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Exploring the dorsal surface of hominoid brain endocasts by stereoplotter and discriminant analysis

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One of the more vexing problems with hominoid endocasts has been to secure reliable information that goes beyond their volumes. One method is explored here, where a large number ($N = 171$) of radial distances from a homologous internal central point to the dorsal endocast surface are measured in a polar coordinate system. From two pilot studies, one with a hominoid sample of $N = 64$, and the other with an enlarged sample of $N = 92$, the following results can be mentioned tentatively: (1) there are residual data that differ taxonomically in different cortical regions once overall endocast size is corrected in allometric fashion; (2) the major cortical regions where these differences appear most strongly are in the lower parietal lobule, anterior occipital zone, and the dorsoanterior region of the frontal lobe; (3) the method shows excellent promise in objectively and quantitatively depicting taxa-specific shape differences in functionally understood cortical regions through multivariate statistical analyses.

Introduction

Brain endocasts, whether 'natural', as found in some of the South African australopithecine sites, or as produced from latex moulds of cranial interiors, are the closest empirical 'windows' to the evolution of the hominid brain that we possess. Apart from their size, however, little if any definitive information has been gleaned from them without considerable speculation. The unfaithfulness of replication of gyral and sulcal relief patterns, at least on hominoid endocasts, is infamous, with but a few minor exceptions. In addition, brain endocasts are very difficult to measure in any meaningful sense. Traditional caliper measurements can be applied to landmarks left by the internal bony table of the cranium, but these have no functional relevance to the underlying brain. Measurements such as length, width, height, whether in chords or arcs, only describe space, and even the measurements or indices devised by Kochetkova (1978) to measure brain lobes are probabilistic guesses, without clear empirical tests, and further run into the abyss of allometric correction.

At the risk of appearing in a Panglossian role, my current research on a large sample of hominoid endocasts ($N = 92$) is suggesting that more information resides in (on) an endocast than its volume and a few morphological features of varying value, such as meningeal patterns, sinus variations, petalial asymmetries, or selected gyral and sulcal patterns such as the lunate sulcus or Broca's 'cap'.

This paper is an updated preliminary and exploratory report on pilot studies that show very considerable promise, objectively and quantitatively, in depicting regional morphological changes that might later be related to our functional knowledge of neurological structure, and which also may provide information useful in taxonomic assignments within the Hominoidea.

Materials and methods

Table 1 is a list of the hominoid endocasts used in the current sample ($N = 92$). Each endocast, with the exception of many of the fossil hominids, was made of latex rubber, as described by Holloway (1978).

Table 1. Hominoid sample breakdown

species or specimen	number	volume/ml
1. *Pan paniscus*	16	327–439
2. *Pan troglodytes*	15	385–449
3. *Gorilla gorilla*	16	422–615
4. *Homo sapiens*	13	1166–1659
5. australopithecines		
(*a*) 'gracile'	4	404–485
1. Taung		404
2. STS 5		485
3. STS 60		436
4. OMO 338		427
(*b*) 'robust'	3	506–530
1. SK 1585		530
2. OH 5		530
3. KNM-ER 732		506
6. *Homo erectus*		
(*a*) *Indonesian*	5	813–1059
(*b*) *Chinese*	4	890–1220
7. Solo	5	1013–1250
8. Neanderthal	4	1350–1641 (La Chapelle, La Ferrassie, La Quina, Neanderthal)
9. unclassified	7	KNM-ER 1470, 1813, 1805, 3733, 3883, OH 9, Rhodesian (S15-1285)
total	92	

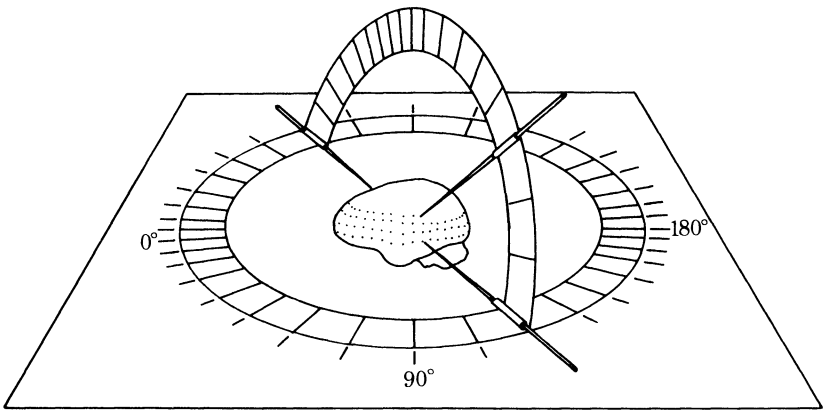

Figure 1. Schematic drawing of the stereoplotting apparatus, originally devised by A. Walker and D. Oyen. (The inner circular element rotates through 360°. The pointer on the vertical arch sweeps 180°.) Measurements are taken to the nearest millimetre.

The measuring device is a coordinate stereoplotter (figure 1), designed by Oyen & Walker (1977), which provides a critical 'localness' of homologous points on the endocast surface that can be initially specified in a polar coordinate system, e.g. two angles and a radial distance. This system permits accurate and replicable measurements to be taken, and provides a large matrix of data, which can be treated in a variety of multivariate statistical ways. This system

has the further advantage of graphic depiction in relation to neuroanatomical and neurophysiological maps.

Each endocast is placed in the apparatus such that: (1) the midsagittal plane is aligned along the 0–180° horizontal axis; and (2) a homologous centrepoint 'within' the endocast is defined as that point exactly midway between frontal and occipital poles, which in hominoids, at least, are homologous structures. The endocasts are then measured every 10° in both horizontal and vertical directions, yielding a total of 171 data points (radial distances from the

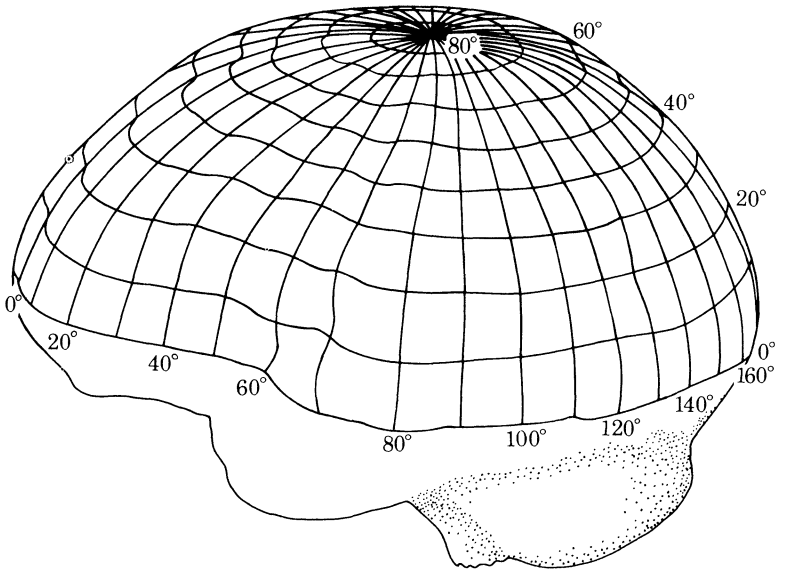

FIGURE 2. Stereoplot 'net' cast over an endocast shape. Each intersection is a point where a radial distance from the surface to a homologous centre point is taken in millimetres.

