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1 **THE EVOLUTIONARY HISTORY OF THE HUMAN FACE**

2

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21

22 **Abstract:** The face is the most distinctive feature used to identify others. Modern humans have  
23 a short, retracted face beneath a large globular brain case that is distinctively different from that  
24 of our closest living relatives. The face is a skeletal complex formed by 14 individual bones  
25 housing parts of the digestive, respiratory, visual, and olfactory systems. A key to understanding  
26 the origin and evolution of the human face is to analyze the faces of extinct taxa in the hominin  
27 clade over the last 6 million years. Yet as new fossils are recovered, and the number of hominin  
28 species grows, the question of how and when the modern human face originated remains  
29 unclear. By examining key features of the facial skeleton, here we evaluate the evolutionary  
30 history of the modern human face in the context of its development, morphology, and function,  
31 and suggest that its appearance is the result of a combination of biomechanical, physiological  
32 and social influences.

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## 44 **Introduction**

45

46 The human face differs across populations and is the most distinctive feature used to identify  
47 and recognize others. Beneath the skin and muscles of facial expression, the face is a skeletal  
48 complex formed by 14 individual bones housing parts of the digestive, respiratory, visual and  
49 olfactory systems. The face plays an important role in social interaction and communication,  
50 signaling more than 20 different categories of emotion via the contraction or relaxation of  
51 muscles<sup>1</sup>. The face begins forming in the human embryo around 24 days via a complex cascade  
52 of molecular interactions. A number of specializations at this level set the face apart, including  
53 the functions of specialized pluripotent cells known as cranial neural crest cells (CNC), the main  
54 contributors to the development of the facial skeleton<sup>2</sup> Facial shape appears to be influenced by  
55 a limited set of candidate genes<sup>3</sup>. Important constraints in the development of the face, or  
56 viscerocranium, are the surrounding cranial structures as facial growth is closely integrated with  
57 the development of the braincase (neurocranium), and other cranial components<sup>4</sup>, highlighting  
58 the interdependence of different morphological traits, or modules, during growth and  
59 development<sup>5,6</sup> (see Box 1).

60

61 A detailed account of the evolution of the human face is a difficult endeavor, largely because of  
62 the intricate and complex nature of its development, and the many factors that influence the  
63 face pre- and post-natally<sup>7</sup>. To constrain our line of inquiry, we suggest here that the  
64 evolutionary changes that occurred on the path to becoming the large-brained, short-faced  
65 hominins we are today, are best interpreted by analyzing the extinct taxa in the hominin clade  
66 over the last ~4 million years (Ma). In this review, we investigate the evolutionary roots of the  
67 modern human face, describing characteristics of the australopiths, early *Homo*, and more  
68 recent hominins to tease apart the morphological transformations that occurred over time and to  
69 discuss factors that have shaped their evolution. We also highlight the earliest evidence of the  
70 *H. sapiens* face and consider the impact of environmental and social factors, population history  
71 and palaeogenomics as well as adaptive explanations, in shaping morphological changes in the  
72 face over time.

73

## 74 **The ancestral facial morphotype**

75

76 That the human and chimpanzee/bonobo lineages shared a most recent common ancestor is  
77 beyond dispute, but no extant African hominoid presents an ideal facial morphotype for the

78 chimp-human ancestor<sup>8</sup>. In their facial morphology, the chimpanzee, bonobo and gorilla differ  
79 from undoubted early hominins (like *Australopithecus*) in fundamental ways. For example, all  
80 three share a distinctive protruding bony arch above the eyes that, in life, sets off the upper rim  
81 of the naked facial mask from the braincase and other parts of the face to which the muscles of  
82 mastication attach. In contrast, the earliest hominins have supraorbital structures that are  
83 weakly differentiated topographically from the braincase, even when there is a distinct  
84 supraorbital torus, as is common in some species of *Homo*<sup>9,10</sup>. As has been suggested for other  
85 ectocranial structures<sup>11</sup>, these differences may reflect a combination of social display  
86 mechanisms and biomechanical performance<sup>12</sup>. As discussed below with respect to the  
87 evolution of the modern human face, the role of social factors in shaping the morphology of the  
88 craniofacial skeleton has received much less attention than those relating to the biomechanics  
89 of the feeding system.

90  
91 In the non-human African great apes (i.e., chimpanzees, bonobos and gorillas), as compared to  
92 known fossil hominins, postnatal growth results in a vertically deep, long and strongly inclined  
93 snout, at the front end of which the prow-like projection of the premaxilla places the expansive  
94 incisor row well forward of the large, tusk-like canine crowns, creating a gap (diastema) between  
95 the lateral incisor and canine. In contrast, the midface of early hominins is shorter with a more  
96 vertical profile seen from the side—a derived condition shared with modern humans—and  
97 although the premaxilla in the most basal hominin species remains primitively prognathic, the  
98 diastema is less frequent. Independent evolution of the maxillary and premaxillary components  
99 of the early hominin midface is consistent with hypotheses of modular development of the  
100 face<sup>13</sup>. The observed differences in prognathism are associated with distinct growth patterns  
101 and remodeling activity of bone cells<sup>14-16</sup> (see Box 2). The derived facial configuration of early  
102 hominins is likely due to a combination of factors including cranial base shortening and canine  
103 crown/root reduction.

104  
105 ***Ardipithecus* vs. *Australopithecus*: Principal morphological shifts - canines vs.**  
106 **mastication**

107  
108 The facial morphologies of *Ardipithecus ramidus* (~4.4 Ma), a candidate basal hominin, and  
109 generalized *Australopithecus* species (best represented by *Australopithecus afarensis*, ~3.7-3.0  
110 Ma) differ in similar ways from the non-human African great ape condition yet they are  
111 distinguishable from one another (Fig. 1a). As in later hominins, including modern humans, the

112 maxilla is vertically short, midfacial projection is reduced and the supraorbital structures are  
113 topographically integrated with the braincase <sup>17</sup>. Both taxa feature shortened basicrania and  
114 reduced, modest sexually dimorphic canine crowns and roots as well as smaller incisors <sup>9,17</sup>. On  
115 the other hand, *Ar. ramidus* and *Au. afarensis* differ from one another in the parts of the face  
116 anchoring the muscles of mastication (Fig. 1a). The *Au. afarensis* face is dominated by  
117 expansive zygomatic (cheek) bones with robust, flaring arches that bridge the face to the  
118 braincase <sup>9</sup>, whereas *Ar. ramidus* shares with the chimpanzee vertically short, lightly built  
119 zygomatic bones and arches <sup>17</sup>. The *Au. afarensis* anatomy is part of a presumptively derived  
120 masticatory system that includes transversely thick mandibular bodies, tall mandibular rami, and  
121 thickly enameled cheek teeth. Although it is tempting to tie these features to the species'  
122 expansive range of dietary-carbon isotopic values, which includes individuals with a significant  
123 component of C4 plants (e.g., grasses, sedges, undergrounds storage organs) in their diet <sup>18</sup>,  
124 the lesser known *Au. anamensis* (~4.2-3.9 Ma), the probable phyletic ancestor of *Au. afarensis*  
125 (see Fig. 1b for the temporal placing of taxa discussed), shares many of these masticatory  
126 features yet it maintained a strongly C3 plant-focused (e.g. fruits, leaves) diet similar to that of  
127 chimpanzees and *Ardipithecus* <sup>19</sup>. The contrast between *Ardipithecus* and early  
128 *Australopithecus* highlights the modularity of facial anatomy in the early part of the hominin  
129 lineage. The initial changes were focused in the central and upper portions of the face, perhaps  
130 in response to changes in the function of the canines and supraorbital region in social signaling,  
131 whereas subsequent changes mainly involved the masticatory apparatus.

132

FIGURE 1 HERE

134

### 135 ***Australopithecus* (incl. *Paranthropus*) craniofacial diversity: Patterns and causes**

136

137 Relative to extant great apes and *Ardipithecus*, *Australopithecus* species (including those some  
138 authors classify within the genus *Paranthropus*) are characterized by a suite of specialized  
139 craniofacial features including the relative expansion of premolar-molar occlusal area, especially  
140 robust mandibular bodies and osteological indications of the enlargement or rearrangement of  
141 the jaw-adductor muscles to maximize vertical bite forces. These derived features have long  
142 been interpreted as adaptations to mechanically tough or hard plant foods that dominated in  
143 African environments during a period of aridification in the late Pliocene ( $\leq 2.8$ - $2.7$  Ma) <sup>20,21</sup>. Yet  
144 incipient expressions of these features can already be seen in the early australopith species  
145 (such as *Au. afarensis* and *Kenyanthropus platyops*), which thrived in the relatively equable,

146 though highly seasonal, environments of the African mid-Pliocene (~3.5-3.0 Ma). Furthermore,  
147 molar microwear, an indicator of food mechanical properties, does not necessarily agree with  
148 suggestions that hard or tough food items were an increasingly common component of the  
149 diet<sup>22</sup>. This is despite progressive changes in the masticatory system (extreme forward shifts in  
150 the origins masseter and temporalis, two large muscles of mastication; increased massiveness  
151 and lateral flare of the zygomatic arches; marked retraction of the dental arches; enhanced  
152 postcanine megadonty and enamel thickness, etc.) among the diverse australopith species after  
153 ~3.0 Ma, culminating in the appearance by ~2.6 Ma of the bizarre “robust” australopith  
154 (= *Paranthropus*) configuration. *Australopithecus africanus* of southern Africa (~2.7-2.3 Ma) and  
155 *Au. garhi* of eastern Africa (~2.5 Ma) appear to represent early stages of this structural  
156 transformation. The younger species *Au. sediba* (~2.0 Ma) from South Africa<sup>23</sup> shares derived  
157 facial features with *Au. africanus*<sup>10</sup>, but its facial remodeling differs from all other  
158 *Australopithecus* facial skeletons (see Box 2, Fig. 2)<sup>15</sup>. Resolving the dissonant dietary signals  
159 from isotopes, microwear, and craniofacial functional morphology should be an important focus  
160 of future research in early hominin paleobiology.

