

Foramen Magnum Position Variation in *Pan troglodytes*, Plio-Pleistocene Hominids, and Recent *Homo sapiens*: Implications for Recognizing the Earliest Hominids

James C.M. Ahern*

Department of Anthropology, University of Wyoming, Laramie, Wyoming 82071

KEY WORDS hominid origins; cranial base; *Sahelanthropus*; *Ardipithecus*; craniometrics

ABSTRACT The anteroposterior position of the foramen magnum distinguishes living *Homo sapiens* from apes, and has been used as evidence for the hominid status of numerable fossils in the history of human paleontology. During the past decade, foramen magnum position has been cited as evidence of the hominid status of *Ardipithecus* and *Sahelanthropus*. Specifically, the basion of *Ardipithecus* is reported to be inline with the bicarotid chord, while the basion of *Sahelanthropus* is reported to both touch the biporion chord and intersect the bicarotid chord. In order to assess the effectiveness of anteroposterior foramen magnum position in distinguishing hominids from nonhominid apes, this study examined whether or not the positions of biporion and bicarotid relative to basion sufficiently distinguished *Pan troglodytes* from recent *Homo sapiens* and Plio-Pleisto-

cene hominids. The distances from basion to the biporion chord (BSBIP) and from basion to the bicarotid chord (BSBIC) were measured on samples of chimpanzee ($n = 69$) and recent human ($n = 42$) crania and a sample of Plio-Pleistocene hominid fossils ($n = 8$). The data were used to test the hypothesis that BSBIP and BSBIC measurements do not sufficiently distinguish *P. troglodytes* from hominids. While basion to biporion (BSBIP) does not effectively distinguish *P. troglodytes* from Plio-Pleistocene hominids and humans when used univariately, basion to bicarotid (BSBIC), when used univariately or bivariate with BSBIP, can be used to test whether or not an unknown specimen is a hominid. These results are used to evaluate the hominid status of *Ardipithecus* and *Sahelanthropus*. *Am J Phys Anthropol* 127:267–276, 2005. © 2005 Wiley-Liss, Inc.

The position of the foramen magnum clearly differs between extant humans and apes (Dean and Wood 1981, 1982; Aiello and Dean, 1990; Luboga and Wood, 1990; Strait et al., 1997; Schaefer, 1999). Humans exhibit anterior foramina magna, while apes exhibit more posterior ones. The gross difference in the position of the foramen magnum likely reflects head position and locomotion posture (Dart, 1925; Broom, 1938; Le Gros Clark, 1954), although the exact nature of this relationship has not been established (Ashton and Zuckerman, 1956; Moore et al., 1973; Masters et al., 1991). The centrally located foramen magnum of humans positions the head so that it is perpendicular with the upright, bipedal body, while the posteriorly located foramen magnum of apes positions the head so that it is inline with the quadrupedal body. Rather than examining the gross difference in foramen magnum position between extant humans and apes, this paper is concerned with how useful foramen magnum position is in distinguishing early bipedal hominids from nonhominid apes.

This is an especially important issue regarding discoveries of the earliest purported hominids. Dart (1925) cited an inferred anterior foramen magnum position as evidence of the hominid status for the earliest known hominid at the time, the Taung fossil. As the hominid fossil record has been pushed

back to the Mio-Pliocene, foramen magnum position has continued to be used to support the hominid status of some of the earliest purported hominids, such as *Sahelanthropus* (Brunet et al., 2002) and *Ardipithecus* (White et al., 1994). According to Brunet et al. (2002, p. 149), the *Sahelanthropus* fossil TM 266-01-060-1 exhibits a biporion line that touches basion and a basion that “is intersected by the bicarotid chord; the basion is posterior in large apes and anterior in some of the later hominids.” Although Brunet et al. (2002) merely described the anatomy and did not explicitly use basion’s relative position as an argument for the hominid status of *Sahelanthropus*, the position of the foramen magnum has figured in the debate surrounding *Sahelanthropus* (e.g., Brunet, 2002; Wolpoff et al., 2002). Between 1.2–2.5 million years younger than

Grant sponsor: University of Wyoming Office of Research.

*Correspondence to: James C.M. Ahern, Department of Anthropology, Dept. 3431, 1000 E. University Ave., University of Wyoming, Laramie, WY 82071-3431. E-mail: jahern@uwyo.edu

Received 21 June 2003; accepted 9 April 2004.

DOI 10.1002/ajpa.20082
Published online 19 November 2004 in Wiley InterScience (www.interscience.wiley.com).

Sahelanthropus, *Ardipithecus* has also been claimed to be one of the earliest hominids; and foramen magnum position of one of the *Ardipithecus* fossils, ARA-VP-1/500, was used to support this contention (White et al., 1994). Regarding ARA-VP-1/500, White et al. (1994, p. 310) stated, "The anterior border of the foramen magnum (basion) is intersected by a bicarotid chord." White et al. (1994, p. 312) suggested that the anterior foramen magnum position in *Ardipithecus* "may correlate with bipedality, although this remains to be demonstrated."

Many studies have addressed foramen magnum position, and Luboga and Wood (1990) provided a good review of this literature, especially in regard to early works by Topinard (1878), (Bolk 1909, 1910), (Schultz 1942, 1955), Weidenreich (1943), Le Gros Clark (1950), and Ashton and Zuckerman (1956). Dean and Wood (1981, 1982), in their extensive metric analyses of the cranial bases of early hominids and apes, reported basion to sphenbasion and basion to biinfratemporal measurements. According to their report, 100% of the examined Plio-Pleistocene hominids fell within the range of their *Pan troglodytes* sample for the variable basion to sphenbasion (Dean and Wood, 1982). Furthermore, 67% of the Plio-Pleistocene sample fell within the range of the *Pan troglodytes* sample for the variable basion to biinfratemporal chord (Dean and Wood, 1982). Using these measurements of foramen magnum position, early hominids cannot be distinguished from extant chimpanzees.

Luboga and Wood (1990) examined variation in foramen magnum position and orientation among recent humans, *Pan troglodytes*, and *Pan paniscus*. They measured relative foramen magnum position with three indices: 1) opisthocranium-basion/opisthocranium-foramen caecum $\cdot 100$, 2) opisthocranium-basion/opisthocranium-subnasale $\cdot 100$, and 3) opisthocranium-basion/opisthocranium-glabella $\cdot 100$. Their work established gross differences between humans and *Pan*, as well as lesser differences between the two species of *Pan*. *P. paniscus* exhibited more anterior foramina magna than did *P. troglodytes*. Additionally, Luboga and Wood (1990) demonstrated that there is a correlation between overall cranial size and distances between basion and three anterior cranial landmarks (foramen caecum, nasion, and subnasale) among recent humans. They reported a more complicated allometric pattern for *Pan*; only one variable (basion-subnasale) significantly correlated with overall cranial size. Luboga and Wood (1990) made an analysis of australopithecine and early *Homo* foramen magnum position, yet poor preservation of most of the hominid fossils studied constrained this aspect of their work. Rather than using basion, they used porion to estimate foramen magnum (Luboga and Wood, 1990). They contend that, within a group such as hominids, the porion-foramen magnum relationship does not vary greatly. Using an index roughly comparable to their index 3

(see above), but with porion substituted for basion, foramen magnum position among the hominids fell closest to the two species of *Pan* and was much more posterior than is found in humans (Luboga and Wood, 1990). As with the measurements of (Dean and Wood, 1981, 1982), those of Luboga and Wood (1990) failed to differentiate hominids from nonhominid apes.

