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THE EVOLUTIONARY HISTORY OF THE HUMAN FACE

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

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

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

The ancestral facial morphotype

That the human and chimpanzee/bonobo lineages shared a most recent common ancestor is beyond dispute, but no extant African hominoid presents an ideal facial morphotype for the chimp-human ancestor [8]. In their facial morphology, the chimpanzee, bonobo and gorilla differ from undoubted early hominins (like *Australopithecus*) in fundamental ways. For example, all three share a distinctive protruding bony arch above the eyes that, in life, sets off the upper rim of the naked facial mask from the braincase and other parts of the face to which the muscles of mastication attach. In contrast, the earliest hominins have supraorbital structures that are weakly differentiated topographically from the braincase, even when there is a distinct supraorbital torus, as is common in some species of *Homo* [9,10]. As has been suggested for other ectocranial structures[11], these differences may reflect a combination of social display mechanisms and biomechanical performance[12]. As discussed below with respect to the evolution of the modern human face, the role of social factors in shaping the morphology of the craniofacial skeleton has received much less attention than those relating to the biomechanics of the feeding system.

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

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

The facial morphologies of *Ardipithecus ramidus* (~4.4 Ma), a candidate basal hominin, and generalized *Australopithecus* species (best represented by *Australopithecus afarensis*, ~3.7-3.0 Ma) differ in similar ways from the non-human African great ape condition yet they are distinguishable from one another (Fig. 1a). As in later hominins, including modern humans, the maxilla is vertically short, midfacial projection is reduced and the supraorbital structures are topographically integrated with the braincase [17]. Both taxa feature shortened basicrania and reduced, modest sexually dimorphic canine crowns and roots as well as smaller incisors [9,17]. On the other hand, *Ar. ramidus* and *Au. afarensis* differ from one another in the parts of the face anchoring the muscles of mastication (Fig. 1a). The *Au. afarensis* face is dominated by expansive zygomatic (cheek) bones with robust, flaring arches that bridge the face to the braincase [9], whereas *Ar. ramidus* shares with the chimpanzee vertically short, lightly built zygomatic bones and arches [17]. The *Au. afarensis* anatomy is part of a presumptively derived masticatory system that includes transversely thick mandibular bodies, tall mandibular rami, and thickly enameled cheek teeth. Although it is tempting to tie these features to the species' expansive range of dietary-carbon isotopic values, which includes individuals with a significant component of C4 plants (e.g., grasses, sedges, undergrounds storage organs) in their diet [18], the lesser known *Au. anamensis* (~4.2-3.9 Ma), the probable phyletic ancestor of *Au. afarensis* (see Fig. 1b for the temporal placing of taxa discussed), shares many of these masticatory features yet it maintained a strongly C3 plant-focused (e.g. fruits, leaves) diet similar to that of chimpanzees and *Ardipithecus* [19]. The contrast between *Ardipithecus* and early *Australopithecus* highlights the modularity of facial anatomy in the early part of the hominin lineage. The initial changes were focused in the central and upper portions of the face, perhaps in response to changes in the function of the canines and supraorbital region in social signaling, whereas subsequent changes mainly involved the masticatory apparatus.

FIGURE 1 HERE

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

Relative to extant great apes and *Ardipithecus*, *Australopithecus* species (including those some authors classify within the genus *Paranthropus*) are characterized by a suite of specialized craniofacial features including the relative expansion of premolar-molar occlusal area, especially robust mandibular bodies and osteological indications of the enlargement or rearrangement of the jaw-adductor muscles to maximize vertical bite forces. These derived features have long been interpreted as adaptations to mechanically tough or hard plant foods that dominated in African environments during a period of aridification in the late Pliocene (≤ 2.8-2.7 Ma) [20,21]. Yet incipient expressions of these features can already be seen in the early australopith species (such as *Au. afarensis* and *Kenyanthropus platyops*), which thrived in the relatively equable, though highly seasonal, environments of the African mid-Pliocene (~3.5-3.0 Ma). Furthermore, molar microwear, an indicator of food mechanical properties, does not necessarily agree with suggestions that hard or tough food items were an increasingly common component of the diet[22]. This is despite progressive changes in the masticatory system (extreme forward shifts in the origins masseter and temporalis, two large muscles of mastication; increased massiveness and lateral flare of the zygomatic arches; marked retraction of the dental arches; enhanced postcanine megadonty and enamel thickness, etc.) among the diverse australopith species after ~3.0 Ma, culminating in the appearance by ~2.6 Ma of the bizarre "robust" australopith (=*Paranthropus*) configuration. *Australopithecus africanus* of southern Africa (~2.7-2.3 Ma) and *Au. garhi* of eastern Africa (~2.5 Ma) appear to represent early stages of this structural transformation. The younger species *Au. sediba* (~2.0 Ma) from South Africa [23] shares derived facial features with *Au. africanus* [10], but its facial remodeling differs from all other *Australopithecus* facial skeletons (see Box 2, Fig. 2)[15]. Resolving the dissonant dietary signals from isotopes, microwear, and craniofacial functional morphology should be an important focus of future research in early hominin paleobiology.

