

# *Gigantopithecus* and Its Relationship to *Australopithecus*<sup>1</sup>

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**ABSTRACT** *Gigantopithecus blacki* and *G. bilaspurensis* are compared to *P. gorilla* and *Australopithecus*. The total morphological pattern of *Gigantopithecus* mandibles is more similar to *Australopithecus* than to *P. gorilla*. Two major points are raised. (1) *G. blacki* might be considered an aberrant hominid rather than an aberrant pongid. (2) *G. bilaspurensis* can be considered an equally likely candidate, along with *Ramapithecus*, for possible hominid ancestry.

Numerous taxonomic and evolutionary statements have been made concerning the genus *Gigantopithecus*. These interpretations have portrayed *Gigantopithecus* as ancestral to hominids, as an over-specialized side-branch of hominids, or as an aberrant pongid, unrelated to hominid evolution. Weidenreich was the main proponent of the ancestor/descendent relationship between *Gigantopithecus* and "Meganthropus" (= *Australopithecus*) ('45, '46, '49). More recently, Eckhardt ('71, '72) has reopened the possibility of *Gigantopithecus* as a hominid forbear. Woo ('62) and von Koenigswald ('52, '58) suggested that *Gigantopithecus* should be considered a hominid, but that the genus represents an over-specialized side-branch which did not contribute to australopithecine evolution, but became extinct. Both of these schemes consider only *G. blacki* and not the recently discovered Middle Pliocene *G. bilaspurensis*.

Simons and Pilbeam ('65) reviewed the *G. blacki* material and concluded that the genus represented an aberrant pongid with peculiar hominid parallelisms. Simons' subsequent discovery of the Indian *Gigantopithecus* (*G. bilaspurensis*) further confirmed, they felt, this aberrant pongid status (Pilbeam, '70; Simons and Ettl, '70; Simons and Chopra, '69a,b; Simons and Pilbeam, '72).

Throughout this debate, however, little substantive information has been given which would indicate the metrical and morphological similarity between *Gigan-*

*topithecus* and *Australopithecus*. Furthermore, a direct comparison between the Middle Pliocene *G. bilaspurensis* and *Australopithecus* has not been done, although Simons and Chopra ('69a) allude to some basic similarities. The metric data presented below combined with a review of morphological data are intended to clarify these relationships.

## DATA

Dental and mandibular measurements of *P. gorilla*, *Australopithecus*, and *Gigantopithecus* appear in Appendices 1-5. Gorilla tooth dimensions were taken by Paul E. Mahler and Milford H. Wolpoff. All mandibular measurements were taken by the author. Since all the Cleveland Museum of Natural History gorilla specimens were wild-shot, reliable sex determinations are possible. The sex of the specimens listed in Appendices 4-5, then, being determined in the field from the carcass, is quite accurate.

Except for noted cases, all australopithecine measurements were taken on the original specimens by Milford H. Wolpoff. These fossils are classified into gracile and robust categories based either on the specific site (e.g., Sterkfontein = gracile) or on published accounts (e.g., robust and gracile forms from Omo). The gracile sample includes South African specimens generally described as *A. africanus* and

<sup>1</sup> This paper is a revised version of paper delivered at the 1971 meeting of the American Association of Physical Anthropologists.

East African Lower Pleistocene specimens described as *Homo*. ER-992 has been included in the gracile sample with reservations. The robust sample consists of specimens published as *A. "robustus"* and *A. "boisei."* Severely crushed and distorted specimens are not included in these groups, but in some cases teeth with post-mortem, matrix-filled cracks are utilized. In these specimens the dimensions of the crack have been subtracted from the overall dimension, rendering a good representation of the true tooth size. The notable case in this regard is the East African robust specimen, ER-818. Formal descriptions of these newly discovered East African hominids appear in Leakey ('71, '72) and Leakey et al. ('71, '72).

With the exception of bicanine breadth, all measurements for *Gigantopithecus blacki* are taken from Woo ('62). To my knowledge published mandibular dimensions for *G. bilaspurensis* do not exist. Consequently, all dimensions on the Bilaspur mandible were taken on the Yale-Peabody Museum cast. Checking dental dimensions from the cast with those published by Simons and Chopra ('69a), the Yale-Peabody Museum case is within 4% of the dimensions on the original specimen. Mandibular dimensions taken from the cast for the Bilaspur mandible are assumed to be within 4% of the true values. Bicanine breadth on *G. blacki* is similarly accurate. Finally, dental dimensions for all *Gigantopithecus* mandibles are published by Simons and Chopra ('69a) and are not duplicated here.

#### METHOD

The indices presented in table 1 are in most cases those used by Simons and Chopra ('69a) in their taxonomic discussion of *G. bilaspurensis* and *G. blacki*. In place of  $P_3-M_3$  length and  $P_3-M_3$  summed areas, I have chosen to substitute  $P_4-M_2$  length and area. This substitution allows for a larger sample size in *Gigantopithecus* (*G. blacki* I and II lack lower third molars) and in *Australopithecus*. It also eliminates the comparison of lower third premolars between known pongids and hominids. Since the lower third premolar in apes is a mesiodistally elongated tooth set at an angle to the tooth row and is not directly involved in grinding and crushing, esti-

mates of posterior tooth size in gorillas are more reliable when considering only the summed areas of  $P_4-M_3$ . I have formulated the same indices using summed  $P_3-M_3$  length and areas and have obtained results similar to those presented in table 1. The inclusion of all the measurements provides data for analysis in either manner.

