Three High Profile Genus *Homo* Discoveries in the Early 21st Century and the Continuing Complexities of Species Designation: A Review—Part II

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Abstract   Human paleontologists are unable to extricate species-level variation from individual, sexual, regional, geographical, pathological, and skull bone variations despite sophisticated statistical methodology. Additionally, true variation within and between groups cannot be generated from a handful of regional and geographical specimens presently used in comparative studies. I therefore conclude that we cannot identify species in the human paleontological record. This conclusion is supported by the analysis and discussion (in this paper) of research conducted on, what I deem to be, three high-profile genus *Homo* fossil discoveries: Dmanisi hominins, *Homo floresiensis*, and *Homo naledi*. The data compiled in these comprehensive studies conclude that Dmanisi, *floresiensis*, and *naledi* share features with all *Homo* and Australopithecine taxa. Specifically, none of these three fossils clustered or aligned definitively with any *Homo* specimens. Consequently, it may now be prudent for us to use numbers or look for gross similarities and differences in hominin fossils to classify them. As such, identifying fossils at the genus level, which was proposed recently, might be a solution worth considering. Using genera will reduce the specificity needed in species identification, but it might be preferable to the chaos we have now in species-level identification. This paper is published in two parts.

Keywords   Dmanisi, Genus, *Homo floresiensis*, *Homo naledi*, Intraspecific Variation, Interspecific Variation, Paleospecies, Species Concepts

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3. *Homo floresiensis*, Liang Bua Cave, Flores, Indonesia

In 2003, a joint Australian-Indonesian team discovered a fossil associated with simple stone tools in a cave called Liang Bua (LB1) on the island of Flores. Most of the skeletal elements for LB1 were recovered in a small area (500 cm^2) at a depth of 5.9 m in Sector 7 of the excavation at Liang Bua [52]. The root of the controversy concerning the taxonomic affiliation of LB1, in my opinion, is the disjunction between its morphology and geological age. LB1 ranges in age from 74,000 to 17,000 years ago using various dating techniques (i.e., ESR/U series date on a *Stegodon* molar, luminescence, and accelerator mass spectrometry) to calibrate the dates. However, redating of the Liang Bua skeletal remains and deposits have produced dates of 100,000 and 60,000 years ago [53]. We all know the dangers of using morphology to infer geological age. *Homo naledi* and even the Miocene ape *Sivapithecus* (dated between 14 million and 7 million years ago) skull, face, teeth, and premaxilla are similar to living orangutans; these are cautionary tales. For instance, Mana Dembo et al. [54] performed a dated Bayesian analysis to generate estimates of the evolutionary relationships and accuracy of age estimates of fossil hominins (including LB1 or its current species designation *Homo floresiensis*) with particular interest in the Dinaledi hominins (before their geological age was known). Using 7.24 million years to present as an a priori, jackknife resampling procedure on dated Bayesian analysis placed the age of LB1 at 19,000 years ago (very recent compared to the lower limits of the new 2016 dates). But its morphology is similar to Australopithecines, particularly the endocranial capacity, which ranges from 417 cm^3 to 430 cm^3 or slightly smaller 380 cm^3 [55-57].

According to Peter Brown et al. [58], *Homo floresiensis* is a nearly complete skeleton with a complete skull. Descriptions of selected features are as follows: the frontal squama is separated from the supraorbital torus by a supraorbital sulcus. The supraorbital torus arches over each orbit (not a straight bar across as in Javan *Homo erectus*), and the superior cranial vault bone is thicker than *Australopithecus* and similar to *Homo erectus* and *Homo*

sapiens. Facial profile is not prognathic, but there are prominent pillars lateral to the nasal aperture formed as a result of large maxillary canine juga. The infraorbital fossae are deep with large infraorbital foramen. Interestingly, there is some asymmetric obelionic flattening, resulting in reduced parietal thickness (prebregmatic depression). Maxillary and mandibular molars are small compared to Australopithecines, and premolars have Tomes root. The mandibular dental arch is narrow anteriorly and long, and the ramus root inserts on the corpus above the lateral prominence.

Furthermore, the iliac blades of the pelvis are broad and wide and the ischial spine is not prominent. The linea aspera of the femur is small and several indices (head size and shape, femur length and sub-trochanteric shaft size) fall within the chimpanzee and Australopithecine range, and the tibia has an oval shaft with slight curvature in the long axis and thick medial-laterally. *Homo floresiensis* height has been estimated to be 3 feet 6 inches based on measurements of its tibia [59]. According to the researchers, these estimates are outside the range of normal modern human height variation and considerably shorter than the average adult height of the smallest modern humans, such as the Mbenga and Mbuti (4 feet 11 inches), the Twa and Semang of the Malay Peninsula (4 feet 6 inches for adult females), or the Andamanese (4 feet 6 inches for adult females) [60, 61]. Moreover, the body mass is estimated to be 55 pounds. This body mass is smaller than modern pygmies and *Homo erectus* (some researchers have suggested that *Homo floresiensis* is either a descendant of *Homo erectus* or a dwarfed version of *Homo erectus*) [62].

