

B. Kenyon-Flatt, Revisiting *Homo* Taxonomy

**Project Title:** Postdoctoral Research Fellowship in Biology: Revisiting *Homo* Taxonomy: A Geometric Morphometric Analysis of the Hominin Skeleton

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**PI:** Brittany Kenyon-Flatt, PhD, Postdoctoral Research Fellow, College of Veterinary Medicine, North Carolina State University

### A. Introduction and Background.

The significant amount of morphological variation observed in genus *Homo* is at the heart of longstanding debates within the field of paleoanthropology (Schroeder and Ackermann 2017; see also Anton et al. 2014; Wood 1992; Wood and Baker 2011). This large amount of morphological variation has suggested that there may be more species represented in the fossils than originally thought (Wood 1992), making the taxonomy of genus *Homo* inaccurate. Previous research suggests that testing this multi-species hypothesis is necessary to draw conclusions about the taxonomy of the genus, though this is relatively complex, as it includes refining definitions regarding the degree and pattern of variability within genus *Homo* (Wood 1992). Other primate species showcase differing levels of sexual dimorphism, and we assume that *Homo* likely exhibits sexual dimorphism as well, though the extent of the dimorphism is unknown. Additionally, differences in ecological landscapes, body mass, or locomotor or dietary behaviors could contribute to the morphological variation seen in *Homo*. Conversely, it has been debated that all *Homo* belong to one single, extremely variable species, known as the Single-Species Hypothesis, based on the fact that, for ecological reasons stemming from cultural adaptations, no more than one culture-bearing hominin species could have arisen or been maintained (Wolpoff 1968). The Single-Species Hypothesis has been repeatedly tested without a clear answer as to its validity (Villamore 2005). Therefore, the defining characteristics of genus *Homo* remain in question, which this proposal seeks to address. Novel methods, such as geometric morphometrics, have yet to be applied to the *Homo* skeleton as a whole. Furthermore, a comparison between a variable extant primate group has not been compared to *Homo* fossils yet, though doing so would provide a useful conceptual link to this on-going debate.

Since the announcement of the discovery of *Homo habilis* fossils from Olduvai Gorge in 1964, paleoanthropologists have attempted to define the morphological characteristics of the genus (Schroeder and Ackermann 2017; Wood 1992). Its tooth and brain size suggests that is more primitive than *Homo erectus* (Leakey et al. 1964), meaning some assume that *Homo habilis* is so primitive it could actually be a member of the *Australopithecus* genus (Wood 1992). More recent fossil evidence has confirmed that *Homo habilis* is a fossil hominin that is distinct from both *Australopithecus* and *Homo erectus* (Chamberlain and Wood 1987; Skelton et al. 1986), though some argue that this is not entirely warranted due to the absence of information regarding the nature and relationship of the species (Wood 1992). There is a large range of morphological variation across fossils assigned to *Homo habilis*, particularly in the post-crania, which begs the question: is this variation large enough to warrant multiple species, or is the defining characteristic of *Homo* that their morphology is exceedingly variable?

The large amount of morphological variation within *Homo* is further evidenced by the geographically extreme and highly variable Dmanisi fossils. The taxonomy of the Dmanisi fossils is highly debated, and DNA analysis is not feasible due to the age of the fossils (Poinar 1999). Therefore, their morphology is the key to elucidating their taxonomic classification. However, it is unknown whether or not they exhibit intra- or inter-taxonomic diversity (see Lordkipanidze et al. 2013; Schwartz et al. 2014; Zollikofer et al. 2014). Several researchers have attempted to taxonomically classify the Dmanisi fossils (Lordkipanidze et al. 2013; Lordkipanidze et al. 2006; Margvelashvili et al. 2013; Rightmire and Lordkipanidze 2010; Schwartz et al. 2014), though since they exhibit an unusually large range of morphological variation, this has proven to be challenging. Cranial morphologies exhibit a high degree of variation, and there are several hypotheses to explain this variation, including age-at-death, sexual dimorphism (Potts et al. 2004; Spoor et al. 2007), and dental wear patterns (Margvelashvili et al. 2013). The general consensus is that these fossils belong to *Homo erectus (sensu lato)*, with some researchers specifically naming this group *Homo erectus ergaster georgicus* (Lordkipanidze et al. 2013; Rightmire and Lordkipanidze 2010). However, there is still a compelling argument that some fossils, such as one of the mandibulae, have such distinct morphology that it should have its own identity as *Homo georgicus* (Schwartz et al. 2014). There is no currently agreed upon nomenclature for the entire group, though most agree that the fossils almost certainly belong to *Homo*, likely having evolved from *Homo habilis* (Vekua et al. 2002).

