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The origin and evolution of *Homo sapiens*

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If we restrict the use of *Homo sapiens* in the fossil record to specimens which share a significant number of derived features in the skeleton with extant *H. sapiens*, the origin of our species would be placed in the African late middle Pleistocene, based on fossils such as Omo Kibish 1, Herto 1 and 2, and the Levantine material from Skhul and Qafzeh. However, genetic data suggest that we and our sister species *Homo neanderthalensis* shared a last common ancestor in the middle Pleistocene approximately 400–700 ka, which is at least 200 000 years earlier than the species origin indicated from the fossils already mentioned. Thus, it is likely that the African fossil record will document early members of the *sapiens* lineage showing only some of the derived features of late members of the lineage. On that basis, I argue that human fossils such as those from Jebel Irhoud, Florisbad, Eliye Springs and Omo Kibish 2 do represent early members of the species, but variation across the African later middle Pleistocene/early Middle Stone Age fossils shows that there was not a simple linear progression towards later *sapiens* morphology, and there was chronological overlap between different 'archaic' and 'modern' morphs. Even in the late Pleistocene within and outside Africa, we find *H. sapiens* specimens which are clearly outside the range of Holocene members of the species, showing the complexity of recent human evolution. The impact on species recognition of late Pleistocene gene flow between the lineages of modern humans, Neanderthals and Denisovans is also discussed, and finally, I reconsider the nature of the middle Pleistocene ancestor of these lineages, based on recent morphological and genetic data.

This article is part of the themed issue 'Major transitions in human evolution'.

1. Introduction: the big questions in modern human origins

The first question which should be addressed in any discussion of the origin and evolution of *Homo sapiens* is which diagnosis of the species is going to be used. A paper using the classic multiregional concept of *H. sapiens* [1,2] would probably need to cover the whole Pleistocene history of the human genus, while the much more restricted usage of authors such as Tattersall & Schwartz [3] might require a focus limited to a small set of middle–late Pleistocene fossils. In this paper, I will use the term *H. sapiens* for material that appears morphologically more closely related to extant humans than to the clade of *Homo neanderthalensis*, one of two potentially closest fossil relatives of extant *H. sapiens* (the other being Denisovans, which are so far virtually unknown from fossil material) [4]. Furthermore, although other researchers, particularly archaeologists, include behavioural factors in their diagnoses of modern humans/*H. sapiens*, I will not do so here.

Extant *H. sapiens* share specific traits such as a high neurocranium, rounded in lateral profile, a small face retracted under the frontal bone, a true chin even in infants, small discontinuous supraorbital tori, a lengthened post-natal growth period and life history, and a narrow trunk and pelvis with short superior pubic rami. Anatomical characterization of the *H. sapiens* lineage should thus be possible from features such as cranial globularity, retrocessive face, basicranial flexion, development of a mental osseum, dental microstructure and pelvic shape [5–8]. In addition, distinctive morphologies of elements of inner ear anatomy are being increasingly well characterized in *H. sapiens* [9]. In the cranial vault, the shape of the parietal region in *H. sapiens* seems particularly distinctive [10–12] and makes a significant contribution to

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globularity in both lateral and occipital views. Basicranial flexion is a more complex feature, but *H. sapiens* certainly appears distinctive in various measurements of this [6,13]. Dental microstructure, especially with the advent of micro-CT and synchrotron technology, is not only demonstrating the extended ontogeny of *H. sapiens*, but also revealing clear differences between *H. sapiens* and other hominin species in features such as enamel thickness and the shape of the enamel–dentine junction [14].

A second major question concerns the mode of evolution of the species *H. sapiens*—whether this was relatively punctuational or gradual. As the African middle Pleistocene hominin record is still sparse and poorly dated, it is not yet possible to tell whether fossils such as Omo Kibish 1 and Herto 1 and 2 represent some of the earliest coalescences of most of the traits we associate with our extant species, or whether more ancient examples remain to be found or dated. In Europe, the recent redating of the Sima de los Huesos fossils to at least 400 ka suggests that many Neanderthal features, particularly in the face, jaws and teeth, were already well developed by that time [15,16], which is more than double the age estimate for Omo Kibish 1 (McDougall) [17]. The subsequent European record had indicated a gradual, though not always precisely ordered, accretion of further Neanderthal synapomorphies [18], though a better absolute chronology is needed to test this properly. So at our present state of knowledge, we cannot yet say if there was an asymmetry between Europe (early) and Africa (late) in the appearance of the most diagnostic traits of the respective Neanderthal and modern human clades (and see further discussion at the end of this paragraph). Weaver [19] discussed three bodies of evidence often used to support a punctuational origin for *H. sapiens* in Africa (the apparent distinctiveness of ‘archaic’ from ‘modern’ fossil morphologies in Africa; the coalescence of extant mtDNAs to approx. 200 ka in Africa; the date of the first African appearance of ‘modern’ morphology apparently lying close to that date). He critiqued this evidence and used population and quantitative genetics theory to show that lengthy process models are also consistent with these data, and provide a viable alternative for modern human origins. A related consideration is whether differences along the respective *neanderthalensis* and *sapiens* lineages arose randomly, as a result of drift, or under the action of selection. Using cranial measurements, Weaver *et al*. [20] demonstrated that the level of difference between the two species could have arisen under drift rather than selection over a timescale of approximately 400 kyr, with the additional possibility that this divergence was relatively unconstrained due to cultural buffering, compared with the morphological divergence shown between crania of subspecies of *Pan troglodytes* [21]. And finally, when considering the rate of evolution of Neanderthal and modern human traits, Trinkaus [22] found that there was asymmetry in the amount of change along the two lineages, with the modern one being more derived than the Neanderthal one. However, limited genetic data seem to suggest the opposite, i.e. the Neanderthal lineage might be the more derived [23].

