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MISCONCEPTIONS ARISING FROM THE MISASSIGNMENT OF NON-HOMINOID TEETH TO THE MIOCENE HOMINOID *SIVAPITHECUS*

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ABSTRACT

Since early in the twentieth century, two distinct upper canine morphologies have been assigned to the fossil hominoid *Sivapithecus* from the Siwaliks of Indo-Pakistan. The canine sample as a whole has been critically important in conceptions of *Sivapithecus* taxonomy and paleobiology. Some specimens of one canine type are associated with other dental and gnathic material of *Sivapithecus*, whereas all specimens of the other type occur as isolated teeth. One unusual feature of all of the latter specimens is the lack of a distal wear facet, even on teeth with an extensive mesial wear facet showing that the teeth were in functional occlusion. This condition is never found in the upper canines of extant anthropoids, indicating that the canines of the second type have been misidentified as hominoid teeth. Comparisons with the canines of other mammals revealed that they are in fact the canines of female suids. Removing these canines from *Sivapithecus* calls into question one recent taxonomic revision of the genus that argued for time-successive species of *Sivapithecus* based on the perceived temporal segregation of the two canine morphologies. It also alters certain perceptions about canine sexual dimorphism in *Sivapithecus*.

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INTRODUCTION

Primate skeletal elements are frequently confused with those of other mammals. This confusion usually occurs with postcranial bones because of the lack of highly specialized locomotor adaptations among primates. Misidentifications of primates with other taxa or vice versa usually involve certain elements of the fairly generalized skeletons of mammals such as carnivores, aardvarks, or even anthracotheres.

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Misidentifications of teeth, at least postcanine teeth, are less frequent because the teeth of most mammals are easily distinguishable, although primate teeth have occasionally been confused with those of suid species that have a simple, bunodont molar morphology (Pickford 1977). Anterior teeth on the other hand (incisors and canines), are often less highly modified than molars or premolars because of similar functional demands across mammalian groups relating to food procurement (incisors) or display, weaponry, and occlusion (canines). Misidentifications are therefore more likely among these teeth.

This paper concerns the regular misidentification for nearly 100 years of a number of non-primate upper canine teeth as belonging to the Miocene, Siwalik hominoid *Sivapithecus.* The same misidentification was repeatedly made by numerous paleontologists who collected in the Siwaliks, beginning with Guy Pilgrim. It went unrecognized by every hominoid expert who has either collected in the Siwaliks or analyzed the Siwalik hominoid collections, including me until recently.

The misidentification of a few non-primate teeth as hominoid might seem a trivial matter, but it has not been trivial in this case. The misidentified canines have been central to efforts to sort out the taxonomy and phylogeny of the Siwalik hominoids (e.g., Greenfield 1979; Kay 1982; Kelley 1986). In the following discussion, I will first detail the history of the misidentifications and the impact of the misidentified teeth in considerations of *Sivapithecus* taxonomy and paleobiology. This will be followed by the evidence for my belated recognition of the errors, and for correctly assigning the misidentified teeth. Finally, I will discuss the taxonomic and other implications of removing these teeth from the hypodigm of *Sivapithecus*.

Specimens discussed here are identified by the following institutional abbreviations: BMNH – British Museum (Natural History) (now the Natural History Museum); BSPhG – Bayerische Staatssammlung für Paläontologie und historische Geologie; GSI–Geological Survey of India; GSP–Geological Survey of Pakistan; YPM–Yale Peabody Museum.

HISTORY OF DISCOVERY

It was recognized early on that the teeth identified here as non-hominoid had an unusual morphology for primate canines, but their hominoid status never seems to have been seriously questioned. The first such specimen, GSI D. 192, was described by Pilgrim (1915, plate 2, figure 3). It was recovered from the Chinji Formation, in the general vicinity of the village of Chinji in the Potwar Plateau of present-day Pakistan (the provenance of specimens has been critical to their impact on *Sivapithecus* taxonomy). Pilgrim said of this specimen, “Though apparently primate, it differs considerably from that of any other genus so far known by the presence of a very distinct cingulum at the postero-internal corner of the tooth” (Pilgrim 1915, p. 48). Interestingly, Pilgrim did not compare this tooth with the canine in the type specimen of *Palaeopithecus* (now *Sivapithecus*) *sivalensis*, GSI D. 1 (Lydekker 1879), which is broken and preserves only the base of the crown. The provenance of the latter is not known with certainty, but it almost certainly comes from the younger Dhok Pathan Formation (J. Barry, personal commun., 1986).