There are three major competing hypotheses: (1) LB1 is a new species, (2) LB1 is a modern human from the Indonesian region (small-bodied) with Down Syndrome; (3) LB1 is an Indonesian *Homo erectus* dwarf. Other secondary hypotheses proposed are that LB1 is (A) a microcephalic pygmy modern human, (B) a modern human with myxoedematous endemic hypothyroidism (cretinism), and (C) a modern human with Laron Syndrome.

The researchers in these different camps are professionals using sophisticated analyses to obtain data; however, they disagree on the interpretation of the morphological variation. For example, facial asymmetry is viewed as disrupted development by proponents of the pathological hypothesis and postmortem taphonomic modification by the new species proponents. Finding a "new" species is always exciting, particularly when the new discovery is widely known in the popular press as the "Hobbit" after characters in a popular fiction book series and fantasy movie trilogy. And contemporary humans seem to prefer fantasy (over reality).

The proponents of the pathological hypotheses were compared indirectly to Rudolf Virchow, who, in 1856, viewed Neanderthal features as rickets in an ancient *modern* human [63]. In defense of the pathological

hypothesis proponents, there was no hominin fossil record in the mid-19th century, and Virchow was a staunch antievolutionist. In my opinion, proponents of the *Homo erectus* dwarf hypothesis attempted to take the most conservative approach.

Let us briefly discuss the findings in each of the three major hypotheses. Dean Falk et al. [64] compared 3-D computed tomographic reconstructions of the internal braincases (virtual endocasts that reproduce details of external brain morphology, brain size, and shape) from a sample of nine microcephalic humans, ten normal humans, LB1, a microcephalic female whose endocast supposedly resembled LB1, and a pathological modern human to test the hypothesis that LB1 represented a microcephalic *Homo sapiens* rather than a new species. The mean cranial capacity recorded for the nine microcephalics was 498 cm^3. The researchers obtained eight measurements electronically from the virtual endocasts and used them to generate four ratios that would discriminate between the two groups: cerebellar protrusion, relative length posterior base, relative cerebellar width, and relative frontal breadth [65]. Subsequently, these four ratios were used to develop discriminant and canonical analyses to study shape differences between microcephalics and normal humans (LB1, the microcephalic female similar to LB1, and the pathological human were not used to develop the discriminant functions). According to the researchers, when the most power discriminators (cerebellar protrusion and relative frontal breadth) were analyzed together, they classified microcephalics and normal humans with 100% success. In fact, LB1 sorted with normal humans and the microcephalic female similar to LB1 and the pathological human classified as microcephalics. The results suggested that LB1's brain shape (frontal breadth relative to cerebellar width and lack of cerebellar protrusion) differs completely from microcephalics.

Falk et al. [66] concluded that while the length of LB1's orbital surface sorted it with *Homo sapiens*, the relative height of its endocast; disparity between its maximum and frontal breadths; relative widths of its caudal and ventral surfaces; small cranial capacity; relative brain size; and ventrally expanded orbital surface show affinities to both *Homo erectus* and *Australopithecus africanus*. Then, they made a giant leap in declaring LB1 a new species: "The above findings for LB1, plus its bilaterally expanded but otherwise normal-appearing gyri in the region of Brodmann's area are consistent with its attribution to a separate species, *H. floresiensis*" [67, p 2516]. We see the same trend as in the Dmanisi hominins that LB1 cannot unequivocally be assigned to any *Homo* or Australopithecine taxa, despite the fact that LB1 has more similarities to *Homo erectus* based on data [68] I used to compare features (thirteen similarities and nine differences) (Table 7). In addition, we do not have, at a minimum, five or ten Liang Bua skulls to understand the range of variation at Liang Bua.

Table 7. Similarities and differences in selected craniodental and postcranial features of other *Homo* and Australopithecine taxa in relation to *Homo floresiensis* (based on description in Brown et al., 2004)

