

Statistical and Biological Definitions of “Anatomically Modern” Humans: Suggestions for a Unified Approach to Modern Morphology

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Much of the recent literature on the origin of modern humans has been plagued by an inability of the participants in the debate to agree on what constitutes “anatomically modern” morphology. An upshot of this disagreement has been an ongoing set of debates over which specimens are or are not anatomically modern and whether various fossil specimens such as the Florisbad cranium, Vindija Neanderthals, Klasies River Mouth mandibles, or Skhul-Qafzeh hominins, all of which arguably possess some supposedly “modern” traits, qualify as genuinely “modern.” Such decisions frequently have implications with regard to how we reconstruct later hominin phylogenies and, ultimately, how we reconstruct the behaviors, adaptations, and evolution of Middle-Late Pleistocene African hominins and their contemporaries.

Over the last two decades, two basic approaches toward definitions of “anatomically modern” morphology have dominated the literature. I term these statistical and biological approaches, but the two are often explicitly or implicitly related. Further elaboration of the theoretical nature of these associations and their implications offers a way forward from the current disagreements.

STATISTICAL APPROACHES

A set of measurements and proportions can be used to define anatomically modern humans. Day and Stringer^{1,2} proposed the most influential formulation of this approach (Table 1). They noted that the crania of most living humans and “modern” fossil individuals share a short, high vault; a long, high parietal arch that expands in length superiorly; a high, fairly vertical frontal bone; and a gently curved rather than angled occipital bone. These morphological features continue to figure prominently in more recent appraisals of cranial vault globularity,^{3,4} which emphasize the developmental roots and morphological integration of these dimensions. This approach to globularity fits among the “biological” definitions of modernity and demonstrates that “statistical” and “biological” definitions are partially related. Day and Stringer¹ stipulated that these characters “are expected to be present in more than 75% of samples” (p. 844) to be considered

anatomically modern. Wolpoff⁵ subsequently challenged this list of characteristics, noting that the crania of some populations of recent humans, such as Australian Aborigines, would not qualify as “anatomically modern” by the criteria.

By 1984, these metrical and discrete traits had been conceptualized as a set of derived features that could be used to define modern humans in a cladistic framework and to separate them from *H. erectus* or Neanderthals.⁶ This work built upon slightly earlier efforts to define cladistic features of modern humans and Neanderthals.^{7–9} More recent work by Schwartz and Tattersall^{10–14} has identified additional features that may be useful in diagnosing crania of “anatomically modern” humans (Table 2). Additional work by Lahr,^{15–17} Habgood,^{18–21} Groves,²² and Lieberman²³ has tested to the extent to which some of the discrete or metrical features that have been argued to provide evidence of multiregional evolution actually support that mode of evolution. Lahr and Wright²⁴ investigated the extent to which these “regional features” covary with patterns of metrical variation in recent human crania.

The lists of metrical characteristics and discrete features that have been proposed to define “anatomically modern” morphology in cladistic analyses are certainly useful in a heuristic sense but, as Wolpoff⁵ demonstrated, they can entail problems when applied to some recent populations. These features and proportions run into more even problems when applied to the earliest candidates for

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TABLE 1. Day and Stringer's (1982) Cranial Dimensions of "Anatomically Modern" Humans^a

1) Basio-bregma height/Glabello-occipital length (BBH/GOL) > 0.70 or BBH/GOL > Vertex radius/Glabello-occipital length (VRR/GOL)
2) Parietal angle (PAA) < 138°
3) Bregma-asterion chord/Biasterionic breadth (BAC/ASB) > 1.19
4) Frontal angle (FRA) < 133°
5) Supraorbital torus weakly developed and torus clearly divided into medial and lateral segments
6) Occipital angle (OCA) > 114°
7) Chin present
8) Limb bones have thin cortical bone and relatively small articular surfaces

^a All measurements defined by Howells.⁴³

"anatomically modern" humans such as the 195,000-year-old Omo Kibish specimens, the Herto crania, or the fossils from Skhul and Qafzeh. Most of these "modern-like" or "near modern" crania do not have the full set, or sometimes even 75%, of the "modern" features. Schwartz and Tattersall's (Table 2) cladistic diagnosis of anatomically modern *Homo sapiens* excludes many of the 100,000-year-old and older candidates for the earliest modern humans. By Schwartz and Tattersall's criteria, none of the Skhul specimens has a truly human chin; neither does Qafzeh 7, Tabun C2, the juvenile specimen Qafzeh 4, or KRM 13400 or 14695 from the Middle Stone Age of South Africa. On the other hand, Schwartz and Tattersall¹² consider Qafzeh 8, 9, and 11, as well as KRM 41815, to have all the components of a chin, as do the much earlier North African specimens of Tighenif 1, 2, and 3, which are generally attributed to *Homo erectus*. Schwartz and Tattersall¹³ describe Omo Kibish 1 and the juvenile mandible Jebel Irhoud 3 as not possessing a true chin. From my personal observation, Omo Kibish 1 has a mental eminence closely resembling that of KRM 41815, the mandible that has the most projecting chin at Klasies River Mouth.²⁵ Perhaps an explanation for these different appraisals lies in the fact that such qualitative judgments always entail a degree of subjectivity and may contain more interobserver error than one might wish.

A second important and nearly ubiquitous finding of multivariate studies of cranial variation in recent and fossil humans is that Pleistocene specimens, including early modern

or nearly modern humans, generally fall outside of the clusters of recent human crania.^{26–35} Middle and early Upper Pleistocene fossils are almost always widely separated in multivariate space from recent populations. The same often applies to postcranial remains of equivalent age.^{36–38}

Figure 1 provides one example of this finding. The figure shows the results of a canonical variates analysis (CVA) on the dimensions of the 160,000-year-old Herto cranium (from the supplementary information of White and colleagues³⁹) versus Howells' males from Teita, East Africa and Mokapu, Hawaii.⁴⁰ The Herto cranium was treated as the mean of "population," a procedure that allows the cranium to express its uniqueness, but that also conflates individual, within-population variation with between-population variation. This statistical effect often tends to make a "population" that is represented by a single specimen appear to be more distinct from the recent populations than was the case for the ancient population from which it was drawn. The measurements suffice to produce complete separation between the groups. Examination of the eigen vectors from the CVA reveals that the great cranial length of the Herto cranium accounts for almost all of its distinctiveness from the recent populations on Axis 2.

Despite the great distances that separate "early modern" crania from recent people, analyses that include a variety of specimens from different geographical locations and times in the late Middle-Upper Pleistocene have produced additional interesting

results, including the fact that European and, to a lesser extent, Near Eastern Neanderthals fall even more distantly from recent humans than do the "early moderns."^{27,29,35,41,42}

Another extremely interesting finding was reported by Stringer,⁴² who calculated Penrose shape distances among several groups of later *Homo* including European Neanderthals, Near Eastern Neanderthals, African late Middle Pleistocene crania (Ngaloba, Jebel Irhoud 1 and 2, Eliye Springs, Singa, and Omo 2), late Middle Pleistocene Chinese crania (Mapa and Dali), Skhul-Qafzeh hominins, and a variety of more recent human groups. Stringer used a subset of 25 of Howells' measurements⁴³ that could be taken on one or more specimens in each of the fossil groups. In common with many other analyses, he found that the African late Middle Pleistocene hominins

TABLE 2. Proposed Cladistic Features of "Anatomically Modern" Skulls^a

Apparent cranial apomorphies of <i>Homo sapiens</i>
• Extension of the tall, thin vaginal or petrous process to the lateral margin of the ectotympanic tube
• Approximation of the vaginal process to the mastoid process
• Extreme lateral placement of the styloid process, with the stylomastoid foramen lying posteromedially at its base
• Narrow, high occipital plane of the occipital bone
• Retention into the adult of a discernible arcuate eminence
• Fully segmented cranial sutures, with some segments deeply interdigitated
• A bipartite supraorbital region
• Symphyseal region of the mandible as seen from below thicker than the corpora on either side
• The uniquely structured chin in the shape of an inverted T
• A subarcuate fossa that is not closed off
• An inferior orbital plane that tilts down and back from the inferior orbital margin

^a This table reproduces a tentative list of cranial apomorphies of *Homo sapiens sensu stricto* circulated at the conference by Dr. Ian Tattersall.

