Modern Human Origins

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INTRODUCTION

The origin of modern humans has long been one of the most dynamic topics in paleoanthropology. In the last few years, however, there has been a dramatic increase in the amount of data that are relevant to the issue. This is partly due to discoveries made in the course of fieldwork (e.g., Duarte et al., 1999; White et al., 2003). But mainly it is a consequence of the development of a range of sophisticated laboratory methods that have allowed us to not only date and compare fossils much more precisely and accurately than was possible before, but also access completely new types of data, including – most remarkably – gene sequences from the fossilized remains of individuals who died over 30,000 years ago (e.g., Krings et al., 1997; Spoor et al., 2003; Harvati, 2009; Richards and Trinkaus, 2009; Reich et al., 2010).

In this chapter, we provide an overview of the current state of research on modern human origins. Conventionally, the evidence pertaining to modern human origins is evaluated in relation to two models – the African replacement model (also known as the Afro-European *sapiens* model, the out of Africa model, the Eve theory, the recent African origin model, or the replacement model) and the multiregional evolution model (also known as the multiregional continuity model) (e.g., Wolpoff and Caspari, 1997; Wood and Baker, 2011). However, it has been argued that treating all the models that have been put forward to explain modern human origins as variants of either the African replacement model or the multiregional evolution model is unhelpful, and that additional models should be recognized (Aiello, 1993; Stringer, 2001). We find this argument convincing, and therefore assess the evidence against several models.

The remainder of this chapter is divided into two main sections. In the first, we outline the four models we think need to be taken into account when discussing modern human origins. In our view, the modern human origins debate has been hampered by ambiguities in the way some of the models in question have been characterized. We discuss these ambiguities and then suggest revisions to the models that reduce the uncertainty. In the other section, we review how well the available anatomical, genetic, and linguistic evidence support the predictions of the models. Anatomical, genetic, and linguistic research on modern human origins has tended to focus on three issues: the structure of living human variation, the timing of the appearance of modern humans, and evidence for the occurrence of gene flow between modern humans and nonmodern hominins. We discuss each of these in turn.

MODELS OF MODERN HUMAN ORIGINS

Two papers are particularly helpful for identifying the models that need to be taken into account when discussing modern human origins: Aiello (1993) and Stringer (2001). Aiello (1993) argued that four models could be identified in the literature dealing with modern human origins: the African replacement model, the (African) hybridization and replacement model, the assimilation model, and the multiregional evolution model. These models, she suggested, differ in relation to three factors: geography, timescale, and process. Aiello (1993: 73–74) summarized the models as follows:

1. *The African replacement model* argues that modern humans first arose in Africa about 100,000 years ago and spread from there throughout the world... Indigenous premodern populations in other areas of the world were replaced by the migrating populations with little, if any, hybridization between the groups.
2. *The (African) hybridization and replacement model* is similar to the above, but allows for a greater or lesser extent of hybridization among the migrating populations and the indigenous premodern populations.
3. *The assimilation model* also accepts an African origin for modern humans. However, it differs from the previous models in denying replacement, or population migration, as a major factor in the appearance of modern humans. Rather, this model emphasizes the importance of gene flow, admixture, changing selection pressures, and resulting directional morphological change. In other words, it accepts the fact that, at least in some areas of Eurasia, local evolution (or continuity) could play an important role in the appearance of modern humans.
4. *The multiregional evolution model* differs from the previous three in denying a recent African origin for modern humans. It emphasizes the role of both genetic continuity over time and gene flow between contemporaneous populations in arguing that modern humans arose not only in Africa but also in Europe and Asia from their Middle Pleistocene forebears.

Stringer (2001) revisited Aiello's (1993) scheme in light of work published in the 1990s that he believed had caused confusion about the differences among the models. He focused particularly on work that had been claimed to support the multiregional evolution model. In some of the studies in question, he argued, the name "multiregional evolution model" had been applied to models that should be considered variants of the assimilation model, while in others the name "multiregional evolution

model" had been applied to a model that does not appear in Aiello's (1993) scheme. The latter model, Stringer (2001) suggested, shares features with the assimilation model and the multiregional evolution model, but is different from both. It is similar to the assimilation model in that it holds that African populations made the largest contribution to the modern human gene pool due to their numerical dominance. Where it differs from the assimilation model and overlaps with the multiregional evolution model is in the timescale involved. Whereas the assimilation model focuses on the Late Pleistocene, the new model contends that the genetic influence of African populations extends throughout the Pleistocene, which is also the timescale the multiregional evolution model operates on. Stringer (2001) went on to suggest that the new model should be dubbed "multiregional evolution 2" and that the original multiregional evolution model should be renamed "multiregional evolution 1."

Generally, we accept the Aiello (1993) / Stringer (2001) scheme. However, we think it needs minor revision. To begin with, the timescale on which the African replacement model and the (African) hybridization and replacement model operate needs to be adjusted. Since the publication of Stringer (2001), the first appearance date of modern humans in Africa has been pushed back on the basis of new finds and re-dating of previously discovered material to between 160 and 195 ka before the present[1] (White et al., 2003; McDougall et al., 2005). As such, both models now argue that modern humans first arose in Africa about 200,000 years ago.

The second revision we wish to propose concerns the model Stringer (2001) called "multiregional 2." It seems to us that this model is better viewed as a variant of the assimilation model than as a version of the multiregional evolution model, and should be renamed accordingly. It is clear from the early work of proponents of the multiregional evolution model not only that they viewed the genetic contributions of nonmodern hominins[2] from Eurasia and Australasia to modern human populations in those areas to be more important than the genetic contributions of African populations, but also that this is a core component of the model. The following quotes from Thorne and Wolpoff (1992: 78–79) illustrate this. Writing about China, Thorne and Wolpoff make the following claim: "Our examinations of the Chinese specimens found no anatomic evidence that typically African features ever replaced those of the ancient Chinese in these regions. Instead there is a smooth transformation of the ancient population into the living peoples of east Asia." They make a similar point about the fossil record of Australasia: "The hominid fossils from Australasia (Indonesia, New Guinea and Australia) show a continuous anatomic sequence that is uninterrupted by African migrants at any time." Given that a dominant contribution from Eurasian and Australasian nonmodern hominins to modern human populations in those regions is central to the multiregional evolution model, it is difficult to see how a model that posits a dominant contribution of African populations to modern human populations in Eurasia and Australasia can be considered to be a variant of the multiregional evolution model. Doing so, in our opinion, effectively strips the multiregional evolution model of one of its key distinguishing features. This problem does not arise if the model that Stringer refers to as multiregional 2 is treated a variant of the assimilation model, because the latter assumes that African populations contribute most to the modern human gene pool. Thus, we prefer to call the model "assimilation 2."