Characteristics	Early *Homo*		H. erectus		Australopithecine		*H. sapiens*	
	similar	different	similar	different	similar	different	similar	different
Small cranium	no	**yes**	no	**yes**	**yes**	no	no	**yes**
Parietal contour (pos. view)	no	**yes**	**yes**	no	no	**yes**	no	**yes**
Cranial base angle flexed	**yes**	no	**yes**[a]	no	no	**yes**	**yes**	no
Thick cranial vault	no	**yes**	**yes**	no	no	**yes**	**yes**	no
Endinion position	no	**yes**	**yes**	no	**yes**	no	no	**yes**
Separation of mastoid process from petrous crest by deep fissure	no	**yes**	**yes**[b]	no	no	**yes**	no	**yes**
Recess between tympanic plate and entoglenoid pyramid	yes[b]	no	**yes**[b]	no	**yes**[b]	no	no	**yes**
Breadth and depth of glenoid fossae	no	**yes**	no	**yes**	no	**yes**	**yes**	no
Angulation of articular eminence	no	**yes**	no	**yes**	no	**yes**	**yes**	no
Inferior surface of petrous pyramid	no	**yes**	**yes**[c]	no	no	**yes**	no	**yes**
Calvaria height and breadth	no	**yes**	**yes**[d]	no	no	**yes**	no	**yes**
Infraorbital region posteriorly oriented	**yes**	no	**yes**	no	no	**yes**	**yes**	no
Curvature of frontal Squama	**yes**	no	**yes**[e]	no	no	**yes**	no	**yes**
Posterior angulation of symphyseal axis	no	**yes**	no	**yes**	**yes**[f]	no	no	**yes**
Double mental foramen	no	**yes**	**yes**[a]	no	no	**yes**	no	**yes**
P$_3$ size and morphology	no	**yes**	**yes**	no	no	**yes**	**yes**	no
P$_3$ and P$_4$ crown and root morphology	**yes**	no	no	**yes**	**yes**	no	no	**yes**
Toomes root	no	**yes**	**yes**[a]	no	no	**yes**	no	**yes**
Femur—lesser trochanter is prominent/strong development of the inter- trochanteric crest	no	**yes**	no	**yes**	no	**yes**	**yes**	no
Fenoral neck long relative to head diameter	**yes**	no	no	**yes**	**yes**	no	no	**yes**
Femur length and sub- trochanteric shaft size	no	**yes**	no	**yes**	**yes**	no	no	**yes**
Tibia mid-shaft and length variation	no	**yes**	no	**yes**	**yes**	no	no	**yes**

[a]Share similarity specifically to Indonesian *H. erectus*

[b]Share similarity specifically to Asian and African *H. erectus* and Pliocene hominins

[c]Share similarity specifically to Zhoukoudian *H. erectus*

[d]Share similarity specifically to Sangiran 2 *H. erectus*, KNM-ER 3733, and KNM-ER 3883

[e]Share similarity specifically to early *Homo* and Dmanisi hominins

[f]Share similarities specifically to LH4 (*A. afarensis*)

boldEarly *Homo*: 6 similarities/16 differences; ***H.erectus*: 13 similarities/9 differences**; Australopith: 8 similarities/14 differences; *H. sapiens*: 7 similarities/ 15 differences

In the early weeks of the LB1 fossil discovery, Maciej Henneberg et al. [69] were cautious about the perceived "uniqueness" of the skeletal features (and the virtual endocast analysis detailed above and shared similarities to other *Homo* and Australopithecine taxa in Table 7 weaken the uniqueness argument). They were not quick to support the naming of another "new" species despite the immediate recognition that it would bring in this age of "light speed" information dissemination. A fossil might seem unique when there are two or fewer specimens in the taxon, where it is impossible to understand the range of variation (i.e., *Homo rudolfensis* is a similar example).

The researchers knew that recent *Homo sapiens* skeletons from Palau exhibit reduced stature and other regional population features similar to those on Flores. Specifically, Palau endocranial volumes scale appropriately to small body dimensions normal for these regional populations and postcrania showed proportions expected for *Homo sapiens*. They used deductive reasoning in documenting general developmental abnormality (i.e., Laron syndrome, cretinism, etc.) until their evidence pointed to a specific abnormality. The evidence pointed to Down Syndrome based on their observation and assessment of craniofacial asymmetry, brain diminution, and limb bone disparities. Henneberg et al. [70] noted that "LB1 phenotype is congruent with [Down Syndrome] being an example of disrupted evolved ontogenetic homeostatic systems" [71, p11968].

The opponents of the pathological hypothesis viewed the craniofacial asymmetry as taphonomic modification [72]. Henneberg et al. [73] described the asymmetry in LB1 (i.e., exaggerated, reversed frontal and occipital petalia with marked palatal rotation, etc.) and emphasized that "the overall craniofacial asymmetry cannot be attributed to postmortem taphonomic modification because it is reflected in asymmetric tooth wear that occurred during life" [74, p11968]. In essence, they believed that "facial asymmetry is a sign of Down Syndrome, with frequency cline of left-right differences increasing from frontal inferiorly through midface to mandible: frontal prominence 11.1%; lateral nasal prominences 43.33%; medial nasal prominences 64.29%; maxillary prominences 95.24%; mandibular prominence 96.67%" [75, p. 11968-11969].

In trying to understand why LB1 had a small brain, Henneberg et al. [76] used the occipitofrontal circumference. They obtained two measurements from respective colleagues (382 mm and 385 mm) and applied the measures to regression formulas. They also used occipitofrontal circumference from local living and skeletal populations near Liang Bua, and with a cranial capacity of 430 cm^3 reported in this study, LB1 seemed to lie within the standard deviation of these populations.

