Journal of Human Evolution 57 (2009) 786–804

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

A comparative study of frontal bone morphology among Pleistocene hominin fossil groups

Sheela Athreya

Department of Anthropology, Texas A&M University, 4352 TAMU, College Station, TX 77843, United States

ARTICLE INFO

Article history:
Received 29 October 2007
Accepted 15 February 2009
Available online xxx

Keywords:
Supraorbital torus
Pleistocene *Homo*
Temporal variation
Multinomial logistic regression
Elliptical Fourier analysis

ABSTRACT

Features of the frontal bone that are conventionally used to distinguish among fossil hominin groups were quantitatively examined. Fifty-five fossil crania dating from the early to the late Pleistocene were analyzed. Using a modified pantograph, outlines of the frontal bone were collected along the midsagittal and two parasagittal planes. The profile from nasion to bregma, as well as two profiles above the medial and lateral sections of the orbit, respectively, extending from the orbital margin to the coronal suture were traced. The outlines were measured using Elliptical Fourier Function Analysis (EFFA), which enabled a quantification of aspects of the frontal bone that have historically been described primarily in nonmetric or linear terms. Four measurements were obtained: 1) overall morphology as expressed in the Fourier harmonic amplitudes; 2) maximum projection of the supraorbital torus at three points along the browridge (glabella and the medial and lateral aspects of the torus above the orbit); 3) maximum distance of the frontal squama from the frontal chord, capturing forehead curvature; and 4) nasion-bregma chord length. The results indicate that the midsagittal profile is significantly different among all Pleistocene groups in analyses that include both size and shape, as well as size-adjusted data. *Homo erectus* is significantly different from the late Pleistocene groups (Neandertals and early modern *H. sapiens*) in glabellar projection. Anatomically modern humans are significantly different from all other groups in both raw and size-standardized analyses of all three outlines that captured overall morphology, as well as forehead curvature and lateral supraorbital torus prominence, and middle Pleistocene *Homo* are significantly different in both medial and lateral overall parasagittal form. However, for the majority of analyses there were no significant differences among the Pleistocene archaic groups in supraorbital torus projection, frontal squama curvature, nasion-bregma chord length, or overall frontal bone morphology.

Introduction

The morphology of the frontal bone, and the supraorbital torus in particular, has been recognized as a distinctive feature of archaic Pleistocene hominins relative to modern humans since the earliest days of paleoanthropology. The original Neandertal fossil, for example, was immediately considered notable due in large part to its unusual browridges (Boule and Vallois, 1957; Trinkaus and Shipman, 1992). Both Schwalbe (1899, 1901, 1906 in Cunningham, 1908) and his student Weidenreich (1941) commented extensively on the distinctiveness of the frontal bone in premodern *Homo*, and Weidenreich (1947) considered this region to be important in the assessment of the relationship of middle Pleistocene *Homo* to Neandertals.

Since that time, features of the frontal bone have been operational in definitions of various Pleistocene hominin species (Clark, 1955; Howells, 1980; Stringer, 1984; Lieberman et al., 2002) and are often a major component of descriptions of new fossil finds (e.g., Boule, 1913; Heim, 1976; Conroy et al., 1978; Stringer et al., 1979; Arsuaga et al., 1997). Traits such as supraorbital torus morphology have been used to characterize entire regional populations, time periods, or lineages (Vallois, 1954; Howells, 1980; Bräuer, 1984; Rightmire, 1984).

In that context, this study offers a quantitative assessment of the strength of these characterizations using a broad sample of Pleistocene hominin fossils and evaluates aspects of the frontal bone that historically have been difficult to measure. Using Elliptical Fourier Analysis to quantify its curvature, a statistical evaluation of the differences in the frontal bone morphology of various Pleistocene hominin groups, particularly those dated to the middle and late Pleistocene, is undertaken in order to identify which aspects

---

E-mail address: athreya@tamu.edu

0047-2484/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jhevol.2009.09.003

are distinctive or even diagnostic between certain groups or time periods.

Previous frontal bone studies

Because of the frontal bone's unusual morphology and the relative paucity of craniometric landmarks on it, accurate quantitative descriptions of its facial-skeletal (supraorbital torus) and neurocranial (frontal squama) parts using standardized linear measurements have been difficult to obtain. The morphology lends itself more to nonmetric or descriptive analyses, although a handful of researchers have used morphometric analyses of its curvilinear aspects (Vacca and Pesce Delfino, 1991; Dean, 1993; Seidler et al., 1995, 1997; Bookstein et al., 1999; Bruner et al., 2004). Recently the availability of computed tomography (CT) scans has also enabled researchers to capture profiles of interest and study both endo- and ecto-cranial aspects of this bone (Seidler et al., 1997; Prossinger et al., 2003; Bruner and Manzi, 2005, 2007).

