General palaeontology, systematics and evolution

Siwalik synopsis: A long stratigraphic sequence for the Later Cenozoic of South Asia

Synopsis Siwalik : longue succession stratigraphique du Cénozoïque moyen et tardif de l'Asie du Sud

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ABSTRACT

The Tertiary sediments of northern Pakistan are an exceptional record of terrestrial sedimentation and represent most of Neogene time. Foremost is the Siwalik Group of the Potwar Plateau, for which multiple, superposed fossil levels span ∼18–6 Ma. Well-developed magnetostratigraphic control provides secure dating so that Siwalik fossil horizons may be interpolated into a time scale with resolution to 100,000 years. We describe the geographic setting of the Potwar, give an overview of the temporal distribution of faunas, and discuss changes in paleohabitat and paleoecology with coinciding faunal change, as seen from the Siwalik viewpoint. The long Siwalik biostratigraphy of many successive assemblages with its resolved time scale may be compared directly with other well-dated sequences. Immigrant arrival and timing of faunal change may be traced. The basins of the Iberian Peninsula show somewhat different timing of introduction of hipparionine horses, and faunal turnover in the Siwaliks clearly precedes the Vallesian crisis in Spain. In contrast to the increasingly seasonal precipitation of the late Miocene Potwar, the paleohabitat of coeval North China appears to have been moist and equable, with high diversity faunas. Continued development and comparison of resolved Neogene records allow increasing resolution of the patterns of faunal change on regional to global levels.

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RÉSUMÉ

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Les sédiments tertiaires du Pakistan septentrional constituent un registre exceptionnel de la sédimentation continentale et représentent la plus grande partie du Néogène. Le groupe Siwalik du plateau du Potwar, en particulier, comporte de multiples niveaux fossilifères entre environ 18 et 6 Ma. Un contrôle magnétostratigraphique approfondi étaie la datation, si bien que les horizons fossilifères Siwalik peuvent être interpolés dans une échelle de temps à la résolution de 100 000 ans. Nous décrivons le cadre géographique du Potwar,

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donnons une vue d'ensemble de la distribution des faunes dans le temps et discutons les changements d'habitat et de paléoécologie coïncidant avec un changement dans la faune du groupe Siwalik. La longue biostratigraphie Siwalik de multiples assemblages successifs, avec son échelle de temps résolue, peut être comparée directement avec d'autres séquences bien datées. L'arrivée d'immigrants et le moment où se produit le changement faunique peuvent être retracés. Les bassins de la péninsule Ibérique indiquent un temps quelque peu différent pour l'introduction des chevaux hipparioninés, et le *turnover* faunique dans les Siwaliks précède la crise valésienne en Espagne. Contrairement aux précipitations saisonnières croissantes au Miocène supérieur dans le Potwar, le paléohabitat concomitant du Nord de la Chine semble avoir été humide et constant, avec une grande diversité faunique. Le développement continu et la comparaison des registres néogènes déterminés permettent une résolution croissante des schémas de changement faunique aux niveaux régional et global.

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1. Introduction

The Indian Subcontinent presents a special setting for paleobiologists. The uplift along the northern margin of the landmass, as its leading edge subducts under the mountainous terrain of the Tibetan Plateau, supplies clastic wedges of terrestrial deposits to the south via major river systems. The relatively continuous process of sediment accumulation under conditions favorable for vertebrate fossil preservation has created a series of fossil horizons, superposed and laterally extensive, spanning much of the second half of the Cenozoic Era. Assemblages represent successive samples of the past biota. The most continuous series of superposed fossil horizons is contained in the Siwalik deposits of the Potwar Plateau, Pakistan. This dense biotic record spanning much of the Neogene can be compared with well-dated biostratigraphies from other biogeographic regions to evaluate mammalian dispersal and turnover, timing of high or low rates of appearance and disappearance events, and response to abiotic factors of temperature, moisture, and tectonics. Research is beginning to address direct comparisons of sequences in Spain and China, for example, because their records comprise increasingly well-dated and resolved faunas.

Sedimentary formations of the Indian Subcontinent include primarily the classical Siwalik Group rocks of northern Pakistan, Nepal and India, of late Early Miocene through Pliocene age. Also relevant and preserving similar faunal assemblages are the Manchar Formation of southern Pakistan (Sindh), and coeval to older Zinda Pir Dome and Bugti sediments of western Pakistan (Baluchistan) (Fig. 1). The oldest of the latter deposits are Oligocene in age (Welcomme et al., 2001). Together they produce a rich record of successive faunas that can be studied for questions on lineage evolution, community structure, and faunal change.

The Siwaliks and related formations have been the subject of field exploration for almost 200 years. Early collecting was sporadic, with little attention paid to provenance, but it provided impetus for later expeditions. Two of these were collecting campaigns under the direction of Barnum Brown of the American Museum of Natural History in the 1920s and G. Edward Lewis of Yale University in the

1930s. Their collecting (Lewis, 1937) was geographically controlled and today we can reconstruct in general where many of their collections were made. Richard Dehm (Dehm et al., 1958), Universität München expeditions of 1939 and 1955–1956, and G.H.R. von Koenigswald, Rijksuniversiteit, Universiteit Utrecht (1966–1967), also recorded data for fossils recovered by their groups. However, the potential for biostratigraphic study of long sections in defined areas was still largely unrealized.

