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SIWALIK PRIMATES

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INTRODUCTION

Primates are present throughout the Siwalik sequence of the Potwar Plateau. At higher taxonomic levels they are highly diverse, with at least six superfamilies represented, but with superfamily and family representation changing through time. The early part of the record (Early to early Middle Miocene) contains only lower primates of small body size, sivaladapids and lorisids, both known from multiple species, and a small, unspecified primitive catarrhine known only from a few teeth. Sivaladapids were almost surely present in the region at the onset of Siwalik sedimentation, as evidenced by their presence near the base of the Kamlial Formation, and in the Oligocene/Early Miocene faunas from Bugti and the Zinda Pir Dome in west-central Pakistan (Marivaux et al. 2002; Lindsay et al. 2005). The earliest lorisid remains postdate those of sivaladapids by more than 1.5 myr and it seems most likely that they immigrated into the region from Africa subsequent to the beginning of Siwalik sedimentation (Phillips and Walker 2000, 2002). Sivaladapids disappear from the Potwar Siwalik record during the Middle Miocene, but some lorisids persist well into the Late Miocene.

The Middle Miocene saw the appearance of the first large-bodied primate, the hominid *Sivapithecus*. *Sivapithecus* was clearly an immigrant to the region, but whether from somewhere in Eurasia, Afro-Arabia, or perhaps even elsewhere in the subcontinent is unknown. Its craniofacial anatomy is distinctive among all known Miocene primates and bears many features otherwise found only in the living orangutan, *Pongo*. In its entirety, its postcranium is also distinctive among Miocene large primates, with a unique combination of ape-like and more primitive features. The postcranium is even less like that of *Pongo* than it is of other Miocene apes. These issues are discussed further below, but they are raised here to underscore the difficulty in determining both the geographic and phyletic origins of *Sivapithecus*. For most of its history in the Potwar Plateau, *Sivapithecus* is one of the more uncommon taxa, but it is nearly always found when total mammalian specimen counts are sufficiently high. A large, very rare, and somewhat enigmatic hominid, *Indopithecus*, is represented by a single tooth from the Potwar Siwaliks, but it is of uncertain provenance. It is known from a more complete specimen from the Indian Siwaliks and is most likely derived from *Sivapithecus*. Another enigmatic primate from the late Middle Miocene is represented by a small proximal humerus that most resembles those of primitive catarrhines or platyrrhines.

The early colobine monkey *Mesopithecus* first appears in the Siwalik record in the Late Miocene, almost one million years after the local extinction of *Sivapithecus* and in the context of progressive faunal change. *Mesopithecus* is widespread throughout southern and central Eurasia in the Late Miocene and spread rapidly from what is either its likely center of origin, or point of entry into Eurasia from Africa, in southwestern Europe. Its first appearance in the Siwaliks is one of the earlier records of its occurrence (Alba et al. 2015). Temporal ranges of all primate taxa recovered from the Potwar Plateau are shown in Figure 12.1.

Primates are also known from several locations in the Siwaliks of India, and a few specimens have been recovered from Early-Middle to perhaps Late Miocene sediments in the Manchar Formation in southern Pakistan. Not surprisingly, these represent many of the same genera as in the Potwar Plateau sequence, but in some cases different species. From Ramnagar and Haritalyangar in India, there are also rare representatives of groups unknown in the Potwar: respectively, Hylobatidae and Pliopithecoidea. Finally, from Early-Middle Miocene sediments in the Manchar Formation is a representative of the Tarsiidae (Zijlstra, Flynn, and Wessels 2013), unknown from the Siwaliks of either Pakistan or India.

STREPSIRRHINI É. GEOFFROY SAINT-HILAIRE, 1812

Fossil Lorisidae and Sivaladapidae have been recovered almost exclusively from screen-washing bulk sediments and are represented primarily by isolated teeth. The exception is a partial skeleton of *Nycticeboides simpsoni* (Jacobs 1981). Despite small samples, the Siwalik small-primate fossils hint at considerable diversity through the sequence. At one locality (Y682), dated

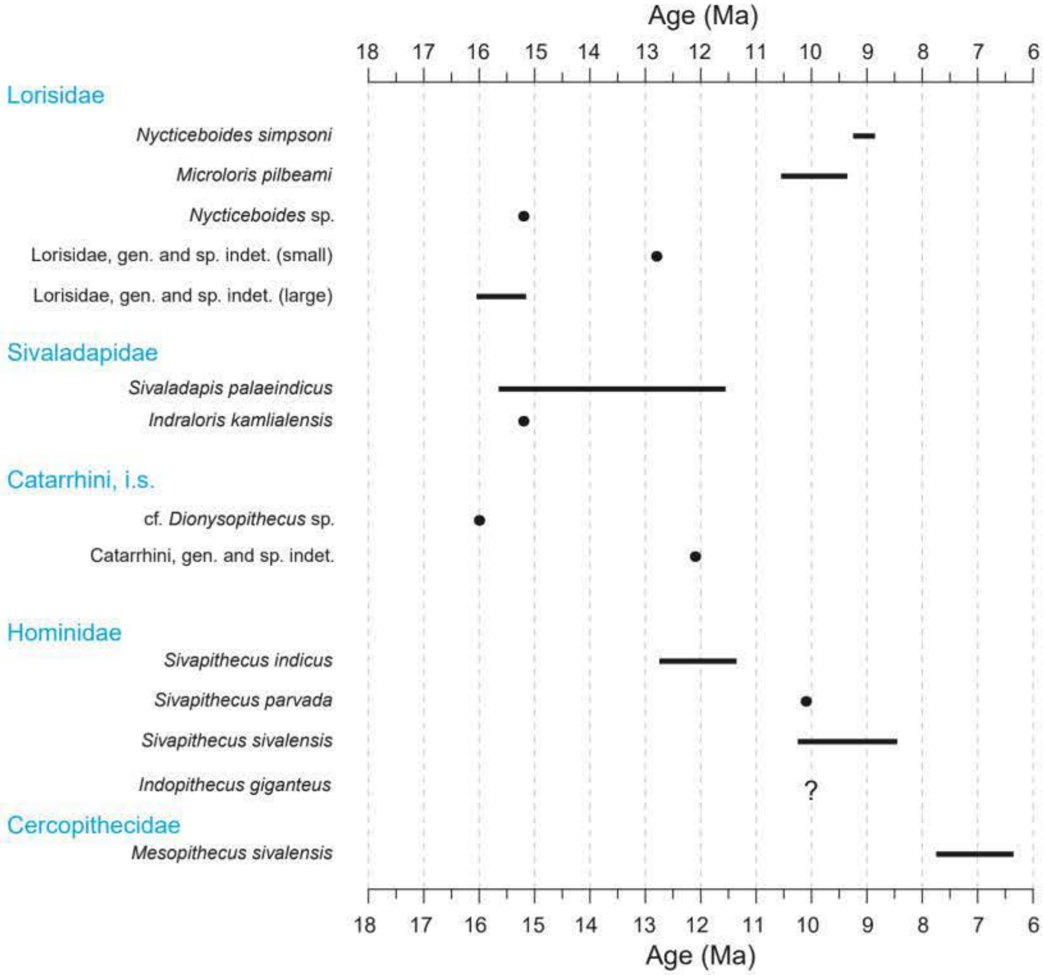

Figure 12.1. Stratigraphic ranges of primate species in the Potwar Plateau, Pakistan.

to 15.2 Ma (million years ago), four species, two lorisids and two sivaladapids, have been identified.

