Endocranial Capacity of Early Hominids

With the use of computed tomography (CT), Glenn C. Conroy *et al.* (*1*) estimate that the endocranial capacity of the *Australopithecus africanus* specimen Stw 505 is 515 cm^3. From this result, they reason that because previous estimates for apparently smaller crania are similar to or higher than that for Stw 505, the necessary downward readjustment of these capacities would require a reevaluation of early hominid brain evolution. We would like to revisit Stw 505 itself.

Computerized imaging techniques, like other forms of measurement in paleontology, are inaccurate unless all sources of postmortem distortion have been taken into account. One of us (C.A.L.) is currently working with P. V. Tobias on the description and primary analysis of Stw 505. This study reveals aspects of damage that were not taken into account by Conroy *et al.* (*1*). The frontal bone has been crushed inward on the left side and the parietals have been flattened and bent downward near midline. The latter contributes to a distorted midsagittal contour that is inconsistent with that of other early hominin crania. In addition, the left half of the neurocranium (especially the temporal bone) has pivoted inward such that the distances between the structures in the middle cranial fossa and the anatomical midline of the cranium are substantially reduced. This effect is also seen beneath the posterior cranial fossa, where a remnant of the left occipital condyle has been pushed into the anatomical midline. As a result of these sources of distortion, which artificially reduce the endocranial capacity of Stw 505, the estimate by Conroy *et al.* of 515 cm^3 must significantly underestimate the actual capacity, perhaps by as much as 10 to 15%. On the other hand, there is no obvious source of artificial expansion of the braincase.

Would a higher cranial capacity for Stw 505 be as unexpected as Conroy *et al.* imply? They criticize anecdotal estimates (*2*) of 600 cm^3 for the Stw 505 endocranial capacity, noting that (p. 1730) "[s]uch an endocranial capacity . . . would be astounding in any australopithecine . . . ." This statement should be placed in a statistical framework. Coefficients of variation (CV) for endocranial capacities in modern great ape and human samples range between 8 and 15% (*3*). The CV for the *A. africanus* sample without Stw 505 is only 5.1% [$n = 6$; (*4*)] and the total range for this small sample is indeed very low (60 cm^3). If Stw 505 did have an endocranial capacity of 600 cm^3, the species sample CV would rise to only 14% with a standard error of 3.4% (*4*). Thus, an endocranial capacity of 600 cm^3 in *A. africanus* should be neither "astounding" nor even unexpected if levels of variation in modern hominoids are any guide.

While the endocranial capacity of Stw 505 remains uncertain, the value provided by Conroy *et al.* (*1*) seems an underestimate, and, in any event, an appreciably higher value would not be unusual for *A. africanus*. Reappraisal of data is always healthy in science, but the endocranial capacity of Stw 505 does not support the conclusion in the report by Conroy et al. (*1*), echoed in Falk's commentary (5), that present views on the tempo and mode of early hominid brain evolution require "reevaluation."

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References and Notes

1. G. C. Conroy *et al.*, *Science* **280**, 1730 (1998).
2. D. C. Johnson and B. Edgar, *From Lucy to Language* (Simon & Schuster, New York, 1996).
3. P. V. Tobias, *The Brain in Hominid Evolution* (Columbia Univ. Press, New York, 1971); , *Olduvai Gorge IV: The Skulls, Endocasts and Teeth of* Homo habilis (Cambridge Univ. Press, Cambridge, 1991); J. A. Miller, *Am. J. Phys. Anthropol.* **84**, 385 (1991).
4. Values of endocranial capacity are from R. Holloway, in *The Functional and Evolutionary Biology of Primates,* R. Tuttle, Ed. (Aldine Atherton, Chicago, 1972), pp. 185–203. Our CVs and standard errors were calculated using the small-sample adjustment suggested by R. R. Sokal and C. A. Braumann [*Syst. Zool.* **29**, 50 (1980)].
5. D. Falk, *Science* **280**, 1714 (1998).

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The three-dimensional CT reconstruction by Conroy *et al.* of the Sterkfontein australopithecine vault Stw 505 (*1*) led to an endocranial volume estimate of 515 cm^3, viewed as either surprisingly small (*1, 2*) or small but not suprising (*3*). Visual inspection and comparisons, however, indicate a large endocranial size for this specimen (Fig. 1). Gross dimensions of the Stw 505 parietal are 10% or more larger than those of Sts 5, the best-preserved Sterkfontein cranium with an endocast volume of 485 cm^3 (*4*), which suggests that the former has an endocranial volume at least 30% greater.

The left parietal of Stw 505 (*5*) is markedly displaced medially along its inferior border and is separated from the temporal squama by more than a centimeter. Also, a marked depression involving the posterior frontal and anterior parietal creates a discontinuity of about a centimeter on the endocranial surface. The parietal midline is notably angled to that of the palate. Symmetric CT reconstruction can be no more precise than allowed by the specimen's condition. Neither this reconstruction nor water displacement performed on existing casts compensates for any of these problems.