Our third proposed revision relates to the distinction between the African replacement model and the (African) hybridization and replacement model. In the way these

models were described by Aiello (1993), there is potential for uncertainty regarding the amount of hybridization between migrating modern humans and nonmodern hominins in Europe, Asia, and Australasia that is consistent with the models. To reiterate, the African replacement model is described as holding that nonmodern hominin populations were replaced by the migrating modern human populations with "little, if any, hybridization between the groups," while the (African) hybridization and replacement model is described as allowing for "a greater or lesser extent of hybridization between the migrating populations and the indigenous premodern populations." The problem here is that it is unclear whether or not the "lesser extent" in the latter description overlaps with the "little" in the former description. If it does, then the two models are effectively identical, because their other components are the same. One way of overcoming this problem, we think, is to focus on the percentage of genes in the contemporary human gene pool that are derived from hominin populations living outside of Africa at 150 ka, which, as we discuss below, is shortly before the first appearance of modern humans outside of Africa. If we focus on this, then the distinction between the African replacement model and the (African) hybridization and replacement model is whether the percentage of genes in the contemporary human gene pool that are derived from hominin populations living outside of Africa at 150 ka is significant or not. Under African replacement model the number of such genes should be insignificant, while it should be significant under the (African) hybridization and replacement model.

The following, then, are the four models against which we will evaluate the anatomical, genetic, and linguistic evidence:

1. *The African replacement model.* This model contends that modern humans arose in Africa around 200 ka. Between 100,000 and 150,000 years later, they expanded out of Africa and colonized Europe, Asia, and Australasia. Eventually, they reached the Americas and Oceania. In the process of colonizing Europe, Asia, and Australasia, modern humans may have encountered nonmodern hominin populations. If they did so, hybridization would have been sufficiently rare and/or infrequently successful that the modern human gene pool is numerically dominated by genes derived from populations that lived in Africa at 150 ka, and contains an insignificant number of genes from populations that lived outside of Africa at that time. This model has been described in numerous publications, including Cann et al. (1987), Stringer and Andrews (1988), Stringer (1989, 1992, 2001), Vigilant et al. (1991), Stringer and Bräuer (1994), Bräuer (2001, 2006, 2007), and Bräuer et al. (2004).

2. *The (African) hybridization and replacement model.* Modern humans arose in Africa about 200 ka. Between 100,000 and 150,000 years later, they expanded out of Africa and colonized Europe, Asia, and Australasia. Eventually, they reached the Americas and Oceania. In the process of colonizing Europe, Asia, and Australasia, modern humans encountered nonmodern hominin populations and interbred with them. Successful hybridization occurred sufficiently frequently that while genes derived from populations that lived in Africa at 150 ka dominate the modern human gene pool, it also contains a significant number of genes from populations that lived outside of Africa at that time. This model is discussed in Bräuer (1989), Churchill and Smith (2000), Kramer et al. (2001), and Smith et al. (2005).

3. *The assimilation model*. Modern humans arose in Africa about 200 ka. Subsequently they interbred with nonmodern hominins in the Middle East. As a consequence of the combined effects of interbreeding and changing selection pressures, the African population's genes spread into the Middle Eastern nonmodern hominin population but also into the nonmodern hominin populations in more distant parts of Europe, Asia, and Australasia. Eventually the genes of the African population came to dominate the gene pools of the hominins populations of Europe, Asia, and Australasia, although the latter continued to contain a significant number of genes that evolved outside of Africa prior to 150 ka. The key difference between this model and the previous two models is that it does not posit a major migration out of Africa. This model was first outlined in Smith (1985). Among the other papers in which it has been discussed are Smith (1992) and Smith et al. (1989).

4. *The multiregional evolution model*. Modern humans do not have a single place of origin. Instead, they evolved in different regions of the Old World from regional nonmodern hominin populations over the course of the last 2 million years. This process was the result of changing selection pressures combined with inter-regional gene flow. Although the latter was extensive, the majority of the genes in the gene pools of regional populations of modern human originated in those regions. Thorne and Wolpoff (1981), Wolpoff et al. (1984), and Wolpoff (1989) are among the publications in which this model has been discussed.

Before we move on to consider the evidence for modern human origins, we want to explain why the example publications we have listed for each model are in some cases different from those listed by Aiello (1993), and why we have listed the publications of some authors under more than one model. The reason for both of these is that the relationship between the models and authors has become complicated since the publication of Aiello's (1993) review. One issue is that some of the individuals that Aiello (1993) identified as proponents of the models in her scheme have changed their views sufficiently that they now effectively support one of the other models in the scheme. The individual that Aiello (1993) identified as the main proponent of the assimilation model, F. H. Smith, is a case in point. Over the last 20 years, Smith has shifted from rejecting the idea that a Late Pleistocene migration out of Africa played a major role in the origins of modern humans in Europe (e.g., Smith et al., 1989) to accepting it (e.g., Churchill and Smith, 2000; Smith et al., 2005). In so doing, he has effectively transitioned from supporting the assimilation model to supporting the (African) hybridization and replacement model, although confusingly he has continued to call his preferred model the assimilation model (e.g., Smith et al., 2005). M. H. Wolpoff is another example. Throughout the 1980s and 1990s, Wolpoff was the leading proponent of the multiregional evolution model. In line with this, Aiello (1993) cited Wolpoff's work in her description of that model. However, in the last few years Wolpoff has clearly accepted that diagnostic modern human traits originated in Africa and spread into the Old World via gene flow (e.g., Wolpoff et al., 2004), which is a core element of the assimilation model rather than the multiregional evolution model as the models were summarized by Aiello (1993). A further complexity is that the researcher that Aiello (1993) identified as the main proponent of the (African) hybridization and replacement model, G. Bräuer, evidently does not see himself as promoting a model that is different from the African replacement model. Over the last few

years, Bräuer has repeatedly made it clear that he does not recognize any substantive difference between the (African) hybridization and replacement model and the African replacement model (e.g., Bräuer et al., 2004; Bräuer, 2007). In other words, since the publication of Aiello's (1993) review, the main proponent of the multiregional evolution model has become a proponent of the assimilation model, the main proponent of the assimilation model has switched to supporting the (African) hybridization and replacement model, and the alleged main proponent of the (African) hybridization and replacement model has made it clear that he thinks of himself as a proponent of the African replacement hypothesis. This is why the example publications we have listed for each model are in some cases different from those listed by Aiello (1993), and why we have linked some authors to more than one model.

