between observed faunal dynamics and changes in the fluvial system, climate, and local habitats. This, however, can only be achieved by first creating a comprehensive chronostratigraphic framework and understanding the biases inherent in the Siwalik fossil record. Therefore, creation of a chronostratigraphic framework, together with determining the taphonomic characteristics of the fossil assemblages, is a critical component of our research program. To that end, this chapter and ongoing related research are steps toward those goals.

In the following, we discuss aspects of Siwalik stratigraphy, with a focus on the depositional system in which the sediments and fossil sites formed. We begin with an overview of the distribution of Siwalik sediments on the Indian Subcontinent and discussion of recent ideas about the depositional system. We then present an outline of the chronological framework constructed for the Siwalik formations on the Potwar Plateau in northern Pakistan and our methods of estimating the ages of the fossil localities. That is followed by preliminary analyses of the temporal distribution of the fossil sites, their taphonomic characteristics, and the implications for biostratigraphy. We end with a brief summary of some of the important changes in the faunas as documented on the Potwar Plateau. All ages cited are based on the Gradstein et al. (Ogg and Smith 2004) calibration of the Geomagnetic Polarity Time Scale.

OVERVIEW OF THE SIWALIKS

The term "Siwalik" is derived from the name of a range of hills lying south of the main ranges of the Himalayas in northwestern India and composed principally of Neogene fluvial sediments. The name has been loosely applied to all Neogene fluvial sediments along the southern margin of the Himalayas and adjacent ranges in Nepal, India, and Pakistan. While the most intensively studied exposures are those of the Punjab region of northern India and northern Pakistan, Siwalik deposits are widely exposed throughout a broad belt stretching eastward from the trans-Indus region of Pakistan (Hussain et al. 1979; Munthe et al. 1979; Swie-Djin and Hussain 1981) through northern India into central Nepal and the Garo Hills of northwest Assam (Pentland 1828), as well as southward to Piram (Perim) Island in the Gulf of Khambhat (Cambay) (see Flynn et al., chapter 14, this volume:fig. 14.1). While not traditionally considered to be "Siwaliks," other areas with Neogene fluvial sediments include the Gaj and Manchar formations in Sind and the Chitarwata and Vihowa formations in Baluchistan and southwestern Punjab. Finally, although in a different tectonic setting, the molassic Irrawaddy Formation in Myanmar (Burma) is often treated as a Siwalik equivalent, especially in the older literature and in conjunction with discussions of fossil material (e.g., Pilgrim 1926; Colbert 1935).

Although typically mantled by Late Pleistocene deposits, in the more arid regions of the Subcontinent the underlying Siwalik formations are often widely exposed as shallowly dipping and undeformed rocks with relatively simple stratigraphic relationships. Particularly on the Potwar Plateau of northern Pakistan, the sediments are exposed as broad belts of outcrop. As a consequence, numerous sections along small cross-cutting streams can be measured, sampled, and correlated laterally by tracing distinctive lithological units that magnetostratigraphic field studies have shown to approximate isochronous horizons over distances of as much as 30 km (McMurtry 1980; Behrensmeyer and Tauxe 1982; Sheikh 1984; Johnson et al. 1988; Badgley and Tauxe 1990; McRae 1990; Kappelman et al. 1991; Friend et al. 2001). Siwalik lithofacies include sandstones, siltstones, mudstones, and rare conglomerates and marls. Formations have been differentiated on the basis of the relative proportions of sandstones and fine-grained units, as well as the thickness of the large sandstone bodies and in some cases mineralogical characteristics. The Potwar sequence can be divided into seven formations (Cheema et al. 1977; Hussain et al. 1992), which are listed in table 15.1 along with estimated ages for their boundaries on the Potwar Plateau. In table 15.1, the overlap in ages between formations represents the approximate degree of known time transgression, but all the formations are likely to be time transgressive to some degree.

Table 15.1
Siwalik Formations and Their Ages on the Potwar Plateau

Formation	Age Range (Ma)
Tatrot	3.5 to 3.3
Samwal[a]	ca. 3.6 to ca. 1.5
Dhok Pathan	9.8 to ca. 3.5
Nagri	11.5 to 9.0
Chinji	14.0 to 11.4
Kamlial/Murree[b]	18.0 to 14.0
Murree	? to 18.0

[a]For a discussion of this unit and the problem of Upper Siwalik Formation nomenclature, see Hussain et al. (1992).

[b]In the Southern Potwar, the Kamlial and Murree formations are not differentiated.

The Potwar Siwalik formations, exposed as a tilted and slightly deformed belt bounded by the Margala Hills and Kala Chitta Hills to the north and the Salt Range to the south (figure 15.1), have had a central role in the development of the lithologic and biostratigraphic nomenclature of the Subcontinent. First used by Pilgrim (1913, 1934) and subsequently by others (Cotter 1933; Colbert 1935; Lewis 1937), five stratigraphic units were recognized on the Potwar Plateau (Kamlial, Chinji, Nagri, Dhok Pathan, and Tatrot "zones") and were an important advance in devising a nomenclature for what came to be recognized as a series of successive faunas. These, together with additional units established in rocks to the east in India, were at first conceived of as faunal units or "zones" that were conceptually most similar to "stages" as used in modern codes of stratigraphic nomenclature and were intended to be used for long-distance correlations throughout the Subcontinent. Thus, Pilgrim referred to fossil collections from the region around Haritalyangar in northwestern India as being of "Nagri" or of "Dhok Pathan" age, although this area is nearly 600 km to the east of the Potwar. Subsequently, Pilgrim's faunal units came to be used as both lithostratigraphic formations and as chronostratigraphic zones, with the distinction not always being made clear and often leading to considerable confusion. The 1977 summary of the stratigraphy of Pakistan (Cheema et al. 1977) establishes the Potwar units as "formations" with distinctions among them based on lithological characteristics, but they still tend to be used as units having chronostratigraphic significance. Fortunately the most recent practice has been to recognize and give different names to local lithological units in distant regions that may be more or less time equivalent. (For further discussion and additional references, see Flynn et al., chapter 14, this volume; for a still relevant discussion of the early history of Siwalik stratigraphic nomenclature, see Colbert 1935:7–19.)

Used in a very broad and loose sense as biostratigraphic units, Pilgrim's faunal zones are still useful, although there are several problems in adapting them to the more demanding requirements of current studies. These problems are separate from the confusion over litho- and biostratigraphic units and stem from the imprecision with

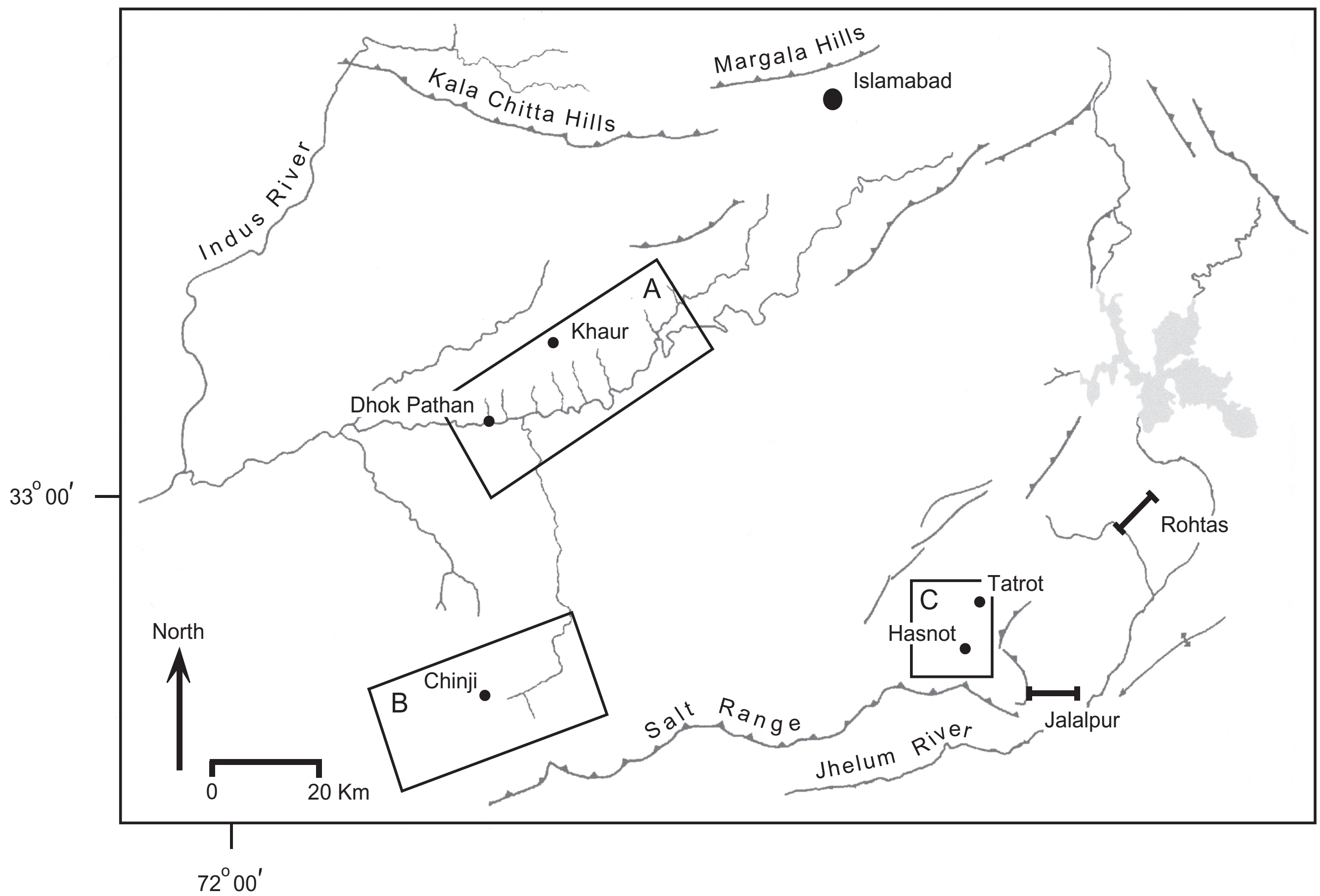

Figure 15.1 Map of the Potwar Plateau in northern Pakistan. Boxes are areas with regional networks of stratigraphic sections: *A*, northern limb of the Soan Synclinorium along the Soan River; *B*, southern limb of the Soan Synclinorium near the Salt Range; *C*, eastern edge of the Potwar Plateau near Hasnot. Isolated sections at Rohtas and Jalalpur are also shown. Barbed lines are the boundaries of thrusts.

which the faunal zones were initially defined. First, only two (the Chinji and Nagri "zones") are in direct superposition in what can be considered to be their type areas. Consequently, it has proved difficult to define the boundaries between the "zones" in precise terms. Secondly, since some of the areas Pilgrim used to characterize his zones are poorly or only modestly fossiliferous, he used fossils from other regions to supplement his faunas. In doing this, Pilgrim must have assumed that his lithological correlations were also chronological correlations, which we now know to be an error. Chief among the problematic units are the Kamlial and Nagri zones. The former was characterized by species from Dera Bugti and the Manchars some 500 km to the south, while the Nagri "fauna" came to include species from Haritalyangar that are now believed to be significantly younger than those of the Nagri Formation on the Potwar Plateau (Johnson et al. 1983; Pillans et al. 2005). Citing these problems, Barry, Lindsay, and Jacobs (1982) established a series of interval zones based on rocks and faunas from the Potwar Plateau, and while the zones were subsequently refined and extended by Hussain et al. (1992), there has not been much further work in this important area of research.

As might be expected for collections formed over 170 yr, fossils from the Siwaliks are scattered among many museums and other institutions and are often without useful stratigraphic data. The initial collections, containing many of the types for Siwalik taxa, are in the British Museum of Natural History and the collections of the Indian Geological Survey in Calcutta. For our work we have primarily relied on material in collections held by the Geological Survey of Pakistan and the Pakistan Museum of Natural History. In addition a number of fossils collected by Barnum Brown and G. Edward Lewis in

1922 and 1932 and now in the American Museum of Natural History and Yale Peabody Museum have been of use, as well as fossils collected in 1935 and divided among the Yale Peabody Museum, the American Museum, and the Geological Survey of India. Other important collections made just before and after World War II are in Munich, Germany, and Utrecht, the Netherlands. (See Dehm et al. 1958 and Hussain 1971 for some discussion of these latter collections.)

THE POTWAR SIWALIK DEPOSITIONAL SYSTEM

Environmental reconstructions of the Siwalik formations are based primarily on sedimentological evidence, using as models the modern analogues provided by the Indus and Ganges Rivers and their tributaries (Behrensmeyer and Tauxe 1982; Behrensmeyer 1987; Badgley and Tauxe 1990; Willis 1993a,b; Willis and Behrensmeyer 1994, 1995; Badgley and Behrensmeyer 1995; Behrensmeyer, Willis, and Quade 1995; Zaleha 1997a, 1997b). Furthermore, while there is essentially no plant or pollen record for the Potwar Siwaliks, insights gained through analysis of stable isotopes and the paleosols (Quade, Cerling, and Bowman 1989; Quade et al. 1995; Retallack 1991; Quade and Cerling 1995; Behrensmeyer et al. 2007; Nelson 2007; Morgan et al. 2009), as well as scattered ecomorphological analyses of selected mammals (e.g., Nelson 2005; Belmaker et al. 2007), have been used to make inferences about the climate and vegetation of the ancient floodplains. Together these studies have been used to develop a conceptual model of local Siwalik deposition and paleoenvironments that potentially can serve as a model for the Neogene fluvial deposits beyond the Potwar Plateau. This model, however, does not apply universally and especially not to the Oligo-Miocene Murree Formation (Najman et al. 2003) nor the Oligo-Miocene Chitarwata Formation (Downing et al. 1993; Welcomme et al 2001; Downing and Lindsay 2005; Métais et al. 2009; Flynn, chapter 14, and Antoine et al., chapter 16, both this volume), and most likely not to the Early Miocene Gaj Formation in the Lower Indus Basin of Sind (Raza et al 1984). Each of these three latter formations apparently includes facies transitional between marine, estuarine, and fluvial environments, and thus include additional and more varied depositional environments.

