Middle and later Pleistocene hominins in Africa and Southwest Asia

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Approximately 700,000 years ago, *Homo erectus* in Africa was giving way to populations with larger brains accompanied by structural adjustments to the vault, cranial base, and face. Such early Middle Pleistocene hominins were not anatomically modern. Their skulls display strong supraorbital tori above projecting faces, flattened frontals, and less parietal expansion than is the case for *Homo sapiens*. Postcranial remains seem also to have archaic features. Subsequently, some groups evolved advanced skeletal morphology, and by *ca.* 200,000 years ago, individuals more similar to recent humans are present in the African record. These fossils are associated with Middle Stone Age lithic assemblages and, in some cases, Acheulean tools. Crania from Herto in Ethiopia carry defleshing cutmarks and superficial scoring that may be indicative of mortuary practices. Despite these signs of behavioral innovation, neither the Herto hominins, nor others from Late Pleistocene sites such as Klasies River in southern Africa and Skhūl/Qafzeh in Israel, can be matched in living populations. Skulls are quite robust, and it is only after ≈35,000 years ago that people with more gracile, fully modern morphology make their appearance. Not surprisingly, many questions concerning this evolutionary history have been raised. Attention has centered on systematics of the mid-Pleistocene hominins, their paleobiology, and the timing of dispersals that spread *H. sapiens* out of Africa and across the Old World. In this report, I discuss structural changes characterizing the skulls from different time periods, possible regional differences in morphology, and the bearing of this evidence on recognizing distinct species.

Homo heidelbergensis | *Homo sapiens* | human evolution | skull morphology | systematics

Stone artifacts and other traces of human activity dating from 700,000 to 130,000 years ago are found across Africa and Eurasia, and a number of sites contain well dated archaeological sequences. Fossils are far less plentiful, particularly compared with the abundant Late Pleistocene Neanderthals. Nevertheless, it is clear that some of the earliest populations differing from *Homo erectus* are documented at localities in Africa and Southwest Asia. One important example is Bodo in the Middle Awash of Ethiopia, where a cranium, a broken parietal, and a humerus were discovered in conglomerates and sands containing mammalian fossils and later Acheulean tools. Radiometric dates point to an age of *ca.* 600,000 years (1). The cranium as reconstructed consists of the face and parts of the braincase. There are resemblances to *H. erectus* in the massive facial skeleton, projecting brow, low and constricted frontal with midline keeling, and parietal angular torus. In other respects, Bodo is advanced in its morphology. Brain size is close to 1,250 cm³ (2) and substantially greater than expected for *H. erectus*. This difference is unlikely to result simply from larger body mass (3). Frontal squama proportions, the arched temporal contour, and some traits of the cranial base are like those of more modern humans. The browridge is divided into medial and lateral segments, the margin of the nose is vertical rather than forward sloping, and the incisive canal opens into the front of the palate. These are derived conditions present also in the face of recent *Homo* (4).

Another ancient cranium and a mandibular fragment were picked up at Elandsfontein in South Africa in 1953. Later, at the site designated Cutting 10, animal bones were uncovered with Acheulean bifaces, cores, and flakes. The fauna from Cutting 10 may not be associated directly with the artifacts, but the contemporaneity of many of the Elandsfontein bones with a later Acheulean industry is not in doubt (5). The fauna includes bovids and other large herbivores, and there are archaic elements such as a dirk-toothed cat, a sivathere, a giant gelada baboon, and at least 4 archaic hartebeest/wildebeest-like antelope species. Some 15 of 48 mammalian species collected at Elandsfontein have no historic descendants, suggesting that this assemblage is 1.0 million to >600,000 years old (6). The human skullcap is cracked and weathered, but as with Bodo, resemblances to *H. erectus* are apparent. At the same time, the parietals are expanded ("bossed"), and the occipital is less angulated than in *H. erectus*. These differences are consistent with an increase in brain volume.

It is likely that the missing Elandsfontein facial parts are mirrored by the cranium from Broken Hill (Kabwe) in Zambia. The Broken Hill face is set forward from the anterior cranial fossa and exhibits very heavy brows. The cranial base is less flexed than is the norm for recent people. Despite the presence of these archaic features, the border of the nose is set vertically, and palatal anatomy is like that of later humans. Also in its occipital proportions and in the temporomandibular joint region, Broken Hill shares derived traits with modern populations. Unfortunately, the cave deposits containing the fossils were long ago quarried away, and circumstances surrounding the 1921 discovery are no longer clear. Associations of the bones and artifacts are uncertain, but a tibia was found near the cranium. Efforts to date the hominins are underway (7), but for the moment the best indications are mammal fossils that suggest an age comparable to Bodo or Elandsfontein (8).