It is now feasible to record precisely the level of occurrence of superposed stratigraphic horizons that produce fossils. The sequence of sites records the local histories of organisms during much of the Miocene Epoch, both changes among members in associated faunas as well as evolution within lineages. The fossil horizons of the Potwar Plateau can be dated relative to one another, and ages can generally be resolved on the scale of 100,000 years for the interval of approximately 18 to 6 Ma (Barry et al., 2013). The record can be extended to about 22 Ma by paleomagnetic correlation of deposits of the Zinda Pir area, and into the Pliocene Upper Siwaliks of the southeastern margin of the Potwar Plateau. Sampling density for fossils is not constant throughout this time, which is critical to note when interpreting recorded faunal change. Fig. 2, based mainly on Potwar records and supplemented by Zinda Pir and Upper Siwalik localities, shows the uneven temporal distribution of Neogene sites in Pakistan.

The Siwaliks present a special geobiological case in which many successive and dated levels can be sampled for their often abundant vertebrate fossils and ecological proxies, affording an excellent opportunity to document changes in landscapes, habitats, and faunas through time. The dimensions of information that can be retrieved from the Siwaliks are considerable compared to other sequences of comparable age.

In the following, we discuss the geological and geographic setting for the major fossil-producing regions of the Indian Subcontinent. We sketch the history of exploration by early workers in the Indian Subcontinent. We touch on major features of the terrestrial deposits and age determination, and then turn to our current assessments of faunas and paleohabitats of the Miocene.
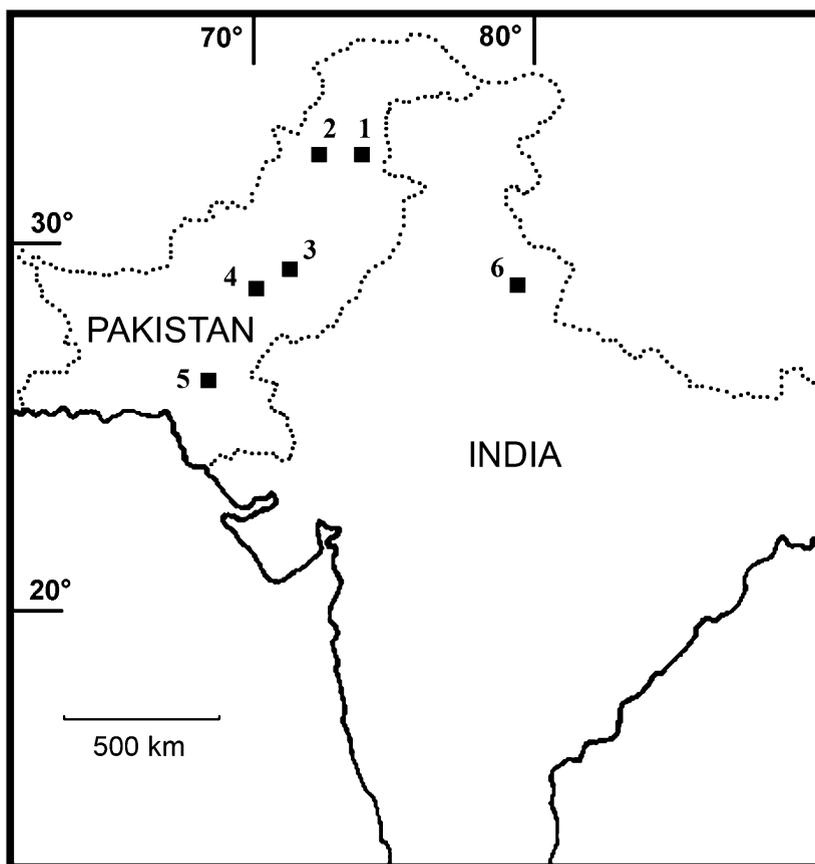
Fig. 1. Major collecting areas of the Indian Subcontinent. 1, Potwar Plateau (Barry et al., 2002, 2013; Flynn et al., 1995); 2, Indus Valley (De Bruijn et al., 1981; Munthe et al., 1979; Wessels et al., 1982); 3, Zinda Pir Dome (Antoine et al., 2013; Lindsay et al., 2005); 4, Bugti, Baluchistan (Welcomme et al., 2001); 5, Manchar Formation, Sindh (Wessels, 2009); 6, Siwalik Hills, one of many areas in India (Patnaik, 2013).
Fig. 1. Principales localités importantes du sous-continent Indien. 1, Plateau du Potwar ; 2, vallée de l'Indus ; 3, dôme Zinda Pir ; 4, Bugti, Baloutchistan ; 5, formation Manchar, Sindh ; 6, collines Siwaliks, Inde.

2. Major fossil-producing sequences and history of exploration

Early fossil collecting involved a gradual realization that fossil resources across the northern part of the Indian Subcontinent are considerable. Cautley and Falconer (1835) reported vertebrates from the "Sivalik" Hills of northern India (Fig. 1, area 6); fossils noted by them and by other early workers (e.g., Pentland, 1828) came to light from field campaigns under the direction of British officers. Vickary (1846) recorded the richness of fossil beds from the Bugti area of Baluchistan. This work was not systematic, but stimulated later study, for example by Pilgrim (1908) and Cooper (1924 and earlier), and much later by Raza et al. (1984). Welcomme et al. (2001) documented the Oligocene age of the oldest Bugti beds, discovering great faunal diversity there, and Antoine et al. (2013) reviewed the Miocene biostratigraphy of the Bugti area (Fig. 1, area 4). Lindsay et al. (2005) concentrated on the Zinda Pir Dome deposits (area 3), finding similar assemblages and adding several superposed early Miocene microfaunas. While earlier collecting tended to mix together fossils by collecting area, regardless of stratigraphy, these recent studies maintained

stratigraphic control to record the succession of assemblages.

