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Extinction of Siwalik fossil apes: a review based on a new fossil tooth and on palaeoecological and palaeoclimatological evidence

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Abstract   We report here a new fossil hominoid tooth from the Late Miocene (~7.8 Ma) of the Hari-Talyangar region, India. The large-sized hominoid M^2 is rather bunodont and its occlusal morphology and size are fairly distinctive from both the *Sivapithecus sivalensis* and *Sivapithecus indicus* conditions. Correlation between upper and lower molar breadth in extant hominoids and *Sivapithecus* species suggests that this upper molar fits within an estimated range of *Indopithecus* (= '*Gigantopithecus*') M^2 variation; a lower M_2 of the same taxon is known from the same region. However, molar size and morphology are also consistent with a *S. parvada* attribution. Therefore its formal taxonomic allocation remains problematic. *Sivapithecus* was primarily a fruit eater and its teeth do not generally show caries, but the present molar exhibits a large caries, indicating a probable diet of grasses and fruits. The supposed diet of the new fossil tooth suggests that these Late Miocene apes of the Hari-Talyangar region lived in a habitat drier than that of *Sivapithecus*. A review based on the present fossil and palaeoecological and palaeoclimatological evidence supports a hypothesis that the Siwalik fossil apes disappeared by the Late Miocene because of a decrease in humidity and an increase in seasonality, aridity, and unpredictable climatic conditions brought about by the intensification of the monsoon system, eventually leading to expansion of grasslands at the expense of rainforests.

Key words: Siwalik, hominoid, *Sivapithecus*, extinction, palaeoclimatology

Introduction

The fluvial sequences of the Siwalik Group are exposed all along the Himalayan foothills from Pakistan in the west to Myanmar in the east. These sedimentary sequences are over 6000 meters in thickness and provide a spectacular laboratory for studies of fluvial dynamics, palaeomagnetic dating, palaeoclimatology, stratigraphic correlation, isotope geochemistry, and vertebrate biochronology spanning the last 20 Ma. The extraordinary fossil record that documents Neogene mammalian evolution includes remains of apes, such as *Sivapithecus*, that are considered ancestral to the orangutan based on facial and palatal morphology (Andrews and Cronin, 1982; Pilbeam, 1982). Recently, however, *Sivapithecus* has been claimed to differ from orangutan in dental and postcranial features (Pilbeam et al., 1990; Ward, 1997).

The Siwalik fossil apes appeared at ~13.5 Ma and disappeared by ~7.5 Ma (Figure 1). This was the time of intense Tibeto-Himalayan uplift (~12–9 Ma) (Amano and Taira, 1992; Prell et al., 1992; Harrison et al., 1993), which probably led to the intensification of the monsoon system in South Asia (Ruddiman and Kutzbach, 1989; Raymo and Ruddiman, 1992; Kutzbach et al., 1993; Hay, 1996; Ramstein et al., 1997). A rapid uplift began at ~10 Ma and ceased after the present elevation (~5 km) was attained at ~5 Ma, indicating that monsoons as strong as today might have started at around 8–7 Ma, when the elevation was half (2.5 km) of the present-day condition (Prell and Kutzbach, 1992). Evidence in support of this hypothesis comes from both oceanic and continental records. At ~8 Ma an endemic foraminiferan and radiolarian fauna is known that suggest upwelling had taken place (Prell et al., 1992). Similar phenomena occur in the modern Indian Ocean; strong summer monsoon winds induce upwelling in the upper water column that controls oceanic primary productivity and promotes the blooming of distinct fauna and flora in different parts of the northern Indian Ocean (Gupta and Melice, 2003). The Indian Ocean diatom record also suggests an intensification of monsoons between 11 and 7 Ma (Schrader, 1974; Burkle, 1989).

