# CRANIAL CAPACITY VARIATION OF PLEISTOCENE HOMO AND POSSIBLE SPECIATION EVENTS

by

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# ABSTRACT

AUTUMN SCARLET HUDOCK. Cranial Capacity Variation of Pleistocene *Homo* and Possible Speciation Events.
(Under the direction of DR. JONATHAN MARKS)

The field of paleoanthropology is tasked with studying the morphology of extinct hominins using fossilized remains. To study the evolution of the human brain, researchers use endocast data derived from fossil skulls, in order to assess when and how our brains have changed throughout time. Endocasts provide the measurement of cranial capacity, a proxy for brain size, and is one investigative avenue to assess human brain evolution. This study gathers fossil endocast data for 156 hominin specimens, as well as other identifying information for each specimen, to gauge how variation of brain size (cranial capacity) has changed throughout our genus. By implementing statistical formulas for rolling window samples, the coefficient of variation (CV) of cranial capacity is calculated across time and species. Rather than assess if cranial capacity has increased throughout time, the current study analyzes variation throughout time, comparing variation throughout the past 2 million years. Comparisons for cranial capacity variation are made with reported values for living apes and modern humans. This analysis is done with the added context of suggested speciation events having occurred in the Pleistocene. This study provides an assessment of variation for this morphological trait across time. The results are interpreted within the context of expected variation represented in living apes and modern humans. Interestingly, cranial capacity variation of Early Pleistocene *Homo* was the highest recorded in this study, followed by moderate variation of the Middle and Late Pleistocene, with moments of increased variation occurring in both periods. The study also demonstrates, that from about 35 Ka to the onset of the Holocene, cranial capacity variation for archaic human populations matched that recorded for modern human populations. Ultimately, this work demonstrates that the most likely speciation event occurred sometime in the Early Pleistocene, possibly coinciding with the taxonomic designations of *Homo georgicus* and *Homo ergaster*.

The cumulative dataset used in this study includes each fossil's original discovery latitudinal and longitudinal coordinates, any other names associated with the fossil, as well as descriptive information of cranial capacity estimates for each specimen. A shortened version of this dataset is listed in appendix A of this work. However, the entire dataset featuring additional information for each specimen is included as a supplementary file, in Microsoft Excel format.

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# DEDICATION

I dedicate this work to my family and my partner, who have been my support system while navigating higher education.

To my mother, who has always believed in me and who has pushed me to believe in myself when I needed it most. Thank you for the countless trips to the museums of Exposition Park where I discovered the love of my life, science.

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# LIST OF ABBREVIATIONS

## General Abbreviations

CC: Cranial Capacity

CV: Coefficient of Variation

ECV: Endocranial Volume

## Taxonomic Abbreviations

ahs: archaic *Homo sapiens*

early h: early *Homo*

h ant: *Homo antecessor*

he: *Homo erectus*

herg: *Homo ergaster*

hg: *Homo georgicus*

hh: *Homo habilis*

hhei: *Homo heidelbergensis*

h rhod: *Homo rhodesiensis*

hrud: *Homo rudolfensis*

hs: *Homo sapiens*

h solo: *Homo soloensis*

n: *Homo neanderthalensis*

pe: *Pithecanthropus erectus*

sp: *Sinanthropus pekinensis*

Dating Method Abbreviations

AMS: Accelerator mass spectrometry

ESR: Electron spin resonance

FT: Fission track

OSL: Optically stimulated luminescence

TL: Thermoluminescence

TT-OSL: Single-grain thermally transferred optically stimulated luminescence

U-series: Uranium series

U-Th series: Uranium-thorium series

# Chapter 1: Introduction

The evolution of the human brain has received significant attention, both in academia and popular culture. With research into the subject spanning centuries and throughout disciplines, the topic of investigation is central to anthropological inquiry. The subfield that specifically studies the brain size and structure of hominins is paleoneurology (Falk 1987). The research behind human brain evolution relies heavily on the study of endocasts (Bruner 2017; Hill et al. 1992), which are 3D or physical representations of the inner cranial vault. Endocasts can provide valuable data pertinent to understanding how the brain has changed throughout hominin evolution, such as brain size, and on occasion, convolutional patterns of the brain that once resided inside fossil skulls (Bruner 2015; Falk 2014). The data provided by endocasts have been used to investigate the pattern and processes of encephalization in human history (Lee and Wolpoff 2003; Shultz et al. 2012; Scott 2014; Van Arsdale and Wolpoff 2013; Villmoare 2005). Recording the brain size of fossil hominins has helped researchers quantify how and when hominin brains have changed through time. However, the past decade has seen a vast increase in hominin fossil discoveries from the Pleistocene era (Asfaw et al. 2002; Baba et al. 2003; Berger et al. 2015; Bruner et al. 2016; Gabunia et al. 2000; Li et al. 2017; Lordkipanidze et al. 2013; Semaw et al. 2020; Spoor et al. 2007; Wu et al. 2014). Additionally, the geographic dispersal of these discoveries has caused researchers to reevaluate assumptions made about human origins, speciation and habitation events, and ancestral relationships between hominin groups (Rightmire 2013; Roberts et al. 2009).