We have estimated endocranial volume by stepwise multiple regression based on endocast volumes of complete australopithecine specimens lacking a sagittal crest (*6*). We used seven linear measurements (Table 1), including our minimal estimate of the Stw 505 cranial breadth (112 mm). A multiple regression of all variables yielded 598 cm^3 for Stw 505. A stepwise regression used only the distance from the auricular point to bregma ($r^2 = 0.974$) and gave 586 ± 23 cm^3 for Stw 505. Two other specimens preserve this measurement (*7*); adding them gave 589 ± 23 cm^3. These determinations fit what the eye can see and are not unexpected because fragmentary *Australopithecus africanus* remains such as MLD 1 are also large.

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Table 1. Specimens and measurements used in the analysis. Linear measurements are in millimeters. All measurements except Stw 505 were taken by one of us (M.H.W.) on the original specimens.

Specimen	Cranial capacity (cm^3)	Nasion-lambda	Glabella-asterion	Basion-bregma	Nasion-auricular point	Bregma-auricular point	Lambda-auricular point	Maximum cranial breadth
STW 505		143	136.6	108.5	103	102	99	112
ER 1813	509	138	133.5	99	100	95	90	114
STS 5	485	132.7	132.4	104	103	96	79	108
STS 71	428	122	122	89	94	88	76	121
ER 1470	752	160	146	104	113	115	114	139
ER 732	506	–	–	–	–	97	–	–
ER 407	510	–	–	–	–	91	–	–

Fig. 1. Comparison to scale of Stw 505 (left) and Sts 5. Both specimens are casts.

References and Notes

1. G. Conroy *et al*., *Science* **280**, 1730 (1998).
2. D. Falk, *idid*., p. 1714.
3. T. White, *ibid*. **281**, 45 (1998).
4. R. Holloway, in *The Functional and Evolutionary Biology of Primates,* R. Tuttle, Ed. (Aldine, Chicago, 1972), pp. 185–203.
5. Almost none of the right parietal of the specimen is preserved.
6. Sts 5, Sts 71, ER 1813, and ER 1470.
7. ER 407 and 732.

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Response: We wish to thank our colleagues for their interest in our work on early hominid brain size and for their thoughtful comments. While in general many of their points are well taken, they do not significantly alter our general conclusions (*1*).

We did, in our report, consider the obvious displacement of the left parietal-temporal bones in our calculations (*1*, p. 1731).

> [T]here is a gap between the left parietal and temporal bones along the squamosal suture that artificially increases the virtual endocast volume by about 8 cm^3, artificially enlarging the total volume by ~16 cm^3.

Furthermore, the slight depression in the frontal bone would have only a minimal effect on total endocranial capacity and would not significantly alter the main point of our report, namely, that endocranial capacity in Stw 505 did not exceed 600 cm^3. In any case, we acknowledged such irregularities in the specimen by reporting the actual volume as *approximately* 515 cm^3, while noting that endocranial capacity estimates varied between 482 to 536 cm^3 in our water displacement experiments.

The observation by Hawks and Wolpoff concerning the angulation of the palate relative to the parietal midline is one we explicitly addressed (*1,* p. 1730).

> Even though there is some plastic deformation in the facial skeleton of Stw 505, particularly in the maxilla, the midsagittal plane of the endocranium is easily identified . . . .

In any event, distortion of the palate is irrelevant to endocranial capacity determinations of Stw 505 because (i) our CT scans were not oriented around the distorted palate, (ii) brain tissue does not normally fill the palate, and (iii) the ANALYZE software we use allows us to interactively query the volume rendered image in any plane of interest (in this case, along the midsagittal plane of the cranium, not the palate).

With regard to the use, by Hawks and Wolpoff, of a multiple regression analysis based on seven linear measurements of broken and distorted fossil skulls they categorize as "complete australopithecine specimens," we observe that (i) their equations are actually based on only two australopithecine specimens (Sts 5 and 71), only one of which (Sts 5) we would describe as "complete" (the two other specimens, ER 1813 and ER 1470, give us some idea of endocranial size and shape in early members of the genus *Homo*, not *Australopithecus*); (ii) two other specimens, ER 732 and 407, preserve only one of their seven linear variables; and (iii) at least three of the endocranial values used in their table 1 are values that have likely been overestimated in the paleoanthropological literature and are themselves in need of reassessment.

The statistical argument presented by Lockwood and Kimbel, while interesting and worthy of further exploration, is not necessarily the most biologically meaningful or appropriate way to approach this problem (there is more than one way to skin a CAT scan). For example, for one to conclude, with the use of the statistical approach of comparing a single specimen with a sample (*2*), that the probability that a specimen of *A. africanus* with a cranial volume of 600+ cm^3 could be drawn from the presently known, and undisputedly *A. africanus*, sample would indeed be "astounding" ($P = 0.00041$). Even if the odds are stacked in favor of Lockwood and Kimbel's argument by artificially tripling the coefficient of variation (CV) of the known *A. africanus* sample from 5 to 15, the probability that a specimen of 600+ cm^3 could be drawn from this expanded *A. africanus* sample would still be less than 5% ($P = 0.03$). [Artificially tripling the CV to 15 gives a standard deviation (SD) of 66 for this "new" *A. africanus* sample; thus, an endocranial volume of 638 cm^3, for example, would be 3 SDs from the mean; a volume of only 572 cm^3 would still be 2 SDs from the sample mean.]

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References

1. G. Conroy *et al*., *Science* **280**, 1730 (1998).
2. R. Sokal and F. Rohlf, *Biometry* (Freeman, New York, ed. 3, 1995).

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