

Comparing Frontal Cranial Profiles in Archaic and Modern *Homo* by Morphometric Analysis

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Archaic and modern human frontal bones are known to be quite distinct externally, by both conventional visual and metric evaluation. Internally this area of the skull has been considerably less well-studied. Here we present results from a comparison of interior, as well as exterior, frontal bone profiles from CT scans of five mid-Pleistocene and Neanderthal crania and 16 modern humans. Analysis was by a new morphometric method, Procrustes analysis of semi-landmarks, that permits the statistical comparison of curves between landmarks. As expected, we found substantial external differences between archaic and modern samples, differences that are mainly confined to the region around the brow ridge. However, in the inner median-sagittal profile, the shape remained remarkably stable over all 21 specimens. This implies that no significant alteration in this region has taken place over a period of a half-million years or more of evolution, even as considerable external change occurred within the hominid clade spanning several species. This confirms that the forms of the inner and outer aspects of the human frontal bone are determined by entirely independent factors, and further indicates unexpected stability in anterior brain morphology over the period during which modern human cognitive capacities emerged. *Anat Rec (New Anat): 257:217–224, 1999.*

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One of the most significant morphological features of mid-Pleistocene fossil hominids and Neanderthals is their

so-called “frontal flattening”—the recession of the frontal bone when compared to the more vertical modern median-sagittal profile.¹⁷ There is a growing body of literature concerning the different developmental bases of the inner and outer tables of the frontal.^{8,10,14,15,20,23} Generally the assumption is that when the profiles of the outer and inner tables differ it is because the former reflects circumorbital morphology, whereas the latter is influenced by the size and shape of the frontal lobes of the brain. However, characterization and quantification of such differences have generally been lacking, a deficiency that we remedy here.

GEOMETRIC MORPHOMETRICS IN THE MEDIAN-SAGITTAL PLANE

To clarify the relationships between hominid internal and external frontal profiles, we examined CT scans of 16 modern human skulls of both sexes:

five from Central Europe, including the more than 32,000-year-old Mladec I,²² three San and two Bantu from Africa, three Chinese, two Australian aboriginals, and one Papuan. To these we added five mid-Pleistocene fossil *Homo* skulls (Fig. 1). These included three *Homo heidelbergensis* specimens: the Ethiopian Bodo I⁷ around 600-kyr-old, and the Zambian Kabwe (Broken Hill) 1²⁵ and Greek Petralona¹² crania, both of uncertain age but probably in excess of 200-kyr-old. The fossil sample also included the Spanish Atapuerca SH5 cranium,¹ about 300-kyr-old and often considered a proto-Neanderthal; and one “classic” *Homo neanderthalensis* skull, the 50-kyr-old Guattari I.² As an outgroup for some of the analyses we also included an australopithecine (the Sts 5⁶ cranium from Sterkfontein, South Africa, about 2.5 million years old), and two modern chimpanzee skulls (*Pan troglodytes*). These latter belong to different taxa and were not used in all analyses in the interests