With the increase in specimens available for study, many researchers have noted that the differences in cranial morphology and size for the genus *Homo* point to evidence of speciation throughout the past 2 million years (Kidder and Durband 2000; 2004; Stringer 1984; Rightmire 2008; Wood 1984). Although the size of the brain is not the only defining characteristic to evaluate when considering derived and ancestral traits, it does offer insight to researchers who wish to compare the trait's variance. These analyses are concerned with whether the diversity of this morphological trait can be explained by intraspecific variation or shifts in morphological form leading to speciation events.

Unfortunately, studies involving fossil hominins have been limited in the past for various reasons, including researchers not having access to some fossil material or not having access to publications describing fossil material for various reasons (De Miguel and Henneberg 2001; Holloway 2008). One limitation for these types of studies stems from the small sample size of the hominin fossil record. Researchers were limited by how they made statistical comparisons of brain size and brain size change due to the small sample size of fossil hominins available for study (Tobias 1971). These limitations were more pronounced when attempting to gauge variation exhibited within and between the samples, depending on how they were divided (by time, region, or sex) (Baab 2008).

Thankfully, the 21st century has allowed for more reliable methods behind these types of studies, such as virtual endocast reconstruction and better relative dating techniques for fossil material (Morley et al. 2020; Nalawade-Chavan et al. 2014; Neubauer 2014; Prossinger et al. 2003). Along with newly discovered fossil remains found throughout Asia, Africa, and Europe, researchers are in a much better place to make more meaningful analyses for the pattern and processes regarding human brain evolution. Currently, the fossil record includes an extensive repository of hominin remains, although the sample size dwindles when excluding only postcranial remains, and even more so when only complete cranial remains are considered.

These changes and additions to the field and fossil record allow for a reevaluation of previous assumptions made about hominin brain evolution and cranial variation within fossil species.

My research applies the newly available data and original publications of fossil specimens to analyze cranial capacity variation for Pleistocene *Homo* and look for evidence of suggested speciation events within the lineage based on variation present in the dataset. The established dataset was created by combining new virtual reconstructions of fossil material, revised age estimates, and original publications outlining metric descriptions of hominin specimens. I employ statistical techniques to remedy possible error margins for relative age estimates associated with fossil specimens. The coefficient of variation was calculated for rolling window samples of hominin cranial capacity data and compared to values for modern humans, living apes, and extinct fossil groups of our genus. This project adds to anthropological knowledge of human brain evolution and the amount of variation present within paleospecies. The project also provides insight into whether there is evidence of multiple species of *Homo* existing throughout the Pleistocene based on the observed amount of cranial capacity variation exhibited within and between groups.

# Chapter 2: Background

## 2.1 History of Paleoanthropological Finds Discussing Cranial Variation of *Homo*

The morphological variation exhibited within Pleistocene *Homo* has long been a subject of debate in paleoanthropology, and with new fossil discoveries, the amount of variation comprising the fossil genus has grown as well (Antón et al. 2016). Fossil discoveries throughout the late 19th and early 20th centuries, now assumed under *Homo erectus*, were given different labels in original publications, notably *Sinanthropus* and *Pithecanthropus*, among others (von Koenigswald and Weidenreich 1939; Weidenreich 1937). Because of the variation present in the existing fossil record of the 19th and early 20th century, some researchers, such as Franz Weidenreich, thought of the fossils as belonging to different populations but not necessarily separate species. However, these early assessments were limited with reasonable comparisons (Wolpoff 1999). The only other hominin fossil group known to paleoanthropologists in the 1890s were Neanderthals, which also showed a great degree of variation in morphology. In the intervening decades, the fossil record expanded exponentially, with researchers claiming fossil discoveries from around the world as belonging to *H. erectus*. This has contributed to the continuing debate surrounding taxonomic categories for fossils attributed to *H. erectus,* now known in Asia, Africa, and Europe, with an estimated existence spanning more than a million years.