Most of the work related to foramen magnum position has focused on the foramen's relationship to overall cranial length measurements (e.g., Bolk, 1909, 1910; Schultz, 1942, 1955; Le Gros Clark, 1950; Ashton and Zuckerman, 1956; Luboga and Wood, 1990; Masters et al., 1991; but see Dean and Wood, 1981, 1982). Yet crania preserving basion and the carotid foramen and/or porion, but insufficiently preserved for overall cranial length measures, are more common in the hominid fossil record, and it is the position of basion relative to the bicarotid (cf. White et al., 1994; Brunet et al., 2002), biporion (cf. Brunet et al., 2002), and/or bitympanic (cf., Dean and Wood, 1982; Aiello and Dean, 1990) chords that is usually cited as differing between hominids and apes. (Dean and Wood, 1981, 1982) described differences in the position of basion relative to the bitympanic chord among hominids and apes, but they did not deal with this relationship metrically. Schaefer (1999) examined the distance between basion and the bicarotid chord among small samples of modern humans ($n = 16$) and *Pan troglodytes* ($n = 19$). This work indicated that the average basion to bicarotid distances significantly differ between humans and chimpanzees, albeit with considerable overlap. There has been no systematic documentation of the variation of basion relative to biporion and bicarotid chords among early hominids and large samples of extant apes and modern humans.

This paper systematically examines the position of basion relative to the biporion and bicarotid chords among *Pan troglodytes*, recent *Homo sapiens*, and Plio-Pleistocene hominids. The relationship of basion to the bitympanic chord was not examined because it has not been cited for recent, purported early, hominids, although basion/biporion (Brunet et al., 2002) and basion/bicarotid (White et al., 1994; Brunet et al., 2002) have been noted. Since, in the case of *Sahelanthropus* and *Ardipithecus*, basion was reported to be inline with biporion and/or bicarotid, the fundamental question to be asked is: how useful are the distances between basion and biporion and between basion and bicarotid for distinguishing hominids from nonhominid apes? In order to answer this question, it is necessary to document the variation of these measurements among hominids and nonhominid apes. Following an assessment of sexual dimorphism and correlation with cranial length, the hypothesis that hominids, as represented by recent humans and Plio-Pleistocene fossils, cannot be sufficiently distinguished from nonhominid apes, as represented by *P. troglodytes*, was tested. Finally, using the results of the analysis of hominid and

TABLE 1. *Samples*

Sample	Specimen	Details
<i>Pan troglodytes</i>		n = 69 ¹
Recent <i>Homo sapiens</i>		n = 42 ²
Plio-Pleistocene hominids		
<i>Australopithecus africanus</i>	MLD 37/38	Fossil ³
	Sts 5	Fossil ⁴
	Sts 19	Fossil ⁴
<i>Australopithecus aethiopicus</i>		
	KNM-WT 17000	Cast ⁵
<i>Australopithecus boisei</i>		
	KNM-ER 406	Cast ⁵
	OH 5	Cast ⁵
Ergasters ⁶		
	KNM-ER 3883	Cast ⁵
	KNM-WT 15000	Cast ⁵

¹ Cleveland Museum of Natural History.

² Human Osteological Repository, University of Wyoming. Sample is a mixture of Amerindian (n = 31), Chinese (n = 3), Euroamerican (n = 2), and uncertain (n = 6) populations.

³ Department of Anatomical Sciences, University of Witwatersrand.

⁴ Transvaal Museum.

⁵ Paleoanthropology Laboratory, University of Michigan.

⁶ Because of continuing controversy concerning taxonomy of early humans in Africa, I chose to use a nontaxonomic term for this sample.

chimpanzee variation, the hominid status of Mio-Pliocene fossils ARA-VP-1/500 (*Ardipithecus ramidus*) and TM 266-01-060-1 (*Sahelanthropus tchadensis*) was assessed.

MATERIALS

Measurements were taken on samples of *Pan troglodytes* (n = 69) and recent *Homo sapiens* (n = 42) crania that included adults of both sexes (Table 1). *Pan troglodytes* was chosen because of its close relationship to hominids (Wildman et al., 2003), and because work by Dean and Wood, 1981, 1982, as well as a preliminary assessment, indicated that *Gorilla gorilla*'s anatomy overlaps with hominids less than does *Pan*'s. All *Pan* specimens were from collections of the Cleveland Museum of Natural History. The *Pan* sample consisted of 45 females, one tentative female, 20 males, and three tentative males. Sex of individual *Pan* crania was taken from the Cleveland Museum of Natural History records and confirmed osteologically. The recent *Homo sapiens* sample consisted of 28 males and 14 females. Sex of individual *Homo sapiens* was taken from the University of Wyoming Human Osteological Repository records and confirmed osteologically. Measurements were also taken on a sample of Plio-Pleistocene hominid fossils (n = 3) and research-quality casts (n = 5) (Table 1). Other Plio-Pleistocene basicrania fossils were not included because of poor preservation (e.g., AL 333-45, KNM-ER 407, SK 83, SK 48, and SKW 18), distortion (e.g., KNM-ER 3733, OH 24, and SK 27), or juvenile age at death (e.g., SK 47, AL 333-105). Based on published descriptions and photographs, the basion to biporion and basion to bicarotid rela-

tionships were also assessed for two Mio-Pliocene fossils: ARA-VP-1-500 and TM 266-01-060-1.

METHODS

Measurements were made on standardized, scaled digital photographs of crania in *norma basilaris*. An exact, standard setup was used for each photograph. A Nikon Coolpix 990 3.4 megapixel digital camera was used. The line-of-sight of the camera was positioned directly perpendicular to the Frankfurt horizontal of each *norma basilaris* cranium, and the external lens surface was 20 cm away from basion. The photographic positions for MLD 37/38 and Sts 19 had to be approximated, because of distortion and/or insufficient preservation to determine the Frankfurt horizontal.

A 30-mm scale was positioned in the same plane as the most superior point of the glenoid fossa. In order to minimize the effects of lens distortion, each basicranium was positioned so that basion lay at the center top of the metering box displayed in the camera's LCD screen when set to "point metering." Focal length was a constant f 8.2 mm, which is the camera's $\times 1$ zoom setting. Lighting was uniform for every photograph, and the shutter speed was set to 1/60 of a second and the F-stop was set to 7.0. Images were recorded at the camera's maximum size of 2,048 \times 1,536 pixels and with "normal" jpeg compression.

