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Cranial vault thickness in primates: *Homo erectus* does not have uniquely thick vault bones

Lynn E. Copes[*, 1], William H. Kimbel

Institute of Human Origins and School of Human Evolution and Social Change, Arizona State University, PO Box 874101, Tempe, AZ 85287-4101, USA

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A B S T R A C T

Extremely thick cranial vaults have been noted as a diagnostic characteristic of *Homo erectus* since the first fossil of the species was identified, but relatively little work has been done on elucidating its etiology or variation across fossils, living humans, or extant non-human primates. Cranial vault thickness (CVT) is not a monolithic trait, and the responsiveness of its layers to environmental stimuli is unknown.

We obtained measurements of cranial vault thickness in fossil hominins from the literature and supplemented those data with additional measurements taken on African fossil specimens. Total CVT and the thickness of the cortical and diploë layers individually were compared to measures of CVT in extant species measured from more than 500 CT scans of human and non-human primates.

Frontal and parietal CVT in fossil primates was compared to a regression of CVT on cranial capacity calculated for extant species. Even after controlling for cranial capacity, African and Asian *H. erectus* do not have uniquely high frontal or parietal thickness residuals, either among hominins or extant primates. Extant primates with residual CVT thickness similar to or exceeding *H. erectus* (depending on the sex and bone analyzed) include *Nycticebus coucang*, *Perodicticus potto*, *Alouatta caraya*, *Lophocebus albigena*, *Galago alleni*, *Mandrillus sphinx*, and *Propithecus diadema*. However, the especially thick vaults of extant non-human primates that overlap with *H. erectus* values are composed primarily of cortical bone, while *H. erectus* and other hominins have diploë-dominated vault bones. Thus, the combination of thick vaults comprised of a thickened diploë layer may be a reliable autapomorphy for members of the genus *Homo*.

1. Introduction

In 1891, Eugene Dubois discovered, near the village of Trinil on the island of Java, the first specimen, a calotte, of the extinct hominin species that would come to be known as *Homo erectus*. Among the characters often used to diagnose the species is a thickened cranial vault (Dubois, 1937; Weidenreich, 1943; Andrews, 1984; Bilsborough and Wood, 1988; Antón, 2002, 2003), which has been considered unique among primates and even mammals (Weidenreich, 1943; Kennedy, 1991). In fact, however, because cranial vault thickness (CVT) is a composite of the thickness of each layer of vault bone (inner and outer cortical tables, sandwiching the spongy diploë), and vault bone composition across extant and extinct primates has never been thoroughly investigated, it remains unclear if a thickened cranial vault in *H. erectus* actually represents a unique trait.

Diploë and cortical bone may be functionally independent, as diploë likely responds to red-blood-cell levels and cortical bone is likely more responsive to mineral-ion levels (Kennedy, 1991). There are additional potentially important reasons to measure the thickness of the diploë layer separately from the total thickness. First, some have suggested that diploë functions to protect the brain by increasing the thickness of the vault while reducing its weight and without proportionally reducing its strength (Anzelmo et al., 2015), so it is possible that selection might act to maintain the ratio of diploë to total thickness, rather than act on absolute thickness of any single layer. Second, it has been shown that the three layers of vault are somewhat independent, with the inner table more responsive to brain growth and the outer table more responsive to muscular loading (Moss and Young, 1960).

Most of the descriptions of modern human cranial robusticity come from clinical studies focused, for example, on quantifying mean CVT for surgical purposes. Published measures of adult cranial vault thickness range from 1.96 mm to 10.6 mm depending on

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[*] Corresponding author.
E-mail address: lynn.copes@quinnipiac.edu (L.E. Copes).
[1] Current address: Frank H. Netter MD School of Medicine, Quinnipiac University, 275 Mt. Carmel Ave, NH-MED, Hamden, CT 06518, USA.

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location on the vault (Adeloye et al., 1975; Brown, 1994; Hwang et al., 1997, 1999; Lynnerup, 2001; Jung et al., 2003; Moreira-Gonzalez et al., 2006). Allograft cranial-bone transplants using cadaver bone have become more common and have spurred increased research on the variation in CVT across the vault. For example, thickness purportedly increases from anterior to posterior across the parietal bone (Moreira-Gonzalez et al., 2006). Many investigators pick specific osteometric landmarks to measure, and most agree that *glabella* is the thickest point on the vault, followed by *vertex*, *opisthion*, and finally *euryon* (Anderson, 1882; Getz, 1960; Adeloye et al., 1975; Hwang et al., 1997, 1999; Friedland and Michel, 2006).

In several recent publications, variation in CVT across the vault (and even across single vault bones) has been assessed using mesh, grid, or semi-landmarks. These papers have found that single-landmark measurements do not capture the true variation of vault thickness (Balzeau, 2013; Marsh, 2013; Anzelmo et al., 2015).

Other work has addressed the question of the ontogeny of CVT in modern *Homo sapiens*, and reported that thickness increases in early life in step with increases in endocranial volume (Anzelmo et al., 2015) until the age of 20 and thereafter remains unchanged through adulthood (Lynnerup, 2001). A lack of an intraspecific scaling relationship between CVT and cranial capacity is not surprising, given frequent weakening of allometric relationships with decreasing taxonomic level (i.e., from order to species) (Copes and Schwartz, 2010).

