Metopic suture of Taung (*Australopithecus africanus*) and its implications for hominin brain evolution

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The type specimen for *Australopithecus africanus* (Taung) includes a natural endocast that reproduces most of the external morphology of the right cerebral hemisphere and a fragment of fossilized face that articulates with the endocast. Despite the fact that Taung died between 3 and 4 y of age, the endocast reproduces a small triangular-shaped remnant of the anterior fontanelle, from which a clear metopic suture (MS) courses rostrally along the midline [Hrdlička A (1925) *Am J Phys Anthropol* 8:379–392]. Here we describe and interpret this feature of Taung in light of comparative fossil and actualistic data on the timing of MS closure. In great apes, the MS normally fuses shortly after birth, such that unfused MS similar to Taung's are rare. In humans, however, MS fuses well after birth, and partially or unfused MS are frequent. In gracile fossil adult hominins that lived between ∼3.0 and 1.5 million y ago, MS are also relatively frequent, indicating that the modern human-like pattern of late MS fusion may have become adaptive during early hominin evolution. Selective pressures favoring delayed fusion might have resulted from three aspects of perinatal ontogeny: (*i*) the difficulty of giving birth to large-headed neonates through birth canals that were reconfigured for bipedalism (the "obstetric dilemma"), (*ii*) high early postnatal brain growth rates, and (*iii*) reorganization and expansion of the frontal neocortex. Overall, our data indicate that hominin brain evolution occurred within a complex network of fetopelvic constraints, which required modification of frontal neurocranial ossification patterns.

brain size evolution | virtual endocast | fossil hominins | frontal cortex | obstetrics

The Taung specimen consists of a natural endocast, a large fragment of fossilized face that articulates with the endocast, and a mandible that occludes with the maxillary dentition of the face (1). Taung died at ∼3.8 y of age (2), although an older age at death was suggested historically (1). Current estimates for Taung's cranial capacity (uncorrected for age) of 382 cm^3 (3) and 402–407 cm^3 (4–6) are in fairly close agreement, especially compared with Dart's earlier estimate of 520 cm^3 (7). Acceptance of *Australopithecus africanus* as a legitimate early hominin took several decades, partly because Dart interpreted the endocast as representing an advanced humanlike pattern of convolutions despite its comparatively small volume (1, 8), which his colleagues found problematic (9). Despite the fact that Dart's general interpretation of Taung is now accepted, debate continues about the morphology and implications of its endocast (10).

Adhering bony fragments and foramina on its basal surface that conduct nerves and vessels have been identified (3). The right temporal and both frontal poles that are embedded in the back of the facial fragment (11, 12) have been incorporated electronically into a virtual reconstruction of Taung's entire endocast (3) (Fig. 1). Comparative measurements of the virtual endocast with other australopithecine endocasts reveal that Taung shares a number of shape features that align it more closely with other *A. africanus* specimens than with *Paranthropus* endocasts, including squared-off frontal lobes and the shape of the temporal poles (3, 13). This finding suggests that, with a brain size that falls within the range for great apes, but represents a higher degree of encephalization, *A. africanus* was neurologically reorganized compared with similarly sized *Paranthropus* brains (13, 14). It is not known, however, whether the brains of *A. africanus* had become reorganized in conjunction with a trend for brain enlargement, because their direct ancestors (and their brain sizes) remain unknown.

Here we describe a previously unanalyzed metopic suture (MS) on the Taung endocast, and compare it with the relevant frontal bone morphology of fetal to adult chimpanzees, bonobos, and *Homo sapiens* (*SI Materials and Methods* and Tables S1 and S2). Data are also provided regarding MS in 58 additional fossil hominins (*SI Materials and Methods, MS in fossil hominins* and Table S3), and we interpret the significance of an unfused or partially fused MS for hominin brain evolution.

Results

The natural endocast of Taung is well preserved and reproduces a small remnant of the anterior fontanelle, from which a clear imprint of a MS courses rostrally along the midline of the endocast (Fig. 1). In a 1925 description of Taung, Hrdlička noted "Posterior 3/5 of frontal (anti-bregmatic) brain surface partly covered by a remnant of bone, shows what appears to be patent metopic suture but no trace on bone (what there is of it) itself" (p. 390 in ref. 15). The MS imprint on the endocast terminates several millimeters above the preserved portion of the frontal squama. The squama does not exhibit traces of MS on its external and internal surfaces, as confirmed with medical CT imaging. The morphology of the MS and anterior fontanelle are consistent with observations from CT studies of humans, in which "fusion of the metopic suture commences at the nasion, proceeds superiorly in progressive fashion, and is completed at the anterior fontanelle in a manner analogous to a zipper closing" (p. 1213 in ref. 16). We thus classify Taung's MS as partially fused. The sagittal (interparietal) and right and left coronal sutures are also clearly represented on the endocast and each intersects with the remnant of the anterior fontanelle.

In chimpanzees and bonobos, MS fusion typically occurs at a faster pace on the internal compared with the external table of the frontal squama, but in humans only minor differences between endocranial and exocranial MS fusion could be observed (Figs. S1 and S2). Endocranial and exocranial MS fusion states thus represent lower and upper ranges for the time of MS fusion. Accordingly, the partially fused MS on the Taung endocast indicates late fusion of MS in this 3- to 4-y-old individual.

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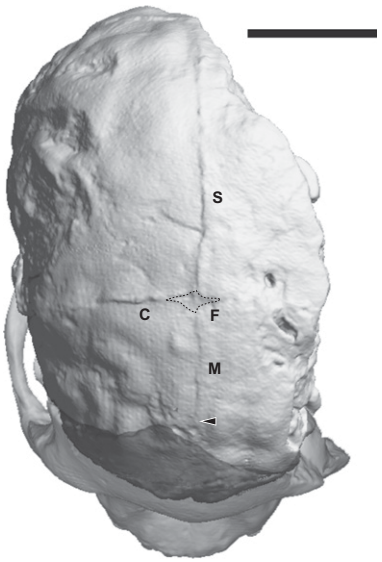

Fig. 1. CT-based superior view of the Taung natural endocast (solid) and face (transparent). Note imprints of sagittal (S, interparietal), coronal (C), and metopic (M) sutures (arrowhead denotes endpoint), and fontanelle (F, area delimited by dashed line). (Scale bar, 30 mm.)

