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Variation in paranasal pneumatisation between Mid-Late Pleistocene hominins

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1 **Title:** Variation in paranasal pneumatization between mid-late Pleistocene hominins

2 **French title:** Variation de la pneumatization paranasale des hominines du Pléistocène moyen
3 finale

4
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19

20 **Keywords:** *Homo heidelbergensis*, sinuses, Neanderthal, Pleistocene, morphology, hominin.

21 **Mots clés:** *Homo heidelbergensis*, sinus, Néandertal, Pléistocène, morphologie, hominine.

22

23

24 **Abstract**

25 There is considerable variation in mid-late Pleistocene hominin paranasal sinuses and in some
26 taxa distinctive craniofacial shape has been linked to sinus size. Extreme frontal sinus size

27 has been reported in mid-Pleistocene specimens often classified as *Homo heidelbergensis* and
28 Neanderthal sinuses are said to be distinctively large, explaining diagnostic Neanderthal
29 facial shape. Here, the sinuses of fossil hominins attributed to several mid-late Pleistocene
30 taxa were compared to those of recent *H. sapiens*. The sinuses were investigated to clarify
31 differences in the extent of pneumatization within this group and the relationship between
32 sinus size and craniofacial variation in hominins from this time period. Frontal and maxillary
33 sinus volumes were measured from CT data and geometric morphometric methods were used
34 to identify and analyse shape variables associated with sinus volume. Some mid-Pleistocene
35 specimens were found to have extremely large frontal sinuses, supporting previous
36 suggestions that this may be a diagnostic characteristic of this group. Contrary to traditional
37 assertions, however, rather than mid-Pleistocene *Homo* or Neanderthals having large
38 maxillary sinuses, this study shows that *H. sapiens* has distinctively small maxillary sinuses.
39 While the causes of large sinuses in mid-Pleistocene *Homo* remains uncertain, small
40 maxillary sinuses in *H. sapiens* most likely result from the derived craniofacial morphology
41 that is diagnostic of our species. These conclusions build on previous studies to over-turn
42 long-standing but unfounded theories about the pneumatic influences on Neanderthal
43 craniofacial form, whilst opening up questions about the ecological correlates of
44 pneumatization in hominins.

45

46 **Résumé :** Les sinus paranasaux des hominines du Pléistocène moyen final présentent une
47 variation morphologique considérable. Chez certains taxons, la taille des sinus semble-t-être
48 liée à une morphologie cranio-faciale particulière. Les fossiles du Pléistocène moyen,
49 souvent rattachés au taxon *H. heidelbergensis*, présentent des sinus frontaux de taille
50 extrêmement importante. Cette caractéristique est partagée avec les Néandertaliens, chez qui
51 une taille importante des sinus frontaux semble expliquer la forme spécifique de leur

52 morphologie faciale. Dans cette étude, nous comparons les sinus d'hominines attribués à
53 plusieurs taxons du Pléistocène moyen –final à ceux d'*H. sapiens* récents. Les sinus ont été
54 étudiés pour clarifier les différences dans l'étendue de la pneumatisation au sein de ce groupe
55 et la relation entre la taille des sinus et la variation cranio-faciale chez les hominines de cette
56 période. Les volumes des sinus frontaux et maxillaires ont été mesurés à partir de données
57 tomодensitométriques et des méthodes de morphométrie géométrique ont été utilisées pour
58 identifier et analyser les variables de conformation associées au volume sinusal. Certains
59 spécimens du Pléistocène moyen ont des sinus frontaux extrêmement grands, ce qui renforce
60 l'hypothèse précédemment suggérée, selon laquelle des sinus de grandes tailles pourrait être
61 diagnostiques de ce groupe. Cependant, et contrairement aux affirmations traditionnelles, les
62 hominines du Pléistocène moyen et les Néandertaliens n'ont pas de grands sinus maxillaires,
63 ce sont les *H. sapiens* qui présentent des sinus maxillaires particulièrement petits. Alors que
64 les raisons expliquant la grande taille des sinus chez les hominines du Pléistocène moyen
65 restent à définir, les petits sinus maxillaires des *H. sapiens* résultent très probablement de la
66 morphologie cranio-faciale dérivée de notre espèce. Ces conclusions contredisent des
67 hypothèses anciennes, mais non fondées, sur l'influence de la pneumatisation sur la
68 morphologie cranio-faciale néandertalienne, tout en ouvrant des perspectives sur les corrélats
69 écologiques de la pneumatisation chez les hominines.

70

71

72 **Introduction**

73 The paranasal sinuses are air-filled cavities between the inner and outer tables of the cranial
74 bones, lined with mucous membrane [1]. Each is recognised by the position of its ostium, the
75 hole through which mucous drains into the nasal cavity, and each is named for the bone it
76 most commonly pneumatizes [2]. There are four types of sinus in hominins: frontal,

77 maxillary, sphenoidal, and ethmoid; maxillary and sphenoidal sinuses are present in all
78 hominoids, whilst the frontal and ethmoid sinuses are only found in hominines [3]. The
79 frontal and maxillary sinuses are investigated here as they are those which are most often
80 asserted to differ between hominin taxa [4-8].

81

82 Mid-late Pleistocene taxa show high levels of variation in craniofacial shape [9]. Here the
83 mid-Pleistocene European and African fossils in our sample (Bodo, Broken Hill [Kabwe],
84 Petralona, Steinheim and Ceprano) are referred to as *H. heidelbergensis*, despite
85 disagreement in the field regarding the alpha taxonomy and indeed, the validity of this
86 species diagnosis [10-12]. It is our intention to investigate the relationship between sinus size
87 and craniofacial shape in these specimens, rather than to diagnose their taxonomy. Mid-
88 Pleistocene specimens from Europe and Africa often attributed to *H. heidelbergensis* [13-19]
89 are differentiated from *H. erectus* by an expanded upper cranial vault and increase in
90 endocranial capacity, a vertical lateral nasal border, and reduced total facial prognathism [16,
91 17, 20]. Massive pneumatization (hyperpneumatization) in some *H. heidelbergensis*
92 specimens has been linked to their craniofacial morphology [6]. For example, comparatively
93 reduced postorbital constriction in Petralona and the anterior orientation of the upper face
94 relative to the anterior cranial fossa in Petralona and Broken Hill have been related to
95 extreme frontal pneumatization [6], though the authors do not make it explicit whether the
96 sinuses are regarded as the cause of craniofacial shape, or vice versa. Here associations
97 between craniofacial morphology and sinus volume are explicitly investigated in these and
98 other mid-Pleistocene hominins.

99

100 The complex of neurocranial features that diagnoses Neanderthals includes a large, long, low
101 cranium, expanded nuchal region with occipital bunning [5, 21] and a supraorbital fossa [22,

102 23]. Facial characteristics include swept-back zygomatics; a great degree of mid-facial
103 prognathism [24]; double-arched supraorbital tori [22] and a large piriform aperture [22, 25].
104 Independently, these features are not unique to Neanderthals, but they are most frequent in
105 this taxon and, in concert differentiate Neanderthal morphology from that of other taxa [26].
106 Neanderthal crania have long been characterised as being hyperpneumatized [5, 27, 28] and it
107 has been asserted that these large sinuses resulted in diagnostic craniofacial shape. The large
108 supraorbital tori of Neanderthals have been said to result from their expanded frontal sinuses
109 [4, 29], and the ‘inflated’ Neanderthal mid-face, which projects and lacks a canine fossa, has
110 been attributed to large maxillary sinuses [4]. This supposed hyperpneumatization has been
111 linked to the species’ assumed adaptation to arctic conditions during the Pleistocene “ice
112 ages”, suggesting that the sinuses have a thermoregulatory role [4], [30]. Subsequent work,
113 however, has demonstrated that sinus volume tends to decrease in cold temperatures [31,
114 34], while quantification of sinus volume relative to facial size shows that relative sinus
115 volumes in the fossil taxon are indistinguishable from those of recent European *H. sapiens*
116 [35, 36], but are substantially different from extant arctic people [37]. Research to date which
117 has questioned the relative hyperpneumatization of Neanderthals [35, 37] has been limited by
118 fairly small and geographically-restricted samples, both of fossils and of recent *H. sapiens*. It
119 is important therefore to test the assumption of Neanderthal hyperpneumatization and the
120 relationship between Neanderthal pneumatization and craniofacial shape with a more
121 comprehensive sample.

122

123 *H. sapiens* is characterised by a globular cranial vault, increased basicranial flexion,
124 anteroposteriorly short and orthognathic face, vertical forehead, presence of a canine fossa,
125 and a true chin [38-44]. Suggested causes for diagnostic *H. sapiens* morphology do not
126 usually include sinus size, yet if it is indeed a key factor governing shape in its close

127 congeners, *H. heidelbergensis* and Neanderthals, it could also be expected to play a part in
128 shaping *H. sapiens* craniofacial shape. These three taxa have been central to theories of
129 hominin sinus function [4, 29, 30], hyperpneumatisation has been argued for both
130 Neanderthals and *H. heidelbergensis* [6, 8, 16], and sinus form has been used as an
131 explanation for Neanderthal and *H. heidelbergensis* characteristic shape [4, 6]. In the current
132 study the differences in frontal and maxillary sinus size between *H. heidelbergensis*,
133 Neanderthals, and *H. sapiens* are measured and the relationship between sinus size and
134 craniofacial shape investigated.

135

136 Based on the literature regarding hominin sinus size, it is hypothesised that there are
137 significant differences between sinus volumes in different taxa, namely that either
138 Neanderthals or *H. heidelbergensis* will be hyperpneumatised, and that these differences will
139 be associated with taxonomically distinctive craniofacial shape. Hyperpneumatisation is
140 clearly a relative term and when used in the literature it is not explained relative to what
141 Neanderthals / *H. heidelbergensis* are thought to show expanded sinuses. For the purposes of
142 this paper, hyperpneumatisation is defined as extreme sinus size in one taxon compared to the
143 other two. If change in sinus volume causes craniofacial morphology to alter, one might
144 expect the taxonomic differences in sinus volume to be larger than those in craniofacial
145 morphology, if the reverse is true and the taxonomic differences in craniofacial morphology
146 are greater than those in sinus volume, this may suggest that the differences in craniofacial
147 morphology are proximal and drive sinus size as a secondary effect. The latter finding would
148 have implications for our understanding of sinus function, or the lack thereof, contributing to
149 a long-standing debate over whether the sinuses are merely evolutionary spandrels (see, [45]
150 for review).

151

152 Previous discussions of pneumatization [6, 45, 46] often assume that sinuses are a
153 functionally and developmentally homogenous group. In fact, there is evidence that this is not
154 necessarily the case; the number and type of sinuses present are not constant between primate
155 species and sinuses have been lost and regained independently on several occasions during
156 the course of primate evolution [3, 47]. This may suggest a degree of functional
157 heterogeneity, or at least modularity. Sinus modularity is also supported by Tillier's [48]
158 observation of a lack of covariation in sinus size between sinus types within hominin
159 individuals. In the current study, the frontal and maxillary sinuses were considered separately
160 to assess the case for treating paranasal pneumatization as a single phenomenon.