A Middle Pleistocene specimen from Salé in Morocco has proved enigmatic, because of distortion due to pathology (9). Another partially reconstructed braincase from Lake Eyasi in Tanzania is low in profile, although the upper scale of the occipital is vertical. The contour of the (left) parietal is rounded when the skull is viewed from the back. More of a cranium from Lake Ndutu is preserved. Reconstructive efforts (10) reveal a vault that is small (1,100 cm³) with side walls that are gently convex. Also, the articular tubercle bounding the mandibular fossa is more prominent than would be the case for *H. erectus*, and the tympanic plate is delicate inferiorly, rather than thickened. The relatively gracile browridge, lack of strong mastoid cresting, and smooth nuchal region suggest identification of Ndutu as a female. A frontal bone from Zuttiyeh Cave in Israel has been interpreted both as an early Neanderthal and as a direct ancestor to the people at Skhūl and Qafzeh. Associated with

Acheulo-Yabrudian artifacts *ca.* 350,000 to 300,000 years old (11), the Zuttiyeh fossil is more likely to represent an archaic population, similar to those in Africa.

Other fossils of later Middle Pleistocene age are linked with Middle Stone Age (MSA) tools. An example is Florisbad in South Africa, where bones and artifacts were recovered from a spring vent. The complex spring deposits and their contents have proved difficult to date, but ESR measurements on a human tooth give an age of *ca.* 260,000 years (12). The Florisbad partial cranium, including the incomplete right side of a face, has been pieced together several times. Clarke's (13) reconstruction corrects some earlier errors, and it is evident that the face is more massive than had been supposed. The supraorbital torus is quite thick. However, the broad frontal is less constricted than that of Broken Hill. Hollowing of the maxillary wall (a "canine fossa") has also been noted, but whether this morphology is "modern" remains uncertain, because the topography of the infraorbital surface is influenced by facial size (14). Unfortunately, neither upper facial height nor the extent of facial projection can be measured.

A more complete cranium from the Ngaloba Beds at Laetoli in Tanzania is also associated with MSA tools. Despite its robust appearance, this individual displays features that are derived compared with the anatomy of Bodo or Broken Hill. The brows are moderately thickened, but the central portion of the torus is clearly set off from the lateral margin by a shallow depression. The parietal vault is broader than the base. The upper scale of the LH 18 occipital is high, rounded, and posteriorly projecting, while the nuchal plane must be relatively short. A cranium similar to LH 18 is known from Ileret in Kenya. KNM-ER 3884 has been dated by gamma-ray spectrometry to *ca.* 270,000 years (15). Parts of the frontal and maxilla are preserved, along with the temporal bones and occiput. Occipital morphology is said to resemble that of later humans (16).

Fragments of a skull and associated postcranial elements (Omo 1), and a second cranium (Omo 2), were collected in the Omo Valley of Ethiopia in 1967. Recent excavations at the Omo 1 locality have produced bones of large mammals, all of which are extant (17). The lithic assemblage contains Levallois (MSA) cores and blades, along with an ovate hand axe (18). On the basis of $^{40}Ar/^{39}Ar$ dating of feldspars, and the correlation of east Mediterranean sapropels with Kibish depositional pulses, all of this material is *ca.* 195,000 years in age (19, 20). As reconstructed, the Omo 1 cranium is globular in form, with expanded parietals and a rounded occipital. Cranial tori are not strongly expressed. The face is very incomplete but appears to be retracted relative to the frontal part of the braincase. The mandible shows either a clear mental eminence (21), or merely the "hint" of a midline bulge externally (22). In any case, there are important markers of anatomical modernity. Postcranial bones demonstrate that Omo 1 has long slender limbs, and body mass is estimated as close to 70 kg (23).