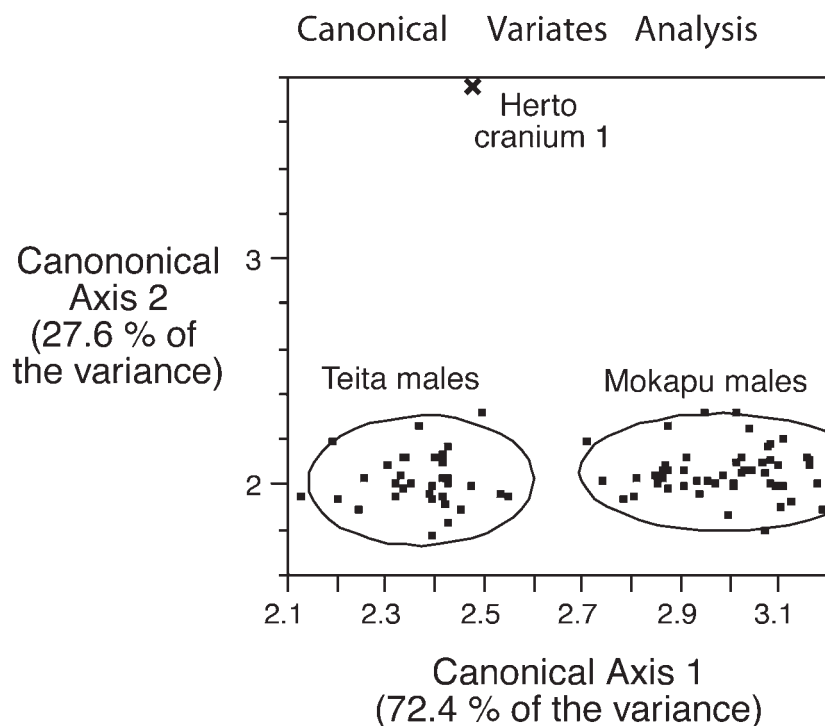


Figure 1. CVA of Herto 1 versus Howells⁴⁰ samples of Teita and Mokapu males. A total of 17 cranial variables (GOL, BNL, BBH, XCB AUB, BPL, NPH, NLH, JUB, NLB, OBH, OBB, DKB, EKB, FRC, PAC, OCC) were used in the analysis. See Howells⁴³ for variable definitions.

were closer to the Skhul-Qafzeh group than were Neanderthals. However, he also found that the Dali-Mapa “group” was only marginally more distant from Skhul-Qafzeh than was the contemporaneous group of African crania. Furthermore, the African and Asian samples of late Middle Pleistocene crania were separated by only a very small shape distance that was similar in size to the shape distances between many of Howells’ groups of recent human crania.

A variety of explanations for this finding have been tendered, including that late Middle Pleistocene gene flow from Asian hominins may have been a key ingredient in the origin of modern humans^{44,45} or that multiple dispersals of hominins brought new genes and morphology to Asia, whether or not admixture with earlier inhabitants also occurred.^{46–51} More work is clearly needed to test these competing hypotheses for the observed pattern of shape distances.

Returning to the issue of the implications for definitions of “anatomically modern” humans, the large dis-

tances between “early moderns” such as the Skhul-Qafzeh hominins and the Herto cranium and recent humans clearly indicate that the fossil specimens are morphologically distinguishable from recent people. However, opinions differ widely on what taxonomic importance (for example, subspecific or specific) these kinds of multivariate distances should be given. Similar debates arise regarding the issue of what the great distances between recent humans and Neanderthals mean for phylogeny.^{52–54} With respect to definitions of “anatomically modern” morphology, an important development was Kidder and colleagues’ proposal³³ that any cranium that could be distinguished metrically at $p < 0.05$ from Howells’ large sample of recent human crania should not be considered “anatomically modern.” In essence, Kidder and colleagues advocated a statistical criterion to operationalize the phylogenetic species concept,⁵⁵ which defines a taxon as a minimum diagnosable unit of organisms.

Application of this criterion led Kidder and colleagues³³ to classify almost all early Upper Pleistocene crania as outside the 95% range of variation in modern humans. Of the putative specimens of early “anatomically modern” humans, only Qafzeh 9 clearly fell within the 95% range of recent humans. Jebel Irhoud 1 also consistently fell outside the 95% range, as did all Neanderthals except Saccopastore 1. In some analyses, a substantial percentage of large and rugged Mesolithic European crania from the site of Ofnet also fell outside of the 95% envelope of recent humans, as did most crania of Upper Paleolithic Europeans.

Kidder and colleagues’ approach has the advantage of proposing a rigorous definition but, from the standpoint of trying to understand the dynamics within an evolving lineage, the simple modern versus nonmodern dichotomy that it offers may be an overly blunt instrument that is of limited utility for producing phylogenetic hypotheses. Wider-ranging phenetic analyses^{17,26,27,29,42} are more flexible and subtle instruments for exploring patterns of phenotypic relationships. Nevertheless, this and other forms of phenetic analysis do not separate homoplasies from synapomorphies, although several authors^{17,26,43,56,57} have made judicious attempts to use metrical data to untangle primitive and derived cranial morphology. Clearly, the phenotypes of the first “anatomically modern humans” differed from those of living people; it remains difficult to decide what phylogenetic significance, if any, that observation should have.

There are many reasons why a 100,000-year-old cranium may differ statistically from 95% of the crania of a recent population. These reasons may include microevolutionary changes and the possibility that quite disparate environmental influences on growth and development acted during the two time periods. Although it is likely that only some of those reasons for the statistical differences are important in a phylogenetic sense, most of them have the potential to provide insights into morphological change. Ideally, one would like to partition morphological

distance into differences due to genetic drift, adaptation, and environmental interactions with ontogeny. Recently, several promising studies have shed light on these issues, including work on the amount of morphological diversity in recent humans that likely reflects genetic drift⁵⁸⁻⁶⁰ and the effects of the toughness of foods on the cranial morphology and occlusion of non-human primates,^{61,62} retrognathic mammals (for example, hyraxes⁶³), and humans from different parts of the world.⁶⁴⁻⁶⁷ Nevertheless, much remains to be done before these relationships become completely clear.

BIOLOGICAL APPROACHES

The second major theoretical approach to defining "anatomically modern" morphology has focused on the developmental processes that produce key differences in cranial morphology between recent people and Middle Pleistocene hominins or between humans and chimpanzees. Many of the proponents of these models stress that one or, at most, a few key changes in growth and development produced modern cranial morphology. Lieberman,^{3,4,68} Krovitz,⁶⁹ Ackermann,^{52,70,71} Williams,⁷² Ponce de León and Zollikofer,⁷³⁻⁷⁶ and Mitteroecker and colleagues⁷⁷ have been prominent recent advocates of this approach, but it is rooted in previous work.⁷⁸⁻⁸¹

Much of the early work on cranial ontogeny in archaic *Homo* focused on contrasts between anatomically modern children and Neanderthals, the best-known group of premodern *Homo*.⁸²⁻⁸⁵ Recent work has increasingly focused on the evolution of hominin life history and the pattern and rate of dental and cranial development in archaic humans in comparison to those in recent human children.⁸⁶⁻⁹⁰

One key finding from this research is that a modern life history evolved surprisingly late, possibly with the origin of modern humans^{81,86,87,91} or in the common ancestor of modern humans and Neanderthals^{88,89}; another is that modern human and Neanderthal crania grow in very similar ways from two years of age onward,

