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► **To cite this version:**

Valéry Zeitoun, Véronique Barriel, Harry Widiyanto. Phylogenetic analysis of the calvaria of *Homo floresiensis*. *Comptes Rendus. Palevol*, 2016, <10.1016/j.crpv.2015.12.002>. <hal-01290521>

HAL Id: hal-01290521

<https://hal.sorbonne-universite.fr/hal-01290521v1>

Submitted on 18 Mar 2016

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Comptes Rendus Palevol

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Human palaeontology and prehistory

Phylogenetic analysis of the calvaria of *Homo floresiensis*

Analyse phylogénétique de la calvaria de *Homo floresiensis*

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ARTICLE INFO

Article history:

Received 26 June 2015

Accepted after revision 15 December 2015

Available online xxx

Handled by Michel Laurin

Keywords:

Cladistics

Alpha taxonomy

Southeast Asia

Palaeoanthropologie

Mots clés :

Cladistique

Alpha taxonomie

Asie du Sud-Est

Paléoanthropologie

ABSTRACT

Because until 2006 the Liang Bua human fossil remains were not available to the entire paleoanthropological community, the taxonomic position of *Homo floresiensis* was only a matter of opinion in publications. From the beginning, two schools of thought prevailed, and this situation persists today. One purports that the Liang Bua human series belongs to a local modern human (*Homo sapiens sapiens*) with anatomical particularities or pathologies that may be due to insular isolation/endogamy. The second argues in favour of the existence of a new species that, depending on the authors, is either a descendant of local *Homo erectus*, or belongs to a much more basal taxon, closer to archaic *Homo* or to australopithecines. Because there are no postcranial remains confidently attributed to *Homo erectus* in the fossil record, and because the *Homo erectus* type specimen is a single and partial calvaria, a cladistic analysis was undertaken using both nonmetric morphological features and metrics of the calvariae of human fossil specimens including LB1 to test if it belongs to this taxon. Our results indicate that LB1 is included in the *Homo erectus* clade.

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RÉSUMÉ

Jusqu'en 2006, plusieurs opinions ont été exprimées à propos du statut taxonomique de *Homo floresiensis*, avant que les paléoanthropologues n'aient directement accès au matériel original de Liang Bua. De nos jours, les points de vue débattus sont davantage fondés sur des études anatomiques quand, par le passé, seules des opinions s'exprimaient sur les travaux des deux équipes ayant eu accès aux fossiles. Il demeure que deux écoles s'affrontent. L'une est partisane de l'existence d'une population d'hommes modernes (*Homo sapiens sapiens*), dont les particularités ou les pathologies sont liées à un isolement et/ou à une endogamie insulaire ; l'autre école défend l'existence d'une nouvelle espèce, qu'elle soit issue d'un *Homo erectus* régional ou qu'il s'agisse de l'ultime représentant d'une lignée archaïque du genre *Homo*, ou même d'un genre différent qui serait proche des Australopithecines. Dans la mesure où aucun reste postcrânien n'est attribuable de manière certaine à *Homo erectus* et, comme le spécimen-type de cette espèce est une calvaria incomplète, une analyse

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<http://dx.doi.org/10.1016/j.crpv.2015.12.002>

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cladistique a été réalisée à partir des données morphologiques métriques et non métriques de la calvaria de plusieurs spécimens fossiles, dont LB1, pour tester son appartenance à ce taxon. Nos conclusions suggèrent une alternative aux hypothèses précédemment discutées et indiquent que ce spécimen n'est, ni un homme moderne ayant une pathologie, ni une nouvelle espèce, mais est inclus dans le clade *Homo erectus*.

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1. Introduction

In September 2003, an Indonesian–Australian team discovered remains of a small fossil hominid (composed of skull and postcranial skeleton) on the island of Flores (Indonesia) that challenged the classical scheme of hominin phylogeny (Brown et al., 2004; Morwood et al., 2004). These remains, including a cranium, mandible, femora, tibiae, fibulae and patellae, partial pelvis, incomplete hands and feet, and fragments of vertebrae, sacrum, ribs, scapulae and clavicles, some of which were still in anatomical articulation, provided sufficient distinctive features according to these authors to erect a new hominin species, *Homo floresiensis*, dated between 90 and 18 ka. This discovery, its presumed taxonomic placement, and its paleobiological interpretations led to reappraisals of the current palaeoanthropological paradigm (Gibbons, 2004; Lahr and Foley, 2004), even more than the discovery of *Australopithecus*, Neanderthal man and *Pithecanthropus* had done in their times, according to De Vos (2009).

A dispute ensued between the team of the discoverers (Argue et al., 2006; Brown et al., 2004; Falk et al., 2005a,b; Morwood et al., 2004, 2005) and the team of Professor Teuku Jacob at Gadjah Mada University (Yogyakarta), who was the authority on palaeoanthropology in Indonesia for many years (Jacob et al., 2006). The dispute concerned both the taxonomic position of the fossils and their availability. At that time, they were the only teams with access to the original fossils; other paleoanthropologists could only offer opinions based on these works (Henneberg and Thorne, 2004; Holloway et al., 2006; Martin et al., 2006a,b; Weber et al., 2005). Thanks to Tony Djubiantono, who was the official curator of the Indonesian fossils, more researchers were given the opportunity to study the specimens, as we did in August 2005 (Zeitoun et al., 2007), after the return of the material from Yogyakarta to Jakarta. Different opinions about Flores man still divide palaeoanthropologists. A couple of recent papers (Eckhardt et al., 2014; Henneberg et al., 2014) reified the pathological hypothesis of a modern human population, which was supported by Jacob et al. (2006), contrary to the new species hypothesis supported by the discoverers (op. cit.).

This question remains unresolved (cf. Montgomery, 2013), and two main competing explanations for the morphology of the Liang Bua human series still exist. The first of these, propounded by several pathologists, considers that these remains merely represent a pathological specimen of a local extant human (e.g. *Homo sapiens sapiens*) (Henneberg and Thorne, 2004; Hershkovitz et al., 2007; Jacob et al., 2006; Martin et al., 2006a, b; Obendorf et al., 2008; Oxnard et al., 2010; Rahmawati et al., 2007; Rauch

et al., 2008; Richards, 2006; Weber et al., 2005 and now Eckhardt et al., 2014 and Henneberg et al., 2014). The second ascribes them to a new species, *Homo floresiensis*, but the phylogenetic position of this lineage is the subject of considerable disagreement, partly because there are so many current gaps in the fossil record, and also because there are no postcranial remains safely attributed to *Homo erectus*. The postcranial data (Jungers et al., 2009a, b; Orr et al., 2013; Tocheri et al., 2007) associated with the small cranial size (Falk et al., 2005a, b) are the most widely used to establish a phylogenetic placement, although no phylogenetic analysis was undertaken until the single work of Argue et al. in 2009.