Omo 2, an isolated surface find, is low in contour with a blunt frontal keel and a strongly angled occiput. Other primitive features include the deep mandibular cavity lacking any distinct articular tubercle, and the absence of a sphenoid spine. Nevertheless, the vault is large overall, with a capacity of ≈1,435 cm³. The frontal bone is broad and relatively unconstricted, and the parietal walls show some outward curvature. The supraorbital torus is extensively damaged, and none of the face is preserved. An important question, still not resolved, is whether Omo 2 can be grouped with the Omo 1 skeleton, or whether these individuals represent separate populations. The morphological differences between them are very substantial. Indeed, Omo 2 has been compared with Broken Hill and Elandsfontein. If the fossils are approximately the same age, then there are 2 possibilities. Omo 2 may be a remarkably robust individual within a highly variable but essentially modern population. More plausibly, this specimen documents an archaic, late-surviving lineage, present alongside near-modern humans. Given the microstratigraphic

evidence placing Omo 2 in uppermost Member 1 of the Kibish Formation (24), it is difficult to argue that this cranium is much older than the first and therefore sampled from an earlier portion of the lineage ancestral to *Homo sapiens*.

Fossils from Herto in the Middle Awash region confirm the presence of *H. sapiens* in northeastern Africa late in the Middle Pleistocene. Bones occur with Acheulean bifaces and Levallois flakes in the Upper Herto sand unit, judged from stratigrapic, geochemical, and radioisotopic evidence to be 160,000 to 154,000 years old (25). One adult cranium (BOU-VP-16/1) is intact, with a brain size estimated as 1,450 cm³ (26). This individual is ruggedly built, with a bilaterally arched glabella, a long vault, and a distinctly flexed occipital. The parietal walls are convex, and the index of neurocranial globularity (27) is high enough to be within the range expected for anatomically modern humans. As a group, the Upper Herto individuals are very robust and thus distinguishable from modern populations.

Aduma, also in the Middle Awash, has produced fragments of 4 crania associated with MSA artifacts, considered to be 105,000 to 79,000 years in age (28). One adult skull cap is partially complete. In its parietal and occipital proportions, ADU-VP-1/3 is similar to Omo 1, LH 18, and Skhūl 5. From Singa in the Sudan, there is another hominin, discovered in 1924. On the basis of U-Th dating of calcrete adhering to the bones, the Singa cranium is >133,000 years old (29). It has a domed frontal, a relatively high vault, and is very broad at the parietal bosses. Here, the parietals are thickened, mostly because of diploic expansion. Great biparietal width is perhaps related to pathology, because the Singa right temporal lacks structures of the bony labyrinth (30).

An assemblage of later Middle Pleistocene age at Jebel Irhoud in Morocco contains human fossils and a Mousterian industry. Recent U-series/ESR measurements on a child's mandible (Irhoud 3) suggest a date of *ca.* 160,000 years. Irhoud 3 has large teeth but possesses the components of a chin. Imaging reveals that this specimen shares a pattern of eruption and dental maturation with recent populations, implying a similar life history (31). An adult cranium (Irhoud 1) is long and low, with thickened brows backed by a convex frontal, and a moderately angled occipital. The facial skeleton is short. The M¹ alveolus is positioned relatively far forward, but in its midsagittal and horizontal profiles, the Irhoud 1 face is not appreciably more projecting than that of modern people (32). The braincase of Irhoud 2 is quite similar to that of Irhoud 1 (9). Remains from Dar es Soltane are not so ancient, although evidence accumulating from several other Aterian sites indicates an age approaching 90,000 years (33). The Dar es Soltane adult has a broad upper face, a prominent glabella, and marked supraorbital development. The midface appears flattened. Overall, there are resemblances to Qafzeh 6.

Two caves in Israel have produced burials along with Mousterian artifacts. On the basis of thermoluminescence of burned flints and ESR measurements from animal teeth, Mousterian levels at both Skhūl and Qafzeh are >100,000 to *ca.* 90,000 years in age (34). Several of the adult crania (Skhūl IX, Qafzeh 6) are ruggedly constructed, with prominent glabellar and supraorbital development. Skhūl IX is relatively low-vaulted, with a flexed occipital that carries a torus-like bulge centrally. These individuals are likely to be males. Other skulls share many features with recent humans. In Qafzeh 9 (a female?), thickening of the brow is restricted to the superciliary eminence. The chin eminence must have tapered superiorly and approached the inverted-T shape said to be diagnostic for *H. sapiens* (35). The cranium is high and long, the parietals are expanded laterally, and the occiput is evenly rounded with no development of a transverse torus. Postcranial bones from Skhūl and Qafzeh are essentially modern. While there is much intragroup variation, all of these hominins differ from Neanderthals (36, 37).