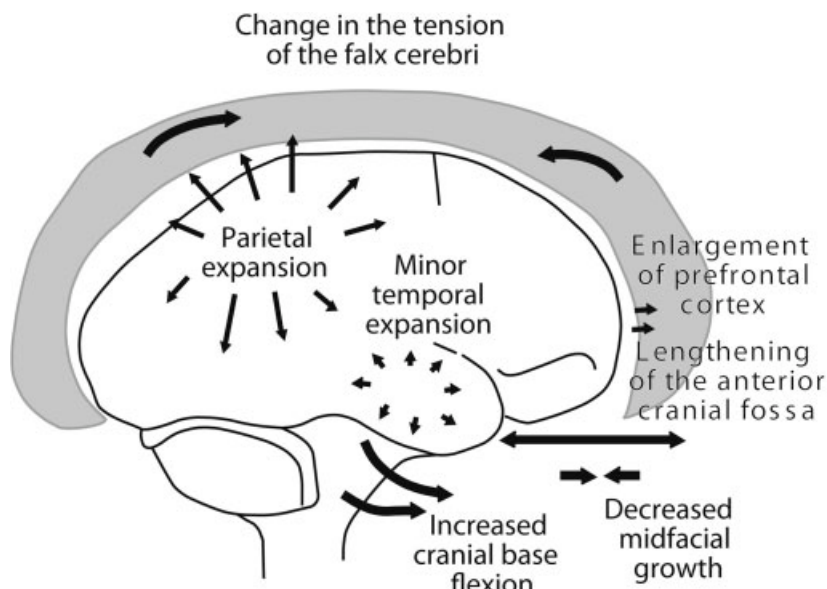


Figure 2. Hypotheses of changes in cranial or brain growth that produced modern morphology.

and quite possibly from birth on.^{69,73,76} Some studies report a faster rate of cranial growth in Neanderthal children, but the pattern of cranial growth is basically similar.^{73,74} Indeed, a similar pattern of growth appears also to characterize australopiths and African apes, whose growth departs from this pattern in comparatively minor ways.^{70,71,77} It is thus quite likely that the archaic African predecessors of modern humans shared the same pattern. Almost all of the differences in proportions that distinguish modern humans from archaic *Homo* may have been established prenatally,⁷⁶ but see McBratney-Owen and Lieberman's⁹² discussion of some of the limitations in this interpretation.

The likelihood that the key morphological differences develop prenatally poses new difficulties for the study of the fossil record because bony remains from this phase of ontogeny are very rarely preserved. The way forward may be to gain a much better understanding of the variability of prenatal growth in modern children, as well as the genetic and epigenetic control of the process. These areas of study are still in their early stages,⁹³ especially with respect to nonpathological variation in morphogenesis.

Despite these difficulties, differences between adult modern and archaic humans can be discerned easily. Various hypotheses have been advanced regarding the growth-related processes that may produce these differences (Fig. 2). A shared challenge for all of these hypotheses is to design nontautological tests of them, something for which the fossil record may be quite useful. All of the novel morphological features related to these proposed ontogenetic changes co-occur in living humans, along with everything else we think to be unique about our species. It can be tempting to suppose that their co-occurrence may mean that they are causally or developmentally intertwined so that they *must* co-occur in *Homo*. This proposition may or may not be the case. The fossil record offers a way to test these kinds of hypotheses either by the direct study of early ontogenetic stages of ancient groups like the Neanderthals or by the study of premodern adults whose morphology can be scrutinized to see if it conforms to ontogenetically based expectations about the interrelationships of the parts of the cranium.

The first type of developmental hypothesis might be termed a "brain-first" hypothesis for its emphasis on

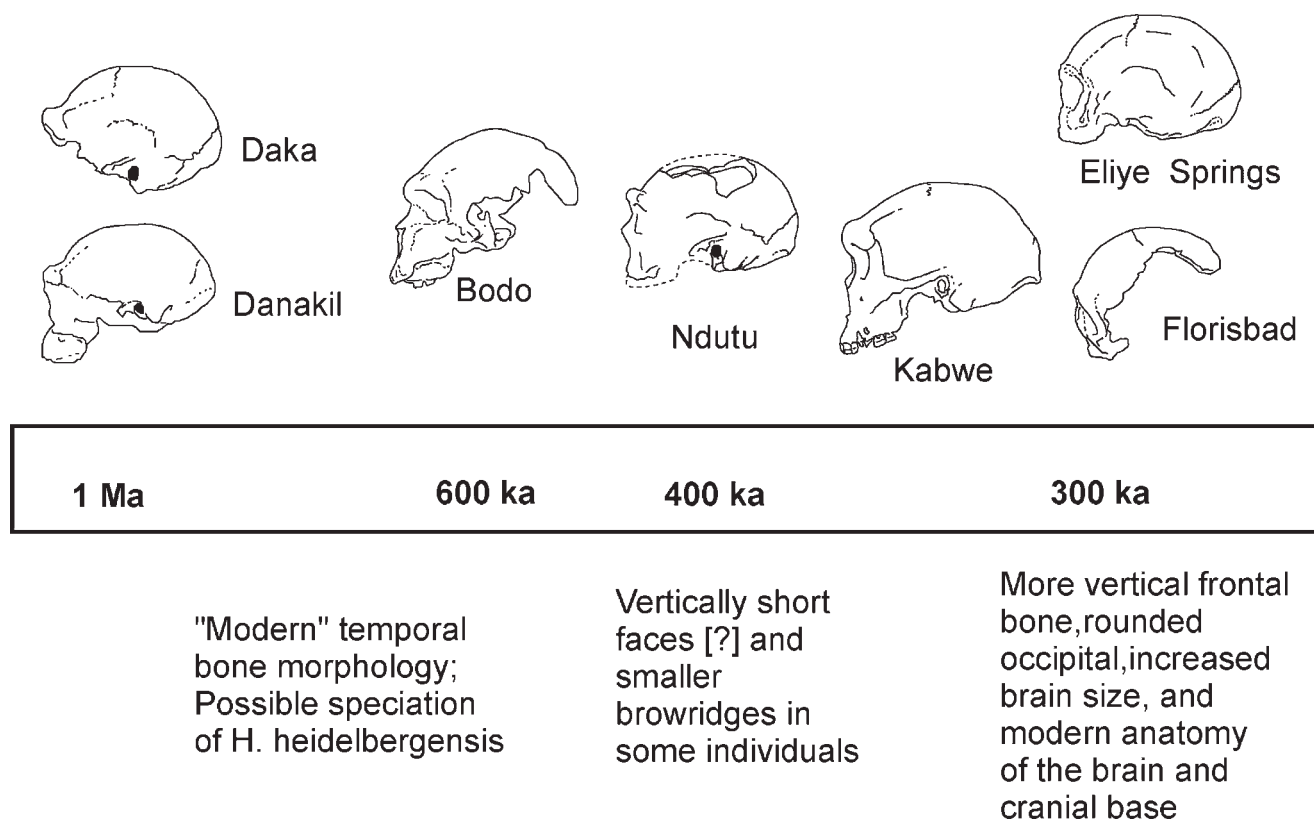


Figure 3. The process of becoming modern. As in de Queiroz's¹⁴ unified concept of speciation, different criteria for what defines "anatomically modern" morphology appear sequentially.

changes in brain size and proportions, frequently depicting brain expansion as the most probable source of influences or constraints that acted to necessitate other morphological changes. A recent example comes from Bruner's^{94,95} studies of the morphometrics of modern and archaic brains. Bruner's studies demonstrate that modern humans and archaic humans, including *H. heidelbergensis* and the larger-brained Neanderthals, did not undergo completely homologous expansion of the different parts of the brain as brain size increased. In particular, Bruner found that modern humans had a species-specific (autapomorphic) expansion of the volume of the parietal lobe.⁹⁵ He speculated that this expansion of the parietal lobe caused dorsal growth and ventral flexion of the brain and, ultimately, a more globular cranium. Alteration of the growth of the brain provides the prime mover in this view of the origin of modern cranial form (see Fig. 2). It

should be noted, however, that such "brain-first" hypotheses acknowledge that changes in other components of the cranial fossa, especially changes in the amount of tension in the falx cerebri, may have interacted with increasing brain size or altered brain proportions to influence the globularity of the cranium.⁹⁵

Other work contradicts Bruner's study, instead finding in comparisons of human and primate brains that only the temporal lobe is larger than expected from patterns of allometric scaling in great apes' brains.⁹⁶⁻¹⁰⁰ Although scenarios for brain change involving the size or proportions of lobes other than the temporal now have a dubious status, brain-centered views of what made humans modern have an added attraction of simultaneously providing an explanation for the change in morphology and offering a possible neurological correlate of some of the cognitive changes, including, perhaps, the final refinement of fully modern language, that

many (but not all) researchers think accompanied the evolution in cranial form.