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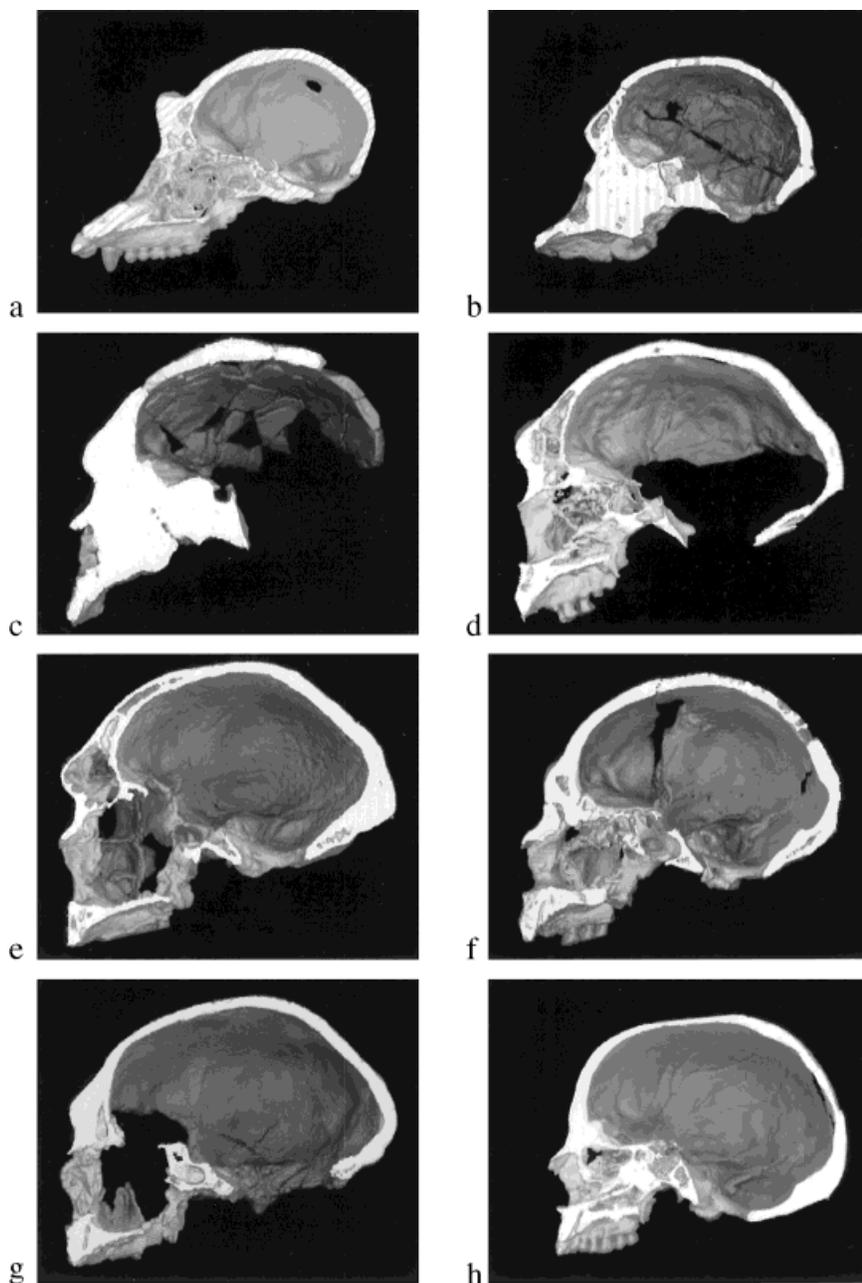


Figure 1. The median-sagittal sections of various crania employed in this study; crania oriented in the Frankfort Horizontal. a: Chimpanzee. b: Sts 5. c: Bodo. d: Kabwe. e: Petralona. f: Atapuerca. g: Guattari. h: *Homo sapiens*.

of clarity of interpretation, but they are shown in Figures 1, 3, 4, and 5.

Using appropriate software,^{5,22} traditional landmarks (Fig. 2, blue dots) were located on each specimen in three dimensions. An estimated mid-sagittal plane (aligned at the anterior cranial base and the anterior vault) was located in each of the scans. Up to seven landmarks were projected onto this plane for each specimen: nasion (the highest point on the nasal bones in the

midline); glabella (the most anterior point of the frontal in the midline); bregma (the external intersection point of the coronal and sagittal sutures); "inner bregma" (the corresponding point on the inside of the braincase); a projection of the optic canals; crista galli; and foramen caecum. Missing landmarks (a total of nine, all from archaic specimens) were estimated by the thin-plate spline relaxation method⁵ using up to nine additional land-

marks from adjacent parts of the specimen.

Ten semi-landmarks were additionally located along the internal curve of the frontal bone in this plane, from foramen caecum to inner bregma, and a further 10 lay along the outer frontal bone from glabella to bregma. These 20 semi-landmarks (Fig. 2, red dots), approximately evenly spaced, were matched to a typical *H. sapiens* specimen along and across the curves in such a way as to minimize the bending energy of the thin plate spline.³ Bending energy is a metaphor borrowed for use in morphometrics from the mechanics of thin metal plates. Imagine a configuration of landmarks that has been printed on an infinite, infinitely thin, flat metal plate, and suppose that the differences in coordinates of these same landmarks in another picture are taken as vertical displacements of this plate perpendicular to itself, one Cartesian coordinate at a time. The bending energy of one of these out-of-plane "shape changes" is the (idealized) energy that would be required to bend the metal plate so that the landmarks were lifted or lowered appropriately.⁴ "Sliding" landmarks are allowed to change their spacing along their curves in order to minimize this energy, and so supply information only in the direction perpendicular to the curve.³ The analyses involved up to 25 points (outer profile: three landmarks and 10 semi-landmarks; inner profile: two landmarks and 10 semi-landmarks). For a typical configuration, see Figure 2. In this way, the semi-landmarks are jointly re-spaced to adjust for the positions of foramen caecum, glabella, and the bregmas along with the shape of the two curves.

