

Eyasi 1 and the Suprainiac Fossa

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ABSTRACT A reexamination of Eyasi 1, a later Middle Pleistocene east African neurocranium, reveals the presence of a suite of midoccipital features, including a modest nuchal torus that is limited to the middle half of the bone, the absence of an external occipital protuberance, and a distinct transversely oval suprainiac fossa. These features, and especially the suprainiac fossa, were

considered to be uniquely derived for the European and western Asian Neandertals. These observations therefore indicate that these features are not limited to Neandertal lineage specimens, and should be assessed in terms of frequency distributions among later archaic humans. *Am J Phys Anthropol* 124:28–32, 2004. © 2004 Wiley-Liss, Inc.

In the late 1970s, following on the work of earlier scholars (e.g., Schwalbe, 1901; Klaatsch, 1902; Gorjanović-Kramberger, 1902; Weidenreich, 1940; Patte, 1955), it was proposed by Hublin (1978a,b) and Santa Luca (1978) that a combination of external features of the posteromiddle of the occipital bone (or iniac region) of the European and western Asian Neandertals was unique to, or uniquely derived for, these Late Pleistocene late archaic humans. These features included the consistent absence of a distinct external occipital protuberance, a modest nuchal torus which was usually present solely in the middle half of the occipital bone (rarely extending laterally), and most importantly, the presence above the inion of a distinct, clearly bounded, transversely oval depression with rugose and porous bone within the concavity, the suprainiac fossa.

Variation in the development of an external occipital protuberance appears to be related to variation in the insertion of the nuchal musculature and its associated connective tissue (Hublin, 1978a), but the functional significance, if any, of the form of the nuchal torus and the suprainiac fossa remains unclear. The degree of development of the torus, but not necessarily its form, appears to be related to the general hypertrophy of neurocranial superstructures (Hublin, 1989). The suprainiac fossa, as an area of external table resorption which emerges early in development (Hublin, 1980; Heim, 1982), remains a morphological marker of unknown etiology.

It was noted by Hublin (1978a,b) and Santa Luca (1978) that this combination of features emerged during the second half of the Middle Pleistocene among archaic *Homo* in Europe (pre-Late Pleistocene human occipital bones remain unknown for western Asia) and is present with varying degrees of development (including variation in both size and number) in all sufficiently preserved Late Pleisto-

cene specimens normally included within the Neandertal group. The degree of development of the suprainiac fossa among Near Eastern mature remains is more variable (Trinkaus, 1983; Condemi, 1992), but the other features appear to characterize that group as well. Furthermore, as noted above, at least the suprainiac fossa has been shown to appear early in development among the Neandertals and their European predecessors (Hublin, 1980; Heim, 1982; Tillier, 1983; Madre-Dupouy, 1992; Arsuaga et al, 1997; Dodo et al., 2002; Ishida and Kondo, 2002).

In the context of this, it is generally maintained that, even though depressions may be present in the occipital bone above the inion in other, non-Neandertal lineage Middle and Late Pleistocene archaic *Homo* remains, these depressions do not exhibit the form seen in Neandertals. In particular, the depressions noted above the inion present in non-Neandertal African and Asian archaic *Homo* appear to be the product primarily of a concavity associated with a clear supratotal sulcus, sometimes with modest porosity, and they lack the distinctive combination of features seen in Neandertals (Hublin, 1978a; Santa Luca, 1978). Similar depressions among Late Pleistocene early modern humans, sometimes with the rugosity and porosity of Neandertal fossae, are frequently associated with a pronounced external occipital protuberance, and they were referred to as “supranuchal fossae” by Sládek (2000). Suprainiac

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fossae similar to those of Neandertals do occasionally appear among these early modern humans (Trinkaus, 2002), but their presence can be explained by some degree of admixture between the Neandertals and indispersing early modern humans (Trinkaus and Zilhão, 2002).