Other developmental hypotheses for the origin of modern cranial morphology have focused on additional aspects of cranial growth, postulating a few key developmental shifts.^{3,4,69-76,101} These studies admit that an increase in brain size during the Middle Pleistocene may have also been an important factor that necessitated some additional alterations in cranial architecture. Lieberman and colleagues^{3,4} described the primary developmental shifts that distinguish "modern" crania from archaic specimens: (1) a more globular cranial vault in the sagittal, coronal, and transverse planes; (2) reduced facial projection linked with a more flexed cranial base and a longer anterior cranial fossa; and (3) a more clearly developed canine fossa. Cranial globularity is hypothesized to develop from an interaction among brain size, cranial base length and width,

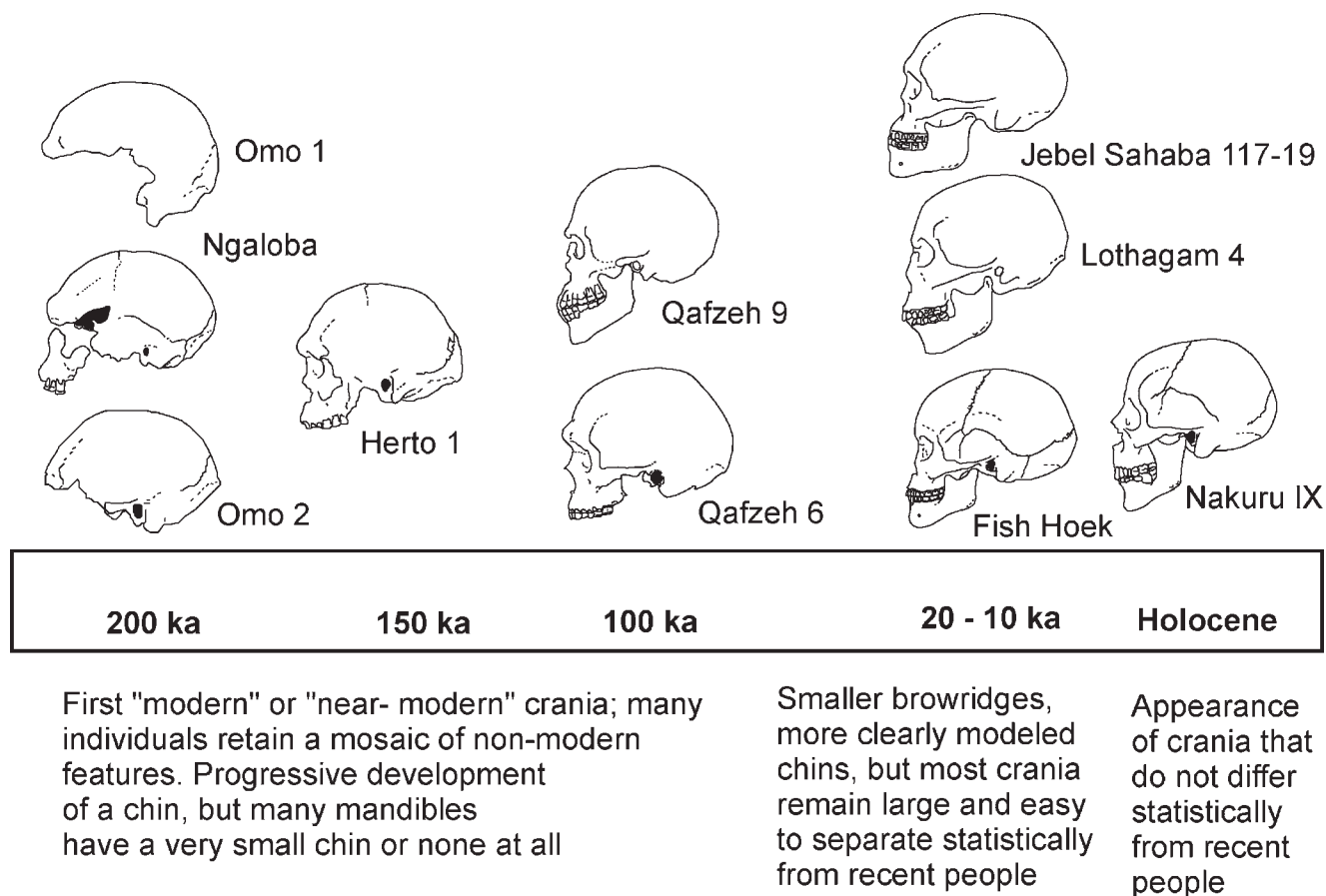


Figure 3. (Continued)

and cranial base angle, which also correlates with facial size.^{3,4,101}

The fossil record also allows us to test, at least partially, hypotheses about morphological integration.^{4,102-104} In the case of the derived features that we can use to distinguish *Homo sapiens sensu stricto* from ca. 1-Ma-old specimens of African *Homo erectus*, Figure 3 shows that the entire suite of characters does not appear as a unified set. It should be noted that Lieberman and colleagues^{3,4} have never claimed that the features evolved in unison, only that they now characterize modern humans and any specimens in the fossil record that can be considered modern. Instead of appearing as a set, these features appeared in the fossil record gradually and in a mosaic fashion. It is highly unlikely, therefore, that the entire suite of features *must* co-occur in the process of development. However, it remains possible that the evolution or ontogeny of later-appearing

traits depended on the evolution of the earlier-appearing traits, and thus may be heavily dependent on one another. This possibility is more difficult to test, but might be amenable to study in 400,000–100,000-year old specimens with mosaics of modern and archaic traits. With regard to the pattern of co-occurrence, however, it is worthwhile to ask how tightly integrated over evolutionary time were the smaller set of features, such as cranial globularity and a vertically short and nonprojecting face, that plausibly stem from developmental shifts.

Gobularity in the transverse plane (that is, brachycephalization) is a recent phenomenon that has accelerated in Holocene populations.¹⁰⁵ Along with a general reduction in overall cranial size, brachycephalization is one of the features that acts to make the crania of the vast majority of living humans highly different, in a statistical sense, from those of

early modern humans from 100,000 or 25,000 years ago. A better case can be made that sagittal and coronal globularity are causally linked because their degree of expression is better correlated in the fossil record.

The fossil record is also informative about the co-evolution of a flexed cranial base; a retracted, vertically short face; a weakly projecting browridge; and a long anterior cranial fossa. A vertically short face may have appeared first (for example, Steinheim, Dali) but the penecontemporaneous specimen Eliye Springs has both a vertically short face and a degree of cranial base flexion that actually exceeds that of modern humans.¹⁰⁶ Eliye Springs has pathological changes of unknown etiology¹⁰⁷ that produced a very thickened vault and may have altered other aspects of its morphology, but Steinheim and Dali are not similarly affected. It is difficult to know how much of this pattern of

decrease in facial size is related to sexual dimorphism in ~300,000–200,000-year-old specimens of *Homo*. Likewise, it has not yet been possible to measure the antero-posterior projection of the face in these early, vertically short-faced specimens, but it is quite possible that the damaged face of Eliye Springs had an antero-posteriorly long face that differs from that of modern humans. In addition, Eliye Springs has a notably antero-posteriorly short anterior cranial fossa.¹⁰⁶ If Eliye Springs is a good guide to the association of these basicranial and facial features, which should be tested rather than assumed, especially given its pathology, this fossil may indicate that a flexed cranial base and vertically short face evolved before a globular cranial form, an antero-posteriorly short face, or an elongated anterior cranial fossa. If so, it is likely that the modern suite of features stems from different or perhaps additive ontogenetic shifts.