Working widely throughout the northern Indian Subcontinent in Neogene age strata, Pilgrim (1910, 1913) distinguished and named successive fossiliferous sequences. He recognized a series of both strata and faunas in the Potwar Plateau of present-day Pakistan and the foothills of northern India. Rocks of the Potwar Plateau from late Early Miocene to early Pliocene came to be designated formally as formations, the Kamlial, Chinji, Nagri, Dhok Pathan, and Tatrot formations. Pilgrim (1910) also noted the older Early Miocene Murree Formation, adjacent to the northern margin of the Potwar. The type area of the Late Pliocene Pinjor Formation lies to the east in India. Prior to the 1970s, the ages of these units were not known, and the faunal content was not only poorly documented, but confounded with fossils from other parts of the subcontinent.

Potwar Plateau formations are stratified, dominantly fluvial sediments. They represent mainly floodplain silts and sands, with lesser components of clays, gravels, and ponded sediments. Vertical variations in lithology appear to be primarily tectonically controlled (Willis, 1993). Formations are distinguished by dominant lithology,
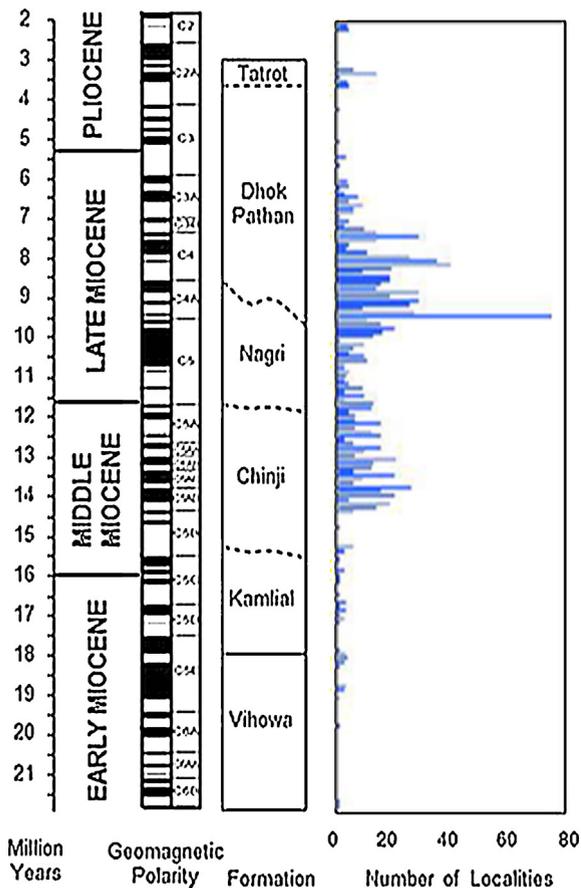
Fig. 2. Distribution through time of numbers of localities documented primarily in the Potwar Plateau, supplemented by information from the Upper Siwaliks of Pakistan, especially near Tatrot, and the Vihowa Formation of the Zinda Pir Dome. Geomagnetic Chrons are plotted on the time scale of Gradstein et al. (2004). This figure illustrates the uneven record, number of sites being a proxy for recorded fossils, but localities differ in productivity. On the right, numbers of localities resolved to 10^5 years are plotted in 100,000 year bins.

Fig. 2. Répartition temporelle des nombres de sites documentés dans le plateau du Potwar, échelle du temps d'après Gradstein et al. (2004). La figure montre un registre inégal, le nombre de sites étant un proxy pour le nombre de fossiles répertoriés, mais les localités diffèrent en productivité. À droite, nombre des localités en bins de cent mille ans.

principally proportions of sand bodies (Khan, 1995). The late early Miocene Kamlial Formation has >50% sand, distinguishing it from the overlying finer-grained red silt of the Chinji Formation, which includes more paleosols and evidence of ponding (Barry et al., 1980; Willis, 1993). In contrast, the younger Late Miocene Nagri Formation is dominated by thick multi-storied sands, while the succeeding finer-grained Dhok Pathan Formation has channel deposits interbedded with floodplain silts. Pliocene Upper Siwalik units include conglomeratic sands (see Barry et al., 2013; Flynn et al., 2013).

Beginning in the 1970s, attention was focused on the Potwar Plateau by teams from the Geological Survey of Pakistan and Yale (later Harvard University), and from Dartmouth and Peshawar universities. For both groups, which later merged, careful biostratigraphic control was

the key goal. Fossils were pinpointed geographically and by stratum, and therefore assemblages were related to one another. A second key innovation was applied: temporal control using paleomagnetic reversal stratigraphy (Johnson et al., 1982; Opdyke et al., 1979; Tauxe and Opdyke, 1982), determining local rock sequence magnetostratigraphy and then correlating the magnetozones to the Geomagnetic Polarity Time Scale. Correlation, while sometimes challenging, is complemented by biostratigraphy and a few radiometric dates, and is anchored by the distinctive and considerable thickness of normally magnetized rock (the long normal, chron C5n.2n). The process included repeated observations that led to a stable, dated magnetostratigraphy for the Potwar Plateau. Magnetic reversal stratigraphy has also been applied successfully in northern India (Patnaik, 2013), to Plio-Pleistocene deposits east of the Potwar, in Pakistan (e.g., Keller et al., 1977), and to the early Miocene of the Zinda Pir Dome (Lindsay et al., 2005).

Simultaneous collaboration with the Howard University project under the direction of S. Taseer Hussain, including scientists of the Rijksuniversiteit at Utrecht and the Milwaukee Public Museum, was also fruitful. Beginning in the late 1970s (Munthe et al., 1979) and primarily during the 1980s (Wessels et al., 1982), fieldwork focused on Early to Middle Miocene deposits near Mianwali and Banda Daud Shah (Indus Valley west of the Potwar), the Manchar Formation of southern Pakistan (Fig. 1, area 5; Wessels, 2009), and Pliocene-Pleistocene deposits southeast of the Potwar Plateau (Hussain et al., 1992). De Bruijn et al. (1981) documented the then-oldest-known, Early Miocene small mammal assemblage from the Murree Formation at Banda Daud Shah. These teams maintained strict control of faunal associations as they carefully documented the localities. The work showed that observed faunal assemblages extended throughout Pakistan (homotaxis), albeit with some local differences.

