Endocranial Capacity of the Bodo Cranium Determined From Three-Dimensional Computed Tomography

GLENN C. CONROY,[1*] GERHARD W. WEBER,[2] HORST SEIDLER,[2] WOLFGANG RECHEIS,[3] DIETER ZUR NEDDEN,[3] AND JARA HAILE MARIAM[4]
[1]*Departments of Anatomy and Neurobiology/Anthropology, Washington University School of Medicine, St. Louis, Missouri 63110*
[2]*Institute of Human Biology, University of Vienna, A1091 Vienna, Austria*
[3]*Department of Radiology II, University of Innsbruck, A-6020 Innsbruck, Austria*
[4]*Office of Conservation and National Heritage, P.O. Box 13247 Addis Ababa, Ethiopia*

KEY WORDS computed tomography; *Homo heidelbergensis*; endocranial capacity; brain evolution

ABSTRACT The 600,000-year-old cranium from Bodo, Ethiopia, is the oldest and most complete early Middle Pleistocene hominid skull from Africa. "Virtual endocast" models created by three-dimensional computed tomography (CT) techniques indicate an endocranial capacity of about 1,250 cc for this cranium (with a reasonable range between ~1,200–1,325 cc, depending on how missing portions of the basicranial region are reconstructed). From these determinations, several important implications emerge concerning current interpretations of "tempo and mode" in early hominid brain evolution: 1) already by the early Middle Pleistocene, at least one African hominid species, *Homo heidelbergensis*, had reached an endocranial capacity within the normal range of modern humans; 2) in spite of its large endocranial capacity, estimates of Bodo's encephalization quotient fall below those found in a large sample of *Homo sapiens* (both fossil and recent) and Neandertals; and 3) the greatest burst of brain expansion in the *Homo* lineage may not have been in the last several hundred thousand years, but rather much earlier in the Lower to early Middle Pleistocene. Am J Phys Anthropol 113:111–118, 2000. © 2000 Wiley-Liss, Inc.

The Bodo cranium is the oldest and most complete representative of an early Middle Pleistocene hominid cranium from Africa (Conroy et al., 1978; Conroy, 1980). Samples from several different vitric tephra horizons (feldspars) within the hominid-bearing Upper Bodo Sand Unit have been dated by laser-fusion $^{40}Ar/^{39}Ar$ techniques to 0.64 ± 0.03 Ma (million years), i.e., roughly contemporaneous with upper members of the Olorgesailie formation in Kenya (Clark et al., 1984). Archeological and paleontological evidence is also consistent with an early Middle Pleistocene age for the cranium (Kalb et al., 1982; Kalb, 1993).

The cranium was found in 1976 during paleontological, archeological, and geological surveys conducted by the Rift Valley Research Mission in Ethiopia headed by Jon Kalb. A separate hominid parietal bone was later found in 1981, and a distal humerus fragment was recovered in 1990 (Asfaw, 1983; Clark et al., 1994). While the Bodo cranium and isolated parietal bone come

*Correspondence to: Glenn C. Conroy, Departments of Anatomy and Neurobiology/Anthropology, Box 8108, Washington University School of Medicine, St. Louis, MO 63110.
E-mail: conroyg@pcg.wustl.edu

Received 27 October 1999; accepted 27 April 2000.

© 2000 WILEY-LISS, INC.

from very robust individuals, the humerus is appreciably smaller than in many modern humans, suggesting that these early Middle Pleistocene Bodo hominids may have been quite sexually dimorphic in overall body size.

Bodo is associated with Acheulean artifacts, including relatively well-made bifacial handaxes and cleavers (Kalb et al., 1982; Clark et al., 1994). Interestingly, while a local shift from Oldowan to Acheulean tools occurred within Ethiopia's Middle Awash sequence about this time, a similar shift in tool types occurred elsewhere in Africa nearly one million years earlier (Asfaw et al., 1992). A particularly notable aspect of the Bodo cranium is the identification of cut marks that closely resemble those caused by cutting fresh bone with stone tools. While hominid-produced cut marks on animal bone may date back some 2.5 million years in Ethiopia (de Heinzelin et al., 1999), the cut marks on the Bodo cranium may be the first documented evidence of intentional postmortem defleshing of human bone in the hominid fossil record (White, 1986).

