

# The Origin of Modern Anatomy: By Speciation or Intraspecific Evolution?

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**“Speciation remains the special case, the less frequent and more elusive phenomenon, often arising by default” (p 164).<sup>1</sup>**

Over the last thirty years, great progress has been made regarding our understanding of *Homo sapiens* evolution in Africa and, in particular, the origin of anatomically modern humans. However, in the mid-1970s, the whole process of *Homo sapiens* evolution in Africa was unclear and confusing. At that time it was widely assumed that very archaic-looking hominins, also called the “Rhodesoids,” which included the specimens from Kabwe (Zambia), Saldanha (South Africa), and Eyasi (Tanzania), were spread over wide parts of the continent as recently as 30,000 or 40,000 years ago. Yet, at the same time, there were also indications from the Omo Kibish skeletal remains (Ethiopia) and the Border Cave specimens (South Africa) that anatomically modern humans had already been present somewhat earlier than 100,000 years B.P.<sup>2,3</sup> Thus, it was puzzling how such early moderns could fit in with the presence of very archaic humans still existing in Eastern and Southern Africa only 30,000 years ago.

During the 1970s, new field work, faunal analyses, and absolute dating began to reveal more and more that the late dates for archaic specimens were incorrect.<sup>4–7</sup> Intensive research also led to a drastic revision of the

archeo-chronology of the African Stone Age and to a dramatic extension in time of the Middle and Later Stone Age, and thus to older dates of the associated hominins.<sup>8,9</sup> The 1970s also saw important Middle Pleistocene hominin discoveries, such as the crania from Ndutu and Laetoli (Tanzania) and Bodo (Ethiopia). In 1978, in view of the accumulating evidence, I started a morphological analysis of the Middle and late Pleistocene hominin material from Africa. This research finally led to a framework of *Homo sapiens* evolution suggesting a mosaic-like, continuous anatomical process of modernization, from an early archaic grade via a more derived late archaic grade to anatomically modern humans.<sup>10–13</sup> This result was a central element of an early version of the Out-of-Africa model,<sup>11</sup> also suggesting that the modernization process in Africa occurred largely in parallel to the Neandertalization process in Europe.

Over the years, the chronological framework for Africa had to be somewhat revised due to new dating evidence and other discoveries. For example, in 1997, we presented a revised scheme<sup>14</sup> in which the time periods of both the early archaic and the late archaic groups had to be somewhat extended because of new absolute dates for the Bodo and Florisbad hominins, among others. The current updated version (Fig. 1) includes the most recently discovered specimens from Ethiopia as well as the latest dating evidence. Looking back over about two and a half decades, no evidence has emerged so far that disproves or contradicts the suggested early origin of modern anatomy in Africa and the continuously evolving lineage during the Middle Pleistocene.<sup>15–19</sup> Also, the current framework appears now to be rather well founded on quite a number of diagnostic hominin specimens, as well as absolute dates (Table 1, Fig. 2).<sup>17</sup>

## EVOLVING LINEAGE

The anatomical modernization process can be divided into three largely diachronic grades of *Homo sapiens* (Fig. 1), each including hominin specimens of similar evolutionary level.<sup>12,13,15,16,20</sup> The specimens in the early archaic *Homo sapiens* category are clearly derived relative to *Homo erectus*, sharing apomorphies with later *Homo sapiens* especially regarding their enlarged braincase, more vertically oriented lateral walls, expanded frontal bone, less strongly angulated occipital bone, more vertically oriented upper scale, higher temporal squama, and

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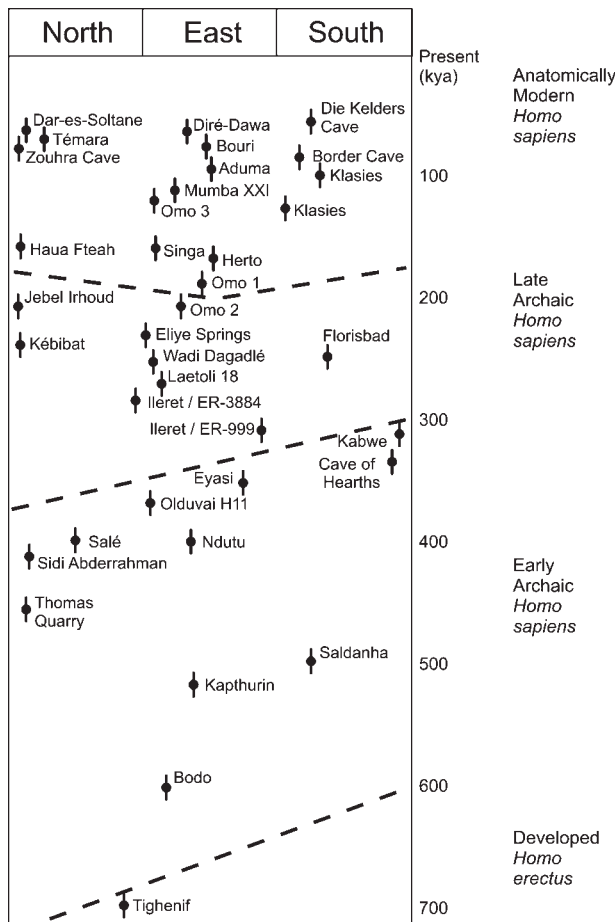


Figure 1. Scheme of *Homo sapiens* evolution in Africa.

reduced development of the supraorbital and occipital tori. The late archaic *Homo sapiens* is clearly more derived as compared to the morphological pattern of the early archaics, as is especially evident in the large cranial capacity, the more reduced supraorbital torus, and the near-modern or modern face, including canine fossa and inframalar incurvature. This grade of evolution is followed by the anatomically modern *Homo sapiens*. The use of these temporally and morphologically overlapping entities is just a way to describe the continuous mosaic-like modernization process.<sup>19</sup> I also favor a gradual pattern for this part of hominin evolution because we are certainly dealing here with diachronic changes within one species. The use of the grade pattern does not suggest anything about the underlying factors of anatomical modernization nor

whether there are parts of the lineage that show more intensive changes toward the modern morphology than do others. Thus, factor analysis and other studies such as those carried out, for example, by Lieberman and coworkers<sup>21,22</sup> are useful in trying to identify major structural elements of this process, such as neurocranial globularity and facial retraction.<sup>23</sup> Indeed, it must be expected that many of the features and aspects characterizing the grades are connected with more general changes or shifts.

### EARLY ARCHAICS

Key evidence of the presence of early archaic *Homo sapiens* (Fig. 3) comes from the hominin specimen from Bodo (Ethiopia), dated by Ar/Ar to ca. 600,000 years B.P.<sup>24</sup> The large cranial capacity of nearly 1,300 cm<sup>3</sup>

is associated with some parietal bossing, a coronally expanded frontal, and derived features of the temporal. The supraorbital torus even appears to show some division into a medial and a lateral portion.<sup>25</sup> Still, the massive face looks rather archaic. Another specimen of similar or slightly younger age<sup>17</sup> is the Saldanha (or Elandsfontein) cranium from South Africa (Fig. 3). Having an estimated cranial capacity of about 1,225 cm<sup>3</sup>, the parietals are well arched and show some bossing. With regard to the parietal arch shape index, the specimen is even close to that of early modern humans from Qafzeh.<sup>26</sup> In addition, the frontal squama is coronally enlarged. The occipital is less angulated than generally is seen in *Homo erectus* and the transverse torus is reduced. Another specimen grouped with the early archaics is the cranium from Ndotu (Tanzania), which is about 400,000 years old or possibly somewhat older.<sup>17,27</sup> In posterior view, the parietal walls are vertically oriented, exhibiting well-developed bossing (Fig. 4). The occipital is clearly derived relative to *Homo erectus* due to its more rounded shape, the relatively long and slightly posteriorly inclined upper scale, and the reduced torus morphology.

