Riddle unravel reprised: the role of LB1 in inferences about human functional morphology and phylogeny

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Abstract – In his paper titled "The unraveled LB1 (*Homo floresiensis*) riddle? Some critical comments on the morphology of LB1" Alfred Czarnetzki (2014) argued that LB1, incorrectly designated as *Homo floresiensis*, is actually a specimen of an orangutan (*Pongo abelii floresiensis*). Although we agree that LB1 is not a member of a new hominin species, we disagree with Dr Czarnetzki's diagnosis. He bases his conclusion on some poorly observable morphological traits such as the oblique line of the lower jaw and condyle tangent angle of the femur, plus unspecific characters including rounded orbits, and arbitrary conversion of continuously distributed traits into discrete traits. Some of these traits of LB1 clearly differ from those of the orangutan, e.g. wide interorbital region, while some others, such as those of wrist bones, vaguely echo those of *Pongo*. As hominoid primates, orangutans show some morphological similarities to humans, but these are not borne out by DNA sequence analyses. Bones and teeth of LB1 yielded only DNA fragments compatible with modern humans, though so far they are interpreted as contamination. Morphological traits of LB1 show disharmony that is a sign of abnormal development and thus LB1 is best interpreted as a pathological modern human.

Keywords – „the hobbit", developmental disharmony, DNA, Flores, species diagnosis

Zusammenfassung – In seinem Aufsatz „The unraveled LB1 (*Homo floresiensis*) riddle? Some critical comments on the morphology of LB1" in dieser Zeitschrift legt Alfred Czarnetzki (2014) dar, dass der als LB1 bezeichnete Knochenkomplex fälschlicherweise als *Homo floresiensis* klassifiziert wird, jedoch tatsächlich als ein Exemplar des Orang-Utan (*Pongo abelii floresiensis*) anzusprechen sei. Wir stimmen mit ihm darin überein, dass LB1 kein Vertreter einer neuen Spezies ist, möchten aber Czarnetzkis Zuordnung zur Spezies der Orang-Utans widersprechen. Czarnetzki stützt seine Diagnose auf einige nur ungenau beobachtbare morphologische Merkmale wie z. B. die schräge Linie des Unterkiefers und den Kondylen-Tangenten-Winkel am Oberschenkelknochen, auf unspezifische Merkmale wie z. B. gerundete Augenhöhlen, und auf eine ad-hoc Umwandlung kontinuierlich verteilter Merkmale in diskrete Merkmale. Es gibt jedoch Merkmale am LB1, die eindeutig nicht zu Orang-Utans passen, z. B. die breite Interorbital-Region, während einige andere Merkmale wie etwa die der Handwurzelknochen der Gattung *Pongo* im Großen und Ganzen entsprechen. Als hominoide Primaten zeigen Orang-Utans in der Tat einige Ähnlichkeiten zu Menschen, welche aber durch DNA-Analysen nicht bestätigt werden. Aus Knochen und Zähnen des LB1 konnten Fragmente von DNA extrahiert werden, die mit denen moderner Menschen übereinstimmen; dies hat man bislang jedoch als Kontamination interpretiert. Die morphologischen Merkmale von LB1 zeigen eine Disharmonie, die von einem abnormalen Wachstum zeugt, weshalb LB1 am besten als ein moderner und pathologisch veränderter Mensch eingeordnet wird.

Schlüsselwörter – der „Hobbit", Entwicklungsstörung, DNA, Flores, Artenbestimmung

Introduction

We regret the death of Alfred Czarnetzki, and thank his widow, along with Winfried Henke for completing the manuscript titled „The unraveled LB1 (*Homo floresiensis*) riddle? Some critical comments on the morphology of LB1." For those of us who value science as an open enterprise, additional perspectives always are welcome, particularly when the underlying set of primary evidence is so limited (Eckhardt et al., 2015) and the access to that evidence is so selectively restricted as to call scientific impartiality into open question (Eckhardt et al. 2014; Eckhardt & Henneberg 2014). We regret that, unlike members of our research group, Dr. Czarnetzki was unable to examine the original specimens. However, it is our position that his inferences merit consideration even though the handicap of his having to work at a remove from the actual bones may explain his shift in opinion from his participation as an author in earlier papers concluding that LB1 manifested microcephaly (Weber et al. 2006; Pusch & Czarnetzki 2008), to the posthumous individual conclusion that „…LB1 could only result in a position close to or within the variability of the genus *Pongo*." This alteration of perspective is surprising, to say the least. Formal response to it on the part of our group is required not only by the magnitude and direction of revised opinion by someone who had been a serious morphologist, but also because of the unusual composite nature of the latest paper published under Dr. Czarnetzki's name. This publication combines a manuscript written before his death on 20 May 2013 (noted as dated 7 May 2012), with the addition by the Editors of references to papers published since then, including ours (Eckhardt et al. 2014; Henneberg et al. 2014). It is legitimate to raise the point of whether the author would have adhered to the posthumously published conclusion in the face of the mass of evidence that we have presented, some of which is immediately pertinent to his inferences about seeming special affinity of LB1 from Liang Bua Cave, Flores, to *Pongo*.

