The Endocast of the One-Million-Year-Old Human Cranium from Buia (UA 31), Danakil Eritrea

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ABSTRACT   *Objectives:* The *Homo erectus*-like cranium from Buia (UA 31) was found in the Eritrean Danakil depression and dated to 1 million years. Its outer morphology displays archaic traits, as well as distinctive and derived characters. The present study provides the description and metric comparison of its endocranial anatomy.

Materials and Methods: UA 31 was originally filled by a diffuse concretion. Following its removal and cleaning, the endocast (995 cc) was reconstructed after physical molding and digital scan. Its morphology is here compared with specimens belonging to different human taxa, taking into account endocranial metrics, cortical traits, and craniovascular features.

Results: The endocast is long and narrow when compared to the *H. erectus/ergaster* hypodigm, although its proportions are compatible with the morphology displayed by all archaic and medium-brained human species. The occipital areas display a pronounced bulging, the cerebellum is located in a posterior position, and the middle meningeal vessels are more developed in the posterior regions. These features are common among specimens attributed to *H. erectus s.l.*, particularly the Middle Pleistocene endocasts from Zhoukoudian. The parietal lobes are markedly bossed. This lateral bulging is associated with the lower parietal circumvolutions, as in other archaic specimens. This pronounced parietal curvature is apparently due to a narrow cranial base, more than to wider parietal areas.

Conclusions: The endocast of UA 31 shows a general plesiomorphic phenotype, with some individual features (e.g., dolichocephaly and rounded lower parietal areas) which confirm a remarkable degree of morphological variability within the *H. erectus/ergaster* hypodigm.

KEY WORDS   paleoneurology; brain evolution; *Homo*; Africa; late Early Pleistocene

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54   The nearly 1,000 m thick late Early to early Middle Pleistocene (Calabrian) fill of the
55   Dandiero basin in the Danakil depression of Eritrea currently represents the only
56   continental succession in the northernmost sector of the African Rift Valley (Afar
57   region). The site produced abundant vertebrate remains, including *Homo* and associated
58   lithic artefacts (Abbate et al., 1998, 2004; Papini et al., 2014; Ghinassi et al., 2015). In
59   terms of thickness of the deposits, preservation quality and density of the
60   paleontological and archaeological remains, the basin is comparable to the
61   penecontemporaneous rift formations of Bouri, in Ethiopia (Gilbert and Asfaw, 2008),
62   Nariokotome (McDougall et al., 2012), Olorgesailie, in Kenya (Owen et al., 2008, 2009,
63   2011), and Olduvai Gorge, in Tanzania (Liutkus and Ashley, 2003; see Ghinassi et al.,
64   2015).

65   Located 35 km inland south of the Gulf of Zula opening into the Red Sea, the
66   Dandiero basin consists of fluvial, deltaic, lacustrine and alluvial fan sediments
67   (Ghinassi et al., 2009, 2013, 2015; Abbate et al., 2012; Papini et al., 2014). Geo-
68   paleontological and paleoanthropological research developed during the last 20 years
69   has mainly focused on the fluvio-deltaic Aalat section outcropping in the northern part
70   of the basin which, together with the Bukra, Wara, Goreya, Aro, and Addai formations,
71   belongs to the so-called Maebele Synthem (Abbate et al., 2004; Ghinassi et al., 2009).
72   The magnetostratigraphic (Abbate et al., 1998; Albianelli and Napoleone, 2004;
73   Ghinassi et al., 2015) and radiometric records (Bigazzi et al., 2004) show that the
74   Jaramillo Subchron is recorded in the upper part of the Bukra and the lower part of the
75   Aalat formations, while the transition from the Matuyama to the Brunhes Chron occurs
76   close to the base of the Aro section. Accordingly, the age of the Aalat deposits is well-
77   constrained around 1 Ma (Ghinassi et al., 2015).