In 1891, when Eugène Dubois discovered a calotte in Trinil, Indonesia, researchers were undecided on whether the fossil could reasonably be accommodated in the family Hominidae based on its morphology (Antón 2003). The Trinil 2 fossil was given the designated taxonomic name of *Pithecanthropus erectus*, which stayed with the specimen for years to come. Many more fossils have been found in Indonesia since then, such as the well-known Sangiran Formation yielding one of the most complete skulls of Asian *H. erectus* (Antón et al. 2016). However, multiple taxonomies were proposed throughout the following decades for hominin fossils discovered throughout Asia well into the 20th century (Antón et al. 2007; Wood 1992).

Throughout the 1930s, Wenchung Pei described hominin fossils from Zhoukoudian Cave in China that exhibited similar traits to those found in Indonesia but still exhibited variation comparatively (Pei 1934; von Koenigswald and Weidenreich 1939). When discussing the morphological differences of the fossil hominins found at the sites throughout Zhoukoudian Cave, Weidenreich acknowledged that the older fossils (now attributed to *H. erectus*) shared many characteristics with modern humans, but the differences between the two seemed too drastic to be direct ancestors of any type (1938-1939). Weidenreich published heavily on the topic of comparing the Asian fossil specimens and packed the former taxonomic divisions given to fossils from Zhoukoudian and Java sites into subspecies of *Homo erectus* in his 1939 publication along with his colleague von Koenigswald (von Koenigswald and Weidenreich 1939). A decade later, he was joined by Ernst Mayr (1950), when he lumped the species designations of *Pithecanthropus, Sinanthropus,* and *Meganthropus,* into *H. erectus*, although acknowledging the amount of morphological variation present throughout the fossils.

In 1964, Wilfrid E. Le Gros Clark was one of the first researchers to claim that the fossils from the Northern Africa site of Ternifine were *H. erectus* and the specimen OH 9 from Olduvai, which was initially given the species name *Homo leakeyi* (1964). The discovery of *H. habilis* from the sites of Olduvai and Koobi Fora, was shortly followed by the claim of some researchers asserting that the fossil ER-1470 belongs to a separate species of early *Homo*, *H. rudolfensis*, and therefore the species should be split in two (Alexeev 1986; Tobias 2009; Wood 1999). Fossil discoveries throughout the 1970s and 1980s from the sites of Koobi Fora and the Turkana Basin in Africa were also deemed to be *H. erectus* (Brown et al. 1985; Leakey and Walker 1976). By the 1980s, *Homo erectus* became an established paleospecies with a wide geographic range and presence throughout the Pleistocene. The 1980s also ignited further debates regarding the validity of *Homo habilis sensu lato*.

Recent decades have also added to the fossil record for *H. erectus*. The Eurasian site of Dmanisi, Georgia, has yielded fossils belonging to individuals from 1.77 Ma (Lordkipanidze et al. 2007), who also exhibit variation in cranial features, such as cranial capacity estimates ranging from 600 to 775 $cm^3$ for the collective fossil sample (Gabunia et al. 2000). A more recent publication featuring the metric description of a fifth cranium found in the Dmanisi fossil assemblage reported a smaller brain size than all other specimens previously attributed to *H. erectus*, with an estimated cranial capacity of 546 $cm^3$ (Lordkipanidze et al. 2013). The collective sample from Georgia represents the smallest of cranial capacities attributed to *H. erectus*, adding even more cranial variation to the fossil record for the species. Although some have argued that the Georgian fossil specimens belong to their own taxonomic category, many researchers still consider them under *H. erectus* and assume the differences in cranial variation may represent pronounced sexual dimorphism of early *Homo* (Baab 2015; Rightmire et al. 2006).

Discoveries in Africa have continued to reinforce *H. erectus* as a morphologically variable species as well. A calvarium found in Ileret, near Lake Turkana, provided with the fossil name KNM-ER 42700, was attributed to *H. erectus* and dated to 1.55 Ma. The fossil shows the most similarity in cranial traits shared with specimens from the Dmanisi and Sambungmacan sites (Spoor et al. 2007). However, prior to the fifth fossil skull found in Georgia, KNM-ER 42700 represented the smallest of adult *H. erectus* skulls with a cranial capacity of 691 cm$^3$. Although Spoor and colleagues acknowledged that the calvarium size was within range of the Dmanisi sample, it also was in the range of estimates of cranial capacity for *H. habilis*. The publication describes this contradiction and challenges the interpretation of *H. habilis* and *H. erectus* as a single evolving anagenetic lineage, along with the assumption that the Georgian fossils are an intermediate between the two species solely based on their “primitive” size. Instead, the researchers state that the small size for KNM-ER 42700 does not limit the fossil in its species designation because the range of variation for cranial capacity within *H. erectus* does not exceed the range of variation found in gorillas. However, it does exceed variation reported for modern humans and chimpanzees. The presence of typically “Asian” *H. erectus* cranial traits regarding KNM-ER 42700 highlights the challenges in separating the Asian and African fossil hypodigms and provides further evidence of *H. erectus* as a paleospecies with a wide range of cranial variation (Neubauer et al. 2018b).