As a result of these observations, it is generally accepted that the morphology of the central occipital region, and in particular the presence and form of the suprainiac fossa, can be used as a uniquely derived complex of Neandertals, at least among Middle and Late Pleistocene archaic members of the genus *Homo*. As such, it has figured prominently in discussions of the identification of uniquely derived Neandertal characteristics (e.g., Hublin, 1978b; Santa Luca, 1978; Stringer et al., 1984; Arsuaga et al., 1997), the evolutionary emergence of Late Pleistocene Neandertals (e.g., Stringer and Hublin, 1999), and the identification of degrees of continuity among Neandertals and early modern humans in Europe (Freyer, 1993; Sládek, 2000; Trinkaus and Zilhão, 2002). However, the number of sufficiently intact later archaic human occipital bones outside of Europe is limited. Since perceptions of diversity are highly sample size-dependent for small samples, it is necessary to account for all available specimens which might have bearing on this issue. With this in mind, the midoccipital region of the east African Eyasi 1 archaic human cranium is reassessed.

THE OCCIPITAL BONE OF EYASI 1

The Eyasi 1 cranium was discovered in 1936 by L. Kohl-Larsen on the shore of Lake Eyasi near the Mumba Hills, Tanzania. It consists of major portions of the posterior neurocranium, fragmentary elements of the frontal bone, numerous isolated cranial fragments, and a few teeth. It was briefly described by Reck and Kohl-Larsen (1936) and Leakey (1936), analyzed in more detail by Weinert (1939), and more recently re-reconstructed and analyzed by Protsch (1981; see also Bräuer, 1984; Bräuer and Mabulla, 1996). The current reconstruction provides most of the superior occipital bone in correct anatomical position, although regions of it, especially laterally, have sustained minor surface erosion. However, the transverse middle of the external occipital plane, from just inferior of the nuchal torus to the region of the lambdoid suture, is well-preserved. Only a few small pieces remain absent, and were restored in plaster (Fig. 1).

The Eyasi human remains were considered in the past to be Late Pleistocene in age on the basis of the associated artifacts and fauna and two amino-acid racemization determinations (Leakey, 1936; Howell, 1978; Protsch, 1975, 1981). Reassessment of the artifacts and especially the fauna of the Eyasi Beds and a critical review of the amino-acid racemization assessments (Mehlman, 1984, 1987), in combination with the dating of the adjacent Mumba Rock Shelter (Bräuer and Mehlman, 1988) and geological assessments of the Eyasi Beds (Bräuer and Mabulla,



Fig. 1. Eyasi 1 neurocranium in occipital view. Note that bone is essentially black, and that relief is achieved principally through light reflecting from glossy surface.

1996), indicate, however, that they predate the Late Pleistocene and most likely derive from the middle or later Middle Pleistocene. The current best estimate of the age of the Eyasi Beds is between ca. 200,000–ca. 400,000 B.P. (Bräuer and Mabulla, 1996). They therefore derive from within the time frame generally occupied by sub-Saharan African later archaic *Homo* specimens such as Broken Hill (Kabwe) 1, the Guomde cranium (KNM-ER 3884), Laetoli 18, Florisbad 1, Ndutu 1, and probably Eliye Springs 1 (KNM-ES 11693), as well as north African specimens such as Irhoud 1 and 2 and Rabat 1.

In his description of the Eyasi 1 occipital region, Protsch (1981) correctly noted the absence of a true external occipital protuberance (there is only a slight inferiorly directed lip near the inion) and the very modest development of the nuchal torus. He described the torus as continuous from asterion to asterion, but reexamination of the preserved portion of the torus indicates that it reduced in prominence as it extended laterally, and was clearly developed only along the middle portion of the occipital bone, as also noted by Bräuer (1984; see also Bräuer and Mabulla, 1996). In these published descriptions, however, there is no explicit mention of the suprainiac region other than to note the modest size of the supratoral sulcus associated with the small nuchal torus.