3. Habitats

The Siwalik mammalian record is characterized by a succession of rich assemblages that approximate past biotic associations, but the fossil assemblages have undergone taphonomic processes and uneven sampling. Consequently, knowledge of paleocommunities is biased to varying degrees. Taken as a whole, Siwalik faunas include elements that, today at the family level, are subtropical in their ranges, with many represented today in Africa and southern Asia. It is important to acknowledge that our interpretation of Siwalik habitats is heavily based on what we know from the Potwar record, while we know very little of the fossil record of Peninsular India, for example.

The latitudinal position of the Potwar during the Miocene at 14 Ma would have been ∼6 degrees farther south, based on a reconstruction of Scotese (1997). Habitats were subtropical with landscapes of generally low relief at low elevation (today generally 300–500 m), characterized by floodplains of major rivers draining highlands to the north (Barry et al., 2002). Fossiliferous Potwar deposits represent secondary and tertiary streams and their associated overbank deposits (Behrensmeyer, 1987). The fossil

record therefore sampled lowland floodplain paleocommunities, not high-relief, high-elevation associations, and faunal diversity is correspondingly high.

Although subtropical and with rich faunal assemblages, the Siwalik habitats were by no means unbroken tropical forest. Faunal assemblages include indicators of both tree-dominated habitat (tree shrews, large body-size primates) as well as partially open terrain (diverse proboscideans, rhinocerotids, bovids). This diversity probably reflects a climate with seasonally varying rainfall. The best evidence for vegetation structure comes from plant remains, which are, unfortunately, uncommon in the Potwar Plateau and other areas of Pakistan. De Franceschi et al. (2008) did recover pollen and wood from the late Oligocene of the Zinda Pir Dome, which indicated tropical lowland rainforest, hills of 2000–2500 m elevation near the region, along with presence of some open-habitat plant taxa.

Knowledge of Miocene age plant ecology comes from sections in Nepal and India. Hoorn et al. (2000) studied pollen from Surai Khola, one area long studied for vertebrates by G. Corvinus (Corvinus and Rimal, 2001). Subtropical to temperate broad-leafed forests with some C3 grasses characterized the Himalayan foothills during the early late Miocene, and tropical forest characterized floodplains. During the late Miocene grasslands replaced woodlands in the foothills, and ultimately C4 grasses dominated the vegetation. Seasonal flooding intensified for Pliocene habitats. A similar progression to the west in the Potwar is likely. There is also some paleobotanical evidence from India. Miocene pollen from the extreme South of peninsular India records humid and tropical habitats (Ramanujan, 1987), while leaves from northern India indicate mixed lowland humid forest (evergreen and deciduous) in the early and middle Miocene (Guleria et al., 2000; Prasad, 1993). Later Miocene pollen from northern India also indicates warm and humid lowland rainforest, but through time, drier conditions and increasing contributions from higher elevation taxa (Sarkar et al., 1994).

Additional lines of evidence are being developed to interpret the paleoenvironments of the Potwar Plateau. Microstratigraphy of the localities producing fossils consistently shows habitats proximal to streams both in and near channels and on associated floodplains (Badgley, 1986). Middle Miocene small mammals occur usually in overbank deposits or crevasse splays from abandoned channels, often with soil development (Badgley et al., 1998). As such, assemblages separated laterally, and even in time, are generally comparable in their paleoecology, and we find great homogeneity in assemblages of similar age. We consider as paleobiologically meaningful observed faunal change through time against a fabric of general continuity among successive assemblages.

Soils preserved in the sedimentary record contain proxy data that offer information on past habitats of the Potwar. Paleosols indicate hiatuses in deposition and subaerial exposure, and thus record geochemical characteristics of plant cover. Stable oxygen and carbon isotopes of paleosol carbonate nodules, which form during seasonal drying, reflect plant biochemistry and general moisture availability on the paleosol surface. Barry et al. (2002) reviewed the Siwalik paleosol record and its significance, noting

evidence for substantial replacement of C3 plants by C4 plants over a period of two million years, beginning about 8 Ma. Behrensmeyer et al. (2007) developed another data set from laterally sampled deposits of late Miocene and Pliocene age. Carbon isotopes show completion there of the transition to C4 floodplain plant cover after 5 Ma, while oxygen isotopes suggest that moisture availability (presumably annual precipitation; see also Nelson, 2007) decreased through the Late Neogene.

For the Potwar Siwaliks, we reconstruct a sequence of subtropical habitats with diverse mammalian assemblages. During the early and middle Miocene, lowland floodplains were dominated by seasonal woodlands with some open habitat and riparian areas of forest. Rainfall was abundant but probably seasonal. Increasing seasonality and decreasing annual rainfall characterized the Late Miocene. Woodlands persisted until after 8 Ma, although types of vegetation may have changed.

Later Miocene landscapes were increasingly dominated by C4 plants, mostly grasses, replacing woodlands and associated C3 grasses.