Other fossils attributed to *H. erectus* in Africa found in recent decades have continued to support previous assumptions regarding the taxonomic debate surrounding the species. One site in Ethiopia reported a calvarium, otherwise known as the Daka calvarium, estimated to be 1 million years old, with a cranial capacity of 995 cm$^3$ (Asfaw et al. 2002). The workers report that the Daka calvarium, whether it is compared morphologically or metrically, aligns with the species designation of *H. erectus*. The Buia specimen, a partial hominin skull from Eritrea dated to 800 Ka, shares derived cranial traits with the Daka specimen and has also been assigned to *H. erectus* (Antón et al. 2007). Some researchers have proposed that the derived traits of the two calvariae, although they compare in overall size for fossils of the same period, represent evidence for a more advanced *H. erectus* that possibly leads into later *Homo*, or that they perhaps belong to a more derived taxon of later *Homo* (Baab 2015). Another recent discovery by Semaw and colleagues (2020) provides further evidence of *H. erectus* cranial capacity variation within the African sample, where researchers reported a cranium from Gona, Ethiopia dated to 1.55 Ma, with a small size of 598 $cm^3$. Although the cranium shares features with other *H. erectus*, such as the Dmanisi fossils and KNM-ER 42700, the fossil is also quite different morphologically from other *H. erectus* found in Africa. These discoveries, among others, highlight the complexity of hominin systematics based on morphological comparisons and how much variation can be accommodated within a single species.

Ultimately, the taxonomic status of *H. erectus*, and other *Homo* fossils from the Early Pleistocene, are essential to studies evaluating the origins of modern humans and the ancestral relationships of these past hominins. Are the Dmanisi hominins truly a separate species? Should *Homo habilis* be split into two species as well? If *H. erectus* was divided into several species globally, what does that mean for models of human evolution? Furthermore, if these fossils to belong to separate species, what does this mean for the hypothesis of a single evolving anagenetic lineage moving from *H. habilis* to *H. erectus* to *H. sapiens*?

## 2.2 The Problem of Taxonomy for Pleistocene *Homo*

Paleontology is tasked with determining the presence of extinct species using the fossil record. However, in biology, the classical definition of a species relies on the ability of members to reproduce with one another. This puts paleontologists in a limiting situation. Because there is no way to determine the ability of fossil species to mate with one another, paleontologists rely on morphological comparisons of fossils to assess the taxonomic status of fossil specimens (Rightmire 2013). The debate surrounding the taxonomy of *Homo erectus* (whether it represents a single species that underwent morphological shifts gradually through time and space or whether multiple speciation events characterized Pleistocene hominin evolution) utilizes comparative data on the level of phenotypic variation represented in the fossil group (Baab 2015; McHenry 1995; Park et al. 2007; Spoor et al. 2007).

As touched on earlier in this paper, supporters of the single species view describe the evolutionary trajectory of *Homo erectus* as experiencing various ecological, geographic, and temporal differences represented in the fossil record, and that morphological variation apparent throughout these fossils can be explained by these differences (Curnoe and Thorne 2003; Curnoe 2006). This viewpoint puts forward that *Homo erectus* was a widespread and biologically variable species, with a presence in Africa, Asia, and Europe. A sect of this argument also indicates that *Homo erectus* and *Homo sapiens* belong to the same species, with modern humans being a continuation of the lineage (Frayer et al. 1993; Wolpoff 1999).