Each index in table 1 intends to show morphological characteristics through metric evaluation. The three genera are represented by measurements presented in indices allowing direct comparison of metric/morphological relationships.

Bicanine breadth divided by the length of the cheekteeth ( $P_4-M_2$ ) compares the maximum external breadth outside the canines to the length of the posterior tooth row. The size of the canine (length  $\times$  breadth) is normalized against the summed areas of the posterior teeth, while the area of the lower second incisor is compared to the area of the lower first molar. I have also compared lower  $I_2$  area with the summed posterior tooth areas as well as lower  $M_2$  area. All indices follow the same pattern, but for the sake of brevity, have not been included in this paper. Maximum symphyseal length is considered in regard to the height of the mandible at  $M_2$ . This index is somewhat different from that described in Simons and Chopra ('69a), but again demonstrates the same morphological relationship as their index of maximum symphyseal length divided by mandible height multiplied by breadth at  $M_2$  and by the summed posterior cheek teeth area. Maximum symphyseal length divided by corpus height at  $M_2$  better separates *Australopithecus* from *P. gorilla* and, for this reason, is used in this analysis. The summed areas of  $P_4-M_2$  divided by height  $\times$  breadth of the mandible at  $M_2$  normalizes the cheek teeth relative to the robusticity of the mandible under  $M_2$ . Area ( $1 \times b$ ) of  $M_1$  divided by height  $\times$  breadth of the corpus under  $M_2$  provides a further check.

These indices are used to demonstrate morphological patterns through metric analysis. They provide excellent sorting criteria for separating australopithecines from gorillas. Student's *t*-tests performed on these two genera (*Australopithecus* and *P. gorilla*) using the six indices all

showed significant differences at the 0.01 level. It follows, then, since the indices separate australopithecines from gorillas, that they are useful criteria for analyzing other hominoid, and possibly related genera.

#### RESULTS

Three major points can be readily seen from an examination of table 1. (1) *Australopithecus* differs widely from gorillas, a fact which has been discussed above and by numerous authors beginning with Dart ('26). Different cultural and dietary adaptations are likely the major reasons for this metric difference. The morphological specialization of *Australopithecus* to small object feeding has been considered in detail by Jolly ('70). The infrequency of range overlap between *Australopithecus* and *P. gorilla* provides new evidence for determining the phylogenetic positions of *G. blacki* and *G. bilaspurensis*.

(2) Except in two cases (relative symphyseal length and relative  $P_1-M_2$  area, both in *G. blacki* II), indices describing *Gigantopithecus* mandibles and tooth size fall completely within the range of *Australopithecus*. Both *G. blacki* and *G. bilaspurensis* overlap extensively with *Australopithecus* but seldom with *P. gorilla*. In those cases where *Gigantopithecus* indices have values within the *P. gorilla* range, *Australopithecus* also has values which overlap with *P. gorilla*.

It is interesting to note that the largest mandible of *Gigantopithecus* (*G. blacki* III), an assumed male (Simons and Chopra, '69a; Woo, '62), is well below the range in all indices describing male gorillas. In canine size, *G. blacki* III has canines which are relatively smaller than the canines of the presumed female, *G. blacki* I. Sexual dimorphism in canine size of *G. blacki* does not follow the common pongid condition where little or no overlap in relative canine size is characteristic. Consequently, relative canine size cannot be used to discriminate male from female *Gigantopithecus*.

The general similarity of *Gigantopithecus* to *Australopithecus* and its dissimilarity in all indices, as well as sexual dimorphism based on relative canine size, to gorillas suggests at least a dietary similarity to *Australopithecus* (Simons and Ettel, '70; Pilbeam, '70; Jolly, '70), but,

contra these authors, does not specifically indicate that gigantopithecines are "aberrant apes." Rather, if one has to resort to such terminology, the close metric similarity between *G. blacki*, *G. bilaspurensis* and *Australopithecus* would better describe an aberrant hominid.

(3) The third observation apparent from table 1 is that *G. blacki* and *G. bilaspurensis* show some different metric relationships. The relative bicanine breadth and relative symphyseal length are both smaller in *G. bilaspurensis* than in *G. blacki* I, II or III, and one would expect the index describing lower incisor area to differ also. In some cases *G. bilaspurensis* closely resembles *Australopithecus*.

This similarity is further emphasized when comparing *G. bilaspurensis* with two robust australopithecines from East Africa (see table 2). Here the major differences between the Bilaspur mandible, Omo 7, and ER-729 relate to absolute canine size. The smaller size of the bicanine breadth in *G. bilaspurensis* reflects the size of the canines rather than the size of the incisors. The internal bicanine breadth (measured from lingual surface on the canine) demonstrates this clearly. The size of the mandibular corpus under  $M_2$  is somewhat more massive in *G. bilaspurensis* than in robust australopithecines although recent East Rudolf finds almost equal it in cross-sectional area, or are larger (see Appendix 1). At least two have mandibles greater in breadth. No gorilla specimen even approaches *G. bilaspurensis* or these large, robust australopithecines in mandibular corpus cross-sectional area at  $M_2$ .