A marked shift in $\delta^{13}C$, accompanied by a shift from C3 vegetation (predominantly forests) to more seasonal water-stressed C4 vegetation (grasslands) at ~8.8–8.6 Ma (according to the timescale of Cande and Kent, 1992), and enrichment of $\delta^{18}O$ and decrease in thickness of leaching zones at 9 Ma led Quade et al. (1989) to propose that there was a change in regional climate (intensification of monsoons). By 7 Ma the C4 plants dominated the Siwalik floodplain biomass (Quade et al., 1989, 1995). All across the Indian subcon-
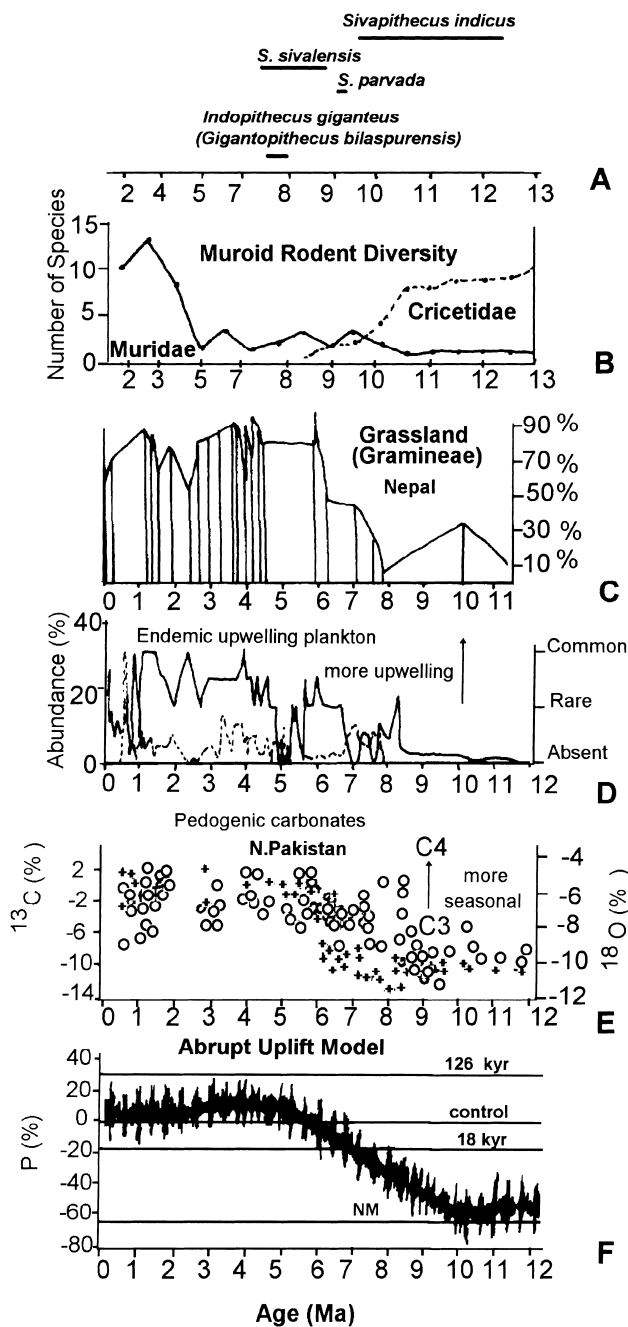
Figure 1. Hominoid occurrences and paleoclimatological and paleoenvironmental indicators of the Siwalik sequence. (A) Age ranges of Siwalik apes, data from this study and Flynn et al. (1995), adjusted following Cande and Kent (1992, 1995). (B) Muroid rodent diversity, from Patnaik (2003). (C) Percentage of grassland, redrawn from Hoorn et al. (2000) Figure 4. (D) Time series of endemic upwelling species of plankton: relative abundance of foraminifera, *Globigerina bulloides* (dotted line), and radiolarian *Actinomma* spp. (solid line), as indices of upwelling induced by monsoon winds, redrawn from Prell and Kutzbach (1992) Figure 4c; arrow indicates direction of increased upwelling. (E) Time series of carbon (crosses) and oxygen (circles) isotopes in soil carbonates in Pakistan as an index of a shift in regional climate and C4 vegetation, redrawn from Prell and Kutzbach (1992) Figure 4d, after Quade et al. (1989); arrow indicates direction of a more arid, highly seasonal environment. (F) Change in precipitation (δP) using the abrupt uplift model, redrawn from Prell and Kutzbach (1992) Figure 4b.