A third question is the nature of the last common ancestor (LCA) of the *sapiens* and *neanderthalensis* lineages, and when that LCA lived. Since 1983, I have built the case that shape resemblances between the Broken Hill and Petralona crania indicate the existence of a widespread middle Pleistocene population which can be called *Homo heidelbergensis* if the Mauer mandible is also included, or *H. rhodesiensis* if it is not [24,25] (see also [26]). Moreover, I have argued that this species represents the most reasonable LCA for the *neanderthalensis* and *sapiens* lineages, with their common origin placed at about 400 ka based on the estimated mtDNA coalescence date of the two lineages [25,27]. A new study using geometric morphometrics of various crania to virtually reconstruct the LCA of Neanderthals and modern humans also found that an Afro-European species (*H. heidelbergensis s.l.*) most closely approached the hypothetically reconstructed LCA, with the added suggestion that the LCA most likely lived in Africa [28]. An alternative model has a much older proposed LCA for the *neanderthalensis* and *sapiens* lineages, based on the ‘modern’ maxillary conformation of the ATD6-69 *H. antecessor* face from Gran Dolina, Atapuerca, dated approximately 850 ka [29]. Such a model would imply that this facial morphology was retained in the descendant *sapiens* lineage, but was lost in that of the Neanderthals. New data are emerging that are relevant to these models concerning the ultimate ancestry of *H. sapiens* and *H. neanderthalensis* (and thus also of the Denisovans), and I will return to this issue in §5.

A fourth question follows from the previous ones. Once the Neanderthal and modern human lineages began to evolve, did more ancient (and perhaps ‘ancestral’) morphologies in Eurasia and Africa soon die away, or could they have persisted alongside their ‘descendants’ for a considerable time? And if the latter, might the contemporaneous lineages have exchanged genes? While such a question poses serious issues for any simple cladistic, phylogenetic or taxonomic schemes, there is growing evidence of the survival of what could be considered as earlier middle Pleistocene morphologies (cf. *H. heidelbergensis* or *H. rhodesiensis*) into at least the later middle Pleistocene of Europe and Africa [8,25]. In addition, recent evidence of late Pleistocene episodes of introgression between different human lineages in Eurasia [30] and perhaps also in Africa [31] shows us that comparable genetic exchanges could also have been occurring in the middle Pleistocene.

2. The African middle–early late Pleistocene fossil record of *Homo sapiens*

The fossil record available to reconstruct the evolution of *H. sapiens* in Africa is still relatively sparse and poorly dated, and is dominated by material from the fossiliferous sedimentary basins of East Africa. Huge expanses of Central and West Africa were clearly inhabited during the later middle Pleistocene, as shown by the evidence of artefacts, but not a single informative fossil has yet been recovered to identify who those early inhabitants were. Thus, the available record is probably highly biased and unrepresentative of the continent as a whole. Nevertheless, we have to work with what is available, and I will now briefly discuss the most complete or significant specimens discovered so far, region by region (figure 1). Wider and more detailed compilations on the material and its dating can be found in Schwartz & Tattersall [32], Millard [33], Klein [34] and Wood [35].

(a) North-west and North Africa

In Morocco, the later middle Pleistocene archaeological record probably changes from non-Aterian Middle Palaeolithic/Middle Stone Age (MSA) industries to those of the Aterian during Marine Isotope Stage (MIS) 6, although it

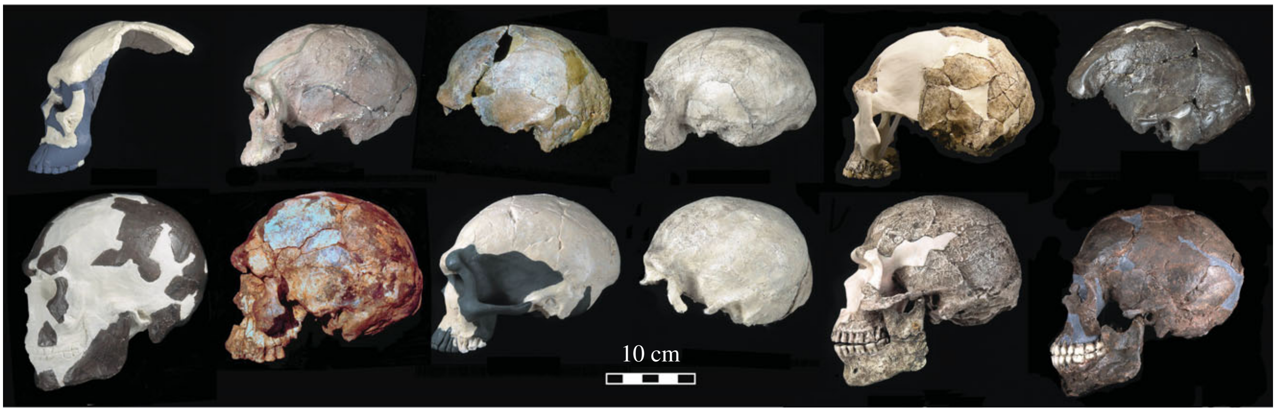

Figure 1. Left lateral views of African and Israeli archaic and early modern *Homo sapiens* crania (replicas unless otherwise stated). Top (L to R): Florisbad, Jebel Irhoud 1, Jebel Irhoud 2 (original), Eliye Springs, Guomde (reversed), Omo 2. Bottom (L to R): Omo 1, Herto (original, reversed), Ngaloba, Singa, Skhul 5, Qafzeh 9.

seems likely that a non-Aterian MSA continues in some regions alongside and even after the Aterian [36,37].

The *Jebel Irhoud* cave was exposed during quarrying operations in a Baryte mine and since 1961 has produced faunal remains, non-Aterian MSA archaeology and at least seven fossil hominins, with several more specimens found since 2007 awaiting publication. The fossil human remains are from low in the stratigraphic sequence, the best known being a cranium (JI1), a calvaria (JI2) and the mandible of a child (JI3) [38]. The cranium is relatively long and low with smooth rather than angular contours. It has a strong continuous supraorbital torus anterior to a somewhat domed frontal, and parallel-sided cranial vault with a capacity of about 1305 cm^3 [39]. The face is large and especially broad in its upper dimensions, with flat angled cheekbones and a broad but low nose, below which is significant alveolar prognathism. JI2 is a somewhat larger, more robust and angular calvaria, with a cranial capacity of approximately 1400 cm^3 [39]. It has a greater occipital projection and angulation, more modern parietal and frontal shape, but equally strong supraorbital development. Although comparisons of midline contours suggest *H. sapiens* affinities for both cranial vaults, multivariate studies indicate somewhat closer affinities for JI2 to recent human samples [40,41]. Both display some phenetic resemblances to early modern specimens such as those from Qafzeh, Skhul and Herto, though they lack their upper parietal expansion. In cranial vault (but not facial) form, there is nevertheless an overall resemblance to the Sima fossils and other early Neanderthals. The JI3 immature mandible presents a rather contrasting gracile body and large posterior teeth, and anteriorly may show incipient chin development. JI4 is a robust partial humerus, despite its immaturity, while there is also a further immature pelvic fragment. Overall, there is enough preserved of JI1 to indicate that it does not represent anatomically modern *H. sapiens*, although there are hints of 'modern' basicranial flexion in the relationship of the face and vault. JI2 and 3 are more difficult to assess because of their incompleteness, but the teeth of Irhoud 3 were subjected to synchrotron analysis which suggested an age at death of about 8 years, and a modern developmental pattern [42]. At the same time, an ESR analysis of its tooth enamel suggested an age of approximately 160 ka, which seems very likely to be a minimum figure.

