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2   **TITLE: A paleoneurological survey of *Homo erectus* endocranial metrics**

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20 **Running title**: Paleoneurology of *Homo erectus*

21 **Keywords**: paleoneurology; endocasts; endocranial morphology; human brain

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23

24 **Abstract**. The taxonomic debate on the phylogenetic coherence of *Homo erectus* as a

25 widespread intercontinental species is constantly put forward, without major

26 agreements. Differences between the African and Asian fossil record as well as

27 differences between the Chinese and Indonesian groups (or even within these two

28 regions) have frequently been used to propose splitting taxonomical alternatives. In this

29 paper we analyze the endocranial variation of African and Asian specimens belonging

30 to the hypodigm of *Homo erectus sensu lato*, to assess whether or not these groups can

31 be characterized in terms of traditional endocranial metrics. According to the basic

32 endocast proportions the three geographic groups largely overlap in their phenotypic

33 distribution and morphological patterns. The morphological affinity or differences

34 among the specimens are largely based on brain size. As already evidenced by using

35   other cranial features, traditional paleoneurological metrics cannot distinguish possible

36   independent groups or trends within the Afro-Asiatic *Homo erectus* hypodigm.

37   Endocranial features and variability are discussed as to provide a general perspective on

38   the paleoneurological traits of this taxon.

39

40   **1. INTRODUCTION**

41

42   Although the description and discovery of fossils associated with *Homo erectus*

43   hypodigm dates back to more than one century, the taxonomic status of this extinct

44   human group remains debated. Apart from problems associated with the never-ending

45   issue on recognition of the species concept in paleontology (e.g., Tattersall, 1986;

46   Turner, 1986; Kimbel, 1991; Plavcan and Cope, 2001; Holliday, 2003; Bruner, 2012),

47   the variation of the so-called *Homo erectus sensu lato* is discussed at two different

48   biogeographical scales. First, it has been hypothesized that the African and Asian

49   populations may belong to different species, with the former described as *H. ergaster*

50   Groves and Mazak, 1975 (see also Wood, 1991; Wood and Collard, 1999). Second, the

51   few populations known in Asia display a marked variability, suggesting that they may

52   belong to isolated and independent groups (Kidder and Durband, 2004). Taking into

53   account the small samples and few individuals available on such a large geographical

54   and chronological scale, many of the questions related to the fine taxonomic status of

55   these populations will probably remain without a definite answer.

56   Despite the fact that there is general agreement on the separation between *H. erectus*

57   and more derived species like *H. heidelbergensis* (Rightmire, 2004, 2008, 2013;

58   Stringer, 2012), the internal variation of the former taxon is hard to classify. In some

59   cases the morphological and phylogenetic boundaries of *H. erectus* are incredibly

60   blurred, displaying in the Dmanisi individuals, depending upon the specimen, characters

61   ranging from earlier species like *H. habilis* (Rightmire et al., 2006) to the most derived

62   Asian sample (Grimaud-Hervé and Lordkipanidze, 2010).

63   The large intra-group variability of this taxon on the one hand, and a lack of patent

64   geographical or chronological trends on the other, leaves most of the phylogenetic

65   problems still open (e.g., Bräuer, 1994; Wood, 1994; Schwartz, 2004; Gilbert and

66   Asfaw, 2008). African and Asian specimens show some metric and non-metric

67   differences in their cranial morphology (Mounier et al., 2011). Nonetheless, such

68   variation can be easily interpreted as the results of a single but widely dispersed

69   polytypic species, formed by regional groups which underwent isolation in both time

70   and space (Rightmire, 1986, 1998; Antón, 2002, 2003; Baab, 2008).

71   Although cranial capacity has been largely studied in these early human groups, the

72   anatomical endocranial traits and general brain proportions have been less investigated.

73   Figure 1 shows some representative specimens from Asia and Africa, with their cranial

74   and endocranial reconstructions.

75   In terms of endocranial morphology *H. erectus sensu lato* displays small cranial

76   capacity (the average figure spanning between 800 and 1000 cc), flat and narrow frontal

77   areas, a parasagittal depression at the upper parietal areas associated with the midline

78   keeling, maximum endocranial width at the posterior temporal lobes, bulging occipital

79   areas, cerebellar lobes in a posterior position, and scarcely reticulated traces of the

80   middle meningeal vessels (Fig. 2; see Weidenreich 1943; Holloway, 1980, 1981;

81   Grimaud-Hervé, 1997, 2004, 2007; Holloway et al., 2004; Wu et al., 2006; Wu and

82   Schepartz, 2010). When compared with earlier hominids they show a relative widening

83   of the temporal and lower parietal areas (Holloway, 1995; Tobias, 1995; Bruner and

84   Holloway, 2010). When compared with large-brained humans (i.e., modern humans and

85   Neandertals) they display flattened parietal lobes, relatively narrow endocrania, and

86   most of all relatively narrow frontal areas (Bruner and Holloway, 2010).

87   The present paper is aimed at reviewing the *H. erectus* paleoneurological metric

88   variation, providing a general perspective of the *H. erectus* endocranial proportions.

89   Traditional arcs and diameters commonly used in paleoneurology will be employed on

90   the endocasts of African, Chinese, and Indonesian specimens representative of the *H.*

91   *ergaster* and *H. erectus* hypodigms, to quantify their variability, to disclose the

92   underlying general structure, and to verify possible geographical differences and

93   patterns, independently from their taxonomic interpretations.