Other well-preserved early archaic crania from Kabwe (Zambia), Eyasi (Tanzania), and Salé (Morocco) date from the same time span between 600,000 and 300,000 years ago and are similar regarding most of their derived conditions.<sup>15,16</sup> The Kabwe specimen (Fig. 4) exhibits an enlarged cranial capacity of ca. 1,280 cm<sup>3</sup>, increased sagittal curvature of the parietal, and coronal expansion of the frontal regions. Other derived features include the vertically oriented upper scale of the occipital bone, the high and superiorly curved temporal squama, and the gracile tympanic nearly aligned with petrous.<sup>28</sup> The Eyasi 1 cranium has an estimated capacity similar to that of Kabwe and rather vertical parietal walls with some bossing. Its occipital is rounded with a relatively vertically oriented upper scale and a weak transverse torus. In spite of pathological changes in the nuchal area and

TABLE 1. Major Middle and Early Late Pleistocene Cranial and Mandibular Remains From Africa

Site	Country	Fossils	Age (Myr)
<b>Eastern Africa</b>			
Bodo	Ethiopia	Partial cranium, temporal fragment	0.6
Ndutu	Tanzania	Partial cranium	0.4
Eyasi	Tanzania	Partial cranium, cranial fragments	0.4–0.3
Olduvai	Tanzania	Maxilla, palate (OH 11)	0.4–0.3
Kapthurin/Baringo	Kenya	2 mandibles	0.5
Laetoli	Tanzania	Cranium (LH 18)	0.3–0.2
Wadi Dagadlé	Djibouti	Maxilla	0.25
Ileret	Kenya	Partial cranium (ER 3884)	0.27
Eliye Springs	Kenya	Cranium	>0.2
Omo Kibish	Ethiopia	Partial cranium, mandible (Omo 1)	0.2
		Partial cranium (Omo 2)	0.2
		Cranial fragment (Omo 3)	0.1
Herto	Ethiopia	Cranium (BOU-VP-16/1)	0.16
		Cranial fragment (16/2, 16/43)	0.16
		Child's cranium (16/5)	0.16
Singa	Sudan	Partial cranium	0.15
Mumba	Tanzania	Teeth	0.13–0.1
Aduma	Ethiopia	Cranial fragment	0.1–0.07
Diré-Dawa	Ethiopia	Partial mandible	0.08–0.06
Bouri	Ethiopia	Cranial fragment	>0.05
<b>Southern Africa</b>			
Saldanha	South Africa	Partial cranium, mandibular fragment	0.6–0.4
Kabwe	Zambia	Cranium (Kabwe 1)	0.35–0.25
		Maxilla (Kabwe 2)	0.35–0.25
Cave of Hearths	South Africa	Partial mandible	0.35–0.25
Florisbad	South Africa	Partial cranium	0.26
Klasies River	South Africa	Several cranial and mandibular fragments	0.12–0.08
Border Cave	South Africa	Partial cranium (BC 1), mandible (BC 2)	0.12–0.09
Die Kelders	South Africa	Teeth	0.08–0.06
<b>Northern Africa</b>			
Thomas Quarry	Morocco	Mandible, cranial fragment	0.6–0.5
Sidi Abderrahman	Morocco	Mandible	0.4
Salé	Morocco	Cranium	0.4
Kébibat	Morocco	Cranial fragment	0.25
Jebel Irhoud	Morocco	Cranium (Jl 1), partial cranium (Jl 2), mandible (Jl 3)	0.19–0.17
Haua Fteah	Libya	2 partial mandibles	0.2–0.08
Zouhra Cave	Morocco	Mandible	0.13–0.04
Témara	Morocco	Cranial and mandibular fragments	0.13–0.04
Dar-es-Soltane	Morocco	Partial cranium, mandible	0.13–0.04

its relatively small cranial capacity, the Salé cranium exhibits a rather convex frontal, expanded parietals and other similarities to the Ndutu hominin.<sup>29,72</sup>

### LATE ARCHAICS

The late archaic grade comprises specimens spreading from northern to southern Africa that are more derived toward the modern morphology than are the early archaics. An example of these near-moderns is the cranium KNM-ER 3884 from Ileret, East Turkana. This specimen was directly dated by gamma-ray spectrometry, which yielded, an U/Th age

of ca. 270,000 years.<sup>14</sup> A previous analysis<sup>30</sup> showed that most of the cranial vault falls both metrically and nonmetrically close to the range of Holocene Africans. However, the cranium also exhibits a continuous supraorbital torus that deviates from the generally rather modern impression of the specimen. As a whole, the cranium is rather close in morphology to that of modern humans (Fig. 5).<sup>15</sup>

During the mid-1990s, further support for the early presence of late archaic *Homo sapiens* emerged based on new absolute dates for the Florisbad hominin from South Africa and the Laetoli Hominid 18 from the Ngaloba Beds in Northern Tanzania.

The Florisbad specimen (Fig. 5) could be directly dated by ESR to ca. 260,000 years B.P.<sup>31</sup> Its derived morphology is evident in the great coronal expansion of the frontal bone, which is associated with a continuous but only slightly projecting supraorbital torus, and the modern facial shape with a well-developed canine fossa. For the LH 18 cranium (Fig. 6), a date of more than 200,000 to 300,000 years was determined by a combined approach using Ar/Ar analysis and the AMS-calibrated amino acid method.<sup>32</sup> This well-preserved specimen exhibits a modern-looking face with a canine fossa and a near-modern braincase with a



Figure 2. Middle and early late Pleistocene hominin sites.

capacity of about 1,350 cm<sup>3</sup>, a rounded occipital bone, and well-developed parietal bossing. It is mainly the frontal that exhibits various archaic features. Among these are the flat, narrow squama and the supraorbital torus, which is rather thick and rounded in its lateral segment. However, the torus shows indications of an incipient division in the mid-orbital region, which might be a tendency toward the fully modern pattern. Although it is not as well dated as the previous three late archaics, the cranium from Eliye Springs, West Lake Turkana, might also belong to this group based on

its combination of archaic and derived conditions.<sup>19,33</sup> A CT-based three-dimensional analysis of the matrix-filled cranium revealed that its cranial capacity measures ca. 1,210 cm<sup>3</sup>.<sup>34</sup>

Important late archaic specimens also exist from Northern Africa, such as the crania from Jebel Irhoud (Morocco), dated to about 170,000 years B.P.<sup>35,36</sup> The better-preserved cranium Jebel Irhoud 1 (Fig. 6) exhibits near-modern morphology of the vault and face.<sup>37</sup> Here again, the most obvious archaic feature is the continuous supraorbital torus. Jebel Irhoud 2, although lacking a face,

appears to have a morphology similar to that of Jebel Irhoud 1.

### EARLY MODERNS

The continuous mosaic-like transition from late archaic to early anatomically modern *Homo sapiens* is also obvious in the available specimens from Ethiopia. The Omo Kibish remains include two reasonably well-preserved crania, Omo 1 and Omo 2. Recent field work at the two sites and new Ar/Ar dating suggests that both the Omo 1 skeleton and the Omo 2 cranium date to around