In African great apes, the MS closes shortly after birth. In chimpanzees, it is completely fused in 65% of all cases before the eruption of the first deciduous molars (dm1) (*Materials and Methods* and Fig. 2*A*). In modern humans, the MS closes comparatively late, in 90% of all cases after the eruption of the dm1 (Fig. 2*B*). In concomitance with late MS closure, human infants and adults exhibit a high proportion of partially fused and unfused MS, but this condition is infrequent in the great apes (Fig. 2). These findings are in line with an earlier survey of "young" human, chimpanzee, and gorilla individuals [i.e., with any permanent teeth erupted, except the third molars (M3)], indicating that 33% of the human sample, but none of the great apes, retained MS (17). By adulthood (complete permanent dentition with appreciable wear), none of 172 chimpanzees or 185 gorillas had any trace of MS, whereas 16% of 2,104 humans had an unfused MS (17).

Data gathered for state of MS fusion in fossil hominins (*SI Materials and Methods, MS in fossil hominins* and Table S3) reveal a clear trend in small-brained gracile hominins that lived in Africa between ~3.0 and 1.5 million y ago (the term "gracile hominins" is used here to indicate fossils attributed to the genus *Australopithecus* and early *Homo*, as opposed to *Paranthropus*). Of five *A. africanus* specimens (Taung, Sts 5, Sts 71, Sts 60, and Sts No. 2 endocasts) and one early *Homo* cranium (SK 27) from South Africa, a partial MS is clearly present in two (Taung, SK 27), We have confirmed an earlier report (18) of partial MS in six East African specimens (KNM-ER 1805, KNM-ER 1813, KNM-ER 3733, KNM-ER 3883, KNM-WT 15000, and OH 24) that have been attributed to early *Homo* (e.g., *Homo ergaster* or *Homo habilis*). To our knowledge, unfused or partially fused MS have not been reported for *Paranthropus aethiopicus*, *Paranthropus boisei*, and *Paranthropus robustus* (for details see Table S3). Taken together, these data suggest that late MS fusion may have evolved in small-brained gracile hominins that lived between ~3.0 and 1.5 million y ago. Comparatively high frequencies of partially fused or unfused MS in *Homo erectus* from Asia and in the Neanderthals indicate that the trend toward late MS fusion continued in mid-to-late Pleistocene hominins (Table S3).

Discussion

The MS normally becomes obliterated later in humans than in chimpanzees (Fig. 2). At the dental age of Taung (first permanent molar erupted), 35% of humans exhibit an unfused or partially fused MS; apes rarely retain a MS similar to Taung's (17) (Fig. 2). Furthermore, unfused or partially fused MS in adults of Neolithic to contemporary human populations are relatively frequent, with a global average around 3–4% (19, 20). Early MS fusion likely represents a primitive feature of haplorhine primates, or even of euprimates (21), and is a feature uniting crown anthropoid primates (22). Late MS fusion in humans thus appears as a derived state, and early fusion, as observed in the great apes, appears as the primitive state.

We hypothesize that late MS fusion and an elevated proportion of partially fused or unfused MS in subadult and adult individuals result from one and the same developmental process. To test this hypothesis, we consider the proportion of fused MS as a function of age in chimpanzees and humans (Fig. 3*A*), and evaluate age-specific rates of MS fusion (Fig. 3*B*). Fig. 3*B* suggests that MS fusion occurs in a probabilistic manner, similar to a survival/death process ("survival" being similar to suture unfused; "death" being similar to suture fused). Peak values of the distributions in Fig. 3*B* indicate that MS fusion in chimpanzees is most likely to occur around birth, but fusion in humans is most likely to occur around the eruption of the second deciduous molar (dm2). Shifting the peak from birth to dm2 results in a longer tail of the probability distribution, and an elevated proportion of late-fusing MS or unfused MS in adult individuals

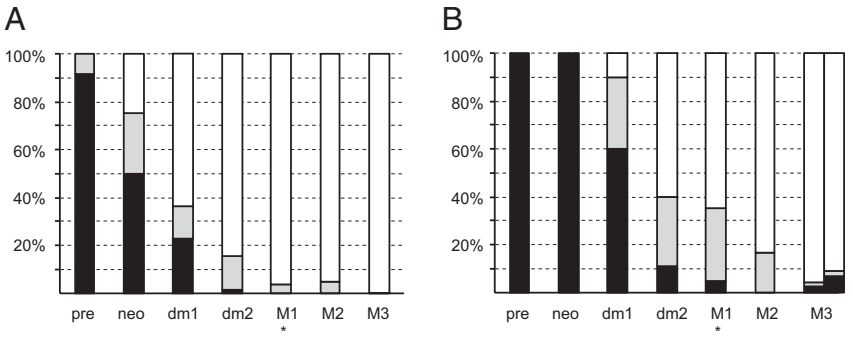

Fig. 2. Prevalence of unfused (black), partially fused (gray), and completely fused (white) internal metopic sutures in ontogenetic series of *P. troglodytes* (*A*) and *H. sapiens* (*B*). Dental age classes are: pre (fetal preterm), neo (neonate to before dental eruption), dm1 (first deciduous molars erupted), dm2 (second deciduous molars erupted), M1/M2/M3: first, second, third permanent molars erupted. The Taung individual belongs to age class M1 (*). Note delayed MS fusion in humans compared with chimpanzees. Prevalence of unfused MS in adult humans varies between populations (the two M3 bars in *B* represent a global sample and a Swiss medieval sample).