ANATOMICAL, GENETIC, AND LINGUISTIC EVIDENCE FOR MODERN HUMAN ORIGINS

As we noted earlier, in this section we review how well the models are supported by the available anatomical, genetic, and linguistic evidence. The review is structured in relation to the three issues that have dominated anatomical and genetic research on modern human origins – the structure of living human variation, the timing of the appearance of modern humans, and evidence for the occurrence of gene flow between modern humans and nonmodern hominins.

The structure of living human variation

A number of modern human origins-related studies have focused on the spatial structure of differences in the amount of variation among regional populations of living humans. However, it is not clear that the main models of modern human origins can in fact be differentiated in relation to the spatial structure of differences in the amount of variation among regional populations.

A number of authors have claimed that the spatial structure of differences in amount of variation among regional populations is useful for differentiating the models of modern human origins (e.g., Harpending and Rogers, 2000; Prugnolle et al., 2005; Manica et al., 2007; Betti et al., 2009; Atkinson, 2011). Their argument derives from population genetic theory. The latter suggests that a small, founder population will not only start off with only a subset of the alleles present in its parent population, but also lose alleles at a faster rate than its parent population. One of the corollaries of this is that a succession of founder events during range expansion should progressively reduce allelic diversity with increasing distance from the point of origin. Thus, measuring allelic diversity in populations from different regions of the Old World and then regressing the allelic diversity values on distance from Africa provides a means of distinguishing between the African replacement model and the multiregional evolution model. The reason for this, so the argument goes, is that the African replacement model predicts a significant negative correlation between distance from Africa and allelic diversity, whereas the multiregional evolution model predicts the existence of several clines.

In some of the studies carried out by these authors microsatellite data have been used to assess regional differences in diversity (e.g., Harpending and Rogers, 2000; Prugnolle et al., 2005). In others, craniometric data have been used in place of genetic data (Manica et al., 2007; Betti et al., 2009). Most recently, Atkinson (2011) argued that the similarities between genes and language are such that the serial founder effect model can be expected to hold for linguistic data as well, and then proceeded to examine the relationship between phoneme diversity and distance from Africa in a worldwide sample of languages. The results of these studies are consistent. They indicate that there is a significant correlation between the amount of variation exhibited by regional populations and their distance from Africa such that populations that live close to Africa are more variable than those that live further away (Harpending and Rogers, 2000; Prugnolle et al., 2005; Manica et al., 2007; Betti et al., 2009; Atkinson, 2011). In line with the rationale outlined in the previous paragraphs, all the authors in question have interpreted this pattern as supporting the African replacement model and refuting the multiregional evolution model.

On the face of it, this conclusion seems reasonable. The African replacement model clearly predicts that diversity should decline with distance from Africa, whereas the term "multiregional evolution" makes it sound as if the model of that name predicts the existence of several clines of diversity rather than one. However, the latter prediction is in fact wrong. In the early 1980s, two of the main proponents of the multiregional evolution model, Alan Thorne and Milford Wolpoff, discussed a concept that they called the "center and edge" hypothesis in connection with the establishment of regional variation (Thorne and Wolpoff, 1981). Drawing on Mayr's (1963) summary of studies examining the impact of colonization on the structure of genetic diversity within fruit fly species, they argued that, due to the combined effects of founder effect, reduced gene flow, and more severe selection, populations at the edges of the range of a polytypic species can be expected to be less genetically and morphologically diverse than populations closer to the center of the species' range. Significantly for present purposes, Thorne and Wolpoff (1981) went on to explain that they regarded Africa as the center of the range of *Homo erectus* and East Asia and Australasia as two of the edges. Thus, for more than 30 years, a core component of the multiregional evolution model has been the idea that African populations should be more diverse than populations from other regions of the Old World, and that diversity should decrease with distance from Africa. The corollary of this is that the multiregional evolution model makes exactly the same prediction regarding the spatial structure of differences in the amount of variation among regional populations of living humans as the African replacement model. This, in turn, means that the spatial structure of differences in the amount of variation among regional populations of living humans is not in fact useful for differentiating among the competing models of modern human origins.

The timing of the appearance of modern human fossils in different regions of the Old World

The geographical pattern of the first appearance dates for modern human fossils in Africa, the Middle East, Europe, Asia, and Australasia also provides an important test of the four models for modern human origins. Because they envisage a migration

of modern humans out of Africa and into the rest of the Old World, the African replacement and (African) hybridization and replacement models both predict that the first appearance date for modern humans in Africa will be earlier than the first appearance date for modern humans in the Middle East, Europe, Asia, and Australasia. In addition, because the Middle East is adjacent to Africa and therefore groups migrating out of Africa and in the rest of the Old World must have passed through it first, the African replacement and (African) hybridization and replacement models also all predict that the first appearance date for modern humans in the Middle East will be earlier than the first appearance date for modern humans in Europe, Asia, and Australasia. The assimilation model makes the same predictions as the African replacement and (African) hybridization and replacement models regarding the geographic pattern of the first appearance dates of modern humans in the different regions of the Old World. Because it envisages modern human traits originating in Africa and then spreading into the rest of the Old World by gene flow, it too predicts that the first appearance date for modern humans in Africa will be earlier than the first appearance date for modern humans in the Middle East, Europe, Asia, and Australasia, and that the first appearance date for modern humans in the Middle East will be earlier than the first appearance date for modern humans in Europe, Asia, and Australasia. In contrast, the multiregional evolution model predicts that the first appearance date for modern humans in Africa, the Middle East, Europe, Asia, and Australasia will be similar. Thus, the geographical pattern of the first appearance dates for modern humans in Africa, the Middle East, Europe, Asia, and Australasia potentially offers a way of discriminating between the African replacement model, the (African) hybridization and replacement model, and the assimilation model on the one hand, and the multiregional evolution model on the other.

Establishing the first appearance dates for modern humans in the different regions of the Old World is complicated by the fact that there is some ambiguity in the literature regarding the use of the term "modern humans" and the species name *Homo sapiens*. The proponents of all four models of modern human origins accept that modern humans are an anatomically distinct group of hominins. However, they disagree about the significance of the anatomical differences between modern humans and nonmodern hominins. Some authors believe the differences are due to modern humans forming a separate species from nonmodern hominins such as the Neanderthals. Consistent with this hypothesis, these authors tend to restrict the species name *H. sapiens* to modern humans. Other authors contend that the differences in question do not exceed those expected for different demes in the same species. Typically, these authors use the name *H. sapiens* to refer not only to modern humans but also to one or more groups of nonmodern hominins. Wolpoff et al. (1994), for example, argue that the name *H. sapiens* should apply to all members of the genus *Homo* apart from the very earliest, the habilines. For present purposes, it does not matter whether modern humans form a separate species from the nonmodern hominins or just a deme. All that matters is that they are sufficiently distinct in their hard-tissue anatomy that they can be identified with confidence in the fossil record.