Some authors suggest that, although close to *Homo erectus*, the new species *Homo floresiensis* is more probably a branch of the human canopy that separated near the origin of *Homo erectus* (Aiello, 2010; Argue et al., 2006, 2009; Baab and McNulty, 2009; Baab et al., 2013; Brown and Maeda, 2009; Gordon et al., 2008). Others (Brown et al., 2004; Hu, 2013; Jungers et al., 2009a, b; Larson et al., 2009; Martinez and Hamsici, 2008) go further and suggest an immediate common ancestor of the Flores specimens with *Australopithecus*. An alternative possibility for the proponents of the new species is that the Liang Bua human fossils are an insular descendant lineage of a local *Homo erectus* (Kaifu et al., 2011; Köhler et al., 2007; Meijer et al., 2010; van Heteren, 2012). Last but not least, Lyras et al. (2009) propose the most original point of view in considering that LB1 cannot be separated from *Homo erectus*.

2. Methods

From a systematic point of view, there is no biological reason to preclude human fossils from being studied in the same way as other taxa (Bonde, 1977; Stringer, 1987; Tassy, 1996). Before considering any evolutionary process and suggesting a scenario, the first step is to consider the evolutionary pattern itself. Following Hennig (1966) (but see also Mayr, 1974, 1986), we consider cladistics the best way to do so but this is far from the rule in palaeoanthropology.

2.1. The palaeoanthropological theoretical context

In the 1960s, palaeoanthropological works focusing on the taxonomy and nomenclature of Hominidae echoed the former works of Dobzhansky (1944) and Mayr (1950), like for instance those of Campbell (1963, 1965, 1972). These studies tended to follow the “syncretistic” school of classification developed in the framework of the Modern Synthesis but, with time, palaeoanthropologists abandoned this framework of classification (Hublin, 2014).

What is true for classification is also true for phylogeny (Zeitoun, 2015), as expressed by Bonde (2012): “Now this has been known as a methodological fact for nearly fifty years since Hennig’s book *Phylogenetic Systematics* (1966), so how come that some ‘scientists’ today can be completely ignorant of that, and how can that be accepted by reviewers of professional journals? Is it really impossible to convey such simple and logical biological methodology to anthropologists—or don’t they care?” Nowadays, the spectrum of current palaeoanthropology is sometimes between ignorance and rejection of cladistics (see below).

The cladistic (phylogenetic) school of thought began to influence some palaeoanthropologists in the 1970s. At that time, debates about diagnoses founded on the “total morphological pattern” were replaced by discussions about the value and polarity of the observed traits. In this way, some authors were influenced by cladistics, which devises cladograms based exclusively on derived characters. Thus some palaeoanthropologists proposed lists of such derived characters (Hublin, 1978, 1986; Stringer, 1984; Wood, 1985), others only proposed cladograms (Collard and Wood, 2001; Delson et al., 1977; Johanson and White, 1979; Olson, 1978; Santa-Luca, 1980; Strait and Wood, 1999; Skelton and McHenry, 1998; White et al., 1981; Wood, 1981; Wood, 1992b; Wood and Collard, 1999) and finally, both lists and cladograms were proposed together by some authors (Andrews, 1984; Andrews and Martin, 1987; Eldredge and Tattersall, 1975; Groves, 1989; Hoffstetter, 1974; Lieberman et al., 1996; Skelton and McHenry, 1992; Strait, 2001; Strait and Grine, 2004; Strait et al., 1997; Wood, 1984, 1992a). But, apart from rare studies (Chamberlain and Wood, 1987; Stringer, 1987), data matrices were rarely available in the palaeoanthropological literature.

In a following phase, discussions about the lack of unequivocal results due to disagreements about the scoring of operational taxonomic units (OTUs) and characters on one hand, and, on the other hand, debates about the methods dealing with the variability or the redundancy of some traits (Andrews and Martin, 1987; Bräuer and Mbua, 1992; Skelton and McHenry, 1992) raised objections that subsequently led palaeoanthropologists to abandon cladistics. Habgood (1989) and Trinkaus (1990) contested the use of cladistics in palaeoanthropology and, in spite of answers by Tassy (1996) to these objections, cladistics was largely ignored or misunderstood by palaeoanthropologists (see Hlusko, 2004). This rejection of cladistics in palaeoanthropology was clearly anticipated by Bonde (1981) and finally, few cladistic analyses of hominids providing a matrix were published in the last two decades (Argue et al., 2009; Asfaw et al., 2002; Caparros, 1997; Curnoe, 2001; González-José et al., 2008; Mounier and Caparros, 2015; Prat, 2002; Smith and Grine, 2008; Widiyanto and Zeitoun, 2003; Zeitoun, 1996, 2000, 2001, 2009; Zeitoun et al., 2010).

In an attempt to settle the decade-long debate about *Homo floresiensis*, we present a thoroughly documented cladistic analysis of the LB1 calvaria.

2.2. One Specimen, one OTU

The phylogenetic pattern of human fossil specimens (as of any fossils) should be resolved before discussing

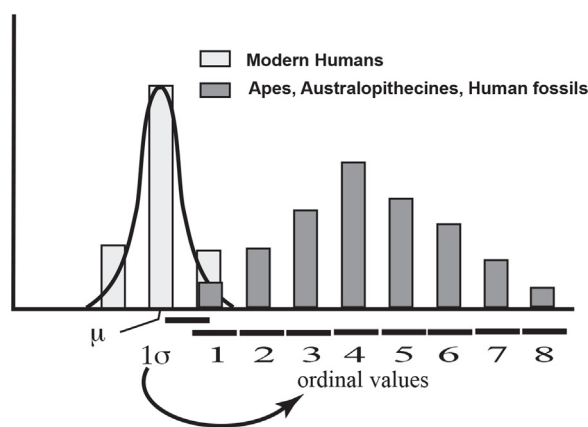


Fig. 1. Coding method. For any given index, the standard deviation(s) and mean of the modern human population are used as a standard and are translated into an ordinal value to score the OTUs (modern and fossil samples and populations).