The Bodo cranium consists of an almost complete face (particularly on the left) and partial neurocranium, as well as part of the basicranium anterior to basion (Conroy et al., 1978; Conroy, 1980; Rightmire, 1996, 1998). Bodo shares a number of craniofacial similarities with *H. erectus*, including a low braincase, broad and robust facial skeleton, thickened cranial bones, projecting and heavily constructed supraorbital tori, and midline frontal bone keeling extending to bregma. It is, however, most similar in overall appearance to other later archaic Middle Pleistocene *Homo* crania like those from Kabwe (Broken Hill), Petralona, and Arago 21. It seems more archaic-looking than the *Homo* crania from Ethiopia's Kibish Formation and Eritrea's Danakil region (Abbate et al., 1998).

Recently, some workers (but certainly not all) have lumped Bodo with varying combinations of other Middle Pleistocene hominids from Africa (e.g., Elandsfontein, Lake Ndutu, Kabwe, and Eyasi) and Europe (e.g., Mauer, Arago, Petralona, Atapuerca (Sima de los Huesos), Steinheim, Bilzingsleben, Vertesszöllös, and Swanscombe) in the species *H. heidelbergensis* (these same fossils are often referred to as "archaic" *H. sapiens*). At present, there are still unresolved questions about the makeup of *H. heidelbergensis*. Some workers suggest that the combined European/African *H. heidelbergensis* sample may represent a single lineage ancestral to both Neandertals and later *H. sapiens* (e.g., Rightmire, 1996, 1998), whereas others suggest that the European sample may be a separate lineage ancestral only to Neandertals (e.g., Arsuaga et al., 1993, 1997). These contrasting views of the role of *H. heidelbergensis* in Middle Pleistocene human evolution are reviewed in Rightmire (1998).

The Bodo cranium (and possibly OH 12 and Saldanha) is the only representative of an early Middle Pleistocene African hominid for which a reasonably accurate endocranial capacity estimate can be determined (specimens such as Kabwe and Florisbad are estimated to be some 300,000–500,000 years younger, as are the European cranial samples from Atapuerca, Petralona, and Steinheim). Indeed, in Africa there is a fossil gap of some half-million to one million years between the earliest *Homo* species like *H. habilis* (e.g., OH 24, KNM-ER 1813), *H. ergaster* (e.g., KNM-ER 3883, 3733, OH 9), and *H. rudolfensis* (e.g., KNM-ER 1470), and *H. heidelbergensis* (= "archaic" *H. sapiens*, e.g., Bodo).

MATERIALS AND METHODS

The accuracy and reliability of three-dimensional (3D) CT for safely and noninvasively studying endocranial capacity in rare early hominids are well-established (Conroy and Vannier, 1985; Conroy et al., 1990, 1998; Seidler et al., 1997; Weber et al., 1998; Zollikofer et al., 1998). To evaluate Bodo's endocranial capacity, transaxial CT scans of the original Bodo specimen were taken at the Radiology Department, University of Innsbruck, Austria, using a Siemens Somotom Plus S40 CT scanner. CT scan parameters were: 1-mm slice thickness, 120 kV, 163 mA, 512 × 512 matrix, 12-bit gray scale, 0.4902-mm pixel size. The 3D reconstructions were obtained by postprocessing the CT data using a Silicon Graphics Workstation running ANALYZE™ software.

Because the cranium is incomplete, "missing" parts were first mirror-imaged from intact contralateral pieces, and then rotated and translated to fit preserved cranial contours. The 3D reconstruction steps were as follows. First, a three-dimensional, geometrically accurate rendering of the original Bodo cranium was produced from the CT scans (Fig. 1a). Second, this 3D rendered cranium was divided into three separate objects that could be independently moved on the computer screen: 1) face; 2) midcranial region; and 3) posterior cranial region. Third, the left side of the face, being virtually complete, was mirror-imaged to produce a geometrically accurate full 3D facial view. The accuracy of this facial reconstruction was tested against known facial dimensions on the original cranium. Fourth, the more complete left lower parietal and temporal area of the midcranial region was mirror-imaged and aligned with the previously rendered, and geometrically accurate, 3D facial segment. Fifth, the more complete right upper parieto-occipital region was mirror-imaged and aligned with the previously rendered and aligned 3D midcranial region. By such repeated mirror imaging, Bodo's cranium could be visualized using the maximal cranial information, regardless of which side the original pieces were on. The final "virtual cranium" is shown in Figure 1b.