161

162

163 **Materials and methods**

164

165 *Materials*

166 The sample consists of clinical and microCT data of recent *H. sapiens* from populations with
167 a wide geographic distribution (133 from 13 populations), early *H. sapiens* (7), *H.*
168 *heidelbergensis* (5) and *H. neanderthalensis* (8) (Table 1). Data collected using the two forms
169 of CT technology were combined to provide the maximum possible sample. The higher
170 resolution of microCT data is likely to enable a more accurate segmentation and
171 measurement of sinus volumes, yet comparison of measurements of the frontal and left
172 maxillary sinuses of the Broken Hill specimen using medical and microCT show a relatively
173 small difference. As measured by a single observer (LTB, see [49]), the difference between
174 measurements of frontal and left maxillary sinus volumes using medical and microCT are
175 4.76% and 1.20% respectively, levels of error that were felt to be acceptable due to the
176 importance of obtaining as large a sample as possible. It is likely that the frontal sinuses are

177 most affected by the poorer resolution of medical CT, due to their more complex shape
178 (particularly in the *H. heidelbergensis* sample), which may be underestimated to some extent.
179 Thus, the level of error seen between the two measurements for Broken Hill is likely at the
180 upper end of that for any specimen.

181

182 In the current sample recent *H. sapiens* are defined as *H. sapiens* less than 25 ka and early *H.*
183 *sapiens* are defined as *H. sapiens* from between 150-25 ka following the rationale of Stringer
184 and Buck [44]. For some of the recent *H. sapiens* groups insufficient individuals were
185 available from one country to make a reasonable sample, thus samples from several countries
186 in the same region were combined if the climate, chronology and method of subsistence were
187 comparable ([50]; Table 1). Since all the recent *H. sapiens* are combined and the goal was to
188 capture as much as possible of global variation in recent *H. sapiens*, differences in levels of
189 intragroup variation between different recent *H. sapiens* samples should not affect the results.

190

191 No significant differences were found between early and recent *H. sapiens* sinus volumes or
192 sinus volume-associated craniofacial shape. Furthermore, the results presented below do not
193 change if early *H. sapiens* are omitted from the *H. sapiens* group. Thus, early and recent *H.*
194 *sapiens* are combined in the results presented here to sample the maximum possible
195 chronological and geographical variation in *H. sapiens* and due to the small sample sizes for
196 early *H. sapiens* in the morphological analyses. The fossils are shown separately in the graphs
197 (Figures 3 and 4) as with the other taxa for consistency and to show where the fossil
198 specimens fall in relation to their younger conspecifics.

199

200 Despite evidence for Neanderthal introgression in the genomes of recent *H. sapiens* [51-53],
201 Neanderthals are treated here as a separate species from *H. sapiens*: *H. neanderthalensis*. It is

202 not uncommon for closely related species to be able to interbreed to some extent [54], and
203 levels of morphological difference between Neanderthals and *H. sapiens* are greater than
204 those seen between many closely related species [55-57]. *H. heidelbergensis* is a disputed
205 category, as mentioned above. In the analyses that follow, *H. heidelbergensis* is defined
206 following Stringer [16], as an Afro-European species.

207

208 Only adult crania were used in these analyses and pathological crania were avoided where
209 possible. Where no alternatives were available (i.e., the fossil sample), pathological crania
210 were used only if the pathology did not appear to alter the regions of interest (e.g., possible
211 pathology affecting the parietals of the early *H. sapiens* fossil Singa). Whilst each recent *H.*
212 *sapiens* sample was chosen to include both males and females, it was not possible to obtain
213 exactly equal numbers without compromising sample size. Butaric et al. [58] have shown
214 that, at least in recent *H. sapiens*, there is no sexual dimorphism in relative maxillary sinus
215 volumes, but this is not known for frontal sinuses. There were generally more male data
216 available, and some populations had no reliable sex information. The sample consisted of
217 crania only (i.e., no postcrania) and no attempt was made to sex individuals based on cranial
218 characteristics since these are very variable between populations and, as they are largely
219 based on levels of robusticity, decisions about sex might bias craniofacial shape analyses.
220 The sexes of the fossils are also mostly unknown; thus even correctly inferring the sex of the
221 recent sample would not eliminate sex as a potentially confounding variable.

222

223

224 *Methods*

225 Sinus volume was used to quantify sinus size [32, 33, 35, 36, 59, 60]. Sinuses were
226 segmented manually from CT scans slice-by-slice by a single observer and their volumes

227 measured in AVIZO versions 5-7 (FEI Visualization Sciences Group, Burlington, MA). A
228 semi-automated method for sinus segmentation is now available [61], which may prove
229 useful for future studies of a similar nature.

230

231 The volumes of both the right and left frontal sinuses were taken where possible (indeed,
232 there is often no demarcation between the two), and the volume was recorded as the sum of
233 both sides, or the only side present multiplied by two, in the instances where only one side
234 was measurable (the Tabun C1 Neanderthal and one Western European recent *H. sapiens*).
235 The left maxillary sinus was used if preserved and the right substituted where necessary,
236 since there is very little bilateral asymmetry in maxillary sinuses [48].

237

238 Only crania with relatively well-preserved sinuses and surrounding craniofacial morphology
239 were included in the study. For all samples, some of the delicate internal bones surrounding
240 the sinuses were broken in many individuals, but by viewing the CT slices in all three planes
241 (transverse, sagittal and coronal) in turn and also inspecting the resulting sinus volume
242 rendered in 3D it was possible to reconstruct the original line of these bones in AVIZO on a
243 slice-by-slice basis (see SI, Figure S1). Error testing (see below) suggests that this
244 reconstruction is robust. Some fossil specimens have sediment in their sinus cavities, but a
245 conservative approach was adopted whereby individuals were only included in the analyses if
246 the sediment was of sufficiently different radio-density from the bone to be clearly visually
247 distinguished from it. Fossil specimens with sinuses rendered and shown in situ are detailed
248 in the Supplementary Information (Figure S2-4).

249

250 To test the precision of the method of measuring sinus volume, the two sinus types (frontal
251 and maxillary) were sectioned out of the same recent *H. sapiens* cranial CT data five times

252 with at least one day elapsing between measurements. These measurements were then
253 compared and error was calculated as the sum of the differences between each individual
254 measurement and their mean, divided by the number of measurements. This error is shown
255 below (Table 2) as a percent of the mean measurement [62].

256

257 The measurement errors (Table 2) are low for each sinus. The recent *H. sapiens* cranium used
258 was reasonably complete and may therefore be easier to measure accurately than some of the
259 more broken specimens (a reasonably intact specimen was chosen to enable measurements of
260 both sinuses on the same individual). However, the medial wall of the maxillary sinus was
261 quite broken, which is reflected in the higher level of error in the volume for that sinus. This
262 damage resulted in the need to estimate the position of the margins of the sinus for numerous
263 slices (SI Figure S1), so the low level of error is reassuring. The scan is also a medical CT
264 scan, so the level of resolution is not as high as for microCT data. For these reasons, it was
265 felt that the error tests demonstrated the method to be sufficiently precise.

266

267 Sinus size has been shown to scale with craniofacial size in *H. sapiens* and other hominoids
268 [36, 63-65]. Therefore, to look at non-isometric differences in volume, measurements must be
269 standardised. Centroid size is one three-dimensional measurement, appropriate for the
270 standardisation of a volume. A centroid size's quality, however, depends on the number and
271 distribution of landmarks used to calculate it and using enough, reasonably spatially
272 distributed, landmarks to obtain a good measure of centroid size on fragmentary specimens is
273 problematic. In the current sample, if only the landmarks preserved on the entire sample were
274 used, centroid size would have to be computed using only four landmarks in the supraorbital
275 region. This would not give a good estimate of overall craniofacial size.

276

277 To test the possibility of using a simpler metric to standardise sinus volume and thus increase
278 sample size, relative sinus volumes calculated using a centroid size (CS) based on a low
279 number of landmarks (see SI, Table S1, Figure S5) were compared to relative sinus volumes
280 calculated using a single linear measurement. A landmark set was devised to include the
281 maximum possible sample with a minimum number of landmarks needed to capture the
282 shape of the entire cranium (6). Despite the low number of landmarks, they are not all
283 preserved in 75% of the fossils and 14% of the recent *H. sapiens*. In previous studies, a
284 simple linear measurement of bi-frontomale temporale breadth was used as a proxy for
285 cranial size to standardise sinus volume [36, 37]. The use of half this measurement (glabella
286 to right frontomale temporale: G-FMT) holds the same information regarding facial size
287 and enables all crania in the current sample to be included in at least one sinus volume
288 analysis [49]. G-FMT was measured in AVIZO and Pearson's correlation tests were run
289 between relative sinus volumes calculated using CS and using G-FMT. Comparison of frontal
290 sinus volume standardisation with CS and with G-FMT produces a very strong, highly
291 significant positive relationship ($r = 0.98$, $p < 0.001$). The relationship for maxillary sinus
292 volumes, although still robust, has a smaller r value ($r = 0.71$, $p < 0.001$). This is perhaps not
293 surprising, as the maxillary region is further from the measurement. Given the number of
294 specimens that would have to be excluded if CS were used to measure size, however, the
295 relationship was judged to be strong enough. It would have been possible to use different CSs
296 for frontal and maxillary relative volumes, but this would have impaired comparisons
297 between sinus types.

298

299 Craniofacial shape related to sinus volume was analysed using geometric morphometric
300 methods (GMM). Preservation (particularly poor in the fossil sample) prevented the inclusion
301 in the GMM analyses of the entire sample used to measure sinus volumes. Thus, reduced

302 samples (Table 1) were used to analyse sinus-specific craniofacial shape and results from the
303 sinus-specific shape analyses on the reduced samples are inferred to apply also to the wider
304 sinus volume samples. To maximise sample sizes, different landmark sets were designed for
305 each sinus and are referred to as frontal/maxillary sinus-specific landmark sets (Table 3 & 4).
306 Sinus-specific landmark sets were chosen to balance the requirements of capturing the shape
307 of interest and including as many specimens as possible in the analyses. The intention was to
308 capture the shape of the region of pneumatization, but also its relationship with the rest of the
309 cranium. For this reason, both landmark sets include a few key landmarks on the face and
310 neurocranium outside the region of their specific sinus.

311

312 The frontal sinus-specific landmark set (Table 3) consisted of ten landmarks, mainly in the
313 supraorbital region, allowing the inclusion of a sample of 110 specimens (Table 1). The
314 maxillary sinus landmark set (Table 4) consisted of 13 landmarks, concentrating on the
315 maxillary region, allowing the inclusion of 88 specimens (Table 1). These are low numbers of
316 landmarks, but they capture shape differences between taxa and they allow the inclusion of
317 many otherwise unusable fossils (see also [84]). Landmarks were digitised on virtual
318 reconstructions of crania created from CT data in AVIZO. The coordinates were exported for
319 use in Morphologika [67] and PAST [68] software. Only one half of the cranium was
320 digitised to remove noise from individual asymmetry. The left side was digitised where there
321 was no difference in preservation; the right was substituted if it was better preserved and
322 mirrored in Morphologika, this allowed larger fossil sample sizes to be included.

323

324 In Morphologika, general Procrustes analyses were performed to superimpose sinus-specific
325 landmark coordinate data for each analysis, and then Principal Components Analyses (PCA)
326 were run. The first seven principal components (PCs), accounting for $\geq 70\%$ of variance, were

327 tested for correlations with the relevant relative sinus volumes from the wider sinus volume
328 sample. The 70% variance cut-off point was based on the visualisation of scree-plots and
329 scrutiny of the eigenvalues. Pearson's correlation tests, rather than regression analyses, were
330 used to test for relationships between shape and relative sinus volume to avoid making
331 assumptions about dependent and independent variables as one of the questions of interest is
332 whether sinus size drives craniofacial shape or vice versa.

