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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 muscles¹. 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 skeleton² Facial shape appears to be influenced by
55 a limited set of candidate genes³. 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 components⁴, highlighting
58 the interdependence of different morphological traits, or modules, during growth and
59 development^{5,6} (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-natally⁷. 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 ancestor⁸. 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*^{9,10}. As has been suggested for other
85 ectocranial structures¹¹, these differences may reflect a combination of social display
86 mechanisms and biomechanical performance¹². 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 face¹³. The observed differences in prognathism are associated with distinct growth patterns
101 and remodeling activity of bone cells¹⁴⁻¹⁶ (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 ¹⁷. Both taxa feature shortened basicrania and
114 reduced, modest sexually dimorphic canine crowns and roots as well as smaller incisors ^{9,17}. 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 ⁹, whereas *Ar. ramidus* shares with the chimpanzee vertically short, lightly built
119 zygomatic bones and arches ¹⁷. 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 ¹⁸,
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* ¹⁹. 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

133

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 (≤ 2.8 - 2.7 Ma) ^{20,21}. 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 diet²². 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 Africa²³ shares derived
157 facial features with *Au. africanus*¹⁰, but its facial remodeling differs from all other
158 *Australopithecus* facial skeletons (see Box 2, Fig. 2)¹⁵. 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*²⁴.

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*²⁵. 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 Ma²⁶,
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* (≤ 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 diet¹⁹. 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 items²⁷.

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 ²⁸.
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 ²⁹⁻³¹. 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
245

***Homo heidelbergensis* as the LCA?**

246 Stringer ³² 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 questioned³³, the nomen *H. rhodesiensis* could be applied^{32,34}.
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 ³⁵). Mounier and Lahr ³⁶ 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 ³⁰. It is possible that allometric factors influence the
263 zygomaxillary morphology when comparing smaller and larger individuals ^{37,38} given the
264 association between body size and facial size in primates³⁹. 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 ⁴⁰. 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 ^{41,42} (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 ATD6-69⁴³ were removed with the finding
283 of similar morphology in fragmentary adult maxillae^{41,44}. 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 trajectories³⁸, 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*¹⁶ (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 deposition⁴⁵. 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 Huesos⁴⁵. 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^{29-31,46}. 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 ancestors⁴⁷, 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 morphology⁴⁷ (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 Ka⁴⁸. 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 Ka⁴⁶). 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 Castro⁴⁴ 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 Ka³¹. 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^{37,38}.
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 Ka⁴⁹, 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 morphology⁵⁰.

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* lineage³¹.

355

356 The transition from MP hominins to modern humans was marked by these changes and
357 gracilisation of the face^{51,52}. As biologists we habitually seek adaptive explanations for such
358 changes^{52,53}, but we must also consider non-adaptive ones, including structure, constraints and
359 neutral evolutionary processes such as drift⁵⁴ and founder effect⁵⁵. 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 demands⁵⁶ and climatic adaptation
362^{57,58}, or on mechanical adaptations to diet, paramasticatory activity^{59,60}, or increase in body size
363⁶¹⁻⁶⁴.

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^{59,60,65,66}. While brow ridges have been considered to arise as a structural consequence of fitting
377 a large face under a retracted frontal (spatial hypothesis)⁶⁷, it has also been argued, but is less
378 likely, that they play a role in resisting loading of the jaws (masticatory loading hypothesis)⁶⁸.
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^{6,69,70}. Although the gracile modern human face is likely less well adapted to
387 powerful, sustained chewing, it has been argued⁷¹ that *H. sapiens* facial skeletons show
388 increased bite force relative to MP hominins^{72,73}, 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 factors⁷⁴, 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^{75,76}. 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 torus⁷⁷. Could some of these
411 features be the result of adaptation to extreme cold⁷⁸? Or, are they simply features that became
412 fixed in the Neanderthal lineage through genetic drift acting on small, isolated populations^{31,79}?
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 processes⁸⁰⁻⁸², the modern human face reflects both
420 phylogenetic and environmental factors⁸¹⁻⁸⁴. 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^{81,82,83}. Additional work has shown that both
427 the external nasal morphology and nasal cavity are related to temperature and humidity^{80,82,85}.
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 air⁸⁴. 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 study⁵⁸.

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 humans⁸⁶ 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 activity⁵². Thus, the modern human face is more sculpted and remodeled,
442 has more complex topography than any other hominin face¹⁶, 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.⁶⁸ 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 likely⁸⁷. 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 humans⁸⁷. 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^{88,89,90}. 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 ⁹¹. Modularity and integration reflect the degree of autonomy and
513 interaction among various cranial components during growth and development ⁶. 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 ⁹². Environmental factors at
519 different stages of development have also been proposed to affect covariation ⁹¹. 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* ⁸⁶, 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 ⁹³. One aspect of this organization in the craniofacial skeleton is the presence of bone growth
523 centers ^{22, 55}, 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 ⁹⁴. 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 ⁹⁴. 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) ⁹⁵. 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 ¹⁷) 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 ¹⁴.
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 ¹⁵. **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 ¹⁴. **d)** The juvenile
572 African *Homo erectus* (*H. ergaster*) KNM-WT 15000 showed only deposition on the limited periosteal bone
573 preserved ¹⁶. 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* ¹⁴. **e)** The oldest
575 known European species, *H. antecessor*, has resorption over the nasoalveolar clivus ¹⁶. This species is also
576 characterized morphologically as being relatively orthognathic and modern human-like ⁴² **f)** Fossils from Sima de
577 los Huesos, Atapuerca are, by contrast, characterized by forming bone surfaces anteriorly ⁴⁵. The Sima de los
578 Huesos population are considered Neanderthal ancestors ⁴⁷ and in keeping with this, Neanderthal faces are also
579 characterized by formation on all anteriorly facing surfaces ⁴⁵ 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 ⁴⁵. 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 Ka³¹, 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 ⁹⁶ where additional details can be found.
620