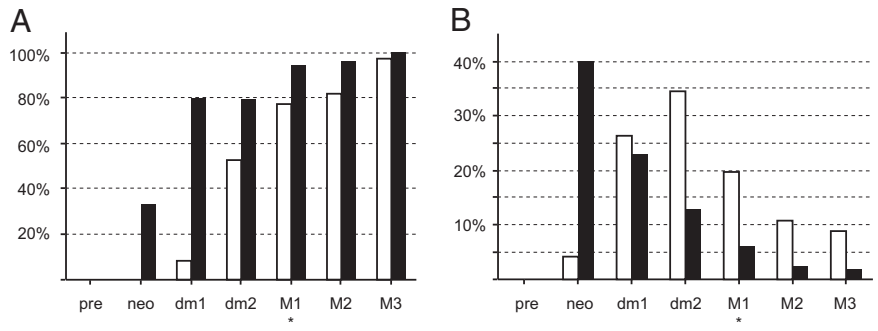

Fig. 3. Metopic suture fusion, empirical and model data. (*A*) Percentage of fused sutures as a function of age class. (*B*) Age class-specific rate (probability) of suture fusion. Black/white bars: chimpanzees/humans; asterisk: dental age class of Taung. Note that *A* represents the cumulative probability distribution of *B*.

(Fig. 3*A*). The presence of a still patent fontanelle and of a partially fused MS in the Taung child, and the incidence of unfused MS in five adult and two other younger *Australopithecus*/early *Homo* specimens (Table S3) is thus taken as evidence that a human-like pattern of late MS fusion was already present in mid-to-late Pliocene gracile hominins.

Already 70 y ago, persistence of the MS was hypothetically related to the evolutionary developmental transformation of the human skull (23, 24), including neurocranial expansion and thinning of the vault bones (23). Hypotheses on the genetic control of MS fusion have also been proposed (24). The large body of modern genetic evidence indicates that a network of at least 10 key genes mediates neurocranial suture fusion, and that these genes act differently on different sutures (25). It is intriguing that the recent sequencing of the Neanderthal genome provides evidence for positive selection in the modern human variant of one of these key genes, *RUNX2*, which is known to affect MS fusion (26). *RUNX2*-related disorders, such as cleidocranial dysplasia, result in delayed MS fusion and pathologies, such as extreme bulging of the forehead and hypertelorism (27). Premature closure of the metopic suture (metopic synostosis), on the other hand, typically results in trigonocephaly: that is, a narrow forehead with an external metopic ridge (keel) extending from glabella to the midforehead, relatively close-set orbits and no lateral browridge (28, 29).

Although various authors regard variation in MS fusion as an adaptively neutral feature (17, 20), the combined comparative evidence provided here for chimpanzees, humans, and fossil hominins supports the hypothesis that the late fusion of MS may have become adaptive relatively early during hominin evolution. Selective pressures favoring late fusion might have resulted from three different, but mutually nonexclusive, aspects of perinatal ontogeny: first, the obstetric dilemma; second, high early postnatal brain growth rates; and third, reorganization of the frontal neocortex.

Obstetric Dilemma. As bipedalism was refined in conjunction with an evolutionary increase in neonate and adult brain sizes, the morphology of the birth canal constrained the size and shape of the neonate (30–32). Although exactly when during hominin evolution the obstetric dilemma arose has been a subject of debate (33, 34), this dilemma is especially severe in humans because of their large-headed (and relatively large-brained) neonates and relatively constricted birth canals. The anterior fontanelle and patent metopic suture of human neonates facilitate parturition. During delivery, contractions of the birth canal cause the edges of the neonate's frontal and parietal bones to overlap and glide together in the region of the anterior fontanelle, which compresses the head and facilitates expulsion of the neonate from the birth canal (35). In early hominins, increased mobility of the neurocranial bones through delayed MS fusion might have represented an adaptive advantage facilitating birth (33).

High Early Postnatal Brain Growth Rates. Compared with chimpanzees, human brains continue to grow at high fetal-like rates throughout the first postnatal year of life, which "may reflect the ontogeny of the 'infrastructure' required for rapid cognitive development" (p. 162 in ref. 36). We hypothesize that late MS closure in modern humans reflects an evolutionary adaptation of the growing frontal neurocranium to keep up with high brain growth rates. When sustained early brain growth appeared during hominin evolution is still a matter of debate (37). The large endocranial volume of the Mojokerto child at an age of < 2 y provides evidence for high early brain growth rates in *H. erectus* (37). Direct evidence for australopith early postnatal cranial ontogeny is currently not available, but evidence for delayed MS fusion in australopiths indicates that early brain growth may already have been fast before the emergence of the genus *Homo*. If so, rapid early postnatal brain growth preceded the increase in brain size in *Homo*, which could be because of the obstetric dilemma shifting prenatal brain growth rates postnatally in association with pelvic modifications for bipedalism, or because of an increase in relative brain size (i.e., increased encephalization) in australopiths compared with their (unknown) ancestors.

Reorganization of the Frontal Cortex. The association of unfused MS with increased interorbital and frontal bone widths in extant humans (38, 39) is intriguing when one considers brain shape and possible neurological reorganization in early hominins (13) in conjunction with the frequencies of unfused MS in different taxa. As noted, a sample of *Australopithecus* and early *Homo* specimens that lived between ~3.0 and 1.5 million y ago shows an unfused MS (Table S3), but no *Paranthropus* specimen does. In keeping with the tendency for an unfused MS in humans, *A. africanus* is characterized by increased interorbital and frontal bone widths compared with *Paranthropus* (40). Also consistent with findings for extant humans with unfused MS, endocasts of *A. africanus* have increased frontal widths in the region of the rostral prefrontal cortex (in addition to an expanded orbital frontal cortex) compared with endocasts of *Paranthropus* (13). It is therefore reasonable to hypothesize that, in addition to reflecting an adaptation to high postnatal brain growth rates, an unfused MS in Taung and other early gracile hominins may have been associated with the evolution of certain morphological (13) and cytoarchitectural features (41) of the prefrontal cortex, parts of which are differentially enlarged in humans and known to be crucial for their advanced cognitive capabilities. [As an aside, it is worth noting that humans also have a unique phase of shape change in their braincases before their deciduous teeth begin to erupt that results in a more general neurocranial globularization compared with chimpanzees (42–45).] If so, the evolution of

increased rates of postnatal brain growth and neurological reorganization were probably entwined in (at least some) species of gracile early hominins.