333

334 PC scores from each sinus-specific analysis showing significant correlation with its
335 respective relative sinus volume (see also [35]) were designated frontal or maxillary sinus
336 volume shape parameters (the frontal SVSP and maxillary SVSP) and used in subsequent
337 analyses (Table 5). Relative frontal sinus volume is correlated with PC6 (explaining 7%
338 variance in shape between the sample), from the frontal sinus-specific landmark analyses this
339 is a significant, negative correlation ($r^2 = -0.12$, $p < 0.001$; remains significant with
340 Bonferroni correction). Relative maxillary sinus volume is correlated with PC3 (explaining
341 11% of variance) from the maxillary sinus-specific landmark analysis, this is a moderate,
342 significant positive correlation ($r^2 = 0.41$, $p < 0.001$; remains significant with Bonferroni
343 correction).

344

345 Wireframe models (Figures 1 and 2) were created in Morphologika to visualise shape
346 changes described by SVSPs. Frontal and maxillary SVSPs were used to determine sinus-
347 related shape differences between taxa. Since it was not the intention of this study to study
348 total craniofacial shape differences between individuals or groups, but to focus only on those
349 aspects of shape differences that are related to sinus volume, only relevant PCs with
350 significant relationships with sinus volume (the SVSPs – Table 5) were analysed. These

351 SVSPs were analysed individually following Zollikofer et al. [35], since this method has been
352 shown to successfully identify relationships between sinus volume and craniofacial shape.

353

354 Given the small size of the fossil samples, the distribution of variation in their sinus volumes
355 is unknown. The very unequal size of the samples is also likely to be problematic for
356 parametric statistics. For these reasons, non-parametric permutation tests, ANOSIMs
357 (analysis of similarity), were performed using PAST [68] to ascertain differences in sinus
358 volumes and SVSP (PC) scores between taxa. An ANOSIM is analogous to an ANOVA in
359 that it compares differences within and between groups [68]. Distances are converted to ranks
360 and the test statistic R gives a measure of relative within group dissimilarity, with more
361 positive numbers showing greater difference [68]. R is interpreted like a correlation
362 coefficient and is a measure of size effect [68]. An effect size of > 0.5 is widely judged to be
363 a large effect [69, 70], a convention followed here. Euclidean distances and 9999
364 permutations were used for ANOSIM analyses.

365

366

367 **Results**

368

369 *Sinus volumes*

370 There are significant differences of moderate size ($R = 0.33$, $p < 0.001$) in relative frontal
371 sinus volumes between taxa (Figure 3). *H. heidelbergensis* has significantly larger relative
372 frontal sinus volumes than either *H. sapiens* or Neanderthals (Table 6).

373

374 There are large, significant differences in relative maxillary sinus volumes (Figure 3)
375 between taxa ($R = 0.55$, $p < 0.001$). *H. sapiens* has significantly smaller relative maxillary
376 sinus volumes than either Neanderthals or *H. heidelbergensis* (Table 7).

377

378 *Sinus-related shape*

379 In the reduced sample analysed for frontal sinus-related shape (Table 1), the frontal SVSP
380 showed a significant, negative correlation with frontal sinus volume ($r^2 = -0.12$, $p = < 0.001$;
381 remains significant with Bonferroni correction). Craniofacial shapes associated with larger
382 frontal sinuses, configurations with lower scores on the frontal SVSP (Figure 4, SI Figure
383 S6), have relatively larger frontal and orbital regions and are taller superoinferiorly in the
384 maxillary region (Figure 5).

385

386 There is a moderate significant difference in frontal SVSP scores (PC scores on PC6, the
387 frontal SVSP, which explains 7% of variation) between taxonomic groups (ANOSIM: $R =$
388 0.45 , $p < 0.005$), due to a significantly higher scores in *H. sapiens* than *H. heidelbergensis*
389 (Figure 4, Table 8, SI Figure S4). There are no significant differences in frontal SVSP scores
390 between Neanderthals and other taxa.

391

392 In the reduced sample analysed for maxillary sinus-related shape, the maxillary SVSP (PC3,
393 maxillary sinus-specific landmark set, which explains 11% of variation) shows a moderate,
394 significant positive correlation with relative maxillary sinus volume ($r^2 = 0.41$, $p < 0.001$;
395 remains significant with Bonferroni correction). Craniofacial shapes associated with
396 relatively larger maxillary sinuses (i.e., higher scores on the maxillary SVSP – see Figure 4,
397 SI Figure S5) have larger, taller, more anteriorly projecting faces relative to their neurocrania
398 than craniofacial shapes associated with relatively smaller maxillary sinuses. The malar

399 region appears superoinferiorly taller in high scoring configurations and the zygomatic arch
400 appears more swept back. Higher scoring configurations also show more dolichocephalic
401 neurocrania (Figure 6).

402

403 There are differences between groups in maxillary sinus-related shape, *H. heidelbergensis*
404 falls beyond the range of variation for other taxa (Figure 4, SI Figure S5) and Neanderthals
405 fall at the upper extreme of the *H. sapiens* range of variation. This is reflected in the very
406 strong, significant difference between taxonomic groups in maxillary sinus-related shape
407 (ANOSIM: $R = 0.78$, $p < 0.001$); *H. sapiens* has significantly lower PC scores on this SVSP
408 than either Neanderthals or *H. heidelbergensis* (see Table 9).

409

410 **Discussion**

411 Paranasal hyperpneumatisation has been discussed as a characteristic of both *H.*
412 *heidelbergensis* [6, 8, 16, 35] and Neanderthals [4, 5, 27-29] and has been used as an
413 explanation for craniofacial morphology in both taxa [4, 6, 29]. Conversely, recent research
414 has suggested that compared to *H. sapiens*, Neanderthals are not hyperpneumatised when
415 craniofacial size is taken into account [35-36]. The aim of this study was to determine the
416 nature of pneumatic variation and its relationship to craniofacial shape in mid-late Pleistocene
417 hominins, by using the largest, most representative sample to date and a more comprehensive
418 method than previously employed. The results presented here support the suggestion that
419 frontal hyperpneumatisation is a characteristic of at least some mid-Pleistocene hominins, yet
420 refute the long-standing assertion that Neanderthals are hyperpneumatised. Further, if the
421 results from the smaller craniofacial shape sample can be extended to the wider sinus volume
422 sample, the relationship between craniofacial shape and maxillary sinus volume suggests that
423 the distinctive small, orthognathic *H. sapiens* face has led to peculiarly small maxillary

424 sinuses in this taxon. This may contribute to resolving long-standing arguments about sinus
425 function [45, 46].

426

427 *Frontal pneumatisation and associated craniofacial shape*

428 The picture of *H. heidelbergensis* frontal pneumatisation from prior research is complicated,
429 in part due to the debate over which specimens should be included in the hypodigm.

430 Petralona, Bodo, and Broken Hill are all known for their large frontal sinuses [6, 8, 35] and

431 similar claims have also been made for other putative *H. heidelbergensis*, such as Steinheim
432 [8], although the current authors see little support for this latter claim based on their

433 examination of the Steinheim CT data. Other middle Pleistocene specimens, such as Ceprano

434 [71] and Arago 21 [48, 72-74], do not necessarily show the same pattern. Arago 21 is a key

435 fossil in the *H. heidelbergensis* hypodigm, linking the mandibular (including the type

436 specimen) and cranial material [13, 18, 20]. Although Arago 21 was unavailable for inclusion

437 in this study, there is evidence from the literature that its frontal sinuses are small [48, 72-74].

438 They also appear to form two widely separated cells that fail to pneumatise the frontal

439 squama [74], which is qualitatively and quantitatively different from the sinuses in Broken

440 Hill / Bodo / Petralona, but similar those of Ceprano (Figure 7). Interestingly, Ceprano and

441 Arago 21 are also shown to be distinctive and closely linked in other recent morphological

442 analyses [10], distancing them from the main Euro-African *H. heidelbergensis* hypodigm

443 (*sensu* Rightmire and Stringer [16, 20, 75, 76]), and supporting a link between external

444 craniofacial shape and frontal sinus form. Thus, from the literature it appears that, despite

445 variation, at least a core group of middle Pleistocene *Homo* from both Europe and Africa

446 show hyperpneumatized frontal sinuses.

447

448 Given the debate surrounding the taxonomic validity of *H. heidelbergensis*, it is difficult to
449 interpret the variation within the mid-Pleistocene sample. If these specimens constitute a
450 single species, the results of the current study support the assertion that the frontal sinuses of
451 *H. heidelbergensis*, relative to those of other fossil and recent hominins, are
452 hyperpneumatized. Most, but not all, of the putative *H. heidelbergensis* individuals analysed
453 have exceptional frontal pneumatization and their overall relative frontal sinus volumes are
454 significantly greater than of the *H. sapiens* or Neanderthal samples. Although one recent *H.*
455 *sapiens* has frontal pneumatization comparable with Broken Hill, nothing in the entire sample
456 (the largest used for a similar study to date) has frontal pneumatization comparable with Bodo
457 or Petralona. The shape and extension of the frontal sinuses of all the putative *H.*
458 *heidelbergensis* in this study, except Ceprano (Figure 7), appear similar and seem
459 qualitatively different from those of the other taxa in the present study and Ceprano has
460 plausibly been excluded from the *H. heidelbergensis* hypodigm based on its craniofacial
461 shape [10, 14, 41, 71, 77]. There is a high degree of variation in recent *H. sapiens* sinuses [6,
462 78, 79] and although *H. sapiens* may be a particularly variable species [80], we should expect
463 at least some variation in *H. heidelbergensis*, particularly given the probable temporal range
464 for the fossil specimens in the sample [75, 81]. Even taking this expected variation into
465 account, the results from the current study suggest that either *H. heidelbergensis* as a species
466 exhibits hyperpneumatized frontals compared to *H. sapiens* and Neanderthals, or that there is
467 a polyphyletic group of mid-Pleistocene hominins from Europe and Africa who share
468 hyperpneumatized frontal sinuses through convergent evolution. The latter is perhaps a more
469 interesting question for the discussion of sinus function, as it could open interesting
470 investigations as to which aspects of ecology (if the sinuses are functional) or craniofacial
471 shape (if the sinuses are spandrels) these specimens share that could have led to

472 hyperpneumatisation. Conversely, these differences in sinus morphology may be due to
473 genetic drift, which should be the null hypothesis for any such future studies [82].

474

475 The statements above assume that hyperpneumatisation is not the primitive condition, yet
476 based on the evidence to date, this is uncertain, given the equivocal knowledge of sinus
477 volume in *H. erectus*. The one *H. erectus* specimen available for sinus volume measurement
478 in the current study (KNM-ER 3883, not included in statistical and shape analyses as the sole
479 representative of its taxon) has a similar relative frontal sinus volume to Broken Hill. Taken
480 alone, this would suggest that large frontal sinuses may be the primitive condition [83].

481 Where it is sufficiently preserved, however, the African *H. erectus* sample in fact suggests
482 that small frontal sinuses restricted to the supraorbital region are the norm for *H. erectus* [84]
483 and the majority of Asian *H. erectus* also have small frontal sinuses that do not extend
484 superiorly past the glabellar region [48, 72, 74, 85-88]. Thus the general impression is of a
485 small frontal sinus in *H. erectus*, with some exceptions such as KNM-ER 3833, quite
486 different from the morphology of at least most *H. heidelbergensis* specimens, as shown in
487 this study. This suggests that frontal hyperpneumatisation is derived in some mid-Pleistocene
488 hominins.