Measurements of the mandible and dentition of *G. bilaspurensis* and *Australopithecus*, then, closely resemble each other. Both have absolutely and relatively narrow bicanine breadths bounded by relatively small canines. The lower incisors are completely unlike gorillas, being considerably reduced. The maximum symphyseal length is greater than the corpus height at the lower second molar, but not to the extent of the condition seen in gorillas. The posterior teeth are both relatively and absolutely large as is the cross-sectional area of the mandible under  $M_2$ . The major metrical difference between the purported aberrant pongid and hominids is the size of the lower canine.

TABLE 1  
 Summary indices for Gigantopithecus, Australopithecus, and Pan gorilla. Sample size is enclosed in brackets. Standard deviations (s.d.) are included where appropriate. All indices are multiplied by 100

	Bicanine Br.		Canine area		Area $l_2$		Max. symph. lt.		Area $P_4M_2$		Area $M_1$	
	Length $P_4M_2$	Area $P_4M_2$	Area $P_4M_2$	Area $M_1$	Area $M_1$	Area $M_1$	Ht. at $M_2$	Ht. at $M_2$	Ht. × br. at $M_2$	Ht. × br. at $M_2$	Ht. × br. at $M_2$	Ht. × br. at $M_2$
<i>G. blacki</i> (I)	89.7	20.9	24.7	126.7	47.1	16.4						
<i>G. blacki</i> (II)	—	—	20.8	145.3	63.2	21.0						
<i>G. blacki</i> (III)	99.3	17.9	22.9	134.0	40.0	12.7						
<i>G. bilaspurensis</i> (IV)	73.2	20.2	—	119.8	41.4	13.5						
<i>Australopithecus</i> (gracile)	99.0 (2)	17.8 (8)	30.7 (7)	114.3 (3)	56.6 (4)	19.5 (5)						
Mean	s.d. = 3.6	s.d. = 2.0	s.d. = 4.1	s.d. = 12.5	s.d. = 8.1	s.d. = 2.7						
Range	(98.7–99.4)	(14.8–21.3)	(23.3–37.1)	(100.6–125.0)	(45.3–64.4)	(15.1–22.2)						
<i>Australopithecus</i> (robust)	79.6 (7)	12.2 (8)	21.4 (4)	123.2 (5)	56.0 (8)	18.8 (8)						
Mean	s.d. = 12.1	s.d. = 2.9	s.d. = 3.7	s.d. = 14.1	s.d. = 9.7	s.d. = 2.9						
Range	(58.2–95.2)	(8.3–16.6)	(16.0–24.1)	(107.9–138.2)	(42.4–71.9)	(13.6–21.7)						
<i>Australopithecus</i> (combined)	84.8 (9)	15.0 (16)	27.3 (11)	119.9 (8)	56.2 (12)	19.1 (13)						
Mean	s.d. = 13.1	s.d. = 3.8	s.d. = 6.0	s.d. = 13.4	s.d. = 8.8	s.d. = 2.7						
Range	(58.2–99.4)	(8.3–21.3)	(16.0–37.1)	(100.6–138.2)	(42.4–71.9)	(13.6–22.2)						
<i>P. gorilla</i> (male)	129.9 (20)	42.3 (20)	44.5 (18)	179.6 (20)	79.8 (20)	26.6 (20)						
Mean	s.d. = 10.7	s.d. = 4.9	s.d. = 5.7	s.d. = 13.6	s.d. = 11.1	s.d. = 3.8						
Range	(113.5–154.8)	(31.8–53.0)	(35.7–54.6)	(156.6–213.8)	(62.6–105.2)	(20.3–35.1)						
<i>P. gorilla</i> (female)	112.7 (20)	23.9 (39)	41.9 (19)	164.0 (20)	82.4 (19)	28.3 (20)						
Mean	s.d. = 9.2	s.d. = 2.2	s.d. = 5.3	s.d. = 11.7	s.d. = 17.6	s.d. = 5.8						
Range	(96.0–129.8)	(20.8–29.5)	(31.6–49.7)	(142.1–186.3)	(62.1–113.5)	(18.4–39.1)						
<i>P. gorilla</i> (male and female)	121.3 (40)	33.4 (39)	43.1 (37)	171.8 (40)	81.1 (39)	27.4 (40)						
Mean	s.d. = 13.2	s.d. = 1.0	s.d. = 5.6	s.d. = 14.8	s.d. = 14.1	s.d. = 4.9						
Range	(96.0–154.8)	(20.8–53.0)	(31.6–54.6)	(142.1–213.8)	(62.1–113.5)	(19.9–39.1)						

TABLE 2

Tooth measurements and indices for two East African australopithecines and *G. bilaspurensis*

	Omo 7	KNM-ER-729	<i>G. bilaspurensis</i>
Areas of mandibular teeth			
Canine	74.9	85.9	148.8
PM3	182.0	150.5	172.3
PM4	221.1	205.9	190.0
M1	314.2	244.9	241.4
M2	291.6	342.0	305.6
M3	269.4	383.4	315.5
Summed cheek teeth	1278.3	1326.7	1224.8
Area P4-M2 Ht. $\times$ br. at M2 $\times$ 100	53.8	58.8	41.4
Bicanine br. Length P4-M2 $\times$ 100	58.2 <sup>1</sup>	76.0	73.2 <sup>2</sup>
Max. symph. lt. Ht. at M2 $\times$ 100	107.9 <sup>1</sup>	112.7	119.8 <sup>2</sup>
Minimum bicanine breadth	20.2	22.5	21.0 <sup>2</sup>

<sup>1</sup> Measurement from cast belonging to F. C. Howell.<sup>2</sup> Measurement from Yale-Peabody cast.