tinent, effected by monsoonal climate, C4 grasses dominate riverine habitats at low elevations. At high temperatures C4 plants are more efficient than C3 plants in CO_2–H_2O exchange accompanying photosynthesis and respiration, allowing C4 plants to function better while under moisture stress during warm season growing (Ehleringer, 1978; Quade and Cerling, 1995). However, $\delta^{13}C$ shifts on a global scale have been noticed ~8–6 Ma ago (Cerling et al., 1993; Quade and Cerling, 1995) and at the Miocene/Pliocene boundary (Cerling et al., 1997). Raymo and Ruddiman (1992) and Quade et al. (1995) opined that regional climates could have affected global CO_2 levels (see also Molnar et al., 1993; Filippelli, 1997).

Hoorn et al. (2000) showed that during the late Middle Miocene to early Late Miocene (~11.5–8 Ma) the Himalayan foothills and the Gangetic floodplain in Nepal were mainly forested with subtropical to temperate broad-leafed and tropical forest taxa, respectively. Between the early to late Late Miocene (~8–6.5 Ma) grassland replaced subtropical and temperate broad-leafed forest in the same regions. Hoorn et al. (2000) suggested that this change may be related to disturbance of the vegetation on the slopes due to uplift, perhaps enhanced by intensification of monsoon. Siwalik palaeosols indicate marked seasonality in rainfall (Retallack, 1991, 1995). Recently, based on inferred first and last occurrences of mammals at 100 kyr resolution, Barry et al. (2002) observed three very brief periods of high faunal turnover at 10.3, 7.8, and 7.37–7.04 Ma. Drastic turnover of Latest Miocene fauna at 7.37 and 7.04 Ma in the Siwaliks of Pakistan were correlated with expansion of C4 grasses, the oxygen isotope and sedimentological evidence indicating an increasingly drier and more seasonal climate (Barry et al., 2002). Patnaik (2003) noted a dramatic change in the diversity of muroid rodents (from cricetid-dominated to murid-dominated) at ~9–8 Ma (Figure 1). This replacement of cricetids by murids in the Late Miocene was attributed to an intensification of the monsoon system (Patnaik, 2003), as most of the present-day murids are found in the monsoon-affected region of the world and their reproduction-oriented life history strategy is better suited to unpredictable and seasonal climatic conditions.

The hominoid fossils from the Siwaliks of Indo-Pakistan, and in particular that of *Sivapithecus* from Hari-Talyangar (India), are a mixture of isolated, fragmentary dentition and partial mandibles and maxillae. The hominoid material from Hari-Talyangar comes from strata dated between 8.7 to 7.3 Ma and is representative of three species: *Sivapithecus indicus* (8.7–8 Ma), *Sivapithecus sivalensis* (8.7–8 Ma), and *Indopithecus giganteus* (7.8–7.3 Ma). *S. indicus* is also known from the Upper Chinji Formation at the Dhara locality (Uttar Pradesh, India) and *S. sivalensis* from the same formation at the Ramnagar locality (Jammu and Kashmir, India) (see Cameron et al., 1999). These two sites have not yet been dated. *I. giganteus* is often referred to *Gigantopithecus*, though Cameron (2001) states that characters shared with the Chinese Pleistocene *Gigantopithecus* species are homoplasies (result of functional convergence). As such, Cameron (2001) resurrected the name *Indopithecus* von Koenigswald (1950) for the Indian Miocene hominoid. The other hominoid that occurs in the Siwaliks is *Sivapithecus*

parvada, which has so far been found only in the Potwar plateau of Pakistan and with an obscure taxonomic position (Kelley, 1988). Many well-preserved specimens of both *S. indicus* and *S. sivalensis* have been found at a number of sites in the Siwaliks, most notably in the Potwar Plateau, Pakistan (Pilbeam et al., 1997, 1980; Madar et al., 2002) and in Nepal (Munthe et al., 1983). In India, an ongoing project at Hari-Talyangar, in particular Dangar and Hari Devi, continues to produce *Sivapithecus* specimens (Patnaik and Cameron, 1997; Cameron et al., 1999).