For the postcranial, the researchers noted that LB1's foot was long relative to the femur and tibia. The fleshy foot length of LB1 is 196 mm. In a sample of more than a thousand women of European ancestry, the average foot length was 240.7 mm and the shortest was 210 mm (LB1 is just 14 mm shorter). Compared with 132 Indonesian females, mean foot length was 230 mm (LB1 is 34 mm shorter). Henneberg et al. [77] noted that LB1's stature of 1,060 mm is shorter than would be predicted from feet of comparable length in living populations, even Rampasasa or Palau peoples. The short femur of LB1 (280 mm) reduced estimated stature, and "this pattern matches the finding from anthropometric data for Down Syndrome patients, in whom the syndrome results in greater shortening of the lower limb than the upper limb" [78, p11970).

Other researchers have argued that the postcranial of LB1 indicated that this individual's upper and lower body movements were slightly different from those of modern humans. Although the difference in upper body movement might have been an advantage in swinging from tree to tree, it was a disadvantage in tool-making and using. Specifically, the top of LB1's ulna twisted 120 degrees, in contrast to a twist of 145–165 degrees in modern humans [79]. When this low twist of the ulna was combined with a short clavicle, the shoulder girdle would be positioned more forward; this would have nothing to do with Laron Syndrome [80]. In other words, tool-making and tool use may have been complicated but not impossible. Analysis of LB1's carpal (wrist) bones indicated that they were similar to African great apes and Australopithecines, and her unusually long and flat feet in relation to her body resulted in a bipedal locomotion that was slightly different compared to modern humans [81, 82].

According to Brown et al. [83], the small body size and brain size of LB1 is the result of selective pressures due to chronic scarcity of dietary resources in the Southeast Asian island ecology. In essence, ancestors of LB1 (possibly *Homo erectus*) made the dangerous water crossing to reach Flores, and over time, there was selection for reduction in body size [84]. Evolutionary changes or evolutionary forces affect every life form in the ecology. Consequently, the phenomenon of "island dwarfing" has been documented for other large-bodied mammals in this region, such as mammoths. Specifically, *Stegodon*, a type of extinct elephant, and komodo dragons were both found in the deposits with *Homo floresiensis* [85]. This subspecies (*Stegodon florensus insularis*)—found in the same layers of Liang Bua cave as LB1—is itself a dwarfed form of its larger and geologically older closest relative, *Stegodon florensus florensis*. The larger *Stegodon* species is rare in the geology of Flores simply because it was difficult for large terrestrial animals to reach islands in the Wallacea region where there is a low level of migration by Asian and Australasian animals to the east and west [86]. It seems that these islands were isolated by strong currents, even when sea levels were low. Furthermore, there are numerous instances of human populations becoming smaller in body size, including on the islands of Southeast Asia. As mentioned in the first paragraph of this section, island dwarfing is often linked to reduced availability of resources in the ecology. Consequently, small body size may be more adaptive in environments of food scarcity.

As I have stated earlier in this section, until we find more fossils like Liang Bua in Indonesia, the "new" species *Homo floresiensis* will remain an enigma.

4. *Homo naledi*, the Rising Star Cave System, South Africa

Between 2013 and 2014, more than 1,550 fossils representing approximately 15 individuals were recovered from a deep chamber (30 meters below ground surface) called the Dinaledi Chamber, and 133 fossils representing approximately three individuals were recovered from a chamber 145 meters (shortest route) from Dinaledi called the Lesedi Chamber [87-89]. Erosional unconformities between the Dinaledi Chamber sedimentary layers enabled researchers to divide these layers into three broad lithostratigraphic units [90]. Subsequently, each unit was further divided into sub-units (i.e., Unit 3 = sub-units 3a, 3b, 3c).

According to the researchers, all fossils in the Dinaledi Chamber were unearthed in sub-unit 3b, which was 20–30 cm deep [91]. This is interesting because the research team claimed that "the [*Homo*] *naledi* fossils are the largest collection of a single species of an ancient human-relative

discovered in Africa" [92, p. 2]. Similar to the single evolving lineage hypothesis proposed for the Dmanisi hominins, the Dinaledi skeletal materials were also discovered in a stratigraphic sequence that was "narrow" both temporally and spatially.

After 2014, the Dinaledi fossils remained undated for just over two years. Consequently, speculation about the age of the fossils was rampant and based on the morphology of the fossils. For example, the Dinaledi fossils shared some features with Australopithecines and early *Homo*, principally small brain size (endocranial capacity range, virtually constructed = 465 cm^3 to 560 cm^3) [93-95]. Predictions range from 2 million years old to 100,000 years old (the actual chronometric date range is 414,000 years to 236,000 years ago).

As I have stated in the previous section, we all know the dangers of using morphology to infer geological age, and examples like the Miocene ape *Sivapithecus*, *Homo floresiensis*, and *Homo naledi* are worth repeating. Nonetheless, before chronometric dates were obtained, an assessment using dated Bayesian phylogenetic methods produced an age of 912,000 years ago. For Dembo et al. [96], two main goals were to find out the taxonomic affinity and geological age of *Homo naledi*. They knew from the initial analysis of the Dinaledi research team that *Homo naledi* shared craniodental and postcranial similarities with several *Homo* taxa [97]. In the study, Dembo et al. [98] used 391 craniodental characters (123 scored for *Homo naledi*) for 22 hominin taxa and two extant hominoids. First, they performed a dated Bayesian analysis and found that *Homo naledi* was in a clade with other *Homo* taxa (*Homo antecessor*, *Homo heidelbergensis*, *Homo neanderthalsis*, *Homo sapiens*) and *Australopithecus sediba*.