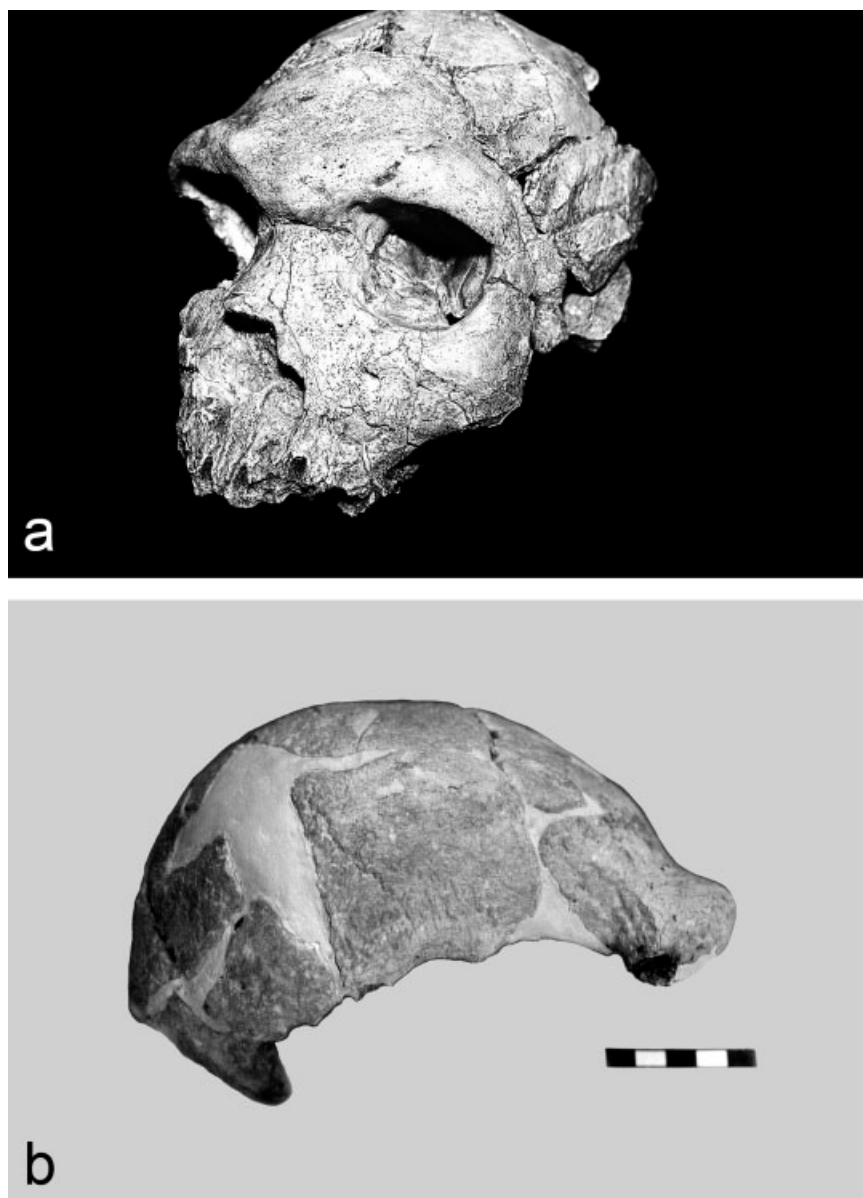


Figure 3. Early archaic *Homo sapiens* specimens from Bodo, Ethiopia, and Saldanha, South Africa.

195,000  $\pm$  5,000 years B.P.<sup>38</sup> Whereas the Omo 1 specimen is fully anatomically modern (Fig. 7) and, according to the most recent dating evidence, the oldest known modern human, the Omo 2 cranium shows a mosaic of modern and archaic features. It exhibits a robust yet basically modern supraorbital morphology. Although this region is very fragmentary, it is clearly visible that the superciliary arch protrudes relative to the more flattened lateral segment. Among the archaic conditions

are the strong mid-sagittal keeling and the angulated occipital bone (Fig. 7). Although the two presumably rather contemporaneous Omo crania illustrate the mosaic-like transitional pattern, recently discovered cranial remains from Herto in the Middle Awash (Ethiopia), dated by Ar/Ar to 154,000–160,000 years B.P., adds further relevant evidence to the process of modernization.<sup>39,40</sup> The large, robust Herto cranium BOU-VP-16/1 (Fig. 7) exhibits a basically modern supraorbital morphology

and modern face combined with a somewhat angulated occipital bone. This feature, however, appears to vary considerably within these early modern or near-modern populations as indicated by the less angled occipital in the other adult specimen, BOU-VP-16/2.<sup>39</sup> The Singa cranium from Sudan, with an age of around 150,000 years B.P.,<sup>41</sup> also belongs to this transitional earliest modern human spectrum.<sup>15</sup>

Other early moderns are known from Southern Africa, especially the Klasies River Mouth Caves on the south coast. Here are the oldest human remains derived from the LBS Member, the lowest member of the Klasies deposits, dated to ca. 120,000 years B.P. These maxillary fragments fall both metrically and morphologically within the range of variation of Holocene Africans.<sup>42</sup> A nearly complete mandible from the Lower SAS Member, a level somewhat higher in the deposits, dates to about 100,000 years and is anatomically modern, as are the other cranial fragments from this site.<sup>15,43</sup>

Regarding the postcranial specimens, the conditions in the Klasies remains can be matched with recent population samples from Southern Africa.<sup>44,45</sup> Some features, such as the relatively low coronoid height of the ulna, could alternatively be retained archaic features reflecting the mosaic pattern of evolution in the postcranial skeleton.<sup>45,46</sup> But it is also possible that such postcranial conditions simply belong to the range of variation of these early modern humans.<sup>47</sup> This latter view finds support in the fact that the Omo 1 ulna has the most “modern” ratio of coronoid to olecranon height of any of the African Middle Stone Age specimens. Moreover, the Skhul/Qafzeh humans display greater coronoid development than do the MSA South African ulnae.<sup>47</sup>

Another important early modern specimen is the Border Cave 1 partial cranium from South Africa, which, if it came from layer 4BS, is about 90,000 years B.P. or, if it came from 5BS, is somewhat older.<sup>48</sup> This reconstructed specimen is basically anatomically modern, with a high, curved frontal bone. The supraorbital morphology is only slightly thickened

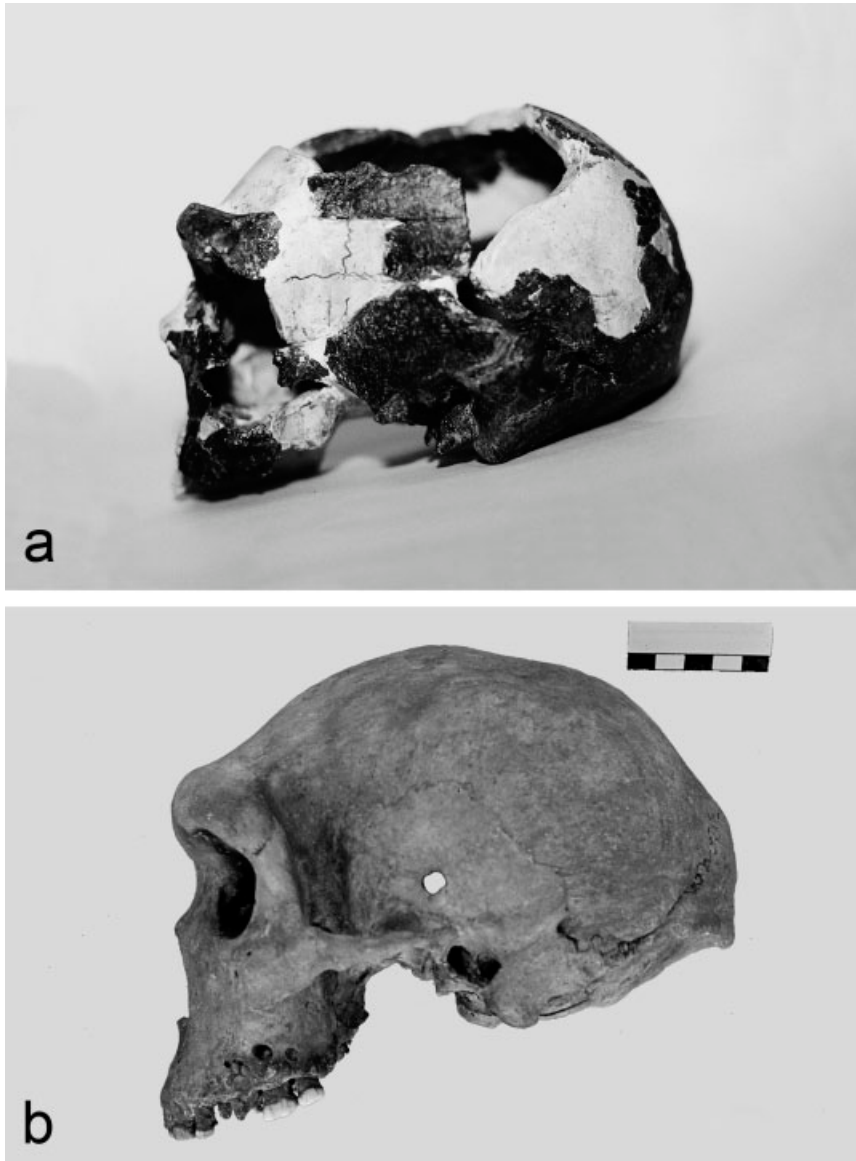


Figure 4. Early archaic *Homo sapiens* specimens from Ndutu, Tanzania, and Kabwe, Zambia.

and anteriorly protrusive. Although it is not clearly divided into medial and lateral portions,<sup>12,49</sup> its strongly reduced condition differs from the tori present in the late archaics.

