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GIGANTOPITHECUS (PONGIDAE, HOMINOIDEA) A NEW SPECIES FROM NORTH INDIA

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ABSTRACT

A nearly complete mandible of *Gigantopithecus* representing a new species, *Gigantopithecus bilaspurensis*, is described. The specimen lacks incisors, left P_4 and the posterior portions of both rami. Even so, it is the most complete Pre-Pleistocene hominoid mandible ever found in the Indian subcontinent. Found in the Dhok Pathan beds northwest of Haritalyangar, India, it is of middle Pliocene age. It is also the most complete higher primate mandible of its age known from any site in the world.

In various ways the new specimen resembles species of *Australopithecus*, *Ramapithecus* and *Dryopithecus* more than does the specialized Chinese Pleistocene species *Gigantopithecus blacki*. In consequence of these resemblances the new Indian find tends to strengthen the close phyletic relationships already suggested by some, on the basis of other finds, for these four genera. It is suggested that in all probability *Gigantopithecus* is derived from a species of *Dryopithecus* and not from *Apidium* via *Oreopithecus* — a position which before this new discovery in India remained a possibility. Thus the new find further demonstrates that *Gigantopithecus*, although well off the line of direct human ancestry, has definite resemblances in the biomechanics of its jaws and teeth to unquestioned Hominidae. Differences in details of this functional system suggest that these features of *Gigantopithecus* may have arisen in parallel with the similar mandibular and dental mechanics of *Ramapithecus* and *Australopithecus*.

HORIZON AND LOCALITY

Upper levels of the Dhok Pathan zone, ?middle Pliocene, north of Haritalyangar, Himachal Pradesh, India.

NATURE OF THE FIND

The specimen, found originally in three associated parts, was identified by G. E. Meyer, co-investigator of the project, in April 1968.¹ The find described here is the first reported scientific result of the joint Chandigarh-Yale research program in search of early hominids and related apes in North India. This description is intended to provide a preliminary statement on the find which will be dealt with in greater detail at a later date. The specimen consists of both horizontal rami of the mandible joined at the symphysis and complete to the base of the ascending ramus on both sides (see Fig. 1). All teeth are preserved intact except that the incisors, left P₄, and anterolateral half of the right canine are broken away. This is the most complete primate fossil ever found in the Miocene/Pliocene sediments of India and one of the most complete Tertiary fossil hominoid specimens ever found in Eurasia.²

SYSTEMATICS

CLASS MAMMALIA

ORDER PRIMATES

SUBORDER ANTHROPOIDEA

SUPERFAMILY HOMINOIDEA

FAMILY PONGIDAE

SUBFAMILY DRYOPITHECINAE

GENUS *GIGANTOPITHECUS* Koenigswald 1935

¹ The authors also wish to acknowledge the services of the remainder of the field staff present at the time of discovery: S. J. Boyer, S. S. Kaul, D. Powers, G. C. Thoron, L. S. Sidhu and P. Singh.

² Although of much greater age and from a different geographical area than the three Chinese mandibles of *Gigantopithecus blacki*, this mandible, for convenience of discussion, will be referred to below as *Gigantopithecus* mandible IV.

TYPE SPECIES. *Gigantopithecus blacki* Koenigswald (1935, p. 874).

INCLUDED SPECIES. *G. blacki*, *G. bilaspurensis* sp. nov.

DISTRIBUTION. South China: Hei-Dong or Black Cave, Tahsin District; teeth of uncertain provenance from Chinese drug stores (possibly from the cooperatives of Nanning, Kwangsi, and Canton, Kwangtung); caves 1, 2, Liucheng, Kwangsi. India: Dhok Pathan zone, Himachal Pradesh.