RESULTS

From Bodo's "virtual cranium," "virtual endocasts" were created using techniques described elsewhere (Fig. 1c) (Conroy and Vannier, 1985; Conroy et al., 1990, 1998; Seidler et al., 1997; Weber et al., 1998). This was relatively straightforward except in the missing basicranial region posterior to basion. Because of the uncertainty of precise cranial contours in this region, several "virtual endocasts" were produced, using slightly different cranial contours. Once each "virtual endocast" was created, its volume could be calculated directly from the ANALYZE™ program. In each case, Bodo's "virtual cranium" was rendered transparent in order to show the "virtual endocast" in situ (Fig. 1c).

Our various "virtual endocast" determinations averaged out to ~1,250 cc, with a low value of ~1,200 cc and a high value of 1,327 cc, depending on the basicranial contours used for the model.[1] The "virtual endocast" in Figure 1c has a volume of 1,248 cc. A value in the low to mid-1,200 cc range seems most likely in light of a second approach to endocranial capacity determination. Using our 3D-CT data of both the Bodo and Kabwe crania, we created a "virtual wall" orthogonal to the median-sagittal plane through bregma and basion, and then calculated the anterior endocranial capacity in both specimens (this did not involve mirror-imaging of any cranial pieces). The resulting anterior endocranial capacity was ~402 cc in Bodo and ~432 cc in Kabwe. Assuming similar proportions between anterior and total endocranial capacity in these two crania, this method would predict Bodo's total endocranial capacity to be somewhat less than Kabwe's published value of 1,270 cc.

DISCUSSION

Several interesting implications emerge from this study. First, it is informative regarding the sometimes dramatic affect that inclusion or exclusion of a single fossil may have on interpretations of "tempo and mode" in early *H. sapiens* (= *heidelbergensis*) brain evolution. For example, the view that early *H. sapiens* was characterized by a high evolutionary rate of change in endocranial capacity may need reevaluation. The addition of Bodo (using a value of 1,250 cc) to one commonly used data set relating endocranial capacity to geologic time in "archaic" *H. sapiens* (Table 3 in Leigh, 1992)[2] reduces the slope of the best-fit line reflecting evolutionary rate of brain size increase in early *H. sapiens* from a very steep value

[1]This is in general agreement with R. Holloway's estimate of ~1,300 cc cited as a personal communication in Rightmire (1996), and much smaller than the +1,500 cc estimate of Adefris (1992). It is also a slight modification of our earlier estimate in Conroy et al. (2000).

[2]The cranial capacity for Sangiran 4 in Table 1 in Leigh's data set should be 908 cc, not 808 cc (S. Leigh, personal communication).