78   Over 200 paleontological and archaeological sites have been identified so far in the
79   area (Abbate et al., 1998; Martini et al., 2004; Delfino et al., 2015; Ghinassi et al.,
80   2015). The terrestrial vertebrate assemblage includes a typical Early to Middle
81   Pleistocene East African fauna and is dominated by a herpetofauna (e.g., Nile crocodile,
82   serrated hinged terrapin, Nile monitor lizard) and mammalian taxa (e.g., hippopotamus,
83   waterbuck, sitatunga, pigs) all characterized by strong water dependence (Ferretti et al.,
84   2003; Delfino et al., 2004; Martínez-Navarro et al., 2004, 2010; Rook et al., 2010, 2013;
85   Medin et al., 2015). As a whole, the sedimentological, pedological, and paleontological
86   records, including the ichthyofauna (Rook et al., 2013), point to a water-rich landscape

87 with grassland- and savannah-dominated environments (Ghinassi et al., 2009, 2013,

88 2015).

89   Fossil remains attributed to *Homo erectus/ergaster* have been discovered nearby the

90 village of Buia in two 4.7 km apart but penecontemporaneous and stratigraphically

91 correlated sites of the Aalat succession: the *Homo* site of Uadi Aalad, identified in 1995,

92 and the site of Mulhuli-Amo, systematically investigated since 2010.

93   The assemblage from Uadi Aalad (UA), which is compatible with a minimum of two

94 adult individuals, consists of a cranium including the face (UA 31), two isolated

95 permanent teeth (UA 222 and UA 369), and three pelvic portions (UA 173, UA 405,

96 UA 466) (Abbate et al. 1998; Macchiarelli et al. 2002, 2004, 2007, 2014; Bondioli et al.

97 2006; Zanolli et al., 2014; Ghinassi et al., 2015). Spread over an area of c. 630 m^2, the

98 site of Mulhuli-Amo (MA) has so far provided 17 fragmentary human cranial remains

99 and a permanent molar crown (Zanolli et al., 2014), likely sampling three juvenile-adult

100 individuals (Coppa et al., 2012, 2014; Rook et al., 2014; Zanolli et al., 2016).

101   The discovery in the Dandiero rift basin of cranial, dental and postcranial human

102 fossil remains adds valuable evidence about the patterns of variation in African *Homo*

103 aff. *erectus* (*sensu* Wood and Leakey, 2011) near the end of the Early Pleistocene

104 (Macchiarelli et al., 2007; Zanolli et al., 2014). Within the scarce and fragmentary

105 penecontemporaneous East African record (Gilbert and Asfaw, 2008; Antón, 2013), the

106 UA 31 cranium represents a find of special interest, notably because of its preserved

107 face. A complete description of the outer morphology of this specimen, especially of its

108 face, has not been finalized yet. Accordingly, in this study also we maintain for UA 31

109 the consensual terminology of *H. erectus*-like representative (or *H. erectus/ergaster*,

110 African *H. erectus*, *H. erectus s.l.*, African *Homo* aff. *erectus*) already used in previous

111 publications (e.g., Abbate el al., 1998; Macchiarelli et al., 2004; Zanolli et al., 2014;

112 Ghinassi et al., 2015).

113   The original description of UA 31 was limited by the presence of a diffuse and

114 locally thick concretion consisting of compacted gray, silty calcareous mudstone. This

115 obscured a considerable portion of its morphology, notably the external neurocranial left

116 aspect, the zygomaxillary and orbital areas, and large parts of the endocranial

117 compartments (Abbate et al., 1998, Fig. 3; Macchiarelli et al., 2004, Fig. 2 and 6).

118 Removal required careful cleaning and reassembly of the specimen, which was

119 performed by M. Chech (Musée de l'Homme, Paris) at the Geo-Paleontological

120   Laboratory set by the Buia Project at the National Museum of Eritrea, Asmara (in

121   Macchiarelli et al., 2004).

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123   **The UA 31 human cranium**

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125   Compared with other Early Pleistocene Eastern African specimens (e.g., KNM-ER

126   3733, KNM-ER 42700, OH 9; Wood 1991; Spoor et al., 2007), including the

127   chronogeographically close calvaria from Daka (Gilbert and Asfaw, 2008), as well as

128   with the Indonesian and Chinese *H. erectus s.s.* hypodigm, UA 31 displays a blend of

129   *H. erectus*-like and derived morphoarchitectural features more commonly found in

130   Middle Pleistocene specimens (Antón, 2013; Rightmire, 2009, 2013; Baab, 2014). The

131   braincase is absolutely long (204 mm), narrow (134.5 mm) and proportionally high

132   (estimated basion-bregma chord: 126 mm). As directly measured on the original

133   specimen by teff seeds and confirmed by repeated measures on the solid cast, its