MSA occupations at Klasies River in South Africa are about the same age as those at Skhūl and Qafzeh (38). Unfortunately, there are no burials. The human material includes broken skull

bones, teeth, an ulna, and several metatarsals. A partial frontal bone (KRM 16425) is very gracile and exhibits none of the brow thickening or supratoral flattening that is present in the case of Florisbad or LH 18. A temporal fragment bears a mandibular fossa that is moderately deep, with a distinct articular eminence. Some lower jaws are massive and do not possess a pronounced chin. Others are smaller but modern in nearly all respects (39). An impression that the Klasies River hominins are essentially modern in their morphology extends also to the few postcranial bones that are preserved. When treated in a multivariate analysis (40), the proximal ulna shows similarities to archaic specimens, but its anatomy can also be matched in recent populations.

Several other later Pleistocene hominins are of interest. One is a complete skeleton from Nazlet Khater in Egypt, probably associated with chert mining activities and Upper Paleolithic tools. The mining site was exploited between 40,000 and 35,000 years ago (41). The cranium can be measured, and the mandible is described as "extremely robust," with a fully developed chin (42). Another specimen, discovered near Hofmeyr in South Africa, has no recorded archaeological associations. This individual has been dated to *ca.* 36,000 years by application of optically stimulated luminescence and U-series methods to sediments filling the braincase (43). The skull is large in relation to that of modern African males, with prominent supraorbital structures and a robust face. A 3D morphometric analysis places Hofmeyr within the ranges of recent human groups and close to crania associated with Upper Paleolithic industries in Eurasia (43). Finally, there are remains from Border Cave, South Africa. These include an adult partial cranium (BC 1), mandibles, an infant burial, and postcranial bones. The significance of this material has been clouded by controversy over provenience and dating. BC 1 was collected from dumps left by guano diggers, and it has not been possible to link the specimen definitively with MSA levels in the cave.

Populations, Skull Measurements, and Variation

Interpretations of the fossils differ in the emphasis placed on specific anatomical traits and in the significance assigned to variation. Human evolution in the Middle and Late Pleistocene is envisioned either as a gradual accumulation of characters within a single species (*H. sapiens*), or as an episodic process effecting important changes in successive populations. Weighing the merits of these proposals is not straightforward, because the paleontological evidence is sparse. Some investigators have elected to consider the fossils as individuals, or to group them broadly by industrial association and geography. In my view, it is important to identify separate paleocommunities, or *p*-demes (44), while emphasizing morphological similarities within groups. Samples rather than single specimens can be compared, and this provides a firmer basis for examining systematic relationships. One grouping places Bodo with Elandsfontein, Broken Hill, Ndutu, and perhaps Eyasi. This is the "early archaic grade" of Bräuer (45), but the fossils are now routinely referred either to *Homo heidelbergensis* or to a closely related species restricted to Africa (46). For reasons adumbrated above, it is appropriate to include both Zuttiyeh and Omo 2 within this sample. The incomplete Florisbad cranium shares features with Omo 2 but may better be sorted to a second *p*-deme, along with LH 18, KNM-ER 3884, Omo 1, and the Irhoud adults. Comparisons are necessarily limited, but Herto, Singa, and ADU-VP-1/3 seem to differ from Florisbad and are treated as a separate group. The collections from Skhūl and Qafzeh are considered together. These Levantine populations can be compared with the geographically distant *p*-demes at Dar es Soltane and Klasies River.

The cranial vault is preserved more frequently than fragile facial bones, and the analysis reflects this bias. Endocranial volume (VOL), glabella-occipital length (GOL), basibregmatic height (BBH), maximum cranial breadth (XCB), least frontal breadth (LFB), maximum biparietal breadth (XPB), biasterionic breadth (ASB), biauricular breadth (AUB), frontal angle (FRA), occipital angle (OCA), lambda-inion chord (LIC), inion-opisthion chord (IOC), supraorbital torus thickness measured centrally (TOR), biorbital breadth (FMB), orbit height (OBH), and upper facial height (NPH) are used. External dimensions are from the original fossils (Bodo, Elandsfontein, Broken Hill, Ndutu, Omo, Florisbad, Laetoli, Skhūl, Qafzeh, Dar es Soltane, Border Cave), casts (Zuttiyeh), or the literature (Irhoud, Nazlet Khater, Herto, Aduma, Hofmeyr). Data for Singa and Ileret were provided by C. Stringer (personal communication) and E. Mbua (personal communication).