To test the strength of the hypothesis generated by the dated analysis, two Bayes factor tests were completed. In the first test *Homo naledi* was part of the clade that included the *Homo* taxa listed above and early *Homo*, *Homo erectus*, and *Australopithecus sediba*, and in the second test *Homo naledi* was a sister group within the *Homo* and *Australopithecus sediba* clade. The results of the first Bayes factor test supported the dated Bayesian analysis that *Homo naledi* "is nested within a clade consisting of the other *Homo* taxa and *Au. sediba*" [99, p22]. In the second Bayes factor test, there was support for *Homo naledi* as a sister taxon of *Homo antecessor*, Asian *Homo erectus*, *Homo habilis*, *Homo floresiensis*, and *Homo sapiens* and not a sister taxon of African *Homo erectus*, Dmanisi hominins, *Homo heidelbergensis*, *Homo neanderthalsis*, and *Homo rudolfensis*.

To estimate age of *Homo naledi*, Dembo et al. [100] used a jackknife resampling method to test the accuracy of the dated Bayesian analysis estimation of 912,000 years ago (morphological clock age estimate). Subsequently, the estimated ages were statistically compared with the geological dates to assess accuracy of the morphological

clock, and the researchers obtained a strong correlation. This analysis, albeit sophisticated, was not immuned from the dangers of morphological dating. In essence, the data generated by Dembo et al. [101] was similar to data in other research in that *Homo naledi* shared craniodental features with several specimens within the *Homo* taxa and was not definitively linked to any one *Homo* species [102-104]. What was different, however, was that *Homo naledi* also formed a close relation to *Australopithecus sediba*. Again, like skull 5 and the other Dmanisi hominins, the taxonomic affiliation of *Homo naledi* remains murky. Dembo et al. [105] stated the following: "The most reasonable conclusion to draw from our phylogenetic results, we think, is that the position of [*Homo*] *naledi* within the clade formed by *Homo* and [*Australopithecus*] *sediba* is currently ambiguous" [106, p24].

Paul Dirks et al. [107] initially began trial dating the Dinaledi Chamber deposits to obtain a rough age of the chamber and the best techniques to apply. In the end, they applied uranium-thorium and electron spin resonance. Uranium-thorium was used to date the flowstones directly above Unit 3 (overlying *Homo naledi* fossils) to obtain an upper age limit (335,000 years ago) and electron spin resonance were applied to three *Homo naledi* teeth and a baboon tooth from sub-unit 3a to obtain a lower age limit (236,000 years ago).

According to the researchers, there was no direct geological connection between the Dinaledi and Lesedi (undated) chambers [108, 109], but they were confident that the hominin remains from both chambers were morphologically consistent with their newly named species *Homo naledi*. In their words, "The collection is a morphologically homogeneous sample that can be attributed to no previously-known hominin species" [110, p3]. The conclusion of a morphologically homogeneous sample was based on an anatomical comparison of skeletal elements for size, curvature, length, shaft morphology, and muscle attachments during the refitting process. Taxonomic affiliation was based on comparison of the craniodental and postcranial metrics and nonmetrics of *Homo naledi* to a sample of *Homo* and Australopithecine taxa.

Out of 15 Dinaledi individuals recognized by the research team, only five individuals (DH1 to DH5) with the requisite cranial and mandibular bones (midface and cranial base were absent from assemblage) were used by various scientists to study variation at Dinaledi and taxonomic affiliation [111, 112]. Dinaledi adult cranial capacities ranged from 465 cm^3 to 560 cm^3 (DH1) and approximately 610 cm^3 for Lesedi 1 (LES1), with well-defined supraorbital torus and supratoral sulcus. Berger et al [113] believed that the variation at Dinaledi (i.e., brain size, nuchal region, supramastoid region, etc.) represents sexual dimorphism rather than different species. Furthermore, the anteroposterior of the cranial vault was short with frontal bossing and prelambdoidal flattening.

Myra Laird et al. [114] obtained sagittal lengths (bregma to lambda) of 79.0 mm for DH1 and 66.0 mm for DH2. In the posterior view, they noted that vault shape was pentagonal with sagittal keeling and parietal bossing. However, the vault breadth was greatest in the supramastoid region (DH1 = 115.0 mm; DH3 = 102.0 mm) and narrowed anteriorly with slight supraorbital constriction (DH3) according to the researchers. There was no observation of zygomatic prominence or flaring, but the researchers did note that the inferior root of the zygomatic process of the maxilla originated anteriorly between P^3 and P^4 and the shape of the palate was broad, parabolic, and deep posteriorly. In analyzing the mandibular torus, the research team observed a parabolic mandibular corpus with a well-developed lateral prominence at M$_2$. They also found a vertical mandibular symphysis, wide mandibular fossa, and wide extramolar sulcus.