In the sections of this paper that follow (Material and method, Results, Discussion, Conclusi-

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on) we present here not our own corresponding manuscript sections, since our evidence and arguments already have been set forth in extensive detail (Eckhardt et al. 2014 and Henneberg et al. 2014; enlarging upon Jacob et al. 2006). Instead, in each section here we offer the results of our own data collection and analysis as the basis for comments on what Dr. Czarnetzki has written. In our assessment his views range from some that are trenchant observations by an experienced morphologist to others that perhaps are best characterized as unclear phrases and unresolved contradictions reflecting thoughts that would be expected in an unfinished manuscript but not one prepared by an experienced author himself for publication.

Material and method

The listed materials are said to comprise published data on LB1, a cast of the LB1 skull, the morphology of 23 skulls and 9 endocasts of microcephalic modern humans (phrasing makes it uncertain whether the study included the actual specimens or published observations on them), and endocasts of another 9 microcephalics, past observations on >5000 worldwide modern human skulls, plus an unspecified number of orangutan skulls (NB, skulls only are mentioned, not postcrania) in the State Collection of Anthropology and Palaeoanatomy in Munich, as well as data in the cited publications. The full extent of comparative data on LB1 and other specimens available to Dr. Czarnetzki is unknown since the 'literature' section is not exhaustive and therefore is unlikely to reflect all sources that were consulted by him. Dr. Czarnetzki made observations of morphological features on a cast of LB1 and on CTs (inferred from Figures in the paper, these observations, at least principally, were of orangutan specimens plus a published CT of LB1, source unspecified).

Results

One observation is best quoted verbatim: „First of all we noted (i) the special course of the oblique line of the lower jaw (*Linea obliqua mandibulae*) compared to *Pithecanthropus*, H.s.s., *Pongo pygmaeus* and LB1 (Fig. 1 a-c)…." The oblique line of the lower jaw begins modestly at the mental tubercle and proceeds posteriorly and superiorly along the external surface of the mandible, passing just below the mental foramen and becoming much more prominent as it nears the ramus. This feature provides attachment for the depressor anguli oris and buccinator muscles. However, only Fig. 1 (b) shows the external (buccal) surface of the mandible, in the form of a drawing by Selenka (1898), in which it is difficult or impossible to distinguish the oblique line. Fig. 1 (a) and Fig. 1 (c) show internal views, in the form of median sagittal CT sections, on which it simply would be impossible to view the *linea obliqua mandibulae*. This reason alone, as well as the author's failure to explain what was intended to be demonstrated by the comparison, render this point moot.

As a parenthetical note that is aside from the main point of Dr. Czarnetzki's paper and our response to it but requested by referees of our paper, we address his use of *Pithecanthropus* as a formal genus name. The taxonomic name Pithecanthropus erectus originally was created by Eugene Dubois to refer to the hominid fossils that he discovered in Java at the end of the 19th Century; as a result of his continued discoveries it came to encompass an extensive and anatomically informative body of fossil remains. These were discussed later in detailed comparative context by Weidenreich. Through at least the 1970s the colloquial term „*pithecanthropine*" often, as by C. Loring Brace in the 1960s and beyond (see Brace 1967), was used to refer collectively to the Javan and somewhat later Chinese populations, as well as non-Asian fossils (such as *Olduvai Hominid 9*) that shared their diagnostic morphological features (skulls that were long and low with marked supraorbital tori, generally with thick vaults). However, the Latinate generic names *Pihecanthropus* and *Sinanthropus* were replaced by the formal taxonomic name *Homo erectus* following a suggestion made by the systematist Ernst Mayr (1950). More recently it has been proposed that because of lineage continuity, *Homo erectus* should be subsumed into *Homo sapiens* (Henneberg 1990; Wolpoff et al. 1994). The lingering, opposite tendency toward splitting suggested by Dr. Czarnetzki's usage of *Pithecanthropus* recalls in the context of this paper the odd suggestion originally made by Peter Brown that the Flores skeletons be designated as Sundanthropus tekagensis. In our judgment, far too little attention has been paid to that proposed oddity of nomenclature and what it implies.