Immature fossil hominins are currently playing a greater role in shaping the ways comparative data from living primates are interpreted (45, 46), and it is within this context that the suture morphology of Taung and other fossil hominins that lived more recently than 3 million y ago is interesting. Although it is beyond the scope of the present article, we hope that future researchers will test and extend the present findings by systematically collecting data on MS, anterior fontanelles, and endocranial size and shape in a wider sample of hominins, including those that lived before ~3 million y ago (e.g., *Australopithecus afarensis*) as well as hominins that lived more recently than the fossils we have sampled. Such data are expected to contribute to a more detailed understanding of when, and in which hominin species, rates of postnatal brain growth first began to increase. This understanding, in turn, may contribute to a better grasp of the relationship between the evolutionary refinement of bipedalism and the evolution of brain size and shape.

Materials and Methods

Sample. The state of MS fusion (unfused, partially fused, fully fused) was observed in ontogenetic samples of wild-shot *Pan troglodytes* (n = 407; CT data acquired on 78 specimens) and *Pan paniscus* (n = 136; CT data for 41 specimens), and in a worldwide ontogenetic sample of modern humans (n = 1060; CT data for 240 specimens). In addition, a sample of n = 376 individuals from Swiss medieval populations was examined. *Pan* data are from the Royal Africa Museum, Tervuren Belgium, and from the Collections of the Anthropological Institute and Museum, University of Zurich. Dental age classes used for developmental seriation were defined as follows: preterm fetal, neonate (from birth to before the eruption of the first teeth), dm1 (first deciduous molars erupted), dm2 (second deciduous molars erupted), M1/M2/M3: first, second, third permanent molars erupted. Details of sample structure and scoring procedures are provided in *SI Materials and Methods* and Tables S1 and S2. Because Taung only preserves endocranial evidence of MS, we use internal MS fusion scores for all comparative analyses in this study. Contrary to earlier studies (summarized in ref. 47, p. 478), we found no statistically significant difference in MS fusion patterns between *P. troglodytes* and *P. paniscus* (see *SI Materials and Methods, MS in chimpanzees, bonobos, and modern humans* and Tables S1 and S2). Suture fusion in Taung was studied on D.F.'s copy of the original endocast and on medical CT scans of the original fossil. Data on MS fusion status in fossil hominins were collected from the literature, D.F.'s collection of hominin endocasts and cranial casts, and from CT data (Table S3).

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Supporting Information

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SI Materials and Methods

Ontogenetic samples of wild-shot *Pan troglodytes* (n = 407; CT data available for 78 specimens) and *Pan paniscus* (n = 136; CT data for 41 specimens) are from the Anthropological Institute and Museum of the University of Zurich (AIMUZ) and the Royal Africa Museum, Tervuren, Belgium (Musée Royal d'Afrique Centrale). The ontogenetic sample of modern humans (n = 1,060 worldwide; n = 376 from Switzerland, mostly from medieval graveyards) is from AIMUZ (CT data available for 240 specimens). Further details on the structure of each sample are provided in Tables S1 and S2.

Dental age classes used for developmental seriation were defined as follows: preterm fetal, neonate (from birth to before the eruption of the first teeth), dm1 (first deciduous molars erupted), dm2 (second deciduous molars erupted), M1/M2/M3 (first, second, third permanent molars erupted). In each specimen, metopic suture (MS) fusion was assessed by direct visual inspection of the external and internal (by means of a dentist's mirror) sides of the frontal squama, and of the bregmatic region. When available, CT data of specimens were examined as well. MS fusion was scored externally and internally with three categories: unfused, partially fused, and fused. Internal fusion advances more rapidly than external fusion, especially in *Pan* (Figs. S1 and S2). Because the Taung specimen only preserves endocranial evidence of MS, we use internal MS fusion scores of the modern comparative sample throughout this study.

MS in chimpanzees, bonobos, and modern humans. Earlier studies (summarized in ref. 1, p. 478) reported differences in MS fusion pattern between *P. troglodytes* and *P. paniscus*, suggesting that MS fusion is delayed in the latter taxon. A statistical comparison of taxon-specific MS fusion patterns for the age range from dm1 to M3 (Tables S1 and S2) with the Chi-Square test does not reveal significant differences between taxa ($P \leq 0.34$).

Fig. S1 shows a modern human specimen (dental stage: before eruption of dm2) with a partially fused MS and a patent fontanelle, which is similar in shape to the fontanelle imprint on the Taung endocast (Fig. 1). Fig. S2 shows a chimpanzee specimen (before eruption of dm1), which has a partially fused MS. MS fusion advances from nasion toward bregma, and more rapidly on the internal than on the external table of the frontal squamae. A sequence of cross sections from nasion to bregma thus serves as a model to illustrate the temporal course of MS fusion.

MS in fossil hominins. The fusion state of the MS was assessed for the fossil specimens listed in Table S3. Observations obtained for this study from computed tomographic data are indicated by "CT" in the data-source column; those from D.F.'s endocast collection are listed as "D.F. endocast." Other observations are noted from the literature. Here we provide additional information on these specimens, and on earlier reports of MS fusion in fossil hominins.

Broom and Robinson (2) mentioned a suture between the frontal bones of a juvenile (dental age class M1) cranium from Swartkrans (SK 27), which has been attributed to early *Homo* sp. (3–5) and, more recently, to the newly proposed species *Homo gautengensis* (6). The suture, which Broom and Robinson illustrated ectocranially (2), is a partial MS that intersects with the right coronal suture near the midsagittal line. More recently, a partial MS has been reported for Sts 5 (7), which is an *Australopithecus africanus* adolescent or adult female (8). However, no mention was made of an MS in the original description of Sts 5 (9) and Sts 5 is reported to have a "metopic ridge" (10), which may indicate a fused rather than patent MS (11). Two scorable *A. africanus* endocasts in D.F.'s collection (the No. 2 specimen from Sterkfontein and Sts 60) show no indication of MS, and CT data for Sts 71 indicate that its MS is also fused. An endocast from *Australopithecus sediba* (MH1) has a crack in it that "obscure(s) potential evidence of a metopic suture" (12). A partially fused or unfused MS was not reported in the original descriptions of the three scorable adult *Paranthropus robustus* crania SK 46 (2), SK 48 (2), or DNH 7 (13), and D.F.'s copy of the SK 1585 natural endocast cannot be scored for MS because it is missing the midline rostral to bregma. The immature SK 54 calvaria (14) (which, like other specimens from Swartkrans, might represent early *Homo*) has a damaged bregmatic region and no evidence of MS.