161

## 162 **Patterns of diversity in the early *Homo* face**

163

164 Evidence from the face constitutes one of the strongest arguments for a taxonomically diverse  
165 fossil record of early *Homo* (~2.1-1.7 Ma), which recognizes *Homo habilis*, *H. rudolfensis* and  
166 early African *H. erectus* (= *H. ergaster* of some authors) as distinct species. If large specimens  
167 such as KNM-ER 1470 and KNM-ER 62000 (usually attributed to *H. rudolfensis*), on the one  
168 hand, and smaller specimens like KNM-ER 1813 and OH 13 (*H. habilis*), on the other, are  
169 combined in a single species, then the implied pattern of sexual dimorphism, in which  
170 divergence in supraorbital form, masticatory structure, and midfacial proportions accompanies  
171 differences in size, is unlike that seen in any of the extant great apes or Old World monkeys  
172 (see Table 1 for specimen attribution). Despite these differences, the faces of all three *Homo*  
173 species are less projecting than those of australopiths, especially in the premaxillary region, and  
174 they show a tendency for the circumnasal plates, the outer rims of the orbits, and the zygomatic  
175 bones to face laterally in fully mature growth stages compared to their front-facing orientation in  
176 the australopiths. While its prominent supraorbital torus is a species hallmark, the face of early  
177 *H. erectus* is more modern human-like than that of either *H. habilis* or *H. rudolfensis*, with a  
178 more vertical profile featuring a retracted subnasal plate and a prominent nasal bridge. In  
179 support of these modifications in the upper face of *H. erectus*, it should also be considered that

180 although *H. habilis* and *H. rudolfensis* have less robust mandibular bodies than do the  
181 australopiths, when scaled against admittedly crude estimates of body mass, neither of them  
182 have mandibular bodies as gracile as those seen in early *H. erectus*<sup>24</sup>.

183

184 There is a tendency to interpret the morphology of the early *Homo* face exclusively in terms of  
185 dietary behavior, but to do so would be an oversimplification. As suggested above for the  
186 earlier, more generalized hominins, there were likely other influences. Nonetheless, historically,  
187 diet has played a large part in explaining changes in facial morphology within the hominin clade,  
188 and particularly in and around the hypothesized origin of the genus *Homo*<sup>25</sup>. These narratives  
189 either explicitly or implicitly suggest that the origin of *Homo* coincides with a grade shift that  
190 includes a change in feeding behavior. Under this scenario, early *Homo* consumed foods that  
191 could be processed without the large postcanine processing area, expanded masticatory  
192 musculature, or robust mandibular bodies that characterized the australopiths. Conventional  
193 wisdom suggests that the relaxation of selection for postcanine megadontia and robust jaws  
194 coincided with a new emphasis on stone tool-assisted meat consumption. Two recent  
195 developments complicate this scenario. First, the earliest known stone tools, at 3.3 Ma<sup>26</sup>,  
196 coincide in time with *Au. afarensis* (and the australopith-grade taxon *K. platyops* of eastern  
197 Africa), predating the earliest fossils of *Homo* by several hundred thousand years—although the  
198 function(s) of these tools is yet unclear, as is their possible use in carnivory. Second, a shift  
199 towards a strong C4 dietary signature occurred in *Homo* with the appearance of early African *H.*  
200 *erectus* ( $\leq 1.7$  Ma), rather than in the earlier species *H. habilis* and *H. rudolfensis*, whose modal  
201 carbon stable isotope signal is similar to that of *Au. afarensis* and *Au. africanus*, suggesting a  
202 mixed C3/C4 diet<sup>19</sup>. These observations are consistent with evidence that early African *H.*  
203 *erectus* was likely the first hominin taxon to show reduction in facial size, postcanine processing  
204 area and mandibular body robusticity—changes that may have resulted from an adaptation to  
205 the routine consumption of foods that require less oral processing. If increased meat  
206 consumption was part of that dietary shift, it would imply that the meat was tenderized before  
207 being ingested. An added component here would be the advent of methods for pre-processing  
208 underground storage organs (e.g. tubers, bulbs), thus reducing the mechanical demands of  
209 masticating these items<sup>27</sup>.

210

FIGURE 2 HERE

211

212 **The faces of the Middle Pleistocene hominins and the LCA**

213 To date, *H. erectus*, is the earliest hominin found outside Africa, in the early Pleistocene <sup>28</sup>.  
214 Following the first dispersal out of Africa, *Homo* evolved into new forms in the Middle  
215 Pleistocene (MP), spreading over parts of Eurasia. MP hominins share a number of facial  
216 characteristics, some of which are present in earlier hominins, but also show a number of new  
217 traits. In some, there is a trend towards increased overall facial robusticity, with enlarged  
218 midfaces, strongly built brows and a large braincase, all seen in the fossil record by ~600  
219 thousand years ago (Ka) (Fig. 3). These MP hominins are a possible ancestral pool for the  
220 emergence of *Homo sapiens*. Hence, MP taxa could include the last common ancestor (LCA) of  
221 *H. sapiens* and other now extinct taxa. But, which of the known MP hominins might be best  
222 suited as the LCA? Importantly also, the LCA should predate the appearance of a modern face,  
223 which begs the question: What is the earliest evidence of a modern human face? In considering  
224 the origins of the human face, we should take into account that mounting genetic and morphological  
225 data support the notion that *H. sapiens* first appeared in Africa <sup>29-31</sup>. But these same data also imply  
226 that while fully fledged *H. sapiens* likely had an African beginning, the evolutionary origins of traits  
227 characteristic of the modern face, represented by the LCA, may be found elsewhere.

228  
229 To address the question of the LCA, we here focus on key features, with an emphasis on  
230 phylogenetic and functional discussions of the modern human zygomaxillary morphology.  
231 Modern human zygomaxillary morphology is quite distinct from that found in MP groups such as  
232 the early Neanderthals (Fig. 3a) and the large crania assigned to *H. heidelbergensis*, including  
233 Petralona (Greece), Bodo 1 (Ethiopia) (Fig. 3b), and Broken Hill 1 (Zambia) (Fig. 3c) (see also  
234 Table 1). In modern humans, the anterior surface of the zygomatic is angled at about 90° to the  
235 midline, the inferior border is either vertically below the superior border or is retracted, and the  
236 inferior border reaches the alveolar process in a sharp inflexion rather than in a more gradual  
237 curvature. There is usually a malar notch, a zygomaxillary tubercle and a canine fossa (a  
238 depression below the orbit). Was the zygomaxillary region in the LCA of the *H. sapiens* and *H.*  
239 *neanderthalensis* lineages more like the modern human or the Neanderthal condition, or was it  
240 intermediate? We will now review potential candidates of the LCA.

241 FIGURE 3 HERE

242  
243  
244 ***Homo heidelbergensis* as the LCA?**  
245

246 Stringer <sup>32</sup> has argued that shape resemblances between the Petralona and Broken Hill 1 crania  
247 indicated the existence of a widespread MP population which, if the Mauer mandible (Germany)  
248 is included, would be called *H. heidelbergensis*. Excluding the Mauer jaw whose diagnostic  
249 credentials have been questioned<sup>33</sup>, the nomen *H. rhodesiensis* could be applied<sup>32,34</sup>.  
250 Furthermore, it was argued that this species represented the best candidate for the LCA of the  
251 *H. sapiens* and *H. neanderthalensis* lineages (see also <sup>35</sup>). Mounier and Lahr <sup>36</sup> produced  
252 several hypothetical virtual reconstructions of the LCA, and these also showed a *H.*  
253 *heidelbergensis*-like facial morphology. One implication of a *H. heidelbergensis*-like LCA would  
254 be that the zygomaxillary morphology found in these large MP crania would have undergone  
255 gracilisation to become the form found in recent *H. sapiens*, and a second trajectory, featuring  
256 increased midfacial projection and maxillary inflation, that led to the facial configuration found in  
257 the Neanderthals.