As is evident in Figure 2, the suprainiac region of Eyasi 1 exhibits a distinct, clearly bounded, transversely oval fossa which is irregularly rugose and porous along the floor of the fossa. It is bordered below by the modest central portion of the nuchal torus, and is bounded superiorly by a rounded elevation arcing over the fossa and blending above into the middle of the occipital plane. The dimensions of the fossa, compared to the same measurements taken on a series of resin casts of mature Middle and Late Pleistocene Neandertal lineage specimens (Ta-



Fig. 2. Detail of Eyasi 1 iniac and suprainiac region, illustrating suprainiac fossa. Image was taken relative to plane of fossa, such that it is modestly more vertically oriented than Figure 1. Scale in centimeters.

ble 1), place the dimensions of the Eyasi 1 fossa below the Neandertal lineage means, but well within its range of variation. Consequently, by the criteria which are normally applied to Neandertals (e.g., Hublin, 1978a; Santa Luca, 1978; Arsuaga et al., 1997), this feature can only be classified as a suprainiac fossa. To exclude it as such would require categorizing a number of Late Pleistocene European and western Asian Neandertal lineage specimens as also lacking a suprainiac fossa.

It should be noted that the fragmentary Eyasi 2 and 4 occipital bones exhibit nuchal torus morphologies similar to that of Eyasi 1 (despite some variation in overall occipital curvature and torus prominence), but they are insufficiently preserved to indicate their configurations at inion and in the suprainiac region (Bräuer and Mabulla, 1996).

DISCUSSION

It is therefore apparent that at least one of the later Middle Pleistocene African late archaic humans exhibits the suite of occipital features considered uniquely derived for the Neandertals. These include the absence of an external occipital protuberance, a modest nuchal torus limited principally to the central region of the occipital bone, and a distinctive, transversely elongated oval suprainiac fossa (although Arsuaga et al. (1997) considered the first feature to be ancestral). By the probable age of Eyasi 1 in the middle or late Middle Pleistocene, this suite of morphological features was well-established among European Neandertal-lineage specimens. It is found in 18 of 21 (85.7%) European specimens between ca. 400–130 ka BP, the majority of which (13) derive from Atapuerca-SH and Krapina (81.3%

($N = 16$) without the terminal Middle Pleistocene Krapina sample). There is nonetheless considerable variation in the degree and pattern of expression of the feature in this sample (Arsuaga et al., 1997).

A review of the later Middle Pleistocene African archaic *Homo* specimens which preserve some or all of the middle occipital bone (observations from Saban, 1975; Rightmire, 1983; Bräuer and Leakey, 1986; Clarke, 1990; Hublin, 1991; Bräuer et al., 1992; personal observations on originals and casts) provides a complex picture of their nuchal and iniac morphology. An external occipital protuberance (or linear tubercle) is present on Broken Hill 1, KNM-ES 11693, and Ndutu 1, but is absent from the other African archaic *Homo* crania. There is a clear, fully transverse nuchal torus on Broken Hill 1 and Ndutu 1, but it is poorly developed and/or limited to the central portion of the occipital bone on the other specimens. In particular, however, a distinct suprainiac fossa is absent from Broken Hill (Kabwe) 1, Irhoud 1 and 2, Laetoli 18, and Ndutu 1, even though the region is partially damaged on Broken Hill 1 and Irhoud 1. It is also too damaged for categorization on the KNM-ER 3884 cranium. However, KNM-ES 11693 and the incomplete occipital bone from the adolescent Rabat 1 exhibit suggestions of suprainiac fossae.

The Eliye Springs cranium has a small (10 mm wide and 4 mm high) distinct oval depression located 20 mm above the inion, which Bräuer and Leakey (1986, p. 303) noted “probably corresponds to a suprainiac fossa,” although Bräuer (personal communication) noted that it may not be homologous with Neandertal suprainiac fossae. Certainly, its small size and more superior location than most suprainiac fossae call into question whether this depression on KNM-ES 11693 is a suprainiac fossa. Moreover, the pathological condition of the KNM-ES 11693 neurocranial vault (Bräuer et al., 2003) calls into question whether the external morphology of its vault can be used for comparative morphological assessments. Along its median break above the inion, the Rabat 1 occipital bone exhibits the rugose and porous bone that is characteristic of a suprainiac fossa, but the original shape of the fossa is uncertain, and it does not appear to have been transversely oval (Saban, 1975).

