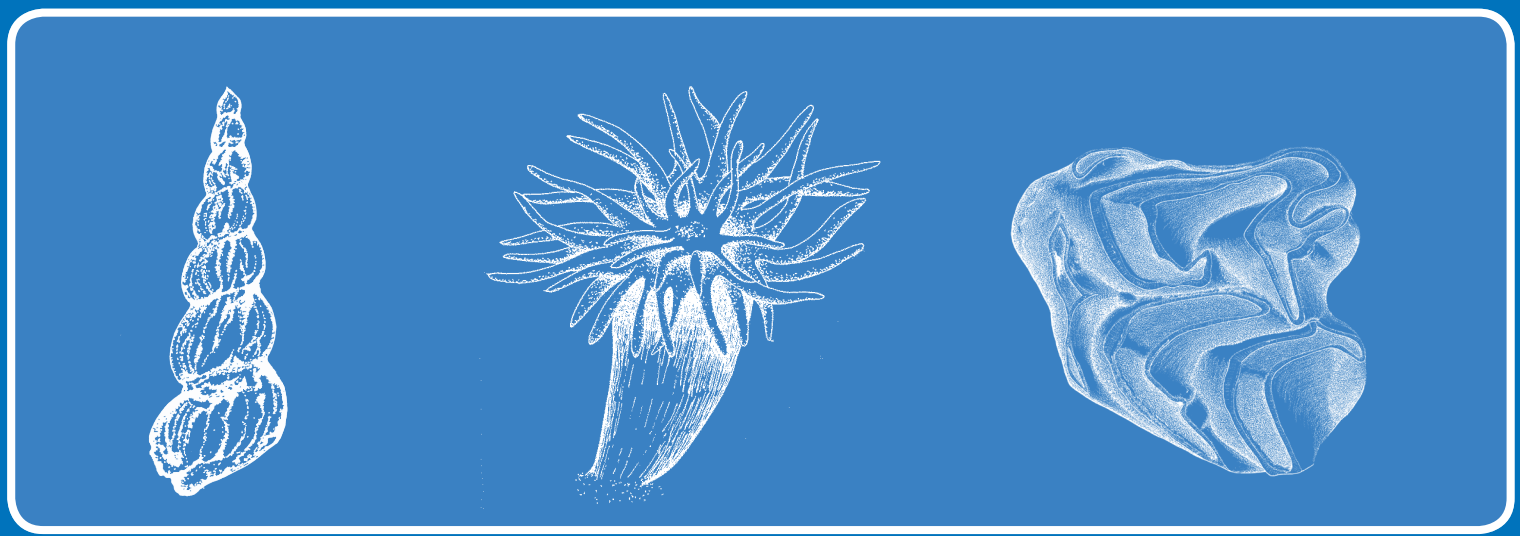
Zitteliana

An International Journal
of Palaeontology and Geobiology

Series A/Reihe A
Mitteilungen der Bayerischen Staatssammlung
für Paläontologie und Geologie

50 Jubilee Volume



München 2010

Zitteliana

An International Journal of Palaeontology and Geobiology

Series A/Reihe A

Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Geologie

50

CONTENTS/INHALT

Zitteliana	A 50	143 Seiten	München, 30.06.2010	ISSN 1612-412X

Editors-in-Chief/Herausgeber: Gert Wörheide, Michael Krings
Production and Layout/Bildbearbeitung und Layout: Martine Focke, Manuela Schellenberger
Bayerische Staatssammlung für Paläontologie und Geologie

Bayerische Staatssammlung für Paläontologie und Geologie
Richard-Wagner-Str. 10, D-80333 München, Deutschland
http://www.palmuc.de
email: zitteliana@lrz.uni-muenchen.de

ISSN 1612-412X
Druck: Gebr. Geiselberger GmbH, Altötting

Cover illustrations: (from left to right) Shell of the gastropod *Loxonema regium* De Koninck from the Carboniferous of Belgium (redrawn from De Koninck 1881); Solitary coral *Caninia* sp. from the Carboniferous of England (redrawn from Ramsbottom in McKerrow 1978); Tooth of the rare ruminant *Orygotherium escheri* von Meyer from the Miocene of Germany (after Rössner & Mörs 2001). **Back cover:** Atrium of the Munich Palaeontological Museum, view from the main entrance.

Umschlagbilder: (von links nach rechts) Gehäuse der Schnecke *Loxonema regium* De Koninck aus dem Karbon von Belgien (neu gezeichnet nach De Koninck 1881); Solitärkoralle *Caninia* sp. aus dem Karbon von England (neu gezeichnet nach Ramsbottom in McKerrow 1978); Zahn des seltenen Wiederkäuers *Orygotherium escheri* von Meyer aus dem Miozän von Deutschland (nach Rössner & Mörs 2001). **Rückseite:** Lichthof des Paläontologischen Museums München, Blick vom Haupteingang.

Zitteliana	A50	111 - 125	12 Figs, 2 Tabs	München, 30.06.2010	ISSN 1612 - 412X

Additions to the Dehm collection of Siwalik hominoids, Pakistan: descriptions and interpretations

By
Martin Pickford*

Collège de France, Paris, France, and UMR 7207 (CR2P) du CNRS, 8, rue Buffon, 75005, Paris, France.

Manuscript received February 15, 2010; revised manuscript accepted May 22, 2010.

Abstract

Richard Dehm collected fossils in the Siwalik Series of Pakistan in 1939, 1952–53 and 1955. Among the multitude of vertebrates that he collected, there were nine hominoid specimens, some from the Chinji Formation in the environs of Chinji Rest House and some from the Nagri Formation at Sethi Nagri. One of the specimens was subsequently identified as a suid canine, reducing the quantity of hominoids in his sample to eight, but recent examination of his collections at the Bayerische Staatssammlung für Paläontologie und Geologie, München, has revealed the presence of two additional teeth, one from Kadirpur, Chinji, and one from Nagri, hitherto misidentified as suids, possibly because of their diminutive dimensions. Following an extensive comparison with most of the fossil hominoid specimens reported from the Indian subcontinent, the Dehm fossils described herein are attributed to two species of *Sivapithecus*, *S. hysudricus* for the Kadirpur specimen, and *S. lewisi* for the Sethi Nagri incisor.

Key words: Pakistan, Chinji, Middle Miocene, hominoid, *Sivapithecus*, Richard Dehm

Zusammenfassung

Von Richard Dehm wurden in 1939, 1952–53 und 1955 Fossilien aus der Siwalik Serie von Pakistan gesammelt. Unter den vielen Wirbeltierresten befinden sich neun Stücke fossiler Hominoiden, einige davon aus der Chinji Formation in der Umgebung des Chinji Rest House, andere aus der Nagri Formation bei Sethi Nagri. Eines der Stücke ist später allerdings als Schweinezahn identifiziert worden, wodurch sich die Anzahl der Hominoidenreste auf acht reduzierte. Im Zuge neuerer Untersuchungen der Dehm-Sammlung in der Bayerischen Staatssammlung für Paläontologie und Geologie, München, wurden zwei zusätzliche Hominoidenzähne entdeckt, einer von Kadirpur, Chinji, der andere von Nagri. Beide Zähne waren bislang als Schweinezähne falsch identifiziert worden, vermutlich auf Grund ihrer geringen Größe. Als Resultat eines umfangreichen Vergleichs mit den meisten der vom Indischen Subkontinent bekannten Hominoidenresten werden die Dehmschen Fossilien in dieser Arbeit beschrieben und zwei verschiedenen Arten der Gattung *Sivapithecus*, nämlich *S. hysudricus* für die Stücke aus Kadirpur und *S. lewisi* für die Sethi Nagri Incisivi, zugeordnet.

Schlüsselwörter: Pakistan, Chinji, Mittel-Miozän, hominoid, *Sivapithecus*, Richard Dehm

1. Introduction

Richard Dehm organised palaeontological expeditions to the Potwar Plateau, Pakistan, in 1939, 1952–53 and 1955, collecting in the region of Chinji (Chinji Formation and basal Nagri Formation, Dhok Pathan and elsewhere). He amassed a comprehensive and representative sample of vertebrate fossils from the classic stratigraphic stages of the Siwaliks of the Indian subcontinent as understood at the time, the subdivisions of the stratigraphic column that he employed (Chinji, Nagri, Dhok Pathan Formations) being based principally on the work of Pilgrim (1913). The fossils are curated at the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG), München. Some of the fossils have been formally described in the scientific literature (Deinotheres, Dehm et al. 1963; Primates, Dehm 1983; Rhinocerotids, Heissig 1972) but many groups remain to be studied. Among these there are important collections of gomphotheres, suids, anthracotheres and ruminants, plus some carnivores and equids.

During a study visit to the BSPG in November, 2009, the author took advantage of the opportunity to browse through the Dehm Siwaliks collection and found two hominoid fossils in the suid collection, having been identified in the field as such. The specimens are a left lower third premolar from "Kadirpur" northeast of Chinji Rest House, and a deciduous upper central incisor from Sethi Nagri.

Dehm (1983) described nine hominoid specimens that his

* *E-mail:* pickford@mnhn.fr

expeditions collected. One of these has subsequently been shown to be a suid canine (Kelley 2005). With the addition of two specimens that had previously escaped notice, this brings to 10 the quantity of hominoid primate fossils that the Dehm expeditions found. The two teeth that have remained unidentified in the collections since 1955 are small within the context of Siwalik hominoids, which explains, in part, why they were not recognised as such by Dehm and other scientists who subsequently arranged the collections by order and family in the storage at the BSPG, München. Both these specimens had been separated from the rest of the suids into small trays with a note by Jan Van der Made that they didn't represent suids.

2. Methods

The Dehm Siwaliks vertebrate collection is stored at the Bayerische Staatssammlung für Paläontologie und Geologie, München.

Measurements are given to the nearest tenth of a mm. It needs to be pointed out that published measurements of the p/3s of hominoids have caused a certain amount of confusion because the way of measuring is usually not specified. Confusion arises because in hominoids, the p/3 is obliquely oriented in the mandible. Pilgrim (1915, 1927) measured the tooth antero-posteriorly and bucco-lingually relative to the long axis of the mandible (Fig. 1), whereas other scientists have measured the greatest diameter (mesio-buccal to disto-lingual) and the transverse diameter. Hooijer (1951) explained clearly the difficulties of obtaining consistent measurements using the method of Pilgrim, especially while measuring isolated teeth, and of the differences of opinion that flow from these difficulties (Fig. 1). Prasad (1968) for example, gave the length and breadth measurements of the p/3 in mandible GSI D 18039 as 9.0 x 9.0 (length/breadth index – 1.0) whereas in the text he described the tooth as "sectorial". Pilgrim (1927) provided measurements for a p/3 (GSI D 190) as 11.2 x 11.2 (length/breadth index – 1.0) for a tooth that is as sectorial as the p/3 in the holotype specimen of *Sivapithecus parvada*. Simons & Chopra (1969) provided measurements of teeth in the Bilaspur mandible that indicate that the breadth of the p/3 is greater than the length. In this paper we use maximum diameter and transverse diameter, which have the merit of being homologous measurements, rather than reflecting the obliquity of the tooth in the mandible. This means that several published measurements of p/3s have to be used with caution for this kind of analysis (Pilgrim 1915, 1927; Prasad 1968; Simons & Chopra 1969) (Tab. 1).