258

259 One complicating factor, often minimized or omitted from these discussions, is the differing and  
260 arguably more *H. sapiens*-like morphology found in smaller individuals sometimes assigned to  
261 *H. heidelbergensis*, including the Thomas Quarry (Morocco) and Ndutu (Tanzania) partial  
262 crania, and the Broken Hill 2 maxilla <sup>30</sup>. It is possible that allometric factors influence the  
263 zygomaxillary morphology when comparing smaller and larger individuals <sup>37,38</sup> given the  
264 association between body size and facial size in primates<sup>39</sup>. Thus, sexual dimorphism could also  
265 be a factor if Thomas Quarry, Ndutu and Broken Hill 2 represent female individuals, and  
266 Petralona, Broken Hill 1 and Bodo much larger males. This issue is further complicated by the  
267 apparent presence of a more *H. sapiens*-like midfacial morphology in Chinese fossils from the  
268 MP, such as Zhoukoudian, Nanjing (Fig. 3d), Dali and Jinniushan <sup>40</sup>. This morphology is  
269 especially apparent in the newly announced (but not yet published scientifically) cranium, said to  
270 be from Harbin, North East China. These examples could perhaps be the result of gene flow or  
271 an independent evolutionary trajectory convergent on that of *H. sapiens*, raising the issue of  
272 whether these differences are phylogenetically meaningful. However, an alternative and  
273 plausible scenario implicates the morphology of the early European hominin species, *H.*  
274 *antecessor*, as we shall discuss.

275

### 276 ***Homo antecessor* as the LCA?**

277 In this scenario, a more ancient and taxonomically distinct LCA for the *H. sapiens* and *H.*  
278 *neanderthalensis* lineages, is based on the claimed “modern” maxillary conformation of the  
279 ATD6-69 *H. antecessor* face from Gran Dolina, Atapuerca, dated at ~850 Ka <sup>41,42</sup> (Fig. 2e). This

280 model implies that a *H. antecessor*-like facial morphology was retained in the descendant *H.*  
281 *sapiens* lineage, but was modified in that of the Neanderthals. Some original reservations  
282 regarding this morphology given the juvenile status of ATD6-69<sup>43</sup> were removed with the finding  
283 of similar morphology in fragmentary adult maxillae<sup>41,44</sup>. The modern appearance of ATD6-69 is  
284 also substantiated by growth simulations of this specimen based on both the Neanderthal and  
285 modern human facial growth trajectories<sup>38</sup>, and by the analysis of the facial growth and  
286 remodeling of ATD6-69, which identified resorptive fields on that maxilla similar to those found  
287 in sub-adult *H. sapiens*<sup>16</sup> (see Box 2, Fig. 2). By contrast, the maxillae of Neanderthals and the  
288 fossils from Sima de los Huesos, Atapuerca (Spain), were similar to those of more ancient  
289 Pliocene hominins showing a pattern of bone deposition<sup>45</sup>. If these analyses of facial  
290 development are correct, deriving the Sima de los Huesos and Neanderthal facial morphologies  
291 from that of a species represented by a specimen like ATD6-69 would require evolutionary  
292 ontogenetic changes in the growth of the face, as illustrated in immature individuals from the  
293 Sima de los Huesos<sup>45</sup>. While these remodeling changes may be construed as evolutionary  
294 reversals, we suggest that this is not the case. Instead, the remodeling changes should be  
295 viewed as a developmental process aligned with the facial morphological characteristics of the  
296 species.

297

### 298 **The LCA, ancient genomes and the earliest *Homo sapiens* face**

299

300 Fossil and ancient DNA data provide further information on the nature and timing of the LCA of  
301 Neanderthals and modern humans<sup>29-31,46</sup>. The clear Neanderthal morphological, ontogenetic  
302 and genetic affinities of the Sima de los Huesos fossils dated to ~430 Ka and regarded as  
303 Neanderthal ancestors<sup>47</sup>, suggest an evolutionary divergence of the Neanderthal lineage  
304 considerably before that date. Comparative analyses on the large sample of 17 crania from  
305 Sima de los Huesos showing a number of shared facial features with Neanderthals, indicate that  
306 modifications in facial shape were one of the first steps in the evolution toward the Neanderthal  
307 morphology<sup>47</sup> (Fig. 4). But, using recently published estimates of the autosomal human  
308 mutation rate, it has been suggested that the divergence date of the *H. neanderthalensis* and *H.*  
309 *sapiens* lineages could indeed be placed earlier — between 550 and 765 Ka<sup>48</sup>. These dates  
310 would be consistent with the oldest suggested examples of *H. heidelbergensis* potentially  
311 representing the LCA, although other estimates are younger (e.g. ~503-565 Ka<sup>46</sup>). An  
312 alternative would be to consider a *H. antecessor*-like facial morphology as more likely for the  
313 LCA of *H. sapiens* and *H. heidelbergensis*, with the *H. heidelbergensis* group exemplified by

314 Petralona, Bodo and Broken Hill 1 having more in common facially with the Sima de los Huesos  
315 fossils and subsequent Neanderthals. When challenging the position of *H. heidelbergensis* as  
316 LCA of *H. sapiens* and *H. neanderthalensis*, and highlighted the significance of the *H. sapiens*-  
317 like facial morphology of *H. antecessor*, Bermúdez de Castro<sup>44</sup> cautioned that other aspects of  
318 *H. heidelbergensis* morphology suggested that it might be a side-branch alongside one of the  
319 early Pleistocene lineages in Eurasia that eventually gave rise to Neanderthals in Europe and to  
320 *H. sapiens* in Africa.

321 FIGURE 4 HERE

322  
323 Further evidence of the antiquity of a *H. sapiens*-like facial morphology is provided by the recent  
324 study and redating of new and old fossil material from Jebel Irhoud (Morocco) (Fig. 3f), now  
325 placed at ~300 Ka<sup>31</sup>. This modern facial morphology, supported by quantitative approaches (Fig.  
326 5), is present in two fossils from Irhoud. This morphology is similar to that shown by Florisbad  
327 (South Africa) and Herto (Ethiopia) (Fig. 3g) at a somewhat later date, Nduvu and Thomas  
328 Quarry at an earlier date, and in the currently undated Eliye Springs (Kenya) and Broken Hill 2  
329 fossils. These specimens show considerable size variation, but a consistency in their *H. sapiens*  
330 -like midfaces. This observation challenges the view that allometric factors and/or sexual  
331 dimorphism might have produced the midfacial variation within a single lineage or species<sup>37,38</sup>.  
332 The evidence instead suggests that the large and non-*H. sapiens*-like faces of Bodo and Broken  
333 Hill 1 (Figs. 3b & c), represent taxonomic diversity in the African MP record, which could exclude  
334 the large fossils assigned to *H. heidelbergensis*/*H. rhodesiensis* as representing an ancestral  
335 morph for *H. sapiens*. Given other shared and more *H. sapiens*-like facial morphologies, ranging  
336 from the late lower Pleistocene of Europe to the MP of China and Africa, it begins to look more  
337 parsimonious to interpret a *H. antecessor*-like facial morphology as primitive for the clade  
338 containing *H. sapiens* and *H. neanderthalensis*. This symplesiomorphic morphology was also  
339 present in at least some fossils assigned to Chinese *H. erectus*, in other archaic Chinese  
340 hominins, and in the lineage of *H. sapiens* present in Africa from ~500 Ky, while it was  
341 apparently lost in the *H. heidelbergensis*/*H. rhodesiensis* and *H. neanderthalensis* lineages. The  
342 more recent fossil material of *H. naledi* from South Africa, dated to ~ 250 Ka<sup>49</sup>, is unfortunately  
343 too incomplete in the face so far to add much to this picture, beyond displaying a transversely  
344 flat but overall very prognathic morphology<sup>50</sup>.

345

346 **Adaptation in MP and modern human faces**

347

348 To consider the impact of functional adaptation in the evolution of the face, we should first revisit  
349 key characteristics of the modern human face. The modern human face is distinct from that of  
350 earlier hominin species in several important ways (Fig. 3h): it is relatively small and non-  
351 projecting, shows a depression - the 'canine fossa' - below the orbit and lacks the pronounced  
352 supraorbital structures and the alveolar and midfacial prognathism exhibited by MP hominins.  
353 These features do not appear all at once in the fossil record, but crucial elements are already in  
354 place among the earliest representatives of the *H. sapiens* lineage<sup>31</sup>.

355  
356 The transition from MP hominins to modern humans was marked by these changes and  
357 gracilisation of the face<sup>51,52</sup>. As biologists we habitually seek adaptive explanations for such  
358 changes<sup>52,53</sup>, but we must also consider non-adaptive ones, including structure, constraints and  
359 neutral evolutionary processes such as drift<sup>54</sup> and founder effect<sup>55</sup>. Adaptive explanations for  
360 an enlarged midface and large brows have focused either on enlargement of the nasal cavity  
361 and paranasal sinuses emphasizing respiratory/energetic demands<sup>56</sup> and climatic adaptation  
362<sup>57,58</sup>, or on mechanical adaptations to diet, paramasticatory activity<sup>59,60</sup>, or increase in body size  
363<sup>61-64</sup>.

364  
365 Thus, in Sima de los Huesos (Fig. 4), *H. heidelbergensis* and Neanderthals (Fig. 3a), there is a  
366 shared large nasal cavity and midfacial configuration, in many cases accompanied by large  
367 paranasal sinuses. Compared to modern humans, the region that most differs is the nasal cavity  
368 itself, suggesting reduction of this is the primary underlying cause of midfacial reduction in  
369 modern humans. As such, midfacial reduction may have arisen simply as a result of loss of pre-  
370 existing selective pressures to maintain a large midface, with cultural adaptations to climate,  
371 feeding and lifestyle being possible factors in reducing these pressures and so allowing drift and  
372 other neutral processes to impact on midfacial form.