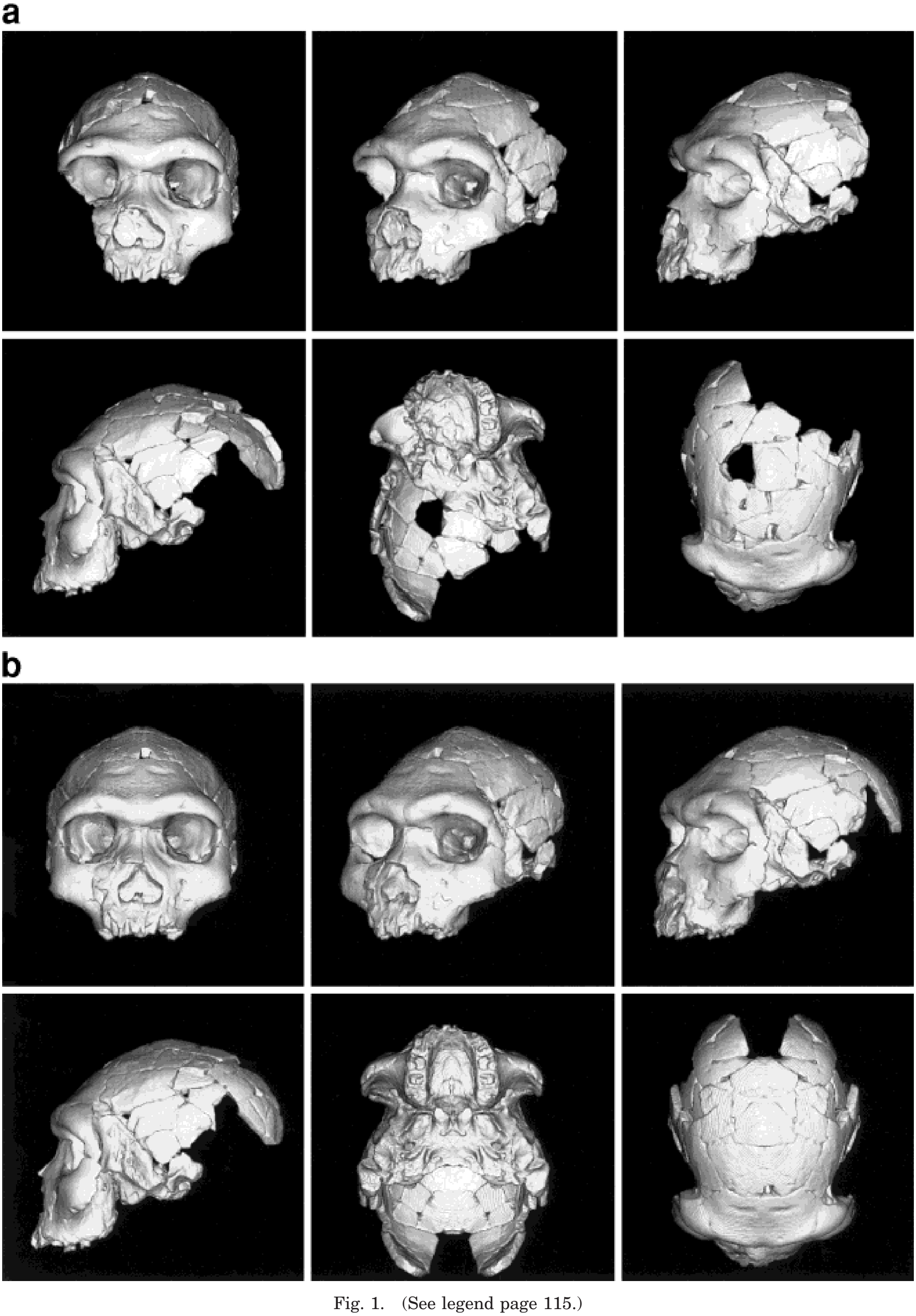


Fig. 1. (See legend page 115.)