The Miocene Siwaliks were deposited as part of a very large river system, one the size of the modern Indus or Ganges systems. While modern rivers of the Punjab region drain southwest into the Indus and contribute to the Indus fan, paleocurrent directions indicate the proto-Ganges system may have extended farther west and drained the Potwar region in the Miocene (Raynolds 1981; Beck and Burbank 1990). Such an ancient proto-Ganges system would have extended several thousand kilometers eastward to the Bay of Bengal, with floodplain widths on the order of 100–500 km. Even if drainage was to the south as a proto-Indus, the whole system would have been very large as it included not only the floodplains but also the more distant mountain source regions and even the deltaic fans of the axial river in either the Arabian Sea or Bay of Bengal. Since the Potwar Plateau is only about 30,000 km^2, it encompasses only a comparatively very small fraction of this much larger area and thus can give us only limited information on the entire Neogene Siwalik system (Willis and Behrensmeyer 1995).

In the Miocene, the Potwar was some 100–200 km southeast of the mountain front where its rivers originated (Zaleha 1997b). At that time the Potwar region was at approximately 29°N latitude, about 4° south of its current position (Tauxe and Opdyke 1982). We infer it had a warm and humid climate, with a monsoonal pattern of circulation and likely marked seasonality. Analysis of Late Miocene paleosols, which are primarily in the Dhok Pathan Formation, indicates they are most like modern soils that form under 25°C mean annual temperature with ca. 1400 mm/yr precipitation (Retallack 1991; Behrensmeyer, Willis, and Quade 1995). At all levels, the paleosols indicate intense oxidation and seasonal differences in the height of the water table, with waterlogging followed by leaching and precipitation of carbonates. The stable isotopes of both the paleosols and teeth indicate there were progressive and marked changes in vegetation and climate, with the most rapid in the latest Miocene (Quade and Cerling 1995; Barry, Lindsay, and Jacobs 2002, Behrensmeyer et al. 2007). Between about 8 Ma and 4.5 Ma there was a shift from floodplain vegetation dominated by C3 plants, which presumably encompassed largely forested habitats of various types, to vegetation dominated by C4 plants, presumably more open grasslands. The transition, however, was complex, with C3 and C4 habitats coexisting on the floodplain in close proximity for several million years (Behrensmeyer et al. 2007).

The various reconstructions of the ancient Potwar rivers all portray them as part of a single large drainage system with a major trunk river the size of the modern Indus running to either the Arabian Sea or the Bay of Bengal. Deposits of the first-order axial trunk river (figure 15.2 [1]) are not preserved, either because it flowed eastward and did not cross the Potwar Plateau or, if flowing southward, was

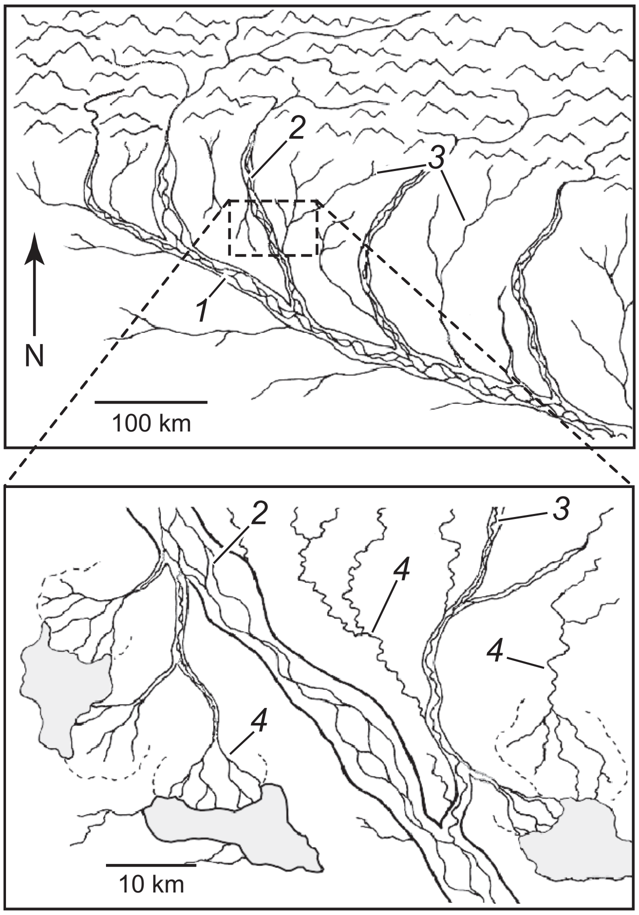

Figure 15.2 Plan view of a reconstructed Siwalik fluvial system. The numbers refer to categories of streams discussed in text: *1*, main trunk river, shown as flowing eastward and not preserved on the Potwar Plateau; *2*, emergent river with origin in northern mountains; *3*, interfan rivers with origins on broad floodplain; *4*, small floodplain streams, some tributary to larger rivers and some draining into swamps or ponds indicated by gray stipple. The outlined box is approximately the size of the Potwar Plateau, indicating the magnitude of the system.

confined to the distant margin of the depositional basin (Willis 1993a, 1993b; Willis and Behrensmeyer 1995).

The channel and floodplain deposits of tributaries to the trunk river are preserved, however. These tributaries are of two types (Willis 1993b; Zaleha 1997b). One type (see figure 15.2 [2]) includes deposits of large rivers the size of the modern Jhelum. These Miocene rivers apparently emerged from the mountains to the north and west at widely spaced intervals and flowed hundreds of kilometers southeast to join the trunk river (see figure 15.2). These second-order rivers, which are referred to as "emergent" or "upland sourced," carried relatively unweathered sediment from the mountains and deposited it in the basin as large, low-gradient fans. The braided channel belts of the emergent rivers were typically more than 5 km wide, with individual channels of 200–400 m. The emergent rivers probably had higher discharge during the spring melt and summer monsoon seasons. Because they were prone to frequent avulsions during flood events, the channels did not migrate laterally to form extensive sand sheets (Behrensmeyer, Willis, and Quade 1995). The Jhelum and Chenab are modern analogues of such rivers.

The second type of tributary (see figure 15.2 [3]) are deposits of smaller rivers that were tributaries of either the trunk river or the emergent rivers (Willis 1993b; Zaleha 1997b). They were braided streams, with channel belts 1–2 km wide and channels of 70–200 m. While a few may have had mountain sources, others had sources in the foothills or the floodplain. Because they were confined by the fan deposits of the larger emergent rivers and carried fine, reworked material eroded from the floodplain, they are referred to as "interfan" or "lowland-source" streams. Since the source of their water was close to or on the floodplains, their flow varied more throughout the year than in the emergent streams, with presumably higher discharge during the summer monsoon (Willis 1993b; Zaleha 1997b). Across the floodplain, floods must have disturbed nearby vegetation, perhaps keeping extensive areas in early stages of ecological succession. The Soan River is a potential modern analogue of an interfan river.

The floodplain was flat, with perhaps at most a few hundred meters difference in elevation across it and local relief of about 10 m (Willis 1993b). Low areas could have been permanent or seasonal ponds and swamps that would have eventually filled with sediment from the second- and third-order channels or from still smaller fourth-order floodplain streams (see figure 15.2 [4]). Preserved floodplain deposits consist chiefly of mudstones, along with minor contributions from crevasse-splays, levees, and smaller floodplain channels. Features of the smallest fourth-order streams indicate that they were 10–100 m wide, smaller than the individual channels of the third-order interfan rivers. Flow in these smallest channels was episodic with, at some times of year, standing water in the channels (Willis 1993a). In all the Siwalik formations, the smaller channels were important sites for fossil bone accumulation, as were the fine-grained fills in the upper parts of the larger channels (Badgley and Behrensmeyer 1980, 1995; Behrensmeyer 1987; Badgley et al. 1995; Behrensmeyer, Willis, and Quade 1995; Willis and Behrensmeyer 1995).

Although not studied extensively, paleosols are common throughout the whole Siwalik sequence. Retallack (1991) described and named nine paleosol types ("series") from two short sections in the lower Dhok Pathan Formation. In these two sections, which are within (9.5–9.4 Ma) and just above (8.8–8.7 Ma) the Nagri–Dhok Pathan transition, he documented differences in the frequencies of soil types that he interpreted as resulting primarily from differences in parent material, local topography, and drainage, as well as local vegetation and the amount of precipitation. Retallack (1991) found no evidence for extensive grasslands in either section, although he suggested that two rare types formed under waterlogged, grassy woodlands. Fewer paleosol types were reported in the younger section, which Retallack (1991) interpreted as evidence for a less varied landscape at that time. Nevertheless, considering the smaller number of recognized soil horizons in the upper section (four paleosol types from 31 horizons versus eight types from 80 horizons in the lower section), the proportions are not different. Nevertheless, between and within stratigraphic levels there is always considerable diversity in paleosol types and by inference considerable diversity in vegetation. Low areas contained seasonal swamps or ephemeral ponds, while other areas had extensive wet upland and lowland forests, dry old-growth deciduous woodlands, tall gallery forest with lush undergrowth, and wet grassy wooded meadows. There were also tracts with secondary growth and early succession (Retallack 1991). These vegetation types would have been common, coexisting elements of the landscape.

Temporal changes in the Siwalik fluvial system have been documented, but whether they are related to climate or subsidence, or simply due to the autocyclic dynamics of the fluvial system, is not clear. The transition between the Chinji and Nagri formations has been interpreted as resulting from the progradation of a second-order emergent system over a smaller, third-order interfan system (Willis 1993b; Zaleha 1997b). The Nagri to Dhok Pathan transition, on the other hand, seems a case of prolonged coexistence of two contemporaneous systems ending with displacement of an emergent system by an interfan system (Behrensmeyer and Tauxe 1982). Although we do not yet fully understand the underlying causes, both of these transitions, and that between the Kamlial and Chinji formations, are likely to be local events without chronostratigraphic significance.

In previous publications (e.g., Barry, Lindsay, and Jacobs 2002), we used two terms to designate the occurrence of fossils: locality and survey block. In our usage, a locality is limited temporally and spatially. In the Siwaliks, concentrations of fossils typically occur in small areas of outcrop of perhaps a few tens or hundreds of square meters extent with a single sedimentary body as the source of the fossils. Between patches there is little or no fossil bone, so that it is usually possible to delineate localities spatially as distinct entities. The duration of accumulation of the fossil material in a given locality is thought to have been brief and was generally between a few tens of years to, rarely, at most fifty thousand years (Behrensmeyer 1982; Badgley 1986; Badgley et al. 1995; Behrensmeyer, Willis, and Quade 1995).

A survey block or collecting level is less limited spatially and temporally, as they are more extensive in area, span a greater stratigraphic thickness, and often include fossils from multiple sedimentary layers. Survey blocks span between 30,000 and 350,000 yr and extend laterally several kilometers. Most survey blocks have been systematically searched with all identifiable surface fossils recorded as part of a program to standardize surface collecting (Behrensmeyer and Barry 2005).

Depositional environments in the Siwaliks include active and abandoned channels of all sizes, levees, crevasse-splays, paleosols, and rarely pond or swamp deposits. These depositional environments are present in all Siwalik formations, but they differ in their frequency of occurrence among the formations. Fossils of both vertebrates and invertebrates are found in nearly all lithologies. The fossils mostly accumulated as attritional assemblages derived from the nearby surroundings, but habitat specific associations of fossils seem to be only rarely preserved (Badgley and Behrensmeyer 1980, 1995; Badgley et al. 1995). Fossil vertebrates are most common in deposits associated with the mid-sized to small floodplain channels, where they occur as concentrations of disarticulated, often fragmentary bones. A very few such concentrations contain a 1000 or more specimens, but the majority have only 5 to 200 fossils each. Because other facies contain only isolated specimens or small, low-density scatters, collections of fossils are biased toward overrepresentation of small channel floodplain sites. This bias, in addition to those introduced by taphonomic processes common to the different facies, may place limits on reconstructions of the living communities (Badgley 1986). This bias may also severely hamper attempts to determine the true temporal ranges of taxa and therefore development of biostratigraphic zonations.

