

Brief Communication: First *Homo erectus* from Turkey and Implications for Migrations into Temperate Eurasia

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ABSTRACT Remains of fossil hominins from temperate regions of the Old World are rare across both time and space, but such specimens are necessary for understanding basic issues in human evolution including linkages between their adaptations and early migration patterns. We report here the remarkable circumstances surrounding the discovery of the first fossil hominin calvaria from Turkey. The specimen was found in the Denizli province of western Turkey and recovered from within a solid block of travertine stone as it was being sawed into tile-sized slabs for the commercial natural stone building market. The new specimen fills an important geographical and temporal gap and displays several anatomical features that are shared with other Middle Pleis-

tocene hominins from both Africa and Asia attributed to *Homo erectus*. It also preserves an unusual pathology on the endocranial surface of the frontal bone that is consistent with a diagnosis of *Leptomenigitis tuberculosa* (TB), and this evidence represents the most ancient example of this disease known for a fossil human. TB is exacerbated in dark-skinned peoples living in northern latitudes by a vitamin D deficiency because of reduced levels of ultraviolet radiation (UVR). Evidence for TB in the new specimen supports the thesis that reduced UVR was one of the many climatic variables presenting an adaptive challenge to ancient hominins during their migration into the temperate regions of Europe and Asia. *Am J Phys Anthropol* 135:110–116, 2008. © 2007 Wiley-Liss, Inc.

The hominin specimen was found in the Büyük Menderes (Fig. 1a,b), a major valley system in western Turkey that initially formed in the Early to Middle Miocene by the collision between the Eurasian and African plates (Koçyigit, 2005; Westaway et al., 2005; Kaymakçi, 2006; Alçiçek et al., in press). The collision forced Asia Minor to the west and produced numerous roughly E-W trending extensional basins along the western margin of Turkey that through time filled with clastic sediments. This region remains tectonically active today (Akyol et al., 2006), and many hot springs that occur at new and/or rejuvenated fissures and faults along the edges of the extensional basins precipitate travertine sediments (Özkul et al., 2002; Altunel and Karabacak, 2005). Some of these travertine deposits are extensive, with perhaps the most famous of these being those at Pamukkale, a famous UNESCO World Heritage site (<http://whc.unesco.org/en/list/485/>).

Discussions with Mr. Galip Vurdaal, manager of the Dalmersan factory (located 20 km east of Denizli) and who gave the hominin specimen to MCA, revealed that the specimen was recovered from a block of travertine mined from a quarry that he rented from Kömürcüoğlu Mermer, a marble and travertine company based in Denizli. This quarry is located north of the village of Kocabaş (Turkish definition: “big head”) (Fig. 1b,c) at N37.86370 E29.38045 (WGS84). Travertines in this area have been dated by the thermoluminescence method and range from 510 ± 0.05 to 330 ± 0.13 Ka (Fig. 1d), with the most likely date for the hominin quarry travertine ranging from 510 ± 0.05 to 490 ± 0.05 Ka (Özkul et al.,

2004b). Other travertines in this region contain occasional vertebrate, invertebrate, and plant fossils. The most common vertebrates are *Equus* aff. *suessenbornensis* Wust, 1901, *Dama* sp., and *Bos* sp. Their Middle Pleistocene age (Özkul et al., 2004a) broadly supports the thermoluminescence dates. Work is underway to test this estimate with paleomagnetic dating.

Given the nature of its discovery in a factory workshop, the hominin was unfortunately reduced to a standard rough-cut tile thickness of about 35 mm (Fig. 2a,b) and is represented by two fragments of the frontal bone that articulate with fragments of the right and left parietals. The question of exactly how much of the calvaria was originally preserved in the travertine block below this cut remains unanswered, but it is probable that a perhaps significant portion was present because the inferior sawn edges of the parietals and left frontal fragments reveal well preserved bone. An estimation of age