There has been some debate about the anatomical traits that distinguish modern humans from nonmodern hominins (Wolpoff, 1989; Lahr, 1996). However, over the last few years a consensus has formed around a list of traits that Lieberman (1998) distilled from the literature. According to Lieberman (1998:158), to be regarded as

anatomically modern human, a skull needs to have "a globular braincase, a vertical forehead, a diminutive browridge, a canine fossa, and a pronounced chin."

The earliest African specimens that exhibit at least some of these traits come from sites in Ethiopia (Table 29.1). One of the specimens in question, Omo I was discovered in 1967 by a team led by Richard Leakey. The site after which the fossil is named, Omo-Kibish, is located in southwest Ethiopia. Omo I is a fragmentary associated skeleton of a young adult male. Initially, Omo I was thought to be around 130 ka based on ^{230}Th/^{234}U dating of *Etheria* shell from the same stratum as Omo I (Butzer et al., 1969). Recently, however, McDougall et al. (2005, 2008) have re-dated Omo I and concluded that it is significantly older than originally thought. Based on ^{40}Ar/^{39}Ar dating of sediments directly above and below the member from which Omo I derives and an assessment of the likely speed of deposition of the member, McDougall et al. contend that Omo I should be considered to date to 195±5 ka. Omo I is considered to be *H. sapiens* because its cranial vault is globular and its forehead is nearly vertical (Wood and Leakey, 2011). In addition, its mandible displays a chin (Day, 1969).

Two other specimens were recovered from Omo-Kibish at the same time as Omo I. One of these specimens, Omo II, is a well-preserved adult male calvaria that is thought to be contemporaneous with Omo I. The other, Omo III, is an adult cranial vault of uncertain sex. Omo III is a surface find, so it is more difficult to date. Depending on which member it derives from, it is either about 195,000 or about 104,000 years old (Wood and Leakey, 2011). Omo III is so fragmentary that little can be said about its affinities other than that it is broadly similar to Omo I (Day, 1969). Omo II, on the other hand, is reasonably well preserved. Its cranial capacity (1,435 ±20 cc) and small supraorbital torus suggest affinities with *H. sapiens* (Wood and Leakey, 2011). However, other features of the specimen are archaic. For example, the occipital bone is strongly angled and the maximum vault breadth is across the supramastoid tubercles. Likewise, the mastoids are mediolaterally thick and the tympanic is robust. The significance of these archaic characters, given the close spatial and temporal proximity of Omo I and II, is unclear.

The other African specimens that exhibit at least some of the traits that are thought to distinguish *H. sapiens* were discovered in 1997 by a team led by Tim White (White et al., 2003). Known as BOU-VP-16/1 and BOU-VP-16/5, these specimens were recovered from sites in the Afar region of northeast Ethiopia. BOU-VP-16/1 is a nearly complete adult cranium (Figure 29.2), while BOU-VP-16/5 is a partial child's cranium. Both specimens were recovered from the Upper Herto Member of the Bouri Formation, which has been dated by ^{40}Ar/^{39}Ar to between 154 and 160 ka. Two other hominin specimens from Herto – BOU-VP-16/2 and BOU-VP-16/43 – were reported by White et al. (2003) but neither specimen is complete enough to allow its affinities to be assessed. The most obvious distinctively modern human traits that BOU-VP-16/1 displays are a vertical forehead and a globular neurocranium. With regard to the latter, metric analyses carried out by White et al. (2003) indicate that the globularity of BOU-VP-16/1's neurocranium falls within the modern human range. In addition, BOU-VP-16/1's greatest cranial breadth occurs high up on the parietals, resulting in a characteristically modern human posterior profile. Assessing the affinities of BOU-VP-16/5 is potentially problematic because it is a juvenile. However, White et al. (2003) have argued that it should be assigned to *H. sapiens* on the grounds that it displays a canine fossa and that its greatest breadth occurs high up on the parietals.

Table 29.1 Key modern human fossil-bearing sites discussed in Chapter 29.

Region	Site	Location	Element	Date	Reference	Notes
Africa	Omo	Omo River, Ethiopia	Partial skeleton and crania	195±5 ka or 104 ka	Day 1969; Wood and Leakey 2011	Omo I is a partial cranium with a globular vault and a vertical forehead. The mandible displays a chin. Omo II is broadly similar to Omo I, but it also has archaic features. These crania are currently the oldest AMH fossils. Omo III is a fragmentary cranial vault. Since this cranium was a surface find, the dating is uncertain.
Africa	Herto	Middle Awash, Ethiopia	Crania	154 ka–160 ka	White et al. 2003	BOU-VP-16/1 is a globular cranium with a vertical forehead and parietal expansion. BOU-VP-16/5 is a juvenile cranium with a canine fossa. The posterior profile of the cranium is similar to modern humans.
Africa	Klasies River Mouth	Klasies River Mouth, South Africa	Skeletal fragments	93·5±10.4 or 88·3±7.8 ka	Cartmill and Smith 2009; Wood and Baker 2011;	There are numerous cranial, mandibular, and postcranial fragments from this site. Several mandibles display a chin. Cranial fragments display modern morphology.
Africa	Border Cave	Lebombo Mountains, South Africa	Partial skeleton, cranial and mandibular fragments	100 ka– 227±11 ka, 53 ka–82 ka	de Villiers 1976; Day 1986; Cartmill and Smith 2009	Border Cave 1 is a fragmentary cranium with features similar to AMH. Border Cave 2 preserves most of the mandibular body without teeth. It is a fully modern mandible. Border Cave 3 is a partial skeleton of an infant that appears to be modern. Border Cave 5 is a fully modern mandibular body with some worn teeth.
Africa	Dar-es-Soultane	Rabat, Morocco	Cranium and mandible	34–127 ka	Ferembach 1976; Hublin 1993, 2000; Cartmill and Smith 2009	Dar-es-Soultane 5 is a partial cranium that is robust with a supraorbital torus. But, it has modern features like reduced dentition.
Africa	Témara	Rabat, Morocco	Cranium and mandible	34–127 ka	Ferembach 1976; Hublin 1993; Cartmill and Smith 2009	Témara 2 is a fragmentary cranium with a rounded occipital, and it lacks a supraorbital torus. The mandible is modern.
Middle East	Skhul	Mount Carmel, Israel	Skeletons	100 ka	Day 1986	There are multiple adult and juvenile skeletons and well-preserved crania. The mandibles have chins.