surface of the endocast to a homologous centre point) *for each side*. In these preliminary studies, only the *left side* of each endocast was measured, except in those obvious cases, such as Taung, SK 1585 etc., where only right-sided endocasts exist, or in those, e.g. Solo, where the right side was less distorted than the left.

Each measurement was first placed on a map of coordinate intersections, and then punched onto data cards, the specimens being arranged according to taxa in a subfile list. Thus, for each endocast, there would be 19 radial distances, one measured every 10° anterior and posterior, for each of the 10° vertical transects between 0° (horizontal) and the 80° level. Figure 2 shows an 'endocast net', as it were, where each intersection represents a coordinate of a radial distance.

For convenient statistical reasons, the original pilot analyses were conducted on a series of individual vertical transects at 20° intervals from anterior to posterior. Thus two sets of data 'decks' were analysed, one called 'evens', composed of a horizontal transect, beginning at the midsagittal plane and containing values at 20° intervals, giving a total of 10 values for each specimen in each of the horizontal transects, and a second set, called 'odds', composed of the intervening 9 values at 20° intervals for each horizontal transect.

The reasons for this division were as follows: (1) the total number of specimens in any one taxonomic group, e.g. *Pan paniscus*, was *less* than 19; (2) there are only ten taxonomic groups,

not counting 'unknowns'. Since discriminant analysis was anticipated as a useful preliminary way of exploring the data, it was decided to keep the number of variables to a minimum in terms of the constraints known for discriminant analysis, e.g. not having more variables than either groups or specimens within groups. Alas, even this was an impossible task, given the low sample sizes of some of the hominid groups. Later analyses were based on selecting the highest univariate *F*-ratios, and choosing only *that* number of variables below the specimen number in the taxonomic group with the lowest number of specimens, e.g. 4 for Neanderthal.

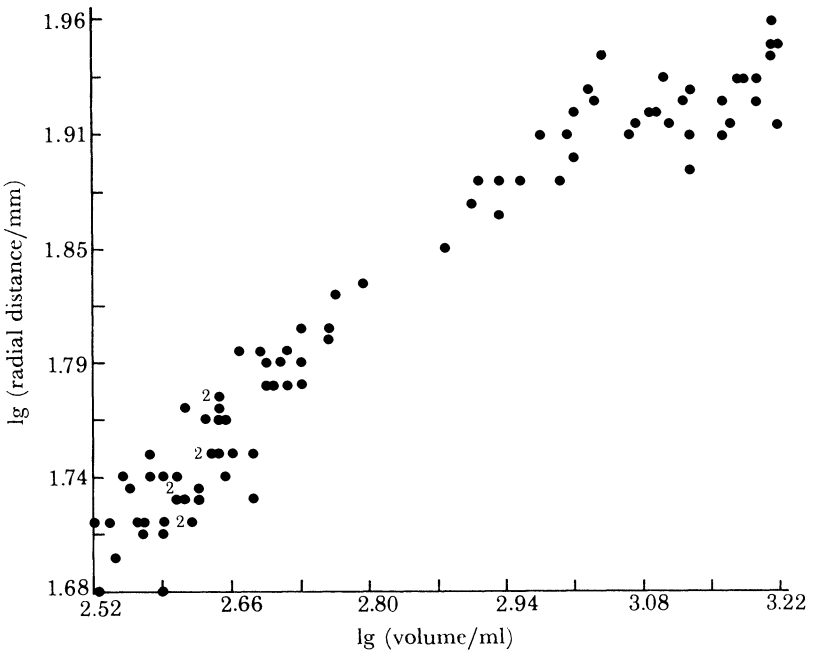

FIGURE 3. A sample output of a bivariate scattergram to illustrate a plot of lg (radial distance) against lg (endocast volume) for 92 hominoid endocasts.

Statistical procedures

It should be apparent that a radial distance from a centre point to the dorsal endocast surface will depend on the size of the endocast, and that, if additional information (shape?) to size is expected, some method of allometric correction must be used.

By the use of a scattergram routine from SPSS, each radial distance and endocranial volume was converted to its logarithmic equivalent, and the same coordinate point for all 92 cases was plotted against volume, yielding a straight-line regression equation of form lg (radial distance) $= k + \alpha$ lg (volume), or radial distance $= k$ (volume)$^{\alpha}$. This was done for each point, generating 171 equations in total, or ten or nine equations for each 'even' or 'odd' transect. These equations were then used to calculate the *expected* value of radial distances for each point, as if they had fallen exactly on the equation line. In other words, each point was considered as an independent variable in the early phase of the analysis.

These *expected* values were next subtracted from the *actual* radial distances, yielding a residual, called DIFF 1, DIFF 2. . . DIFF 10, etc., depending on its angular location. In other words, the DIFFS are the residual values of the allometric corrections, and each 'even' deck gives ten DIFFS

at 20° intervals, and each 'odd' deck nine DIFFS at 20° intervals. Thus for one side of an endocast there result 171 DIFFS.

The correlation coefficients were all high, but varied in different locations on the dorsal endocast surface, ranging from 0.93 to 0.98. All were significant at the 10^{-5} level. The exponents (slopes, α) also varied, from about 0.28 to 0.50, again depending on the particular point and angular transect. The overall average was about 0.33, as would be expected from geometrical considerations (i.e. the cube of the radius would approximate volume).

The DIFFS, as described above, thus became the variables analysed by means of a variety of statistical techniques, mainly (1) ANOVA, (2) discriminant analysis, and (3) factor analysis.

Hypothesis and preliminary results

Two basic questions were being asked of the data: (1) if allometric corrections were made, would the residual information pattern itself in a meaningful way?; and (2) would it be possible to translate this (these) pattern(s) into one(s) having functional meaning neurologically?