489

490 In addition to the clear difference in relative frontal sinus volumes discussed above, inter-
491 taxonomic differences were also found in the reduced sample analysis of frontal sinus-related
492 craniofacial shape (*H. heidelbergensis* sample: Broken Hill and Petralona). It has been argued
493 that hyperpneumatisation is a cause of the distinctive *H. heidelbergensis* craniofacial shape
494 [6]. Conversely, the shape of the frontal bone [74], the orbital [35] and supraorbital regions
495 [79] have been suggested as influences on frontal sinus form. In the reduced *H.*
496 *heidelbergensis* sample specimens show significant differences in frontal sinus-related

497 craniofacial shape from *H. sapiens*: *H. heidelbergensis* specimens have taller supraorbital
498 regions and deeper, taller faces than *H. sapiens*. *H. heidelbergensis* specimens often have
499 remarkably large supraorbital tori [16] and, in common with earlier *Homo*, *H.*
500 *heidelbergensis* fossils have larger faces than either *H. sapiens* or Neanderthals [17]. The
501 particularly small, retracted face of *H. sapiens* is more derived, compared to earlier *Homo*,
502 than the distinctive face of Neanderthals [89, 90]. It is likely that the analyses of frontal sinus-
503 related craniofacial shape in the current study reflect these differences between *H. sapiens*
504 and *H. heidelbergensis*. The lack of a difference in this variable between *H. heidelbergensis*
505 and Neanderthals may be caused by an insufficient number of landmarks to pick up on this
506 relatively smaller shape difference.

507

508 The statistical difference between taxa in the frontal sinus-related shape analysis has a
509 smaller effect size than for frontal sinus volume analysis. This could be construed as
510 suggesting that the greater size of *H. heidelbergensis* frontal sinuses compared to *H. sapiens*
511 is not only because of their differences in craniofacial shape (contra [3, 101, 107]) and could
512 even perhaps be interpreted as supporting the idea that differences in craniofacial shape
513 between *H. heidelbergensis* and *H. sapiens* are affected by degree of frontal pneumatisation
514 (cf. [6, 7]). However, the relatively few landmarks used in the present study could affect the
515 quality of the shape data captured and the results may be affected by sample composition.
516 Therefore, conclusions about the relative sizes effects in the two types of data should be made
517 with caution pending further investigation. It seems unlikely that differences in
518 pneumatisation lead to the differences in supraorbital form between *H. sapiens* and *H.*
519 *heidelbergensis*, given that Neanderthals and *H. erectus* both have larger (although
520 differently shaped) supraorbital tori than *H. sapiens*, yet show no relative difference in frontal
521 sinus volume compared to *H. sapiens*.

522

523 Contrary to traditional theories regarding the cause of the supraorbital tori in Neanderthals [4,
524 29], but in accordance with more recent findings [35-37], Neanderthal frontal sinuses were
525 not found to be relatively larger than those of *H. sapiens*, and thus Neanderthal frontal
526 sinuses are not hyperpneumatised. This is despite the much greater size and geographic range
527 of the *H. sapiens* sample in the current study compared with previous research [35-37].
528 Several studies, including this one, have now shown that Neanderthals do not have relatively
529 larger frontal sinus volumes than *H. sapiens* and there is thus no evidence that differences
530 between *H. sapiens* and Neanderthal supraorbital shape are caused by large frontal sinuses
531 (c.f., [9, 22, 105]). It seems reasonable, therefore, that this idea should be abandoned. What
532 were asserted to be large sinuses in Neanderthals were used for many years to prop up
533 theories that the Neanderthal face resulted from cold adaptation [4, 29, 30]. The lack of
534 evidence for Neanderthal hyperpneumatisation thus also weakens the argument that their
535 craniofacial shape is the result of hyperpolar adaptation [36, 91], (but see [92]). Although
536 these results do not necessarily rule out the possibility that relatively extreme pneumatisation
537 was due to cold adaptation at some point in *H. heidelbergensis* evolution (depending on the
538 location, and environmental conditions, of the origin of this taxon), experimental [34] and
539 naturalistic [33] data from other primates / mammals strongly suggest that relative sinus size
540 would not have increased in response to low temperatures.

541

542 **Maxillary pneumatisation and associated craniofacial shape**

543 In contrast to their frontal pneumatisation, *H. heidelbergensis* specimens in the current study
544 do not show distinctively large maxillary sinuses compared to closely related species.
545 However, *H. sapiens* do have significantly smaller relative maxillary sinus volumes than the
546 other taxa (Figure 8). This provides novel evidence that *H. sapiens* has hypopneumatised

547 maxillary sinuses compared to its closest congeners. This is contrary to previous research,
548 which not only suggested that *H. heidelbergensis* maxillary sinuses are distinctively large
549 [e.g., 77], but also that maxillary hyperpneumatisation is a diagnostic feature and a cause of
550 Neanderthal craniofacial morphology [e.g., 21].

551

552 In addition to differences between taxa in the full maxillary sinus volume sample, differences
553 were also found in the reduced sample used in the maxillary sinus-related shape analyses
554 between *H. sapiens* and the other taxa. Differences in maxillary sinus-related craniofacial
555 shape coincide with some of the differences that are well-established as diagnosing *H.*
556 *sapiens*: differences in neurocranium globularity, facial size and flatness [38-43, 93]. The
557 strength of the shape differences resulting from these derived characteristics in *H. sapiens* is
558 demonstrated by their identification by the present analyses, despite the relatively few
559 landmarks used and the fact that the maxillary sinus-specific shape variable does not describe
560 the greatest shape variation in the sample (it is PC3, explaining 11% of variance). The
561 characteristic shape of *H. sapiens* (as described by the maxillary sinus-related shape variable)
562 is associated with smaller maxillary sinuses. Despite the reduced sample size, the size effect
563 of the difference between *H. sapiens* and Neanderthals / *H. heidelbergensis* in maxillary
564 sinus-associated shape is much larger than that of the difference in the relative maxillary
565 sinus volumes themselves. This offers important evidence that the derived facial shape of *H.*
566 *sapiens* leads to the distinctively small maxillary sinuses seen in our species. These results
567 may also support theories suggesting the maxillary sinuses are in themselves functionless,
568 their volume resulting from surrounding craniofacial form [33, 58, 60, 94, 95].

569

570 **Conclusions**

571 This study aimed to test the hypotheses that there are differences in sinus size between mid-
572 late Pleistocene hominin taxa and that these differences are related to craniofacial shape.
573 Sinus volume and sinus volume-associated craniofacial shape in mid-late Pleistocene
574 hominins were compared to investigate variation in paranasal pneumatization and its effect on
575 craniofacial form. As construed in this study, *H. heidelbergensis* on average has a
576 hyperpneumatized frontal compared to Neanderthals and *H. sapiens*, although it is not of
577 homogenous size throughout the taxon as currently described. In addition to sinus volume
578 differences, there are differences between taxa in frontal sinus-related craniofacial shape.
579 These differences are related to supraorbital torus and facial size differences used to
580 differentiate *H. heidelbergensis* from *H. sapiens* and Neanderthals [42, 89, 90]. Larger
581 taxonomic differences in frontal sinus-related shape than in volumes themselves could be
582 argued to offer support for the assertion that hyperpneumatization has shaped the distinctive
583 craniofacial shape of these specimens [6, 7], but this seems implausible given the similarly
584 sized external, but not internal, supraorbital morphology of Neanderthals and *H. erectus*.
585 Contrary to long-standing beliefs about frontal hyperpneumatization in Neanderthals,
586 Neanderthals do not have larger relative frontal sinuses than *H. sapiens*. This negates the role
587 of the frontal sinuses in the large supraorbital tori of Neanderthals and does not support
588 theories explaining distinctive Neanderthal craniofacial form as resulting from hyperpolar
589 adaptation via pneumatization.

590

591 In contrast to their enlarged frontal sinuses, the maxillary sinuses of *H. heidelbergensis* are
592 not hyperpneumatized. Conversely, it can be said that the maxillary sinuses of *H. sapiens* are
593 hypopneumatized compared to Neanderthals / *H. heidelbergensis*. The greater size effect of
594 the taxonomic difference in facial shape, compared to the difference in sinus size itself
595 suggests this is a characteristic that can be explained partly by the distinctive craniofacial

596 shape of our species. This finding overturns historical pneumatic explanations for
597 Neanderthal maxillary shape, as the lack of significant difference in relative frontal sinus
598 volumes between Neanderthals and *H. sapiens* does for Neanderthal supraorbital shape. The
599 relationship between relative maxillary sinus volume and maxillary sinus-related craniofacial
600 shape provides support for the hypothesised relationship between craniofacial shape and
601 maxillary sinus size, but suggests that it is craniofacial shape that is the driver of maxillary
602 sinus size, rather than the converse. This may support assertions that the maxillary sinuses are
603 functionless, but act as zones of accommodation, allowing modularity in the cranium [33, 58,
604 60, 94, 95]. The difference in relationship between face shape and sinus volume in frontal and
605 maxillary sinuses within these taxa supports the assertion [48, 72] that the different individual
606 sinuses may be modular and their size governed by different stimuli.

607

608

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625

626

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877 the origin of modern human behavior. J Hum Evol 39(5):453-563

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880 **List of Tables**

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882 **Table 1:** Sample details. FVS: included in frontal sinus volume sample, FSS: included in
883 frontal sinus-specific shape sample, MVS: included in maxillary sinus volume sample, MSS:
884 included in maxillary sinus-specific shape sample. Y: included in analysis, N: not included in
885 analysis. The sole *H. erectus* specimen, KNM-ER 3883, was not included in statistical
886 analyses or figures, but is mentioned in the Discussion with reference to the potential
887 phylogenetic significance of sinus size in *H. heidelbergensis*. NMK: National Museum of
888 Kenya; DAFH: Digital Archive of Fossil Hominins, University of Vienna; USL: Università
889 La Sapienza, Rome; NHM: Natural History Museum, London; UV: University of Vienna;
890 AUT: Aristotle University of Thessaloniki; MNPE: Museo Nazionale Preistorico Etnografico
891 "Luigi Pigorini", Rome; MHP: Musée de l'Homme, Paris; UZ: University of Zurich; Ernst-
892 Morritz-Arndt University, Greifswald.

893 **Table 1:** *Détails de l'échantillon. FVS: spécimens inclus dans l'échantillon de volume du*
894 *sinus frontal, FSS: spécimens inclus dans l'échantillon de conformation cranio-faciale*
895 *spécifique au sinus frontal, MVS: spécimens inclus dans l'échantillon de volume du sinus*

896 *maxillaire, MSS: spécimens inclus dans l'échantillon de conformation cranio-faciale sinus*
897 *maxillaire spécifique. Y: spécimens inclus dans l'analyse, N: spécimens non inclus dans*
898 *l'analyse. Le seul spécimen d'*H. erectus*, KNM-ER 3883, n'a pas été inclus dans les analyses*
899 *statistiques, mais il est discuté dans la discussion en ce qui concerne la signification*
900 *phylogénétique potentielle de la taille des sinus chez *H. heidelbergensis*. NMK: National*
901 *Museum of Kenya; DAFH: Digital Archive of Fossil Hominins, University of Vienna; USL:*
902 *Università La Sapienza, Rome; NHM: Natural History Museum, London; UV: University of*
903 *Vienna; AUT: Aristotle University of Thessaloniki; MNPE: Museo Nazionale Preistorico*
904 *Etnografico "Luigi Pigorini", Rome; MHP: Musée de l'Homme, Paris; UZ: University of*
905 *Zurich; Ernst-Morritz-Arndt University, Greifswald.*

906

907 **Table 2:** Error test for sinus volume measurements. Results (mm³) for five repetitions of
908 sinus volume measurement (raw volume, not relative volume) and percentage error.