Fig. 1. Codage. Pour un indice donné, l'écart-type (s) et la moyenne dans la population des hommes modernes prise comme référence sont utilisés comme standards et servent à transcrire les données en valeurs ordinales pour effectuer le codage des caractères métriques des OTUs.

the evolutionary processes leading to such a pattern. Yet, phylogenetic hypotheses in palaeoanthropology almost exclusively result from the analysis of group of specimens lumped together according to the weight of tradition. Because the grouping of specimens under taxonomic names is controversial, we decided to treat every specimen as a different OTU, which corresponds to the original definition of OTUs (Sneath and Sokal, 1973; Sokal and Sneath, 1963).

2.3. Coding the metrics and nonmetric morphological characters

We consider together both metric and nonmetric morphological characters in our analysis. Several techniques have been proposed to translate metrics in cladistics (Almeida and Bisby, 1985; Archie, 1985; Chapill, 1989; Mickevich and Johnson, 1976; Strait et al., 1997; Thiele, 1993), but it would take too long to explain each of them, along with their limitations. Apart from Strait et al. (1997), who proposed a solution, the main problem of these techniques is that they are not applicable by considering one OTU for each specimen.

A metric coding sequence was established by comparing the range of values of the metrics for an extant human (*Homo sapiens sapiens*) sample taken as a standard (Zeitoun, 2000). For convenience we summarize this coding method here. Because we are mainly considering human taxa, we chose an extant human sample to standardize the amount of variation within each state of the characters for each calculated index. From the extreme value (minimum and maximum) gathered for the sample, the amplitude of variation is divided into segments equivalent to the value of the standard deviation (Fig. 1). Each segment therefore corresponds to a state for the character defined by the index. Among all possible indices calculated from 38 classical cranial anatomical landmarks in physical

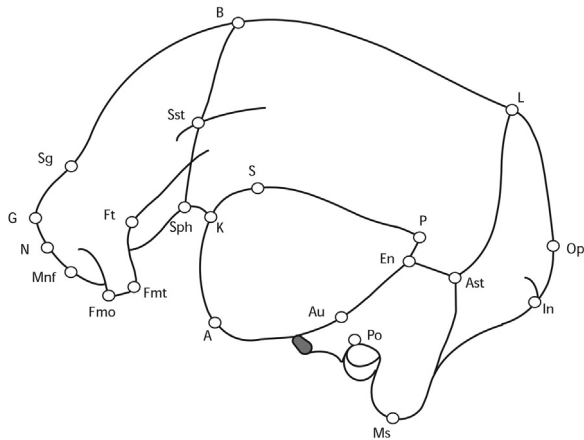


Fig. 2. Anatomical landmarks. G: Glabella; Sg: supraglabellare; B: bregma; L: lambda; Op: opisthocranium; In: inion; Sst: suprastephanion; Sph: sphenion; K: krotaphion; Ast: asterion; En: entomion; Au: auriculare; Po: porion; Ft: fontotemporale; N: nasion; Mnf: maxilonasofrontale; Ms: mastoideale; Fmt: frontomale temporale; Fmo: frontomale orbitale; A: anterior point of the temporal scale; P: posterior point of the temporal scale; S: upper point of the temporal scale.

Fig. 2. Points de références anatomiques. G : Glabella ; Sg : supraglabellare ; B : bregma ; L : lambda ; Op : opisthocranium ; In : inion ; Sst : suprastephanion ; Sph : sphenion ; K : krotaphion ; Ast : asterion ; En : entomion ; Au : auriculare ; Po : porion ; Ft : fontotemporale ; N : nasion ; Mnf : maxilonasofrontale ; Ms : mastoideale ; Fmt : frontomale temporale ; Fmo : frontomale orbitale ; A : point antérieure de l'écaille temporale ; P : point postérieure de l'écaille temporale ; S : point supérieur de l'écaille temporale.

anthropology (Fig. 2), two current anthropological types of indices were considered: type I=(arch AB - chord AB)/chord AB and type II=(chord AB/chord CD). Bearing in mind that the bilateral data are reduced to one single parameter and to bones taken individually, 2264 indices were calculated *per* complete individual.

2.4. Parsimony and simplification

Many of the numerous initial possible metric indices ($N=2264$) were rejected because no differences were found between apes, australopithecines and *Homo* ($N_{\text{rejected}} = 1919$ e.g. 84.7% of the data). Besides, it can still appear that among the morphological characters several have been described for a single structure, such as the cranial keeling, the eyebrow or the temporo-mandibular articulation. From a strictly anatomical point of view, we took into consideration all the anatomical elements that have been discussed by several anthropologists to describe and distinguish different fossil hominid specimens. Our coding of the states of these non-metric morphological characters can also be used for partially preserved specimens.

3. Materials

Reconstructing hominid phylogeny should involve examining the largest possible number of fossils, but in order to avoid the problems resulting from the large amount of missing data (since most fossils are incomplete) we focus this study on the best-preserved human fossil

calvaria (Table 1). Thus we consider 4 outgroups including two extant taxa, *Pan troglodytes* and *Gorilla gorilla*, and two extinct taxa, *Paranthropus* (based on Knmer 406) and *Australopithecus* (based on Sts 5). Among the other OTUs, 26 are human fossil specimens, including LB1, and one is an extant series of modern humans. Our choice to restrict our phylogenetic analysis to the calvaria of LB1 is legitimate given the fact that we compare this specimen to *Homo erectus*, for which the type-specimen is an incomplete calvaria, in keeping with the fact that “The species hypodigms examined do not include postcranial remains because, with the exception of partial skeletons, such specimens can only rarely be attributed to particular species with a high degree of confidence. Moreover, the postcranial skeletons of most species are poorly known, and thus the cladistics utility of postcranial features would be compromised” (Strait and Grine, 2004). The morphological characters of the calvaria taken into account are those usually described and debated by morphologists in palaeoanthropological studies. These characters are defined and listed in Appendix 1.

When ontogenetic information is available to propose a transformation series of the character states, this information is added to the treatment of the matrix. Among the 123 non-metric morphological characters, there are two ways to treat the multistate characters: ordered or unordered. When the states of a character follow an ontogenetic sequence in modern humans, the character is ordered. In the other cases, unordered treatment is selected. Multistate characters account for 74% of the characters, and among them 23% are ordered (nonmetrical morphological characters 2, 4, 18, 32, 92, 99, 103, 106, 108, 109, 114, 119, 120 and metrical characters 125, 126, 129, 130, 137, 140, 142, 143, 145, 146, 147, 148, 149, 152, 153, 154, 155, 156, 165, 166, 167, 179, 182, 183, 184, 192, 193, 194, 199, 200, 201, 202, 226, 227, 237, 240, 246, 259, 260, 261, 283, 286, 291, 293, 294, 297, 300, 301, 303, 304, 305, 306, 307, 308, 309, 330, 384, 385, 388, 389, 416, 423, 424, 435, 437 and 441).