373  
374 Alternatively, it can be argued that the large midface, chinless jaws and enlarged brow ridges of  
375 MP hominins make up a suite of features adapted to masticatory or paramasticatory uses  
376<sup>59,60,65,66</sup>. While brow ridges have been considered to arise as a structural consequence of fitting  
377 a large face under a retracted frontal (spatial hypothesis)<sup>67</sup>, it has also been argued, but is less  
378 likely, that they play a role in resisting loading of the jaws (masticatory loading hypothesis)<sup>68</sup>.  
379 Could the reduction of brows, midfaces, jaws and the development of a chin in modern humans  
380 be a response to altered jaw loading?

381

382 One way of addressing this question is to assess the impact of diet as a driver for facial  
383 changes in *H. sapiens*. The main mode of subsistence in modern human populations (i.e.  
384 agricultural vs non-agricultural diet; plant-based vs meat-based diet) is recognized as playing an  
385 important role in shaping the face, with masticatory stress particularly affecting the mandible  
386 and lower face<sup>6,69,70</sup>. Although the gracile modern human face is likely less well adapted to  
387 powerful, sustained chewing, it has been argued<sup>71</sup> that *H. sapiens* facial skeletons show  
388 increased bite force relative to MP hominins<sup>72,73</sup>, which could be an advantage in fracturing  
389 hard objects. Alternatively, because *H. sapiens* shows decreased ability to resist masticatory  
390 loading despite increased bite force, the increased bite force may simply be a by-product of  
391 facial reduction, driven by other factors<sup>74</sup>, as we will further discuss below.

392 FIGURE 5 HERE

### 393 **Population history and climatic adaptation shape the face**

394  
395 We have stated earlier that, although the face is the most distinctive feature used to identify and  
396 recognize others, the human face differs across populations. In fact, it is recognized that  
397 modern humans have a high degree of cranial variation exceeding that found in other primate  
398 species, with the face being an important contributor to this variation<sup>75,76</sup>. For this reason,  
399 several hypotheses have considered the influence of population history, subsistence and  
400 climate adaptation in shaping the human facial skeleton. To address the contribution of these  
401 sources, a major question is whether facial morphology accurately reflects population history  
402 and genetic relatedness or, alternatively, predominantly represents responses to external  
403 conditions through plastic response or genetic adaptation. This issue also has implications for  
404 interpreting the MP faces: if facial anatomy is found to be plastic or highly responsive to  
405 environmental conditions among modern humans, this would suggest that the facial morphology  
406 of MP hominins and the LCA may also have been, to some degree, affected by external factors  
407 rather than genetically determined or indicative of phylogeny. An illustration of this conundrum is  
408 the well-studied Neanderthal face, which shows a distinctive combination of features discussed  
409 above, including a large nasal opening and cavity, a projecting midface, a “puffy” maxilla and  
410 infraorbital region, and a double-arched, continuous supraorbital torus<sup>77</sup>. Could some of these  
411 features be the result of adaptation to extreme cold<sup>78</sup>? Or, are they simply features that became  
412 fixed in the Neanderthal lineage through genetic drift acting on small, isolated populations<sup>31,79</sup>?  
413 The answer lies in developing a deeper understanding of this type of variation among modern  
414 humans.

415

416 In recent years, several studies have been conducted using quantitative genetic approaches to  
417 evaluate the effects of different factors on facial phenotypic expression. Together, they indicate  
418 a complex pattern of influences. While the modern human cranium, overall, appears to be  
419 mainly shaped by neutral evolutionary processes<sup>80-82</sup>, the modern human face reflects both  
420 phylogenetic and environmental factors<sup>81-84</sup>. The latter appear to act on different parts of the  
421 cranium in varying ways and to differentially affect facial features. Early studies compared the  
422 overall shape of cranial regions, including the basicranium, neurocranium and face, among a set  
423 of modern human populations to neutral genetic and climate data for the same (or closely  
424 related) groups. Results indicated that while facial morphology does carry a neutral genetic or  
425 population history signal, it is more strongly affected by climatic conditions than other parts of  
426 the cranium, especially in high latitude populations<sup>81,82,83</sup>. Additional work has shown that both  
427 the external nasal morphology and nasal cavity are related to temperature and humidity<sup>80,82,85</sup>.  
428 This effect is particularly pronounced in populations living in extreme cold, where the internal  
429 nasal morphology plays a crucial role in warming and humidifying the inspired air<sup>84</sup>. It appears  
430 to affect the dimensions as well as the projection of the nasal cavity and external nose.  
431 Therefore, climate may have been an important contributor to the evolution of the Eurasian MP  
432 face, and computational fluid dynamic modelling might provide a useful way of relating midfacial  
433 morphology to air-flow and energetic demands, as has been demonstrated in a recent study<sup>58</sup>.

434

#### 435 **A cultural/social component for the evolution of the face?**

436

437 The substantial relative reduction in the size of the face compared to the neurocranium in  
438 modern humans<sup>86</sup> has been implicated in, and attributed to, cultural and social change. In  
439 addition to diet, respiratory physiology and climate, as highlighted above, facial reduction since  
440 the MP has also been attributed to the evolution of enhanced social tolerance as well as to  
441 reduced androgen activity<sup>52</sup>. Thus, the modern human face is more sculpted and remodeled,  
442 has more complex topography than any other hominin face<sup>16</sup>, and has considerably more  
443 topographic relief than the “inflated” midfaces of MP fossils. MP crania such as Bodo, Arago 21  
444 (France), Petralona or Broken Hill 1, for example, have a facial skeleton that has the  
445 appearance of a stiff “facial mask” rather than the more “expressive” human face. Does this  
446 suggest that our face evolved to provide more possibilities for gestural (nonverbal)  
447 communication?

448

449 It is of interest in this regard that brow ridge reduction accompanied midfacial reduction. Russell  
450 et al.<sup>68</sup> noted that the supraorbital torus has been implicated in many functions. Of particular  
451 interest is its role in the proposed threat display in Neanderthals. Similarly, after excluding  
452 spatial and masticatory loading resistance roles for the extremely large brow ridges of the  
453 Broken Hill 1 cranium, a recent study suggested that a social signaling role, particularly in  
454 relation to dominance/aggression, was likely<sup>87</sup>. It was also noted that reduction of the brow  
455 ridge and retraction of the midface under the frontal bone would have likely increased the range  
456 of visible motion of the eyebrows among modern humans<sup>87</sup>. Whatever the cause of this  
457 reduction, such a shift in eyebrow mobility could have enabled a wider range of subtler social  
458 signals, enhancing social communication. These considerations raise the possibility that the role  
459 of the face in social signaling may have been an important contributor to its later evolution, as  
460 we have suggested (see above) for the earliest stages of the hominin record as well. This  
461 possibility remains under- studied.

462

## 463 **Conclusion**

464

465 The evolutionary history of the human face involved many intermediate morphological  
466 transformations leading to the short-faced cranium with a large globular brain case of modern  
467 humans. We have explored facial evolution over the past 4 Ma, from *Ardipithecus* and the early  
468 australopiths to the earliest known examples of a *H. sapiens*-like faces found ~300 Ka. The  
469 earliest changes during the australopith to early *Homo* transition may have been driven, in part,  
470 by abiotic environmental factors but also by the social context, since some sexually dimorphic  
471 structures (e.g. canines, browridges) reduced in size over time. In more recent fossil *Homo*,  
472 facial projection decreased further, with a moderate but cumulative increase in brain size. A  
473 striking feature observed in the MP hominins is that the face evolved more rapidly than other  
474 cranial components, as illustrated by the facial characteristics of *H. antecessor*, a key LCA  
475 candidate, presenting modern facial features while retaining some primitive characters  
476 elsewhere in the cranium. This is also evidenced in Asian specimens such as Nanjing. These  
477 new faces continued to evolve during challenges by their environment, impacted increasingly by  
478 culture and social factors. Over time, the face became more gracile, potentially gaining an ability  
479 to generate more diverse facial expressions, likely enhancing non-verbal communication.

480

481 Multidisciplinary efforts are required to reach a detailed understanding of the complex  
482 evolutionary history of the face. Looking at future challenges, important areas that remain to be

483 elucidated include how to integrate potentially conflicting evidence from craniofacial  
484 biomechanics, occlusal-microwear and stable isotopes into hypotheses about early hominin  
485 dietary behavior. Further, resolution of the debate over whether simulated stress patterns in the  
486 australopith craniofacial skeleton faithfully track feeding adaptations will be critical to the  
487 success of this venture<sup>88,89,90</sup>. Moreover, we must disentangle the complex effects of shared  
488 ancestry, climate adaptation and the influence of subsistence in shaping the evolution of the  
489 human face.

