Part II

South and Southeast Asia

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Chapter 14

The Siwaliks and Neogene Evolutionary Biology in South Asia

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The extensive, superposed stratigraphic record of the Siwaliks of southern Asia applies broadly to questions in evolutionary biology. In coordination with Barry et al. (chapter 15, this volume), this chapter focuses on the distribution of fossiliferous terrestrial deposits of late Cenozoic age across the Indian Subcontinent, the development of a chronostratigraphic framework in Pakistan and India, and the significance of the Siwalik deposits as a window on a subtropical ecosystem of the Miocene world, a window that was open during the late Paleogene and most of the Neogene. Retrievable information is paleontological, sedimentological, and geochemical, and it is relevant to systematics, biochronology, paleoecology, and paleobiogeography. Tightly constrained spatial and temporal data integrated with paleobiological and geological information provide unifying themes. The wealth of information bears on evolutionary questions from the level of the microevolutionary scale of population changes to the macroevolutionary scale of phenomena such as the dynamics of faunal responses to environmental change.

Vertebrate fossils from southern Asia became known to the Western world as early as the 1830s, primarily from Siwalik deposits of the Indian Subcontinent, and led to the steady accumulation of specimens in natural history collections in Calcutta and London. Virtually all the fossils the nineteenth century were obtained second- or third-hand by travelers passing through that part of the world. Cautley and Falconer (1835) and Medlicott (1864) applied the term "Sivalik" or "Sewalik" or "Shevallik" to these fossils, and later Pilgrim (1913) defined a succession of strata and fossils (Kamlial, Chinji, Dhok Pathan, Tatrot, and Pinjor) from the Potwar Plateau of Pakistan and the Siwalik Hills in northern India, which produced most of the fossils. This stratigraphic-chronologic framework became used widely by numerous authors (Pilgrim 1926, 1934; Colbert 1935; Lewis 1937; Hussain 1971; Cheema, Raza, and Ahmed 1977). Barry et al. (chapter 15, this volume) interpret the stratigraphy of the Potwar Plateau as it is observed, without prior assumptions of the chronologic significance of Pilgrim's units.

Early in the twentieth century, the ages of Siwalik deposits were estimated from stage of evolution and presence of key mammalian immigrants. The long stratigraphic sequence produced fossils of the horses *Equus* and *Hipparion*, then thought of as indicators of Pleistocene and Pliocene age, respectively. *Equus* occurs in the Pinjor Formation and hipparionine horses appear in the Nagri Formation, but Colbert (1935) believed early collections indicated *Hipparion* in the older Chinji Formation. This led to the idea in the older literature that Chinji strata would be Pliocene in age. We now know that hipparionines do not occur in the Chinji Formation and that these horses entered the Old World in the Late Miocene; the Chinji Formation is mainly Middle Miocene in age, and the underlying Kamlial Formation extends into the Early Miocene. The transformative factor that led to accurate dating of the Siwaliks was the application of magnetostratigraphy to detailed biostratigraphic sections, the development of which we will explore.

The Siwalik sequence of terrestrial deposits of the Indian Subcontinent can be likened to a laboratory in which the evolution of subtropical terrestrial fauna proceeded for over 20 million years. The quality of the Siwalik fossil record resides in its extraordinary time depth, rather than richness of fossil horizons, although specific horizons do contain unusual numbers of well-preserved remains. Fossil assemblages are distributed throughout, and by careful stratigraphic control successive samples can be used to reconstruct a time series that records mammalian community evolution over many millions of years.

TERRESTRIAL DEPOSITS IN THE INDIAN SUBCONTINENT

The term "Siwalik" refers to molasse eroded from the Himalaya-Karakorum ranges and deposited in the foreland basin south of the mountain front. Sediments of the Siwalik Group are kilometers-thick accumulations of terrestrial deposits best exposed along a northwest–southeast belt from northern Pakistan (about 33°N latitude today) through north India and southern Nepal to the Garo Hills of Assam (about 25°N), a distance of over 2000 km (figure 14.1). In total, the Siwaliks record relatively continuous deposition throughout Neogene time. Barry et al. (chapter 15, this volume) present the stratigraphy of the Siwaliks observed on the Potwar Plateau of northern Pakistan and the tectonic setting of accumulation. Collectively, the Siwaliks of northern Pakistan are a clastic wedge that thins southward (Mascle and Hérail 1982). The Irrawaddy Formation of related origin and similar age occurs southeastward in Burma (Myanmar; see Chavasseau et al., chapter 19, this volume). Late Neogene terrestrial deposits in Afghanistan are not part of the Siwaliks, but also result from the tectonics of Indian plate collision.

Siwalik sediments are dominantly sandstones and siltstones, with lesser components of conglomerates and claystones, the latter often red in color. Continuously accumulating floodplain sediments and channel avulsions in the aggrading fluvial systems of the sub-Himalayan foreland basin set the stage for frequent burial and preservation of vertebrate remains. Rapid burial of skeletal remains and favorable post-burial pH conditions resulted in a long sequence of fossil-bearing horizons preserved in partially indurated strata. Most fossils are associated with paleo-channels and abandoned-channel environments (Badgley 1986a; Rajpar 1993; Badgley and Behrensmeyer 1995). Small mammal concentrations occur in abandoned channels and crevasse splay deposits (Badgley, Downs, and Flynn 1998).

Taphonomic analysis of Siwalik fossil assemblages of Pakistan explains the fragmentary nature of the Siwalik vertebrate record. Most vertebrate fossils were preserved in either fluvially transported assemblages of disassociated, fragmentary remains or in attritional, untransported assemblages of biological origin such as sites of repeated predation or other causes of mortality (e.g., waterholes; Badgley 1986a, 1986b; Behrensmeyer 1987). In both taphonomic contexts, vertebrate remains are typically disarticulated and fragmentary, with low levels of association. No instances of mass death followed by rapid burial have been found, except for rare beds of articulated fish remains. The fragmentary nature of the fossil record results from both biological processes—including predation, scavenging, and trampling—and fluvial processes resulting in transport, abrasion, and sorting.

That superposed assemblages of the Potwar Plateau crop out over a limited area presents both limitations and possibilities. Siwalik fossil assemblages there repeatedly sample low-elevation floodplain habitat; they represent communities living near perennial rivers, smaller-scale streams, and ponds. Therefore, the Potwar Siwaliks do not usually preserve faunal elements of the Indian Subcontinent from dry upland or estuarine environments. This is why comparative studies of faunas from distant areas of the Indian Subcontinent representing different environments will be complementary in the future.

The Siwaliks of the Potwar Plateau present a record of how lowland floodplain communities changed through millions of years. Superposed assemblages sample long-term environmental change that affected the broad sub-Himalayan alluvial plain, making the Siwalik record highly applicable to studies of vertebrate evolution. Because temporal sampling is dense, the time scale on which changes can be resolved is short (10^5 yr for the Potwar Plateau; Barry et al. 2002; Badgley et al. 2008). The scale of paleobiological questions that can be addressed through the Siwalik fossil record represents the level of Gould's (1985) "second tier" (see also Jablonski 2008), and helps to "bridge microevolution and macroevolution" (Reznick and Ricklefs 2009).

The Potwar Plateau

Pilgrim's (1913) units were formally designated formations (see Cheema, Raza, and Ahmed 1977) clustered as the Rawalpindi Group and Siwalik Group. The older Rawalpindi Group includes the Kamlial Formation and underlying Murree Formation. The Chinji, Nagri, Dhok Pathan, and (in Pakistan) Soan formations constitute the

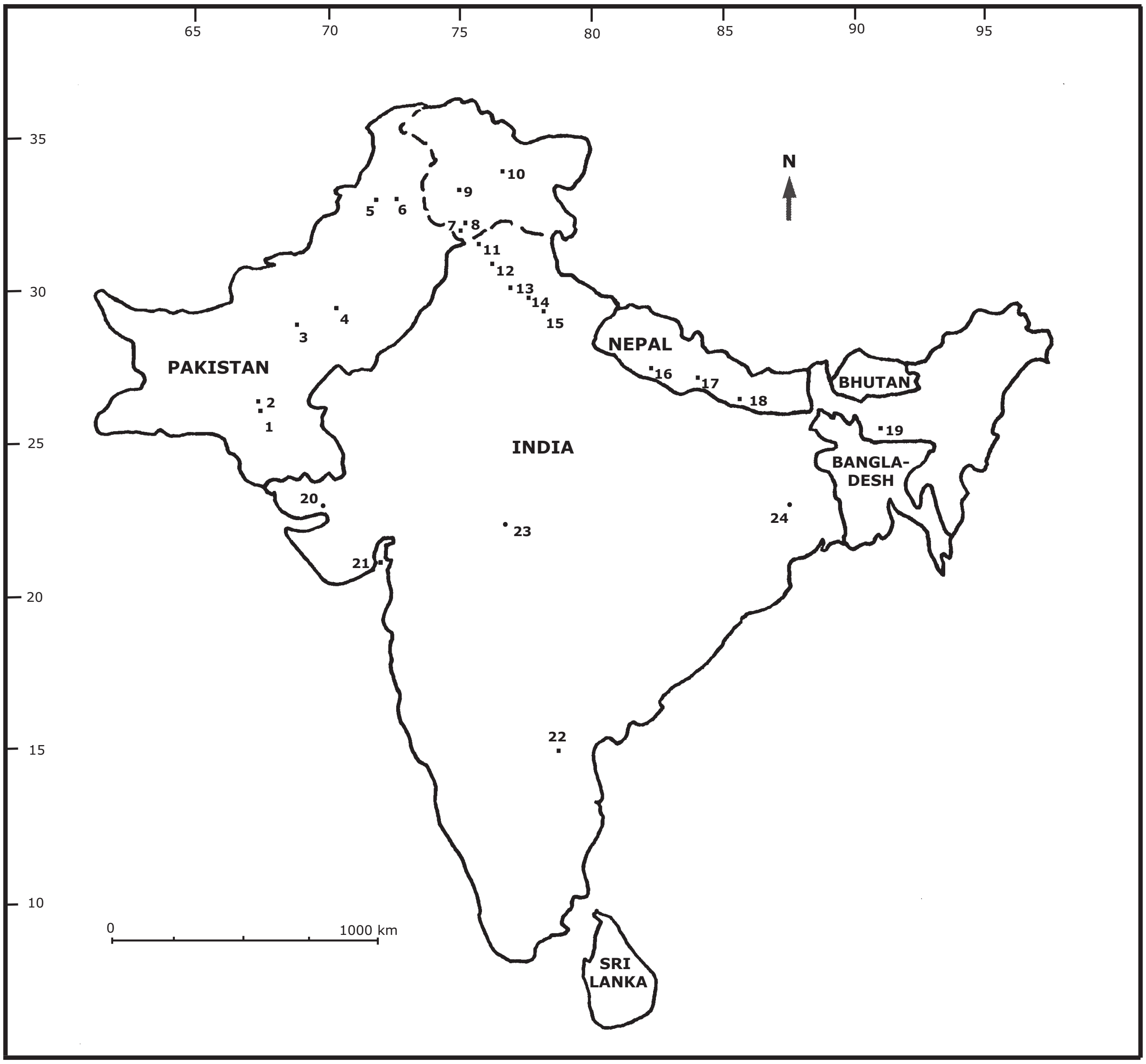

Figure 14.1 Location map for representative fossil localities of the Indian Subcontinent. Sites discussed in the text are the Sehwan (*1*) and Gaj (*2*) sections of the Manchar Formation, Bugti (*3*) and Zinda Pir Dome (*4*) of Balochistan, Kohat (*5*) and the Potwar Plateau (*6*) of the Punjab, Jammu (*7*), Ramnagar (*8*), Karewa (*9*) and Kargil (*10*) in Jammu-Kashmir, Nurpur (*11*), Haritalyangar (*12*), Pinjor (*13*), Saketi (*14*) and Kalagarh (*15*) of northern India, Dang Valley–Surai Khola (*16*), Tinau Khola (*17*) and Rato Khola (*18*) of Nepal, Garo Hills (*19*) in Assam, Kutch (*20*) and Perim Island (*21*) in western India, and the Pleistocene localities Kurnool Caves (*22*), Narmada Valley (*23*), and Bankura, West Bengal (*24*). Some locations, like Bugti (*3*), the Potwar Plateau (*6*), and the Jammu area (*7*), are general positions for multiple fossil sites, clusters of which can be recognized. Latitude and longitude indicated.