134   endocranial volume is 995 cc (Macchiarelli et al., 2008, 2014; Bruner et al., 2011a). In

135   upper view, its dolium-shaped profile results from an anteroposteriorly and laterally

136   projecting supraorbital torus, a marked postorbital constriction, an increasingly

137   posterolateral enlargement of the parietal contour, a smooth profile of the parietoccipital

138   region with no occipital torus. Laterally, it shows relative frontal dominance and

139   opisthocranion coincident with inion. While the braincase displays intercristal

140   positioning of the greatest breadth, in coronal view it also shows modest lateral

141   protrusion of the mastoid-supramastoid-auriculare complex, high positioning of the

142   maximum parietal breadth and from sub-vertical to slightly downwards converging

143   parietal walls, a combination of morphostructurally related features which is unique in

144   the penecontemporary fossil record (Macchiarelli et al., 2004; Friess et al., 2013). In

145   fact, in UA 31 the difference between the greatest calvarial breadth (134.5 mm) and the

146   biparietal breadth (128 mm) is only about 6.5 mm, which is lower than measured in all

147   other Early Pleistocene specimens reported so far (Ghinassi et al., 2015).

148   UA 31 shows a flexed base (estimated basion-sella-foramen caecum angle: 133.6°;

149   Ghinassi et al., 2015). For the face, there is an especially large zygomatic process filled

150   by a voluminous maxillary sinus. The height of the maxilla is the largest found among

151   the few known African Early Pleistocene human faces. Unlike any other Early to

152   Middle Pleistocene African and Asian specimen, the orbits are tall, representing over

153   90% of the orbital breadth, and the sockets are deep and voluminous - 37 cc in UA 31

vs. 23.2-31.3 cc in extant humans (Bondioli et al., 2007; comparative data in Brown and Maeda, 2004). Compared to the more posteriorly-set pattern commonly observed in the *H. erectus*-like hypodigm, an anteriorly-placed incisive canal opening is a derived feature of this specimen (Macchiarelli et al., 2014).

The first high-quality resin cast of the outer cranial morphology was made in 2002 and, once completely freed of its original matrix, the endocranial morphology was molded in 2003. Endocasts provide information on the general anatomy of the brain, as well as on some aspects of the sulcal patterns and of the meningeal vascular morphology (Holloway et al., 2004). The endocranial form is influenced by cerebral and cranial factors combining, in evolutionary terms, effects due to primary neural adaptations and secondary bone constraints (Bruner, 2015). Although endocranial morphology can supply only gross morphological data, it represents the only direct neuroanatomical evidence available for fossil species.

Following a preliminary paleoneurological survey (Bruner et al., 2011a), here we provide the anatomical description of the UA 31 endocast, with a comparative morphometric analysis to evaluate its general proportions within the Early to Late Pleistocene human phenotypic variation.

MATERIALS AND METHODS

In the present study we used a high-quality resin cast of the UA 31 endocranium and the digital replica of the endocast obtained after synchrotron radiation microtomography (SR-µCT) at the European Synchrotron Radiation Facility of Grenoble, France (isometric voxel size: 350 µm). The fossil was previously CT scanned in 2002 at the Sembel Hospital of Asmara by a Tomoscan ET Phylips equipment (2 mm slice thickness/spacing) (Macchiarelli et al., 2004), and µCT scanned in 2006 with a portable microtomographic equipment temporary set at the National Museum of Asmara by physicists of the University of Bologna (Xray tube Microfocus Hamamatsu with a focal spot of 20 µm (source); CsI panel coupled with a camera Apogee Usb32, ccd 2184x1472, 1092x736 image size, operating at -8 °C (detector); 150 kV voltage, 200 µA current, Cu filter of 0.3 mm, 720 projections over 360°; 16 bit format and isometric voxel size of 285 µm). However, because of local technical constraints and of the preservation conditions of the specimen, the quality of both the CT and the µCT records

uniquely grants gross anatomical observations on the endocranial surface. Here, those data have been used only for visual purposes.