The first test was to ascertain that the DIFFS, or residuals, were related to taxonomic groups *and not to volumes*. Thus the ANOVA procedure was used, in which each DIFF was the dependent variable, with the taxonomic groups as independent variable, and lg (volume) a covariate. The resulting *F*-ratios (between-group-to-within-group variance ratio), after allowance for covariance between the DIFFS and lg (volume), were all high and significant, indicating that no further significant relation between the DIFFS and lg (volume) existed, and that the patterns of DIFFS were explainable by their taxonomic group.† Furthermore, the values of the *F*-ratios varied considerably depending on the location of the points on the endocast. In other words, it was possible to map the univariate *F*-ratios for all 171 locations and study the placement of highest and lowest values. By and large, the highest *F*-ratios were in locations of considerable neuroanatomical interest, such as the inferior parietal–anterior occipital zone, the superior parietal zone and a small portion of the frontal lobe. These findings will be described in greater detail in the discussion section of this paper.

Discriminant analyses were performed, again by means of the SPSS package, for each horizontal transect, 'even', and 'odd'. The explicit hypothesis tested was: if there was no further relevant information after allometric correction, the DIFFS (residuals) should *not* show any meaningful taxonomic classification results: i.e. the percentage of classifications correct should be random, or approximately 50. In fact, the classification scores varied for each transect, depending on the transect and on whether nine or ten DIFFS were being used. Classification results were higher when ten rather than nine variables were used. The classification results were *also* very dependent upon the combinations of taxonomic groups used.‡

† This was particularly true when ANOVA was used on all groups. No significant variation was found that could be related to the base 10 logarithm of the endocast volume. A warning here is in order. For other group combinations, e.g. extant only or fossils only, the relations of the DIFFS to volume do change, and some of the ANOVA results suggest that some of the DIFFS are related to the covariate as well as to the taxonomic group. The statistical tables are misleading, however. When the DIFFS for the extant group are plotted against (volume) there are two large clusters: one for pongids, and one for *Homo sapiens*, with a huge gap in between. This amounts to plotting a line with only two points (or centroids): there are no such relations within the pongid or *Homo* groups. Nevertheless, some of the DIFFS do show weak, but sometimes significant, correlations with lg (volume).

‡ If all the decks are combined, and data points linearly arranged, one can select those coordinates where *F*-ratios are highest. While not reported here, these runs have yielded higher classification scores for all three of the group combinations discussed, and permit one to avoid non-singular covariance matrices.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 2 indicates the variability of classification scores for each transect, when different groups are used. 'Unknown' specimens such as KNM-ER 1813, 1805, 1470, 3733, 3883, OH9, and the Rhodesian endocast were not classified on the trial runs but were retained as a group for later predictions.

TABLE 2. DISCRIMINANT ANALYSIS† CLASSIFICATION RESULTS (PERCENTAGE CORRECT)

Grouping A: all subfiles, extant + fossil.
Grouping B: extant species only (*Pan paniscus*, *Pan troglodytes*, *Gorilla*, *Homo sapiens*).
Grouping C: fossil hominids only (Indonesian + Chinese *Homo erectus*, Solo, australopiths, Neanderthal).
Parenthesized values are for the stepwise method, based on the method of Wilks (Λ).)

transect	grouping A	grouping B	grouping C
0° horiz.	89 (87)	92 (87)	100 (96)
10° even	73 (63)	73 (68)	88 (80)
10° odd	62 (62)	67 (65)	96 (80)
20° even	74 (69)	73 (72)	100 (92)
20° odd	65 (66)	75 (70)	84 (76)
30° even	67 (62)	73 (70)	88 (84)
30° odd	56 (49)	63 (65)	84 (80)
40° even	58 (59)	80 (73)	80 (64)
40° odd	63 (62)	80 (78)	80 (84)
50° even	75 (68)	83 (85)	84 (64)
50° odd	56 (49)	67 (65)	92 (72)
60° even	61 (60)	68 (70)	92 (92)
60° odd	52 (45)	71 (69)	88 (84)
70° even	56 (43)	63 (55)	96 (76)
70° odd	46 (39)	60 (52)	84 (64)
80° even	51 (46)	62 (53)	80 (72)
80° odd	36 (33)	55 (58)	84 (72)

† Based on direct method.

It should be mentioned that the discriminant analyses were done in two ways: (1) direct method, in which all nine or ten DIFFS were entered; (2) the stepwise method, in which only several were selected for inclusion, depending on their *F*-values and the results of their inclusion on lowering the Wilks Λ value at each step.‡ As table 2 suggests, the classifications are highest in the lower transects, i.e. 0 (horizontal, 19 values), 10, 20, 30, and the highest univariate. *F*-ratios are in the posterior coordinates. *Most* of the misclassifications occur between *Pan paniscus* and *Pan troglodytes*, or between *Homo erectus* (Java) and *Homo erectus* (China). Curiously, the classifications between *Australopithecus africanus* and *Australopithecus robustus* are often very high, e.g. 100%. However, the sample sizes for these taxa are very low ($N = 4, 3$, respectively) and their covariance matrices are non-singular, and so considerable caution must be exercised in interpreting these results as truly significant (see also table 3).

Space forbids a full discussion of the factor analytic explorations. The point in trying these techniques was to reduce the data to some number of factor scores lower than the number of specimens in any one taxonomic group (i.e. $N = 4$). Discriminant analyses were tried on the

‡ I have hesitated to go beyond the very shallow analyses offered here because I am not yet comfortable with the statistical methods employed. If the MAHAL method (also stepwise) is used, the classification results vary slightly, and the SPSS (Nie *et al.* 1975) set of options, provides a great number of different routines. For example, if individual group covariance matrices are used for classification, rather than a pooled-with-group matrix, the classifications improve slightly, although the discriminant functions and scores do not change. Classifications will also change depending on the *a priori* probabilities assigned for each group. In the data provided in this paper, all groups have been given *equal* probabilities, and have not been weighted by group sizes. I assume that this is a more robust test.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

factor scores, and, in general, there was a loss of information, which reduced the classification scores. (Factoring was done by the PA1 principal components technique of SPSS, with Varimax rotation.)

Discussion

I must stress that these results are only preliminary and of a tentative nature. I believe that they are encouraging and show considerable promise, provided that our sample sizes for certain taxonomic groups improve and that further statistical refinements are made.

Hopefully, the choice of the central point as a 'homologous centre' is reasonable, as all evidence points to both frontal and occipital poles being homologous points in both a structural and functional sense, between pongids and hominids.†

Some of the difficulties of these studies, however, should be explicitly stated. The underlying assumption is that the shape differences between the various taxa are due to evolutionary changes of the brain rather than other adaptive processes such as craniobasal flexion, postural adjustments, masticatory functions etc. At the moment, I do not know how to test this assumption, nor how to weight the various possibilities. It depends very much on our basic understanding of such postural-masticatory influences on the cerebrum, rather than on exocranial structure. My own belief is that those influences are minimal.