REFERENCES

- 621
622
- 623 1 Du, S., Tao, Y. & Martinez, A. M. Compound facial expressions of emotion. *Proc. Natl. Acad. Sci. USA* **111**, E1454-1462 (2014).
- 624
625 2 Cordero, D. R. *et al.* Cranial neural crest cells on the move: their roles in craniofacial
626 development. *Am. J. Med. Genet. A* **155A**, 270-279 (2011).
- 627 3 Liu, F. *et al.* A genome-wide association study identifies five loci influencing facial
628 morphology in Europeans. *PLoS Genet.* **8**, e1002932 (2012).
- 629 4 Marcucio, R. S., Young, N. M., Hu, D. & Hallgrímsson, B. Mechanisms that underlie co-
630 variation of the brain and face. *Genesis* **49**, 177-189 (2011).
- 631 5 Ackermann, R. R. Ontogenetic integration of the hominoid face. *J. Hum. Evol.* **48**, 175-
632 197 (2005).
- 633 6 Lieberman, D. E. *The Evolution of the Human Head. Cambridge: Harvard University*
634 *Press.*
- 635 7 Wilkins, A. *Making Faces: The Evolutionary Origins of the Human Face. The Belknap*
636 *Press of Harvard University Press (2017).*
- 637 8 Cobb, S. N. The facial skeleton of the chimpanzee-human last common ancestor. *J. Anat.*
638 **212**, 469-485 (2008).
- 639 9 Kimbel, W. H., Y, R. & DC, J. *The skull of Australopithecus afarensis. Oxford University*
640 *Press (2004).*
- 641 10 Kimbel, W. H. & Rak, Y. *Australopithecus sediba* and the emergence of *Homo*:
642 Questionable evidence from the cranium of the juvenile holotype MH 1. *J. Hum. Evol.*
643 **107**, 94-106 (2017).
- 644 11 Balolia, K. L., Soligo, C. & Wood, B. Sagittal crest formation in great apes and gibbons. *J.*
645 *Anat.* **230**, 820-832 (2017).
- 646 12 Ravosa, M. J., Vinyard, C. J. & Hylander, W. L. Stressed out: masticatory forces and
647 primate circumorbital form. *Anat. Rec.* **261**, 173-175 (2000).
- 648 13 Villmoare, B. A. *et al.* Craniofacial modularity, character analysis, and the evolution of
649 the premaxilla in early African hominins. *J. Hum. Evol.* **77**, 143-154 (2014).
- 650 14 Bromage, T. G. Ontogeny of the Early Hominid Face. *J. Hum. Evol.* **18**, 751-773 (1989).
- 651 15 Lacruz, R. S. *et al.* Distinct growth of the nasomaxillary complex in *Au. sediba*. *Sci. Rep.* **5**,
652 15175 (2015).
- 653 16 Lacruz, R. S. *et al.* Facial morphogenesis of the earliest europeans. *PLoS One* **8**, e65199
654 (2013).
- 655 17 Suwa, G. *et al.* The *Ardipithecus ramidus* skull and its implications for hominid origins.
656 *Science* **326**, 68e61-67 (2009).
- 657 18 Wynn, J. G. *et al.* Diet of *Australopithecus afarensis* from the Pliocene Hadar Formation,
658 Ethiopia. *Proc. Natl. Acad. Sci. USA* **110**, 10495-10500 (2013).
- 659 19 Cerling, T. E. *et al.* Stable isotope-based diet reconstructions of Turkana Basin hominins.
660 *Proc. Natl. Acad. Sci. USA* **110**, 10501-10506 (2013).
- 661 20 deMenocal, P. B. Plio-Pleistocene African climate. *Science* **270**, 53-59 (1995).
- 662 21 Trauth, M. H. *et al.* High- and low-latitude forcing of Plio-Pleistocene East African
663 climate and human evolution. *J. Hum. Evol.* **53**, 475-486 (2007).
- 664 22 Ungar, P. S. & Sponheimer, M. The diets of early hominins. *Science* **334**, 190-193 (2011).

665 23 Berger, L. R. *et al.* *Australopithecus sediba*: a new species of *Homo*-like australopith from
666 South Africa. *Science* **328**, 195-204 (2010).

667 24 Wood, B. & Aiello, L. C. Taxonomic and functional implications of mandibular scaling in
668 early hominins. *Am. J. Phys. Anthropol.* **105**, 523-538 (1998).

669 25 Ungar, P. S., Grine, F. E., Teaford, M. F. & El Zaatari, S. Dental microwear and diets of
670 African early *Homo*. *J. Hum. Evol.* **50**, 78-95 (2006).

671 26 Harmand, S. *et al.* 3.3-million-year-old stone tools from Lomekwi 3, West Turkana,
672 Kenya. *Nature* **521**, 310-315, doi:10.1038/nature14464 (2015).

673 27 Dominy, N., Vogel, E. R., Yeakel, J. D., Constantino, P. & Lucas, P. W. Mechanical
674 Properties of Plant Underground Storage Organs and Implications for Dietary Models of
675 Early Hominins. *Evol. Biol.* **35**, 159–175 (2008).

676 28 Ferring, R. *et al.* Earliest human occupations at Dmanisi (Georgian Caucasus) dated to
677 1.85-1.78 Ma. *Proc. Natl. Acad. Sci. USA* **108**, 10432-10436 (2011).

678 29 Skoglund, P. & Mathieson, I. Ancient Genomics of Modern Humans: The First Decade.
679 *Annu. Rev. Genom. Hum. G* **19**, 381-404 (2018).

680 30 Stringer, C. The origin and evolution of *Homo sapiens*. *Philos. Trans. R. Soc. Lond. B Biol.*
681 *Sci.* **371** (2016).

682 31 Hublin, J. J. *et al.* New fossils from Jebel Irhoud, Morocco and the pan-African origin of
683 *Homo sapiens*. *Nature* **546**, 289-292 (2017).

684 32 Stringer, C. B. Some further notes on the morphology and dating of the Petralona
685 hominid. *J. Hum. Evol.* **12**, 731–742 (1983).