We used 613 measurements to produce metric (ratio) characters that represent the frontal bone (154 measurements), the parietal (84), the temporal (72), the occipital (51), and the calvaria as a whole (252). These data (chords and arches, measured between all the landmarks on a calvaria) are transformed into 345 metrical indices (Appendix 2) and allow to discriminate the various taxa (e.g. modern humans, human fossils, *Paranthropus*, *Australopithecus*, *Gorilla* and *Pan*). The metric characters have 2 to 9 states. Finally, after this coding step, a cladistic analysis is carried out with 345 metrical morphological characters and 123 non-metric morphological characters. The final matrix concerns 31 OTUs and 468 characters (Appendices 3 and 4).

4. Results

Analysis carried out with a heuristic search in PAUP 3.1.1 (Swofford, 1993) using tree bisection reconnection branch swapping (TBR) and 100 random addition sequences (RAS) produce only one parsimonious tree (Length = 2953 steps; CI = 0.386; RI = 0.426).

Table 1

List of the OTUs including their usual taxonomic attribution and chronology (original specimens in regular, casts in italic).

Tableau 1

Liste des UTO avec leurs attributions taxonomiques et chronologie (spécimens originaux en caractère normal, moulages en italique).

Specimen	Current Taxonomical attribution	Taxonomical references	Taxonomical result	Location	Dating	Chronological references
KNMER 1470	<i>Homo rudolfensis</i>	Groves (1989)	<i>Homo rudolfensis</i>	Kenya	1,6–2,5 Ma	Fitch et al. (1996)
KNMER 1813	<i>Homo ergaster</i>	Groves (1989)	<i>Homo ergaster</i>	Kenya	> 1,88–1,90 Ma	Feibel et al. (1989)
KNMER 3733	<i>Homo cf Homo ergaster</i>	Wood (1992)	<i>Homo nov sp1</i>	Kenya	1,78 Ma	Wood (1991)
KNMER 3883	<i>Homo cf Homo ergaster</i>	Wood (1992)	<i>Homo nov sp2</i>	Kenya	1,5–1,65 Ma	Wood (1991)
KNMWT 15000	<i>Homo cf Homo ergaster</i>	Wood (1992)	<i>Homo erectus</i>	Kenya	1,53 Ma	Walker & Leakey (1994)
Trinil 2	<i>Homo erectus</i>	Dubois (1893)	<i>Homo erectus</i>	Java	1,0–07 Ma	Van den Bergh et al. (2001)
LB 1	<i>Homo floresiensis</i>	Morwood et al. (2004)	<i>Homo erectus</i>	Flores	95–17 ka	Morwood et al., 2004
Sangiran 2	<i>Homo erectus</i>	Weidenreich (1943)	<i>Homo erectus</i>	Java	1,27–1,20 Ma	Larick et al. (2001)
Sangiran 17	<i>Homo erectus</i>	Weidenreich (1943)	<i>Homo erectus</i>	Java	1,3–1,02 Ma	Larick et al. (2001)
Laetoli H18	Archaic <i>Homo sapiens</i>	Bräuer & Rimbach (1990)	<i>Homo sapiens rhodesiensis</i>	Tanzanie	129–90 ka	Bräuer (1989)
Kabwe 1	<i>Homo rhodesiensis</i>	Woodward (1921)	<i>Homo sapiens rhodesiensis</i>	Zambie	> isotopic stage 6	Day (1986)
Omo Kibish 2	Archaic <i>Homo sapiens</i>	Bräuer and Leakey (1986)	<i>Homo sapiens rhodesiensis</i>	Ethiopia	?	
Sambungmachan 1	Archaic <i>Homo sapiens</i>	Bräuer & Mbua (1992)	<i>Homo sapiens soloensis</i>	Java	37 ± 12 ka	Yokoyama et al. (2008)
Ngandong VI	<i>Homo soloensis</i>	Bräuer & Mbua (1992)	<i>Homo sapiens soloensis</i>	Java	47 ± 18 ka	Yokoyama et al. (2008)
Ngandong XI	<i>Homo soloensis</i>	Bräuer & Mbua (1992)	<i>Homo sapiens soloensis</i>	Java	52–27 ka	Swisher et al. (1996)
Ngawi	Archaic <i>Homo sapiens</i>	Widianto & Zeitoun (2003)	<i>Homo sapiens soloensis</i>	Java	?	
Sinanthropus III	<i>Homo pekinensis</i>	Black (1927)	<i>Homo sapiens pekinensis</i>	China (Lower fissure)	> 460 ka	Wu & Dong (1983)
Sinanthropus XI	<i>Homo pekinensis</i>	Black (1927)	<i>Homo sapiens pekinensis</i>	China (couche 8–9)	420 ka	Pope (1992)
Bodo 1	<i>Homo sapiens</i>	Rightmire (1986)	<i>Homo sapiens</i>	Ethiopia	Isotopic stage 11	Bräuer (1989)
Petalona 1	Archaic <i>Homo sapiens</i>	Stringer et al. (1979)	<i>Homo sapiens</i>	Greece	240–160 ka	Hennig et al. (1981)
Arago XXI + XLVII	<i>Homo erectus</i>	Lumley & Lumley (1971)	<i>Homo sapiens</i>	France	450 ka	Lumley et al. (1984)
Dali	<i>Homo sapiens daliensis</i>	Zhou et al. (1982)	<i>Homo sapiens daliensis</i>	China	230–190 ka	Wu (1991)
Monte Circeo I	<i>Homo sapiens neanderthalensis</i>	Blanc (1939)	<i>Homo sapiens neanderthalensis</i>	Italy	> 50–60 ka	Grün & Stringer (1991)
La Chapelle-aux-Saints 1	<i>Homo sapiens neanderthalensis</i>	Vandermeersch (1965)	<i>Homo sapiens neanderthalensis</i>	France	60–44 ka	Raynal (1990)
Amud I	<i>Homo sapiens neanderthalensis</i>	Suzuki (1970)	<i>Homo sapiens neanderthalensis</i>	Palestine	54–38 ka	Grün & Stringer (1991)
Skhùl V	<i>Homo sapiens sapiens</i>	Vandermeersch (1981)	<i>Homo sapiens sapiens</i>	Palestine	113–66 ka	Mercier et al. (1993)
Modern human	<i>Homo sapiens sapiens</i>		<i>Homo sapiens sapiens</i>	Indonesia	Actual	
STS 5	<i>Australopithecus africanus</i>	Broom & Robinson (1947)	OUTGROUP	South Africa	3,3 Ma	Partridge (1973)
KNMER 406	<i>Paranthropus boisei</i>	Wood (1992)	OUTGROUP	Kenya	1,65–1,7 Ma	Wood (1991)
Gorilla gorilla	<i>Gorilla gorilla</i>		OUTGROUP	West Africa	Actual	
Pan troglodytes	<i>Pan troglodytes</i>		OUTGROUP	West Africa	Actual	