Since *S. indicus* and *S. sivalensis* have almost identical dentitions, their identification depends on the size of the teeth, with *S. indicus* being the larger of the two (Kelley and Pilbeam, 1986; Kelley, 1988). Dating of deposits containing *S. indicus* and *S. sivalensis*, mainly in Pakistan, indicates that these species are temporally distinct. *S. indicus* derives from older deposits that range from 12.5 to 9.3 Ma (Kappelman et al., 1991) and *S. sivalensis* from younger deposits dated between 8.8 and 7.4 Ma (Flynn et al., 1995). These dates are based on the time scale of Berggren et al. (1985)

and should be ~1 Ma older if we follow the more acceptable timescale of Cande and Kent (1992, 1995). Therefore, *Sivapithecus* in Pakistan ranges from 13.5 to 8.4 Ma. *Indopithecus* was a very large hominoid, about the size of extant gorillas. To date, the representative fossil is a mandibular specimen which was found in the Hari-Talyangar region (Simons and Chopra, 1969).

Hominoid Specimen and Locality from Hari Devi

The Hari Devi I locality (31° 31' 54.0" N, 76° 38' 14.7" E) is located approximately 100 meters north of the Dangar I locality (VPL-1), and is stratigraphically placed above Dangar I (Figure 2A). Both localities are part of the Cuesta scarp as described by Johnson et al. (1983) and Patnaik and Cameron (1997). As suggested by the stratigraphic work of Johnson et al. (1983), Hari Devi I is considered to be around half a million years younger than Dangar I based on palaeomagnetic stratigraphy (Figure 2B). A preliminary geological survey by the Siwalik Hominid Project also supports the
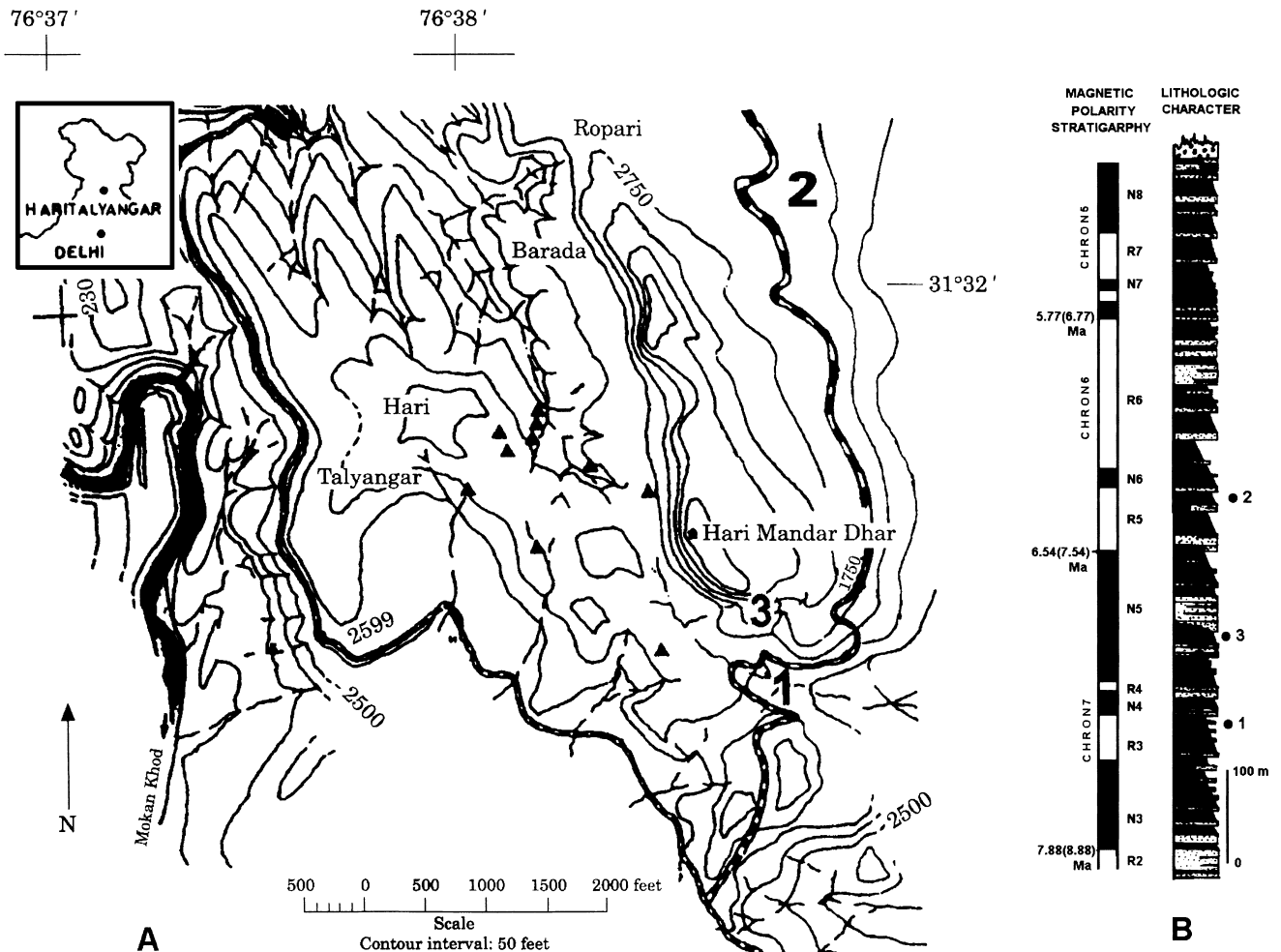