The UA 31 endocast morphology was compared with adult specimens from different geographical, taxonomical, and chronological ranges associated with the variation of the human genus, including African *H. erectus/ergaster* (KNM-ER 3733, OH 9) and Middle Pleistocene archaic humans (Salé 1), Asian *Homo erectus s.s.* from Indonesia (Sangiran 2, Trinil 2, Sambungmacan 3) and China (Zhoukoudian 3, 10, 12), European *H. heidelbergensis* (Sima de los Huesos 4 and 5, possibly among the earliest representatives of the Neandertal lineage from OIS 12), Neandertals (Saccopastore 1, La Ferrassie 1, Guattari 1, Feldhofer 1, La Chapelle-aux-Saints), and Upper Paleolithic *H. sapiens* (Předmostí 3, 4, 9, 10, Combe Capelle 1, Vatte di Zambana 1). Data are from Bruner et al. (2003), except maximum width and length for KNM-ER 3773, OH9, and Sambungmacan 3, from Holloway et al. (2004).

Bivariate correlations were computed for the endocranial maximum length and frontal and maximum widths. Nine endocranial chords were used for a Principal Component Analysis (PCA): maximum hemispheric length (averaged hemispheres), maximum endocranial width, maximum frontal width (at the Broca's cap), frontal lobe chord (from frontal pole to estimated central sulcus), parietal lobe chord (from estimated central sulcus to estimated parieto-occipital sulcus), occipital lobe chord (from estimated parieto-occipital sulcus to the center of the internal occipital protuberance), and three vault heights calculated at 25%, 50%, and 75% of the fronto-occipital chord (see Bruner et al., 2003 for further details). PCA was computed on the correlation matrix, to normalize variables. Supplementary traditional metric variables are provided for a general description, following Holloway et al. (2004). Statistical analyses were computed with PAST 2.17c (Hammer et al., 2001) and Statistica 12 (StatSoft Inc).

RESULTS

General morphology of the endocast

The endocast is complete and there is no evidence of deformation (Fig. 1). Because of the many fractures of the braincase and because of the removal of the original encrustations on the endocranial table, unfortunately the surface is not sufficiently

221 smooth to allow the subtle recognition of minor details of the sulcal patterns. However,
222 the main cortical areas can be identified and localized.

223 The hemispheres are elongated anteroposteriorly, and the whole endocast looks
224 especially long (dolichocephalic) and narrow, matching the ectocranial features. In
225 lateral view, it looks similar to OH 9, even if in Buia the curvature of the frontal and
226 parietal outlines looks slightly more pronounced (Fig. 2). The elongation of the
227 anteroposterior axis is more evident when considering the occipital lobes, which are
228 patently bulging and projecting backward. The occipital projection is also evident
229 because of a clear midsagittal flexion of the surface at the parieto-occipital boundary.

230 The cerebellar lobes are not located below the temporal lobes, but in a more posterior
231 position along the neurocranial axis. Although they do not reach the occipital poles,
232 they are largely positioned under the occipital areas, with their major axis slightly
233 angled relative to the midsagittal plane. The frontal lobes are narrower than the
234 maximum endocranial width, although the difference is modest. The prefrontal area is
235 not located above the orbits, but in a more posterior position, and the orbital roof is
236 partially separated by the floor of the anterior cranial fossa (Fig. 3). The upper parietal
237 areas show a slight parasagittal depression, while the lower ones display a marked
238 lateral bossing associated with the supramarginal gyrus and with the angular gyrus. This
239 pronounced lateral bossing of the lower parietal areas, apparent in posterior view, is
240 remarkably distinct from the morphology observed in specimens like OH 9 and
241 Zhoukoudian 12, in which the parietal surface does not bulge over the temporal areas
242 (see Fig. 2). In UA 31, this parietal bossing is associated with a pronounced narrowing
243 of the temporal and cerebellar areas, i.e. of the cranial base. The maximum endocranial
244 width is positioned in the lower parietal areas, at the supramarginal gyrus.

245 Concerning asymmetries, the right frontal lobe is larger than its counterpart, and the
246 left occipital lobe is larger and more projecting than the right side. The posterior tract of
247 the third frontal circumvolution is more bossed and projecting on the left side. Because
248 of the difference in size of the right and left occipital areas, the left cerebellar lobe is
249 positioned more posterior than the right one. The parietal area is more bulging on the
250 right hemisphere, and the upper parasagittal depression is more pronounced on the left
251 side.