As an aid in paleoecological and biostratigraphic analysis, a classification system has recently been developed for the depositional environments of Siwalik localities (Behrensmeyer et al. 2005). The classification recognizes four major groups (major channel, floodplain channel, sheet deposits, and floodplain), with all but the sheet deposit category being further subdivided (table 15.2). The criteria for classification are based only physical characteristics, such as lithology or sedimentary structures, and the geometry and relationships of the beds, not proper-

Table 15.2
Depositional Categories

Abbreviation	Primary Context	Secondary Context	Lithologies/Depositional Setting	Number of Localities
MC-L	Major channel	Lower two-thirds of channel	Basal lag and bar	3
MC-U1	Major channel	Upper third of channel	Channel bar	8
MC-U2a	Major channel	Upper third of channel	Large scale, coarse fill: gravel and coarse sand lens, mudclasts, reworked carbonate nodules	11
MC-U2b	Major channel	Upper third of channel	Large scale, fine fill: laminated and cross-stratified sands and silts, fining upwards into mudstones	12
MC-U3a	Major channel	Upper third of channel	Small scale, coarse fill: sand, grit	12
MC-U3b	Major channle	Upper third of channel	Small scale, fine fill: mudstones, siltstone	6
FC-C1	Floodplain channel	Complex fill	Basal lag and bar in lower part of channel	19
FC-C2	Floodplain channel	Complex fill	Cross cutting lens of mixed lithologies within channel	43
FC-S1	Floodplain channel	Simple fill	Basal lag and bar in active channels	20
FC-S2	Floodplain channel	Simple fill	Mixed lithologies with inclined bedding, silts and fine sand, mudclast gravels	37
FC-S3	Floodplain channel	Simple fill	Fine grained mudstones and clays, laminated or pedogenically altered	16
FP-P	Floodplain	Patchy	Laterally continuous paleosols with concentrations of bone	37
FP-C	Floodplain	Continuous	Laterally continuous paleosols with extensive bone throughout	10
FP-L	Floodplain	Laminated	Temporary or seasonal water bodies	4
SD	Sheet deposit		Crevasse-splay, levee, or sheet wash deposits	17

NOTE: The total of the number of localities in the last column is fewer than 321 because the secondary context of all localities is not known.

ties of the fossil assemblages such as taphonomic character or taxonomic composition.

Most major channel (MC) and floodplain channel (FC) localities are part of infillings of abandoned channels. Major channels approximately correspond to the second- and third-order channels of the emergent and interfan system deposits, while the floodplain channels correspond to the small, fourth-order channels of the interfan floodplain. The floodplain (FP) localities mostly occur in paleosols, as either discrete patches or dispersed concentrations, or very rarely as laminated deposits in ponds or swales. The localities of the sheet deposits (SD) formed in crevasse-splays, levees, or in sheet-wash deposits.

Research based on this classification of depositional settings is just beginning. In a later section, we present some new data on the relative frequency of the types and subtypes and discuss some of the implications for biochronology.

THE CHRONOLOGICAL FRAMEWORK AND ESTIMATION OF AGES OF LOCALITIES

The Siwaliks comprise not only a thick sequence but also one that had relatively continuous deposition of sediment with fossils at many horizons and easily determined superpositional relationships between individual localities. The thickness and continuity of deposition has allowed the development of a detailed paleomagnetic reversal stratigraphy and as a consequence a reliable chronostratigraphic framework for much of the region (Barndt 1977; Barndt et al 1978;Opdyke et al. 1979; Barry, Behrensmeyer, and Monaghan 1980; McMurtry

1980; Behrensmeyer and Tauxe 1982; Johnson et al 1982; Stix 1982; Tauxe and Opdyke 1982; Johnson et al. 1985; Tauxe and Badgley 1988; Willis 1993a, 1993b). See also Barry, Lindsay, and Jacobs (2002:appendix 1).

At present, our chronostratigraphic framework for the Potwar Plateau is based on 29 measured sections between 250 m and 3200 m thick, as well as 34 shorter sections. Twenty-four of the 29 long sections and 23 of the 34 short sections have determined magnetic polarity stratigraphies. Except for outliers at Rohtas and Jalalpur (Opdyke et al. 1979; Johnson et al. 1982; Behrensmeyer et al 2007), the 63 sections form three regional networks (see figure 15.1) corresponding to the classic Potwar areas of Pilgrim and subsequent collectors. Two networks are on the northern and southern limbs of the Soan Synclinorium, and the third lies at the eastern edge of the Potwar Plateau near Hasnot. In each region, exposures are vertically and laterally continuous, and individual sections can be correlated lithologically as well as by magnetic polarity. However, because of the absence of connecting exposures between regions, correlations among the regions depend on the magnetic polarity stratigraphy. No sections on the Potwar have been correlated on the basis of biostratigraphy.

In the Potwar Siwaliks, individual measured sections over 250 m usually have at least six or seven magnetic polarity transitions and can be independently correlated to the Geomagnetic Polarity Time Scale (GPTS; Johnson and McGee 1983). The shorter sections having fewer polarity zones typically cannot be directly matched to the GPTS, but they can still be reliably placed in the stratigraphic framework by determining their relationships to the long sections. We have correlated between adjacent sections by either tracing magnetic polarity transitions or by tracing sandstone bodies or paleosols; lithological units that have been shown in different parts of the sequence to be approximately isochronous (McMurtry 1980; Behrensmeyer and Tauxe 1982; Johnson et al. 1988; Badgley and Tauxe 1990; McRae 1990; Kappelman et al. 1991, Friend et al. 2001).

When correlating to the GPTS, it is not possible to match every observed magnetic transition to a GPTS magnetic boundary (Johnson and McGee 1983; Kappelman et al. 1991). Nevertheless, the algorithm we use to estimate dates for localities is based on interpolation between two points of known age, and these need not be successive geomagnetic transitions. In principle, radiometric dates, isotopic events, or even biostratigraphic zone boundaries of known age could also be used. Here, all ages are based on the ages for geomagnetic chrons in the Gradstein et al. (Ogg and Smith 2004) calibration of the Geomagnetic Polarity Time Scale.

Detailed analyses of lithological facies, in several cases accompanied by tracing paleomagnetic transitions laterally between multiple adjacent sections, have been made at five horizons in the Potwar Siwaliks (McMurtry 1980; Behrensmeyer and Tauxe 1982; Sheikh 1984; Kappelman 1986; Johnson et al. 1988; McRae 1990; Kappelman et al. 1991; Friend et al. 2001; Behrensmeyer et al. 2007). These five more detailed studies demonstrate that there was considerable lithological and paleoenvironmental variation across the floodplain at all times. Irregular channel and floodplain deposition combined with contemporaneous periods of nondeposition and erosion to create a complex stratigraphic architecture and on very short timescales produced highly variable rates of sediment accumulation. Consequently, adjacent sections may either record or miss particular magnetic transitions, have differences in apparent thickness of geomagnetic chrons, or even capture otherwise unknown brief geomagnetic events (Johnson et al. 1985; Kappelman 1986; McRae 1990; Kappelman et al. 1991). On longer time scales, however, the sediment accumulation rate was steadier and a more faithful recorder of the history of geomagnetic reversals (Johnson and McGee 1983; Johnson et al. 1988; McRae 1990).

Correlation of the Late Miocene and Pliocene Siwalik sections to the Geomagnetic Polarity Time Scale was discussed in Barry, Lindsay, and Jacobs (2002). Other than for publication of a section at Rohtas (Behrensmeyer et al. 2007), we have not altered those stratigraphic correlations and consider them to still be reliable. We have, however, changed the calibration of the time scale. Previously we used the Cande and Kent (1995) calibration of the GPTS (Barry, Lindsay, and Jacobs 2002). Here, all ages are based on the Gradstein et al. calibration (Ogg and Smith 2004). It is, of course, straightforward to substitute one calibration for another and recalculate ages of localities using the original stratigraphic data.

Our previous work focused on the Late Miocene part of the Siwalik sequence (Barry, Lindsay, and Jacobs 2002). The current focus of our efforts is now on the Kamlial and Chinji formations, which comprise the Early and Middle Miocene portions of the sequence. We have extended the correlations made in Barry, Lindsay, and Jacobs (2002), developed new ones for the older formations, and added age estimates for 471 localities to our database. We analyze this nearly doubled sample of dated localities in the next section.

Compared to the Nagri and Dhok Pathan formations, correlations of the older Chinji and Kamlial formations to the GPTS are made more difficult by the overall lower rates of sedimentation and possibly less steady rates of accumulation (McRae 1990). The middle of the Chinji Formation has been particularly problematic. In the upper part of the formation, chrons C5r and C5An (11.040–12.415 Ma using the Gradstein et al. calibration) are consistently identified (Johnson et al. 1985, 1988; Kappelman et al. 1991), as are C5AB and C5ACn (13.369–14.095 Ma) in the lower Chinji (Sheikh 1984; McRae 1990). The intervening intervals C5Ar and C5AA (12.415–13.369 Ma), however, are more irregular in their expression (Johnson et al. 1985; Johnson et al. 1988), and it is only at the western edge of the Chinji exposures that an easily interpretable sequence has been documented (Kappelman et al. 1991). Similarly at the base of the Chinji Formation and the top of the Kamlial Formation, chron C5ACr (14.095–14.194 Ma) is only occasionally recorded, and researchers have found an otherwise unknown very short reversed cryptochron within C5ACn (13.734–14.095 Ma) that can be confused with C5ACr. Recognition of this new reversal has altered the correlations of the eastern lower Chinji sections (McRae 1990) slightly, but not that of the Chitaparwala section (Johnson et al. 1985). We still place the local base of the Kamlial Formation in chron C5Dr, but now estimate its age at approximately 17.9 Ma using the Gradstein et al. calibration (Ogg and Smith 2004).

Fossil sites are typically at most only a few kilometers away from the nearest measured section and can be placed on that reference section by laterally tracing lithological markers. As noted, these marker horizons are types of lithologies that have been demonstrated to be isochronous at timescales of 10^3 yr over the distances involved (Behrensmeyer and Tauxe 1982), but the correlations have various degrees of uncertainty that are specific for each locality. In order to preserve the uncertainty, we recorded the stratigraphic position of each locality as bracketed by upper- and lowermost bounds in the section. These are the highest and lowest possible levels where the locality could occur in the reference section (figure 15.3). We have been conservative in these judgments, giving localities a wide range of possible ages. We assume that the locality could occur with equal likelihood at any horizon within the bracketed interval.

To order localities temporally, each is assigned an absolute age determined from its stratigraphic position relative to the Geomagnetic Polarity Time Scale. Ages are estimated with varying degrees of accuracy depending on both the precision of the stratigraphic position of the locality and how precisely the stratigraphic levels of the magnetic polarity transitions have been located in the stratigraphic sections. Most ages are based on interpolations between two levels of known age—that is, identified magnetic polarity transitions of the GPTS. However, some localities are in magnetozones truncated at either the top or bottom. In such cases the ages are extrapolated, using the rate of sediment accumulation of sub- or superjacent magnetic intervals.

Ages are determined for both the upper and lower limits of each locality's stratigraphic position, a practice that incorporates the uncertainty in the correlation of the locality to a stratigraphic section. In addition, although it is conventional to place magnetic polarity transitions midway between sites of differing polarity, in calculating ages for localities we instead use the highest and lowest possible positions of the magnetic transitions in the lithological sections (see figure 15.3). By so doing, we can incorporate uncertainties in the stratigraphic positions of the magnetic transitions as well. When a locality's stratigraphic level is precisely determined and the magnetic transitions are stratigraphically tightly constrained, the oldest and youngest age estimates will converge. Taken together, these two refinements produce conservative estimates for a pair of maximum and minimum ages for each locality and thus the largest reasonable range of possible ages. In the following analyzes and discussion, we average the oldest and youngest ages for each locality ("midpoint age") and calculate the difference between them ("delta age").

Both interpolation and extrapolation assume constant rates of sediment accumulation within polarity chrons. This assumption is certainly incorrect, as fluvial sequences are by nature episodic with many short intervals of erosion and nondeposition that leave hiatuses. However, as long as the hiatuses are short relative to the duration of the geomagnetic polarity chron and are evenly distributed within it, the approach will produce reliable results (Johnson and McGee 1983; Johnson et al. 1988).

ANALYSIS OF THE LOCALITY DATA

The variety of depositional environments and the biased preservation of fossils in those different settings (Behrensmeyer et al. 2005) suggest the possibility of imposed biases on the representation of taxa in our collections, with implications for both paleoecology and biostratigraphy. In the following, we first document how the localities and various depositional types are temporally distributed, and then use that information to examine the relationships between the depositional environment and faunal composition of the localities.

