Frontal sinuses and human evolution
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To cite this version:
Antoine Balzeau, Lou Albessard-Ball, Anna Maria Kubicka, Andréa Filippo, Amélie Beaudet, et al.. Frontal sinuses and human evolution. Science Advances, 2022, 8 (42), 10.1126/sciadv.abp9767. hal-03891924

HAL Id: hal-03891924
https://hal.science/hal-03891924v1
Submitted on 23 Mar 2023

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INTRODUCTION

Sinus presence and morphology have been used in systematics in phylogenetically disparate taxa (1, 2), and there is some evidence that pneumatic variation may be diagnostic in Middle and Late Pleistocene hominins (3–6). Relationships between hominins remain far from clear and potentially phylogenetically informative characters such as frontal sinus morphology that may be useful in elucidating them. Among extant primates, ethmoidally derived frontal sinuses are present only in Gorilla, Pan, and Homo (7, 8), and we have recently characterized morphology in these genera (9). Knowledge of the variation in size and shape of frontal pneumatization during human evolution, however, is limited. In original specimens, pneumatization is usually only directly observable when they are fragmented. In this context, most of the evidence resides in brief descriptions that appear occasionally as part of detailed presentations of fossil individuals. The few comparative studies of hominin frontal sinuses to date have been based on restricted samples and focused either on comparing Homo neanderthalensis to Homo sapiens or on the distinctive sinuses of Middle Pleistocene Homo (3, 6, 10, 11). Moreover, frontal sinus shapes show great complexity and extreme levels of variation within and between taxa. Imaging and quantification of such variation are difficult, and most studies have therefore focused on quantitative analysis of size. Here, we apply a simple, repeatable method for quantifying and comparing sinus shape and position and additionally quantify and compare frontal sinus size in a large sample of extinct hominins and extant nonhuman African apes.

In addition to uncertainty regarding the taxonomic patterning of frontal sinus variation, debate continues over their potential function. Many varied explanations have been proposed for sinus function (12–14), from aquatic adaptation (15) to acoustic adaptations (16). Two hypotheses of enduring popularity are that sinuses are a thermoregulatory adaptation [e.g., (17)] or that they serve to disperse masticatory strain [e.g., (18)]. An alternative is that sinuses have no function at all and are evolutionary spandrels in the sense described by Gould and Lewontin (19). The different hominin sinus types (frontal, maxillary, sphenoidal, and ethmoidal) are not functionally or developmentally homologous (6, 20); thus, we focus here solely on the frontal sinuses. Although we do not explicitly test functional hypotheses, our results from comparisons of frontal sinus morphology among hominin and nonhuman primate taxa are informative in the context of this debate.

The present study aims to (i) quantify variation in frontal sinus shape and size for each available hominin species, using linear and volumetric measurements, and to compare these results to large samples of extant hominines; and (ii) to describe and quantify patterns of bilateral variation in the frontal sinuses to investigate the possible relationship between sinus form and the position of the underlying frontal lobes of the brain (as reflected by the endocast) following patterns suggested by our previous investigation of extant taxa (9).

Our results bring original and previously unknown insights to understanding the origin of hominin frontal pneumatization by highlighting the phylogenetic importance of this character and its relationship with other aspects of the cranium. Our study also contributes strongly to the characterization of hominin cranial anatomy in different taxa.

RESULTS

Sinus size and shape variation

Descriptive information illustrating variation in frontal sinus morphology between and within a total of 21 hominin species (69 fossil hominin specimens) is given in the Supplementary Materials
Paranthropus (Bou-VP-12/130), Australopithecus prometheus (StW 71, StW 505), Australopithecus africanus, Sahelanthropus tchadensis (TM 266-01-060-1), Australopithecus africanus (Sts 5 and 71, StW 505), Australopithecus garhi (Bou-VP-12/130), Australopithecus sediba (U.W. 88), Paranthropus robustus (DHN 155), and Paranthropus boisei (OH 5). Two Homo individuals also plot within this variation: the Homo naledi individual Lesedi 1 and D4500 from Dmanisi. Early Homo fossils would probably also plot in this distribution if we could measure both their endocranial size and the volume of their frontal sinuses. Other hominin species, with larger brains, do not follow this pattern and plot outside of this distribution. H. sapiens (that includes large samples of recent individuals and several fossil individuals with all the characteristic features of our species) has a particular position in relation with restricted pneumatization compared to other species, in terms of both the absolute extension and the proportion of unpneumatized individuals.