94

95   **2. MATERIALS AND METHODS**

96

97   *2. 1 Sample*

98   Diameters and arcs have been measured on 23 *Homo erectus* endocasts (Table 1).

99   Specimens were selected according to their degree of completeness, trying to maximize

100   the number of available variables and the reliability of the endocranial morphology. The

101   sample includes specimens from Africa (N = 6), China (N = 8), and Indonesia (N = 9).

102   The African sample includes specimens usually assigned to *H. ergaster* (KNM-ER

103   3733, KNM-ER 3833, WT 15000) and specimens displaying more derived characters

104   like Daka, Salé, and OH9. According to the available metrics, KNM-ER 3733, KNM-

105   ER 3883, and WT15000 (Kenya) display similar endocranial morphology (Begun and

106   Walker, 1993). OH9 (Tanzania) displays features affine to the Asian morphotypes

107   (Wood, 1994). KNM-ER 3733 and KNM-ER 3883 endocasts show a cranial capacity of

108   804 cc 848 cc respectively, but they both have poor preservation of the internal bony

109   table. The WT 15000 and OH 9 specimens have volumes of 900 cc and 1059 cc

110   respectively, but with major damage at the cranial base in WT 15000 and, despite the

111   reliable reconstruction, large missing portions for OH9. In this group, the most complete

112   and best preserved of these specimens is the Daka cranium (Gilbert et al., 2008), with an

113   estimated endocranial volume of 998 cc. The skull and endocast from Daka (Ethiopia),

114   despite a general affinity with *H. erectus*, display many specific traits like the large

115   browridge and domed parietal bosses (Gilbert and Asfaw, 2008). Despite the lack of

116   agreement on its taxonomic status, the endocast of Salé (Morocco) has been used as

117   reference for the basic *Homo* endocranial form because of its standard human

118   morphology and absence of any visible derived traits (Bruner, 2004). Accordingly, we

119   have included this specimen in the analysis, to be compared with the rest of the African

120   sample.

121   The Indonesian record is limited to the island of Java. The sample includes specimens

122   from the four main Javanese sites: Sangiran, Trinil, Ngandong and Sambungmacan.

123   The sample spans from around 1.6 Ma for the oldest skull from the Pucangan layer of

124   Sangiran dome to 70-40 Ka for the most recent found in Ngandong site along the Solo

125   River (Sémah et al. 2000; Yokoyama et al. 2008). Sangiran and Trinil display similar

126   cranial morphology, sharing also the oldest chronology and smaller cranial capacity

127   (Rightmire, 1988; Antón, 2002). The average estimated cranial capacity is 949 cc. The

128   most recent Javanese *H. erectus* group include the specimens from Ngandong and

129   Sambungmacan (Yokoyama et al. 2008). The average estimated cranial capacity is 1085

130   cc. The endocranial shape is more ovoid, with wider frontal lobes. Sambungmacan 3

131   displays a more globular braincase when compared with the platycephalic morphology

132   of other *Homo erectus* specimens (Broadfield et al., 2001; Delson et al., 2001), as

133   Sambungmacan 4 (Baba et al, 2003). Apart from the relationships between the

134   Indonesian population and the rest of the hypodigm, there is also debate on whether or

135   not the most recent specimens from the sites of Ngandong and Sambungmacan could be

136   a distinct taxon, namely *H. soloensis* (Zeitoun et al., 2010).

137   The Chinese sample is largely represented by the Zhoukoudian specimens. Average

138   cranial capacity is estimated to be 1058 cc, ranging from 915 ml (ZKD III) to 1225 ml

139   (ZKD XII). The Zhoukoudian specimens come from a single locality I, Longgushan, in

140   the north of China. Electron Spin Resonance (ESR) dating of mammal teeth suggest a

141   geological dating of 0.28 – 0.58 Ma from the upper to lower strata (Grün et al., 1997).

142   More recently, thermal ionization mass spectrometric (TIMS) 230Th/234U dating on

143   intercalated speleothem samples suggests that the age of the ZKD fossils ranges from

144   0.4 to 0.8 My (Shen et al., 2009). We also included the endocast from Hexian and

145   Nanjing 1. The Hexian specimen came from Longtandong, in southern China (Wu and

146   Dong, 1982). An age of 412 ka was estimated based on ESR and U-series analyses

147   (Grün et al., 1998). Zhoukoudian and Hexian endocasts share most of the general *H.*

148   *erectus* archaic traits, and they also display a more prominent projection of the occipital

149   lobes, with a patent midsagittal flexion at the parieto-occipital junction. Hexian also

150   shows a relatively wider and ovoid endocranial shape, contrasting with the relatively

151   long and narrow morphology of the Zhoukoudian endocasts. Overall, Hexian endocast

152   resembles the Zhoukoudian ones both for the general morphology and for the metric

153   patterns, and their differences were suggested to be the result of local variations (Wu et

154   al., 2006). Nanjing 1 was discovered in 1993 in South China, and it is dated to 0.58-0.62

155   Ma (Wu et al., 2011). The estimated cranial capacity is 876 cc.

156

157   *2.2 Morphometrics*

158   Ten variables have been used to accounts for the general size and proportions of the

159   endocasts, representing common arcs and chords traditionally used in paleoneurology

160   (Fig. 3; for details see Bruner, 2004, Holloway *et al*., 2004, Bruner and Holloway,

161   2010): basion-bregma (BB); biasterionic chord (BAC); frontal width (FW); hemispheric

162   length lateral arc (HLL); hemispheric length chord (HLC); hemispheric length dorsal

163   arc (HLD); maximum cerebellar width (MCW); maximum width arc (MWA);

164   maximum width chord (MWC); vertex-lowest temporal (VT). These variables have

165   been selected according to their availability in the sample, so as to optimize the number

166   of specimens to be compared in the analysis without using missing data. Nonetheless, it

167   is worth noting that paleoneurology (as all the other paleontological fields) deals

168   necessarily with reconstructed specimens, and hence the results may be partially

169   influenced by the anatomical decisions taken during the reconstruction.