4. Fauna

Classical Siwalik faunas span much of the Neogene of Indo-Pakistan and are well known for the 18 to 2 Ma interval. Faunal composition is diverse, and small mammals include tree shrews, shrews, hedgehogs, squirrels, gundis (ctenodactylids), dormice, bamboo rats (rhizomyines), hamsters, gerbils, mice, rats, and in the Late Miocene porcupines and rabbits. Typical carnivores, primates and ungulates are hyaenids, felids, viverrids, creodonts (until the early late Miocene), lorises, sivaladapids, hominids (*Sivapithecus*), hipparionine horses (late Miocene onward), diverse rhinocerotids and proboscideans, chalicotheres, suoids, anthracotheres, giraffids, tragulids, and many bovid groups. Certain archaic lineages persist later here than elsewhere in the Old World, for example, creodonts and sivaladapids. A few rare lineages are also present (e.g., aardvarks and diatomyid rodents), as well as bats, and reptiles and birds, but preservation is so uneven for these groups that temporal ranges of genera are unknown. Some mammals that are characteristic of other biogeographic regions, such as cervids and ursids, appear in the Indian Subcontinent only in the last few million years.

Many of the large mammal groups have not been revised for many years, although primates and hipparionines have had deserved attention (e.g., Morgan et al., 2015; Wolf et al., 2013). Stratigraphically controlled collecting has built large collections with excellent provenance data, especially for suoids and ruminants, now undergoing systematic revision (e.g., Barry, 2014). Some of the carnivore groups, rhinocerotids, and proboscideans also have enough material distributed through the sequence to offer useful data on ecomorphology, systematics, and stratigraphic ranges.

4.1. Diversity

The combined effect of large collections amassed over many field campaigns, and controlled stratigraphy to maintain distinct assemblages, results in greater diversity in

some well-defined clades than was previously apparent. This is perhaps most evident in single groups such as rhinocerotids, which show surprising diversity of six to eight coexisting species in the middle to early late Miocene (Heissig, 1972). Hipparionine horses also diversify; whereas a single species is present at the earliest appearance of the group in the Siwaliks, two and then three species co-occur later in the Late Miocene (Wolf et al., 2013).

Terrestrial artiodactyls (non-cetacean Cetartiodactyla) are the most species-rich higher group of large mammals in the Siwalik record. Successive faunas are dominated by long lineages of suoids, anthracotheres, giraffoids, tragulids, and bovids (Barry et al., 2013). Their history reflects the successful radiation of ruminants and records the emergence of bovid tribes. Throughout the middle and early late Miocene, there were at least twenty co-existing species of artiodactyls in Siwalik habitats (Flynn et al., 2014).

Perceived diversity is dependent on sampling density and applies to both the species level within genera and to groups of closely related genera. Siwalik tragulids (*Dorcabune, Siamotragulus*, and *Dorcatherium*) are an example. While this family of ruminants might seemed at first to be low in species richness, current analyses (Barry, 2014) combine dental and postcranial material and demonstrate that up to four species of *Dorcatherium* co-existed at a single time in the middle Miocene. This is also the case for small bamboo rats of the genera *Prokanisamys* and *Kanisamys* for which single Chinji Formation sites (middle Miocene) produce four species, although they do not show major morphological differences other than size. Co-occurring at one site, this suggests microhabitat partitioning within a small range area by the bamboo rats. The combination of large collections with precise stratigraphic control provides a view, although still incomplete, of the complexity of past Siwalik habitats, which were rich enough to support multiple closely related species.

Beginning in the late 1970s, a fuller appreciation of Siwalik faunal composition was revealed by applying screening techniques to retrieve very small vertebrates. Localized sedimentary concentrations with small bones and teeth were quarried, soaked in water, and sifted through fine mesh. Microfauna (fish, herpetofauna, small mammals) revealed an aspect of Siwalik assemblages previously largely hidden. Jacobs (1978) and Munthe (1980) reported high diversity in the small mammal Siwalik community, especially for rodents. Squirrels, muroids and other rodents had been virtually unknown, but showed high diversity along with evolutionary change at multiple biostratigraphic levels (Kimura et al., 2013). We have developed in excess of 100 productive screen washing horizons throughout Siwalik Group rocks. These document diversities of 25 to 30 species of rodents at single localities of middle Miocene age. It is unlikely that all small mammal species in the paleofauna are sampled, but the consistency in faunal composition through time shows that comparisons of successive assemblages offer meaningful information on species temporal ranges and faunal change.

For rodents, screening efforts throughout the stratigraphic record reveal a rich record of muroid clades, diverse squirrels, and long-lived conservative lineages of gundis, dormice, and thryonomyids (Flynn and Wessels, 2013; Flynn et al., 1995; Wessels, 2009). Muroid fossils include an array of cricetid and similar relatives of hamsters, with some forms close to African dendromurines, and murids embracing early gerbils as well as true mice and rats (Jacobs and Flynn, 2005; Lindsay, 1988). The record documents the early radiation and initial diversification of crown murines, the early evolution of stem bamboo rats, and emergence of fully fossorial crown Rhizomyini (Flynn, 2009).

4.2. Ecology

Several lines of investigation focus on understanding the ecology of key taxa; knowledge of certain mammals sheds light on the roles played by other mammals. An example is *Sivapithecus*. This is a moderate-size, dimorphic ape genus, with males about the size of female chimpanzees and females about the size of male baboons (Morgan et al., 2015). Like modern apes, *it* was arboreal and a frugivore. Thus its success until the middle of the late Miocene implies tree cover including at least riparian woodlands bearing fruit. Indeed, Nelson (2005) ties the disappearance of *Sivapithecus* to increasing monsoon seasonality and a more significant dry season, leading to a loss of favorable plant resources. Analyses of postcranial remains summarized in Morgan et al. (2015) indicate arboreal locomotor adaptations for *Sivapithecus*, reflecting above-branch pronograde positional behaviors.

While *Sivapithecus* lived in wooded habitats, other faunal elements indicate more open terrain. High diversity of proboscideans, rhinocerotids, and bovids suggests exploitation of a wide range of habitats. Tooth microwear and premaxilla shape (Solounias and Moelleken, 1993) are ecomorphological clues that can be used to judge preferred habitat of extinct genera. Carnivorans occupying equally varied habitats contribute to fossil assemblages. Dominant predators are large-bodied hyaena-like percrocutids, felids, and creodonts. Smaller bone-crushing hyaenids, sabertooth cats, and the proviverrine creodont *Dissopsalis* (Barry, 1988) complement these large forms, coexisting on the landscape. Small viverrids and mustelids round out the carnivoran guild.