GENERIC DIAGNOSIS (modified from Simons and Pilbeam 1965, p. 134-5). Largest genus of dryopithecine.³ Exhibits markedly reduced lower incisors and somewhat reduced and low-crowned canines. Simian shelf typically shorter (front to back), relative to absolute mandibular size, than in most modern apes; cross-section similar to that of *Australopithecus robustus*. Greatest length of symphyseal section shorter (in both presumed male and female *Gigantopithecus*), relative to an absolute size index combining length of $P_3 - M_3$ and depth and breadth of mandible at M_2 , than is typical of gorillas including *G. g. beringei* both male and female. Mandible deeper and more robust, relative to tooth size, than in any other ape and typically increasing in vertical height of horizontal ramus posteriorly. Incisors crowded between canines, vertically emplaced and with as small a bicanine breadth, relative to the length of cheek-teeth ($P_3 - M_3$), as in *A. robustus*. Lower canine crowns comparatively reduced and vertically implanted rather than flaring out laterally as is typical of a majority of Recent apes, i.e. in hominids canine roots are typically more than twice the length of unworn crown. Lower premolars only slightly heteromorphic with distinct internal cusps (metaconids) on P_3 as well as P_4 and with relative reduction of anterolateral face of P_3 correlative with distinct shortening and size reduction of upper canine compared to other apes. Molars absolutely larger than in any other extinct hominoid genus; larger than in most gorillas.

³ Hominid placement of this genus as advocated by Koenigswald (1952) Weidenreich (1945), Dart (1960) and Woo (1962), among others, is not impossible, but placement among Pongidae, following Remane (1950, 1960) and Simons and Pilbeam (1965), is continued here pending more complete fossil finds of this animal and of early hominids.

*Gigantopithecus bilaspurensis*⁴ sp. nov.

Figures 1-4

TYPE. Chandigarh-Yale Project No. 359/68, both horizontal rami of mandible joined at symphysis containing left C, P₃, M₁₋₃ and posterior half right C, P₃₋₄, M₁₋₃. Horizontal rami are broken off just posterior to third molars.

DISTRIBUTION. North India, early or middle Pliocene.

HYPODIGM. Type only.

SPECIFIC DIAGNOSIS. Mandible smaller in absolute size than smallest known *G. blacki*, but showing relatively even smaller anterior teeth. Teeth preserved (C through M₃) are little worn and lack characteristic polycuspidation of unworn *G. blacki* teeth. In this cusp simplicity these teeth resemble some *Dryopithecus*, for instance most *D. sivalensis* and *D. indicus*. Unlike *G. blacki* molars or the large molar of *D. indicus* from Alipur, India, GSI D-175⁵; lower molar protoconid distinctly smaller than metaconid, and apices of lower molar cusps more laterally placed—such a distinction also separates most *Dryopithecus* from *Ramapithecus*. Teeth much less hypsodont than *G. blacki*. Resembles *Ramapithecus punjabicus*, *G. blacki*, and most hominids in having lingually and labially expanded cheek tooth occlusal faces so that sides of teeth are oriented in a more nearly vertical plane, not rounded out as in most *Dryopithecus* species and *G. blacki*. Molars not strongly divided into trigonid and talonid portions by a lingual indentation between metaconid and entoconid as is typical of *G. blacki*.

DISCUSSION

SIZE. The new mandible represents a very large primate species. Although it is somewhat smaller than the geologically younger Chinese Pleistocene species of *Gigantopithecus*, the Himachal

⁴ Named from its provenance in the former Hill State of Bilaspur; Himachal Pradesh, India and in honor of H.H. Sir Anand Chand, Maharajah of Bilaspur.

⁵ This specimen is the type of *D. gigantius* Pilgrim, 1915, which was later proposed as type of a distinct genus and species *Indopithecus gigantius* (Koenigswald, 1949). Hooijer (1951), however, challenged the propriety of establishing a distinct genus on two unassociated teeth.