Abbreviations in the text are as follows: dI1/ – upper deciduous central incisor, p/3 – lower third premolar, M – upper molar, m – lower molar, md – mesio-distal, Ll – labio-lingual, max – maximum, trs – transversal. GPTS – geomagnetic polarity time scale. Institutional abbreviations are: AMNH – American Museum of Natural History, BSPG – Bayerische

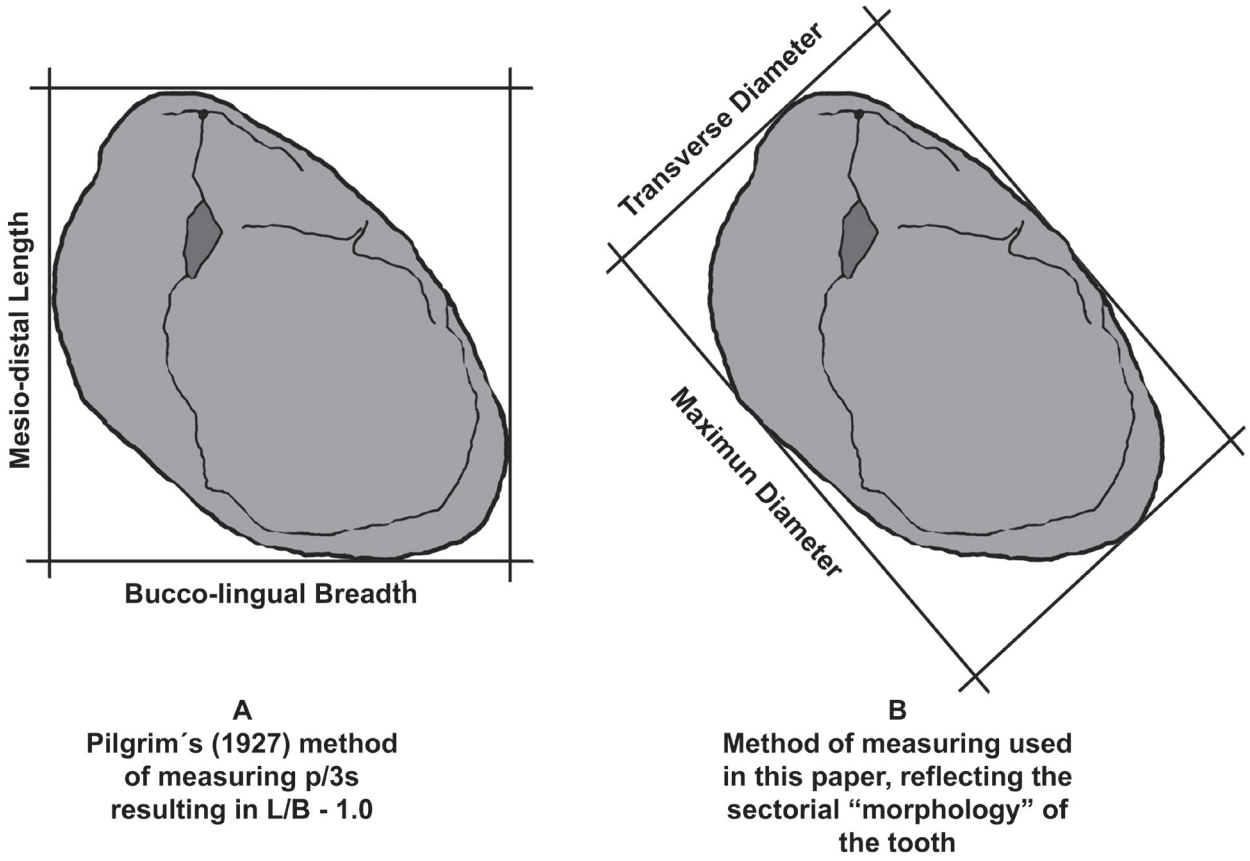


Figure 1: Methods of measuring p/3s of hominoids. Pilgrim's (1927) method (A) results in a length to breadth index of 1.0, whereas the method employed in this paper (B) reflects the "sectorial" aspect of the tooth.

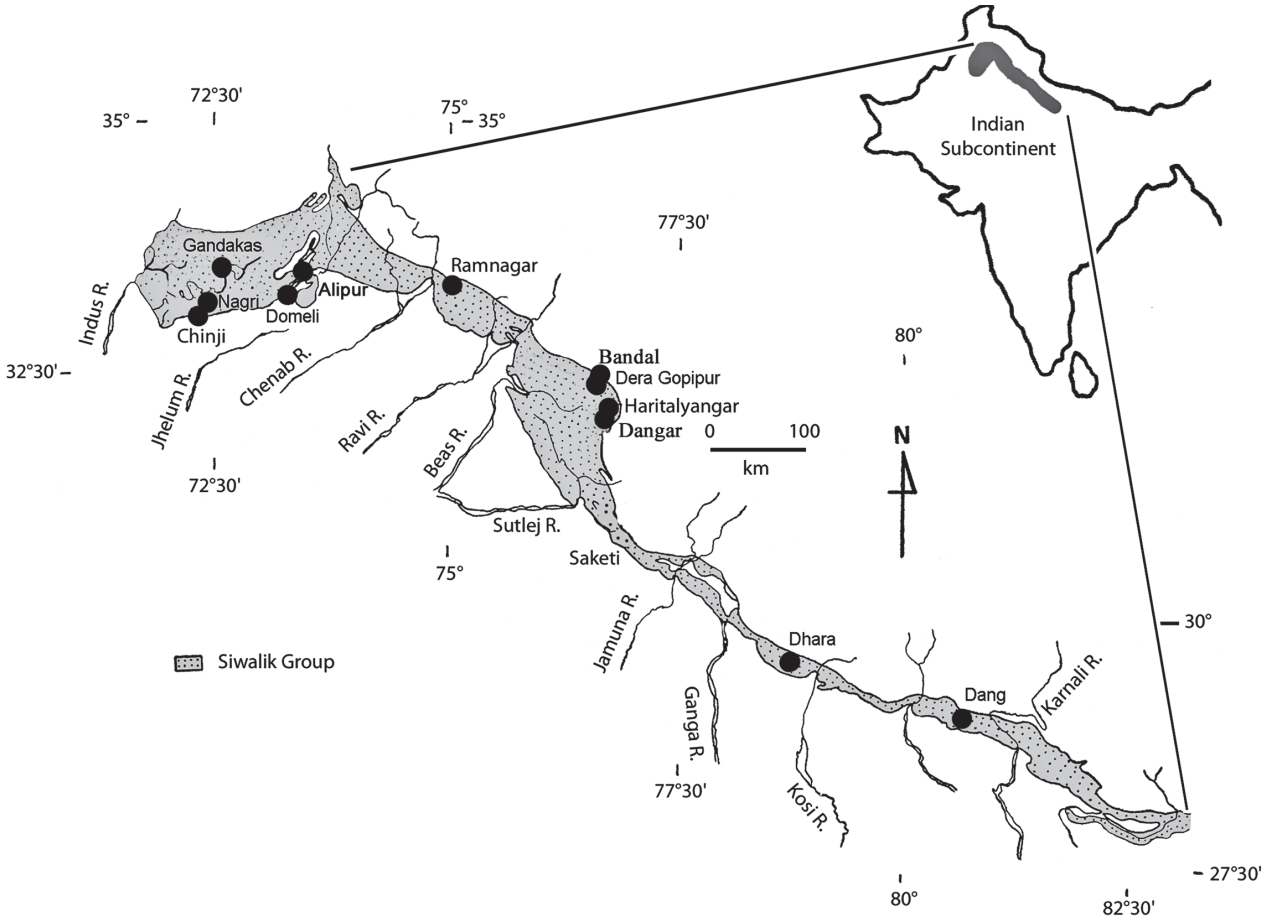


Figure 2: Distribution of Siwalik Group sediments along the southern margin of the Himalayas, highlighting sites that have yielded Miocene hominoids. Kadirpur is close to Chinji, in Pakistan.

Staatssammlung für Paläontologie und Geologie, CYP – Chandigarh Yale Palaeontology , GSI – Geological Survey of India, GSP – Geological Survey of Pakistan, ONGC – Oil and Natural Gas Commission, Dehra Dun; PUA – Punjab University Anthropology Department, SFP – Saketi Fossil Park, YPM – Yale Peabody Museum.

3. Biochronology and geological context

The Kadirpur hominoid lower premolar is from deposits northeast of Chinji Rest House where the Dehm expedition collected a comprehensive sample of vertebrate fossils. The locality is south of the village of Kadirpur (modern spelling – Qadirpur) and is positioned near the top of the Chinji Formation (Fig. 2). Johnson et al. (1982) estimated the age of the Chinji-Nagri boundary to be about 10.1 Ma, based on the GPTS available at the time of their study. Recalculating the palaeomagnetic position relative to more recent GPTS yields an age of ca 11 Ma for this boundary, which accords better with the arrival of *Hipparion* in the region (absent in the Chinji Formation – present in the Nagri Formation) (Pickford 1998). Of biochronological importance in the sample from this site are the suids *Conohyus sindiensis*, *Hyotherium pilgrimi* and *Listriodon pentapotamiae*, all three of which are species characteristic of the Chinji zone in its type locality close to the Chinji Rest House (indeed, Kadirpur could be said to lie within the type area; Fig. 3). *L. pentapotamiae* and *H. pilgrimi* died out before the beginning of the Nagri zone (Pickford 1988) and *C. sindiensis* gave rise to *C. indicus* by the time that the the Nagri Formation accumulated. The stratigraphic position of the hominoid left lower p/3 is therefore relatively well constrained, indicating that it is of "Chinji" age, correlative to European zone MN 7/8, close to 12 Ma (+/- 1 Ma) (Pickford 1998). The same locality yielded a mandible of *Archaeobelodon* and a large diversity of ruminants, anthracotheres, gomphotheres and other mammals such as amphicyonids (personal observation of fossils in the BSPG).

The Nagri hominoid deciduous incisor was associated with an abundant fauna of upper Nagri age, including *Sivapithecus lewisi* (previously identified as *S. parvada*). Subsequent studies of the stratigraphy of the region (Barry 1986; Johnson et al. 1982, 1985) indicate a correlation of the Nagri deposits to MN 10 of the European mammal scale, and the Sethi Nagri site at ca. 9.5 Ma (+/-1 Ma), late Vallesian equivalent (Fig. 3).