Region	Site	Location	Specimen	Date	References	Description
Middle East	Qafzeh	Jebel Qafzeh, Israel	Skeletons	92ka	Day 1986	There are multiple skeletons of adult and juvenile individuals. The cranium is robust and large, but it has a rounded vault.
Europe	Peştera cu Oase	Carpathian Mountains, Romania	Crania, mandible	34–36ka	Trinkaus et al. 2003	There are multiple individuals represented. The mandible is robust and has a prominent chin. Some researchers have argued that these specimens represent evidence for interbreeding with non-modern hominins.
Europe	Kostenki	Don River, Russia	Skeletons	32–33ka	Richards et al. 2001; Klein 2009	There are numerous skeletons from multiple sites along the Don River. Kostenki XIV cranium is distinctively modern with a slight alveolar prognathism.
Europe	Brassempouy	Landes, France	Skeletal fragments, but mostly teeth	30–33.5ka	Henry-Gambier et al. 2004; Bailey et al. 2009	The specimens are associated with early Aurignacian industry.
Europe	La Quina Aval	Charente, France	Skeletal fragments	32–33ka	Dujardin 2003; Verna et al. 2012	There are multiple fragmentary specimens representing various anatomical elements associated with Aurignacian material.
Europe	Mladeč	Olomouc, Czech Republic	Skeletons	31ka	Wild et al. 2005; Cartmill and Smith 2009	There are multiple adult and juvenile AMH skeletons from this site.
Asia	Liujian	Guangxi, China	Partial skeleton	67ka	Brown 1992; Cartmill and Smith 2009	The date associated with the Liujian skull is debated. This may be the oldest AMH fossil from East Asia if the dating is accepted.
Asia	Niah Cave	Sarawak, Malaysia	Cranium, femur, tibia	39–45ka	Barker et al. 2007; Klein 2009	This site has yielded a juvenile specimen with modern features. Currently, this is the oldest AMH cranium from SE Asia.
Asia	Tianyuan Cave	Fangshan, China	Partial skeleton	39–42ka	Shang et al. 2007; Cartmill and Smith 2009	The specimen from this site is the most reliably dated AMH from East Asia. The mandible displays a chin with a gracile mandibular body. The postcrania appear modern.
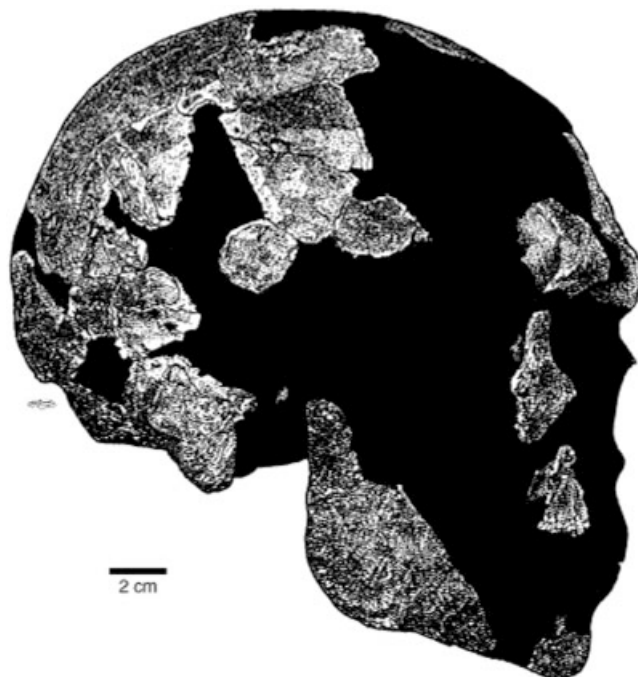
Figure 29.1   Lateral view of Omo Kibish 1 skull. Drawing © Matt Cartmill, used with permission from *The Human Lineage*, by Matt Cartmill and Fred H. Smith (2009).
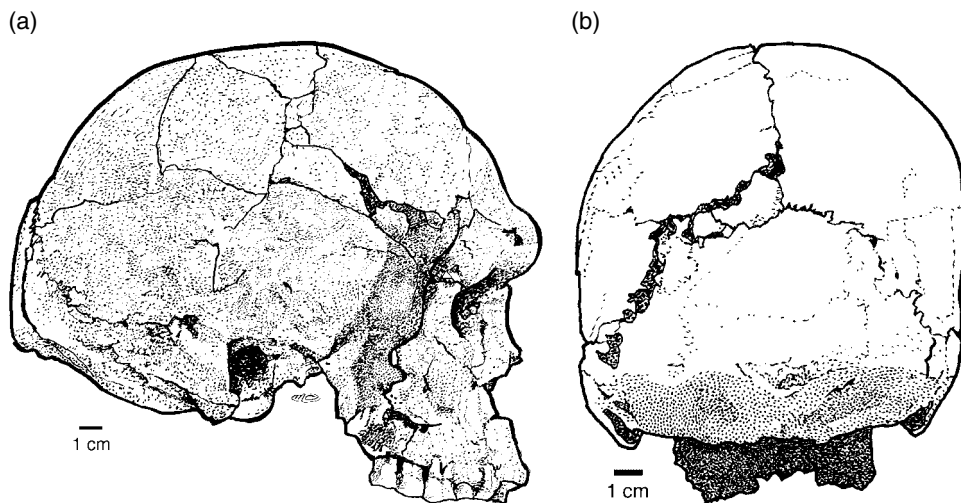
Figure 29.2   (a) Lateral and (b) occipital views of Herto 1 cranium. Drawing © Matt Cartmill, used with permission from *The Human Lineage*, by Matt Cartmill and Fred H. Smith (2009).

Sites in South and North Africa have also produced fossils that are widely considered to be the remains of early anatomically modern humans (Table 29.1). Klasies River Mouth in the Eastern Cape Province of the Republic of South Africa is one such site. Klasies River Mouth has yielded 26 hominin specimens. These specimens have

been dated by the electron spin resonance (ESR) method to around 93·5±10·4 or 88·3±7·8 ka (Wood and Baker, 2011). The majority of the Klasies River Mouth fossils cannot be confidently assigned to a species because they are too fragmentary. However, several of the mandibles unearthed at the site display a chin and therefore can be assigned to *H. sapiens* (e.g., Stringer and Andrews, 1988; Bräuer, 1989; Schwartz and Tattersall, 2003).