Lorisoidea Gray, 1821

Nycticeboides simpsoni. The type specimen of *Nycticeboides simpsoni*, YGSP 8091 (Figure 12.2), is a fragmentary cranium, mandible, and partial skeleton (Jacobs 1981; MacPhee and Jacobs 1986). *N. simpsoni* was probably similar in size to extant *Nycticebus pygmaeus* at around 400 g (MacPhee and Jacobs 1986; Ravosa 1998). Jacobs (1981) reconstructed *N. simpsoni* as a slow-moving arboreal quadruped primarily on the basis of features of the humerus. MacPhee and Jacobs (1986) inferred from tooth morphology and body size that *N. simpsoni* likely consumed insects, exudates, and fruit.

Microloris pilbeami. The type specimen of *Microloris pilbeami* is YGSP 26006, a left M2 (Flynn and Morgan 2005). *M. pilbeami* is much smaller than living *Nycticebus*. Its teeth are similar in size to those of *Galagoides demidovii*, which weighs less than 100 g (Nowak and Paradiso 1983). The molar morphology of *M. pilbeami* suggests an insectivorous diet, although a concave wear facet on the upper P2 might indicate lateral stripping of vegetation (Flynn and Morgan 2005). Sussman, Rasmussen, and Raven (2012) note that among extant species, even small lorises are omnivorous.

At least four additional lorisoid species are represented in the Siwaliks. These have not been formally named due to the fragmentary material but are distinct from both *Nycticeboides simpsoni* and *Microloris pilbeami* in morphology or size (Flynn and Morgan 2005).

Nycticeboides sp. YGSP 48029, a left m1 from Locality Y682 (15.2 Ma), is similar to *Nycticeboides simpsoni* but much smaller. This specimen considerably extends the temporal range of *Nycticeboides* in the Siwaliks.

cf. *Nycticeboides* sp. YGSP 26009, a left p4 from Locality Y182 (9.2 Ma), is somewhat similar to *Nycticeboides simpsoni*, also represented at this locality, but it clearly represents a different species (MacPhee and Jacobs 1986; Flynn and Morgan 2005).

Lorisidae, unnamed small genus and species. YGSP 53266, a left p2 from Locality Y714 (12.8 Ma), is smaller than *Microloris pilbeami* and has a blunt cusp (Flynn and Morgan 2005). The specimen extends the temporal range of small lorisids into the Chinji Formation.

Figure 12.2. Mandible of the type specimen of *Nycticeboides simpsoni*, YGSP 8091, from Locality Y363 dated to about 9 Ma. Scale bar = 1 cm.

Lorisidae, unnamed large genus and species. Two lower molars from the Kamlial Formation, YGSP 19069, a left m2 from Locality Y592 (16.0 Ma), and YGSP 33156, a right m3 from Locality Y682 (15.2 Ma), represent a large lorisid (Flynn and Morgan 2005), larger dentally than living *Nycticebus coucang* and therefore probably weighing more than 2 kg (Nowak and Paradiso 1983). The size and bulbous shape of the molar cusps suggest a largely frugivorous diet.

Lorisoid Evolution and Biogeography

Comparative genetic data suggest a late Middle Eocene origin for Lorisoidea (Yoder and Yang 2004). Several lorisoid genera have been described from the Early and Middle Miocene of East Africa (Phillips and Walker 2002) and, based on this record, Seiffert (2007) and Seiffert, Simons, and Attia (2003) have also suggested a late Middle Eocene Afro-Arabian origin for the group. A late Early Miocene specimen from Thailand attributed to "?*Nycticebus*" (Mein and Ginsburg 1997) is the earliest record of Lorisoidea in southern Asia. Lorisoids were present for at least 7 million years in the Potwar Plateau (minimum range of 16.0 to 8.9 Ma). Dental and postcranial morphology of the Potwar fossil specimens, as well as the size range, suggest similarities with both galagids and lorisids (Flynn and Morgan 2005).

Sivaladapidae Thomas and Verma, 1979

Sivaladapis palaeindicus. The type specimen of *Sivaladapis palaeindicus*, GSI D224, is a partial mandible from an unknown locality near Chinji Village (Pilgrim 1932; Gingerich and Sahni 1979). Body size likely exceeded 3 kg, similar to large species of *Lemur* and *Varecia* (Flynn and Morgan 2005).

Indraloris kamlialensis. The type specimen of *Indraloris kamlialensis*, YGSP 44443, is a lower right molar, probably m1, from Locality Y682 (15.2 Ma). A handful of other teeth from this and nearby localities at the same stratigraphic level are about 20% smaller than specimens of *Indraloris himalayensis* from the Late Miocene at Haritalyangar, India (Gingerich and Sahni 1979; Flynn and Morgan 2005).

Indraloris large species. Two specimens of a large *Indraloris* have been identified from the Kamlial Formation (Flynn and Morgan 2005). These are larger than *I. kamlialensis* and similar in size to *I. himalayensis* (Gingerich and Sahni 1979).

Sivaladapid Evolution and Biogeography

Sivaladapids are also present in the Indian Siwaliks at Ramnagar and Haritalyangar. Ramnagar has not been paleomagnetically dated but is faunally equivalent to the Chinji Formation in the Potwar Plateau (~14–11 Ma), perhaps correlating to the lower half of that range (Gilbert et al. 2019), but most likely in the middle of the range. Primate-bearing sediments at Haritalyangar are dated to ~9.2–8.6 Ma (Pillans et al. 2005). Ramnagar contains *S. palaeindicus* and the newly named *Ramadapis sahnii* (Gilbert et al. 2017). *Sivaladapis nagrii* from Haritalyangar differs from *S. palaeindicus* in having a more derived molar morphology, including higher cusps and more molariform lower premolars, and is interpreted to have been a mixed frugivore-folivore (Patnaik et al. 2014). It is also smaller than *S. palaeindicus* and is plausibly derived from it (Gingerich and Sahni 1979, 1984; Flynn and Morgan 2005). *Indraloris himalayensis* is represented by two specimens from Haritalyangar (Gingerich and Sahni 1979). Thus, of the six sivaladapid species known from Siwalik sediments, *S. palaeindicus* is the only one common to both the Potwar Plateau and the Indian Siwaliks, despite Ramnagar and Haritalyangar being, respectively, only ~150 and 400 km to the east of the Potwar. The presence of *Sivaladapis* and *Indraloris* at Haritalyangar reveals that both genera were present for several million years in the Indian subcontinent and persisted later in the Indian Siwaliks than in the Potwar Plateau.