Alternatively, other researchers have claimed that the morphological differences within this group are too variable for one species, and therefore, the shifts in morphology should be quantified as speciation events throughout the fossil record (Antón 2003; Baab 2008; Bräuer 2008; Rightmire 2013). Some proponents of this theory support the distinct taxonomic divisions of *Homo heidelbergensis*, *Homo ergaster*, and *Homo georgicus* as separate from *Homo erectus* (de Lumley et al. 2006). There are also variations of this theory, with some researchers siding with multiple hominin species represented throughout the Pleistocene (Martinón-Torres et al. 2007; Rightmire et al. 2006), and others only accepting a two-species model. There is also debate for fossil specimens originally deemed *H. habilis*, with some researchers asserting that certain fossils from this group belong to a separate taxonomic species called *H. rudolfensis* (Alexeev 1986).

Although there is variation in the postcranial morphology of Pleistocene *Homo* fossils, cranial variation in *Homo erectus* has been used as evidence for multiple distinct taxonomic species by some researchers. The evolutionary pattern of encephalization has been a focal point in the investigation of hominin phylogenetic trees (Antón 2002; Hofman 1983; Lee and Wolpoff 2003; Rightmire 2013). Although it is apparent that increases in cranial capacity characterize the genus *Homo* through time, the same trend, although on a lesser scale, was observed in australopiths leading to the appearance of *Homo* (Park et al. 2007). With the fossil specimens of *Homo erectus* existing within a broad temporal and spatial spectrum, some researchers have pointed to the high degree of cranial variation for the species as a product of geographic or time related differences (Villmoare 2005) rather than speciation events (Leigh 1992). With a growing fossil record, the increase in data allows for further investigation into these claims, and any evolutionary trends relevant to brain size increase over time.

The theory of speciation in the global *Homo erectus* sample has been subject to studies evaluating the variation of cranial capacity, among other nonmetric, metric, and linear measurements of fossil hominins, to assess the validity of *Homo heidelbergensis*, *Homo georgicus*, and *Homo ergaster* as separate and distinct species from *Homo erectus* (Donnelly and Kramer 1999; Kidder and Durband 2000, 2004; Lee 2005; Lee and Wolpoff 2003; Rightmire 2008; Scott 2014; Van Arsdale and Wolpoff 2013). European fossils featuring larger cranial capacities, but more “primitive” morphology reinforced the taxonomic separation of *H. heidelbergensis* from Neanderthals and “archaic” *H. sapiens*, with later additions of African fossils also attributed to the taxon (Cartmill and Smith 2009). Initially, the Georgian hominins were thought to be a different species than *H. erectus*, as some researchers suggested multiple species within the fossil assemblage, citing the small cranial capacities throughout the skeletal sample (Rightmire et al. 2006). The taxonomic group, *Homo ergaster*, has been used for the African hominin fossils that are otherwise considered *H. erectus*, based on the absence of specific cranial characteristics typically associated with Asian *H. erectus* from earlier studies. This has caused some to assert a multiple species explanation. In contrast, others claim the differences are due to geographic variation with the African fossils still conforming to the Asian *H. erectus* cranial 'bauplan' (Antón et al. 2007; Asfaw et al. 2002). Along with the African discoveries of a calvarium with a large cranial capacity of 995 $cm^3$ and another with the second smallest cranial capacity of *H. erectus* estimated at 691 $cm^3$, both being assumed into the same species, the range of cranial variation exhibited within *H. erectus* is extensive (Baab 2008).

### *2.2.1 Homo habilis and Homo rudolfensis*

*Homo habilis* is the first member belonging to the genus encompassing our species, and the fossils belonging to this group have been described as intermediate between an ancestral species of *Australopithecus* and *Homo erectus*. Specimens known as *H. habilis* include those found at the Olduvai Gorge in Tanzania. Upon its initial description in Nature, *Homo habilis* (meaning "handy man") was thought to be the first who used crafted tools in the hominin lineage (Leakey et al. 1965). Brain volume is slightly larger in this group compared to earlier hominins; however, some members fall well within the range observed for australopiths, ranging around 500 – 700 $cm^3$ (Lieberman 2011). Interestingly, the criteria to be considered into the *Homo* genus was revised once the *Homo habilis* specimens were discovered, one example being the minimum brain size as the fossils fell below the previous threshold (Wood 1992). The sovereignty of this species is also debated within the field of paleoanthropology, with some researchers subscribing to the view that the fossils attributed to this group should be split into two, *H. habilis* and *H. rudolfensis* (Schrenk et al. 1993).