Another area of uncertainty is the method of using residual (DIFFS) information from allometric corrections based on log–log regressions. It should be immediately evident that there is a certain *relativity* in this method, as the corrections depend on the construction of the base line. Certain taxonomic groups heavily weight the regressions, such as two species of *Pan*, *Gorilla* and *Homo sapiens*. One can argue that, after all, 92 examples give a very good representation of the hominoids; on the other hand, one could argue that the inclusion of values *to be tested* is not maximally appropriate. Still, it is the best base line that we have.

The relativity question must be given serious consideration, since classification scores *and* *F*-ratios change considerably depending on the groups compared. Figures 4–6 show the mappings of univariate *F*-ratios in three different combinations of taxonomic groups: (1) all groups ($N = 10$) without 'unknowns'; (2) only extant species, *Pan paniscus*, *Pan troglodytes*, *Gorilla* and *Homo sapiens*; (3) fossil groups only, where Indonesian and Chinese *Homo erectus* are combined, Solo is separate, australopithecines are combined and neanderthals are separate ($N = 4$). Table 3 shows the different classifications possibilities depending on such selections of groups. In these cases, there are no non-singular matrices.

I have included two additional diagrams to illustrate some of the depictional possibilities of these methods. Figure 7 is a map of the probabilities from *t*-tests on each coordinate between *Homo erectus* and *Homo sapiens*, with all *p*-values lower than 0.05 encircled. It is intriguing that the major differences are in those regions of the endocast that we normally associate with posterior and inferior parietal lobe (Wernicke's area, in part?), and the dorsal anterior part of the frontal lobe. My point here, I must stress, is not that these values are correct or proof of significant cerebral neurological differences between the two groups, as the sample sizes are pathetically small. Rather, it represents an interesting depictional possibility. Similarly, figure 8 is a Cartesian, and thus distorted, rendition of Brodmann's areas, as applied to a human

† Some effort has been made to check the internal 'centre' point, to see if its location is also homologous. Unfortunately, precise stereographic atlases do not exist for most primates. Median sagittal sections of both human and chimpanzee brains, as illustrated in a variety of anatomy books, indicate that the centre point does consistently fall in the thalamus zone, just anterior to the posterior commissure.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

TABLE 3. SOME SAMPLE DISCRIMINANT ANALYSIS CLASSIFICATIONS (PERCENTAGE† CORRECT) FOR VARIOUS TAXONOMIC COMBINATIONS, BASED ON SELECTING HIGHEST *F*-RATIO VALUES‡

grouping	direct	stepwise
Panp, Pant, Gorilla§	95.7	85.1
Panp+, Pant, Gorilla	100.0	97.9
Pith+Sina, Solo, Aust+Robt, Nean	64.0	84.0
Panp, Pant, Gorilla, Homo§	78.3	75.0
Panp+Pant+Gorilla, Aust+Robt	96.3	94.4
Panp+Pant, Gorilla, Aust+Robt	83.3	77.8
Pith+Sina, Solo, Nean	72.2	100.0
Homo sapiens, Nean	100.0	100.0
Pith+Sina, Aust+Robt	100.0	100.0

† The percentage values are for both direct and stepwise solutions, by the methods of Wilks (Λ).

‡ Each grouping yields its own univariate *F*-ratios for each 171 points. These are ordered according to rank, and the highest ratios are selected for discriminant analysis. In these runs, there were no non-singular covariance matrices, as the number of variables selected was always $N-1$, the lowest number of specimens within a taxonomic group.

§ Almost all misclassifications occur between *Pan paniscus* and *Pan troglodytes*.

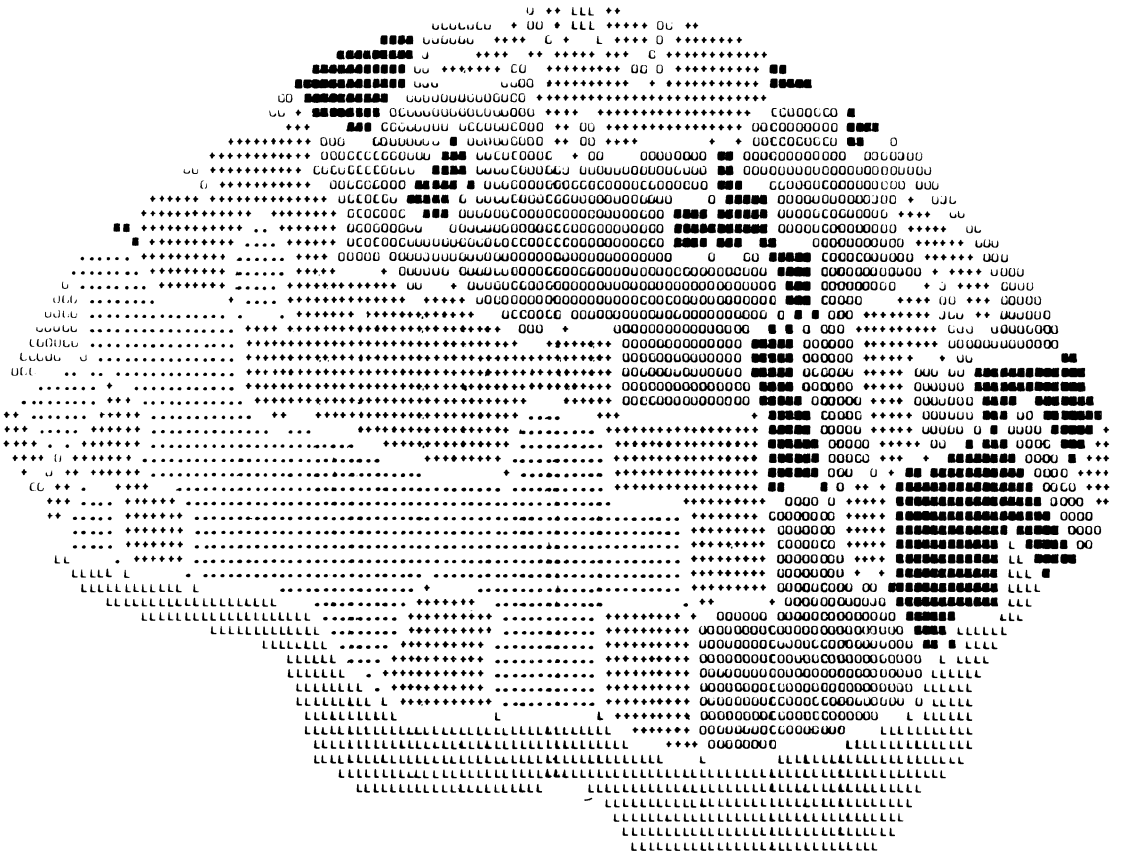

FIGURE 4. A SYNMAP of 171 univariate *F*-ratios plotted within an endocast shape. The darkest areas have the highest *F*-ratio values, ranging from 8.5 to 12.7, and significant at less than the 10^{-5} level. This map is for all groups combined, i.e. fossil and extant species

