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

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Abstract Human paleontologists are unable to extricate species-level variation from individual, sexual, 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

1. Introduction

In part 1 of this paper, I discuss the Dmanisi hominins. In part 2, published in a separate issue, I complete the paper with a discussion of *Homo floresiensis*, *Homo naledi*, and

possible solutions to this complex problem.

In 2009, I wrote a paper on the excessive naming of new hominin species in the fossil record. On reflection, the paper was somewhat arrogant and ignored other researchers' freedom and courage to name new species based on their interpretation of the morphology. It goes without saying that "we must do something" and not just "stand on the sidelines throwing stones." We all agree that fossils must be analyzed and the data interpreted. At the same time, we all disagree on the length of time needed before a secure taxonomic determination is made. Many researchers make an initial taxonomic determination within a few months to a year. Essentially, researchers place their new discovery into a "suspense account," fueling debate until a new discovery changes conventional thinking [1].

One good example is the discovery of *Ardipithecus ramidus* in 1994. In its first publication in the journal *Nature* in 1994, this fossil was designated *Australopithecus ramidus*. But on subsequent analysis the original genus designation was changed to *Ardipithecus*. Will other high-profile hominin discoveries such as *Homo floresiensis*, Dmanisi *Homo erectus*, or *Homo naledi* have their current taxonomic names changed in the next five or ten years on subsequent analyses? It is certainly possible based on calls for reassignment of the Dmanisi hominins; *Homo floresiensis*; a mandible (KNM-ER 1802) attributed to *Homo rudolfensis*; a mandible (KNM-ER 60000) attributed to *Homo erectus*; and a cranial bone (KNM-ER 42700) attributed to *Homo erectus*, to name a few [2-6].

I am comforted by the knowledge that over time, the new generation building on the results of the previous generation—with better technology—will be able to reduce the complexities in hominin paleontology. In the meantime, this generation has to deal with the complexities, and I use these three high-profile hominin discoveries and their controversial taxonomic designations to discuss their complexities and suggest solutions.

I chose these three fossil taxa because they have caused

and still are causing heated debates at national and international conferences and in the literature. Furthermore, the mosaic nature of their morphological characteristics is generating new questions about the diversity of the genus *Homo* and reasons for it. For instance, Schroeder et al. [7] have noted, “It has become increasingly clear in recent years that the genus *Homo* is highly variable, with the discovery of [*Homo*] *naledi* once again expanding this range of variation” [8, p133]. *Homo floresiensis* and *Homo naledi* in particular are causing the most conflicts within hominin paleontology because of their small brains and their mid-to-late Pleistocene age. This disjunction between morphological age and geological age has caused much confusion. Nonetheless, it is important to remember the caution expressed by Albrecht and Miller: “Theoretically, there is no necessary, predictable, or required relationship between evolutionary divergence and morphological change” [9, p149].

Although the tone of my 2009 paper seemed self-righteous, I, nonetheless, emphasized chronic problems such as misinterpretation of the variation, limited fossils, limited comparative taxa, fragmentary fossils, missing skeletal elements, and substantial time dimension accompanied by the interaction of evolutionary, environmental, and cultural forces. I also proposed some temporary solutions.

I am pessimistic about attempts to find any definitive solution in understanding and distinguishing morphological variation within and between hominin taxa (taking into account relative differences between individuals, sexes, demes, subspecies, and species) despite the numerous sophisticated analyses used [10]. For example, researchers use geometric morphometrics (Procrustes distances) to write about the tremendous overlap in inter- and intra-group variability in skull diversity in the genus *Homo*: “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” [11].

In another example, researchers analyzing shape variables from Dmanisi and other *Homo* specimens emphasize taxonomic problems: “Analysis based on shape variables obtained from the dental arcade places KNM-ER 60000 closer to D2600 and other specimens from Dmanisi than to KNM-ER 1482, thus raising a question as to whether KNM-ER 60000 might actually represent *H. erectus*. . . If this is the case, comparisons of D2600 with KNM-ER 60000 reflect variation among conspecifics rather than resemblances/ differences between species”. [12]

Furthermore, Laird et al. [13] detailed some overlap in the Dinaledi hominins craniofacial characteristics with

Australopithecines (this included the robust Australopithecines or *Paranthropus*) and most species in the genus *Homo*. Specifically, they emphasized the following: *Homo naledi* range in cranial capacity from 465 cm³ to 560 cm³, which was similar to *Australopithecus* but overlapped with *Homo habilis* (KNM-ER 1813: 478 cm³), *Homo erectus* (D4500: 546 cm³), and *Homo floresiensis* (LB1: 426 cm³). The face of *Homo naledi* overlapped in superior facial breadth with the more gracile Dmanisi hominins; the tall alveolar height of *Homo naledi* overlapped with one *Homo habilis* hominin (AL666-1); the articular eminence depth of *Homo naledi* overlapped with *Homo habilis*; the maxilla-alveolar breadth of *Homo naledi* overlapped with *Australopithecus africanus*; and the maxillary incisor and premolar tooth row lengths and canine alveolus length of *Homo naledi* overlapped with *Australopithecus africanus*. Additionally, in selective dental and postcranial (i.e., clavicular anatomy, ribs, wrist bones, femora, feet) morphology comparisons there were shared features between *Homo floresiensis*, Dmanisi *Homo erectus*, *Australopithecus sediba*, and *Homo naledi* and among other Australopithecines and *Homo* species.