Later, Pilgrim did compare GSI D. 192 to a second, minimally damaged canine of *Sivapithecus*, GSI D. 196 (Pilgrim 1927, figure 1). Like the canine in the *S. sivalensis* type specimen, this tooth was also in place in a maxilla so its assignment to *Sivapithecus* was unambiguous. The new specimen was from Haritalyangar, in present-day India, from sediments that are also younger than those in the Chinji area of the Potwar Plateau. Pilgrim recognized that this newer specimen was very different morphologically from GSI D. 192, and that its greatest resemblance (among both living and fossil primates) was to the partial canine preserved in GSI D. 1. He described GSI D. 196 as having a convex buccal surface, a rounded mesial outline interrupted by a deep sulcus, a concave disto-lingual surface, and being covered with coarse wrinkles. D. 192, by contrast, he described as being only slightly convex buccally and having only a slight sulcus. He therefore assigned D. 192 to a different genus, *Dryopithecus*, which was then considered to be present in the Siwaliks. Thus, it was also recognized early on that there were two distinct morphologies within the presumed hominoid upper canine sample from the Siwaliks.

For ease of reference in the ensuing discussion, the misidentified non-hominoid canines will be referred to as the “atypical” or “unusual” canines (Table 1), whereas the genuine hominoid canines will be referred to as “typical” hominoid canines, or simply as “*Sivapithecus* canines,” since several, like the *Sivapithecus* type specimen, are in maxillae assignable to *Sivapithecus*.

A second atypical canine, YPM 13809, also from the Chinji area and nearly identical in morphology to GSI D. 192, was described by Lewis (1934, plate 1, figure 3). Lewis also recognized the morphological differences between these and the typical *Sivapithecus* canines and agreed with Pilgrim that the atypical canines did not belong to

Table 1. Atypical Siwalik upper canines assigned to *Sivapithecus.*

Specimen	Original description
GSI D.192	Pilgrim 1915
YPM 13809	Lewis 1934
GSI D.307	Gregory et al. 1938
GSI D.308	Gregory et al. 1938
GSI K56/681	Dutta et al. 1976
BSPhG 1956 II 38	Dehm 1983
GSP 17121	Raza et al. 1983
GSP 17122	Raza et al. 1983
GSP 23124	Unpublished

Sivapithecus. With regard to assigning them to *Dryopithecus*, he noted only that the Indian material regarded to be *Dryopithecus* was quite different from *Dryopithecus* specimens from Europe.

Two additional atypical canines, K 23/212 (now GSI D. 307) and K 22/448 (now GSI D. 308) were described shortly thereafter by Gregory et al. (1938, plate 2, figures 1, 2, A, B; plate 7, figures A-C). GSI D. 307 is from the Chinji Formation, whereas GSI D. 308 was described as being from older, Kamlial Formation sediments, but was shown in tables 2 and 4 of Gregory et al. as being from "(?) Chinji" (no other hominoid specimens have been reported from the Kamlial Formation). Their discussion of the morphology of these canines is terse and somewhat ambiguous, as they were clearly more focused on size than on morphology.

In the same publication, Gregory et al. (1938) described the first (and still the only) female upper canines of *Sivapithecus*, from the associated dentition K 29/466 (now GSI D. 299/300) from Haritalyangar (Gregory et al. 1938, plate 1, figure 1; plate 2, figures C-E). Although they acknowledged that the greatest morphological similarity in certain features was between the atypical canines GSI D. 307 and GSI D. 308, they included D. 307 (smaller than D. 308) along with the even smaller GSI D. 299/300 in *S. sivalensis*, as male and female, respectively. The taxonomic status of the larger GSI D. 308 was left unresolved, but they tentatively assigned it to a different species of *Sivapithecus*, *S. indicus*. They were clearly cognizant of the morphological differences among the larger teeth in the Siwalik upper-canine sample described by Pilgrim, but opted to include both morphologies within the genus *Sivapithecus*. One morphology was described as "massive with posterior shear and deep anterior vertical groove" (represented by GSI D. 196), and the other as "more slender with less accented characters" (represented by GSI D. 307 and D. 308; Gregory et al. 1938, p. 10).