Siwalik Group. This sequence is particularly well exposed on the Potwar Plateau, a large area of about 12,000 km^2 in northern Pakistan, north of the Salt Range (Barry et al., chapter 15, this volume). Unlike the stratigraphy of southern Pakistan, where the Siwaliks grade downward to near-shore marine deposits, the Siwalik clastic wedge of the Potwar Plateau lies unconformably on Eocene marine limestones and represents alluvial filling of the sub-Himalayan foreland basin formed by the northward movement of the Indian sub-continent and the uplift of the Himalayas along the major boundary faults. Near and west of Islamabad, the thick sands with few vertebrate localities of the Murree Formation characterize the base of the Potwar Siwaliks. This unit is less distinctive nearer the Salt Range and is usually not differentiated there from the overlying Kamlial Formation. In total, the Siwaliks are thousands of meters thick, with some composite sections in the north estimated to be up to 6 or 7 km thick. One detailed study of a continuous section (Willis 1993; not the thickest portion of the wedge) recorded 2100 m of sediment from much of the Lower and Middle Siwaliks; the complete sequence there would be over 3000 m.

The Early Miocene onset of terrestrial deposition probably came earlier in the northern, proximal part of the clastic wedge than nearer the Salt Range, judging from a primitive small mammal assemblage from the Murree Formation of Kohat (de Bruijn, Tasser Hussain, and Leinders 1981). The Kohat area (see figure 14.1 [5]) includes a thick set of Lower and Middle Siwalik sediments above the Murree Formation. In the Potwar Plateau, sediments immediately overlying Eocene marine units are dominated by dark-gray fluvial sandstones, sometimes cross bedded, with intervening red mudstones.

The Siwaliks of the Potwar Plateau contain the type areas for several formations (Barry et al., chapter 15, this volume). The uplifted sequence abutting on the Salt Range is a succession of formations (from oldest to youngest Kamlial, Chinji, Nagri, and Dhok Pathan) named for villages separated by no more than 60 km. The Kamlial and the overlying Chinji formations are lumped in some contexts as the Lower Siwaliks (particularly older publications, e.g., Colbert 1935). The Nagri and interfingering (see Behrensmeyer and Tauxe 1982) Dhok Pathan formations informally constitute the Middle Siwaliks. Upper Siwalik rocks occur on the Potwar Plateau and adjacent Pabbi Hills (Jacobs 1978) and Mangla Dam areas, but they are best developed in the famous Saketi Park of northern India, southeast of the type area of the Pliocene Pinjor Formation. Other bodies of Upper Siwalik rock bear formation names, including the fossiliferous Tatrot Formation of the Potwar Plateau. The Tatrot Formation is local and thin (60 m) and spans a short time (a single magnetozone), and a local unconformity separates it from the subjacent Dhok Pathan Formation (Opdyke et al. 1979). More widespread in northern Pakistan is the Upper Siwalik Soan Formation, named for coarse clastic deposits along the Soan River of the Potwar, which overlies the Dhok Pathan Formation.

The successive Kamlial, Chinji, Nagri, and Dhok Pathan formations span the Miocene without significant hiatus and are distinguished by the proportion and nature of their sand content (Khan 1995). Much of the Kamlial section is sandy, but red siltstones increase toward the top of the unit. The overlying Middle Miocene Chinji Formation, dominantly red silts and clays, contains gray cross-bedded sandstones, but the red sediments are very well developed, contain paleosols, and are reminiscent of Early to Middle Miocene age redbeds in China. There is no indication that the Chinji red clays are aeolian in origin, however. Above the Chinji Formation, the Nagri Formation is characterized by massive, multistoried blue-gray sands with lesser amounts of red silt and smaller channel deposits. Upward, a change to more frequent buff-colored sand bodies with associated mudstones and fewer blue-gray sands indicates interfingering with the overlying Dhok Pathan Formation (Behrensmeyer and Tauxe 1982; Behrensmeyer 1987). The sand bodies and their mineralogical composition indicate two different drainage systems (mountain-sourced vs. foothill-sourced) that had differing taphonomic effects on fossil preservation (Badgley 1986b; Behrensmeyer 1987). Upper Siwalik units (Tatrot, Pinjor, and Soan formations) are recognized by significant gravel components.

Like most bodies of sedimentary rock, Siwalik formations are time transgressive. In any one section, they are successive, but age assumptions about fossils from laterally distant localities should not depend on dominant lithology (Pilbeam et al. 1996). Some marker beds extending over kilometers do approximate time lines in the Siwaliks (Behrensmeyer and Tauxe 1982). Typically, these are paleosols or thin, resistant, and continuous sheet sands (representing widespread flood events) and can be used to trace localities into master sections (Barry et al., chapter 15, this volume).

The fundamental key to age control on the Potwar Plateau is magnetostratigraphy applied to precise biostratigraphic sections and used successfully to correlate the Siwalik sequence to the geomagnetic polarity time scale. Long, continuous stratigraphic sections of the Potwar Plateau near the town of Khaur, plus sections in the Hasnot, Jalalpur, and Rohtas areas (Barry et al. 2002:fig. 1), provide the backbone for the biostratigraphy and historical geology of the area (Opdyke et al. 1979; N. M. Johnson et al. 1982; Johnson et al. 1985). The great length of the composite secures correlations to chrons C5Dr to C3An.2n, 17.9 Ma to 6.4 Ma on the Gradstein et al. (2004) time scale. The extensive lateral exposures allow multiple coeval sections, enabling secure correlations across tens of kilometers. Parallel sections recording the same magnetozones and reversal events (time lines) allow correlation of localities to a precision of up to 10^4 yr in some instances (Flynn et al. 1990). The Upper Siwaliks also have magnetostratigraphic control in addition to radiometric dates on tuffs at Kotal Kund, Pabbi Hills, Rohtas Anticline, and elsewhere (Opdyke et al. 1979; G.

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D. Johnson et al. 1982), bringing the dated record to less than 1 Ma.

Other Neogene Deposits of the Indian Subcontinent

Other Neogene terrestrial deposits of the Indian Subcontinent may be considered local manifestations of the Siwaliks insofar as their origin is loosely related to the same tectonic history as the formally named units. Usually they bear other formation names (figure 14.2). For example, Pliocene age deposits of the Potwar Plateau are generally undifferentiated as "Upper Siwaliks" or referred to as Soan Formation, but elsewhere as around Mangla Dam (Mirpur and Lehri towns), Upper Siwaliks have been designated as the successive Samwal, Kakra, and Mirpur formations. Important fossils from this area have paleomagnetic control (Johnson et al. 1979) and supplement the Potwar record (e.g., Hussain et al. 1992; Steensma and Hussain 1992; Cheema, Raza, and Flynn 1997; Cheema, Flynn, and Rajpar 2003).

Northern India

The Upper Siwaliks are best exposed and highly fossiliferous along a 400-km, northwest–southeast band of outcrops in northern India and Kashmir. The type area for the Late Pliocene–Early Pleistocene Pinjor Formation is about 10 km northeast of Chandigarh (see figure 14.1 [13]). The Saketi region, 40 km to the southeast and established as a national historical park, has magnetic control (Azzaroli and Napoleone 1981; Tandon et al. 1984). In the Jammu area (see figure 14.1 [7]), the Nagrota Formation is the name usually applied to rocks of the Upper Siwaliks, although other units have been proposed. Basu (2004) related Pliocene faunal assemblages from the Nagrota (=Uttarbani) Formation to a 2.5 Ma tuff. Gupta and Prasad (2001) reported diverse Pliocene microfauna from the Nagrota Formation 10 km north of Jammu. Patnaik (chapter 17, this volume) presents the details of faunal occurrences for this band of Upper Siwaliks.

Gupta and Verma (1988) named the Mansar, Dewal, Mohargarh, Uttarbani, and Dughor formations (oldest to youngest) for an impressive package of molassic sediments 20 km southeast of Jammu, and they noted fossils of late Miocene through Pliocene ages. Recently, Early Miocene deposits north of Jammu have been shown to yield small mammals (Kumar and Kad 2002).

There are also significant high-elevation fossil resources in Kashmir. South of Srinagar (see figure 14.1 [9]), Plio-Pleistocene deposits of the intermontane Karewa Formation, with fission-track dating and a paleomagnetic record for the last 3 myr produce a late Neogene *Equus-Cervus-Canis-Elephas hysudricus* fauna (Kotlia 1990). Micromammals include arvicolines, reflecting high elevation by the late Pliocene (Kotlia and von Koenigswald 1992). Farther east and higher into the hills of Ladakh, the Kargil Formation produces mid-Tertiary fauna including anthracotheres and small mammals (Kumar, Nanda, and Tiwari 1996; see figure 14.1 [10]). A derived diatomyid rodent from the Kargil Formation (Nanda and Sahni 1998) suggests Late Oligocene age, by comparison with Early Oligocene *Fallomus* (see Marivaux and Welcomme 2003).

Middle to Late Miocene age sediments of northern India were at one time considered to represent the formations that are recognized on the Potwar Plateau. The red siltstones of the well-known Ramnagar hominoid locality (40 km east of Jammu; see figure 14.1 [8]) are reminiscent of the Chinji Formation, but they are currently referred loosely to the Lower Siwaliks. The faunal content, including *Sivapithecus*, is very much like that of type—Chinji assemblages, with some notable differences—for example, occurrence at Ramnagar of the rare hystricid *Sivacanthion*, which has not been found anywhere in the Potwar since 1922 (one Chinji area specimen, Colbert 1935). Basu (2004) and Patnaik (chapter 17, this volume) advance the biostratigraphy of Ramnagar significantly and show that it compares well with assemblages of about 13 Ma on the Potwar Plateau.

Exposures near Haritalyangar (100 km north of Chandigarh; see figure 14.1 [12]), yield rich assemblages, including relatively abundant hominoid primates. Despite lithological similarity to the Nagri and Dhok Pathan formations of the Potwar, identical ages should not be assumed, and Indian geologists (Patnaik, chapter 17, this volume) recognize local lithological units for the sequence. The most productive deposits, assigned without differentiation to the Middle Siwaliks, lie above a local sand unit (the Nahan Sandstone; Prasad 1968) that was formerly thought of as equivalent to the Nagri Formation (and probably is of about the same age). The magnetostratigraphy of Haritalyangar (Johnson et al. 1983), supplemented and reinterpreted by Pillans et al. (2005), shows that most of the fossil material derives from an interval of about 9.3 Ma to 8.1 Ma, making this the chronological equivalent of lower part of the Dhok Pathan Formation in the Potwar Plateau.