We applied the standard Procrustes analysis method,^{4,9} which is a least-squares method for standardizing size, position, and orientation in the course of a multivariate analysis of shape. First we generated a "consensus skull" for the twelve points of the inner profile based on the recent *Homo sapiens* specimens. The two landmarks and 10 semi-landmarks along the inner arc of the archaic skull profiles were then fitted to the same 12 points of the modern ones. These profiles fit so well that they are essentially indistinguish-

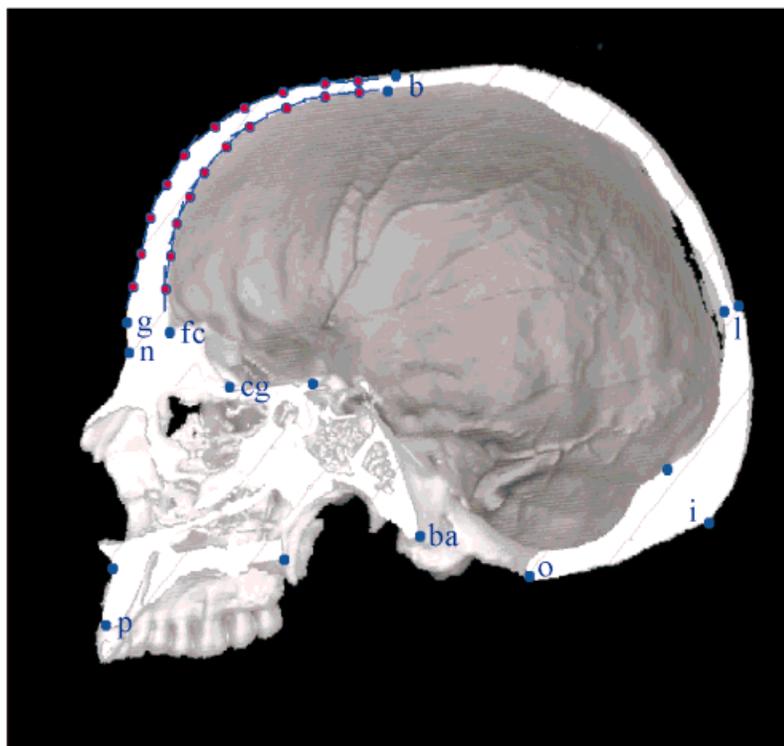


Figure 2. Digitizing scheme for a typical skull (a modern European). Blue dots, landmark points; red dots, semi-landmarks free to slide in the directions indicated by the blue segments. Selected landmarks: g, glabella; n, nasion; fc, foramen caecum; cg, crista galli; ba, basion; o, opisthion; i, inion; l, lambda; p, prosthion.

able in an optimally superimposed scatter. Figure 3 shows these superimposed profiles, along with the superimpositions of the 13-point outer profiles using the same (inner-profile) Procrustes fit, for all 24 forms. This multivariate statistical display is a variant of the Procrustes method that encourages permutation tests of “Procrustes distance” (the square root of the sum of the squared distances between corresponding positions of landmarks when the two skulls have been optimally superimposed this way), rather than conventional forms of multivariate analysis of the separate coordinates. In a permutation test, the significance level of a hypothesized group difference is the frequency with which a random permutation of the group labels over the cases yields a “group difference” at least as large. The permutation approach is unaffected by the excess of shape variables (here, 50 coordinates) over sample size (16 vs. 5).

The comparison of the Procrustes fits of the full complement of points suggests that one region, the interior frontal profile, is unusually conserva-

tive in evolutionary terms (Fig. 3). The Procrustes fit of the inner 12 points is homogeneous across the full sample of 21 skulls: the internal *Homo sapiens* profiles are indistinguishable by this method from those of the archaic forms. On the other hand, the subsample of the five archaic skulls turned out to be strikingly different from the *Homo sapiens* in the outer profile of 13 points from nasion to bregma along the frontal bone (Fig. 4). The Procrustes distance between the mean of 16 and the mean of 5 is never exceeded in 4,000 random permutations of the actual group membership. That is, the significance level is estimated as $P < 1/4000$ up to sampling of the permutations themselves. The fraction of Procrustes variance between recent and archaic sample means explained in the outer profile in this registration is 0.53, vs. a fraction of only 0.10 for the inner frontal profile on which these registrations were based. This latter contrast is not statistically significant ($P > 0.10$) by a similar permutation test. This means that whereas the separation of the two groups of outer fron-

tals is highly unlikely to have arisen by chance, that of the inner frontals could very well have arisen so.

In a Procrustes analysis of the 12 outer boundary points by themselves, recent vs. archaic differences perpendicular to the mean curve (the mean shape in our analysis) average 3.5 times the pooled within-group standard deviation (sd). By contrast, in similar analyses of the inner boundary, the differences average only 0.95 times the pooled within-group sd, and only one of the differences exceeds 1.2 sd. Again, although the outer skull profile (i.e., the externally visible forehead) differed markedly between the samples, internally the frontal midsagittal profiles remained uniform when centered and scaled appropriately. This stability is extraordinary for so extensive a region observed worldwide over a period in excess of half a million years. Indeed, this feature remains stable even when Sts 5 and *Pan* are incorporated into the analysis (Fig. 3). In contrast, external frontal shape is distinctly different in the out-group.