Patterns of diversity in the early *Homo* face

Evidence from the face constitutes one of the strongest arguments for a taxonomically diverse fossil record of early *Homo* (~2.1-1.7 Ma), which recognizes *Homo habilis*, *H. rudolfensis* and early African *H. erectus* (=*H. ergaster* of some authors) as distinct species. If large specimens such as KNM-ER 1470 and KNM-ER 62000 (usually attributed to *H. rudolfensis*), on the one hand, and smaller specimens like KNM-ER 1813 and OH 13 (*H. habilis*), on the other, are combined in a single species, then the implied pattern of sexual dimorphism, in which divergence in supraorbital form, masticatory structure, and midfacial proportions accompanies differences in size, is unlike that seen in any of the extant great apes or Old World monkeys (see Table 1 for specimen attribution). Despite these differences, the faces of all three *Homo* species are less projecting than those of australopiths, especially in the premaxillary region, and they show a tendency for the circumnasal plates, the outer rims of the orbits, and the zygomatic bones to face laterally in fully mature growth stages compared to their front-facing orientation in the australopiths. While its prominent supraorbital torus is a species hallmark, the face of early *H. erectus* is more modern human-like than that of either *H. habilis* or *H. rudolfensis,* with a more vertical profile featuring a retracted subnasal plate and a prominent nasal bridge. In support of these modifications in the upper face of *H. erectus*, it should also be considered that although *H. habilis* and *H. rudolfensis* have less robust mandibular bodies than do the australopiths, when scaled against admittedly crude estimates of body mass, neither of them have mandibular bodies as gracile as those seen in early *H. erectus* [24].

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

FIGURE 2 HERE

The faces of the Middle Pleistocene hominins and the LCA

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

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

FIGURE 3 HERE

Homo heidelbergensis as the LCA?

Stringer [32] has argued that shape resemblances between the Petralona and Broken Hill 1 crania indicated the existence of a widespread MP population which, if the Mauer mandible (Germany) is included, would be called *H. heidelbergensis.* Excluding the Mauer jaw whose diagnostic credentials have been questioned[33], the nomen *H. rhodesiensis* could be applied[32,34].

Furthermore, it was argued that this species represented the best candidate for the LCA of the *H. sapiens* and *H. neanderthalensis* lineages (see also [35]). Mounier and Lahr [36] produced several hypothetical virtual reconstructions of the LCA, and these also showed a *H. heidelbergensis*-like facial morphology. One implication of a *H. heidelbergensis*-like LCA would be that the zygomaxillary morphology found in these large MP crania would have undergone gracilisation to become the form found in recent *H. sapiens*, and a second trajectory, featuring increased midfacial projection and maxillary inflation, that led to the facial configuration found in the Neanderthals.

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

***Homo antecessor* as the LCA?**

In this scenario, a more ancient and taxonomically distinct LCA for the *H. sapiens* and *H. neanderthalensis* lineages, is based on the claimed “modern” maxillary conformation of the ATD6-69 *H. antecessor* face from Gran Dolina, Atapuerca, dated at ~850 Ka [41,42] (Fig. 2e). This model implies that a *H. antecessor*-like facial morphology was retained in the descendant *H. sapiens* lineage, but was modified in that of the Neanderthals. Some original reservations regarding this morphology given the juvenile status of ATD6-69[43] were removed with the finding of similar morphology in fragmentary adult maxillae[41,44]. The modern appearance of ATD6-69 is also substantiated by growth simulations of this specimen based on both the Neanderthal and modern human facial growth trajectories[38], and by the analysis of the facial growth and remodeling of ATD6-69, which identified resorptive fields on that maxilla similar to those found in sub-adult *H. sapiens* [16] (see Box 2, Fig. 2). By contrast, the maxillae of Neanderthals and the fossils from Sima de los Huesos, Atapuerca (Spain), were similar to those of more ancient Pliocene hominins showing a pattern of bone deposition[45]. If these analyses of facial development are correct, deriving the Sima de los Huesos and Neanderthal facial morphologies from that of a species represented by a specimen like ATD6-69 would require evolutionary ontogenetic changes in the growth of the face, as illustrated in immature individuals from the Sima de los Huesos [45]. While these remodeling changes may be construed as evolutionary reversals, we suggest that this is not the case. Instead, the remodeling changes should be viewed as a developmental process aligned with the facial morphological characteristics of the species.