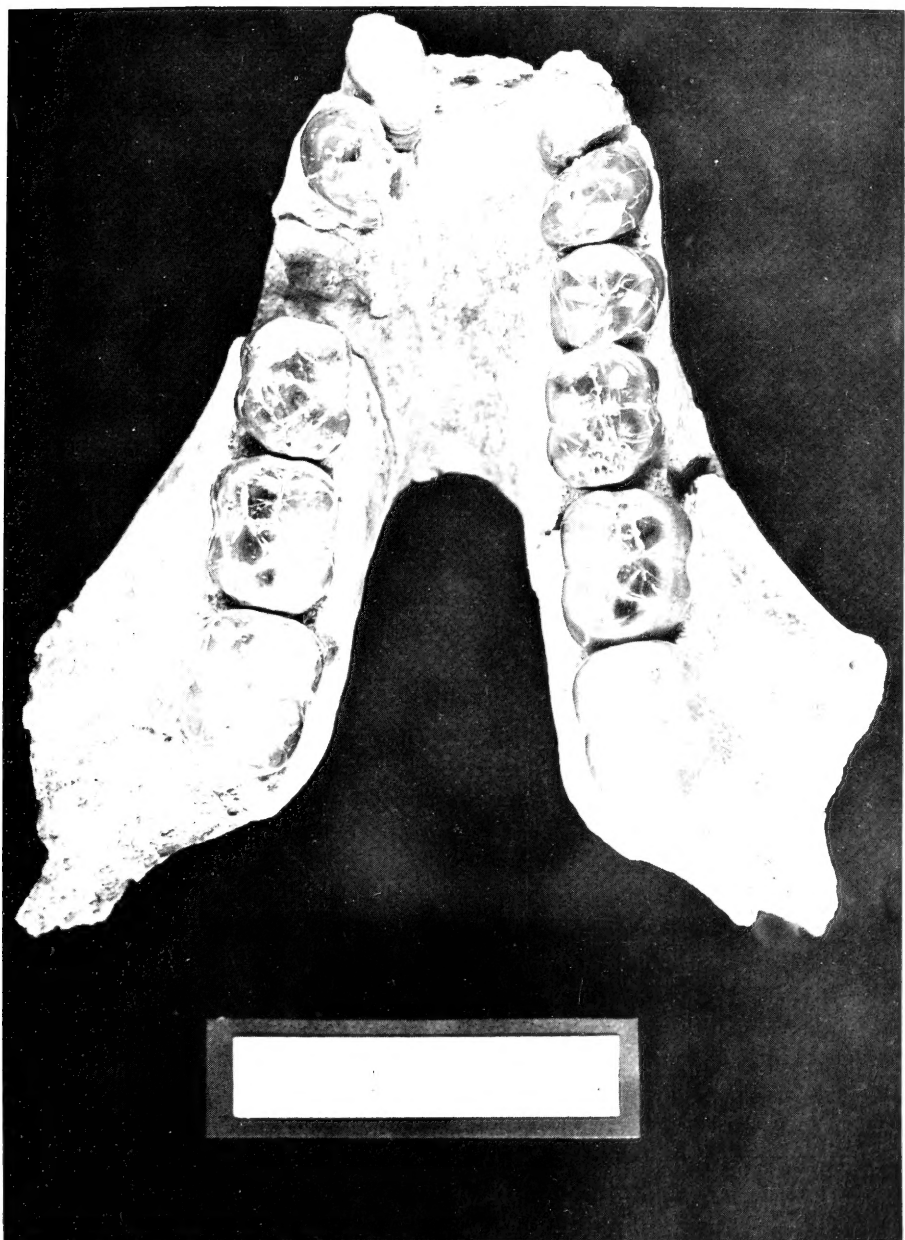


FIGURE 1. Occlusal view of the teeth and mandible of the type specimen of *Gigantopithecus bilaspurensis*, XI.

Pradesh specimen has larger premolars and molars than are typical of most hominoids. Ever since Remane's report (1921) it has been clear that variation in the absolute size of cheek-teeth among given hominoid species is great. Even so these are very large. The general robustness of the horizontal rami of the mandibles under premolars and molars is well above the range for living *G. gorilla*, including *G. g. beringei*. The contrast between the mandibles of *G. blacki* and *G. bilaspurensis* and those of living apes may be seen by comparing *Gigantopithecus* (Fig. 2) with male and female members of the largest living race of apes, the mountain gorilla, *G. g. beringei*. The male mountain gorilla, AMNH 115609 of this figure, in most cheek-tooth measurements is above the 95% confidence limits calculated by Pilbeam (in press) for a sample of 20 *G. g. gorilla* males. In these measurements it is also above the upper ranges for *Gorilla* given by Remane (1960). The M_{1-3} length is greater than in a gorilla with exceptionally large teeth described by Schultz (1964). There must then be few if any gorilla mandibles of larger size. Even so it is clear from Figure 2 that the horizontal rami of all four *Gigantopithecus* are both absolutely and relatively deeper than those of the living ape with cheek-teeth of approximately the same size.