Northwestern Africa is also a potential region for an early presence of modern humans. However, much depends here on the unclear dating evidence for the Aterian and the associated anatomically modern human remains such as those from Dar-es-Soltane, Témara, and Zouhra Cave (Morocco).<sup>37</sup> Ages between 40,000 and even more than 100,000

years ago are possible for these modern specimens. Current research might contribute to further clarifying the age of these diagnostic and relevant remains.

#### MODE OF MODERNIZATION

Considering the morphological and chronological evidence together, there is good fossil documentation of a continuous evolutionary change in Africa. This does not mean that the modernization process occurred

simultaneously all over the continent. Based on the current evidence, it seems likely that the earliest transition to anatomically modern humans occurred in Eastern Africa. However, future dating and new discoveries may change this impression. Indeed, a mode of continuous evolution without speciation events has been supported by a recent comprehensive analysis of the Middle Pleistocene hominins showing clear temporal trends from early archaic up to modern *Homo sapiens* in many metrical and nonmetrical cranial features.<sup>50</sup> These include, for example, major dimensions of the frontal, parietal, and occipital bones, as well as nonmetrical traits of the supraorbitals, parietal expansion, temporal squama and mastoid region, occipital shape, and facial features. Many of these changes certainly correlate with increasing rounding of the vault or a reduction and retraction of the face. However, since these changes can be observed in a mosaic-like pattern over some hundreds of thousands of years, it does not appear very likely that the origin of the anatomically modern skull shape was the result of just a few evolutionary adjustments within a short period associated with a speciation event as Lieberman, McBratney, and Krovitz<sup>21</sup> suggested. In her comment on such an interpretation, Brooks (cited by Balter<sup>51</sup>) emphasized that “we don’t see any sudden leaps” in the emergence of modern humans. Instead, she sees a gradual process of both physical and behavioral change. Also commenting on Lieberman’s results, Aiello (cited by Balter<sup>51</sup>) raised the question of whether these innovations in skull anatomy really add up to make humans a truly different species; that is, a separate group that could not breed with Neandertals or other extinct humans. Her answer was, “Nobody’s cracked this question yet (p. 1222).” In my view, Lieberman, McBratney, and Krovitz’s<sup>21</sup> interpretation that anatomical modernization can be boiled down to just a few autapomorphies or genetic changes will be difficult to accom-

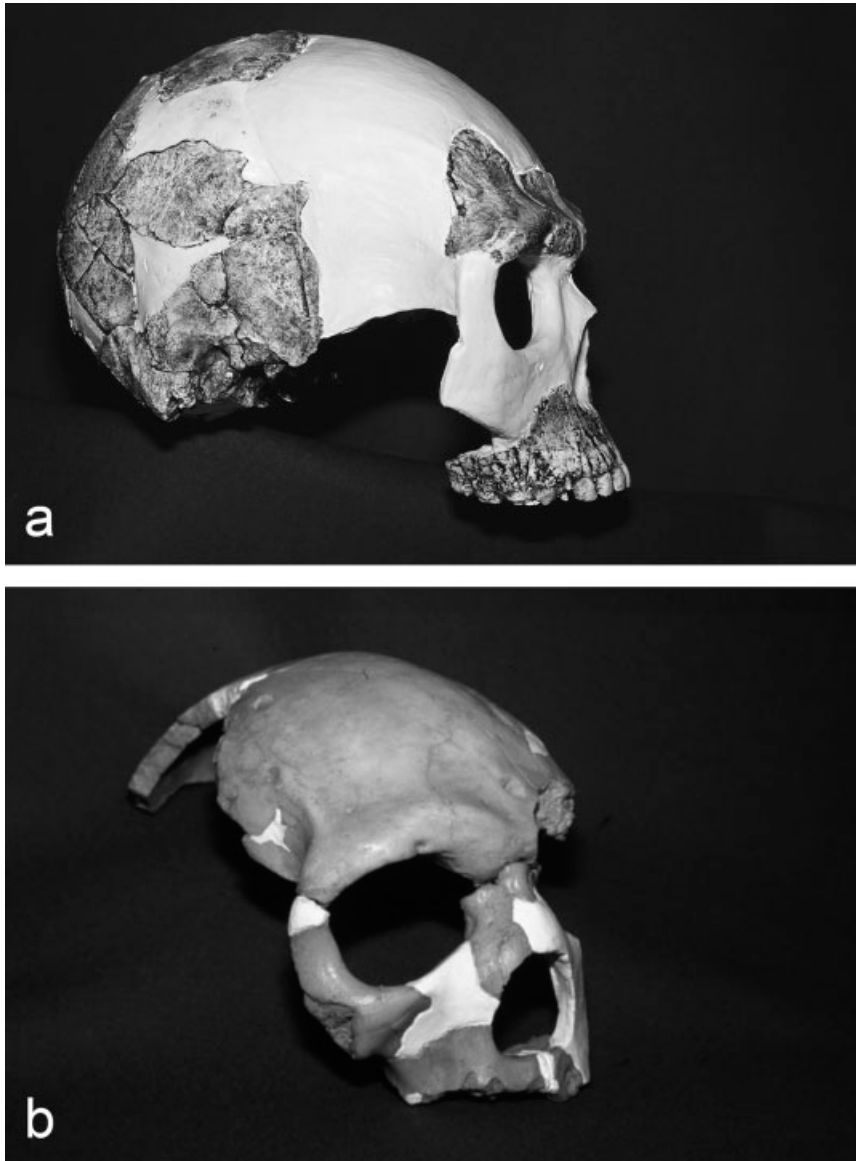


Figure 5. Late archaic *Homo sapiens* specimens from Ileret, Kenya, and Florisbad, South Africa.

modate within the current fossil evidence.

As suggested in the previous section, the Middle Pleistocene fossil record from Africa can be morphologically subdivided into three grades or groups of an evolving species, *Homo sapiens*. The recognition of three groups is well founded and widely accepted, as the discussion at the Stony Brook Symposium and Workshop revealed. Also, Howell's<sup>52,53</sup> suggestion of paleo-demes, spatially and temporally bounded entities below the species level, is basically in agreement with the sequence sug-

gested here. Howell<sup>53</sup> recognized an early p-deme represented by Kabwe and associated specimens like Saldanha, Ndotu, Bodo, Baringo/Kapthurin, and Eyasi (here assigned as early archaic *Homo sapiens*). The specimens from Jebel Irhoud and Florisbad are seen as major representatives of two later p-demes, the latter including specimens such as Laetoli Hominid 18, Eliye Springs, Ileret/ER 3884, and Omo 2. Regarding this p-deme, "all the specimens exhibit substantially derived aspects of cranial morphology vis-à-vis antecedent African p-demes...."

(p. 208).<sup>53</sup> Finally, three further p-demes around Klasies, Dar-es-Soltane, and possibly Singa are distinguished as representing early modern humans. However, current disagreements exist regarding the taxonomic level on which the major groups or entities should be distinguished and consequently, about the resulting phylogenetic scenarios. Therefore, some current alternative views are discussed here.

#### HOMO HELMEI

According to Foley,<sup>54</sup> the three major groups should be classified as *Homo heidelbergensis*, *Homo helmei*, and *Homo sapiens*. Although this indicates a separation on the "species" level, he concedes that the

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derived descendent taxa of *Homo heidelbergensis* are problematic because of the continuity that can be found between them and *Homo heidelbergensis*: "These seem to be species in the sense that Simpson meant—lineages with independent trajectories—but both the details of the fossil record and the scale of the process seem to rule out any punctuated events. Indeed, continuity between them, rather than discontinuity, is the reason for the persistent problem of delimiting the taxonomic units in the later stages of human evolution and gives rise to the question of whether the species concept, which lies at the heart of macroevolutionary theory, is sufficiently fine-tuned to cope with evolution at this scale. The lineages of later human evolu-



Figure 6. Late archaic *Homo sapiens* specimens from Laetoli, Tanzania, and Jebel Irhoud, Morocco.

tion seem to show simultaneously *continuously evolving lineages* and very distinctive derived endpoints, . . . They certainly highlight the problems of reconciling terminology with process (p. 9–10).<sup>54</sup> This statement indicates that a distinction of three species would, in fact, be an artificial division of a *continuously evolving lineage* in Africa. Stringer,<sup>18</sup> as well, recognizes here a gradual mosaic-like evolution to modern humans in Africa, using the term “archaic *Homo sapiens*” for the late archaic specimens. In fact, there appears to be lit-

tle justification in distinguishing this transitional<sup>55</sup> or late archaic group as a distinct species, *Homo helmei*.