4. Systematic palaeontology

The systematics and taxonomy of Siwalik hominoids have an

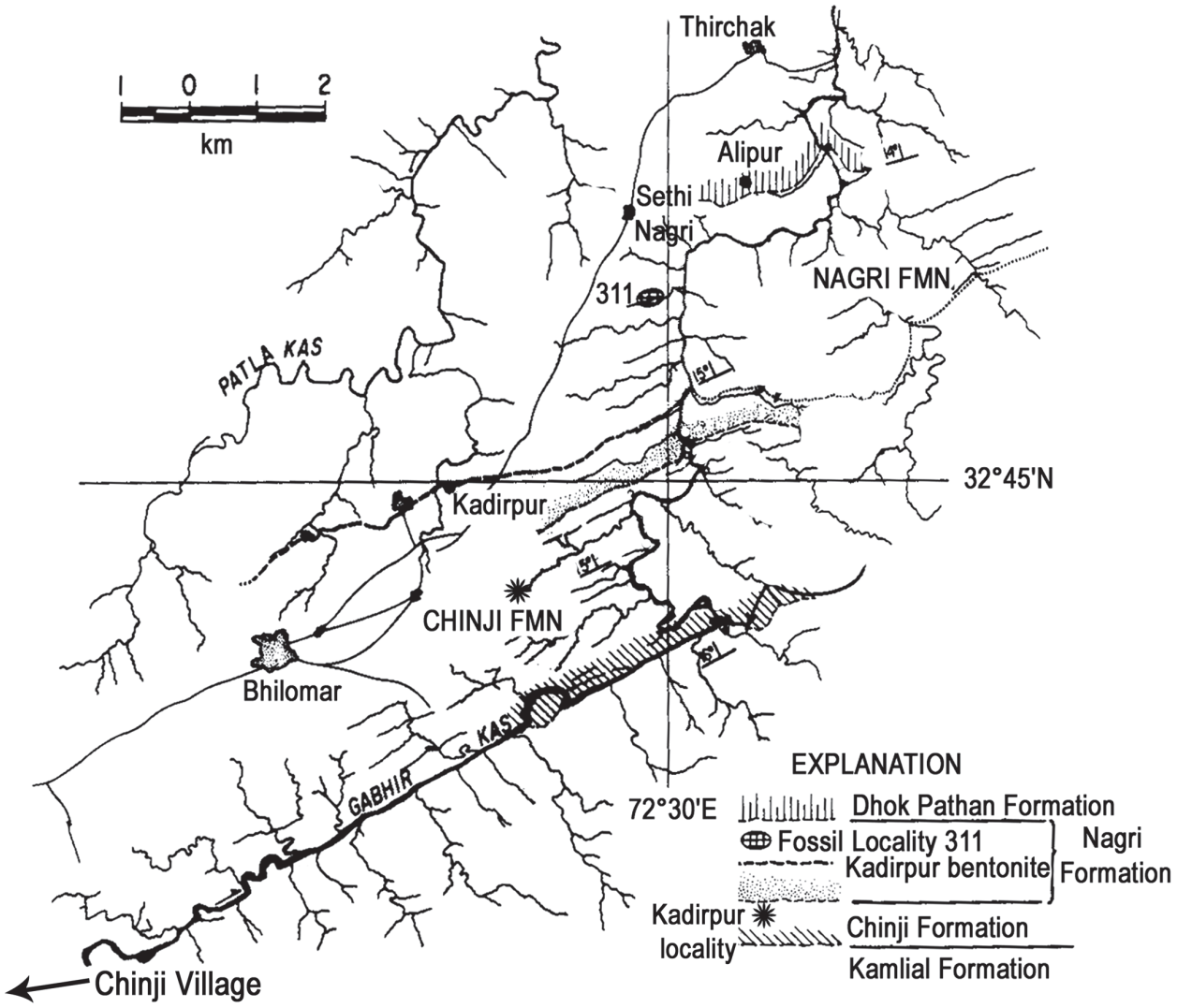


Figure 3: Location of the Kadirpur and Sethi Nagri (311) fossil localities (Kadirpur fossil locality is approximate only, but is near the top of the Chinji Formation). (Map modified from Johnson et al. 1982).

exceedingly complicated history (Brown et al. 1924; Cameron 1997, 2001, 2003; Cameron et al. 1999 ; Chopra 1983; Chopra & Kaul 1975; Dehm 1983; Dutta et al. 1976; Falconer 1868; Gregory & Hellman 1926; Gregory et al. 1938; Gupta 1969; Gupta et al. 1979, 1982; Hooijer 1951; Kappelman et al. 1991; Kay 1982; Kelley 1988, 2002, 2005; Kelley et al. 1995; Lewis 1934, 1936, 1937; Lydekker 1884; Munthe et al. 1983; Pandey & Sastri 1968; Patnaik & Cameron 1997; Patnaik et al. 2005; Pilbeam et al. 1977, 1980; Pilbeam & Smith 1981; Pilgrim 1910, 1915, 1927; Pillans et al. 2005; Prasad 1962, 1964, 1968; Pruess 1982; Raza et al. 1983; Sahni et al. 1974, 1980, 1983; Sahni & Tiwari 1979; Sankhyan 1985; Simons & Chopra 1969; Simons & Ettel 1970; Simons & Pilbeam 1965; Tattersall & Simons 1969; Tiwari & Kumar 1984; Verma & Gupta 1997; Verma et al. 2002; von Koenigswald 1950, 1951, 1981, 1983; Wadia & Aiyengar 1938).

There has been a tendency to name new genera and species on the basis of isolated teeth or fragments of jaw, and historically there has been an alternation between excessive splitting and excessive lumping, flavoured until about 1990, with a preoccupation for discovering early hominids. A better appreciation of morphological and metric variation, taking into account sexual dimorphism and bimodality, resulted in the realisation that *Ramapithecus*, which for about four decades was interpreted by many palaeoanthropologists as an early hominid, represents the females of *Sivapithecus*, but even with this clarification there remained several problems, which are evoked below. Collections during the last quarter of the 20th Century greatly enhanced the sample of hominoids from the Indian Subcontinent, and for some taxa, the samples are now sufficient to resolve many of the taxonomic issues. However, since the preliminary revision of the Dryopithecinae by Simons & Pilbeam in 1965, most palaeoanthropologists appear to have lost sight of specimens which were declared in that work either to be nomina dubia or to be synonyms of other species. The new samples now available permit some of the proposals in that revision to be tested.

Order: Primates Linnaeus, 1758
Superfamily: Hominoidea Gray, 1825

Genus: *Sivapithecus* Pilgrim, 1910

Type species: *Sivapithecus indicus* Pilgrim, 1910

Species: *Sivapithecus hysudricus* (Pilgrim, 1927)

*v.	1927	*Hylopithecus hysudricus* nov. gen. nov. sp. – Pilgrim, p. 9, Pl.1 , fig. 3.
v.	1934	*Bramapithecus thorpei* nov. sp. – Lewis, p. 173.
part.v	1965	*Dryopithecus laietanus* (Villalta & Crusafont, 1944) – Simons & Pilbeam, pp. 120, 143.
v.	1982	*Sivapithecus simonsi* nov. sp. – Kay, pp. 130–133, figs 4, 5.

Diagnosis: *S. hysudricus* resembles other *Sivapithecus* in having thicker molar enamel than *Dryopithecus*. It has significantly smaller maxillary and mandibular premolars and molars than *Sivapithecus sivalensis* (modified from Kay 1982).

Type locality: Haritalyangar (31°32'E: 76°38'N), India. The stratigraphic succession at Haritalyangar is 1,600 metres thick (Pillans et al. 2005). The holotype of *S. hysudricus* was probably collected from the levels yielding *Conohyus chinjiensis* (Pilgrim 1913, 1927; Prasad 1962).

Hypodigm: GSI D 200, right m/1 from Hari Talyangar, India (holotype); YPM 13814, from Hasnot, Pakistan (type specimen of *Bramapithecus thorpei* Lewis, 1934, considered by Simons 1964, and Simons & Pilbeam 1965, to represent *Ramapithecus punjabicus*); M 15423, left mandible containing roots of p/3 and crowns of p/4-m/2, from Domeli, Pakistan (= M 15243 in Simons & Pilbeam 1965, *Dryopithecus laietanus*); BSPG 1939 X 1, right M1/, Kundal Nala; BSPG 1956 II 2366 (Field N° 750 (9-12-55)), left p/3 from Kadirpur, Pakistan; GSI D 298, right mandible with p/3-m/2 from Kundal Nala, near Chinji, Pakistan (= GSI D 618 in Simons & Pilbeam 1965, *Dryopithecus laietanus* ; = type specimen of *Sivapithecus simonsi* Kay, 1982); GSI D 185, right maxilla containing P3/-M2/, from Hari Talyangar, India; SFP 187 – left M2/, SFP 188 – right M2/, SFP 189 – right m/2, SFP 190 – left p/3, SFP 191 – right m/1 fragment, SFP 192 – left P3/ fragment, from Dera Gopipur, India (Gupta et al. 1982; Pickford & Tiwari in prep.).

Localities: Pakistan – Kundal Nala, near Chinji; Kadirpur, near Chinji; Domeli; Hasnot: India – Dera Gopipur; Haritalyangar.

Age: Late Middle Miocene equivalent to MN 7/8 of the European Land Mammal Zonation, (ca. 12 Ma +/- 1 Ma) and perhaps the base of the Late Miocene (MN 9 equivalent).

Other species included: *Sivapithecus sivalensis* (Lydekker, 1879), *Sivapithecus lewisi* Pandey & Sastri, 1968 (= *S. parvada* Kelley, 1988).

Note: The holotype of *Hylopithecus hysudricus* Pilgrim, 1927 was declared to be a nomen dubium by Simons & Pilbeam (1965), who, on the basis of its dimensions wrote that "its small size alone strongly suggests that specimen in question is not a dryopithecine, but there is some liklihood that it is, or is closely related to *Pliopithecus*". In fact its dimensions do not rule out its attribution to Dryopithecinae: at least two specimens attributed to *Ramapithecus punjabicus* by Simons & Pilbeam (1965) but now attributed to *Sivapithecus*, have first molars as small as the type specimen. The holotype of *S. hysudricus*, GSI D 200, is a right lower permanent molar from Hari Talyangar, which was illustrated and described by Pigrim (1927). Whilst it is not a very convenient type specimen, Pilgrim (1927) noted that the tooth was smaller than all other Siwalik hominoid teeth that had passed through his hands, which is a valid observation, and he wished to perennise the fact. He can be criticised for naming a new genus and species on the basis of the holotype which is a damaged and worn lower molar, but his observation that the tooth represents a species of small hominoid is correct. Comparison with lower molars in mandibles attributed to *Sivapithecus*

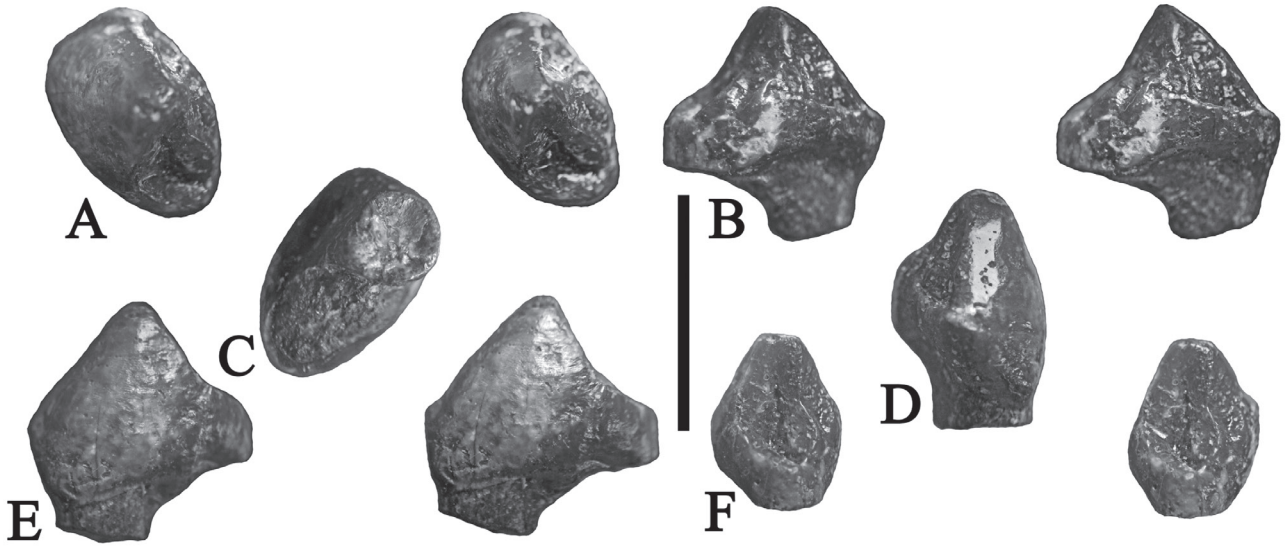


Figure 4: BSPG 1956 II 2366 *Sivapithecus hysudricus*, left p/3 from Kadirpur, Chinji Formation, Pakistan. A) stereo occlusal, B) stereo lingual, C) radicular, D) mesial view to show honing facet, E) stereo buccal, and F) stereo distal views (Scale bar: 10 mm).

simonsi, reveals that the type specimen of *S. hysudricus* has a high probability of belonging to the same species on account of its similar dimensions and morphology. It has a very low probability of belonging to a pliopithecid on account of its overall morphology and the thickness of the enamel. It is not a deciduous tooth, as shown by the crown morphology and the presence of a well developed, vertical distal root (Pilgrim 1927).