Lauren Schroeder et al. [115] performed geometric morphometric (generalized Procrustes, principal component analysis, and multivariate allometry) comparative analyses of the overall shape of the Dinaledi hominins cranial and mandibular elements to find out (1) if they were indeed a new species; (2) if they belonged to early *Homo*, *Homo erectus*, or Australopithecines; and (3) the age of the fossils based on skull morphology (there were no dates for the Dinaledi hominins during the writing of the Schroeder et al. 2017 paper).

In all four analyses of cranial shape variation, DH1, DH2, and DH3 fell outside the *Homo erectus* convex hull; DH3, specifically, was clustered with other *Homo erectus* specimens (KNM-ER 3883 and KNM-WT 15000) and Dmanisi skull 1, reflecting similarities in cranial height and frontal angle (PC1). Interestingly, DH3 also clustered with *Australopithecus sediba*, reflecting similar positions of parietal notch (PC2). In cranial analysis two, DH3 clustered with Dmanisi skulls 1 and 3 and *Homo rudolfensis*, reflecting similar anteroposterior elongation of calvaria (PC2). In cranial analysis three, DH2 was aligned with *Homo erectus* (KNM-ER 3883) and Dmanisi skull 3, reflecting posterior cranial height and position of parietal notch (PC1 and 2). At this point, there was no definitive taxonomic affiliation for the Dinaledi hominins. This outcome mirrors the Dmanisi skull 5 discussed earlier in the paper. Finally, cranial analysis four showed DH1 clustered close to KNM-ER 1813 (*Homo habilis*), reflecting prognathism and cranial breadth (PC1), and KNM-WT 15000, reflecting calvaria length (PC2).

I ask the question again: Do these cranial dimensions and features (i.e., cranial height, parietal notch, calvaria length, frontal angle, etc.) affect mating and fertility? This question also relates to the mandibular analysis, where the results showed alignment with *Homo rudolfensis*, *Homo floresiensis*, and a few Australopithecine specimens [116].

For instance, DH1 clustered with *Australopithecus africanus* (Sts 36) and *Australopithecus* (*Paranthropus*) *boisei* (KNM-ER 729), reflecting corpus thickness and mental protuberance projection (PC1), and was close to *Homo rudolfensis* (KNM-ER 60000), *Homo floresiensis*, and *Australopithecus sediba*.

It is important to note at this point that the age of the fossils based on skull morphology suggested "an older origin for this taxon, at least in terms of overall skull shape prior to the emergence of *Homo erectus*, but postdating *H. habilis*" [117, p133]. The chronometric dates and the dangers of morphological dating were discussed earlier in this section.

When the research team investigated allometric relationships (shape and size), DH3 (for cranial analysis one and two) was outside the 95% confidence ellipse for *Homo erectus* and distant from all *Homo erectus* specimens for shape. Schroeder et al. [118] noted that "This indicates that in these two analyses, *H. naledi* does not appear to follow a *Homo erectus* allometric trajectory, contradicting the proposal that *H. naledi* could be a small variant of *H. erectus*" [119, p127]. Interestingly, cranial analysis 3 showed DH2 within the 95% confidence ellipse for *Homo erectus* and clustered with KNM-ER 42700 and Dmanisi skull 3. In the mandibular analysis, *Homo erectus* and *Homo sapiens* 95% confidence ellipses were overlapping and *Homo naledi* fell within this complexity. Are dietary (masticatory) and intra- and interspecific variations merging to create a complicated picture? For shape and size, DH1 was similar to *Australopithecus sediba* and *Homo habilis* (OH 13). For shape alone, DH1 aligned with early *Homo*, *Homo erectus*, and Australopithecines (and robust Australopithecines).

Furthermore, Schroeder et al. [120] compared Procrustes distances between individuals of *Homo naledi* and *Homo erectus* to the 95% confidence interval distributions of distances between individuals within and between a sample of *Homo sapiens* and *Pan troglodytes*. The results were inconclusive. The researchers stated the following: "The range of inter-group distances calculated between *H. naledi* and *H. erectus* in this analysis is larger than the distances between *P. troglodytes* and *H. sapiens*, which may indicate that either the *H. erectus* sample has a large degree of intra-group variability or that this variability may be inter-specific" (121, p131). This statement encapsulates the intractable problem plaguing primate evolution in general and human paleontology in particular.

Table 8 shows ratios of bivariate measurements published by Laird et al. [122]. Based on the results, we see the same trend as in other analyses [123-126]: *Homo naledi* shares features—more or less—with *Australopithecus sediba*, *Homo habilis*, *Homo rudolfensis*, and *Homo erectus*.