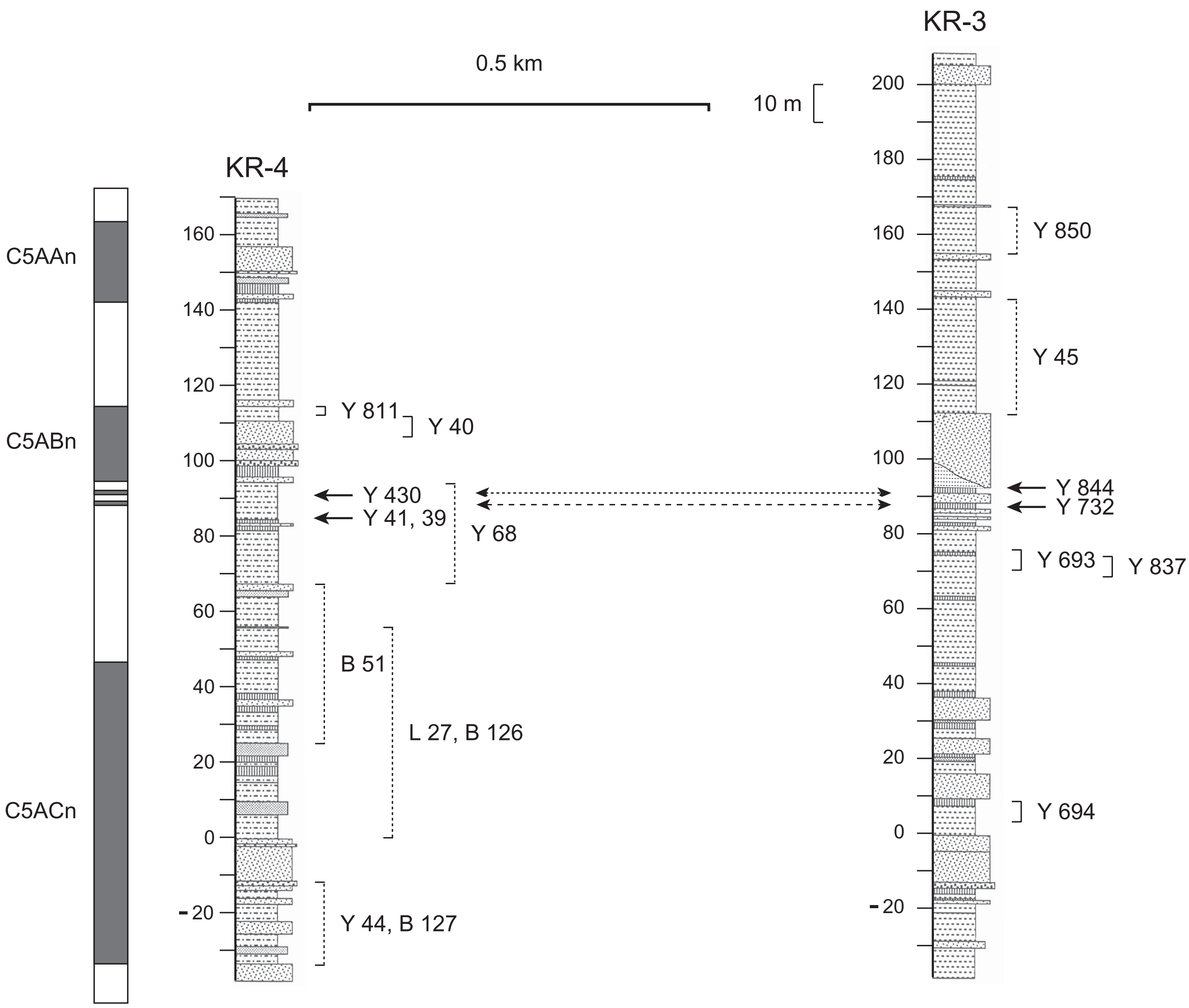

Figure 15.3 Two lower Chinji Formation reference sections (KR-4 and KR-4) with correlated localities shown by letters and numbers. Dashed connecting lines show levels of two paleosols traced between the sections. Correlation of the local magnetostratigraphy of section KR-4 to the Geomagnetic Polarity Time Scale shown on left. Locality stratigraphic positions shown by brackets or arrows.

Our Siwalik database currently has 1375 Miocene localities from northern Pakistan and India, plus another 97 localities from the Chitarwata, Vihowa, Gaj, and Manchar formations in southern Pakistan. The northern group, the majority of which are on the Potwar Plateau, include localities discovered by B. Brown and G.E. Lewis in 1922 and 1932, localities discovered by the Dartmouth–Peshawar University project, and localities discovered by parties of the Harvard–Geological Survey of Pakistan project. Not included are the many localities located in northern India or Jammu and Kashmir, a substantial number of which are of Late Pliocene and Pleistocene age, time periods not well represented on the Potwar Plateau. (For references and discussion, see Flynn et al., chapter 14, this volume.)

Thirteen hundred of the northern localities have been assigned to one of the Potwar Siwalik formations (see table 15.1), and of these, 1026 (75%) currently have estimated absolute ages. We anticipate that eventually we will be able to incorporate an additional 100 to 200 of the undated residue into our chronostratigraphic framework, at least half of which will be from the Chinji Formation.

Thus, we eventually expect to have 85–90% of the localities in our database with an estimate of absolute age. Nevertheless, there remains a substantial number of localities (and therefore fossils of interest) that are either too poorly located geographically and stratigraphically or else lie outside the area in which we have focused our research. Some of these, especially localities near Haritalyangar, India, potentially could be incorporated into a chronostratigraphic framework such as that of Pillans et al. (2005). (For discussion and additional references on this topic, see Patnaik, chapter 17, this volume.)

Figure 15.4 shows the total number of localities in each formation, from which it is apparent that while the time encompassed by each formation (see table 15.1) differs by at most only a factor of 3, there is as much as a 9-fold difference in the number of localities among formations. This difference is also reflected in the number of fossils from different horizons (Barry, Lindsay, and Jacobs 2002) and is related to the megafacies of each formation. The channel-dominated Kamlial and Nagri formations have few localities, while the floodplain-dominated Chinji and Dhok Pathan formations have many. Figure 15.4 also shows relative proportions of dated and undated sites for each formation. The intensively studied Nagri and Dhok Pathan formations presently have the largest proportion of dated sites, but we expect the other formations to eventually match them.

The youngest dated Potwar site in our database is D 54, the Haro River Quarry of Saunders and Dawson (1998), a site also excavated by de Terra and Teilhard de Chardin in 1935. It has a midpoint age of 1.420 Ma. (Midpoint ages are expressed to the nearest thousand years. This is only to preserve the fine-scale superposition of localities in the measured sections, not because the age estimates have that degree of precision. The upper and lower estimated ages of D 54, for example, are 1.070 Ma and 1.770 Ma—hardly 10^3 precision!) The oldest dated localities are Y 590 and Y 739, at the base of the Kamlial Formation in the Salt Range. Both have midpoint estimates of 17.899 Ma (17.736–18.061 Ma). There is, however, a Murree Formation locality (Y 405) on the northern flank of the Khairi-Murat Ridge south of Fatehjang that is likely to be still older (Barry and Cheema 1984). Unfortunately, it cannot be inserted into any of our stratigraphic sections in that area.

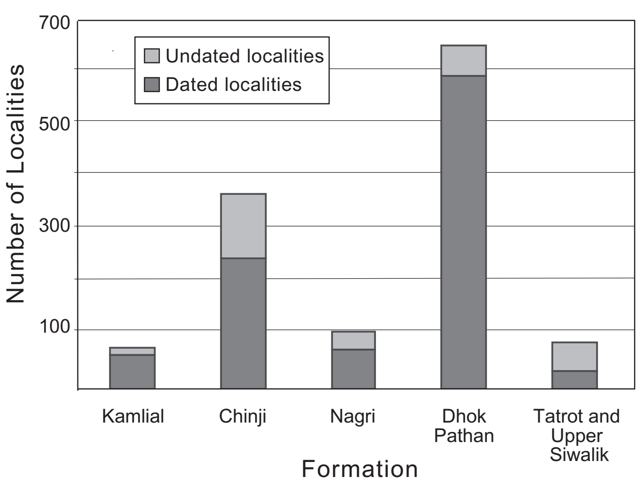

Figure15.4 Number of localities by formation. Dark gray indicates the number of localities with absolute ages; light gray the number of localities without absolute ages.

The precision of our age estimates—that is, the difference between the maximum and minimum estimates for each locality ("delta age")—varies considerably. The longest span is over 1 myr duration, but the ages of most localities are much more tightly constrained (figure 15.5). Fifty-four percent ($n = 554$) of the 1026 dated localities have a temporal resolution of 100,000 yr or less, while 80% ($n = 822$) have a resolution of 200,000 yr or less.

Following Barry, Lindsay, and Jacobs (2002) we have assigned each locality from the Potwar Plateau to a 100,000-yr-long interval using the following protocol. Two hundred and forty-eight (24%) of the 1012 dated localities have both minimum and maximum age estimates falling in the same 100,000 yr interval and can be unambiguously assigned to that interval (figure 15.6 [Class I]). Another 306 (30%) localities have a difference between maximum and minimum estimates of less than or equal to 100,000 yr but straddle two intervals (see figure 15.6 [Class II]). This class of localities cannot be assigned unambiguously to a single interval. An additional class containing 268 (26%) localities have maximum–minimum differences between 100,000 and 200,000 yrs and straddle either two or three 100,000 yr intervals (see figure 15.6 [Class III]). These localities are also ambiguous as to interval. Nevertheless, the Class II and III localities do have at least 50% of their range in a single 100,000 yr interval. If the percent of overlap is equivalent to the probability that the true age lies within the interval, then localities of both Classes II and III can be assigned to the interval with the greatest overlap—which will be the interval containing the midpoint age. Two hundred and four (20%) localities fail to meet this criterion (see figure 15.6 [Class IV]) and are left unassigned and are excluded from most of the following synthesis. The unassigned localities may have important fossils and can enter into discussions of specific taxa. However, they are not useful in investigations of turnover dynamics.

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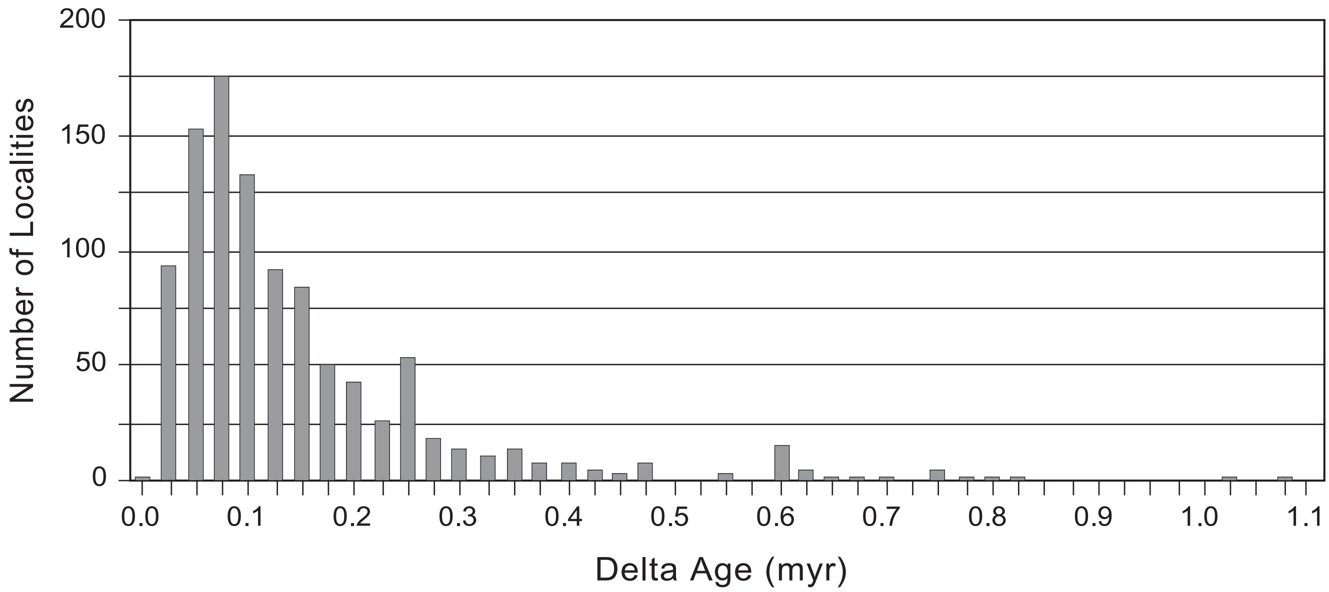

Figure 15.5 Differences between estimated maximum and minimum ages (Delta Age) of 1026 localities. The ages were calculated using the Gradstein et al. 2004 calibration of the Geomagnetic Polarity Time Scale (Ogg and Smith 2004).

The number of localities meeting the above criterion and assigned to a 100 kyr interval ($n = 822$) is shown in figure 15.7. The figure shows that the number of localities per interval varies from 0 to nearly 70 throughout the sequence, with the richest intervals between the upper Kamlial Formation (ca. 14.3 Ma) to the middle of the Dhok Pathan Formation (ca. 6.0 Ma). In this span of more than 8 myr, all but three (6.2, 6.7, and 11.0) of the 100 kyr intervals have at least one fossil locality. Before 14.3 Ma and after 6.0 Ma, the record is sparse and dominated by clusters of localities near 17 Ma and 3.4 Ma—the latter occurring in the Tatrot Formation. The variation in numbers of localities (and by inference numbers of fossils) is due to numerous factors. Some, such as the size of the animals, are biotic in origin. From a geological and sampling perspective, however, critical factors include the area of outcrop, dip of the beds, amount of vegetation on the exposures, ease of access to outcrops, collecting effort, and the types and frequency of depositional environments. Among these factors, the variety of depositional environments and their relative frequencies have the greatest influence in determining the patterns of locality and fossil occurrences over time. These two factors are examined in more detail in a later section.

The Chinji and Dhok Pathan formations are both characterized by abundant and diverse overbank and floodplain channel deposits. The more modestly fossiliferous Kamlial and Nagri formations, on the other hand, are dominated by the multiple, stacked channels of large emergent and interfan streams. These, in contrast to the overbank deposits, offer few opportunities for preservation of fossils (Badgley and Behrensmeyer 1995; Behrensmeyer et al. 2005). The upper part of the Dhok Pathan Formation (ca. 6.0–3.5 Ma) is a special case. In these rocks, lithologies that are broadly similar to normally productive lithologies are nearly barren.