686 33 Balter, M. Paleoanthropology. RIP for a key *Homo* species? *Science* **345**, 129 (2014).

687 34 Stringer, C. The status of *Homo heidelbergensis* (Schoetensack 1908). *Evol. Anthropol.*
688 **21**, 101-107 (2012).

689 35 Rightmire, G. P. Human evolution in the Middle Pleistocene: The role of *Homo*
690 *heidelbergensis*. *Evol. Anthropol.* **6**, 218–227 (1998).

691 36 Mounier, A. & Lahr, M. M. Virtual ancestor reconstruction: Revealing the ancestor of
692 modern humans and Neandertals. *J. Hum. Evol.* **91**, 57-72 (2016).

693 37 Maddux, S. D. & Franciscus, R. G. Allometric scaling of infraorbital surface topography in
694 *Homo*. *J. Hum. Evol.* **56**, 161-174 (2009).

695 38 Freidline, S. E., Gunz, P., Harvati, K. & Hublin, J. J. Evaluating developmental shape
696 changes in *Homo antecessor* subadult facial morphology. *J. Hum. Evol.* **65**, 404-423
697 (2013).

698 39 Dobson, S. D. Allometry of Facial Mobility in Anthropoid Primates: Implications for the
699 Evolution of Facial Expression. *Am. J. Phys. Anthropol.* **138**, 70-81 (2009).

700 40 Vialet, A. *et al.* *Homo erectus* from the Yunxian and Nankin Chinese sites:
701 ANthropological insights using 3D virtual imaging techniques. *Comptes Rendus Palevol* **9**,
702 331-339 (2010).

703 41 Bermúdez de Castro, J. M. *et al.* The Atapuerca sites and their contribution to the
704 knowledge of human evolution in Europe. *Evol. Anthropol.* **13**, 25–41 (2004).

705 42 Bermudez de Castro, J. M. *et al.* A hominid from the lower Pleistocene of Atapuerca,
706 Spain: possible ancestor to Neandertals and modern humans. *Science* **276**, 1392-1395
707 (1997).

708 43 Stringer, C. Modern human origins: progress and prospects. *Philos. Trans. R. Soc. Lond. B*
709 *Biol. Sci.* **357**, 563-579 (2002).

710 44 Bermúdez de Castro, J. M. & Martínón-Torres, M. Evolutionary interpretation of the
711 modern human-like facial morphology of the Atapuerca Gran Dolina-TD6 hominins.
712 *Anthropol. Sci.* **122**, 149-155 (2014).

713 45 Lacruz, R. S. *et al.* Ontogeny of the maxilla in Neanderthals and their ancestors. *Nat.*
714 *Commun.* **6**, 8996 (2015).

715 46 Hajdinjak, M. *et al.* Reconstructing the genetic history of late Neanderthals. *Nature* **555**,
716 652-656 (2018).

717 47 Arsuaga, J. L. *et al.* Neandertal roots: Cranial and chronological evidence from Sima de
718 los Huesos. *Science* **344**, 1358-1363 (2014).

719 48 Meyer, M. *et al.* Nuclear DNA sequences from the Middle Pleistocene Sima de los
720 Huesos hominins. *Nature* **531**, 504-507 (2016).

721 49 Dirks, P. H. *et al.* The age of *Homo naledi* and associated sediments in the Rising Star
722 Cave, South Africa. *Elife* **6** eLife.24231 (2017).

723 50 Berger, L. R. *et al.* *Homo naledi*, a new species of the genus *Homo* from the Dinaledi
724 Chamber, South Africa. *Elife* **4** eLife.09560 (2015).

725 51 Groves, C. The origins of modern humans. *Science* **19**, 23-34 (1994).

726 52 Cieri, R. L., Churchill, S. E., Franciscus, R. G., Tan, J. & Hare, B. Craniofacial feminization,
727 social tolerance, and the origins of behavioral modernity. *Current Anthropol.* **55** (2014).

728 53 Ledogar, J. A. *et al.* Human feeding biomechanics: performance, variation, and
729 functional constraints. *PeerJ* **4**, e2242 (2016).

730 54 Smith, H. F. The role of genetic drift in shaping modern human cranial evolution: a test
731 using microevolutionary modeling. *Int. J. Evol. Biol.* **2011**, 145262 (2011).

732 55 Lieberman, D. E. Speculations about the selective basis for modern human craniofacial
733 form. *Evol. Anthropol.* **17**, 55-68 (2008).

734 56 Garcia-Martinez, D. *et al.* Ribcage measurements indicate greater lung capacity in
735 Neanderthals and Lower Pleistocene hominins compared to modern humans. *Commun.*
736 *Biol* **1**, 117 (2018).

737 57 Churchill, S. E. Bioenergetic perspectives on Neanderthal thermoregulatory and activity
738 budgets. *In: Neanderthals revisited: new approaches and perspectives*, pp. 113-133
739 (2006).

740 58 Wroe, S. *et al.* Computer simulations show that Neanderthal facial morphology
741 represents adaptation to cold and high energy demands, but not heavy biting. *Proc. Biol.*
742 *Sci.* **285** (2018).

743 59 Rak, Y. The Neanderthal - a New Look at an Old Face. *J. Hum. Evol.* **15**, 151-164 (1986).

744 60 Demes, B. Another Look at an Old Face - Biomechanics of the Neanderthal Facial Skeleton
745 Reconsidered. *J. Hum. Evol.* **16**, 297-303 (1987).

746 61 Holton, N. E., Yokley, T. R., Froehle, A. W. & Southard, T. E. Ontogenetic scaling of the
747 human nose in a longitudinal sample: implications for genus *Homo* facial evolution. *Am.*
748 *J. Phys. Anthropol.* **153**, 52-60 (2014).

749 62 Bastir, M. & Rosas, A. Cranial base topology and basic trends in the facial evolution of
750 *Homo*. *J. Hum. Evol.* **91**, 26-35 (2016).