Table 1 gives cranial indices and angles registering sagittal curvature. The relative brain size index, calculated as $VOL^{.33}/OBH$, averages 2.77 for Bodo and Broken Hill and is within the range observed for *H. erectus* (3). Other samples register slight increases, and ranges for the Herto and Levantine groups overlap with recent humans. Indices measuring vault shape document trends that are generally expected. Height/length (BBH/GOL) is low in the Bodo and Florisbad groups, slightly greater in the Herto group and Skhūl V, and comparable to recent humans in the case of Hofmeyr. Crania of Middle Pleistocene hominins (particularly Irhoud 2) are relatively broad, but XCB/BBH is reduced in the few Late Pleistocene crania that are intact. An index of overall globularity ($XCB \times BBH/GOL^2$) seems to set Bodo and Broken Hill apart from the Irhoud 2 and Singa crania, while Herto and Skhūl V have intermediate scores. Later Pleistocene specimens resemble modern humans in this feature, identified as an important marker for our species (27).

TOR averages 17.1 mm in the Bodo group but is less for Florisbad, LH 18, KNM-ER 3884, and Irhoud. Three Skhūl crania average 11.1 mm. Other Skhūl/Qafzeh individuals exhibit development of the glabellar prominence and superciliary arch varying from substantial (Qafzeh 6, Qafzeh 3) to relatively slight (Qafzeh 9). In these cases, vertical thickness of the torus is difficult to quantify. The brow ridge is massive in Dar es Soltane, but further reduction of the superciliary eminence and flattening of the lateral plate are apparent in specimens from Nazlet Khater and Border Cave. Change is evident through the later Pleistocene, but there is no clear separation of populations showing "archaic" morphology from others that approach the "modern" condition.

Postorbital constriction (LFB/FMB) is marked in Bodo and Broken Hill, while the frontal is broader in Omo 2. Postorbital narrowing is also characteristic of Florisbad, Singa, and Irhoud 1. There is more variation at Skhūl/Qafzeh, where a number of individuals have frontal breadth proportions resembling those of recent people. In sagittal profile, the frontal is flattened in the Bodo and Florisbad groups, where FRA is close to 140^0. This angle is lower for the Irhoud specimens and in the Herto and Skhūl/Qafzeh assemblages, indicating that the forehead is more domed in shape. The Late Pleistocene Nazlet Khater and Hofmeyr crania both display high, relatively rounded vaults, and the BC 1 frontal is strongly convex, even in relation to that of recent South Africans.

Parietal proportions have been a key element in most lists of modern human features. While the *H. erectus* skull is broadest at the supramastoid crests, with inward-sloping sides, *H. sapiens* has a relatively narrow cranial base underlying an expanded neurocranium. Parietal "bossing" is usually pronounced. An index of parietal expansion (XPB/AUB) is low (mean = 106.2) in the Bodo group, aligning these specimens with *H. erectus*. For Irhoud 1, the ratio is 107.5. In the case of LH 18, Herto, Singa, and Skhūl/Qafzeh, the index ranges from 109 to 118. Here, there is no overlap with the condition in the Bodo *p*-deme, and parietal expansion is comparable with that of recent populations.

Table 1. Relative brain size, vault proportions, and facial measurements for Middle and Late Pleistocene African hominins