These recent studies build upon a set of structural/functional studies that were done in the 1980s and 1990s that provided information on potential sources of variation in frontal bone morphology. Models were developed that sought to explain the ontogenetic basis of frontal morphology, particularly the supraorbital torus, on the basis of a number of variables including craniofacial architecture (Cunningham, 1908; Moss and Young, 1960; Shea, 1986; Ravosa, 1988, 1991a,; Enlow and Hans, 1996; May and Sheffer, 1999; Lieberman, 2000; Fiscella and Smith, 2006), allometric changes related to encephalization (Weidenreich, 1941; Leigh, 1992; Ruff et al., 1997), or biomechanical and functional stressors. For the latter, some researchers (Endo, 1970; Oyen et al., 1979; Russell, 1985; Hilloowala and Trent, 1988) have argued that loading during mastication influences frontal bone morphology. However, a series of analyses using *in vivo* bone strain studies have provided evidence against this hypothesis (Picq and Hylander, 1989; Hylander et al., 1991) in primates, and while some have not eliminated this model entirely from consideration (Prossinger et al., 2000), a comprehensive review of potential sources of browridge variation by Lieberman (2000) suggests that browridge growth is not a plastic response to mechanical loading during mastication. Finally, some studies have proposed the idea that systemic developmental changes, including those that contribute to overall skeletal robusticity, could explain the presence of a prominent browridge (Tillier, 1977; Hublin, 1987; Lahr and Wright, 1996; Lieberman, 1996).

The results of these studies suggest that morphological variation in the supraorbital morphology of human and nonhuman primates is almost certainly not a plastic, *in vivo* response to high loading levels, and therefore, is not primarily a reflection of differences in activity patterns or levels among individuals (Ravosa, 1988, 1991a, b; Lieberman, 2000). Supraorbital morphology is most likely related to changing spatial relationships between the neurocranium, splanchnocranium, and basicranium (Lieberman, 2000; Fiscella and Smith, 2006). Studies focusing on modern humans similarly support this model (Vinyard and Smith, 1997, 2001), as do those investigating the emergence and definition of modern human craniofacial form (Lieberman, 2000; Lieberman et al., 2002; Tillier, 2007; Pearson, 2008). For the purposes of this study, these previous analyses provide an indication as to the source of differentiation in the traits being tested. If certain defining traits in frontal bone morphology are found for a particular group, they most likely reflect systemic ontogenetic differences.

In addition to biomechanical and craniofacial architecture studies, the frontal bone has also been included in studies that examine the evolutionary relationships of hominin groups throughout the Pleistocene. Several studies have used characters on the frontal bone to support competing interpretations of the fossil record (Rightmire, 1985; Spitery, 1985; Bräuer and Mbua, 1992; Smith, 1992; Lahr, 1994; Lieberman, 1995). Most of these studies consider supraorbital torus morphology in particular to be distinctive, even diagnostic, between African and Asian *H. erectus*, Neandertals, and modern humans (Cunningham, 1908; Weidenreich, 1951; Lahr and Wright, 1996). In addition, definitions of fossil groups often include characters on the frontal bone (Weidenreich, 1947; Howells, 1980; Day and Stringer, 1982). While many of the traits are neither unique to an individual fossil population, nor independent of each other (Bräuer and Mbua, 1992), they have nonetheless been interpreted by some as being phylogenetically significant (Spitery, 1985; Lieberman, 1995).

Many of the studies that make phylogenetic inferences have been based primarily on qualitative descriptions of the frontal bone, although a few are based on quantitative analyses of the endo- and ectocranial surface of the bone (Seidler et al., 1997; Prossinger et al., 2003; Bruner and Manzi, 2005, 2007). This study builds on this previous research in three ways. First, it expands the existing database to provide information on several parasagittal dimensions of the entire frontal bone, as well as standardized projection measurements of the supraorbital torus. Second, the focus here is not on one individual or a small group of fossils, but a broad sample of Pleistocene specimens. Third, group differences (both temporal and regional), as well as intra-group variation, are explored in order to provide a detailed picture of the nature of frontal bone variation throughout the Pleistocene.

Fossil sample

Fifty-five fossils were analyzed (Table 1**)**. Half of these ($n = 27$) were original specimens, and the remainder were research-quality casts housed at various museums, as well as the research collection at Washington University in St. Louis, MO. The casts are considered good representations of the original fossil morphology based on a strong relationship between linear measurements taken on the casts and those published for the originals. A comparison between the frontal chord values generated by this data collection method and those obtained from the original fossils, following published monographs and papers, is presented in the Supplemental Online Material (SOM; supplementary data associated with this article can be found in the online version at doi:10.1016/j.jhevol.2009.09.003). The results show that the average difference between the two is 1.55 mm, or a 1.35% difference.

The specimens date from the early to late Pleistocene (1.8 Ma–19 ka), with the majority from the middle and late Pleistocene. Only adult, nonpathological specimens were used. Age was assessed using the original descriptions of the fossils. Due to the difficulty in sexing fossil hominins—and in particular the tendency to use supraorbital torus robusticity as a measure of sex—the sex of the fossils was not taken into account so as to avoid potential circular reasoning.

Since one goal of this study was to examine differences between fossil groups, it was necessary to develop criteria by which the specimens would be grouped together. The ongoing debates regarding the taxonomy and systematics of Pleistocene hominins (Mayr, 1963; Howells, 1980; Stringer, 1984; Wolpoff, 1989; Kramer, 1993; Wood and Collard, 1999; Rightmire, 2001b; Tattersall and Schwartz, 2006; Trinkaus, 2007) mean that such an exercise will inevitably yield groups that are objectionably defined to some. Three taxa that are widely accepted as valid in paleoanthropology are *Homo erectus* sensu stricto, Neandertals, and anatomically modern *Homo sapiens* (AMHS). Regardless of what their relationship to other fossil groups is believed to be, most scholars agree upon the assignment of certain Chinese and Indonesian specimens