Yet there are more problems with regard to Foley and Lahr’s<sup>56</sup> use of *Homo helmei*, because they also included European fossils in their hypodigm. Stringer<sup>18</sup> clearly addressed the problems:<sup>11</sup> “First, Neanderthal characteristics were already evolving in Europe prior to the hypothesized appearance of “*H. helmei*,” e.g., in the Swanscombe specimen, dated to *ca.* 400 kyr. Second, African specimens such as Florisbad and

Jebel Irhoud make unparsimonious ancestors for the Neanderthals, since not only do they post-date the appearance of Neanderthal clade characters in Europe, but they appear to lack Neanderthal morphological characteristics that might be expected in a common ancestor (p. 567).”

Another problem of Foley and Lahr’s proposal is that they also included technological aspects in their species definition. Stringer<sup>18</sup> criticized their use of Mode 3 technology as an ancestral “taxonomic” characteristic not only “because technologies might transfer between distinct populations or even different species . . . , but also because the time and place of origin of prepared core techniques are currently unknown.” Similar criticism comes from McBrearty and Brooks.<sup>27</sup> They regard it “a curious departure from normal taxonomic practice [that] Lahr and Foley (1998: 157) have included certain European fossils in *H. helmei* on the basis of their ages (isotopic stages 6, 7 and 8) and presumed associated technology (“mode 3”).<sup>27</sup> Moreover, McBrearty and Brooks<sup>27</sup> regard *Homo helmei* in general as a problematic taxon with no formal diagnosis. In contrast to Foley and Lahr, they merely used the name *Homo helmei* or *Homo sapiens* for their morphologically intermediate “Group 2” of African fossils, which is equivalent to “late archaic *Homo sapiens*.” In summary, it appears obvious that the species *Homo helmei sensu* Foley and Lahr hardly helps to clarify the issue.<sup>57</sup> In view of the generally agreed transitional character of this derived pre-modern group,<sup>55</sup> it is much more appropriate to include this morph within the species *Homo sapiens* as a late archaic group, an intermediate stage,<sup>36</sup> or a somehow labeled chrono-subspecies.

### HOMO HEIDELBERGENSIS

Problems also exist with regard to a possible species *Homo heidelbergensis* in Africa. The oldest, most relevant African specimen that some have assigned to this taxon is the Bodo hominin. However, Adefris,<sup>58</sup>



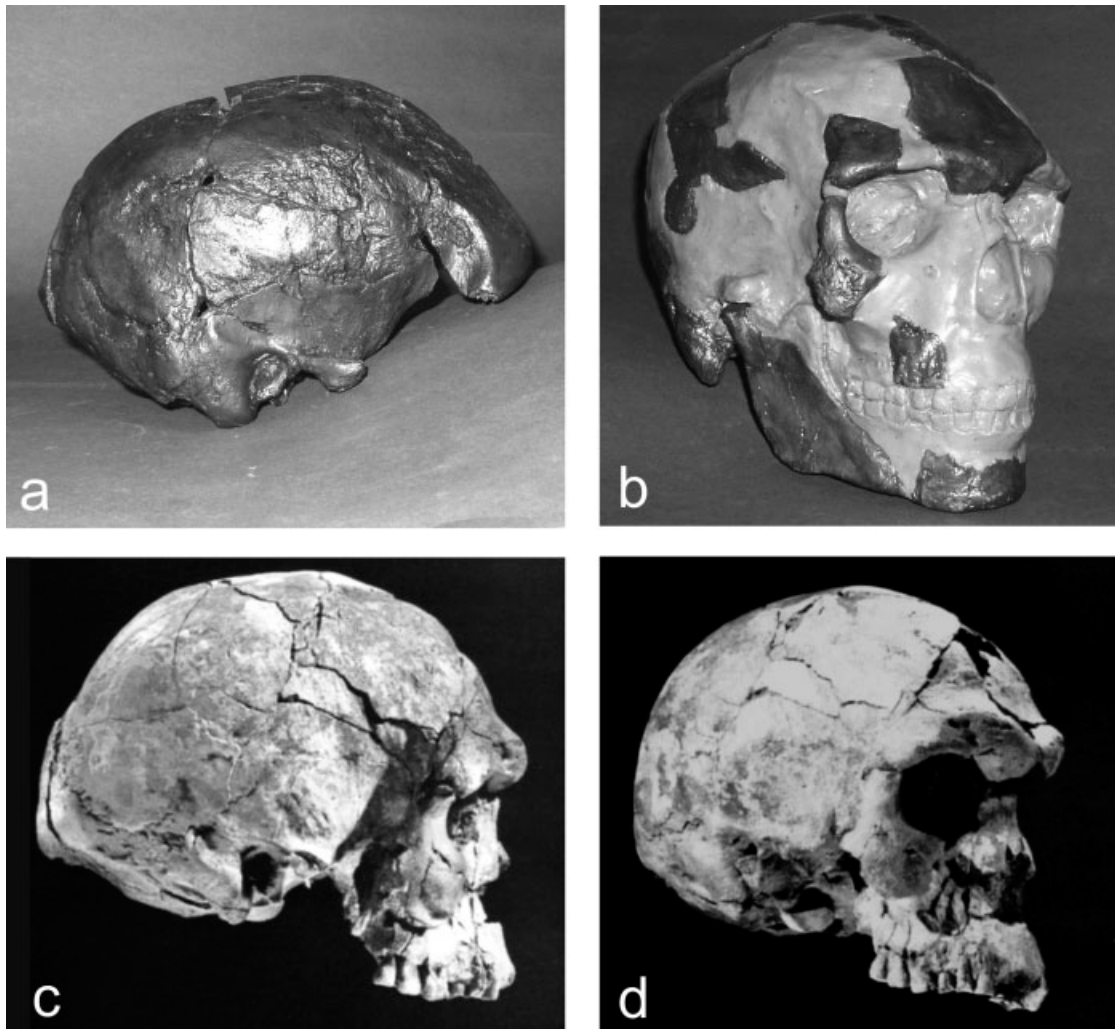


Figure 7. Late archaic transitional and early modern specimens from Ethiopia: a) Omo 2; b) Omo 1; c) and d) Herto BOU-VP-16/1 (courtesy of T. White).

based on her detailed anatomical study of this cranium, arrived in 1992 at the conclusion that it should be classified as an “archaic *Homo sapiens*.” Only a short time later, Rightmire<sup>25</sup> regarded it more reasonable to refer to Bodo as a *Homo heidelbergensis*, together with Mauer, Arago, Petralona, Kabwe, Ndutu, and others. Rightmire<sup>59</sup> suggested a speciation event between *Homo erectus* and *Homo heidelbergensis* in Africa at around 800,000 to 700,000 years ago. This speciation refers to the same event that I recognize between *Homo erectus* and (archaic) *Homo sapiens*,<sup>15,16</sup> since Rightmire<sup>25</sup> also supports a single polytypic species *Homo erectus* in Asia and Africa. Thus, I agree with Rightmire on the

more derived morphology of the post-*erectus* species. But the major contrast (Fig. 8) is that Rightmire’s scenario suggests two further, largely sympatric speciations, one in Europe from *Homo heidelbergensis* to *Homo neanderthalensis* at ca. 300,000 years ago and another in Africa from *Homo heidelbergensis* to *Homo sapiens* at ca. 150,000 or 200,000 years ago.<sup>59,60</sup>

As outlined, however, the evidence from Africa rather shows a continuous gradual process of anatomical modernization without any clear subdivisions on the species level, especially at the transition to anatomically moderns. In view of the many shared derived features of late archaics and early moderns, it can

hardly be plausible, for example, to classify Omo 2 or Florisbad together with Bodo (and the possible *Homo erectus* from Ceprano, Italy<sup>61</sup>) as *Homo heidelbergensis* and Omo 1 as *Homo sapiens*, as indicated by Rightmire.<sup>60</sup> Assigning the two Omo specimens to two different species would inadequately exaggerate the differences. If they are indeed so close in age, Trinkaus<sup>62</sup> would rather see a reflection of considerable intrapopulation variation.