Morphological details of *Australopithecus* and *G. bilaspurensis* are also quite similar. Besides the metrical details of the horizontal ramus under M<sub>2</sub>, other characters of the mandibular body can be duplicated in australopithecines. Symphyseal cross-sections of Natron, ER-729, and ER-818, as well as other early hominids, show essentially the same morphological features. The middle symphyseal area is buttressed by two transverse tori, one running superior and one inferior to the genial-glossal fossa. Above the superior torus is a shelf-like area which is characteristic of most australopithecines and pongids, both fossil and recent. The inferior transverse torus of *G. bilaspurensis* forms a short simian shelf, more vertical than in *P. gorilla* with a relatively higher placement of the genial-glossal fossa.

The origin of the ascending ramus in *G. bilaspurensis* arises at M<sub>1</sub> a considerable distance lateral to the buccal aspect of the tooth. The result of the condition is a wide buccinator groove similar to those found in some robust australopithecines. In the later *G. blacki* mandibles, the ascending ramus begins further posterior at M<sub>2</sub> and the buccinator groove is narrower and less marked. The horizontal ramus of *G. bilaspurensis* increases in

depth posteriorly. This characteristic is similar to East African robust forms, ER-403, 404, and 726, but different from others. ER-818, for example, sharply decreases posteriorly in horizontal ramus depth.

The two major differences between *G. bilaspurensis* and *Australopithecus* in mandibular morphological details are the angle of the symphyseal region and the shape of the dental arcade. In most australopithecines the symphyseal angle is nearly perpendicular to the horizontal ramus, while in the Bilaspur mandible the area is at a 45° angle to the horizontal ramus. It is noteworthy that *Ramapithecus* also has a non-perpendicular symphyseal angle (Andrews, '71). The contour of the tooth row in the Bilaspur mandible is V-shaped, resembling its probable mid-Miocene dryopithecine ancestors which all have anteriorly convergent dental arcades. This feature differs from *Australopithecus* and is not unlike the palatal shape in *Ramapithecus*. With decrease in size of the canines and shortening of the mandible the palatal contour of *G. bilaspurensis* would probably resemble *Australopithecus*.

*G. bilaspurensis* has a P<sub>4</sub>, M<sub>1</sub>, M<sub>2</sub>, and M<sub>3</sub> of similar shape to *Australopithecus*, but the teeth lack crenulations on the occlusal surfaces. Unworn molars are longer

than broad with bulging lingual and buccal aspects (see table 3). Comparing heavily-worn molars of *Australopithecus* to those of *G. bilaspurensis* as Simons does ('72:258) only confuses the similarity of molar shape with australopithecines. On the average, *G. bilaspurensis* has length/breadth ratios at the upper end of the *Australopithecus* range or just slightly beyond it.

Occlusally, the molars of *G. bilaspurensis* are less similar to *Australopithecus*, but are also completely unlike *P. gorilla*. The occlusal surfaces of the teeth in the Bilaspur mandible are characterized by low, broad cusps with shallow fovea separating each cusp. These teeth are not characterized by highly crenulated surfaces, although the cusp pattern can be duplicated in several robust australopithecines.

The occlusal morphology on the lower molars is strikingly similar to the description of the Ngorora M<sup>2</sup> found in Pliocene deposits in East Africa (Bishop and Chapman, '70). This upper molar described by Leakey is also bunodont with low rounded cusps and distinct fovea separating the cusps, and appears to be about the same geological age as *G. bilaspurensis*. Due to the lack of other African middle Pliocene forms, this relationship is certainly tenuous.

Another similarity in dental morphology is the "plate-like" premolar and molar roots of both genera. From breaks and erosions in the Bilaspur mandible one can observe a left P<sub>4</sub> anterior root, a left M<sub>1</sub> anterior root, and a right M<sub>3</sub> posterior root, all of which are "plate-like." Leakey et al. ('71) have noted "plate-like" roots in ER-404, and Wolpoff has observed them in the originals of ER-725, 726, and 733a, and ER-818 (personal comm.).

These similarities are not meant to imply, however, that there are no differences between *G. bilaspurensis* and *Australopithecus*. There appear to me to be four main differences, three of which are functionally interrelated. (1) The size of the canine has been noted above. Simons has demonstrated that the angle of occlusal wear on the lower canines of *G. bilaspurensis* is lower than on the canines of *G. blacki*, but higher than on the canines of *Australopithecus* (Simons and

Chopra, '69a). A steeply inclined wear facet on the lower canine would indicate that a maxillary canine, through occlusion with the mandibular canine, was acting in life to sharpen the distal edge of the lower canine. Since the lower canines of *G. bilaspurensis* are truncated more than sharpened and since the lower third premolar lacks a large well-defined mesial contact facet, it is reasonable to infer that the maxillary canine was not large, nor similar in function compared to gorillas. Rather, since the mandibular canine was truncated during life, masticatory actions performed at the canine appear to be more involved with grinding, than with shearing and gripping functions. The absolute size, wear, and morphology of the mandibular canines on the Bilaspur mandible, then, do not completely match either *P. gorilla* or *Australopithecus*.