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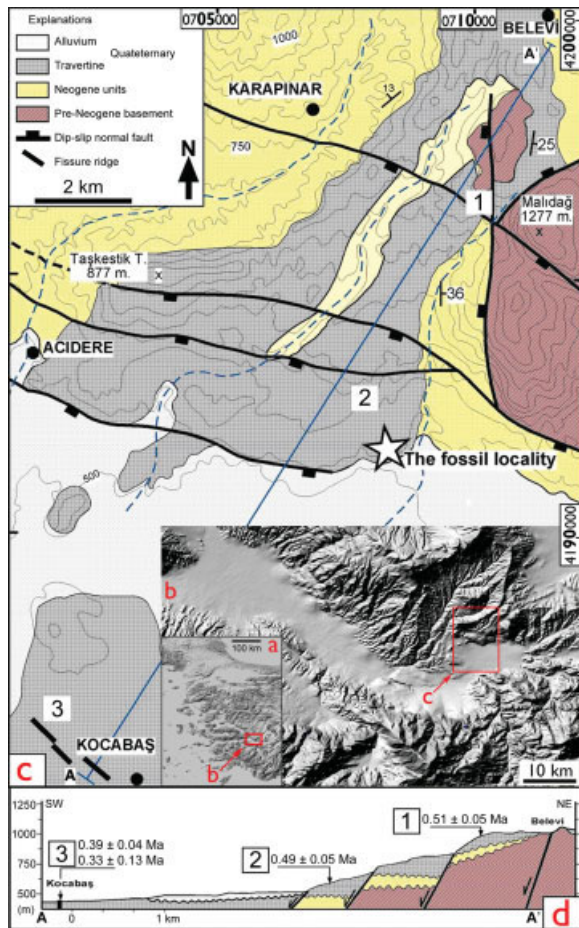


Fig. 1. Maps showing the Kocabaş hominin fossil locality. (a) Digital elevation model (DEM) showing western Turkey from the Shuttle Radar Topography Mission (SRTM). (b) DEM showing the Büyük Menderes Graben. (c) Geologic map showing the hominin locality (star). Note that the faulted morphology of the graben is filled with abundant travertines. (d) The geologic cross-section from (c) shows the location of the TL dated travertines (Özkul et al., 2004b) with (2) at the travertine quarry containing the fossil locality.

at death can be derived from the degree of suture closure of cranial elements as based on a comparison with modern humans, and endo- rather than ectocranial closure is generally a better indicator of younger ages (Acsádi and Nemeskéri, 1970). Preservation of the endocranial surfaces is excellent (Fig. 2c) but a reliable age assessment requires scoring the complete lengths of the sagittal, coronal, and lambdoid sutures, none of which are preserved in their entirety. All elements easily separate from one another (Fig. 2a), and the degree of closure of the partially preserved endocranial sagittal and coronal sutures is scored as open to incipient closure. This minimal degree of closure suggests that the individual was in the range of late juvenile to young adult, for a rough estimate of about 15–40 years of age. Other support for this age range is found in the morphology of the frontal sinus (Fig. 2d,e). This sinus is extensive, multifocal, and very invasive in the Kocabaş hominin, extending superiorly into the right torus by a depth of 15.2 mm. The frontal sinus achieves maximum size by about 16 years of age in males and 14 in females (Brown et al., 1984)