Kay's (1982) revision of sivapithecines, in which he erected the species *Sivapithecus simonsi*, does not mention the existence of *Hylopithecus hysudricus* Pilgrim, 1927, nor of *Bramapithecus thorpei* Lewis, 1934, which is part of the hypodigm of *S. hysudricus* as understood in this paper (neither of these papers was cited by Kay 1982). It is interesting to note that Hari Talyangar yielded a maxilla belonging to this species (Kay 1982, referred this maxilla to the species *S. simonsi* with some hesitation). This maxilla was initially attributed to *Dryopithecus punjabicus* by Pilgrim (1915), but was subsequently transferred to *Ramapithecus punjabicus* by Simons & Pilbeam (1965) as an early hominid.

Simons & Pilbeam (1965) attributed two specimens from the Siwaliks of Indo-Pakistan to *Dryopithecus laietanus* (Crusafont & Villalta 1944). Both are here attributed to *Sivapithecus hysudricus*. It is necessary to discuss here the attribution to *Ramapithecus punjabicus* by Simons & Pilbeam (1965) of several of the specimens listed above. The type specimen of *R. punjabicus* (GSI D 118 left mandible fragment with m/2 + GSI D 119 right mandible fragment with m/3) was originally attributed to the genus *Dryopithecus* by Pilgrim (1910). In

Table 1: Metric comparison (in mm) of lower third premolars of Miocene hominoids from the Indian Subcontinent (data and identifications for specimens in the left columns (from Ramnagar, Hari-Talyangar and the Potwar Plateau) are from Cameron et al. (1999) who gleaned values from (a) Gregory & Hellman (1926); (b) Chopra & Kaul (1975); (c) Pilgrim (1927); (d) Prasad (1968); (e) Pilbeam et al. (1980); (f) Preuss (1982); (g) Kay (1982); (h) Kelley (1988) ; and (i) Simons & Chopra (1969). In bold are specimens measured by the Pilgrim (1927) method; other measurements are maximum diameter and transverse diameters (Fig. 1). The two right hand columns of measurements are by the author. Note the large discrepancy in values yielded by the two methods, making comparisons between them meaningless (Hooijer 1951) (e = estimated measurement from roots or damaged crown) (I have omitted GSP 13445, as I was not able to examine this tooth. Published measurements (10.4 x 6.5, Pilbeam et al. 1980) plot with *S. sivalensis*) (* = estimated measurement).

Location and specimen number	Length published	Breadth published	Length (max) own	Breadth (trs) own	Identifications and notes
Dera Gopipur, India					
SFP 190	-	-	8.8	6.5	*S. hysudricus*
Rammagar, India					
AMNH 19411 a	11.3	7.2	11.4	7.2	*S. sivalensis*
Hari Talyangar, India					
PUA 1047-69 b	11.9	7.8	-	-	*S. sivalensis*
GSI D-197 c	**11.2**	**11.2**	13	8.5	*S. indicus*
YPM 13828/ D-189/190 c	14.1	11.6	15.4	10.3	*S. indicus*
GSI-18039 d	9.0	9.0	14	8.3	*S. indicus*
CYP 359-68 i left	**11.8**	**14.6**	17	12	*I. giganteus*
CYP 359-68 right	-	-	16.4	11	*I. giganteus*
ONGC/V/790	-	-	16*	9.2*	*S. lewisi* Holotype
Potwar Plateau, Pakistan					
AMNH 19412 b	11.3	7.5	11.4	7.2	*S. sivalensis*
GSP 9563 e	11.5	6.3	11.6	6.4	*S. sivalensis*
GSP 6160 e	11.1	6.5	11	7	*S. sivalensis*
GSP 15000f left	13.4	8.7	14.5	7.8	*S. indicus*
GSP 15000 right	-	-	14	8	*S. indicus*
GSI D-298 g	9.8	5.5	9.4	4.6	*S. hysudricus;* *S. simonsi* Holotype
BSPG 1939 X 4 h left	17.4	9.9	16.3	9.7	*S. lewisi; S. parvada* Holotype
BSPG 1939 X 4 right	-	-	18*	9.9	*S. lewisi; S. parvada* Holotype
BSPG 1956 II 2366	-	-	9.8	5.6	*S. hysudricus*
YPM 13811	-	-	11.6	6.3	*S. sivalensis; Sugrivapithecus salmontanus* Holotype

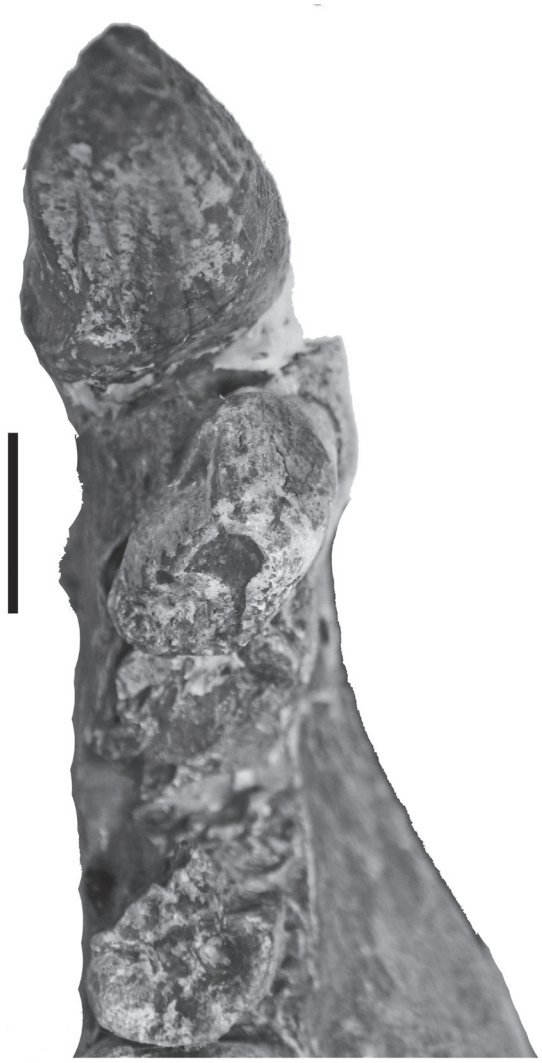


Figure 5: BSPG 1939 X 4, right mandible, part of holotype of *Sivapithecus lewisi*, Sethi Nagri, Nagri Formation, Pakistan, showing the elongated and narrow p/3 (scale: 10 mm).

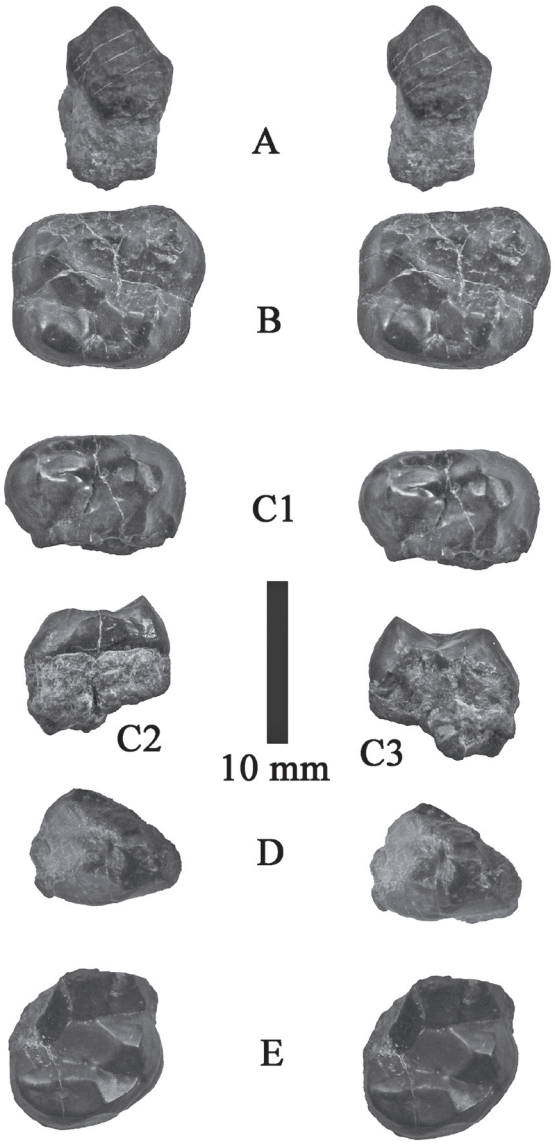


Figure 6: Hominoid teeth from Dera Gopipur, Himachal Pradesh, India. A – SFP 192, left P3/ stereo buccal view; B – SFP 188, left M2/, stereo occlusal view; C – SFP 187, right M2/, C1 – stereo occlusal view, C2 – anterior view; C3 – distal view; D – SFP 190, damaged left p/3 stereo occlusal view; E – SFP 189, right m/2, stereo occlusal view.

bivariate plots these two specimens fall at the lower end of the range of variation of *Sivapithecus sivalensis*. KAY (1982) excluded them from *Sivapithecus simonsi*, and I agree that they are more likely to represent *Sivapithecus sivalensis* than *S. hysudricus*. If, however, D 118 + D 119 are shown in future analyses to represent the same species as *S. hysudricus*, then the species would have to be called *Sivapithecus punjabicus* (PILGRIM, 1910). Presently available evidence suggests that the specimens represents a female of *S. sivalensis*.

As PILGRIM (1915, 1927) wrote on several occasions, the status of many Siwalik species of primates and other mammals would become clearer with additional discoveries. This is the case in the present study, and, although the species *Sivapithecus hysudricus* still remains relatively poorly known, it is clear that there was indeed a small hominoid in the Indian Subcontinent about 12 million years ago. The association of upper and lower teeth of this species at Dera Gopipur, India (GUPTA et al. 1982), is important, and the well preserved Kadipur specimen described here provides additional evidence supporting PILGRIM's original observation.

Description: The Kadirpur hominoid lower premolar had just come into wear when the individual died (Fig. 4). As such it is the best preserved tooth attributed to the species. There are wear facets along the antero-buccal crest (the honing facet), down the distal face of the main cusp and the low protoconid, passing at a distinct and sharp angle onto the distal cingulum.