(2) As mentioned above, the third lower premolar of *G. bilaspurensis* also differs from hominids. This tooth in addition to having only a very small mesial contact facet, is set at an angle to the tooth row and displays at least three cusps. Most investigators have argued that this tooth is pongid-like, considering it somewhat modified from a true sectorial lower third premolar. It is important to note, however, that the model of a Pliocene hominid ancestor with bicuspid lower third premolars, is no longer supported by the data, since the Fort Ternan ramapithecine has a sectorial lower third premolar (Andrews, '71). This tooth is also set at an angle to the tooth row, and further differs from *G. bilaspurensis* in having a long, mesial contact facet for occlusion with the maxillary canine. The morphology of P<sub>3</sub> on *G. bilaspurensis* can not be used to exclude it from the status of a possible hominid ancestor.

(3) Another morphological feature that is not found within the australopithecines is the posteriorly diverging tooth row of *G. bilaspurensis*. This condition demonstrates the undeniable links of the Bilaspur mandible with late Miocene/early Pliocene dryopithecines (Pilbeam, '70), but again does not eliminate it from ancestral status. Reduction in molar length and increase in molar breadth accompanying canine reduction would probably produce a more parabolic dental arcade.

(4) Lower molars of *G. bilaspurensis* lack the complex crenulations of the occlusal surfaces that are so characteristic of *Australopithecus*. These teeth tend to be long compared to breadth (see table 3), but are not without parallels in the australopithecines. Simons and Chopra ('69a) point out that the molars are *unlike* apes in that they have low broad cusps, and that they seem to more "closely parallel hominids and perhaps *Pongo*" ('69a:13).

In summary, the major differences between *Australopithecus* and *G. bilaspurensis* are the absolute size, wear, and morphology of the canine, the polycuspid lower third premolar, the posteriorly diverging dental arcade, and the lack of heavily crenulated but mesio-distally long molars. All but the last are related primarily to the anterior dentition and suggest a complex not unlike *Ramapithecus*, and, in light of the other similarities, not particularly crucial to the decision to accept or reject it as a possible hominid ancestor (see Andrew's reasons for retaining *Ramapithecus*, '71). A minimum amount of selection to reduce canine size could very plausibly produce an East Rudolf-like australopithecine from something like *G. bilaspurensis*.

#### DISCUSSION

Recently, Eckhardt ('71, '72) has proposed that the genus *Gigantopithecus* could be ancestral to hominids. His main argument concerning the amount of time required for morphological change may be valid, but the inclusion of *G. blacki* as an ancestor is certainly debatable. From all indications, *G. blacki* is no earlier than the late Pliocene and probably as recent as Middle Pleistocene. In all probability it overlaps with *Australopithecus* from Africa, and very likely overlaps with *Homo erectus* (Pei, '60; Kahlke, '61; von Koenigswald, '52; Woo, '62). Because of this time overlap, *G. blacki* cannot be considered ancestral to australopithecines.

*G. bilaspurensis*, however, is considerably earlier (at least Late Miocene) (Simons and Chopra, '69a,b; Simons and Pilbeam, '72) and as has been demonstrated, is metrically and morphologically similar to australopithecines. It is described by most authors as a pongid occupying a savannah niche without de-

pendence upon tools. But what would happen in the Early or Middle Pliocene if a hypothetical African *G. bilaspurensis* began to use tools? First, the large body size which could be construed as a defensive mechanism could become smaller. Canines would reduce in size in responding to tool manipulation or possibly in response to Jolly's "phase I" adaptation ('70). Whatever the case, with smaller canines *G. bilaspurensis* or something similar to it would look very much like an ER-729 or ER-818. The mandible would lose anterior robusticity due to the smaller canines, and length reduction and breadth expansion of cheek teeth related to selection pressures of heavy mastication would result to counteract interstitial wear.

From table 3 it can be seen that *G. bilaspurensis* has a larger L/B index for  $M_1$ ,  $M_2$ , or  $M_3$  than any *G. blacki* or the mean of either robust or gracile australopithecines. Reduction of mesio-distal length and increase in buccal-lingual breadth is reasonable when considering the amount of interstitial wear of both *Australopithecus* and *Gigantopithecus* (Wolpoff, '71b). By increasing buccal-lingual breadth, the amount of occlusal area lost by interstitial wear would be considerably less, and, hence, selectively important. Coupled with this, reduction in  $P_3$ - $M_3$  length would be the mechanical advantage of a shorter mandible with more forward placement of *m. temporalis* and *m. masseter* (Andrews, '71). With shorter  $P_3$ - $M_3$  length, canine reduction and greater breadth of all the cheek teeth, a parabolic arcade would be produced. Both *G. blacki* and *Australopithecus* demonstrate this change. In each the form of the tooth row is unquestionably parabolic (see Eckhardt, '72:103).