To further complicate *Homo* taxonomy, the newly described *Homo naledi* fossils from South Africa once again expand the range of phenotypic variation throughout genus *Homo*. Unlike the Dmanisi fossils, the variation seen within the population from the Dinaledi chamber unquestionably represents a single

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population (Berger et al. 2015). *Homo naledi* is thought to be an anatomical mosaic, featuring anatomical characteristics shared with *Australopithecus* and *Homo* but also showing new features not observed before (Berger et al. 2015). The cranium, mandible, and teeth are consistent with other fossils in genus *Homo* (Laird et al. 2016), though the pelvis is flared like *Australopithecus afarensis* (VanSickle et al. 2017). The lower limb is more consistent with observations seen in modern humans (Marchi et al. 2016), though the scapula is more akin to *Homo erectus* in some ways (i.e. scapular position) and *Australopithecus* in others due to its more primitive morphologies (Feurriegel et al. 2016). It has been indisputably argued that the Dinaledi chamber contains the richest assemblage of fossil hominins ever discovered in Africa, though the analyses of these fossils also highlights our ignorance about the interplay of taxonomy and morphology of *Homo*-like hominins (Berger et al. 2015).

As seen with the above examples, decades of research regarding *Homo* taxonomy and relationships have confirmed that there is an unusually large level of morphological variation throughout the genus (see Kramer et al. 1995; Leakey et al. 1964; Lieberman et al. 1996; Miller 1991; 2000; Wood 1993). Additional discoveries such as the oldest *Homo* specimen from Ledi-Geraru, Ethiopia (Villamore et al. 2015); the controversial small-bodied *Homo floresiensis* from Flores, Indonesia (Brown et al. 2004); and myriad of robust *Homo neandertalensis* from around Europe (Drell 2000) prove the point that *Homo* is an exceedingly diverse and hard to define genus. This increased knowledge about the morphological diversity in the *Homo* lineage means that our previous attempts to define *Homo* are no longer appropriate (Schroeder and Ackermann 2017), and thus new, comparative approaches must be taken.

Previous studies investigating the transition to early *Homo* and the diversification within the lineage suggest that selective forces may have played a significant role in shaping diversity (Schroeder and Ackermann 2017). Thus, scientists are beginning to understand the underlying evolutionary processes for species diversification in *Homo*, however, there is still a question of how to define genus *Homo*. Some would argue that there is considerable evolutionary experimentation within our lineage, and thus genus *Homo* may just truly be an exceptionally morphologically and behaviorally diverse genus. However, most of the work that has defined the genus has focused on the crania, and therefore left the postcrania largely unexplored. Though the genus has been studied for decades, how to taxonomically define genus *Homo* remains one of the largest debates within biology, and the application of new methods to this age-old question is sure to illuminate our current understanding of the genus, and aid in providing a more solid definition of *Homo*.

### **B. Research Objectives and Methods.**

The overall objective of this research is to apply novel geometric morphometric methods to the *Homo* fossil record, in order to assess the interplay of morphological variation and taxonomy. This will be done by addressing the following questions:

**Aim 1: Do the levels of morphological variation seen in *Homo* mimic or exceed what is observed intra-generically in comparable primate species?**

**Aim 2: Given the sparse fossil record, how can we develop models for accurate taxonomic assessment based on morphological variation?**