One can carry out principal component analysis of the coordinates in Figure 3 as an ordinary set of 50 variables. (That is, one does not need to worry about the Procrustes standardization or the sliding step that preceded.) This is called the method of relative warps.⁴ Relative warps analyses of the two curves separately yield exactly the same conclusion about the groups that arose from the tests of Procrustes distance and the displays of Procrustes shape coordinates. For the outer table analysis, Figure 5a, the first relative warp score (first principal component) separates the two subsamples perfectly. For the inner table, Figure 5b, there is substantial overlap and no significant difference. Note how Sts 5 clusters with *Pan* in Figure 5b.

In Figure 4, the *H. sapiens* outer profiles lie markedly more posterior than the others when registered on the inner profile; the closer to nasion, the greater the difference. Furthermore, the *H. sapiens* outer profiles have less variation than the archaic. By *F*-test, the differences of variance of frontal thickness, recent versus archaic, are not significant for the upper half of the outline, but are significant at better

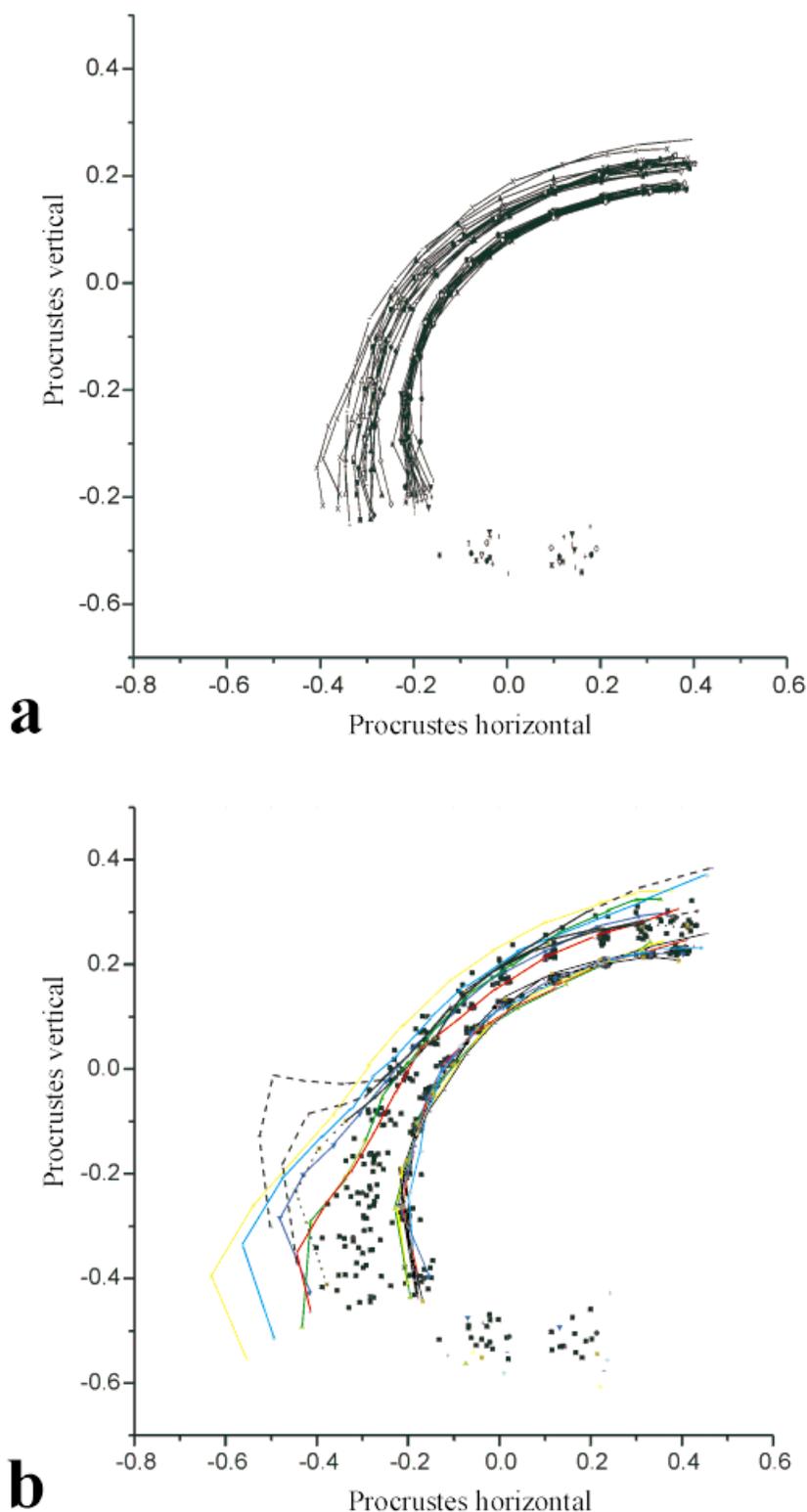


Figure 3. Procrustes fits of all 24 specimens using the 12 points (two landmarks and ten sliding points) of the inner frontal profile. The Procrustes reference is the average (consensus) of the sixteen modern specimens. Outer points, whether archaic or modern, were fitted according to the Procrustes registration dictated by the twelve inner points. The archaic and modern samples are indistinguishable in the structure used for this registration. **a:** Modern forms only. **b:** Archaic hominids, australopithecines and *Pan*. Color, archaic *Homo*; short dashes, Sts 5; long dashes, *Pan troglodytes*.

than $P < 0.05$ for the last four points next to glabella.

That the inner profiles of the frontal bone are statistically indistinguishable implies that mid-sagittal vault morphology may likewise have remained remarkably conservative in the genus *Homo* since the mid-Pleistocene, in spite of considerable change in Centroid Size.