Turning to East Africa, a partial ectocranial MS has recently been reported for six Plio-Pleistocene hominins by Prat (7). This sample includes KNM-ER 1805, consistent with earlier reports of MS in that specimen (15, 16), which is an "enigmatic" adult specimen from Kenya that is attributed to early *Homo* or *Australopithecus* (17), but not to *Paranthropus* (18). Prat's sample also includes one juvenile (KNM-WT 15000) and three adult (KNM-ER 3733, KNM-ER 3883, and KNM-ER 1813) *Homo ergaster/erectus* crania from Kenya (7). Earlier, Leakey and Walker (19) mentioned traces of MS in the glabellar region of KNM-ER 3733 and KNM-ER 3883, and Chamberlain (20) (cited in ref. 16) noted that there may have been an "accessory bone" near bregma on KNM-ER 3733, an observation that may well be associated with an unfused MS. Although we have found no mention of MS in the earlier literature for KNM-ER 1813, D.F.'s copy of the skull reveals a clear trace of MS in the glabellar region. Despite the fact that Walker and Leakey do not mention MS in their description of KNM-WT 15000, their photograph of a dorsal view of that specimen suggests that a trace of MS may have been present (21). Our observations of CT data confirm partial MS in all five of these specimens. The sixth specimen in Prat's sample of early East African hominins with partial MS is an adult from Tanzania, OH 24 (*Homo habilis*). Although the original description of OH 24 does not mention a partial MS (22), D.F.'s copy of a cast of the skull suggests that Prat's observation is correct.

Wood's meticulous descriptions of the relevant areas in East African *Paranthropus boisei* specimens KNM-ER 406, 407, and 732 (16) suggest that their ectocranial MS were fused, as does Tobias's thorough description of OH 5, which includes a survey of its cranial sutures (23). A fused MS is also apparent for KNM-ER 23000 and KNM-ER 13750 (24). CT data confirm that MS is fused in KNM-ER 406 and OH 5, and also indicate that MS is fused in KNM-WT 17000 (*Paranthropus aethiopicus*). As far as we are aware, an unfused or partially fused MS has not been reported for any other East African *Paranthropus* specimen, which is consistent with the fact that MS appears to be fused on two scorable *P. boisei* endocasts in D.F.'s collection (KNM-ER 23000 and KNM-WT 17400).

To summarize, of six gracile specimens that are scored from South Africa (Taung, SK 27, Sts 5, Sts 71, and the No. 2 and Sts 60 endocasts), a persistent MS is clearly present in two (Taung, SK 27), and we know of no reports of an unfused or partially fused MS for *P robustus*. Having examined the literature, CT data, and D.F.'s collection of endocasts and copies of skulls, we have confirmed Prat's recent report of partial MS in six East African specimens (KNM-ER 1805, KNM-ER 1813, KNM-ER 3733, KNM-ER 3883, KNM-WT 15000, and OH 24) (7). Reports from the literature for five *P. boisei* crania (KNM-ER 406, KNM-ER 407, KNM-ER 732, KNM-ER 13750, and OH 5) and three

P. robustus crania (SK 46, SK 48, and DNH 7) do not include observations of unfused or partially fused MS, consistent with observations of fused MS on two endocasts (KNM-ER 23000 and KNM-WT 17400) of *P. boisei* and another endocast from *P. aethiopicus* (KNM-WT 17000). Taken together, these data suggest that late MS fusion and a persistent MS may already have been a normal derived variation in small-brained gracile hominins that lived between ~3.0 and 1.5 million y ago. (The term "gracile hominins" is used here to indicate fossils attributed to the genus *Australopithecus* or early *Homo*, as opposed to *Paranthropus*.)

This trend continued among adult *H. erectus* specimens from Eurasia and East Asia, some of which lived as recently as ~0.3–0.5 million y ago (Table S3). The Dmanisi adult D3444 has a small bregmatic remnant of a MS (Table S3), and Hexian (25), *Sinanthropus* ZKD XI (skull LII) (26), and Ngawi 1 (27; MS illustrated on pp. 163–164) are reported to have partial or unfused MS ectocranially. D.F.'s endocast from *Sinanthropus* adolescent ZKD III (skull E1) suggests that it may also have had a trace of a partial MS near bregma, although this was not reported or illustrated in Davidson Black's 1932 description of the skull (28). D.F.'s endocasts for ZKD X (skull LI), ZKD XII (skull LIII), and the Trinil 2 *H. erectus* endocast from Java show no sign of MS. CT data reveal a partial MS in Sambungmacan 3. The Mojokerto child (Perning I) is estimated to have been less than 2 y old (29; but see 30 for an older age estimate). The bregmatic region of this specimen bears evidence of a fontanelle ["a gap of 3.5 mm can either be interpreted as a fontanelle in its final stage of closure or as post-mortem damage" (29)]. CT images provide clear evidence that the parietal bones near bregma did not yet have a diploic layer, a condition that characterizes the time before or shortly after closure of the fontanelle. Thus, of the 14 (mostly adult) *H. erectus* specimens scored, as many as five may have partially fused MS and another one (ZKD XI) could have an unfused rather than partial MS.

An ontogenetic series of $n = 21$ Neanderthals was scored for MS state (Table S3). MS is unfused in the two neonates (Mezmaiskaya 1, Le Moustier 1), two of five dm2 specimens (Pech de l'Azé 1, Subalyuk 2), and one of three M1 specimens (Krapina A). MS is partially fused in one dm1 specimen (Dederiyeh 2) and probably one (Spy 2) of eight adults.