Another major difference between *Gigantopithecus* and the three largest ape species relates to the marked reduction in size of the front teeth in *G. blacki* and *G. bilaspurensis* when compared to *Gorilla g. beringei*. The frequent spacing out of incisors and lateral flare of canines often seen in male gorillas is wholly different from the crowded incisors and vertically implanted canines of the presumed male of *Gigantopithecus*. Distinct differences also exist in this region between female *G. g. beringei* and the type of *G. bilaspurensis*, a probable female. The same distinctions from female *Gorilla* are to be seen in mandible I from the South Chinese Pleistocene site in Kwangsi, which has been assumed by Woo (1962) and others to be female. From Table 1 it is clear that although measurements of the incisors and canines of *Gigantopithecus* are near the minima for gorillas, the lengths and breadths of cheek-teeth of *Gigantopithecus* are close to or exceed the maxima known for *Gorilla*.

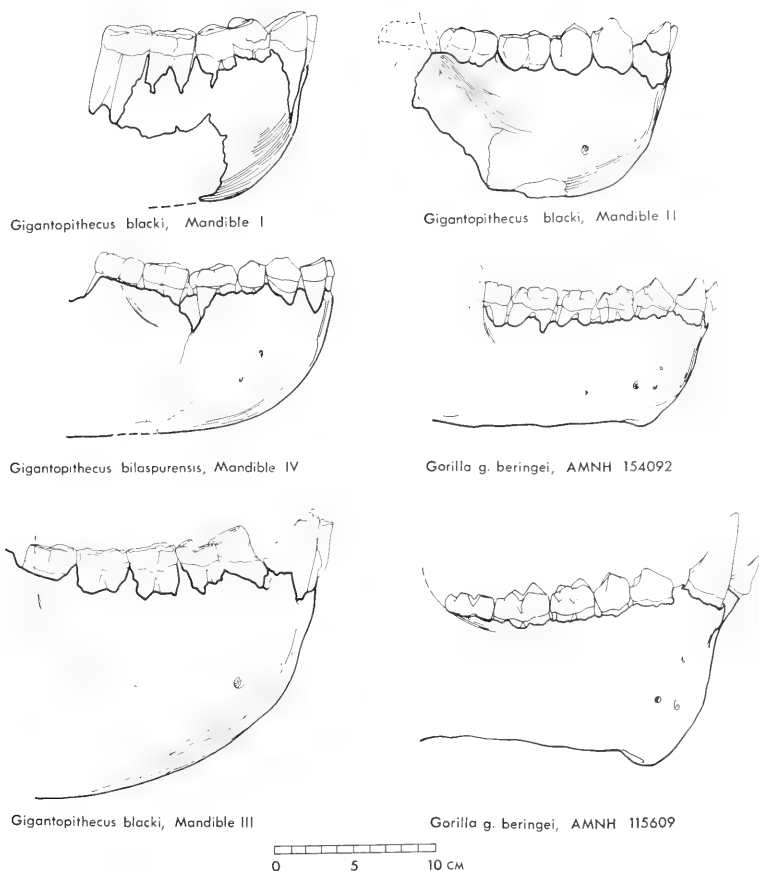


FIGURE 2. The four mandibles of *Gigantopithecus* compared with specimens of the largest living ape, *Gorilla gorilla beringei*. The male mountain gorilla, AMNH 115609, has the longest molars on record for a gorilla.

TABLE 1⁶. Measurements comparing the four *Gigantopithecus* lower dentitions with minima and maxima of *Gorilla* males.