One of the most crucial questions concerning the relationship of *G. bilaspurensis* to *Australopithecus* is the sex of the Bilaspur mandible. Previous studies have sexed the mandible as female (Simons and Chopra, '69a: p. 6; and Simons and Ettl, '70: p. 79). I submit that the sex of a single specimen which is the sole representation of a new species cannot be accurately assessed beyond the 50% level, i.e., a guess. The Bilaspur mandible is no less likely a male, and, if it is, one would expect to find smaller females which would

TABLE 3

Length/breadth indices for lower molars of *G. blacki*, *G. bilaspurensis*, and *Australopithecus*. All indices are multiplied by 100. Bracketed number following mean refers to sample size. All dental measurements for *Australopithecus* are listed in Appendix

	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
<i>G. blacki</i> I	106.0	106.9	—
<i>G. blacki</i> II	116.9	112.7	—
<i>G. blacki</i> III	102.2	101.0	113.8
<i>G. bilaspurensis</i> IV	119.7	119.4	121.0
<i>Australopithecus</i> (robust)			
Mean	102.1 (28)	106.1 (29)	114.2 (17)
s.d. = 6.8		s.d. = 5.1	s.d. = 5.9
Range	(86.1–113.7)	(90.0–116.3)	(101.8–123.0)
<i>Australopithecus</i> (gracile)			
Mean	106.2 (23)	106.8 (22)	108.9 (11)
s.d. = 9.3		s.d. = 7.6	s.d. = 10.9
Range	(80.8–119.3)	(87.6–119.2)	(94.8–134.7)

even more closely resemble australopithecines.

In the middle and late Miocene there were, at least, two possible hominid ancestors, *Ramapithecus* and *G. bilaspurensis*. Until now, no one has recognized the possibility of the species represented by the Bilaspur mandible as being ancestral to early hominids. I feel that *G. bilaspurensis* is a better candidate for an australopithecine forbear in that body size is an important adaptive mechanism in creatures that are exploiting a terrestrial-niche without dependence on tools. Livingstone ('62) as well as Weidenreich ('45) have previously suggested the importance of size and reduction of size in human evolution.

*G. bilaspurensis* closely follows an australopithecine morphological pattern in both metric and non-metric characteristics. Its only major differences are not crucial in eliminating it as a hominid ancestor since *Ramapithecus* evinces the same morphological differences, and in many other respects, is more apelike.

*Gigantopithecus blacki*, on the other hand, can best be explained as an Asiatic hominoid (an aberrant hominid) which did not use tools, but rather continued to increase in body size as it adapted to the forest conditions. From the number of teeth found in China, it would seem that this specific adaptation (size *vs* tools) was quite adequate. Survival into the mid-Pleistocene attests to this. *Australopithecus* with smaller size and a non-hunting industrial technology could not drive *G. blacki* into extinction. *Homo erectus*,

though, with effective hunting technology could have caused extermination, as could have competition with the giant panda (Simons, '72). The late existence of these large primates proves their effective adaptation through size.

As a hypothesis, this suggestion will stand or fall as new specimens are discovered. It is important to realize that the issue of man's Pliocene ancestry is far from closed, and that the present evidence does not yet allow a clear decision between *Ramapithecus* and *G. bilaspurensis*. It is important that viable alternative hypotheses be considered as additional evidence is discovered.

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## APPENDIX 1

*Mandibular dimensions for Australopithecus (gracile and robust) and Gigantopithecus. Except where noted, all measurements are from the original specimen. Abbreviations signify the site or area where the fossil was discovered. (SK, Swarthkrans; STS, Sterkfontein; MLD, Makapansgat; TM, Kromdraai; Sterkfontein; ER, East Rudolf; OH, Olduvai). (In mm)*

Specimen	External bicanine breadth	Maximum symphyseal length	Corpus height at M <sub>2</sub>	Corpus breadth at M <sub>2</sub>	Length P <sub>4</sub> -M <sub>2</sub>
<i>Australopithecus (robust)</i>					
TM-1517			33.8	28.3	39.4
SK-12	31.0	50.0	41.0	34.0	40.0
SK-23	32.8	48.5	35.1	27.8	39.4
SK-34			41.0	22.0	43.1
SK-74	36.0				37.8
SK-858	37.0				40.7
Omo-7-125 <sup>1</sup>	26.0 <sup>1</sup>	50.7 <sup>1</sup>	47.0	32.7	44.7
ER-403			46.6	31.8	42.8
ER-404			48.3	35.8	
ER-725			40.0	31.4	42.5
ER-726			44.5	29.5	51.0
ER-728			37.5	25.8	
ER-729	36.1	51.5	45.7	29.5	47.5
ER-810			38.0	27.3	44.0
ER-818			51.0	36.0	50.8
Natron	35.0	50.6	36.7	31.5	46.0
<i>Australopithecus (gracile)</i>					
MLD-18	35.2		32.4	25.4	35.4
MLD-40			35.4	29.5	38.0
STS-7		45.0	36.0		37.5
STS-36			36.0	23.4	
STS-52		36.7			39.5
ER-730	31.7	32.7	33.2	18.8	32.1
ER-992		38.5	34.0	23.2	34.6
<i>Gigantopithecus</i>					
<i>G. blacki</i> I	45.3 <sup>2</sup>	76.0	60.0	30.0	50.5
<i>G. blacki</i> II	—	77.0	53.0	31.0 <sup>3</sup>	57.7
<i>G. blacki</i> III	56.7 <sup>2</sup>	108.5	81.0	34.0	57.1
<i>G. bilaspurensis</i>	36.0 <sup>2</sup>	62.4 <sup>2</sup>	52.1 <sup>2</sup>	34.2 <sup>2</sup>	49.2

<sup>1</sup> From Howell ('69) or from cast belonging to Howell.