The SYNMAP symbols have been chosen such that L represents non-significant *F*-ratios, and the five gradations, of darkness represent increasingly significant *F*-ratios, roughly at the 5×10^{-2} to 10^{-2}, 10^{-3}, 10^{-4} and 10^{-5} levels. The outline of the endocast is only approximate, based on the figure 2 'net' shape. In reality, there are no data points *below* the horizontal plane passing through frontal and occipital poles.

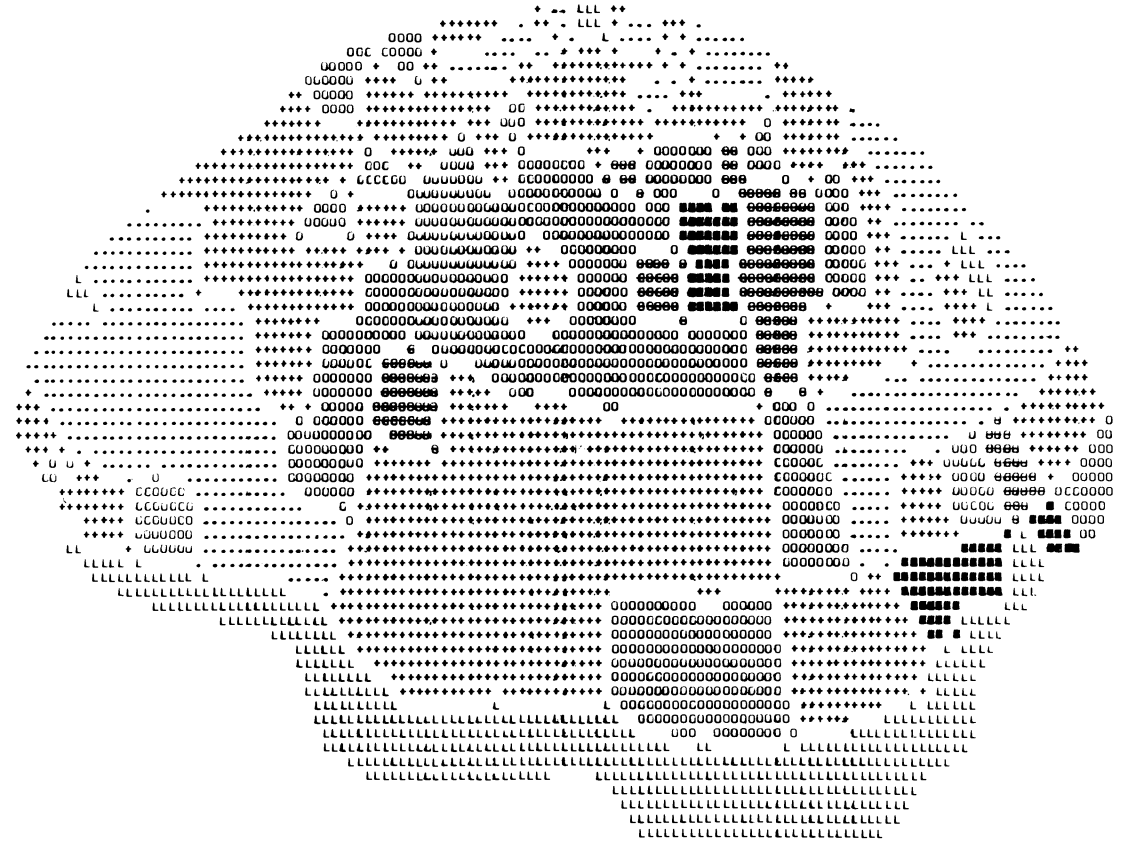

FIGURE 5. As in figure 4, except that these *F*-ratios are for extant species only. The darkest areas have *F*-values ranging from 12.6 to 18.0.

FIGURE 6. As in figures 4 and 5, except that these *F*-ratios are for the fossil hominids only. Darkest area has *F*-values ranging from 15.0 to 21.3.

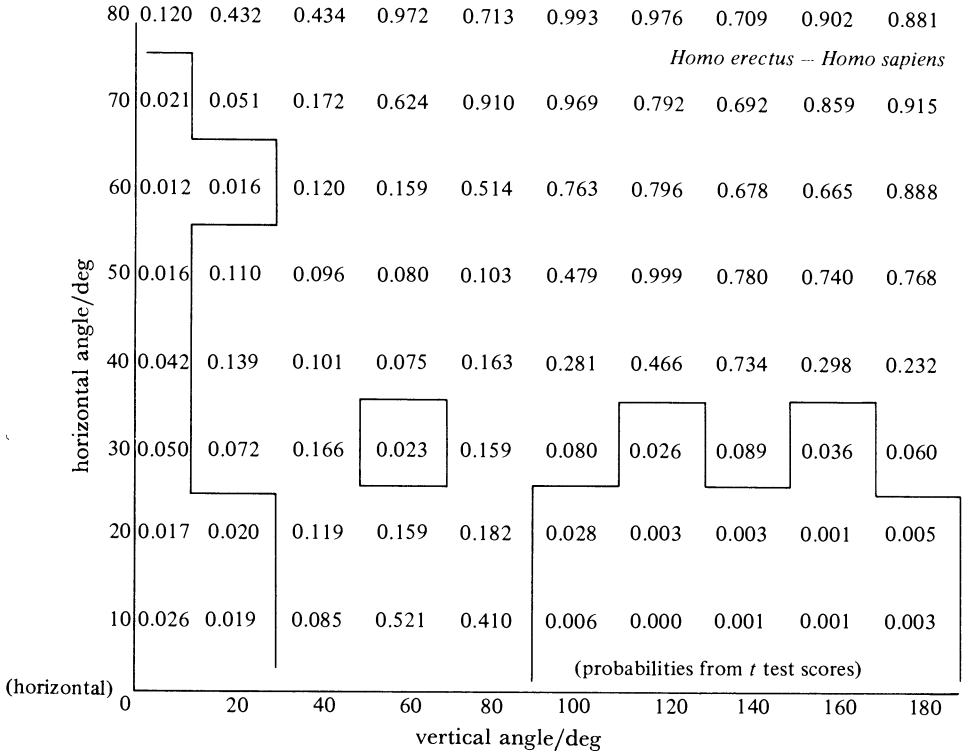

FIGURE 7. A tentative plot, every 20°, of the *p*-values associated with 'student' *t*-tests of the DIFFS between *Homo erectus* and *Homo sapiens* (for depictional purposes only).