	Bodo group*, N mean range	Florisbad group†, N mean range	Herto group‡, N mean range	Skhūl/Qafzeh§, N mean range	Dar es Soltane (N = 1)	Nazlet Khater Hofmeyr Border Cave, N mean range	Recent humans World	Zulu, male	Zulu, female
VOL.^{33}/OBH	2 2.77 (2.7–2.8)	1 3.03	2 3.23 (3.1–3.3)	2 3.4 (3.3–3.5)	—	—	3.3	—	—
BBH/GOL	2 62.9 (61.7–64)	1 62.8	2 67.4 (67–67.6)	1 65.6	—	1 70.1	72.7	72.2	71.7
XCB/BBH	2 117 (112–122)	1 132	2 112.5 (105–120)	1 114	—	1 108	105	100	102
XCB × BBH/GOL^2	2 46.6 (43–50.5)	1 52.2	2 51.3 (47.4–55)	1 49.2	—	1 53.1	55.4	52.3	52.7
TOR	5 17.1 (13.5–22)	5 12.8 (10–15)	—	3 11.1 (9–12)	16	—	—	–	—
LFB/FMB	4 85.6 (79–94.7)	2 92.3 (91–93.5)	1 92.1	3 94.7 (87.8–98)	96.5	2 92.3 (88–96.4)	—	96.1	97.6
FRA	3 140 (139–141)	4 136.4 (131–143)	2 133 (132–134)	3 133.3 (130–137)	132	1 122	129.2	126.3	125.1
XPB/AUB	3 106.2 (105–108)	2 109.8 (108–112)	2 115.3 (112–118)	3 113.5 (109–116)	—	—	113.2	115.4	116.8
OCA	2 108.5 (106–111)	2 121.9 (117–127)	2 106 (103–109)	3 119 (109–133)	—	—	118.8	121.6	119.8
LIC/ASB	3 51.5 (46.5–54)	3 54.1 (51–59.5)	1 50.8	2 55.2 (53–57.5)	—	—	—	59.4	—
IOC/LIC	3 80.7 (73.7–90)	1 62.5	—	3 76.8 (63–85.5)	—	—	—	67.2	—
NPH/GMN	2 80.7 (79–81.8)	1 72.2	1 71.3	3 70.7 (70–72.1)	67.7	2 71.8 (65.7–78)	69.9	70.0	67.8

*Bodo; Broken Hill; Elandsfontein; Ndutu; Omo 2; Zuttiyeh.
†Florisbad; LH 18; KNM-ER 3884; Omo 1; Irhoud 1, 2.
‡Herto (BOU-VP-16/1); Singa; Aduma (ADU-VP-1/3).
§Skhul IV, V, IX; Qafzeh 3, 6, 9.

Occipital angulation is less marked in *H. heidelbergensis* than in *H. erectus* (46). For Ndutu and Omo 2, and for Herto and Singa, values of OCA are relatively low. Angles measured for the Florisbad group are greater, indicating more rounding of the occiput. At Skhūl/Qafzeh, there is much individual variation. In general, OCA provides little basis for distinguishing the mid and later Pleistocene populations from one another or from living people. Occipital height proportions also fluctuate throughout this interval. The LIC/ASB ratio averages 51.5 in the Bodo group. Increases in the Florisbad and Skhūl/Qafzeh assemblages suggest a slightly taller occiput, but this change is not registered in the Herto *p*-deme. Measurements for the later Pleistocene specimens are not available. However, the LIC/ASB index does increase in a sample of recent humans, offering support for the claim that a high occipital plane is uniquely derived for *H. sapiens*, narrowly defined (47). The occipital scale index (IOC/LIC) averages 80.7 for the Bodo population. This value is lower than expected for *H. erectus*, indicating relative reduction of the nuchal plane (46). The index is still lower (62.5) for Omo 1 but much higher for several of the Skhūl/Qafzeh individuals. Given this variation in samples from different time periods, it is difficult to discern any long term trend.

Facial size and orientation are often cited as criteria for anatomical modernity, and a vertically short, nonprojecting face is considered to be a principal distinguishing feature of our species (27, 48). Facial retraction cannot be measured satisfactorily without lateral radiographs, but NPH can be obtained directly from the fossils. For Table 1, values of NPH are standardized using the geometric mean (GMN) of 4 variables (GOL, XCB, FMB, and OBH). For Bodo and Broken Hill, NPH/GMN averages 80.7, and scaled facial heights are close to those of *H. erectus*. The index is significantly reduced in Irhoud 1, Herto, the Skhūl/Qafzeh assemblage, and Dar es Soltane. Only in the Late Pleistocene specimen from Hofmeyr is the face long in relation to overall size of the cranium.

Discussion

There is agreement that earlier Middle Pleistocene hominins share primitive traits with *H. erectus*. Later populations display more derived features, and the skeletons from Qafzeh and Klasies River are near-modern in their morphology. Toward the close of the Pleistocene, skulls appear increasingly similar to those of living humans. However, there is no consensus concerning the tempo of this progression, or the extent to which