⁹ Centroid Size, the square root of the sum of squared distances of the landmarks from the center-of-mass of all the landmarks, is a good surrogate for the intuitive assessment of size of the object under investigation. Our statistical analysis shows that the change in size from pre-Pleistocene to the present does not alter the shape of the inner frontal bone. During the time period covered by our *Homo* specimens, inner frontal size changed by 11%, $P > 0.002$, between these samples, vs. 3% (not significant) for outer frontal size.

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ASPECTS OF THE MORPHOLOGY OF THE ANTERIOR CRANIAL FOSSA

These counterintuitive results agree with an observation made in 1931 by Schultz¹⁶ that a median-sagittal cross section of an endocast of Kabwe yielded a curve similar to that of *Homo sapiens*. Schultz was convinced by this observation that, despite a smaller volume of the forebrain in the latter, the morphologies of *Homo sapiens* and Kabwe, as well as other fossil specimens he investigated, were not substantially different. However, Schultz did claim one anthropologically significant novel acquisition by *Homo sapi-*

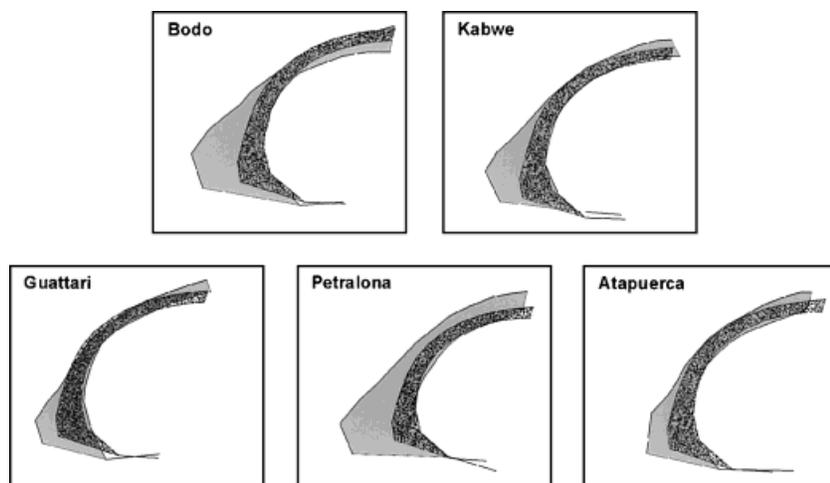


Figure 4. The five archaic crania superimposed on the consensus profiles (inner and outer) of the 16 *Homo sapiens* profiles obtained by full Procrustes fit to the inner ones. The speckled (narrow) band is the consensus bone cross section between inner and outer profile (approximated by 25 points) in the mid-sagittal plane, while the grey band approximates the individual cross section for each archaic cranium.

ens: the enlargement and verticalization of the parietal part of the brain, an observation that still needs careful corroboration.¹⁶

Semendeferi et al.¹⁸ have recently argued that, contrary to the general belief that the human frontal lobes are uniquely large, relative to overall brain size the volumes of chimpanzee frontal lobes fall within the human range. While it is still unclear exactly which elements of the frontal lobe complex differ significantly among hominoids, these authors argue, as did Spatz¹⁹ earlier, that certain morphological structures on the frontal lobe surface, and especially on the basal neocortex and the basal region of the prefrontal and orbital cortex, may be significant in this context.