The handful of fossils that encompass *H. rudolfensis* were initially assigned to *H. habilis* and were reappraised after researchers analyzed the highly variable fossil sample. When considered together as one species, studies revealed that the early *Homo* sample is more anatomically variable than any other living ape species, even when considering the possibility of extreme sexual dimorphism (Wood 1999). Comparatively, *H. rudolfensis* was found to have a larger brain size of 775 $cm^3$, compared to the size of the Olduvai specimens. In addition, the face of *H. rudolfensis* is wide and flat, as well as slightly prognathic compared to *H. habilis* specimens (Lieberman 2011). However, there are no postcranial remains that belong to the *H. rudolfensis* specimens, and therefore researchers cannot make inferences into how features such as relative brain size would scale with body size (Cartmill and Smith 2009). Additionally, specimens belonging to both groups overlap in age estimates. For these reasons, the taxonomic debate for early *Homo* in Africa continues to be played out in paleoanthropology.

### *2.2.2 Homo ergaster*

*Homo ergaster* is made up of a handful of fossil specimens found in Eastern Africa and is associated with the dates of 1.9 to 1.55 Ma (Bilsborough 2005). Although some researchers argued for the specimens to be placed under *H. erectus*, and at the time of their initial discovery were deemed *H. erectus*, others supported a distinct species designation in articles published by

Stringer (1984) and Wood (1984). This assertion was based on the wavering definition of *H. erectus* morphology and comparisons made with Asian *H. erectus* specimens. Both Wood and Stringer attempted to establish a list of criteria for cranial features and morphology that the *H. ergaster* specimens did not meet. Alternatively, the presence of primitive cranial morphology could be due to their age. Others have used this as evidence that *H. ergaster*, being that the fossils attributed to the group are among the oldest *Homo* fossils in Africa, has a "primitive" morphology because they are early representatives of *H. erectus* (Cartmill and Smith 2009).

Studies that followed Wood (1984) and Stringer's (1984) work, have investigated the cranial variation within the fossil sample, and ultimately support the viewpoint that they should be subsumed under *H. erectus*. For example, Philip Rightmire, who combined samples of *H. habilis*, and Asian and African *H. erectus*, analyzed different cranial features with the conclusion that the traits demonstrate continued variation throughout time, and specimens could not be ruled out of *H. erectus* based on the presence or absence of these features (1993). Andrew Kramer (1993) compared the variation of *H. erectus* cranial morphology (combining both Asian and African samples) to the fossil samples of *H. ergaster* and modern human populations. They ultimately demonstrated that the degree and patterning of variation for the entirety of *H. erectus* (including *H. ergaster*) did not warrant a separate species explanation as the sample resembles the amount of variation present within a single species (Kramer 1993). A study done by Liu and colleagues (2005) has also supported *H. ergaster* as *H. erectus*, with their principal-components analysis of cranial measurements pointing to shared affinities between the East African fossils and Asian *H. erectus*.

### *2.2.3 Homo georgicus*

The hominin fossils found in the 1990s in Dmanisi, Georgia, have complicated the systematics of *Homo erectus* (Gabunia et al. 2000). The fossils exhibit small cranial capacities and share craniofacial characteristics with *H. habilis* but have been likened to African *H. erectus* and Javan *H. erectus* with other morphological similarities. This has led some researchers to refer to the fossils as *H. erectus* (Vekua et al. 2002), with others claiming that the sample constitutes a distinct taxonomic category, *H. georgicus*. The age of the fossils has also complicated previous assumptions regarding hominin brain evolution for earlier *Homo* species (Ferring et al. 2011; Rightmire 2013). The “primitive” cranial traits maintained in the Dmanisi sample may be explained by the existence of plesiomorphic retentions or can be explained by growth-related processes that affect particular cranial and facial morphology (Rightmire et al. 2006). If these explanations are taken into account, there is little basis for asserting a *H. habilis* designation, based on all other comparisons pointing toward an *erectus* morphology. Additionally, the variation in facial morphology and cranial capacity of the fossil specimens may be due to sexual dimorphism in early *Homo* (Lordkipanidze et al. 2013). For these reasons, the taxonomic place of the Dmanisi hominins remains a continuous debate.

### *2.2.4 Homo heidelbergensis*

Ian Tattersall proposed using *H. heidelbergensis* as the species designation for fossils that were otherwise referred to as “archaic” *H. sapiens* in the European fossil record (1986). This suggestion was furthered by the disconnect in morphology when comparing the fossils to *H.*

*erectus* from Asia and Africa. *Homo heidelbergensis* is made up of fossil specimens with cranial capacities within the modern human range but shares a “primitive” cranial morphology otherwise (Cartmill and Smith 2009). Around the same time, the employment of cladistics gained popularity in paleoanthropology. This led to a further reappraisal of fossil specimens, which coincided with additional discoveries from Africa, including the specimens Bodo, Ndutu, and Elandsfontein, resulting in more fossils being subsumed under *H. heidelbergensis* (Rightmire 1998). *Homo heidelbergensis* was considered the representative taxon that was likely the last common ancestor to the Neanderthal lineage in Europe and “archaic” *H. sapiens* in Africa. However, *H. heidelbergensis* as a distinct species has consistently been debated, citing inconsistencies with morphological requirements and other phenotypic traits across specimens (Lieberman 2011; McCarthy et al. 2007; Rightmire 1996).