I will address these issues in greater detail later in the paper. Some may agree that the variation among the handful of fossils listed above may represent differences among individuals, sexes, geographical demes, subspecies, species, or some combination of these [14]. Moreover, one researcher has summarized all of this as follows: “Early on, I noted that speciation is a complex process or, rather, menu of processes, that does not necessarily result in morphological shifts of the kind we would expect to pick up in the bones and teeth that are preserved as fossils” [15, p116].

This overlap of morphological features within and between hominin taxa in general and among the four high-profile hominins in particular—the subject of this paper—brings us back to the critical problem, which is interpreting and understanding the variation or the range of variation. As such, some have suggested that we need to consider relegating some present fossils to other species or genera [16, 17]. However, there is an important disagreement between researchers who claim little to no craniodental differences between primate subspecies of the same species and other researchers who claim that the combined effect of intraspecific variation can be remarkable based on their study of geographic variation in primates [18-21].

Gene Albrecht and Joseph Miller [22] use the Hanuman langur, *Presbytis entellas*, to support their claim of what geographic variation might look like in a fossil species (Figure 1). The Hanuman langurs are distributed across the Indian subcontinent from Sri Lanka in the south to the Himalayas in the north. I conducted a classroom exercise using an image of six Hanuman langur skulls, the outcome of which was interesting but predictable. On viewing the image of the skulls, students in my Human Origins course

believed that they were looking at two or more monkey species and did not realize that the skulls represented individuals from a single species. For instance, based on shape and size of the skull, females from the extreme north (bottom right in Figure 1) and extreme south (bottom left in Figure 1) could be attributed to different species. Similarly, males from the extreme north (top right) and extreme south (top left) can be attributed to different species. Even more remarkable, the females with the smallest crania and the males with the largest crania could be attributed to different genera. This leads, in my opinion, to an important question: What do the craniofacial, dental, and postcranial metrics and nonmetrics really tell us about taxonomic affiliation (Tables 1 and 2)? Some of these metrics and features are

affected by climate, diet, and locomotion. We know that these analyses, in addition to the sophisticated 3-D morphometrics, give us information about shape and size dimensions and the frequency of specific features within and between sample groups. But, what do endocranial capacity—albeit, a trait used frequently in defining species—or other skeletal and dental traits tell us about mating structures or fertility? Do craniofacial, dental, or postcranial shape and size affect mating and fertility? Hominins are a diurnal primate species; consequently, mating will depend on external characteristics. However, mating does not equal fertility, and fertile hybrids complicate the picture.

Figure 1. The Hanuman langurs are distributed across the Indian subcontinent from Sri Lanka in the south to the Himalayas in the north: a) males from extreme south (top left); b) males from the extreme north (top right); c) females from extreme south (bottom left); d) females from the extreme north (bottom right)

Table 1. Selected osteometrics and nonmetrics used by researchers analyzing *Homo floresiensis*, Dmanisi hominins, *Australopithecus sediba*, and *Homo naledi* in comparison to other Australopithec and *Homo* species to obtain information on inter and intra specific variation; size and shape; and taxonomic affiliation/designation. (adapted from Brown et al., 2004; Falk et al., 2007; 2004; Berger et al., 2010; Lordkipanidze et al., 2013; Henneberg et al., 2014; Dembo et al., 2016; Hawks et al., 2017; Rightmire et al., 2017; Schroeder et al., 2017; Laird et al., 2017)