252 Vascular traces associated with the middle meningeal artery are visible, although the
253 many fractures confound the recognition of some minor vessels (Fig. 4). The vascular
254 pattern is generally simple, with few bifurcations and with the posterior branches more

developed than the anterior ones. In the right hemisphere, the middle ramus originates from the posterior branch. In the left hemisphere, the middle ramus is the main element of the posterior network and the lambdatic ramus is a minor vessel branching from the obelic one. Apparently, there is a long horizontal anastomotic channel bridging the middle and anterior branches. The traces of the venous sinuses are not clearly recognizable on the endocranial surface.

Morphometrics

The endocast has a mean hemispheric length of 167 mm, hemispheric dorsal arc of 229 mm, and hemispheric lateral arc of 212 mm. The main widths are 91 mm at the Broca's cap and 116 mm at the maximum endocranial width. Basion-vertex height is 100 mm and basion-bregma height is 104 mm. The bregma-lambda chord is 94 mm. The estimated length of the vault lobes is 116, 50, and 57 mm, respectively for the frontal, parietal, and occipital chords.

Figure 5a shows a bivariate comparison plotting endocranial length and widths in UA 31 and in some selected Early to Late Pleistocene specimens from Africa and Asia. In this context, UA 31 shows a longer and narrower braincase, with the hemispheric length similar to larger specimens (like Zhoukoudian 12 and OH 9), but widths comparable with the smaller endocasts of this sample. The difference is more evident for the maximum width, which shows the largest residual from the regression with the hemispheric length. Actually, the ratio between frontal and maximum width in UA 31 (0.78) is higher when compared with the distribution of the other specimens (0.75 $\pm$ 0.04), suggesting that the frontal narrowing is less pronounced than in other archaic phenotypes.

When the chords of the entire comparative sample used in this study are analyzed together with a Principal Component Analysis, UA 31 largely fits the non-modern allometric trajectory (Fig. 5b). The first component, which explains 77% of the variance, is a size-related vector. The second component (13% of the variance) separates modern humans because of their larger parietal areas and higher vault. Non-modern humans are aligned along a size-related pattern, associated with the increase of all the other variables. Within this space, accounting for the 90% of the variation, UA 31 is positioned in the middle of the *H. erectus s.l.* spatial range and close to Sima de

los Huesos 5. The following components are below a random threshold of variation and explain less than 5% of the variance and thus cannot be considered as reliable vectors.

Analyzing only the archaic sample and therefore excluding modern humans and Neandertals results do not change: only the size-related PC1 remains significant and UA 31 shows again a phenotypic affinity with Sima de los Huesos 5, bridging small-sized and large-sized *H. erectus* specimens.

DISCUSSION

Within the genus *Homo*, the only noticeable change of the endocranial form beyond variations in brain size is due to the bulging of the parietal areas characteristic of modern humans (Lieberman et al., 2002; Bruner et al., 2003, 2011b; Bruner 2004; Gunz et al., 2010). Neandertals, beyond a large allometric component shared with their ancestors (Bruner et al., 2006), displayed a more modest but consistent lateral widening of the upper parietal (Bruner et al., 2003; Bruner and Manzi, 2008) and frontal (Bruner and Holloway, 2010) areas. In contrast, for most of the earlier human species (here generally termed "archaic humans") we still lack, beyond size differences, quantitative evidence of form changes (Bruner et al., 2015). In *H. erectus/ergaster*, size is the main apparent factor generating a recognizable pattern of variation (Rightmire, 2013) and most Afro-Asiatic specimens show a shared neurocranial organization (Baab, 2016).

Concerning the current analysis it is worth noting that, beyond a size-related vector (PC1) and the specific difference associated with modern human parietal size (PC2), no significant multivariate axis can be detected. Therefore, any normalization aimed at eliminating these two factors will not be able to supply any further stable and significant component, and the resulting statistical ordination would be largely sensitive to random and individual effects.

Beyond cranial capacity, even endocranial differences between *H. erectus s.l.* and *H. heidelbergensis* have not yet been identified and indications from other species (e.g., *H. habilis*) are even scantier. This lack of evidence can be interpreted as the absence of any other specific factor channeling brain morphology beyond size and allometric variability. However, it is worth noting that the current limits in sample size when dealing with the paleoneurological record can seriously hamper a proper statistical analysis of subtle differences, which can remain undetected.