c

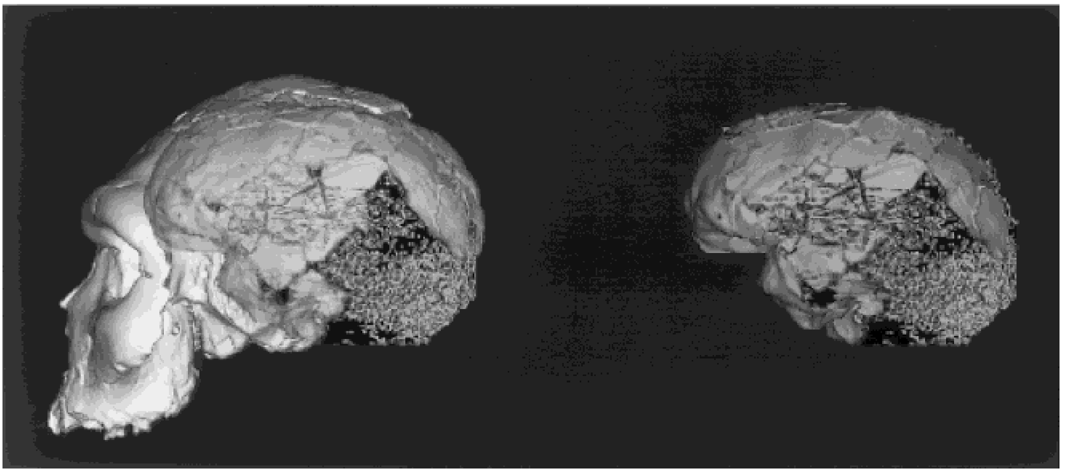


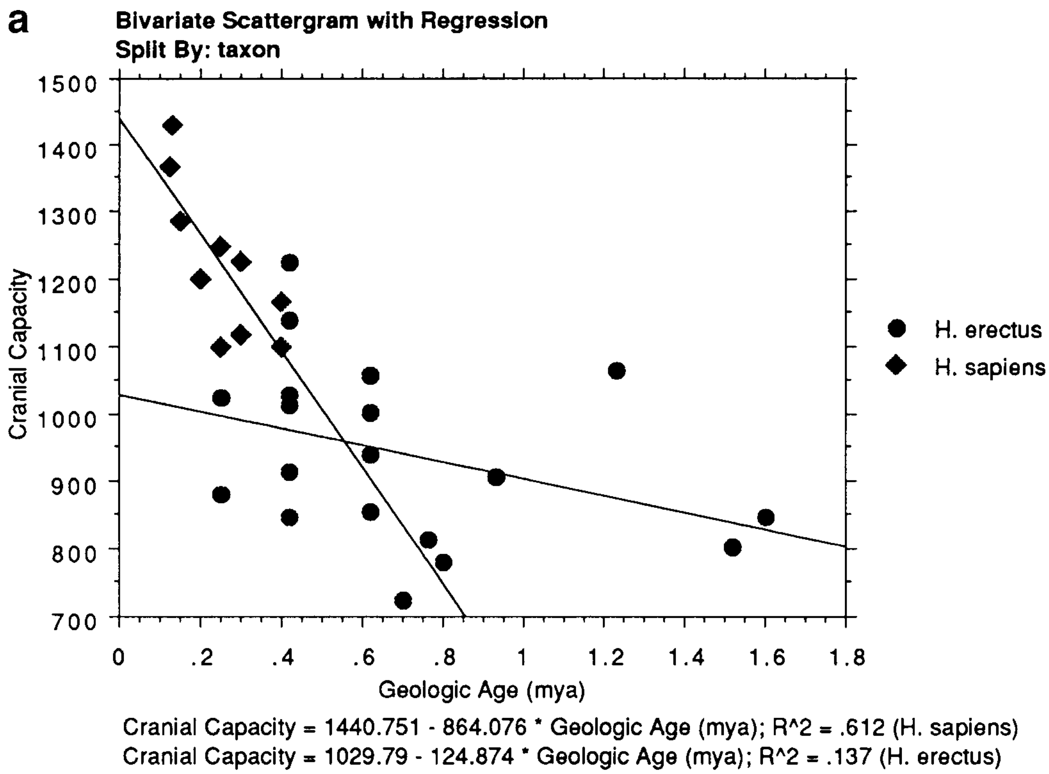
Fig. 1. **a:** Three-dimensional reconstructions of the original Bodo cranium produced from a contiguous series of 1-mm transaxial CT slices (the cranium is rotated through 30° in the first four images). **b:** 3D-CT reconstruction of the Bodo cranium after mirror-imaging various portions of the original specimen. Compare with a. **c:** Left, Bodo cranium rendered transparent to view the "virtual endocast" in situ; right, "virtual endocast" isolated from the cranium. The volume of this "virtual endocast" is 1,248 cc.

of −864 to a much more modest value of −353, reduces the R^2 value from 0.61 to 0.22, and changes the *P*-value for slope (rate of change) from <0.007 to 0.14 (Fig. 2).

Without the inclusion of Bodo, one might have interpreted the above-mentioned data set as suggesting a "punctuated equilibrium" event in brain size evolution between *H. erectus* and "archaic" *H. sapiens*, since an analysis of covariance for homogeneity of slopes between these two taxa approaches statistical significance ($P = 0.056$) (Fig. 2). However, inclusion of Bodo's endocranial capacity and geologic age into this data set changes this interpretation dramatically: using an endocranial capacity value of 1,250 cc gives highly nonsignificant values for homogeneity of slope ($P = 0.40$). In other words, with Bodo in the data set, one might conclude that there has been a gradual, rather than punctuational, change in brain size between *H. erectus* and "archaic" *H. sapiens*, since one cannot reject the hypothesis of homogeneity of slopes between these two taxa.

Second, Bodo's cranial capacity of ~1,250 cc is evidence that by the early Middle Pleistocene, at least one African hominid species, *H. heidelbergensis*, had reached an endocranial capacity well within the range of normal modern humans. Mean endocranial capacity from over a dozen widely distributed modern human samples ranges from 1,147–1,505 cc (cranial capacity translated from brain mass means of 1,111–1,450 g, using the formula: brain mass = 1.147 × cranial capacity$^{0.976}$) (Pakkenberg and Voigt, 1964; Martin, 1990; Smith et al., 1995; Falk et al., 1999).