Another apparent atypical hominoid canine, GSI K56/681, was reported by Dutta et al. (1976, figure 5) from Ramnagar in India, from sediments that are roughly contemporaneous with those in the upper part of the Chinji Formation. Dutta et al. actually figured two upper canines, both with broken crowns. GSI K56/681 preserves nearly the entire root with the crown base and appears to have the same morphology as GSI D. 192 and the other atypical canines. The second canine, GSI K56/680 (Dutta et al. 1976, figure 3), is the basal half of a crown that appears to have the deep mesial groove and heavily wrinkled enamel of the typical *Sivapithecus* canines, such as GSI D. 1 and D. 196. No comments were made concerning the morphology of either canine.

It is important at this point to note the recovery during this same time span of more of the typical *Sivapithecus* upper canines, identical in morphology to GSI D. 1 and D. 196. One specimen, GSI D. 238, is listed in the compendium of Siwalik primates by Wadia and Aiyengar (1938), but appears not to have been otherwise published. They report it as having been collected in the vicinity of Chinji village and it is catalogued as such at the GSI. Another specimen, GSI 18066, from Haritalyangar was described by Prasad (1964, plate 20, figure 2, but mislabeled as 18065) as having a deep anterior groove, coarse wrinkles and a well preserved lingual cingulum. Lastly, Pilbeam et al. (1977, 1980) described several mostly worn or broken canines (11 total, including two pairs of antimeres in palates), all collected from younger sediments of the Dhok Pathan Formation in the Khaur area of the Potwar Plateau. One of these specimens, however, GSP 11003, is complete and minimally worn and virtually identical to GSI D. 238.

Finally, three more of the atypical canines were described in 1983, two, GSP 17121 and 17122, by Raza et al. (1983, figure 1b) and one, BSPhG 1956 II 38, by Dehm (1983, figure 1H), all from localities in the Chinji Formation. Raza et al. (1983) provided the most complete description yet of the morphological differences between the two types of canines from the Siwaliks, with the atypical canines having less well developed mesial grooves, lower crowns, a sinuous crown-root junction, roots that taper to a triangular apex, and a crown that is more "flexed" with respect to the root compared to the typical *Sivapithecus* canines. With the greatly expanded sample of typical *Sivapithecus* canines now at hand, Raza et al. also postulated for the first time that the two morphologies segregated temporally, with the atypical canines

being from Chinji sediments and the typical *Sivapithecus* canines being from younger sediments of the Dhok Pathan Formation, exposed mostly in the area around Khaur and at Haritalyangar. Raza et al. appear not to have been aware of Dutta's specimen K56/680 (again, with apparently typical *Sivapithecus* morphology) from sediments at Ramnagar contemporaneous with the Chinji Formation, or chose to ignore it because they could not be certain of its morphology based on the published photograph. However, among the Chinji canines listed by them is GSI D. 238, which is one of the typical *Sivapithecus* canines that are otherwise associated with younger sediments. They did not discuss possible taxonomic implications of this purported temporal segregation of the two canine morphologies.

CANINES AND *SIVAPITHECUS* TAXONOMY AND PALEOBIOLOGY

The Siwalik canines were central to Greenfield's (1979) arguments for the synonymy of *Ramapithecus* with *Sivapithecus*. Following Gregory et al. (1938), Greenfield recognized the morphology of the small GSI D. 299/300 canines as female, but he also regarded all of the atypical canines to be those of males. Size differences among these presumed male canines were critical to his demonstration that there were three species of *Sivapithecus* that differed only in body size and male relative canine size. Moreover, Greenfield failed to recognize the morphological differences between the atypical canines and the more typical *Sivapithecus* canines. Thus, one of his *Sivapithecus* species had canines of both types included in its hypodigm. Greenfield did, however, make one critical observation, which he did not pursue further and which was ignored by later workers, including me initially. That observation was the complete lack of a distal "posterior attrition" facet on any of the three atypical canines that he had at his disposal (YPM 13809, GSI D. 192, and GSI D. 308), canines that had clearly been in occlusion as shown by anterior wear facets. Regarding this curious feature, Greenfield (1979) stated, "Whether or not this is an important trend bearing on functional or phylogenetic questions cannot be ascertained until detailed comparisons with extant pongines are made." (p. 534); these comparisons were apparently never carried out.

