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What do cranial bones of LB1 tell us about *Homo floresiensis*?

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ABSTRACT

Cranial vault thickness (CVT) of Liang Bua 1, the specimen that is proposed to be the holotype of *Homo floresiensis*, has not yet been described in detail and compared with samples of fossil hominins, anatomically modern humans or microcephalic skulls. In addition, a complete description from a forensic and pathological point of view has not yet been carried out. It is important to evaluate scientifically if features related to CVT bring new information concerning the possible pathological status of LB1, and if it helps to recognize affinities with any hominin species and particularly if the specimen could belong to the species *Homo sapiens*.

Medical examination of the skull based on a micro-CT examination clearly brings to light the presence of a sincipital T (a non-metrical variant of normal anatomy), a scar from an old frontal trauma without any evident functional consequence, and a severe bilateral hyperostosis frontalis interna that may have modified the anterior morphology of the endocranium of LB1. We also show that LB1 displays characteristics, related to the distribution of bone thickness and arrangements of cranial structures, that are plesiomorphic traits for hominins, at least for *Homo erectus s.l.* relative to *Homo neanderthalensis* and *H. sapiens*. All the microcephalic skulls analyzed here share the derived condition of anatomically modern *H. sapiens*. Cranial vault thickness does not help to clarify the definition of the species *H. floresiensis* but it also does not support an attribution of LB1 to *H. sapiens*. We conclude that there is no support for the attribution of LB1 to *H. sapiens* as there is no evidence of systemic pathology and because it does not have any of the apomorphic traits of our species.

RÉSUMÉ

L'épaisseur du crâne de Liang Bua 1, le spécimen proposé comme holotype de l'espèce *Homo floresiensis*, n'avait pas été décrite et analysée dans le détail, ni comparée avec des échantillons d'homininés fossiles, d'Hommes anatomiquement modernes et de microcéphales. Par ailleurs, la description paléopathologique du spécimen demeurait superficielle. Il était important d'évaluer si les caractères liés à l'épaisseur crânienne apportent de nouvelles informations sur l'état pathologique de LB1 et si cela aide à reconnaitre des affinités avec d'autres espèces d'homininés.

L'étude avec un regard médical à partir de données microtomographiques permet d'établir plusieurs diagnostic rétrospectifs: sincipital T correspondant à une variation anatomique sans caractère pathologique; séquelle d'un traumatisme ancien frontal sans conséquence fonctionnelle évidente; hyperostose frontale interne sévère bilatérale qui a pu modifier la morphologie frontale antérieure de l'endocrâne de LB1. Nous montrons aussi que LB1 a des états pour les caractères étudiés, en relation avec la distribution de l'épaisseur osseuse, sa constitution interne et la configuration des structures crâniennes, qui sont plésiomorphes chez les homininés, du moins lorsque *H. erectus s.l.* est considéré relativement à *H. neanderthalensis* et *H. sapiens*. En complément, tous les crânes de microcéphales étudiés partagent les caractéristiques dérivées observées chez les Hommes modernes.

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Nous concluons qu'il n'y a aucun support à une attribution de LB1 à *H. sapiens* puisque son crâne ne ressemble à aucune pathologie connue et qu'il n'a aucun des caractères apomorphes de notre espèce. En revanche, les données d'épaisseur osseuse ne permettent pas de clarifier la définition de l'espèce *H. floresiensis*, ni de proposer d'hypothèses concernant l'espèce fossile dont ce petit Homme a hérité ses caractéristiques.

1. Introduction

The hominins from the Liang Bua cave on the island of Flores, South-East Asia, Indonesia, have been a matter of passionate debate since their discovery in 2003. The material comprises a relatively complete skeleton (LB1 for Liang Bua 1), and several bones representing a total of possibly 14 individuals (Morwood et al., 2005). The fossils come from layers dated between 95 and 74 to 17 ka (Morwood et al., 2009; Roberts et al., 2009). LB1 has a stature estimated to be around 106 cm and a cranial capacity of 426 cm^3 (Kubo et al., 2013). The debate (e.g., Aiello, 2010) concerns the attribution of the specimens to a new hominin fossil species, *Homo floresiensis* (e.g., Brown et al., 2004; Morwood et al., 2004, 2005), and its relationships with other hominin species (e.g., Argue et al., 2006, 2009; Gordon et al., 2008; Kaifu et al., 2011; Baab et al., 2013), or if they might represent pathological modern humans (e.g., Henneberg and Thorne, 2004; Weber et al., 2005; Jacob et al., 2006; Martin et al., 2006a,b; Richards, 2006; Hershkovitz et al., 2007, Obendorf et al., 2008; Eckhardt and Henneberg, 2010; Vannucci et al., 2011; Oxnard et al., 2012; Eckhardt et al., 2014; Henneberg et al., 2014). Indeed, several pathologies have been suggested, including growth and development anomalies, Laron syndrome, hypothyroid or myxoedematous cretinism, microcephaly and Down syndrome.