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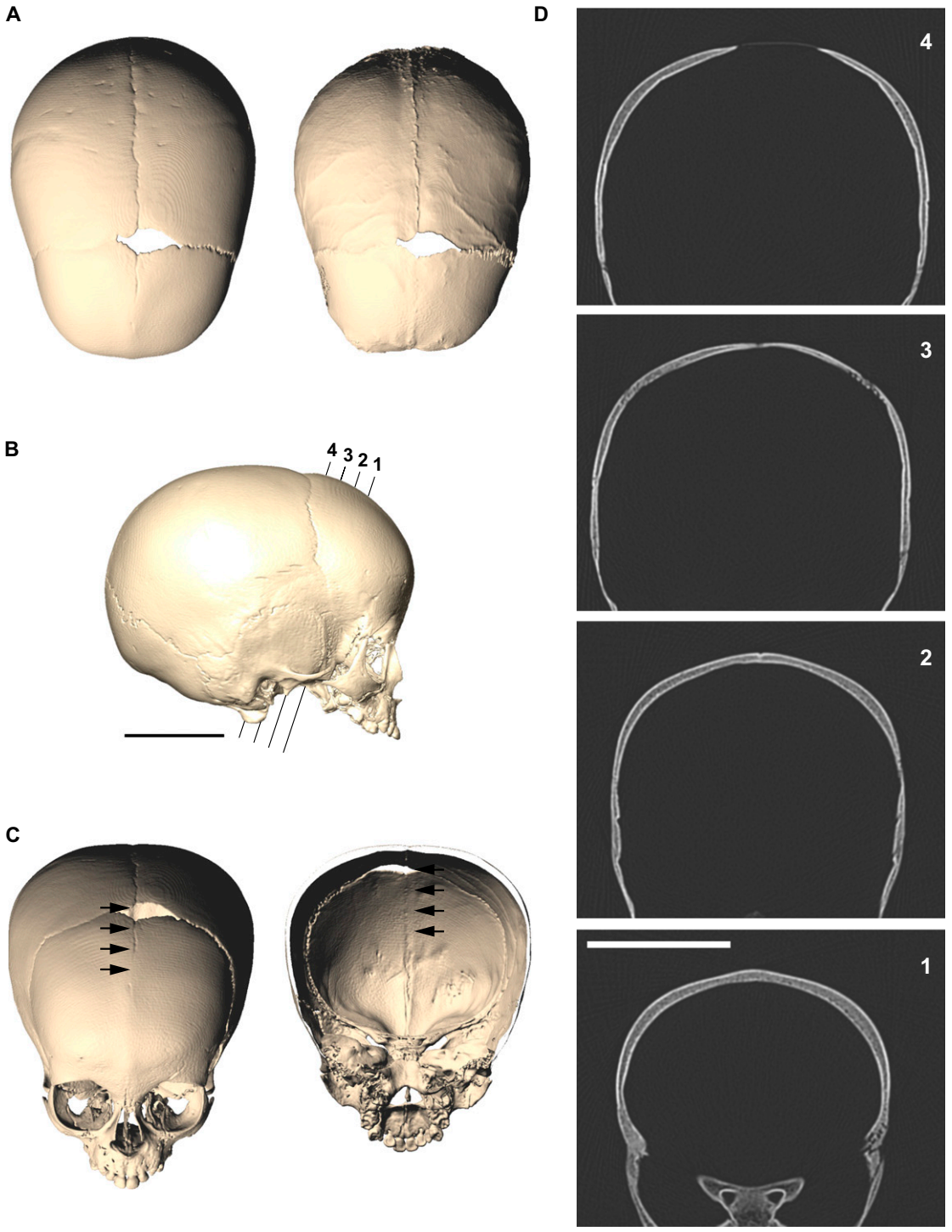

Fig. S1. Metopic suture in a modern human child cranium (CT data of dry skull). (*A*) Superior views of the external cranial surface and of the endocast. (*B*) Lateral view indicating the location of the four cross-sections shown in *D*. (*C*) External and internal aspects of the frontal squama (arrows indicate location of cross-sections in *D*). (*D*) Cross-sections. 1: fully fused MS; 2: fusion slightly more advanced on the internal compared with external surface; 3: MS not yet fused in the vicinity of the fontanelle (connection between left and right bony margins consists of dried soft tissue); 4: fontanelle region; note tapering of the frontal squamae toward fontanelle margin. (Scale bar, 5 cm.)