In a taxonomic revision of *Sivapithecus* a few years later, Kay (1982) either did not notice any morphological variation in the canine sample or chose not to assess it. He expressed the opinion that the allocation of Siwalik hominoid maxillary canines "to a particular species (let alone a particular sex) is impossible" (Kay 1982, p. 150). He included the atypical canines in a metric analysis of *Sivapithecus* canines, from which he concluded that canine sexual dimorphism in all species of *Sivapithecus* was quite low.

My work on hominoid canines began in early 1981. Although I had access to the Siwalik collections housed at Yale University and had read Greenfield's 1979 paper, my earliest notes on Siwalik canines – dating from a visit to the Geological Survey of India in February, 1981 – indicate no prior awareness of the details of Siwalik hominoid canine morphology and wear, nor any recollection of the specifics of Greenfield's comments on the Siwalik canines. In my examination of the GSI material, I noted both the presence of two distinct upper canine morphologies in the Siwalik sample, one including GSI D. 196, D. 238 and 18066 and the other D. 192, D. 307 and D. 308, as well as the oddly curious feature of the lack of a distal wear facet among the specimens of the latter group. My characterizations of the two upper canine morphologies in my notes were as follows (see Figure 1 and Figure 2):

> (GSI D. 196, D. 238, 18066) Highly crenulated enamel, especially disto-lingually, lingual surface strongly concave mesiodistally, deep mesio-lingual groove with slight to moderate development of a mesial wear facet and early development of a distal wear facet along the entire crown length, a more or less straight cemento-enamel junction [cej] lingually, a robust crown relative to crown height, especially in bucco-lingual breadth, and a circular/ovoid root at the cej with the root remaining robust toward its apex;
>
> (GSI D. 192, D. 307, D. 308) Smooth enamel, lingual surface strongly convex mesiodistally, a shallow mesial groove with a marked wear facet, no distal wear facet, a sigmoid shaped cej lingually, a relatively gracile crown compared to crown height, and a more or less triangular root at the cej with the root tapering strongly toward the apex.

By the time of the publication by Raza et al. in 1983 describing two more atypical canines, I had also adopted the viewpoint expressed by them that the two canine morphologies segregated temporally, with the atypical canines being restricted to the earlier Chinji Formation localities, while the more typical *Sivapithecus* canines came from younger localities, mostly of the Dhok Pathan Formation. I was strongly influenced in this assessment by the fact that all the canines for which provenance was certain, that is, all those collected

Figure 1. Examples of the two Siwalik upper canine morphologies, lingual view. Left: GSP 11003, a typical *Sivapithecus* canine; right: GSP 17121, an atypical canine. Note the wrinkled enamel, concave lingual face, deep mesial groove, straight cemento-enamel junction (cej), and stout root of GSP 11003, and the smooth enamel, convex lingual face, minimal or no mesial groove, sigmoid cej, and tapering root of GSP 17121. Actual specimen lengths: GSP 11003 = 44.7 mm; GSP 17121 = 41.7 mm.

Figure 2. Same two specimens as in Figure 1, angled to show the deep mesial groove in GSP 11003, with an incipient mesial wear facet confined to the apical part of the crown, and the distinct mesial wear facet on GSP 17121.

after the early part of the century and particularly the many canines recovered by the Harvard-Geological Survey of Pakistan Project headed by David Pilbeam, segregated in this fashion. I therefore assumed that the reported provenance of GSI D. 238 (a typical canine) as being from the Chinji Formation was probably an error, as its collector, Mr. Vinayak Rao, had also collected from younger sediments at Haritalyangar (Pilgrim 1915; Wadia and Aiyengar 1938), and as this specimen had not in fact been described by Pilgrim. There was also the apparently more typical hominoid canine fragment (GSI K56/680) from the Chinji-equivalent sediments at Ramnagar, which I had not seen and the morphology of which I could not confidently ascertain from the photograph published by Dutta et al. (1976). Finally, a broken canine housed at the Natural History Museum, London (BMNH M34438) has a typical *Sivapithecus* morphology and was catalogued as being from Chinji, but it was also collected early in the century. Given the uncertainties concerning these canines, it was easy for me to rationalize away any evidence that might have contradicted the notion of temporal segregation of the two canine morphologies, which later became an instructive lesson in self-deception.