The *Rabat* (*Kebibat*) hominin from Morocco consists of a very fragmentary cranial vault with more complete upper and lower jaws. The large teeth are typical of middle Pleistocene specimens from North Africa, but the mandible has elements of a mental trigone and a vertical symphysis, while the occipital region is high and relatively rounded [38]. However, the individual is subadult and so caution must be exercised in interpreting its morphology. Faunal correlation places the Rabat specimen in the late middle Pleistocene.

The Moroccan cave of *Dar-es-Soltan II* has produced an immature calvaria, an adolescent mandible and the anterior part of a skull with associated hemimandible. The anterior vault of DeS5 is high and very large, with a strong but divided supraorbital torus over a low, broad and flat face, with a low but broad nose. There are indications of a canine fossa and of alveolar prognathism. The mandible and the preserved posterior dentition are also large, but illustrations are deceptive in indicating the lack of a chin—the symphysial region is in fact broken off. Deciding on how to classify DeS5 is difficult—it has a rather modern-looking face and frontal bone shape, but both are very large in size, as is the supraorbital development. Although previous assessments have suggested that it could represent an Aterian intermediate between the MSA-associated Irhoud specimens and those of the Iberomaurusian (i.e. local late Upper Palaeolithic), morphometric analyses place it closer to Jebel Irhoud 1 and the Qafzeh crania than to the late Pleistocene fossils [36].

The caves of *El-Aliya* and *Témara* (Morocco) have produced fragmentary human cranial fossils from MSA/Aterian contexts. The Aliya material includes a large maxilla and teeth, but despite previous assertions, the preserved cheek morphology seems rather flat and non-Neanderthal [43]. However, not enough is preserved for definitive statements about the affinities of the material. The Témara specimens consist of some vault fragments, lacking a supraorbital torus and a mandible, which can more definitely be allied with modern *H. sapiens*.

A number of other Aterian sites have produced dental material which was analysed by Hublin *et al.* [43]. The cave of Zouhrah at *El Harhoura* yielded a mandible and canine during excavations in 1977, while the *Grotte des Contrabandiers* (Temara) has been under intermittent excavation since 1955 with early discoveries of material such as a robust and large-toothed mandible (in 2009 a still-unpublished immature human skeleton was recovered from Aterian levels apparently dated to MIS5). The Aterian dental samples generally display very large dimensions compared with late Pleistocene *H. sapiens* and Neanderthals. However, a relatively smaller anterior dentition and thicker enamel on the molars are more modern traits. While crown morphologies are generally complex, they resemble material like Skhul and Qafzeh more closely in pattern than the Neanderthals.

In contrast to the large and complex molar morphology found in the Moroccan Aterian material, the only teeth in the posterior mandible fragments recovered from 'levalloiso-mousterian' deposits in the Libyan cave of *Haua Fteah* in the 1950s are small and simple-crowned. The mandible fragments both have rather low rami and no evidence of retromolar spaces. As far as can be judged from the limited morphology preserved, these appear to represent *H. sapiens*, with an age now estimated at approximately 70 ka, within the early part of MIS4 [44]. Another possibly MSA-associated specimen which lacks the dental size and complexity of the Moroccan Aterian material is the cranium and fragmentary skeleton of a child recovered within sand deposits on the top of *Taramsa Hill*, Egypt [45]. Enough of the cranial vault is preserved to indicate a modern shape, even before cleaning, but the postcranial skeleton was highly friable and little of it survives. The MSA age of the specimen could not be definitively confirmed by direct dating [46].

(b) Southern Africa

The *Florisbad* 'cranium' (in fact only the anterior part of a skull and face) was found at this open locality in South Africa in 1932, stratified in a long sequence which remained poorly dated until 1996, when ESR on an enamel fragment from the human fossil provided an age estimate of approximately 259 ka [47]. The frontal bone is wide, thick and relatively receding, and the supraorbital torus is high but not strongly projecting, with lateral reduction. The face is incomplete but is certainly very broad in its upper proportions, with some expression of a canine fossa. In R. Clarke's reconstruction, it is low relative to its great breadth, but allowing for a complete anterior dentition, as in P. Cohen's unpublished reconstruction (figure 1), it may well have been closer to the Broken Hill cranium in facial height. Florisbad has sometimes been seen as morphologically allied to Broken Hill, at other times as an early member of the *H. sapiens* clade, and at yet other times as possibly representing a distinct late Middle Pleistocene species *H. helmei*, either a precursor species to *H. sapiens* [48], or as the LCA of the Neanderthal and modern clades, and the originating species of Mode 3 (levallois) lithic technology [49]. While too incomplete for definitive assignment, like the Irhoud material this fossil probably represents an archaic part of the *H. sapiens* clade.

The *Klasies River Mouth* fossil human material has been recovered over a period of more than 40 years in a variety of MSA-related stratigraphic contexts from an interrelated complex of caves on the southern coast of South Africa [34]. The material is fragmentary and represents mandibular, maxillary, facial, cranial vault and postcranial elements. The mandibles display great variation, ranging from large and chinless through ones with an apparently modern symphysial morphology, to a very small, albeit robust corpus with tiny teeth. Two maxillary fossils show comparable variation in size, while an isolated zygomatic is robust but of modern aspect, despite claims to the contrary. An apparently adult frontal fragment displays a wide interorbital breadth but centrally has a modern supraorbital profile. The few recovered postcranial bones indicate small-bodied individuals, although a proximal ulna has relatively large joint surfaces. Some elements of the Klasies assemblages clearly conform to the modern *H. sapiens* pattern, but other material cannot be so readily assigned on the parts preserved.