In lateral view the p/3 is triangular in profile with a gently convex anterior margin. The buccal surface is convex and smooth except for the development of a low fold of enamel rising from the cervix towards the mesial edge of the distal fovea. Perikymata are clearly visible on the buccal surface. The honing facet is developed along the leading edge of the buccal surface, but it is so lightly worn that it has barely altered the profile of the tooth, unlike the heavy wear facet that is present in the holotype of *Sivapithecus parvada*. The crown height

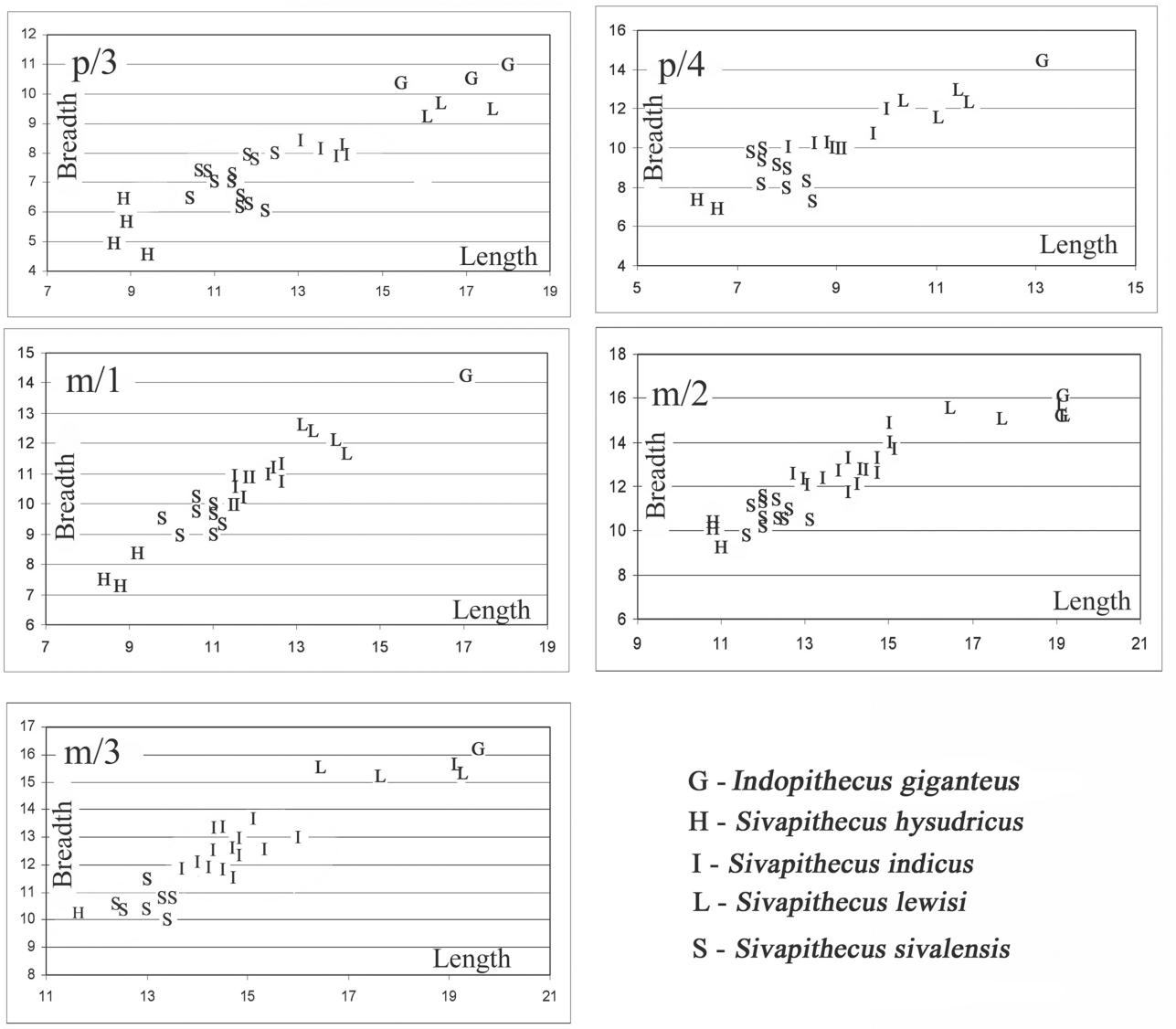


Figure 7: Bivariate plot of lower cheek teeth of Siwalik hominoids (*Sivapithecus* and *Indopithecus* species). The Kadirpur tooth plots close to the very small holotype of *S. simonsi* from Kundal Nala, which is here attributed to *Sivapithecus hysudricus* and with the specimens from Domeli and Hasnot, Pakistan, and Dera Gopipur, India. It has previously been argued that the holotype of *S. simonsi* could represent a female of *S. sivalensis*, but this would make the range of variation of the species greater than that of *Sivapithecus indicus*. The gap between the clouds of points here interpreted as representing *S. sivalensis* and *S. hysudricus*, supports the two species hypothesis.

measured from the cervix to apex along the mesial edge of the tooth is 8.2 mm. In lingual view, the crown shows a prominent main cusp, on the lingual side of which there is a low protoconid slightly distal to and lower than the apex of the main cusp. Mesial to the protoconid there is a weak cusplet (the lingual tubercle) rising from the base of the mesial fovea, and the enamel on the surface of the mesial fovea in front of the tubercle is heavily wrinkled. The distal fovea is bordered lingually by the cingulum which extends all along the lingual side of the tooth rising anteriorly to form a low cusplet or "shoulder" at the mesial extremity of the tooth. In occlusal view, it is possible to observe that this "shoulder" is formed where the lingual cingulum meets the buccal cingulum which is steep and short, extending to the base of the tooth anteriorly but not extending buccally or distally to any extent.

In occlusal view the crown of the Kadirpur p/3 is ovoid in outline, with a centrally positioned main cusp, a prominent distal fovea bordered buccally, distally and lingually by the cingulum, and mesially by the main cusp and protoconid. The low point, or "spout" of the distal fovea is in the disto-lingual corner of the tooth. Between the main cusp and the protoconid there is a vertical groove that continues into the base of the fovea. In distal view, the distal interstitial facet caused by abrasion against the p/4 is present; and its position reveals that the p/3 was markedly obliquely oriented in the mandible, such that the almost circular mesial root was antero-lateral to the obliquely oval distal root. For this reason, the maximum and minimum crown dimensions do not correspond to the mesio-distal and bucco-lingual measurements (Tab. 1). Thus the orientation of this tooth complies with the usual situation in hominoid p/3s.

Comparisons: The Kadirpur hominoid p/3 is basically a

Table 2: Hominoid teeth from Dera Gopipur, Himachal Pradesh, India, curated at the Saketi Fossil Park, with measurements (in mm) by the author (* = estimated measurement).

Specimen number	Gupta *et al.*, (1982)	This paper	Length (mm)	Breadth (mm)
SFP 187	Right M1/	Left M2/	9.7	11.7
SFP 188	Left M2/	Right M2/	--	11.4
SFP 189	Right m/2	Right m/2	--	9.6*
SFP 190	P3/(?)	Left p/3	8.8	6.5
SFP 191	Left i/2	Right m/1 fragment	--	--
SFP 192	Left C1/	Left P3/	6.2	--
SFP 193	Left c/1	Indeterminate	--	--

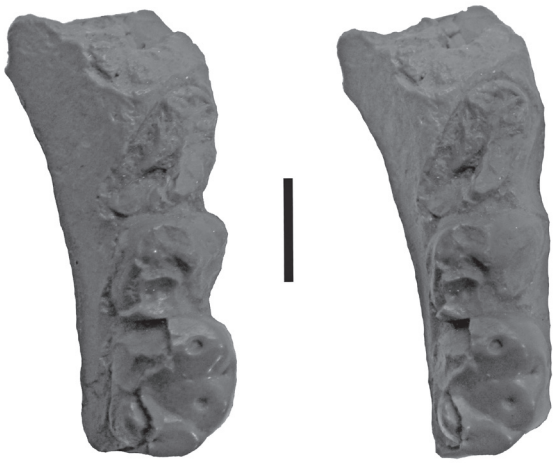


Figure 8: *Sivapithecus lewisi*, ONGC/V/790, holotype, right mandible fragment containing the roots of canine and p/3 and the crowns of p/4 (lacking most of the enamel) and m/1, from Bandal, India, stereo occlusal view (scale: 10 mm).

miniature version of the corresponding tooth in the specimens of *Sivapithecus lewisi* Pandey & Sastri (1968) which was collected by the Dehm expedition at Sethi Nagri, Pakistan (Fig. 5). The morphology of the specimen corresponds closely with that of BSPG 1939 X 4, taking into account the greater degree of wear in the *S. lewisi* specimen. The Kadirpur specimen is however, just above half the dimensions (Tab. 1) of the geologically younger specimen from Sethi Nagri.

The Kadirpur p/3 is close in dimensions and morphology to a tooth from Dera Gopipur, India (Gupta et al. 1982) (Fig. 6) and to the holotype specimen of *Sivapithecus simonsi* (Kay, 1982) from Kundal Nala, near Chinji, Pakistan (Fig. 10; Tab. 1). The Dera Gopipur specimen is part of an association of hominoid teeth from a single individual with representation of both upper and lower teeth (Pickford and Tiwari in prep.) (Tab. 2) and is thus a particularly valuable sample. The Dera Gopipur specimens are associated with an extremely poor fauna, but the deposits were correlated to the Chinji zone by the discoverers, on the basis of the lithology of the sediments from which the teeth had evidently eroded.

Pilgrim (1927) erected *Hylopithecus hysudricus* for a small lower first molar from Hari Talyangar, India (GSI D 200: 8.7 x 7.4 mm). Small Siwalik hominoids were attributed to *Sivapithecus simonsi* Kay, 1982, but the name has not found universal acceptance (Kelley 2002). Nevertheless, the small hominoids from Chinji levels and from Hari Talyangar do appear to be smaller than material attributed to *Sivapithecus sivalensis*, and if they are considered to belong to *S. sivalensis*, then this species would become substantially more variable in premolar and molar dimensions than *Sivapithecus indicus* (Fig. 7). The gap between the two clouds of points of *S. hysudricus* and *S. sivalensis* in Figure 7, supports the hypothesis that the fossils represent two species.

Species: *Sivapithecus lewisi* Pandey & Sastri, 1968

Holotype: ONGC/V/790 right mandible fragment containing the roots of canine and p/3 and the crowns of p/4 (missing much of the enamel) and m/1.

Diagnosis: Similar to other Siwalik *Sivapithecus* species in known dental-gnathic and postcranial morphology, but significantly larger; size, as determined from postcranial elements, approximately between that of male chimpanzees and female gorillas. Dentally, it is approximately the size of small female gorillas. Compared to other *Sivapithecus* species, P4/ is expanded lingually, the lower premolars and m/3 are large relative to m/1 and m/2, and p/3 has an inflated disto-lingual ridge (from Kelley 1988).

Type locality: Bandal (32°01'55"E: 76°16'15"N), India.

Age: Nagri Formation, equivalent to MN 10 of the European Land Mammal Zonation (ca 9.5 +/- 1 Ma).

Material and measurements: BSPG 1956 II 2367, (15-12-55) left dI1/ – 6.9 x 4.9 mm.

Note: The holotype of *Sivapithecus lewisi* Pandey & Sastri, 1968 (ONGC/V/790, a right mandible with roots of the canine and p/3, crowns of p/4 and m/1) (Fig. 8) is close in dimensions and morphology to the type specimen of *Sivapithecus parvada*, and is appreciably larger than any specimens attributed to *Sivapithecus indicus*. *S. parvada* Kelley, 1988, is therefore a junior synonym of *S. lewisi* Pandey & Sastri, 1968. The type specimen of *Sivapithecus aiyengari* Prasad,

Figure 9: BSPG 1956 II 2367, *Sivapithecus lewisi* left dI1/ from Sethi Nagri, Nagri Formation, Pakistan. A) lingual, B) occlusal, and C) labial views (scale bar: 10 mm).