909 **Table 2:** *Test d'erreur pour les mesures de volume sinusal. Résultats (mm³) pour cinq*
910 *répétitions de mesure du volume sinusal (volume brut, volume non relatif) et pourcentage*
911 *d'erreur.*

912

913 **Table 3:** Landmarks used in frontal sinus-specific landmark set analyses.

914 **Table 3:** *Points repères utilisés pour l'analyse de conformation cranio-faciale spécifique au*
915 *sinus frontal.*

916

917 **Table 4:** Landmarks used in maxillary sinus-specific landmark set analyses.

918 **Table 4:** *Points repères utilisés pour l'analyse de conformation cranio-faciale spécifique au*
919 *sinus maxillaire.*

920

921 **Table 5:** Sinus volume shape parameters (SVSPs). PC: principal component from
922 frontal/maxillary sinus-specific GMM landmark analysis. Bonferroni correction: remains
923 significant if a Bonferroni correction is applied to reduce the likelihood of type II errors.

924 **Table 5:** *Paramètres de conformation associés au volume sinusal (SVSP). PC: composante*
925 *principale de l'analyse par morphométrie géométrique de conformation cranio-faciale*
926 *spécifique au sinus frontal / maxillaire. Correction de Bonferroni: est significatif si une*
927 *correction de Bonferroni est appliquée pour réduire la probabilité d'erreurs de type II.*

928

929 **Table 6:** ANOSIM comparing relative frontal sinus volumes between taxa. The matrix is
930 symmetrical; numbers above the trace are R values, numbers below the trace are p values. *:
931 significant, $\alpha < 0.05$. **Bold:** remains significant if a Bonferroni correction is applied.

932 **Table 6:** *Résultats de l'ANOSIM comparant les volumes relatifs des sinus frontaux entre les*
933 *taxons. La matrice est symétrique ; les nombres au-dessus de la trace sont des valeurs de R,*
934 *les nombres au-dessous de la trace sont des valeurs de p. *: significatif, $\alpha < 0,05$. Gras: est*
935 *significatif si une correction de Bonferroni est appliquée.*

936

937

938 **Table 7:** ANOSIM of relative maxillary sinus volume differences between taxa. The matrix
939 is symmetrical. Above the trace are R values, below the trace are p values; *: significant, $\alpha <$
940 0.05 , **Bold:** remains significant if a Bonferroni correction is applied.

941 **Table 7:** *Résultats de l'ANOSIM comparant les volumes relatifs des sinus maxillaire entre les*
942 *taxons. La matrice est symétrique ; les nombres au-dessus de la trace sont des valeurs de R,*

943 *les nombres au-dessous de la trace sont des valeurs de p. *: significatif, $\alpha < 0,05$. **Gras**: est*
944 *significatif si une correction de Bonferroni est appliquée.*

945

946

947 **Table 8:** ANOSIM of taxonomic position on the frontal SVSP. Matrix is symmetrical;
948 numbers above trace are R values, and numbers below trace are p values. *: significant, $\alpha <$
949 0.05. **Bold:** remains significant if a Bonferroni correction is applied.

950 **Table 8:** *Résultats de l'ANOSIM comparant la position taxonomique sur le SVSP frontal. La*
951 *matrice est symétrique ; les nombres au-dessus de la trace sont des valeurs de R, les nombres*
952 *au-dessous de la trace sont des valeurs de p. *: significatif, $\alpha < 0,05$. **Gras**: est significatif si*
953 *une correction de Bonferroni est appliquée.*

954

955

956 **Table 9:** ANOSIM of taxonomic position on the maxillary SVSP. Matrix is symmetrical,
957 numbers above trace are R values, and numbers below trace are p values. *: significant, $\alpha <$
958 0.05, **Bold:** remains significant if a Bonferroni correction is applied.

959 **Table 9:** *Résultats de l'ANOSIM comparant la position taxonomique sur le SVSP maxillaire.*
960 *La matrice est symétrique ; les nombres au-dessus de la trace sont des valeurs de R, les*
961 *nombres au-dessous de la trace sont des valeurs de p. *: significatif, $\alpha < 0,05$. **Gras**: est*
962 *significatif si une correction de Bonferroni est appliquée.*

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966 **List of Figures**

967

968 **Figure 1:** Landmarks and wireframe used for frontal sinus-specific landmark set. Numbered
969 landmarks (Table 3) of the frontal sinus-specific landmark set seen in *norma frontalis* (left)
970 and *norma lateralis* (right). Wireframe shows which landmarks are joined to illustrate shape
971 changes in later figures. Dashed lines indicate links between landmarks that are not visible
972 when the cranium is shown.

973

974 **Figure 1:** Points repères utilisés pour décrire la conformation cranio-faciale spécifique au
975 sinus frontal. Points repères numérotés (Tableau 3) de conformation cranio-faciale
976 spécifique au sinus frontal en *norma frontalis* (à gauche) et *norma lateralis* (à droite). Les
977 points de repère sont reliés pour illustrer les changements de conformation dans les figures
978 ultérieures. Les lignes pointillées indiquent les liens entre les points de repère qui ne sont pas
979 visibles lorsque le crâne est affiché.

980

981 **Figure 2:** Landmarks and wireframe used for maxillary sinus-specific landmark set.
982 Numbered landmarks (Table 4) of maxillary sinus-specific landmark seen in *norma frontalis*
983 (left) and *norma lateralis* (right). Wireframe shows which landmarks are joined to illustrate
984 shape changes in later figures. Dashed lines indicate links between landmarks that are not
985 visible when the cranium is shown.

986

987 **Figure 2** Points repères utilisés pour décrire la conformation cranio-faciale spécifique au
988 sinus maxillaire. Points repères numérotés (Tableau 3) de conformation cranio-faciale
989 spécifique au sinus maxillaire observés en *norma frontalis* (à gauche) et *norma lateralis* (à
990 droite). Les points de repère sont reliés pour illustrer les changements de conformation dans
991 les figures ultérieures. Les lignes pointillées indiquent les liens entre les points de repère qui
992 ne sont pas visibles lorsque le crâne est affiché.

993

994 **Figure 3:** Variation in sinus size in full sample. Top: Relative (size-corrected) frontal sinus
995 volume by taxon. Bottom: relative maxillary sinus volume by taxon. Red, R H.s: recent *H.*
996 *sapiens*; blue, E H.s: early *H. sapiens*; green, H.n: *H. neanderthalensis*; magenta, H. h: *H.*
997 *heidelbergensis*. CroM: Cro-Magnon, Sing: Singa, Mlad: Mladeč 1, Skh: Skhul, LaF: La
998 Ferrassie, LaC: La Chapelle, Krap: Krapina, Feld: Feldhofer, Tab: Tabun C1, FQ: Forbes
999 Quarry, LaQ: La Quina, Pet: Petralona, Bod: Bodo, Kab: Broken Hill, Cep: Ceprano. Recent
1000 and early *H. sapiens* shown separately in Figure, although pooled for analyses following
1001 rationale explained in Methods.

1002

1003 **Figure 3:** *Variation de la taille des sinus dans l'échantillon complet. En haut: Volume relatif*
1004 *du sinus frontal relatif (corrigé en fonction de la taille) par taxon. En bas: volume relatif du*
1005 *sinus maxillaire par taxon. Rouge, R H.s: H. sapiens récent; bleu, EH: H. sapiens ancien;*
1006 *vert, H.n: H. neanderthalensis; magenta, H. h: H. heidelbergensis. CroM: Cro-Magnon, Sing:*
1007 *Singa, Mlad: Mladeč 1, Skh: Skhul, LaF: La Ferrassie, LaC: La Chapelle, Krap: Krapina,*
1008 *Feld: Feldhofer, Tab: Tabun C1, FQ: Carrière de Forbes, LaQ: La Quina, Pet: Petralona,*
1009 *Bod: Bodo, Kab: Broken Hill, Cep: Ceprano. Les H. sapiens récent et ancien sont montrés*
1010 *séparément dans la figure, mais regroupés dans les analyses suivant la justification expliquée*
1011 *dans la section Méthodes.*

1012

1013 **Figure 4:** Variation in sinus-specific craniofacial shape in reduced sample (Table 1). Left:
1014 PCA showing frontal sinus-related craniofacial shape (Frontal SVSP, PC6 of the frontal
1015 sinus-specific landmark set analysis explaining 7% of variance) on x axis. Right: PCA of
1016 maxillary sinus-related craniofacial shape (Maxillary SVSP, PC3 of the maxillary sinus-
1017 specific landmark set analyses explaining 11% of variance) on x axis. SVSPs (x axes) are

1018 shown against PC2 on y axes as this spreads the data more than PC1 and aids visualisation of
1019 group differences, PC2 is not correlated with frontal or maxillary sinus volume. Red
1020 triangles, R H.s: recent *H. sapiens*; blue diamonds, E. H.s: early *H. sapiens*; green squares,
1021 H.n: *H. neanderthalensis*; magenta circles, H.h: *H. heidelbergensis*. Recent and early *H.*
1022 *sapiens* shown separately in Figure, although pooled for analyses following rationale
1023 explained in Methods. For shape changes described by frontal and maxillary SVSPs, see
1024 Figures 5 and 6. Fossil names as above.

1025

1026 **Figure 4:** *Variation de la forme cranio-faciale sinus-spécifique dans l'échantillon réduit*
1027 *(Tableau 1). A gauche: ACP montrant la forme cranio-faciale associé avec le sinus frontal*
1028 *(SVSP frontal, CP6 de l'analyse du sinus frontal) sur l'axe des x. À droite: ACP de la forme*
1029 *cranio-faciale associé avec le sinus maxillaire (Maxillary SVSP, CP3 des analyses du sinus*
1030 *maxillaire) sur l'axe des x. Les SVSP (axes x) sont représentés par rapport à la CP2 sur les*
1031 *axes y car cela répartit mieux les données que la CP1 et facilite la visualisation des*
1032 *différences entre groupes, CP2 n'est pas corrélé avec le volume sinusal frontal ou maxillaire.*
1033 *Triangles rouges, R H.s: H. sapiens récent; diamants bleus, E.H.: H. sapiens ancien; carrés*
1034 *verts, H.n: H. neanderthalensis; cercles magenta, H.h: H. heidelbergensis. Les H. sapiens*
1035 *récent et ancien sont montrés séparément sur la figure, mais regroupés dans les analyses*
1036 *suivant la justification expliquée dans la section Méthodes. Pour les changements de*
1037 *conformations décrits par les SVSP frontal et maxillaire, voir les figures 5 et 6. Noms de*
1038 *fossiles comme ci-dessus.*

1039

1040 **Figure 5:** Shape changes along frontal sinus volume shape parameter (SVSP). Wireframe
1041 (Figure 1) created in Morphologika showing shape changes in frontal sinus specific landmark
1042 configuration along the frontal SVSP. Left: mean configuration warped to lowest extreme of

1043 SVSP, right: mean configuration warped to highest extreme of SVSP (Figure 4). Top: norma
1044 frontalis, middle: norma lateralis.