For Rightmire’s view on *Homo heidelbergensis*, however, it is also essential whether a speciation can be assumed in Europe. Yet here, as well, there is little support for a conclusive speciation event along the pre-Neandertal/Neandertal lineage.

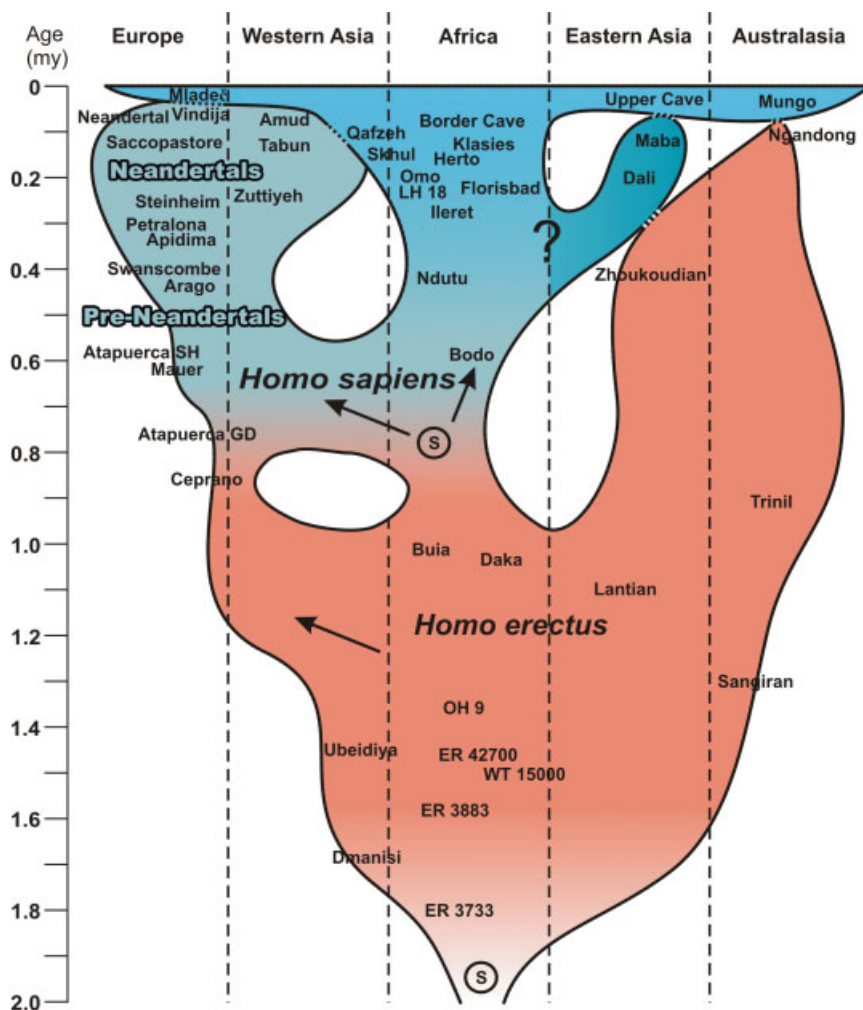


Figure 8. Suggested scenario of *Homo erectus* and *Homo sapiens* evolution. (S) = speciation event. (Color figure can be viewed in the online issue, which is available at [www.interscience.wiley.com](http://www.interscience.wiley.com).)

In fact, there is wide agreement that “the development of the Neandertal morphology results from an accretion phenomenon beginning in the middle of the Middle Pleistocene, around 450,000 or a bit before (p. 301).”<sup>63</sup> “Considering the mosaic nature of the accretion phenomenon, tracing clear divisions along the pre-Neandertals/Neandertals lineage is quite artificial (p. 302).”<sup>63</sup> Most recent U-series dates using inductively coupled plasma multicollector mass spectrometry (ICP-MS) yielded an age of about 600,000 years B.P. for the pre-Neandertals from Atapuerca Sima de los Huesos,<sup>64</sup> indicating that the Neandertalization process might have already started in the early Middle Pleistocene. The accretion pro-

cess resulted from an increase in the frequency of derived Neandertal conditions in the pre-Neandertal/Neandertal lineage (see also Stringer<sup>18</sup>) or, as Klein<sup>65</sup> put it, the European lineage is “marked by the progressive accumulation of Neandertal features.” Manzi also speaks of an *anagenetic* sequence, “which could be more reasonably considered a sequence of chrono-subspecies.”<sup>66</sup> In addition Condemi<sup>67</sup> suggested an evolutionary lineage that can be divided into early pre-Neandertals, late pre-Neandertals, and proto-Neandertals. In fact, over hundreds of thousands of years, this Neandertalization process might have occurred without a speciation event in parallel with and largely isolated from the

anatomical modernization process in Africa. Thus, Rightmire’s view of *Homo heidelbergensis* and two subsequent speciation events is, in my view, hardly supported by the fossil evidence.

In addition, *Homo heidelbergensis sensu* Rightmire is just one of quite a number of different definitions of this “species.” Stringer<sup>18</sup> favors a similar widespread species but excludes African late archaic *Homo sapiens* from his hypodigm. Lahr and Foley<sup>68</sup> exclude late archaic Africans as well, but classify these hominins together with some pre-Neandertals as *Homo helmei*. In view of the previously noted problems with *Homo helmei*, such a definition of *Homo heidelbergensis* appears highly problematic.<sup>57</sup> Manzi,<sup>66</sup> on the other hand, disagrees with such a single widespread species in Africa, Europe, and parts of East Asia, because it “may obscure the occurrence of separate lineages at a macro-regional scale and different patterns of adaptations and evolution.” Therefore, he and other researchers, including Bermúdez de Castro and coworkers<sup>69</sup> favor a separate morph, *Homo rhodesiensis*, for African *Homo heidelbergensis sensu* Rightmire and regard *Homo heidelbergensis* as a chronospecies or, “more reasonably,” a chrono-subspecies of the anagenetic Neandertal lineage.<sup>66</sup>

McBrearty and Brooks<sup>27</sup> also rejected the name *Homo heidelbergensis* for Africa but, in contrast to Manzi, used the term *Homo rhodesiensis* only for African specimens equivalent to early archaic *Homo sapiens*, thus excluding the late archaics.<sup>27</sup> White and colleagues,<sup>39</sup> although using the species name for early archaics as well, put it in quotation marks (*Homo rhodesiensis*). Hublin<sup>63</sup> even doubted the appropriateness of *Homo heidelbergensis* for Europe: “If, in Europe, a taxon anatomically distinguishable from *Homo erectus sensu lato* was present before the development of the Neandertal lineage, its hypodigm should be restricted to the populations anterior to the development of the first Neandertal apomorphies. In this case, the term *Homo heidelbergensis* itself, with the Mauer mandible as a type specimen, would be inappropriate.

Considering its fragmentary nature, this specimen is at least to be regarded as an *insertae sedis*, if it is not one of the first representatives of *Homo neanderthalensis* (p. 302).” Tattersall and Schwartz<sup>70</sup> used the species name in a broad sense but, at the same time, emphasized that *Homo heidelbergensis* only serves as a useful umbrella for a diversity of fossils not necessarily belonging to one species. The obviously great diversity in using the name *Homo heidelbergensis* reveals that it is hardly a well-defined taxon proving that speciation events occurred within the Neanderthal or modern human lineages.