Border Cave, which is located in the Lebombo Mountains near the border between the Republic of South Africa and the Kingdom of Swaziland, has also produced fossils that are widely accepted to be the remains of early modern humans (e.g., de Villiers, 1976; Bräuer, 1989; Stringer and Andrews, 1988; Schwartz and Tattersall, 2003). Two of the Border Cave specimens, BC 1 (a calvaria) and BC 2 (a partial adult mandible), are thought to date between 100 ka and 227±11 ka, although there are doubts about their provenance. Two other specimens, BC 3 (an infant skeleton) and BC 5 (nearly complete adult mandible), have been dated to between 82 ka and 53 ka. It has been suggested that these specimens are intrusive, but ESR dating of a tooth fragment from BC 5 has yielded an age of 74±5 ka (Grün et al., 2003; Grün, 2006), which indicates that BC 5, at least, is not from a later time period. The remaining four hominin fossils from Border Cave date to the Iron Age (i.e., around 1 ka). The BC 1 calvaria has been assigned to *H. sapiens* on account of its high forehead and rounded cranial contours (Day, 1986). The two adult mandibles, BC 2 and 5, are considered to belong to *H. sapiens* because of their size and shape, and also because they have chins defined by distinctive mental trigones (de Villiers, 1976).

The most compelling early anatomically modern human fossils from North Africa come from the sites of Dar-es-Soultane and Témara in Morocco. Dar-es-Soultane 5 consists of a partial cranium and the left side of an associated mandible. The specimen is robust but modern, according to Ferembach (1976) and Hublin (1993, 2000). This assessment, which is widely accepted (e.g., Schwartz and Tattersall, 2003; Cartmill and Smith, 2009; Wood and Baker, 2011), is based primarily on the fact that the specimen has a relatively high forehead, an angled zygomaticoalveolar margin, a large and robust mastoid, and an orthognathic face (Ferembach, 1976). The specimens from Témara are more fragmentary than Dar-es-Soultane 5. However, they include a frontal bone whose supraorbital region displays a flattened supraorbital trigone and a mandible with a chin, and thus can be confidently assigned to *H. sapiens* (Ferembach, 1976; Hublin, 1993). Currently, there are no radiometric dates for either site. Thus, the dating of Dar-es-Soultane 5 and the hominin specimens from Témara is based solely on their association with an archeological industry known as the Aterian. The time span of the Aterian is such that Dar-es-Soultane 5 and the Témara specimens can only be said to date between 34 and 127 ka.

In sum, then, individuals displaying diagnostic modern human traits were present in East Africa between 150 and 200 ka. By 80–90 ka, individuals displaying diagnostic modern human traits were also living in South Africa and may have been present in North Africa too.

The first appearance date for modern humans in the Middle East is considerably later than the first appearance date for modern humans in Africa (Table 29.1). The earliest Middle Eastern specimens with diagnostic modern human traits come from the sites of Skhul and Qafzeh in Israel (Figures 29.3 and 29.4). Skhul is a cave located in the Mount Carmel mountain range in northern Israel. Between 1929 and 1935,
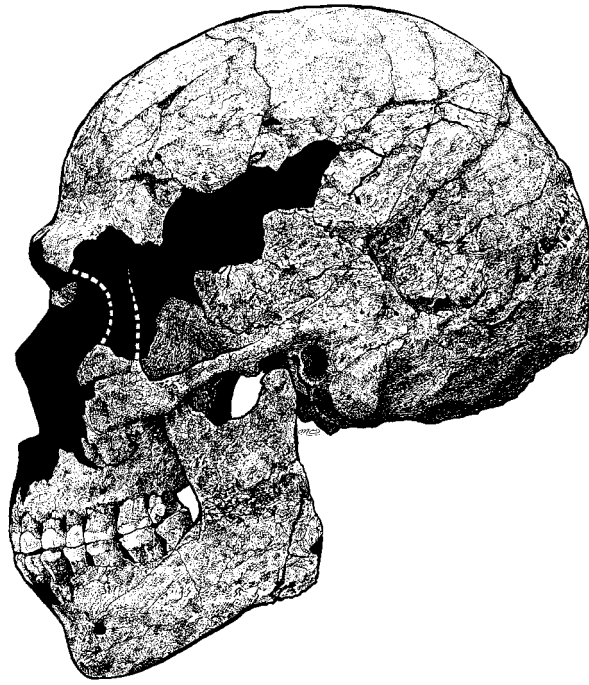
Figure 29.3 Lateral view of Skhul 5 skull. Drawing © Matt Cartmill, used with permission from *The Human Lineage*, by Matt Cartmill and Fred H. Smith (2009).

Figure 29.4 Lateral view of Qafzeh 9 skull. Drawing © Matt Cartmill, used with permission from *The Human Lineage*, by Matt Cartmill and Fred H. Smith (2009).

Layer B at the site yielded the remains of at least ten modern humans. For many years, these specimens were thought to be about 40,000 years old. However, in the early 1990s they were re-dated by Grün and Stringer (1991) using electron spin resonance (ESR) and thermoluminesence (TL) dating, and found to be considerably older. Grün and Stringer's (1991) ESR analyses suggested that Layer B dates to between 81 and 101 ka. Their TL analyses suggested an even earlier date for Layer B. The average of the TL dates for Layer B was 118 ka. Because ESR dates tend to be more precise than TL dates, the current consensus is that the early modern human specimens from Skhul are around 100,000 years old. Qafzeh is a cave site too. Also known as Jebel Qafzeh, it is located in Mount Qafzeh, which lies to the north of Mount Carmel. To date, Qafzeh has yielded the remains of 12 modern human specimens associated with Middle Paleolithic artifacts, including a well-preserved skull (Qafzeh 6) and several partial skeletons (Qafzeh 3, 8, 9, 10, and 11) (Day, 1985). As with the Skhul early modern human material, the date for these specimens has been pushed back recently. In the 1970s, they were estimated to be 27,000–33,000 years old (Bada and Helfman, 1976). Today, as a result of an archeological reappraisal of the age of the site (Bar Yosef and Vandermeersch, 1981) and a radiometric dating study (Grün and Stringer, 1991), they are accepted to be around 92,000 years old. Thus, the first appearance date for modern humans in the Middle East is 90–100 ka.