<sup>2</sup> Measured from casts produced by Yale University.

<sup>3</sup> Behind P<sub>4</sub>.

## APPENDIX 2

*Dental measurements of mandibular teeth*<sup>2</sup> *of gracile australopithecines. All measurements are from the original specimens unless otherwise indicated. (In mm)*

Specimen	Incisor 2		Canine		Premolar 3		Premolar 4		Molar 1		Molar 2		Molar 3	
	l	b	l	b	l	b	l	b	l	b	l	b	l	b
Omo-75 <sup>1</sup>					11.3	12.3	11.4	12.7	15.6	14.1	17.5	15.4	15.1	14.1
Omo-Kalam 7 <sup>1</sup>									15.1	13.4				
Omo-75 S.15 <sup>1</sup>									14.0	13.0				
Omo-WS-508 <sup>1</sup>									13.3	12.2				
Omo-WS-752 <sup>1</sup>									14.1	13.0				
Omo-L2-89 <sup>1</sup>									13.7	11.5				
Omo-L45-2 <sup>1</sup>									12.9	12.0				
Omo-L51-1 <sup>1</sup>											14.0	12.6		
Omo-L26-1 <sup>1</sup>											15.5	13.0		
Omo-L28-30/31 <sup>1</sup>											15.0	13.0	16.7	12.4
OH-7	7.2	7.4	8.9	9.8	9.5	10.2	10.3	10.6	14.1	12.5	15.8	13.8		
OH-16	7.6	7.6	9.9	10.1	10.3	11.5	10.1	11.0	14.3	12.8	15.3	14.7	15.8	14.4
OH-30	6.8		7.8	7.7					16.5	14.5				
ER-730									11.3	12.0	11.6	11.8	13.0	11.6
ER-992	7.1	7.0	9.0	9.2	9.3	11.5	8.6	11.4	12.3	10.9	12.8	12.3	13.1	12.5
STS-4											14.4	13.3		
STS-6											14.3	14.0		
STS-7	5.5	8.5	9.2	11.0	10.9	13.2	10.7	12.5	14.3	14.0	15.0	14.6	15.3	14.7
STS-9									14.9	13.0				
STS-18									15.3	14.5				
STS-24	7.6	6.5							13.6	11.4				
STS-36			9.5	10.5	9.5	13.3	9.0	13.3	11.8	14.6	14.8	16.9	16.3	17.2
STS-52b	7.0	8.1	7.9	10.2	9.1	11.9	10.0	11.6	13.5	13.1	14.5	13.4	13.8	12.7
STS-55b											15.2	13.3		
TM-1515					9.0	13.0	10.4		13.0		16.9	16.4		
TM-1518									14.3	13.2				
Taung											16.9	16.4		
MLD-2					10.0	12.6	11.1		14.7	14.1	16.8	15.1		
MLD-18	5.8	8.0	8.9	8.9	8.3	11.4	8.4	12.0	12.4	13.1	14.6	14.8	14.0	13.9
MLD-22											13.5	14.3	15.8	15.2
MLD-24											15.0	14.0		
MLD-29							9.0	12.0	12.5	13.4				
MLD-40			7.7	9.1	8.9	11.4	9.5	11.4	12.8	12.3	15.0	13.8	16.5	14.1

<sup>1</sup> From Howell ('69).

<sup>2</sup> Only isolated M<sub>1</sub> and M<sub>2</sub> are included.

## APPENDIX 3

*Dental measurements of mandibular teeth<sup>2</sup> of robust australopithecines. All measurements are from original specimens unless otherwise indicated. (In mm)*