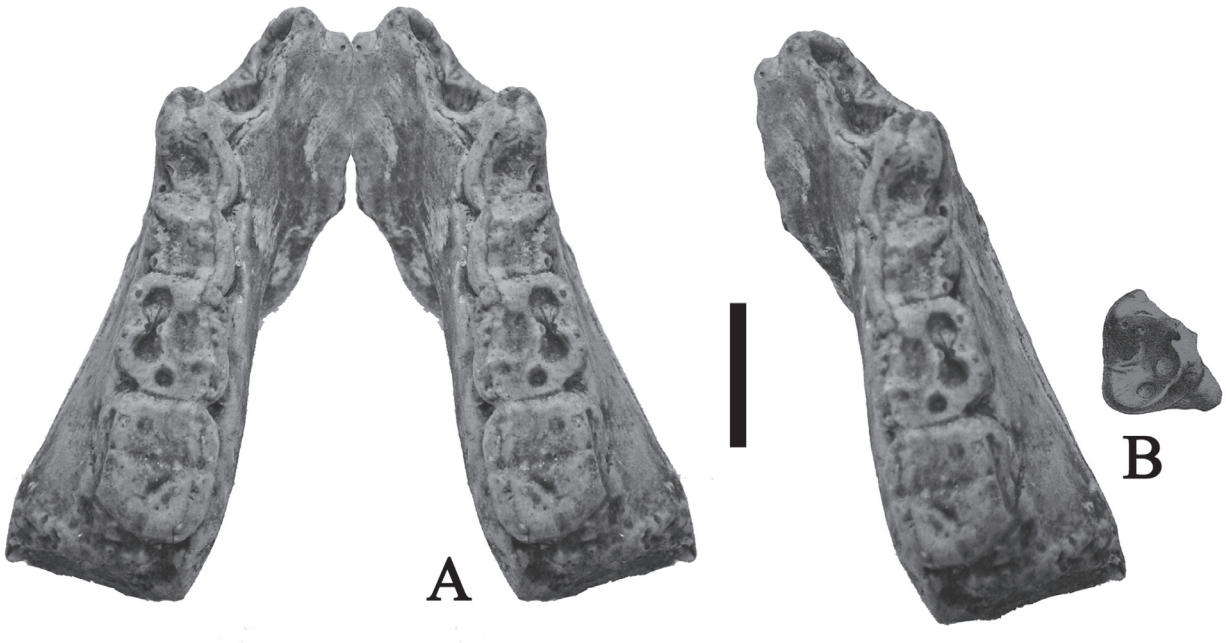


Figure 10: *Sivapithecus hysudricus*, A) GSI D 298, Kundal Nala, Pakistan, cast of right mandible containing p/3-m/2 (with mirror image), right side in stereo, B) GSI D 200, holotype right m/1 of *Sivapithecus hysudricus* (Pilgrim, 1927) (scale: 10 mm).

1962, falls into the range of morphological and metric variation of *Sivapithecus indicus* as was correctly observed by Kelley (1988).

Description: The deciduous upper central incisor from Sethi Nagri is in medium wear (Fig. 9). The crown is slightly spatulate, with lightly inflated labial and lingual surfaces and it has a small root. It has lost perhaps a quarter of its height to wear.

Comparisons: No other deciduous incisors of hominoids have been described from the Siwaliks, so it is not possible to make comparisons with the specimen from Sethi Nagri. Judging from its dimensions, the tooth is compatible with the species *Sivapithecus parvada*, the only hominoid species found at the site (Kelley 1988) but here treated as a junior synonym of *S. lewisi* Pandey & Sastri, 1968. The Sethi Nagri locality has yielded several dento-gnathic elements of juvenile hominoids, notably a left mandible containing the erupted dp/3 and the

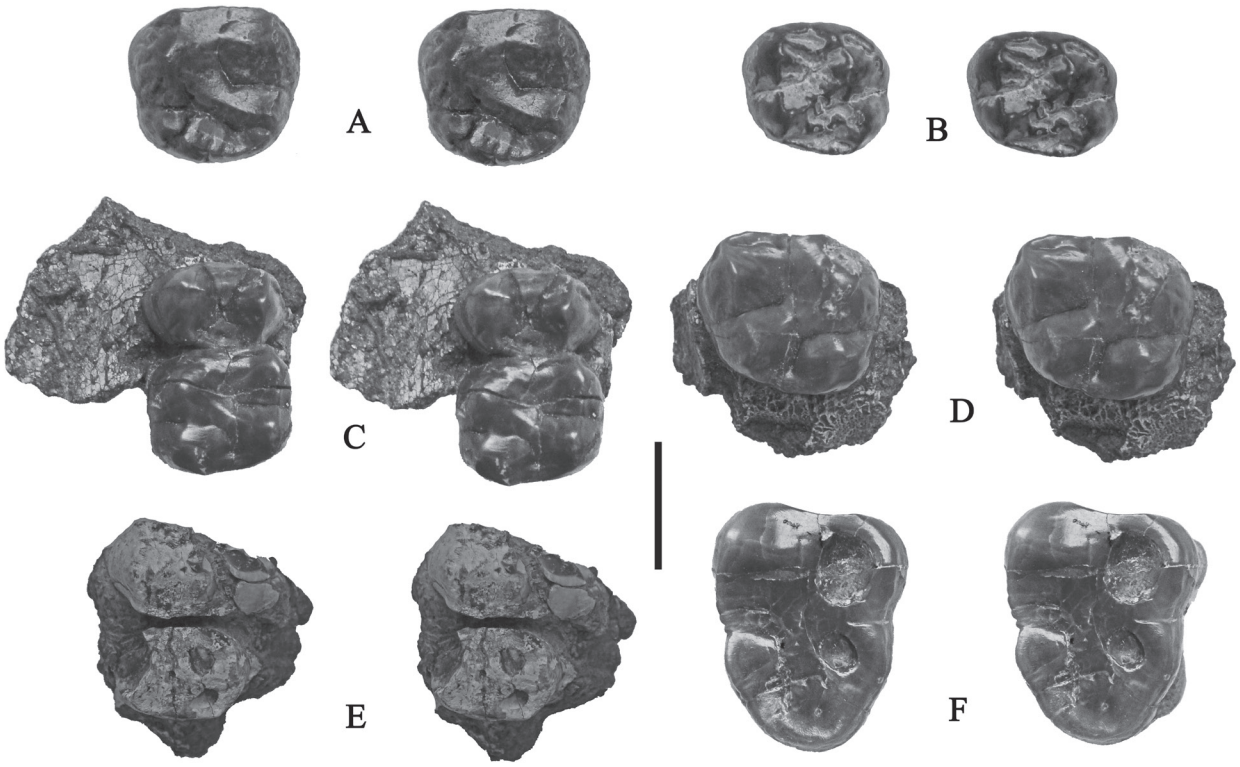


Figure 11: *Sivapithecus* teeth collected by Richard DEHM in the Chinji and Nagri Formations, Pakistan, stereo occlusal views. A) BSPG 1939 X 3, Sosianwali, Chinji zone, left upper molar; B) BSPG 1939 X 1 Kundal Nala, Chinji zone, left upper molar; C) BSPG 1939 X 2, Parrewali, Chinji zone, left P4/ and M1/ in maxilla fragment; D) BSPG 1939 X 2 same individual as C, right upper molar; E) BSPG 1956 II 37, Sosianwali, Chinji zone, right P3/ and P4/ in maxilla fragment; G) BSPG 1956 II 40, Sethi Nagri, right m/3 Of these teeth, B) probably belongs to *S. hysudricus*, A) and C–E) to *S. sivalensis*, and F) to *S. lewisi*. (Scale: 10 mm).

permanent premolars and incisors in their crypts (KELLEY 1988), and a maxilla containing unerupted incisors (KELLEY et al. 1995). So far there is no duplication of deciduous elements, raising the possibility that the deciduous upper incisor described here may belong to the same inividual as the other juvenile specimens from the site.

5. Discussion

Several points emerge from the present study. Firstly, it is never a waste of time to examine fossil collections, even those that have been studied intensively. The current mode for transferring fossil collections to dépôts far from the parent institutions will make it less likely that they will receive the sort of attention from visiting and local scientists that lead to such discoveries as the ones reported in this contribution.

Secondly, most of the DEHM Siwaliks collection is in need of further research, several of the groups being well represented in the BSPG München, but not yet having been published (carnivores, gomphotheres, equids, suids, anthracotheres, suids, ruminants). Study of these fossils would help to provide a more secure biochronological and palaeoenvironmental background to the important hominoid fossils that DEHM's expeditions collected, among which are an extremely large (*S. lewisi*), a medium sized (*S. sivalensis*) and a small form (*S. hysudricus*) of the genus *Sivapithecus*. Such studies might throw light on the factors (environmental, climatic etc.) that, between 12 and 9 Ma (+/- 1 Ma), accompanied an enormous increase in dimensions of the species classed in *Sivapithecus* as represented by the Kadirpur and Sethi Nagri specimens. This trend apparently continued during the Late Miocene and Plio-Pleistocene with the evolution of the genus *Indopithecus* by 8–7 Ma (*Indopithecus giganteus*, Haritalyangar, India ca 7 Ma) (Fig. 7) which culminated in the species *Gigantopithecus blacki* (Pleistocene, China) the largest primate that ever existed.

It has been noted that the suid *Conohyus* increased in dimensions at the same time as species of *Sivapithecus* (*Conohyus sindiensis* at Chinji, *Conohyus indicus* at Nagri), and that the suid genus *Tetraconodon* (present in the Dehm collection from Chinji) also experienced a similar trend of increasing dimensions throughout the same period (PICKFORD 1988; VON KOENIGSWALD 1983). In contrast the suid genus *Listriodon*, which was extremely common during the Chinji time period, went extinct before the onset of Nagri times. The same period witnessed the arrival of the equid *Hipparion* in the Indian subcontinent. One might pose the question whether these changes were all related aspects of a long term trend in palaeoclimatic (and thus palaeoenvironmental) change (PICKFORD & MORALES 1994), or whether they were due to biogeographic shifts of

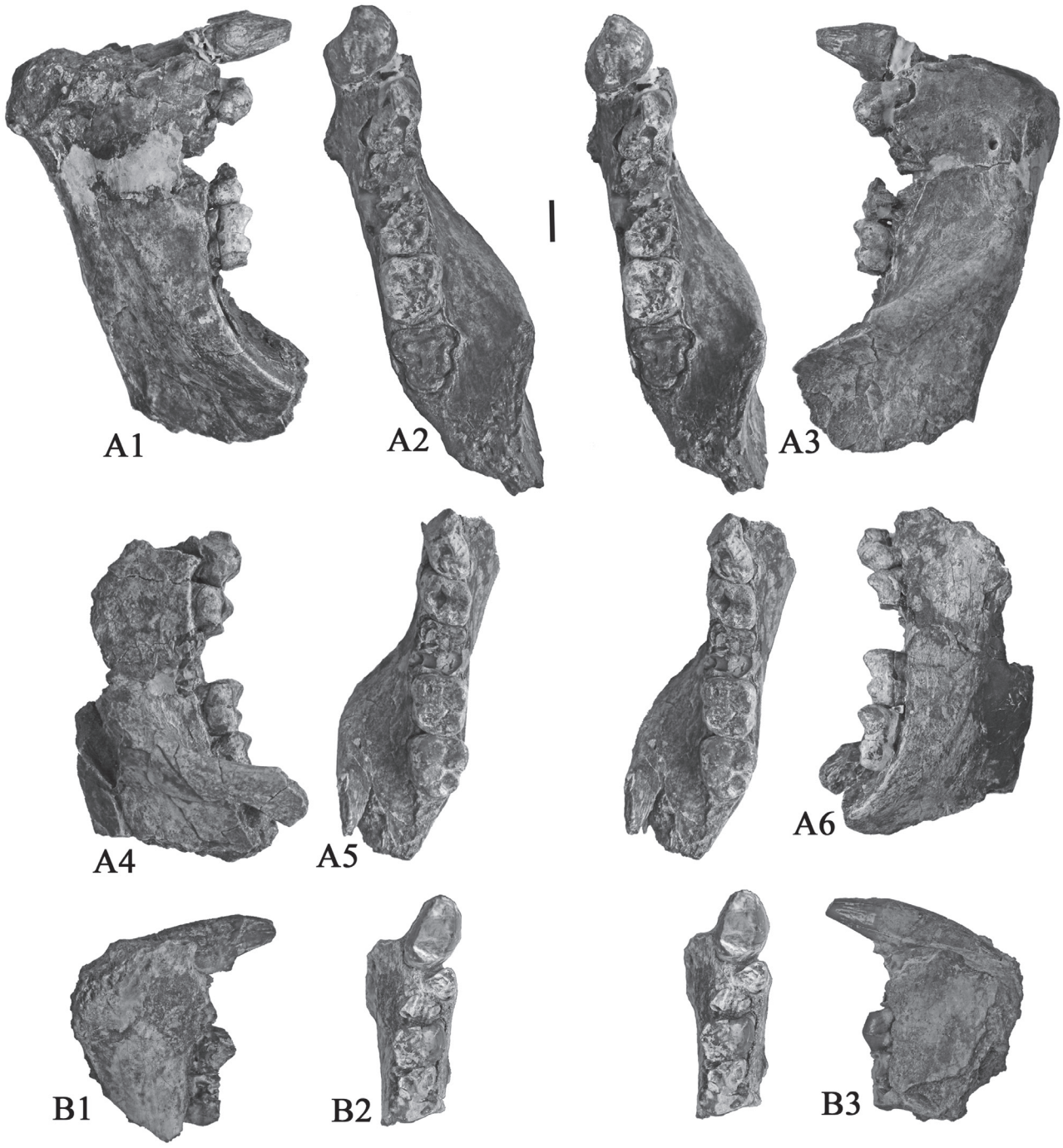


Figure 12: Mandibles of *Sivapithecus lewisi* collected from Sethi Nagri, Pakistan, by Richard Dehm. A) BSPG 1939 X 4 left and right rami of a single individual (A1: lingual, A2: stereo occlusal, A3: buccal views of right mandible, A4: buccal, A5: stereo occlusal and A6: lingual views of left mandible); B) BSPG 1956 II 39, right mandible fragment containing c/1, p/4 and m/1 (B1: lingual, B2: stereo occlusal, and B3: buccal views). (Scale: 10 mm)