The variation of theories surrounding the taxonomy of *Homo* fossils from this time are extensive. For some experts, the best way to divide the hominin fossils taxonomically is to put all African “archaics” into *H. heidelbergensis* and the oldest specimens from Europe, with the later European specimens designated to Neanderthals, such as Swanscombe (Tattersall and Schwartz 2001). Some researchers support the taxonomic distinction of *H. heidelbergensis* as “pre-Neanderthal” for European specimens (Bermúdez de Castro et al. 1997), with others claiming that all European fossils should be considered Neanderthal, and the African fossils as *H. sapiens* (Klein 1999). There has even been an effort by McCarthy and colleagues (2007) to consider at least two species within all the fossils attributed to *H. heidelbergensis*, based on the amount of cranial variation exhibited throughout the sample.

## 2.3 Alternative Explanations for Cranial Capacity Variation

Addressing sources of variation in the fossil record without invoking separate species can be done by understanding alternative explanations for why there is morphological variation within a group. Factoring in the influence of these causes can help researchers understand the extent of variation that cannot be accounted for otherwise (Plavcan and Cope 2001). It is also important to point out that variation in cranial capacity in modern humans can be used as a basis for understanding past trends of variation in the genus *Homo*. One variable that can affect total cranial capacity in hominins is the overall body size of an individual. With a bigger body size, brain size also tends to be larger, with a scaling relationship between the two reported in mammals and in humans (Kappelman 1996; Ruff et al. 1997). Although recent research suggests that this relationship may not be positively correlated in modern humans, with evidence pointing to a negative relationship between increasing brain size and decreasing body size for our species as a whole (Smaers et al. 2021). More examples that may contribute to variation in brain size for humans and hominins are discussed below.

### *2.3.1 Ontogeny*

One source contributing to variation in terms of cranial capacity is ontogeny. By only including adult specimens, clearer parameters are set for expected variation, as infant specimens would significantly impact the data as cranial capacity is directly influenced by physical development in hominins (Balzeau et al. 2005; Coqueugniot and Hublin 2012). Cranial variation is not exempt from this rule, as human brain development does not conclude after birth. The human brain continues to change and develop in both size and structure throughout one's life (Shepherd et al. 2017). Between the ages of 2 and 6, human brains grow four times in size and represent about 90% of their adult size by that time (Stiles and Jernigan 2010).

By age 10.5 (average age for females) or 14.5 (average age for males), brains reach their peak size in humans (Giedd et al. 2015). However, during an individual's 20s and 30s, gray matter volume steadily declines. Other age-related changes to brain size include the doubling of cerebral spinal fluid throughout one's life, from occupying around 7% of a child's total endocranial cavity to around 14% by 80 years old (Coqueugniot and Hublin 2012). Therefore, age is just one factor that can alter the size of the human brain. Because of these possible interferences for brain size in humans, it is important to quantify brain size variation in extinct hominins of the human lineage. For these reasons, it can be justified to include juvenile specimens when assessing cranial capacity, as they are comparable in size with adult specimens.

### *2.3.2 Sexual Dimorphism*

The best way to avoid mistaking variation of cranial capacity as evidence of speciation in the context of sexual dimorphism would be to use a trait that is not expected to vastly differ based on sex. However, cranial capacity can be affected by sexual dimorphism, in the aspect of absolute brain size correlating with body size, with hominin females estimated to be smaller in stature compared to males (Ruff et al. 1997; Ruff 2002). Assessing sex in fossil species, especially hominins, is a challenging task for researchers (Bello et al. 2006). In some cases, most of the fossil specimen is missing, and therefore cannot be efficiently assessed for sex, or the fossil specimen is so fragmentary that sex assessment cannot be done reliably and can even prove difficult when most of the skeleton is present (Rosenberg et al. 2006).