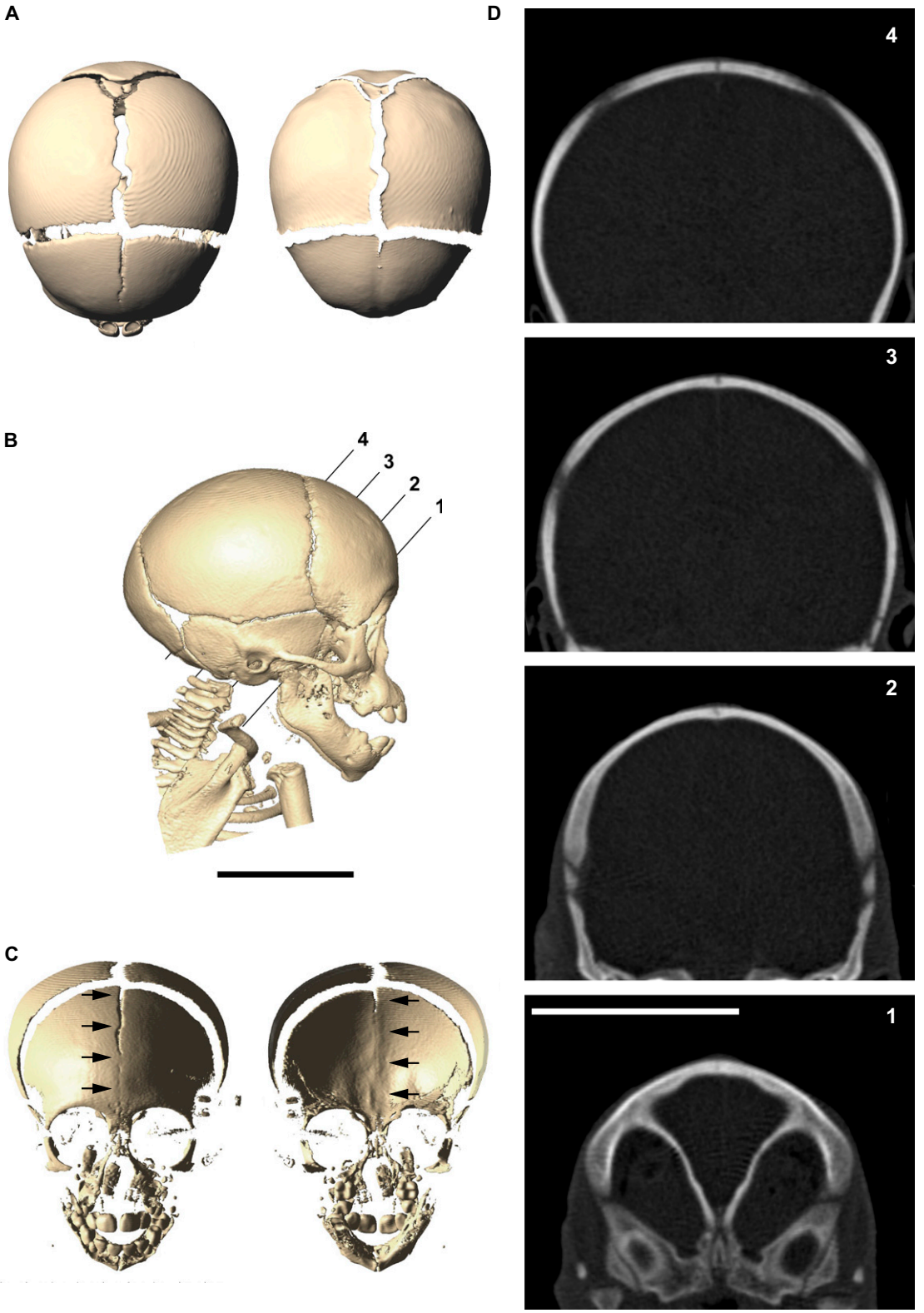

Fig. S2. Metopic suture in an immature chimpanzee cranium (CT data of frozen specimen). (*A*) Superior views of the external cranial surface and of the endocast. (*B*) Lateral view indicating the location of the four cross sections shown in *D*. (*C*) External and internal aspects of the frontal squama (arrows indicate location of cross sections in *D*); note more advanced state of fusion on the internal compared with external table. (*D*) Cross-sections. 1: fused MS, but cancellous bone of the diploe is less dense at the location of the former MS; 2: fusion more advanced on the internal compared with external surface; 3: external MS unfused, internal MS fused; 4: MS unfused externally and internally. (Scale bar, 5 cm.)

Table S1. Sample structure: *H. sapiens* subsamples per region

Age class	S. Africa	Egypt	Europe	Asia	Sahul	N. America	S. America	No id	Switzerland	Total
pre	2	0	5	5	0	0	0	3	0	15
neo	3	0	3	4	0	0	0	0	0	10
dm1	6	1	3	0	0	0	0	0	0	10
dm2	8	0	15	0	3	0	1	0	0	27
M1	2	4	5	1	6	1	1	0	2	22
M2	1	0	38	4	3	1	1	0	2	50
M3	165	229	154	173	106	59	44	0	372	1,302
Total	187	234	223	187	118	61	47	3	376	1,436

Table S2. Sample structures

	Metopic suture fusion state			
Age class	Unfused	Partial	Fused	Total
H. sapiens global sample (without Switzerland)				
pre	15	0	0	15
neo	10	0	0	10
dm1	6	3	1	10
dm2	3	8	16	27
M1	1	6	13	20
M2	0	8	40	48
M3	24	18	888	930
Total	59	43	958	1,060
H. sapiens Swiss sample				
M1	0	2	0	2
M2	0	2	0	2
M3	26	8	338	372
Total	26	12	338	376
Pan troglodytes				
pre	5	0	0	5
neo	10	3	2	15
dm1	6	2	14	22
dm2	1	9	54	64
M1	0	3	79	82
M2	0	3	61	64
M3	0	0	155	155
Total	22	20	365	407
Pan paniscus				
pre	0	0	0	0
neo	1	0	0	1
dm1	0	1	2	3
dm2	1	3	18	22
M1	1	1	28	30
M2	2	1	27	30
M3	1	0	49	50
Total	6	6	124	136