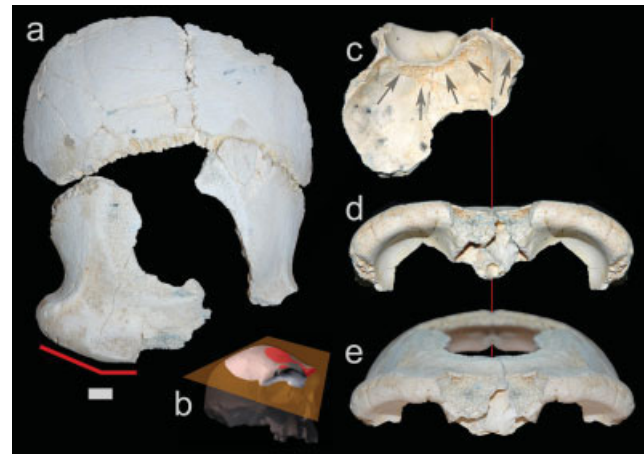


Fig. 2. The Kocabaş hominin calvaria. (a) Superior view shows that right and left parietals articulate with each other along the sagittal suture, and the right and left fragments of the frontal articulate with the parietals along the coronal suture. The presence of the frontal crest (position shown by red vertical line at right) facilitates repositioning the two frontal fragments relative to one another, with midline established by aligning the frontal crest with the sagittal suture, and the distance from midline to the temporal line on the right side used to position the left frontal fragment relative to midline. Red lines show obtuse angle of outermost anterior aspect of SOT. Scale bar 1 cm. (b) Plane of the inferior roughly transversely inclined saw cut superimposed on the Kabwe calvaria to show extent of preserved specimen; superior cut is parallel to lower cut and approximately 3.5 cm higher. The superior cut removed the medial portion of the right SOT and the central portion of the frontal squama immediately anterior to bregma. The thickness of bone removed from the frontal bone by the superior saw cut is estimated to be less than 1 cm in thickness. The plane of the inferior saw cut runs through the right and left parietals and left frontal fragment and is about 50 mm posterior to bregma along the sagittal suture, with slightly more bone preserved on the right than left side because of an upper left to lower right incline to the sectioned plane. (c) Endocranial surface of the right frontal fragment preserves the frontal crest. Arrows point to extensive lesions around the base of the anterior wall that are detailed in Figure 4. (d, e) The right frontal and parietal fragments are more completely represented than the left fragments and can be mirrored to offer a reconstruction of the specimen.

but there is some indication that its development in early hominins may be completed at an earlier age (Arsuaga et al., 1999). The size and extent of the frontal sinus adds supports to the estimate of a late juvenile to young adult age.

Perhaps the most striking aspect of the Kocabaş hominin is its prominent supraorbital torus (SOT), a feature commonly known as the browridge (Fig. 2d,e). The SOT is not complete because of its superior medial surface slightly lateral to and above the supraorbital notch was sawed away while the midline portion was broken away. The thickness of the SOT at its central and lateral points is massive (Tables 1 and 2). SOT size is clearly related to cranial size (see Fig. 3) and it is also likely that it is a sexually dimorphic feature. On the basis of size alone, it appears that the Kocabaş hominin was a male, but without other associated cranial features that better facilitate sex identification (e.g., mastoid region), this assignment should be considered a preliminary determination.

TABLE 1. *Calvaria measurements*

Measurements for Kocabaş calvaria	mm
Biorbital chord (Fma–Fma)	116 ± 1 ^a
Minimum frontal breadth (Ft–Ft)	92 ± 1 ^a
Maximum–Minimum breadth across temporal fossae of frontal	99 ± 1 ^a
Frontal supraorbital torus breadth	124 ± 1 ^a
Supraorbital torus thickness central	[18 ± 1]
Supraorbital torus thickness lateral	16
Orbit breadth	36
Interorbital breadth	31 ^a
Maximum biparietal breadth (chord)	140 ^a
Vault thickness near bregma	10

^a Right side, mirror image estimate, [] estimate based on SOT contour extended to sawed region; *italics*: *parietal incomplete*, so *minimum value*.

Aspects of the frontal bone underscore some of the challenges in sorting out the affinities of Middle Pleistocene hominins (Potts et al., 2003). For example, when viewed superiorly, the outer anterior aspect of the SOT forms an obtuse angle with midline (Fig. 2a), and in this feature the Kocabaş hominin differs from Chinese *H. erectus* and more closely resembles specimens from Java (Antón, 2002) and Africa attributed to *Homo erectus*. Since glabella is not preserved, it is unknown if the SOT continued medially to form a curved and superiorly thickened central arch with a depressed glabella as in Daka calvaria (BOU-VP-2/66) from Ethiopia (Asfaw et al., 2002) or was instead a horizontal bar of nearly uniform thickness as in Sangiran 17 from Java. The Kocabaş specimen has a distinct supratatorial sulcus. The sulcus begins just above the strongly crested temporal line as a small depression and shallows as it continues in a gentle arc across midline. This region does not protrude in a shelf-like manner as in OH9 from Tanzania but arches upward to join the frontal squama. Unfortunately, the plane of the superior saw cut removed the central portion of the frontal squama so it is unknown if there was any keeling in this region. However, the fragment of the left frontal preserved superior to the temporal line is more curved than flat, and this morphology suggests that the frontal squama was somewhat rounded. Sagittal keeling along the parietals is slight and parasagittal depressions are found along the length of the preserved portion of the sagittal suture.