It is therefore the presence of a marked, reasonably large, distinctive transversely oval suprainiac fossa on Eyasi 1, albeit in combination with its nuchal torus and external iniac morphology, which separates it from the Broken Hill, Irhoud, Laetoli, and Ndutu remains (and possibly Rabat 1), and aligns it with the Neandertals. Given the otherwise non-Neandertal morphology of the remaining portions of the Eyasi 1 neurocranium, in which it generally resembles other sub-Saharan Middle Pleistocene specimens (Howell, 1978; Protsch, 1981; Bräuer, 1984; Bräuer and Mabulla, 1996), these observations on its occipital morphology suggest that there was more variation in some of these purport-

TABLE 1. Transverse breadth and vertical height of Eyasi 1 suprainiac fossa, and comparative data for sample of late Middle and Late Pleistocene Neandertal crania¹

	Breadth (mm)	Height (mm)	Area (mm ²)
Eyasi 1	30.5	12.5	299.5
Neandertals	40.0 ± 7.4 (10)	17.5 ± 3.5 (11)	543.1 ± 171.0 (10)
Eyasi 1 z-scores	1.28	1.43	1.43

¹ Area is computed using an ellipse formula. For Neandertal sample, mean ± standard deviation (N) is provided. Z-scores are number of standard deviations between Eyasi 1 value and Neandertal mean. Eyasi 1 measurements are approximate (±0.5 mm), given irregular margins of suprainiac fossa.

TABLE 2. Fisher's exact test P-values, calculated as an exact value (Mehta and Patel, 1999), for European vs. African Middle Pleistocene samples with respect to presence/absence of suprainiac fossa¹

	Including Krapina (N = 21)	Without Krapina (N = 16)
Ignoring KNM-ES11693 and Rabat 1 (N = 6)	0.004	0.011
Including Rabat 1 but not KNM-ES 11693 (N = 7)	0.009	0.024

¹ Using a sequentially rejective Bonferroni multiple comparison, all remain significant at $\alpha = 0.05$.

edly regional characteristics of later archaic *Homo* than was previously recognized.

Nonetheless, given current samples of middle and late Middle Pleistocene specimens, the African vs. European distributions of the presence of a suprainiac fossa remain significantly different, whether or not the terminal Middle Pleistocene Krapina sample is included (Table 2). Even if Rabat 1 is included in the African sample as possessing suprainiac fossae, the samples remain significantly different at $P < 0.05$ (Table 2); the Eliye Springs specimen is not included in this assessment, given its ambiguous morphology and pathological condition.

Given that the suprainiac fossa has remained prominent in discussions of Middle and Late Pleistocene European human phylogeny, it is appropriate to query whether this observation changes our current perceptions of either late Middle or Late Pleistocene human phylogeny. Current models of later archaic *Homo* regional differentiation through isolation-by-distance, such as the accretion model for Europe (Hublin, 1998; see also Stringer and Hublin, 1999; Hawks and Wolpoff, 2001), remain valid, since they address the accumulation of regional contrasts in terms of shifting frequencies of traits. Discussions of modern human phylogenetic emergence within the Neandertal range are unaffected, since the concern there is whether Neandertal features (such as suprainiac fossae), that are absent from representatives of the ancestral northwestern Old World early modern humans (e.g., Omo-Kibish 1 and the Qafzeh and Skhul samples), appear in earlier Upper Paleolithic early modern humans in Europe and western Asia (e.g., Frayer, 1993; Sládek, 2000; Trinkaus and Zilhão, 2002). The presence of the suite of "Neandertal" occipital features in Eyasi 1 serves mainly to focus the discussion of later Pleistocene human re-

gional differentiation and evolution to the evaluation of distributional patterns.

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