A principal components analysis (PCA) of all the linear measurements computed on the data before adjustment for size illustrates the strong influence of sinus size on distinguishing extant and fossil groups. Separation on the first axis is mainly due not only to size (Fig. 4) but also to shape, particularly in the antero-posterior and lateral dimensions, which separate out Gorilla from the other taxa, and in the supero-inferior dimensions, which separate out recent H. sapiens. Pan and fossil hominins have an intermediate position on the first axis. Broken Hill 1, Petralona, and Bodo have large values on the first axis and are isolated on this axis. A PCA computed on relative (size-adjusted) data distinguishes well on the second axis between recent/fossil H. sapiens and Pan/Gorilla, while, again, fossil hominin species have intermediate positions (Fig. 5).

In the analyses of both absolute and relative measurements, the early hominin individuals, which include Sahelanthropus, Australopithecus, and Paranthropus, plot together and fall between Pan and Gorilla.
on the one hand and the later hominins on the other. H. naledi plots in the center of the distribution of Homo erectus for both the absolute and relative size analyses. H. erectus s.l. shares with H. sapiens a higher degree of variation in sinus extension. The H. neanderthalensis and most European Middle Pleistocene hominin distributions overlap partly in both analyses. A group composed of Broken Hill 1, Bodo, and Petralona plots outside of the distribution of all other hominin samples due to their much larger sinuses (Fig. 4). In terms of relative dimensions, these three fossils plot at the intersection of early hominins and H. erectus because of their relatively large antero-posterior sinus dimensions compared to other hominin species (Fig. 5). The individual attributed to Homo antecessor plots well within the distribution of other Middle Pleistocene hominins for both absolute and relative analyses. TD6-15 has absolutely smaller sinuses, possibly relating to its individual age, than the H. neanderthalensis individuals (table S3, Fig. 4, and fig. S34) but falls within the H. neanderthalensis range of variation for the relative data (Fig. 5). Fossil and recent H. sapiens have relatively small sinuses of distinctively great height (supero-inferior dimensions). These morphometric results complement the visible variation in sinus shape (Supplementary Text and table S4).

Morphometric trends between H. sapiens populations

When a linear discriminant analysis of the different geographic samples of recent H. sapiens was computed on the dataset of absolute measurements, the resulting confusion matrix showed a proportion of correctly classified individuals of 33.9%. This low level of correct classification illustrates the large variation observed within samples and a lack of geographic partitioning in sinus size/shape. A multi-variate analysis of variance, however, shows some significant differences between pairs of samples that were investigated through additional analyses. The resulting squared Mahalanobis distances (table S5) highlight some closer affinities and differences between groups, but there is no clear geographic patterning. Last, we tested for a potential correlation between sinus dimensions and geography. To do so, a PCA was calculated on sinus dimensions of the different samples of extant H. sapiens. PC1 accounts for 91.95% of the variation in this extant human sample. Spatial autocorrelation was not observed in the dataset (Mantel test, \( P = 0.1662 \)), which means that the frontal sinus measurements in one population are not more similar to those of geographic neighbors than they are to groups at a greater distance. We also calculated a generalized linear model (table S6) to see whether individuals from various regions differed in the measurements of...
their frontal sinuses. These results illustrate that, although the Mantel tests showed that the dimensions of the frontal sinuses are not spatially autocorrelated, they differed significantly between geographic regions (see P values in table S6).

**Bilateral variation in sinus and brain anatomy**

Within the recent *H. sapiens* sample, among 345 individuals, 41 do not have sinuses (aplasia), 24 have no sinus on the right side, and 9 have no sinus on the left side. There is a tendency toward greater sinus extension toward the left, resulting in significant directional asymmetry (DA). The mean values right minus left (R-L) for anterior length (AL) and superior length (SL) are $-2.23$ and $-2.25$ mm ($t = -4.3113$, $P = 2.2 \times 10^{-6}$, $t = -3.806$, $P = 0.0002$, respectively). This shows that frontal sinuses in *H. sapiens* tend to be larger on the left side, as mean values (R-L) for AL and SL are negative and significantly different from zero. Asymmetrical sinus development in recent *H. sapiens* has been shown to be associated with right petalia (frontal lobe expansion in the brain) (9). On the left side, it appears that sinus development takes advantage of the greater space available, resulting in greater pneumatization. In *Pan* and *Gorilla*, no DA was detected for all the dimensions of the frontal sinuses (9), while petalias in these taxa do show some degree of asymmetry (21).