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

Fossil and ancient DNA data provide further information on the nature and timing of the LCA of Neanderthals and modern humans [29-31,46]. The clear Neanderthal morphological, ontogenetic and genetic affinities of the Sima de los Huesos fossils dated to ~430 Ka and regarded as Neanderthal ancestors [47], suggest an evolutionary divergence of the Neanderthal lineage considerably before that date. Comparative analyses on the large sample of 17 crania from Sima de los Huesos showing a number of shared facial features with Neanderthals, indicate that modifications in facial shape were one of the first steps in the evolution toward the Neanderthal morphology [47] (Fig. 4). But, using recently published estimates of the autosomal human mutation rate, it has been suggested that the divergence date of the *H. neanderthalensis* and *H. sapiens* lineages could indeed be placed earlier — between 550 and 765 Ka[48]. These dates would be consistent with the oldest suggested examples of *H. heidelbergensis* potentially representing the LCA, although other estimates are younger (e.g. ~503-565 Ka[46]). An alternative would be to consider a *H. antecessor*-like facial morphology as more likely for the LCA of *H. sapiens* and *H. heidelbergensis,* with the *H. heidelbergensis* group exemplified by Petralona, Bodo and Broken Hill 1 having more in common facially with the Sima de los Huesos fossils and subsequent Neanderthals. When challenging the position of *H. heidelbergensis* as LCA of *H. sapiens* and *H. neanderthalensis,* and highlighted the significance of the *H. sapiens*-like facial morphology of *H. antecessor*, Bermúdez de Castro[44] cautioned that other aspects of *H. heidelbergensis* morphology suggested that it might be a side-branch alongside one of the early Pleistocene lineages in Eurasia that eventually gave rise to Neanderthals in Europe and to *H. sapiens* in Africa.

FIGURE 4 HERE

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

Adaptation in MP and modern human faces

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

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

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

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

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

FIGURE 5 HERE

Population history and climatic adaptation shape the face

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

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

A cultural/social component for the evolution of the face?

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

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

Conclusion

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

Multidisciplinary efforts are required to reach a detailed understanding of the complex evolutionary history of the face. Looking at future challenges, important areas that remain to be elucidated include how to integrate potentially conflicting evidence from craniofacial biomechanics, occlusal-microwear and stable isotopes into hypotheses about early hominin dietary behavior. Further, resolution of the debate over whether simulated stress patterns in the australopith craniofacial skeleton faithfully track feeding adaptations will be critical to the success of this venture [88,89,90]. Moreover, we must disentangle the complex effects of shared ancestry, climate adaptation and the influence of subsistence in shaping the evolution of the human face.

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

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

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

Table legend:

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

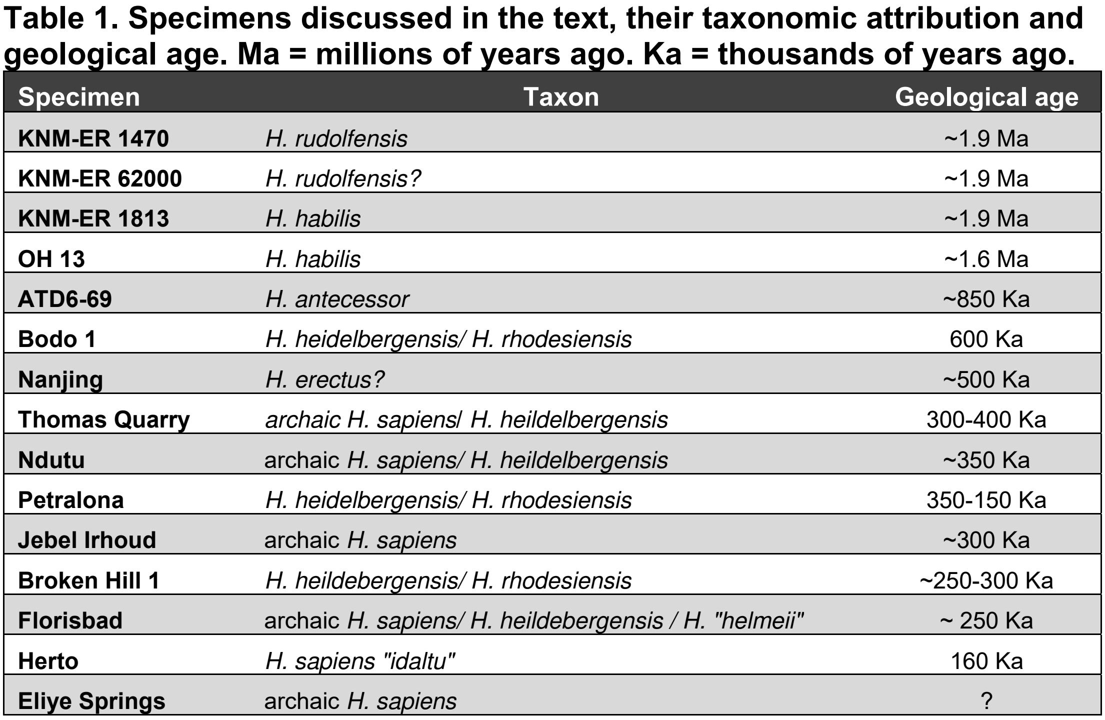


Table 1. Specimens discussed in the text, their taxonomic attribution and geological age. Ma = millions of years ago. Ka = thousands of years ago.

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

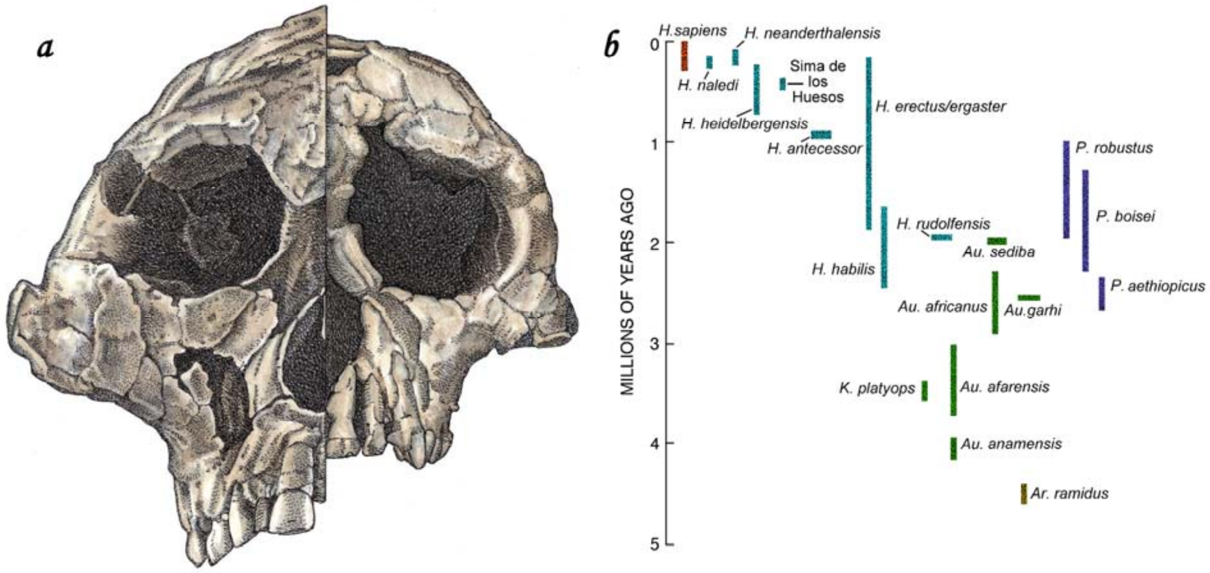
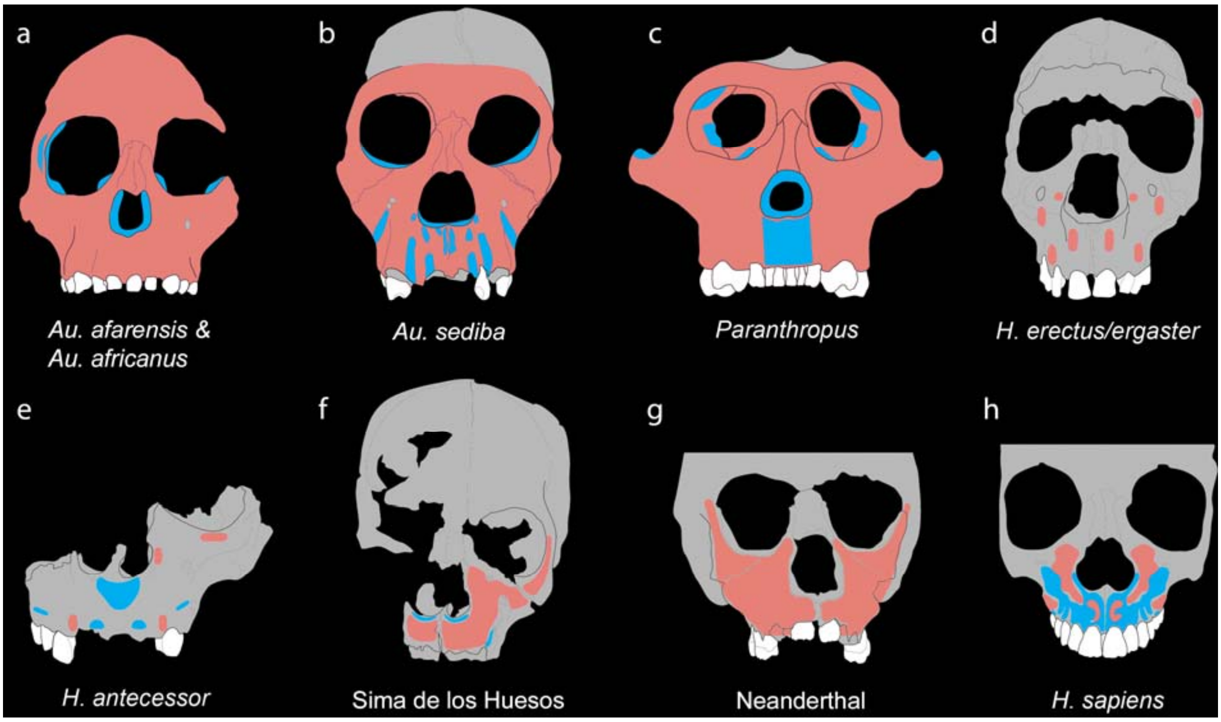