Craniofacial metrics	Craniofacial nonmetrics	Postcranial metrics/nonmetrics
Endocranial volume (cm ³)*	Cranial vault shape ^c	Clavicle: deltoid crest morphology
Glabella-occipital length ^c	Frontal bone morphology ^c	Clavicle: conoid tubercle morphology
Porion-vertex height ^c	Parietal morphology ^c	Clavicle: subclavian sulcus morphology
Max. cranial breadth ^c	Occipital morphology*	Humerus: bicipital groove morphology
Supraorbital torus thickness*	Sagittal keel!	Humerus: lesser tubercle morphology
Min. frontal breadth	Bregma morphology	Humerus: torsion angle
Postorbital breadth ^c	Lambdoidal morphology	Ulna: olecranon process morphology
Max. frontal breadth	Postorbital morphology ^c	Ulna: trochlear notch morphology
Nasion-bregma chord ^c	Supraorbital torus morphology ^c	Metacarpal morphology
Nasion-bregma arc	Supratrochlear sulcus morphology	Thoracic vertebra morphology
Glabella-bregma arc ^c	Nasal aperture morphology	-vertebral body
Frontal angle ^c	Infraorbital fossa morphology	-spinal canal
Max. biparietal breadth ^c	Infraorbital foramen morphology	-spinous process
Bregma-lambda chord ^c	Zygomaxillary region morphology	-transverse process
Bregma-lambda arc ^c	Subnasal region morphology	-pedicles
Lambda-asterion chord	Palate morphology	-facets; articular and costal
Lambda-asterion arc	Root of zygomatic morphology (temp. bone) ^c	Rib morphology
Biasterrion breadth ^c	Mandibular fossa morphology ^c	Os coxae: iliac morphology
Lambda-opisthion chord ^c	External auditory meatus morphology ^c	Ischium morphology
Occipital angle ^c	Postglenoid morphology ^c	Femur: max. length ^d
Inion-opisthion chord	Mastoid process morphology*	Femur: mid-shaft ant-pos. diameter ^d
Biauricular breadth ^c	Articular eminence morphology	Femur: mid-shaft med-lat. diameter ^d
Foramen magnum area	Mandibular ramus morphology	Femur: mid-shaft circumference ^d
Cranial base angle	Mandibular corpus morphology ^c	Femur: bicondylar angle ^a
Mandibular fossa breadth ^c	Symphyseal region (axis) morphology ^c	Femur: biomechanical neck length ^a
Basion-prosthion length*	Coronoid process morphology	Femur: intertrochanteric crest morphology ^d
Nasion-prosthion height*	Extramolar sulcus morphology	Femur: neck-shaft angle ^a
Biorbital chord*	Alveolar planum morphology	Femur: neck- head junction morphology ^d
Nasal angle*	Diagastic fossa morphology	Femur: head diameter+
Nasal breadth	Mental foramen morphology ^c	Femur: head size-midshaft circumference ^d
Nasorbital angle*	Masseteric tuberosity morphology	Femur: length-subtrochanteric shaft ^d
Clivus length*	Masseteric fossa morphology	Femur: linea aspera morphology
Bimaxillary chord*	Gonial region morphology	Tibia: max. length ^d
Max. malar height	Pharyngeal crest morphology	Tibia: midshaft circumference ^d
Palate length*	Mylohyoid groove morphology	
Palate breadth	Pterygoid fossa morphology	
Palate depth at M ² *	Incisor and canine juga morphology*	
Symphysis height*	Head circumference ^c	
Symphysis thickness*	Skull asymmetry ^c	
Min. corpus height at P ₃ *	Cranial bone thickness ^c	
Maxillo-alveolar breadth at M ² *	Bicondylar br./biparietal br. ratios ^c	

*Are these features sensitive to sexual or taxonomic affiliation? ^dAre these features used in climate adaptation and body mass?

^cAre these features sensitive to taxonomic affiliation or impact mating/fertility? ^aAre these features used in locomotion?

Table 2. Selected dental osteometrics and nonmetrics used by researchers analyzing *Homo floresiensis*, Dmanisi hominins, *Australopithecus sediba*, and *Homo naledi* in comparison to other Australopithec and *Homo* species to obtain information on inter and intra specific variation; size and shape; and taxonomic affiliation/designation (adapted from Brown et al., 2004; Hawks et al., 2017; Rightmire et al., 2017).

Dental metrics (mesiodistal length [MD] and buccolingual breadth[BL]) and Nonmetrics	
Maxillary teeth	Mandibular teeth
Central incisor (I ¹)	Central incisor (I ₁)
Lateral incisor (I ²)	Lateral incisor (I ₂)
Canine (UC)	Canine (LC)
Third premolar (P ³)	Third premolar (P ₃)
Fourth premolar (P ⁴)	Fourth premolar (P ₄)
First molar (M ¹)	First molar (M ₁)
Second molar (M ²)	Second molar (M ₂)
Third molar (M ³)	Third molar (M ₃)
Labial curvature	Tome's root (P ₃) ^b
Shovel-shaped I ¹	Lingual cusps LP ₂
Double shovel-shaped I ¹	Anterior fovea LM ₁
Bushman canine	Cusps number LM ₁
Distal accessory ridge (UC)Protostylid LM ₁	Distal accessory ridge (UC)Protostylid LM ₁
Root number (P ³) ^b Cusp 7 (LM ₁)	Root number (P ₃) ^b Cusp 7 (LM ₁)
Hypocone (M ¹)	Root number (P ₄) ^b
Carabelli's cusp (M ¹)	Root number (LM ₁)
Cusp 5 (M ¹)	Groove pattern (LM ₂)
Enamel extension (M ¹)	Cusp number (M ₂)
Hypocone (M ²)	Root number (M ₂)
Agenesis (M ³)	Torsomolar angle (M ₃)
Canine root morphology*	Canine root morphology*

*Are these features sensitive to sexual or taxonomic affiliation?