To identify potential relationships between sinus and cranial or brain morphology in fossil hominin taxa, we investigated several features at the individual level among our sample, including bilateral variation in sinus dimensions (relative to their preservation), the shape of the supraorbital torus (as directly observed for each individual), and the position of the underlying frontal lobes of the brain as reflected by the endocranial cast (including the petalia, i.e., the relative extension of respectively the right and left frontal poles). It was necessary to consider specimens individually due to poor preservation in many individuals precluding sample-wide analysis. In Sts 5 and StW 505 (*A. africanus*), there appears to be a left frontal petalia of the brain associated with a smaller sinus on the left side. In U.W. 88 (*A. sediba*), a right frontal petalia is associated with a larger left sinus. We observe a tendency among our sample of Asian *H. erectus* for the left sinus to be larger than the right sinus, and most of these fossils show a right frontal petalia. The exception is Sangiran 17, which has a left frontal petalia. In Middle Pleistocene hominins, the left sinus tends to be larger than the right sinus, and a right frontal petalia is observed in all individuals that allow evaluation of this trait. In *H. neanderthalensis*, there is no clear asymmetric tendency in the sinuses at the scale of the sample, which might result from the incomplete preservation in many individuals. Nevertheless, a right frontal petalia is the most common pattern and appears to be paired with qualitatively greater extension of the left sinuses (R petalia and L > R sinus) in La Ferrassie 1, Gibraltar 1, Krapina 3, and Spy 1.

**DISCUSSION**

**Frontal bone pneumatization and phylogenetic implications**

With regard to the relationship between sinus size and endocranial size, early hominins, including *Sahelanthropus* and various species of *Australopithecus* and *Paranthropus*, plot comfortably within the range of variation observed for *Pan* and *Gorilla* and at some distance from the distribution of *Homo* individuals (Fig. 3). This pattern is maintained in multivariate analyses of sinus dimensions (Figs. 4 and 5). The underlying frontal lobes do not appear to influence sinus shape and expansion in *Pan*, *Gorilla*, and early hominins,
while the large frontal superstructures in these taxa give the sinuses the opportunity to develop isometrically relative to brain size, in contrast to the condition observed among Homo species. This morphology, shared not only between Pan and Gorilla (9) but also with Sahelanthropus, Australopithecus, and Paranthropus, could be seen as a primitive trait in contrast with the different conditions observed in Homo individuals. Nevertheless, with the potential exception of Stw 53, which has been tentatively attributed to Homo gautengensis (22) but more conventionally to Homo erectus s.l.; light orange: G. gorilla; small pink dots: extant H. sapiens; purple: Sahelanthropus, Australopithecus, and Paranthropus; gray: H. naledi; green: H. erectus s.l.; light blue: H. heidelbergensis; light green: H. rhodesiensis; dark blue: H. neanderthalensis; pink: fossil H. sapiens); the pink lines show the variation and the mean for recent H. sapiens. The black line shows the regression of both variables in Pan and Gorilla (slope = 1.36, r = 0.72, P = 10 × 10⁻²³). Labels for fossil hominins are as follows: TM 266-01-060-01 (Toumai), To; Sts 5, S5; Stw 505, S505; Sts 71, S71; Stw 573, S573; UW 88-50, U88; BOU-VP-12/130, BOU; SK 48, S48; DNH 155, D155; OH 5, O5; Stw 53, S53; KNM-ER 3883, ER; OH 9, O9; D2280, D1; D2282, D2; D3444, D3; D4500, D4; Trinil 2, T; Sambungmacan 4, S4; Sangiran 17, S17; Skull IX, SIX; Ngandong 1, N1; Ngandong 7, N7; Ngandong 12, N12; Ngawi 1, Nw1; Lesedi 1, Les; La Ferrassie 1, LF; La Quina H5, LQ; Guattari, Gu; Forbes’ Quarry 1, Gi; Krapina 3, K3; Krapina 6, K6; La Chapelle aux Saints, LCP; Spy 1, St; Spy 10, SX; Feldhofer, F; Amud, Am; Tabun C1, Tc1; light orange: H. erectus s.l.; dark orange: H. neanderthalensis; light orange: H. erectus s.l.; light green: H. rhodesiensis; pink: fossil H. sapiens; while the large frontal superstructures in these taxa give the sinuses the opportunity to develop isometrically relative to brain size, in contrast to the condition observed among Homo species. This morphology, shared not only between Pan and Gorilla (9) but also with Sahelanthropus, Australopithecus, and Paranthropus, could be seen as a primitive trait in contrast with the different conditions observed in Homo individuals. Nevertheless, with the potential exception of Stw 53, which has been tentatively attributed to Homo gautengensis (22) but more conventionally to Australopithecus sp. (23) or Homo cf. habilis (24, 25) and shows the primitive frontal sinus size and shape, we feel that this finding cannot be used to clarify the taxonomic attribution of disputed early hominin fossils. With regard to Stw 53, its primitive sinus morphology may support its exclusion from the genus Homo.