Sivaladapids are known from elsewhere in Asia during the Miocene—*Siamodapis* from Thailand, dated to 13.3–13.1 Ma (Chaimanee et al. 2008), and *Sinoadapis* from Lufeng in southern China, dated to 6.9–6.2 Ma (Pan and Wu 1985; Wu and Pan 1986; Yue and Zhang 2006), the latter being the latest record of the family. They are also known from Eocene and Oligocene localities in China, Myanmar, and Pakistan (Beard et al. 2007; Marivaux et al. 2002, 2008; Qi and Beard 1998), which gives the group a temporal range of more than 30 million years. The known geographic range of sivaladapids indicates that they were likely endemic to southern and eastern Asia.

CATARRHINI É. GEOFFROY SAINT-HILAIRE, 1812

Siwalik fossil catarrhines include primitive catarrhines of uncertain status, a pliopithecoid, a hylobatid, hominids, and cercopithecids, all unevenly distributed through space and time. By far the most abundant remains are those of the hominid *Sivapithecus*, while primitive catarrhines, the hylobatid, and the pliopithecoid are known from only one or a few specimens each.

Sivapithecus Pilgrim, 1910

The taxonomy of *Sivapithecus* has proven quite vexing from its earliest description (see Kelley 2002), and there is still no consensus about the number of species or the allocation of specimens to species (Kelley 2005). This is a consequence of *Sivapithecus* being relatively uncommon and the sample comprising, apart from a partial skull, YGSP 15000 (Figure 12.3), mostly fragmentary remains. There is general agreement about the validity of two of the three first-named Siwalik *Sivapithecus* species, *S. sivalensis* Lydekker, 1879 and *S. indicus* Pilgrim, 1910, but not about their hypodigms. The types of both of these species are from the Potwar Plateau, while that of the third, *S.* ("*Ramapithecus*") *punjabicus*, now regarded as a junior synonym of *S. sivalensis,* is from Haritalyangar in India. The traditional conception is of a large (*S. indicus*) and small (*S. sivalensis*) species pair (e.g., Simons and Pilbeam 1965; Greenfield 1979; Kay 1982), but there is no consistency among those using this taxonomy in the assignment of specimens in the middle of the overall size range. Moreover, acknowledgment of the implications of this taxonomic scheme for dental, and by extension, body-size sexual dimorphism, is rare; these would have been quite low by extant ape standards, given the overall size range in each of these species. An alternative taxonomy followed here sees time-successive species (Kelley 1986, 1988, 2005)—the earlier *S. indicus* from the Chinji Formation and the later *S. sivalensis* from the Nagri and Dhok Pathan Formations (see Fig. 12.1). In this taxonomy, both species contain large (male) and small (female) specimens, and dental sexual dimorphism in both is substantial, more or less equivalent to that found in extant *Gorilla* or *Pongo* (Kelley 2005). The two species are nearly identical in known dento-gnathic morphology, but there are differences in molar proportions, and the teeth of *S. indicus* are, on average, slightly smaller

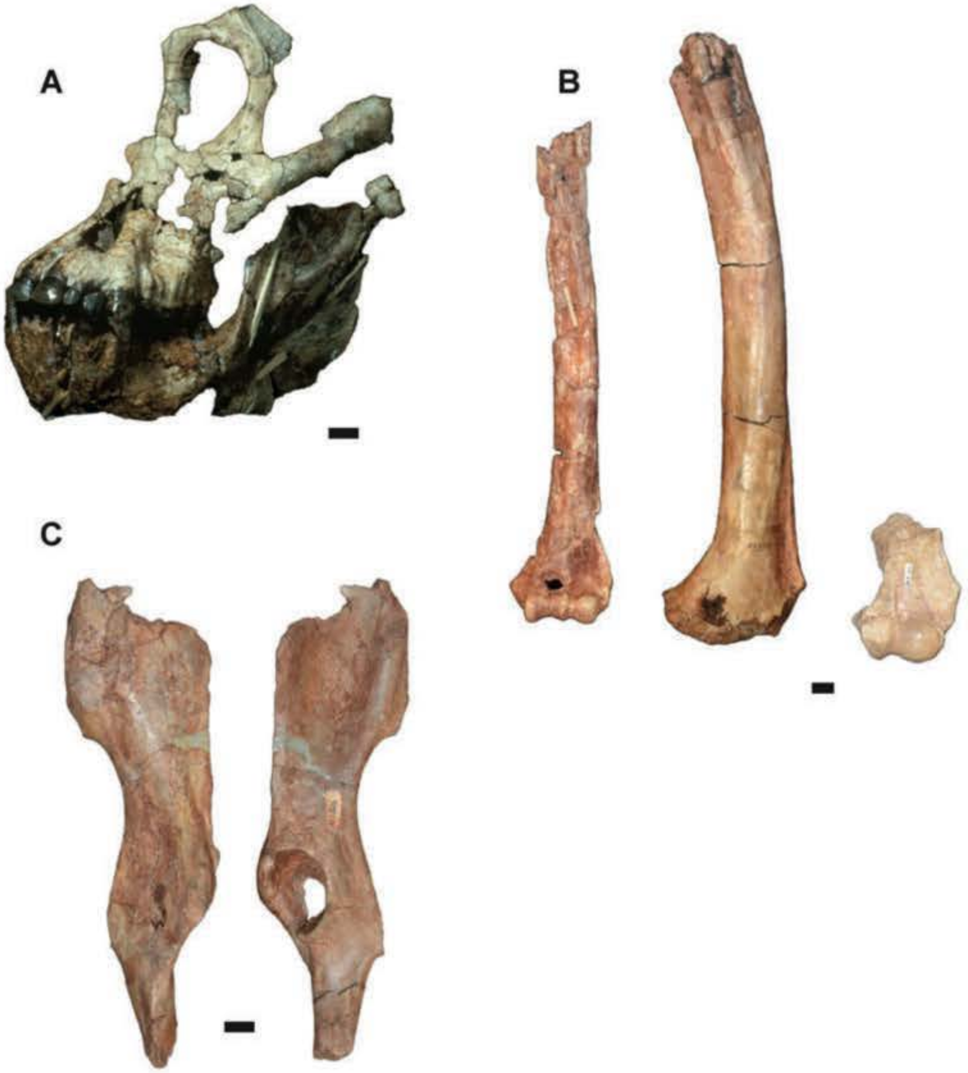

Figure 12.3. Sivapithecus: A. partial skull of *S. sivalensis*, YGSP 15000 from Locality Y410 dating to 9.4 Ma; B. humeri, from left to right: YGSP 30730, left humerus of *S. indicus* from Locality Y76 dated to 11.4 Ma, YGSP 30754 (left humerus) and YGSP 12271 (right humerus, reversed) of *S. parvada* from Locality Y311 dated to 10.1 Ma; C. partial left innominate of *S. indicus*, YGSP 41216 from Locality Y647 dated to 12.4 Ma. Scale bars = 1 cm.

than those of *S. sivalensis* (Kelley 2005). There are also differences between the one partial palate of *S. indicus* and those of *S. sivalensis* (Begun and Güleç 1998), but whether these reflect inter-individual variation or species-specific morphology is not clear. There are few shared elements among the postcranial samples of the two species, and those that are shared (humerus, calcaneus) show no meaningful differences.