Figure 1: a) *Australopithecus* and *Ardipithecus* faces compared: Anterior views of hemisected crania, *Australopithecus afarensis* (A.L. 822-1, left) and *Ardipithecus ramidus* (ARA-VP 6/500 reconstruction, right -from ref [17]) illustrating the fundamental characteristics of facial shape. Note similarities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



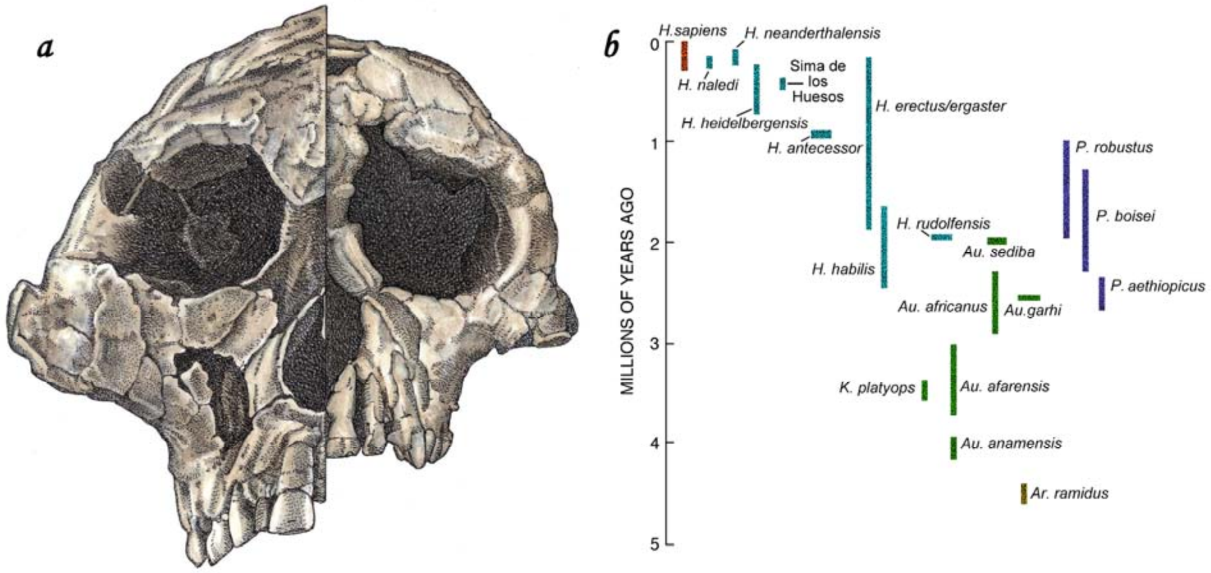


Figure 2: Summary of growth remodeling maps in fossil hominins compared to *H. sapiens*. Bone resorption is represented in blue and deposition is pink. **a)** *Au. africanus* and *Au. afarensis* facial skeletons show a depositional pattern in all anteriorly-facing surfaces of the face, in keeping with the growth of a prognathic facial skeleton [14]. Only the anterior border of the mandibular ascending ramus is resorbing, which is a mechanism to relocate the ramus to the borders of the pharynx in compensation for anterior displacement caused by condylar growth. **b)** The more recent species *Au. sediba* (~2.0 My) illustrates some vertically oriented resorption over the maxilla contributing to its less prognathic face compared to *Au. afarensis* and *Au. africanus*, and represents an evolutionary modification in facial