1045

1046 **Figure 5:** *Changements de conformation du paramètre de forme du volume sinusal frontal*

1047 *(SVSP). Wireframe (Figure 1) créé dans Morphologika montrent des changements de*

1048 *conformation dans la configuration du point repère du sinus frontal dans la SVSP frontale.*

1049 *Gauche: configuration moyenne déformée au plus bas extrême de SVSP, à droite:*

1050 *configuration moyenne déformée au plus haut extrême de SVSP (Figure 4). En haut: norma*

1051 *frontalis, milieu: norma lateralis.*

1052

1053

1054 **Figure 6:** Shape changes along maxillary sinus volume shape parameter (SVSP). Wireframe

1055 (Figure 2) created in Morphologika showing shape changes in maxillary sinus-specific

1056 landmark configurations along the maxillary SVSP. Left: mean configuration warped to

1057 lowest extreme of SVSP, right: mean configuration warped to highest extreme of SVSP. Top:

1058 *norma frontalis, middle: norma lateralis.*

1059

1060 **Figure 6:** *Changements de conformation du paramètre de forme du volume sinusal maxillaire*

1061 *(SVSP). Wireframe (Figure 2) créé dans Morphologika montrent des changements de*

1062 *conformation dans la configuration du point repère du sinus maxillaire spécifique dans la*

1063 *SVSP maxillaire. Gauche: configuration moyenne déformée au plus bas extrême de SVSP, à*

1064 *droite: configuration moyenne déformée au plus haut extrême de SVSP (Figure 4). En haut:*

1065 *norma frontalis, milieu: norma lateralis.*

1066

1067

1068 **Figure 7:** Frontal sinuses in the *H. heidelbergensis* sample. Images of the virtually
1069 reconstructed crania rendered transparent with frontal sinuses sectioned out and rendered in
1070 black. Crania scaled to approximately the same size in order to show relative size of frontal
1071 sinuses to crania, scale bars under crania = 1cm. A: Bodo, B: Ceprano, C: Petralona, D:
1072 Broken Hill. Detail of qualitatively different Ceprano frontal sinus inset, shown from
1073 aspectus superialis. With the exception of Ceprano, all four specimens' frontal sinuses are
1074 single and continuous.

1075

1076 **Figure 7:** *Les sinus frontaux dans l'échantillon d'H. heidelbergensis. Images du crâne*
1077 *reconstitué montrant les sinus frontaux en noir. Les crânes ont été mis à l'échelle pour*
1078 *apparaître à la même taille approximative afin de montrer la taille relative des sinus*
1079 *frontaux, les barres d'échelle sous les crânes = 1cm. A: Bodo, B: Ceprano, C: Petralona, D:*
1080 *Broken Hill. Détail de l'insert du sinus frontal de Ceprano dont la forme est différente,*
1081 *montré en aspectus superialis. À l'exception de Ceprano, les sinus frontaux des quatre*
1082 *échantillons sont uniques et continus.*

1083

1084 **Figure 8:** A comparison of maxillary sinuses between species. Virtual reconstructions of
1085 crania showing sectioned out maxillary sinuses rendered in black in (A-C) Petralona (*H.*
1086 *heidelbergensis*), Guattari (*H. neanderthalensis*) and a recent *H. sapiens* from Mexico. Left
1087 view: norma frontalis, right view: norma lateralis. The norma lateralis view for Petralona is
1088 flipped horizontally for consistency and ease of comparison, since only the left maxillary
1089 sinus is fully preserved in this fossil. Crania scaled to approximately the same size in order to
1090 show relative size of maxillary sinuses, scale bars under crania = 1cm.

1091

1092 **Figure 8:** *Comparaison des sinus maxillaires entre les espèces. Reconstructions virtuelles de*
1093 *crânes montrant les sinus maxillaires en noir (A-C) Petralona (H. heidelbergensis), Guattari*
1094 *(H. neanderthalensis) et un H. sapiens récent du Mexique. A gauche: norma frontalis, à*
1095 *droite: norma lateralis. La vue en norma lateralis pour Petralona est inversée*
1096 *horizontalement pour faciliter la e comparaison, puisque seule sinus maxillaire gauche est*
1097 *entièrement préservé chez ce fossile. Les crânes ont été mis à l'échelle pour apparaître à la*
1098 *même taille approximative afin de montrer la taille relative des sinus maxillaires, les barres*
1099 *d'échelle sous les crânes = 1cm.*

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1102

1103 **Tables**

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Specimen/Group	Taxonomic group	Geographic location	Date	Number in sample	Medical/microCT	Source	FVS Y/N (sample n where >1)	FSS Y/N (sample n where >1)	MVS Y/N (sample n where >1)	MSS Y/N (sample n where >1)
KNM-ER 3883	<i>H. erectus</i>	Kenya	1.5-6 Ma [96]	1	Medical	KNM	N	N	N	N
Steinheim	<i>H. heidelbergensis</i>	Germany	>300 ka, MIS 9 [97]	1	Medical	UV	N	Y	N	N
Broken Hill	<i>H. heidelbergensis</i>	Zambia	~250-300 ka [98]	1	Medical	NHM	Y	Y	Y	Y
Bodo	<i>H. heidelbergensis</i>	Ethiopia	~600 ka [81]	1	Medical	UV	Y	N	Y	N
Petralona	<i>H. heidelbergensis</i>	Greece	~400 ka [75]	1	Medical	UV/UT	Y	Y	Y	Y
Ceprano	<i>H. heidelbergensis</i>	Italy	430-385 ka [99]	1	Medical	ULS	Y	N	N	N
Guattari	<i>H. neanderthalensis</i>	Italy	57-51 ka [100]	1	Medical	MNPE	Y	N	Y	N
Krapina 3	<i>H. neanderthalensis</i>	Croatia	~130 ka [101]	1	Medical	NESPOS	Y	N	N	N
Tabun C1	<i>H. neanderthalensis</i>	Israel	~122 ka [102]	1	Medical	NHM	Y	N	N	N
Forbes' Quarry	<i>H. neanderthalensis</i>	Gibraltar	~ 50 ka [103]	1	Medical	NHM	Y	N	Y	N
La Chapelle-aux-Saints 1	<i>H. neanderthalensis</i>	France	~ 50 ka [104]	1	Medical	MH	Y	Y	Y	Y
La Ferrassie 1	<i>H. neanderthalensis</i>	France	75 – 60 ka [105]	1	Medical	MH	Y	Y	Y	Y
La Quina 5	<i>H. neanderthalensis</i>	France	75-48 ka [105], [106]	1	Medical	MH	Y	N	N	N
Feldhofer Neanderthal	<i>H. neanderthalensis</i>	Germany	~40 ka [107]	1	Medical	UZ	Y	N	N	N
Skhul 5	Early <i>H. sapiens</i>	Israel	130-100 ka [108]	1	Medical	NESPOS	Y	N	N	N
Singa	Early <i>H. sapiens</i>	Sudan	>131-135 ka [104]	1	micro	NHM	Y	N	N	N

Mladeč 1	Early <i>H. sapiens</i>	Czech Republic	~37.5-34.75 ka [109]	1	Medical	UV	Y	N	Y	Y
Cro-Magnon 1	Early <i>H. sapiens</i>	France	<28 ka [110]	1	Medical	MH	Y	N	Y	N
Cro-Magnon 2	Early <i>H. sapiens</i>	France	<28 Ka [110]	1	Medical	MH	Y	Y	N	N
Cro-Magnon 3	Early <i>H. sapiens</i>	France	<28 Ka [110]	1	Medical	MH	Y	N	N	N
Ngaloba	Early <i>H. sapiens</i>	Tanzania	50-120 ka [111], [112]	1	Medical	UV	Y	N	N	N
Lithuania	Recent <i>H. sapiens</i>	Lithuania	<25 ka	14	Medical	TK	Y (11)	Y (10)	Y (11)	Y (8)
Western Africa	Recent <i>H. sapiens</i>	Angola, Liberia, Nigeria	<25 ka	13	Medical	ORSA	Y (13)	Y (8)	Y (12)	Y (8)
Western Europe	Recent <i>H. sapiens</i>	Germany, The Netherlands, Norway, Sweden	<25 ka	12	Medical	NESPOS	Y (11)	Y (10)	Y (10)	Y (10)
India	Recent <i>H. sapiens</i>	India	<25 ka	12	Medical	ORSA	Y (11)	Y (10)	Y (10)	Y (5)
Greenland	Recent <i>H. sapiens</i>	Greenland	<25 ka	7	micro	NHM	Y (7)	Y (7)	Y (7)	Y (7)
Russia	Recent <i>H. sapiens</i>	Russia	<25 ka	4	Medical	ORSA	Y (4)	Y (4)	Y (4)	Y (2)
North Africa	Recent <i>H. sapiens</i>	Algeria, Morocco	<25 ka	7	Medical	IPH	Y (7)	Y (3)	Y (2)	Y (1)
Tasmania	Recent <i>H. sapiens</i>	Tasmania	<25 ka	8	micro	NHM	Y (8)	Y (5)	Y (8)	Y (3)
Torres Straits Islands	Recent <i>H. sapiens</i>	Torres Straits Islands	<25 ka	15	micro	NHM	Y (12)	Y (10)	Y (12)	Y (8)
Peru	Recent <i>H. sapiens</i>	Peru	<25 ka	10	Medical	ORSA	Y (10)	Y (10)	Y (10)	Y (10)

China	Recent <i>H. sapiens</i>	China	<25 ka	10	Medical	ORSA	Y (9)	Y (9)	Y (10)	Y (8)
Hawaii	Recent <i>H. sapiens</i>	Hawaii	<25 ka	11	micro	NHM	Y (11)	Y (10)	Y (10)	Y (8)
Mexico	Recent <i>H. sapiens</i>	Mexico	<25 ka	10	Medical	ORSA	Y (10)	Y (8)	Y (9)	Y (5)

Replication	Frontal	Maxillary
1	7616.8	17214.2
2	7785.7	16947.0
3	7353.4	16688.7
4	7598.5	16735.8
5	7751.4	18416.8
Mean	7621.2	17200.5
Standard deviation	170.5	710.9
% error	1.8	2.9

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Landmark	Definition	Number in frontal sinus-specific landmark set
Bregma	Point where coronal & sagittal sutures intersect	1
Glabella	Most anterior point on frontal bone	2
Nasion	Point of intersection of nasofrontal suture & midsagittal plane	3
C/P3	Most inferior external point between maxillary canine (C) and first pre-molar (P3)	4
Frontomalare orbitale	Point where zygomaticofrontal suture crosses orbital margin	5
Zygoorbitale	Point where zygomaticomaxillary suture intersects with inferior orbital margin	6
Frontotemporale	Point on frontal bone where temporal line reaches its most anteromedial position	7
Frontomalare temporale	Most lateral point on zygomaticofrontal suture	8
Porion	Most superior point on margin of external auditory meatus	9
Lambda	Point where sagittal & lambdoid sutures intersect	10

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Landmark	Definitions	Number in maxillary sinus-specific landmark set
Bregma	Point where coronal & sagittal sutures intersect	1
Glabella	Most anterior point on frontal bone	2
Nasion	Point of intersection of nasofrontal suture & midsagittal plane	3
Alare	Most lateral point on nasal aperture taken perpendicular to nasal height	4
C/P3	Most inferior external point between maxillary canine (C) and first premolar (P3)	5
Zygoorbitale	Point where zygomaticomaxillary suture intersects with inferior orbital margin	6
Zygion	Most lateral point on surface of zygomatic arch	7
Zygomaxillare	Most inferoanterior point on zygomaticomaxillary suture	8
Molars pos.	Most inferoposterior point on external maxillary alveolus (posterior to M3)	9
Porion	Most superior point on margin of external auditory meatus	10
Lambda	Point where sagittal & lambdoid sutures intersect	11
Ectomolare	Most lateral point on outer surface of alveolar margin of maxilla	12
Orale	Point of intersection on palate with line tangent to posterior margins of central incisor alveoli	13