321   The interpretation of such shared endocranial morphology among archaic human
322   species is further constrained by two limits. First, for many endocranial traits we still
323   lack general information on their morphogenetic or functional aspects, including in our
324   own species. Second, many endocranial traits are extremely variable and differences
325   among groups, if any, show a consistent overlap. All this suggests that, mostly when
326   dealing with archaic species, endocasts can be barely used for taxonomic or
327   phylogenetic analyses. It is not surprising that, when analyzed within a multivariate
328   context, UA 31 fits the general human allometric trend as a "medium sized archaic
329   specimen".

330   Also asymmetries cannot provide further inferences. The pattern expressed in UA 31
331   (right frontal - left occipital petalia), although generally associated with language and
332   handedness, is the most frequent found in every species of the human genus (Holloway
333   and De La Coste-Lareymondie, 1982; Holloway, 1995; Balzeau et al., 2012a, b). Taking
334   into account that these hemispheric asymmetries represent a plesiomorphic trait, that the
335   differences between humans and apes may be largely allometric (Gómez-Robles et al.,
336   2013) and that the structural causes of these geometrical asymmetries are not currently
337   known (Bruner, 2015), these characters cannot at present supply any specific
338   information.

339   When compared with other specimens of similar volume from the *H.*
340   *erectus/ergaster* assemblage (Holloway et al., 2004), the Eritrean endocast is markedly
341   dolichocephalic, i.e., its braincase is relatively and absolutely narrow respect to its
342   hemispheric length. As evidenced by the bivariate analyses, such proportions are
343   distinctive when compared with the trend observed in archaic humans, although still
344   reasonably compatible with their variation. However, the marked dolichocephalic
345   proportions in UA 31 are especially noticeable when this specimen is compared with
346   Daka, a *H. erectus* braincase found in the same geographical area and dated to the same
347   period (Asfaw et al., 2002; Gilbert and Asfaw, 2008). Although they have virtually the
348   same brain size (995 cc), the two crania display different proportions. The percent ratio
349   between UA 31 and Daka endocranial metrics (Asfaw et al., 2008; Gilbert et al., 2008)
350   shows that the former is longer (108%), narrower (94%) and less tall (84%).
351   Interestingly, they apparently have roughly the same parietal length on the endocranial
352   surface, although Buia has a longer parietal bone (111%). Despite their general archaic
353   morphology, both Buia and Daka show a phenotypic affinity with European Middle
354   Pleistocene specimens like Sima de los Huesos 5, in their brain (this study) and

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braincase (Baab, 2016) form. It cannot be ruled out that such similarity could be only a matter of allometric factors and individual variation. Nonetheless, also because of their chronological and geographical position, the possibility of a phylogenetic relationship with later human species (i.e., *H. heidelbergensis*) has been formerly mentioned (Ghinassi et al., 2015; Baab, 2016). This suggests that a more inclusive analysis of these two specimens is needed, contrasting their endo- and ectocranial morphology with respect to the Middle Pleistocene variation. A study of the UA 31 ectocranial anatomy is currently in progress, to evaluate characters which may be useful to provide further taxonomic and phylogenetic information.

The anteroposterior elongation of the braincase in UA 31 is further stressed because of a noticeable bulging and projection of the occipital lobes. As in many archaic specimens, the cerebellar lobes are positioned under the occipital areas, and not under the parietal and temporal areas as in more derived taxa (Grimaud-Hervé, 1997). Many Asian *H. erectus* have relatively large occipital areas, and the posterior regions in UA 31 (occipital morphology, cerebellar position, and vascular patterns) show archaic traits which are particularly evident in many Zhoukoudian endocasts (Grimaud-Hervé, 1997; Bruner, 2004; Wu et al., 2010; Balzeau et al., 2012b; Bruner et al., 2015). Zhoukoudian specimens, as UA-31, also display long and narrow fronto-occipital areas (Kidder and Durband, 2004). It remains to be established whether this morphology in UA 31 is the primary result of brain form variation or a secondary effect of cranial structural features (platycephaly and cranial base morphology) influencing brain spatial organization and not associated with any concrete neural factors (Bruner et al., 2011a; Friess et al., 2013; Ghinassi et al., 2015). Whatever the primary cause of such morphology, cerebral or cranial, it is likely that the bulging of the occipital areas, the posterior displacement of the cerebellar lobes and the dominance of the posterior vascular branches in the specimen from Buia are part of an integrated pattern due to larger longitudinal proportions of the posterior endocranial regions. In terms of bones, an inverse relationship between parietal and occipital bulging is based on an integrated pattern of shape variation (Gunz and Harvati, 2007), clearly expressed in the morphology of UA 31.