Third, by using estimates of body weight predicted by orbital aperture area (Kappelman, 1996) and the formula Encephalization quotient (EQ) = brain mass(g)/(11.22 × body mass (kg)$^{0.76}$), Bodo's EQ would be ~3.6, based on a predicted body mass of 87,265 g and a predicted brain mass of 1,208 g (= cranial capacity of 1,250 cc) (Martin, 1981; Ruff et al., 1997). Using the lower 95% confidence limit of Bodo's predicted body weight (80,311 g), EQ would equal ~3.8; using the upper 95% confidence limit of Bodo's predicted body weight (171,138 g), EQ would equal ~2.2 (these body weights, particularly the latter, are obviously extreme, thus making it extremely unlikely that EQ values for Bodo would lie beyond the values of 3.8 and 2.2). In spite of Bodo's modern human-sized brain, these EQ esti-


a
Bivariate Scattergram with Regression
Split By: taxon
Cranial Capacity
1500
1400
1300
1200
1100
1000
900
800
700
0
.2
.4
.6
.8
1
1.2
1.4
1.6
1.8
Geologic Age (mya)
H. erectus
H. sapiens
Cranial Capacity = 1440.751 - 864.076 * Geologic Age (mya); R^2 = .612 (H. sapiens)
Cranial Capacity = 1029.79 - 124.874 * Geologic Age (mya); R^2 = .137 (H. erectus)

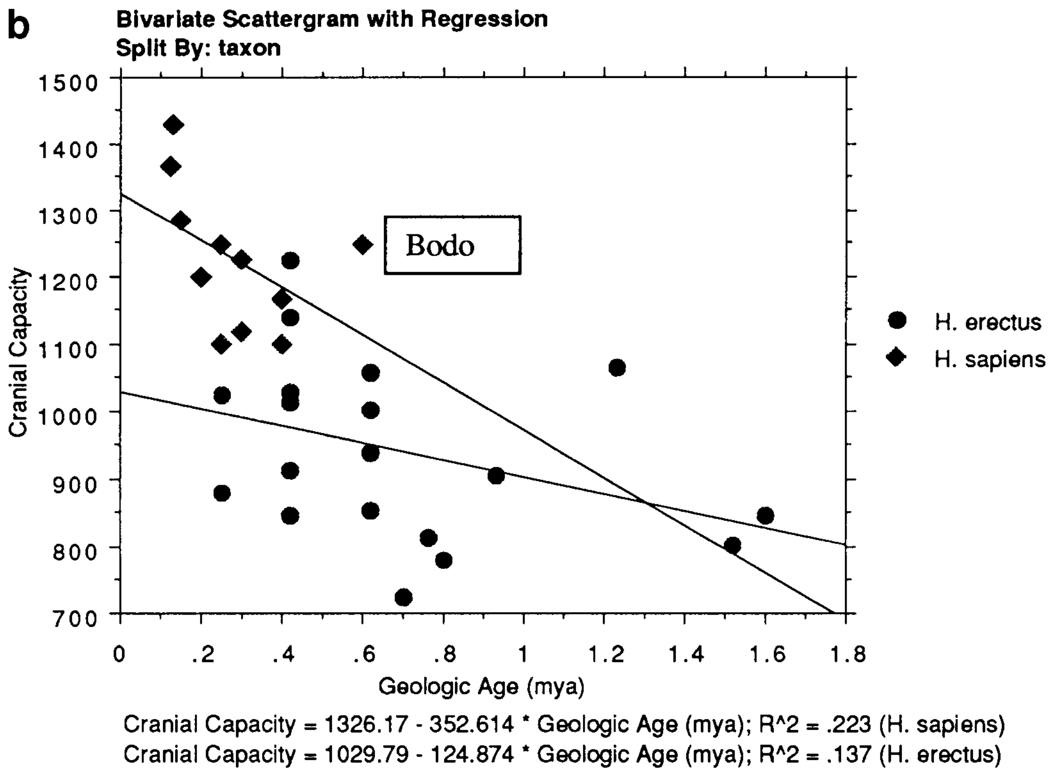

b
Bivariate Scattergram with Regression
Split By: taxon
Bodo
Cranial Capacity
1500
1400
1300
1200
1100
1000
900
800
700
0
.2
.4
.6
.8
1
1.2
1.4
1.6
1.8
Geologic Age (mya)
H. erectus
H. sapiens
Cranial Capacity = 1326.17 - 352.614 * Geologic Age (mya); R^2 = .223 (H. sapiens)
Cranial Capacity = 1029.79 - 124.874 * Geologic Age (mya); R^2 = .137 (H. erectus)

Fig. 2.