In contrast to the relative homogeneity of sinus morphology in nonhuman apes and early hominins, we observe differences in frontal sinus size and shape between H. erectus s.l., H. neanderthalensis, Middle Pleistocene hominins, and fossil H. sapiens. Our results suggest that frontal pneumatization develops in Homo species in relation to new and variable constraints related to factors such as the integration between the vault and the upper face, brain, and frontal sinuses. These groups of Homo share a reduced antero-posterior extension of the sinuses compared to early hominins and show variation in the extension of the sinuses in the lateral and vertical directions, depending on taxon (table S4). These differences may be an indirect consequence of the differences in cranial morphology between taxa, as already suggested [e.g., (6, 10)], and of different evolutionary trajectories. However, that does not prevent their potential utility in taxonomic analyses.

Despite its relatively small brain size, H. naledi does not follow the pattern of frontal pneumatization seen in other small-brained hominins but is in the center of the range of variation observed for H. erectus s.l. both for multivariate analyses of absolute and relative
Data. This is a previously unknown and important observation for this species and supports its inclusion in the genus *Homo* notwithstanding many primitive aspects of its morphology (26).

Both *H. erectus* s.l. and *H. sapiens* show relatively great variation in the size and shape of the frontal sinuses (table S4), including a sizeable proportion of aplasia. The Zhoukoudian, Ngandong, and Sambungmacan individuals tend to have small sinuses, and several exhibit aplasia (tables S2 and S3). Sinuses are larger in the more ancient Indonesian and African *H. erectus* individuals. The five Dmanisi individuals constitute an interesting illustration of the level of sinus morphology variation that can be observed in *H. erectus* s.l. They show a very high degree of intraindividual sinus morphology variation, although they come from a unique stratigraphic layer from the same site. This is congruent with the elevated craniofacial variability observed in this sample (27). High levels of variation in craniodental anatomy in *H. erectus* as a species have been noted [e.g. (28, 29)] and have caused some to argue that the taxon should be divided (30, 31). However, many see this level of variation as commensurate with what should be expected in a long-lived, geographically widespread primate species (28, 32).

High levels of variation in sinus size and shape are visible among Middle Pleistocene hominins, particularly because of the huge pneumatization of Bodo, Broken Hill 1, and Petralona. These individuals are unique in terms of the size and shape of their sinuses, which might support their grouping in a separate taxon that could be called *Homo rhodesiensis* due to the presence of the holotype of the species in the group (i.e., Broken Hill 1). Regarding the debated taxonomic position of Zuttiyeh ([33] versus [34]), the individuals’ frontal pneumatization shares more affinities with *H. neanderthalensis* than with *H. erectus* s.l. The other European Middle Pleistocene specimens (to the exclusion of Broken Hill 1, Bodo, and Petralona, if grouped into *H. rhodesiensis*) exhibit a coherent morphological pattern of frontal pneumatization, which differs from the other groups. For this reason, these fossils are grouped here into *Homo heidelbergensis* for ease of discussion (but note that not all authors of this paper agree on the use of *H. heidelbergensis* for all specimens within this group).

In terms of absolute data, these individuals form a group close to *H. neanderthalensis* except for Sima de los Huesos 13 and 17, in which the sinuses are smaller, and Steinheim, which plots with *H. erectus*. The morphology of the frontal pneumatization of Steinheim may nevertheless reflect taphonomic alteration. When relative dimensions are considered, the *H. heidelbergensis* fossils are slightly further outside the range of *H. neanderthalensis*.