170   Correlations between variables were investigated by Pearson's coefficients.

171   Hemispheric length, frontal width, and maximum width were analyzed with analysis of

172   covariance, being informative in terms of species-specific differences (Bruner and

173   Holloway, 2010; Bruner et al., 2011). A Cluster Analysis (UPGMA) was computed on

174   normalized values (z-scores), to show phenotypic similarities between specimens. The

175   dataset was analyzed by Principal Component Analysis (PCA) computed on the

176   correlation matrix, to evaluate the morphological affinity, degree of variation, and

177   patterns of covariation, within the sample. We also computed between-group PCA, to

178   evaluate intra-group variation according to inter-group covariation structure

179   (Mitteroecker and Bookstein, 2011). When dealing with small samples or other

180   statistical limits associated with the covariance structure or representativeness of the

181   sample, inferential methods like discrimination analysis or canonical variates analysis

182   may be seriously misleading. Between-group PCA allows to investigate the group

183   variation according to higher ranks covariation patterns, by using an explorative

184   ordination method, evidencing major differences among the defined groups within the

185   multivariate space (e.g., Gunz et al., 2012). Statistics were performed with PAST 2.12

186   (Hammer et al., 2001).

187

188   **3. RESULTS**

189

190   Table 2 shows the descriptive statistics for the endocranial variables. Table 3 shows the

191   correlation between variables, and the log-log correlations between variables and cranial

192   capacity. The correlations between the variables used in the present study are generally

193   moderate, with a mean coefficient of correlation $R = 0.56 \pm 0.17$. Cranial capacity is

194   correlated to all the variables, but mostly to the hemispheric length arcs and chord, as

195   well as to the frontal width ($R \approx 0.89$). Hemispheric length is therefore confirmed to be

196   a good linear proxy for brain size (Bruner, 2010). Analysis of covariance with

197   hemispheric length using frontal width and maximum width as covariate fails to

198   evidence any significant differences in both slopes and intercepts among the three

199   groups.

200   Following cluster analysis (Fig. 4), specimens are not patently grouped according to

201   their geographical origin. Two groups are mainly divided following general size,

202   separating one large-brained and one small-brained cluster.

203   After PCA, only the first three components explain more than 5% each, and are

204   furthermore above a Jolliffe threshold (Fig. 5). These values are generally used to retain

205   stable components and discard noisy vectors. However, only the first component is

206   above the broken stick threshold, thus above the probability of non-random values. This

207   first component (62% of the variance) largely polarizes the morphological space, while

208   the following two explains a much reduced percentage of variation (13% and 9%,

209   respectively). A steep change can be recognized in the scree plot after the third

210   component, with the fourth component explaining less than 5% of the variance.

211   Accordingly, we can consider here the overall resulting multivariate space formed by

212   one dominant component and two secondary components, which must be however

213   interpreted with caution. The three geographic groups largely overlap along the three

214   components (Fig. 5). Table 4 shows the loadings for the first three components.

215   PC1 is a size vector, with all the loadings increasing almost equally. This vector is

216   strongly correlated with cranial capacity (R = 0.96; p < 0.0001). PC2 is associated with

217   increase of the endocranial heights (BB, VT) and decrease of the posterior width

218   (MWC, MCW, BAC). Daka and WT15000 stand out of the general variability because

219   of their tall and narrow endocast, while Hexian exceeds the opposite pattern. PC3 is

220   associated with increase in the basicranial widths and decrease of the parietal width. All

221   the African specimens display large values for this axis, except Salé. ZKD II shows the

222   largest value along this vector, exceeding the variation of the rest of the sample. PC2

223   and PC3 are not correlated with cranial capacity. Taking into consideration the summed

224   standard deviation of each geographical group along these three axes, it can be noted

225   that the African group shows the largest variation within the morphological space

226   (5.07), followed by the Chinese group (4.21) and the Indonesian group (3.79).

227   Between-group PCA confirms a lack of differences among the three groups, even when

228   the multivariate space is obtained by their respective means (Fig. 6). In the

229   bidimensional space obtained by the correlation matrix of the three mean values, the

230   groups largely overlap, with the African sample showing the largest variation.

231

232   **4. DISCUSSION**

233

234　The taxonomic status of Afro-Asiatic *H. erectus* populations has been debated for

235　decades. From one side, some authors identify discrete differences between these two

236　groups. According to this view, the Asian populations represent a local, widespread, and

237　variable species, while the African counterpart is phylogenetically related to the

238　following speciation events associated with more derived taxa (Wood, 1992). However,

239　specimens like OH9 may suggest that the Asian morphotype could have been also

240　present in Africa, making the scenario more complex (Wood, 1994). On the other hand,

241　other authors do not recognize two different species, assuming that most of the

242　differences are due to a marked intra-specific and intra-population variability (Bräuer,

243　1994; Rightmire, 1998). The present study is aimed at providing a review of the

244　paleoneurological traits of *Homo erectus*, investigating whether traditional endocranial

245　metrics are able to reveal differences between the main geographic groups.