faunas related to the opening up of intercontinental migration pathways due to global tectonics (Pickford & Morales 1994).

Although hominoids have long been known to occur in the Chinji levels of Pakistan and India (Ramnagar, Dera Gopipur), the available samples are rather limited, especially when they are compared with the more abundant material collected from the Nagri levels. The Kadirpur discovery represents a new locality for Siwalik hominoids and is thus a precious addition to the archives of fossil hominoids from the Indian Subcontinent.

The pristine, almost unworn, state of preservation of the p/3 from the Kadirpur site permits detailed comparisons with other fossil hominoids. It resolves the debate about the status of the poorly known species *Sivapithecus hysudricus* (= *Bramapithecus thorpei* Lewis, 1934, = *Sivapithecus simonsi* Kay, 1982) (Fig. 10) tilting the balance in favour of the hypothesis that this species is valid, mainly because, if these teeth represent *S. sivalensis* as reported in the literature (Kelley 1988) then the species would be substantially more variable

in p/3 and other dental dimensions than *Sivapithecus indicus* is (Fig. 7).

Over the years, many genus names have been proposed for Siwalik hominoids, most of them based on species for which the holotype is an isolated tooth. For pragmatic reasons, most of these genus names have been considered to be synonyms of *Sivapithecus* (Simons & Pilbeam 1965; Kelley 2002). *Chinjipithecus* von Koenigswald, 1981, is one such genus (type species *C. atavus*, type specimen: a lower right molar) and *Indopithecus* von Koenigswald, 1950, is another (type species *I. giganteus* (Pilgrim, 1915), type specimen: GSI D-175, a right lower molar) although for a while it was considered to represent *Gigantopithecus*, in recent literature it has been attributed to *Indopithecus*. *Palaeosimia* Pilgrim, 1915, is another (type species *P. rugosidens*, type specimen: GSI D-188, isolated upper molar). Others are: *Hylopithecus* Pilgrim, 1927 (type species *H. hysudricus*, type specimen GSI D 200: isolated right m/1) (reported to be a *nomen dubium* by Simons & Pilbeam, 1965, but compatible in dimensions and morphology with the holotype of *Sivapithecus simonsi*); *Sugrivapithecus* Lewis, 1934 (type species *S. salmontanus*, type specimen: YPM 13811, left mandible lacking the p/3 crown (roots are present) but with complete p/4-m/2, here considered to represent *Sivapithecus sivalensis*); *Bramapithecus* Lewis, 1934 (type species *B. thorpei*, type specimen: YPM 13814, mandible lacking the premolars and first molar); *Ramapithecus* Lewis, 1934 (type species *R. brevirostris*, type specimen: YPM 13799, right maxilla); *Sivasimia* Chopra, 1983 (type species *Sivasimia chinjiensis*, type specimen: PUA 187-76, a fragmentary lower molar thought by its describer to be an upper molar). The type specimen of *Adaetontherium incognitum* Lewis, 1934, originally interpreted as a hominoid (Tattersall & Simons 1969), is the rear half of a lower molar of *Conohyus sindiensis* (Pickford, 1977).

The morphology of GSI D 200 is close to that of other species of the genus *Sivapithecus*, which makes it unlikely that the species *hysudricus* should be retained in a separate genus, *Hylopithecus*, as originally proposed by Pilgrim (1927). Three species of small hominoid from the Siwaliks of the Indian Subcontinent have been named, but it is evident that all the material belongs to a single taxon, the name with priority being *Sivapithecus hysudricus* (Pilgrim, 1927). *Bramapithecus thorpei* Lewis, 1934, and *Sivapithecus simonsi* Kay, 1982, are here considered to be junior synonyms of *Sivapithecus hysudricus*.

A very large species of *Sivapithecus* exists in the Siwaliks of Pakistan and India (Fig. 6–8) for which two names have been proposed, *Sivapithecus lewisi* Pandey & Sastri, 1968, and *Sivapithecus parvada* Kelley, 1988. Kelley (1988) excluded the holotype of *S. lewisi* from *S. parvada*, on the basis of minor morphological differences, but examination of a good cast housed at the Natural History Museum, London, (Fig. 8) reveals that the Bandal specimen of *S. lewisi* falls comfortably within the known range of morphological and metric variation of the Sethi Nagri *S. parvada*. The latter is thus a synonym of *S. lewisi*.

6. Conclusions

Two hitherto undescribed hominoid teeth from the Siwaliks of Pakistan collected by Richard Dehm in 1955 are attributed to two distinct species of *Sivapithecus*, a small tooth from Kadirpur, to *Sivapithecus hysudricus* (Pilgrim, 1927) and a deciduous upper central incisor from Sethi Nagri, to *Sivapithecus lewisi* Pandey & Sastri, 1968.

It appears from the various reports of fossils from the Chinji area, Pakistan, that there is a broad size range of hominoids from the deposits (Pilbeam et al. 1980) (Fig. 11). The smallest species is represented by the p/3 from Kadirpur collected by Dehm, described in this paper and attributed to *Sivapithecus hysudricus* (Pilgrim, 1927) and by the holotype of *Sivapithecus simonsi* collected from Kundal Nala (Kay 1982) which is a junior synonym of *S. hysudricus*. Medium sized specimens are represented by teeth from various sites (Parrewali, West of Chinji, Kundal Nala, NW of Chinji, Bhuriwala SE of Chinji, and Sosianwali NW of Chinji, attributed by Dehm (1983) to various species of *Sivapithecus* (*orientalis*, *indicus*, *sivalensis*), but at least one of the specimens (BSPG 1939 X 1) is likely to belong to *S. hysudricus*, and the large species by the type specimen of *Chinjipithecus atavus* from an unknown locality near Chinji (von Koenigswald 1981). If the tooth of *C. atavus* came from Sethi Nagri, which is not very far from Chinji (Fig. 3), then it could belong to *S. lewisi*.

Metric analysis of the lower teeth of Siwalik hominoids (Fig. 7) reveals that there are five taxa in total, four of *Sivapithecus* and one of *Indopithecus*. The species of *Sivapithecus* span a broad range of sizes from the small *S. hysudricus*, which was smaller than a female chimpanzee, through *S. sivalensis* which was about the same size as a chimpanzee, to *S. indicus* which would correspond in body size to large chimpanzees, and ending with *S. lewisi* which was the size of female gorillas (Fig. 12). *Indopithecus giganteus* was the largest of the Siwalik hominoids, although in some tooth positions it overlaps in dimensions with *S. lewisi*.

Finally, the Kadirpur lower third premolar effectively refutes the hypothesis that the small Siwalik hominoids are human ancestors (Simons & Pilbeam 1965). The mandibles attributed to *Ramapithecus punjabicus* by these authors, and for a long time considered to be those of early hominids, have poorly preserved p/3s or are lacking this tooth. Where comparisons can be made, the morphology of the Kadirpur specimen is the same as that of other species of *Sivapithecus* (*S. sivalensis*, *S. indicus*, *S. lewisi*) and it is similar in dimensions to the p/3s in the mandibles formerly attributed to *Ramapithecus punjabicus*. I have little hesitation in attributing the specimen to a small species of *Sivapithecus*, for which the name with priority is *Sivapithecus hysudricus* (Pilgrim, 1927).

Acknowledgements

I am anxious to thank Gertrud Rössner at the BSPG München for according me access to the fossil collections in her care. I benefitted from the detailed knowledge that Kurt Heissig has of the Siwalik collections at München. Thanks to the Collège de France, the Muséum National d'Histoire Naturelle, Paris, and UMR 7202 (CR2P) du CNRS for support. Thanks also to Robert Kruszinski and Pip Brewer at the Natural History Museum, London, for providing access to fossils and casts of hominoids in their care.

7. References

Barry, J. (1986): A review of the chronology of Siwalik hominoids. – In: J. G. Else & P. C. Lee (Eds), Primate Evolution; London (Cambridge University Press), pp. 93–106.

Brown, B. Gregory, W. & Hellmann, M. (1924): On three incomplete anthropoid jaws from the Siwaliks, India. – American Museum Novitates, **130:** 1–9.

Cameron, D. (1997): A revised systematic scheme for the Eurasian Miocene fossil Hominidae. – Journal of Human Evolution, **33:** 449–478.

Cameron, D. (2001): The taxonomic status of the Siwalik late Miocene hominid *Indopithecus* (= *Gigantopithecus*). – Himalayan Geology, **22:** 29–34.

Cameron, D. (2003): A functional and phylogenetic interpretation of the late Miocene Siwalik hominid *Indopithecus* and the Chinese Pleistocene hominid *Gigantopithecus*. – Himalayan Geology, **24:** 19–28.

Cameron, D., Patnaik, R. & Sahni, A. (1999): *Sivapithecus* dental specimens from Dhara locality, Kalgarh District, Uttar Pradesh, Siwaliks, Northern India. – Journal of Human Evolution, **37:** 861–868.

Chopra, S. R. K. (1983): Significance of recent hominoid discoveries from the Siwalik Hills of India. – In: R. Ciochon & R. Corruccini (Eds), New Interpretations of Ape and Human Ancestry; New York (Plenum), pp. 539–557.

Chopra, S. R. K. & Kaul, S. (1975): New fossil *Dryopithecus* material from the Nagri Beds at Haritalyangar (H.P.), India. – In: S. Kondo, M. Kawai & A. Ehara (Eds), Contemporary Primatology; Basel (S. Karger), pp. 2–11.

Dehm, R. (1983): Miocene hominoid primate dental remains from the Siwaliks of Pakistan. – In: R. Ciochon & R. Corruccini (Eds), New Interpretations of Ape and Human Ancestry; New York (Plenum), pp. 527–538.

Dehm, R. Oettingen-Spielberg, T. & Vidal, H. (1963): Paläontologische und geologische Untersuchungen im Tertiär von Pakistan, 3. *Deinotherium* im der Chinji-stufe der Unteren Siwalik-Schichten. – Abhandlungen der Bayerischen Akademie der Wissenschaften, München, mathematische-naturwissenschaftliche Klasse, **114:** 1–34.