Patnaik (1994, chapter 17, this volume) reviews the biostratigraphy of Haritalyangar and Dangar and shows the potential for comparing observed temporal ranges of species in North India with those seen 500 km away on

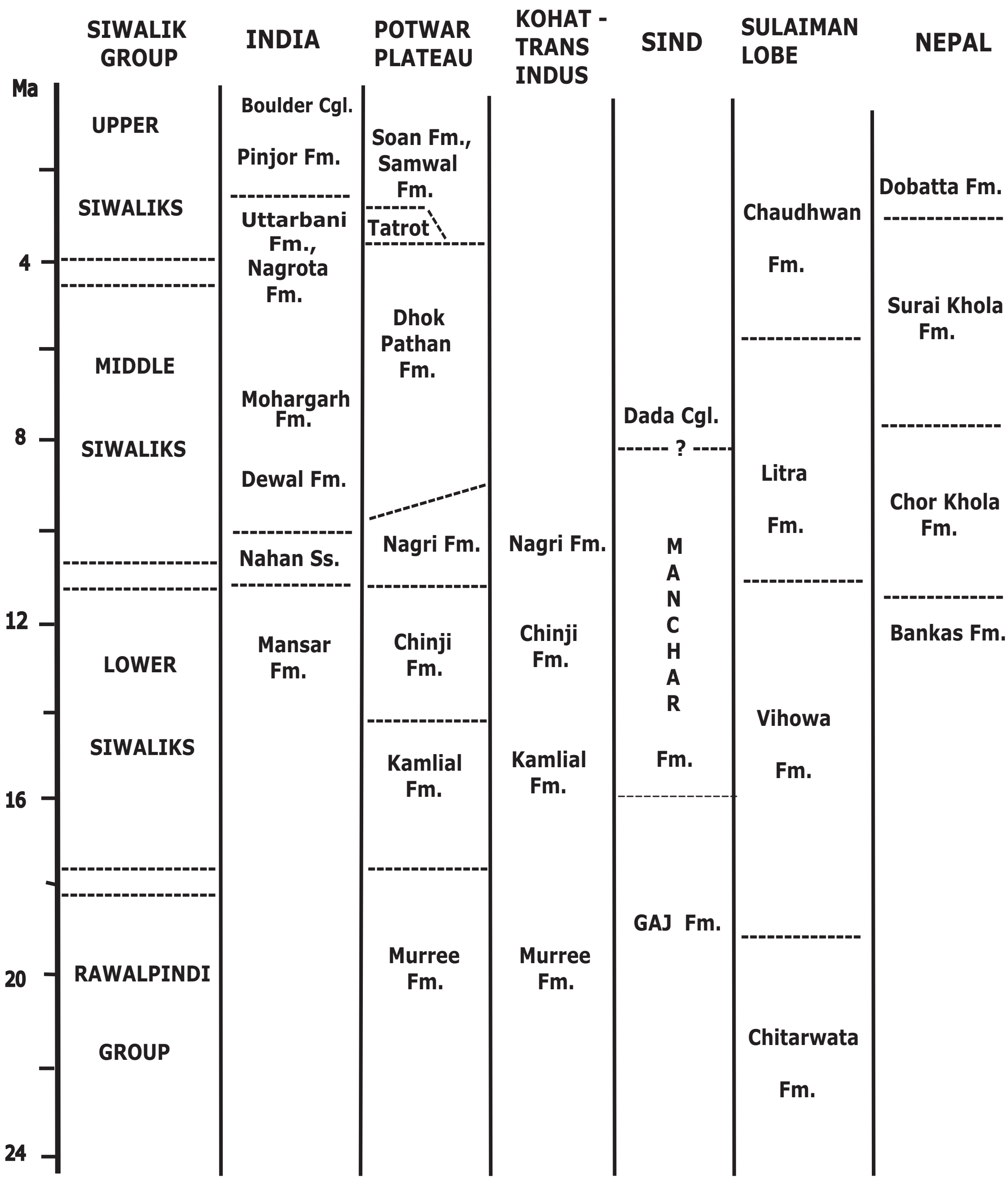

Figure 14.2 Stratigraphic correlation chart for the Indian Subcontinent. Time scale (Ma) adjusted to GTS2004. Geographic areas of the Indian Subcontinent are compared to the generalized succession in the left column. Dashed lines are meant to show that ages of stratigraphic boundaries are approximate and known to transgress time. In northern India, the Boulder Conglomerate is a local unit, and various formation names have been applied in different areas; the rock succession is a composite of units from several areas. On the Potwar Plateau, the Nagri Formation interfingers with the Dhok Pathan Formation, and the Tatrot Formation is local in distribution. In some areas, such as Sind or Kohat, the succession of units is known, but the ages are approximate, according to faunal content. In Nepal, paleomagnetic plus faunal data are the source for the age assessment.

the Potwar Plateau. Any differences will raise interesting questions. Flynn and Morgan (2005) noted that the primate *Sivaladapis* persisted much later at Haritalyangar than in the Potwar Plateau. Does this reflect limitations due to sampling bias, or real differences in paleoecology across the Indian Subcontinent? This may be answerable by ongoing work.

The vertebrate record for Late Miocene deposits of northern India is growing. Recent work near Nurpur and Kalagarh (see figure 14.1 [11 and 15]) complements the biostratigraphic information available from the vicinity of Haritalyangar. Ranga Rao (1993) provides a foundation for beginning direct comparison of the deposits at Nurpur with the Potwar Dhok Pathan Formation. The potential is great to compare local observed biostratigraphies at a high level of resolution when the fossil horizons are tied to a resolved magnetostratigraphy (Patnaik, chapter 17, this volume).

Peninsular India

The later Cenozoic fossiliferous deposits of the Indian Subcontinent are generally northern in distribution, while the fossil record of Peninsular India is poorly represented by Neogene assemblages. The obvious exception for the Miocene is the more southerly assemblage from Perim Island (Falconer 1845; see figure 14.1 [22]), which contains many of the taxa found in northern localities. A recent review of fauna from Kutch (Bhandari et al. 2009:area 21) reveals the same Cetartiodactyla species as encountered in Pakistan. Whether the vertebrate fauna of Peninsular India evolved in an ecological setting similar to that of the north remains to be examined.

Pleistocene localities are distributed broadly in India, including the famous Narmada Valley hominin localities, Bankura District sites, and Pleistocene cave deposits of Kurnool (see figure 14.1; Sahni and Mitra 1980; Patnaik, Badam, and Murty 2008). The Kurnool caves yield a fauna of modern murines, porcupines, and leporids, comparable to that found today in India.

Nepal

Corvinus and Rimal (2001) and West, Hutchinson, and Munthe (1991) developed understanding of the lithostratigraphic sequence and fossil productivity of the Siwaliks in Nepal, focusing on the exposures of Surai Khola, Tinau Khola, and Rato Khola along the southwestern margin of Nepal. The magnetic interpretation of Corvinus and Rimal (2001) places the fossiliferous sediments in the 12 Ma to 2 Ma range, with the most productive portion of the sequence being the Surai Khola and Dobatta formations, about 7.5 Ma to 2 Ma. Fossils are consistent with Potwar assemblages of similar age. Patnaik (chapter 17, this volume) reviews these and other occurrences of vertebrate fossils in Nepal. Corvinus and Rimal (2001) also present important summaries of studies on Nepalese paleofloras, and Hoorn, Ohja, and Quade (2000) use the palynological record to reconstruct a subtropical to tropical ecosystem that gave way to grasslands in the late Miocene. Pliocene conditions in Nepal appear to have involved seasonal flooding and local ponding, which may contrast with a drier, grass-dominated paleohabitat of the Siwalik Hills and northern Pakistan (Quade and Cerling 1995).

Pakistan South of the Potwar

Rocks southwest of the Potwar Plateau are Oligocene and Early Miocene to Late Miocene in age. In Sind Province, vertebrate fossils occur in the Manchar Formation, principally in two areas, Gaj and Sehwan. The long sections there include Miocene faunas comparable to Kamlial, Chinji, and Nagri assemblages (Pilgrim 1912; Raza et al. 1984; van der Made and Hussain 1992), but small mammal fossils show that the early Miocene base of the Gaj section predates the earliest assemblages near the Salt Range (de Bruijn and Hussain 1984; de Bruijn, Boon, and Hussain 1989; Wessels and de Bruijn 2001; Wessels 2009).

In and adjacent to Balochistan in the Sulaiman Lobe of western Pakistan, thick terrestrial accumulations contain Oligocene vertebrate assemblages that pass into early and late Miocene faunas. Welcomme et al. (1999, 2001) established the Oligocene age of the famous Bugti Bone Bed (see figure 14.1 [3]) and demonstrated the Miocene ages of the overlying succession of vertebrate assemblages. Antoine et al. (chapter 16, this volume) resolve the Early Miocene biostratigraphy observed at Bugti and the Dalana area to the east as it pertains to the pattern of emplacement of Siwalik faunas.

The stratigraphy and named stratigraphic units in this part of Pakistan differ from those observed to the north, so distinct stratigraphic units are recognized (Chitarwata and overlying Vihowa formations). The Oligocene to early Miocene Chitarwata Formation represents low-lying terrestrial delta deposits interfingering with lagoonal, brackish water deposits containing sharks and marine shell beds (Downing et al. 1993). The environment of deposition becomes increasingly terrestrial upward. Higher stratigraphically, thick, prominent, gray sandstones with interbedded red mudstones constitute the Vihowa Formation. Lowest Vihowa beds near Dalana are early

Miocene, predating the Kamlial Formation, based on the paleomagnetic and faunal analysis of Lindsay et al. (2005; see following discussion).

Raza et al. (2002) extended knowledge of the Miocene faunal sequence of the Dalana area with explorations through the Vihowa Formation into the overlying Litra and Chaudhwan formations, in all well over 3000 m of sediments recording terrestrial deposition. They showed that the Litra Formation produces fossils consistent with early Late Miocene age, including *Cormohipparion*, *Listriodon*, and a large giraffid perhaps representing *Bramatherium*.

CHRONOLOGY

The wealth of the Siwalik fossil record made it imperative to develop well-resolved temporal control. However, knowledge of the approximate age of the Siwaliks eluded scientists until the later part of the twentieth century. The widespread occurrence of hipparionine horses in upper levels (Nagri Formation and higher) had indicated later Tertiary time, but age control was poor, and the time span of the Siwalik sequence was underestimated. The very few and dispersed tephra of the Siwaliks offered only limited help when radiometric dating became feasible. By the 1970s, the main hope for developing a time frame for the Siwaliks lay in application of magnetostratigraphy in conjunction with biostratigraphy for correlation to the developing geomagnetic polarity time scale.

Magnetochronology

In 1973, Noye Johnson (Dartmouth College) initiated a project funded by the Smithsonian Foreign Currency Program for paleomagnetic correlation of Siwalik deposits in Pakistan with those of North America and the mid-Atlantic ridge system, the standard magnetostratigraphic reference of the time. The magnetic polarity sequence had been established for the Late Neogene (Cox, Doell, and Dalrymple 1963), but at the time it was believed that magnetic reversals older than 5 Ma could not be dated accurately because the limits of radiometric dating would not precisely constrain placement of an unknown magnetozone to a particular magnetic event of that age. Noye Johnson and his colleagues would prove this wrong by determining the magnetic sequence in Siwalik rocks of age greatly exceeding 5 Ma.

Also in 1973, the Yale University (later Harvard University) project in evolutionary biology had begun in the Potwar Plateau, in part searching for early records of hominoid fossils of southern Asia. In addition, S. Taseer Hussain, Howard University, and colleagues from Universiteit Utrecht, Netherlands, became interested in searching for Cenozoic vertebrate fossils in terrestrial deposits. We soon saw that the geology of Pakistan provided a long terrestrial sequence with multiple fossil horizons that offered documentation and dating of a densely sampled biostratigraphy. Cooperation along lines of mutual interest proved very productive over the next decades.

Key to developing the biochronology of the Potwar Plateau Siwaliks was its dating. The magnetostratigraphic framework used here as the current standard for the GPTS is that of Gradstein, Ogg, and Smith (2004; designated GTS2004), which incorporates numerous refinements of the last 50 years. Earlier time scales were used in many older publications, yielding different ages for localities in some instances. GTS2004 is based on biologic and magnetic data from deep-sea cores, terrestrial magnetostratigraphy, radiometric dating, and astronomical tuning of cyclic phenomena recorded in sediments. The Neogene part of the time scale is thoroughly reviewed by Lourens et al. (2004), who note that one of the least secure parts of GTS2004 is the interval between the Oligocene–Miocene boundary and the Middle Miocene, about 13 Ma.

Potwar Magnetostratigraphy

N. M. Johnson et al. (1982) built their composite magnetostratigraphic framework for the Middle and Upper Siwaliks (figure 14.3) using six long sections correlated with a thick normal magnetozone (N_0) that included a volcanic tuff with fission track age of 9.50 ± 0.63 Ma (G. D. Johnson et al. 1982). Formation boundaries in relation to magnetozones were consistent in each of the sections. The Upper Siwaliks, with late Neogene fauna, were found to include a 2.53 ± 0.35 Ma tuff (G. D. Johnson et al. 1982), and a paleomagnetic reversal pattern characteristic for the Plio-Pleistocene sequence spanning chrons C2n to C3r (current chron designations). The Middle Siwaliks together encompass chrons C3An to C5n.2n. chron C5n.2n is the long normal magnetozone (N_0). Opdyke et al. (1979) and Tauxe and Opdyke (1982) extended this work to other sections, developing fine scale temporal control over large areas around the towns of Jhelum and Khaur.