^bAre these features sensitive to taxonomic affiliation? Impact mating/fertility?

In this two-part paper, I begin by analyzing and discussing the research conducted on the Dmanisi *Homo erectus* and in the second part I continue with *Homo floresiensis* and *Homo naledi* emphasizing — in these three fossils — the complexities and futility of trying to identify species in the hominin fossil record because of the combined effects of ontogenetic, individual, sexual, geographical, pathological, and skull shape (calvarium, face, and cranial base) variation in closely related taxa. Also in part two, I discuss the possibility of using numbers or identifying fossils at the genus level where morphological distinctions are unequivocal, as opposed to the sharpness required for species distinctions. I also raise the question of adding a third genus between *Australopithecus* and *Homo*.

2. Dmanisi, Georgian Caucasus Hominin Skull 5

Over the past 20 years, Georgian paleoanthropologist David Lordkipanidze and his team have recovered hominin cranial, postcranial, and stone tools (Oldowan) from a site called Dmanisi in the Georgian Caucasus in Eastern Europe. In 1991 and 1999, a mandible and two crania (both mandible and crania attributed to the *Homo* taxon) were discovered at the site [23, 24]. Skull 5—the most complete

specimen of the assemblage—was discovered in 2005. During the refitting of current and new skeletal elements, the mandible discovered fourteen years earlier was a good fit in size and shape to skull 5. The researchers believed that the skeletal materials represented at least five individuals: skull 1 (D2280): an adolescent of unknown sex; skull 2 (D2282/D211): an adult male; skull 3 (D2700/D2735): a young female; skull 4 (D3444/D3900): an elderly toothless male; and skull 5 (D4500/2600): an adult male [25]. Argon isotopes were used to date the site to 1.77 million to 1.85 million years ago (date of possible occupation of the site), which meant that Dmanisi preserved one of the oldest genus *Homo* outside of Africa.

In the final analysis of the Dmanisi discovery, published in 2013, the research team concluded that the great variations among all Dmanisi skulls were no greater than what is seen within modern *Homo sapiens* and most (not all) *Pan* demes, indicating that the Dmanisi hominins represented a single, variable species [26]. At that time, this belief was supported by several important analyses. Adam Van Arsdale and Lordkipanidze [27] combined resampling statistics with geometric morphometric data and found that the Dmanisi hominin variation was similar to individuals within a dimorphic ape population. When they compared calvaria shape variation with variation in samples of *Pan troglodytes*, *Pan paniscus*, and modern *Homo sapiens*, the Dmanisi maximum inter-individual distance was greater

than the resampled maximum distance in 347/1,000 cases for *Pan troglodytes*, 779/1,000 cases for *Pan troglodytes verus*, 1,000/1,000 cases for *Pan troglodytes schweinfurthii*, 747/1,000 cases for *Pan paniscus*, and 804/1,000 cases for *Homo sapiens*. Additionally, their analysis of the whole crania showed that the maximum phenetic distance between Dmanisi hominins was below the 95th percentile values in all *Pan troglodytes* demes and close to the 95th percentile value for *Pan paniscus* and *Homo sapiens*.

In the case of skull 5, Lordkipanidze et al. [28] stated that the craniomandibular morphology of this fossil was massive and it shared plesiomorphic characteristics with Australopithecine species. In fact, their resampling analyses had shown that for some measurements of the corpus and dental arcade of mandibular pairs D2600/D211, the level of size variation may be greater than in *Homo sapiens*, *Pan troglodytes*, and even *Gorilla gorilla* [29]. However, the small cranial capacity (endocranial volume = 546 +/- 5 cc, smallest of Dmanisi skulls 1 to 4 ranging from 601 cm³ to 730 cm³) and large prognathic face were all in the normal range of variation for early *Homo*. Specifically, the researchers believed that the midface of skull 5 exhibited morphological similarities to the AL 666-1 maxilla from Hadar, the SK 847 partial cranium from Swartkrans, and the OH 65 palate [30]. Other researchers claimed that “. . . several of the Dmanisi skulls resemble KNMM-ER 3733 and other *H. erectus* individuals from the Turkana basin. . . . [A]ll of these specimens share a suite of features that is near-universally accepted as diagnostic for the genus *Homo*. These observations reinforce the strong African affinities of the Dmanisi population and appear to place it within *H. erectus*” [31, p.51]. Stature and body mass estimates from the postcranial bones of skull 5 placed

this individual in the range of variation for early *Homo*, *Homo erectus*, and modern humans according to the past analysis [32].