**Aim 3: What behaviors drive the morphological variation seen throughout genus *Homo*?**

Materials consist of 3D scans of original fossils, or first-generation fossil casts when the original fossil material is unavailable. Some early *Homo* scans are available to me via Dr. Chris Walker, modern *Homo sapiens* scans, and chimpanzee and gorilla scans are available for my use from other colleagues. Several data collection trips to biological collections will be necessary to complete this research including visits to: University of Witwatersrand in South Africa; Cleveland Natural History Museum in Cleveland, OH; American Museum of Natural History in New York City, NY; Smithsonian Institution in Washington, DC;

Scans will be collected using an HDI 120 structured light scanner (available through the NC State University Hominin Evolution Lab), and photographs of each fossil will be taken for reference when constructing 3D models. This step is not always necessary, but given the fragmentary nature of the fossils

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and the capacity for the scan processing software to “hole fill” any missing parts of a scan, I want to ensure that the 3D model accurately represents the fossil including any missing parts.

Upon completion of the scanning, 3D models will be processed using the software *FlexScan* and models will be exported as .ply files. Landmarks will be placed on each 3D surface scan using *Landmark* (Wiley et al. 2005) and coordinate data will be exported for statistical analysis. Landmarks were specifically chosen to assess the overall bone shape and allow for an assessment of functionally-important morphology (i.e., load-bearing regions or muscle attachment sites). However, given that the fossils are fragmentary, a good portion of the project will be spent developing a landmarking scheme that represents the fewest number of landmarks necessary for morphological analysis, and highlights a landmarking scheme representing the portions of the bone most likely to be complete.

All landmark configurations will be registered using Generalized Procrustes Analysis using MorphoJ (Klingenberg 2011) and resultant shape variables will be subject to a Principal Components Analyses (PCA) to investigate average shape variation among individuals (Zelditch et al. 2004) as well as how variation is partitioned within and among taxa (Harvati 2003). Resultant principal component (PC) scores generated in MorphoJ (Klingenberg 2011) will be exported into a Microsoft Excel spreadsheet for analysis. A multivariate analysis of variance (MANOVA) will be performed on the PC scores, using the software PAST, to determine which taxa (if any) show significant shape differences. Thereafter, a Canonical Variate Analysis (CVA) will be employed to maximize inter-group differences (Zelditch et al. 2004). Once it is determined that the canonical variates (CVs) of shape variables are useful for distinguishing samples and assigning them to groups, it will be necessary to explore what shape differentiations the CVs represent; results from these tests will be used to analyze general shape differences among species.

To test aim 1, we will use Mahalanobis distances to determine if the difference between *Homo* is greater than or the same as the differences between *Macaca*, following Harvati (2003). This project will collect a sample of *Homo* scans, which will be compared to the macaque data collected for my dissertation. Both *Homo* and *Macaca* are geographically widespread throughout Eurasia and Africa and thus different species exhibit morphologies consistent with particular behaviors or climates. The same landmarks will be used on the *Homo* sample that were used on the *Macaca* sample and therefore the Mahalanobis distances can be directly compared. Since I will be working with fossils and therefore some data will be missing, some levels of data reconstruction will be considered through estimation of the position of the structure of interest using the morphology preserved in surrounding areas (Harvati 2003).

Aim 2 will expand on reconstructing some of the missing data, in order to have the most accurate fossil models for analysis. Several comparisons of landmarking protocols will be developed and tested in order to develop a landmarking scheme that is still accurate for taxonomic assessment though also uses the fewest number of landmarks possible, given that some fossils are typically missing quite a bit of bone. While data reconstruction is useful, it is not perfect since it makes statistical assumptions. Therefore, sets of landmarks that has proven to be useful in other fossil species will be tested on hominins to create the most accurate landmarking scheme possible (e.g. Bonnan 2004; 2007).

As a further test for aim 2, I will develop a method by which to systematically and statistically test post-cranial remains for taxonomic assessment. Historically, the cranium has been thought to best reflect taxonomic distinction (Fleagle et al. 2010). However, my doctoral research suggested that other bones such as the os coxa or scapula may be equally as good at taxonomic assessment as the cranium. For fossils, this is particularly important since a cranium is not always found. This will be done by running a discriminant function analysis (DFA) based on the PC scores that explain 95% of overall shape information (Mitteroecker and Bookstein 2008) and will be performed in SPSS (IBM Corp, 2017). Each bone will be subjected to a DFA, and results will predict categorical (i.e. species) memberships, thus determining the extent to which specimens are classified or misclassified. Since complete fossil hominins are rarely, if ever, found, it is equally important to understand how single elements differentiate and predict taxa.