Arguably, as an artifact of the history of discovery of fossil specimens,¹⁰⁸ the presence of a canine fossa had, by the early 1980s, become one of the derived traits used to characterize modern morphology.^{1,2,6} This practice now appears to be inaccurate. A well-developed canine fossa appears in the 800,000-year-old *H. antecessor* juvenile,¹⁰⁹ some *H. heidelbergensis* specimens from Sima de los Huesos,¹¹⁰ and the second, smaller adult maxilla from Broken Hill.¹¹¹ Thus, development of a canine fossa appears to be a very old trait in archaic *Homo*. Interestingly, canine fossae also seem to be more prevalent in smaller adult faces (for example, Steinheim, Dali, and Florisbad) and juveniles. However, a canine fossa is rarely present in larger, presumably male crania such as Bodo, Kabwe, Sima de los Huesos 5, and Petralona, which have heavily influenced conceptions of the morphology of *Homo heidelbergensis*.¹¹²

Empirically, the presence of a canine fossa does not depend on the presence of a globular cranial vault. Canine fossae may also occur in conjunction with highly projecting brow-ridges, as in Steinheim and Dali, so those two features are unlikely to

be developmentally or functionally linked. An association between the presence of canine fossae and a flexed cranial base and long anterior cranial fossa is much more difficult to test. Nevertheless, an association between canine fossae and vertically short faces, whether in small adults or juveniles, is present in the fossil record, but not uniformly. For example, juvenile Neanderthals have small faces without canine fossae.^{82,113} In sum, the development of a canine fossa does not seem to result directly from the presence of any one of the features that define modern crania

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and thus is less likely to be a functional or developmental byproduct of the other shifts. Its association with a vertically short, wide face *may* have a functional or developmental basis, but this hypothesis should be tested further.

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and Schwartz’s cladistic approach or fall outside of a confidence region containing 95% of more recent crania. These paradigmatic differences have resulted in the current disagreements about how to define “anatomically modern” morphology.

INTEGRATION

Perhaps the evolution of modern humans should be viewed as a process rather than as an event, although it may have involved one or more periods of rapid morphological change due to drift during population bottlenecks, selection for new, advantageous traits or genes, or some combination of the two. De Queiroz¹¹⁴ has proposed a philosophically useful view of speciation as just such a process, during which various criteria for what constitutes a “species” differentiate the members of an evolving lineage from its closest living relatives. According to that model, early in the divergence of populations that will become different species, separation usually occurs, followed in turn (but not always in the same order) by the establishment of criteria needed to identify species according to differing definitions: establishment of a given level of average phenetic or genetic difference, establishment of diagnosability (which de Queiroz¹¹⁴ considers one or more fixed differences), development of different apomorphies, selection against hybrid individuals, the establishment of differing mate recognition systems, reproductive isolation, and ultimately a complete lack of viability of hybrids. Given enough time, all of the criteria will eventually apply to two lineages that have diverged.

De Queiroz’s insight can be applied to the *process* of the origin of “anatomically modern” morphology and the origin of modern humans in Africa, whether or not that process involved speciation. As shown in Figure 3, the process of becoming “modern” likely occurred as a series of steps, regardless of whether one considers these different steps to be different taxa in a bushy phylogeny or merely different grades in a single evolving lineage. At different points in this process, different criteria for

what defines an "anatomically modern" skull would allow one to diagnose some or all of the specimens from a given segment of time or in a given clade as "anatomically modern."

Study of the order in which "modern" traits appear is also highly useful because it can allow preliminary tests of hypotheses about how the various features are integrated. Unfortunately, aside from the Herto and Jebel Irhoud juveniles, the fossil record for the period in Africa is largely restricted to adults. However, as adult morphology results from ontogeny, the study of the co-occurrence of features in adults can yield at least some insights into the underlying process of growth and development, or at least lead to more informed hypotheses about those processes.

With respect to the various morphological features that can be used to define modern humans, perhaps the initial changes are an increase in the brain size of African *H. erectus* between 1.0 Ma and 600 ka, and the evolution of "modern" temporal bone morphology^{8,9} during the same interval. Vertically shorter faces appear in at least some individuals by 400–300 ka; these faces include Ndutu, the second maxilla from Kabwe (if it is genuinely this old), Eliye Springs, KNM-ER 3884,¹¹⁵ and Florisbad.^{28,115,116} Between 400 and 300 ka, there appears to have been a continued but probably slow expansion in brain size and a reduction in facial size.

Evolution of crania that display the "modern" apomorphies of a more globular cranial vault, flexed cranial base, enlarged middle cranial fossa, lengthened anterior cranial fossa, and antero-posteriorly short midface^{3,4,92} occurs by 200 ka. Evolution of more pronounced mental eminences, some of which obtain the morphological condition described by Schwartz and Tattersall¹² as an inverted T, first appear between 200–100 ka, but may date back to the Middle Pleistocene *H. erectus* specimens from Tighenif. Even at 100 ka, however, many "modern" or "near-modern"¹¹⁷ mandibles in Africa and the Levant have weakly developed

chins; the feature clearly continued to become more prominent and more common in humans between 100 ka and ca 20 ka.

In Africa, there is a long gap in the hominin fossil record between ca 80–20 ka, from which few specimens are known. The exceptions are Taramsa Hill¹¹⁸ and Hofmeyr.¹¹⁹ This gap in the fossil record is unfortunate, causing us to have almost no insights into the process of morphological diversification of anatomically human populations in Africa. After

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the gap, it is clear that several morphologically distinguishable populations existed within Africa. In common with many other parts of the world,^{26,30,32,33} crania that have dimensions or suites of morphological traits that make them statistically indistinguishable from the living populations appear only during the Holocene.^{18,30,31,120–129}

Holocene crania tend to be smaller and less ruggedly built than are their Pleistocene predecessors and tend to have much more pronounced chins than do Middle Stone Age early moderns. This nearly universal pattern of gracilization is associated with the marked reduction in size that apparently occurred in the Upper Pleistocene in the ancestors of the Khoesan

in southern Africa^{130,131} and the cranial gracilization that accompanied the spread of agriculture through the continent.^{132,133} This is the latest step in human morphological evolution in Africa.

Just as in de Queiroz's¹¹⁴ unified view of speciation, at various points in this process, different criteria for what defines "anatomically modern" morphology apply and would allow one to identify most of the specimens from that point on as "anatomically modern" humans. It is worth remembering, however, that the simplest view of the process *assumes* a specific alpha taxonomy of the specimens in question, namely that they all belonged to a single evolving lineage. By implication, all of the specimens would represent steps in the process of our species' evolution. Although this assumption rests on a precedent established by other researchers,^{28,115,116} the alpha taxonomy of Middle Pleistocene hominins is still a matter of considerable debate. Rather than one evolving hominin lineage in Africa, other workers prefer to recognize many distinct species, morphs, or paleodemes.^{13,14,48,134,135}

As Tattersall wisely emphasized at the conference, a solid alpha taxonomy is of crucial importance, for only when we understand who the actors were, whether species or sub-specific but morphologically divergent populations, will we be able to understand what happened in human evolution. A key factor in appraisals of Middle Pleistocene taxa is how one should deal with intrapopulation morphological variability.^{110,136–138} Much remains to be done before the experts are likely to reach a consensus on the alpha taxonomy of Middle Pleistocene hominins in Africa or the rest of the world. In this regard, the new emphasis on the study of the developmental basis of cranial traits is very welcome. A better understanding of the developmental and genetic basis of adult morphology should help to clarify many of these phylogenetic relationships or at least provide us with insights into which features may be the most useful for phylogenetic reconstructions.