A few workers have investigated the thickness of the diploë, either relative to total CVT or to age in modern humans. Lynnerup et al (2005) found a significant correlation between diploë thickness and total CVT in an autopsy sample of 64 modern humans, but failed to find significant associations between diploë thickness and age, height, or weight. Diploë thickness was measured on x-rays of trephined biopsies taken at four locations on dried skulls. Hatipolgu et al (2008) measured diploë thickness at seven landmarks on MR scans of 107 live adult subjects and reported significant linear correlations between age and diploë thickness at each landmark.

Variation in CVT among non-human primates has, to the best of our knowledge, been thoroughly investigated in only one study (Gauld, 1996). The goal of Gauld's study was to determine 1) if primate species are characterized by consistent patterns of interspecific variation in cranial thickness; 2) whether patterns of thickness in hominin species are concordant with those of other primates; or 3) whether deviations from typical patterns of cranial thickness occur with predictable regularity. Gauld chose to compare CVT with body mass. One of the most important aspects of an organism's biology is its body mass, which is highly correlated with certain key adaptations, including diet, locomotion, energetics, ecology, life history, morphology, and physiology. Body mass is thus one of the most commonly used metrics for exploring morphological allometric relationships.

Gauld (1992) found statistically significant relationships between CVT and body mass across her anthropoid sample (r values ranging from 0.94 to 0.97). She analyzed the relationships between body mass and CVT at different landmarks separately (rather than averaging all CVT measures), and in extant anthropoids the relationships were mostly positively allometric (slopes ranging from 0.40 to 0.53, where the slope for isometry is 0.33). Gauld did not test the relationship between vault or brain size and CVT, nor was she able to examine each bone layer individually. Her sample also did not include strepsirrhines.

When Gauld (1992) included *Australopithecus africanus*, “archaic” *H. sapiens*, and various regional groups of *H. erectus* in the regressions, slopes dramatically increased compared to the extant anthropoid analyses (0.45–2.63). Gauld's body masses of fossil hominins came from McHenry (1992) and Rightmire (1986), both of whom used postcranial size regressions to arrive at their estimates. While such analyses are ubiquitous in paleoanthropology, the use of cranial features such as cranial capacity or orbit size to estimate body mass have been argued to be both more practical (given the relative dearth of associated cranial and postcranial remains in the hominin fossil record) and as accurate as estimates relying on postcranial element scaling (Aiello and Wood, 1994; Kappelman, 1996; Plavcan, 2003).

Antón et al. (2007) explored the relationship between CVT at multiple landmarks and cranial capacity in fossil hominins. They reported a significant association within *H. erectus* between cranial capacity and bone thickness at *lambda* ($r^2 = 0.357$, slope $= 0.862$), thickness at the external occipital protuberance ($r^2 = 0.280$, slope $= 0.930$), and thickness at *asterion* ($r^2 = 0.509$, slope $= 1.61$). They reported no significant relationship between cranial capacity and thickness at midfrontal, *bregma*, or the parietal eminence.

Balzeau (2006, 2013) is one of the few workers to examine diploë thickness in fossil hominins. In 2006, he measured diploë and total CVT along the mid-sagittal plane from CT scans of four Ngandong and Sambungmacan fossils of *H. erectus* and compared them to measures taken on 12 modern *H. sapiens*. He produced a map of outer table, diploë, and inner table thickness along the mid-sagittal plane from *glabella* to opisthocranion, and was able to determine that whereas diploë constituted the majority of frontal bone thickness in most of the specimens he examined, all three layers contributed approximately equally to occipital thickness. Diploë thickness in the parietal region was not measurable, due to the presence of the sagittal suture. In his 2013 paper, Balzeau used a similar protocol to measure total CVT and quantify sagittal keeling in 120 specimens of recent and archaic *H. sapiens* and extant *Pan paniscus*, but he did not measure the thickness of each table separately.

Given previous suggestions regarding CVT in *H. erectus*, we here test two hypotheses:

1) Relative CVT is uniquely high in African and Asian *H. erectus* compared to other extant human and non-human primates; and
2) The vault composition of African and Asian *H. erectus* (quantified as the ratio of diploë to total thickness) is unique among primates.

Data collected for this endeavor allow for a previously impossible in-depth exploration of variation in CVT in the fossil record and across extant primates. These data will also be useful to test mechanistic hypotheses for increased CVT in the future.

2. Materials and methods

2.1. Non-human primate sample

A total of 452 non-human primate skulls housed at the Museum of Comparative Zoology and the Peabody Museum of Anthropology at Harvard University were microCT (μCT) scanned at Harvard's Center for Nanoscale Systems (CNS). From this sample, 255 female and 111 male adults were included in these analyses. Adulthood was determined by full eruption of the permanent third molars and canines. Any specimen with signs of bony pathology that might have impacted vault or facial growth was excluded. Specimens listed as captive were also not included. Specimens included in the final analyses came from 53 species representing all major families in the order Primates. The only major groups not included are *Phaner*, *Mirza*, *Allocebus*, and *Cheirogaleus* of the Cheirogaleiidae, *Lepilemur* of the Lepilemuridae, or any genus of Daubentoniidae or Tarsiidae. A summary of the sample size by sex per species is listed in Table 1.