When considered with respect to the endocranial width, the lateral extension of the frontal lobes in UA 31 is larger than the average figures of most archaic human specimens. However, this ratio shows considerable variation (Bruner and Holloway, 2010) and the condition in UA 31 is largely due to the relatively small endocranial

389 breadth, more than to an actual increase of the frontal width. The frontal profile looks

390 also somewhat more curved than observed in other *H. erectus/ergaster* specimens.

391 However, the midsagittal curvature of the anterior cranial fossa does not show

392 noticeable trends within the human genus (Bookstein et al., 1999). As for the lateral

393 proportions, even though modern humans display a more curved frontal profile, the

394 intraspecific variation is remarkable and there is overlap among the ranges of different

395 taxa (Bruner et al., 2013). Furthermore, as described above, the frontal lobes in UA 31

396 are positioned behind the orbital roof, like in all archaic human species (Fig. 3). This

397 spatial relationship between prefrontal cortex and upper facial areas represents a

398 plesiomorphic condition for the human genus (Bookstein et al., 1999; Bruner and

399 Manzi, 2005). Therefore, we conclude that also the frontal lobes in UA 31 do not

400 display apparent derived characters when compared with *H. erectus/ergaster*, and their

401 morphology is compatible with the phenotype associated with other medium-brained

402 human taxa.

403 As systematically reported since the first description of its outer morphology (Abbate

404 et al., 1998; see also Macchiarelli et al., 2004; Friess et al., 2013; Ghinassi et al., 2015),

405 a peculiar trait of the UA 31 endocast is represented by its parietal bossing, which is

406 more pronounced than in other Early to early Middle Pleistocene African specimens

407 (Holloway et al., 2004). In particular, despite their similar appearance and dimensions in

408 lateral view, UA 31 and OH 9 differ remarkably in the rear view, with the Tanzanian

409 specimen very similar to the Indonesian and Chinese hypodigm (Holloway et al., 2004),

410 suggesting a shared Afro-Asiatic phenotype. On the contrary, UA 31 shows a sub-

411 rounded outline when viewed posteriorly (Figs. 1, 2b), while OH 9 (Fig. 2b) and

412 Zhoukoudian 12 display a more typical "tent-like" profile.

413 A "tent-like" posterior outline, where the upper parietal walls distinctly diverge

414 downwards, nearly invariably characterizes the outer and inner morphology of the *H.

415 erectus s.l.* cranial hypodigm (e.g. Rightmire, 1990; Grimaud-Hervé, 1997; Holloway et

416 al., 2004). However, while this feature is marked in the Indonesian and Chinese

417 assemblages and in OH 9, it is more moderately expressed in some African

418 representatives, such as KNM-ER 3733 and Daka (Asfaw et al., 2008: plate 13.5;

419 Gilbert et al., 2008: plate 14.4), and virtually absent in UA 31 (Abbate et al. 1998;

420 Macchiarelli et al., 2004; see Gilbert, 2008: fig. 15.1). Nonetheless, also in the Eritrean

421 specimen the maximum endocranial width is localized at the boundaries between the

422 lower parietal and temporal areas (Abbate et al. 1998; Macchiarelli et al., 2004), as in

13

423   all archaic species (Holloway et al., 2004). Taking into account that the biparietal width

424   of UA 31 is not particularly large when compared with the estimates of other archaic

425   human specimens with similar brain size (cf. Wood, 1991; Spoor et al., 2007: tab. S1.1;

426   Lordkipanidze et al., 2013: tab. S2A), it is likely that its peculiar outline is associated

427   with narrow endocranial base and temporal lobes, more than with wider parietal lobes.