There is also general agreement about a third, very large species of *Sivapithecus*, *S. parvada* Kelley, 1988, known from a single Potwar locality, Y311, and not known from outside the Potwar Plateau. In addition to the inferred body mass of *S. parvada* being substantially greater than that of both *S. indicus* and *S. sivalensis* (Table 12.1 and below), *S. parvada* also differs from both in having relatively large premolars in relation to molars and different upper central incisor morphology (Kelley 1988; Kelley et al. 1995).

While the temporal range of *S. parvada* is confined to the depositional period of the Y311 locality, perhaps several tens of thousands of years at ~10.1 Ma, the narrow stratigraphic interval that has produced most of the remains spans perhaps no more than a few hundred years (Behrensmeyer 1987). Both *S. indicus* and *S. sivalensis* are known from numerous localities, but their relative rarity, combined with the low quality of the Potwar fossil record during long stretches of time (Barry et al. 1995, 2002), make it difficult to precisely delimit their temporal ranges. The first appearance of *S. indicus* (12.7 Ma) and the last appearance of *S. sivalensis* (8.5 Ma) are preceded and followed, respectively, by several 100,000-year intervals[1] of high record quality (large numbers of mammal specimens and numerous species represented) in which they are not found, making these dates highly reliable. In contrast, the quality of the record over the interval in which *S. indicus* last appeared and *S. sivalensis* first appeared (or during which anagenesis occurred—see below) is relatively poor and specimens are few. Thus, the precise temporal ranges of *S. indicus* and *S. sivalensis* remain unknown.

Finally, there is a long history of discussion regarding the possible presence of a fourth, very small species of *Sivapithecus* (see Kelley 2002, 2005; Bhandari et al. 2018). The few suggested hypodigms for this species all contain only a handful of specimens, some from the Potwar Plateau and some from Haritalyangar in India, and all include specimens that extend over much of the temporal and geographic range of *Sivapithecus* as a whole. While there are certainly some quite small dental and mandibular specimens in the greater Siwalik sample (including India), there are no obvious breaks in the continuity of dental metric distributions by which this species, if it exists, might be easily delimited. If a very small species is present, naming it will depend on which specimens are included in the hypodigm (Kelley 2005; Bhandari et al. 2018).

Body Size and Body-Size Dimorphism

Postcranial remains are known for all three *Sivapithecus* species, and for all three, most or all postcranial elements broadly fall into two size groups corresponding to males and females (see Table 12.1; see also DeSilva et al. 2009). Based on comparisons to extant primates, male and female body-size estimates for the three *Sivapithecus* species are: *S. parvada*, ~60–70 kg and ~30–35 kg; *S. sivalensis*, ~50–55 kg and ~25–30 kg; *S. indicus*, ~30–45 kg and ~20–25 kg. Body-size dimorphism in all three species is therefore estimated to have been about 2:1 or similar to that in *Pongo pygmaeus*.

Locomotion and Substrate Use

As shown in Table 12.1, there is not a great deal of overlap in postcranial elements among the three *Sivapithecus* species. However, where it occurs (humerus, calcaneus), the morphology is remarkably consistent among species, in spite of the considerable size disparity between *S. parvada* and the other two species. These and all other elements present a consistent picture regarding positional behavior, locomotion, and substrate use in *Sivapithecus*: a generalized, above-branch, arboreal quadruped that was capable of engaging to some degree in a variety of other arboreal locomotor modes such as climbing and certain forms of suspension (Rose 1984, 1986, 1989, 1994, 1997; Pilbeam et al. 1980, 1990; Madar et al. 2002; DeSilva et al. 2009; Morgan et al. 2015). Even occasional terrestriality may have been practiced (Spoor, Sondar, and Hussain 1991; Madar et al. 2002), although we find evidence that *Sivapithecus* was a habitual knuckle-walker (Begun and Kivell 2011) unconvincing. That *Sivapithecus* engaged primarily in monkey-like quadrupedal locomotion rather than the suspensory behaviors common in modern apes is particularly borne out by the morphology of the humeral diaphysis and pelvis (Figure 12.3).

In addition, it has been proposed that *Sivapithecus* relied on a mechanism of balance that may have been peculiar to a number of other mostly quadrupedal arboreal Miocene apes, but not utilized by any living anthropoid. It is presumed that *Sivapithecus*, like other apes, did not possess a tail, so that balance was maintained by maneuvering the torso and the center of gravity from secure hand and foot holds held in a variety of orientations, rather than by reliance on a tail as a counterweight or counter force (Kelley 1997; Morgan et al. 2015; see also Larsen and Stern 2006). Such a mechanism is compatible with postcranial features in *Sivapithecus* that are associated with enhanced limb mobility, especially distally (Rose 1986; Pilbeam et al. 1980, 1990; Madar et al. 2002), and with powerfully grasping hands and feet, enhanced by hallux and pollex elements that are both relatively long and robust (Pilbeam et al. 1980; Madar et al. 2002).

Diet

Tooth morphology, microwear, and carbon and oxygen isotopes from enamel support a predominantly frugivorous diet derived largely from upper-canopy forage (Nelson 2003, 2007). Intraspecific variation in *Sivapithecus sivalensis* microwear suggests that the fruits consumed varied in hardness, including both fruits softer in consistency, like those ordinarily consumed by chimpanzees, and some harder fruits, as often consumed by orangutans (Teaford and Walker 1984; Nelson 2003).

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[1] 100,000-year intervals are the standard for analysis of the Potwar Plateau faunal record.