The key Siwalik Gabhir Kas/Chita Parwala magnetostratigraphic section (figure 14.4) extended the composite record downward from the Middle Siwaliks through the Chinji Formation to the base of the Kamlial Formation, where Siwalik deposits are underlain by Eocene limestone and marls. The magnetic traverse passes near

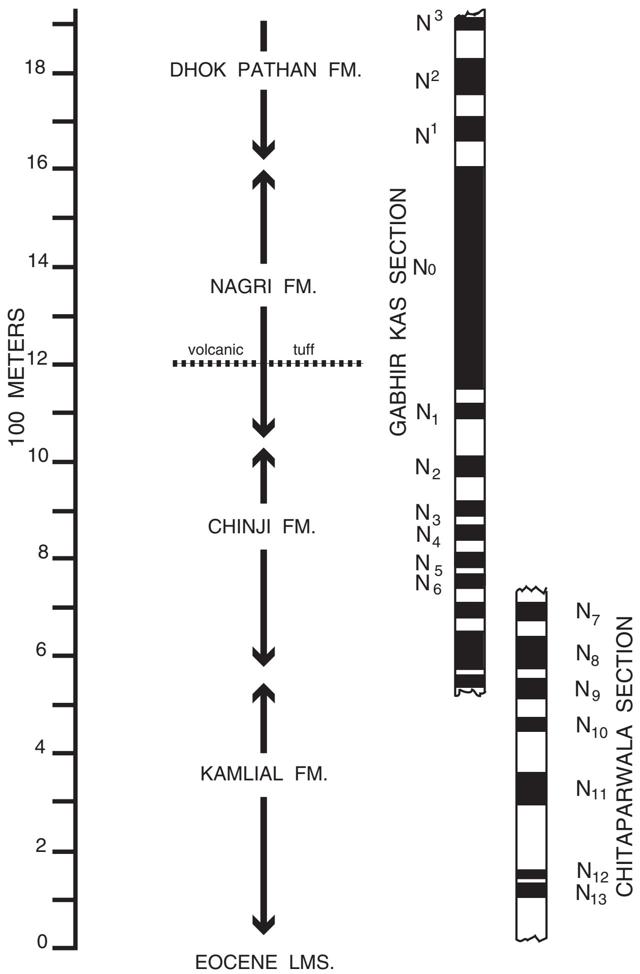

Figure 14.3 Stratigraphic sequence of the Siwaliks, with observed magnetostratigraphy, near the village of Chinji on the Potwar Plateau, Pakistan. Modified from Johnson et al. (1985).

the historical towns of Chinji and Sethi Nagri. Johnson et al. (1985) correlated the base of the Kamlial Formation in their Chita Parwala section with chron 17 of the Mankinen and Dalrymple (1979) time scale (=chron C5Dr), yielding an age for the base of the Siwalik sequence of 18.3 Ma on that time scale, 17.9 Ma on GTS2004.

Chitarwata Magnetostratigraphy

Fieldwork in the Zinda Pir Dome was initiated in 1989 along the Dalana Nala, west of Dera Ghazi Khan in Punjab Province, near Balochistan. This is in the southern part of the area studied in detail by Hemphill and Kidwai (1973) as part of cooperative mapping by the United States Geological Survey and the Geological Survey of Pakistan (GSP). The Zinda Pir Dome is a folded structure in the eastern foothills of the NE–SW trending Sulaiman Range. The Sulaiman Range bends to the west at its southern extent, flexes to the north, and loops back to the south in a tight fold before it continues southward as the Kirthar Range. Within the loop at the southern end of the Sulaiman Range folded sediments are exposed near the town of Bugti; these are the Bugti beds of early workers beginning with Vickary (1846), and the Chitarwata Formation of Hemphill and Kidwai (1973) and Antoine et al. (chapter 16, this volume). The Chitarwata Formation is overlain by Siwalik-like fluvial sediments that wedge southward from the Himalaya Mountains and eastward from the Sulaiman Range (in ascending order, the Vihowa, Litra, and Chaudhwan formations of Hemphill and Kidwai 1973). Thick exposures of strata assigned to the Chitarwata and Vihowa formations are unconformably superposed on marine Eocene deposits near Dalana in the southern part of the Zinda Pir Dome.

Downing et al. (1993) recognized three units in the Chitarwata Formation, characterizing the lower unit (unconformable on the Eocene marine Kirthar Formation) as representing estuarine habitat, with abundant molluscan borings in highly oxidized sediments located in and above the basal contact (these diminish upward). The middle unit indicated a strandplain habitat, dominated by sands with abundant tabular and trough crossbeds, and the upper unit was characterized as a tidal flat with mostly fine-grained sediments interspersed by shallow channels. Discontinuous but thin shell beds occur throughout the upper unit, which was interpreted to represent storm beds, recording repeated shallow incursions of marine sediments onto the delta plain. The Vihowa Formation disconformably overlies the Chitarwata Formation with a thick, massive sandstone at its base, grading up into silts and thin discontinuous sands.

Friedman et al. (1992) published a paleomagnetic analysis of the Chitarwata Formation and the lower part of the Vihowa Formation near Dalana, noting difficulty in determining reliable results. Lindsay et al. (2005:fig. 4) measured and sampled two more complete sections in the Chitarwata Formation. The three complete Chitarwata sections near Dalana averaged about 420 m thick. Magnetic data from the two new Chitarwata sections were combined with the results of Friedman et al. (1992) to assemble a composite sequence (Lindsay et al. 2005). Again, correlation of the Chitarwata magnetostratigraphy to the Geomagnetic Polarity Time Scale (GPTS) (figure 14.5) is very difficult, due to suspected hiatuses and lack of reliable magnetic samples in some parts of the section (primarily in the middle of the Chitarwata Formation). Lind-say et al. (2005) interpreted a hiatus of unknown

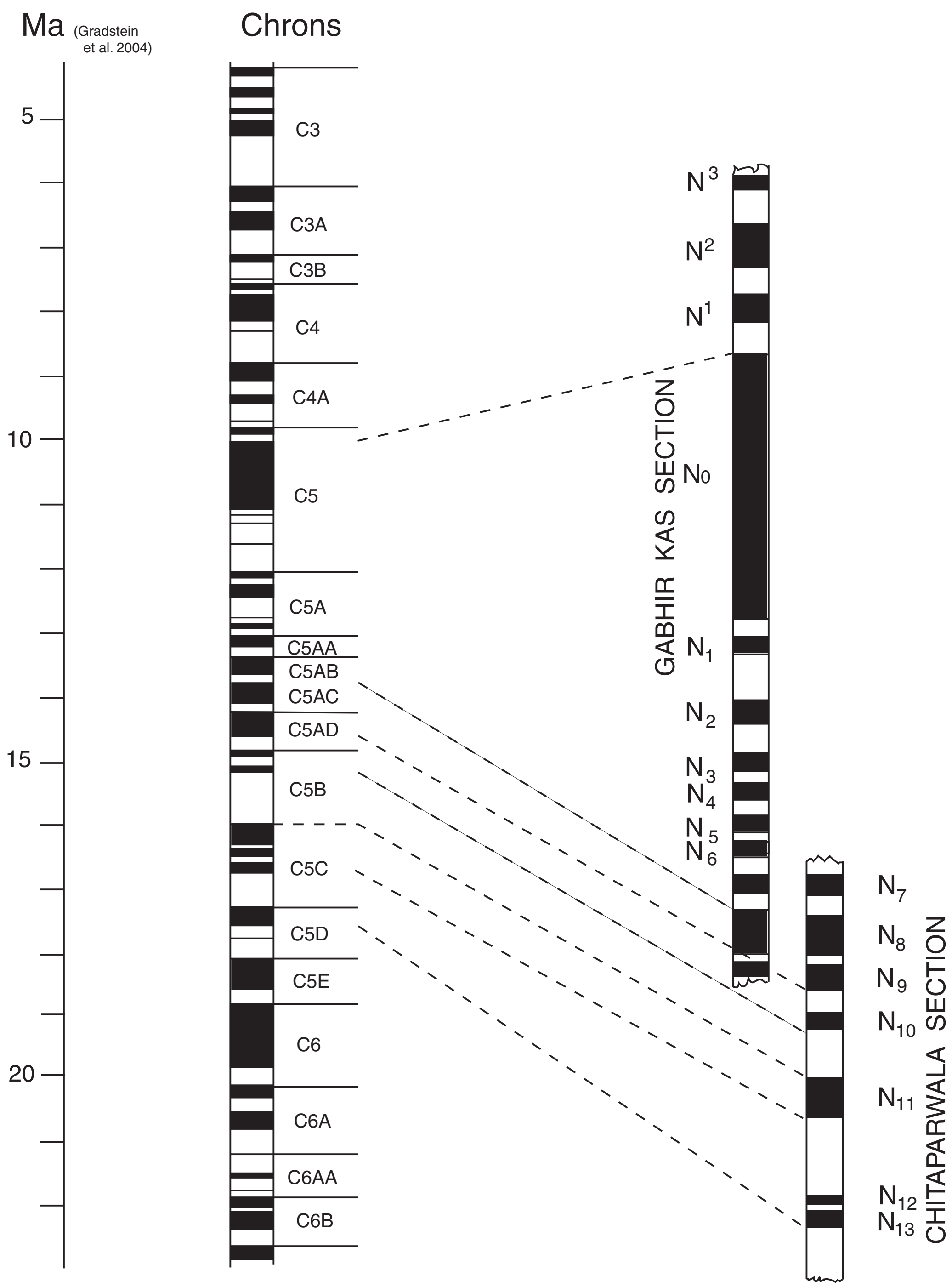

Figure 14.4 Correlation of the Gabhir Kas and Chita Parwala Kas magnetostratigraphic sequence with GTS2004.

duration (and unknown number of reversals) at the Vihowa/Chitarwata unconformity and proposed alternative correlations. Figure 14.5 is a revised correlation that minimizes the hiatus but implies others throughout the section. It is supported by new evidence from associated fossils (Antoine et al., chapter 16, this volume).