To test aim 3, it will be necessary to compare morphological data to behavioral data, which is unavailable when using fossils, and therefore this will be based on the reconstruction of paleoenvironments and hominin behavior. Here, I seek to reconstruct the fossil hominin body mass and limb proportions using the landmark protocols developed with aim 2. These protocols can aid in the estimation of bone length, which will be

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compared to small-bodied, related modern species (i.e. chimpanzees, bonobos). The estimated body mass will be used to reconstruct hominin behaviors following Walker et al. (2017), Holliday et al. (2018), and Churchill et al. (2016).

Then, the estimated behaviors will be compared to the collected morphological data. Based on methods developed in my dissertation, I will conduct pair-wise among-species matrices based on the morphological or behavioral data. Mahalanobis distances ( $D^2$ ) will be calculated among species based on morphological data (PC scores) (Zelditch et al. 2004). Geographic distances will be calculated among species as great circle distances in kilometers between latitude and longitude coordinates (Ramachandran et al. 2005), temperature distances will be calculated as average differences paleotemperatures, while the locomotor and dietary data for each species will be coded and converted to Euclidean distance matrices (von Cramon-Taubadel 2011). Mantel tests will be used to test for significant correlations between the morphological distance and distances representing geography, climate, locomotor behavior, and diet.

## C. Training Objectives and Career Goals.

**Research Goals.** Correct taxonomy is at the heart of understanding the evolutionary origins of any organism. As such, developing methodologies in order to accurately assess the taxonomy of previously contentious or unknown organisms is central to my research. Ultimately, I seek to better understand the guiding principles of how morphological variation evolves in order to make informed inferences about past evolutionary history, where genetic data is not and may not ever, be available. Furthermore, I aim to better understand the primary behavioral causes of morphological variation and thus learn more about the interaction between the environment and the skeleton, particularly the post-cranial skeleton. I have been working to develop these methods using extant primates as models, but the next step is to apply these methods and results to the hominin fossil record. I aim to spend my career revisiting taxonomic nomenclature methods with newer technologies and statistical modeling analyses, and hope to develop a set of methods that will aid future scientists in determining accurate taxonomic assessment when new fossils are discovered.

**Teaching and Mentorship Goals.** Mentoring anatomists and biologists to use new technology and novel theoretical approaches to address age-old questions will be the central focus of my career as a tenure-track professor at a major research institution. Therefore, a large section of this postdoctoral fellowship will be learning the skills necessary to teach the next generation of scientists how to incorporate new technology into their work, how to think through advanced theories with new eyes, and how to collect data from biological research collections. The Hominin Evolution Lab at NC State University is actively recruiting and mentoring undergraduate students to aid in its research projects. As part of my mentoring plan, I will become the primary research advisor for some of these students, with the goal using newer technologies such as 3D scanning to address questions of hominin origins. As part of my teaching plan, I will aid in the teaching of the Veterinary Anatomy I course and develop a syllabus for an undergraduate course entitled “Geometric Morphometrics for Anatomists” where the goal of the course is to introduce students to microscribing and 3D scanning, and then subsequent analysis in statistical programs such as morphogika, MorphoJ, R, PAST, and others; the course will purposefully focus on freeware in an effort to keep statistical scientific tools available for anyone.

**Career Development.** The proposed work is a natural extension of the statistical and biological skills that I developed during my PhD, while giving me numerous new skills in paleontology. This fellowship will represent a shift in my work from working with extant primates to working with broader questions regarding the largest questions within human evolution. At the start of the fellowship, Dr. Walker and I will have a meeting to formalize my training plan, focusing on 1) publication record, 2) teaching anatomy and mentoring students, and 3) proposal writing. Dr. Walker and I will have meetings once per semester thereafter to discuss progress in these three areas. As I near the end of the fellowship, these meetings will shift towards the development of application materials for tenure-track positions in anatomy.