Both microwear and mesowear of teeth offer insight into the diet and behavior of individual taxa. Nelson (2003) found that, like Miocene *Sivapithecus*, tragulids and contemporary bovids depended on fallen fruit and soft vegetation. Many of the largely frugivorous artiodactyls declined about the time that *Sivapithecus* disappeared from the record (Nelson, 2003). Microwear shows that the Bovidae present after fossil apes disappeared depended more on grazing. Mesowear analyses of equid teeth also document an increase in the abrasiveness of the consumed forage between 10 and 7 Ma (Wolf et al., 2013).

Stable isotopes of paleosol carbonates and tooth enamel show profound ecological change for the Siwaliks. Paleosol carbonate nodules average the effects of plant cover over the period of their formation, usually hundreds to several thousand years, masking the complex biological pattern of plant replacement. Barry et al. (2002) analyze the evidence for a dramatic change in plant composition, specifically replacement of a large proportion of vegetation

utilizing the C3 photosynthetic pathway by C4 photosynthesizing vegetation. C3 plants include trees, shrubs, and some grasses; C4 plants include many grasses and sedges that are favored in regions with warm growing seasons. C3 and C4 plants are distinguished isotopically by their differential fractionation of carbon; C4 plants discriminate less against incorporation of carbon-13 than C3 plants (Smith, 1972). This isotopic fractionation pattern is reflected in paleosol carbonates, and in animal consumers (Cerling et al., 1989; Lee-Thorp et al., 1989). In the Siwaliks, C4 plant cover became significant at about 8 Ma but it was not until a million years later that paleosols dominated by C3 declined (Barry et al., 2002).

Most of the dominant Siwalik herbivores have been studied for stable isotope analysis of tooth enamel. A number of mammal species exploiting C3 vegetation disappeared during the transition, whereas newly appearing taxa were C4 grazers. In a few cases, single lineages showed change from a C3 to a C4 diet (Badgley et al., 2008). Morgan et al. (1994, 2012) traced changes in the isotopic signatures of mammalian groups during the Late Miocene and demonstrated that hipparionine horses showed adoption of C4 vegetation into their diet beginning about 10 Ma, well in advance of other mammals. Fine-scale differences in carbon and oxygen isotope values likely reflect different intake strategies for food and water (Nelson, 2005), and can be used to distinguish taxa isotopically from one another (Morgan et al., 2012). Kimura et al. (2013) showed isotopic divergence of two mouse lineages beginning around 8 Ma.

Both microwear and stable isotopes offer complementary data that are beginning to be incorporated into the paleoecological synthesis, and other paleoecological signals are also under study, such as dental mesowear features, frequency of presence of lophodonty, dimorphism in ungulates, and limb proportion indices. We mention one other phenomenon here. Later Miocene herbivores display increased body size (Morgan et al., 1995), and some appear to have larger cheek tooth batteries than would be predicted for herbivores of their body size as based on postcranial measurements. These patterns reflect changing climate or plant productivity in ways as yet poorly understood.

5. Faunal change

We noted at the outset that the Pakistan Siwaliks present an extraordinary terrestrial record of mammalian evolution in that many successive fossil horizons are present in one area, with paleobiological representation for many of the 100,000 year intervals over the span of 18 to 6 Ma. Younger and older rocks (Fig. 2) are less well sampled in Pakistan. In the preceding, we have discussed general habitats, paleoecology, faunal composition, and long term trends recorded in the densely sampled sequence. An additional field of study focuses on details of faunal change, including stasis and turnover, and on reconstructing paleocommunity composition and structure.

Badgley et al. (2016) explore the interplay of mode of faunal change with climatic stability or change, and presence or absence of physical barriers. Degree of faunal turnover appears to reflect both. Barry et al. (1995) analyzed faunal change in 500,000 year intervals, recognizing the effects of an uneven record on perceived timing of change. After applying confidence intervals on measured taxon ranges, maxima of first appearance and last appearance events could be more meaningfully evaluated. This was carried further in Barry et al. (2002) where faunal change between 10.7 and 5.7 Ma was analyzed at a finer scale of resolution, 100,000 years. Considerable change among large mammals peaked at about 10.3 Ma and after 8 Ma, especially about 7.3 to 7 Ma. The disappearance of C3 dominated landscapes before 7 Ma, coincides with the last phase of faunal turnover, perhaps the strongest in the Siwalik record (Barry et al., 2002). Late Miocene small mammal lineages also show diverging dental changes (Kimura et al., 2013).

Given a densely sampled biostratigraphy, species longevity can also be studied using the observed Potwar sequence as an approximate record of residence times for small and large mammals (Flynn et al., 1995). Modal longevities for rodents and artiodactyls appear in line with estimates derived from other data.

5.1. Endemism vs. immigration

How does faunal composition change through time? Flynn et al. (2014) reviewed biostratigraphic ranges for the species-rich rodents and artiodactyls, and assessed the changing contributions to the fauna of endemic and immigrant appearances over time (Fig. 3). Given tight temporal control, especially for the well-sampled 18 to 6 Ma Potwar record, we examined Siwalik assemblages at two million year intervals. We added the Zinda Pir rodent record back to 22 Ma (Fig. 3a). We did not estimate appearances and disappearances, but set out to record presences at specific times and used the range-through concept to count as present those species found in preceding and succeeding intervals. Because the counts for time slices pooled data from adjacent 100 Ky bins, sample size is not directly related to richness. Both rodents and artiodactyls occur in early Miocene deposits, but this analysis, in effect a series of censuses, required assessment of rodent and artiodactyl species as recurring residents either or *as* immigrant or as endemic new arrivals. Earlier species, especially early Miocene artiodactyls, are as yet unresolved for this (Fig. 3b).