In my Ph.D. dissertation, I made features of the *Sivapithecus* canines the diagnostic characters in a taxonomic revision that recognized a temporal segregation between what were regarded as the two most common species, *S. sivalensis* and *S. indicus* (Kelley 1986). This scheme was alluded to but not formally proposed by Kelley and Pilbeam (1986). By the early 1980s, *Sivapithecus* taxonomy had come to be based largely or entirely on size, regardless of the number of species recognized or their nomenclature (Simons and Pilbeam 1965; Pilbeam et al. 1977; Greenfield 1979; Kay 1982; Kay and Simons 1983; Martin 1983). However, it had become clear to me that sized-based taxa in many instances simply separated males from females of the same species (Kelley 1986). The proposal of time-successive species therefore took shape in the context of a more comprehensive effort to revise *Sivapithecus* taxonomy to unite male and female individuals of the same species. Since the upper canines were the only teeth in the *Sivapithecus* sample that showed clear, discrete variation, and since this variation seemed to segregate temporally, large and small specimens from the younger Dhok Pathan Formation were placed in one species, while those from the older Chinji Formation were placed in another. As noted above, a specimen of the more typical hominoid canine mor-

Figure 3. GSP 11003, showing the extensive distal wear facet in a tooth that had only just begun to develop a mesial wear facet.

Figure 4. Distal view of GSP 11003 (left) and GSP 17121 (right). Note the sharp, unworn distal ridge of GSP 17121 compared to the elongate distal wear facet on GSP 11003 (see also Figure 3). Figure 1 shows that there is also no wear on the lingual margin of the distal ridge of GSP 17121. The broad mesial wear facet of GSP 17121 (Figure 2) demonstrates that the tooth had been in occlusion for some time.

phology occurs in the type specimen of *S. sivalensis*, which is from the Dhok Pathan Formation, so this name was applied to the younger species. None of the described atypical canines is associated with other dental or gnathic remains (one maxillary specimen from the Chinji Formation preserves an embedded canine root, which Raza et al. (1983) incorrectly claimed has a triangular outline characteristic of the atypical canines), but since the name *S. indicus* has priority among type specimens from the Chinji Formation, this name was applied to the older species (Kelley 1986).

A few years later, I began a study of anthropoid canine morphology in an attempt to discern if there were features by which male and female canines could be reliably distinguished (Kelley 1995a, 1995b). During this study, I incidentally observed that, because the distal margin of the upper canine occludes with the mesial face of the lower anterior premolar (either P_2 or P_3) in all anthropoids, a distal wear facet invariably begins to develop on the upper canine as soon as occlusion is achieved with the lower premolar (Figure 3). *None* of the atypical canines that I had seen (eight, including one more recent find of the Harvard-GSP Project, GSP 23124) had a distal wear facet, although all bore a large mesial wear facet demonstrating that they had been in occlusion (Figure 4). This confirmed Greenfield's (1979) observation based on three of these canines, an observation that had passed unnoticed by virtually everyone else. At this time I became convinced that these canines could not possibly be hominoid canines, but I had no idea as to which animal they did belong.

Figure 5. Comparison of GSP 17121 with GSP 11205, a female suid canine from the Dhok Pathan Formation. The light area at the base of the distal ridge of GSP 11205 is discoloration rather than wear. Note also the exposure of the mesial wear facet, most of which cannot be seen in this view, at the crown tip of GSP 11205. GSP 11205 is 32.7 mm long.

ATTRIBUTION OF THE CHINJI ATYPICAL "HOMINOID" CANINES

The atypical upper canines are, in fact, suid canines. The first evidence of this came when I began to search through the Siwalik collections at the Geological Survey of Pakistan during the 1993 field season. In the suid collections, I found an isolated upper canine (from a Dhok Pathan locality) that is nearly identical to the atypical Chinji canines in every respect, differing only in being strongly compressed bucco-lingually (Figure 5). Like the atypical canines, it has a distinct mesial wear facet but no distal wear.