Furthermore, this “single evolving lineage hypothesis” for the Dmanisi hominins was to some extent based on the geology, in that the skeletal materials were discovered in a stratigraphic sequence that was “narrow” temporally and spatially: skulls 4 and 5 were found in stratum B1y and skull 3 was found 50 cm below in stratum B1x. The logical conclusion or parsimonious explanation was that this fossil sample was a paleodeme. Nonetheless, independent resampling analyses of these fossils by researchers internationally have been ambiguous and have produced no definitive taxonomic affiliation. There are, however, loud and numerous calls for the taxonomic splitting of the Dmanisi hominins (Table 3).

In 2017, a comprehensive study of skull 5 and other Dmanisi specimens within the assemblage was conducted to understand the variation within the Dmanisi fossil assemblage and to retain or reject the null hypothesis that this fossil assemblage is best grouped within the regionally diverse *Homo erectus* taxon [33]. To accomplish their study, the research team compared the Dmanisi hominins to *Homo erectus* fossils from Africa and Asia, early *Homo*, *Australopithecus* (and robust *Australopithecines* or *Paranthropus*), and sub-Saharan African modern *Homo sapiens* using the coefficient of variation (CV) and principal components analysis (PCA) on size-adjusted cranial measurements and nonmetric features [34]. They studied in detail missing skeletal elements and teeth, dental attrition, damage, distortion due to preservation, and pathological variation (due to age and trauma). In general, the Dmanisi fossils were in fair to good condition.

Table 3. Call for taxonomic splitting of the Dmanisi hominins by various researchers (adapted from Rightmire et al., 2017).

Researchers	General Statements
Schwartz, 2000; Schwartz and Tattersall, 2003;	Two distinct taxa at the site as opposed to age and sex
Skinner et al., 2006	
variation	
Skinner et al., 2006	On basis of mandibular measurements, D2600 should be grouped separately from the other specimens
Martinón-Torres et al., 2008:	Unusual morphology of D2600 suggesting two distinct paleodemes at the site
Bermúdez de Castro et al., 2014: and	The small Dmanisi mandibles are similar to <i>Homo habilis</i> and <i>Homo ergaster</i> , but D2600 has a different growth pattern
Bermúdez de Castro et al., 2014:	Skull 5 should be referred to as <i>Homo georgicus</i>
Schwartz et al., 2014; Gabunia et al. 2002	
Schwartz et al., 2014:	Not giving skull 5 a different taxonomic designation “is effectively to deny the utility of morphology in systematics, a radical proposition to which few would subscribe” (p. 360)
Tattersall, 2016:	Small-brained Dmanisi hominins fall outside the limits of “any morphological or behavioral characterization of the genus <i>Homo</i> ” (p. 3)
Tattersall, 2017	“...there is little morphological rationale for forcing the Dmanisi 2600/4500 fossil (or indeed, any of the other tiny-brained Dmanisi hominids) into our genus <i>Homo</i> , at least partly on the grounds that they are not <i>Australopithecus</i> ... Expanding <i>Homo</i> in this way not only makes the genus surpassingly difficult to define in any morphologically coherent manner, but also obscures whatever phylogenetic signal the fossils involved might actually encode” (p.117)

Initially, the researchers tackled the variation due to age and sex. They acknowledged the well-known difficulties: “For non-modern populations, or for archaic species where patterns of growth and maturation almost certainly differed from the norms established within *H. sapiens*, the utility of standards based on living humans is uncertain” [35, p54]. Nonetheless, based on ectocranial suture closure, spheno-occipital synchondrosis fusion, and coronal and sagittal suture closures, the researchers estimated that the skull 5 individual died in middle age.

As far as sex, prominent cranial superstructures (i.e., large glabella, supraorbital region, mastoid and supramastoid crests, and occipital torus) normally indicate male. But the researchers were cautious: “Patterns established for modern humans, or other reference populations, should not be assumed uncritically to be appropriate templates applicable to ancient *Homo*” [36, p54]. The critical problem, as discussed in the introduction, is to extricate individual variation (i.e., diet, age, pathology) from variation due to sex and from variation due to species differences. For instance, skull 1 (D2280) has an endocranial capacity of 730cm³ accompanied by a large supraorbital torus in contrast to skull 5 (4500), which has an endocranial capacity of 546 cm³ with a very big face and prominent juga associated with large canine roots. Are skulls 1 and 5 female and male of the same species or different species? Or, are skulls 2 and 4 female and male or different species? Skull 2 (D2282) possessed a small supraorbital torus and small mastoid process compared with skull 4 (D3444) where the glabella region (including the supraorbital torus, mastoid process, and occipital torus) were large.