The distances from basion to the biporion chord (BSBIP) and basion to the bicarotid chord (BSBIC) were measured on the image for each basicranium, using ImageJ 1.28v (<http://rsb.info.nih.gov/ij/>). After adjusting the measuring units to the scale in each image, each porion point was approximated by the midpoint of a line drawn across the external margin of the external acoustic meatus. Once the left and right porion points were marked, a 1-pixel-wide biporion line was drawn to connect them (Fig. 1). Although Dean and Wood (1981) defined the carotid points as the center of the carotid foramen as determined by the intersection of the maximum anteroposterior and mediolateral diameters of the carotid foramen, the medialmost point, because of its distinctiveness, was chosen. A 1-pixel-thick bicarotid line was then drawn (Fig. 1). The variance with the definition by Dean and Wood (1981) of the carotid point was not a problem for the present work, since this analysis was not interested in the length of the bicarotid chord, but instead was interested in accurately determining the anteroposterior position of this chord relative to basion. Using ImageJ's line tool combined with its "measure" command, the distances from basion to each of the two lines were measured. Measurements where the biporion or bicarotid chord was anterior to basion were recorded as positive values, while measurements where biporion or bicarotid were posterior to basion were recorded as negative values.

Three Plio-Pleistocene specimens were measured as original fossils, while the rest were examined as

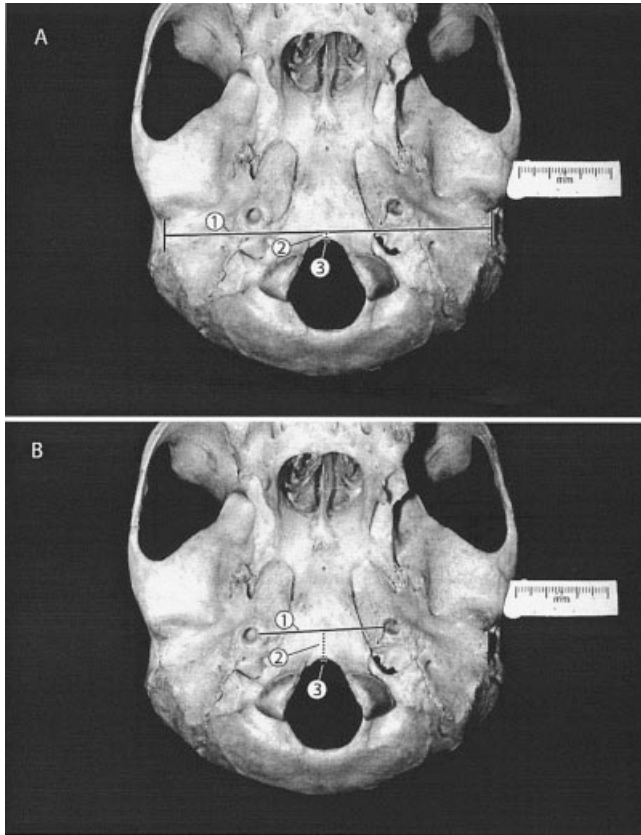


Fig. 1. Illustration of chords and metric points used in study. **A:** 1, biporion chord; 2, basion-biporion chord; 3, basion. **B:** 1, bicarotid chord; 2, basion-bicarotid chord; 3, basion. Specimen pictured is B1703 (*Pan troglodytes*).

research-quality casts. Of the three fossils, only one, Sts 5, could be positioned in the Frankfurt horizontal with certainty because of preservation. The Frankfurt horizontal for the other two fossils, MLD 37/38 and Sts 19, was estimated with enough accuracy for measurement. The five fossils examined as casts could all be accurately placed in the Frankfurt horizontal. The measurements of these casts were deemed accurate reflections of the originals, since shrinkage would be minimal across the spans being measured. Nevertheless, the measurements from casts should be regarded as tentative until proper measurements are made of the original fossils.

Neither the originals nor casts of the two Mio-Pliocene specimens were available for study, and the estimates for their BSBIP and BSBIC measurements should be regarded as gross approximations. Measurements of ARA-VP-1-500 were made from the published, scaled photograph of the specimen (White et al., 1994). The BSBIC measurement from the photograph (0 mm) is consistent with the description by White et al. (1994) (basion is inline with bicarotid). However, both measurements of this specimen should be regarded as rough estimates, since it is unclear whether or not the fossil is in correct anatomical position in the published photo-

graph, a task which would prove difficult given the fossil's preservation. The values used for the Toumaï fossil, TM 266-01-060-1, are interpretations of the description by Brunet et al. (2002). They reported that the specimen's basion is inline with both biporion and bicarotid. Measurements of the published basal photograph of the fossil were not used. The cranial base of TM 266-01-060-1 is severely distorted, and if the positioning of the fossil in the other published photographs is any indication (especially the lateral view image; Brunet et al., 2002, their Fig. 1b), the fossil is unlikely in *norma basilaris* in the published basal view image (Brunet et al., 2002, their Fig. 1d). Given the pattern of distortion, the interpretation by Brunet et al. (2002) that TM 266-01-060-1's basion is inline with biporion and bicarotid seems unlikely. The distortion anteriorly misplaced the basioccipital relative to the temporal bones, and the actual, original position of basion was likely well posterior to biporion and bicarotid (Wolpoff et al., unpublished findings). Thus, TM 266-01-060-1's foramen magnum position as reported and as used here is likely incorrect, and the specimen probably had a more ape-like position.

Since the *P. troglodytes* sample has an overrepresentation of females (female $n = 46$, male $n = 23$) and the recent human sample has an overrepresentation of males (male $n = 28$, female $n = 14$), it was necessary to test the hypothesis that males and females in both taxa do not differ in terms of their basion to biporion and basion to bicarotid relationships. Among standard, conventional test statistics, Student's *t*-test (Sokal and Rohlf, 1994) is often used to test a relationship between a continuous variable and a dichotomous variable such as sex. However, Student's *t*-test only compares the means of two groups. A more appropriate test is point biserial correlation (Tate, 1954, 1955). The formula for the point biserial correlation coefficient, r_{pb} , is:

$$r = (pq)^{1/2}(\bar{y}_1 - \bar{y}_0)/s_y$$

where $(x_1, y_1), (x_2, y_2), \dots, (x_n, y_n)$ is a sample from the (X, Y) population; \bar{y}_1 and \bar{y}_0 are the mean y -values of observations having $x_i = 1$ and $x_i = 0$, respectively; s_y is the sample standard deviation of Y ; and p is the proportion of the X -sample with $x_i = 1$, ($q = 1 - p$). A *t*-statistic is used to test the null hypothesis that there is no correlation. The *t*-statistic used is:

$$t = (n - 2)^{1/2} r(1 - r^2)^{-1/2}$$

with $n - 2$ degrees of freedom (df). Point biserial correlation is preferable to a two-sample *t*-test of means, since it directly addresses the degree of relationship between the two elements of a category and a given continuous variable.

The hypothesis that there was no relationship between each of the variables (basion-biporion and basion-bicarotid) and maximum cranial length was also tested in order to roughly assess the variables' relationship to cranial size. Maximum cranial

length, M1 (Martin and Saller, 1957), was treated as the independent variable, while basion-biporion and basion-bicarotid were treated as the dependent variables in linear regression. All data were logarithmically transformed prior to linear regressions. Since many of the BSBIP and BSBIC measurements were negative, a constant (10.0 mm) was added to all BSBIP and BSBIC values before they were logarithmically transformed.