Border Cave, South Africa, has produced a number of fossil or subfossil human remains of actual or possible MSA antiquity [50]. In the 1940s, a humerus, ulna fragment and two metatarsals were recovered out of context in a spoil heap but have been argued on preservation grounds to be of MSA age. Their size and robusticity suggest that they might represent the same individual as the Border Cave 1 partial skull also found in spoil. This 'skull' actually consists of only part of the upper face and vault, but enough is preserved to show its large size, domed frontal, small supraorbital development and wide interorbital breadth. Although it appears of modern aspect, its large size and frontal and upper facial shape discriminate it from recent populations, and the possibly associated humerus and ulna display a few archaic traits. An edentulous mandible (BC2) recovered around the same time is small and more lightly built and appears assignable to anatomically modern *H. sapiens* on size and symphysial morphology. The infant skeleton BC3 certainly appears to represent *H. sapiens*, and has an important association with perforated *Conus* shells and red pigment [51]. Like BC2, the BC5 partial mandible is small and has a modern symphysial morphology, and its importance has been enhanced by direct ESR dating, providing an age estimate of approximately 74 ka [50].

(c) East Africa

The *Eliye Springs* (ES-11693) cranium was discovered by tourists after rapid changes in lake levels at West Turkana, Kenya [52]. The cranium had suffered anterior erosion, particularly of the face, but enough is preserved to reveal an archaic morphology. The vault is long and inferiorly broad, with limited upper parietal expansion, parallel-sided in rear view. There is slight frontal keeling but cranial buttressing is not strongly expressed, although it is not possible to assess the full extent of supraorbital torus development due to erosion, which has exposed the frontal sinuses. The occipital contour is rather rounded with minimal development of an occipital torus. Although heavily eroded, the face appears to resemble some late middle Pleistocene African crania in being relatively short, flat and broad, and there are signs of the slight development of a canine fossa. Although ES-11693 was discovered with faunal remains, the lack of any secure context or associated archaeology means that it remains undated. What is preserved of the specimen does not suggest particular *H. sapiens* affinities, although there are regional characteristics in facial shape and vault form that may relate it to other middle Pleistocene African crania such as Florisbad, Jebel Irhoud 1, Singa and Ngaloba. However, like Singa (see below, this section) its shape may have been affected by pathology [53].

Seven fragmentary cranial and mandibular fossils have been recovered from sediments bordering Lake *Eyasi* in Tanzania since the 1930s. Possible association with Acheulian artefacts had suggested an earlier rather than later middle

Pleistocene age, but limited ESR and U-series age estimates from fauna associated with frontal 7 suggest an age approximately between 88 and 130 ka. Eyasi 1 has a projecting but not massive supraorbital torus on its frontal, while its occipital is more modern in torus formation compared with a much stronger development in Eyasi 2, even displaying a possible suprainiac fossa. Frontal 7, like Eyasi 1, shows a rather low frontal bone with a distinct but not massive torus. The fragmentary condition of the material and difficulties of reconstruction limit the information available beyond indications that these specimens are apparently not assignable to anatomically modern *H. sapiens* [54,55], despite the later Pleistocene date suggested for some of them.

Ngaloba Laetoli Hominid 18 was recovered from the Ngaloba beds in the Laetoli region of Tanzania [56]. This partial cranium may date from the late middle or early late Pleistocene [57]. It is relatively long and low with an elongated and receding frontal bone. It is rather rounded posteriorly in both rear and lateral views, with negligible development of an occipital torus, but anteriorly there is a prominent but thin supraorbital torus. The occipitomastoid region is interesting for its resemblance to that of Neanderthals in the relation of mastoid and juxtamastoid eminences. The face cannot be properly articulated with the vault, but it is evidently rather low, broad and flat in the midface, with canine fossae, giving way to a prognathic subnasal region. The reconstruction by Cohen [58] confirms the relative gracility of the face, but suggests a greater height than in other depictions. Workers such as Rightmire [59] have classified LH18 as fundamentally modern, but it does not conform to anatomically modern *H. sapiens* in overall morphology, despite a suggestive facial and parietal shape.

Three *Omo Kibish* fossil hominins were discovered in 1967 in separate localities and contexts. Omo 1 was a partial skeleton in Member I of the Kibish Formation, Omo 2 an isolated surface find of a calvaria and Omo 3 a frontal fragment from member III [60]. More recently, an American-led expedition has located the original sites of Omo 2 and Omo 1, recovering more human material, including further parts of Omo 1, and additional fossils [61,62]. The fragmented skull from the Omo 1 assemblage has been the subject of several reconstructions but all concur in indicating a high, rounded and voluminous cranial vault with an occipital morphology of *sapiens* configuration, albeit with a wide frontal bone and strong but partitioned brow ridges. The face, dentition and mandible are much more fragmentary but evidence a canine fossa and mental eminence [63]. The postcranial remains include fragmentary limb bones which are largely of modern aspect, although with some distinctive features also noted in Neanderthal, Skhul-Qafzeh and Upper Palaeolithic individuals [61], and with proportions comparable with those of recent East Africans [64]. Omo 2 also has a very large braincase, with an endocranial capacity of approximately 1435 cm^3, but is narrower, with parallel-sided rather than superiorly expanded parietals, and a strongly angled occipital bone bearing a high but not especially projecting occipital torus. It also displays parasagittal flattening either side of a midline keel. In contrast with these archaic features, the supraorbital torus is a weakly expressed prominence at the anterior end of a flat, broad and receding frontal bone. The ages of Omo 1 and 2 have been sources of much controversy, but now seem well established at approximately 195 ka [17,65]. Classifying the Omo material is difficult. It is evident that Omo 1 can be assigned to modern *H. sapiens* from the preserved parts, but Omo 2 can only be tentatively placed in the clade through the apomorphy of supraorbital reduction.

The two separate human fossils found in the *Guomde* Formation of East Turkana in 1971 and 1976 consist of a proximal femur fragment KNM-ER 999 and a partial skull KNM-ER 3884 [66]. The femur is strongly built but seemingly of modern aspect in shaft shape and cross section [67] while the partial skull seems to combine characteristics found in Omo Kibish 1 and 2. It is similarly large and high, with a rounded modern-looking occipital region like Omo 1, but looking much more like Omo 2 in rear profile, high, with vertical walls. The supraorbital torus, as reconstructed, is evenly thick and projecting. Direct uranium-series dating of the material suggests an age of more than 180 ka [68].