Specimen	Incisor 2		Canine		Premolar 3		Premolar 4		Molar 1		Molar 2		Molar 3	
	l	b	l	b	l	b	l	b	l	b	l	b	l	b
Omo-L7-125 <sup>1</sup>			7.8	9.6	10.4	17.5	11.7	18.9	16.8	18.7	16.2	18.0	18.2	14.8
Omo 74 <sup>1</sup>			8.8	9.7			13.0	13.8						
Natron	6.0	6.3	7.5	8.0	9.3	13.4	14.0	15.0	15.4	15.3	17.0	16.1	18.0	16.0
TM-1517			9.4	8.8	10.3	12.7	10.8	12.9	13.8	13.2	15.4	14.4	16.4	14.0
TM-1536									12.5	11.8				
TM-1600					9.9	12.1					15.0	14.8	15.9	14.8
SK-1											17.0	15.3		
SK-5											14.9	14.2		
SK-6					13.0	10.3	10.7	12.9	15.9	15.4	16.9	16.3	18.5	15.4
SK-12					10.0	12.0	10.5	12.0	15.0	14.4	15.8	15.8	16.0	15.2
SK-15									12.0	12.0	13.0	12.7	14.3	12.7
SK-20									14.7	14.2				
SK-23	7.0	6.6	8.2	8.0	9.1	11.3	10.0	14.2	14.5	14.6	14.9	14.8	16.0	13.2
SK-25								11.4	13.2	14.7	14.0	16.3	14.7	
SK-34	6.6	7.0	8.9	8.8	9.7	12.8	13.0	14.0	13.5	14.5	16.6	16.3	17.0	16.7
SK-37											16.5	14.7		
SK-45									11.3		12.6	12.3		
SK-55					10.0	10.3			14.6	13.7	16.1	14.3	15.5	13.8
SK-61									15.0	14.0				
SK-63									13.7	13.5				
SK-74		8.1	7.6	9.2	8.8	10.1	10.1	12.1	13.2	13.5	14.5	14.3		
SK-81					9.1	10.6	10.6	13.3	14.3	15.8	16.0	16.0	17.0	15.0
SK-104											14.9	13.9		
SK-828									15.4	14.2				
SK-838b									14.1	13.0				
SK-843									14.4	13.4	15.9	14.0	17.3	15.0
SK-846a									14.6	13.7				
SK-858	6.7	7.5	8.5	8.0	10.0	13.7	11.0		13.9	15.0	15.8	15.0		
SK-876			9.0	10.8	10.0	11.7	10.5	12.5	13.0	15.1	17.0	15.1	18.5	15.7
SK-1586									13.7		15.0	14.0	16.5	15.0
SK-1587								10.4	11.0	13.3	13.0	15.0	12.9	
SK-1588								10.5	11.6	14.1	12.4			
SK-1648									12.5		15.7	14.6		
SK-3974									14.8	13.5				
SK-3976											17.4	16.0		
ER-729			8.5	10.1	11.4	13.2	14.2	14.5	15.6	15.7	19.0	18.0	20.5	18.7
ER-801							13.8	14.5			18.1	16.5	18.8	15.5
ER-810													17.4	15.6
ER-818					13.4		13.9	15.1	16.4	15.2	18.5	18.0	21.5	18.4
ER-1171/2											18.8	16.9		

<sup>1</sup> From Howell ('69).

<sup>2</sup> Only isolated M<sub>1</sub> and M<sub>2</sub> are included.

## APPENDIX 4

*Mandibular dimensions of P. gorilla (male and female). Specimen numbers refer to individual catalogue numbers in the Cleveland Museum of Natural History. (In mm)*

Specimen	External bicanine breadth	Maximum symphyseal length	Corpus height at M <sub>2</sub>	Corpus breadth at M <sub>2</sub>	Length P <sub>4</sub> -M <sub>2</sub>
<i>P. gorilla (male)</i>					
B-647	51.5	59.7	31.7	17.9	43.2
B-1076	60.5	63.2	39.7	20.7	48.7
B-1402	55.2	62.0	35.8	20.2	45.1
B-1404	56.7	73.3	40.6	18.6	45.6
B-1405	62.4	68.0	38.9	20.0	40.3
B-1731	54.7	65.2	39.6	19.6	40.3
B-1736	61.0	75.2	40.8	19.8	40.9
B-1746	62.3	72.2	38.9	22.1	44.3
B-1784	54.6	72.0	40.7	18.6	46.3
B-2000	57.9	76.2	43.2	22.8	43.9
B-2029	56.8	69.1	37.1	19.9	43.2
B-2766	61.6	69.1	38.2	21.0	46.5
B-2767	56.5	74.6	43.2	20.8	46.2
B-2826	62.2	75.4	40.4	23.6	46.4
B-3410	52.3	68.4	33.6	21.1	46.1
B-3415	61.3	62.0	39.6	19.9	45.8
B-3420	57.0	72.2	38.9	27.7	50.0
B-3431	54.5	62.2	36.5	18.4	40.6
B-3547	51.9	69.9	32.7	21.4	40.3
B-3557	59.1	65.7	39.3	25.1	44.9
<i>P. gorilla (female)</i>					
B-1398	43.1	56.6	35.8	21.5	41.1
B-1399	50.5	55.9	33.9	22.0	44.2
B-1400	46.0	58.9	38.1	23.0	43.3
B-1419	45.6	50.7	31.8	21.5	42.2
B-1690	47.3	57.4	32.8	23.9	43.5
B-1710	46.0	49.5	32.6	21.4	35.9
B-1725	50.3	54.8	34.1	26.8	42.0
B-1756	49.0	53.4	31.9	24.4	39.6
B-1851	47.6	53.4	35.4	26.8	41.2
B-1996	47.8	53.2	30.2	19.5	43.5
B-2782	43.7	51.7	32.4	20.3	44.8
B-2785	47.6	54.0	34.0	19.3	44.6
B-2799	42.6	50.1	32.1	18.8	44.4
B-2818	44.0	54.6	31.4	21.7	41.4
B-2820	46.8	49.0	32.0	18.7	41.0
B-3393	45.9	51.2	29.4	16.8	40.7
B-3405	49.0	53.8	29.7	24.8	38.9
B-3424	43.6	47.6	33.5	18.7	40.0
B-3426	44.0	50.3	27.0	17.3	40.4
B-3562	48.7	57.8	32.8	20.2	42.9