Once the nature of any relationships of foramen magnum position with sex and maximum cranial length was established, the hypothesis that humans cannot be distinguished from *P. troglodytes* in terms of BSBIP and BSBIC was tested. Student's *t*-tests were used to examine mean difference, since if the human and chimpanzee means are not significantly different, then the variable tested does not have any utility for distinguishing humans and perhaps other hominids from chimpanzees. If a significant difference was found, then 95% confidence ranges (mean $\pm 2s$) were calculated for each variable for each sample. The mean $- 2s$ for the sample with the larger mean and the mean $+ 2s$ for the sample with the smaller mean were used to demarcate the range of overlap between the *P. troglodytes* and *H. sapiens* samples. The Plio-Pleistocene hominid BSBIP and BSBIC measures were compared with those of the *P. troglodytes* and *H. sapiens* samples, and each fossil was designated as falling in the clearly *H. sapiens* range, the clearly *P. troglodytes* range, or the range of ambiguity. Finally, the Mio-Pliocene fossils ARA-VP-1/500 and TM 266-01-060-1 were assessed relative to the Plio-Pleistocene hominids and the *P. troglodytes* and *H. sapiens* confidence ranges.

Since some fossils preserve both BSBIP and BSBIC, it is potentially helpful to examine the issue bivariate in addition to the univariate procedure outlined above. Ninety-five percent bivariate equal-frequency ellipses were calculated and plotted for each sex subset of *H. sapiens* and *P. troglodytes* samples. The procedure for determining equal-frequency ellipses followed that of Sokal and Rohlf (1994). Those Plio-Pleistocene and Mio-Pliocene fossils for which both measurements could be assessed were plotted for comparison. Furthermore, a bivariate discriminant analysis was run (using SPSS 11.0) to establish an appropriate function separating humans and chimpanzees. Equal sex-ratio subsets of the original *P. troglodytes* and *H. sapiens* data were used for the discriminant analysis, since sex significantly covaried with one of the variables, BSBIC (see Results, below). While the bivariate 95% equal frequency ellipses provided a conservative assessment for any specimen that fell within the ellipses, the $z = 0$ discriminant function line served as the sectioning point for specimens that fell outside of the ellipses.

RESULTS

Using point biserial correlation, sex covariance with basion to biporion (BSBIP) and basion to bica-

TABLE 2. Linear regression results for basion to biporion (BSBIP) and basion to bicarotid (BSBIC) vs. maximum cranial length (M1)¹ in *Pan troglodytes* ($n = 62$) and *Homo sapiens* ($n = 44$)¹

	n	r ²	F	P
<i>Pan troglodytes</i>				
BSBIP and M1	62	0.022	1.354	0.249
BCBIC and M1	62	0.019	1.188	0.280
<i>Homo sapiens</i>				
BSBIP and M1	44	0.001	0.013	0.911
BCBIC and M1	44	0.001	0.054	0.818

¹ Variables were logarithmically transformed. Because there were negative BSBIP and BSBIC values, a constant (10.0 mm) was added to all BSBIP and BSBIC values before logarithmic transformation.

rotid (BSBIC) was analyzed for the *P. troglodytes* and *H. sapiens* samples. Among chimpanzees, sex significantly covaries with BSBIC ($r = 0.42$, $df = 66$, $t = 3.80$, $P < 0.01$). Male chimpanzees tend to have bicarotid chords which lie more anterior to basion than do females. Sex and BSBIP do not significantly covary at $\alpha = 0.05$ ($r = 0.16$, $df = 63$, $t = 1.31$, $P = 0.10$). For the recent human sample, neither BSBIP ($r = 0.16$, $df = 40$, $t = 1.05$, $P = 0.15$) nor BSBIC ($r = 0.03$, $df = 40$, $t = 0.20$, $P = 0.42$) significantly covaries with sex. Additionally, neither variable, BSBIP nor BSBIC, significantly correlates with maximum cranial length (Table 2). These nonsignificant correlations do not necessarily indicate that the measurements do not allometrically vary. As demonstrated by Luboga and Wood (1990), larger measurements related to foramen magnum position do vary allometrically.

Summary statistics for the BSBIP and BSBIC measurements are given in Table 3. Because one of the variables significantly covaries with sex among *Pan*, equal-sex weighted means and standard deviations are given in addition to nonweighted statistics. The weighted statistics for both variables and both samples were used to calculate the 95% (mean ± 2 standard deviations) confidence intervals, as opposed to just using weighted statistics for BSBIC. *Pan troglodytes* and *Homo sapiens* means significantly differ for BSBIP ($t = 10.07$, $df = 107$, $P < 0.01$) and for BSBIC ($t = 8.41$, $df = 108$, $P < 0.01$). However, there is a considerable degree of overlap between the two samples for both variables (Table 3 and Figs. 2, 3).

Figure 2 plots *P. troglodytes* and *H. sapiens* BSBIP means with bars for ± 2 standard deviations. BSBIP values that fall below the range of ambiguity (as determined by the *P. troglodytes* mean $- 2s$ as the lower end and the *H. sapiens* mean $+ 2s$ as the upper end) are clearly in the *H. sapiens* range, while values that fall above the range of ambiguity are clearly in the *P. troglodytes* range. Five Plio-Pleistocene hominids (KNM-ER 3883, KNM-WT 15000, Sts 5, and KNM-ER 406) fall in the ambiguous range for BSBIP, while the remaining four (OH 5, MLD 37/38, Sts 19, and KNM-WT 17000) fall in the

TABLE 3. Basion-biporion and basion-bicarotid summary statistics

	Basion-biporion (mm) ¹	Basion-bicarotid (mm) ¹
<i>Pan troglodytes</i>		
Mean	4.7	8.1
s	3.2	2.1
95% interval (-2s to +2s) (not weighted)	-1.7 to 11.1	3.9-12.3
Mean (weighted, sex equalized)	4.8	8.4
s (weighted/sex-equalized)	3.2	2.2
95% interval (-2s to +2s) (weighted, sex-equalized)	-1.6 to 11.2	4.0-12.8
n	69	68
<i>Homo sapiens</i>		
Mean	-0.4	5.0
s	2.3	1.9
95% interval (-2s to +2s) (not weighted)	-5.0 to 4.2	1.2-8.8
Mean (weighted, sex-equalized)	-0.4	5.1
s (weighted/sex-equalized)	2.2	1.8
95% interval (-2s to +2s) (weighted, sex-equalized)	-4.8 to 4.0	1.5-8.7
n	42	42
Plio-Pleistocene hominids		
MLD 37/38 ²	-3.7	0.0
Sts 5	2.9	3.5
Sts 19	-3.8	0.5
KNM-WT 17000 (cast)	-2.8	4.7
KNM-ER 406 (cast)	0.0	5.3
OH 5 (cast)	-6.2	0.0
KNM-ER 3883 (cast)	-1.0	-0.3
KNM-WT 15000 (cast)	0.8	-1.0
Mio-Pliocene fossils		
ARA-VP-1-500	-1.6 ³	0.0 ³
TM 266-01-060-1 (as reported)	≈0.0 ⁴	≈0.0 ⁴

¹ See text for method of measurement.

² Base of MLD 37/38 is asymmetrically distorted. Values given are based on using undistorted side only.

³ See Methods for description of how these values were determined.