The most recent step in the evolution of the forebrain is documented by the presence of “digital impressions,” i.e., indentations of the inner skull surface made by evaginations of the basal neocortical surface, which contribute to the neural cell mass without discernibly enlarging the brain case or cranial capacity (Fig. 6). And while our results show that the shape of the inner frontal bone in the median-sagittal plane is effectively invariant among all the investigated specimens of genus *Homo*, there is potentially significant variation in these impressions. As has recently been noted,¹⁷ in the specimen Kabwe Hill there are only slight surface features of the or-

bital plate corresponding to the digital impressions, while they are pronounced in the probably more ancient Bodo specimen, producing an astonishingly modern morphology (Fig. 6a vs. b). The functional and systematic significances of these variations have yet to be resolved. Although these features add only a few cubic centimeters to overall brain volume, they may prove to be the key to the modern development of the prefrontal cortex and its interconnections with the cerebellum—the neural substrate that may have made *Homo* become *sapiens*.

PHYLOGENETIC AND FUNCTIONAL INFLUENCES ON ANTERIOR CRANIAL SHAPE

We observed not only discordance between anterior endocranial and exocranial shape among hominids, but also temporal stability in the former and variation in the latter. What factors influence these differences? According to widely accepted theories of neuro-orbital disjunction²³ and of the functional matrices¹⁴ involved, the inner frontal table mirrors the shape of the frontal lobes of the brain, while the form of the outer table reflects brow-ridge structure. Topographically, this relationship is suggested metrically by the linear measurements presented in Table 1, which quantify the relationships between the surfaces. The neuro-

orbital disjunction can be evaluated, for example, by referring to the nasion-foramen caecum distance, which reflects browridge size. In Bodo, Kabwe and Petralona this distance is increased; the very large brow ridges house remarkably large frontal sinuses that penetrate far into the frontal bone. This is particularly notable in Petralona, where these holes also extend so far laterally as to form a “post-orbital” sinus.¹⁷ On the other hand, both the Atapuerca specimen, often considered a proto-Neanderthal, and the Neanderthal fossil from Guattari exhibit a reduced nasion-foramen caecum distance. This reduction appears less derived (in the cladistic sense) than what is seen in the *Homo heidelbergensis* specimens. In terms of internal profile, in contrast, the distances given in Table 1 differ only slightly

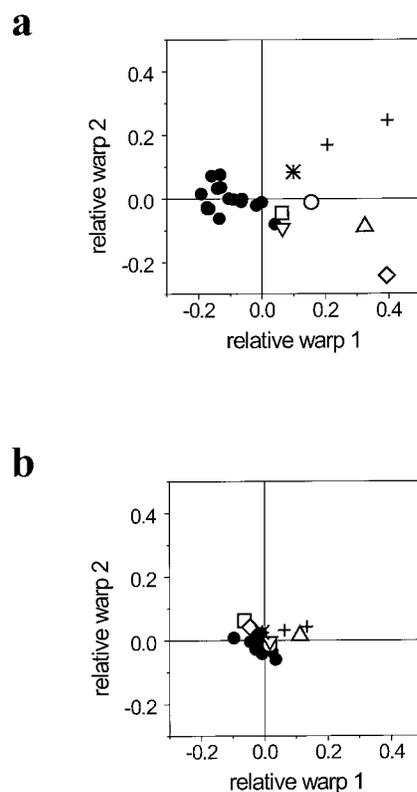


Figure 5. Relative warp scores (principal component scores for Procrustes-registered shape co-ordinates) of the mid-sagittal frontal profiles. Solid symbols: *Homo sapiens*; open symbols: fossil *Homo* (Bodo, Kabwe, Atapuerca, Petralona, Guattari), * Mrs. Ples, + *Pan troglodytes*. Axes are in units of Procrustes length throughout. **a:** The samples are widely separated on the first relative warp of outer profile shape. **b:** The relative warp scores for inner profile shape show overlap between the samples.