490

491 Finally, although projecting evolution is fraught with difficulties, given the impact of the softer  
492 diets of industrialized societies on facial shape, it is possible that the face will continue to  
493 decrease in size somewhat in the coming millennia. In addition, some projections of global  
494 warming suggest humans could soon be living on a planet that is 4° C warmer than today, with  
495 somewhat different atmospheric composition, which would certainly affect human physiology.  
496 Yet, there are important limitations in the amount of change as breathing requires a sufficiently  
497 large nasal cavity and upper respiratory tract. In addition, the size of the jaws is restricted by  
498 the housing of teeth. It is also important to recognize the role of gene flow associated with  
499 migrations across the globe, which will likely affect the pace of evolutionary change. Within  
500 these and other limitations on the amount of change, the evolution of the human face is likely to  
501 continue as long as our species survives, migrates and encounters new environmental, social  
502 and cultural conditions.

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511 **Box 1. Modularity and Integration of the Craniofacial Complex:** The mammalian skull is developmentally  
512 complex and a highly integrated structure <sup>91</sup>. Modularity and integration reflect the degree of autonomy and  
513 interaction among various cranial components during growth and development <sup>6</sup>. Modularity refers to the relative  
514 independence of components, ranging from the molecular units that code for programmed growth to capsular  
515 matrices such as the brain, orbital, oral, and nasal capsules. Integration refers to the connectedness or  
516 interdependence among these components during development, and throughout mature life. Integration, or  
517 covariation, among morphological units can be quantitated, enabling the development of mathematical models that  
518 predict how changes of individual units may occur in response to changes in other units <sup>92</sup>. Environmental factors at  
519 different stages of development have also been proposed to affect covariation <sup>91</sup>. In the evolution of the human skull,  
520 it has been predicted that the shortening of the human face, one of the main characteristics of *H. sapiens* <sup>86</sup>, could be  
521 explained by three major changes: increased flexion of the cranial base, a relatively longer anterior cranial base, and  
522 a shorter upper face <sup>93</sup>. One aspect of this organization in the craniofacial skeleton is the presence of bone growth  
523 centers <sup>22, 55</sup>, which are situated to optimize the organism's physiological requirements through the actions of  
524 integrating factors over time. Such factors include biomolecular and mechanical signals that trigger coordinated  
525 bone forming and bone resorbing activity during growth (see Box 2).

526

527 **Box 2. Facial Growth and Remodeling of the Hominin Face:** Growth remodeling (bone formation and bone  
528 resorption) is an integral process of craniofacial growth that relates to maintaining the shape and proportions of the  
529 face during development <sup>94</sup>. Growth remodeling can be determined by analysis of the distribution of *depository* and  
530 *resorptive* fields on bone surfaces due to the activities of osteoblasts and osteoclasts, respectively. Genetic,  
531 mechanical and hormonal signals determine the distribution of these fields <sup>94</sup>. Such developmental signatures are  
532 best characterized in sub-adult individuals. In modern humans, there is a predominance of widely-spread resorptive  
533 fields variously spread over the maxilla, infraorbital and anterior zygoma as well as the mental region and coronoid  
534 process of the mandible, contributing to facial retraction (orthognathy) (see Fig. 2) <sup>95</sup>. In prognathic faces such as in  
535 chimpanzees or early *Australopithecus*, this prognathism is characterized by a pattern of bone deposition.

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545 **Table legend:**

546 **Table 1. List of key specimens discussed in the text, taxonomic attribution and geological age. Ma= million**  
547 **years ago. Ka=thousand years ago.**

548

549 **Figure legends:**

550

551 **Figure 1: a) *Australopithecus* and *Ardipithecus* faces compared:** Anterior views of hemisected crania,  
552 *Australopithecus afarensis* (A.L. 822-1, left) and *Ardipithecus ramidus* (ARA-VP 6/500 reconstruction, right -from  
553 ref <sup>17</sup>) illustrating the fundamental characteristics of facial shape. Note similarities in frontal/supraorbital form and  
554 inferior maxillary depth (corresponding to the limited extension of the canine roots), but pronounced differences in  
555 the lateral flare and vertical depth of the infraorbital and zygomaxillary regions (reflecting enhancement of the  
556 masticatory system in *Au. afarensis*). Specimens oriented on Frankfurt Horizontal and reproduced at equivalent  
557 orbital breadths. **b) Species recognized in hominin taxonomy discussed in the text.** The height of the lines  
558 represents currently accepted geological ages for each group or species. Abbreviations: *Ar* = *Ardipithecus*; *Au.* =  
559 *Australopithecus*; *K.* = *Kenyanthropus*; *P.* = *Paranthropus*; *H.* = *Homo*. Note: Sima de los Huesos fossils are  
560 currently unassigned to species.

561

562 **Figure 2: Summary of growth remodeling maps in fossil hominins compared to *H. sapiens*.** Bone resorption is  
563 represented in blue and deposition is pink. **a) *Au. africanus* and *Au. afarensis*** facial skeletons show a depositional  
564 pattern in all anteriorly-facing surfaces of the face, in keeping with the growth of a prognathic facial skeleton <sup>14</sup>.  
565 Only the anterior border of the mandibular ascending ramus is resorbing, which is a mechanism to relocate the  
566 ramus to the borders of the pharynx in compensation for anterior displacement caused by condylar growth. **b)** The  
567 more recent species *Au. sediba* (~2.0 My) illustrates some vertically oriented resorption over the maxilla  
568 contributing to its less prognathic face compared to *Au. afarensis* and *Au. africanus*, and represents an evolutionary  
569 modification in facial ontogeny <sup>15</sup>. **c) *Paranthropus* (*P. boisei* and *P. robustus*)** together, differ from  
570 *Australopithecus* showing narrow fields of resorption along the nasoalveolar clivus and in the vicinity of the canines  
571 of the lower jaw, indicative of some posterior relocation of the jaws, and reduced prognathism <sup>14</sup>. **d)** The juvenile  
572 African *Homo erectus* (*H. ergaster*) KNM-WT 15000 showed only deposition on the limited periosteal bone  
573 preserved <sup>16</sup>. To our present knowledge, all anteriorly-facing surfaces were forming in African *H. habilis*,  
574 reminiscent of those surfaces found in the more prognathic species of the genus *Australopithecus* <sup>14</sup>. **e)** The oldest  
575 known European species, *H. antecessor*, has resorption over the nasoalveolar clivus <sup>16</sup>. This species is also  
576 characterized morphologically as being relatively orthognathic and modern human-like <sup>42</sup> **f)** Fossils from Sima de  
577 los Huesos, Atapuerca are, by contrast, characterized by forming bone surfaces anteriorly <sup>45</sup>. The Sima de los  
578 Huesos population are considered Neanderthal ancestors <sup>47</sup> and in keeping with this, Neanderthal faces are also  
579 characterized by formation on all anteriorly facing surfaces <sup>45</sup> as shown in **g)**. The forwardly placed midface and  
580 nasal aperture of the Neanderthals resulted in a more anterior positioning of the tooth row *en bloc*, taking with it the  
581 maxillary tuberosity and generating the retromolar space characteristic of Neanderthals <sup>45</sup>. By the anterior

582 repositioning of the entire midface, the Neanderthal achieved relative orthognathy. **h)** An example of a recent 12-  
583 year old *H. sapiens* individual showing widely distributed field of bone resorption.

584 **Figure 3: Middle-Late Pleistocene hominin crania compared to *H. sapiens*:** **a)** La Ferrassie 1 Neanderthal dated  
585 to ~ 60-40 Ka. **b)** Bodo (Ethiopia) dated to ~ 600 Ka. **b)** Broken Hill 1 (Zambia) dated to ~250-300 Ka. **d)** Nanjing,  
586 China, dated to ~400 Ka. **e)** ATD6-69 maxilla, the holotype of *H. antecessor*, dated to ~850 Ka. **f)** *H. sapiens* from  
587 Jebel Irhoud 1 (Morocco) dated to ~ 300 Ka. **g)** *H. sapiens idaltu* from Herto (Ethiopia) dated to ~ 160 Ka. **h)** *H.*  
588 *sapiens* Abri Pataud, France (dated to ~20 Ka). Skulls not to scale.

589  
590 **Figure 4: Sima de los Huesos fossils show facial differences from Neanderthals.** In this frontal view of the adult  
591 specimen Cranium 17 from Sima de los Huesos (SH) (Atapuerca, Spain), the face is reminiscent of that of the  
592 Neanderthals in its marked nasal projection and a supraorbital torus that is continuous through the glabellar region as  
593 shown by **A**. However, there are also key differences from “classic” Neanderthal specimens (i.e., late Middle and  
594 Late Pleistocene Neanderthals). In particular, SH 17 (and the rest of the SH faces) shows the following archaic  
595 features: **1)** a root of the zygomaticoalveolar crest that is placed higher than in “classic” Neanderthals” (making the  
596 crest more curved); **2)** there is some “flexion” (depression) of the maxillae at the infraorbital foramen and groove  
597 (instead of being completely flat); **3)** the orbits are rectangular (and not truncated in the lower and medial corner);  
598 and **4)** there is a prenasal groove (i.e., the lateral nasal crests are placed in front of the spinal crests, instead of being  
599 continuous with them).