	Teeth							
	I ₁	I ₂	C	P ₃	P ₄	M ₁	M ₂	M ₃
Anteroposterior length								
<i>Gorilla</i> (minima)	7.2	7.8	12.6	14.8	9.8	13.0	14.6	14.7
<i>Gorilla</i> (maxima)	9.4	11.1	18.0	20.4	13.5	18.3	21.0	22.0
<i>Gigantopithecus</i> I	6.0	7.7	11.5	15.1	14.2	17.7	18.6	—
<i>Gigantopithecus</i> II	—	7.2	—	16.4	16.3	20.1	21.3	—
<i>Gigantopithecus</i> III	—	8.0	13.1	16.5	17.0	18.9	21.2	21.4
<i>Gigantopithecus</i> IV	—	—	9.3	11.8	13.1	17.0	19.1	19.6
Labiolingual breadth								
<i>Gorilla</i> (minima)	8.7	9.9	14.2	9.2	11.5	11.7	13.2	13.0
<i>Gorilla</i> (maxima)	11.0	13.2	24.0	14.8	17.0	16.2	17.8	18.7
<i>Gigantopithecus</i> I	8.7	9.5	15.4	15.0	16.1	16.7	17.4	—
<i>Gigantopithecus</i> II	—	10.0	—	16.0	17.8	17.2	18.9	—
<i>Gigantopithecus</i> III	—	10.0	15.0	16.9	18.0	18.5	21.0	18.8
<i>Gigantopithecus</i> IV	—	—	16.0	14.6	14.5	14.2	16.0	16.2

DENTITION

INCISORS. Although the incisors of *G. bilaspurensis* are missing, the breadth across these four teeth can be measured because the mesiolabial corner of the left canine bears a wear facet formed by interstitial attrition with the distal border of I₂. This attrition indicates the degree of crowding in the front teeth, a feature also noted by Woo (1962) for all three Chinese Pleistocene mandibles. The position of this facet also shows that in life the lateral incisor was appressed to the mesiolabial face of the canine and situated so that the outer face of this incisor projected well forward of a line drawn between the anterior faces of the lower canines. Such an orientation of the left lateral incisor is preserved in Chinese mandible I as well as in the *Gigantopithecus* mandible III right lateral incisor, see Woo, 1962, plate IX. This establishes that the incisors of *Gigantopithecus* formed a compressed anterior-facing

⁶ Measurements of *Gorilla* from Schultz (1964) after Remane (1960), with addition of new molar length maxima from AMNH 115609.

arc. At least after some wear, in *G. bilaspurensis* there was no longer a gap between the crowns of I_2 and C as is typical of *G. g. beringei* and most other modern pongids even when these teeth are in contact at the base. The *Gigantopithecus* mandible I shows that a continuous plane of wear has truncated the six front teeth so that the outer, or leading edges of the occlusal faces of these six front teeth form a continuous row. The same arrangement of incisors and canines appears to have been true of *Gigantopithecus* mandible IV.

Relative to the extreme robustness of the horizontal ramus of the mandible and the large size of the cheek-teeth, the incisors of *Gigantopithecus* are unlike all other pongids in their relatively small size and closely compressed condition. The narrow breadth of the four incisors correlates with a remarkably constricted space between the canines and premolars above the planum alveolare.

CANINES. As was previously evident from the canines in mandibles I and III as well as isolated canine teeth described by Koenigswald (1952) and by Woo (1962) the canine is more reduced in this genus (relative to size of mandible and cheek-teeth) than in any other ape. In consequence the canines would have barely overlapped when unworn upper and lower dentitions were in occlusion, as seen in female *G. g. beringei*, Fig. 2. Nevertheless, after eruption of the full adult dentition, the course of wear is subsequently rather different in *G. g. beringei* females and both male and female *Gigantopithecus*. In *Gigantopithecus* the whole top of the canine crown appears to have been worn off early in the life of the individual. This phenomenon, which would permit greater transverse movement of the anterior dentition during mastication, is best demonstrated in the mandible under consideration (*Gigantopithecus* IV). This specimen is of much younger dental age than are either of the two Chinese *Gigantopithecus* mandibles whose canines are preserved, and the molars are so little worn that only on the protoconid of the first molars has the enamel been significantly penetrated, yet the canine is already completely truncated, see Fig. 3. Viewed directly from above, the canine of *Gigantopithecus* IV, *G. bilaspurensis*, is roughly ovoid, with the long axis of the tooth situated at an angle of about 45° to the sagittal plane of the mandible. Recently Leakey (1968) has argued that possession of an anteroposteriorly compressed canine of this



FIGURE 3. Composite of individual close-up photographs of the *Gigantopithecus bilc. purensis* superimposed on the outline of the mandible.