The specimens and their geochronological/cultural contexts have been published in detail (e.g., Moore et al., 2009; Falk et al., 2005a,b, 2007, 2009a,b, 2010; Tocheri et al., 2007; Jungers et al., 2009a,b; Kaifu et al., 2009, 2011; Larson et al., 2009; Morwood and Jungers, 2009; Roberts et al., 2009; Westaway et al., 2009a,b; Brown, 2012; Baab et al., 2013; Kubo et al., 2013; Orr et al., 2013; Daegling et al., 2014). However, some aspects of the anatomy of the skull of LB1 have still not been fully detailed, evaluated and compared with appropriate samples. A forensic and pathological evaluation remains to be done and features related to cranial vault thickness (CVT) and internal structure remain to be studied.

CVT is often discussed in analyses of fossil hominins particularly when dealing with *Homo erectus* (Weidenreich, 1943; Le Gros Clark, 1964; Hublin, 1978; Andrews, 1984; Wood, 1984). A variety of results have been obtained and several interpretations proposed (Kennedy, 1991; Kennedy et al., 1991; Bräuer and Mbua, 1992; Brown, 1994; Gauld, 1996; Antón, 1997; Balzeau, 2006, 2007, 2013), yet CVT is still used to discuss taxonomic attribution (e.g., Kennedy et al., 1991; Baba et al., 2003; Manzi et al., 2003; Kappelman et al., 2008; Indriati and Antón, 2010; Grimaud-Hervé et al., 2012; Curnoe and Green, 2013). In the case of *H. floresiensis*, most studies have included at least a short statement about CVT. In the initial publication about LB1, the authors mentioned that its "superior cranial vault bone (is) thicker than *Australopithecus* and similar to *H. erectus* and *Homo sapiens*" (Brown et al., 2004: p. 1055). The anatomical description of the skull has been completed (Kaifu et al., 2011) and CVT at isolated points and comparison with other hominins and samples for recent modern humans have been provided (Brown et al., 2004; Kaifu et al., 2011). However, the proposed similarity with *H. erectus* and *H. sapiens* for CVT does not help to answer the question about the attribution of LB1 to an extinct/extant hominin species and/or its proposed pathological state for these features.

Studies have mentioned aspects of CVT and bone composition to support a similarity between LB1 and microcephalic modern humans or other pathologies. They generally concern vague statements whose phylogenetic or pathological implications are not fully evaluated. Among these features are the supposedly "high level of suture closure and obliteration (in LB1 that) is atypical for any species of *Homo*, *Australopithecus*, and most nonhuman primates" (Jacob et al., 2006: p. 13423) or the "absence of or undersized frontal sinuses" (Hershkovitz et al., 2007) that would be a feature shared between LB1 and microcephalic modern humans. Non-pneumatised (acellular) mastoid process … and small paranasal sinuses would be characteristic of Laron syndrome (LS) (Kornreich et al., 2003; Hershkovitz et al., 2007). Hershkovitz and collaborators (2007: p. 200) state that "the thickness of the bones of the cranial vault is normal in LS and LB1 …". In the same vein, Obendorf and collaborators (2008) report that "adult African (Uele) ME cretins have open anterior fontanelles, also evident in DC, HC and possibly replicated in the damaged LB1. The vault is thick in DC (a 28-year-old European male, Dolega's case) and LB1 … frontal sinuses are absent in European sporadic cretins (6–35 years old), African ME cretins, DC and LB1" (Obendorf et al., 2008: p. 1288). It was also proposed that individuals with Down syndrome have "hypoplasia and non-pneumatisation of the paranasal sinus" (Henneberg et al., 2014:SI p. 4). This list of proposed resemblances between various modern pathologic cases and LB1 is not exhaustive (e.g., Van Heteren, 2013). The limitation of most of these statements is the lack of comparison with LB1, inconsistent evaluation of thin, normal or thick vault thickness for various pathologies and absence of quantification, but also the limited quality of the data used to evaluate the features. For example, the medical CT used to evaluate the pneumatisation of the internal carotid structure (e.g., Brown, 2012) has a resolution that does not allow accurate estimation of these features (see below).

This study will therefore fill several lacunae in our knowledge of the anatomy of the skull of LB1, and our study has two main objectives. First, we expect to complete the anatomical description of the skull of LB1 by detailing features that have not been completely addressed, including bone thickness distribution of the vault and internal bone composition and structure. We also detail anatomical features from a pathological point of view to evaluate the origin of some features of LB1 that have not been properly identified. By doing so, we want to clarify which features are in a normal range of variation, which ones may be related to diseases and which may have a taphonomical origin. We also aim to clarify aspects that are subject to conflicting interpretations. The second objective is to compare the features related to bone thickness and composition with comparative samples of fossil hominins and anatomically modern humans including a relatively large sample of microcephalic humans. This approach will permit us to analyse the possible resemblance of LB1 to fossil hominins and modern humans. More importantly, it will also permit us to identify the polarity of the