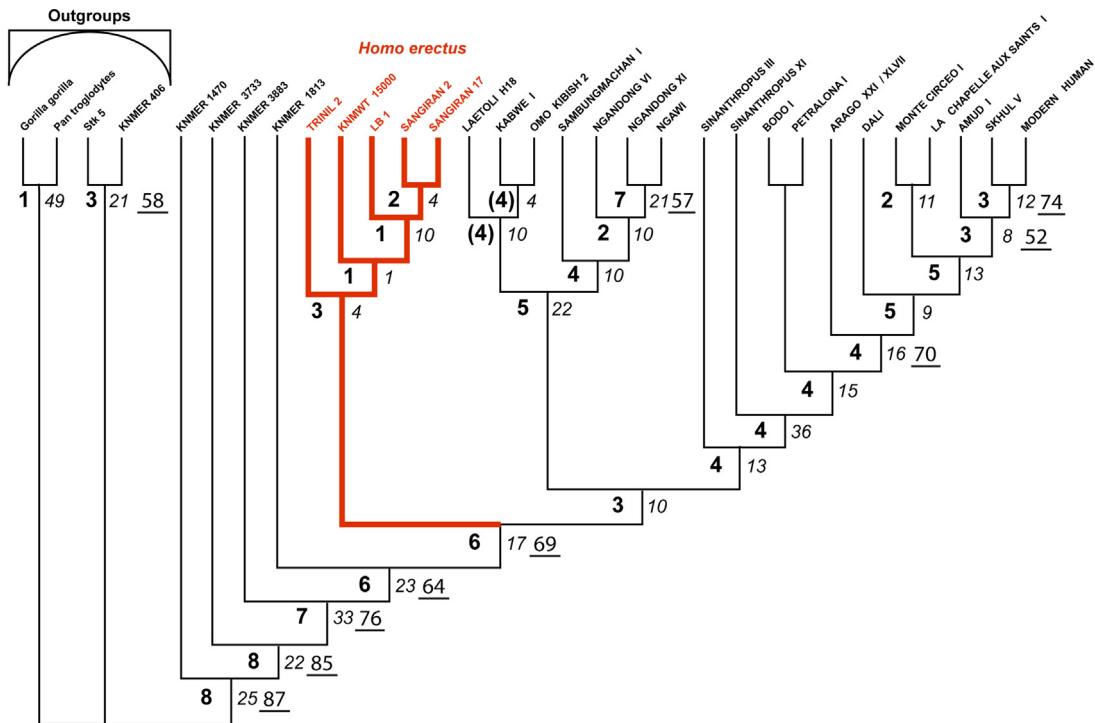


Fig. 3. Single tree with its characteristics: Length of the tree: 2953 steps; CI: 0.386; RI 0.426. Number of unambiguous synapomorphies: **x**, Bremer support: **x**, and bootstrap values: **x** (only provided if > 50%).

Fig. 3. Arbre unique. Longueur de l'arbre : 2953 pas. Indice de cohérence : IC=0,386 ; indice de rétention : IR=0,426. Nombre de synapomorphies non ambiguës : **x** ; indice de Bremer : **x** et valeurs de bootstrap : **x** (indiquées seulement si > 50 %).

Clade supports are assessed based on Bremer support (Bremer, 1994) and bootstrapping (Felsenstein, 1985). Bremer support values is calculated from the suboptimal Trees 1–8 steps longer than the shortest tree and are indicated on the parsimonious tree. Standard bootstrap resampling is carried out with a traditional search, producing 1000 replicates with absolute frequencies but no values are statistically significant (all are inferior to 95%). The minimum (unambiguous change) lengths of the branches for each node are also provided on Fig. 3.

The analysis shows that the calvaria of LB1 is close to the specimen KNM-WT 15000 and to the Trinil-Sangiran series and is more distantly related to the Solo series (Ngandong, Ngawi, Sambungmacan) and to extant humans. Phylogenetic positioning therefore demonstrates that LB1 belongs to the clade that can be called *Homo erectus* (Dubois, 1893). It should be noted that although a single tree has been obtained, its RI and CI are weak. However, the *Homo erectus* clade including LB1 is supported by 4 unambiguous changes and up to 58 maximum changes (Table 2), and the smallest clade that includes the Solo series and extant humans is supported by a Bremer index of 10. Together, these findings provide fairly strong evidence that LB1 is not a dwarf modern human. Based on the skull size, which was not taken into account by our way of coding the characters, whatever the causality of the process (hypophysary nanism or insular nanism etc.), we simply propose that LB1 is a small *Homo erectus* who also appears to be the geologically most recent known specimen of that clade.

5. Discussion

5.1. Questioning the single former cladistic analysis of LB1

Argue et al.'s (2009) study took into account only a non-metric morphological dataset and is based on the *a priori* grouping of specimens that may not reflect their phylogenetic affinities. In that study (Argue et al., 2009), *Homo erectus* was represented by three specimens (Sangiran 2, Sangiran 17, Trinil 2), *Homo ergaster* by two specimens (KNM-ER3733 and KNM-ER 3883), *Homo rhodesiensis* by a single specimen (Kabwe 1), *Homo habilis* by two specimens (KNM-ER 1813 and OH 24), and finally, *Australopithecus africanus* was represented by three specimens (Stw 505, Sts 71 and Sts 5). On the basis of these OTUs defined *a priori*, Argue et al.'s cladistic analysis suggests that LB1 is the sister group of the australopithecines (e.g. Stw 505, Sts 71 and Sts 5) and that the new taxon *Homo floresiensis* is characterized by four autapomorphies: the presence of an obelionic depression, the absence of a postglenoid process, an orifice of the incisive canal that is on a plane with the second premolar, and a P4 Tomes'root.