Dutta, A., Basu, P. & Sastry, M. (1976): On the new finds of hominids and additional finds of pongids from the Siwaliks of Ramnagar area, Udhampur District, J & K State. – Indian Journal of Earth Sciences, **3:** 234–235.

Falconer, H. (1868): Palaeontological Memoirs and Notes of the Late Hugh Falconer, vol. 1, Fauna Antiqua Sivalensis; London (C. Murchinson), 145 pp.

Gregory, W. & Hellman, M. (1926): The dentition of *Dryopithecus* and the origin of man. – Anthropological Papers of the American Museum of Natural History, **28:** 1–125.

Gregory, W., Hellmann, M. & Lewis, G. (1938): Fossil anthropoids of the Yale-Cambridge India Expedition of 1935. – Publications of the Carnegie Institute, Washington, **495:** 1–27.

Gupta, V. J. (1969): Fossil Primates from the lower Siwaliks of Kangra District, H.P. – Research Bulletin (new series) of the Panjab University, India, **20:** 577–578.

Gupta, S. S. Verma, B. C. & Tewari, A. P. (1979): New fossil hominoid material from the Middle Siwaliks of Kangra District, Himachal Pradesh. – International Geological Correlation Programme, IGCP-41. Neogene/Quaternary Boundary: Field Conference, India, **1979:** p. 11.

Gupta, S. S. Verma, B. C. & Tewari, A. P. (1982): New fossil hominoid material from the Siwaliks of Kangra District, Himachal Pradesh. – Journal of the Palaeontological Society of India, **27:** 111–115.

Heissig, K. (1972): Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 5 – Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-schichten. – Abhandlungen der Bayerischen Akademie der Wissenschaften, München, mathematische-naturwissenschaftliche Klasse, **152:** 1–112.

Hooijer, D. (1951): Questions relating to a new large anthropoid ape from the Mio-Pliocene of the Siwaliks. – American Journal of Physical Anthropology, **9:** 79–94.

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

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

Kappelman, J., Kelley, J., Pilbeam, D., Sheikh, K., Ward, S., Anwar, M., Barry, J., Brown, B., Hake, P., Johnson, N., Raza, S. M. & Shah, S. (1991): The earlist occurrence of *Sivapithecus* from the Middle Miocene Chinji Formation of Pakistan. – Journal of Human Evolution, **21:** 61–73.

Kay, R. (1982): *Sivapithecus simonsi*, a new species of Miocene hominoid with comments on the phylogenetic status of the Ramapithecinae. – International Journal of Primatology, **3:** 113–174.

Kelley, J. (1988): A new large species of *Sivapithecus* from the Siwaliks of Pakistan. – Journal of Human Evolution, **17:** 305–324.

Kelley, J. (2002): The hominoid radiation in Asia. – In: W. C. Harwig (Ed.), The Primate Fossil Record; Cambridge (Cambridge University Press), pp. 369–384.

Kelley, J. (2005): Misconceptions arising from the misassignment of non-hominoid teeth to the Miocene hominoid *Sivapithecus*. – Palaeontologia Electronica, **8/1:** 16A: 1–19.

Kelley, J., Anwar, M., McCollum, M. & Ward, S. (1995): The anterior dentition of *Sivapithecus parvada* with comments on the phylogenetic significance of incisor heteromorphy in hominoids. – Journal of Human Evolution, **28:** 503–517.

Koenigswald, G. von (1950): Bemerkungen zu *Dryopithecus giganteus* Pilgrim. – Eclogae geologicae Helvetiae, **42:** 515–519.

Koenigswald, G. von (1951): Remarks on *Indopithecus*: A reply. – American Journal of Physical Anthropology. **9/4**: 1–4.

Koenigswald, G. von (1981): A possible ancestral form of *Gigantopithecus* (Mammalia, Hominoidea) from the Chinji layers of Pakistan. – Journal of Human Evolution, **10:** 511–515.

Koenigswald, G. von (1983): The significance of hitherto undescribed Miocene hominoids from the Siwaliks of Pakistan in the Senckenberg Museum, Frankfurt. – In: R. Ciochon & R. Corruccini (Eds), New Interpretations of Ape and Human Ancestry; New York (Plenum), pp. 517–526.

Lewis, G. (1934): Preliminary notice of new man-like apes from India. – American Journal of Science, **27:** 167–179.

Lewis, G. (1936): A new species of *Sugrivapithecus*. – American Journal of Science, **31:** 450–452.

Lewis, G. (1937): Taxonomic syllabus of Siwalik fossil anthropoids. – American Journal of Science, **34:** 139–147.

Lydekker, R. (1879): Further notices of Siwalik Mammalia. – Records of the geological Survey of India, **12:** 33–52.

Lydekker, R. (1884): Indian Tertiary and post-Tertiary Vertebrata. Siwalik and Narbada Bunodont Suina. – Memoirs of the Geological Survey of India, Palaeontologica indica, **10/3/2:** 35–104.

Munthe, J., Dongol, B., Hutchison, J., Kean, W., Munthe, K. & West, R. (1983): New fossil discoveries from the Miocene of Nepal including a hominoid. – Nature, **303:** 331–333.

Pandey, J., & Sastri, V. V. (1968): On a new species of *Sivapithecus* from the Siwalik rocks of India – Journal of the Geological Society of India, **9:** 206–211.

Patnaik, R. & Cameron, D. (1997): New Miocene fossil ape locality, Dangar, Hari-Talyangar region, Siwaliks, Northern India. – Journal of Human Evolution, **32:** 93–97.

Patnaik, R., Cameron, D., Sharma, J. C. & Hogarth, J. (2005): Extinction of Siwalik fossil apes: a review based on a new fossil tooth and on palaeoecological and palaeoclimatological evidence. – Anthropological Science, **113:** 65–72.

Pickford, M. (1977): The status of *Adaetontherium incognitum* Lewis, 1934 from the middle Miocene of Pakistan. – Tertiary Research, **1:** 67–68.

Pickford, M. (1988): Revision of the Miocene Suidae of the Indian Subcontinent. – Münchner Geowissenschaftliche Abhandlungen, **12:** 1–91.

Pickford, M. (1998): Dating of the Neogene Old World anthropoid fossil record: essential base for phylogenetic analysis, biogeogra-

phy and palaeoecology. – Primatologie, **1:** 27–92.

Pickford, M. & Morales, J. (1994): Biostratigraphy and palaeobiogeography of East Africa and the Iberian Peninsula. – Palaeogeography, Palaeoclimatology, Palaeoecology, **112:** 297–322.

Pickford, M. & Tiwari, B. N. (In prep.): Precisions concerning the distribution and identification of Miocene hominoids from India.

Pilbeam, D., Meyer, G., Badgley, C., Rose, M., Pickford, M., Behrensmeyer, K. & Shah, S. (1977): New hominoid primates and their bearing on hominoid evolution. – Nature, **270:** 684–689.

Pilbeam, D. R., Rose, M. D., Badgley, C. & Lipschutz, B. (1980): Miocene Hominoids from Pakistan. – Postilla, **181:** 1–94.

Pilbeam, D. & Smith, R. (1981): New skull remains of *Sivapithecus* from Pakistan. – Memoir of the Geological Survey of Pakistan, **11:** 1–13.

Pilgrim, G. E. (1910): Notices of new Mammalian genera and species from the Tertiaries of India. – Records of the Geological Survey of India, **40:** 63–71.

Pilgrim, G. E. (1913): The correlation of the Siwaliks with the mammal horizons of Europe. – Records of the Geological Survey of India, **43:** 264–325.

Pilgrim, G. E. (1915): New Siwalik Primates and their bearing on the question of the evolution of man and the Anthropoidea. – Records of the Geological Survey of India, **45:** 1–74.

Pilgrim, G. E. (1927): A *Sivapithecus* palate and other primate fossils from India. – Palaeontologica indica, **14:** 1–26.

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

Prasad, K. N. (1962): Fossil primates from the Siwalik Beds near Haritalyangar, Himachal Pradesh, India. – Journal of the Geological Society of India, **3:** 86–96.

Prasad, K. N. (1964): Upper Miocene anthropoids from the Siwalik Beds of Haritalyangar, Himachal Pradesh, India. – Palaeontology, **7:** 124–134.

Prasad, K. N. (1968): The vertebrate fauna from the Siwalik Beds of Haritalyangar, Himachal Pradesh, India. – Palaeontologica indica, **39:** 1–77.

Preuss, T. M. (1982): The face of *Sivapithecus indicus*: Description of a new, relatively complete specimen from the Siwaliks of Pakistan. – Folia primatologica, **38:** 141–157.

Raza, S. M., Barry, J., Pilbeam, D., Rose, M., Shah, I. & Ward, S. (1983): New hominoid primates from the Middle Miocene Chinji Formation, Potwar Plateau, Pakistan. – Nature, **306:** 52–54.

Sahni, A., Kumar, V. & Srivastava, V. C. (1974): *Dryopithecus* (subgenus: *Sivapithecus*) and associated vertebrates from the Lower Siwaliks of Uttar Pradesh. – Bulletin of the Indian Geological Association, **7:** p. 54.

Sahni, A. & Tiwari, B. N. (1979): Lower Siwalik vertebrates from Kalagarh District Pauri Garwhal, U.P. – Himalayan Geology, **9:** 339–347.

Sahni, A., Tiwari, B. N. & Kumar, K. (1980): An additional Lower Siwalik vertebrate fauna from the Kalagarh Area, District Pauri Garhwal, Uttar Pradesh. – Proceedings of the 3rd Indian Geological Congress, Poona, pp. 81–90.

Sahni, A., Tiwari, B. N. & Kumar, K. (1983): A report on the occurrence of *Ramapithecus punjabicus* (Hominoidea) from the Uttar Pradesh Siwaliks. – Himalayan Geology, **11:** 193–197.

Sankhyan, A. R. (1985): Late occurrence of *Sivapithecus* in Indian Siwaliks. – Journal of Human Evolution, **14:** 573–578.

Simons, E. L. (1964): On the mandible of *Ramapithecus*. – Proceedings of the National Academy of Sciences, **51:** 528–535.

Simons, E. L. & Chopra, S. R. K. (1969): *Gigantopithecus* (Pongidae, Hominoidea): A new species from Northern India. – Postilla, **138:** 1–8.

Simons, E. & Ettel, P. (1970): *Gigantopithecus*. – Scientific American, **222:** 77–85.

Simons, E. & Pilbeam, D. (1965): Preliminary revision of the Dryopithecinae (Pongidae, Anthropoidea). – Folia primatologica, **3:** 81–152.

Tattersall, I., & Simons, E. (1969): Notes on some little-known primate fossils from India. – Folia primatologica, **10:** 146–153.

Tiwari, B. N. & Kumar, K. (1984): A new locality for *Ramapithecus* (Hominoidea): Lower Siwaliks of the Dhara Reserve Forest, Uttar Pradesh. – Man and Environment, Pune, **8:** 8–12.

Verma, B. & Gupta, S. (1997): New light on the antiquity of Siwalik great apes. – Current Science, **72:** 302–303.

Verma, B. C., Mishra, V. P. & Gupta, S. S. (2002): Pictorial Catalogue of Siwalik Vertebrate Fossils from Northwest Himalaya. – Geological Survey of India Catalogue Series, **5:** 1–378.

Villalta, J. & Crusafont, M. (1944): Dos nuevos antropomorfos del Mioceno español y su situacion dentro de la moderna sistematica de los simidos. – Notas del Comision de investigationes geologicas y mineralogicas, **13:** 91–139.

Wadia, D. & Aiyengar, N. (1938): Fossil anthropoids of India: A list of the fossil material hitherto discovered from the Tertiary deposits of India. – Records of the Geological Survey of India, **72,** 467–494.