246　Previous analyses have shown that a large part of the endocranial form variation in non-

247　modern human taxa is mostly associated with brain size and allometric changes (Bruner

248　et al., 2003; Bruner, 2004). Along such allometric trajectory, endocasts from *H. erectus*

249　represent the smaller figures, and morphological similarities or differences are largely

250　based on size and associated shape variation. Taking into consideration that in the

251　whole genus *Homo* most of the endocranial morphological variation is size-related, it is

252　not surprising to find that also in *H. erectus* size is the major source of variability. In the

253　present analysis, size differences are actually the only robust vector of variation,

254　accounting for the 62% of the variance. The rest of the variability is associated with

255　minor covariance axes which may be influenced by the small sample size and random

256　factors. Hence, we must assume that size is the only relevant component of form

257　variation in this sample, and the rest of the variability is not the result of influent

258　morphological patterns that can patently channel and integrate the group variation.

259　There is no evidence to discard the view that the differences observed in the current

260　sample can be interpreted in terms of individual idiosyncratic differences or in terms of

261　strictly local (site-specific) traits. No clear phylogenetic or geographic patterns can be

262　evidenced, at least by using these traditional endocranial variables.

263　*H. erectus* has been hypothesized to show a trend in increasing cranial capacity not

264　because of a process of encephalization, but rather as a secondary consequence of

265　increasing body size (e.g., Holloway, 1995, 1996; Tobias, 1995; Ruff et al., 1997). It is

266　supposed that this process was somewhat progressive during time and, because of this

267　shared allometric trend, the earliest African specimens are pretty similar to the most

268 archaic Indonesian ones. This study reveals morphological similarities in the

269 endocranial proportions within and beyond this common size-related factor, but without

270 showing any recognizable structure behind this morphological affinity.

271 According to the arcs and chords used in this analysis, Daka, WT15000, and Hexian,

272 display the most divergent morphology when compared with the rest of the sample,

273 because of their vertical proportions. OH9 and Salé, despite their debated taxonomy, fit

274 within the normal *H. erectus* variability. Also Sambungmacan 3, although its endocast

275 is more globular than the rest of the Asian specimens, shows normal *H. erectus*

276 proportions when analyzed through multivariate analysis.

277 It is worth noting that the metric variables used in this study show only a moderate

278 correlation between them, suggesting once more a marked individual variability and the

279 absence of patent patterns of morphological integration. The absence of strong

280 morphological shared components (apart from size) and the idiosyncratic individual

281 variation are probably the causes of many disagreements on the interpretations of these

282 groups. That is, the fossil record is currently based on few and rather heterogeneous

283 specimens. It remains to be understood how much of this variability is associated with

284 phylogenetic differences, geographic variations, or even to limits of the reconstructions.

285 Actually, endocasts from *H. erectus* used to be largely reconstructed, because of

286 missing parts, fragmentation, and deformation. Particularly, the elements of the

287 endocranial base (temporal and cerebellar areas) are poorly preserved. Hence, apart

288 from the large geographical and chronological range, errors in estimations or

289 interpolations of the anatomical elements are supposed to introduce a further source of

290 noise within the analysis of morphological variation. In this analysis Daka, WT15000,

291 and Hexian, show an endocranial morphology that departs from the rest of the sample.

292 It must be assessed whether this is the results of a marked individual variation,

293 phylogeny, or bias in their reconstruction. Fossil reconstruction can decisively influence

294 the morphological analyses. In this sense, it is worth noting that multivariate approaches

295 (like PCA) are able not only to detect underlying patterns of variability, but also

296 departures from these patterns. Such outliers may be the result of individual variations,

297 but also specimens with biases in the interpretation of their original anatomy. Therefore,

298 multivariate statistics may also represent a very useful tool to reveal incorrect

299 reconstructions, and to investigate the reliability of fossil replicas (e.g. Neubauer et al.,

300 2012).

301 According to the distribution along the main axes of covariance, the African sample is

302 the most variable in terms of endocranial form. The Indonesian sample is the less

303 variable, and it may be hypothesized that the geographical isolation of the populations

304 occupying marginal territories may have had a role in this sense. At least in this case,

305 the magnitude of the variation basically follows the order of rough geographical

306 extension of the group areas, although no general rule can be inferred with this limited

307 number of groups and samples.

308 The issue of biological representativeness of the sample is another important limiting

309 factor in paleoanthropology. As a matter of fact, even large samples may not necessarily

310 represent a species in term of actual variation. In this case, we should for example take

311 into consideration that the available African record is very scattered in time and space,

312 while the Asian record is largely associated with a single population (Zhoukoudian).

313 Both extreme situations can introduce biases in the actual estimation of the group

314 morphology. Although a geographic comparison represents the easiest way to compare

315 *H. erectus*, we must stress that the resulting groups are not relatively homogeneous. In

316 China, the Zhoukoudian sample is different from the rest of the *H. erectus* sample,

317 while the skull from Hexian is more affine to the rest of the hypodigm (Kidder and

318 Durband, 2004). In Indonesia, as already mentioned, there are two distinct groups,

319 separated both from chronology and morphology. Finally, the African population

320 analyzed here refers to a wide geographic and chronological range, and it is possible

321 that the specimens used here can belong to different taxonomic unit. Therefore, it must

322 be taken into consideration that a general distinction among these geographical

323 categories is but a very gross separation into groups which are not expected to be

324 necessarily homogeneous in evolutionary terms.