sort is a hominid feature. Admittedly the canine in the African apes is usually "pear-shaped" ("triangular" in Leakey's terms) in cross-section at the base of the enamel with the larger bulge located anterolaterally, but an ovoid, parallel-sided canine cross-section is not rare among Pongidae, and indeed is a regular occurrence in the Orangutan. One final observation of some significance is that the canines of modern female apes do not wear down in the manner seen in *G. bilaspurensis*. The plane of wear on lower canines of great apes (whether heavily worn or not) slopes steeply downward typically at angles of from 50° to 75° relative to the plane of the long axis of the tooth row. In *G. bilaspurensis* this angle is much lower at about 18° . In *G. blacki* these angles are somewhat higher than in *G. bilaspurensis* but are lower than is typical in modern apes or *Dryopithecus*. *Gigantopithecus* mandible I, a probable female, has an angle of 29° and in the old male *G. blacki* (III) this angle is 46° (left C).

PREMOLARS. P_3 . The anterior premolar of *G. bilaspurensis* is remarkable for an ape in that the tooth does not exhibit an anterolateral extension for sectorial or sharpening action against the posterior wear facet of the upper canine. This is to be expected in a form in which the absolute size of canines has been relatively reduced. Consequently P_3 is not much larger than P_4 but in such females this tooth nevertheless retains an anterolateral boss against which the back of the upper canine shears. In *Gorilla* of the dental age of *G. bilaspurensis* a wear facet on the anterolateral boss of P_3 is usually detectable. Another difference between the P_3 of *Gigantopithecus* and that of most apes is that the inner, metaconid cusp is well-developed. This is most clearly seen in P_3 of mandibles II and IV and gives the premolars a bicusped, hominid look. This could be taken as a special indication of affinities with hominids but since small metaconids do occur on P_3 in at least some *Dryopithecus*, as well as *Oreopithecus*, the secondary enlargement of the cusp could have taken place in this line independent of a similar development among hominid ancestors. Such a parallelism may have occurred because in both lineages there could have been a similar reorganization of function and relative proportions in the anterior dentition, particularly P_3 , consequent to canine and incisor reduction. This tooth is reminiscent of *Dryopithecus* in outline and general proportions but differs from *Dryopithecus* and

species of the three genera of great apes as well in having an extremely low, flattened metaconid and protoconid lacking all but the slightest expression of the ridges or crenulations which radiate from the apices of these cusps in most unworn hominoid premolars. Although one could maintain that such crenulations might have been somewhat obscured by wear on the crown, had they ever been present, some evidence of this character would probably remain in the talonid basin. In addition to these differences the trigonid portion of P_4 is greatly expanded while the talonid is much reduced over what is typical of apes. In *Gorilla* there is often a well-developed posterointernal cusp of P_4 . In *G. bilaspurensis* the heel of this tooth is hardly more than a cingulum. Moreover this tooth differs markedly from *G. blacki* and from *Gorilla* in the extreme lowness of the trigonid.

MOLARS. M_1 — M_3 . As is typical in *Aegyptopithecus* and early *Dryopithecus*, the molars of *G. bilaspurensis* increase in size posteriorly, both in breadth and length. This is apparently a primitive character among Pongidae. In *G. blacki* the M_3 of mandible III is distinctly narrower than M_2 . Although the M_1 in mandible III is barely longer than M_2 , interstitial wear has undoubtedly shortened lengths of M_1 and M_2 which would render Woo's published measurements somewhat doubtful (see Table 1). In mandible I, M_2 is barely larger than M_1 , which does not suggest a posterior size increase in molars. Nevertheless the sample of *Gigantopithecus* jaws is too small for one to be sure that the two species of *Gigantopithecus* differed consistently in the degree of molar size-increase posteriorly.

A particularly distinctive feature of the molars of *G. bilaspurensis* is the extraordinary flatness of their occlusal surfaces which is most closely paralleled elsewhere among Anthropoidea by hominids and perhaps *Pongo*. These teeth lack the deeply incised crenulations and polycuspitation of molars and premolars seen in newly erupted teeth of *G. blacki* (mandible II and isolated unworn teeth). In *G. bilaspurensis* all the molar cusps are delineated on the occlusal face by shallow grooves, but even before wear the apices of the cusps could not have risen to an extent in any way similar to cusp height in most apes (other than some *Pongo*) because the enamel has only been perforated by wear on the protoconid and hypoconid of both M_1 's. Considering the

length and breadth of these molars, molar crown height is extremely low, resembling Hominidae and not *G. blacki*, which as Weidenreich (1945) and Koenigswald (1952, p. 318) have pointed out shows incipient hypsodonty. Thus the molar breadth-height indices for the two species of *Gigantopithecus* are at nearly opposite extremes among Hominoidea (see Table 2).