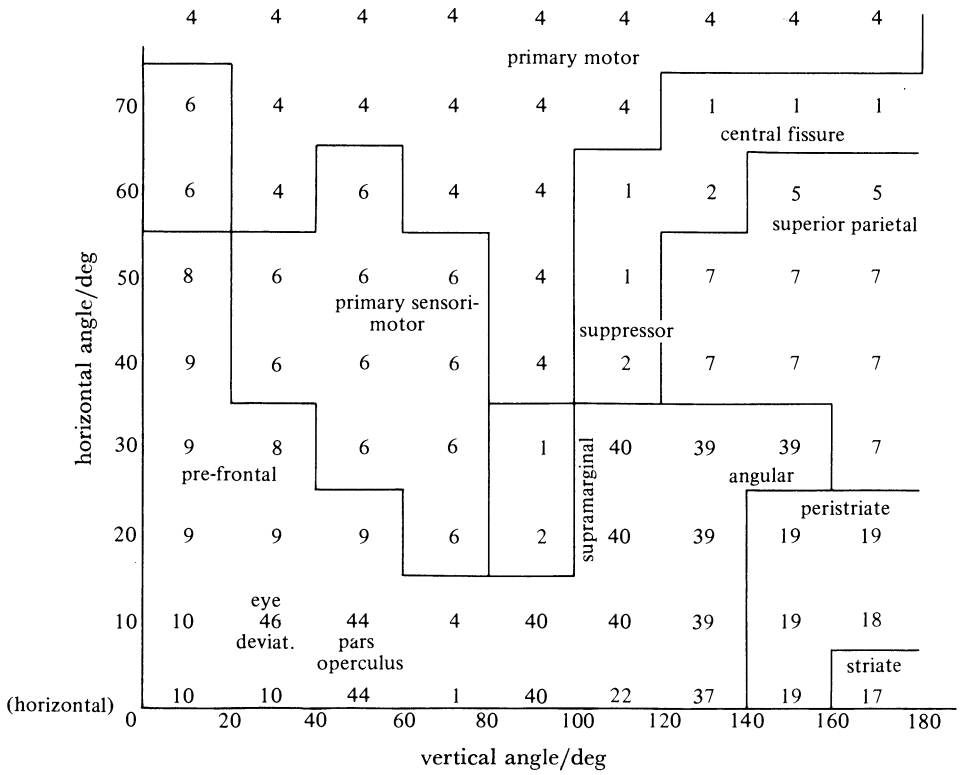

FIGURE 8. The coordinates of Brodmann's areas as based on a human brain. Note the distortion of primary motor and sensory cortex in particular, when the coordinate net is transformed to Cartesian coordinates.

brain (not endocast) cast. More work is needed on actual brain casts to ascertain the locational variation of gyral and sulcal patterns.

Space forbids adequate discussion of the meaning of these results. While the first size correction leaves DIFFS with useful information, it does *not* mean that size has been totally disregarded. In fact, if for certain taxonomic groups the DIFFS with the highest F-ratios are plotted against lg (volume), there are clear trends, with multiple R of about 12 to 20 %. I interpret these findings to mean that certain regions show size differentials above and below the expected allometric-corrected values. These are, however, only *relative* to those particular groups being compared. It is too early to be certain that this interpretation is correct, but it does appear to be the most promising and reasonable explanation to date. Thus, with reference to figure 4, the highest F-ratios are distributed mainly in those areas of Brodmann's that are 'peristriate', i.e. 19, 37, and 8, which is prefrontal, and in areas 5 and 7, which is the superior parietal region. Given the complex composition of groups (i.e. all extant *and* fossil groups as separate samples), no evolutionary interpretation should be made. It should be remembered that the F-ratios are only a measure of between-group-to-within-group variances.

With regard to figure 5, extant species only, the F-ratios are highest in areas 19–37 and 17–19 (striate and peristriate). If the DIFFS for the highest F-ratios are plotted against $\log_{10}$ (volume) the highest multiple R (R^2) is about 0.22, with most values being between 0.05 and 0.10, and non-significant. In this case, the sample sizes are $N = 13$ or greater for each species, and the tentative conclusion that I would draw is that the inferior parietal region shows the most significant variations once 'size' is removed.

Figure 6, which depicts the distribution of F-ratios for the fossil hominids only, suggests that the greatest degree of change has occurred in areas 5, 7 and 4, the first two being the superior parietal region. In this case, however, plotting the DIFFS against lg (volume) gives R^2 values of approximately 0.65, with negative correlations, and all significant. These results suggest, tentatively, that the major changes in endocast surface morphology since the australopithecines have been in the superior parietal region and that, furthermore, the increments have been somewhat *less* than would be expected on a purely allometric basis. This, in obverse terms, would mean that significant changes from apes to hominids have been directed towards enlargement of the superior parietal lobule. Indeed, if F-ratios are plotted for pongids (each group separate) and australopithecines only, areas 5 and 7 show the highest values. If *Pan paniscus* and *P. troglodytes* are combined, *Gorilla* being kept as a separate taxon, the F-ratios show that areas 8, 9, 6 and 19–37 score highest, the latter moiety representing inferior parietal lobule.

Unfortunately, it is beyond the scope of this paper to discuss all combinations of groups adequately, and in particular the patterns of classifications for the 'unknowns' listed in table 1. For those interested, KNM-ER 1470 is most frequently classified as an australopith, as are 1805 and 1813. KNM-ER 3733 and 3883, and OH9 are classified as *Homo erectus*, and the Rhodesian endocast as a Neanderthal. These results are wholly tentative, of course, and are based on small samples. They are found without *a priori* probability weighting of group membership, that is, each 'unknown' has an initial equal probability of being classified in any of the fossil groups. This is a very robust 'test', and the results are admittedly gratifying, but they should be taken with extreme caution until the sample sizes are enlarged and the statistical procedures are refined.

In summary, stereoplotting of the dorsal endocast surface of hominoids is showing consider-

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

able promise in objectively and quantitatively delineating those regions of the cerebral surface that have undergone differential expansion during the course of hominid evolution.

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REFERENCES (Holloway)

Dudik, E. E. 1972 *Synmap; user's reference manual*. Cambridge: Laboratory for Computer Graphics and Spatial Analysis (Harvard University).