Table 8.   Select ratios of bivariate measurements (x100) (adapted from Laird et al., 2017)

Measurements	*H. naledi*				*A. africanus*	*A. sediba*	*H. habilis*	*H. rudolfensis*	*H. erectus*
	Mean	DH1	DH2	DH3	Mean	MH1	Mean	Mean	Mean
Cranial ht./porionic br.	79	77	76	85[a*]	72	67	72	74	74
Supra-mastoid br./temporal br	103[b]	105[b]	105[b]	99	111	109 108	104[b]	105[b]	103[b]
Postorbital br./superior facial br.				79[b]	69	81[b]	73	74	80[b]
Temporal lines/parietal br	51	52	45	55[b]	27	56[b]	32	43	57[b]
Squamous suture ht./br				67[a]	52	42	42	58	52
Mandibular fossa lg./br.				96[a]	60	52	58	79	75
Mandibular fossa depth/lg.				21[a]	48	50	52	32	51
Articular eminence br./mandibular fossa br.				80[a]	106	104	111	100	117
Bi-ento-glenoid br./temporal br.				58[b]	62	57	55	58[b]	54
Supra-orbital torus br. – chord/arc				75[a]	84	86	88	87	85
Anterior interorbital br./bi-orbital br				27[b]	22	26[b]	23	24	25[b]
Anterior interorbital br./orbital br.				72[a]	53	65	58	61	62
Maxillo-alveolar lg./br.	93[b]				107	100	95[b]	96[b]	98
Mental foramen ht./corpus ht. at P$_4$	40[a]	42			53	50	46	49	48

[a]These measures alone support the new species designation, *H. naledi* for the Dinaledi hominins. *H. naledi* appears distinct from all *Homo* taxa in cranial vault, temporal, and mandibular fossa/corpus.

[a*]This measure makes DH3 distinct from all other Dinaledi hominins.

[b]These measures alone suggest that *H. naledi* shares features with *H. rudolfensis*, *H. habilis*, *H. erectus*, and *A. sediba* in cranial vault and temporal.

If we were to eliminate some data in Table 7 and use others, how would interpretation of the data change? An example is instructive. If squamous suture height/breadth, mandibular fossa length/breadth, mandibular fossa depth/length, articular eminence breadth/mandibular, supra-orbital torus breadth–chord/arc, anterior interorbital breadth/orbital breadth, and mental foramen height/corpus height at P$_4$ were the only measurements used to compare the Dinaledi hominins to *Homo* and Australopithecine taxa, one could understand the research team's decision to name a new species—*Homo naledi*—based on these suite of traits (cranial vault, temporal, and mandibular fossa/corpus) that differed from other hominins. [127, 128] In cranial height/porionic breadth DH3 was different from the other Dinaledi hominins and more similar to the middle Pleistocene *Homo* sample group.

Alternatively, supramastoid breadth/temporal breadth, postorbital breadth/superior facial breadth, temporal lines/parietal breadth, bi-ento-glenoid breadth/temporal breadth, anterior interorbital breadth/biorbital breadth, and maxilla alveolar length/breadth used exclusively would cluster *Homo naledi* with *Homo rudolfensis*, *Homo habilis*, *Homo erectus*, and *Australopithecus sediba* (in cranial vault and temporal) creating an ambiguous picture and weakening the support for the new species designation. The postcranial bones (clavicle, ribs, carpals, pelvis, and femur) also present a picture of ambiguous taxonomic affiliation.

5. Discussion

5.1. What Shall We Call Them?

Analyzing the data resulting from the studies on the Dmanisi hominins (part one), LB1 (*Homo floresiensis*), and *Homo naledi* (part two) has convinced me, with great regret, that we are not able to identify species in human paleontological record. As an unrepentant "lumper", I am forced to agree with Tattersall [129] when he makes the following statement: "[T]here is no specifiable amount of morphological displacement between any two closely related fossils that will reliably indicate that they belonged to different species – no matter how sophisticated the algorithms or statistical methodologies we may bring to bear on the issue". [130, p116] The Dmanisi hominins, LB1, and *Homo naledi* all share features, to some extent (but cannot be ignored), with *Homo habilis*, *Homo rudolfensis*, *Homo erectus*, and Australopithecines.

In the discussion sections of these studies, I assessed that the Dmanisi hominins, or *Homo naledi,* could not be definitively aligned with any *Homo* or Australopithecine taxa or specimens. As for LB1, its endocast classified with modern humans (as opposed to microcephalics) based on shape, but the disagreements were largely on whether the craniofacial and postcranial features were the result of pathology or shared similarities with *Homo erectus* and/or Australopithecines. The "big picture" implications of small brain in the late Pleistocene—especially if one accepts the

sharing of *Homo* features or *Homo erectus*-shape cranium according to some researchers—are that the genus *Homo* as a taxa may need to be reexamined. As such, this leads to an action that most lumpers hate but may have to endure, which is the possibility of "splitting" the *Homo* taxa in general and the *Homo erectus* taxon in particular due to the wide range of variation.