Several cranial and dental human fossils were recovered from an open site at *Herto* in Ethiopia in 1997 [69]. The most significant consist of a nearly complete adult skull, an immature calvaria and parts of another cranial vault, probably adult. All are very large in size, the adult skull having a capacity of approximately 1450 cm^3. The length of the skull is outside the range of over 5000 modern crania, but its high and relatively globular shape (except for the occipital) conforms to the *H. sapiens* pattern. The supraorbital torus is strong and projecting, although divided into lateral and central parts, but the angled occipital with its centrally strong torus is reminiscent of that of Broken Hill 1 and Jebel Irhoud 2. The rear of the separate cranial fragments indicates an even greater size and robusticity than the most complete cranium. Univariate and multivariate analyses showed that the combination of features of the adult skull differentiate it from recent humans, but in terms of cranial shape, cranial angles and neurocranial globularity, it can be classified as *H. sapiens*, perhaps of comparable grade to material from Qafzeh & Skhul [70]. Its modernity was reaffirmed in metrical studies by Lubsen & Corruccini [71] and McCarthy & Lucas [72]. However, the addition of the subspecific nomen *idaltu* [69] does not seem justified.

The *Singa* calvaria was discovered in a block of calcrete in the seasonally dry bed of the Blue Nile in Sudan in 1924. It was notable for its strong parietal bosses, which were argued by some workers to link it to Khoisan origins, despite its great distance from southern Africa [73]. It has a well marked but centrally divided supraorbital torus, flat upper face and wide interorbital spacing, while the frontal is quite high. However, the parietals are very short and the occipital is also short and protruding, without showing a transverse torus. Natural breakage allowed removal of calcrete filling the endocranium, revealing the parietal bosses were abnormally thickened by diploic bone. An endocranial mould indicated a cranial capacity of about 1400 cm^3, while its asymmetry suggested a left-handed individual [74]. CT-scanning revealed further evidence of pathology in the unilateral absence of the inner ear on the right side, and Spoor *et al.* [75] suggested labyrinthine ossification had occurred, following an infection of the labyrinth membrane. This may have been due to a blood-borne infection (such as septicaemia) or a blood disorder such as anaemia, which fits with some explanations for the parietal pathology. Because of its pathology, it is unclear how abnormal is the shape of the calvaria. Overall, the anterior cranial morphology looks fairly modern, but the parietals are abnormal, preventing proper taxonomic assessment. The fossil is dated to a minimum age of 131–135 ka by U-series dating on sediments from the inside of the calvaria, and ESR analyses on associated faunal remains [76].

(d) Western Asia (Skhul and Qafzeh)

Although not in Africa, the adjacent Levant has clearly been a conduit for ancient population movement between Africa and Eurasia. Material such as the Zuttiyeh fronto-facial fragment, probably from the middle Pleistocene, remains difficult to classify, but in my view it does not show clear Neanderthal or modern human affinities, as can also be argued for the approximately 400 ka dental sample from Qesem [77]. Later and more clearly diagnosable material usually assigned to MIS5 also comes from Israel, in the form of the Tabun 1 Neanderthal skeleton, and the material I will discuss in more detail from the caves of Skhul and Qafzeh.

The site of Mugharet es-Skhul comprises a small cave, and a larger external rock-shelter and terrace, with most of the archaeological and hominin remains coming from the latter. The Skhul fossils, comprising 10 individuals, were discovered by Ted McCown in 1931–1932 as part of a larger rescue dig in the Mount Carmel area directed by Dorothy Garrod [78]. There is evidence that at least some of the Skhul individuals were intentionally buried [79], which may explain their relatively good preservation. Skhul 4 and 5 have significant portions of cranial and postcranial material preserved, while Skhul 9 consists of a more fragmentary calvaria and face with fragments of the pelvis and a femur. At one stage, Skhul was believed to be only around 40 ka in age, based on faunal and lithic similarities to Tabun, the Middle Palaeolithic levels of which had supposedly been dated to about 40 ka using radiocarbon. However, the Skhul material (Skhul 2, 5 and 9) has now been dated to between approximately 100 and 130 ka using ESR, U-series and luminescence analyses [80]. Nevertheless, it remains possible that Skhul 9 is older than the other fossils, as suggested by its morphology and lower stratigraphic position [48,80].

The first discoveries from Qafzeh Cave and its terrace (including Qafzeh 6) were made in the 1930s, but the full study and publication of the Qafzeh specimens only really began in the 1970s, by which time new excavations were greatly enlarging the Middle Palaeolithic-associated sample to 16 individuals. Vandermeersch's monographic work on the still-growing series [81] demonstrated that the Skhul and Qafzeh samples shared Middle Palaeolithic associations, the apparent presence of symbolic burials, and significant skeletal similarities. In terms of morphology, Vandermeersch highlighted the *H. sapiens* (*sensu stricto*) affinities of both groups of hominins from their cranial and mandibular shape to their pelves and limb bones. Non-metric, metric and morphometric analyses have regularly supported the view that the cranial, dental and postcranial anatomy of the combined Skhul-Qafzeh sample represents an early form of *H. sapiens sensu stricto*, albeit with robust or primitive features (e.g. [82–88]). As with Skhul, the application of luminescence, ESR and U-series dating has also placed the Middle Palaeolithic material into MIS5, with age estimates ranging approximately from 90 to 120 ka [89].

While the Skhul and Qafzeh series show clear derived traits in cranial and postcranial anatomy shared with Upper Palaeolithic and recent humans, they also display considerable variation, and differ in aspects of cranial shape and morphology, both within and between the samples (e.g. [3,48]). Given the wide error ranges on the available physical dating of the sites and skeletal and archaeological material [57], it is currently impossible to determine whether the Skhul and Qafzeh specimens represent different samples from essentially the same variable MIS5 population, as is often assumed in palaeoanthropological studies, two distinct populations, perhaps separated by many millennia, or even a sample of hominins covering a long period of time at both sites.