⁴ Estimates for this specimen are an interpretation of Brunet et al. (2002) describing it as having basion in line with biporion and bicarotid. However, pattern of distortion of TM 266-01-060-1's cranial base seems to indicate that measurements given here actually overestimate how anterior foramen magnum is in this fossil.

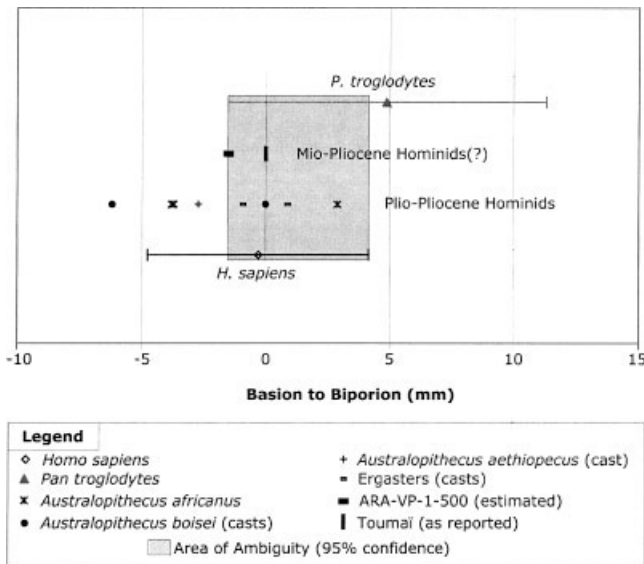


Fig. 2. Plot of basion to biporion (BSBIP). Means \pm 2 standard deviations are plotted for *P. troglodytes* and *H. sapiens* samples, while individual fossil specimens are plotted. Note that in five Plio-Pleistocene hominids estimates, two Mio-Pliocene hominid fossils fall within area of statistical overlap between *P. troglodytes* and *H. sapiens* (see text for concerns regarding TM 266-01-060-1). Three Plio-Pleistocene fossils that fall clearly in *H. sapiens* range are OH 5, MLD 37/38, Sts 19, and KNM-WT 17000. OH 5's difference from conspecific KNM-ER 406 is likely due to exaggerated degree of cranial base flexion in its reconstruction (Wolpoff, personal communication).

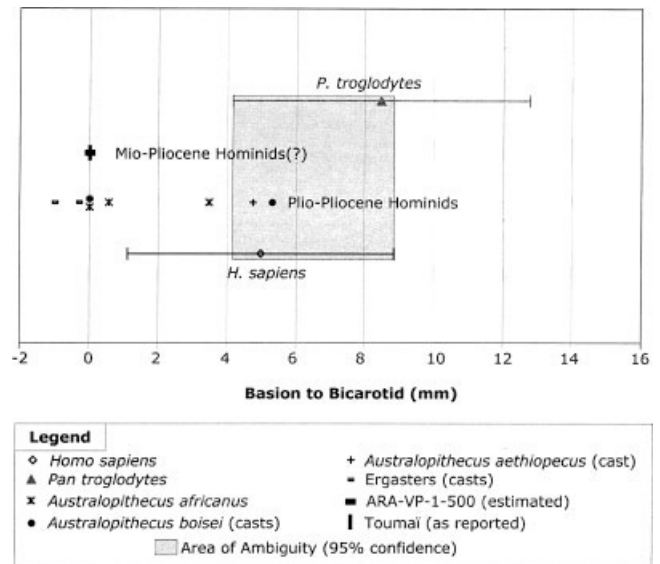


Fig. 3. Plot of basion to bicarotid (BSBIC). Means \pm 2 standard deviations are plotted for *P. troglodytes* and *H. sapiens* samples, while individual fossil specimens are plotted. Note that estimates for Mio-Pliocene fossils (see text for concerns regarding TM 266-01-060-1) and all but two Plio-Pleistocene hominids fall clearly in *H. sapiens* range. KNM-WT 17000 and KNM-ER 406 fall in ambiguous range. OH 5's extreme difference from conspecific KNM-ER 406 is likely due to exaggerated degree of cranial base flexion in its reconstruction (Wolpoff, personal communication).

clearly *H. sapiens* range. A metric estimate of the reported relative position of basion to biporion for the Toumaï specimen (TM 266-01-060-1) falls in the ambiguous range, while the approximate BSBIP measurement of the Aramis specimen (ARA-VP-1/500) falls on the border between the ambiguous and *H. sapiens* ranges. Thus, if these metric estimates are close to being correct, then the two Mio-Pliocene fossils cannot be conclusively regarded as hominid. However, as a testimony to the inefficacy of using BSBIP for discrimination, most of the Plio-Pleistocene hominid specimens also cannot be conclusively regarded as hominids based solely upon BSBIP.

Basion to bicarotid (BSBIC) appears to do a better job at discriminating between hominids and *P. troglodytes*. Figure 3 plots *P. troglodytes* and *H. sapiens* BSBIC means with bars for ± 2 standard deviations. BSBIC values that fall below the range of ambiguity (as determined by the *P. troglodytes* mean $- 2s$ as the lower end and the *H. sapiens* mean $+ 2s$ as the upper end) are clearly in the *H. sapiens* range, while values that fall above the range of ambiguity are clearly in the *P. troglodytes* range. Only two Plio-Pleistocene fossils, KNM-WT 17000 and KNM-ER 406, fall within the ambiguous range for BSBIC. All the other fossils, including the estimated values of the two Mio-Pliocene specimens, fall in the clearly *H. sapiens* range.

When examined bivariately, there is a considerable degree of overlap between the *P. troglodytes* and *H. sapiens* samples (Fig. 4). Eighty-three percent ($n = 35$) of the *H. sapiens* observations fall within the *P. troglodytes* male and/or female 95% equal-frequency ellipses. Forty-three percent ($n = 29$) of the chimpanzee observations fall within the human male and/or female 95% equal-frequency ellipses. Although the chimpanzee and human samples overlap considerably, most of the Plio-Pleistocene hominids fall well outside of the chimpanzee equal-frequency ellipses. MLD 37/38, Sts 5, and OH 5 (which might be spurious; see Discussion, below) exhibit biporion chords which are behind basion, and bicarotid chords that fall very near to basion. Ergaster specimens, KNM-ER 3883 and KNM-WT 15000, and the estimated Mio-Pliocene fossils fall outside of both the chimpanzee and human ellipses. These four specimens exhibit biporion chords that fall near basion and bicarotid chords at or slightly posterior to basion.

Figure 4 also shows a $z = 0$ line for the discriminant function formula $z = 0.243\text{BSBIP} + 0.186\text{BSBIC} - 2.001$. This formula is based on a discriminant analysis of the *P. troglodytes* and *H. sapiens* samples, with each sample having an equal number of males and females within it. Tests of equality of group means demonstrate that both variables, BSBIP and BSBIC, significantly ($P < 0.001$) contribute to the discriminant model. The discriminant model is significantly better than chance (Wilk's $\lambda = 0.537$, $\chi^2 = 44.180$, $df = 2$, $P < 0.001$) at discriminating between the two groups.