325 The third limit of this these approaches is represented by the sample size, generally

326 hampering definite statistical conclusions. For example considering the present study, to

327 assess the differences in cranial capacity between the African and Indonesian groups

328 according to their current values and with standard thresholds ($\alpha < 0.05$ and $\beta < 0.90$) a

329 power analysis suggests the necessity of a minimum of 37 specimens per groups, to

330 reach a statistical significance. Taking into account that differences in brain volumes in

331 this case are even more obvious than other subtle metric differences in brain

332 proportions, it is evident that in this case paleontology can give only descriptive results,

333 avoiding numerical inferences. For group-wise multivariate approaches (like for

334 example Canonical variates Analysis) a rule of thumb to reach stable and reliable results

335   suggests using at least a sample of three to four times the number of variables per group,

336   which for ten variables means 30-40 specimens per group. These limits must be

337   necessarily considered when providing paleoanthropological hypotheses. Of course this

338   does not mean that we must exclude such information, but only that we have to avoid

339   strict conclusions in our analytical approaches. In the case of *H. erectus*, our 22 total

340   specimens are undoubtedly a relevant source of information, apart from being the only

341   one we have on this important extinct human taxon. Nonetheless, analyses can only

342   provide comparisons strictly referred to these specimens, avoiding generalizations,

343   stringent hypotheses, or conclusive statements.

344   Future analyses should take into account specific traits. For example, many Asian *H.*

345   *erectus* (most of all the endocasts from Zhoukoudian) have projecting occipital lobes,

346   namely their occipital lobes display a marked posterior bulging. A recent

347   comprehensive analytical review on cranial integration in *Homo erectus* suggests that

348   this feature may be allometric within the variation of this group (Rightmire, 2013).

349   However, the limited sample available does not allow a population (within-group)

350   approach in this sense. Furthermore, the occipital bulging should be however interpreted

351   more in terms of functional craniology than of brain changes. From one side, the

352   posterior fossa is part of the endocranial base, influenced by several different functional

353   and structural non-neural factors (Bruner and Ripani, 2008). At the same time, the

354   occipital bone is integrated with the parietal bone (Gunz and Harvati, 2007). Evidence

355   of integration between the deep areas of the parietal and occipital lobes have been also

356   described for modern humans, and tentatively interpreted according to the structural role

357   of the tentorium cerebelli (Bruner et al,. 2010; 2012). Accordingly, it is likely that such

358   occipital projection in Asian *H. erectus* may be related to the marked platycephaly, and

359   not to brain specific features. Another trait possibly associated with these structural

360   relationships is the posterior position of the cerebellar lobes in *Homo erectus*, mostly in

361   the Asian specimens. In modern humans the cerebellar lobes, because of the globular

362   form of the brain, are positioned below the temporal areas. In Neandertals, which lack

363   such globularity, they are positioned more posteriorly, at the base of the temporal areas.

364   In *H. erectus* the cerebellar lobes are positioned almost below the occipital lobes

365   (Grimaud-Hervé, 1997). Hence, it can be hypothesized that the integration between

366   parietal and occipital areas and the integration between the occipital and cerebellar areas

367   can generate the endocranial morphology characterized by flat parietals, bulging

368   occipital, and posterior cerebellar lobes.

369 We have previously used traditional endocranial metrics to evidence some species-
370 specific differences among human groups (e.g., Bruner and Holloway, 2010; Bruner et
371 al., 2011a). However, when differences are more subtle, traditional metrics fails to
372 detect significant changes, dealing largely with size variation (e.g. Bruner et al., 2003,
373 2006). Furthermore, preliminary comparisons between cranial and brain landmarks
374 suggests that there is an important level of independence between cranial and brain
375 boundaries, and the former are hence not necessarily a good proxy for estimating brain
376 proportions (Bruner et al., 2014). Therefore, beyond the simple chords and arcs used in
377 this study, more information should be also achieved by taking into consideration the
378 overall endocranial shape (e.g., Neubauer et al., 2009; Gunz et al., 2010).

379 As a final note, we must remark that the current variation should be also considered
380 according to an even wider interpretation of the *H. erectus* hypodigm, often extended to
381 all the "archaic", "early", or "small brained" humans. Two extreme morphotypes in this
382 sense are represented by the Ceprano and Buia specimens. Ceprano has many archaic
383 features only displayed by *H. erectus*, but it is definitely wider in terms of endocranial
384 morphology, when compared with African and Asian specimens (Bruner and Manzi,
385 2005, 2007). On the opposite side the endocast of Buia, although relatively long and
386 narrow, displays most of the traits associated with small-brained hominids, and can be
387 regarded as an extremely dolichocephalic archaic human braincase (Bruner et al.,
388 2011b). A special case concerns the specimen from the island of Flores, which is not
389 included in this study because of the total disagreement on its evolutionary context (e.g.,
390 Aiello, 2010; Baab et al., 2013; Kubo et al., 2013; Vannucci et al., 2013). Whether or
391 not it represents a separate species or a pathological individual, its peculiar and
392 diminutive size puts it outside of the common variation of *Homo erectus*, and it must be
393 considered separately.