Table S3. MS fusion state in fossil hominins

Specimen	Taxon	Age (dental)	MS state	Ectocranial	Endocranial	Data source	Main reference	Text in main reference	Second reference	Third reference
TM266	*Sahelanthropus. tchadensis*	Adult	Fused			CT	(1)			
ARA-VP-6/500	*Ardipithecus ramidus*	Adult	Fused			Main reference	(2)			
Taung	*Australopithecus africanus*	M1	Partial	Bregma region not preserved	Unfused upper two-thirds	CT	(3), p. 390			
SK 27	*Homo* sp.	M1	Partial	Partial MS that intersects with the right coronal suture near the midsagittal line		Main reference	(4) p. 28			
Sts 5	*A. africanus*	Young adult	Fused			CT	(5), p. 447	"prominent metopic ridge"	(6)	
Sts No. 2	*A. africanus*	Adult	Fused			D.F. endocast				
Sts 60	*A. africanus*	Adult	Fused			D.F. endocast				
Sts 71	*A. africanus*	Adult	Fused			CT				
MH1	*Australopithecus sediba*	M2	?	Crack		Main reference	(7)			
KNM-ER 1805	*Homo habilis (?) or A.*	Adult	Partial	Remnants of suture from n to b	Remnants of suture above n	CT	(8), p. 388	"traces of metopic suture"	(6)	(9)
KNM-ER 3733	*Homo ergaster*	Adult	Partial	Bregmatic region,accessory bone near bregma (or fragmentation)	Bregmatic region	CT	(10), p. 148	"trace of a metopic suture"	(11) cited in ref. 9, p. 94	(6)
KNM-ER 3883	*H. ergaster*	Adult	Partial	Bregmatic region	Small remnant of suture ant. to bregma	CT	(10), p. 154	"faint trace of the metopic suture"	(6)	
KNM-WT 15000	*H. ergaster*	M2	Partial	One-third above nasion	Small bregmatic remnant (bone broken close to the midline)	CT	(12), p. 70		(6)	
KNM-ER 1813	*H. habilis*	Adult	Partial	Glabellar region	Glabellar region	CT, D.F. cranial cast	(6)			
OH 24	*H. habilis*	Adult	Partial	Bregmatic region	?	D.F. cranial cast	(6)			
KNM-ER 406	*Paranthropus boisei*	Adult	Fused			CT	(9)			
KNM-ER 407	*P. boisei*	Adult	Fused				(9)			
KNM-ER 732	*P. boisei*	Adult	Fused				(9)			
KNM-ER 13750	*P. boisei*	Adult	Fused			Illustration in main reference	(13)			
KNM-WT 17400	*P. boisei*		Fused			D.F. endocast				
KNM-ER 23000	*P. boisei*	Adult	Fused			D.F. endocast, cast, photographs in main reference	(13)			
OH5	*P. boisei*	Adult	Fused			CT	(14)			
SK46	*Paranthropus robustus*	Adult	Fused				(4)			
SK48	*P. robustus*	Adult	Fused				(4)			
SK54	*P. robustus* or early *Homo*?	Immature	Fused	Bregmatic region damaged		D.F. cranial cast	(15)			

Table S3. Cont.

Specimen	Taxon	Age (dental)	MS state	Ectocranial	Endocranial	Data source	Main reference	Text in main reference	Second reference	Third reference
SK1585	*P. robustus*	Adult	(Fused?)	Bregmatic part missing		D.F. endocast				
DNH 7	*P. robustus*	Adult	Fused				(16)			
KNM-WT 17000	*Paranthropus aethiopicus*	Adult	Fused			CT				
D2280	*Homo erectus*	Adult	Fused			CT				
D2282	*H. erectus*	Adult	Fused			CT				
D2700	*H. erectus*	M2	Fused			CT				
D3444	*H. erectus*	Adult	Partial	Bregmatic remnant (~10 mm)	Bregmatic remnant (<10 mm)	CT				
ZKD III (skull E1)	*H. erectus*	adolescent	Partial ?		Small remnant near bregma ?	D.F. endocast	(17)			
ZKD XI (skull LII)	*H. erectus*	Adult	Unfused	Unfused	Unfused	Main reference, D.F. endocast	(18), p. 332	"the metopic suture is well preserved"		
ZKD XII (skull LIII)	*H. erectus*	Adult	Fused			D.F. endocast				
ZKD X (skull LI)	*H. erectus*	Adult	Fused			D.F. endocast				
Trinil 2	*H. erectus*	Adult	Fused			D.F. endocast				
Sambungmacan 3	*H. erectus*	Adult	Partial	Bregmatic remnant of MS	None	CT				
Sambungmacan 4	*H. erectus*	Adult	Fused				(19)			
Ngawi	*H. erectus*	Adult	Partial	Extends 33 mm from bregma	Extends 5 mm from bregma	CT	(20), p. 341	"A metopical suture runs over a length of 28 mm, from 5 mm to the left of the bregma"		
Mojokerto	*H. erectus*	1.5 y (?)	Fused	Possible fontanelle	Possible fontanelle	Cast, main reference	(21), p. 301	"a gap of 3.5 mm can either be interpreted as a fontanelle in its final stage of closure or as post-mortem damage"	(22)	
Hexian	*H. erectus (or H. sp.)*	Adult	Partial		Upper 50%	Main reference	(23), p. 447	"impression of the metopic suture is visible between the frontal pole and bregma"		
Mezmaiskaya	*Homo neanderthalensis*	Neonate	Unfused	Unfused		CT	(24)			
Le Moustier 2	*H. neanderthalensis*	Neonate	Unfused	Unfused		CT	(25)			
Dederiyeh 1	*H. neanderthalensis*	dm1	—	Frontal squama not preserved		CT	(24)			
Dederiyeh 2	*H. neanderthalensis*	dm1	Partial	Remnants of fontanelle, metop. sut. trace below bregma	Bregmatic region	CT	(24)			
Pech de l'Azé 1	*H. neanderthalensis*	dm2	Unfused			Cast	(26)			
Subalyuk 2	*H. neanderthalensis*	dm2	Unfused			CT	(27)			
Roc de Marsal	*H. neanderthalensis*	dm2	Fused			CT				
Gibraltar 2	*H. neanderthalensis*	dm2	Fused			CT				

Table S3. Cont.

Specimen	Taxon	Age (dental)	MS state	Ectocranial	Endocranial	Data source	Main reference	Text in main reference	Second reference	Third reference
Engis 2	*H. neanderthalensis*	dm2	Fused			CT				
Krapina A	*H. neanderthalensis*	M1(?)	Unfused			Main reference	(28)			
La Quina	*H. neanderthalensis*	M1	Fused			Cast				
Teshik Tash	*H. neanderthalensis*	M1	Fused			CT				
Le Moustier 1	*H. neanderthalensis*	M2	Fused			CT				
Gibraltar 1	*H. neanderthalensis*	Adult	Fused	Frontla squama only partially preserved		CT				
Neanderthal	*H. neanderthalensis*	Adult	Fused			CT				
La Ferrassie	*H. neanderthalensis*	Adult	Fused			CT				
La Chapelle	*H. neanderthalensis*	Adult	Fused			CT				
Spy1	*H. neanderthalensis*	Adult	Fused			CT				
Spy2	*H. neanderthalensis*	Adult	Partial?	Possibly fracture around bregma		CT				
Amud1	*H. neanderthalensis*	Adult	Fused			CT				
Tabun1	*H. neanderthalensis*	Adult	?	Frontal squama heavily fractured		CT				

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