Observation (ii), rounded shape of the orbits, is nonspecific and undiagnostic of taxonomic affinity, particularly when considered in isolation from logically related features such as the interorbital region, moderately wide in LB1 (see Fig. 4b) and strikingly much narrower in *Pongo* (see Fig. 3a and Fig. 3b, as well as Fig. 4a). Comparisons of individual traits in isolation, or even as elements in a list of traits that are not considered as functional wholes, are likely to be extremely misleading.

Next, three features are noted as „not in good agreement with one another." The general point intended by this observation again is unclear. Point 1 concerning „the low degree of dental prognathism" is contradicted within this paper itself. Feature 8 in Table 1 is „Protrusion of the upper incisors" (scored as shared by LB1, *Pongo*, and *Sivapithecus*, but not by *Pithecanthropus erectus erectus* or *Homo sapiens sapiens*, either normal or microcephalic). However, later in discussion of Fig. 4 the author notes correctly that „…the part of the socket for the incisors (premaxillary bone) is missing [on LB1] due to weathering." The evidential weight of inferences about the character states, shared or unshared, of missing – and hence unobservable – elements cannot be reckoned as high. Points 2 and 3, relating to low degree of suture fusion [most cranial sutures of LB1 are obliterated] in contrast to the fully developed dentition, hint at conflicting signals of biological maturation. These disparate data have been commented on widely by previous authors, though most commonly without drawing an obvious inference, that (as we maintain) such disharmony arguably is an unambiguous sign of abnormal development (JACOB ET AL. 2006; ECKHARDT & HENNEBERG 2010; ECKHARDT ET AL. 2014).

Trait lists such as Table 1 are problematical, since they tend to suffer from the same intrinsic limitation as cladograms based on morphological features: that is, the outcomes generally appear to be more or less predetermined by trait selection, criteria for which rarely are specified. A lesser but non-trivial defect is the tendency to represent as discrete character states some features that in reality are continuously distributed morphologies (Feature 1, Less developed supraorbital torus; Feature 18, Low degree of humeral torsion [understated in text as 110°, really at least 120° and hence within the range of living humans]; and a great many more) or polymorphisms as discrete, taxon-specific identifier (features 11 and 12; see Eckhardt (1987) and Eckhardt (2003) for the empirical counterpoise).

Larson et al. (2007) provide comparative data for humeral torsion in various living human populations. Unfortunately formal summary statistics such as mean and standard deviations are not provided there. However, their Fig. 4 shows that the value of 120° falls within the 95% confidence intervals of East Central African Pygmies (N=14), West Central African Pygmies (N=15), Australians (N=4), Melanesians (N=14), and Senoi (N=4); note, moreover, that these are small samples. Even if the value of LB1 humeral torsion were as low as the 110° as originally reported erroneously, it still would fall within the 95% confidence of the small Australian and African Pygmy samples. See also Eckhardt et al. (2014, p. SI 6). This is yet another example of our point that, despite repeated statements, the reportedly „unique" anatomical features of LB1 simply are not unique at all, and its supposed blend of unique and „primitive" characteristics reflects a pattern that is common in the case of developmental conditions reflected in atavisms.

Some of the pertinent examples of exceedingly broad but rather unlikely conclusions in concerning the hypothetical species *„Homo floresiensis"* are the two simultaneously published but flatly contradictory cladograms supposedly representing the affinities of LB1 (ARGUE ET AL. 2007; ZEITOUN ET AL. 2007), as well as the enduringly baffling subjective preference for the orangutan as the nearest human ancestor despite overwhelming molecular evidence to the contrary. An additional but minor point concerning Dr. Czarnetzki's results is that Fig. 2 is mislabeled. The „schematic drawing of the positive chin of modern man (c)" really refers to Fig. 2d. This technical flaw masks a more serious conceptual error in Fig. 2: propagation of the idea that modern humans uniformly manifest positive chins, despite data published repeatedly to the contrary (ECKHARDT ET AL. 2014; HENNEBERG ET AL. 2014 are among the references added after death of Dr. Czarnetzki, but this point had been documented clearly for some years before, e.g. JACOB ET AL. 2006; HATSUTI ET AL. 2007).