A greater degree of variation is observed in earlier European fossils, but they also share clear affinities in sinus shape with the most recent *H. neanderthalensis*, which exhibit reduced variation in sinus shape and size compared to other fossil populations. The specimens from Sima de los Huesos slightly expand the observed variation in the *H. neanderthalensis* sample if included therein. *H. neanderthalensis* do not have absolutely or relatively larger sinuses compared to other hominins (6, 10, 35). These observations on frontal sinuses are consistent with a potential phylogenetic relationship between at least some fossils named here *H. heidelbergensis* and *H. neanderthalensis*, as suggested by craniofacial morphological evidence from the Sima de los Huesos, Steinheim, and Ehringsdorf individuals [e.g., (5, 30, 36, 37)] and by genetic data from the Sima de los Huesos hominins (38). Other members of the group described here as *H. heidelbergensis* may show different taxonomic affinities. Analyses of temporal bone pneumatization have also shown very low levels of morphological variation in *H. neanderthalensis* (39). This is interesting in the context of ancient DNA studies, which have demonstrated low levels of genetic diversity and a high frequency of inbreeding within later representatives of *H. neanderthalensis* (38, 40).

Causes and modalities of expression of the frontal sinuses

Our results illustrate various patterns of sinus variation in *Gorilla*, *Pan*, and hominin species. We see different sinus morphologies between taxa likely undergoing relatively similar masticatory strain regimes, such as *H. erectus* s.l. and Middle Pleistocene hominins (41, 42). On the basis of these observations and previous evidence (41, 42), it is very unlikely that sinus size and shape are driven by masticatory strains in hominins.

Our results, along with multiple strands of evidence in the literature (6, 10, 35), demonstrate that *H. neanderthalensis* individuals
are not hyperpneumatized compared to *H. sapiens, H. erectus*, or other hominin samples in terms of absolute or relative frontal pneumatization. In addition, there is no clear support for a functional or a climatic origin of *H. neanderthalensis* pneumatization when all of the evidence (43), including observed variation among hominins, is considered. On the basis of this multiple evidence, we, therefore, propose that the long-standing hypothesis that the frontal sinuses of *H. neanderthalensis* are an adaptation to cold climate [e.g., (17, 44, 45)], should be definitively rejected.

Moreover, our results obtained from large, diverse samples of *H. sapiens* (Supplementary Text and tables S5 and S6) show that the dimensions of the sinuses are not spatially autocorrelated, despite significant differences between geographic regions. In other words, no direct link is observed between geographic origin and the size and shape of frontal sinuses, i.e., individuals from colder climates are not characterized by significantly larger/smaller frontal sinuses than populations from warmer areas. The observed differences within the analyzed sample appear to be related to other factors besides climate. We propose then that climate does not seem to directly explain the development of frontal sinuses in our species. It is nevertheless likely that sinus shape and variation in living populations around the world may reflect some aspects of the recent history of our species including migrations, genetic drift, and local adaptations. Whether these factors exert selective pressures on the sinuses themselves or indirectly via their effects on craniofacial morphology remains to be determined.

**Does frontal lobe shape influence sinus shape?**

A more anterior, lateral extension of the right frontal lobe of the brain, as reflected by the endocranial cast, compared to the contralateral side is a general pattern in hominins that becomes consistent brain, as reflected by the endocranial cast, compared to the contra-

A new perspective on frontal sinuses and human evolution

This research opens original perspectives for the study of frontal sinuses. A limiting factor in this analysis of complex internal anatomical traits during human evolution is the available information for the hominin fossil record. Moreover, the comparison of the different features of bilateral frontal sinus morphology among fossil hominins is complicated. Several fossils do not have fully preserved bilateral pneumatization, and taphonomic alteration may alter the shape and size of the sinuses on each side, complicating the analyses of subtle bilateral differences. The small sample size for fossil hominins also prevents large-scale analyses of directional and fluctuating asymmetry. This is why we have considered here several features at the individual level among our fossil hominin sample, including the bilateral variation of the dimensions of the sinuses in relation to their preservation, the shape of the torus, and the position of the underlying frontal lobes to identify potential relationships between anatomical features and repeated patterns among hominin samples. More generally, fossil preservation and relatively low resolution for imaging datasets are problematic for paleoanthropological research. Data access is another issue. Fortunately, we had here access to a unique database to study the variation and evolution of the hominin anatomy, yet there are still taxa that we were unable to access. The sample for this study is more complete and diverse, in terms of hominin species and fossil individuals included, than any previous study on paranasal pneumatization. The internal preservation of the crania and the capacity of the imaging data to allow visualization of the features studied have to be considered, nevertheless. Our simple and pragmatic protocol allows for a large, precise, and detailed study of this complex fossil record. In this context, we revise previous incomplete or erroneous characterizations of sinus morphology for some fossil individuals or species and obtain original information on the majority of the material (see Supplementary Text).