Reflecting the degree of overlap, however, the function misclassifies 26.5% ($n = 18$) of the chimpanzee individuals and 11.9% ($n = 5$) of the humans when all specimens are included, including those excluded during the discriminant analysis for equalizing the sex ratios of the samples. Classification results for the Plio-Pleistocene and Mio-Pliocene fossils are given in Table 4. All of the Plio-Pleistocene fossils are "correctly" classified as human rather than as chimpanzee. Both of the estimates for the Mio-Pliocene fossils are also classified with humans, rather than chimpanzees.

DISCUSSION

As demonstrated by univariate, bivariate, and discriminant function results, there is considerable overlap between *P. troglodytes* and *H. sapiens* for both the variables examined in this study. The range of overlap between the chimpanzee and human 95% intervals is similar for each variable (5.6 mm for BSBIP, and 4.8 mm for BSBIC). Furthermore, each variable contributes similarly to the discriminant function model. However, when it comes to discriminating between the Plio-Pleistocene hominids and the chimpanzees, basion to bicarotid (BSBIC) is clearly more effective. While only 50% ($n = 4$) of the Plio-Pleistocene hominids fell in the clearly human range for BSBIP, 75% ($n = 6$) of the Plio-Pleistocene fossils did so for BSBIC. If univariate assessment can be made of a fossil's antero-posterior basion position, BSBIC should be preferred compared to BSBIP. If a specimen has a BSBIC value of < 4.0 mm, then it falls below the 95% range for *P. troglodytes* and is likely a hominid. If a specimen's BSBIP is < -1.6 mm then it is likely a hominid, as well. Preferably, however, a bivariate assessment of a specimen can be made. If a specimen falls outside of the chimpanzee 95% equal-frequency ellipses on the *H. sapiens* side of the $z = 0$ discriminant function line, it can be confidently assigned as hominid as opposed to chimpanzee.

The present study's BSBIC results for humans and *Pan* are similar to those reported by Schaefer (1999) on smaller samples. The 95% confidence range for Schaefer's *Pan* sample was 3.3–13.7 mm, compared to the present study's 4.0–12.8 mm. The means did not significantly differ ($t = 0.1682$, $df = 85$, $P = 0.867$). The 95% confidence range for the *H. sapiens* sample of Schaefer (1999) was 1.8–10.6 mm, compared to the present study's 1.5–8.7 mm. The two studies' human sample means were barely significantly different ($t = 2.061$, $df = 59$, $P = 0.043$). Thus the study by Schaefer (1999) showed slightly more overlap between humans and chimpanzees in terms of BSBIC. This might suggest that more caution is warranted when using BSBIC to distinguish humans from chimpanzees than what the present study indicates. However, the samples of Schaefer (1999) were considerably smaller and their sex compositions were unreported. Given that BSBIC significantly covaries with sex among chim-

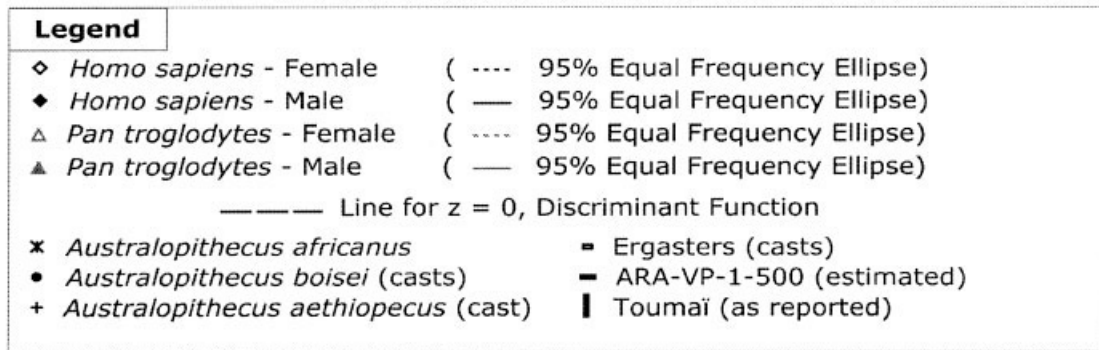
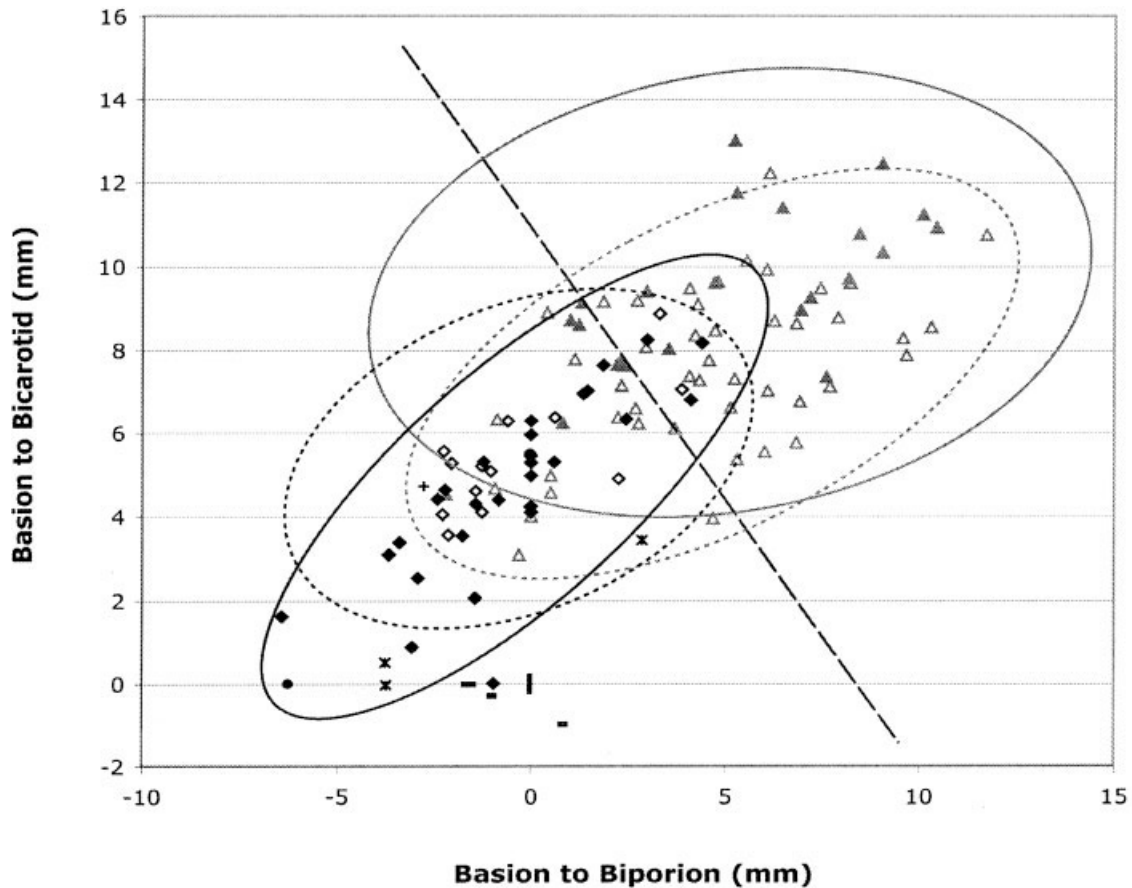


Fig. 4. Bivariate plot of basion to biporion (BSBIP) and basion to bicarotid (BSBIC), with 95% equal-frequency ellipses around each sex for *P. troglodytes* and *H. sapiens*. Discriminant function line is for $z = 0$ in equation $z = 0.243\text{BSBIP} + 0.186\text{BSBIC} - 2.001$. This equation is derived from discriminant function analysis of *P. troglodytes* and *H. sapiens* samples. While discriminant function used equal sex-ratio subsets of human and chimpanzee samples, all individuals are plotted here. Note that most fossils fall well away from *P. troglodytes* samples (see text for concerns regarding TM 266-01-060-1). However, KNM-ER 406 falls in area of overlap for all extant samples, and Sts 5 falls in area of overlap between *H. sapiens* and *P. troglodytes* females.

panzees, it is possible that the results of Schaefer (1999) were slightly skewed by an unequal sex ratio.