751 63 Rosas, A., Bastir, M., Martinez-Maza, C., Garcia-Taberner, A. & Lalueza-Fox, C. Inquiries
752 into Neanderthal craniofacial development and evolution: "accretion" versus
753 "organismic" models. *In K. Harvati and T Harrison (eds) Neanderthals Revisited: New*
754 *Approaches and Perspectives. Springer, 37-70 (2006).*

755 64 Bastir, M. Back to Basics: Morphological Analysis in Paleoanthropology. *In: Schwartz J,*
756 *editor. Biological Theory. Boston: MIT-press, 205-227. (in press).*

757 65 Groning, F., Liu, J., Fagan, M. J. & O'Higgins, P. Why do humans have chins? Testing the
758 mechanical significance of modern human symphyseal morphology with finite element
759 analysis. *Am. J. Phys. Anthropol.* **144**, 593-606 (2011).

760 66 Pampush, J. D. & Daegling, D. J. The enduring puzzle of the human chin. *Evol. Anthropol.*
761 **2**, 20-35 (2016).

762 67 Moss, M. L. & Young, R. W. A functional approach to craniology. *Am. J. Phys. Anthropol.*
763 **18**, 281-292 (1960).

764 68 Russell, M. D. *et al.* The Supraorbital Torus:" A Most Remarkable Peculiarity. *Current*
765 *Anthropol.* **26**, 337-360 (1985).

766 69 von Cramon-Taubadel, N. Global human mandibular variation reflects differences in
767 agricultural and hunter-gatherer subsistence strategies. *Proc. Natl. Acad. Sci. U A* **108**,
768 19546-19551 (2011).

769 70 Noback, M. L. & Harvati, K. The contribution of subsistence to global human cranial
770 variation. *J. Hum. Evol.* **80**, 34-50 (2015).

771 71 Wroe, S., Ferrara, T. L., McHenry, C. R., Curnoe, D. & Chamoli, U. The craniomandibular
772 mechanics of being human. *Proc. Biol. Sci.* **277**, 3579-3586 (2010).

773 72 Anton, S. C. Neandertals and the anterior dental loading hypothesis: a biomechanical
774 evaluation of bite force production. *Kroeber Anthropol. Soc. Papers* **71-72**, 67-76 (1990).

775 73 O'Connor, C. F., Franciscus, R. G. & Holton, N. E. Bite force production capability and
776 efficiency in Neandertals and modern humans. *Am. J. Phys. Anthropol.* **127**, 129-151
777 (2005).

778 74 Godinho, R. M. *et al.* The biting performance of *Homo sapiens* and *Homo*
779 *heidelbergensis*. *J Hum Evol* **118**, 56-71 (2018).

780 75 Harvati, K. The Neanderthal taxonomic position: models of intra- and inter-specific
781 craniofacial variation. *J. Hum. Evol.* **44**, 107-132 (2003).

782 76 Harvati, K., Frost, S. R. & McNulty, K. P. Neanderthal taxonomy reconsidered:
783 implications of 3D primate models of intra- and interspecific differences. *Proc. Natl.*
784 *Acad. Sci. USA* **101**, 1147-1152 (2004).

785 77 Harvati, K. H. Neanderthals and their contemporaries. *Handbook of Paleoanthropology*
786 **Springer**, 2243-2279 (2014).

787 78 Dean, M. C. Another look at the nose and the functional significance of the face and
788 nasal mucous membrane for cooling the brain in fossil hominids. *J. Hum. Evol.* **17**, 715–
789 718 (1988).

790 79 Stewart, J. R. & Stringer, C. B. Human evolution out of Africa: the role of refugia and
791 climate change. *Science* **335**, 1317-1321 (2012).

792 80 von Cramon-Taubadel, N. Evolutionary insights into global patterns of human cranial
793 diversity: population history, climatic and dietary effects. *J. Anthropol. Sci.* **93**, 43-77
794 (2014).

795 81 Harvati, K. & Weaver, T. D. Human cranial anatomy and the differential preservation of
796 population history and climate signatures. *Anat. Rec. A Discov. Mol. Cell. Evol. Biol.* **288**,
797 1225-1233 (2006).

798 82 Hubbe, M., Hanihara, T. & Harvati, K. Climate signatures in the morphological
799 differentiation of worldwide modern human populations. *Anat. Rec. (Hoboken)* **292**,
800 1720-1733 (2009).

801 83 Reyes-Centeno, H., Harvati, K. & Jager, G. Tracking modern human population history
802 from linguistic and cranial phenotype. *Sci. Rep.* **6**, 36645 (2016).

803 84 Evteev, A., Cardini, A. L., Morozova, I. & O'Higgins, P. Extreme climate, rather than
804 population history, explains mid-facial morphology of Northern Asians. *Am. J. Phys.*
805 *Anthropol.* **153**, 449-462 (2014).

806 85 Noback, M. L., Harvati, K. & Spoor, F. Climate-related variation of the human nasal
807 cavity. *Am. J. Phys. Anthropol.* **145**, 599-614 (2011).

808 86 Lieberman, D. E., McBratney, B. M. & Krovitz, G. The evolution and development of
809 cranial form in *Homo sapiens*. *Proc. Natl. Acad. Sci. USA* **99**, 1134-1139 (2002).

810 87 Godinho, R. M., Spikins, P. & O'Higgins, P. Supraorbital morphology and social dynamics
811 in human evolution. *Nat. Ecol. Evol.* s41559-018-0528-0 (2018).

812 88 Strait, D. S. *et al.* Viewpoints: diet and dietary adaptations in early hominins: the hard
813 food perspective. *Am. J. Phys. Anthropol.* **151**, 339-355 (2013).

814 89 Daegling, D. J. *et al.* Viewpoints: feeding mechanics, diet, and dietary adaptations in
815 early hominins. *Am. J. Phys. Anthropol.* **151**, 356-371 (2013).

816 90 Grine, F. E. & Daegling, D. J. Functional morphology, biomechanics and the retrodiction
817 of early hominin diets. *Comptes Rendus Palevol* **16**, 613-631 (2017).