We propose a simple, repeatable methodology for the anatomical description and quantification of sinus size and shape, as well as a global comparative morphometric and anatomic framework for nearly all the identified hominin species. We hope that this will encourage authors of future descriptions of key hominin skulls to report detailed information about the morphology and dimensions of the sinuses. This does not prevent researchers from doing additional comparative analyses of their individuals but provides the paleoanthropological community with basic knowledge of a potentially important area of anatomy in fossil hominins.

On the basis of the available evidence, we conclude that large frontal superstructures induce weak constraints related to the position of the face and the brain and give the sinuses the opportunity to expand allometrically in all directions into the available space in the genera Gorilla, Pan, Sahelanthropus, Australopithecus, and Paranthropus. In later hominins, new and variable constraints related to developmental integration between the cranium, brain, and frontal sinuses as well as the timing of growth and development of all these structures result in limitations in the opportunistic expansion of the sinuses into the osseous structures of the frontal bone. This different condition results in a lower antero-posterior extension of the sinuses compared to early hominins and Pan/Gorilla. However, differences in sinus shape and size are also observed among later Homo species, and these may have some implications for phylogenetic discussions and open original perspectives for specific studies to better interpret the origin of these different patterns (e.g., to investigate the role of the face). Future research on extant species should compare the shape and size of the skull, the face, and the base together with the observed variations for frontal sinuses, but application to the fossil record will be, in essence, difficult. Concerning the causes and modalities of the expression of the sinuses, our results are in agreement with the assertion that sinus size and shape are not driven by adaptation to masticatory strains in hominins nor due to climatic adaptation.

**MATERIALS AND METHODS**

Our materials consist of imaging datasets, including a large number of fossil hominins (N = 94; table S2) that are separated into different geographic and/or chronological groups as follows (species names that have been proposed are also mentioned): early hominins: TM 266-01-060-1 (S. tchadensis), Taung, Sts 5, Sts 71, StW 505 (A. africanus), StW 573 (A. prometheus), BOU-VP-12/130 (A. garhi), U.W. 88 (A. sediba), KNM-WT 17000 (Paranthropus aethiopicus), DNH 7,
et al. Variation in paranasal pneumatisation (CV = SD/mean) was corrected for a small sample size using the V* parameter, which is calculated as [(1 + 1/4 N) × CV] and expressed in percentages (56, 57). Linear regressions were calculated with the reduced major axis algorithm (58), which minimizes the errors in both variables (59). Figures for the PCA and linear regression were computed in R (R Core Team, 2014).

### SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at https://doi.org/10.1126/sciadv.abp9767

View/request a protocol for this paper from Bio-protocol.