3. Interpreting the African middle–late Pleistocene fossil human record

During the past 25 years, the Recent African Origin model has increasingly dominated discussions about the evolution of *H. sapiens*, but with the recent modifications to it demanded by evidence of introgression from archaic humans such as Neanderthals and Denisovans outside Africa [90]. The date of origin of *H. sapiens* in this model has also changed in the face of new discoveries and dating work and is now often placed at about 200 ka, with the generally accepted first appearance of 'anatomically modern humans' (that is to say fossils that predominantly share the skeletal morphology of extant humans) in the form of the Omo Kibish 1 skeleton and the somewhat younger Herto material. This usage is consistent with my previous only partly successful attempts at diagnosing *H. sapiens* through a 'working definition' delimited by recent skeletal, and particularly, cranial variation in traits such as a domed neurocranium, reduction in facial size and projection, and increased basicranial flexion [63,91,92].

If it is accepted that *H. sapiens* is a relatively young species, distinct from Neanderthals and from the putative LCA, *H. heidelbergensis*, there are a number of possible schemes for the evolution of *H. sapiens*, three of which are illustrated in figure 2. One possibility would be to limit the species diagnoses of both *H. neanderthalensis* and *H. sapiens* to those samples which predominantly share the morphological traits of the terminal members of the Neanderthal and modern human clades, e.g. post-MIS8 Neanderthals, and post-MIS8 *H. sapiens*. Primitive members of the Neanderthal and *sapiens* clades that showed only some of the diagnostic features of the terminal species could then be given a separate species name. If this scheme were to be followed, the species 'intermediate' between *H. heidelbergensis* and *H. sapiens* would probably by priority be *H. helmei*, based on the Florisbad partial cranium [48]—note that this is a distinct usage of the species name from that of Foley & Lahr, [49]. The equivalent nomen for specimens 'intermediate' between *H. heidelbergensis* and *H. neanderthalensis* would probably then be *H. steinheimensis* by priority (figure 2*a*). Yet as explained in Stringer & Buck [4], unless there is truly punctuational change at each species origination, there would undoubtedly be blurred and probably unworkable boundaries between *helmei* and *sapiens*, and between *steinheimensis* and *neanderthalensis*. Given that there are already difficulties in distinguishing the LCA from the early stages of evolution along the respective *sapiens* and *neanderthalensis* lineages, creating further taxonomic divisions for such relatively short-lived populations would merely atomize the taxonomic problems rather than solve them.

Another option would be to employ looser definitions of *H. sapiens* and *H. neanderthalensis* to encompass all the

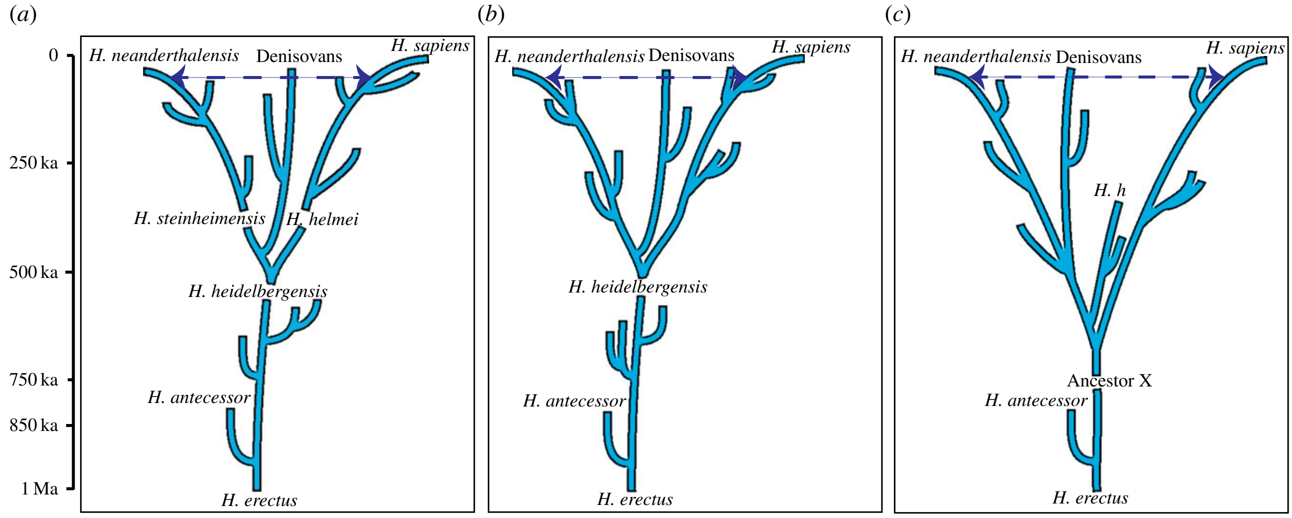

Figure 2. (*a*) *H. sapiens* and *H. neanderthalensis* as species represented only as terminal taxa, with all the traits judged to be diagnostic. *H. helmei* and *H. steinheimensis* as intermediate species between each terminal species and LCA, here suggested to be *H. heidelbergensis*. (*b*) Looser diagnoses of *H. sapiens* and *H. neanderthalensis* including all populations after the split from the LCA. Both species encompass considerable morphological variation along their lineages and populations which go extinct without issue. The overall topography of both trees and the estimated divergence and LCA 'dates' are derived from a study of whole mtDNA genomic data [25,27]. (*c*) A tree which uses the new date and Neanderthal-like morphology of the Sima sample, plus an inferred deeper divergence date based on new genomic mutation rate estimates [93]. Here, a hypothetical and older 'Ancestor X' replaces *heidelbergensis* as the LCA. The Denisovans are also shown on the diagram, as an early derivative of the Neanderthal clade. Their taxonomic status is still unclear [30]. Late Pleistocene inter-lineage gene flow is indicated by the dashed arrows [30,94,95].

samples which lie on the respective lineages after their separation from the LCA (figure 2*b*). The early members of the modern human lineage could be informally termed 'archaic *H. sapiens*', and the early members of the Neanderthal lineage 'early *H. neanderthalensis*' (figure 2*b*) which, although it lacks taxonomic precision, is my present preference. Unfortunately, the term 'archaic *H. sapiens*' has previously been used much more loosely, often referring to specimens as different as Broken Hill and La Chapelle-aux-Saints, but I think its use could be restricted to specimens with a predominance of archaic features but which nevertheless demonstrably belong to the phylogenetic clade of extant *H. sapiens*. One day we may be able to map more fossils onto their respective lineages through their aDNA, as has now proved possible for the Sima specimens, placed within the Neanderthal clade via genomic DNA [93]. However, this method would be entirely dependent on aDNA preservation, and is likely to prove impractical for much of the material recovered from warmer depositional environments. The early parts of both the *H. sapiens* and *H. neanderthalensis* lineages are also likely to show some of the lost diversity that once existed and will thus contain populations which might ultimately not be ancestral to late members of either species, as shown notionally in figure 2—but see further discussion in §4.