The most conservative approach is to provisionally attribute the Kocabaş specimen to *H. erectus* but the combination of features in the Kocabaş hominin highlights the ongoing controversy about whether Pleistocene hominins attributed to the genus *Homo* represent a polytypic species with an Old World range (Asfaw et al., 2002) or instead provide evidence for multiple lineages with more limited temporal and geographical distributions (Schwartz, 2004). A single specimen clearly cannot answer this question, and it seems likely that the ongoing controversy will extend past the sample traditionally referred to *H. erectus* and on into that referred to *H. heidelbergensis*.

Even though most of the orbital plate of the frontal is missing, its endocranial surface at the angle between the anterior wall and the base of the anterior cranial fossa preserves numerous small, roundish to ellipsoidal, flat granular impressions with a relatively smooth surface (Fig. 4a). Single impressions average about 1–2 mm in diameter but coalesce to form groups distributed all along the contour of this region (Fig. 4b,c). Since only a

TABLE 2. *Measurements of comparative calvaria (mm)*

	ASIA																AFRICA												Europe			
	Kocabaş	D2280	D2282	D2700	D3444	Trinil 2	San 2	San 17	San X	Zhou XI	Zhou XII	Sam 1	Sam 3	Sam 4	Sam 5	Ng 1	Ng 7	Ng 11	Ng 12													
Minimum frontal breadth (Ft–Ft)	92 ± 1	75	66	67	67.5	85	82	95	89	84	91	102	101	110	106	103	103	112	103													
Supraorbital thickness	[18 ± 1]	11	10.5	8	10	13 ^a	12	17	16.5	13.2	14.6	15	13	14.5	13	15	15	12	14													
Maximum biparietal breadth (chord)	140	119	116	117	122	131	137	142	137	136	140	146	127	156	149	141	141	147	139													
Supplemental references	T1	1	1	1	2	3	3	3	3	3	3	3	4	5	3	3	3	3	3													
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Italics = estimate.

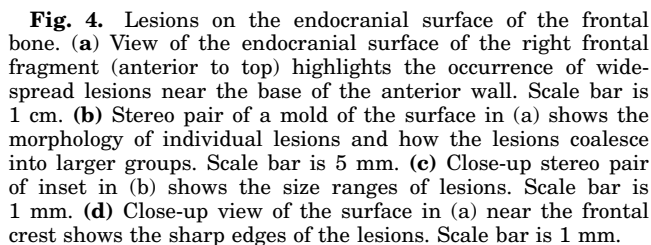
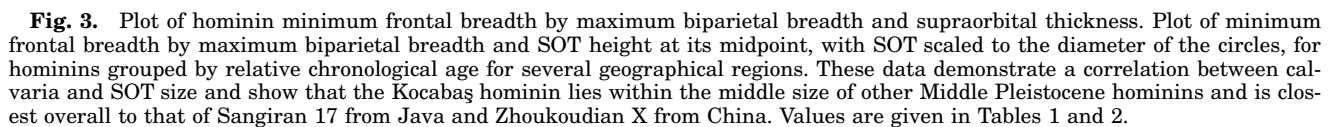
T1 See T. 1 for key to Kocabaş measurements, 1, Rightmire et al., 2006; 2, Lordkipanidze et al., 2006; 3, Rightmire, 1990; 4, Márquez et al., 2001; 5, Baba et al., 2003; 6, Spoor et al., 2007, and pers. comm. (<f.spoor@ucl.ac.uk>); 7, Roberto Macchiarelli, pers. comm. (<Roberto.Macchiarelli@univ-poitiers.fr>); 8, Asfaw et al., 2002; 9, Rightmire, 1996; 10, Ascenzi et al., 2000.