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Landmark set	PC	Variance explained (%)	Direction of relationship	r²	p	Bonferroni correction
Frontal sinus-specific	6	7	Negative	0.12	< 0.001	Yes
Maxillary sinus-specific	3	11	Positive	0.41	< 0.001	Yes

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	<i>H. sapiens</i>	<i>H. neanderthalensis</i>	<i>H. heidelbergensis</i>
<i>H. sapiens</i>		0.05848	0.6914*
<i>H. neanderthalensis</i>	1		0.6930*
<i>H. heidelbergensis</i>	0.0006*	0.0186*	

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	<i>H. sapiens</i>	<i>H. neanderthalensis</i>	<i>H. heidelbergensis</i>
<i>H. sapiens</i>		0.6059*	0.4542*
<i>H. neanderthalensis</i>	0.0001*		-0.0714
<i>H. heidelbergensis</i>	0.0147*	0.5275	

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	<i>H. sapiens</i>	<i>H. neanderthalensis</i>	<i>H. heidelbergensis</i>
<i>H. sapiens</i>		0.311	0.591*
<i>H. neanderthalensis</i>	0.194		-0.25
<i>H. heidelbergensis</i>	0.015*	1	

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	<i>H. sapiens</i>	<i>H. neanderthalensis</i>	<i>H. heidelbergensis</i>
<i>H. sapiens</i>		0.9599*	0.6119*
<i>H. neanderthalensis</i>	0.0001*		1
<i>H. heidelbergensis</i>	0.0062*	0.3447	

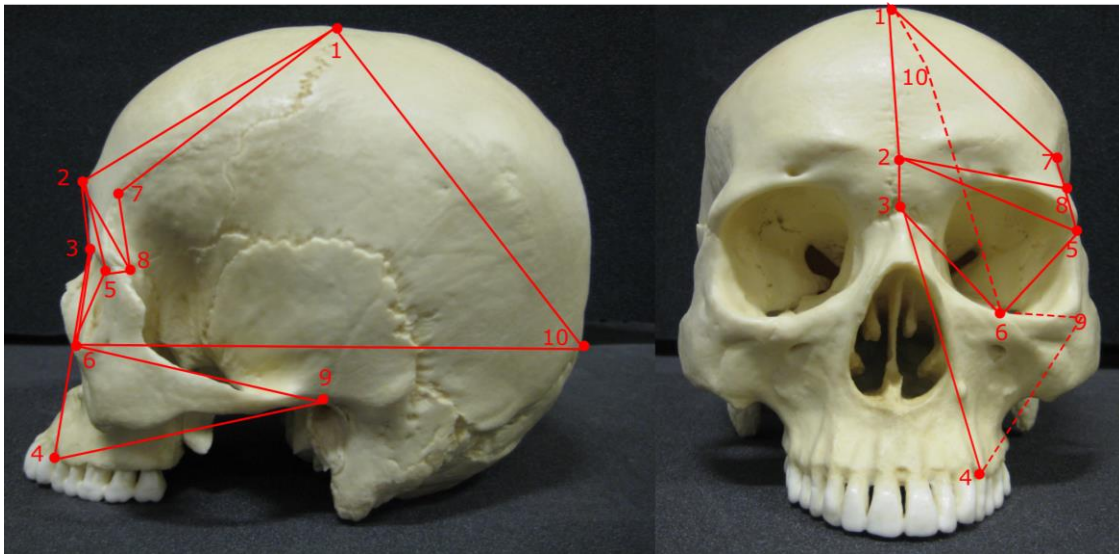
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1130 **Figures**

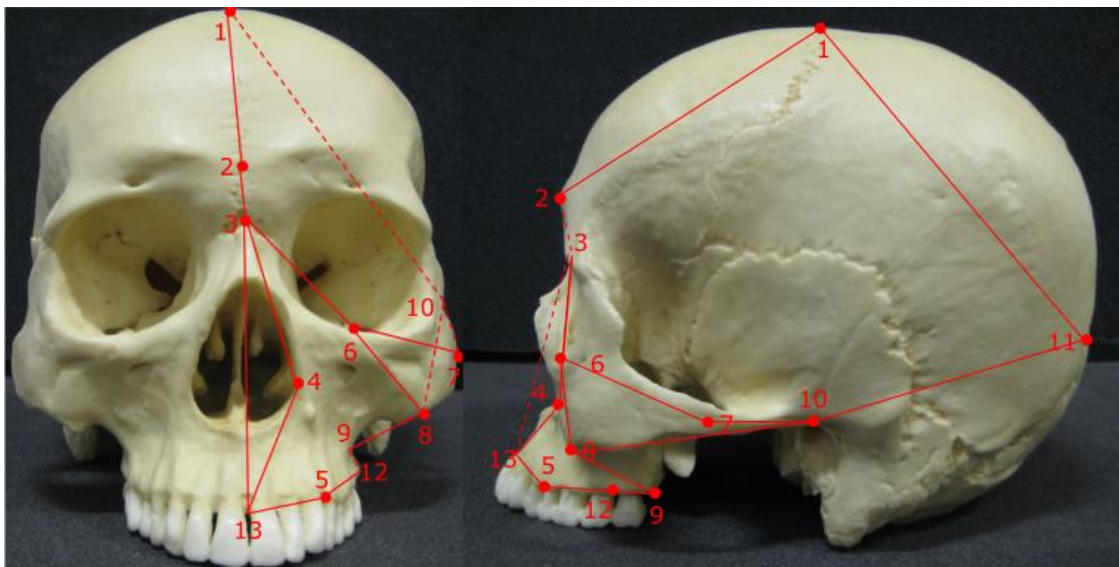
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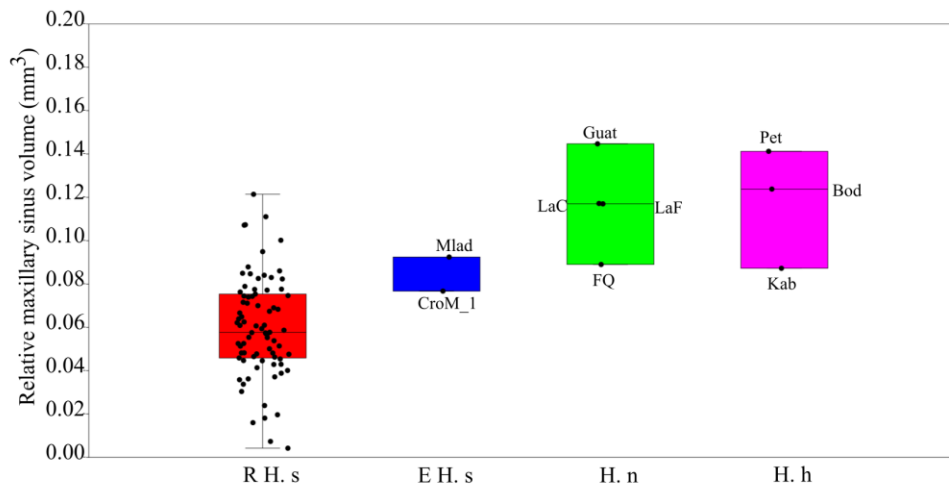
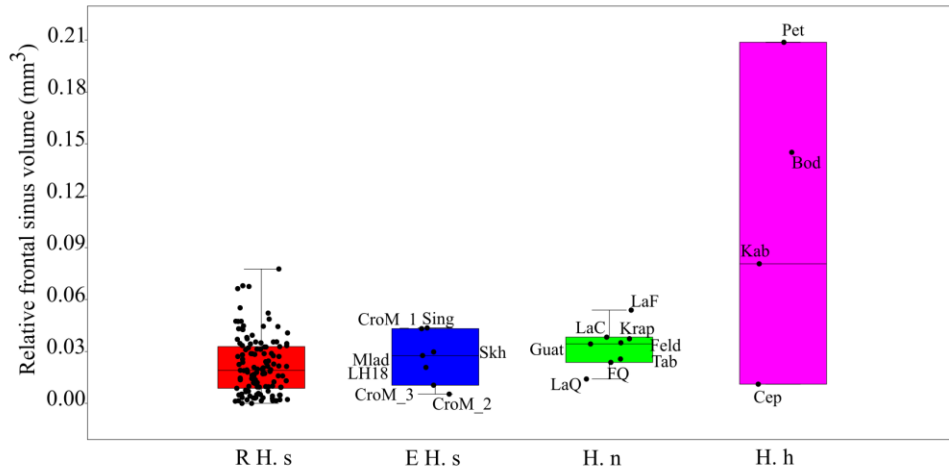
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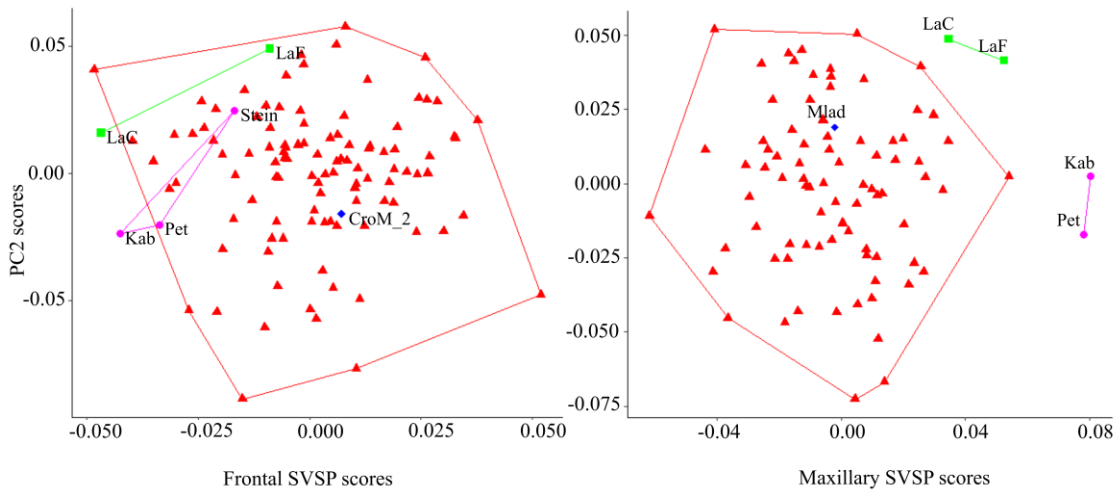
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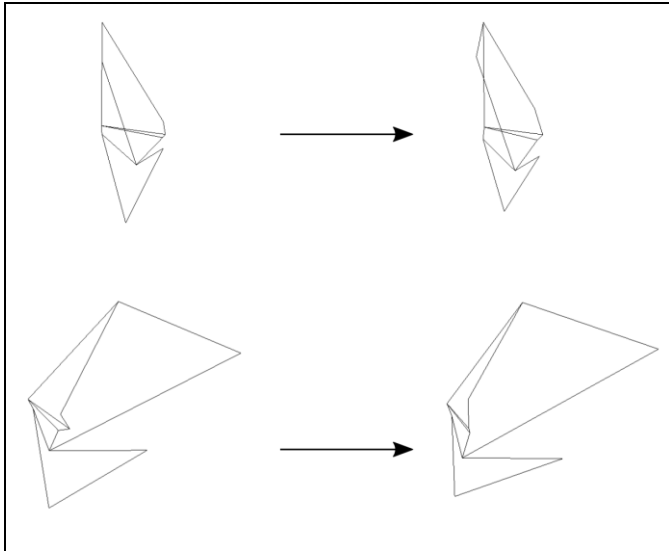
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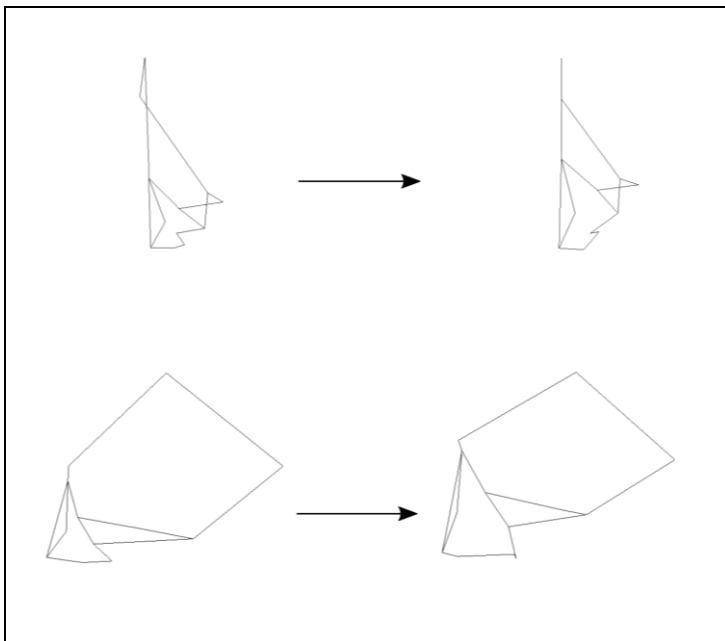
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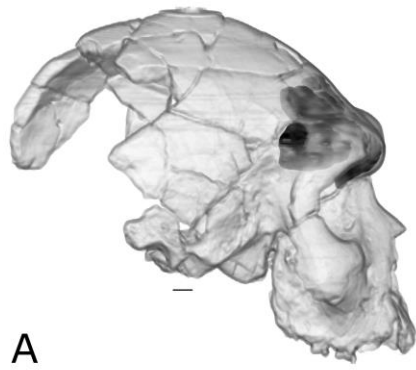
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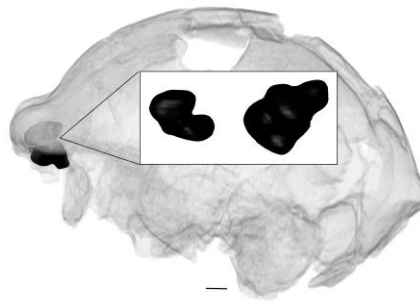
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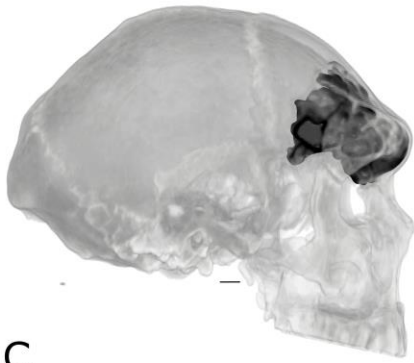
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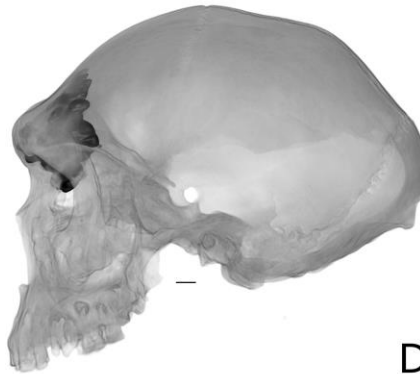
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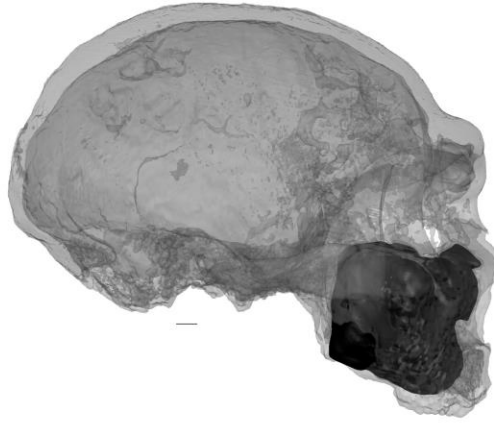
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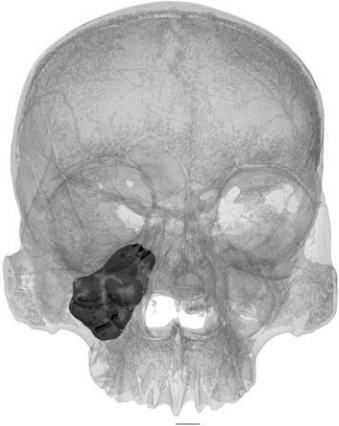
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C