818 91 Hallgrímsson, B., Lieberman, D. E., Young, N. M., Parsons, T. & Wat, S. Evolution of
819 covariance in the mammalian skull. *Novartis Found. Symp.* **284**, 164-185; discussion 185-
820 190 (2007).

821 92 Cheverud, J. M. Genetics and analysis of quantitative traits. *Am. J. Phys. Anthropol.* **108**,
822 375-376 (1999).

823 93 Lieberman, D. E., Krovitz, G. E. & McBratney-Owen, B. Testing hypotheses about
824 tinkering in the fossil record: The case of the human skull. *J. Exp. Zool. Part B* **302b**, 284-
825 301 (2004).

826 94 Enlow, D. H. Facial growth and development. *Int. J. Oral Myol.* **5**, 7-10 (1979).

827 95 Kurihara, S., Enlow, D. H. & Rangel, R. D. Remodeling reversals in anterior parts of the
828 human mandible and maxilla. *Angle Orthod.* **50**, 98-106 (1980).

829 96 Harvati, K. & Hublin, J.-J. Morphological continuity of the face in the late Middle and
830 Upper Pleistocene Hominins from Northwestern Africa – A 3-D geometric morphometric
831 analysis. *Modern Origins: A North African perspective Springer Verlag*, 179-188 (2012).
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859 **Author contributions**

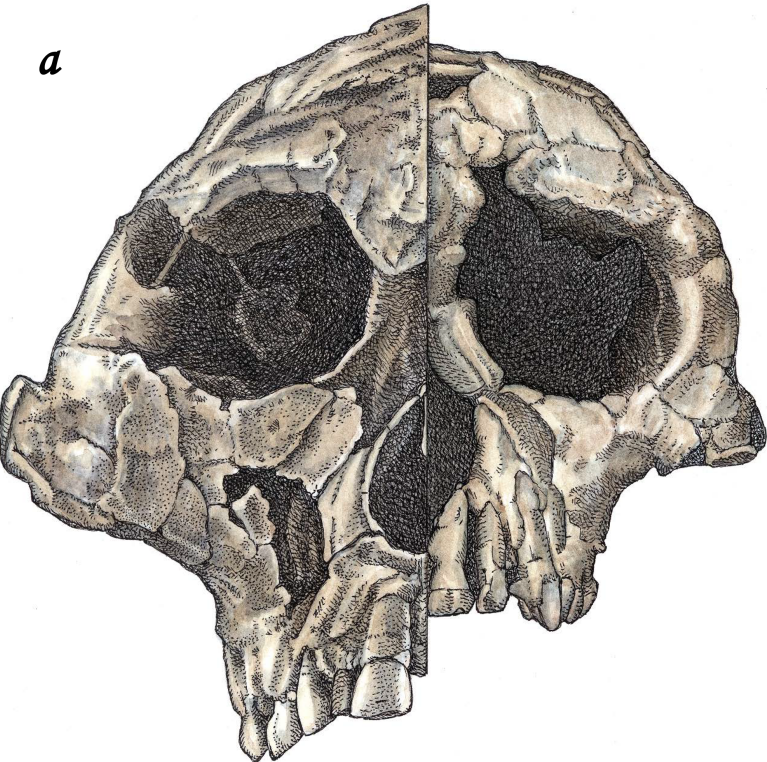
860 Author order reflects the relative size of the contributions made. All authors included contributed
861 to the development of the study and wrote the paper.

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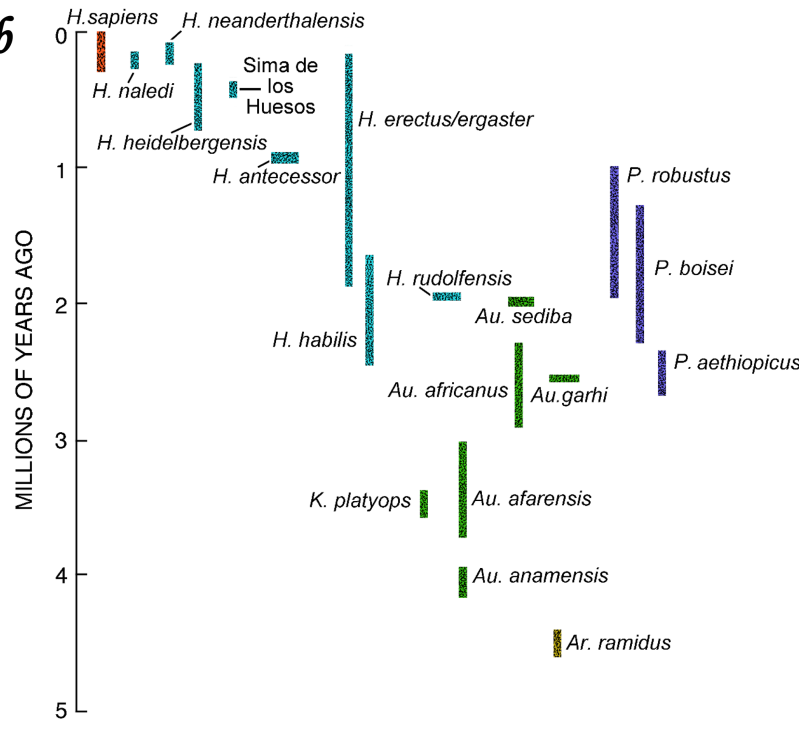
863 **Competing interests**