^a JK measurement on cast = minimum.

^b Average of R and L slides.

^c JK measurement on cast; ref. 9 reports 16.

^d JK measurement on cast.



(Fig. 4d) leave no doubt that these alterations are intravital in origin. Lesions of this type are known to form in response to an inflammatory process of the meninges, sometimes originating in the frontal or maxillary sinuses, the middle ear region, or even as a even as a primary meningeal reaction, such as bacterial meningitis; however, the macro-morphology of these granular impressions and their location are characteristic of the vestiges of *Leptomeningitis tuberculosa* (Schultz, 1999, 2001). Tuberculosis (TB) of the meninges is characterized by inflammatory changes which, as a rule, are localized at the base of the brain in the meninges with the characteristic tubercles forming small granular impressions in the internal surface of the cranial bones because of pressure atrophy. While this condition is not uncommon in modern humans, the Kocabaş specimen presents the most ancient example of TB known for a fossil hominin. A recent genetic analysis of the *Mycobacterium* genus by Gutierrez et al. (2005) estimates tubercle bacilli divergence at 2.6–2.8 Ma with a possible origin in East Africa; TB may then have afflicted some of the very earliest hominins.

The age estimate of $490\text{--}510 \pm 0.05$ Ka for the Kocabaşı specimen falls near the beginning of Marine Isotope Stage 13, a warm interglacial that was preceded and followed by two of the coldest glacial stages of the past million years (Bassinot et al., 1994; Oppo et al., 1998). Even as interglacials probably facilitated the northward migration of early hominins into the temperate regions of Europe and Asia during the Middle Pleistocene, these equatorial species would have had to successfully adapt to the highly variable climates and associated differences in available food resources in order to maintain viable populations (Dennell, 2003).

One adaptive response that the northward migration of early hominins seems certain to have required is a lightening of skin color in response to lower ultraviolet radiation (UVR) in order to maintain adequate levels of vitamin D (Murray, 1934; Loomis, 1967). Earlier discussions about the function of vitamin D were usually limited to photoprotection along with mineral homeostasis and skeletal integrity, with detrimental effects for the latter functions (e.g., rickets) resulting from reduced UVB-induced synthesis of the active vitamin D₃ (1,25-dihydroxyvitamin D₃; 1,25(OH)₂D₃) from the previtamin D₃ (25-hydroxyvitamin D₃; 25(OH)D₃) because of the interaction between the lower incidence of UVR especially in temperate regions often compounded by the filtering effect of melanin in dark skin that further impedes UVB absorption (Jablonski and Chaplin, 2000; Chaplin, 2004; Jablonski, 2006).

New work demonstrates that vitamin D has a wide variety of noncalcemic functions (Holick, 2004; Nagpal et al., 2005), with perhaps the most important of these being that the active form of vitamin D, 1,25-dihydroxyvitamin D₃, serves as an immunoregulatory hormone (Tsoukas et al., 1984). Liu et al. (2006) elucidated the innate antimicrobial mechanism by which the activation of Toll-like receptors produces the enzyme Cyp27B1 which catalyzes active vitamin D₃ that in turn triggers the induction of cathelicidin mRNA that, in this particular study, kills *Mycobacterium tuberculosis*. Liu et al. (2006) also demonstrated that dark-skinned African Americans had significantly lower levels of 25(OH)D₃ than the Caucasians in their study cohort which resulted in a significantly lower induction of cathelicidin RNA, thus providing an explanation for Stead et al.'s (1990) observation that African Americans have a higher susceptibility to *M. tuberculosis*. The link between a vitamin D deficiency in dark-skinned peoples living at high latitude and TB has been raised before in, for example, a high TB incidence in a Gujarati Asian population living in London (Wilkinson et al., 2000) and the case of a Marshall Island adoptee child living in North Dakota (Stead, 2000; and see Curtis et al., 1999); it might also have played a role in the high incidence of TB infection in native Senegalese troops that increased with the amount of time that the battalion was barracked in France during WWI (Borrel, 1920), and a TB infection rate 68 times higher for Somali immigrants living in Minnesota than the national Caucasian rate (Kempainen et al., 2001). Furthermore, the reemergence of TB as a global killer and its high incidence in co-infected HIV patients (Bloom and Murray, 1992) underscores the role that immunosuppression plays in the spread of this disease. Although the exact role that UV radiation plays in the vitamin D-mediated immunity response has only recently been demonstrated, it is important to note that increased exposure to sunlight was one of the most widely accepted treatment regimens for TB in past centuries (Woodcock, 1924; Vrooman, 1928; Dormandy, 1999) and was in fact at the heart of the sanatorium movement (MacCarthy, 2001). In the case of the Kocabaş hominin, the probable evidence of *Leptomeningitis tuberculosa* permits us to speculate that a case of TB was exacerbated by the reduced level of UVR encountered during the expansion of a low-latitude population of dark-skinned *Homo* into temperate Turkey during the warm interval of MIS 13.