394

5. CONCLUSIONS

396

397 Traditional endocranial metrics are not able to distinguish groups within specimens
398 included in *H. erectus sensu lato*. Endocranial morphology does not show phylogenetic
399 or geographical patterns than can be observed or even statistically tested. Brain form
400 differences or similarities among specimens are largely based on size, without major
401 channelled patterns of variation. Morphometric analyses on the geometrical
402 organization of the brain areas suggests that in the human brain there are only weak

403 levels of integration, which are mostly based on spatial proximity (Bruner et al., 2010; 404 Gomez-Robles et al., 2014). According to these general trends in brain and skull 405 morphology, it is hence not surprising to find a lack of determinant pattern of variation 406 within a human group which is definitely homogeneous, at least when considered within 407 the whole of hominid variability. We must also remark that, despite the differences in 408 brain size and possibly some different cranial integration patterns (Rightmire, 2014), we 409 still miss a clear evidence of difference in endocranial brain proportions between *H.* 410 *erectus* and *H. heidelbergensis* (e.g., Bruner et al., 2003), largely because of the limited 411 sample size and taxonomical uncertainties associated with this latter taxon.

412 Taking into consideration the marked individual differences associated with the lack of 413 morphological trends or cluster, there is no paleoneurological evidence to support 414 different brain morphology among major geographical groups. This result cannot reject 415 the hypothesis of a unique but diversified morphotype, as suggested by different 416 analysis on cranial variation. As previously noted for other aspects of the cranial 417 morphology (Rightmire, 1998; Antón, 2003; Baab 2008), there is marked individual 418 variability that further hampers conclusive statistical approaches. Nonetheless, we 419 cannot rule out the existence of distinct phylogenetic groups sharing the same overall 420 brain form, or the existence of subtle differences that cannot be revealed because of the 421 limited sample size or because associated with traits not described by the variables used 422 here. Given the limits in the relationship between morphological characters and 423 phylogeny (Tattersall, 1986; Collard and Wood, 2000; Bruner, 2012), this analysis must 424 not be intended in terms of taxonomic inferences. The absence of evidenced differences 425 in the endocranial proportions cannot support or else deny the presence of two or more 426 species or lineages within this group. Here we only argue that, independently upon their 427 taxonomic status or phylogenetic relationships, the current fossil record does not allow 428 us to recognize endocranial metric features *specific* for the main geographic groups of 429 the Afro-Asiatic *H. erectus* hypodigm.

430

431 **ACKNOWLEDGMENTS**

432

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642   **Table 1.** Sample and labels

643

Africa

KNM-ER 3733	KNM3733
KNM-ER 3883	KNM3883
WT 15000	WT15000
Daka	DAK
Salé	SAL
OH9	OH9

Indonesia

Sangiran 4	SNG4
Sangiran 2	SNG2
Sangiran 12	SNG12
Sangiran 17	SNG17
Trinil 2	TRN2
Sambungmacan 3	SMB3
Solo 5	SOLO5
Solo 6	SOLO6
Solo 11	SOLO11

China

Zhoukoudian II	ZKDII
Zhoukoudian III	ZKDIII
Zhoukoudian V	ZKDV
Zhoukoudian X	ZKDX
Zhoukoudian XI	ZKDXI
Zhoukoudian XII	ZKDXII
Hexian	HEX
Nanjing 1	NANJ

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647   **Table 2**. Descriptive statistics (N = 23)

648

	Mean	St Dev	Min	25th	Median	75th	Max
CC	987	119	804	890	1001	1067	1250
HLD	161	8	145	156	161	166	177
HLA	216	12	191	208	216	220	243
HLL	207	11	190	199	205	214	229
FW	94	7	84	88	95	99	108
MWC	125	5	115	121	125	130	134
MWA	202	12	181	192	201	214	219
BB	109	7	96	103	110	114	124
BAC	97	5	85	94	98	101	105
VT	100	5	92	95	99	105	110
MCW	101	4	95	97	101	104	110

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651   **Table 3. Correlations between variables (R/p) and between cranial capacity**

652   **and variables (log-log).**

653

	HLC	HLD	HLL	FW	MWC	MWA	BB	BAC	VT	MCW
HLC		0.000	0.000	0.000	0.002	0.005	0.034	0.007	0.001	0.002
HLD	0.78		0.000	0.000	0.004	0.009	0.003	0.067	0.002	0.043
HLL	0.93	0.75		0.000	0.000	0.006	0.093	0.004	0.006	0.002
FW	0.79	0.67	0.82		0.000	0.000	0.008	0.009	0.001	0.003
MWC	0.62	0.57	0.68	0.74		0.075	0.406	0.047	0.110	0.001
MWA	0.57	0.53	0.56	0.71	0.38		0.008	0.005	0.005	0.021
BB	0.44	0.59	0.36	0.54	0.18	0.54		0.202	0.001	0.813
BAC	0.55	0.39	0.58	0.53	0.42	0.56	0.28		0.009	0.000
VT	0.64	0.62	0.55	0.64	0.34	0.57	0.66	0.53		0.008
MCW	0.62	0.43	0.61	0.58	0.66	0.48	0.05	0.76	0.54	
CC	0.90	0.88	0.89	0.89	0.73	0.68	0.63	0.55	0.73	0.63