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REFERENCES

- 1 Day MH, Stringer CB. 1982. A reconsideration of the Omo Kibish remains and the erectus-sapiens transition: 1er Congr Internat Paleont Hum, Prétirage. Nice, p 814–846.
- 2 Day MH, Stringer CB. 1991. Les restes crâniens d'Omo-Kibish et leur classification à l'intérieur du genre Homo. L'Anthropol 95: 573–594.
- 3 Lieberman DE, McBratney BM, Krovitz G. 2002. The evolution and development of cranial form in *Homo sapiens*. Proc Natl Acad Sci USA 99:1134–1139.
- 4 Lieberman DE, Krovitz GE, McBratney-Owen B. 2004. Testing hypothesis about tinkering in the fossil record: the case of the human skull. J Exper Zool 302B:284–301.
- 5 Wolpoff MH. 1986. Describing anatomically modern *Homo sapiens*: a distinction without a definable difference. Anthropos (Brno) 23:41–53.
- 6 Stringer CB, Hublin JJ, Vandermeersch B. 1984. The origin of anatomically modern humans in Western Europe. In: Smith FH, Spencer F, editors. The origins of modern humans: a world survey of the fossil evidence. New York: Alan R. Liss, p 51–135.
- 7 Hublin JJ. 1978. Quelques caractères apomorphes du crâne néandertalien et leur interprétation phylogénétique. C R Acad Sci Paris série D 287:923–926.
- 8 Santa Luca AP. 1978. A re-examination of presumed Neandertal-like fossils. J Hum Evol 7:619–636.
- 9 Santa Luca AP. 1980. The Ngandong fossil hominids: a comparative study of a Far Eastern *Homo erectus* group. Yale University Publications Anthropol 78:1–175.
- 10 Schwartz JH, Tattersall I. 1996. Toward distinguishing *Homo neanderthalensis* from *Homo sapiens* and vice versa. Anthropologie (Brno) 34:79–88.
- 11 Schwartz JH, Tattersall I. 1996. Toward a definition of *Homo neanderthalensis* and *Homo sapiens*: II. The petromastoid region. Am J Phys Anthropol 22(Suppl):211–212.
- 12 Schwartz JH, Tattersall I. 2000. The human chin revisited: what is it and who has it? J Hum Evol 38:367–409.
- 13 Schwartz JH, Tattersall I. 2003. The human fossil record; vol. 2. Craniodental morphology of the genus Homo (Africa and Asia). New York: Wiley-Liss.
- 14 Tattersall I, Schwartz JH. 2008. The morphological distinctiveness of *Homo sapiens* and its recognition in the fossil record: clarifying the problem. Evol Anthropol 17:49–54.
- 15 Lahr MM. 1994. The multiregional model of modern human origins: a reassessment of its morphological basis. J Hum Evol 26:23–56.
- 16 Lahr MM. 1995. Patterns of modern human diversification: implications for Amerindian origins. Year book Phys Anthropol 38:163–198.
- 17 Lahr MM. 1996. The evolution of modern human diversity: a study of cranial variation. Cambridge: Cambridge University Press.
- 18 Habgood PJ. 1989. An examination of regional features on Middle and early Late Pleistocene Sub-Saharan African hominids. S Afr Archaeol Bull 44:17–22.
- 19 Habgood PJ. 1989. The origin of anatomically-modern-humans in Australia. In: Mellars P, Stringer C, editors. The human revolution: behavioural and biological perspectives on the origins of modern humans. Princeton: Princeton University Press. p 245–274.
- 20 Habgood PJ. 1989. An investigation into the usefulness of a cladistic approach to the study of the origin of anatomically modern humans. Hum Evol 4:241–252.
- 21 Habgood PJ. 1992. The origin of anatomically modern humans in East Asia. In: Bräuer G, Smith FH, editors. Continuity or replacement: controversies in *Homo sapiens* evolution. Rotterdam: Balkema. p 273–288.
- 22 Groves CP. 1989. A regional approach to the problem of the origin of modern humans in Australia. In: Mellars P, Stringer C, editors. The human revolution: behavioural and biological perspectives on the origins of modern humans. Princeton: Princeton University Press. p 274–285.
- 23 Lieberman DE. 1995. Testing hypotheses about recent human evolution from skulls. Curr Anthropol 36:159–197.
- 24 Lahr MM, Wright RVS. 1996. The question of robusticity and the relationship between cranial size and shape in *Homo sapiens*. J Hum Evol 31:157–191.
- 25 Lam YM, Pearson OM, Smith CM. 1996. Chin morphology and sexual dimorphism in the fossil hominid mandible sample from Klasies River Mouth. Am J Phys Anthropol 100: 545–557.
- 26 Howells WW. 1989. Skull shapes and the map: craniometric analysis of modern Homo. Cambridge: Harvard.
- 27 Stringer CB. 1974. Population relationships of later Pleistocene hominids: a multivariate study of available crania. J Archaeol Sci 1:317–342.
- 28 Bräuer G. 1984. A craniological approach to the origin of anatomically modern *Homo sapiens* in Africa and implications for the appearance of modern Europeans. In: Smith FH, Spencer F, editors. The origins of modern humans: a world survey of the fossil evidence. New York: Alan R. Liss. p 327–410.
- 29 Bräuer G, Rimbach KW. 1990. Late archaic and modern *Homo sapiens* from Europe, Africa, and Southwest Asia: phylogenetic implications. J Hum Evol 19:789–807.
- 30 de Villiers H, Fatti LP. 1982. The antiquity of the negro. S Afr J Sci 78:321–332.
- 31 Van Vark GN, Bilsborough A, Dijkema J. 1989. A further study of the Border Cave 1 cranium, with special reference to the origin of modern man. Anthropol Préhist 100:43–56.
- 32 Van Vark GN, Bilsborough A, Henke W. 1992. Affinities of European Upper Paleolithic *Homo sapiens* and later human evolution. J Hum Evol 23:401–417.
- 33 Kidder JH, Jantz RL, Smith FH. 1992. Defining modern humans: a multivariate approach. In: Bräuer G, Smith FH, editors. Continuity or replacement: controversies in *Homo sapiens* evolution. Rotterdam: Balkema. p 157–177.
- 34 Corruccini RS. 1992. Metrical reconsideration of the Skhul IV and IX and Border Cave 1 crania in the context of modern human origins. Am J Phys Anthropol 87:433–445.
- 35 Turbón D, Pérez-Pérez A, Stringer CB. 1997. A multivariate analysis of Pleistocene hominids: testing hypotheses of European origins. J Hum Evol 32:449–468.
- 36 Churchill SE, Pearson OM, Grine FE, Trinkaus E, Holliday TW. 1996. Morphological affinities of the proximal ulna from Klasies River Mouth main site: archaic or modern? J Hum Evol 31:213–237.
- 37 Pearson OM, Grine FE. 1997. Re-analysis of the hominid radii from Cave of Hearths and Klasies River Mouth, South Africa. J Hum Evol 32:577–592.
- 38 Pearson OM. 2000. Postcranial remains and the origin of modern humans. Evol Anthropol 9:229–247.
- 39 White TD, Asfaw B, DeGusta D, Gilbert H, Richards GD, Suwa G, Howell FC. 2003. Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. Nature 423:742–747.
- 40 Howells WW. 1996. Howells' craniometric data on the Internet. Am J Phys Anthropol 101:441–442.
- 41 Stringer CB. 1989. The origin of early modern humans: a comparison of the European and non-European evidence. In: Mellars P, Stringer C, editors. The human revolution: behavioural and biological perspectives on the origins of modern humans. Princeton: Princeton University Press. p 232–244.
- 42 Stringer CB. 1993. Reconstructing recent human evolution. In: Aitken MJ, Stringer CB, Mellars PA, editors. The origin of modern humans and the impact of chronometric dating. Princeton: Princeton University Press. p 179–195.
- 43 Howells WW. 1973. Cranial variation in man: a study by multivariate analysis of pattern of differences among recent human populations. Cambridge: Harvard.
- 44 Pope GG. 1992. Craniofacial evidence for the origin of modern humans in China. Yearbook Phys Anthropol 35:243–289.
- 45 Sohn S, Wolpoff MH. 1993. Zuttiyeh face: a view from the east. Am J Phys Anthropol 91:325–347.
- 46 Lahr MM, Foley R. 1994. Multiple dispersals and modern human origins. Evol Anthropol 3:48–58.
- 47 Lahr MM, Foley RA. 2003. Demography, dispersal and human evolution in the Last Glacial period. In: van Andel TH, Davis W, editors. Neanderthals and modern humans in the European landscape during the last glaciation: archaeological results of the Stage 3 Project. Cambridge: McDonald Institute for Archaeological Research. p 241–256.
- 48 Tattersall I. 1997. Out of Africa again ... and again? Sci Am 276:46–53.
- 49 Templeton AR. 2002. Out of Africa again and again. Nature 416:45–51.
- 50 Relethford JH, Harpending HC. 1994. Craniometric variation, genetic theory, and modern human origins. Am J Phys Anthropol 95:249–270.
- 51 Relethford JH. 2001. Genetics and the search for modern human origins. New York: Wiley-Liss.
- 52 Ackermann RR. 2005. Variation in Neanderthals: a response to Harvati (2003). J Hum Evol 48:643–646.
- 53 Ahern JCM, Hawks JD, Lee S-H. 2005. Neandertal taxonomy reconsidered...again: a response to Harvati et al. (2004). J Hum Evol 48:647–652.