The magnetic sequence in the lower part of the Vihowa Formation (magnetozones R_1 through N_4U of Lindsay et al. 2005) in the Zinda Pir Dome matches fairly well with the Early Miocene chrons C5Cr to C6n of GTS2004. Small mammals from low in the Vihowa are consistent with Early Miocene age in that they appear to

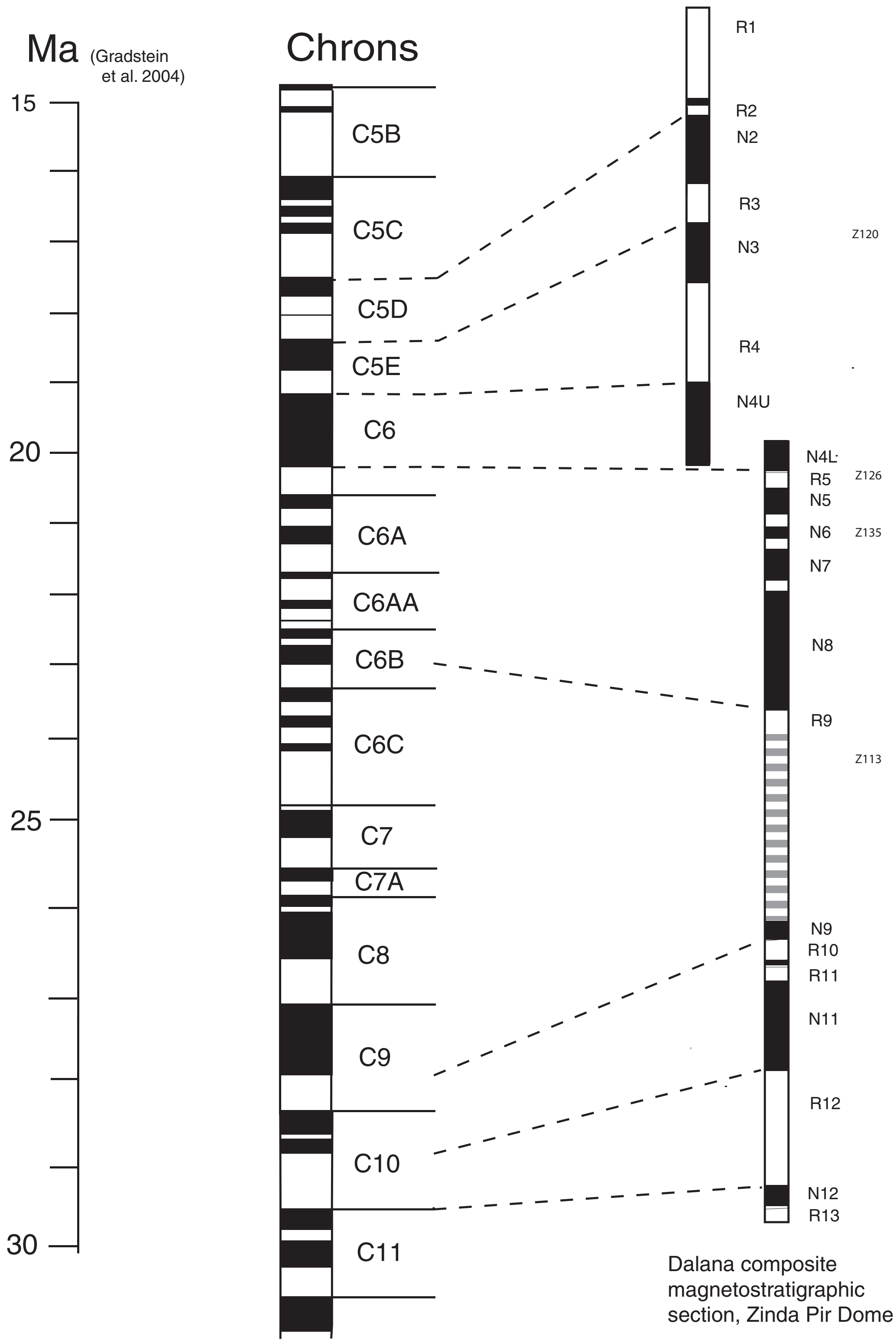

Figure 14.5 Correlation of the lower Vihowa and Chitarwata sections near Dalana, Zinda Pir Dome, with GTS2004. Revised from Lindsay et al. (2005). Key fossil sites, Z numbers, are noted on the right.

be somewhat older than the lowest (chron C5Dr, 17.8 Ma) Kamlial assemblages. Our highest small mammal site in the Vihowa Formation (locality Z120) occurs about 21m above the base of the Vihowa Formation, near the top of magnetozone N_3, which we correlate with chron C5En of GTS2004 (18.4 Ma). Therefore, a gap of 0.6 myr occurs between our lowest records of small mammals in the Kamlial Formation and our highest record in the Vihowa Formation. Deposition of the Vihowa Formation would have begun in the Dalana area of the Sulaiman Range about 1.8 myr earlier than fluvial Siwalik deposition was initiated in the Chita Parwala section, north of the Salt Range of the Potwar Plateau.

The top of the Chitarwata Formation is early Miocene, but its magnetostratigraphic match to the GPTS is controversial. We correlate the top normal magnetozone (N_4L) to part of chron C6n (see figure 14.5), but we previously considered C6Bn a possibility. Our present interpretation is supported by small mammals from Zinda Pir site Z126, just before N_4L, which indicate late Early Miocene age. Antoine et al. (chapter 16, this volume) agree, estimating early Miocene ages for levels of the upper unit of the Chitarwata Formation, based primarily on rhinocerotid fossils. Orliac et al. (2010), studying suoid fossils, project the Miocene–Oligocene boundary to below level M-3bis at Bugti and correlate this horizon with the bottom of the upper member of the Chitarwata, well below Z135 and somewhat above Z113. Therefore, the Z135 microsite should be early Early Miocene, and its short normal magnetozone (N_6) could correlate to a short normal such as chron C6AAr.1n, at about 22.2 Ma.

Z113 (although itself in indeterminate rock) falls below a significant normal magnetozone that likely is chron C6Bn, the base of the Miocene. The Z113 rodent fauna is demonstrably more primitive than that of Z135 and is reasonably latest Oligocene (approximately 23.5 Ma). Significant hiatuses below Z113 are likely. The oldest part of the Chitarwata Formation near Dalana includes site Z108 (base of N_{11}) with Bugti Member fauna that appears to correlate with Early Oligocene chron C10n. The latter interpretation agrees with the biochronological conclusion of Welcomme et al. (2001), who assigned an Early Oligocene age for fauna from the base of the Chitarwata Formation in the Bugti area.

APPLYING THE RECORD

Having developed the Siwalik and pre-Siwalik lithostratigraphy and its magnetochronology in Pakistan, the contained biotic record can be analyzed in detail. Sufficient control is established to develop the biostratigraphy on a regional basis (relating localities separated by up to tens of kilometers) and to interpret occurrence patterns, biochronology, evolutionary histories of lineages, and paleoecological changes in the fauna.

Biochronology

Siwalik faunal assemblages changed through time, and we have documented changes for the Potwar Plateau against its observed chronology. Efforts to analyze change include study of observed ranges (Flynn et al. 1995 for micromammals; Barry et al. 2002; Badgley et al. 2008 for large and small mammals). In these works, we examine change without reference to formation boundaries. Other analyses examine primarily rates of turnover and significance of peaks in turnover (Barry, Flynn, and Pilbeam 1990; Barry et al. 1991; Barry et al. 1995). We are currently working toward an understanding of how representative the observed fossil record is of change in Indian Subcontinent faunal communities of the past, focusing on measures of mammalian diversity, dietary adaptation, and patterns of evolution, immigration, and extinction.

Lowest Stratigraphic Datum

The temporal distributions of abundant taxa reveal paleocommunity change. Recording the appearances of distinctive and more common taxa allows ongoing testing of the observed biostratigraphy: Are observed ranges repeatedly supported? This sort of analysis is most precise if performed at the species level, but genera or taxa of higher rank may also be relevant, particularly if they are immigrants. Based on previous work and building on occurrence data in Barry et al. (2002:appendix 4) and Lindsay et al. (2005), we list a series of observed LSDs (lowest stratigraphic datum) for the Potwar Plateau and Sulaiman area of the Zinda Pir Dome, Pakistan, and date them according to GTS2004 (table 14.1). These LSDs are faunal events, as described by Barry and Flynn (1990); the age assigned to each LSD usually differs slightly from previous designations, partly due to recalibration of the time scale, and to new fossils.

For example, the *Elephas planifrons* datum is extended downward from that perceived by Barry, Lindsay, and Jacobs (1982), following Hussain et al. (1992) to 3.5 Ma (see table 14.1). This is also an example of a datum that coincides approximately with other prominent events—in this case, the entry of Cervidae and *Stegodon* into the Siwalik record. Table 14.1 includes key small

Table 14.1
Lowest Stratigraphic Datums (LSDs) for Selected Mammal Fossils Recorded in Neogene Sediments of the Potwar Plateau and Zinda Pir Dome

Taxon	Age Estimate	Magnetic Chron
Equus sp.	2.6 Ma	chron C2r base
Elephas planifrons	3.5 Ma	chron C2An.3n base
Family Cervidae	3.5 Ma	chron C2An.3n base
Hexaprotodon sivalensis	6.2 Ma	chron C3An.1n bottom
Family Leporidae (*Alilepus*)	7.4 Ma	chron C3Br.3r middle
Hystrix sivalensis	8.1 Ma	chron C4r.1r top
Giraffa punjabiensis	9.1 Ma	chron C4An base
Selenoportax spp.	10.5 Ma	chron C5n.2n middle
Hippotherium s.l.	10.8 Ma	chron C5n.2n lower third
Progonomys hussaini	11.7 Ma	chron C5r.3r top
Sayimys chinjiensis	12.3 Ma	chron C5An.2n middle
Family Gliridae (*Myomimus*)	13.8 Ma	chron C5ACn.1n top
Listriodon pentapotamiae	14.1 Ma	chron C5ACr top
Sayimys sivalensis	15.2 Ma	chron C5Br top
Kochalia geespei	16.1 Ma	chron C5Cn.1n top
Sayimys intermedius (Z122)*	19.0 Ma	chron C5Er lower third
Listriodon guptai (Z124)*	19.1 Ma	chron C6n top
Myocricetodontinae (Z124)*	19.1 Ma	chron C6n top
Prokanisamys arifi (Z126)*	20.1 Ma	chron C6n base
Democricetodon sp. (Z135)*	~22 Ma	?chron C6AAr.1n
Prokanisamys sp. (Z135)*	~22 Ma	?chron C6AAr.1n
Prodeinotherium sp. (Z129)*	~23 Ma	low chron C6Bn
Primus sp. (Z113)*	~23.5 Ma	?below chron C6Br
Prosayimys (Z113)*	~23.5 Ma	?below chron C6Br

*Zinda Pir Dome localities.

SOURCES: Data from Opdyke et al. (1979); Barry, Lindsay, and Jacobs (1982); Hussain et al. (1992); Baskin (1996); Barry et al. (2002); Jacobs and Flynn (2005); Lindsay et al. (2005); Orliac et al. (2010).

mammal appearances, most of which have been presented in previous publications, but ages are refined here. These include Late Miocene appearances of leporids and *Hystrix*, and the Middle Miocene appearance of dormice (Gliridae). Species in a long lineage of ctenodactylid rodents (genus *Sayimys*) are distinctive, as was suggested by de Bruijn, Boon, and Hussain (1989). Key Miocene large-mammal appearances include species of *Listriodon* and *Deinotherium*.

Table 14.1 includes Zinda Pir Dome LSD events that precede the Potwar record. Small mammal sites low in the Vihowa Formation record the appearance of the modern ctenodactyline *Sayimys intermedius* at 19 Ma. Older small mammal LSDs include *Prokanisamys arifi* at about 20 Ma, and the modern grade cricetid *Democricetodon* at Z135, about 22 Ma. We find early *Primus* and *Prosayimys* as old as 23.5 Ma at locality Z113, along with the early spalacid *Eumyarion kowalskii*. If these correlations are correct, then the earlier Oligocene Bugti fauna in the Zinda Pir area, where the diatomyid *Fallomus* is common, would date to about 28.5 Ma (locality Z108 in chron C10n). All first appearances are testable by future field studies in which new localities are placed in dated sections.

Interval Zones and Biochrons

A logical extension of the observed LSD is establishment of biochronological units, after sufficient testing shows the usefulness of key taxa as temporal indicators. Such units are meant to have more widespread time significance, beyond the basin of initial observation, and in the case of the Siwaliks, across a large part of South Asia. Barry, Lindsay, and Jacobs (1982) developed this concept in proposing "interval zones" for upper and middle Siwalik deposits, dating from about 11 Ma to 1 Ma. These were designed as contiguous biostratigraphic interval zones based at that time on mammalian stratigraphic ranges plotted on the N. M. Johnson et al. (1982) paleomagnetic section. The rationale for placing stratigraphic levels into a composite chronologic framework is discussed in Barry et al. (2002:12–14). Siwalik interval zones of Barry, Lindsay, and Jacobs (1982), defined by appearance of the name-sake taxon, include from oldest to youngest (1) the *Hipparion* s.l. interval zone, (2) the *Selenoportax lydekkeri* interval zone, (3) the *Hexaprotodon sivalensis* interval zone, and (4) the *Elephas planifrons* interval zone.