This exercise is not biostratigraphic but rather a means to evaluate rodent and artiodactyl richness and judge degree of endemism at successive time intervals. What proportions of recorded taxa are long-term residents or new appearances, and among the latter, are they immigrants or had they evolved within the biogeographic province as endemics?

Successive two-million-year censuses (Fig. 3) indicate faunal richness building at the end of the Early Miocene, high middle Miocene diversity, turnover (after 11 Ma) largely completed before 10 Ma, and recovery for artiodactyls during the middle late Miocene. There is some evidence that large and small mammals do not always show the same pattern of change. In particular, during the late Miocene, while artiodactyls rebound with a return to diverse faunas (in part more grazers), rodents show steady decline from middle Miocene high diversity. As to
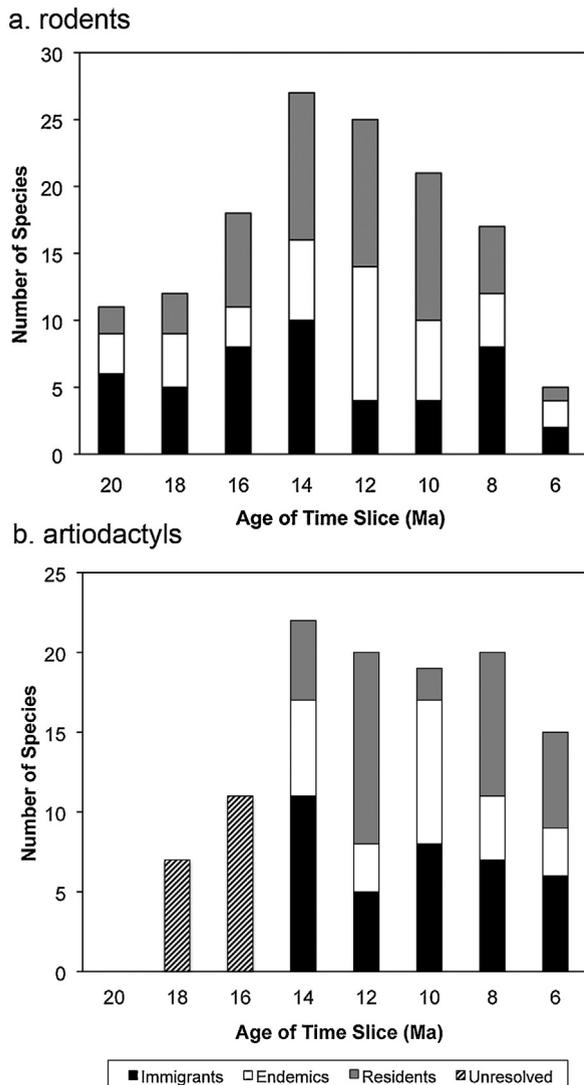
a. rodents

b. artiodactyls

Legend: ■ Immigrants □ Endemics ▨ Residents ▨ Unresolved

Fig. 3. Rodents (a) and artiodactyls (b) recorded at time slices centered at 2 m.y. intervals. Species are classified as residents or newcomers, newcomers being of endemic or immigrant origin. These categories are defined in Flynn et al. (2014), from which the figure is modified. Older and younger rodents and artiodactyls are known but are not part of the analysis; artiodactyl diversity for the 16 and 18 Ma time slices is indicated, but relationships to younger species are unresolved (cross hatch symbol). The underrepresented oldest and youngest time slices are affected by the few known localities of those ages (see Fig. 2).

Fig. 3. Rongeurs (a) et artiodactyles (b) enregistrés par tranches de temps de 2 millions d'années. Les espèces sont classifiées en espèces résidentes ou nouvellement arrivées, ces dernières étant d'origine endémique ou immigrante. Ces catégories ont été définies par Flynn et al. (2014), d'où la figure modifiée est issue. Des rongeurs et artiodactyles plus anciens et plus jeunes sont connus, mais ne font pas partie de l'analyse ; la diversité chez les artiodactyles est indiquée par tranches de temps de 16 et 18 Ma, mais la relation aux plus jeunes espèces n'est pas résolue (symboles barres croisées). Les tranches de temps les plus anciennes et les plus récentes sont sous-représentées, en raison du peu de localités connues pour ces âges (voir Fig. 2).

components of the faunas, large mammals show many new appearances, both endemics and immigrants, during the early middle and early late Miocene, and a dominance of residents (indicating stability) at the 12 Ma and 8 Ma time

slices. Rodents show many immigrants in the early Middle Miocene, and a large proportion of continuing residents (a measure of stability despite declining richness) from 14 to 10 Ma. Late Miocene richness is lower for rodent species and nearly half are immigrants, a pattern quite unlike that of the artiodactyls.

This analysis indicates ongoing change for Siwalik mammals through time, and a discontinuous pattern of diversity and relative proportions of endemics and newcomers vs. holdovers. The trends differ for rodents and artiodactyls and may help to reveal the dynamics of turnover events, and offer clues as to how faunas change.

5.2. Inter-regional and intercontinental comparisons

Stratigraphic control of long records over deep time opens new avenues to compare terrestrial faunal events from different biogeographic regions at fine time resolution. Dated biostratigraphies from distinct areas can be correlated on time scales considerably shorter than one million years, allowing evaluation of the timing and players in faunal change against the backdrop of local tectonics and regional to global climatic events. Patnaik (2013) evaluated differences in species ranges for the adjacent Potwar and North Indian fossil records. Faunal change in distinct theaters of evolution also may be assessed independently of taxonomy: as Neogene records from Spain and China become increasingly well dated, great potential emerges for detailed comparisons.