Figure 2.   Geographical and chronological placement of the new hominoid molar. (A) Fossil ape localities of the Hari-Talyangar area, modified after Johnson et al. (1983) and Patnaik and Cameron (1997): (1) the Dangar I locality; (2) the *Indopithecus giganteus* (= *Gigantopithecus bilaspurensis*) locality; (3) the new hominoid molar site Hari Devi I; triangles denote other major hominoid localities. (B) Lithostratigraphy and magnetic polarity stratigraphy near Hari-Talyangar, modified after Johnson et al. (1983). Dates in parenthesis were readjusted following Cande and Kent (1992).

younger date suggested for this locality. A hominoid right M[2] was recovered from a new locality (Hari Devi I). The M[2] is designated VPL/Hari Devi I (1). The specimen was not excavated but was lying on the surface of the exposed outcrop; it is likely to have originated from the maroon mudstone sediments, which are the major fossiliferous deposits in this area (Patnaik and Cameron, 1997; Cameron et al., 1999). Other taxa found at this locality include *Hipparion* sp. and teeth of Bovidae sp. indet.

The new hominoid molar is thought to be an M[2] because the hypocone is reduced in height but not to the degree observed in upper third molars (Figure 3). There is minor occlusal wear that does not reach the dentine. The surface enamel is smooth and lacks extensive enamel wrinkling as commonly observed in *Sivapithecus* specimens from the same area. The mesial crown has a large portion of enamel missing due to a pathological condition (it is damaged with a large caries). Tooth roots are preserved with two buccal and a single large lingual root.