The specific depositional contexts of the localities are also important, because differences over time in the frequency of occurrence of types have the potential to introduce biases in both biostratigraphic and paleoecological analyses (Behrensmeyer et al. 2005). We currently have information on the environment of deposition for 321 localities. Most localities are in a single depositional environment, but 18 sites are more complex with fossils coming from two or even three different facies. We have not yet developed a simple protocol for such localities, largely because the source of the surface collected fossils—which form the bulk of our collections—cannot easily be determined. Thus, it is not easy to assess the relative importance of individual depositional facies in complex localities—if in fact one facies predominates over the others. However, there are no apparent patterns in the combinations of depositional environments in complex localities. Environments belonging to different major categories co-occur (e.g., Loc Y 310: MC-U1 [major channel bar] and FC-S [floodplain channel, simple fill]) as well as ones belonging to the same category (e.g., Loc. Y 735: MC-U1 [major channel bar] and MC-U3b [major channel with small scale fine fill of a sub-channel]). In the following, we have assigned the 18 complex localities to the type that seems most important.

Grouping the localities by major depositional categories (table 15.3; figure 15.8), floodplain channels (FC) comprise nearly half the localities, followed by localities associated with major channels (MC) and those in floodplain soils (FP). Localities in sheet deposits (SD) are notably rare in all formations, although crevasse-splay deposits in general are common in the floodplain sequences of the Chinji and Dhok Pathan formations. With the exception of sheet deposits in the Kamlial Formation, this pattern holds both within and between formations (figure 15.8*B*). As is true for the localities overall, the Chinji and Dhok Pathan formations have many more of the subset of classified localities than either the Kamlial or Nagri formations.

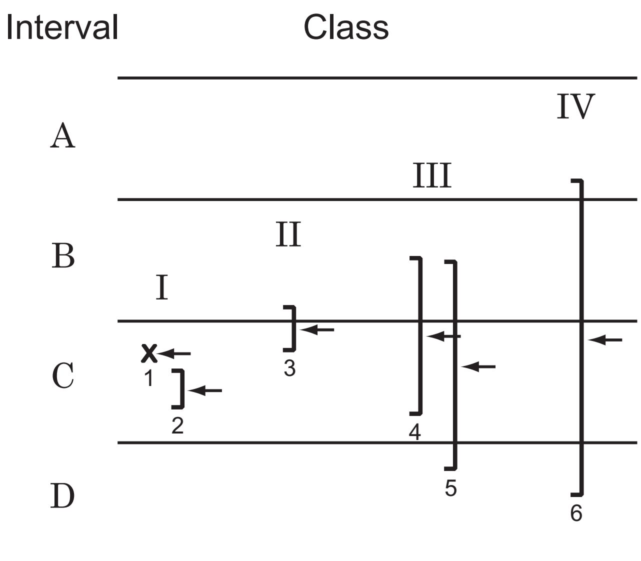

Figure 15.6 Hypothetical examples illustrating different classes of localities. Intervals A–D are of 100,000 yr duration, and midpoint ages of the localities, as indicated by small arrows, are all in interval C. *1*, Locality with maximum estimated age the same as the minimum estimated age; *2*, locality with difference between maximum and minimum estimated ages (delta age) less than 100,000 yr and both falling in the same 100,000 yr interval; *3*, locality with difference between maximum and minimum estimated ages also less than 100,000 yr, but falling in different 100,000 yr intervals; *4*, locality with difference between maximum and minimum estimated ages greater than 100,000 yr and less than 200,000 yr and falling in adjacent 100,000 yr intervals; *5*, locality with difference between maximum and minimum estimated ages greater than 100,000 yr and less than 200,000 yr, but not falling in adjacent 100,000 yr intervals; *6*, locality with difference between maximum and minimum estimated ages greater than 200,000 yr and spanning three or more 100,000 intervals. Localities 1, 2, 3, 4, and 5 would be assigned to Interval C. Locality 6 would not be assigned to any interval, although its midpoint lies in Interval C.

In table 15.4 and figure 15.9, we have rearranged the subtypes of the major depositional environments to reflect cross-category depositional similarities, with the basal lag and channel bar facies (MC-L, FC-C1, FC-S1, MC-U1), upper channel fills (MC-U2a,b, MC-U3a,b, FC-C2, FC-S2, FC-S3), floodplain (FP-P, FP-C, FP-l), and sheet deposits (SD) forming four groups. The temporal distribution of these depositional subtypes is shown in figure 15.9, from which it is apparent that, after allowing for sample size differences among the formations, most depositional environments are present throughout the sequence. For example, while the small floodplain channel deposits (FC-C2 and FC-S2) have many more localities in the floodplain-dominated Chinji and Dhok Pathan formations, these two highly productive facies are also present in the major channel-dominated Kamlial and Nagri formations. There are, however, significant exceptions. Sites in sheet deposits (SD) are absent between 13.8 Ma and 9.8 Ma, a period that encompasses the Chinji Formation and much of the lower Nagri Formation. Other exceptions include the near absence after 9 Ma of basal lag and channel bar sites in floodplain channels (FC-C1 and FC-S1), the sparse record between approximately 12 Ma and 10 Ma of patchy floodplain sites (FP-P), and the relatively few Chinji Formation (ca. 14–11 Ma) sites in the upper parts of the larger major channels (MC-U2a and MC-U2b). Most of these exceptions are only modestly productive facies, but patchy floodplain sites (FP-P) are the third most productive facies overall and are of major importance.

The distribution of localities among depositional subtypes is contrasted in figure 15.10 for the Chinji and Dhok Pathan formations, which have the largest numbers of localities. Overall the figure shows the profiles of the two floodplain-dominated formations are similar, with by far the largest number of localities being infillings in the top of smaller floodplain channels. These are typically channels that have either been abandoned (FC-S2, FC-S3) or are in late stages of flow activity (FC-C2) (Behrensmeyer et al. 2005). Such localities would be ones most likely to preserve autochthonous (nontransported) bone assemblages with relatively minor allochthonous (transported) constituents and temporal and spatial averaging on the order of 10^2 to 10^4 yr and 10^2 to 10^3 m^2 (Behrensmeyer et al. 2005). Both formations also have large numbers of patchy floodplain localities (FP-P), which

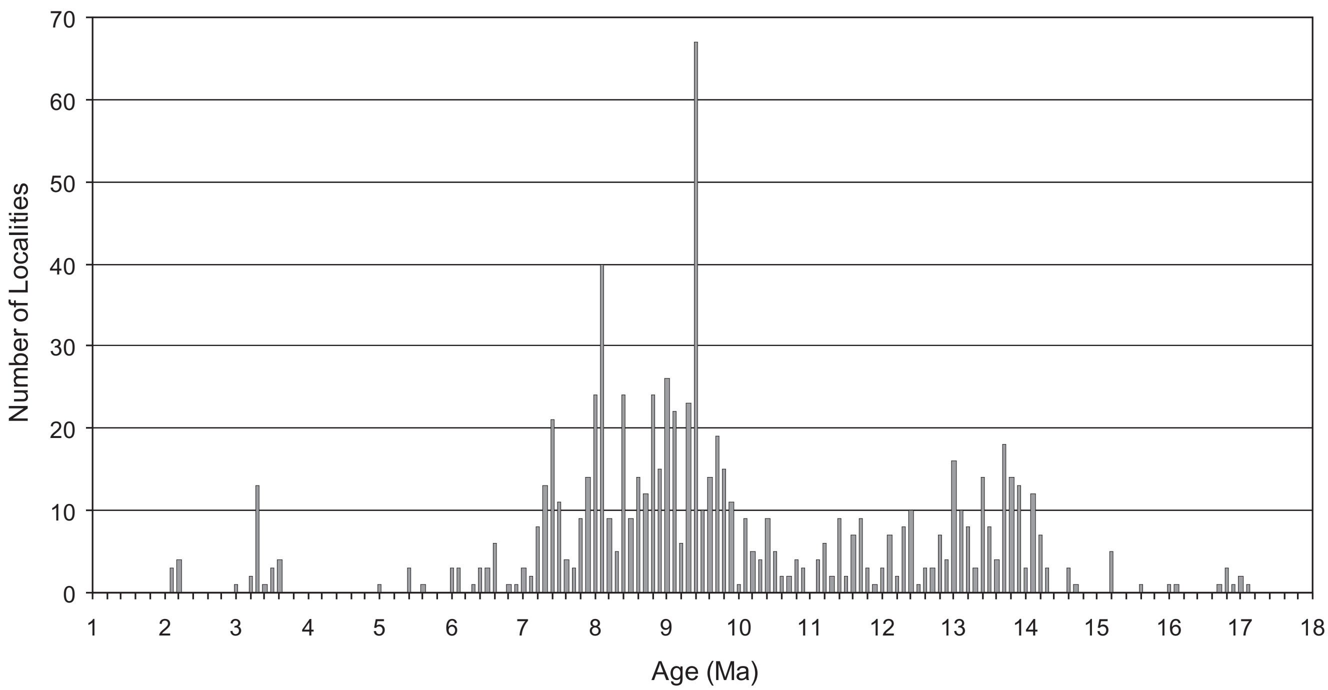

Figure 15.7 Number of localities per 100,000 yr interval. Data selected to include only localities assigned to a 100,000 yr interval (*n* = 822. The ages were calculated using the Gradstein et al. 2004 calibration of the Geomagnetic Polarity Time Scale (Ogg and Smith 2004).

Table 15.3
Number of Localities by Formation and Primary Depositional Environment

	Kamlial Fm.		Chinji Fm.		Nagri Fm.		Dhok Pathan Fm.		Row Totals	
Major Channel	6	24.0%	35	28.5%	11	37.9%	40	27.8%	92	28.7%
Floodplain Channel	10	40.0%	62	50.4%	15	51.7%	61	42.4%	148	46.1%
Floodplain	4	16.0%	25	20.3%	3	10.3%	32	22.2%	64	19.9%
Sheet Deposit	5	20.0%	1	0.8%	0	0.0%	11	7.6%	17	5.3%
Column Totals	25		123		29		144		321	

NOTE: Percentages are for within each formation.

typically have few individuals but high proportions of autochthonous faunal elements. Nevertheless, both formations also have substantial numbers of channel lag and bar localities (FC-C1, FC-S1). These, having formed in high-energy regimes with much reworking, are expected to have fossil assemblages dominated by allochthonous components.

Although similar in many aspects there are also noteworthy differences in the representation of depositional facies in the Chinji and Dhok Pathan formations (see figure 15.10 and table 15.4). Small, complex floodplain channels with mixed lithologies (FC-C2) are the first-ranked facies in the Chinji Formation, comprising 22.8% of the localities. In the Dhok Pathan Formation, they are the fourth-ranked facies, at 10.4%. Small, simple floodplain channels with fine-grained fill (FC-S3) are the fourth-ranked Chinji Formation facies, comprising 9.9% of localities, while in the Dhok Pathan Formation they are only the tenth ranked. Sheet deposits (SD) are the third-ranked Dhok Pathan Formation facies at 10.4%,

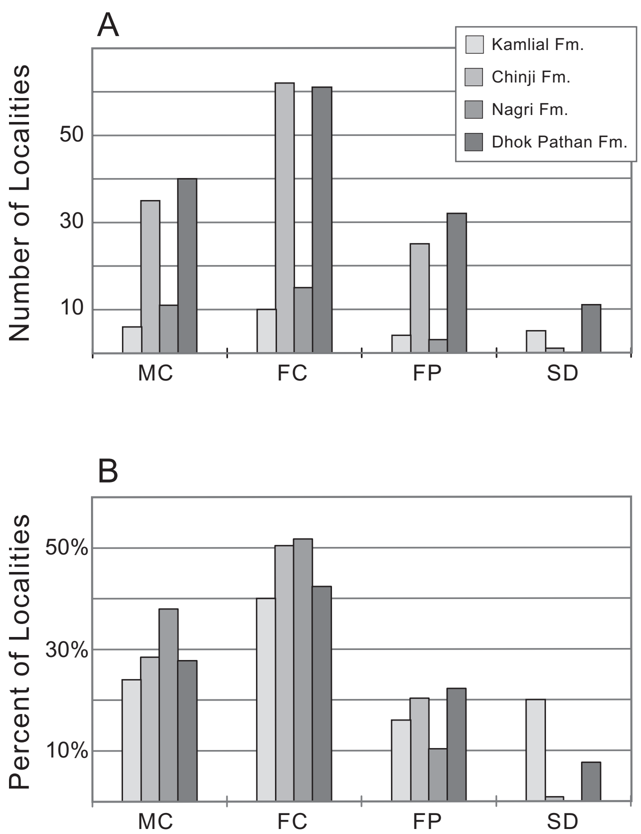

Figure 15.8 Number of localities in each major depositional category. (*A*) Number of localities. (*B*) Percent of localities. MC = major channel; FC = floodplain channel; FP = floodplain; SD = sheet deposit. Data from table 15.3 (*n* = 321).