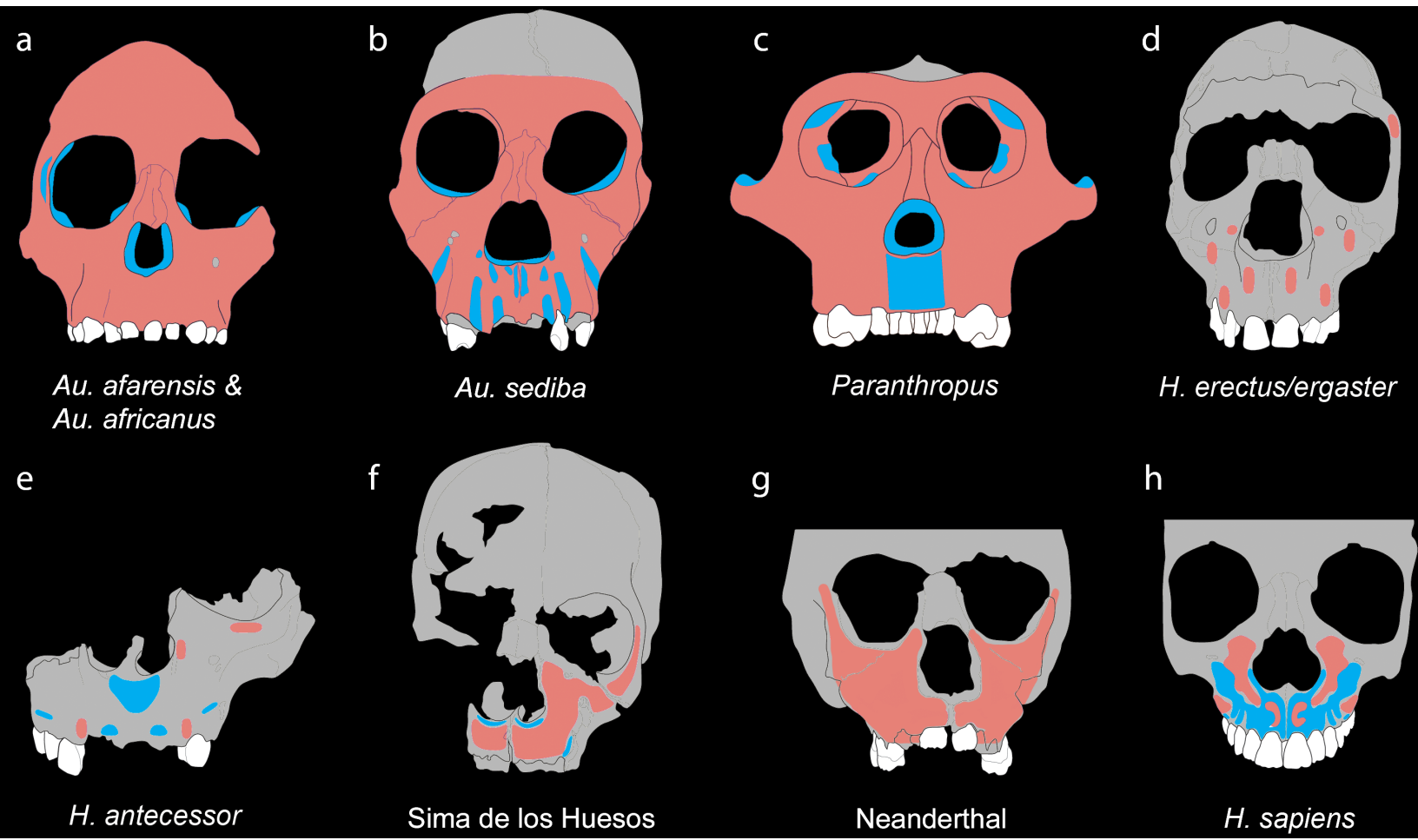
864 The authors declare no competing interests