The tooth is rectangular in occlusal outline, broader than long. Each buccal cusp is anteriorly placed relative to its opposite lingual cusp, giving a rhomboid appearance to the tooth (Figure 3). The mesial fovea cannot be identified because of the missing enamel. It is evident, however, that a preparastyle existed slightly anterior to the paracone. The paracone and protocone are of similar size and are higher than the distal cusps. Both the metacone and hypocone are reduced in size. Cristae are undeveloped and the tooth has a simple bunodont morphology. The crista obliqua is identified as a low relief. There is no posterior transverse crista, as is commonly observed in *S. sivalensis* specimens from the same region (Cameron et al., 1999). The tooth has a slight lingual cingulum below and between the buccal cusps. There is waisting of the tooth, but lingual and buccal fissures do not continue onto the occlusal surface. The overall simple appearance of this tooth is more similar to the condition observed in *S. parvada* specimens from Pakistan than that of *S. sivalensis* specimens from the Hari-Talyangar area, whose

molar morphology is characterized by complicated cristae formation (Patnaik and Cameron, 1997; Cameron et al., 1999).

Measurements taken from the specimen, VPL/Hari Devi I (1), are shown in Table 1, as are values from other *Sivapithecus* M[2] teeth. This tooth is large, especially compared with other hominoid specimens from the Hari-Talyangar region. A bivariate plot of *Sivapithecus* M[2] length and breadth demonstrates the larger size of the new specimen relative to *S. sivalensis* and *S. indicus* (Figure 4). It clearly falls between the ranges of *S. indicus* and *S. parvada*.

Phylogenetic Position of the New Fossil Tooth from Hari Devi I

Kelley (1988), in his description of *S. parvada*, focused on the lower dentition of this species, although in his hypodigm he allocated the maxillary fragment SM-I (with P[3]–M[3]) to *S. parvada*. The upper molars of the SM-I specimen are characterized by their large size and uncomplicated occlusal morphology (von Koenigswald, 1950). As described above, a similar character set is found in the Hari Devi I specimen. It is not to say, however, that the new specimen represents a later 'Indian' deme of *S. parvada*, as the apparent temporal gap between the Pakistan and Indian localities suggests that this is unlikely (though not impossible). Sethi Nagri deposits in Pakistan are dated to ~9.0 Ma, (Kelley, 1988), while the Hari Devi I locality is currently thought to be ~7.8 Ma. Indeed, the large size and bunodont morphology with thick enamel might also be characteristic of the upper molars of *Indopithecus*, as suggested by the mandibular dentition of this genus. Specimens assigned to *Indopithecus* have been recovered from a site in the Hari-Talyangar region, the age of which was estimated to be close to that of the Hari Devi I tooth.

Because no upper molars of Siwalik *Indopithecus* have yet been found, the allocation of the Hari Devi I tooth to either species is problematic. The extant hominoids show a
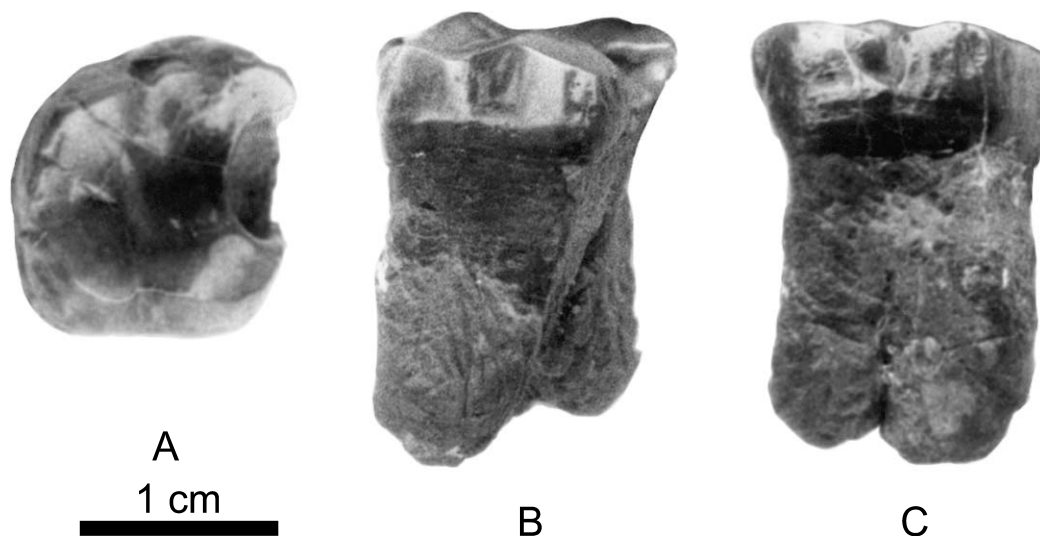

Figure 3.   Hominoid M[2] specimen VPL/Hari Devi I (1). (A) Occlusal view; (B) lingual view; (C) buccal view.