Table 15.4
Number of Localities by Formation and Secondary Context

	Kamlial Fm.		Chinji Fm.		Nagri Fm.		Dhok Pathan Fm.	
MC-L	0	0.0%	1	1.0%	2	8.0%	0	0.0%
FC-C1	3	13.0%	5	5.0%	2	8.0%	9	8.5%
FC-S1	1	4.3%	9	8.9%	2	8.0%	8	7.5%
MC-U1	0	0.0%	3	3.0%	1	4.0%	4	3.8%
MC-U2a	0	0.0%	1	1.0%	3	12.0%	7	6.6%
MC-U2b	0	0.0%	4	4.0%	2	8.0%	6	5.7%
MC-U3a	2	8.7%	5	5.0%	0	0.0%	5	4.7%
MC-U3b	2	8.7%	2	2.0%	0	0.0%	2	1.9%
FC-C2	1	4.3%	23	22.8%	8	32.0%	11	10.4%
FC-S2	4	17.4%	14	13.9%	1	4.0%	18	17.0%
FC-S3	1	4.3%	10	9.9%	1	4.0%	4	3.8%
FP-P	4	17.4%	16	15.8%	2	8.0%	15	14.2%
FP-C	0	0.0%	5	5.0%	0	0.0%	5	4.7%
FP-L	0	0.0%	2	2.0%	1	4.0%	1	0.9%
SD	5	21.7%	1	1.0%	0	0.0%	11	10.4%
Totals	23		101		25		106	

NOTE: The total of the number of localities in the table is fewer than 321 because the secondary context of all localities is not known. Percentages are for within each formation.

but in the Chinji Formation they surprisingly comprise only 1.0% of localities. The coarse fills of large channels (MC-U2a) are a minor component of Dhok Pathan Formation localities at 6.6%, but in the Chinji only an insignificant 1.0%. And, finally, in the Dhok Pathan Formation, basal lag and bar deposits of complex floodplain channels (FC-C1) make up 8.5% of the localities, while in the Chinji Formation they comprise 5.0%, a difference of 3.8%.

Interpretation of these differences is inconclusive, as there is no consistent pattern. However, the differences in the frequency of occurrence of depositional facies between all four formations have the potential to bias both biostratigraphic and paleoecological analyses, including patterns of diversity and faunal turnover. Chief among potential biases are those affecting the size spectrum of species and the degree of allochthonous versus autochthonous mixing of species from different habitats on the floodplain. Examination of such biases is a research priority, and the next two sections are steps in that direction.

The 321 fossil sites with depositional data can be divided into four groups based on the number of large and small mammal specimens they contain: (I) sites with few large or small mammals; (II) sites with many small mammals but few large mammals; (III) sites with few small mammals but many large mammals; and (IV) sites with both many small and many large mammals. (Small mammals include all rodents, bats, insectivores, and strepsirhine primates. Large mammals include all other taxa.) The data are presented in table 15.5. Localities with more than 24 large mammal specimens are classified as having many large mammals, and those with more than 9 small mammal specimens are classified as having many small mammals. Localities with 10 or more small mammal specimens are all productive screen-wash sites. Those with fewer than 5 small mammal specimens are typically sites where the small mammals were surface collected, while those with 5 to 9 specimens are mostly less productive screenwash sites. (Screen-washing is a technique for extracting very small fossils from bulk samples of sediment. Large specimens are rare in such bulk samples compared to the number of small fossils, which is the main criterion for our subdivisions.)

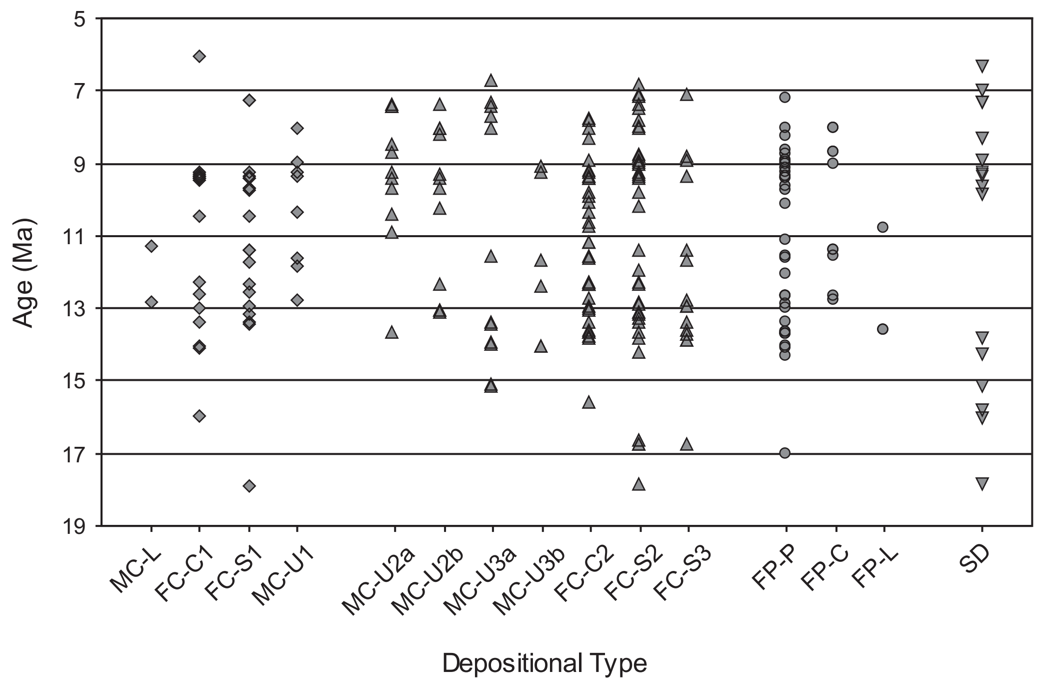

Figure 15.9 Distribution of finer depositional subcategories over time, ordered from left to right by cross-category depositional similarities. ◇ = basal lag and channel bar facies; △ = upper channel fill facies; ○= floodplain facies; ▽= sheet deposits. Figure shows only localities with a determined secondary depositional context and known age. Data taken selectively from table 15.4 ($n = 210$).

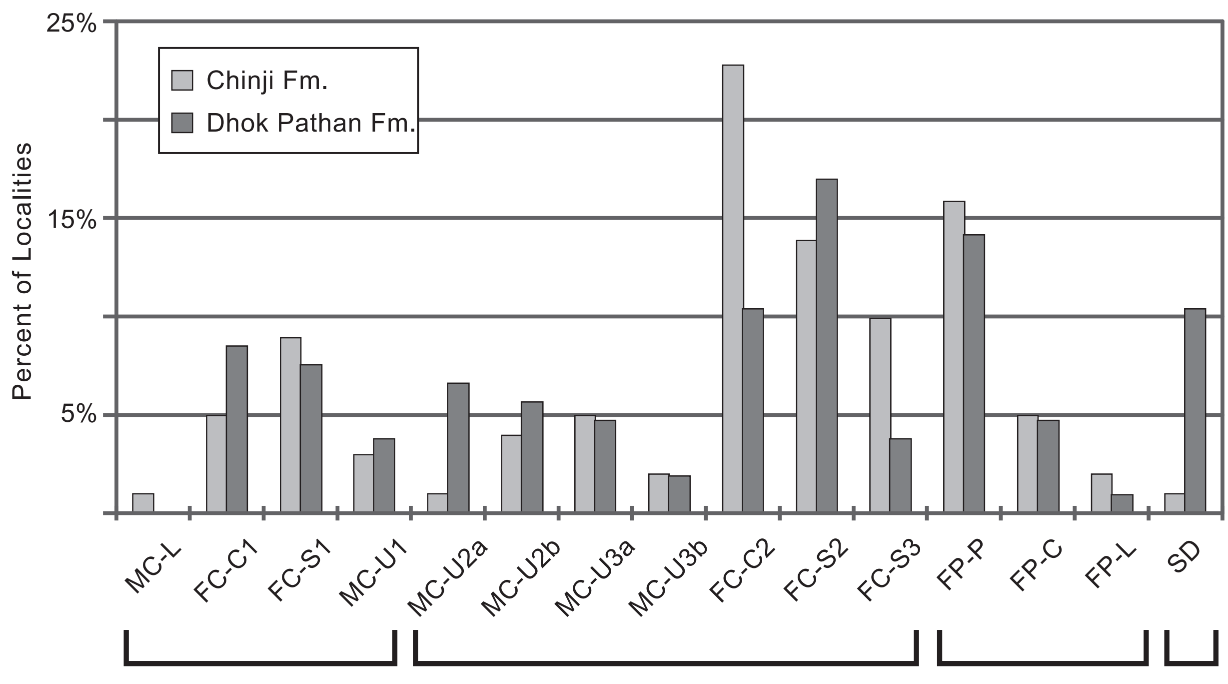

Figure 15.10 Comparison of depositional environments of the Chinji and Dhok Pathan formations. Data from table 15.4. Abbreviations listed in table 15.2; brackets at bottom mark the four cross-category depositional groups, from left to right: basal lag and channel bar facies, upper channel fill facies, floodplain facies, sheet deposits.

Table 15.5
Number of Localities by Major Depositional Environment and Number of Large or Small Mammal Specimens

Type	Description	MC		FC		FP		SD		Row Totals
I	Few small or large mammals	48	25.8%	84	45.2%	46	24.7%	8	4.3%	186
II	Many small, few large mammals	4	26.7%	3	20.0%	6	40.0%	2	13.3%	15
II	Few small, many large mammals	27	32.1%	41	48.8%	11	13.1%	5	6.0%	84
IV	Many small and large mammals	13	36.1%	20	55.6%	1	2.8%	2	5.6%	36
	Column totals	92		148		64		17		321

NOTE: Percentages are for within each type.

These four groups can be compared in terms of depositional facies (see table 15.5), with the expectation that sites with many small mammals occur in depositional environments different from those containing many large mammals and that sites with many fossils occur in different depositional environments than those with few fossils. Inspection of table 15.5 indicates that the first expectation is borne out, as there are large contrasts between the predominantly small mammal (type II) and predominantly large mammal (type III) sites. Because of the large differences in the number of sites in each category this is best seen in the relative frequencies (%). Sites with many large and few small mammals (type III) are mainly in the small channels of the floodplain (48.8% vs. 20.0%), while those with many small and few large mammals (type II) are largely in the floodplain paleosols (40.0% vs. 13.1%). An even larger difference is seen in the group of sites with both many large and many small mammals (type IV) (see table 15.5), where almost 56% of the sites are in the small floodplain channels and less than 3% are in floodplain paleosols. The differences among all four types and all four depositional categories (see table 15.5) are significantly different ($\chi^2 = 19.397$, $p = 0.022$). Even stronger differences are apparent if the depositional categories are collapsed into channel (MC + FC) and nonchannel (FP + SD) contexts, where again sites with many large mammals (types III + IV) are found mostly in channel settings (101 of 120) rather than nonchannel settings (19 of 120), while the predominantly small mammal sites (type II) are as likely to be in nonchannel (8 of 15) as channel settings (7 of 15). The differences are highly significant ($\chi^2 = 14.854$, $p = 0.002$).

From an analysis of the depositional settings of 13 sites with small mammals in the lower third of the Chinji Formation, Badgley et al (1998) concluded that the small mammals were mostly coming from localities in the fill of small-to-large abandoned channels; a conclusion apparently at variance with that reached here. However, with the one exception of locality Y 430, the 13 localities of that study also had large mammals as Badgley et al (1998) were contrasting sites with many small mammals to those without, irrespective of the number of large mammals. Most of their sites, therefore, were in the group of sites with both many small and many large mammals, a group that shows a very strong tendency to occur in channel contexts.

The second expectation, that sites with few fossils differ in depositional context from those with many, is only weakly supported. Collapsing the data of table 15.5 into sites with few fossils overall (type I) and sites with many (types II, III, and IV), shows small differences between the depositional settings, with the most marked being the difference in occurrence in the floodplain paleosols (46 of 186 for type I vs. 18 of 135 for types II–IV; $\chi^2 = 7.266$, $p = 0.064$), a difference that while large is not significant at a .05 level.

The preceding two cases focused on size-class distribution of the fossils, an attribute that is strongly influenced by taphonomic factors and collecting technique. It is, however, also of interest to examine potential biases in preservation of individual species, biases that are likely to vary among species and possibly are connected to a species' ecology. In order to explore possible biases, we have selected four suoids of moderate body mass as subjects. The observed range, estimated body mass, and number of sites with the species in each depositional environment ("observed") are listed in table 15.6. Three species (*Listriodon pentapotamiae*, *Conohyus sindiensis*, and *Merycopotamus nanus*) overlap considerably in their observed stratigraphic ranges, while the fourth (*Merycopotamus medioximus*) is closely related to *M. nanus* but is younger. Although not abundant, the four species are

Table 15.6
Distribution of Occurrences by Depositional Environment for Four Suoid Species

	Listriodon pentapotamiae		*Conohyus sindiensis*		*Merycopotamus nanus*		*Merycopotamus medioximus*	
Observed Range	14.1–10.4 Ma		14.6–10.4 Ma		15.1–11.4 Ma		10.2–8.5 Ma	
Estimated Body Mass	80 kg		40 kg		110 kg		150 kg	
	Obs.	Overall	Obs.	Overall	Obs.	Overall	Obs.	Overall
MC-L	-	2	-	2	-	1	-	-
FC-C1	2	7	3	7	2	6	6	9
FC-S1	4	10	2	10	2	9	3	7
MC-U1	2	3	2	4	3	3	1	3
MC-U2	14	18	11	18	16	16	1	10
MC-U3	2	9	3	9	3	10	1	3
FC-C2	13	27	11	27	12	23	4	10
FC-S2	7	12	8	12	6	12	3	11
FC-S3	6	10	2	10	-	10	-	3
FP-P	9	19	-	18	3	17	1	13
FP-C	-	5	-	5	1	5	1	3
FP-L	-	3	-	3	-	2	-	-
SD	1	2	-	2	2	3	2	6
Total	60	127	42	127	50	117	23	78
Number of categories	10	13	9	13	10	13	10	11

NOTE: For each species, the tabulated numbers are: *Observed*, the number of sites with the species for each depositional category; *Overall*, the number of sites, with or without the species, for each depositional category tallied over the known stratigraphic range of the species.

fairly common within their observed ranges. *Conohyus sindiensis* is the rarest, as well as smallest, species.