Holloway, R. L. 1978 The relevance of endocasts for studying primate brain evolution. In *Sensory systems in primates* (ed. C. R. Noback), pp. 181–200. New York: Academic Press.

Kochetkova, V. I. 1978 *Paleoneurology*. Washington, D.C.: J. H. Winston. New York: John Wiley.

Nie, H. N., Hull, C. H., Jenkins, J. G., Steinbrenner, K. & Bent, D. H. 1975 SPSS. *Statistical package for the social sciences*. New York: McGraw-Hill.

Oyen, O. J. & Walker, A. 1977 Stereometric craniometry. *Am. J. phys. Anthrop.* **46**, 177–182.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

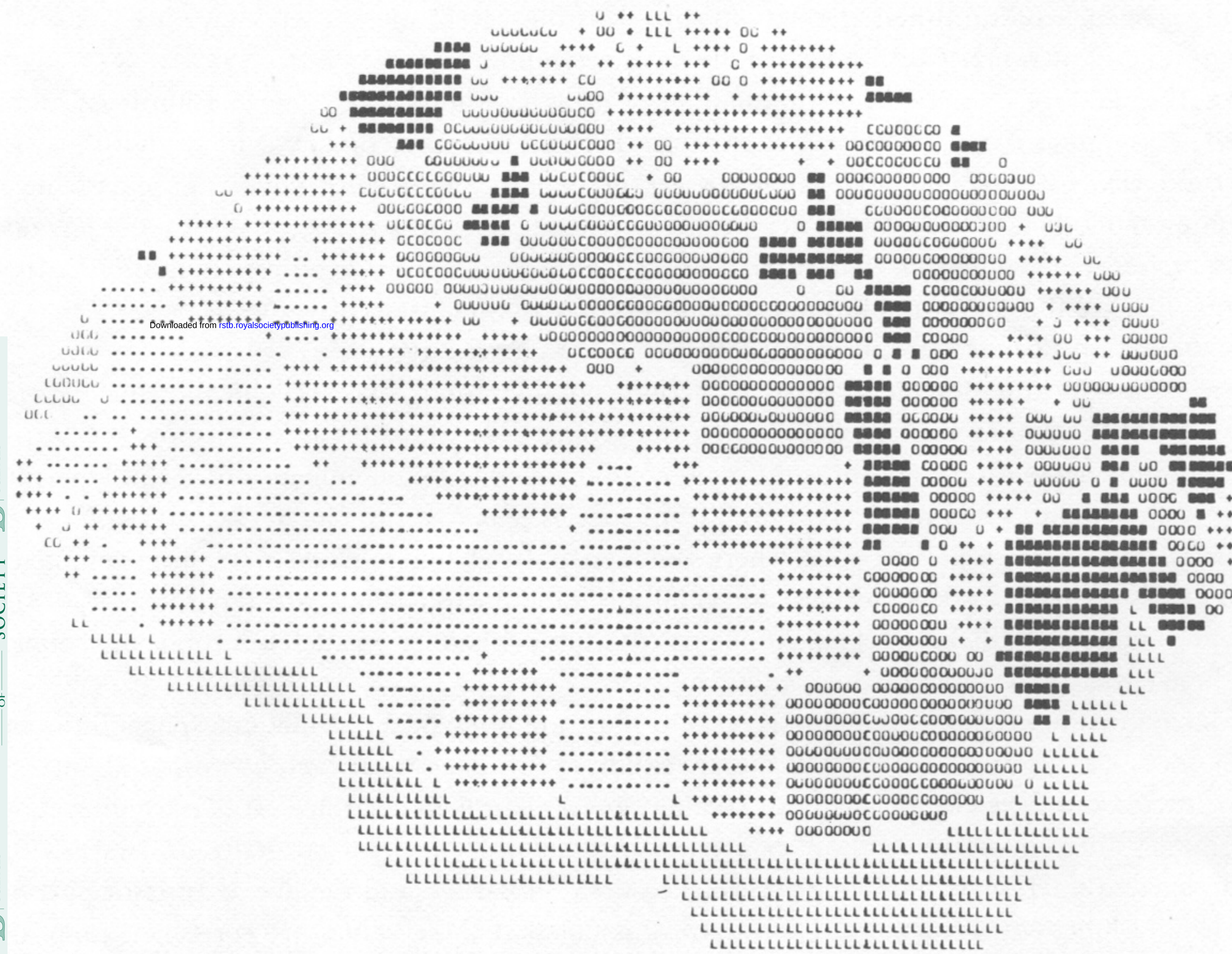

FIGURE 4. A SYNMAP of 171 univariate *F*-ratios plotted within an endocast shape. The darkest areas have the highest *F*-ratio values, ranging from 8.5 to 12.7, and significant at less than the 10^{-5} level. This map is for all groups combined, i.e. fossil and extant species

The SYNMAP symbols have been chosen such that L represents non-significant *F*-ratios, and the five gradations, of darkness represent increasingly significant *F*-ratios, roughly at the 5×10^{-2} to 10^{-2}, 10^{-3}, 10^{-4} and 10^{-5} levels. The outline of the endocast is only approximate, based on the figure 2 'net' shape. In reality, there are no data points *below* the horizontal plane passing through frontal and occipital poles.