Table 12.1. Body Mass Estimation in *Sivapithecus*

	Element	Comparison to Extant Primate Species
S. indicus		
YGSP 1656	Distal tibia	Similar to male proboscis monkey: ~20 kg
YGSP 17118	Ectocuneiform	Similar to small male chimpanzee: ~45–50 kg
YGSP 17119	Capitate	Slightly smaller than male & female bonobos: ~30–40 kg
YGSP 28230	Calcaneus	Similar to male proboscis monkey: ~20 kg
YGSP 30730	Humerus	Similar to male baboon: ~25 kg
YGSP 41216	Innominate	Similar to male proboscis monkey & baboon: ~20–25 kg
YGSP 46459	Navicular	Similar to male proboscis monkey: ~20 kg
S. parvada		
NG 933	Metacarpal I	Head slightly larger than male chimpanzee, shaft as stout as male gorilla: ~65–70 kg
NG 940	Hamate	Slightly larger and stouter than male chimpanzee: ~60 kg
YGSP 6454	Int. cuneiform	Similar to male baboon: ~25 kg
YGSP 6663	Distal humerus	Similar to male baboon; slightly smaller than female chimpanzee: ~25–30 kg
YGSP 6664	Pollical prox. phalanx	Slightly larger than male gorilla; relationship of phalanges to body mass uncertain
YGSP 12271	Distal humerus	Similar to male orangutan: ~70 kg
YGSP 17152	Calcaneus	Similar to male chimpanzee: ~60 kg
YGSP 17606	Calcaneus	Similar to small female chimpanzee: ~30–35 kg
YGSP 19905	Cuboid	Slightly larger than male baboon: ~30 kg
YGSP 30754	Humerus	Slightly smaller than male orangutan: ~65 kg
YGSP 47700	Hallucal dist. phalanx	Similar to male gorilla; relationship of phalanges to body mass uncertain
YGSP 51344	Pollical prox. phalanx	Similar to male gorilla; relationship of phalanges to body mass uncertain
S. sivalensis		
YGSP 4664	Calcaneus	Larger than siamang; smaller than male baboon: ~15–20 kg
YGSP 6178	Femoral head	Intermediate between siamang and female chimpanzee: ~20–25 kg
YGSP 10785	Talus	Larger than siamang; much smaller than male baboon: ~15–18 kg
YGSP 11867	Femoral head	Slightly larger than male baboon: ~25 kg
YGSP 13420	Femoral shaft	Similar to male baboon: ~25 kg
YGSP 13506	Distal humerus	Similar to small female chimpanzee but less robust: ~30 kg
YGSP 13929	Femoral head	Intermediate between siamang and female chimpanzee: ~20–25 kg
YGSP 14046	Hallux	Metatarsal head slightly smaller than male chimpanzee; phalanges larger than female chimpanzee: ~50 kg
YGSP 15782	Femoral head	Slightly larger than male baboon: ~25–30 kg
YGSP 47025	Distal femur	Slightly larger than male baboon: ~25–30 kg

Habitat Preference

The Potwar Siwalik sequence preserves very few plant remains and lacks pollen. Reconstruction of habitats associated with *Sivapithecus* between ~13 and ~8 Ma relies therefore on carbon and oxygen isotopic analyses of paleosols and mammalian teeth, on mammalian ecomorphology, and on inferences from sedimentology. Habitats over the interval when *Sivapithecus* was part of the mammal community are reconstructed as mosaic, with probable gallery forests, woodlands of varying density, and some grassland, while climates would have been subtropical and seasonal although not strongly so (Behrensmeyer, Willis, and Quade 1995; Scott, Kappelman, and Kelley 1999; Barry et al. 2002; Nelson 2005, 2007; Behrensmeyer 2007; Badgley et al. 2008; Morgan et al. 2009). Given the inferred positional repertoire of *Sivapithecus*, together with indications that a substantial amount of feeding took place in the upper canopy (Nelson 2005, 2007), it is likely that *Sivapithecus* was highly dependent on forests and denser woodlands.

Life History

Life history in *Sivapithecus parvada* has been examined using the chronology of dental development derived from the remains of a juvenile, YGSP 11536 and YGSP 46460, that died shortly after the first molars erupted. From the incremental growth features preserved on the upper incisors (Figure 12.4), it was possible to estimate a likely age at first molar emergence of 40–41 months, which falls within the ranges of extant great apes (Kelley 1997). Since age at first-molar emergence is a useful proxy for the overall schedule of development in primates (Smith 1989; Kelley and Schwartz 2010), the estimated age at death for this individual reveals that life history in *Sivapithecus* would have been broadly the same as the prolonged life histories of extant apes.

Indopithecus von Koenigswald, 1950

Indopithecus giganteus (Pilgrim 1915) is known from only two specimens, of which the type, an m2, is from the Potwar Plateau but is of uncertain provenance. The other specimen, a relatively

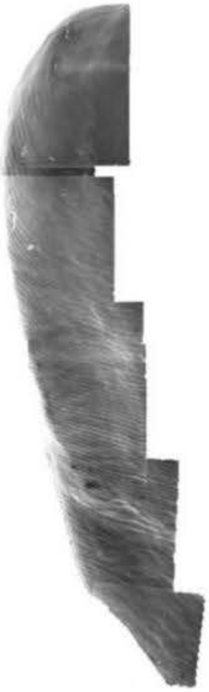

Figure 12.4. Incremental growth features on upper incisor enamel of juvenile *Sivapithecus parvada* (YGSP 46460, from Locality Y311 dated to 10.1 Ma).

complete mandible, is from Haritalyangar in India. The mandible was described as representing a species of *Gigantopithecus*, *G. bilaspurensis* (Simons and Chopra 1969). Szalay and Delson (1979) combined the two specimens as *G. giganteus*, but they were returned to the resurrected *Indopithecus* by Cameron (2001). At ~8.6 Ma (Pillans et al. 2005), the Haritalyangar mandible is the youngest hominid specimen recovered from that sequence and is among the youngest hominids from the Siwaliks.

Cf. *Dionysopithecus* Li, 1978/Primitive Catarrhine

A small upper molar from ~16.0 Ma in the Kamlial Formation was regarded by Barry, Jacobs, and Kelley (1986) as taxonomically indeterminate, being equally similar to the early Middle Miocene *Dionysopithecus* from China and Early Miocene *Micropithecus* from East Africa. *Dionysopithecus* is possibly a primitive pliopithecoid (Harrison and Gu 1999), while *Micropithecus* is generally regarded as a primitive catarrhine and is placed in the superfamily Dendropithecoidea by Harrison (2010).

A small proximal humerus from the Chinji Formation bears similarities to a variety of primitive catarrhines or even platyrrhines such as *Cebus* (Rose 1989). Whether it represents the same taxon as the Kamlial molar cannot be determined, but it is additional evidence for the rare presence of small, non-hominoid, non-cercopithecoid catarrhines in the early Potwar record.

Mesopithecus Wagner, 1839

Over decades of collecting, a small number of cercopithecid primates have been recovered from the Late Miocene of the Potwar Plateau. Only four of these have reliable provenance, three recovered by the Harvard-GSP project from localities in the Kaulial Kas area and one collected by G. E. Lewis in the 1930s from Locality L082 near Hasnot, and range in age from 7.7 to 7.0 Ma. The best preserved of these is YGSP 14043, a partial mandible (Figure 12.5). Several other fragmentary specimens were also recovered by earlier researchers, mainly from deposits in the Hasnot area, estimated to range in age from 7.2 to 6.4 Ma (J. Barry, pers. comm., revised from Barry 1987). Two species were named from this earlier material, the first being *Macaca sivalensis* Lydekker, 1878, but this and the other remains were eventually all recognized to be colobine (Simons 1970). Delson (1975, 1994) and Szalay and Delson (1979) combined all the specimens into a single species, which Harrison and Delson (2007) later tentatively assigned to the cosmopolitan Late Miocene genus *Mesopithecus*, as *M. sivalensis*. However, the available material is too fragmentary and insufficiently studied to say anything about the paleobiology of this species.