If the fossil occurrences of a species are unrelated to the depositional context (i.e., its occurrences are random with respect to the depositional facies), then the observed distribution of a species' occurrences should mimic the related "overall" distribution. As a result, for each species in table 15.6 the "overall" distribution can be used to calculate an "expected" frequency distribution, against which the "observed" frequencies can be compared.

Figure 15.11 shows the distribution for each species by depositional environments as well as the "expected" distribution for sites within the observed range of each species. To make comparisons among the species easier, both distributions have been recast as percentages, based on the frequencies in the "observed" and "overall" columns of table 15.6. Comparisons of the panels of figure 15.11 then indicate the following:

1. Each species is found in a variety of depositional environments, rather than being mostly concentrated in one. Nevertheless, three or four categories together typically have nearly 70% of the occurrences.

2. The observed and expected for each category are generally similar, although all species have at least one facies where either the observed greatly exceeds the expected or the expected exceeds the observed.

3. *Listriodon pentapotamiae*, *Conohyus sindiensis*, and *Merycopotamus nanus* have generally similar patterns of occurrence that differ markedly from that of *Merycopotamus medioximus*. Presumably, their profiles are similar because the three species ranges overlap considerably and they come from much the same suite of localities. There are, however, important differences in the pattern of occurrences among the four species.

4. The observed occurrences of *L. pentapotamiae* come the closest to matching the expected occurrences, al-

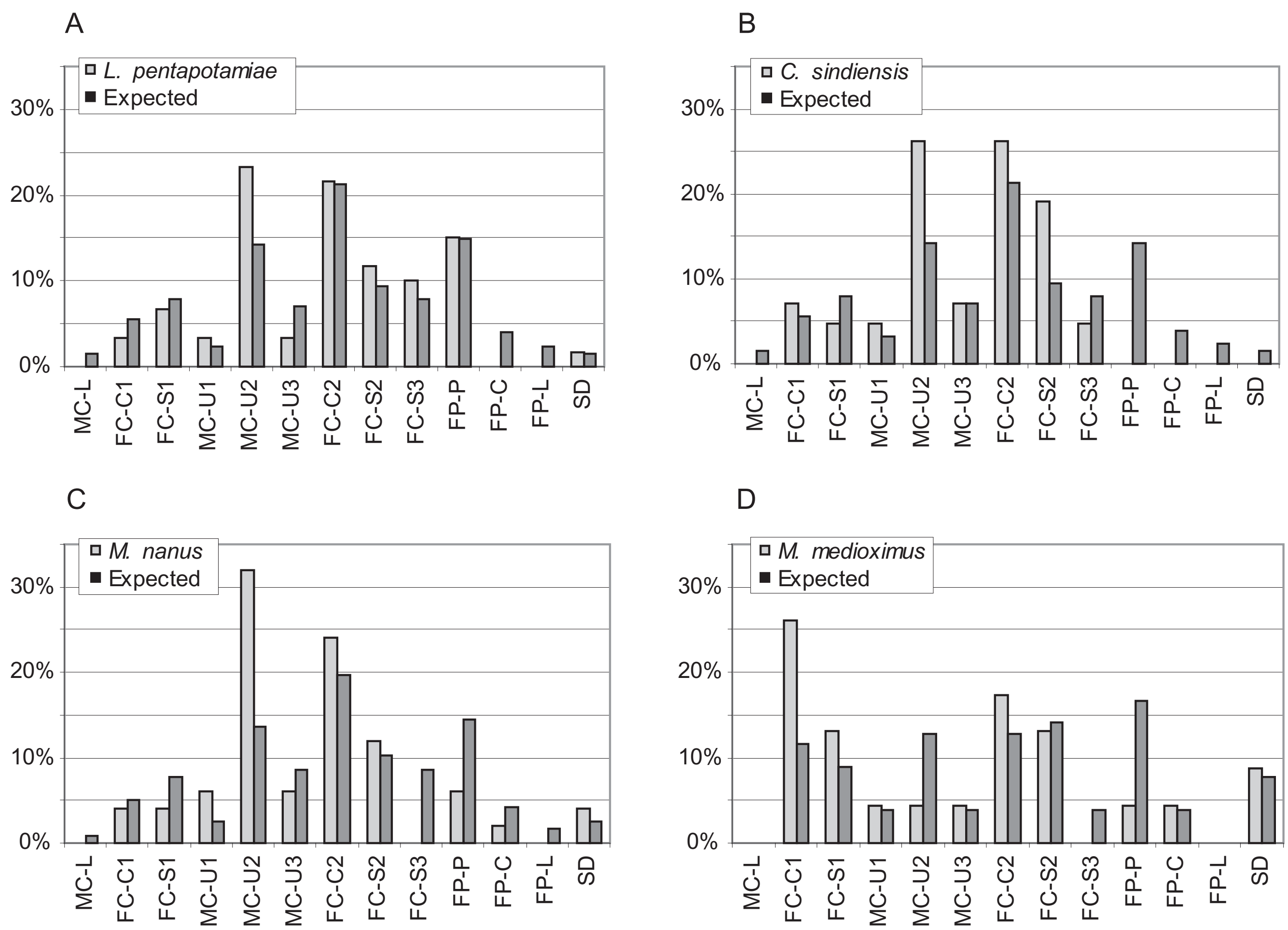

Figure 15.11 Distribution of occurrences by depositional environment for four suoid species. Percentages are based on the frequencies in the "Observed" and "Overall" columns of table 15.6.

though there is a major discrepancy in its being overrepresented in the MC-U2 facies. The other suid, *C. sindiensis*, is also overrepresented in the MC-U2 facies, but unlike *L. pentapotamiae* it is not present in the FP-P facies at all and is overrepresented in the FC-S2 facies.

5. *M. nanus* is similar to the two suids but is even more strongly overrepresented in the MC-U2 facies and slightly underrepresented in the FP-P facies. *M. medioximus* departs considerably from the suids and the closely related *M. nanus*. It generally matches its expected distribution, occurring more frequently in the more energetic facies and less frequently in the lower-energy facies. Unlike its close relative, *M. medioximus* is overrepresented in the FC-C1 facies and underrepresented in MC-U2. *M. medioximus* is also underrepresented in the FP-P facies, a similarity shared with *M. nanus*.

There is clearly a strong signal in the species distributions related to the frequency and productivity of different facies in the formations. The overrepresentation of *L. pentapotamiae*, *C. sindiensis*, and *M. nanus* in the MC-U2 facies, which includes localities that formed in the complex fills at the top of large channels, may simply reflect how productive these settings are of large fossil accumulations in the Chinji Formation. Such large accumulations are more likely to have many taxa, including the less common species such as suoids. In the Dhok Pathan Formation, localities in the same setting occur as frequently as in the Chinji Formation, but they are not so productive and rarely if ever host very large assemblages of fossils. Consequently, in the Dhok Pathan Formation relatively uncommon taxa such as *M. medioximus* are not frequently found in this particular facies and the facies does not contribute a significant number of specimens to the *M. medioximus* collection.

Differences in the patterns of occurrence among the two suids and *M. nanus* should reflect aspects of their habitats and ecology. Otherwise, the species should show similar preservational biases, since they are approximately the same size, have comparable relative abundance, and overlap stratigraphically. The absence or near absence of *C. sindiensis* and *M. nanus* from floodplain facies is the most suggestive of differences between them and *L. pentapotamiae*. Also suggestive of differences among the species are the overrepresentation of *C. sindiensis* in the FC-S2 and FC-C2 facies and the absence of *M. nanus* from the FC-S3 facies. In contrast to *L. pentapotamiae*, which is found at expected frequencies in all facies but one, *C. sindiensis* and *M. nanus* may have been more restricted in which habitats they occupied.

Our analyses have identified several areas of potential bias that have implications for biostratigraphy. These include biases in the size classes preserved in different depositional environments and differences in the number of specimens from localities in different facies. There is also evidence of differential preservation of species in different facies, with some species occurring at higher frequencies that expected and other species at lower frequencies—a conclusion we expect will prove more general once a larger number of species have been examined. These differences in the temporal distribution of depositional facies potentially could alter the observed stratigraphic range of the species, although the effects are likely to be subtle.

FAUNAL TURNOVER AMONG THE ARTIODACTYLA

Because they are common with numerous and distinctive species, artiodactyls are potentially very useful for defining biostratigraphic zonations. As a step toward defining biostratigraphic zones, in the following we present a brief summary of what is currently known about Siwalik artiodactyls. However, several groups, including all the ruminant families, are undergoing major revision and we expect there will be significant changes in the species lists. In addition, we do not attempt to infer first and last appearances from the fossil occurrence data, as was done in Barry, Lindsay, and Jacobs (2002), although determining accurate first and last appearances is central to any biostratigraphic study. Even with these caveats, the broad outlines of our taxonomic and stratigraphic studies are now evident and the general patterns should be robust. Unless otherwise noted, all ages cited are first or last occurrences, that is the age of the oldest or youngest known specimen. In many cases, the inferred first or last appearances are beyond those limits. All cited ages have been converted to the Gradstein et al. 2004 time scale (Ogg and Smith 2004).

Siwalik suoids include five subordinate taxa: anthracotheres, hippopotamuses, sanitheres, palaeochoerids, and suids. Of these five, anthracotheres consist of a diverse, but not very abundant, group of species. While gigantic anthracotherines are typical of the upper Chitarwata and Vihowa formations (Antoine et al., chapter 16, this volume), they are not present in the lower levels of the Kamlial Formation. The long-ranging and much smaller *Microbunodon silistrensis* is, however, present from the base of the Kamlial Formation (ca. 17.8 Ma) until 11.4 Ma (Lihoreau et al. 2004a). It is succeeded by *Microbunodon milaensis*, which is best known from sites dated at 9.3 Ma and 9.4 Ma, but extends down to 10.4 Ma (Lihoreau et al. 2004a).

Bothriodontine anthracotheres include two lineages in the Late Oligocene and earliest Miocene Chitarwata and Vihowa formations that continue into the base of the Kamlial Formation. *Sivameryx palaeindicus*, which is the dominant Chitarwata and Vihowa selenodont species, is also the most abundant in the Early Miocene of the Potwar Plateau, with first and last occurrences at 17.8 Ma and 15.6 Ma. The much larger *Hemimeryx blanfordi*, on the other hand, is only known from postcranials at one Potwar Plateau site close to the base of the Kamlial Formation (17.8 Ma). Finally, species of *Merycopotamus* are first known from the upper Kamlial Formation (15.1 Ma) and continue well into the Pliocene Tatrot Formation (3.3 Ma). Three successive species were recognized by Lihoreau et al. (2004b 2007); *M. nanus* (15.1–11.4 Ma), *M. medioximus* (10.2–8.5 Ma), and *M. dissimilus* (7.8–3.3 Ma). The two gaps between the species' ranges are artifacts, as there are nondiagnostic fossils of *Merycopotamus* from both.

Hippopotamuses are represented in the latest Miocene and Pliocene by *Hexaprotodon sivalensis*. The species' first occurrence is most definitely documented at 6.2 Ma. However, a fragment of what might be a *Hexaprotodon* molar has been collected from a site that is between 6.5 Ma and 6.7 Ma, while a second, more securely identified molar in the Yale collections could be as old as 7.3 Ma. Hippopotamuses are typically very common as well as easily recognized fossils, but other than these two doubtful records, there are no specimens older than 6.2 Ma. *Hexaprotodon sivalensis* and *Merycopotamus dissimilus* overlap stratigraphically.

On the Potwar Plateau, sanitheres are represented by a single species, *Sanitherium schlagintweiti*, first known from the base of the Kamlial Formation (17.9 Ma) and common until it disappears between 14.2 Ma and ca. 14.0 Ma in the uppermost Kamlial Formation or lowermost Chinji Formation. Palaeochoerids are also a family with few species. While *Pecarichoerus* is recorded in the Early Oligocene Chitarwata Formation (Orliac et al. 2010), the only known Potwar Plateau specimen is the holotype of *Pecarichoerus orientalis* described by Colbert (1933) from a ca. 14.0-Ma-old site near the base of the Chinji Formation. A second palaeochoerid, *Schizochoerus gandakasensis*, has inferred first and last appearances at 11.3 Ma and 8.1 Ma (Barry, Lindsay, and Jacobs 2002).

Suids comprise a species-rich family, with at least nine distinctive lineages. They are also relatively common as fossils, giving them considerable biostratigraphic potential. *Listriodon* is first represented by sublophodont species in the earliest Miocene part of the upper Chitarwata and Vihowa formations (Orliac et al. 2010; Antoine et al., chapter 16, this volume), with *Listriodon guptai* subsequently found in the Kamlial Formation. The material is very sparse and fragmentary, but *Listriodon guptai* seems to range from 17.8 Ma to at least 15.8 Ma. The fully lophodont *Listriodon pentapotamiae*, which is very common within its time range, first occurs at 14.1 Ma and perhaps as early as 14.3 Ma. Systematic revision may alter these dates, as the earliest specimens are similar to *Listriodon guptai*. The inferred last appearance of *Listriodon pentapotamiae* is at 10.4 Ma, overlapping with the first appearance of equids (Barry, Lindsay, and Jacobs 2002).