Brown & Maeda (2009) are believed by some to show a position contrary to our statement that positive chins are not universal features of modern humans. In fact Brown & Maeda (2009) did not show the contrary; they stated a contrary proposition, but did so in a manner that is insupportable observationally and logically. We previously have made this point at length (HENNEBERG ET AL. 2014, p. SI4), but it bears quoting here. The contention that some Australomelanesians lack external chins is made by Brown & Maeda (2009) „ …in their figure 19 and its legend in ref. 57, which purports to disprove our documentation of the existence of a reduced (neutral or negative) chin in some Australomelanesians (frequencies of which obviously vary from population to population in the region) by showing a lateral radiograph on one unidentified Australomelanesian with a projecting bony mental tuberosity supposedly within a facial phenotype that has the „appearance of a receding chin given by external soft tissue." The argument fails logically, because other than in a typological framework, the phenotypic characteristics of any single specimen cannot disprove by proxy the existence of traits found in other individuals among multiple populations in an entire geographic region. Moreover, there is reason to be skeptical of this particular example because the soft tissue profile is so tenuous that Brown and Maeda felt the need to delineate its contours with a line that is drawn in, obscuring if not altering the appearance of the soft tissue itself. Even if we do not reject the augmented evidence provided by this single unidentified specimen (photographic evidence thus modified is prohibited by some journals), it is obvious logically that the existence of any individual Australomelanesian with some bony chin projection covered by soft tissue that gives it a receding appearance cannot establish the generality of that hypothetical or actual anatomical conformation. Fortunately, it is unnecessary to speculate in this matter, or to rely on a single dubious specimen. There is abundant evidence contrary to the position of Brown and Maeda (2009). Among 76 adult Rampasasa, 93.4% exhibited neutral or negative chins externally, on the basis of their soft tissue configuration. In the entire sample, only eight subjects (15.35%) showed a positive bony chin that appeared neutral on the basis of its soft tissue covering, and no subject exhibited a negative soft tissue chin that concealed a salient underlying bony chin. These findings (Hastuti et al 2007) were presented to a large international audience (including Michael Morwood and many other supporters of „*Homo floresiensis*") without rebuttal and were published fully illustrated in the set of CD roms supplied to all conference participants. Because they were not published subsequently in a journal that would make them more widely available, we now have posted on our own web site (www.LiangBuaCave.org [19.5.2015]) the photographic and radiographic data that demonstrate the occurrence of neutral and negative chins in the Rampasasa of Flores. Despite our repeated efforts to show the morphological evidence for the normal absence of non-projecting chins in some extant human populations, some supporters of „*Homo floresiensis*" continue to deny this inconvenient truth (Michael Westaway and colleagues; see Eckhardt et al. 2015).

Against the background provided by these substantive critiques, it is obvious that we cannot concur that „On the basis of the unrivalled summary of *Pongo*-like features these skeletal remains should be assigned to the more gracile variant from Sumatra, *Pongo abelii floresiensis*."

Discussion

It has been argued, based on the arbitrary selection of morphological traits, that *Pongo* is the closest hominoid to modern humans (Schwartz 1984, 1988, 2005). This conclusion accepted by Dr. Czarnetzki is as good as stating that LB1 represents *Homo sapiens*. What Dr. Czarnetzki omitted to show is that LB1 fits *Homo sapiens* better than it fits *Pongo*. Had a different suite of morphological traits been selected for phylogenetic analysis, it would produce a finding that LB1 is similar to *Plio-/Pleistocene hominins* such as Australopithecus or the earliest Homo (Argue et al. 2007, 2009). All that these phylogenetic analyses establish is that if a sizeable number of morphological traits of LB1 is selected arbitrarily, some similarity to some hominoid can be found. Clearly, a more rigorous analytical method needs to be applied to resolve the status of LB1. It is worth noting, to provide context for Dr. Czarnetzki's unexpectedly revised conclusions about LB1 (from developmentally abnormal recent human to island-isolated *Pongo* subspecies), that his inferences appear to have been influenced heavily by the highly selective data presented repeatedly by Schwartz (1984, 1988, 2005). The phylogenies of Schwartz long have been at variance with much more extensively data-based papers (e.g. Goodman et al. 1971, 1983; Goldman et al. 1987; Bradley 2008); that is, abundant molecular findings published by many different investigators have falsified the view of Schwartz that the orangutan is the nearest living relative of humans. These contradictions have been published over the entire time period ranging from before, through contemporaneous with, to succeeding his formulations.

We have commented previously, though only to a limited extent since that is all that is possible in our brief response here, on the remark by Dr. Czarnetzki that „morphological similarities between *Pongo* and Homo can be observed much more frequently than those between Homo, Pan, and Gorilla." Matters of morphological trait selection, scoring (commonly involving the treatment of continuous variates as discrete traits), tabulation, evaluation, and quantitative assessment, all points that are central to cladistic and phylogenetic determinations, commonly are overlooked, with the implication that they are self-evident. The unexamined reality that they are not at all self-evident will continue to produce the striking contrast between some morphological vs. many molecular inferences, as in the case here as well as the works of Schwartz (1984, 1988, 2005).