4. Early *Homo sapiens* in Africa

Figure 1 illustrates the wide morphological variation in fossil human crania associated (or potentially associated) with early MSA archaeology in Africa, ranging from material like Florisbad and Jebel Irhoud through to Ngaloba and Herto. The figure also includes examples from Skhul and Qafzeh. This array of fossils shows differing combinations of archaic and derived (recent *H. sapiens*-like) traits, and illustrates some of the variation displayed even at closely related sites.

As discussed, Omo Kibish 1 and 2 contrast strongly in cranial shape. A transition between their morphologies would provide a different model of *H. sapiens* evolution from that suggested by Herto, and this is perhaps exemplified in the ER-3884 partial cranium from Guomde which shows features found in both the Kibish crania. These potential variations already suggest that there is probably not a simple, linear relationship between an ancestral *heidelbergensis*-like morphology and that of *H. sapiens*. Alternatively, as suggested by Stringer [2,8,70], this variation might instead reflect the coexistence of morphologically distinct populations during the later middle Pleistocene in Africa. Evolution may at times have progressed independently in different areas, with morphological substructure leading on to the eventual coalescence of the full suite of *H. sapiens* characteristics, comparable with the pattern seen in the genetic data. I have called this an 'African multiregionalism', with many potentially interfertile subdivisions of the evolving *sapiens* species across Africa [2,8,70]. Others (e.g. [96]) have used the analogy of a braided stream for what they consider to be an open genetic network for different human lineages across the whole Old World, but I think the most appropriate application for this analogy is in the middle Pleistocene of Africa. The imperfect chronological control over the African middle Pleistocene record provides only very limited support for an ordered progression from 'archaic *sapiens*' to 'modern *sapiens*' through time. Instead we see morphologically varied fossils such as Broken Hill, Florisbad and Omo Kibish 1 apparently juxtaposed in close temporal proximity [8]. There is also growing evidence of the survival of even younger elements of archaic morphology into the late Pleistocene at sites like Eyasi, Iwo Eleru and Lukenya Hill (e.g. [40,41,97–99]).

While later Pleistocene Eurasia suffered both large-scale and sharp millennial-scale climatic oscillations, which were especially reflected in fluctuations of temperature, these changes in Africa were expressed much more in terms of precipitation (e.g. [100,101]). This would have led to the creation or removal of biogeographic barriers such as tropical rainforests and deserts—both probably largely impenetrable to early humans [8,100,102]. In turn, this could have had direct demographic effects on human populations. For example, the middle of MIS6 (approx. 150 ka) was predominantly arid, with the probable isolation or even extinction of small human populations across Africa. By contrast, the warmest part of MIS5 (approx. 120 ka) may have been a time of population expansions and interconnections. However, this may not always have led to homogenization, as Scerri *et al*. note for the 'green' Sahara [37], where distinct palaeobiomes may have catalysed enduring subdivisions. Refugia in which populations could weather the worst of climatic downturns have been suggested as a key driver of morphological and perhaps adaptive behavioural changes in Eurasia [8,103], but in Africa climatic ameliorations could have been equally important in seeding denser and more networked populations, facilitating both genetic and cultural changes [8,101,104]. The result of these processes was the composite we call modern *H. sapiens*, genetically, morphologically and behaviourally, but there was never a single centre of origin, and despite later homogenization [82], some ancient substructure could have persisted.

Several relatively late Pleistocene African sites contain fossils that exhibit combinations of archaic and recent *H. sapiens* traits. In my doctoral research, I found that, despite its Late Stone Age associations and overall 'modern' shape, the Iwo Eleru fossil from Nigeria was idiosyncratic, since it also showed affinities to archaic fossils such as Ngandong, Saccopastore 1 and Omo 2 [10,11]. Its dating was recently confirmed as late Pleistocene (approx. 14 ka) but also confirmed was its morphological distinctiveness from recent African crania. Despite its late date, it showed morphometric shape affinities to the much older Elandsfontein, Ngaloba, and Skhul and Qafzeh fossils [40,41]. A comparable though slightly earlier example of late Pleistocene distinctiveness (approx. 22 ka) is the Lukenya Hill partial calvaria from Kenya, which was restudied by Tryon *et al*. [98], showing a similar mix of more archaic and recent elements of cranial shape. These specimens emphasize how little we still know about late Pleistocene morphological variation across much of the African continent. These fossils may indicate deep Pleistocene population substructural variation, possibly including hybridization between late *H. sapiens* and surviving archaic hominin lineages [8,30,40,92], variation which was subsequently lost.

5. Discussion

Based on this research, there are genetic traces in extant *H. sapiens* of earlier introgression from at least three extinct human groups [30,92,94,95]. So how does this affect any definition of *H. sapiens* in the fossil record? As Jolly [105, p. 129] stated in comparing the taxonomy of recent papionins and of fossil hominins 'The message . . . is to concentrate on biology, avoid semantic traps and realize that any species-level taxonomy based on fossil material is going to be only an approximate reflection of real-world complexities'. As long as the biological species concept (which does not operate well for many closely related extant species of birds and mammals) is not imposed, species can be recognized in the fossil record as evolutionary lineages which maintain their identity through significant periods of time (and in the face of *small* amounts of introgression). On that basis, I consider that both *H. neanderthalensis* and *H. sapiens* can be treated as species with a time depth that stretches back into the middle Pleistocene. However, that pragmatic use of the term 'species' must be tempered with a recognition that these 'species' were not genetically impermeable.