### HOMO ANTECESSOR

In addition to these different views, another hypothesis suggests that the last common ancestor of the Neanderthal and modern lineages is represented by a new species, *Homo antecessor*.<sup>69,71</sup> This species was suggested on the basis of the hominin remains from the ca. 800,000-year-old TD6 level of Gran Dolina, Atapuerca (Spain). Mainly, the modern-looking face and primitive aspects of the dentition led to the suggestion that it is ancestral to the later Afro-European hominins and originated from *Homo ergaster*. However, the material is very fragmentary. Indeed, it might appear more likely that this material represents a late *Homo erectus* or a transitional form between *Homo erectus* and subsequent archaic *Homo sapiens* or “*Homo heidelbergensis*.”<sup>18,60</sup>

The progressive traits of the face, including the canine fossa, could be due to subadult status, since the fossa is less developed in the adult Gran Dolina specimen. This feature in general shows great variation among Middle Pleistocene hominins from Africa and Europe. Also, no Neanderthal features can be detected in the Gran Dolina material. Instead, many dental features appear to show great similarities to those of the roughly contemporaneous late *Homo erectus* from Tighenif, Algeria.<sup>72</sup> The ATD6-96 partial mandible exhibits close affinities to Chinese *Homo erectus*.<sup>73</sup> Moreover, the distinction

between the suggested ancestor of *Homo antecessor*, *Homo ergaster*, and *Homo erectus* could not be supported by many studies during the 1990s or more recent ones.<sup>60,74–81</sup> There also is no evidence of a separate species *Homo antecessor* in Africa, although such a species is assumed to have originated there more than 1 million years ago.<sup>69</sup> According to Tattersall and Schwartz,<sup>82</sup> it is, in fact, difficult to demonstrate, on the basis of the small sample of Gran Dolina hominins, that this material represents the common ancestor of both the Neanderthal and modern human lineages.

### CLUES FROM EXTANT PRIMATES

If the diverse alternatives should not just express personal tastes or

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**The obviously great diversity in using the name *Homo heidelbergensis* reveals that it is hardly a well-defined taxon proving that speciation events occurred within the Neanderthal or modern human lineages.**

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views of groupings and splittings, but are meant to approach the species problem, comparisons with living taxa might be useful. Studies on extant primates led Jolly<sup>83</sup> to conclude that Neanderthals, Afro-Arabian “premodern” populations, and modern humans are, roughly speaking, biological subspecies, comparable to interfertile allopatric taxa or phylogenetic species of baboons. Based on research in contemporary zones of hybridization such as the Awash *anubis-hamadryas* hybrid zone, Jolly<sup>84</sup> concluded “that unless an undocumented, radical genetic event occurred in the 600 ka since they

shared mtDNA ancestry with the Neanderthals, premodern humans were certainly able to interbreed with them and produce viable, fertile, offspring, as hamadryas and anubis baboons do.” Moreover, according to Jolly<sup>83</sup> “the other message from catarrhine hybridization is that recognizably distinct species that originated <2 million or even <4 million years previously cannot be assumed to be incapable of exchanging genes. Such exchange may have results ranging from minor parallelism to the formation of new, hybrid species (p. 663).”

Based on the evidence from living primates, it appears plausible to regard European pre-Neanderthals/Neanderthals and the African Middle Pleistocene lineage from Bodo to modern humans as belonging to one polytypic species, *Homo sapiens*, as it is widely agreed to do with regard to *Homo erectus* as well (Fig. 8).<sup>75,76,78–81</sup> In such a scenario, it still remains unclear whether the post-*erectus* archaic group in China (Jinniushan, Dali, Maba) also resulted from a dispersal of archaic *Homo sapiens*, had regional *Homo erectus* ancestors, or is even a kind of hybrid population. “Speciation remains the special case, the less frequent and more elusive phenomenon, often arising by default” (p. 164).<sup>1</sup>

### DNA AND ADMIXTURE

Studies of mitochondrial DNA from several Neanderthals have indicated that the Neanderthal and modern lineages might have separated at about 500,000 years ago (between 300,000 and 700,000 years ago).<sup>85–87</sup> Most recent analyses of Neanderthal nuclear DNA have supported these estimates. The study of one million base pairs of Neanderthal nuclear DNA and comparison with the human and chimpanzee genomes suggest a divergence time of about 500,000 years ago.<sup>88</sup> Another study of about 65,000 base pairs of Neanderthal nuclear DNA places the most recent common ancestor at roughly 700,000 years ago and the split between human and Neanderthal pop-

ulations at ca. 370,000 years ago.<sup>89,90</sup> Because the taxonomic significance of the genetic differences is ambiguous, the separate evolutionary lineages during the Middle Pleistocene can hardly prove that two different biological species emerged. Stringer<sup>18</sup> argues that the DNA data available “can be used to support a placing of Neanderthals and recent humans in either the same or different species, given the recency of common ancestry.” The discussion among molecular biologists and paleoanthropologists has focused instead on whether or not there is evidence of admixture in the DNA or in the morphology of the fossils and whether the evidence indicates that any Neandertal contribution to the early modern gene pool was significant or minor.

An analysis of ancient mtDNA of five Neandertals and five early moderns yielded DNA sequences in all Neandertals that were similar to each other but absent from the five early modern humans, as well as from recent humans.<sup>91,92</sup> Using a simple model of a constant human effective population size, contribution of Neandertal mtDNA to early modern Europeans larger than 25% was statistically excluded. Under a more realistic scenario of an expansion of the population during and after the colonization of Europe, a smaller Neandertal contribution can be excluded, but such estimates depend on when and how the expansion occurred.<sup>91</sup> Assuming a late survival, with Neandertals contributing for 10,000 years (40,000–30,000 years ago) and a rapid growth model, the Neandertal admixture would be very small.<sup>93</sup> According to another complex demographic simulation of Neandertal-modern interaction and replacement, the maximum genetic contribution appears to be only about 0.1%.<sup>94</sup> Certainly, further sequencing of the Neandertal nuclear DNA will provide more clarity on the level of possible Neandertal-modern gene flow.

Over many years the continuous debate, between supporters of the Multiregional Evolution and Out-of-Africa models about whether evidence for significant Neandertal-

modern gene flow exists<sup>62,95,96</sup> has led to more clarity. Re-examination of proposed morphological indications of admixture have shown that many of these suggestions are equivocal or problematic.<sup>16,18,97–100</sup> The relatively scarce evidence of possible admixture in the fossil record, for example in some early modern remains from Romania,<sup>62,98,99,101</sup> can be seen to agree with the current molecular evidence pointing to a small rate of possible Neandertal-modern gene flow. According to Lieberman,<sup>119</sup> the question of gene flow is relevant to the species question: “If one can find good evidence that humans and Neandertals interbred and that modern humans have some Neandertal autapomorphies, then, by all means, let’s include Neandertals in our species” (p. 665). In fact, there

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**In fact, there is no evidence from extant primates, current DNA results, or the fossils that would exclude Neandertals from having interbred with modern *Homo sapiens*.**

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is no evidence from extant primates, current DNA results, or the fossils that would exclude Neandertals from having interbred with modern *Homo sapiens*. In spite of the Neandertal-modern differences in genes and morphology, there is no unequivocal evidence to classify these closely related taxa into two different species.<sup>102,103</sup>

#### CLADISTICS AND PITFALLS

The major reason for the many attempts over the last two decades to split taxa into new morphs or species is the application of cladistics in paleoanthropology. Foley,<sup>54</sup> for example, emphasized that *Homo heidelbergensis* has a “strong cladistic

basis” and that *Homo ergaster* is “the best example of a taxon arising out of cladistics.” Yet, as shown, there is, in fact, a lot of confusion about *Homo heidelbergensis*, which can hardly be regarded a reliable or well-defined species.<sup>104</sup> Intensive research has also revealed that the original assumptions used in the mid-1980s for splitting *Homo erectus* into *Homo ergaster* and *Homo erectus* are not tenable. All of the suggested East Asian *Homo erectus* autapomorphies occur in the African specimens as well, and morphometric analyses were not able to distinguish between so-called *Homo ergaster* fossils like KNM-ER 3733 and KNM-ER 3883 and East Asian specimens.<sup>59,74–81,105</sup> In fact, for several reasons “the majority of researchers do not regard the *H. ergaster* hypodigm as worthy of a separate species.”<sup>104</sup> Instead, it appears more plausible that “geographic subdivision of early *H. erectus* into separate species lineages is biologically misleading, artificially inflating early Pleistocene species diversity.”<sup>80</sup>

This has most recently been underscored by a study of *Homo erectus* features that also considered body and brain size.<sup>81</sup> Antón and co-workers<sup>81</sup> arrived at the conclusion that “cranial characters, particularly those related to vault thickness and development of the supraorbital torus and many of those related to differentiating African from Asian *H. erectus*, scale with brain size in *H. erectus* yielding little support for a differentiation between *H. erectus* and *H. ergaster*.” Antón<sup>106</sup> rather finds “the most useful approach to the taxonomy of *H. erectus* to be that proposed by Jolly,<sup>84</sup> who recognized both the complexity of species boundaries in living organisms and that the fossil record is magnitudes too incomplete to test alternative interpretations (if indeed it ever could). Jolly<sup>84</sup> suggested avoiding arguments over definitionally induced differences in favor of recognizing geographically replacing allotaxa. Such a move recognizes the likelihood that morphological differences may arise among allotaxa, but allows for hybridization between them. This aptly reflects the situation in *H. erectus*.”