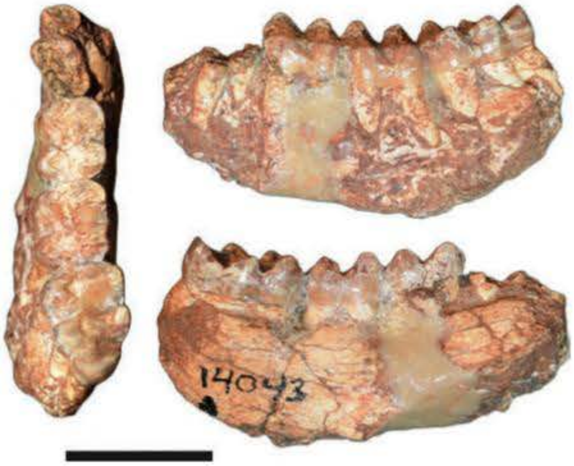

Figure 12.5. Partial mandible of *Mesopithecus* (YGSP 14043 from Locality Y370 dated to 7.2 Ma) in occlusal, lingual and labial views. Scale bar = 1 cm.

More recently, additional cercopithecid dento-gnathic specimens were recovered from the Hasnot area, dated to ~7.9–7.0 Ma and assigned to cf. *Mesopithecus* sp., pending comparison to the earlier material (Khan et al. 2020).

Catarrhime Primates from the Indian Siwaliks, Southern Pakistan, and Nepal

Catarrhine primates are also known from the more easterly regions of the Siwaliks in India. Among hominids, these include, in addition to *Indopithecus*, both *S. indicus* from the Ramnagar area and *S. sivalensis* from the vicinity of Haritalyangar and farther east (Kelley 2002 and references therein; Cameron, Patnaik, and Sahni 1999; Patnaik 2013; Gilbert et al. 2019). The sample from the Haritalyangar area contains several specimens that are larger than any *S. sivalensis* specimens from the Potwar Plateau, although more similar in size to the latter than to *S. parvada* (Kelley 1988), as well as some that are among the smallest, which makes the taxonomy of the sample difficult to interpret (Kelley 2005; Scott, Schrein and Kelley 2009). If the largest specimens are in fact *S. sivalensis*, they appear to represent a larger regional variant than in the Potwar Plateau. Both Ramnagar and Haritalyangar also preserve catarrhines unknown from the Potwar Siwalik sequence. A single m3 from Ramnagar, representing a new genus and species, *Kapi ramnagarensis*, has been assigned to Hylobatidae (Gilbert et al. 2020). If this assignment is accurate (see Ji et al. 2022; Gilbert et al. 2023), it would nearly double the temporal range of fossil hylobatids to between ~12 and ~13 Ma and represent the first record of the family outside southeastern Asia (Pan 2006; Harrison 2016). The pliopithecoid from Haritalyangar, *Krishnapithecus krishnaii* Chopra and Kaul, 1979 is highly derived and, dentally, is one of the largest pliopithecoids (Sankhyan, Kelley, and Harrison 2017).

Six cercopithecid dento-gnathic specimens, one partial maxilla and five partial mandibles, have also been recovered from (younger) Indian Siwalik sediments. The maxilla was the first fossil primate to be described from the subcontinent and the first fossil to have been recognized as primate (Baker and Durand 1836); it was named *Semnopithecus subhimalayanus* in a catalog by von Meyer (1848) but is now generally assigned to *Procynocephalus*. The mandibular fragments, three of which were described by Falconer and Cautley (1837), have a checkered taxonomic history (Lydekker 1884, 1886; Verma 1969; Delson 1973, 1975; Szalay and Delson 1979). There is still disagreement about species attribution and, for two specimens, subfamily attribution (Delson 1973, 1975; Jablonski 2002).

A single hominid molar has been recovered from sediments in Nepal that appear to be faunally equivalent to the Chinji Formation of the Potwar Plateau (Munthe et al. 1983).

Primate teeth have also been recovered from the (mostly) early Middle Miocene Manchar Formation at Sehwan in southern Pakistan (Raza et al. 1984; Bernor et al. 1988). The smaller teeth were provisionally assigned to *Dionysopithecus*, but this has been questioned by Harrison and Gu (1999). In size and morphology, they are compatible with the unassigned molar from the Kamlial Formation in the Potwar Plateau described by Barry, Jacobs, and Kelley (1986) and offer further evidence for the widespread occurrence of small, primitive catarrhine primates in South Asia at this time. Two of the Manchar Formation teeth, however, are larger. One (GSP S214) is a large hominid molar from near the top of the local section, which also produced teeth of *Hipparion*, so it is Late Miocene in age and contemporaneous with later hominid-bearing sediments in the Potwar Plateau. The other (GSP S100) is a worn molar fragment that cannot be definitively identified as hominid or even hominoid. If it is, its position from much lower in the section would establish the presence of large hominoids in the subcontinent considerably earlier than the first appearance of *Sivapithecus* in the Potwar Plateau at 12.8 Ma, and perhaps among the earliest in Eurasia (see Raza et al. 1984).

Finally, a poorly preserved maxillary fragment from Kutch, Gujarat state in western India, assigned to *Sivapithecus* sp., is dated faunally to younger than 10.8 Ma (Bhandari et al. 2018). This is the only definitive occurrence of *Sivapithecus* outside the Siwaliks and extends its range southwestward by roughly 1,000 km, although much less than this if either of the two large catarrhine teeth from Sehwan in southern Pakistan is *Sivapithecus*.

Siwalik Catarrhine Evolution and Biogeography

There are no obvious precursors to *Sivapithecus* in the fossil record, although the record of hominoids in Eurasia is quite sparse prior to its first appearance at 12.8 Ma. The only earlier sample with more than a handful of specimens is from Paşalar, at 14–15 Ma, while the earliest hominoids from the Vallès Penedès Basin in Spain are ~12 Ma (Casanovas-Vilar et al. 2011). The two species in the large Paşalar sample, *Kenyapithecus kizili* and *Griphopithecus alpani*, are known almost entirely from teeth (Alpagut, Andrews, and Martin 1990; Martin and Andrews 1993; Gençturk, Alpagut, and Andrews 2008), which, along with the few cranial and mandibular remains, are largely uninformative with respect to *Sivapithecus* ancestry. One specimen reveals a rather large palatal incisive foramen (Kelley, Andrews, and Alpagut 2008), unlike the more restricted foramen in *Sivapithecus*, which is part of a derived subnasal morphological complex that is distinctive for *Sivapithecus* and the later *Khoratpithecus* from Thailand and Myanmar (Chaimanee et al. 2019) among Miocene hominoids. None among the very large number of catarrhine species from the Early and Middle Miocene of East Africa shows any particular affinity with *Sivapithecus*.