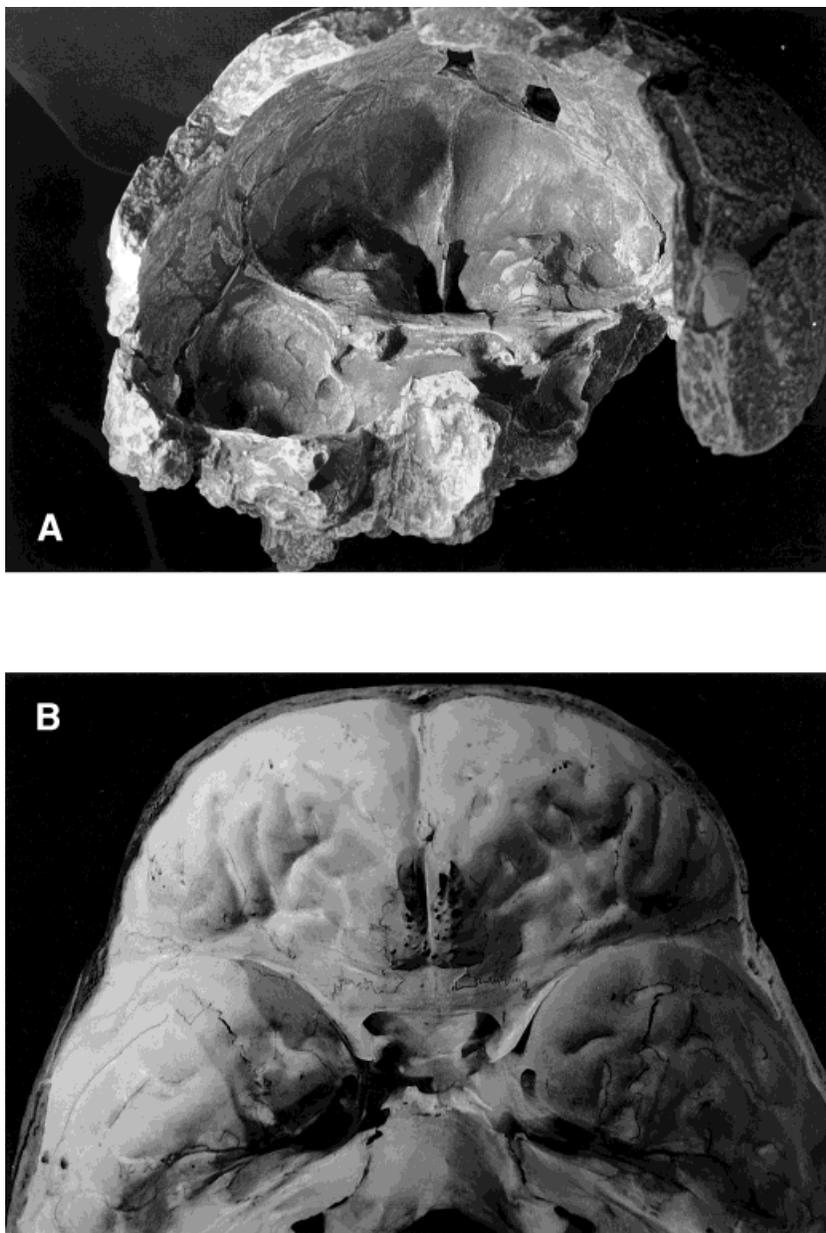


Figure 6. “Digital impressions” of the anterior lobes. a: Bodo (cast). b: *Homo sapiens* (skull with calotte removed).

between the fossil and modern specimens. There is one exception: the small distance from optic canal to endobregma in Petralona falls not only outside the modern range, but outside that of the other fossils too. Why Petralona should be an outlier in this regard is unclear.

Earlier workers have suggested that the external form of the browridges is related to the need to resolve the stresses in the face that are induced by mastication. We agree, and thus disagree with critics such as Ravosa¹⁵ and Hylander,¹¹ in part owing to the inner morphology of the frontal si-

nuses evident in the CT scans (Fig. 7). Notice that the anterior and posterior walls of the sinuses are quite thin—a few millimeters at most—as are the thin bony lamellae that separate the air chambers.¹⁷ The thinning minimizes bone mass without compromising the necessary strength, suggesting that the externally enormous supraorbital structures do relate to masticatory stresses.

While the numerous small walls may help to absorb the masticatory stresses, there may be more to this variation of the external form of the frontal than simple structural resolution of chew-

ing forces through mass minimization. In contrast, the low variation in internal frontal profile across this heterogeneous sample of hominids suggests that the morphology of this area is indeed closely related to development of the anterior brain structures.

SUMMARY

The discordance between the internal and external features of hominid frontal profiles raises the obvious question of whether there has been co-evolution or syn-evolution between the two structural complexes. This question, along with determination of precisely which features of the frontal bone are primitive and which derived, will be the focus of future research by our group. At present we can say that there is a disjunction both topographical and evolutionary between the inner and outer curvatures of the mid-sagittal profile. While the curvature of the inner frontal vault remains remarkably conservative, external morphology in this area is much more diverse. We were able to clarify this disjunction because our quantitative method allowed an appropriately local superposition of mid-sagittal profiles. This

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is in contrast to more inflexible traditional orientations, such as the Frankfurt Horizontal, a superimposition on a porion-orbitale plane. Indeed, studies using this plane as a basis of orientation have totally obscured the main finding presented here.^{13,24}

A major advantage of the Procrustes approach is its independence of predefined orientations. It is therefore