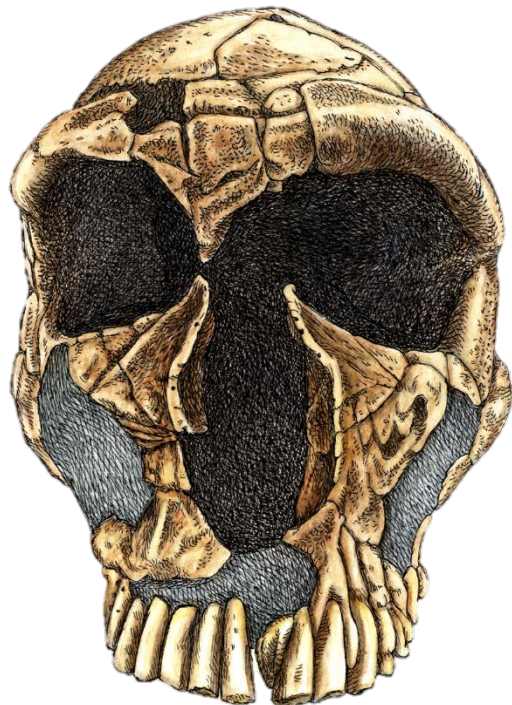
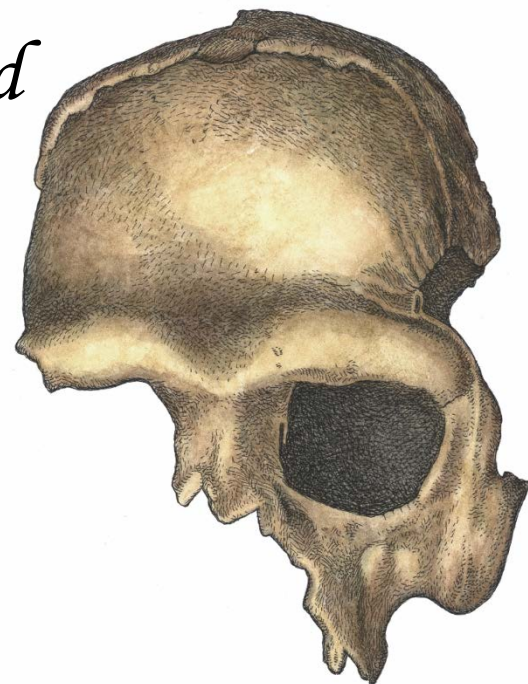
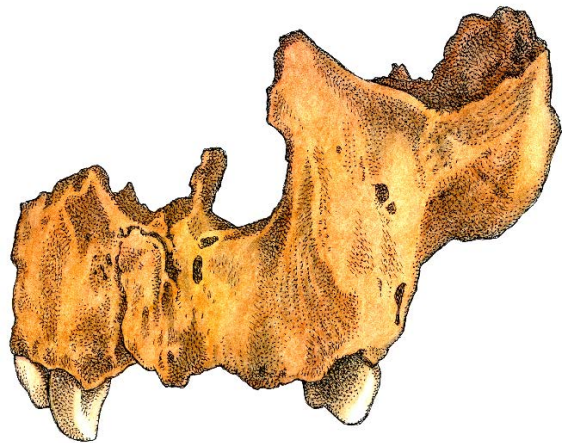
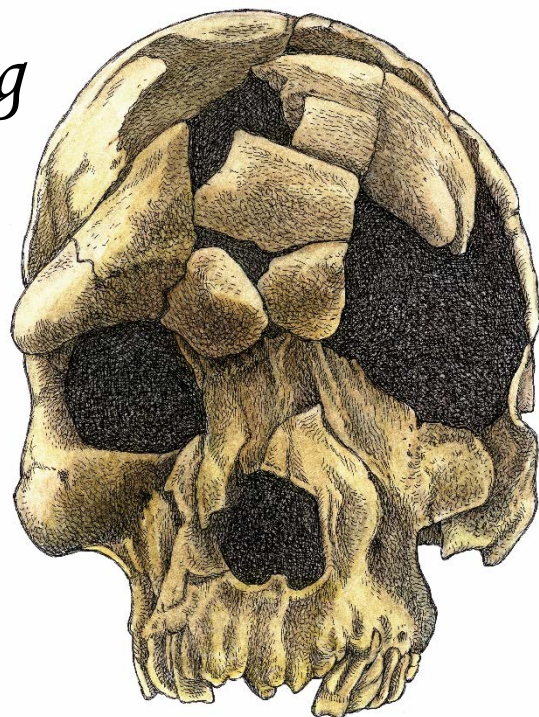
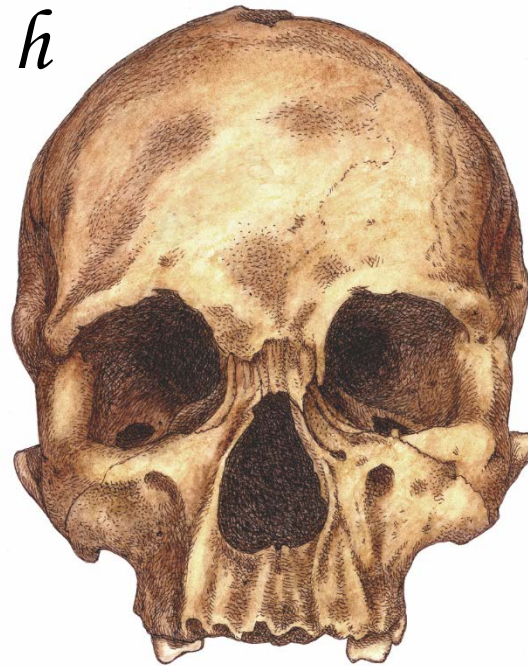
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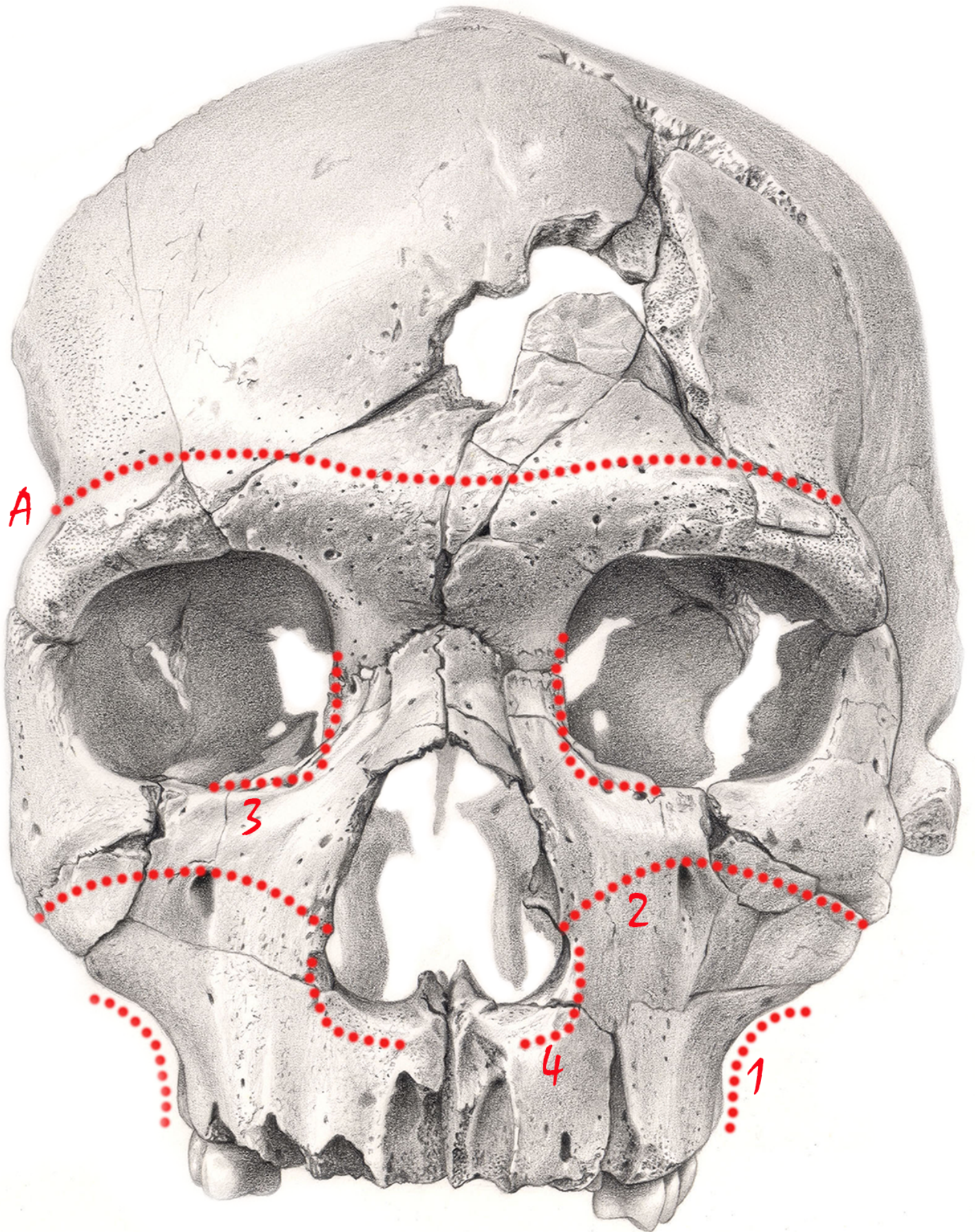