We disagree that these four characters are diagnostic of *Homo floresiensis*. We also observed an obelionic depression (character 28, state 2) on LB1, but this feature is present in the modern population as well as in some African human fossils and does not appear to be an autapomorphy in our analysis. The LB1 tympanal contributes almost exclusively

Table 2List of the unambiguous (minimum changes) synapomorphies supporting the *Homo erectus* clade, as defined here.**Tableau 2**Liste des synapomorphies non ambiguës soutenant le clade *Homo erectus*, tel que reconnu ici.

Node <i>Homo erectus</i> : 4 unambiguous (minimum changes) synapomorphies (maximum changes = 58)					
character	state	CI	RI	Character state description	
31	2	0.333	0.455	Presence of a postcoronal depression	
47	0	0.167	0.167	Median lateral extension of the <i>torus occipitalis</i>	
129	1	0.200	0.200	BSst \leq 0.05	
130	1	0.167	0.375	BFt \leq 0.06	

Node (LB1 (Sangiran2, Sangiran 17)): 10 unambiguous (minimum changes) synapomorphies (maximum changes = 58)					
Character	State	CI	RI	Character state description	
33	0	0.125	0.462	No thrust of the temporal band after the coronal suture	
107	0	0.250	0.400	Entoglenoidal formation and <i>tuberculum zygomaticum</i> median to the <i>fossa mandibularis</i>	
119	1	0.222	0.632	Small <i>processus postglenoidalis</i>	
134	2	0.500	0.250	FtFmo 0.18 to 0.22	
369	2	0.500	0.571	PoK/EnS > 0.74	
385	2	0.333	0.250	EnPo/PMs > 0.88 to 0.97	
387	0	0.333	0.333	EnMs/EnA < 0.50	
423	1	0.333	0.200	AstAu/PMs 1.41 to 1.28	
430	0	0.273	0.385	LIn < 0.16	
435	0	0.250	0.400	LAst/LMs > 0.75	

to the rear wall of the mandibular fossa (character 81, state 1), but there is a small but transversally stretched out *processus postglenoidalis* (character 119, state 1). It is weak (character 120, state 0) and it laterally overtakes the end of the tympanal (character 121, state 1). It is rounded in anterior view (character 122, state 1) and triangular in lateral view (character 123, state 0).

The incisive (nasopalatine) foramen at the second premolars is a part of the normal human variation observed among Australo-Melanesian populations and is illustrated in Milicerowa (1955). We did not consider dental characters, but according to Haile-Selassie (2001), a P4 with Tomes' root is present in the Miocene *Ardipithecus ramidus* and in another hominin from the Atapuerca site. Indeed, Carbonell et al. (2008) indicated that the C, P3 and P4 of the ATE9-1 mandible exhibit single Tomes' roots with a groove along the mesiolingual root surface. Moreover, in Jacob (1973) described the Sangiran 8 mandible with a Tomes root on the P3 and, finally Jacob et al. (2006) claimed that the Tomes' roots on LB1 in P3 and P4 are completely within expectations for extant human populations from the region. These data suggest that the characters interpreted as autapomorphies by Argue et al. (2009) have a broader taxonomic distribution.

According to our analysis, the LB1 specimen belongs to a clade that can be named *Homo erectus*, which contradicts both main alternatives discussed: a microcephalic modern human hypothesis or a new species.

Our hypothesis that LB1 belongs to *Homo erectus* appears to be compatible with additional anatomical parts not taken into account in our phylogenetic analysis. On the one hand, according to Brown and Maeda (2009), both of the Liang Bua mandibles share symplesiomorphic characters with *Australopithecus* and early *Homo* and on the other hand, even if the postcranial remains of *Homo erectus* are poorly known (Donlon et al., 2006), recent studies of the foot, hand, and shoulder provide evidence that features

found in the postcranial remains of the Liang Bua series are similar to the primitive morphology of earlier hominins (Jungers et al., 2009a, b; Larson, 2007; Larson et al., 2007, 2009; Orr et al., 2013; Tocheri et al., 2007). In both cases (mandible and postcranial), from a cladist point of view, primitive characters do not provide evidence of close affinities.

Other elements seem to support our conclusion. Following the results provided by Balzeau et al. (2005), the endocast of LB1 resembles the endocast of a juvenile *Homo erectus* more than that of an adult *Homo erectus*, according to van Heteren (2008). Moreover, on the basis of the exocranial anatomy, when taking all principal components into account with the use of Euclidean distances, Liang Bua only clusters with *Homo erectus* (Argue et al., 2006; Lyras et al., 2009). Gordon et al. (2008) acknowledged that their metric analyses of LB1, in which they found it to be similar to *Homo erectus* (and, to a lesser extent, *Homo habilis*), might be affected by scaling relationships for crania as small as LB1. Thus, finally should it be hypothesized that LB1 is a small (possibly pathological) *Homo erectus*?

5.2. A question of size

Even under our hypothesis, the small size of LB1 raises questions about the underlying evolutionary process. Holliday and Franciscus (2009) conclude that the small body size of LB1 cannot be explained exclusively by the retention of primitive (*Australopithecus*-like) traits. So, how to explain such a small size?

The biological significance of size variation has long been debated in the context of the origins and evolution of *Homo*, thus playing a key role in discussions concerning species recognition, sexual dimorphism, life history, and phenomena such as Allen's and Bergmann's rules, secular patterns in diet and nutrition, local adaptation to variations in climate, resource availability, and selection

Table 3

Comparison between the height of modern Indonesians and pathological individuals with LB1 specimen and comparison of cranial capacity between specimens usually attributed to "Homo erectus" and LB1.

Tableau 3

Comparaison de la taille des hommes modernes indonésiens et des individus pathologiques avec le spécimen LB1 et comparaison de la capacité crânienne entre des spécimens habituellement attribués à *Homo erectus* et le spécimen LB1.