- 54 Harvati K, Frost SR, McNulty KP. 2005. Neandertal variation and taxonomy, a reply to Ackermann (2005) and Ahern et al. (2005). *J Hum Evol* 48:653–660.
- 55 Cracraft J. 1983. Species concepts and speciation analysis. *Curr Ornithol* 1:159–187.
- 56 Hanihara T. 1994. Craniofacial continuity and discontinuity of Far Easterners in the late Pleistocene and Holocene. *J Hum Evol* 27:417–441.
- 57 Hanihara T. 1996. Comparison of craniofacial features of major human groups. *Am J Phys Anthropol* 99:389–412.
- 58 Roseman CC, Weaver TD. 2004. Multivariate apportionment of global human craniometric diversity. *Am J Phys Anthropol* 125:257–263.
- 59 Roseman CC. 2004. Detecting interregionally diversifying natural selection on modern human cranial form by using matched molecular and morphometric data. *Proc Natl Acad Sci USA* 101:12824–12829.
- 60 Weaver TD, Roseman CC, Stringer CB. 2007. Were neandertal and modern human cranial differences produced by natural selection or genetic drift? *J Hum Evol* 53:135–145.
- 61 Corruccini RS, Beecher RM. 1982. Occlusal variation related to soft diet in a nonhuman primate. *Science* 218:74–76.
- 62 Beecher RM, Corruccini RS, Freeman M. 1983. Craniofacial correlates of dietary consistency in a nonhuman primate. *J Craniofacial Genet Dev Biol* 3:193–202.
- 63 Lieberman DE, Krovitz GE, Yates FW, Devlin M, Claire MS. 2004. Effects of food processing on masticatory strain and craniofacial growth in a retrognathic face. *J Hum Evol* 46:655–677.
- 64 Corruccini RS, Henderson AM, Kaul SS. 1985. Bite-force variation related to occlusal variation in rural and urban Punjabis (North India). *Archs Oral Biol* 30:65–69.
- 65 Corruccini RS, Whitley LD, Kaul SS, Flander LB, Morrow CA. 1985. Facial height and breadth relative to dietary consistency and oral breathing in two populations (North India and U.S.). *Hum Biol* 57:151–161.
- 66 Corruccini RS, Townsend GC, Brown T. 1990. Occlusal variation in Australian Aborigines. *Am J Phys Anthropol* 82:257–265.
- 67 Corruccini RS, Townsend GC, Richards LC, Brown T. 1990. Genetic and environmental determinants of dental occlusal variation in twins of different nationalities. *Hum Biol* 62:353–367.
- 68 Lieberman DE. 1998. Sphenoid shortening and the evolution of modern human cranial shape. *Nature* 393:158–162.
- 69 Krovitz GE. 2003. Shape and growth differences between Neandertals and modern humans: grounds for a species-level distinction? In: Thompson JL, Krovitz GE, Nelson AJ, editors. *Patterns of growth and development in the genus Homo*. Cambridge: Cambridge University Press. p 320–342.
- 70 Ackermann RR. 2002. Patterns of covariation in the hominoid craniofacial skeleton: implications for paleanthropological models. *J Hum Evol* 43:167–187.
- 71 Ackermann RR. 2005. Ontogenetic integration of the hominoid face. *J Hum Evol* 48:175–197.
- 72 Williams FL, Godfrey LR, Sutherland MR. 2003. Diagnosing heterochronic perturbations in the craniofacial evolution of *Homo* (Neandertals and modern humans) and *Pan* (*P. troglodytes* and *P. paniscus*). In: Thompson JL, Krovitz GE, Nelson AJ, editors. *Patterns of growth and development in the genus Homo*. Cambridge: Cambridge University Press. p 295–319.
- 73 Ponce de León MS, Zollikofer CPE. 2001. Neandertal cranial ontogeny and its implications for late hominid diversity. *Nature* 412:534–537.
- 74 Ponce de León MS, Zollikofer CPE. 2006. Neandertals and modern humans: chimps and bonobos: similarities and differences in development and evolution. In: Harvati K, Harrison T, editors. *Neandertals revisited: new approaches and perspectives*. New York: Springer. p 71–88.
- 75 Zollikofer CPE, Ponce de León MS. 2004. Kinematics of cranial ontogeny: heterotopy, heterochrony, and geometric morphometric analysis of growth models. *J Exp Zool (Mol Dev Evol)* 302B:322–340.
- 76 Zollikofer CPE, Ponce de León MS. 2006. Cranial growth models: heterochrony, heterotopy, and the kinematics of ontogeny. In: Harvati K, Harrison T, editors. *Neandertals revisited: new approaches and perspectives*. New York: Springer. p 89–112.
- 77 Mitteroecker P, Gunz P, Bernhard M, Schaefer K, Bookstein FL. 2004. Comparison of cranial ontogenetic trajectories among great apes and humans. *J Hum Evol* 46:679–698.
- 78 Moss ML, Young RW. 1960. A functional approach to craniology. *Am J Phys Anthropol* 18:281–292.
- 79 Enlow D. 1990. *Facial growth*, 3rd ed. Philadelphia: W. B. Saunders.
- 80 Ravosa MJ. 1991. Interspecific perspective on mechanical and non-mechanical models of primate circumorbital morphology. *Am J Phys Anthropol* 86:369–396.
- 81 Smith FH, Paquette SP. 1989. The adaptive basis of Neandertal facial form, with some thoughts on the nature of modern human origins. In: Trinkaus E, editor. *The emergence of modern humans: biocultural adaptations in the Later Pleistocene*. Cambridge: Cambridge University Press. p 181–211.
- 82 Tillier A-M. 1988. A propos de sequences phylogénique et ontogénique chez les neandertaliens. In: Trinkaus E, editor. *L'Homme de Neandertal*, vol. 3, *L'Anatomie*. Liège. p 125–135.
- 83 Minugh-Purvis N. 1988. Patterns of craniofacial growth and development in Upper Pleistocene hominids. Ph.D. dissertation, University of Pennsylvania, Philadelphia.
- 84 Thompson JL, Nelson AJ. 2000. The place of Neandertals in the evolution of hominid patterns of growth and development. *J Hum Evol* 38:475–495.
- 85 Akazawa T, Muhesen S, editors. 2002. *Neandertal burials: excavations of the Dederiyeh Cave, Afrin, Syria*. Kyoto: International Research Center for Japanese Studies.
- 86 Ramirez Rozzi FV, Bermúdez de Castro JM. 2004. Surprisingly rapid growth in Neandertals. *Nature* 428:936–939.
- 87 Ramirez Rozzi FV, Sardi M. 2007. Crown-formation time in Neandertal anterior teeth revisited. *J Hum Evol* 53:108–113.
- 88 Guatelli-Steinberg D, Reid DJ, Bishop TA. 2007. Did the lateral enamel of Neandertal anterior teeth grow differently from that of modern humans? *J Hum Evol* 52:72–84.
- 89 Guatelli-Steinberg D, Reid DJ, Bishop TA, Larsen CS. 2007. Not so fast: a reply to Ramirez Rozzi and Sardi (2007). *J Hum Evol* 53:114–118.
- 90 Smith TM, Tafforeau P, Reid DJ, Grün R, Eggins S, Boutakiout M, Hublin J-J. 2007. Earliest evidence of modern life history in North American early *Homo sapiens*. *Proc Natl Acad Sci USA* 104:6128–6133.
- 91 Dean C, Leakey MG, Reid D, Schrenk F, Schwartz GT, Stringer C, Walker A. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature* 414:628–631.
- 92 McBratney-Owen B, Lieberman DE. 2003. Postnatal ontogeny of facial position in *Homo sapiens* and *Pan troglodytes*. In: Thompson JL, Krovitz GE, Nelson AJ, editors. *Patterns of growth and development in the genus Homo*. Cambridge: Cambridge University Press. p 45–72.
- 93 Jeffrey N, Spoor F. 2004. Ossification and midline shape changes of the human fetal cranial base. *Am J Phys Anthropol* 123:78–90.
- 94 Bruner E, Manzi G, Arsuaga JL. 2003. Encephalization and allometric trajectories in the genus *Homo*: evidence from the Neandertal and modern lineages. *Proc Natl Acad Sci USA* 100:15335–15340.
- 95 Bruner E. 2004. Geometric morphometrics and paleoneurology: brain shape evolution in the genus *Homo*. *J Hum Evol* 47:279–303.
- 96 Semendeferi K, Damasio H, Frank R, Van Hoesen GW. 1997. The evolution of the frontal lobes: a volumetric analysis based on three-dimensional reconstructions of magnetic resonance scans of human and ape brains. *J Hum Evol* 32:375–388.
- 97 Semendeferi K, Damasio H. 2000. The brain and its main anatomical subdivisions in living hominoids using magnetic resonance imaging. *J Hum Evol* 38:317–332.
- 98 Rilling JK, Insel TR. 1999. The primate neocortex in comparative perspective using magnetic resonance imaging. *J Hum Evol* 37:191–223.
- 99 Rilling JK, Seligman RA. 2002. A quantitative morphometric comparative analysis of the primate temporal lobe. *J Hum Evol* 42:505–533.
- 100 Rilling JK. 2006. Human and nonhuman primate brains: are they allometrically scaled versions of the same design? *Evol Anthropol* 15:65–77.
- 101 Lieberman DE, Pearson OM, Mowbray KM. 2000. Basicranial influence on overall cranial shape. *J Hum Evol* 38:291–315.
- 102 Strait DS. 2001. Integration, phylogeny, and the hominid cranial base. *Am J Phys Anthropol* 114:273–297.
- 103 McCollum MA. 1999. The robust australopithecine face: a morphogenetic perspective. *Science* 284:301–305.
- 104 McCollum MA, Sharpe PT. 2001. Developmental genetics and early hominid craniodental evolution. *BioEssays* 23:481–493.
- 105 Weidenreich F. 1945. The brachycephalization of recent mankind. *Southwest J Anthropol* 1:1–54.
- 106 Bräuer B, Groden C, Gröning F, Kroll A, Kupczik K, Mbua E, Pommert A, Schiemann T. 2004. Virtual study of the endocranial morphology of the matrix-filled cranium from Eliye Springs, Kenya. *Anat Rec Part A* 276A:113–133.
- 107 Bräuer G, Groden C, Delling G, Kupczik K, Mbua E. 2003. Pathological alterations in the archaic *Homo sapiens* cranium from Eliye Springs, Kenya. *Am J Phys Anthropol* 120:200–204.
- 108 Tattersall I. 1995. The fossil trail: how we think we know what we think we know about human evolution. New York: Oxford University Press.
- 109 Bermúdez de Castro JM, Arsuaga JL, Carbonell E, Rosas A, Martínez I, Mosquera M. 1997. A hominid from the Lower Pleistocene of Atapuerca, Spain: possible ancestor to Neandertals and modern humans. *Science* 276:1392–1395.