Fig. 2. Comparisons relating rate of change in endocranial capacity over geologic time in early *H. sapiens* (= *heidelbergensis*) and *H. erectus* through the Middle to Late Pleistocene. **a:** Without Bodo. **b:** With Bodo (data from Table 3 in Leigh, 1992). The addition of Bodo (1,250 cc) reduces the slope of the best-fit line reflecting evolutionary rate of brain size increase in early *H. sapiens* from a very steep −864 to a more modest −353, reduces the R^2 value from 0.61 to 0.22, and changes the *P*-value for slope (rate of change) from <0.007 to 0.14. Inclusion of Bodo may also change interpretations of "tempo and mode" of brain evolution. With Bodo in the data set, one might conclude that there had been a gradual, rather than punctuational, change in brain size between *H. erectus* and *H. sapiens*, since one cannot reject the hypothesis of homogeneity of slopes between these two taxa ($P = 0.40$).

mates fall below EQ values found in large samples of early Late Pleistocene to modern *Homo sapiens* (both fossil and recent) and Neandertals (Ruff et al., 1997).

CONCLUSIONS

In summary, our results support the view expressed by Ruff et al. (1997) that the greatest period of brain expansion in the *Homo* lineage occurred in the earlier, rather than the later, Pleistocene. Even so, *Homo*'s attainment of essentially normal modern human brain size by the early Middle Pleistocene ~600,000 kya postdated by approximately one million years other significant evolutionary changes such as the transition from Oldowan to Acheulean industries (Asfaw et al., 1992; Clark, 1994) and to more modern human body size and shape (Ruff and Walker, 1993), both of which occurred approximately 1.5 mya. If the Bodo cranium is any guide, expansion in the absolute size of the human brain over the last several hundred thousand years has been relatively minimal.

ACKNOWLEDGMENTS

We thank the Office of Conservation and National Heritage of Ethiopia and the National Museum of Ethiopia for permission to study the Bodo specimen, and we thank G. Muluneh, B. Brunsden, and E. Trinkaus for their contributions to various aspects of this project.

LITERATURE CITED

Abbate E, Albianelli A, Azzaroli A, Benvenuti M, Tesfamariam B, Bruni P, Cipriani N, Clarke R, Ficcarelli G, Macchiarelli R, Napoleone G, Papini M, Rook L, Sagri M, Tecle T, Torre D, Villa I. 1998. A one-million-year-old *Homo* cranium from the Danakil (Afar) Depression of Eritrea. Nature 393:458–460.

Adefris T. 1992. A description of the Bodo cranium: an archaic *Homo sapiens* from Ethiopia. Ph.D. thesis, New York University.

Arsuaga J, Martínez I, Gracia A, Carretero J-M, Carbonell E. 1993. Three new human skulls from the Sima de los Huesos Middle Pleistocene site in Sierra de Atapuerca, Spain. Nature 362:534–537.

Arsuaga J, Martínez I, Gracia A, Lorenzo C. 1997. The Sima de los Huesos crania (Sierra de Atapuerca, Spain). A comparative study. J Hum Evol 33:219–281.

Asfaw B. 1983. A new hominid parietal from Bodo, Middle Awash Valley, Ethiopia. Am J Phys Anthropol 61:367–371.

Asfaw B, Beyene Y, Suwa G, Walter R, White T, Wolde-Gabriel G, Yemane T. 1992. The earliest Acheulean from Konso-Gardula. Nature 360:732–735.

Clark J. 1994. The Acheulian industrial complex in Africa and elsewhere. In: Corruccini R, Ciochon R, editors. Integrative paths to the past. Englewood Cliffs: Prentice Hall. p 451–469.

Clark J, Asfaw B, Assefa G, Harris J, Kurashina H, Walter R, White T, Williams M. 1984. Palaeoanthropological discoveries in the Middle Awash valley, Ethiopia. Nature 307:423–428.