Human category	Stature in m	Cranial capacity in cm ³	References
Modern human (Indonesia)		1350	Beals et al. (1984)
Female	1.62		Chuan et al. (2010)
Male	1.63		Bargain & Zeidan (2014)
Rampasa population			
Female	1.44		Rahmawati et al. (2007)
Male	1.49		Rahmawati et al. (2007)
Pathological modern human <i>pituitary hypoplasia (dwarfism of Sindh)</i>	1.19	1000	Maheshwari et al. (1988)
	1.24		Murray et al. (2000)
Trinil 2		930	Grimaud-Hervé and Lordkipanidze (2010)
		943	Holloway (1975)
Sangiran 2		840	Grimaud & Lordkipanidze (2010)
		815	Holloway (1975)
Sangiran 10		840	Grimaud & Lordkipanidze (2010)
		855	Holloway (1978)
Sangiran 12		1,059.	Holloway (1978)
Sangiran 17		960	Grimaud & Lordkipanidze (2010)
		1,004	Holloway (1978)
Sinanthropus II		995	Grimaud & Lordkipanidze (2010)
		1,030	Weidenreich (1943)
Sinanthropus III		915	Grimaud & Lordkipanidze (2010)
		915	Weidenreich (1943)
Sinanthropus V		1,140	Chiu et al. (1973)
Sinanthropus VI		850	Weidenreich (1943)
Sinanthropus X		1,245	Grimaud & Lordkipanidze (2010)
		1,225	Weidenreich (1943)
Sinanthropus XI		1,020	Grimaud & Lordkipanidze (2010)
		1,015	Weidenreich (1943)
Sinanthropus XII		1,020	Grimaud & Lordkipanidze (2010)
		1,030	Weidenreich (1943)
D 2280		790	Grimaud & Lordkipanidze (2010)
		775	Gabounia et al. (2000)
D 2282		625	Lumley et al. (2006)
D 2700		645	Vekua et al. (2002)
		600	Lee (2005)
D 3444		625-650	Lordkipanidze et al. (2006)
D 4500		546	Lordkipanidze et al. (2013)
KNMER 42700		691	Spoor et al., 2007
KNMWT 15000		885	Grimaud & Lordkipanidze (2010)
		880	Begun & Walker (1993)
KNMER 3883		785	Grimaud & Lordkipanidze (2010)
		804	Holloway (1983)
KNMER 3733		715	Grimaud & Lordkipanidze (2010)
		848	Holloway (1983)
KNMER 1470		760	Grimaud & Lordkipanidze (2010)
		752	Holloway (1978)
KNMER 1813		500	Grimaud & Lordkipanidze (2010)
		510	Holloway (1978)
Homo erectus mean value		860	
Liang Bua		426	Kubo et al. (2013)
		417	Falk et al. (2005)
	1.2	430	Jacob et al. (2006)
	1	380	Brown et al. (2004)
	1.06		Morwood et al. (2005)
	1.26		Henneberg et al. (2014)
Theoretical Pathological <i>Homo erectus</i>			
Theoretical pathological effect on Dmanisi D4500	$(1.24/1625) \times 1.50 = 1.14$	$(1000/1350) \times 860 = 637$	
Theoretical pathological effect on KNMER 1813		404	
		378	

driven by diseases or environmental and behavioural factors (Plavcan, 2012). With a height of a little more than one meter and a cranial volume comparable to that of a chimpanzee, the well-known mechanism of “insular nanism” initially evoked by Brown et al. (2004) is advanced as the most likely explanation by some authors (Meijer et al., 2010; van Heteren, 2012) for the Liang Bua series. Body size is used as a criterion for erecting a new species among various taxa (Tintant, 1972), as exemplified by the distinction between *Cervus simplicidens* and *Cervus elaphus* by Guadelli (1996).

If we examine the raw data again, we observe significant differences of interpretation of body size of the Liang Bua series among authors (Table 3). Several human fossils have small brains, and sometimes this criterion has been used to erect new taxa. The KNM-ER 1813 specimen was considered the paratype of the species *Homo ergaster* by Groves (1989), but because of its brain size (510 cm³), Fergusson (1995) erected the name *Homo microcranous*, based on this specimen. Notwithstanding, nobody followed Fergusson and, in other human fossil series, some specimens have a small cranial volume but authors did not systematically erect new species for these. The human series of Dmanisi was initially attributed to *Homo ergaster* (Gabunia, 1992), but the discovery of a large mandible (D2600) in this assemblage was used to erect the species *Homo georgicus* (Gabounia et al., 2002). Subsequently, because of the discovery that a complete small (546 cm³) calvarium (D4500) and a large mandible (D2600) belong to the same specimen, Lordkipanidze et al. (2013) abandoned *Homo georgicus* to designate the Dmanisi series. Thus, they put *Homo georgicus* into synonymy with *Homo ergaster*. We also suggest abandoning the name *Homo floresiensis* to designate small *Homo erectus* and we recommend putting *Homo floresiensis* into synonymy with *Homo erectus*.

5.3. Pathology and size effect

On the basis of the overall shape analysis of the cranial morphology of several fossils, Lyras et al. (2009) also postulate that the Liang Bua series is distinct from modern humans, including microcephalic specimens, Neolithic specimens from Flores Island, and Melanesian specimens. LB1 cannot be assigned to a modern microcephalic human on the basis of its endocranial (Falk et al., 2005a, b, 2007, 2009) or exocranial (Argue et al., 2006) anatomy. Eckhardt et al. (2014) considered that the new species hypothesis results from the conflation and misinterpretation. Henneberg et al. (2014) suggested that LB1 had a disturbed developmental homeostasis reflecting Down syndrome. Our phylogenetic results suggest a third explanation.

It is a cardinal rule of systematics that a new species can be erected only from a non-pathological specimen, and this question has to be considered for LB1. Even determining the stature of the Liang Bua series is challenging; Eckhardt et al. (2014), for instance, considered that it is a mistake estimate the stature of LB1 by extrapolation, using the femur length with a formula derived from an African pygmy population. The most astonishing feature of the anatomy of the Flores specimens is not its height (see Jacob et al., 2006 and Henneberg et al., 2014), but rather, its tiny cranial

capacity (Brown et al., 2004; Conroy and Smith, 2007; Falk et al., 2005a, b, 2007; Kubo et al., 2013; Martin et al., 2006a, b; Richards, 2006).

For *Homo erectus sensu lato*, height has been estimated at around 1.50 m, with a mean cranial capacity of 904 cm³ (Rightmire, 2004). Local (Indonesian) *Homo sapiens sapiens* have a mean height of 1.63 m (Bargain and Zeidan, 2014) and a mean cranial capacity value of 1350 cm³ (Beals et al., 1984). The height of the pathological cases described by Maheshwari et al. (1988) and Murray et al. (2000) among present populations (1.20 m) is comparable to the stature of the Liang Bua series, but not the cranial capacity (1000 cm³, vs about 400 for LB1). Rahmawati et al. (2007) showed that at 5.5 SD below the combined sex mean of the people living at Rampasasa around the Liang Bua cave (1.49 m for males and 1.44 m for females), LB1 is, a clear outlier. Data about the skull size of the entire human data set leads to similar conclusions (Plavcan, 2012). However, the cranial volume of LB1 can be estimated only with moderate precision (Table 3).