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Acknowledgments: For permission to access specimens and help in collecting CT data, we thank numerous colleagues and institutions over the world. For details, see references for individual samples in the Supplementary Materials. We thank the Trustees of the Natural History Museum; M. Skinner for scanning assistance; the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology; as well as T. White, G. Suwa, and B. Asfaw. L.T.B. would like to thank the University of Roehampton, The Primate Society of Great Britain (Charles A. Lockwood Memorial Prize), and The Leakey Trust for funding during her PhD data collection from which some of these data are taken (see 6 for details). K.H. would like to thank the Centre for Early Sapiens Behaviour (SapienCE), Department of Archaeology, History, Cultural Studies and Religion, University of Bergen, Norway. Last, we thank the editorial team and the reviewers who provided very helpful comments to improve our paper. Funding: This work is part of the PaleoBRAIN project financed by the Agence Nationale de la Recherche, grant ANR-20-CE27-0009 (A.Bal.); fyssen foundation (L.A.-B.); the Calleva Foundation and the Human Origins Research Fund (C.S.); Shota Rustaveli National Science Foundation of Georgia, grant YS-21-1959 (A.Ma.); European Research Council, grants ERC-CoG-724703 and ERC AdG 101019659 (K.H.); and Deutsche Forschungsgemeinschaft, grant DFG FOR 2237 (K.H.). Funding for the Atapuerca hominin analyses was from the Dirección General de Investigación of the Ministerio de Ciencia e Innovación, grant numbers PGC2018-103925-B-C33 and C33 (MCI/AEI/FEDER, UE). Author contributions: Conceptualization: A. Bal, L.A.-B., A.M.K., and L.T.B. Contribution to osteological, archeological, and paleoanthropological material: A.Bal., J.Ha., A.H., J.-J.H., J.Hu., R.I., J.A.J., Y.K., M.K., D.L., A.Ma., J.M., M.M.-T., H.M., A.Mo., A.d.P., T.R., C.R., M.S., P.S., D.S., C.S., M.T., H.T., E.T., J.Z., B.Z., and L.T.B. Contribution to sampling from which some of these data are taken [see (6) for details]. K.H. would like to thank the Centre for Early Sapiens Behaviour (SapienCE), Department of Archaeology, History, Cultural Studies and Religion, University of Bergen, Norway. Last, we thank the editorial team and the reviewers who provided very helpful comments to improve our paper. Funding: This work is part of the PaleoBRAIN project financed by the Agence Nationale de la Recherche, grant ANR-20-CE27-0009 (A.Bal.); Fyssen foundation (L.A.-B.); the Calleva Foundation and the Human Origins Research Fund (C.S.); Shota Rustaveli National Science Foundation of Georgia, grant YS-21-1959 (A.Ma.); European Research Council, grants ERC-CoG-724703 and ERC AdG 101019659 (K.H.); and Deutsche Forschungsgemeinschaft, grant DFG FOR 2237 (K.H.). Funding for the Atapuerca hominin analyses was from the Dirección General de Investigación of the Ministerio de Ciencia e Innovación, grant numbers PGC2018-103925-B-C33 and C33 (MCI/AEI/FEDER, UE). Author contributions: Conceptualization: A. Bal, L.A.-B., A.M.K., and L.T.B. Contribution to osteological, archeological, and paleoanthropological material: A.Bal., A.Be., A.M.K., E.S., T.B., J.-J.H., J.A., J.A.J., Y.K., M.K., D.L., A.Ma., J.M., M.M.-T., H.M., A.Mo., A.P., T.R., C.R., M.S., P.S., D.S., C.S., M.T., H.T., E.T., J.Z., and B.Z. Investigation (performed research): A.Bal., L.A.-B., A.M.K., A.F., A.B., L.E.S., T.B., A.Ma., and L.T.B. Data analysis: A.Bal., L.A.-B., and J.A.J. Writing—original draft: A.Bal., L.A.-B., A.M.K., and L.T.B. Writing—review and editing: A.Bal., L.A.-B., A.F., A.B., E.S., T.B., J.-J.H., J.A., J.A.J., Y.K., M.K., D.L., A.Ma., J.M., M.M.-T., H.M., A.Mo., A.D.P., T.R., C.R., M.S., P.S., D.S., C.S., M.T., H.T., E.T., J.Z., B.Z., and L.T.B. Competing interests: The authors declare that they have no competing interests. Data and materials availability: All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials.
Frontal sinuses and human evolution

Antoine Balzeau, Lou Albessard-Ball, Anna Maria Kubicka, Andra Filippo, Amlie Beaudet, Elena Santos, Thibault Bienvenu, Juan-Luis Arsuaga, Antonis Bartsiokas, Lee Berger, Jos Mara Bermdez de Castro, Michel Brunet, Kristian J. Carlson, Joan Daura, Vassilis G. Gorgoulis, Frederick E. Grine, Katerina Harvati, John Hawks, Andy Herries, Jean-Jacques Hublin, Jiaming Hui, Rachel Ives, Josephine A. Joordens, Yousuke Kaifu, Mirsini Kouloukoussa, Baptiste Lger, David Lordkipanidze, Ann Margvelashvili, Jesse Martin, Mara Martinn-Torres, Hila May, Aurlien Mounier, Anton du Plessis, Todd Rae, Carolin Rding, Montserrat Sanz, Patrick Semal, Dominic Stratford, Chris Stringer, Mirriam Tawane, Heiko Temming, Evangelia Tsoukala, Joo Zilho, Bernhard Zipfel, and Laura T. Buck

Sci. Adv., 8 (42), eabp9767.
DOI: 10.1126/sciadv.abp9767

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