ontogeny [15]. c) *Paranthropus* (*P. boisei* and *P. robustus*) together, differ from *Australopithecus* showing narrow fields of resorption along the nasoalveolar clivus and in the vicinity of the canines of the lower jaw, indicative of some posterior relocation of the jaws, and reduced prognathism [14]. **d)** The juvenile African *Homo erectus* (*H. ergaster*) KNM-WT 15000 showed only deposition on the limited periosteal bone preserved [16]. To our present knowledge, all anteriorly-facing surfaces were forming in African *H. habilis*, reminiscent of those surfaces found in the more prognathic species of the genus *Australopithecus* [14]. **e)** The oldest known European species, *H. antecessor*, has resorption over the nasoalveolar clivus [16]**.** This species is also characterized morphologically as being relatively orthognathic and modern human-like [42] **f)** Fossils from Sima de los Huesos, Atapuerca are, by contrast, characterized by forming bone surfaces anteriorly [45]. The Sima de los Huesos population are considered Neanderthal ancestors [47] and in keeping with this, Neanderthal faces are also characterized by formation on all anteriorly facing surfaces [45] as shown in **g)**. The forwardly placed midface and nasal aperture of the Neanderthals resulted in a more anterior positioning of the tooth row *en bloc*, taking with it the maxillary tuberosity and generating the retromolar space characteristic of Neanderthals [45]. By the anterior repositioning of the entire midface, the Neanderthal achieved relative orthognathy. **h)** An example of a recent 12-year old *H. sapiens* individual showing widely distributed field of bone resorption.