A remaining task is defining the regional extent of the Potwar-based Siwalik biochronology. Biochrons apply to biogeographic provinces and their distinctiveness outside these areas is limited. Siwalik biochrons likely apply throughout the Indian Subcontinent and eastward, with diminishing relevance, toward Myanmar, Thailand, and South China (Yunnan; see Dong and Qi, chapter 11, and Chavasseau et al., chapter 19, both this volume). This region presages the modern Oriental Biogeographic Province. Its boundary is distinct northward where it is defined by mountains. In China, the northern limit of the Oriental Biogeographic Province is less distinct and was inconstant through time, although major rivers played a role. Mountains and aridity are also westward barriers that separate the Oriental province from a distinct Eurasian biogeographic province. During the Late Miocene, this Eurasian province to the west had characteristic vertebrate assemblages, the Pikermian chronofauna (Eronen et al. 2009), which contrasted with Siwalik faunas.

Modes of Deposition and Preservation

Careful attention to microstratigraphy by Badgley (1986a), Behrensmeyer (1987), and Behrensmeyer et al. (2007) showed that vertebrate fossils are frequently associated with a subset of fluvial deposits, especially the fillings of abandoned channels. These low-lying settings adjacent to major streams were characterized by rapid but gentle burial in a protected, well-watered habitat. They preserved time-averaged (on a scale up to thousands of years) vertebrate assemblages sampled from local paleocommunities. One ongoing line of inquiry is the degree of taxonomic variation present in contemporaneous assemblages, both from similar and different sub-habitats. Assuming that the better-sampled assemblages represent local communities, how do taxon associations vary among similar age fossil sites, and is this variation correlated to depositional regime or other ecological factors (e.g., scale of the abandoned channel swale or distance from a major channel)?

Some intermittently flooded settings preserved small mammals abundantly, and these settings are highly comparable throughout the Siwalik sequence, since they repeatedly sample similar environments of deposition (Badgley, Downs, and Flynn 1998). We think they recorded community composition (and possibly relative abundances) with reasonable faithfulness. Small mammal sites are characterized by disassociated, isolated teeth plus occasional jaws and postcrania. The high frequency of isolated teeth suggests a period of subaerial exposure after concentration of small mammal remains by predators and local effects of gentle currents and pooling of water. In some cases, teeth appear to indicate origin from the same individual, but usually this cannot be demonstrated conclusively. Therefore, MNI (minimum number of individuals) underestimates actual numbers of individuals represented in these paleofaunas.

Through paleomagnetic control, Behrensmeyer (1987) showed that Chinji through Dhok Pathan formation net accumulation rates of sediment increased from 14 to 50 cm/kyr, with correlated change in dominant depositional sources and in fossil productivity. Microstratigraphic control laterally over kilometers allowed Behrensmeyer (1987) to trace individual paleosols with great precision and show that laterally equivalent fossil concentrations had consistent relationships to the soils and were essentially contemporaneous within estimated time spans of 10^3–10^4 yr. Applying sediment accumulation rates calculated from magnetozone thickness, she estimated that durations of individual paleosols averaged no more than 24 kyr. Therefore, reworking of remains accumulated on or in these soils into contemporaneous fluvial channel deposits would represent <24 kyr of time averaging.

Habitat Change and Stable Isotopes

Combining stable isotope geochemistry with precisely controlled stratigraphy and fossil provenance, Quade and Cerling (1995) and Cerling et al. (1997) documented a major shift in carbon isotopes derived from a shift from C3 to C4 plant dominance in the late Miocene Siwaliks, which led to its detection elsewhere on a global scale. The change was initially tracked in soil carbonate nodules, from which both carbon and oxygen isotopes can be extracted and analyzed for paleoclimatic signals. The carbon shift was also recognized in the dental enamel of ungulates, which tracks the dominant vegetation type of the paleohabitat. Vegetation changed in the late Miocene from forest to grassland, and this was reflected in carbon isotopes of both soils and teeth. However, mammalian enamel shows a complex range of diets across the paleohabitat (Morgan, Kingston, and Marino 1994; Barry et al. 2002). Painstaking lateral sampling of sections across the late Miocene carbon shift in the Rohtas Anticline showed that vegetation change was slow and patchy, not sudden and monotonic (Behrensmeyer et al. 2007). Lateral variation in carbon isotopes from large herbivorous mammals sampled across the landscape at about 9.2 Ma (Morgan et al. 2009) provides evidence for an environmental gradient prior to the main shift to C4 plants. This gradient indicates lateral variation in soil moisture and, presumably, dominant plant types of the paleohabitat over tens of kilometers. The consistent association of carbon-isotope values with location on the floodplain implies strong site fidelity during the lifetimes of mammalian ungulates and hominoids (they did not disperse far during their lives).

Isotopic changes in carbonate nodules within the Siwalik paleosols intensified, especially in the interval between 6 Ma and 10 Ma, where $\delta^{13}C$ values record a significant shift in vegetation and habitat. More recent analyses, again made possible only by high-resolution spatial and stratigraphic control of fossil localities against the paleomagnetic time scale, have shown a relationship between regional vegetation change and faunal turnover. Barry et al. (2002) analyzed sustained faunal change over the million years of vegetational shift from dominantly C_3, to mixed C_3/C_4, to dominantly and then exclusively C_4. The change was found to coincide with a peak in faunal turnover. Badgley et al. (2008) took the analysis further to show that dietary preference determined the sequence of lineage extinctions during the vegetational transition. Isotopic evidence from mammalian herbivores showed that in some lineages (e.g., the anthracothere *Merycopotamus* or hipparionine equids) the predominant vegetation in the diet shifted from C_3 to C_4; other taxa such as frugivores feeding exclusively on C_3 plants (e.g., the ape *Sivapithecus* or tragulid artiodactyls) declined in abundance or disappeared.

Change at Faunal and Lineage Levels

Precise biostratigraphy with age control has made study of trends on the scale of 10^5 yr possible for the Siwaliks. Barry et al. (1985) related initial observations on faunal turnover to sea-level curves, proposing that some of the turnover pattern reflected immigration at low sea-level stands. Later studies (Barry, Flynn, and Pilbeam 1990; Barry et al. 1991; Barry et al. 1995; Barry et al. 2002) refined the scale of analysis to distinguish trends in species richness and pulses of appearances (mostly immigration) and extinction on the Potwar Plateau. Peaks in appearances and extinction were separated by longer intervals of low rates of change and did not always coincide. In some cases, elevated rates of change appeared to coincide with global climatic events, but their timing was not always clearly linked to events as then recognized. Given improved understanding of global changes in the marine record (Zachos et al. 2001), we are now reexamining possible correlations, particularly the effects of dramatic cooling on terrestrial faunas at about 14 Ma.

Siwalik data have the potential of resolving macroevolutionary issues in paleobiology. For this subtropical Miocene setting, species properties intrinsic to taxa distinguished by body size may be emerging. Flynn et al. (1995) evaluated lineage duration (residence time) in relation to environmental change and showed that small mammals had shorter species durations than did large mammals in the Siwalik data set. Morgan et al. (1995) examined size increase across taxa, large and small, during the later Miocene, concluding that changes were climatically driven and likely reflected within-group competition.

Flynn et al. (1998) expanded the analysis of trends in species richness in small mammal assemblages throughout the Siwaliks and found evidence for high diversity in the middle Miocene, higher than expected in modern faunas at the same latitude. Faunal change after 11 Ma included decline in species richness over time and suggested that late Miocene species generally had shorter temporal ranges than middle Miocene species (Flynn et al. 1995). The biotic signal in the fossil record, therefore, includes evidence that diversity patterns in deep time differed from those observed today and that rates of species turnover during the Cenozoic (typical longevities observed in lineages) were not constant.

Our agenda of research is targeted at deriving the highest level of precision achievable from the Siwalik biotic record. This level of refinement bridges the gulf between macroevolutionary patterns and microevolutionary processes (cf. Reznick and Ricklefs 2009). We cannot capture actual records of microevolution of species transforming into one or more descendants (except possibly for extraordinary brief stratigraphic intervals), but we can garner data relevant to the microevolutionary process by observing change in intraspecific character variation (e.g., dental variation) in successive populations.

Fine-scale biostratigraphy and dense fossil sampling provide the raw materials for phylogenetic analysis and for interpretation of the tempo and mode of evolutionary processes that are manifested in phenotypic change. Stasis in tooth size and morphology dominated the histories of most lineages of small mammals—for example, species of the primitive bamboo rat genus *Kanisamys*, in which crown height changed in punctuated events after long periods of stability (Flynn 1986; Flynn et al. 1995). More gradual change is evident in other rodents (Flynn 1985).

The Siwaliks fortuitously preserve fossils that show the pattern and timing of the origin and initial diversification of murine and other rodent groups. Multiple superposed small mammal assemblages in the Chinji Formation capture the mode of acquisition of the murine synapomorphy (a third row of cusps on upper molars), and younger sites show diversification with this novelty.

Jacobs and Flynn (2005) extended previous work (Jacobs and Downs 1994) to constrain the timing of murine evolution. This fossil record not only sets minima for dates of genetic splitting but also indicates maxima beyond which certain splits are unlikely. For the *Mus–Rattus* split, for example, an age greater than 12 Ma is highly unlikely because the only ancestor of that age evident in the fossil record from anywhere in the world is *Antemus*, clearly a primitive murine. This age is consistent with the molecular estimate of Steppan, Adkins, and Anderson (2004); a younger age for this split (10–11 Ma) is quite conceivable from the viewpoint of the fossil record.

CONCLUSION

The Siwalik Group is a thick and laterally expansive wedge of sub-Himalayan nonmarine clastic deposits best developed in the northern Indian Subcontinent, extending southeastward through Nepal and into Assam. The Siwaliks span the Neogene, but the most fossiliferous parts are late Early Miocene to Pliocene in age. Temporal equivalents and older deposits occur southward in Pakistan toward distal parts of the clastic wedge. Pliocene deposits are best developed in northern India. Biostratigraphies and age control are refined to the scale of 10^5 yr, thanks to a relatively complete sedimentary record conducive to paleomagnetic analysis.

The Siwaliks are not only a long, continuous sequence, but they are characterized by abundant, superimposed fossiliferous strata that invite analyses of fossil productivity correlated to depositional setting and lithology. Most productive fossil sites of similar age in the Siwaliks yield comparable assemblages because they derive from generally similar depositional regimes: floodplain settings often affiliated with crevasse splay deposits and fine-grained filling of abandoned channels.

Because the Siwaliks record successive faunal assemblages, the sequence invites biochronological analysis. We use interval zones to demarcate times characterized by key taxa. The Siwalik biogeographic province is South Asian in scale, from Pakistan and India on the west, to Yunnan in the east, where the biogeographic identity weakens. This province, a predecessor of the Oriental Biogeographic Province, is sharply bounded by mountains and high elevations to the north, and mountainous, dry habitat to the west.

The rich scale of fossil representation in the Siwaliks, its temporal duration, and its high density of fossil levels in many intervals, make the sequence an ideal laboratory for examining the evolution of terrestrial vertebrates. Data are relevant for both macroevolutionary phenomena and for finer scale issues, those that form a bridge to microevolution. Observations at the macroevolutionary level concern faunal composition, species richness, longevity patterns, turnover, and size trends. Data reflecting microevolutionary processes include changing frequencies of characters within successive samples of single lineages, which approximate transformation of the phenotype. Given tight temporal control, the Siwalik sequence is relevant for constraining various aspects of the evolutionary time scale, specifically estimating times of lineage splitting.

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REFERENCES

Azzarolli, A. and G. Napoleone. 1981. Magnetostratigraphic investigation of the Upper Sivaliks near Pinjor, India. *Rivista Italiana di Paleontoligia e Stratigrafia* 87(4):739–762.

Badgley, C. 1986a. Taphonomy of mammalian fossil remains from Siwalik rocks of Pakistan. *Paleobiology* 12:119–142.

Badgley, C. 1986b. Counting individuals in mammalian fossil assemblages from fluvial environments. *Palaios* 1:328–338.

Badgley, C., J. C. Barry, M. E. Morgan, S. V. Nelson, A. K. Behrensmeyer, T. E. Cerling, and D. Pilbeam. 2008. Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing. *Proceedings of the National Academy of Sciences* 105(34):12145–12149.

Badgley, C. and A. K. Behrensmeyer. 1995. Preservational, paleoecological, and evolutionary patterns in the Paleogene of Wyoming—Montana and the Neogene of Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 115:319–340.