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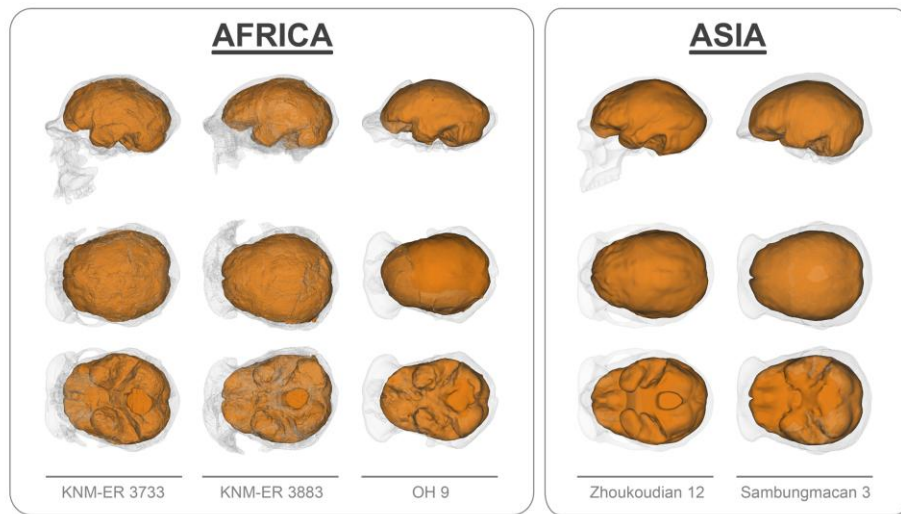658   **Table 4.** Loadings of the variables for the first three principal components

659

	Loadings		
	PC1	PC2	PC3
HLC	0.36	-0.03	-0.22
HLD	0.33	0.20	-0.33
HLL	0.36	-0.12	-0.27
FW	0.37	0.02	-0.15
MWC	0.29	-0.35	-0.38
MWA	0.30	0.18	0.31
BB	0.23	0.66	0.06
BAC	0.29	-0.24	0.57
VT	0.31	0.28	0.29
MCW	0.30	-0.47	0.30

