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 the species sample CV for the Stw 505 endocranial capacity, 3.4% (4). Thus, an endocranial capacity of 600 cm$^3$ in *A. africanaus* should be neither “astonishing” 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. africanaus*. 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

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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.

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

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 surprising (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 endocranial casts 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 africanaus* remains such as MLD 1 are also large.
Fig. 1. Comparison to scale of Stw 505 (left) and Sts 5. Both specimens are casts.

References and Notes
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 (I).

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

There is a gap between the left parietal and temporal bones along the squamosal suture that artificially increases the virtual endocast volume by about 8 cm³, artificially enlarging the total volume by ~16 cm³.

Furthermore, the slight depression in the frontal bone would have only a minimal effect on total endocast capacity and would not significantly alter the main point of our report, namely, that endocast capacity in Stw 505 did not exceed 600 cm³. In any case, we acknowledged such irregularities in the specimen by reporting the actual volume as approximately 515 cm³, while noting that endocast capacity estimates varied between 482 to 536 cm³ 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 (I, 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 endocast is easily identified.

In any event, distortion of the palate is irrelevant to endocast 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) would we describe as “complete” (the two other specimens, ER 1813 and ER 1470, give us some idea of endocast 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 endocast 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+ cm³ 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+ cm³ 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 endocast volume of 638 cm³, for example, would be 3 SDs from the mean; a volume of only 572 cm³ would still be 2 SDs from the sample mean.]

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