Initially, Falk et al. (2005a, b) argued that LB1 cannot be considered a microcephal because it is different from their studied specimens, while other authors (Martin et al., 2006a, b; Weber et al., 2005) consider that the former studies could not conclusively reject this hypothesis. From the beginning of this debate, pathologists have suggested various possible pathologies to explain LB1: microcephaly (Martin et al., 2006a, b), Laron Syndrome (Hershkovitz et al., 2007), cretinism (Obendorf et al., 2008; Oxnard et al., 2010), or microcephalic osteodysplastic primordial dwarfism type II (MOPD II) (Hall et al., 2004; Rauch et al., 2008).

Brown (2012) asserted that LB1 matched none of the known pathological traits and metrics, and van Heteren (2013) provides convincing and detailed elements to reject the hypotheses interpreting LB1 as a pathological modern human. Nevertheless, Henneberg et al. (2014) gave fresh impetus to the debate by associating facial asymmetry, small endocranial volume, brachycephaly, disproportionately short femora, flat feet and other characteristics to Down syndrome. The hypothesis of hypophysal nanism described by Murray et al. (2000), which is a very rare syndrome that leads to an allometrically conservative reduction of the whole individual, has not yet been tested. This pathology is known in Asia and is suspected to occur in the Pacific (Zeitoun et al., 2007). According to Maheshwari et al. (1988), this rare disease occurs at higher frequencies in endogamous populations, and endogamy is favoured by geographic isolation, as on islands such as Flores.

6. Conclusion

The suggestion that *Homo floresiensis* is not a pathological modern human has remarkable consequences and raises exciting questions. This suggests that modern humans coexisted with another hominine species until much more recently than previously thought (Lahr and Foley, 2004); *id est* –18,000 years instead of –30,000 years ago (the latter date is the demise of Solo men in Far East Asia and of Neanderthals in Far western Eurasia; Zeitoun et al., 2010). This hypothesis suggests that, until recently, the phenotype of humankind remained very malleable

to environmental constraints, despite the development of the technological skills seen in the human fossils of Liang Bua (Moore et al., 2009). Our findings suggest a coexistence of two species of hominines within *Homo* until very recently, and raise questions about the selective pressures that reduced body size in the lineage leading to LB1.

“The task of palaeoanthropologists is to reconstruct the evolutionary history of the period between our species, *Homo sapiens*, and the ancestral species we share exclusively with chimpanzees and bonobos” (Wood, 2012), but most paleoanthropologists instead aim to tackle the evolutionary process directly rather than first assessing the evolutionary pattern. An elaborate review of the current debate led Aiello (2010) to conclude that the most parsimonious explanation for the morphology of Liang Bua series is that *Homo floresiensis* is a descendent of an early australopithecine-like hominin. The new species hypothesis promoted by several authors (Aiello, 2010; Argue et al., 2009; Brown and Maeda, 2009; Jungers et al., 2009a, b) is mainly based on the fact that the Liang Bua specimens arguably possess both derived and primitive characters, which were produced by mosaic evolution, or heterobathmy of characters, a trivial phenomenon. The external morphology of the LB1 skull is significantly different from that of modern humans and similar to that of archaic *Homo*, according to Baab and McNulty (2009), and in particular to *Homo erectus* (Gordon et al., 2008; Lyras et al., 2009). However, similarity includes shared primitive characters, derived characters and homoplasy, and these distinctions were not made by these authors.

The only previous phylogenetic analysis of LB1 is that of Argue et al. (2009), but as we have shown, none of the four autapomorphies described by these authors can be retained. Our phylogenetic analysis of the LB1 calvaria suggests that it is included in the clade *Homo erectus*, which is restricted to the Trinil-Sangiran series and to the African specimen KNMWT 15000. Whereas the Solo series was initially considered distinct from *Homo erectus* (Campbell, 1963; Oppenoorth, 1932), since Jacob (1967), various authors included the series in *Homo erectus* (but see Bräuer and Mbua, 1992; Durband, 2007; Santa-Luca, 1980; Stringer, 1987; Zeitoun et al., 2010). We do not identify any autapomorphic feature for the LB1 calvaria, and comparisons of facial or postcranial characters are difficult due to the lack of available remains reliably attributed to *Homo erectus sensu stricto* (Donlon et al., 2006). Studies on mandibles (Brown and Maeda, 2009) or even hand, foot and shoulder (Jungers et al., 2009a, b; Larson, 2007; Larson et al., 2007, 2009; Orr et al., 2013; Tocheri et al., 2007) led us to recognize symplesiomorphic characters with *Australopithecus* and early *Homo* that only suggest that LB1 is not a *Homo sapiens*.

Several authors (Henneberg and Thorne, 2004; Hershkovitz et al., 2007; Jacob et al., 2006; Obendorf et al., 2008; Oxnard et al., 2010; Martin et al., 2006a; Rauch et al., 2008; Richards, 2006; Weber et al., 2005) have suggested that the small body size and most especially the low cranial capacity of LB1 (considered an extant human by these authors) may be pathological. Down syndrome, as described by Henneberg et al. (2014) and Eckhardt et al. (2014) on the one hand, or the pituitary hypophylasia

described by Maheshwari et al. (1988) and Murray et al. (2000), on the other hand, are interesting hypotheses to explain the small skull size of the LB1. Thus, the evolutionary pattern indicates that LB1 is a *Homo erectus*, which does not necessarily exclude the possibility that its size could be due to a pathological effect. Nevertheless, the frequency of occurrence of these diseases could be exploited to rule out this possibility, if they are very rare, even in isolated populations. Finally, we conclude that the process leading to such a small size is still unanswered.

Acknowledgments

We would like to thank Tony Djubiantono for his authorisation to study the Liang Bua specimens and Patrick Semal for his interesting information concerning the Pacific area. We thank Maciej Henneberg and Robert Eckhardt for informative data and discussions, as well as Louise Byrne and Kevin Padian for improving our English and four reviewers for their constructive comments. Last but not least, thanks to Michel Laurin for his advice. The initial stage of this work was supported by the Fyssen Foundation.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2015.12.002>.

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