TABLE 2. Mean molar breadth-height indices for samples of various hominoid species, arranged in ascending order of magnitude.

<i>Pongo pygmaeus</i>	41.37
<i>Gigantopithecus bilaspurensis</i>	46.5
<i>Gorilla gorilla</i>	54.3
<i>Homo erectus</i>	ca. 55.0
<i>Pan troglodytes</i>	58.8
<i>Homo sapiens</i>	61.2
<i>Gigantopithecus blacki</i>	73.6

In view of the fact that nearly all *Dryopithecus* species tend to show lower cusps than do the modern great apes, the brachyodonty of Pliocene *G. bilaspurensis* is a feature which it shares with earlier apes of the Miocene epoch.

THE PHYLETIC POSITION OF GIGANTOPITHECUS

There have been two primary views among earlier workers as to the affinities of *Gigantopithecus*. These are: 1) that it is an aberrant pongid with some distinctive dental features which either: a) adapt it to a novel manner of feeding, or b) are due to allometric changes related to its large absolute size; and 2) that the genus should be placed in Hominidae, either: a) ancestral to later hominids, or b) as an extinct side branch of Hominidae which existed in South East Asia as an apparent contemporary of *Australopithecus* and, or *Homo*. The uncertain age of the *Stegodon*—*Ailuropoda* fauna of South China in which *G. blacki* occurs, is discussed by Kahlke (1961).

⁷ All values from Weidenreich (1945) apart from those of *Gigantopithecus* (*G. blacki* value from Koenigswald, 1952).

Of these choices 2a has been generally abandoned. Without going into the whole history of study in this short paper the alternative views of authors can be tabulated as follows:

In Hominidae	In Pongidae
Weidenreich (1945)	Koenigswald (1935)
Koenigswald (1949, 1952, 1958)	Pei and Woo (1956)
Heberer (1959 a and b)	Pei and Li (1959)
Dart (1960)	Remane (1950, 1960)
Woo (1962)	Ti-Cheng (1962)
	Simons and Pilbeam (1965)

This study of *G. bilaspurensis* makes it seem probable that *Gigantopithecus* represents a side branch of Asian apes which achieved a dental mechanism approximating to some extent that of hominids. These functional similarities, however, are not as close to *Australopithecus* and *Homo* as are those of *Ramapithecus*, and the latter remains the best candidate for ancestral relationship to *Australopithecus*. Figure 4 gives evidence that the symphyseal cross-section can no longer be considered a discriminant between apes and hominids. The symphyseal cross-sections of Figure 4 do not clearly separate *Gigantopithecus* and *Gorilla* and are also similar to such sections of *Australopithecus* and *Dryopithecus* mandibles. Both *G. bilaspurensis* and *Ramapithecus punjabicus* show morphological ties with *Dryopithecus*, particularly with *D. indicus* which has rather flat cheek teeth. Evidence is thus accumulating that both these genera arose from an early species of *Dryopithecus*. The latter in turn is apparently derived from Oligocene *Aegyptopithecus*.

Simons (1960) suggested that the possibility of a relationship between *Oreopithecus* and *Gigantopithecus* should be examined. This was mainly because of the common possession in these two forms of extremely deep mandibles relative to tooth size, and particularly polycuspidate molars with distinct centroconids in both *Oreopithecus bambolii* and *G. blacki*. In addition, the molar trigonids and talonids of *G. blacki* are clearly separated by a vertical interior and exterior groove into fairly distinct trigonid and talonid lobes much as is the case in *Oreopithecus*. It is now evident that polycuspidation and central pinching of the molars of *Gigantopithecus* must have been late developments in this line