428   No data about basicranial size and proportions in UA 31 have been reported so far

429   with respect to the data from extant and fossil humans (e.g., Dean and Wood, 1982;

430   Wood, 1991; Bastir et al., 2011; Kimbel et al., 2014). The cranial base in UA 31 is

431   particularly flexed (Ghinassi et al., 2015), more than measured in Sambungmacan 4

432   (Baba et al., 2003) and near to the extant human figures (Baba et al., 2003), but less

433   than reported for Daka (Gilbert et al., 2008). Given that the cranial base is a major

434   morphological constraint for the whole cranial architecture (Lieberman et al., 2000,

435   2002), it should be considered that the individual endocranial traits in UA 31, like

436   marked dolichocephaly and parietal bossing, may be secondary consequences of a

437   particular basicranial anatomy and consequent spatial adjustments. It is worth nothing

438   that UA 31 also displays distinct facial traits, which may be relevant to the relationships

439   between endocranial base and facial morphology (see Bastir et al., 2010; Bastir and

440   Rosas, 2016). In this sense, future studies integrating endocranial and ectocranial data

441   will provide a more comprehensive perspective on the overall organization of this

442   specimen.

443

444   **CONCLUSIONS**

445

446   The endocranial morphology of UA 31 is compatible with the archaic human range

447   of variation and similar to specimens generally included in the *H. erectus/ergaster*

448   hypodigm (e.g., Holloway, 1980, 1981). The posterior morphology of the endocast,

449   including the occipital lobes, the cerebellar lobes and the vascular traces are reminiscent

450   of the phenotype observed in the Zhoukoudian samples (Grimaud-Hervé, 1997; Wu et

451   al., 2014). At present, we cannot dismiss that the marked dolichocephaly and parietal

452   bossing characterizing the specimen from Buia could represent individual traits, with no

453   taxonomic or phylogenetic significance. In any case, it is likely that they represent

454   secondary adjustments due to basicranial constraints and not primary neural variations.

455   While current paleoneurological evidence cannot exclude the existence of multiple

456   lineages and phylogenetic trends within the available *H. erectus s.l.* assemblage, the

hypothesis of a wide intraspecific braincase variability (e.g., Rightmire, 1998; Antón, 2003; Baab 2008; 2016; Bruner et al., 2015) cannot be rejected.

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original UA 31 specimen by the "wizard" Mario Chech (see Supporting Information SI1 and SI2), this study would have simply not been possible. All former and present members of the Buia Project sincerely acknowledge the unforgettable contribution of our recently deceased colleague.

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751

Captions

753

754   **Fig. 1.** The digital endocast of the UA 31 cranium from Buia (average endocranial
755 length 167 mm, maximum endocranial width 116 mm).

756

757   **Fig. 2.** Above: The UA 31 endocast (right) compared in lateral (upper) and superior
758 (lower) views with the endocasts from three Early Pleistocene African (KNM-ER 3733,
759 KNM-ER 3883, OH 9) and one Middle Pleistocene Chinese (ZKD 12) specimens
760 included in the *H. erectus/ergaster* variation (for visual purposes, images are scaled to
761 similar endocranial length). Below: Posterior view of the endocranial reconstruction of
762 OH 9 and UA 31 (images scaled to similar endocranial width). Digital replicas after
763 Bruner et al. (2015).

764

765   **Fig. 3.** Digital reconstruction of the UA 31 cranium in transparency (left), showing
766 the spatial relationships between the endocranial cavity (red) and the orbital space
767 (blue), and compared with the orbit position in KNM-ER 3733 (a) and in a modern
768 human cranium (b) (redrawn after Bruner et al., 2014 - images not to scale). In UA 31,
769 as in other archaic human species, the orbital roof (OR) is largely separated by the
770 prefrontal cortex (PF).

771

772   **Fig. 4.** Drawing of the lateral views of UA 31 endocast, emphasizing the morphology
773 and position of the main vascular traces.

774

775   **Fig. 5.** a) Comparison between hemispheric length (HL), frontal width (FW) and
776 maximum endocranial width (MW) (lines: least square regression). b) Biplot showing
777 first and second principal components computed on nine chords (green: UA 31; red: *H.*
778 *erectus s.l.*; purple: Sima de los Huesos; blue: Neandertals; pink: fossil *H. sapiens*).
779 Specimens: SAL: Salé; SBM: Sambungmacan; SH: Sima de los Huesos; SNG:
780 Sangiran; TRN: Trinil; UA 31: Buia; ZKD: Zhoukoudian. Variables: FC: frontal chord;
781 FW: frontal width; H1, H2, H3: vault heights; HL: hemispheric length; MW: maximum
782 width; OC: occipital chord; PC: parietal chord.

783

784   **Supplementary Figs. 1, 2.** Mario Chech restoring the UA 31 cranium in 2002 at the
785 National Museum of Eritrea, Asmara.