Siwalik tetraconodontines include the small *Conohyus sindiensis*, which resembles *Listriodon pentapotamiae* in both being very common and overlapping with equids. It has a first occurrence in the upper Kamlial formation at 14.6 Ma and a last occurrence of at least 10.4 Ma, and possibly younger. The gigantic tetraconodontines *Tetraconodon magnus* and *Sivachoerus prior*, in contrast, have much more restricted ranges. Their known ranges are 10.0 Ma to 9.4 Ma and 3.5 Ma to 2.1 Ma, respectively.

Suines are the most diverse of the Siwalik suids. The oldest species is "*Hyotherium*" *pilgrimi*, which first occurs at 13.7 Ma and is last known at 11.1 Ma. Succeeding "*Hyotherium*" *pilgrimi* in the Late Miocene are species of *Hippopotamodon*, *Propotamochoerus*, *Hippohyus*, *Potamochoerus*, and early *Sus*. Species of *Hippopotamodon* were inferred by Barry, Lindsay, and Jacobs (2002) to range from 11.5 Ma to 7.3 Ma, but the genus might still have been present at ca. 6.3 Ma. The earliest *Hippopotamodon* is a relatively small form, likely to be a different species from later *Hippopotamodon sivalense*. The transition between the two forms is at ca. 10.4 Ma. Material presently identified as *Hippopotamodon sivalense* shows a strong trend toward increasing size and may well encompass two distinct species. Similarly, material identified as *Propotamochoerus hysudricus*, which has an inferred range of 10.3 Ma to 6.7 Ma, may belong to more than one species. Species of *Hippohyus*, *Potamochoerus*, and *Sus* all appear much later at the end of the Miocene, but their first occurrences are difficult to determine because of the sparse latest Miocene record and fragmentary material. The oldest record of *Hippohyus* is between 6.6 Ma and 6.4 Ma, that of *Potamochoerus* is at 6.0 Ma, and our oldest record of *Sus* is at 6.5 Ma. These three taxa are still present in the Tatrot Formation at about 3.3 Ma, but they might well have persisted until much later. Pliocene suids include a taxon similar to *Kolpochoerus* and the small *Sivahyus punjabiensis*, both of which are present in the Tatrot Formation (ca. 3.5–3.3 Ma). In addition, a few other, typically very small, taxa are present. In most cases, these are only known from a few specimens of uncertain identity. Most notable among them are a very small suine known from six localities that range in age from 10.1 Ma to 7.5 Ma and a tiny lophodont species from a single locality at 11.4 Ma. Both likely weighed only around 10–15 kg.

Fossil camels are not known in the Miocene of northern Pakistan, but West (1981) reports an Upper Pliocene occurrence in the Marwat Formation. The age is based on faunal correlations and the specimen should be between 3 and 2 million yr old.

Common Siwalik ruminants include tragulids, giraffoids, and bovids. Cervids are also known, but not until the Pliocene, with a first occurrence at 3.5 Ma (Flynn et al., chapter 14, this volume). Although common in the earliest Miocene of the upper Chitarwata Formation, species of the enigmatic *Bugtimeryx* are not known from the Potwar Plateau. The genus, however, can only be recognized on the basis of its teeth because the postcranials are virtually identical with those of early bovids.

Tragulids are known from the Early Oligocene of the lower Chitarwata Formation (Antoine et al., chapter 16, this volume) and presumably have a continuing, but poorly documented, presence on the Subcontinent. On the Potwar Plateau, at least one small species of *Dorcabune* is present throughout the Kamlial Formation. The oldest record is at 16.8 Ma, but Antoine et al. (chapter 16, this volume) record *Dorcabune* in the lowermost Vihowa Formation at Dera Bugti, which is probably slightly older

—-1
—0
—+1

than the base of the Kamlial Formation. Small *Dorcabune* range up into the Chinji Formation, with a last occurrence at 13.6 Ma. The very much larger *Dorcabune anthracotherioides* first occurs at 13.6 Ma and persists until 10.6 Ma, after which the much smaller *Dorcabune nagrii* first occurs. This latter species is the last of the *Dorcabune* lineage, with an inferred last appearance of about 8.4 Ma (Barry, Lindsay, and Jacobs 2002).

The systematics of *Dorcatherium* is more complex. There are numerous species that generally have to be distinguished on the basis of size, while the relationships between the smaller species of *Dorcatherium* and *Siamotragulus* have yet to be resolved. *Dorcatherium* (or perhaps *Siamotragulus*) is present in the latest Oligocene and earliest Miocene of the Chitarwata and Vihowa formations, while one medium-size species is present at the base of the Kamlial Formation (17.8 Ma). More than two coexisting species of *Dorcatherium* are not known until about 14 Ma, but throughout the rest of the Miocene there are typically three species present; a very small, a medium, and in the Late Miocene what becomes a very large species. The smallest forms constitute three or four separate species that are not likely ancestor–descendent pairs. By ca. 12 Ma, they have a foot structure similar to that of *Tragulus*. Tragulids are a major component of Middle Miocene Siwalik faunas, at some sites being nearly as abundant as bovids. After about 9.5 Ma, they have become markedly rarer as fossils. The younger species tend toward being high crowned, and the youngest species in the Tatrot Formation (3.3 Ma) could well be placed in a different genus.

Giraffoids have a long Siwalik record and, while having low species richness, are consistently found starting in the earliest Miocene part of the Chitarwata Formation and continuing well into the Pliocene. *Progiraffa exigua*, which we consider a primitive giraffoid, is the common large ruminant of the upper Chitarwata and Vihowa formations. It is also present throughout the Kamlial Formation, although the evidence suggests there may be as many as three time-successive species that differ in size (Barry et al. 2005). The youngest specimens assigned to *Progiraffa* are at least 13.6 Ma and maybe as young as 13.2 Ma. The Middle and Late Miocene giraffids of the Potwar Plateau are currently under study by N. Solounias. While in the past the material has been treated as comprising a small earlier species (*Giraffokeryx punjabiensis*) and a later large species (*Bramatherium megacephalum*; e.g., Barry, Lindsay, and Jacobs 2002), Solounias (pers. comm. February 2011) suggests there is evidence for more species, some of which may coexist. Specifically, the material from the uppermost Kamlial Formation (ca. 14.0 Ma) to the lower Nagri Formation (10.4 Ma), which had been referred to *Giraffokeryx punjabiensis*, must belong to at least two species. Similarly, the large sivatheres of the Nagri through Dhok Pathan Formations (10.4–7.3 Ma) appear to be a pair of time-successive species, with the younger form being considerably larger than the older. Finally, *Giraffa punjabiensis* has been inferred to have a first appearance of 9.1 Ma (Barry, Lindsay, and Jacobs 2002). The youngest fossils of it are 7.2 Ma.

Bovids constitute a very abundant and diverse set of species that are currently undergoing major revision. They have a complex and not-yet-well-understood history on the Subcontinent, and here we only make the most general statements about them.

As the name suggests, hypsodontines are characterized by extremely high-crowned teeth. While there is not a consensus as to their phylogenetic affinities, they are generally placed with the Bovidae because they possess unbranched horncores covered by a sheath. *Palaeohypsodontus zinensis* is known from the Early and Late Oligocene of the Chitarwata Formation and earliest Miocene Vihowa Formation (Antoine et al., chapter 16, this volume). Hypsodontines are not, however, known on the Potwar Plateau until 15.2 Ma, undoubtedly because of the dearth of fossils in the Kamlial Formation. Many horncores and teeth of *Hypsodontus sokolovi* have been recovered from the uppermost Kamlial Formation /lowermost Chinji Formation. Most of the material comes from a single site between 14.2 Ma and 14.0 Ma and is comparable in size to the Kamlial material. A larger second species, *Hypsodontus pronaticornis*, occurs between 13.6 Ma and 12.1 Ma.

Bovids other than hypsodontines first occur at early Miocene Vihowa Formation sites on the order of 19 Ma (Barry et al. 2005; Flynn et al., chapter 14, and Antoine et al., chapter 16, both this volume). Antoine et al. (chapter 16, this volume) also reports bovids from the earliest Miocene of the Chitarwata Formation, although the records are based on postcranials that are difficult to distinguish from those of *Bugtimeryx*. The Vihowa bovids include at least two species belonging to divergent taxa. One referred to *Eotragus* has round horncores, while the other has a more compressed horn. On the Potwar Plateau, *Eotragus* occurs at the base of the Kamlial Formation at 17.8 Ma. Teeth and postcranials indicate the presence of several small unidentified species between 17.8 Ma and 15.1 Ma.

The fossil record improves markedly at the base of the Chinji Formation (ca. 14.0 Ma), and at that juncture there is much greater richness of small- to medium-size bovid species that are well represented by horncores, teeth, and postcranials—an increase that is certainly an artifact of the record. Between 14 Ma and 11 Ma, species of four medium-size genera (*Strepsiportax*, *Sivaceros*, *Sivoreas*, and *Helicoportax*) are common. Additionally, there are two or even three antilopines, a small boselaphine, and a few specimens of *Protoryx* and *Tethytragus*. All of these taxa disappear from the Potwar Plateau Siwalik record by 11.3 Ma, after which time *Selenoportax vexillarius*, "*Tragocerides*" *pilgrimi*, *Elachistoceras khauristanensis*, and a small *Gazella* are most common. During the Late Miocene, there is turnover of species in both *Selenoportax* and "*Tragocerides*," and additional species appear, including antilopines other than *Gazella* and reduncines. There is a noticeable trend toward increase in size among the Late Miocene bovids, and several species have very brief durations compared to the more common species.

Further changes in the bovid fauna at the end of the Miocene are apparent, but they are much obscured by the deteriorating quality of the fossil record on the Potwar Plateau. We therefore do not review them here.

CONCLUSION

Neogene age sediments exist over a wide area in Pakistan, India, and Nepal, with contemporaneous and equivalent sediments in Myanmar (Burma). Throughout this area the Siwaliks are the fluvial phase of infilling of foreland basins created by the collision of peninsular India with mainland Asia. In some regions, sediments exist that represent a transitional phase between marine and fluvial deposition. These are best represented by the Chitarwata Formation and perhaps the Gaj and Murree formations, all in Pakistan.

On the Potwar Plateau of northern Pakistan, and probably elsewhere, the fluvial Siwaliks were deposited by a very large river system. This ancient system bears many similarities to the modern Indus and Ganges systems, with their broad floodplains and multitudes of tributaries. The preserved parts of the system—at least on the Potwar Plateau—include large and medium size tributary rivers that originated in the adjacent northern mountains or on the floodplain itself. These tributary rivers left thick sandstones and minor associated overbank deposits. Such deposits are major constituents of all four formations, but they are particularly important in the Nagri and Kamlial formations. There were, in addition, smaller floodplain streams and their associated levees, crevasse-splays, and paleosols. These predominate in the Chinji and Dhok Pathan formations.

Vertebrate and invertebrate fossils typically occur in the Siwaliks as distinct clusters of small areal extent that originate from a very limited stratigraphic horizon. Such clusters or localities may contain from a very few to, in rare cases, over a thousand fossils. The fossils are usually the disarticulated remains of terrestrial and aquatic vertebrates, but bivalves, gastropods, and crabs also occur. Plant remains, whether pollen or body fossils, are very rare. Paleosols and stable isotopes provide indirect evidence of the vegetation. Localities with more than a few fossils ordinarily have several species.

The fossils mostly occur in the infillings at the top of channels and especially the channels of the smaller streams. However, fossils are common in other lithologies, including paleosol, crevasse-splay, and levee deposits and even in the basal lag of the very largest sandstones. A classification of depositional facies recognizes four main types and 15 subcategories. Of the subcategories, the small floodplain channels (FC-C2 and FC-S2) and paleosols with patchy concentrations (FP-P) are consistently the most productive facies. Sheet deposits (SD) are also important in the Kamlial and Dhok Pathan formations. A preliminary analysis indicates that localities with only fossils of small mammal species are most often found in the floodplain paleosols, while large species (with or without many small species) are more often in the various small floodplain channel facies. In addition, there is strong evidence that the occurrences of individual species are not random with respect to the depositional facies. In some cases, this is a result of large differences of the number of fossils in highly productive facies, which entails more frequent recovery of rarer species. In other cases, the patterns of occurrence among species are likely to reflect aspects of their habitats and ecology

At present our Siwalik database includes over 1400 localities, the majority of which are on the Potwar Plateau. Of these, 810 localities have absolute ages precise enough to be assigned to a 100 kyr interval. Ages of localities range from 1.4 Ma to 17.9 Ma, but there are significantly older localities in the Murree, Chitarwata, and perhaps Gaj formations that have not yet been given absolute ages. On the Potwar Plateau, the segment between 14.3 Ma and 6.0 Ma has the most localities and is the most complete, with only three 100 kyr intervals having no localities.

The long and well-dated sequence of Siwalik sediments and fauna offers an opportunity to document changes in diversity and patterns of faunal turnover in sufficient detail that they can be used to test the relationships between environmental change and the ecological and evolutionary responses of the biota. Long-term research goals therefore include study of those relationships as well as the usual focus on the evolutionary histories of species and clades and reconstruction of the paleoecology of individual species. In all of these endeavors, special concerns are 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 geomagnetic polarity time-scale calibrations, and uneven taxonomic treatment across groups.

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