As this paper includes the origin of *H. sapiens* in its title, it seems appropriate to return to this topic, with relevant new data to add to the picture. For some time, it has been recognized that the immature ATD6-69 face which forms part of the hypodigm of *H. antecessor* displays apparent resemblances to extant *H. sapiens* in the confirmation of the zygomaxillary area. For example, its anterior surface is angled at about 90° to the midline, its inferior border is retracted and runs approximately horizontally, with a malar notch and zygomaxillary tubercle, and there is a canine fossa in the infraorbital area. For some, this morphology in a fossil dated at more than 800 ka may reflect the ancestral condition for *H. sapiens* [29]. Previously [2], I questioned whether this morphology would have been maintained in the adult, and whether there would have been population variation in its expression, but it does seem to be expressed in three more fragmentary subadult and adult specimens from Gran Dolina [106]. Issues have also been raised about allometric effects on the zygomaxillary area such that larger archaic faces would show an inflated maxillary morphology more like that of the massive Bodo and Petralona crania [107]. Friedline *et al*. [108] conducted a wide-ranging morphometric study of the faces of various fossil crania in order to better place ATD6-69 developmentally and phylogenetically. They confirmed that its morphology was largely shared with *H. sapiens* and that this would probably have persisted into adulthood. However, they argued that this morphology was largely primitive and that it had probably evolved and re-evolved several times in human evolution, and therefore had to be used with caution phylogenetically. In their view, the true 'modern' zygomaxillary morphology could only be reliably traced back to later middle Pleistocene fossils such as Jebel Irhoud 1.

But there are further relevant data. First, microscopic study of the facial growth of the immature ATD6-69 *antecessor* fossil confirmed that it does show homologies with the maxillary developmental pattern of recent *H. sapiens*, a pattern argued to be derived, not primitive [109], while a second study has concluded that the facial ontogeny of immature Sima de los Huesos fossils (dated approx. 400 ka) instead show homologies with later *neanderthalensis* specimens [110]. Thus, deriving the Sima and Neanderthal facial morphologies from that of the Gran Dolina child would demand evolutionary reversals in their ontogeny, while deriving *H. sapiens* from it would apparently not. And it has been recognized for some time (e.g. [32]) that if we examine the African middle Pleistocene record we find the majority of fossils with the area preserved share much of the zygomaxillary morphology of most extant *H. sapiens* in having an anterior surface angled at about 90° to the midline, an approximately horizontal lower border, and a flat or retracted infraorbital surface in lateral view (which may include a canine fossa). However, African fossils that I assign to *H. heidelbergensis*/*rhodesiensis* are divided into ones which although damaged or incomplete, apparently display a more *sapiens*-like zygomaxillary morphology (Thomas Quarry and Ndutu), and those that do not (Bodo, Broken Hill). If this is not a reflection of sexual dimorphism or allometric factors at work in the large faces of Bodo 1 and

Broken Hill 1 (as I have sometimes argued), it may indicate taxonomic diversity in the African middle Pleistocene record which could exclude those fossils from representing an ancestral morph for *H. sapiens*.

New genetic data add further complexity to reconstructing the nature and dating of the LCA of Neanderthals and modern humans. As already mentioned, mtDNA indicates that the LCA lived approximately 400 ka, consistent with a *heidelbergensis* origin [27]. However, as also discussed, the clear Neanderthal morphological and genetic affinities of the Sima fossils, now dated to at least 400 ka, suggest there was probably an evolutionary divergence well before that date. Moreover, using the latest estimates of the autosomal human mutation rate, the divergence date of the *neanderthalensis* and *sapiens* lineages can indeed be placed earlier, between 550 and 765 ka, which would be consistent with only the oldest suggested examples of *heidelbergensis* as potentially representing the LCA [93]. An alternative would be to consider a *H. antecessor*-like morphology as more likely for the LCA of *H. sapiens* and *H. heidelbergensis*, with the *heidelbergensis* group exemplified by Arago, Petralona, Bodo and Broken Hill having more in common facially with the Sima fossils and subsequent Neanderthals (figure 2*c*).

It has been suggested that the *antecessor* material also displays a derived *sapiens*-like pattern of dental development [111], as well as some similarities in postcranial morphology [106], but in other respects there are Neanderthal-like features such as in the mastoid region, hypertrophied medial pterygoid tubercle, M^1 shape, clavicle and humerus. Bermúdez de Castro & Martinón-Torres [106] concluded that *antecessor* was a side-branch of a lower Pleistocene radiation of lineages in Eurasia that eventually gave rise to Neanderthals in Europe and to *H. sapiens* in Africa. If *heidelbergensis* (*sensu* Stringer [25]) is *not* the LCA for *sapiens* and *neanderthalensis* because of a derived facial morphology and because the known fossils post-date the actual divergence date, then what did the LCA look like (Ancestor X in figure 2*c*). It may have displayed a morphology of the lower face more like *antecessor* than *heidelbergensis*, but what about the rest of the cranium and the dentition? Mounier *et al*. [112] argued that, despite its younger age, the Ceprano calvaria displays the most primitive morphology of the *heidelbergensis* group. Unfortunately, it lacks the crucial facial region, but perhaps its cranial form is a retention of the shape that typified the LCA in the early middle Pleistocene. In considering dental morphology, we are severely limited by the lack of good data for this period from sub-Saharan Africa, while further north the Tighennif fossils from Algeria have been considered more primitive than the *antecessor* material [113]. However, endostructurally, the Tighennif dentitions were considered close to the status of a Neanderthal-modern LCA by Zanolli & Mazurier [114].

There are perhaps also clues in the form of the Qesem teeth from Israel, which are of comparable age to or slightly younger than the Sima de los Huesos fossils (approx. 400 ka). According to Hershkovitz *et al*. [77], these teeth combine features found in the Neanderthals with some typical of the early modern Skhul and Qafzeh samples. Given the much earlier presence of Neanderthal-like traits in the *antecessor* and Tighennif materials, we should consider the possibility that the LCA did display some Neanderthal-like features dentally. In the past, I have tended to envisage the LCA as ideally totally plesiomorphous, and thus lacking the derived features of either Neanderthals or modern humans. But in reality, the LCA may in fact have shown a mosaic of primitive and derived traits, with the latter differentially inherited in the descendant lineages. Thus, the cranial vault may have been Ceprano-like, the facial morphology *antecessor*-like and retained in the *sapiens* line in Africa, while the dentition may have been more Neanderthal-like than previously envisaged, and then increasingly modified in the modern human lineage. New studies and discoveries should allow the proper testing of these ideas in the next few years.

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