The first appearance dates for modern humans in Europe, Asia, and Australasia are later than the first appearance date of modern humans in Africa and the Middle East (Table 29.1). The earliest European modern human fossil comes from the site of Peştera cu Oase in Romania. The specimen in question is a mandible and dates to 34–36 ka (Trinkaus et al. 2003). A number of other Europe sites have yielded modern human specimens with similar dates. These include Kostenki in Russia, Brassempouy and La Quina Aval in France, and Mladeč in the Czech Republic. Kostenki has produced a modern human tibia and a modern fibula that date to 32–33 ka (Richards et al. 2001). Brassempouy has yielded modern human teeth and phalanges that date between 30 and 33·5 ka (Henry-Gambier et al. 2004). La Quina Aval has produced a partial mandible of a modern juvenile that has been dated to 32–33 ka (Dujardin 2003). Mladeč has yielded the remains of four modern humans that date to 31 ka (Figure 29.5; Wild et al. 2005). Thus, modern humans appear in Europe around 30–35 ka, some 70,000 years after they appear in the Middle East and nearly 170,000 years after they appear in Africa.

Establishing the first appearance date of modern humans in East Asia is difficult because few sites have been reliably dated. The Liujian skull, dated to 67 ka, has been claimed to be the earliest evidence of modern humans in China. However, this date remains controversial because it is not directly associated with the Liujian skull (Brown 1992). More widely accepted dates for modern humans in Asia come from Niah Cave in Borneo, and Tianyuan Cave in northern China. Niah Cave has yielded an anatomically modern partial cranium, a femur, and a tibial fragment that date between 39 and 45 ka (Barker et al., 2007). Tianyuan Cave has produced a partial modern human skeleton that has been dated to between 39 and 42 ka (Shang et al., 2007). Thus, the currently available evidence suggests that modern humans have been in East Asia since at least 39 ka.

Establishing the first appearance date for humans in Australasia is aided by the fact that there is no evidence of nonmodern hominins having colonized Sahul, the landmass

Figure 29.5   Lateral view of Mladeč 5 cranium. Drawing © Matt Cartmill, used with permission from *The Human Lineage*, by Matt Cartmill and Fred H. Smith (2009).

formed by Australia and Papua New Guinea during the Late Pleistocene. The corollary of this is that both fossils and archaeological artifacts can be used to establish the first appearance of modern humans in Australia and Papua New Guinea. The timing of the entry of modern humans into Sahul has been the subject of controversy for a number of years. Some researchers have suggested that it occurred during or even before Oxygen Isotope Stage 4 (57–71 ka) (Thorne et al., 1999). Others have argued in favor of a date of 50 ka (Roberts et al. 1990; Bowler et al., 2003). Still others have averred that the oldest dates are unreliable and that the entry cannot be pushed back beyond 40–45 ka with any confidence (O'Connell and Allen, 2004). Currently, it appears that the majority of specialists find the second of these hypotheses most convincing (Klein, 2009). No matter which hypothesis is preferred, however, it is clear that the first appearance date of modern humans in Australasia is also tens of thousands of years later than the first appearance dates of modern humans in Africa and the Middle East.

Currently, then, modern human fossils appear in Africa some 50,000 to 100,000 years before they appear in the Middle East, Europe, Asia, or Australasia. Modern human fossils also appear in the Middle East between 50,000 and 60,000 years before they appear in Europe, Asia, or Australasia. This pattern is consistent with the predictions of the African replacement model, the (African) hybridization and replacement model, and the assimilation model, but inconsistent with the predictions of the multiregional evolution model. Thus, the geographic pattern of first appearance dates for modern humans in the different regions of the Old World supports the African replacement model, the (African) hybridization and replacement model, and the assimilation model, but not the multiregional evolution model.

Evidence for the occurrence of gene flow between modern humans and nonmodern hominins

The four models of modern human origins we have been discussing make markedly different predictions about the existence and nature of evidence for gene flow between modern humans and nonmodern hominins. The African replacement model contends

that if modern human encountered nonmodern hominin populations as they expanded out of Africa they would have interbred with them sufficiently rarely that the modern human gene pool is numerically dominated by genes derived from populations that lived in Africa at 150 ka, and contains an insignificant number of genes from populations that lived outside of Africa at that time. The African replacement model therefore predicts that there should be little or no evidence for hybridization between modern humans and nonmodern hominins outside of Africa. The (African) hybridization and replacement model holds that hybridization occurred sufficiently frequently that while genes derived from populations that lived in Africa at 150 ka dominate the modern human gene pool, it also contains a significant number of genes from populations that lived outside of Africa at that time. Thus, the (African) hybridization and replacement model predicts that there should be evidence for a small but significant amount of hybridization between modern humans and nonmodern hominins outside of Africa. The assimilation model and the multiregional evolution model both deny the occurrence of a major out of Africa migration during the Late Pleistocene, and argue instead that modern human genes spread via gene flow. As such, they predict much more extensive interbreeding between modern humans and nonmodern hominins in Europe, Asia, and Australasia than either the African replacement model or the (African) hybridization and replacement model. Where the assimilation model and the multiregional evolution differ is in their expectations regarding the nature of the gene flow. The assimilation model predicts that the majority of derived modern human genes spread from Africa after 150 ka, whereas the multiregional model predicts that different modern human genes spread from different regions of the world at different times over the last two million years.

Traditionally, palaeoanthropologists have relied on comparisons of qualitative skeletal characters recorded on modern human and nonhuman hominin specimens from Europe, Asia, and Australasia to investigate whether gene flow occurred between modern humans and nonmodern hominins (e.g., Wolpoff et al., 1984; Stringer and Andrews, 1988; Wolpoff, 1989, 2001; Frayer et al., 1993; Lahr, 1994; Duarte et al., 1999; Hawks et al., 2000; Bräuer et al., 2004). However, this approach has not been particularly successful. Indeed, we know of no case in which a qualitative skeletal character has been accepted as unambiguous evidence of gene flow between modern humans and nonmodern hominins. Instead, every time a character has been argued to be shared between a modern human population and a nonmodern hominin taxon in a given region as a consequence of gene flow, other researchers have countered that the character in question is not informative with regard to gene flow either because it is a retention from the last common ancestor of modern humans and the nonmodern hominin taxon or because it is not homologous, and the character's status as an indicator of gene flow has ended up being a matter of preference. Authors who favor the multiregional evolution model or the assimilation model typically view the character as evidence of gene flow, while authors who favor the (African) hybridization and replacement model or the African replacement model tend to view it as a symplesiomorphy or a homoplasy.

Fortunately, the traditional approach has been supplemented by other, less subjective approaches in recent years. One of these approaches involves the use of quantitative data derived from the crania to assess the degree of morphological and by extension genetic difference between modern humans and nonmodern hominins.