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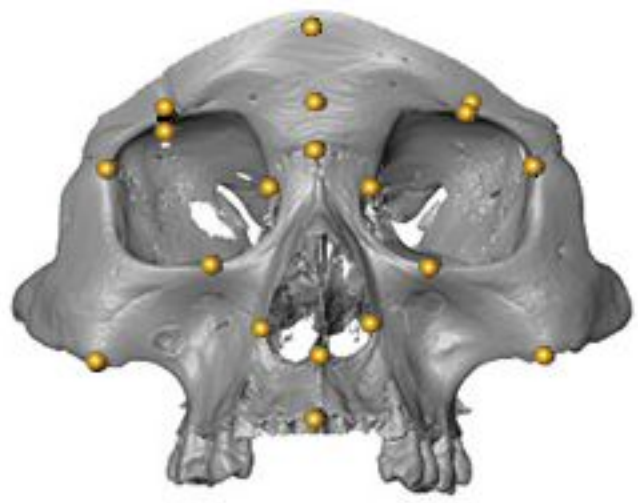




a*b**c**d**e**f**g**h*



E. Spitz-1h



Shape changes along PC2

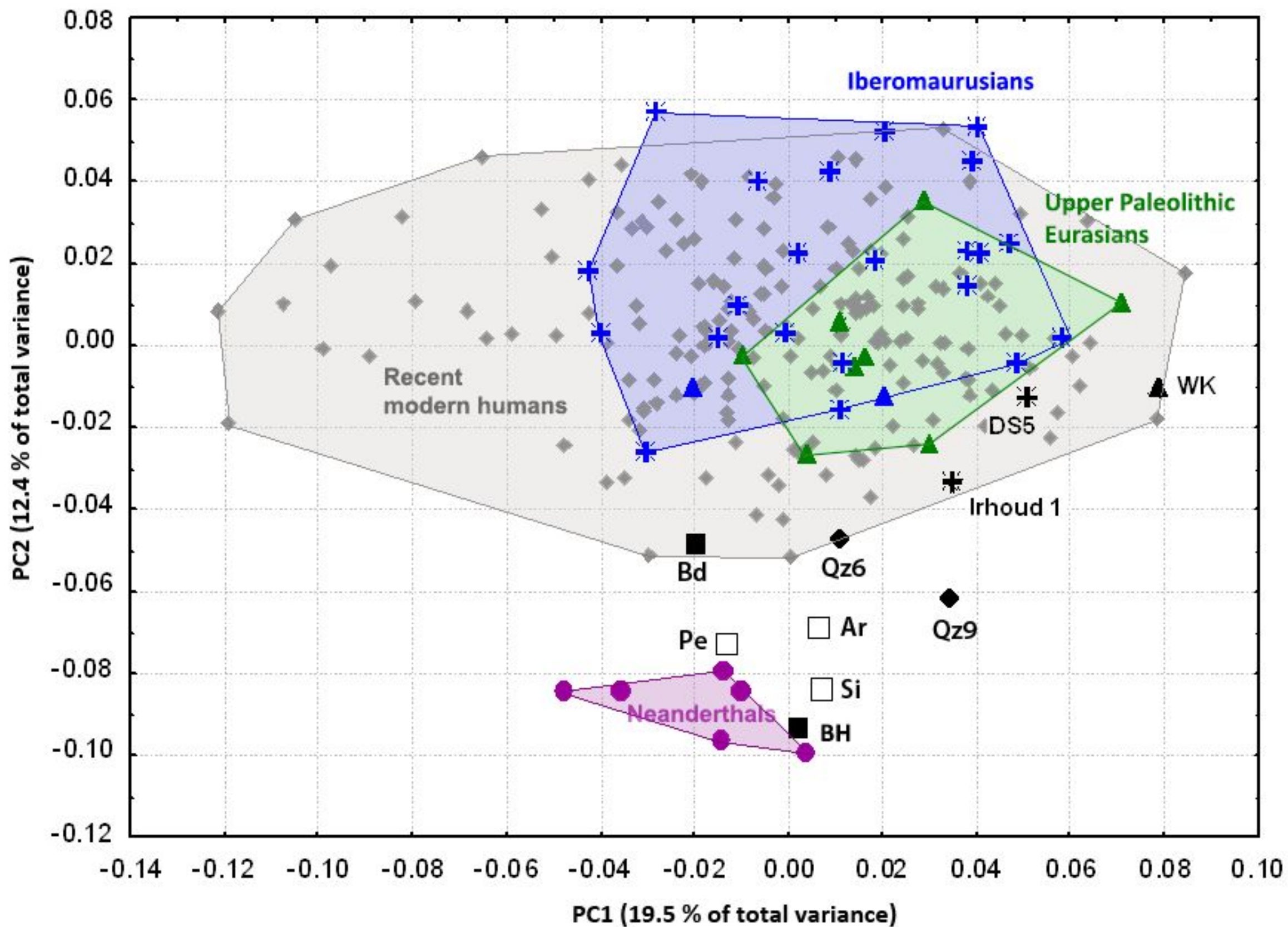


Table 1. Specimens discussed in the text, their taxonomic attribution and geological age. Ma = millions of years ago. Ka = thousands of years ago.

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