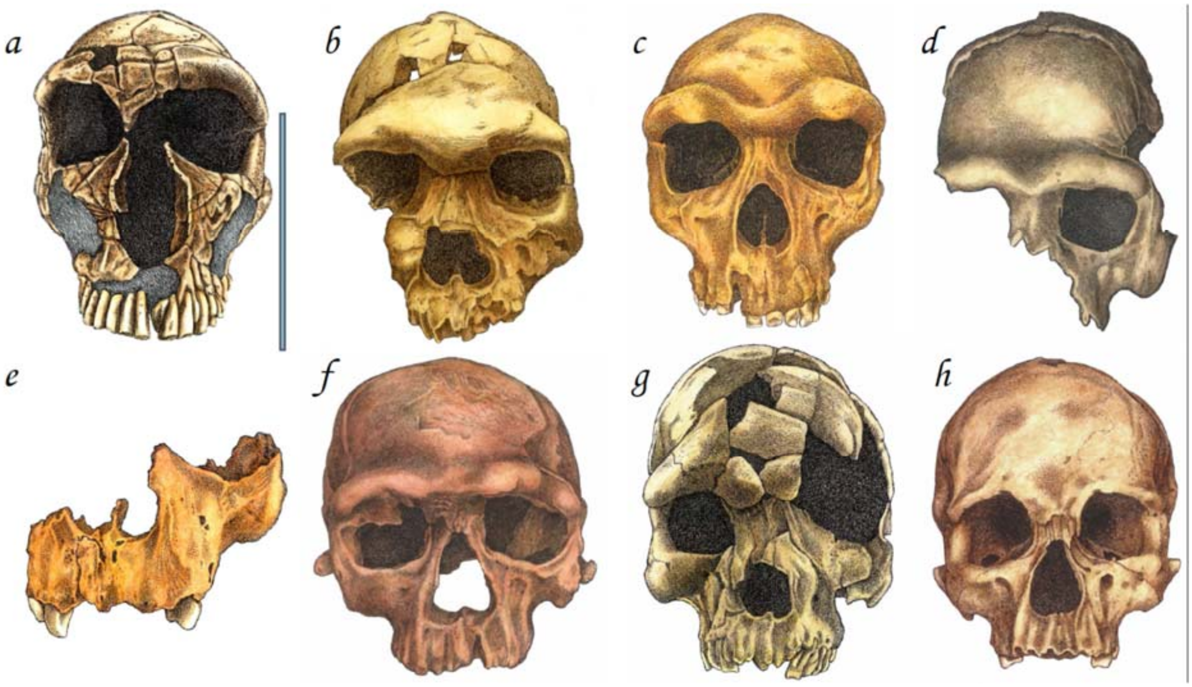


Figure 3: Middle-Late Pleistocene hominin crania compared to *H. sapiens*: a) La Ferrassie 1 Neanderthal dated to ~ 60-40 Ka. **b**) Bodo (Ethiopia) dated to ~ 600 Ka. **b)** Broken Hill 1 (Zambia) dated to ~250-300 Ka. **d)** Nanjing, China, dated to ~400 Ka. **e)** ATD6-69 maxilla, the holotype of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

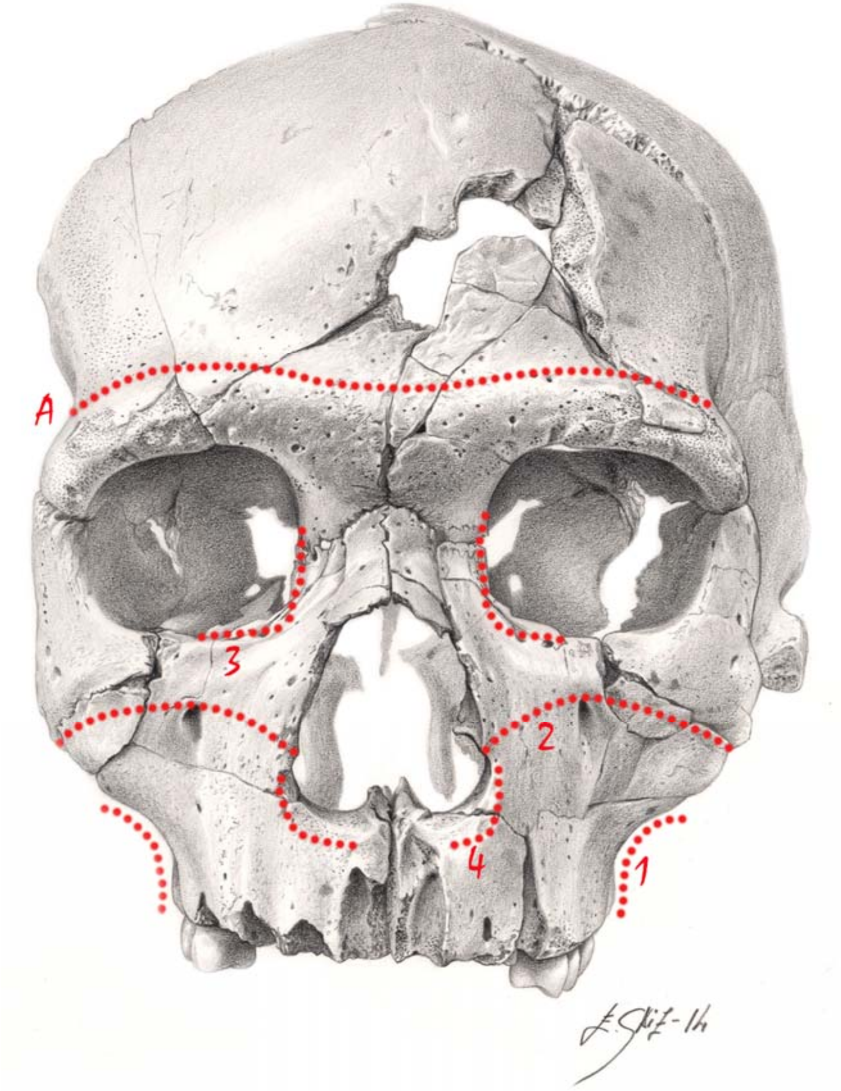


Figure 4: Sima de los Huesos fossils show facial differences from Neanderthals. In this frontal view of the adult specimen Cranium 17 from Sima de los Huesos (SH) (Atapuerca, Spain), the face is reminiscent of that of the Neanderthals in its marked nasal projection and a supraorbital torus that is continuous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