Badgley, C., W. Downs, and L. J. Flynn. 1998. Taphonomy of small-mammal fossil assemblages from the middle Miocene Chinji Formation, Siwalik Group, Pakistan. In *Advances in Vertebrate Paleontology and Geochronology*, ed. Y. Tomida, L. J. Flynn, L. L. Jacobs, pp. 145–166. National Science Museum Monograph 14. Tokyo: National Science Museum.

Barry, J. C. and L. J. Flynn. 1990. Key Biostratigraphic Events in the Siwalik Sequence. In *European Neogene Mammal Chronology*, ed. E. H. Lindsay, V. Fahlbusch, and P. Mein, 557–571. New York: Plenum Press.

Barry, J. C., L. J. Flynn, and D. Pilbeam. 1990. Faunal diversity and turnover in a Miocene terrestrial sequence. In *Causes of Evolution: A Paleontological Perspective*, ed. R. M. Ross and W. D. Allmon, pp. 381–421. Chicago: University of Chicago Press.

Barry, J. C., N. M. Johnson, S. M. Raza, and L. L. Jacobs. 1985. Neogene mammalian faunal change in southern Asia: Correlations with climatic, tectonic and eustatic events. *Geology* 13:637–640.

Barry, J. C., E. H. Lindsay, and L. L. Jacobs. 1982. A biostratigraphic zonation of the Middle and Upper Siwaliks of the Potwar Plateau of northern Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37:95–130.

Barry, J. C., M. E. Morgan, L. J. Flynn, D. Pilbeam, A. K. Behrensmeyer, S. Mahmood Raza, A. Imran Khan, C. Badgley, J. Hicks, and J. Kelley. 2002. Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. *Paleobiology* Memoir 3:1–71.

Barry, J. C., M. E. Morgan, L. J. Flynn, D. Pilbeam, L. L. Jacobs, E. H. Lindsay, S. Mahmood Raza, and N. Solounias. 1995. Patterns of faunal turnover and diversity in the Neogene Siwaliks of northern Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 115:209–226.

Barry, J. C., M. E. Morgan, A. J. Winkler, L. J. Flynn, E. H. Lindsay, L. L. Jacobs, and D. Pilbeam. 1991. Faunal interchange and Miocene terrestrial vertebrates of southern Asia. *Paleobiology* 17(3):231–245.

Baskin, J. A. 1996. Systematic revision of Ctenodactylidae (Mammalia, Rodentia) from the Miocene of Pakistan. *Palaeovertebrata* 25:1–49.

Basu, P. K., 2004. Siwalik mammals of the Jammu Sub-Himalaya, India: An appraisal of their diversity and habitats. *Quaternary International* 117:105–118.

Behrensmeyer, A. K. 1987. Miocene fluvial facies and vertebrate taphonomy in northern Pakistan. *Society of Economic Paleontologists and Mineralogists, Special Publication* 39:169–176.

Behrensmeyer, A. K., J. Quade, T. E. Cerling, J. Kappelman, I. A. Khan, P. Copeland, L. Roe, J. Hicks, P. Stubblefield, B. J. Willis, and C. Latorre. 2007. The structure and rate of late Miocene expansion of C4 plants: Evidence from lateral variation in stable isotopes in paleosols of the Siwalik Group, northern Pakistan. *Geological Society of America Bulletin* 119:1486–1505.

Behrensmeyer, A. K. and L. Tauxe 1982. Isochronous fluvial systems in Miocene deposits of northern Pakistan. *Sedimentology* 29:331–352.

Bhandari, A., D. M. Mohabey, S. Bajpai, B. N. Tiwari, and M. Pickford. 2009. Early Miocene mammals from central Kutch (Gujarat), Western India: Implications for geochronology, biogeography, eustacy and intercontinental dispersals. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 256(1):69–97.

Cautley, P. T. and H. Falconer, 1835. Synopsis of fossil genera and species from the upper deposits of the Tertiary strata of the Siválik Hills, in the collection of the authors. *Journal of the Asiatic Society* 4:706–707.

Cerling, T. E., J. M Harris, B. J. MacFadden, M. G. Leakey, J. Quade, V. Eisenmann, and J. R. Ehleringer. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389:153–158.

Cheema, I. U., L. J. Flynn, and A. R. Rajpar. 2003. Late Pliocene murid rodents from Lehri, Jhelum District, northern Pakistan. In *Advances in Vertebrate Paleontology "Hen to Panta": A Tribute to Constantin Rădulescu and Petre Mihai Samson*, ed. A. Petculescu and E. Ştiudcă, pp. 85–92. Bucharest: Roumanan Academy Emil Racovită Institute of Speleology.

Cheema, I. U., S. Mahmood Raza, and L. J. Flynn. 1997. Note on Pliocene small mammals from the Mirpur District, Azad Kashmir, Pakistan. *Géobios* 30:115–119.

Cheema, M. R., S. M. Raza, and H. Ahmed. 1977. Cainozoic. In *Stratigraphy of Pakistan*, ed. S. M. I. Shah. *Memoirs of the Geological Survey of Pakistan* 12:56–98.

Colbert, E. H. 1935. Siwalik mammals in the American Museum of Natural History. *Transactions of the American Philosophical Society* 27:1–401.

Corvinus, G. and L. N. Rimal. 2001. Biostratigraphy and geology of the Neogene Siwalik Group of the Surai Khola and Rato Khola areas in Nepal. *Palaeogeography, Palaeoclimatology, Palaeoecology* 165:251–279.

Cox, A., R. R. Doell, and G. B. Dalrymple. 1963. Geomagnetic Polarity Epochs and Pleistocene Geochronometry. *Nature* 198 (4885):1049–1051.

de Bruijn, H., E. Boon, and S. T. Hussain. 1989. Evolutionary trends in *Sayimys* (Ctenodactylidae, Rodentia) from the Lower Manchar Formation (Sind, Pakistan). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* B92(3):191–214.

de Bruijn, H. and S. Taseer Hussain. 1984. The succession of rodent faunas from the lower Manchar Formation, southern Pakistan, and its relevance for the biostratigraphy of the Mediterranean Miocene. Montpellier: *Paléobiologie Continentale* 14(2):191–204.

de Bruijn, H., S. Taseer Hussain, and J. J. M. Leinders. 1981. Fossil rodents from the Murree Formation near Banda Daud Shah, Kohat, Pakistan. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* B84(1):71–99.

Downing, K. F., E. H. Lindsay, W. R. Downs, and S. E. Speyer. 1993. Lithostratigraphy and vertebrate biostratigraphy of the Early Miocene Himalayan Foreland, Zinda Pir Dome, Pakistan. *Sedimentary Geology* 87:25–37.

Eronen, J. T., M. Mirzaie Ataabadi, A. Micheels, A. Karme, R. L. Bernor, and M. Fortelius. 2009. Distribution history and climatic controls of the Late Miocene Pikermian chronofauna. *Proceedings of the National Academy of Sciences* 106(29):11867–11871.

Falconer, H. 1845. Description of some fossil remains of *Dinotherium*, giraffe, and other Mammalia, from the Gulf of Cambay, western coast of India, chiefly from the collection presented by Captain Fulljames of the Bombay Engineers. *Quarterly Journal of the Geological Society of London* 1:356–372

Flynn, L. J. 1985. Evolutionary patterns and rates in Siwalik Rhizomyidae. In *Acta Zoologica Fennica* 170:140–144.

Flynn, L. J. 1986. Species longevity, stasis, and stairsteps in rhizomyid rodents. In *Vertebrates Phylogeny, and Philosophy: Contributions to Geology*, ed. K. M. Flanagan and J. A. Lillegraven, pp. 273–285. Special Paper 3. Laramie: University of Wyoming.

Flynn, L. J., J. C. Barry, M. E. Morgan, D. Pilbeam, L. L. Jacobs, and E. H. Lindsay. 1995. Neogene Siwalik mammalian lineages: Species longevities, rates of change, and modes of speciation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 115:249–264.

Flynn, L. J., W. Downs, M. E. Morgan, J. C. Barry, and D. Pilbeam. 1998. High Miocene species richness in the Siwaliks of Pakistan. In *Advances in Vertebrate Paleontology and Geochronology*, ed. Y. Tomida, L. J. Flynn, and L. L. Jacobs, pp. 167–180. National Science Museum Monograph 14. Tokyo: National Science Museum.

Flynn, L. J., and M. E. Morgan. 2005. New lower Primates from the Miocene Siwaliks of Pakistan. In *Interpreting the Past: Essays on Human, Primate, and Mammal Evolution in Honor of David Pilbeam*, ed. D. E. Lieberman, R.J. Smith, and J. Kelley, pp. 81–101. American School of Prehistoric Research Monograph 5. Boston: Brill.

Flynn, L. J., D. Pilbeam, L. L. Jacobs, J. C. Barry, A. K. Behrensmeyer, and J. W. Kappelman. 1990. The Siwaliks of Pakistan: Time and faunas in a Miocene terrestrial setting. *Journal of Geology* 98:589–604.

Friedman, R., J. Gee, L. Tauxe, K. Downing, and E. Lindsay. 1992. The magnetostratigraphy of the Chitarwata and lower Vihowa Formations of the Dera Ghazi Khan area, Pakistan. *Sedimentary Geology* 81:253–268.

Gould, S. J. 1985. The paradox of the first tier: An agenda for paleobiology. *Paleobiology* 11:2–12.

Gradstein, F. M., J. G. Ogg, and A. G. Smith. 2004. *A Geologic Time Scale 2004*. Cambridge: Cambridge University Press.

Gupta, S. S. and G. V. R. Prasad. 2001. Micromammals from the Upper Siwalik subgroup of the Jammu region, Jammu and Kashmir State, India: Some constraints on age. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 220(2):153–187.

Gupta, S. S. and B. C. Verma. 1988. Stratigraphy and vertebrate fauna of the Siwalik Group, Mansar-Uttarbaini section, Jammu District, J&K. *Journal of the Palaeontological Society of India* 33:117–124.

Hemphill, W. R. and A. H. Kidwai. 1973. Stratigraphy of the Bannu and Dera Ismail Khan areas, Pakistan. *U.S. Geological Survey Professional Paper* 716B:1–36.

Hoorn, C., T. Ohja, and J. Quade. 2000. Palynological evidence for vegetation development and climatic change in the Sub-Himalayan Zone (Neogene, Central Nepal). *Palaeogeography, Palaeoclimatology, Palaeoecology* 163:133–161.

Hussain, S. T. 1971. Revision of *Hipparion* (Equidae, Mammalia) from the Siwalik Hills of Pakistan and India. *Abhandlungen Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse (Neue Folge)* 147:1–68.

Hussain, S. T., G. D. van den Bergh, K. J. Steensma, J. A. de Visser, J. de Vos, M. Arif, J. van Dam, P. Y. Sondaar, and S. B. Malik. 1992. Biostratigraphy of the Plio-Pleistocene continental sediments (Upper Siwaliks) of the Mangla-Samwal Anticline, Asad Kashmir, Pakistan. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* 95:65–80.

Jablonski, D. 2008. Biotic interactions and macroevolution: Extensions and mismatches across scales and levels. *Evolution* 62:715–739.

Jacobs, L. L. 1978. Fossil rodents (Rhizomyidae and Muridae) from Neogene Siwalik deposits, Pakistan. *Museum of Northern Arizona Press Bulletin Series* 52:1–103.

Jacobs, L. L., and W. Downs. 1994. The Evolution of murine rodents in Asia. In *Rodent and Lagomorph Families of Asian Origins and Diversification*, ed. Y. Tomida, C. Li, and T. Setoguchi, pp. 149–156. National Science Museum Monograph 8. Tokyo: National Science Museum.

Jacobs, L. L., and L. J. Flynn. 2005. Of mice . . . again: The Siwalik rodent record, murine distribution, and molecular clocks. In *Interpreting the Past: Essays on Human, Primate, and Mammal Evolution in Honor of David Pilbeam*, ed. D. E. Lieberman, R. J. Smith, and J. Kelley, pp. 63–80. American School of Prehistoric Research Monograph 5. Boston: Brill.