## D. Justification for Sponsoring Scientist.

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Dr. Christopher Walker is a leading paleoanthropologist and anatomist based at North Carolina State University with expertise in hominin paleontology and functional morphology of the postcranial skeleton, making him an ideal sponsor for this project. One of Dr. Walker’s main research interests is to examine the hominin postcranial skeleton in an effort to better understand how morphology varies with behavior and how information gathered from the postcranial skeleton aids in evaluating evolutionary relationships (see Walker et al. 2019; Friedl et al. 2019; DeSilva et al. 2018; Marchi et al. 2016; Feurriegel et al. 2016). Dr. Walker will be an excellent mentor for this project given his direct experience working with both *Au. sediba* *H. naledi*, and other hominin fossils. This study is built around the examination of hominin postcranial remains to understand morphological variation, and then uses this information to explore how variation is driven by locomotory patterns or other behaviors. The methods we will follow are based on Dr. Walker’s previous work relating to biomechanics and functional morphology (see DeSilva *et al.*, 2013). A key issue when studying hominin postcrania is the lack of available specimens, which could ultimately hinder parts of this project, and thus we will use Dr. Walker’s experience with modeling body size and limb proportions in modern humans for application to the fossil record specifically to test aim 3 (see Walker *et al.*, 2018; Holliday *et al.*, 2018; Yapuncich *et al.*, 2018).

Dr. Walker holds joint appointments in the Department of Molecular Biological Sciences in the College of Veterinary Medicine and the Department of Sociology and Anthropology at North Carolina State University. Additionally, he holds affiliations with the Department of Evolutionary Anthropology at Duke University and the Evolutionary Studies Institute at the University of Witwatersrand (Johannesburg, South Africa); these four appointments also give me direct access to the resources held by these institutions through Dr. Walker. However, the main host institution for this postdoctoral fellowship will be the Department of Molecular Biological Sciences in the College of Veterinary Medicine at North Carolina State University, which has excellent infrastructure in place for postdoctoral fellows. The Office of Postdoctoral Affairs provides administrative resources for postdoctoral fellows, professional development opportunities, and networking. In concert with the Postdoctoral Association, the Office hosts the Postdoctoral Research Symposium which is a yearly research symposium for all current postdoctoral fellows to present their current work to fellow NC State University colleagues. I will be working in the Hominin Evolution Lab (directed by Dr. Walker), which provides desk space and associated infrastructure, a suite of software (Geomagic Design X, Avizo), scanning equipment (HDI 120 structured light scanner, Artec Spider, David SLS-3), 3D printing equipment, and high-graphics desktop computers, all of which are necessities for the proposed research.

## F. Timetable.

	<b>Year 1</b>	<b>Year 2</b>	<b>Year 3</b>
<b>Research Goals</b>	Conduct pilot study on available scans from MorphoSource; plan data collection trips; data collection; learn fossil description process	Finish data collection; data processing; learn/develop methods for landmarking fragmented fossil scans; preliminary analysis	Complete statistical analyses for the entire skeleton; learn/develop limb bone modeling; draw final conclusions
<b>Training Goals</b>	Plan manuscript submissions; serve as guest lecturer for Veterinary Anatomy; begin mentorship of undergraduate students	Continue mentoring undergraduate student projects; develop “Geometric Morphometrics for Anatomists” syllabus	Finish mentorship for undergraduate projects; finalize job application materials; apply to tenure-track anatomy jobs
<b>Broader Impacts</b>	Recruit undergraduate assistants; write and submit blog to <i>Science</i>	Write and submit blog post to <i>IFL Science</i> and <i>Sapiens</i> ; write	Write and submit blog post to <i>Scientific American</i> ; NC Museum of Natural Science Science Café presentation;

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	<i>Trends</i> ; write lecture 1 & lesson plans	lecture 2 & lesson plans	write lecture 3 & lesson plans; publish all lesson plans
<b>Dissemination</b>	Submit the pilot study for publication; presentation of pilot study results at scientific meetings	Submit manuscripts; presentations at scientific meeting	Make 3D scans of fossils publicly available; submit final manuscripts; submit and chair “Hominin Postcranial Morphology” symposium