In the end, the research team tentatively assigned skull 5 as male. I use the adverb *tentatively* because the researchers will continue their study of the Dmanisi hominins beyond 2019 and revisit this issue. For now, I will discuss some of their present interpretation of the variation within Dmanisi and how this variation compares to what is seen within and between other *Homo* and Australopithecine taxa.

The researchers measured and described many features on all bone elements of skull 5, including the maxillary and mandibular dentition, to get a better understanding, in my opinion, of the Dmanisi variation in general versus the variation between the Dmanisi skulls in particular (and a comparative sample of *Homo* and Australopithecine taxa). Skull 5, for instance, showed greater postorbital constriction than other Dmanisi crania but its supraorbital—broad anteroposteriorly as in most *Homo* specimens—was similar to skull 4 but different from skull

1 (adolescent) where the supraorbital outline was straighter. Skull 5’s occipital was high and narrow with a rugged torus, nuchal plane (and elevated external crest), and large occipital condyles with convex articular surfaces that differ from other Dmanisi individuals but found, to some extent, in a few African and Asian *Homo erectus* specimens [37]. Skull 5’s mastoid process was long and rectangular in contrast to skull 4, whose mastoid process was short and cylindrical according to the researchers.

In addition, they noted that as in skull 1, skull 5’s mastoid wall was fused anteriorly to the tympanic plate with no intervening tympanomastoid fissure. They noted that the massive zygomatic root, large supramastoid crest, broad temporal gutter, and a bony ridge external to the obliquus superior impression forming a raised oblique line posterior to the superior nuchal line created a strong relief that “constitutes a distinctive suite of morphologies emphasizing the extreme robusticity of the new skull in relation to other Dmanisi individuals”. [38, p57]

Furthermore, the mandibular fossa of skull 5 was shallow compared to skulls 1 and 4. The researchers noted that “similar morphology is present in some [*Homo*] *habilis* (OH 13, KNM-ER 1805, KNM-ER 1813) and African [*Homo*] *erectus* (KNM-ER 3733)” [39, p58]. The anterior wall of the fossa was low and curved forward centrally, unlike skull 1 where the wall was steeper, and skull 5’s postglenoid tubercle was more prominent than other Dmanisi crania. Additionally, the researchers noted that nearly two-thirds of the mandibular articular surface was beyond the external wall of the vault, positioned below the protruding zygomatic shelf. They stated that “Similar morphology occurs in other [*Homo*] *erectus* specimens, but in D4500 it is expressed to an extreme degree” [40, p58].

Skull 5’s face was broad centrally and prognathic. The cheekbones were massive and outwardly flaring with a wide nasal aperture. Specific facial measurements (basion-prosthion length, nasion-prosthion height, biorbital chord, nasion angle, mid-orbital chord, naso-orbital angle, clivus length, bimaxillary chord, prosthion angle, palate length, and palate depth at M²) are listed in Table 4. If these 11 measurements were the only facial measurements used, the Dmanisi hominids could potentially be assigned to different species. Alternatively, are these measurements giving information about sexual variation? The coefficient of variation analyses discussed later show interesting results. Meanwhile, skull 5’s midline facial angles indicated that the nasal saddle was concave and less elevated, and the interorbital pillar was less robust compared with skull 1.

Table 4. Facial measurements (linear dimensions in mm, angles in degrees) in Dmanisi specimens (adapted from Rightmire et al., 2017)

Measurements	D2282	D2700	D3444	D4500
	(skull 2)	(Skull 3)	(Skull 4)	(Skull 5)
Basion-prosthion length	-	100	-	126.7
Nasion-prosthion height	-	69	-	74
Biorbital chord	96	90	98	102
Nasion angle	-	136	142	147
Midorbital chord	-	55	51	60
Naso-orbital angle	-	129	130	146
Clivus length	28	>20	-	33
Bimaxillary chord	91	97	93	110
Prosthion angle	107	107	-	102
Palate length	54	55	-	68
Palate depth at M ²	15	12.5	-	18

The researchers also stated that the nasal bones were narrow in the middle and broad below, and in the profile view, they were concave compared with skull 4. The piriform aperture was broad compared with skulls 3 and 4, and the length of the maxillary clivus (nasospinale to prosthion) is greater than in skulls 2 and 3. They noted that “Alveolar prognathism is pronounced, and the clivus joins FH at an angle at an angle of 39° (versus 90° in *H. sapiens*)” [41, p59]. This prognathism was reflected in the long and narrow palate. Additionally, they noted that the palate surface appeared shallow at the front but sloped upward creating a high arch at the level of the molar teeth, and, “in this respect, D4500 resembles AL 666-1 from Hadar . . . but differs from other Dmanisi specimens and also from the shallower *H. habilis* palates from Olduvai (OH 13, OH 24) and Koobi Fora (KNM-ER 1813)”. [42, p59]