This is not to say that molecular approaches are inherently superior or inerrant, but rather that the „traits" used in them are enormously more abundant quantitatively and far less subject to selection bias than morphological traits that are expressed at phenotypic levels much farther removed from DNA base sequences and consequently much less subject to environmental modifications of their expression. In this context we note that attempts were made at extraction and analysis of DNA from LB1 bones and teeth. Results of these studies, however, remain unpublished because only *Homo sapiens* DNA fragments were found (Henneberg et al. 2010, p. 143), which, in the words of Alan Cooper whose laboratory has run some of these analyses, is taken to mean that no DNA of the hypothetical „new species" was found while fragments that were found represent contamination.

The discrepancy in quantity and quality of evidence is a large part of the reason, we posit, for the shift in Dr. Czarnezki's assessment of LB1 (which is only part of the sample of the bones from Liang Bua Cave) from abnormal development producing microcephaly among other signs, to paedomorphic transformation of a local *Pongo* population in the context of island isolation (for which the author cites Bromham et al. 2007). Flores, being a part of a tightly clustered chain of islands separated only by narrow straits that sometimes disappear as a result of low sea levels, is not a geographical form that can be conducive to island isolation of large-bodied primates. In the context of the Liang Bua Cave bones, island isolation has been invoked to explain so many disparate outcomes that logically it is unlikely to explain convincingly any of them. Its invocation in this scientific conundrum seems analogous to the belief by every partisan group in a religious war that God uniquely is on their side.

The odd scatter of *Pongo*-like features in LB1 at least have been dealt with more forthrightly by Dr. Czarnetzki than by some others writing on the subject. Convergence on *Pongo* morphologies in some features have been found elsewhere, but these awkward phylogenetic implications have been dealt with on the part of others by avoidance of their probable meaning. Here we note, for example, plots of the canonical variables derived from the LB1 trapezoid and capitate. These data (e.g. Tocheri et al. 2007) fall most solidly – and quite counter-intuitively, if not to say embarrassingly for the advocates of „*Homo floresiensis*" – into the point distribution of *Pongo* specimens. Much more data and much less subjective analyses are needed to resolve this conundrum definitively, but until such empirical work (not just more repetitive, formulaic analyses of the same limited sample as offered so far [Orr et al. 2011, 2013]) has been done we suggest the far less unlikely view that the few and fragmentary Liang Bua Cave carpals reflect scaling effects, with the possible additional or alternative contribution of atavism, a common observation in developmental abnormalities of the sort that mark the LB1 specimen. Here some of the comments by Dr. Czarnetzki (2014, p. 6) on the wrist bones are highly pertinent: „The differences in the articular surface of the wrist bones can, in contrast to the similarities of the scaphoid and capitatum between *Pongo* and LB1 (Tocheri et al 2007), never be an argument for a species specific differentiation, because it is known that these features vary even within a species…."

A reviewer of this manuscript has raised several points about our comments concerning the relevance of the carpal bones from Liang Bua Cave for interpretations of the problem:

- „Please explain why geometric morphometric analyses are called „subjective". Common sense suggests that this is one of the most objective analytical method in comparative anatomy. The fact that the point clouds of modern humans, chimpanzees and gorillas are separated from each other in Tocheri et al. 2007 implies that the method is well suitable to differentiate the morphologies and hence is not subjective. On the other hand, it should also be noted that chimpanzees cluster with *Pongo* in many of these analyses and that also early hominins fall in the range of variation of great apes and close to LB1 with respect to these analyses, but outside the distribution of modern humans."
- „Please note that at least one other individual from Liang Bua (LB 21/22) in addition to LB1 shares the same ape-like morphology of the wrist bones. Thus, the sample is not so limited as claimed here."
- „Scaling effects are in fact an extremely unlikely explanation as the influence of body size is removed by 3D shape analyses. This is also supported by a close examination of the published analyses."
- „This citation (Czarnetzki 2014, p. 6) suggests that Czarnetzki also did not understand the power of 3D shape analyses. It is therefore not 'highly pertinent', it's just untrue."