Why this one canine should have been placed with the Suidae is unclear. It may be because this was the first canine of this type discovered by Harvard-GSP team members, who, as noted earlier, had found a number of genuine *Sivapithecus* upper canines, including some still in jaws, and who may have correctly recognized this canine as non-hominoid. According to its catalogue number, it was

found several years before GSP 23124 and the two atypical canines described by Raza et al. (1983). Nevertheless, this canine was itself unassociated, so it was possible that its assignment to the Suidae was incorrect.

More definitive evidence that this canine and the atypical canines from the Chinji Formation were those of suids came during a search of the suid collections at the Kenya National Museums in 1996. This search produced a skull of the early Miocene suid *Hyotherium dartevellai* with the upper canines in place (figured in Cooke and Wilkinson 1978, figure 22.4). These closely resemble the Siwalik atypical canines morphologically and also have mesial wear facets but no distal wear facets. Confirmation came soon after with the publication of van der Made's (1996) monograph on the Listriodontidae, in which are figured and described a number of female suid canines that are similar or identical to the atypical Siwalik canines from the Chinji Formation. Figured canines of *Bunolistriodon* from Maboko (van der Made 1996, plate 26) and Paşalar (plate 19), and *Listriodon* canines from Paşalar (plate 35) and Arroyo del Val IV (plate 38), in particular closely resemble the atypical Siwalik canines. While a few heavily worn canines figured by van der Made have both mesial and distal wear facets, most have only a mesial facet like all the atypical Siwalik canines. Interestingly, in van der Made's description of *Listriodon pentapotamiae* from the Siwalik Chinji Formation, there is no mention of female canine morphology, presumably because all of the female canines were in the hominoid collection. In fact, it is almost surely to this species that the atypical Chinji canines belong, rather than to the other Chinji suid, the non-listriodont *Conohyus sindiensis*.

IMPLICATIONS OF REMOVING THE ATYPICAL (SUID) CANINES FROM *SIVAPITHECUS*

The most significant implication of removing the atypical canines from *Sivapithecus* is that there is no longer any clear morphological justification for recognizing *S. indicus* and *S. sivalensis* as time-successive species. Accepting the stated provenance of the two Chinji canines with a typical *Sivapithecus* morphology, GSI D. 238 and BMNH M34438, there are no discernable differences in hominoid upper-canine size or morphology between older and younger levels in the Siwaliks. While there are suggestions of other differences in the *Sivapithecus* samples from the Chinji and Dhok Pathan Formations, for example in tooth proportions (Kelley 1988), that might indicate the presence of different species, these have not been systematically assessed. Nevertheless, Begun and Güleç (1998) have suggested that the hominoids from the Chinji Formation might not even be attributable to *Sivapithecus*. This argument is based on perceived differences between the only known palatal specimen from the Chinji Formation, GSP 16075, and the palates from the Dhok Pathan Formation, particularly GSP 15000. However, GSP 16075 is incomplete and damaged, and it is not clear that the noted differences between it and GSP 15000, even if all accurately portrayed, reflect anything more than normal intraspecific variation.

The characterizations of canine sexual dimorphism in *Sivapithecus*, both morphological and metric, put forward by Greenfield (1979) and Kay (1982) must also be reconsidered. Unfortunately, whereas several *Sivapithecus* male upper canines have been recovered (Pilbeam et al. 1980), there is still only one female canine (actually an antimere pair), GSI D299/300 (Kelley 1995b). The degree of canine height dimorphism in *Sivapithecus* based on these specimens is relatively high and on a par with that found in gorillas or orangutans (Kelley 1995a, 1995b), in contrast to the claim for relatively low canine dimorphism in *Sivapithecus* species made by Kay (1982) based on overall metric variation in the canine sample. Thus, the level of canine dimorphism in *Sivapithecus* appears to be similar to that of all other large-bodied Miocene hominoids for which measures of canine dimorphism can be calculated (Kelley 1995b; Kelley and Alpagut 1999).

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