Skull 5’s mandible (D2600) length matched the long palate length with parallel tooth rows. The measurements obtained by the research team indicated that symphyseal height (49 mm), symphyseal thickness (21 mm), corpus height (min) at P₃ (44.1 mm), and corpus height (min) at M₁ (41 mm) were greater than the same measurements on mandibles belonging to skull 2 (30.8 mm, 16.8 mm, 27.5 mm) and skull 3 (34 mm, 16 mm, 26.5 mm, 22.5 mm). But the robusticity index (corpus breadth/height at M₁ ratio) for skull 3’s mandible was much greater (84.4 mm) than skull 5’s mandible (51.2 mm). It seemed that the greater the corpus height, the lower the robusticity. Are these differences in mandibular dimension a function of interspecific variation, sexual dimorphism, or dietary variation?

Sexual dimorphism, dietary adaptation, and attrition are all important factors considered when we analyze dentition in prehistoric sample groups. As such, the researchers reported that skull 5’s maxillary and mandibular dentition were “heavily worn and in poor condition” [43, p61]. This fact did not hinder some dental metrics and nonmetrics. Analysis of skull 5’s maxillary third premolars showed

three roots and the fourth premolars had two roots (with the buccal root exhibiting two canals). In contrast, skull 3’s third premolar had single fused buccal and lingual roots, and skull 2’s fourth premolar had a single mesiodistally compressed root. Such variation, according to the researchers, “is common in early *Homo* populations. The P³ of OH 16 has a single flat root with a bifid tip; OH 13 exhibits a double root, and OH 24 presents three roots (two buccal, one lingual). . . . This polymorphism has persisted for a long period, and P³s with one, two, and three roots continued to occur at widely different frequencies among populations of modern *H. sapiens*” [44, p61]. Skull 5’s mandibular third premolars had two divergent roots, whereas skull 2’s third premolars were single-rooted, and skull 3 had two deeply grooved mesial roots, according to the researchers.

Due to dental attrition, the researchers could only obtain labiolingual diameters for the upper incisors and buccolingual breadths for the other teeth. Nonetheless, they found that skull 5’s maxillary fourth premolar crown area was very large (137mm²) compared with skull 1 (93mm²) and skull 3 (78mm²). For mandibular teeth (D2600), they found that skull 5’s canines, third premolars, and second and third molars were larger than in the other Dmanisi individuals. The researchers noted that “In addition to such differences, it is important to point out that neither D4500 nor D2600 exhibits any size reduction of the M3s relative to the M2s. In this respect, skull 5 is unique within the Dmanisi assemblage”. [45, p61]

It was interesting to note that the polymorphic nature of premolar root morphology and dimorphic teeth such as third premolars and canines were each complex problems on their own. These problems existed together making it difficult to interpret the type of variation; nonetheless, the dental data indicated that the buccolingual dimensions of skull 5’s maxillary premolars and first molars were similar to the same dimensions in *Homo habilis*, but the maxillary canines and molars were larger than in other early *Homo*

contemporaries. The researchers noted that “The Dmanisi M³ crown stands out as the largest in the early *Homo* inventory, falling just within the range for *P. boisei*.” [46, p66]. J. Michael Plavcan [47], who has used tooth-size variability to help discrimination between species in the fossil record, provided the following caution:

[D]imorphic teeth such as P3 or canines should not be used to test a multiple species hypothesis, since sample variation due to dimorphism is often as great as that due to interspecific differences in tooth size. If tooth-size variation in a fossil sample exceeds that in all living species, we have little choice but to infer that the sample is composed of more than one species, rather than two sexes, unless there is other strong evidence to support the dimorphism hypothesis [48, p255, 259].

To compare the variation in dimensions of the cranial vault, base, and face within Dmanisi and other *Homo* and Australopithecine taxa, the researchers applied CV and

modified this statistic for small sample sizes (unbiased V*) (Table 5). The results give “no indication that variation within the Dmanisi paleodeme is excessive, relative to that of most other hominins. Overall, the V* values reported convey few clear signals that the Dmanisi crania are excessively variable in comparison to recent to recent *H. sapiens*” [49, p62].