Table 1. Length and breadth measurements of the new and other Sivapithecus M2 specimens

Specimen	Length	Breadth	L/B
Hari-Talyangar localities, India			
VPL/Hari Devi I (1)	(13.8)	15.8	0.87
S. sivalensis			
GSI D-1 (type)	11.3	12.9	0.88
GSI D-185	10.6	11.4	0.93
GSI 18064	12.0	13.0	0.92
YPM 13799	9.9	11.9	0.83
YMP 13807	11.2	12.7	0.88
Mean	11.0	12.4	0.89
S. indicus			
GSI D-176 (type)	10.9	12.7	0.86
GSI D-196	12.8	14.2	0.90
Mean	11.9	13.5	0.88
Potwar-Plateau localities, Pakistan			
S. indicus			
GSP 6206	(12.3)	13.0	0.95
GPS 9896	9.9	11.7	0.87
GSP 9969	(12.9)	13.4	0.96
GSP 9972	—	13.7	—
GSP 9977	(13.4)	13.4	1.00
GSP 9986	(13.0)	14.0	0.93
GSP 10500	(15.0)	—	—
GSP 11786	11.9	13.5	0.88
GSP 11708	(13.9)	14.0	0.99
GSP 15000	12.8	14.4	0.89
Mean	12.8	13.5	0.93
S. parvada			
SM I	14.4	17.6	0.82
GSP 10500	13.5	—	—
GSP 13162	16.0	—	—
GSP 20450	13.6	(16.9)	0.80
Mean	14.4	17.3	0.81

Values taken from Pilgrim (1927), Lewis (1937), Prasad (1968), Pilbeam et al. (1980), Pilbeam (1982), and Kelley (1988).
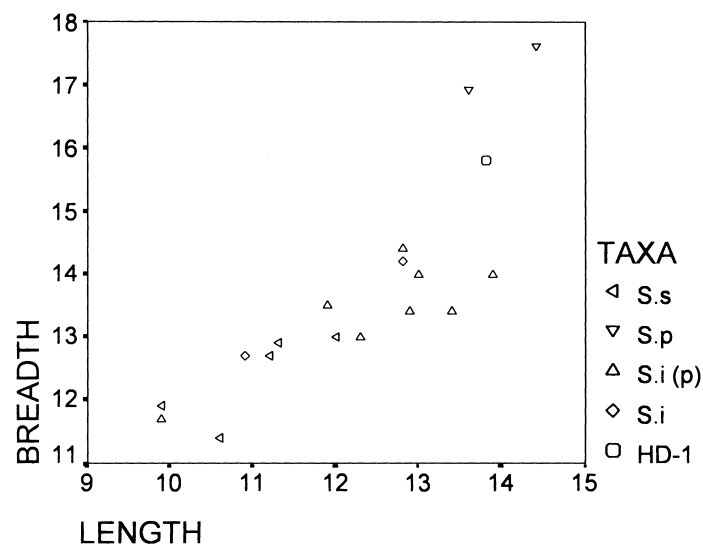

Figure 4.   Bivariate plot of *Sivapithecus* M² length and breadth. S.s, *S. sivalensis* (India); S.i, *S. indicus* (India); S.i(p), *S. indicus* (Pakistan); S.p, *S. parvada*; HD-1, VPL/Hari Devi I (1).