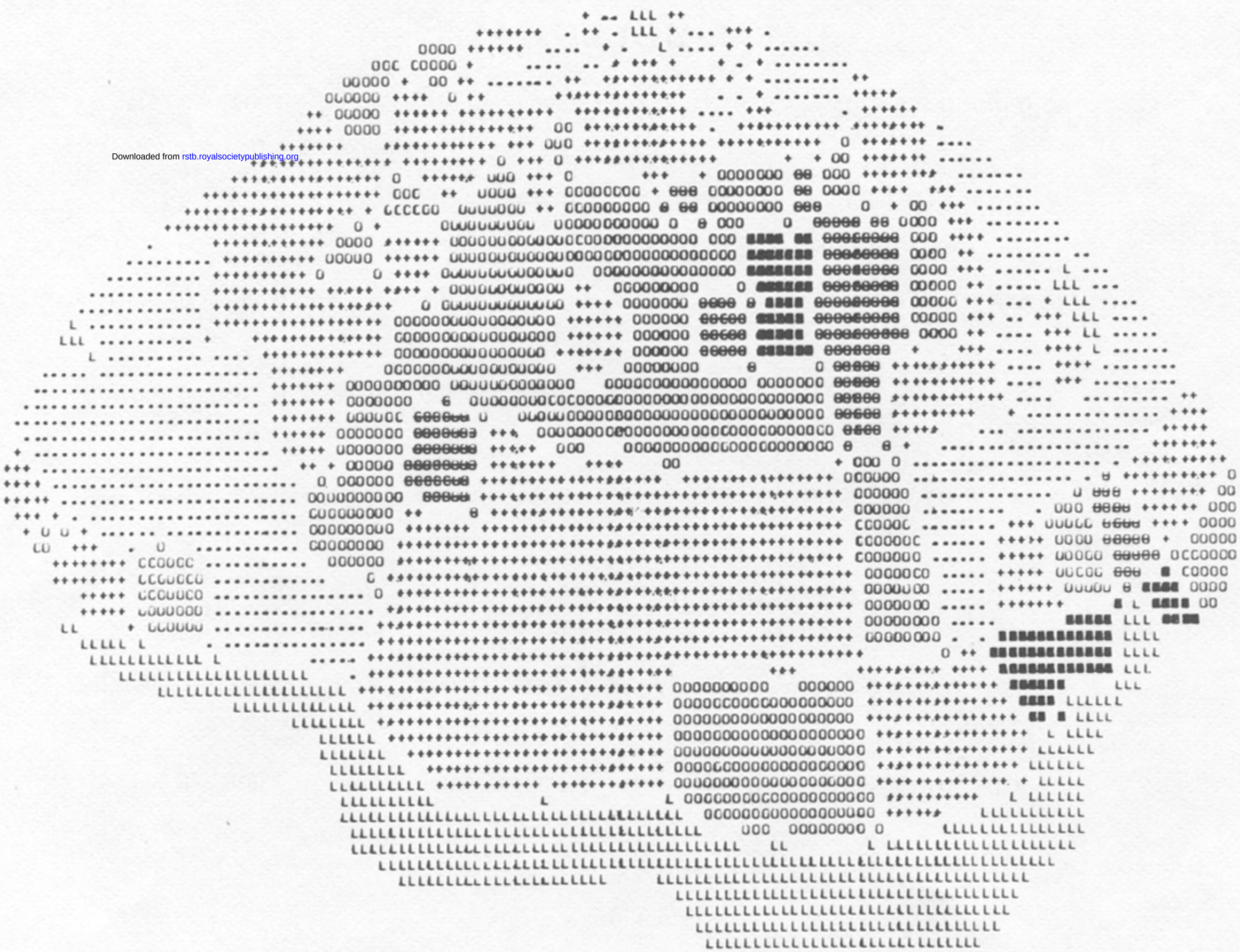

FIGURE 5. As in figure 4, except that these *F*-ratios are for extant species only. The darkest areas have *F*-values ranging from 12.6 to 18.0.

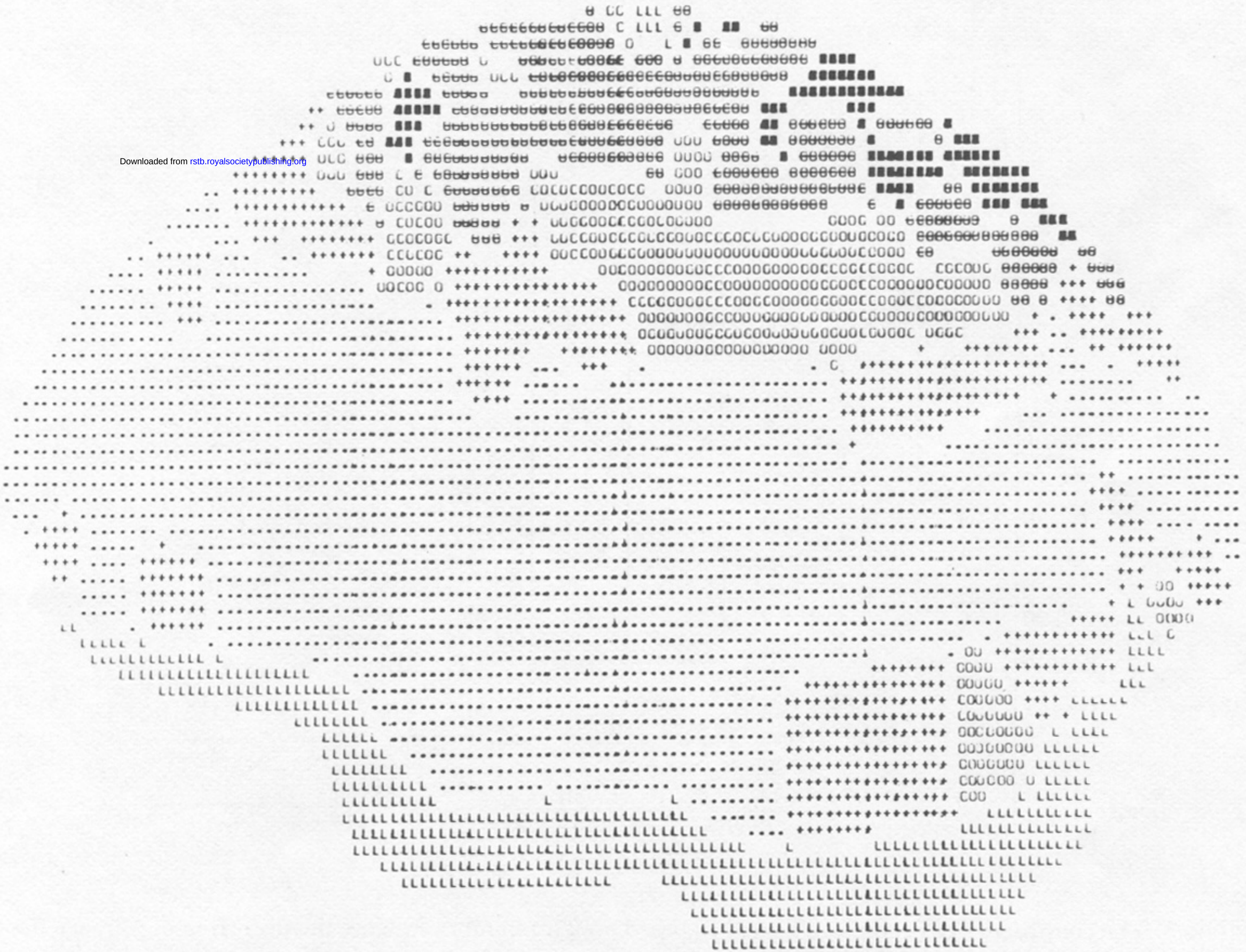

FIGURE 6. As in figures 4 and 5, except that these *F*-ratios are for the fossil hominids only. Darkest area has *F*-values ranging from 15.0 to 21.3.