Clark J, de Heinzelin J, Schick K, Hart W, White T, Wolde-Gabriel G, Walter R, Suwa G, Asfaw B, Vrba E, Selassie Y. 1994. African *Homo erectus*: old radiometric ages and young Oldowan assemblages in the Middle Awash Valley, Ethiopia. Science 264:1907–1910.

Conroy G. 1980. New evidence of Middle Pleistocene hominids from the Afar Desert, Ethiopia. Anthropos 7:96–107.

Conroy G, Vannier M. 1985. Endocranial volume determination of matrix filled fossil skulls using high resolution computed tomography. In: Tobias, P editor. Hominid evolution: past, present and future. New York: Alan R. Liss. p 419–426.

Conroy G, Jolly C, Cramer D, Kalb J. 1978. Newly discovered fossil hominid skull from the Afar depression, Ethiopia. Nature 275:67–70.

Conroy G, Vannier M, Tobias P. 1990. Endocranial features of *Australopithecus africanus* revealed by 2 and 3-D computed tomography. Science 247:838–841.

Conroy G, Weber G, Seidler H, Tobias P, Kane A, Brunsden B. 1998. Endocranial capacity in an early hominid cranium from Sterkfonetin, South Africa. Science 280:1730–1731.

Conroy G, Weber G, Seidler H, Recheis W, zur Nedden D, Mariam J. 2000 Endocranial capacity of "Bodo man" by 3D-CT. Am J Phys Anthropol [Suppl] 30: 129–130

de Heinzelin J, Clark J, White T, Hart W, Renne P, Wolde-Gabriel G, Beyene Y, Vrba E. 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. Science 284:625–629.

Falk D, Froese N, Sade D, Dudek B. 1999. Sex differences in brain/body relationships of Rhesus monkeys and humans. J Hum Evol 36:233–238.

Kalb J. 1993. Refined stratigraphy of the hominid-bearing Awash Group, Middle Awash Valley, Afar Depression, Ethiopia. Newslett Stratigr 29:21–62.

Kalb J, Jolly C, Mebrate A, Tebedge S, Smart C, Oswald E, Cramer D, Whitehead P, Wood C, Conroy G, Adefris T, Sperling L, Kana B. 1982. Fossil mammals and artefacts from the Middle Awash valley, Ethiopia. Nature 298:25–29.

Kappelman J. 1996. The evolution of body mass and relative brain size in fossil hominids. J Hum Evol 30:243–276.

Leigh S. 1992. Cranial capacity evolution in *Homo erectus* and early *Homo sapiens*. Am J Phys Anthropol 87:1–13.

Martin R. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. Nature 293:57–60.

Martin R. 1990. Primate origins and evolution. Princeton: Princeton University Press.

Pakkenberg H, Voigt J. 1964. Brain weight of the Danes. Acta Anat (Basel) 56:297–307.

Rightmire G. 1996. The human cranium from Bodo, Ethiopia: evidence for speciation in the Middle Pleistocene? J Hum Evol 31:21–39.

Rightmire G. 1998. Human evolution in the Middle Pleistocene: the role of *Homo heidelbergensis*. Evol Anthropol 6:218–227.

Ruff C, Walker A. 1993. The body size and body shape of KNM-WT 15000. In: Walker A, Leakey R, editors. The Nariokotome *Homo erectus* skeleton. Cambridge: Harvard University Press. p 234–265.

Ruff C, Trinkaus E, Holliday T. 1997. Body mass and encephalization in Pleistocene *Homo*. Nature 387:173–176.

Seidler H, Falk D, Stringer C, Wilfing H, Müller G, zur Nedden D, Weber G, Reicheis W, Arsuaga J-L. 1997. A comparative study of stereolithographically modelled skulls of Petralona and Broken Hill: implications for future studies of middle Pleistocene hominid evolution. J Hum Evol 33:691–703.

Smith R, Gannon P, Smith B. 1995. Ontogeny of australopithecines and early *Homo*: evidence from cranial capacity and dental eruption. J Hum Evol 29:155–168.

Weber G, Recheis W, Seidler H, Scholze T. 1998. "Virtual anthropology"—methodological aspects of measurements. Am J Phys Anthropol [Suppl] 26:228–229.

White T. 1986. Cut marks on the Bodo cranium: a case of prehistoric defleshing. Am J Phys Anthropol 69:503–509.

Zollikofer C, Ponce de León M, Martin R. 1998. Computer-assisted paleoanthropology. Evol Anthropol 6:41–54.