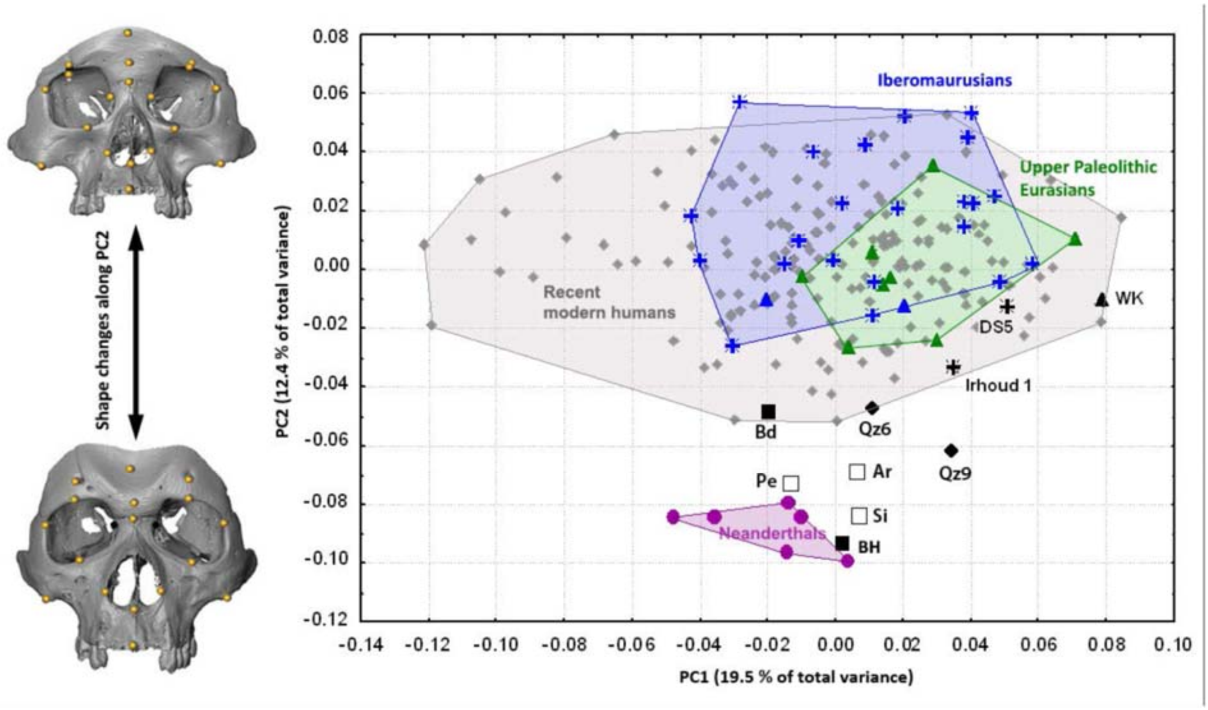


Figure 5: Morphometric analysis of the face discriminates Pleistocene fossils. We here show a principal components analysis of nineteen facial three-dimensional landmarks (illustrated as black points on the faces shown in the left panel) of a number of Middle-Late Pleistocene fossils and a sample of modern humans, revealing clusters of fossils based on facial shape. Shape differences between modern humans (high PC2 scores) on the one hand, and Neanderthals and other Pleistocene fossils (low PC2 scores) are illustrated in the left panel. Modern humans are distinguished by a flat and anteriorly oriented face, angled zygomatic, and gracile browridge (top left), contrasting with the large browridge and 'puffy' midface of the Neanderthals (bottom left). These quantitative analyses also indicate the morphological proximity of some these fossils to modern humans. Irhoud 1, found in Morocco and recently dated to ~300 Ka [31], is likely an early member of the *Homo sapiens* lineage, and unlike Neanderthals and other MP crania (Petralona, Bodo, Broken Hill 1, Sima de los Huesos), Irhoud 1 already shows almost completely modern human-like facial morphology. Other examples of *H. sapiens* include Qafzeh from Israel ~100 Ka, Wadi Kubbaniya from Egypt (~18 Ka) and possibly also the Moroccan fossils of Dar es Soltane (110-125 Ka). Grey diamonds: recent modern humans; black diamonds: early anatomically modern humans; green triangles: European Upper Paleolithic modern humans; red triangles: African Late Paleolithic modern humans; blue stars: North African Iberomaurusians; black solid squares: African Middle Pleistocene fossils; Black open squares: European Middle Pleistocene fossils; purple dots: Neanderthals. Labels as follows: Ar: Arago 21 (France); Bd: Bodo (Ethiopia); Pe: Petralona (Greece); Si: Sima 5 (Spain); BH: Broken Hill 1 (Zambia); Qz6 and Qz9: Qafzeh (Israel); WK: Wadi Kubbaniya (Egypt); DS5: Dar es Soltane 5 (Morocco). Plot produced using data collected by KH, previously analyzed in ref [96] where additional details can be found.

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Author contributions

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

Competing interests

The authors declare no competing interests