Some of these studies have compared the degree of divergence between modern humans and Neanderthals with the degree of divergence among modern human populations (Turbón et al., 1997), while others have compared the level of divergence between modern humans and Neanderthals with the level of divergence between nonhuman primate species (Schillaci and Froehlich, 2001; Havarti, 2003; Havarti et al., 2004). The rationale for the latter approach is that, if the level of divergence between modern humans and Neanderthals is as great or greater than the level of divergence between the nonhuman primate species, then modern humans and Neanderthals are likely to have been reproductively isolated from one another and therefore should be considered to be separate species. The results of these studies are remarkably consistent. Turbón et al.'s (1997) analyses of data derived from 25 facial measurements separated Neanderthals not only from recent modern humans but also from the 90–100,000-year-old modern human specimens from the sites of Skhul and Qafzeh in Israel. Schillaci and Froehlich's (2001) analysis of ten craniometric variables indicated that the differences between Neanderthals and Pleistocene modern humans are significantly greater than the differences between macaque species that do not hybridize in the wild. Subsequently, Havarti (2003) analyzed three-dimensional (3D) craniometric data from modern humans, Neanderthals, chimpanzees, and bonobos, and found that modern humans and Neanderthals are more different than chimpanzees and bonobos, which are widely considered to be distinct species. More recently still, Havarti and colleagues (2004) have shown that 3D craniometric differences between modern humans and Neanderthals exceed those observed between conspecifics in ten catarrhine nonhuman primate species. Thus, the craniometric assessments of the degree of morphological and genetic divergence between modern humans and Neanderthals suggest that they are not simply distinct from one another but distinct enough to be considered different, reproductively isolated species. One implication of this is that gene flow between modern humans and Neanderthals would have been limited, if it occurred at all.

The development of techniques for extracting DNA from fossil remains over the last 20 years has also provided a more objective means of assessing the extent to which modern humans and nonmodern hominins interbred. To date, most of the ancient DNA work on fossil hominins has focused on the relationship between modern humans and the Neanderthals (e.g., Krings et al., 1997; Serre et al., 2004). Some of these studies suggest that there was no interbreeding between modern humans and Neanderthals. In the first study of fossil hominin ancient DNA, for example, Krings et al. (1997) found no evidence of interbreeding between Neanderthals and the ancestors of any modern human population in the portion of mitochondrial DNA (mtDNA) control region known as the hypervariable region I. All of the modern human sequences in their sample were more closely related to one another than any of them was to the Neanderthal sequence. Similar results have been obtained by Ovchinnikov et al. (2000), Lalueza-Fox et al. (2006), Orlando et al. (2006), and Krause et al. (2007) in analyses employing additional Neanderthal mtDNA sequences. Early analyses of Neanderthal nuclear DNA (nDNA) also did found no evidence that Neanderthals interbred with modern humans (Noonan et al., 2006). However, more recent analyses based on the first full draft of the Neanderthal genome have yielded evidence of a Neanderthal genetic contribution to European, East Asian, and Australasian modern human populations ranging from 1 percent to 4 percent (Green et al., 2010).

A similar pattern of results has been obtained in analyses of mtDNA and nDNA obtained from unattributed fossil hominin specimens from Denisova Cave in Siberia. The mtDNA data indicate that the Denisova specimens are distinct from both modern humans and Neanderthals (Krause et al., 2010), while the nDNA data suggest that the population represented by the Denisova specimens contributed 4–6 percent of their nuclear genes to the genomes of Australasian modern humans (Reich et al., 2010). At first glance, the results of the mtDNA and nDNA analyses appear difficult to reconcile with respect to the question of whether modern humans interbred with nonmodern hominins. However, Currat and Excoffier (2011) have recently shown with the aid of spatially explicit simulations that the absence of evidence of mtDNA introgression from Neanderthals to modern humans and the 1–4 percent level of Neanderthal to modern human nDNA introgression that has been inferred from the full draft of the Neanderthal genome imply the existence of very strong barriers to gene flow between Neanderthals and modern humans.

In sum, then, the available evidence suggests that there was some gene flow between modern humans and nonmodern hominins in Europe, Asia, and Australasia, but it was limited. This is incompatible with the multiregional evolution model and the assimilation model, both of which posit the existence of extensive gene flow between modern humans and nonmodern hominins. At the moment, it is not clear whether the evidence pertaining to gene flow is most compatible with the African replacement model or the (African) hybridization and replacement model. It depends on whether the small amount of introgression from the Neanderthals and Denisovans to modern humans is significant. Further work will be required to determine this.

CONCLUSIONS

Progress in paleoanthropology requires not only additional fossils and new analytical techniques but also improved theory. The modern human origins debate illustrates this clearly, we think. In the last 20 years, the amount of fossil evidence pertaining to modern human origins has increased substantially and so has the range of analytical techniques available to researchers. Yet, the level of disagreement among specialists has not declined appreciably. All sides in the debate have claimed that the new data support their position. An important reason for this confusing state of affairs, we suspect, is that insufficient attention has been paid to the theories of modern human origins, and especially to what distinguishes them from each other and what they predict in relation to a given analysis. With this in mind, in first part of the present chapter we analyzed the four models that we think need to be taken into account when discussing modern human origins and sought to characterize them in such a way that their differences are clear. Subsequently, we examined how consistent the available anatomical, genetic, and linguistic evidence is with the predictions of the models.

Clarifying the differences among the models and paying close attention to their predictions lead to two important conclusions regarding the modern human origins debate. The first is that one of the main issues that researchers have investigated in an effort to shed light on modern human origins – the structure of living human anatomical, genetic, and linguistic variation – is not informative regarding which of the

models is most likely correct. The reason for this is that the models' predictions concerning the structure of living human variation are not different. The second conclusion is that, contrary to the impression given by the recent literature on the topic, it is possible to choose among the models of modern human origins. The available evidence pertaining to the other main issues that researchers have investigated in an effort to shed light on modern human origins – the timing of the appearance of modern humans, and evidence for the occurrence of gene flow between modern humans and nonmodern hominins – are clearly consistent with the predictions of the African replacement and the African hybridization and replacement models, and equally clearly inconsistent with the predictions of the multiregional evolution and assimilation models.

NOTES

1 All dates are given as ka (thousands of years before the present).
2 We use the term "nonmodern hominin" rather than "premodern hominin" because, unlike "premodern hominin", it does not imply anything about such a hominin's phylogenetic relationship to modern humans, or its temporal distribution compared to that of modern humans.

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