Johnson, G. D., N. M. Johnson, N. D. Opdyke, and R. A. K. Tahirkheli. 1979. Magnetic reversal stratigraphy and sedimentary tectonic history of the Upper Siwalik group, eastern Salt Range and southwestern Kashmir. In *Geodynamics of Pakistan*, ed. A. Farah and K. A. de Jong, pp. 149–165. Memoirs of the Geological Survey of Pakistan 11. Islamabad: Geological Survey of Pakistan.

Johnson, G. D., N. D. Opdyke, S. K. Tandon, and A. C. Nanda. 1983. The magnetic polarity stratigraphy of the Siwalik Group at Haritalyangar (India) and a new last appearance datum for *Ramapithecus* and *Sivapithecus* in Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 44:223–249.

Johnson, G. D., P. Zeitler, C. W. Naeser, N. M. Johnson, D. M. Summers, C. D. Frost, N. D. Opdyke, and R. A. K. Tahirkheli. 1982. The occurrence and fission-track ages of late Neogene and Quaternary volcanic sediments, Siwalik Group, Northern Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37:63–93.

Johnson, N. M., N. D. Opdyke, G. D. Johnson, E. H. Lindsay, and R. A. K. Tahirkheli. 1982. Magnetic polarity stratigraphy and ages of Siwalik Group rocks of the Potwar Plateau, Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37:17–42.

Johnson, N. M., J. Stix, L. Tauxe, P. F. Cerveny, and R. A. K. Tahirkheli. 1985. Paleomagnetic chronology, fluvial processes, and tectonic implications of the Siwalik deposits near Chinji Village, Pakistan. *Journal of Geology* 93:27–40.

Khan, I. A. 1995. Complexity in stratigraphic division of fluviatile successions. *Pakistan Journal of Mineral Sciences* 7:23–34.

Kotlia, B. S. 1990. Large mammals from the Plio-Pleistocene of Kashmir Intermontane Basin, India, with reference to their status in magnetic polarity time scale. *Eiszeitalter und Gegenwart* 40:38–52.

Kotlia, B. S. and W. von Koenigswald. 1992. Plio-Pleistocene arvicolids (Rodentia, Mammalia) from Kashmir Intermontane Basin, Northwestern India. *Palaeontolgraphica* A223:103–135.

Kumar, K. and S. Kad. 2002. Early Miocene cricetid rodent (Mammalia) from the Murree Group of Kalakot, Rajauri District, Jammu and Kashmir, India. *Current Science* 82(6):736–740.

Kumar, K., A. C. Nanda, and B. N. Tiwari. 1996. Rodents from the Oligo-Miocene Kargil Formation, Ladakh, India: Biochronologic and paleobiogeographic implications. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 202(3):383–407.

Lewis, G. E. 1937. A new Siwalik correlation (India). *American Journal of Science*, 5th ser., 33:191–204.

Lindsay, E. H., L. J. Flynn, I. U. Cheema, J. C. Barry, K. F. Downing, A. R. Rajpar, and S. Mahmood Raza. 2005. Will Downs and the Zinda Pir Dome. *Palaeontologia Electronica* 8(1)19A:1–19, 1MB; http:palaeo-electronica.org/toc.htm.

Lourens, L., F. Hilgen, N. J. Shackleton, J. Laskar, and D. Wilson. 2004. The Neogene Period. In *A Geologic Time Scale*, ed. F. Gradstein, J. Ogg, and A. Smith, pp. 409–440. Cambridge: Cambridge University Press.

Mankinen, E. A. and G. D. Dalrymple. 1979. Revised geomagnetic polarity time scale for the interval 0–5 m.y. B.P. *Journal of Geological Research* 84:615–626.

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Marivaux, L. and J.-L. Welcomme. 2003. New diatomyid and baluchimyine rodents from the Oligocene of Pakistan (Bugti Hills, Balochistan): Systematic and paleobiogeographic implications. *Journal of Vertebrate Paleontology* 23(2):420–434.

Mascle, G. and G. Hérail. 1982. Les Siwaliks: le prisme d'accrétion tectonique associé à la seduction intracontinentale himalayenne. *Géologie Alpine* 58:95–103.

Medlicott, H. B. 1864. On the geological structure and relations of the southern portions of the Himalayan ranges between the Rivers Ganges and Ravee. *Memoirs of the Geological Survey of India* 3(4):1–206.

Morgan, M. E., C. Badgley, G. F. Gunnell, P. D. Gingerich, J. W. Kappelman, and M. C. Maas. 1995. Comparative paleoecology of Paleogene and Neogene mammalian faunas: Body-size structure. *Palaeogeography, Palaeoclimatology, Palaeoecology* 115:287–317.

Morgan, M. E., A. K. Behrensmeyer, C. Badgley, J. C. Barry, S. Nelson, and D. Pilbeam. 2009. Lateral trends in carbon isotope ratios reveal a Miocene vegetation gradient in the Siwaliks of Pakistan. *Geology* 37(2):103–106.

Morgan, M. E., J. D. Kingston, and B. D. Marino. 1994. Carbon isotopic evidence for the emergence of C4 plants in the Neogene from Pakistan and Kenya. *Nature* 367:162–165.

Nanda, A. C. and A. Sahni. 1998. Ctenodactyloid rodent assemblage from Kargil Formation, Ladakh molasse group: Age and palaeobiogeographic implications for the Indian Subcontinent in the Oligo-Miocene. *Géobios* 31(4):533–544.

Opdyke, N. D., E. Lindsay, G. D. Johnson, N. Johnson, R. A. K. Tahirkheli, and M. A. Mirza. 1979. Magnetic polarity stratigraphy and vertebrate paleontology of the Upper Siwalik Subgroup of Northern Pakisatan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 27:1–34.

Orliac, M. J, P.-O. Antoine, G. Roohi, and J.-L. Welcomme. 2010. Suoidea (Mammalia, Cetartiodactyla) from the Early Oligocene of the Bugti Hills, Balochistan, Pakistan. *Journal of Vertebrate Paleontology* 30(4):1300–1305.

Patnaik, R. 1994. Find of a *Ramapithecus punjabicus* premolar from a palaeosol unit exposed near Village Dangar, Dist. Bilaspur, HP. *Current Science* 67(7):538–539.

Patnaik, R., G. L. Badam, and M. L. K. Murty. 2008. Additional vertebrate remains from one of the Late Pleistocene-Holocene Kurnool Caves (Muchchatla Chintamanu Gavi) of South India. *Quaternary International* 192:43–51.

Pilbeam, D., M. Morgan, J. C. Barry, and L. J. Flynn. 1996. European MN units and the Siwalik faunal sequence in Pakistan. In *The Evolution of Western Eurasian Neogene Mammal Faunas*, ed. R. L. Bernor, V. Fahlbusch, and H.-W. Mittman, pp. 96–105. New York: Columbia University Press.

Pilgrim, G. E. 1912. The vertebrate fauna of the Gaj Series in the Bugti Hills and the Punjab. *Geological Survey of India Memoirs, Palaeontologia Indica*, n. s., 4(2):1–83.

Pilgrim, G.E. 1913. The correlation of the Siwaliks with mammal horizons of Europe. *Records of the Geological Survey of India* 43:264–326.

Pilgrim, G. E. 1926. The fossil Suidae of India. *Memoirs of the Geological Survey of India*, n. s., 8:1–65.

Pilgrim, G. E. 1934. Correlation of the ossiferous sections in the Upper Cenozoic of India. *American Museum of Natural History Novitates* 704:1–5.

Pillans, B., M. Williams, C. Cameron, R. Patnaik, J. Hogarth, A. Sahni, J. C. Sharma, F. Williams, and R. L. Bernor. 2005. Revised correlation of the Haritalyangar magnetostratigraphy, Indian Siwaliks: Implications for the age of the Miocene hominids *Indopithecus* and *Sivapithecus*, with a note on a new hominid tooth. *Journal of Human Evolution* 48:507–515.

Prasad, K. N. 1968. The vertebrate fauna from the Siwalik beds of Haritalyangar, Himachal Pradesh. *Palaeontologia Indica* (New Series) 39:1–55.

Quade, J. and T. E. Cerling. 1995. Expansion of C_4 grasses in the Late Miocene of northern Pakistan: Evidence from stable isotopes in paleosols. In *Long Records of Continental Ecosystems*, ed. C. Badgley and A. K. Behrensmeyer, pp. 91–116. *Palaeogeography, Palaeoclimatology, Palaeoecology* 115.

Rajpar, A. R. 1993. Taphonomy of a Pliocene Quarry in the Upper Siwalik, near Mirpur, Azad Jammu Kashmir. *Pakistan Journal of Zoology* 25(3):243–247.

Ranga Rao, A. 1993. Magnetic-polarity stratigraphy of Upper Siwalik of north-western Himalayan foothills. *Current Science* 64(11–12):863–873.

Raza, S. M., J. C. Barrry, G. E. Meyer, and L. Martin. 1984. Preliminary report on the geology and vertebrate fauna of the Miocene Manchar Formation, Sind, Pakistan. *Journal of Vertebrate Paleontology* 4:584–599.

Raza, S. M., I. U. Cheema, W. R. Downs, A. R. Rajpar, and S. C. Ward. 2002. Miocene stratigraphy and mammal fauna from the Sulaiman Range, Southwestern Himalayas, Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 186:185–197.

Reznick, D. N. and R. E. Ricklefs. 2009. Darwin's bridge between microevolution and macroevolution. *Nature* 457:837–842.

Sahni, A. and H. C. Mitra. 1980. Neogene paleobiogeography of the Indian Subcontinent with special reference to fossil vertebrates. *Journal of Human Evolution* 31:39–62.

Steensma, K. J. and S. Taseer Hussain. 1992. *Merycopotamus dissimilis* (Artiodactyla, Mammalia) from the Upper Siwalik Subgroup and its affinities with Asian and African forms. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* 95(1):97–108.

Steppan, S. J., R. M. Adkins, and J. Anderson. 2004. Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. *Systematic Biology* 53(4):533–553.

Tandon, S. K., R. Kumar, M. Koyama, and N. Niitsuma. 1984. Magnetic polarity stratigraphy of the Upper Siwalik subgroup, east of Chandigarh, Punjab, Sub-Himalaya, India. *Journal of the Geological Society of India* 25(1):45–55.

Tauxe, L. and N. D. Opdyke. 1982. A time framework based on magnetostratigraphy for the Siwalik sediments of the Khaur area, northern Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37:43–61.

van der Made, J. and S. Taseer Hussain. 1992. Sanitheres from the Miocene Manchar Formation of Sind, Pakistan, and remarks on sanithere taxonomy and stratigraphy. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* 95(1):81–95.

Vickary, N. 1846. Geological report on a portion of the Baluchistan Hills. *Quarterly Journal of the Geological Society of London* 2:260–265.

Welcomme, J-L., M. Benammi, J-Y. Crochet, L. Marivaux, G. Metais, P-O. Antoine, and Ibrahim Baloch. 2001. Himalayan forelands: Paleontological evidence for Oligocene detrital deposits in the Bugti Hills (Balochistan, Pakistan). *Geological Magazine* 138(4):397–405.

Welcomme, J.-L., L. Marivaux, P.-O. Antoine, and M. Bennami. 1999. Mammifères fossiles des collines Bugti (Balochistan, Pakistan): Nouvelles données. *Bulletin Société Histoire Naturelle, Toulouse* 135:135–139.

Wessels, W. 2009. Miocene rodent evolution and migration: Muroidea from Pakistan, Turkey, and northern Africa. *Geologica Ultraiectina* 307:1–290.

Wessels, W. and H. de Bruijn. 2001. Rhizomyidae from the Lower Manchar Formation (Miocene, Pakistan). *Annals of Carnegie Museum* 70:143–168.

West, R. M., J. H. Hutchinson, and J. Munthe. 1991. Miocene vertebrates from the Siwalik Group, western Nepal. *Journal of Vertebrate Paleontology* 11(1):108–129.

Willis, B. J. 1993. Evolution of Miocene fluvial systems in the Himalayan foredeep through a two kilometer-thick succession in northern Pakistan. *Sedimentary Geology* 88:77–121.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to Present. *Nature* 292:686–693.