strong correlation between the breadth of their upper and lower second molars. This is also applicable to *S. indicus* specimen GSP15000 and the means of this species. In the case of *S. sivalensis* and *S. parvada*, however, there is a trend in upper molars being moderately broader than lower molars, on average. Comparison of the new Siwalik (Hari Devi I) specimen with the lower molar of *Indopithecus* indicates a similar correlation to that observed in the extant hominoids and *S. indicus*. While we have associated dentitions for extant species, we have few associated upper and lower teeth for fossil hominoids. We have problems related not only to small sample size, but also to sexual dimorphism and ranges of species variation. The morphology of the Hari Devi I specimen, its size, and suggested correlation with lower molars suggest that it is a specimen either of *S. parvada* or *Indopithecus*. Taking account of its geographical location within the Hari-Talyangar region and age (~7.8 Ma), the most parsimonious allocation of the Hari Devi I specimen is to consider it a specimen of *Indopithecus* (= *Gigantopithecus*). The fact that large caries are quite common in *Gigantopithecus* from Pleistocene deposits of China (Han and Zhao, 2002) may give a hint to our classification.

Disappearance of the Siwalik Apes

While *Sivapithecus* disappeared from Pakistan by 8.4 Ma, in India (Hari-Talyangar) it survived until 8 Ma. *Indopithecus* (= *Gigantopithecus*) is thought to have survived until ~7.8 and ~7.3 Ma in Pakistan and India, respectively. Opal phytoliths in molar enamel of *Gigantopithecus* teeth from China probably indicates a varied diet of grasses (possibly bamboo) and fruits (Ciochon et al., 1990). The new *Indopithecus* tooth with a large caries indicates that a habitat drier than that preferred by *Sivapithecus* existed at the Late Miocene in India. Associated fauna, *Hipparion* sp. and Bovidae sp. indet., point towards the presence of a mosaic environment including grasslands and more open, forest-like areas close by (see Morgan et al., 1995). *Sivapithecus*, on the other hand, was primarily frugivorous (Nelson, 2003). Dental microwear studies and isotopic analysis of tooth enamel led Nelson (2003) to propose that *Sivapithecus* thrived in a wet monsoonal forest. Nelson (2003) noticed a shift from wet to dry monsoonal forest from 10 to 6.3 Ma in the Potwar plateau, Pakistan and concluded that this shift combined with replacement of forests by open habitat might have led to the extinction of frugivorous sivapithecines.

Late Miocene tropical grasslands spread from Africa to the Indian subcontinent (Retallack, 1991). Within the Indian subcontinent, a difference in the timing of the C3–C4 ecological shift has been observed. At Potwar in Pakistan, it occurred at ~8 Ma, in Surai Khola, western Nepal, at ~7.4 Ma (timescale after Cande and Kent, 1992), and at Bakia Khola in central Nepal it was at ~6.6 or ~5.9 Ma (Harrison et al., 1993; Quade et al., 1995). The disappearance of hominoids appears to be correlated with the destruction of their forest habitats by encroaching grasslands. It has been observed that in the Late Miocene of the Siwaliks murid rodents replaced cricetid rodents (Patnaik, 2003). The climatic change (intensification of monsoon) in the Late Miocene, leading to decrease in humidity and increase in seasonality, aridity, and unpredictability, might have allowed the reproduction-oriented murids to replace the survival-oriented cricetids in both abundance and diversity (Patnaik, 2003; see also van Dam, 1997). The unpredictable monsoonal climatic condition, characterized by long, dry months and heavy rainy seasons, does not suit the present-day great apes, and probably did not favour *Sivapithecus* either.

Current fieldwork in the Hari-Talyangar region by members of the Siwalik Hominid Project will help to add information about the palaeohabitats occupied by *Indopithecus* and *Sivapithecus*. During recent surveys and excavations a number of new fossiliferous localities with in situ material has been identified. They are located within the Kursai region (3 km north of Hari-Talyangar). During fieldwork in 2003 these localities have been geologically mapped and samples for palaeomagnetic dating have also been obtained. A great deal of work remains to be done to find answers to the unresolved questions about the origin, evolution, paleobiology, and extinction of fossil great apes.

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