- 110** Arsuaga JL, Martínez I, Gracia A, Lorenzo C. 1997. The Sima de los Huesos crania (Sierra de Atapuerca, Spain): a comparative study. *J Hum Evol* 33:219–281.
- 111** Wells LH. 1947. A note on the maxillary fragment from the Broken Hill Cave. *J R Anthropol Inst* 77:11–12.
- 112** Rightmire GP. 1996. The human cranium from Bodo, Ethiopia: evidence for speciation in the Middle Pleistocene? *J Hum Evol* 31:21–39.
- 113** Tillier A-M. 1999. Les Enfants Moustériens de Qafzeh: Interprétation Phylogénétique et Paléoaurologique. Paris: CNRS Éditions.
- 114** de Queiroz K. 1998. The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. In: Howard DJ, Berlocher SH, editors. *Endless forms: species and speciation*. New York: Oxford University Press. p 57–75.
- 115** Bräuer G. 2001. The KNM-ER 3884 hominid and the emergence of modern anatomy in Africa. In: Tobias PV, Raath MA, Moggi-Cecchi J, Doyle GA, editors. *Humanity from African naissance to coming millennia*. Firenze: Firenze University Press. p 191–197.
- 116** Rightmire GP. 1984. *Homo sapiens* in sub-Saharan Africa. In: Smith FH, Spencer F, editors. *The origins of modern humans: a world survey of the fossil evidence*. New York: Alan R. Liss. p 295–325.
- 117** Klein RG. 1999. *The human career*, 2nd ed. Chicago: University of Chicago Press.
- 118** Vermeersch PM, Paulissen E, Stokes S, Charlier C, Van Peer P, Stringer C, Lindsay W. 1998. A Middle Palaeolithic burial of a modern human at Taramsa Hill, Egypt. *Antiquity* 72: 475–484.
- 119** Grine FE, Bailey RM, Harvati K, Nathan P, Morris AG, Henderson GM, Ribot I, Pike AWG. 2007. Late Pleistocene human skull from Hofmeyr, South Africa, and modern human origins. *Science* 315:226–229.
- 120** Angel JL, Kelly JO. 1986. Description and comparison of the skeleton. In: Wendorf F, Schild R, editors. *The Wadi Kubbaniya skeleton: a Late Paleolithic burial from Southern Egypt*. Dallas: Southern Methodist University Press. p 53–70.
- 121** Angel JL, Phenice TW, Robbins LH, Lynch BM. 1980. Lopoy and Lothagam. No. 2: Late Stone-Age fishermen of Lothagam, Kenya. East Lansing, MI: Michigan State University.
- 122** Rightmire GP. 1975. New studies of post-Pleistocene human skeletal remains from the Rift Valley, Kenya. *Am J Phys Anthropol* 42: 351–370.
- 123** Rightmire GP. 1975. Problems in the study of later Pleistocene man in Africa. *Am Anthropol* 77:28–52.
- 124** Rightmire GP. 1978. Human skeletal remains from the Southern Cape Province and their bearing on the stone age prehistory of South Africa. *Quaternary Res* 9:219–230.
- 125** Rightmire GP. 1979. Implications of the Border Cave skeletal remains for Later Pleistocene human evolution. *Curr Anthropol* 20:23–35.
- 126** Rightmire GP. 1981. Later Pleistocene hominids of eastern and southern Africa. *Anthropologie (Brno)* 19:15–26.
- 127** Rightmire GP. 1981. More on the study of the Border Cave remains. *Curr Anthropol* 22: 199–200.
- 128** Brothwell D, Shaw T. 1971. A late Upper Pleistocene proto-West African negro from Nigeria. *Man* 6:221–227.
- 129** Anderson JE. 1968. Late Paleolithic skeletal remains from Nubia. In: Wendorf F, editor. *The prehistory of Nubia*. Dallas: Fort Burgwin Research Center and Southern Methodist University Press. p 996–1039.
- 130** Keith A. 1925. *The antiquity of man*. London: Williams and Norgate.
- 131** Keith A. 1931. *New discoveries relating to the antiquity of man*. London: Williams and Norgate.
- 132** Masticatory function and Post-Pleistocene evolution in Nubia. *Am J Phys Anthropol* 46: 495–506.
- 133** Rightmire GP. 1984. Human skeletal remains from Eastern Africa. In: Clark JD, Brandt SA, editors. *From hunters to farmers*. Berkeley: University of California Press. p 191–199.
- 134** Howell FC. 1994. A chronostratigraphic and taxonomic framework of the origins of modern humans. In: Nitecki MH, Nitecki DV, editors. *Origins of anatomically modern humans*. New York: Plenum. p 253–319.
- 135** Howell FC. 1999. Paleo-demes, species clades, and extinctions in the Pleistocene hominin record. *J Anthropol Res* 55:191–243.
- 136** Bräuer G, Mbua E. 1992. *Homo erectus* features used in cladistics and their variability in Asian and African hominids. *J Hum Evol* 22:79–108.
- 137** Wolpoff MH. 1993. Implications of *Homo heidelbergensis*: a new record set of homoplasies in mammalian evolution? *Am J Phys Anthropol* 16(suppl):210.
- 138** Stringer C. 1993. Secrets of the pit of the bones. *Nature* 362:501–502.