*tus sensu lato*, in which evident regional variation exists in cranial morphology and yet in which a total morphological pattern is shared across regions” (p. 154). According to Jolly,<sup>84</sup> most allotaxa are subspecies by the biological species concept, so there is little reason to assume a different mode for the species *Homo sapiens sensu lato*. Certainly, the cladistic approach has useful elements for analyzing phylogeny, but it reveals little about when speciation occurred because characters normally change within a species. There are no direct relationships between change of morphological features and speciation<sup>107</sup> or, as Grubb<sup>1</sup> put it: “Cladogenetic events may need to accumulate before it is possible to achieve speciation, the less frequent and often less tangible phenomenon (p. 163).”

When using cladistics, however, one has to be aware of various problems and pitfalls,<sup>76,108–111</sup> which are likely to make results based on fossil material less clear than many supporters of this approach appear to believe. Only a few of these problems can be addressed here. For example, the assessment of features as present or absent might in many cases be an inadequate simplification of the extant variation and might lead to inadequate character states and even to the assessment of a feature as absent when, in fact, it is clearly present as, for example, the frontal keel on KNM-ER 3733 or Bodo.<sup>66,76,112</sup> Also, the traits used are often functionally interrelated and cannot be regarded as independent features. Used in a cladistic analysis, such nonindependent characters will produce a numerical bias that influences conclusions about the most parsimonious set of evolutionary relationships among taxa and which traits one interprets as homoplasy and synapomorphies.

Intraspecific polymorphism is also widely ignored. Hublin<sup>63</sup> illustrated this problem by stating that “the mosaic of derived and primitive features may be different in two contemporaneous specimens. But this does not mean that we have two different contemporary taxa in Europe. As a matter of fact, the mosaic can

also be different from one individual to another *within the same population* as documented by the Middle Pleistocene sites of Arago and Atapuerca SH (p. 301).” Species definitions and phylogenies are often based on selected features or anatomical regions, but evolutionary changes are likely to differ from one anatomical area to another. Furthermore, as demonstrated earlier with *Homo heidelbergensis* and *Homo helmei*, the operational taxonomic units are largely arbitrarily defined, so that exclusion or inclusion of specimens will lead to different results.

It is often difficult to determine the autapomorphic status of morphological features, as has been shown with regard to the suggested *Homo erectus* autapomorphies<sup>76</sup> and as is likely the case with regard to a recent definition of *Homo sapiens* by Schwartz and Tattersall.<sup>49,113,114</sup> These authors suggested “nine features of the skull that do appear among hominoids to be autapomorphic for *Homo sapiens* (p. 599).”<sup>49</sup> These anatomical details include, for example, extreme lateral placement of the styloid process; a narrow, high occipital plane of the occipital bone; a bipartite brow (glabellar butterfly); and the inverted-T-shaped chin. Based on these details, Schwartz and Tattersall<sup>49</sup> concluded that many specimens that have in the past been identified as modern *Homo sapiens* should now be distinguished from *Homo sapiens*. These hominins include, for example, most but not all Klasies specimens, Omo 1, some but not all of the Qafzeh specimens, Skhul, and even the undated, possibly post-Pleistocene Boskop and Fish Hoek crania from South Africa. In the mandible of some Qafzeh specimens, much as in Skhul, “there is a teardrop-shaped bulge low down on the external symphysis, but no keel” (p. 600),<sup>49</sup> which would exclude them from being *Homo sapiens*. In contrast, Lieberman’s analyses, presented at the Stony Brook Workshop in 2004, based on relatively complete cranial vaults and faces and using different autapomorphies, found that Omo 1 and Skhul 5 fall within modern *Homo sapiens*. Schwartz and Tattersall’s typological approach is a

recent example of the fact that, just by looking for unique derived traits, one can arrive at a view that excludes clearly anatomically modern humans from being *Homo sapiens*. Regarding such cladistic definitions, Foley,<sup>115</sup> however, reminds us that *variability and polymorphisms* in both ancestral and descendent taxa often make such autapomorphies hard to demonstrate (see also the criticism by Stringer<sup>116</sup>). In fact, a look into a recent human skeletal collection reveals that there is obviously great variability in chin morphology, with many specimens lacking an inverted-T-shape. This clearly shows that the feature is too narrowly defined and thus problematic for taxonomic classifications (see also Pearson<sup>19</sup>).

Moreover, according to Foley<sup>115</sup> “it is unlikely that the species concept itself will be the most useful tool for unraveling what is in effect ... a very small-scale event, especially in its later stages (the last half million years).” In view of all these problems, it should come as no surprise that there are large disagreements regarding the definitions used for *Homo ergaster*, *Homo heidelbergensis*, *Homo rhodesiensis*, *Homo helmei*, *Homo neanderthalensis*, and even *Homo sapiens*. Thus, how to define species and how many species or morphs should be assumed appears to be largely subjective. In contrast to the various attempts to split Middle Pleistocene hominins into several species, Wolpoff and colleagues<sup>117,118</sup> proposed an extremely opposite view by even including *Homo erectus* in the species *Homo sapiens*. A major reason for such a wide definition is seen by these authors in a mix of *erectus* and *sapiens* characteristics in many of the Middle Pleistocene specimens from Africa, Europe, and Asia. However, the presence of plesiomorphic *erectus* features in a specimen does not necessarily exclude it from belonging to a different, more derived species.

## CONCLUSIONS

As demonstrated in the present paper, both the African and European fossil records represent long continu-

ous lineages through most of the Middle Pleistocene; these lineages cannot consistently or reasonably be subdivided into different species. It is likely that the lineages diverged some time after the speciation of *Homo sapiens* from *Homo erectus* in Africa about 700,000 or 800,000 years ago, and thus are closely related. This makes it reasonable to assume that the African Middle Pleistocene lineage represents the species

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**This makes it reasonable to assume that the African Middle Pleistocene lineage represents the species *Homo sapiens* and that the European Neandertal lineage, which derived from early African *Homo sapiens*, belongs to the same species except that there would be unequivocal evidence that Neandertals and modern humans were too different to be one species. This, however, cannot be seen by many specialists.**

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*Homo sapiens* and that the European Neandertal lineage, which derived from early African *Homo sapiens*, belongs to the same species<sup>120</sup> except that there would be unequivocal evidence that Neandertals and modern humans were too different to be one species. This, however, cannot be seen by many specialists. As with the much longer existing, widespread, and polytypic species *Homo erectus*,

it appears plausible here, as well, not to split *Homo sapiens* into further species. The variety of alternative scenarios discussed here can hardly be regarded as having convincingly demonstrated that more than one species was involved in this process, even if this might be unsatisfactory for some splitters. This is a major reason why the use of archaic *Homo sapiens*<sup>120</sup> still appears adequate and plausible. Archaic *Homo sapiens* is not a “wastebasket” for diverse Middle Pleistocene hominin specimens, as some like to believe. Such a designation could then also be used for *Homo heidelbergensis* in its predominant sense, since it includes most of the same phenetically diverse specimens from Africa, Europe, and China.

Clearly, Middle and late Pleistocene hominins in Africa and Europe show morphological differences in time and space. It is necessary to explore the evolutionary pattern by detecting groups, grades, steps, paleo-demes, morphs, or subspecies. Yet it only causes confusion, and is indeed unsatisfactory, to call any unit, no matter how it is defined, a species and, based on this, to suggest phylogenetic trees that are unrealistic and misleading. This even becomes worse when it enters popular science.

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