There are two unresolved issues that require further understanding before the basion-bicarotid relationship can effectively be used to distinguish non-hominids from hominids. First, we need a better understanding of foramen magnum position variation among early hominids. Two of the hominid samples used in this study are *Australopithecus boisei*. According to Dean and Wood (1982), robust australo-

pithecines have more anterior foramina magna than many living humans (Dean and Wood, 1982). Basion to biporion and bicarotid relationships of one of the *A. boisei* specimens, OH 5, seem to reflect this. However, the second specimen, KNM-ER 406, is second only to Sts 5 in how chimpanzee-like its BSBIP and BSBIC measurements are of any of the fossils examined. Furthermore, it falls well within the chimpanzee 95% confidence ellipses, although still in the area of overlap with the *H. sapiens* sample.

TABLE 4. Discriminant function classification results for Plio-Pleistocene and Mio-Pleistocene fossils

	Score ¹	Predicted group ²
Plio-Pleistocene		
MLD 37/38	-2.91	<i>H. sapiens</i>
Sts 5	-0.66	<i>H. sapiens</i>
Sts 19	-2.82	<i>H. sapiens</i>
KNM-WT 17000 (cast)	-1.80	<i>H. sapiens</i>
KNM-ER 406 (cast)	-1.02	<i>H. sapiens</i>
OH 5 (cast)	-3.52	<i>H. sapiens</i>
KNM-ER 3883 (cast)	-2.29	<i>H. sapiens</i>
KNM-WT 15000 (cast)	-1.98	<i>H. sapiens</i>
Mio-Pliocene		
ARA-VP-1-500 (estimated)	-2.39	<i>H. sapiens</i>
TM 266-01-060-1 (as reported) ³	-2.00	<i>H. sapiens</i>

¹ Calculated as $z = 0.243\text{BSBIP} + 0.186\text{BSBIC} - 2.001$.

² Possible groups are *P. troglodytes* and *H. sapiens*.

³ This likely underestimates Toumaï fossils nonhominid affinities, since reported basion position underestimates how posterior basion actually was relative to biporion and bicarotid (Wolpoff et al., unpublished findings).

According to Wolpoff (personal communication), the OH 5 reconstruction, of which a cast was measured for this study, exhibits an artificially marked degree of cranial base flexion. Thus, it is possible that OH 5's measurements are grossly inaccurate, and the measurements of KNM-ER 406 may be more typical of *A. boisei*. KNM-ER 407, which cannot be accurately measured because basion is missing (but can still be roughly assessed), appears to have basion to biporion and bicarotid relationships more similar to OH 5. Discovery of additional basicranial fossils will bring a better understanding of Plio-Pleistocene foramen magnum position.

A second unresolved issue is that it is possible that *P. troglodytes* is not the ideal ape species to examine, even though it is a close living relative of humans. Since there is no indisputable fossil record for chimpanzees (or any African ape, for that matter), we cannot be sure that the chimpanzee condition would be the same as in late Miocene and early Pliocene apes, those that we might mistake for hominids. For example, it is possible that the degree of overlap between chimpanzees and hominids in terms of BSBIP and especially BSBIC evolved recently and was not characteristic of Mio-Pliocene nonhominid ape contemporaries of the earliest hominids. On the other hand, it may be equally likely that Mio-Pliocene apes were similar to chimpanzees or even more hominid-like in terms of their foramina magna positions. Luboga and Wood (1990) reported that *P. paniscus* exhibits foramina magna that are even more anterior relative to overall cranial length than those found among *P. troglodytes*. Basion-bicarotid and basion-biporion relationships among *P. paniscus* need to be examined, since it is possible that the apes contemporary to Mio-Pliocene hominids may have had a *P. paniscus*-like foramen magnum position.

According to Brunet et al. (2002), both biporion and bicarotid lie inline with basion on the *Sahelanthropus* fossil, TM 266-01-060-1. For the purposes of

the current study, this description was translated into estimated BSBIP and BSBIC measurements of 0 mm. Brunet et al. (2002) did not explain how they assessed foramen magnum position (e.g., was the fossil in the Frankfurt horizontal or some other position?), and the fossil is heavily distorted, which has affected the relationships of basion, bicarotid, and biporion. If the assessment by Brunet et al. (2002) was made in the Frankfurt horizontal and if distortion did not affect the assessment, the results of this current work would indicate that: 1) the basion-biporion relationship, by itself, does not demonstrate a hominid status for *Sahelanthropus*, and 2) the basion-bicarotid relationship and bivariate relationship of BSBIP and BSBIC might demonstrate hominid status for this specimen, if contemporary nonhominid apes followed a chimp-like (or more divergent from hominids) basion-bicarotid pattern. If the *Sahelanthropus* specimen, TM 266-01-060-1, could be demonstrated hominid based on other aspects of anatomy, it could shed light upon the Mio-Pliocene ape or earliest hominid condition regarding the position of the foramen magnum. Yet almost every hominid-like feature exhibited by TM 266-01-060-1 cited by Brunet et al. (2002) was recently contested by Wolpoff et al. (2002). Thus, the situation is a "catch-22." If we knew that Mio-Pliocene apes had posteriorly placed foramina magna relative to biporion and/or bicarotid, then TM 266-01-060-1's reported foramen magnum position would bolster its hominid status. If we knew that TM 266-01-060-1 was, in fact, one of those Mio-Pliocene apes and not a hominid, then we would know that basion's relative position to biporion (and bicarotid) could not be used to distinguish Mio-Pliocene apes from early hominids.

White et al. (1994) did not explain how they assessed the basion-bicarotid relationship for the *Ardipithecus* basicranial fossil, ARA-VP-1/500, but they reported that bicarotid is inline with basion. This can be readily confirmed from the published photograph of the fragmentary but undistorted fossil, but it is unclear how preservation has affected the orientation of the fossil in the photograph. If the fossil is roughly in Frankfurt horizontal, then not only is bicarotid inline with basion (BSBIC \approx 0.0 mm), but biporion lies approximately 1.6 mm posterior to basion. Using these estimated measures, the Aramis fossil falls well outside of the *Pan* range. Taken by itself, the *Ardipithecus* specimen might leave us in the same situation as *Sahelanthropus*: the basion-bicarotid and basion-biporion relationships are not *P. troglodytes*-like, but how do they differ from contemporary nonhominid apes? If ARA-VP-1/500 is the same species as the other fossils from the site as indicated by White et al. (1994), then based on the postcranial remains, it is a hominid, and at least some early Pliocene hominids had a foramen magnum position like the majority of Plio-Pleistocene hominids. There is no reason to

think that ARA-VP-1/500 is a different taxon from at least some of the other Aramis remains.