**G. Significance.**

**Intellectual Merits.** One of the defining characteristics of *Homo* is that it is exceedingly variable. However, it is not currently known how this variation affects the taxonomy of the genus. Given the direct link to humans, it is of the utmost importance to have a firm grasp on how to define genus *Homo*, given that doing so aids in defining who humans are. This project seeks to firstly compare the levels of variation seen within a different species of *Homo* and compare them to the levels of variation seen in *Macaca*, a primate with the largest geographical range aside from *Homo*. Scientists have called for a comparative population of extant primates by which to compare *Homo* against, and this project seeks to answer that call (see Zollikofer et al. 2014). Secondly, the project aims to develop better classification schemes for accurate assessment of future fossils. Additionally, the use of postcranial remains in taxonomic research has large been ignored, and given that newer research suggests that these bones can be as accurate as the cranium, it is imperative that there are techniques developed in order to accurately assess post-cranial remains for taxonomic signals. Lastly, the project seeks to begin exploring the behaviors that drive this variation, and a better understanding of these behaviors leads to a better understanding of the hominin family tree. Results from this project promise to substantially contribute to the current knowledge base surrounding *Homo* morphology and taxonomy, and as such will be published in high-impact journals such as *The American Journal of Physical Anthropology*, *The Journal of Human Evolution*, and *Evolutionary Anthropology*.

**Broader Impacts.** A main goal of this research is to gain a better understanding of *Homo* skeletal variation, and given that humans are categorized under genus *Homo*, there is a wide audience by which to disperse results. As such, results issuing from this project will be shared in three main ways: (1) submission to popular science blogs and websites, (2) local Science Cafes, and (3) develop lesson plans for use in North Carolina public schools for three target grade levels (kindergarten, grades 4-6, and high school biology). Blogs are a relatively popular way to engage the general public in scientific research because the writing is more accessible. I wrote my own blog during my field school (2012) and contributed to the Turkana Basin Institute’s blog during my tenure. Since May 2019, I have been working with *Science News* to publish a blog post relating to my research. As such, I have gained the skills necessary to produce blog posts, and intend to submit to *Science Trends* (year 1), *Sapiens* and *IFL Science* (year 2), and *Scientific American* (year 3). The order of submissions is based on each blog’s prestige and relevance to the project, with a planned submission to the popular *IFL Science*, who has a strong social media presence, halfway through the project in order to garner interest. The North Carolina Science Museum located in Raleigh, NC hosts bi-monthly Science Cafes, or casual public events meant to be particularly engaging for the general public.

Lastly, I will develop a series of three lesson plans and corresponding lectures for three main grade levels: kindergarten, grades 4-6, and high school which I will be available to teach, but will also be made available online via my webpage and the lab’s webpage for use by any teacher. These lessons will be based on the North Carolina Standard Course of Study (NCSOC), particularly based on the Essential Standards of Science, though contain valuable information for students in any state. The kindergarten lesson will meet the K.L.1 standard: “comparing characteristics of animals that make them alike and different from other animals and non-living things.” The grade 4-6 lesson will meet the 4.L.1 standard: “Understand the effects of environmental changes, adaptations and behaviors that enable animals (including humans) to survive in changing habitats” and the final series will be geared towards high school biology, meeting the Bio.3.4

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standard and Bio.3.5 standard, which focus on understanding the theory of evolution by natural selection and how classification systems are developed.

**H. Hominins and Biological Collections.** This application is for the biological collections program, which is the most natural fit for this project. After excavation, fossils and bones are stored in museums or universities for future researchers to study. Thus, all data for this project will be collected from global biological collections. Data for the project will be collected in the form of 3D scans and photographs, which is imperative to the preservation of these fossils. As seen with the fire at the National Museum of Brazil, or with the fires currently threatening California, natural history objects are under threat. While the original fossils are the best model, in the event of fire or other natural disaster, 3D models and photographs of the objects are invaluable resources. I have worked in the biological collections in over 10 museums and archives and am therefore well-equipped to conduct collections-based research.