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Figure 1. Some representative specimens of African and Asian *Homo erectus*, with their reconstructed skull and endocasts, in lateral, upper, and lower view.
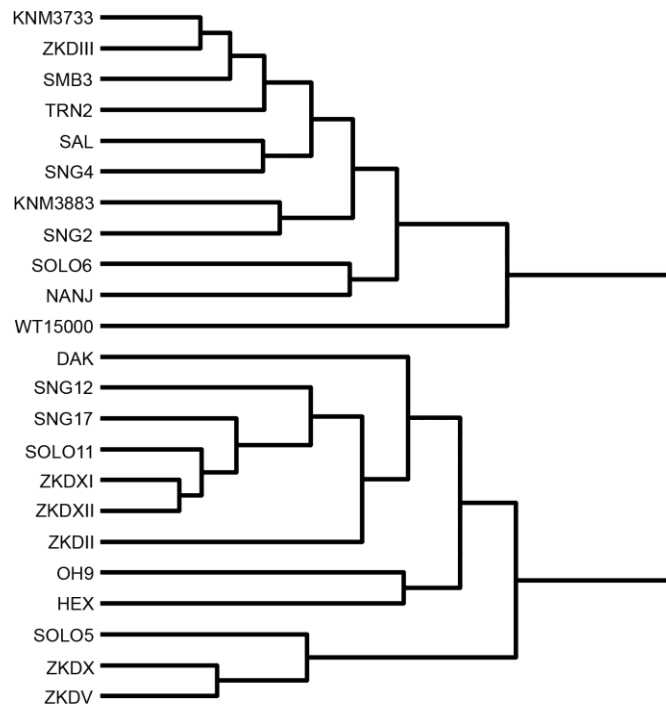
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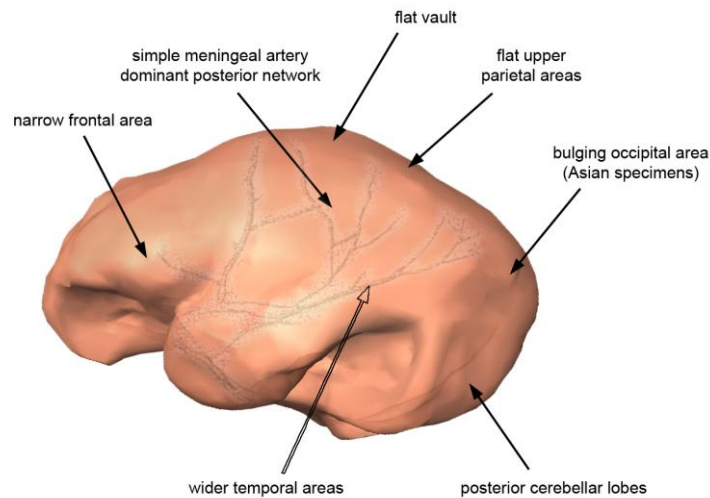
Figure 2. The main characteristics of *Homo erectus* endocranial morphology are shown on the Zhoukoudian XII laser scanned endocast. Black arrows: differences from modern humans and Neandertals; White arrow: differences from *Australopithecus*.
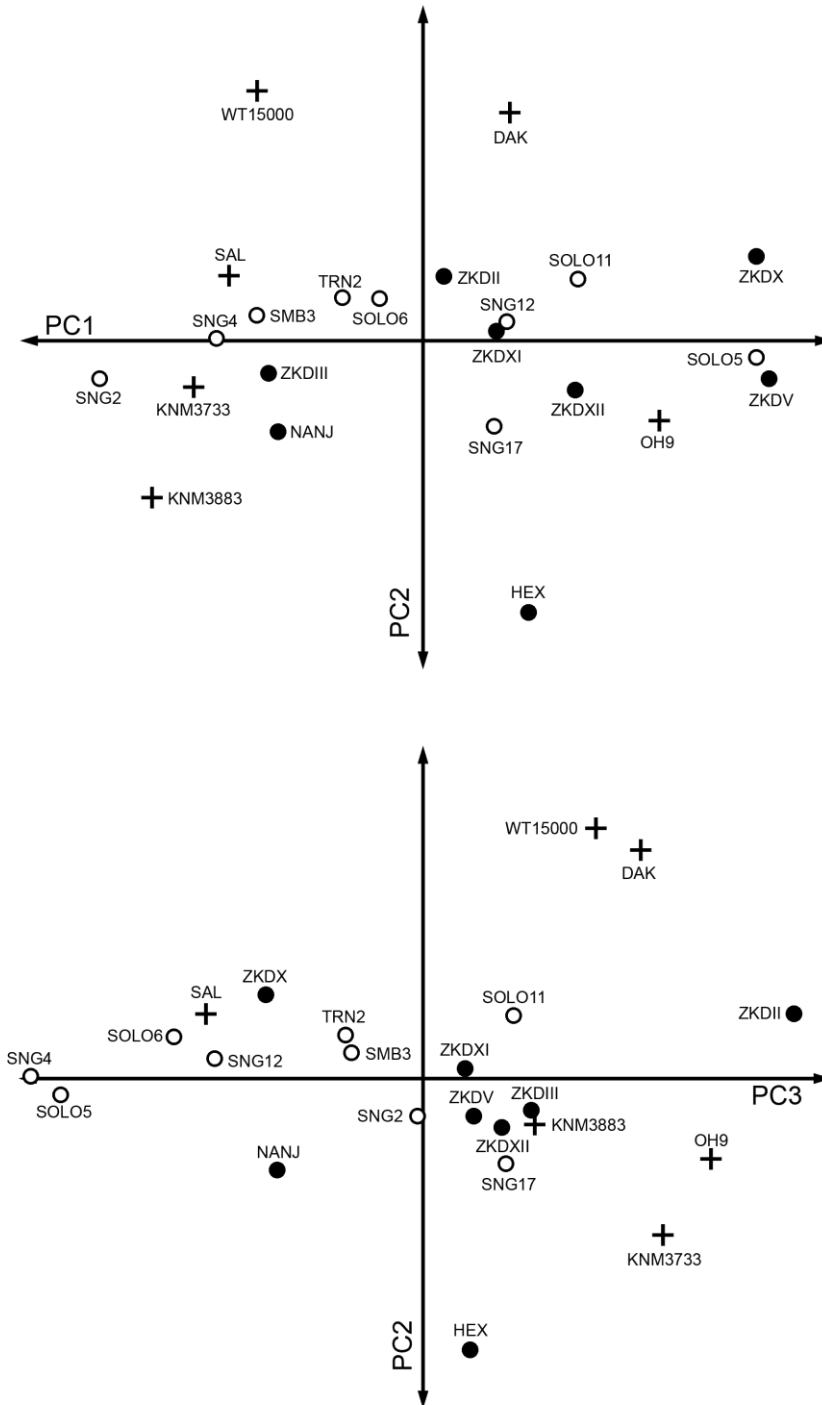
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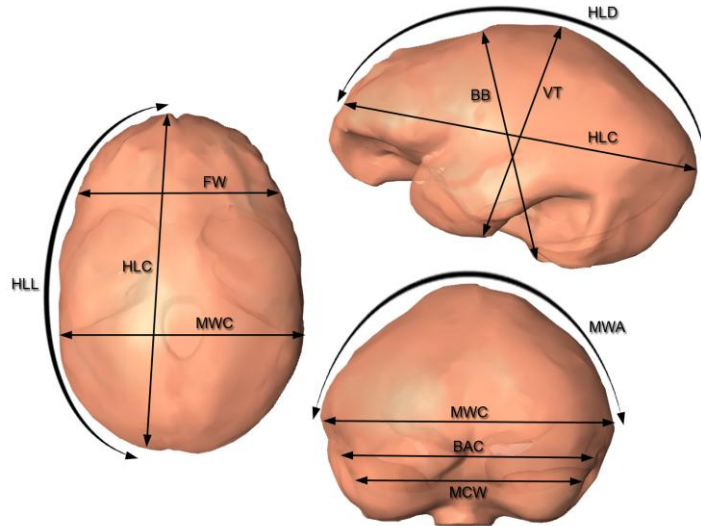
676   **Figure 3.** Metric variables used in this analysis (see text for labels).

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679

680   **Figure 4.** UPGMA cluster procedure on normalized values (z-scores). See Table 1 for
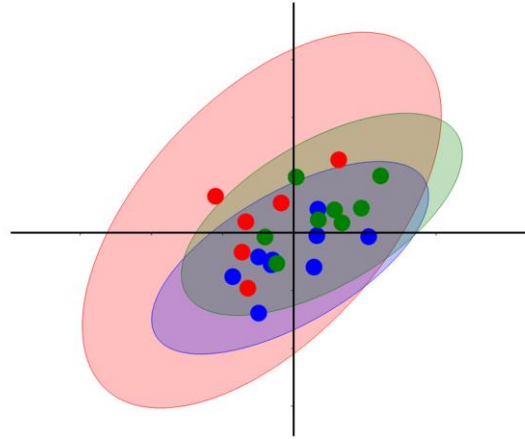
681   labels.

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685 **Figure 5.** First, second, and third principal components for the whole sample: crosses:

686 Africa; black dots: China; white dots: Indonesia. See Table 1 for labels. See Table 3 for

687 loadings.

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Figure 6. Between-group PCA, showing the distribution (95% probability ellipses) of the African (red), Indonesian (blue) and Chinese (green) samples after PCA of their respective means.

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