CONCLUSIONS

Although basion to biporion (BSBIP) does not sufficiently distinguish hominids from *P. troglodytes*, basion to bicarotid (BSBIC), when treated univariately or bivariately with basion to biporion, does sufficiently distinguish hominids from *P. troglodytes*. Based on the results, it is recommended that BSBIP not be used to assess the hominid status of a fossil, unless it is used bivariately with BSBIC. Based on the criteria developed here, the *Ardipithecus* specimen ARA-VP-1/500 is clearly a hominid. The hominid status of the *Sahelanthropus* specimen TM 266-01-060-1, however, is unclear. If the description by Brunet et al. (2002) of the fossil's basion to biporion and bicarotid relationships is correct and does not reflect distortion, then the Toumaï *Sahelanthropus* fossil is likely a hominid. However, the pattern of cranial base distortion of this fossil, with its artificially anteriorly placed basioccipital relative to the temporals (Wolpoff et al., unpublished findings), indicates that the fossil's undistorted basion position might have been more ape-like.

The criteria and conclusions given here are tentative and await a better understanding of variation in early hominids and contemporary nonhominid apes before any definitive criteria can be developed. Since such an understanding of variation will only come with the discoveries of associated basicranial and postcranial fossils, the results of this study may serve as a yardstick until such discoveries are made.

ACKNOWLEDGMENTS

Thanks go to L. Jellema and B. Latimer of the Cleveland Museum of Natural History; H. Fourie, S. Potze, and F. Thackeray of the Transvaal Museum; R. Clarke, B. Kramer, and P.V. Tobias of the Department of Sciences, University of Witwatersrand; and D. de Ruiter of the Bernard Price Institute of Paleontology, University of Witwatersrand, for access to collections in their care. M.H. Wolpoff and J. Hawks provided insightful discussions regarding this project. Thanks also go to M.H. Wolpoff for access to casts in his care. Thorough comments from C.S. Larsen, F.H. Smith, G. Gill, and two anonymous reviewers greatly improved this paper. S.-H. Lee graciously let me use her maximum cranial length data for the Cleveland Museum of Natural History chimpanzee sample.

LITERATURE CITED

- Aiello L, Dean C. 1990. An introduction to human evolutionary anatomy. New York: Academic Press.
- Ashton EH, Zuckerman S. 1956. Age changes in the position of the foramen magnum in hominids. *Proc Zool Soc Lond* 126:315–325.
- Bolk L. 1909. On the position and displacement of the foramen magnum in the primates. *Kon Akad Wet Amst* 12:362–377.
- Bolk L. 1910. On the slope of the foramen magnum in primates. *Kon Akad Wet Amst* 12:525–534.
- Broom R. 1938. The Pleistocene anthropoid apes of South Africa. *Nature* 142:377–379.
- Brunet M. 2002. Reply to “*Sahelanthropus* or ‘*Sahelpithecus*’” by Wolpoff et al., 2002. *Nature* 419:582.
- Brunet M, Guy F, Pilbeam D, Mackaye HT, Likius A, Ahounta D, Beauvilain A, Blondel C, Bocherens H, Boisserie J-R, de Bonis L, Coppens Y, Dejax J, Denys C, Dusinger P, Eisenmann V, Fanone G, Fronty P, Geraads D, Lehmann T, Lihoreau F, Louchart A, Mahamat A, Merceron G, Mouchelin G, Otero O, Campomanes PP, Ponce De Leon M, Rage J-C, Sapanet M, Schuster M, Sudre J, Tassy P, Valentin X, Vignaud P, Viriot L, Zazzo A, Zollikofer C. 2002. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* 418:145–151.
- Dart R. 1925. *Australopithecus africanus*: the man-ape of South Africa. *Nature* 115:195–199.
- Dean MC, Wood BA. 1981. Metrical analysis of the basicranium of extant hominoids and *Australopithecus*. *Am J Phys Anthropol* 54:63–71.
- Dean MC, Wood BA. 1982. Basicranial anatomy of Plio-Pleistocene hominids from East and South Africa. *Am J Phys Anthropol* 59:157–174.
- Le Gros Clark WE. 1950. New palaeontological evidence bearing on the evolution of the Hominoidea. *Q J Geol Soc Lond* 105:225–264.
- Le Gros Clark WE. 1954. Reason and fallacy in the study of fossil man. *Adv Sci Lond* 43:1–13.
- Luboga SA, Wood BA. 1990. Position and orientation of the foramen magnum in higher primates. *Am J Phys Anthropol* 81:67–76.
- Martin R, Saller K. 1957. *Lehrbuch der Anthropologie*. Stuttgart: Gustav Fischer.
- Masters AV, Falk D, Gage TB. 1991. Effects of age and gender on the location and orientation of the foramen magnum in rhesus macaques (*Macaca mulatta*). *Am J Phys Anthropol* 86:75–80.
- Moore WJ, Adams LM, Lavelle CLB. 1973. Head posture in the Hominoidea. *Zool Lond* 169:409–416.
- Schaefer MS. 1999. Brief communication: foramen magnum-carotid foramen relationship: is it useful for species designation? *Am J Phys Anthropol* 110:467–471.
- Schultz AH. 1942. Conditions for balancing the head in primates. *Am J Phys Anthropol* 29:483–497.
- Schultz AH. 1955. The position of the occipital condyles and the face relative to the skull base in primates. *Am J Phys Anthropol* 13:97–120.
- Sokal RR, Rohlf FJ. 1994. *Biometry*. 3rd ed. New York: W.H. Freeman.
- Strait DS, Grine FE, Moniz MA. 1997. A reappraisal of early hominid phylogeny. *J Hum Evol* 32:17–82.
- Tate RF. 1954. Correlation between a discrete and a continuous variable: point biserial correlation. *Ann Math Stat* 2:603–607.
- Tate RF. 1955. The theory of correlation between two continuous variables when one is dichotomized. *Biometrika* 42:205–216.
- Topinard P. 1878. *Anthropology*. Philadelphia: J.B. Lippincott and Co.
- Weidenreich F. 1943. The skull of *Sinanthropus pekinensis*: a comparative study on a primitive hominid skull. *Palaeont Sin New Ser D* 127:1–484.
- White TD, Suwa G, Asfaw B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 371:306–312.
- Wildman DE, Uddin M, Liu G, Grossman LI, Goodman M. 2003. Implications of natural selection in shaping 99.4% nonsynonymous DNA identity between humans and chimpanzees: enlarging the genus *Homo*. *Proc Natl Acad Sci USA* 100:7181–7188.
- Wolpoff MH, Senut B, Pickford M, Hawks J. 2002. *Sahelanthropus* or “*Sahelpithecus*.” *Nature* 419:581–582.