If the origins of *Sivapithecus* are uncertain, its phylogenetic position within Hominoidea seems clearer, but even that comes with caveats. As noted, *Sivapithecus* uniquely shares with extant *Pongo* a suite of craniofacial features that are widely interpreted as confirming membership in the Ponginae (see Figure 12.3). These include vertically elongate orbits; a narrow interorbital septum lacking ethmoid sinuses; absence of a frontal sinus; a continuously concave upper and midfacial profile combined with pronounced nasoalveolar prognathism; a subnasal morphology characterized by a premaxilla that extends well into the nasal cavity; a smooth transition from the premaxilla to the palate; a reduced incisive fossa, narrow incisive canal, and a slit-like incisive foramen (Andrews and Cronin 1982; Pilbeam 1982; Ward and Kimbel 1983, Ward and Pilbeam 1983; Ward and Brown 1986, McCollum et al. 1993, Brown, Kappelman, and Ward 2005). In contrast, the teeth and mandible do not bear any particular resemblance to those of *Pongo*, with the possible exception of upper central incisor morphology and premolar/molar proportions in *S. parvada* (Kelley 1988; Kelley et al. 1995). Likewise, while many individual features among the *Sivapithecus* postcranial elements are broadly like those of extant great apes (and many more that are not), none is exclusively like those of *Pongo* (Madar et al. 2002 and references therein; Morgan et al. 2015), nor, as noted, is overall postcranial morphology at all like that of extant great apes. While we tend to favor the view that the shared craniofacial features of *Sivapithecus* and *Pongo* represent homologies while much of the shared postcranial morphology of extant great apes results from homoplasy, we acknowledge that there are no clear biological criteria for deciding such questions (Morgan et al. 2015).

Regarding other Miocene apes, there is little morphological similarity between *Sivapithecus* and most other fossil taxa, especially cranially, even among taxa considered by some to be in the *Pongo* clade. *Ankarapithecus* from Turkey bears some similarity in a few cranial features, but overall has a fundamentally different morphology and mostly lacks the numerous *Pongo*-like features evident in *Sivapithecus* (Begun and Guleç 1998; Alpagut et al. 1996; Kappelman et al. 2003; Brown, Kappelman, and Ward 2005). Species of *Lufengpithecus* from southern China are even more dissimilar and show no compelling evidence to support membership in the *Pongo* clade (Kelley and Gao 2012; Ji et al. 2013). Other Eurasian fossil apes with more than a few postcranial remains (*Hispanopithecus* and *Pierolapithecus* from Spain; *Rudapithecus* from Hungary) show a fundamentally different body plan, one more compatible with orthogrady and the frequent use of suspensory behaviors (Moyà Solà and Köhler 1996; Moyà Solà et al. 2004; Kivell and Begun 2009; Begun 2010; Alba 2012; Alba et al. 2012; Begun, Nargolwalla, and Kordos 2012; Ward et al. 2019).

An exception to this lack of similarity is *Khoratpithecus*, which is known from the late Middle and Late Miocene of Thailand and Myanmar. While the first published remains of *Khoratpithecus* were limited to two mandibles and a small number of teeth that are either unlike those of *Sivapithecus* or show no particular affinity (Chaimanee et al. 2003, 2004, 2006; Jaeger et al. 2011), a more recently recovered partial maxilla (Chaimanee et al. 2019) broadly displays the same diagnostic subnasal morphology otherwise evident only in *Pongo* and *Sivapithecus* (Ward and Kimbel 1983).

Beyond origins and phylogeny, some of the more intriguing questions regarding *Sivapithecus* concern the occurrence and abundance of the different species in space and through time, particularly *S. parvada*. Given that species of *Sivapithecus* were probably continuously present in the region for more than 4 myr, the restriction of *S. parvada* to the Y311 locality is noteworthy. Y311 is unusual both for its abundance of fossils and its depositional environment within the Potwar sequence, as the facies associated with fossil concentrations in the Chinji and Dhok Pathan Formations are uncommon in the Nagri Formation (Behrensmeyer 1987: Y311 designated as Level 3; Willis 1993a, 1993b). The massive channel system represented by the Nagri Formation would almost surely have offered a different mix of habitats, or at least in different proportions, than those most frequently associated with other formations. Whether or not the presence of *S. parvada* was dependent on such factors is unknown, and its restriction to this single locality is a conundrum.

The Y311 locality is also unusual for the abundance of *Sivapithecus* specimens relative to other mammalian fossils. For the 25 hundred-thousand-year intervals from the 12.8 to 8.5 Ma *Sivapithecus* time range that have produced at least 150 total mammalian specimens (24 of these intervals have produced at least 200), the average proportion of *Sivapithecus* specimens among all specimens is 0.22 (range: 0–0.66); the value for Y311, which accounts for nearly all the mammal remains in the 10.1–10.0 Ma interval, is 1.18. There are three other hundred-thousand-year intervals with a high relative abundance of *Sivapithecus* remains (*S. sivalensis*), all clustered around the U-level sandstone at ~9.4-9.2 Ma. The values for these are, respectively, 1.20, 4.89 and 3.49. Since these comparisons are restricted to intervals in which record quality is good, the exceptional abundance of *Sivapithecus* within these few time intervals, particularly at 9.3–9.2 Ma, would appear to be real. While the Y311 locality is somewhat unusual as noted above, there is nothing obvious about either the depositional environments or the faunas from localities clustered around the U-level that might explain the exceptional abundance of *Sivapithecus* during this period.

Regarding relationships among species of *Sivapithecus*, it was suggested earlier that *S. indicus* and *S. sivalensis* might be anagenetic species, with *S. parvada* showing no closer relationship to one or the other. However, this is based on little more than the two former species being essentially the same size while the latter is substantially larger. There is nothing in the morphology of the three species to favor any particular hypothesis of relationships among them. Resolving these relationships is made even more intractable by the near absence of any *Sivapithecus* remains between 11.4 and 9.4 Ma, much of this period being of low record quality, other than those of *S. parvada*.

There is little that can be inferred about the evolution and biogeography of other Siwalik catarrhines. Few morphological features distinguish the dentition of *Indopithecus* from that of *Sivapithecus*, although dental proportions differ, with *Indopithecus* having relatively very small canines and incisors (Simons and Chopra 1969). Further, despite its great size, the *Indopithecus* mandible is closely matched morphologically by some mandibles of *S. sivalensis*. It is most reasonable, therefore, to regard *Indopithecus* as a derived taxon within the *Sivapithecus* radiation. The affinities of the small, primitive catarrhine teeth from the Kamlial and Manchar Formations could as easily be with some Early Miocene catarrhine from East Africa as with *Dionysopithecus* from eastern Asia (Barry et al. 1986). Seemingly, a single species of *Mesopithecus*, *M. pentelicus*, ranges from Spain to southwestern China during the Late Miocene (Alba et al. 2015; Jablonski et al. 2020). Further comparative study of the Siwalik *Mesopithecus* will be necessary to determine if it does in fact represent a different species.

PRIMATE EXTINCTIONS IN THE POTWAR PLATEAU

The local extinction of sivaladapids in the Potwar Plateau sequence at 11.6 Ma occurred during a period of low faunal extinction overall, but this was followed by a period of significantly higher rates of extinction that peaked at around 11 Ma (Badgley et al. 2016). It may be that sivaladapids were particularly sensitive to whatever conditions led to this subsequent wave of extinctions.

The conditions that led to the local extinction of other primate groups are clearer. Marked change in habitat from predominantly forests and woodlands to more open woodlands and grasslands, inferred primarily from stable isotope analysis of paleosol carbonates and mammalian enamel, began around 8 Ma on the Potwar Plateau (Behrensmeyer et al. 2007). This change is correlated with significant faunal change, in which most closed-habitat frugivorous and browsing mammals disappear from the record, or with shifts in dietary habits among herbivorous mammals from consuming browse and other C_3 vegetation to increasing reliance on C_4 grasses (Barry et al. 2002; Behrensmeyer et al. 2007; Badgley et al. 2008). A similar pattern and timing of habitat change, from predominantly closed to more open habitats, is documented in the paleobotanical and palynological records of India and Nepal (Hoorn, Ohja, and Quade 2000).