600  
601 **Figure 5: Morphometric analysis of the face discriminates Pleistocene fossils.** We here show a principal  
602 components analysis of nineteen facial three-dimensional landmarks (illustrated as black points on the faces shown  
603 in the left panel) of a number of Middle-Late Pleistocene fossils and a sample of modern humans, revealing clusters  
604 of fossils based on facial shape. Shape differences between modern humans (high PC2 scores) on the one hand, and  
605 Neanderthals and other Pleistocene fossils (low PC2 scores) are illustrated in the left panel. Modern humans are  
606 distinguished by a flat and anteriorly oriented face, angled zygomatic, and gracile browridge (top left), contrasting  
607 with the large browridge and ‘puffy’ midface of the Neanderthals (bottom left). These quantitative analyses also  
608 indicate the morphological proximity of some these fossils to modern humans. Irhoud 1, found in Morocco and  
609 recently dated to ~300 Ka<sup>31</sup>, is likely an early member of the *Homo sapiens* lineage, and unlike Neanderthals and  
610 other MP crania (Petalona, Bodo, Broken Hill 1, Sima de los Huesos), Irhoud 1 already shows almost completely  
611 modern human-like facial morphology. Other examples of *H. sapiens* include Qafzeh from Israel ~100 Ka, Wadi  
612 Kubbania from Egypt (~18 Ka) and possibly also the Moroccan fossils of Dar es Soltane (110-125 Ka). Grey  
613 diamonds: recent modern humans; black diamonds: early anatomically modern humans; green triangles: European  
614 Upper Paleolithic modern humans; red triangles: African Late Paleolithic modern humans; blue stars: North African  
615 Iberomaurusians; black solid squares: African Middle Pleistocene fossils; Black open squares: European Middle  
616 Pleistocene fossils; purple dots: Neanderthals. Labels as follows: Ar: Arago 21 (France); Bd: Bodo (Ethiopia); Pe:  
617 Petralona (Greece); Si: Sima 5 (Spain); BH: Broken Hill 1 (Zambia); Qz6 and Qz9: Qafzeh (Israel); WK: Wadi

618 Kubbaniya (Egypt); DS5: Dar es Soltane 5 (Morocco). Plot produced using data collected by KH, previously  
619 analyzed in ref <sup>96</sup> where additional details can be found.  
620

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858

859 **Author contributions**

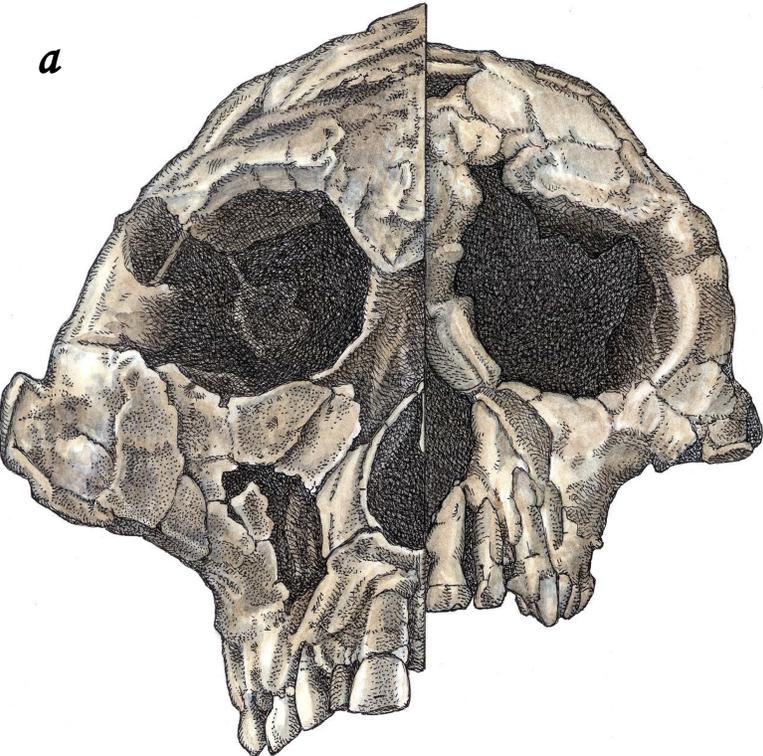
860 Author order reflects the relative size of the contributions made. All authors included contributed  
861 to the development of the study and wrote the paper.

862

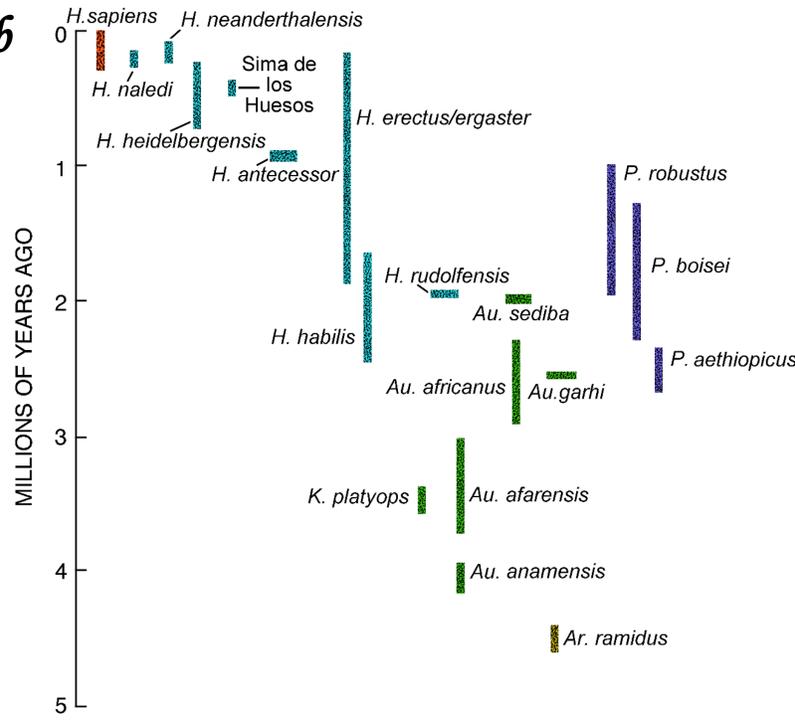
863 **Competing interests**

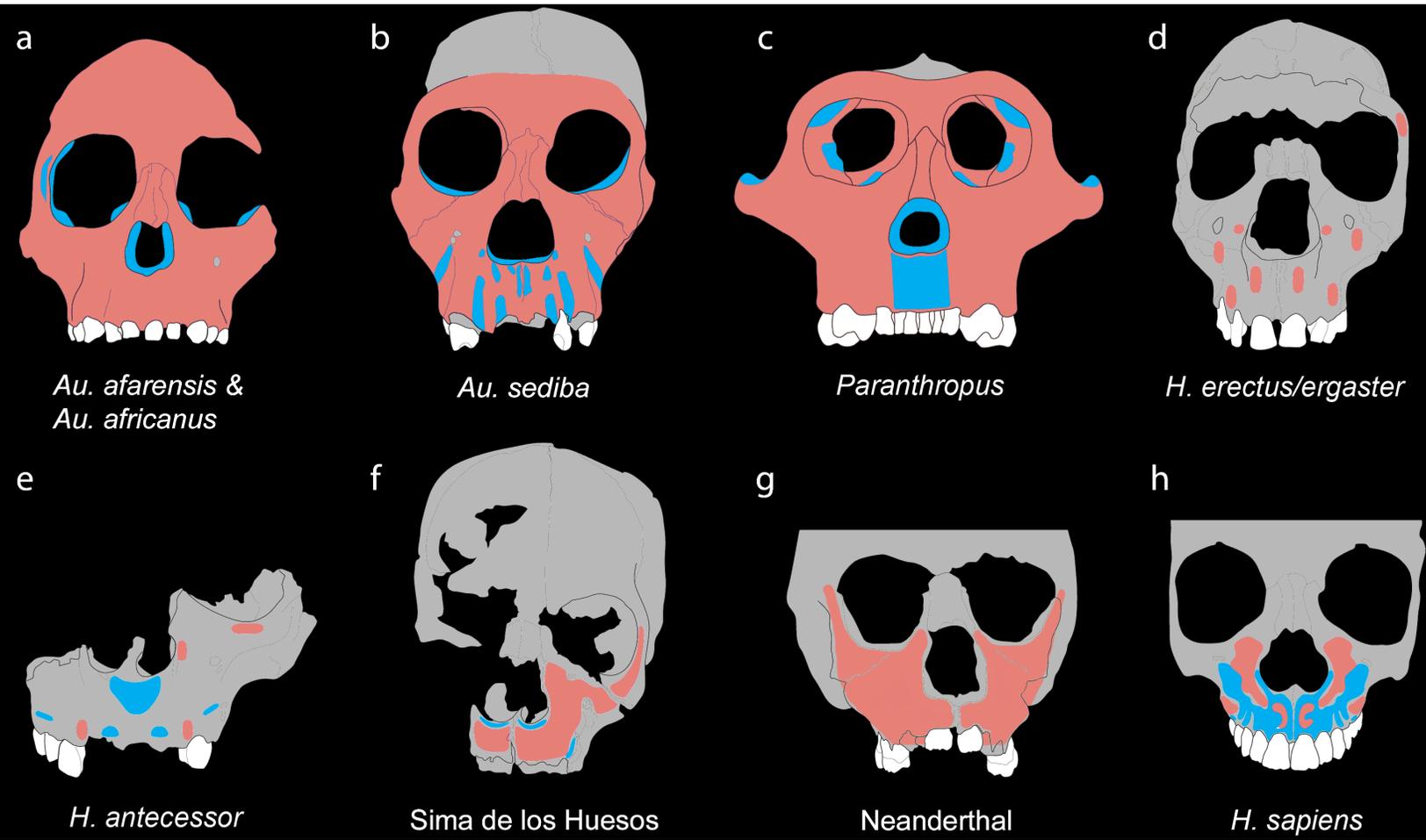
864 The authors declare no competing interests