Several comments are pertinent here. The first is that the carpal bones of LB1 (and subsequently LB6) entered into the discussion of the Liang Bua Cave remains only after the two most central defining features of „*Homo floresiensis*" (very low endocranial volume and stature) were shown to have been mis-estimated substantially. Endocranial volume is 430 ml rather than 380 ml (Jacob et al. 200, with several subsequent independent confirmations), and stature is far more likely to be in the range of 1.25 to 1.35 m rather than 1.06 m (Jacob et al. 2006, Eckhardt et al. 2014, Henneberg et al. 2014, De Klerk 2012). The chief explanatory hypothesis of island isolation also did not hold up (Jacob et al. 2006), a matter that has been accepted somewhat awkwardly and differentially, with some scholars seemingly able to believe simultaneously in island isolation as the explanation for small brain and body size as well as other features, but also in the origin of small brain and body size prior to arrival on Flores. Against this conflicting background, the carpal bone analysis of Tocheri et al. (2007) provided a convenient, skeletal-based anchor point from which the „new species" interpretation could pivot in a different direction, to the idea that the Liang Bua Cave skeletal remains instead were those of a late australopithecine or early Homo population caught in a time warp on Flores. In fact, no tangible evidence links them to a hypothetical (and still not clearly specified) ancestor on another continent separated by more than a million years in time.

A second comment is that the points concerning the 3-D analyses of the LB1 and LB6 (probably comprising LB20, LB21, LB22) carpal bones raised by the referee were dealt with in detail (three pages of discussion as Supplementary Information file SI5) in Eckhardt et al. (2014). For that reason we will respond to the referee comments here only to a limited extent, and hope that future readers will read our earlier paper, which we took pains and expense to publish as open access so it would be readily available.

Our more detailed response

1. As far as „Common sense suggests that this is one of the most objective analytical method in comparative anatomy", of course, as long as the measurements in question are made accurately and the statistical techniques are used competently, there is an element of objectivity. However, data are not collected, analysed, and interpreted in a philosophical vacuum. How does subjectivity enter? For one thing, in the selection of the specimens that form the basis of comparison for the several carpal bones of LB1 and LB6. For a decade we have noted in conference papers and posters as well as published papers that the core attributes of LB1 (short stature, unusually small brain size, asymmetry) are shared in common by several hundred abnormalities and pathologies. To date, taking into account all of the papers published by supporters of „*Homo floresiensis*," fewer than ten of these syndromes or conditions have been examined in any detail, and among the few that have been considered, a priori many of them do not make any sense at all, as is the case of the recent paper by Orr et al (2013). It is difficult to conceive of what hypothesis is being tested in the comparison of a pituitary giant with the Flores carpals, and one suspects that such specimens are included so that it can be said that some developmental abnormalities were considered in the analysis.

   Similarly, by their very complex nature, the geometric morphometric analyses make it possible for subjectivity to arise in their interpretation. For example, Orr et al. (2013) compared multiple data points and angles on LB1 and LB6 (debatedly referred to as fossil hominids, with four individually identified earlier true fossil hominids (AL 288, AL 333, TM 1526, KNM-WT 22994H), and eight later fossil hominids (Neandertals). The individual points and angles then were combined into three canonical variates that were plotted in pairwise comparisons. The results of these operations are complex swarms of points that show variable but extensive overlap.

   The numbers of verbal descriptions (which reflect the visual impressions of the plots) are very high indeed. That said, there are some repeating patterns that raise problems that are difficult to dismiss by those who advocate the position that the Liang Bua Cave carpals have any special affinity to the small sample of genuine early fossil hominids.

   Here is just one set of comparisons among a great many that could be teased out for the capitate: In the plot of can1 vs. can3, LB1 and LB 20 plot extremely close to each other, which should be expected. But both of these specimens sit virtually immediately on top of several *Pongo* individuals, which all together are grouped in a small swarm of points surrounded by Pan and *Pongo*. Nearby (higher and to the right on the plot) are AL288 and KNM-WT 22994H; however, AL333 is roughly five to six times further away from AL288 (to which it is much closer evolutionarily and even taxonomically) than it is from KNM-WT 22994H. Whatever does that set of spatial relationships signal? Again, on the same plot, LB1 and LB20 are about as close to two of the Neandertal specimens (below and to the right) as they are to TM 1526. We are at a loss to know what that pattern tells us, other than that we need a lot more specimens, of fossil hominids as well as individuals with developmental abnormalities, to test clearly formulated hypotheses.

For the hamate metrics the pattern is even more problematical for advocates of the position that carpal bone geometric morphometric comparisons provide clear support for the existence of „*Homo floresiensis*." In the plot of hamate can2 vs. can1, LB21+22 is closer to one Neandertal specimen, and to at least five *Pongo* specimens and two Gorilla specimens than it is to any early fossil hominid (only AL 333 being shown). In the same manner, in the plot of hamate can3 vs. can1, LB21+22 falls right on top of one Gorilla specimen and in the midst of about half a dozen more Gorilla specimens. It is further from AL 333 than it is from one Neandertal specimen and a large number of Pan and *Pongo* specimens.