Notably, isotopic evidence, especially from mammalian tooth enamel, also indicates that these habitat changes began much earlier, by 10 Ma or even earlier (Quade, Cerling and Bowman 1989; Morgan, Kingston and Marino 1994; Behrensmeyer et al. 2007), but the isotopic shifts were initially subtle, with as-yet uncertain effects on faunal composition. *Sivapithecus* and other ripe-fruit dependent or extensive closed-canopy-dependent species appear to have been the earliest affected as these changes accelerated (Nelson 2003, 2005, 2007; Badgley et al. 2008), with lorisoids last recorded at 8.9 Ma and *Sivapithecus* at 8.5 Ma. The first appearance of *Mesopithecus* is at 7.7 Ma, roughly at the midpoint of the accelerated period of isotope transition, and postdates the last record of *Sivapithecus* by nearly 1 myr. Thus, the "replacement" of apes by monkeys in the Siwaliks is driven entirely by the differing ecological requirements of the two groups and owes nothing to competition between them.

PRIMATE FAUNAS OF THE POTWAR PLATEAU AND THE INDIAN SIWALIKS

One of the more interesting aspects of the Siwalik primate record is the differences between the primate faunas of the Potwar Plateau and those of the Indian Siwaliks throughout the entirety of this record, despite the relatively small distances between the various Indian sites and the Potwar. These include mostly different sivaladapid species and the persistence of the group in India for more than 2 myr longer than in the Potwar; the absence of *S. parvada* in the Indian record (although possibly being due to an unrepresented time interval); apparent differences in the body size of *Sivapithecus* in the two regions ~9 Ma, perhaps reflecting the appearance of a different, larger species in the Indian Siwaliks at this time; and the presence of both a pliopithecoid and a probable hylobatid in the Indian Siwaliks but not in the Potwar. The absence of lorisoids from the Indian Siwalik record is likely an artifact of infrequent sediment screen-washing by groups who have collected there. The reasons for the other differences have not been explored and remain a potential informative line of inquiry into the history of Siwalik primates and into overall regional differences in the biogeography of the Siwalik sequence of South Asia.

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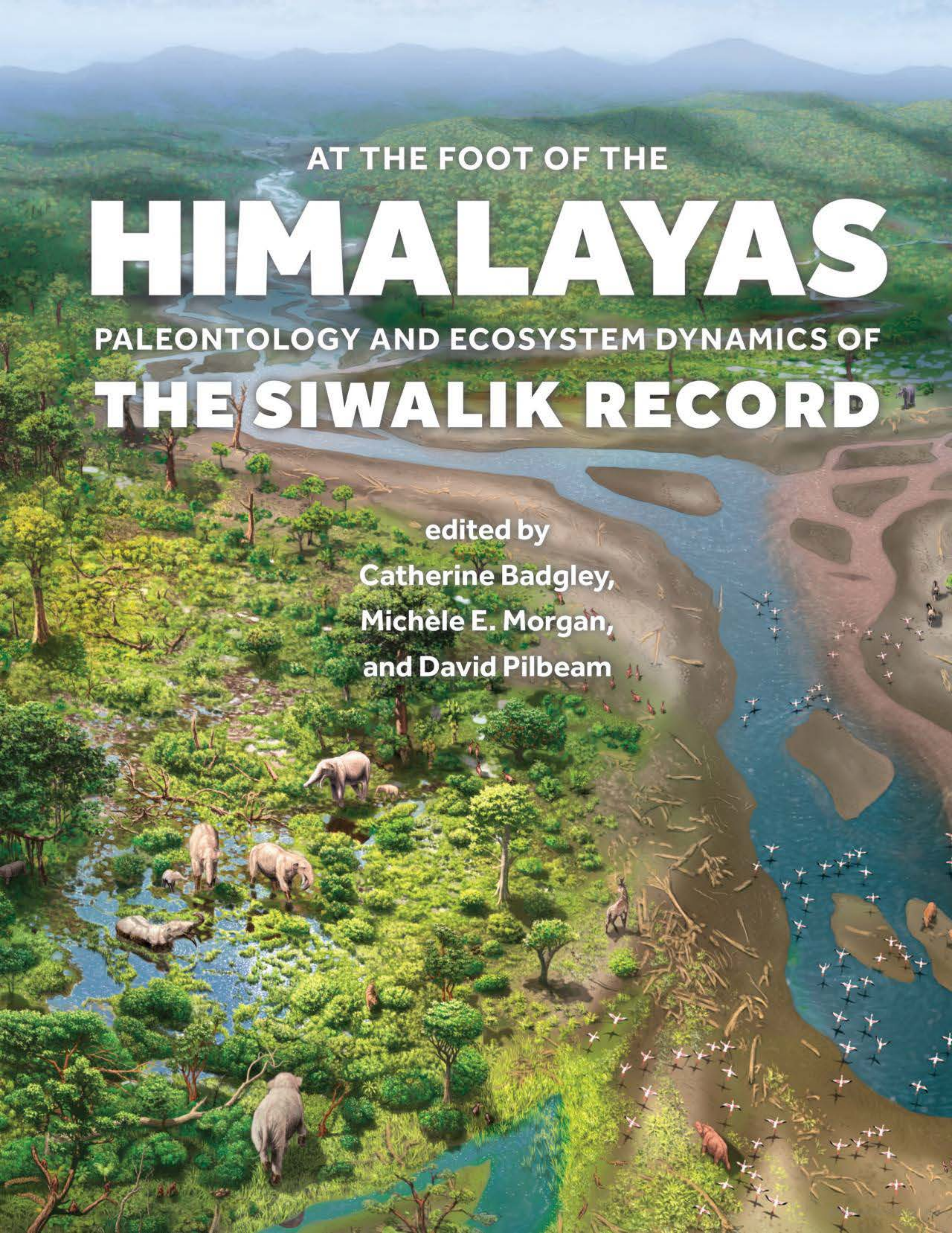

AT THE FOOT OF THE HIMALAYAS

PALEONTOLOGY AND ECOSYSTEM DYNAMICS OF THE SIWALIK RECORD

edited by
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Cover illustration: The western Siwalik sub-Himalayan alluvial plain ecosystem at ~9 Ma (similar in age to Locality Y182, Fig. 24.11). The reconstruction is based on scientific evidence discussed in this book and illustrated by Julius Csotonyi. The view is toward the north, with a large, mountain-sourced river entering from the upper left and a smaller, foothill-sourced tributary entering from the upper right. The scene occurs after the end of the rainy season and shows ponding, sediment deposition, and debris from recent flooding, with smoke from a wildfire visible in a drier area on the upper right. Low hills are visible in the near distance and higher mountains in the far distance.

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