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1157 **Supplementary**

1158

1159 **Figure S1:** Illustration of estimation of sinus volume in partially broken maxillary sinus (Broken
1160 Hill). A: rendered right maxillary sinus volume. B: virtual reconstruction of cranium with rendered
1161 sinuses in situ (right maxillary sinus in red), coloured lines show positions of slices shown below. C:
1162 CT slices showing maxillary sinus area manually selected in red. Left / green: coronal slice, middle /
1163 blue: sagittal slice, right / red: transverse slice. See also sediment within the sinus cavity that can be
1164 distinguished from bone due to its location, shape and radio-density (greyscale values).

1165

1166 *Figure S1: Illustration de l'estimation du volume sinusal dans le sinus maxillaire partiellement cassé*
1167 *(Broken Hill). A: volume sinusal maxillaire droit. B: reconstruction virtuelle du crâne avec des sinus*
1168 *rendus in situ (sinus maxillaire droit en rouge), les lignes colorées montrent les positions des tranches*
1169 *illustrées ci-dessous. C: des coupes de tomodynamométrie montrant la zone de sinus maxillaire*
1170 *sélectionnée manuellement en rouge. Gauche / vert: coupe coronale, milieu / bleu: coupe sagittale,*
1171 *droite / rouge: coupe transversale. Voir aussi les sédiments dans la cavité sinusale qui peuvent être*
1172 *distingués des os en raison de leur emplacement, de leur forme et de leur densité radio (valeurs de*
1173 *niveaux de gris).*

1174

1175 **Figure S2:** All preserved sinuses in *H. heidelbergensis* sample. A: Bodo, B: Broken Hill (Kabwe), C:
1176 Ceprano, D: Petralona. Left: front view, right: side view. Bodo lateral view is flipped horizontally for
1177 ease of comparison with other fossils. All specimens scaled to approximately same size to illustrate
1178 relative sinus size.

1179

1180 *Figure S2: Tous les sinus conservés dans l'échantillon de H. heidelbergensis. A: Bodo, B: Broken Hill*
1181 *(Kabwe), C: Ceprano, D: Petralona. Gauche: vue de face, à droite: vue latérale. La vue latérale de*
1182 *Bodo est retournée horizontalement pour faciliter la comparaison avec les autres fossiles. Tous les*
1183 *spécimens ont une taille approximative identique pour illustrer la taille des sinus.*

1184

1185 **Figure S3:** All preserved sinuses in *H. neanderthalensis* sample. A: Guattari 1, B: Feldhofer 1, C:
1186 Forbes' Quarry, D: Krapina 3, E: La Ferrassie 1, F: La Chapelle-aux-Saints 1, G: Tabun C1. Left:
1187 front view, right: side view. Guattari lateral view is flipped horizontally for ease of comparison with
1188 other fossils. All specimens scaled to approximately same size to illustrate relative sinus size.

1189

1190 *Figure S3: Tous les sinus préservés dans l'échantillon d' H. neanderthalensis. A: Guattari 1, B:*
1191 *Feldhofer 1, C: Forbes' Quarry, D: Krapina 3, E: La Ferrassie 1, F: La Chapelle-aux-Saints 1, G:*
1192 *Tabun C1. Gauche: vue de face, à droite: vue latérale. La vue latérale de Guattari est retournée*
1193 *horizontalement pour faciliter la comparaison avec les autres fossiles. Tous les spécimens ont une*
1194 *taille approximativement identique pour illustrer la taille relative des sinus*

1196

1197 **Figure S4:** All preserved sinuses in early *H. sapiens* sample. A: Cro-Magnon 1, B: Cro-Magnon 2, C:
1198 Cro-Magnon 3, D: Ngaloba, E: Mladeč 1, F: Singa, G: Skhul V. Left: front view, right: side view.
1199 Cro-Magnon1 lateral view is flipped horizontally for ease of comparison with other fossils. All
1200 specimens scaled to approximately same size to illustrate relative sinus size.

1201 *Figure S4: Tous les sinus conservés dans l'échantillon H. sapiens anciens. A: Cro-Magnon 1, B: Cro-*
1202 *Magnon 2, C: Cro-Magnon 3, D: Ngaloba, E: Mladeč 1, F: Singa, G: Skhul V. Gauche: vue de face,*

1203 à droite: vue latérale. La vue latérale de Cro-Magnon 1 est retournée horizontalement pour faciliter
1204 la comparaison avec d'autres fossiles. Tous les spécimens ont une taille approximativement identique
1205 pour illustrer la taille de sinus relative.
1206

1207 **Figure S5:** Landmarks used to calculate centroid size to calculate relative sinus volumes (see Table
1208 S1).

1209
1210 *Figure S5: Points de repères utilisés pour calculer la taille du centroïde afin de calculer les volumes*
1211 *sinusaux relatifs (voir tableau S1).*

1212
1213 **Figure S6:** Relative frontal sinus volume against frontal sinus shape parameter (PC6) in reduced
1214 sample. Red triangles: recent *H. sapiens*, blue diamond: early *H. sapiens*, green square: Neanderthals,
1215 magenta circles: *H. heidelbergensis*. For sample composition see Table 1, main text.

1216 *Figure S6: Volume de sinus frontal relatif par rapport au paramètre de forme de sinus frontal (CP6)*
1217 *dans un échantillon réduit. Triangles rouges: H. sapiens récents, diamant bleu: H. sapiens anciens,*
1218 *carré vert: néandertaliens, cercles magenta: H. heidelbergensis. Pour la composition de l'échantillon,*
1219 *voir le tableau 1, texte principal.*

1220

1221 **Figure S7:** Relative maxillary sinus volume against maxillary sinus shape parameter (PC3) in reduced
1222 sample. Red triangles: recent *H. sapiens*, blue diamond: early *H. sapiens*, green square: Neanderthals,
1223 magenta circles: *H. heidelbergensis*. For sample composition see Table 1, main text.

1224

1225 *Figure S7: Volume du sinus maxillaire relatif par rapport au paramètre de la forme du sinus*
1226 *maxillaire (PC3) dans un échantillon réduit. Triangles rouges: H. sapiens récents, diamant bleu: H.*
1227 *sapiens anciens, carré vert: néandertaliens, cercles magenta: H. heidelbergensis. Pour la composition*
1228 *de l'échantillon, voir tableau 1, texte principal*

1229 **Table S1:** Landmarks used to calculate centroid size to standardise sinus volume.

1230

1231 *Tableau S1: Repères utilisés pour calculer la taille du centroïde afin de normaliser le volume sinusal.*

1232 **Table S2:** Absolute frontal sinus volumes.

1233

1234 *Tableau S2: Volumes absolus de sinus frontal.*

1235

1236 **Table S3 :** Absolute maxillary sinus volumes.

1237 *Tableau S3: Volumes absolus de sinus maxillare.*

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