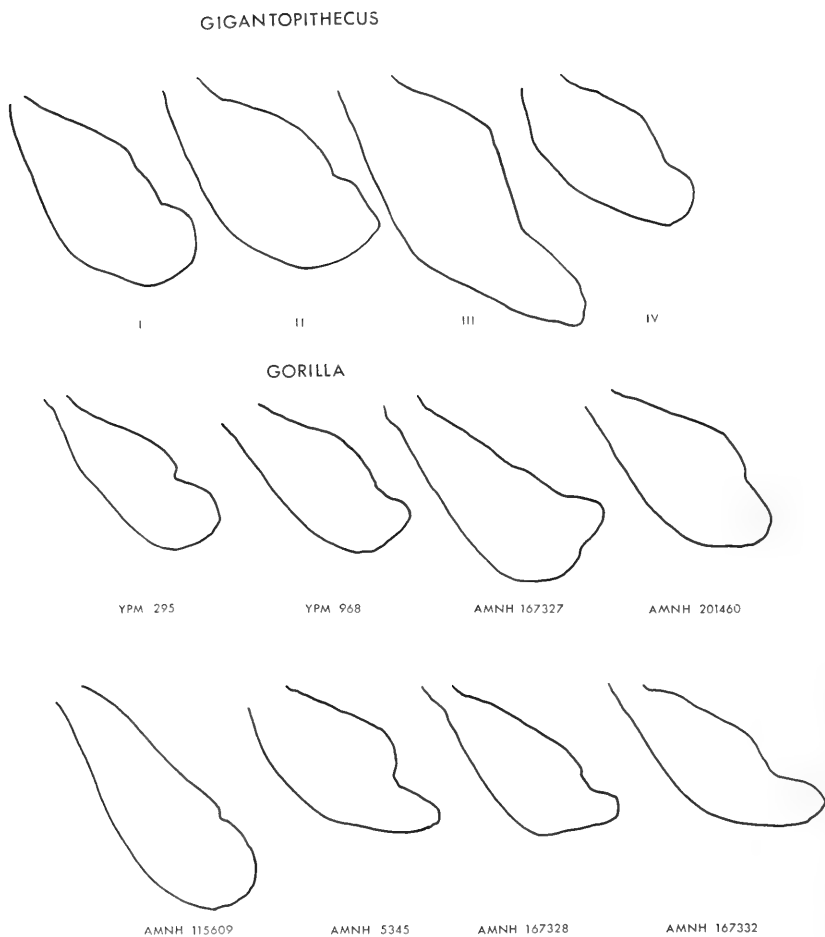


FIGURE 4. Symphyseal cross-sections of the four *Gigantopithecus* mandibles (top row) compared with those of eight large gorillas (second and third rows) showing close correspondence in outline of this section. *Australopithecus robustus* has similar sections.

since they are absent in *G. bilaspurensis*. Other late developments were the acquisition of a high index of hypsodonty and a relatively deeper mandible in *G. blacki*.

Thus this new and much older species of *Gigantopithecus*, *G. bilaspurensis*, does not indicate a derivation of *Gigantopithecus* from *Oreopithecus*, but from *Dryopithecus*.

In sum, it would appear that *Gigantopithecus* represents a divergent branch of the Pongidae with distinctive dental specializations which perhaps fitted it for foraging in open country. It may have been derived from earlier rather gorilla-like forest dwelling ancestors such as *D. indicus*.

ACKNOWLEDGEMENTS

We wish to express our sincere thanks to V.K.R.K. Rao, Minister of Education, Government of India, and H. R. H. Anand Chand M. P., inaugurators of our co-operative project; to the Vice-Chancellor of Panjab University, Mr. Suraj Bhan, for his help in initiating the work; to the Smithsonian Foreign Currency Program (Grant No. 37); and the National Science Foundation (Grant No. G.S. 1817) for providing the funds which have made our research program possible. The photographs were prepared by Mr. Baldev Singh, photographer of the Department of Anthropology, Panjab University and the figures by Mrs. Susan Weeks, Division of Vertebrate Paleontology, Peabody Museum. The senior author would like to acknowledge a brief discussion regarding the text of this paper with the junior author, and the assistance while preparing the manuscript of Ian Tattersall and David R. Pilbeam of the Peabody Museum.

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