adjustments in the cranial base, braincase, and face are correlated within discrete assemblages as evidence for developmental integration. It has become clear that anatomically modern humans evolved in Africa, but the process or event(s) underlying this emergence are poorly understood. One view is that of Bräuer (e.g., ref. 45), who discerns "a mosaic-like, continuous anatomical process of modernization" from an archaic grade via a later group to recent humans. Here, each grade can be defined by advances in brain size and skull form. Although changes accumulate in a mosaic pattern, early and late grades follow one another seamlessly, as segments of a single evolving lineage. A very different opinion is held by Tattersall and Schwartz (47), who regard living humans as unique morphologically. Derived features can be identified in the tympanic plate, petrous bone, vault sutures, occipital squama, supraorbital region, and mandibular symphysis. The authors allow that a fossil otherwise clearly representative of *H. sapiens* may lack 1 or more of these traits, but on balance, individuals that do not share this suite of morphologies can be excluded from our species. Multiple, distinct taxa should be recognized within *Homo*, and speciation must have occurred repeatedly throughout the Pleistocene.

Metric comparisons (Table 1) offer a way to evaluate these disparate hypotheses. Of course, such small samples may not adequately represent past populations. Where trends are apparent, caution is appropriate when judging the significance of paired differences. Several cranial features are quite variable. The supraorbital torus is massive in the Bodo group but fluctuates in later populations. Evidently, expression of the brow is influenced by facial projection and other aspects of structure not considered here (see ref. 49). Vaults are broad relative to height in the Pleistocene groups, while this ratio is reduced in recent humans. Only one of the Levantine individuals (Skhūl V) can be measured, but XCB/BBH falls within the range for the Bodo *p*-deme. The occipital angle is low in the Bodo and Herto groups but reaches modern values in the Florisbad assemblage. The IOC/LIC ratio also fluctuates within and between groups, and there are no clear trends. In other instances, skull form seems to change gradually over time, as predicted by the scenario of Bräuer (45). Globularity and postorbital constriction may be examples. Also, the frontal profile is relatively flattened in the earlier groups, while sagittal curvature increases in later populations. Two additional indices suggest a pattern of slight change throughout much of the Pleistocene, followed by a shift toward the modern condition. Such a shift is consistent with the hypothesis of Tattersall and Schwartz (47). The BBH/GOL ratio is low in the

ancient groups. Vaults are higher for Herto and Skhūl/Qafzeh, but there is no overlap with Late Pleistocene or recent samples. Also, LIC relative to ASB fluctuates in the Bodo, Florisbad, Herto, and Skhūl/Qafzeh groups. This index cannot be calculated for later Pleistocene individuals, but it is high in recent humans.

Other features separate the Bodo group more consistently from all later hominins. Relative brain volume is low for Bodo and Broken Hill. This measure is greater for the Florisbad group, and in the Herto and Levantine assemblages, it rises approximately to the level seen in recent people. Neurocranial globularity increases through time. These data may document gradual change, but it can be argued that near-modern cranial form is established in the Florisbad and Herto p-demes, even if there is variation. The frontal is constricted in the Bodo group but broader in all later populations. A similar pattern is apparent for both parietal expansion (XPB/AUB) and size-adjusted facial height. Here, correlations help to clarify the role of brain size increase. In fact, $VOL^{.33}/OBH$ is not significantly associated with globularity, parietal expansion, or facial height within this small sample of Pleistocene crania. Globularity influences frontal breadth (Spearman's $\rho = 1.0$, $P < 0.001$), and parietal expansion is associated with decreasing facial height ($\rho = -0.97$, $P < 0.004$), but most indices are not significantly correlated. If an increase in relative brain size, greater cranial

globularity, reduced postorbital constriction, and facial shortening can be documented from the time of Florisbad, Laetoli, and Irhoud, then these fossils share key traits with recent humans. Elements of a chin are also present, probably in Omo 1 and more definitely at Skhūl/Qafzeh and Dar es Soltane. This evidence suggests a speciation event, giving rise to hominins distinct from *H. heidelbergensis*. Even if the chin is variably developed at Skhūl or within the Klasies River assemblage, it will not be reasonable to exclude individuals selectively from this constellation of near-modern and recent populations. The systematic status of Florisbad itself may remain uncertain, but for (all) the other fossils, *H. sapiens* is the appropriate taxonomic designation. Given the *ca.* 195,000-year age for the Upper Member of the Kibish Formation, it is likely that 2 lineages coexisted in the Middle Pleistocene. Archaic *H. heidelbergensis* may have persisted through much of this interval, before going extinct. *H. sapiens* evolved earlier than has been supposed and was present in Africa for a substantial period before dispersing into other regions.

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