Geometric means (GMs) based on linear measurements for skull 5 and other early *Homo*, *Homo erectus*, and Australopithecine specimens’ face and cranial vault were calculated to obtain an overall measure of face (GM_{face}) in relation to overall measure of braincase (GM_{vault}). For skull 5, the researchers calculated GM_{face} = 68.8 and GM_{vault} = 96.3, so that facial size is 71.4% of braincase size. This percentage is larger than some *Homo* taxa, but surprisingly close to Sts 5, *Australopithecus africanus* (Table 6). For the selected *Homo* taxa used for this geometric mean analysis, facial size “is reduced in relation to the vault”. [50, p65]

Table 5. Relative variation in dimensions of the cranial vault, base, and facial skeleton (adapted from Rightmire et al., 2017)

Measurements	Dmanisi		<i>H. erectus</i>	
	N	V*	N	V*
Endocranial capacity	5	11.3 ^c	27	12.8
Glabella-opisthocranium	4	5.9	25	5.4
Porion-vertex height	4	10.2 ^c	26	6.0
Glabella-bregma arc	5	4.6 ^c	22	5.9
Bregma-lambda arc	5	9.8 ^c	25	7.1
Lambda-opisthion arc	4	6.3 ^c	22	5.4
Maximum cranial breadth	4	3.7 ^c	26	4.2
Maximum biparietal breadth	5	4.0 ^c	27	5.2
Biauricular breadth	4	5.5	25	5.3
Biasterionic breadth	5	5.1	27	5.7
Mandibular fossa breadth	4	3.5 ^c	18	23.6
Supraorbital torus thickness	5	15.1	25	18.2
Biorbital chord	5	5.5	16	5.9

^cVariation that is high and moderately high compared to *H. erectus*

Table 6. Geometric means calculated from face and braincase dimensions for Dmanisi, other *Homo*, and Australopithecines (including the robust forms) (adapted from Rightmire et al., 2017).

	D2700	D4500	OH 5	Sts 5	ER1470	ER1813	ER3733	S 17
GM (face)	60.9	68.8*	81.9	65.0*	73.3	60.1	69.7	72.2
GM (vault)	98.1	96.3*	93.8	86.0*	109.5	92.6	114.0	126.7
% of facial size to braincase size	62.1%	71.4%*	87.3%	75.6%*	67.0%	65.0%	61.1%	57.2%

*D4500 and Sts 5 similar in overall measure face and vault

Finally, the researchers used principal component analysis to study cranial shape at Dmanisi compared to a sample of early *Homo* and *Homo erectus* taxa. Dimensions of the braincase and the base were collected from the Dmanisi skulls and a selected sample of the *Homo* taxa. Specifically, they used endocranial volume, biauricular (base) breadth, and supraorbital thickness because these metrics provided information about overall size. Glabella-occipital length, maximum cranial breadth, and vertex height provided information about overall cranial proportions; postorbital breadth provided information of anterior frontal narrowing; biasterionic chord and occipital angle provided information about width and curvature of the posterior vault; and mandibular fossa breadth is very variable within and between the *Homo* taxa. Shape variables were obtained by adjusting the linear measurements for size using geometric mean calculated from the measurements listed directly above.

The first principal component was influenced strongly and negatively by mandibular fossa breadth and contributions from postorbital breadth, endocranial volume, and vertex height. The second principal component was influenced strongly and negatively by supraorbital thickness and significant contributions from maximum cranial breadth and biauricular breadth; the third principal component was influenced strongly and negatively by biasterionic width and significant contributions from glabella-occipital length and biauricular breadth; and the fourth principal component had significant loadings for occipital angle and vertex height.

In general, the Dmanisi individuals clustered in braincase and base with various early *Homo* and *Homo erectus* taxa. Specifically, on the first and second principal components Dmanisi skulls 3 and 5, two *Homo habilis* specimens (KNM-ER 1813 and OH 24), and *Homo rudolfensis* (KNM-ER 1470) were outside the 95% density ellipse constructed for the *Homo erectus* sample. Interestingly, the third principal component showed Dmanisi skulls 1, 3, and 4, and *Homo habilis* crania within the 95% density ellipse constructed for the *Homo erectus* sample, but Dmanisi skull 5 was distant from the *Homo* taxa and the other Dmanisi individuals.

In the end, the researchers had only weak support for their null hypothesis that Dmanisi hominins were best grouped with the *Homo erectus* taxon because of the conflicting data. They stated that “Overall, the PC results seem to provide little support for the hypothesis grouping Dmanisi within the *H. erectus* hypodigm” [51, p74]. Several analyses, particularly of the principal components, indicated that some Dmanisi individuals (skulls 3, 4, and 5) clustered with *Homo habilis* for mandibular fossa breadth, vertex height, postorbital breadth, supraorbital, cranial length, and cranial base breadth. But only skull 5 was distant from all other Dmanisi individuals and *Homo* taxa for cranial length, cranial base breadth, and asterionic breadth. Which of these features are good taxonomic discriminators? Does cranial shape and size prevent mating

or fertility? These questions go to the heart of identifying, if possible, fossil species.

*To continue see Part II in *Sociology and Anthropology* Vol.7 No.6

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