TABLE 1. Linear distances of the anterior cranial fossa (in millimeters)*

	N-FC	CO-Endobregma	Wing Breadth	FC-CO	Lat. Chord
Bodo	27	78	106	46	79
Kabwe	30	82	99	33	83
Petralona	35	68	101		83
Atapuerca	23	72	100	45	78
Guattari	24	82	111	37	85
<i>H. sapiens</i> (n = 16)	8-21	78-89	97-121	34-43	71-91

*CO, Tangent over the anterior edges of the two optic canals at the cross point with the median sagittal plane. This is the most posterior point on the orbital plate, close to the limbus. N, Nasion; FC, foramen caecum. Wing breadth, Distance between the lesser wings of the anterior cranial fossa from the left and right lateral merge points with the parietal bone. Lat. chord, Distance from the right and the left points where the lesser wings reach the parietal to the bregma (actually, the calculated means between the right and left distances). Endobregma often has to be approximated.

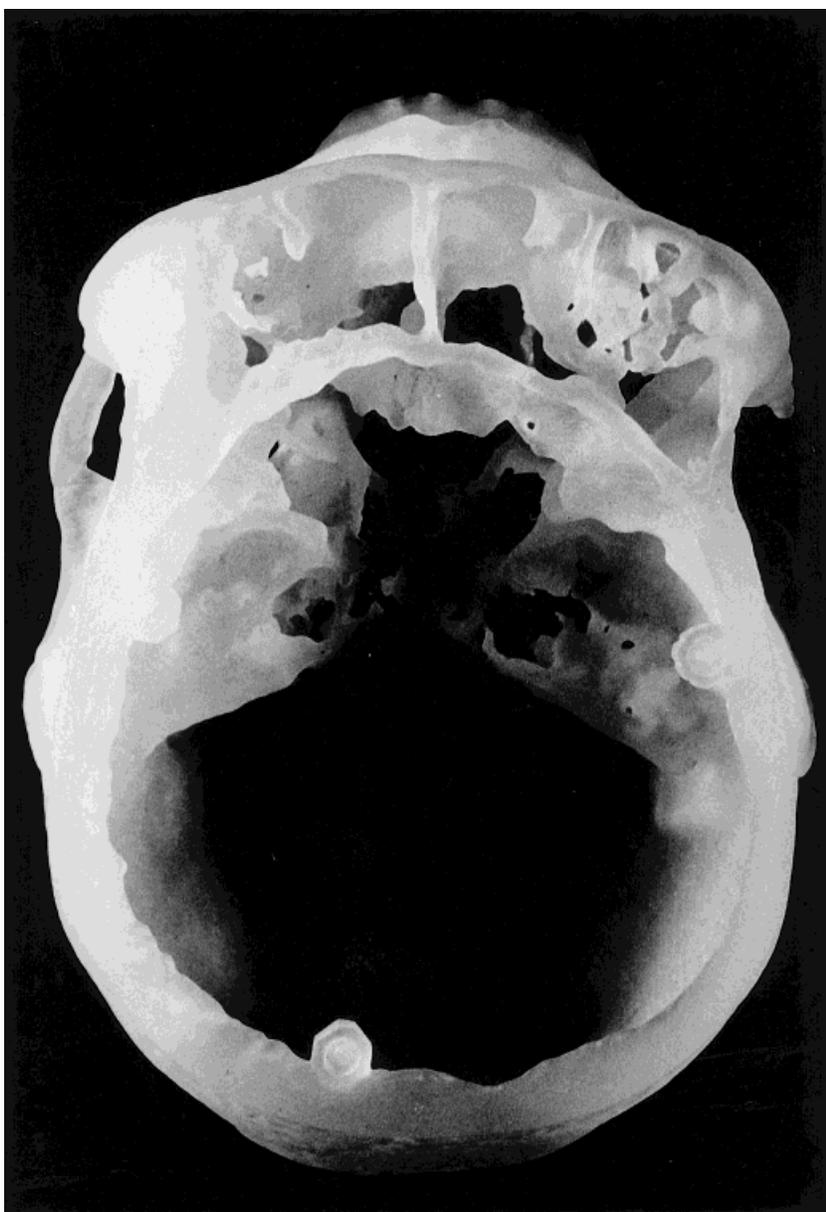


Figure 7. The remarkable pneumatization of the frontal sinus in the Petralona cranium, as revealed in a superior view of a stereolithograph¹⁷ with the calotte removed.

also suited for the morphometric analysis of fragmentary fossils, such as Bodo, in which large parts of the neurocranium are missing. We believe that the work reported here is only a preliminary example of the many ways in which refinements in methods of morphometric analysis will lead to new perspectives on phylogenetic and functional relationships among hominids of the middle and late Pleistocene.

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