This specific call for change is not new. For instance, Bernard Wood and Mark Collard [131] suggested that we should rethink the definition of *Homo* and reassign current fossils to other genera. One example noted in Rightmire et al. [132] is the similarities in symphyseal and corpus heights and robusticity between Dmanisi skull 3 and KNM-ER 60000 (assigned as *Homo rudolfensis* a few years ago). Shape analysis using features on the dental arcade places KNM-ER 60000 closer to the Dmanisi mandible (skull 5) than to KNM-ER 1482 (*Homo rudolfensis*), raising the possibility of the reassignment of KNM-ER 60000 to the *Homo erectus* taxon. Another example is the *Homo rudolfensis* taxon, with only two specimens (KNM-ER 1470 and KNM-62000) that are secure (for now) in their assignment and one mandible (KNM-ER 1802) whose assignment is being questioned.

Like *Homo floresiensis* (LB1), we do not really know the range of variation in *Homo rudolfensis*. Should *rudolfensis* be assigned to a new genus? In Rightmire et al. (2017) principal components analysis based on vault measurements, the Dmanisi crania cluster with *Homo habilis* and *Homo erectus* (at the negative pole of axis 1), but *Homo rudolfensis* (KNM-ER 1470) was extremely distant (at the extremely positive pole of axis 2). Other researchers prefer assigning A.L. 66-1, OH 62, and Stw 53 outside the genus *Homo* [133]. There are others examples indicating this growing movement in the field.

What about the features we traditionally use in our analyses? Tables 1 and 2 present a list of metric and nonmetric craniodental features. Do these features, particularly the features used frequently in taxonomic affiliation, affect mating or fertility? The intractable problem is interpretation of the interspecific and intraspecific variation in primate paleontology. Additionally, the complex interaction between cranial vault, brain size, face, and cranial base in shape variation increases the murkiness of taxonomic affiliation, including the small numbers of hominin specimens, and the lack of clear knowledge of the range of variation within and between geographic regions exacerbates the problem. Nonetheless, Albrecht and Miller [134] noted that even in studies using large samples, interpretation of the variation is still difficult:

> Non-Sulawesi macaques are characterized by conservative changes in skull morphology (mostly size related) despite a long evolutionary history (about 5 million years), substantial taxonomic variety (numerous subspecies, 12 species, and 4 species groups), substantial taxonomic variety (numerous subspecies, 12 species, and 4 species groups), wide geographic range (across southern Asia and a relict species in northwestern Africa), and considerable habitat diversity (deciduous temperate forests to evergreen tropical forests). In contrast, the seven Sulawesi macaques display extremes in skull shape suggestive of generic differences among other primates, despite their relatively recent evolution (about 1 million years), close taxonomic affinities (some combination of subspecies and species), restricted distribution (about 2% of the genus range), and homogeneity of environment (equatorial forests) [135, p150].

The above quote emphasizes the difficulty (and possible futility) in trying to identify species in the human paleontology record. So what do we do? We could adopt a solution proposed years ago, which I mentioned in a previous article and now restate:

> In the case of fossils the first individual who is clearly dissimilar to others is given a nickname. When other fossils resembling this one are discovered they may be designated similar of this individual if they do not resemble fossils described earlier. A collection of similar (a similum) is given a name of the first individual and is a "slice" of a lineage. While species can be created for a single individual by a process of deduction it takes a minimum of two individuals to define a similum [136, p278].

Or, we can simply use numbers for example, middle Pleistocene Atapuerca *Homo*, late Pleistocene Dmanisi *Homo* 5, late Pleistocene Liang Bua *Homo* 1, Hadar *Australopithecus* 333, Sterkfontein *Australopithecus* 17, early Pleistocene Koobi Fora *Homo* 1470, etc. This solution is not perfect because we encounter wordiness and ambiguity problems, but the use of genera is prominent in these examples. The ambiguity in the examples above is that we are confined to only two large, diverse genera: *Homo* and *Australopithecus*. I was intrigued by Tattersall's proposal that genera would be easier to identify (compared to species) in the fossil record. He states that, "Because of the greater morphological distances among them, genera should be more robustly recognizable in the fossil record than species are" [137, p116].

In our work, we sometimes become so focused on one idea that we are afraid to look up (in this case, higher in the taxonomy) to see a commonsense solution. In the genera scenario, should LB1 be assigned to a new genus? If so, what name should we use: *Lianganthropus*, *Floresanthropus*, or the first-favored genus *Sundanthropus*? However, we cannot unequivocally assign LB1 to any taxa—*Homo* and *Australopithecine*—or any proposed genus until more Liang Bua-like specimens are found (as mentioned earlier in this paper). Finding genera in the human fossil record will appeal to lumpers because it is similar to lumping, or being more inclusive. We will lose specificity, but "a minor loss of resolution is infinitely

preferable to the distortion that inevitable arises from incorrectly recognizing our basic units of analysis" [138, p117]. Finally, until we find large samples (N ≥ 40) of Australopithecine, *Homo habilis*, *Homo erectus*, *Homo rudolfensis*, middle Pleistocene hominins, etc., in a peat bog or mass grave, we will not be able to identify species in the human paleontological fossil record.

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