The long stratigraphic record of Spain is a composite from several basins, individual sections of which have excellent control and magnetostratigraphy. Evolutionary events, introductions of exotic elements (e.g., equids or murids), and turnover maxima can be compared between Spain and Pakistan on time scales of ca. 10^5 years, more fine-scale than was previously available. The records are developing for comparison, but already we think that a keystone group, hipparionine horses, immigrated to the Vallès Penedés Basin (∼11.1 Ma; Garces et al., 1996) significantly before the Potwar (∼10.7 Ma; Pilbeam et al., 1996). Yet within Spain diachrony is apparent: the interior Iberian Daroca area records its first *Hipparion* later than in the Vallès Penedés Basin (Garces et al., 2003).

Does the 11 to 10 Ma Siwalik turnover have a counterpart in Spain? Among Siwalik artiodactyls, by 10 Ma many continuing species had become extinct and newly appearing taxa involved roughly equally immigrants and endemics (Morgan et al., 2013). Potwar rodents showed mainly decreasing diversity, with diminished immigration among the fewer first appearances. The Spanish record reveals a pattern of change offset with respect to the Siwaliks, with maximum change later in time, after 10 Ma (Agusti et al., 2013; Domingo et al., 2014). After adjusting for unevenness in the fossil record, the Vallesian crisis in the Spanish fossil record is seen to be less abrupt than previously thought, but still significant, and postdates Siwalik events (Casanovas-Vilar et al., 2014, 2016).

As for Spain, the basins of North China together record faunal events of the Neogene. North China is part of the Palaearctic biogeographic region, in contrast to the Indian Subcontinent of the Oriental region. Faunal composition

at the species level is distinct, but comparisons of faunal change may reflect larger continental conditions. The Miocene Tunggur fauna of Inner Mongolia (Qiu et al., 2013) may be compared with Chinji Fm. assemblages of the Potwar Plateau. Twenty Tunggur rodent species represent richness on a par with Potwar assemblages, but the nine artiodactyls suggest considerably lower diversity in this continental interior setting. In contrast, while the later late Miocene of the Potwar saw increasing accentuation of its dry season and possible cooling (Tang et al., 2015), with decreased micromammal diversity, moist conditions in North China (Fortelius et al., 2014) led to high diversity among both ungulates and small mammals (see also Flynn et al., 2011). These differences likely reflect shifts in overall precipitation patterns correlated with monsoon strength. Comparisons like these stand to enrich knowledge of biotic events on a spatial scale well beyond that of the local basin.

6. Conclusions

The Siwalik deposits of the Potwar Plateau and adjacent areas are outstanding for their entombed record of Neogene terrestrial vertebrates of South Asia. Superposed Potwar deposits contain many successive fossil assemblages that provide a wealth of paleobiological data spanning 18 to 6 Ma, with dating resolved in most cases to 100,000 years. Strata of the Zinda Pir Dome to the southwest add complementary early Miocene assemblages, and deposits east of the Potwar contain important Pliocene faunas. Together, these reveal the history of faunal succession of a constrained area, northern Pakistan, which models the terrestrial biotic history of the Indian Subcontinent biogeographic subregion.

Siwalik habitats represent mainly low-elevation floodplains of large river systems. The fauna is diverse, with high species richness especially in the middle Miocene. Siwalik mammals include extinct groups and surviving families. There is strong evidence for local subtropical woodland habitat (many arboreal vertebrates) and we hypothesize nearby open terrain (to accommodate grazers of C3 and, later, C4 vegetation) between riparian settings rather than continuous canopy. Both the shift in vegetation and faunal turnover suggest changing ecology, which we think involved increasing seasonality, especially of moisture, with development of an extended dry season.

While fossil sites are distributed densely at some intervals, the quality (richness) of the fossil record is uneven throughout much of the Miocene. This affects fossil recovery and the perceived biostratigraphy of fossil taxa. Well represented times offer much fuller pictures of past assemblages, and temporal ranges of species can be extended by estimated confidence intervals.

Faunal change is observed to be continuous during the Miocene. We see adjustments in total diversity and, among the continuing taxa, changing proportions of species of endemic vs. immigrant origin. Both diversity and endemism appear to be related to ecological stability and degree of isolation of the biogeographic subregion. Data on small and large mammals suggest that they do not necessarily show the same trends; for example, both groups show maximum richness in the middle Miocene,

but rodents steadily decline thereafter, while artiodactyls rebound in diversity after a phase of turnover.

Deep time control on biostratigraphy invites comparisons with like records from separate biogeographic regions and evaluation of continental to global controlling factors of climatic change. Correlation with other records on a time scale resolved to 10^5 years yields information on biogeographic dispersal, mammalian turnover, and response to abiotic drivers (temperature, moisture distribution, sea level, tectonics). The timing of introduction of exotic elements (e.g., hipparionine horses) may be traced at this time scale. The Vallès-Penedès Basin and other regions of Spain show trends that contrast with the Potwar record. The Late Vallesian faunal turnover, although attenuated, is not seen in the Siwaliks. Rather, faunal turnover in northern Pakistan preceded the Vallès-Penedès events, and Potwar habitat supporting ape faunas continued well into the late Miocene, to 8.5 Ma. North China provides a complementary comparison with the Potwar: while North China habitats experienced increasing vegetation cover after 8 Ma, the Potwar likely saw an increase in seasonality of precipitation and possibly cooler temperatures. These contrasting trends at the end of the Miocene may prove to reflect development of the monsoon systems of modern climate.

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