2. What about the referee's comment „that at least one other individual from Liang Bua (LB 21/22) in addition to LB1 shares the same ape-like morphology of the wrist bones. Thus, the sample is not as limited as claimed here"? It appears that the referee is unaware that we already had noted the second individual (LB20, LB21, and LB22 are attributed to LB6). To the extent that the members of this small sample of carpal bones can be analysed, their consistently pervasive resemblance is not especially to the early hominid specimens, and not to any single great ape taxon but to several, and often to *Pongo* in particular, would seem to be a much greater problem for advocates of „*Homo floresiensis*" than generally is admitted.
3. The referee states that „Scaling effects are in fact an extremely unlikely explanation as the influence of body size is removed by 3D shape analyses. This is also supported by a close examination of the published analyses." These assertions are debatable. They are based on a confusion between statistical adjustments to dimensions after death of individuals, based on a given sample of bones distributed over a size range on the one hand; and the developmental genesis of bones (reflected partially in relative differences among various dimensions) during the life histories of different individual organisms. These retrospective and prospective processes emphatically are not the same.

This is not the place to develop the pertinent responses in full detail that would be needed to understand the geometric morphometric analyses of carpal morphology. After all, what we set out to do in our response to Dr. Czarnetzki's paper was to attempt an understanding of why a respected colleague who was a distinguished morphologist would shift his interpretation of the LB1 individual so radically, from a sign of developmental abnormality (microcephaly) to a regional variant of a different hominoid primate genus (*Pongo*). But neither can we avoid responding in a meaningful manner to suggestions that we do not understand the applications and implications of geometric morphometric analysis. We do understand these methods, and have used them ourselves, so have working knowledge not only of their intrinsic nature, but also their very real limitations. Discussion follows.

In the recent carpal bone study by Orr et al. (2013) the total sample was stated to comprise 67 specimens for the capitate, 66 for the hamate (NB: These numbers are incorrect in the original publication, being reversed; Fig. 6 shows a plot of the canonical variate scores for the capitate metrics, which includes the pituitary giant but not the pituitary dwarf; Fig. 8 includes points for the pituitary dwarf as well as the pituitary giant). Reportedly two individuals from Flores were included in the sample, but it was not specified whether they were Rampasasa, other known small-bodied individuals, or individuals larger in stature; the recent population of Flores is diverse in its composition, and this information as well as identification of these specimens on the various plots might have been informative.

There are several problems with the sample and its analysis. First, as noted immediately above, the sample is weighted toward large-bodied subjects. Second, as also noted, it contains at least one evident example of specimen misidentification; experience teaches that where one error is encountered in a study, others are likely to have been overlooked by referees as well as the authors. Third, the failure to include in the sample more than one or two token subjects with developmental abnormalities limits severely the inferences that can be made from it, given that it is offered as a test of the hypothesis that one or more Liang Bua Cave specimens manifest developmental abnormality.

Addressing the referee statement „Scaling effects are in fact an extremely unlikely explanation as the influence of body size is removed by 3D shape analyses" from another perspective, that of actual results, we observe that in

Orr et al. (2013), in the plots of can2 vs. can1 and can3 vs. can1 as part of their Figure 9, the point for LB21+22 is twice as far from the pituitary giant point than it is from the pituitary dwarf point. Our doubts that the canonical plots reflect shape independent of body size are reinforced directly and strongly by the fact that in Figure 13 B the plot of hamulus angle against total surface area shows the point for LB22 literally on top of the point for the pituitary dwarf (and both just at the boundary of the 95% confidence ellipse) and far distant from that of the pituitary giant (which is shown as having total surface area that is so great that it is placed outside the 95% confidence ellipse for the human sample). Another way of stating this observation is that in the Figure 13D plot, a known human with a developmental abnormality is more distant from the 95% confidence limits of the sample than is LB22, which is dismissed as being a hypothetical human with a developmental abnormality. Quite similarly, in Figure 13C, specimens labelled as LB22 and LB21+22 composite [the labelling here is confusing and again possibly incorrect] are far closer in hamulus breadth and hamulus width to the pituitary dwarf than they are to the rest of the plotted points for human specimens, including particularly the pituitary giant. In Figure 13A much the same pattern holds, while the pituitary giant specimen is not labelled. All of these observations are at variance with the referee's rote contention that „the influence of body size is removed by 3D shape analyses."

Our research group now is beginning to expand a research initiative begun on a pilot basis several years ago (Eckhardt et al. 2010), designed to study specifically an array of human subjects not limited by the need to work only with skeletal samples. We use methods already developed in biomedical contexts to explore the in vivo relationships among form and function in complex structures such as the carpals, thus having many more diverse subject available to us than those that turn up in museum samples.