Other evidence documenting the effects of reduced UVR on early hominins living in temperate regions may already exist. For example, dental enamel hypoplasia

(EH), a developmental defect produced by physiological stress (Schultz et al., 1998), is common in Eurasian fossil hominins including later Neanderthals and modern humans (Guatelli-Steinberg et al., 2004). Most studies ascribe EH to nutritional stresses including perhaps a vitamin A deficiency (Skinner, 1996), the effects of weaning (Ogilvie et al., 1989; Cunha et al., 2004), and/or seasonal changes in food availability (Guatelli-Steinberg, 2001) or moisture cycles (Skinner and Hopwood, 2004). However, EH can also be produced by a vitamin D deficiency (Purvis et al., 1973) because of the role that vitamin D plays as a regulator of calcium metabolism. Detailed studies of EH might prove to be able to distinguish among these different vectors. For example, Stamp and Round (1974) first documented marked seasonal variation in vitamin D deficiency, and linked winter and early spring hypovitaminosis D to differences to seasonal variations in solar insolation; subsequent work has supported this conclusion and provided more detail about seasonal differences including those between men and women (Hyppönen and Power, 2007), among different age classes (Tangpricha et al., 2002), and between light and dark-skinned people of different age classes from high (Harris and Dawson-Hughes, 1998; Rucker et al., 2002; Gordon et al., 2004; Weiler et al., 2007) and low (Willis et al., 2007) latitudes within the temperate zone. Given that seasonal differences in solar insolation vary by latitude and are even witnessed in equatorial regions (see NASA Total Ozone Mapping Spectrometer (TOMS) Mission, http://toms.gsfc.nasa.gov/ery_uv/euv_v8.html), EH produced by insolation-driven seasonal deficiencies in vitamin D should be manifested in: 1) trends whose amplitudes are predicted to be stronger at higher than lower latitudes; and 2) a more regular periodicity through time that should stand in strong contrast to, for example, a sharp weaning signal or diet-based deficiencies whose periods and/or amplitudes should vary more between and across seasons, or differences in diet that might change with increasing age. Detailed counts and statistical analyses of daily enamel increments might prove to be able to identify the effect of an insolation-driven seasonal deficiency in vitamin D.

The discovery of the first hominin calvaria at Kocabaş complements Turkey's rich Lower through Middle Paleolithic archaeological record (Kuhn, 2002) and adds to earlier evidence for the presence of early *Homo* in this region of the world (Gülec, 1997; Otte et al., 1998). Because Turkey lies at the crossroads of the Old World, this specimen fills a long standing gap in the geographical distribution of fossil hominins. The role that climatic variables played in limiting the migration and expansion of ancient human populations is often raised but only rarely is testable; the case presented here suggests that investigations of the direct and indirect effects of vitamin D deficiencies on the skeleton and dentition as driven by reduced UVR can aid our understanding of how *Homo* adapted to the challenges of life in temperate regions.

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