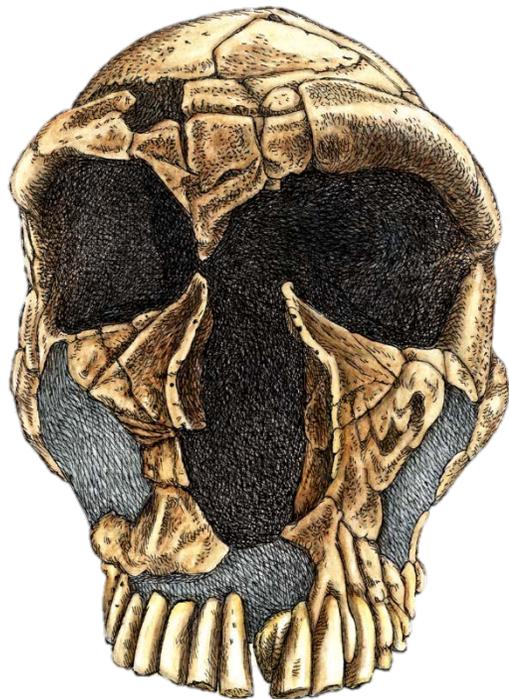
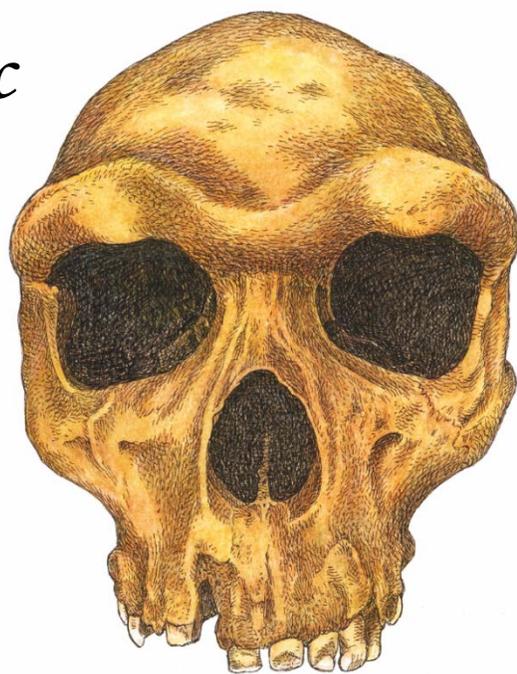
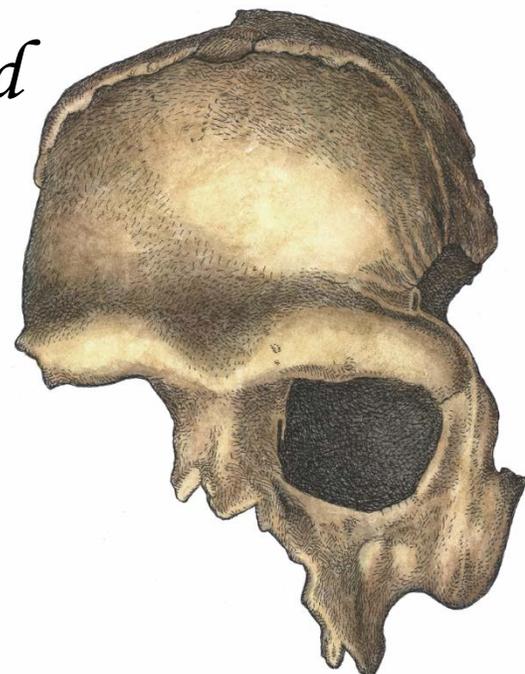
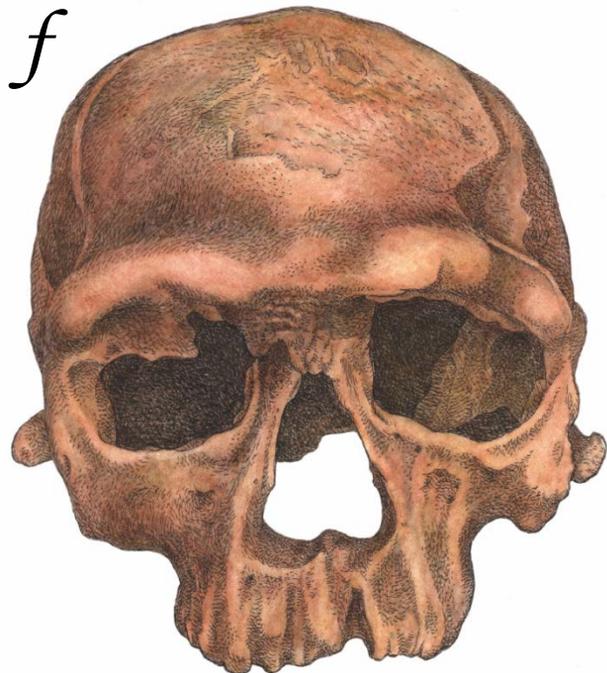
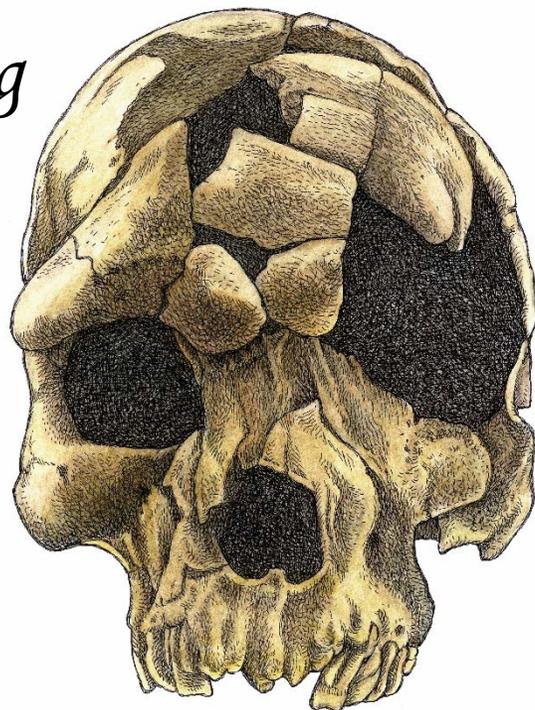
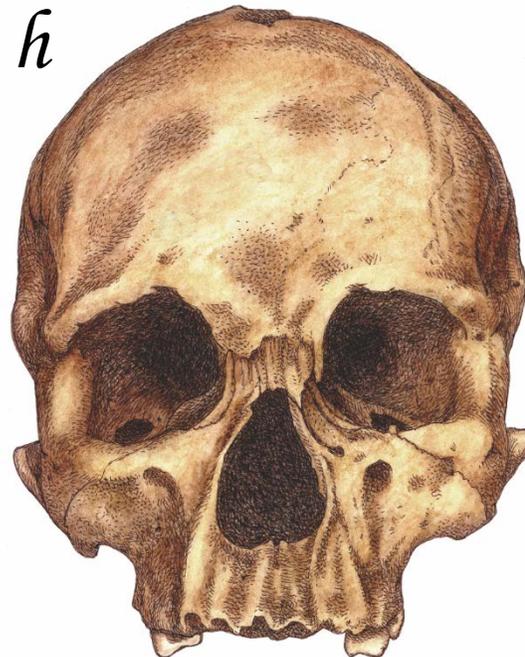
*a*