4. The referee stated „This citation (Czarnetzki 2014, p. 6) suggests that Czarnetzki also did not understand the power of 3D shape analyses. It is therefore not 'highly pertinent', it's just untrue." It is not clear to us what point the referee is disputing. We do not have any independent knowledge of Dr. Czarnetzki's understanding of 3D shape analysis, which does not in any case seem to be pertinent to our response. If the referee is disputing Dr. Czarnetzki's statement that „these features [articular features of the scaphoid and capitatum] vary even within a species" and hence can „never be an argument for a species specific differentiation" then we are far more in agreement with Dr. Czarnetzki than with the referee. There is a rich orthopaedic surgical as well as anatomical literature documenting a high level of variation in joint surface shapes and areas. Whether or not hypothetical invariance of such features can be used to differentiate among species is beyond our knowledge, and we suspect that is beyond that of the referee as well. We know of no case in which morphological features of one or more carpal bones has been used to define a hominin species; stating that to be sufficient evidence to establish the reality of „*Homo floresiensis*" amounts to asserting as true the precise point that is being disputed.

   In discussing the form of locomotion inferred for LB1, Dr. Czarnetzki comments on the „specialized locomotion" of the orangutan, which „applies especially to the condyle tangent angle of the distal epicondyles of the femur... that can be observed only in non-human primates, but never in humans." Fig. 8 on page 8 illustrates the tangent angles of the distal epicondyles of the femur in *Homo sapiens sapiens* (H.s.s.), Gorilla, Pan, and *Pongo*. It is understandable that the figure is presented to show the difference in the inclination of the condyle tangent angle between H.s.s. and primates. However, it can be misleading to present only one figure as an example for each group, as this neglects variation within a group unless condyle tangent angles are included quantitatively (average condyle tangent angle +/- S.D., as well as maximum and minimum of the samples). Moreover, the paper did not clearly show how LB1 fits in more with *Pongo* based on condyle tangent angle. The condyle tangent angle or a CT cross-section of the LB1 femur are not presented. Even if these were presented, attempting to fit LB1 into either one of the groups, great apes or modern humans, based on condyle tangent angle may not be persuasive especially if the variation on the condyle tangent angle is large for each group, because LB1 is just one individual which could be on the extreme end of the range (recall that there are no femora in the Liang Bua Cave sample other than those of LB1). Dr. Czarnetzki's intended meaning, perhaps quite insightful, is undeveloped and hence although not necessarily wrong, remains elusive.

As further ironies in the debate over the taxonomic and phylogenetic status of LB1 as emblematic for all of the Liang Bua Cave bones, just as molecular evidence (Perry et al., 2014) is showing that environmental influences (including but not limited to isolation) can produce dwarfing in humans, the same evidence shows unequivocally that speciation is not a necessary part of the island population differentiation package. Gene based phenotypic differences can underlie morphological change without requiring reproductive isolation. These findings come even as advocates of „*Homo floresiensis*" have been abandoning island isolation as an explanatory device for other reasons (Eckhardt et al., 2014). In the event the „new species" advocates are devising alternative explanations (derivation from earlier Homo species from a million or more years ago) based largely on the failure of island isolation to explain existing evidence, which no longer supports uniqueness of the originally key defining features of low endocranial volume and short stature.

One last indication of the tension in Dr. Czanetzki's paper between opinions received from others and the framework of his own earlier and more reliable inferences is exemplified by his remark on „The contrast between the tiny stature and the big foot…." This erroneous observation (the foot is not objectively large, but only appears so in comparison with the abnormally short femur; see Henneberg et al., 2014) is contradicted by his own reconstruction of the stature of LB1: „For a femoral length of 280 mm, the average must be between 128.0 and 132.8 cm." This stature range is higher than that of 1.06 m extrapolated for LB1 since the earliest publications (Brown et al., 2004) and widely reiterated uncritically since. Dr. Czarnetzki's statue estimate falls in the same range as our own reconstructions (see Eckhardt et al., 2014 for citation of previous papers going back nearly a decade) as well as remarks by De Klerk (2012). These higher statures estimated for LB1 are within the range of living humans in the region.

Conclusion

Dr. Czarnetzki concluded that „…the phylogenetic positioning of LB1 could only result in a position close to or within the variability of the genus *Pongo*… features of the extremities… are in best agreement with the laws of functional anatomy for the locomotion of a pongo-like Hominoid." For the many reasons cited above, it is impossible for us to concur with this sharp revision in opinion. We suggest that the inferences made by Dr. Czarnetzki and many other scientists probably would be different, and at least would be better grounded empirically, if access to the Liang Bua Cave bones were open to all scientists rather than selectively restricted to those who continue to advocate the existence of a new hominin species even as the evidence for it has been shown increasingly to be untenable.

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