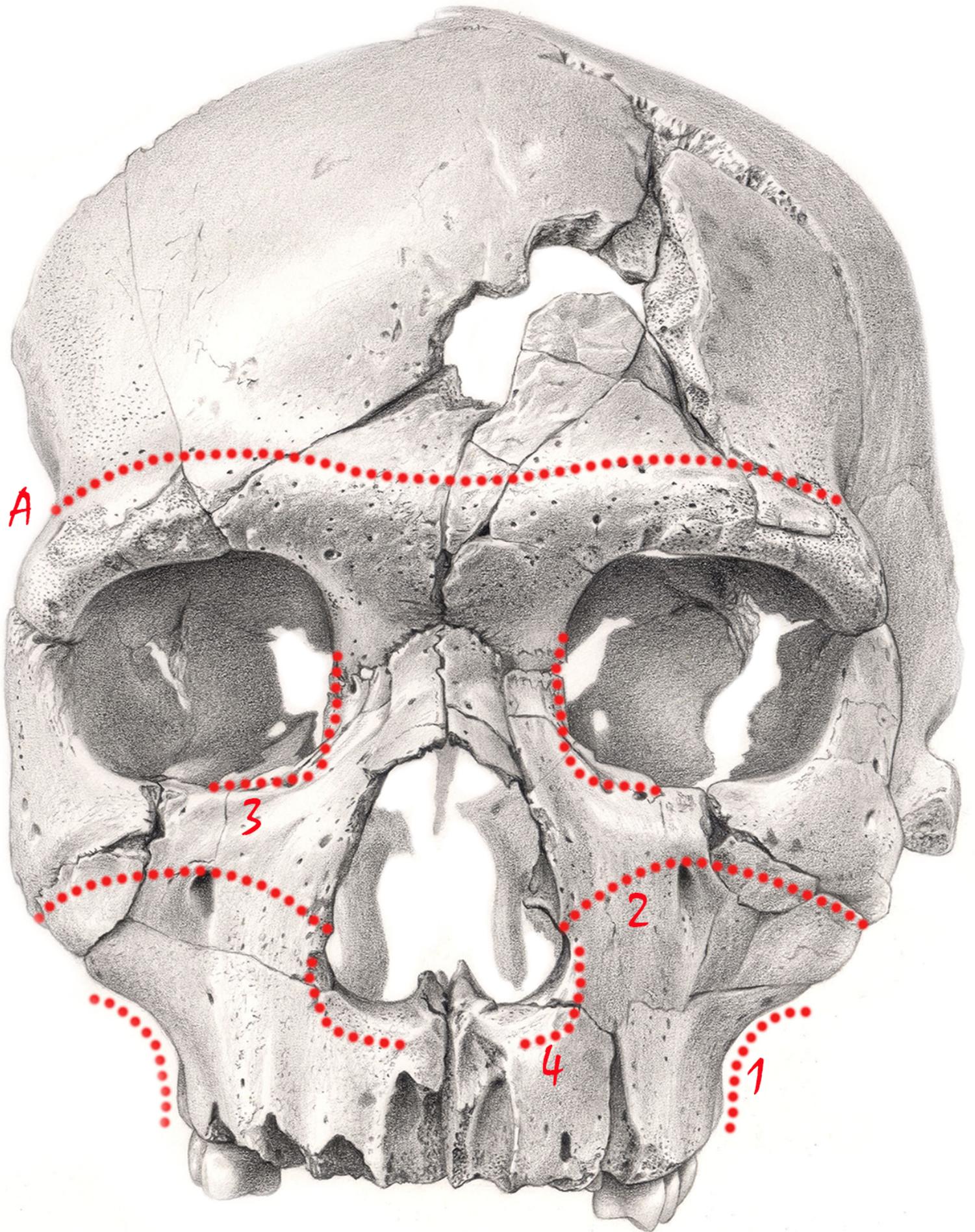


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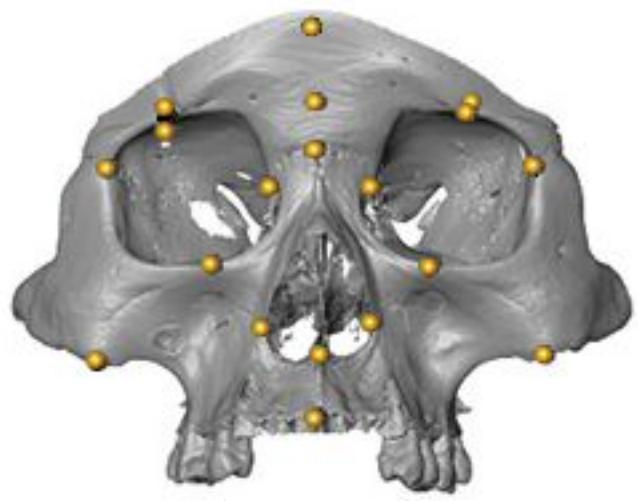




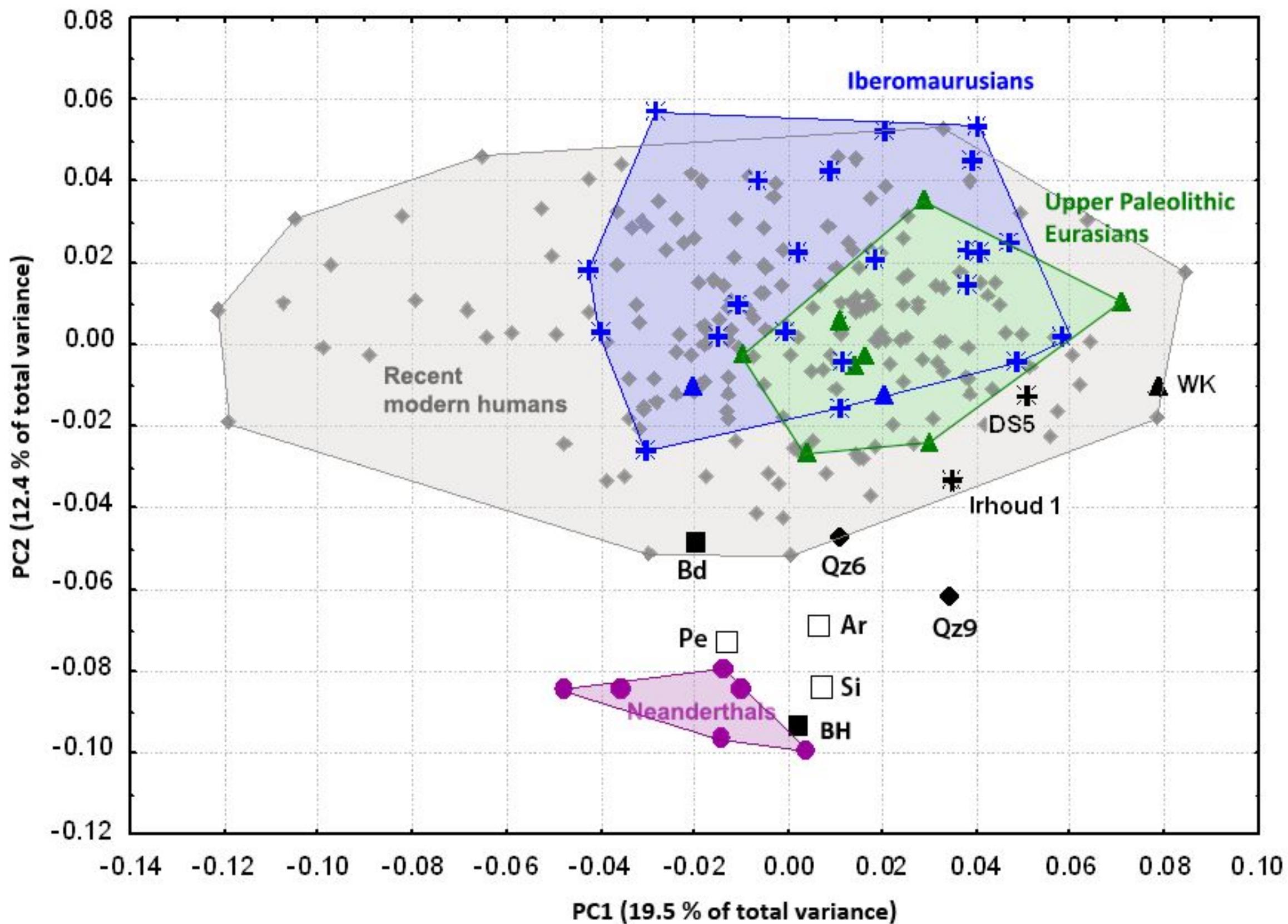
*a**b**c**d**e**f**g**h*



*E. Spitz-1h*



Shape changes along PC2



**Table 1. Specimens discussed in the text, their taxonomic attribution and geological age. Ma = millions of years ago. Ka = thousands of years ago.**

<b>Specimen</b>	<b>Taxon</b>	<b>Geological age</b>
<b>KNM-ER 1470</b>	<i>H. rudolfensis</i>	~1.9 Ma
<b>KNM-ER 62000</b>	<i>H. rudolfensis?</i>	~1.9 Ma
<b>KNM-ER 1813</b>	<i>H. habilis</i>	~1.9 Ma
<b>OH 13</b>	<i>H. habilis</i>	~1.6 Ma
<b>ATD6-69</b>	<i>H. antecessor</i>	~850 Ka
<b>Bodo 1</b>	<i>H. heidelbergensis/ H. rhodesiensis</i>	600 Ka
<b>Nanjing</b>	<i>H. erectus?</i>	~500 Ka
<b>Thomas Quarry</b>	archaic <i>H. sapiens/ H. heidelbergensis</i>	300-400 Ka
<b>Ndutu</b>	archaic <i>H. sapiens/ H. heidelbergensis</i>	~350 Ka
<b>Petralona</b>	<i>H. heidelbergensis/ H. rhodesiensis</i>	350-150 Ka
<b>Jebel Irhoud</b>	archaic <i>H. sapiens</i>	~300 Ka
<b>Broken Hill 1</b>	<i>H. heidelbergensis/ H. rhodesiensis</i>	~250-300 Ka
<b>Florisbad</b>	archaic <i>H. sapiens/ H. heidelbergensis / H. "helmeii"</i>	~ 250 Ka
<b>Herto</b>	<i>H. sapiens "idaltu"</i>	160 Ka
<b>Eliye Springs</b>	archaic <i>H. sapiens</i>	?