The fossil record for Pleistocene *Homo* is much more expansive in recent times but still considered to be a small dataset, nonetheless. Therefore, we cannot afford to rule out specimens due to the uncertainty of sex when evaluating cranial variation. Additionally, using a mixed sample for analysis provides a more comprehensive picture of cranial capacity variation for an entire species. Because this analysis uses fossils designated to *Homo habilis* and to *Homo erectus* (or *H. georgicus*/ *H. heidelbergensis*/ *H. ergaster*), there is less likelihood of cranial capacity ranges being drastically different from modern values that include both males and females. *Homo habilis* is not known to be as sexually dimorphic as *Australopithecus*, and as time goes on, later *Homo* species resemble values closer to modern humans than to orangutans, chimpanzees, or gorillas (Lieberman 2011).

Studies that analyzed modern human populations also justify assessing cranial capacity variance exhibited in our species, despite some degree of sexual dimorphism. One heavily cited study evaluated cranial capacity separately based on sex for various global populations of adult humans and compared variation overall for the trait (Henneberg 1990). It was found that female cranial capacity, on average, differed from the male sample by a standard deviation of 72.1 $cm^3$. On average, modern female cranial capacity was reported at 1272 $cm^3$, and modern male cranial capacity at 1426.6 $cm^3$. The study also found that the degree of sexual dimorphism of cranial capacity only contributed less than 25% of the overall variance present. In addition, cranial capacities of modern humans overlap in values for male and females (Hawks 2011; Henneberg 1990; Lieberman 2011; Ruff et al. 1997), which underlines a justification for using cranial capacity as a measure of speciation in fossil species that is representative of living populations.

### *2.3.3 Geography and Climate*

Different climates can affect body size in mammals, which ultimately affects brain size. This is referred to as Bergmann's rule, which is an ecogeographic principle stating that species throughout widespread geographic areas tend to have increased body size in higher latitudes (and therefore colder climates) as an adaptation to reduce surface area, resulting in enhanced regulation of the animal's body temperature (Rosenberg et al. 2006; Ruff 2002). This principle extends to brain size since brain size and body size are correlated in mammals. In humans, this scaling relationship is often understood with the computed EQ of an individual or group (encephalization quotient). Harry Jerison (1973) first proposed the EQ formula based on the assumption that within the mammalian group, brain mass scales to body mass to the power of 2/3. Therefore, EQ is used to predict brain mass under these assumptions. Later studies have reported that brain mass across the mammalian group scales to body mass to a degree of 3/4 (Martin 1981). Under these principles, researchers have studied how this scaling relationship, in addition to climatic influences, may factor into the observed cranial capacity for hominins and humans.

Whether the environmental influences resulting in cranial capacity differences between modern humans belonging to different geographic areas are due to varying selection pressures or ecological ones, the values remain relatively similar when compared. Most notably, studies have found that brain size was the largest among human populations living in colder and dryer climates, accompanied by higher latitudes (Beals et al. 1984; Kappelman 1996; Katz et al. 2016). Henneberg reported modern comparisons of human cranial capacity made between different geographic populations and found that differences in geography only contributed to less than

30% of the overall observed cranial capacity variance (1990). In another study, Beals and colleagues (1984) determined that population differences of cranial capacity only differed by less than one standard deviation in most cases when population means were compared, demonstrating that geographic differences only account for a small amount of variation pertaining to brain size in modern humans.

## 2.4 Estimating Cranial Capacity for Fossil Hominins and Humans

Evaluating brain size has been a significant point of inquiry into the evolution of the hominid brain, one reason being that other features are almost impossible to distinguish on fossilized specimens. However, estimating brain size is done in different ways. There are different types of measurements for the human brain, absolute and relative. Researchers either measure brain size in mass or volume, resulting in similar values but calculated using different methodologies. One way to measure brain size is the displacement method where a brain is placed in water (or some other fluid), then a measurement of the displaced fluid is calculated, estimating the volume of the brain (Holloway et al. 2004). Another manner of measuring brain size in volume is done by calculating ECV, which is done by measuring the volume of the endocranial cavity from outer measurements of the skull or virtual measurements from 3D models (Lieberman 2011). This method is often used for fossil hominins because it is impossible for the actual brain to be preserved for direct measurement, as is the case with living animals. Another method of estimating cranial capacity can be done by regression formulas which account for deformations or missing portions of unrestored fossil skulls (Wu and Zhang 2019).

ECV and brain size are not the same thing. Because the ECV measures the skull's entire cavity, the estimated ECV also factors in the cerebral fluid and the presence of the brain's vascular system. Therefore, ECV is not entirely representative of brain size (Neubauer 2014). Because brain mass specifically refers to only the weight of the brain, mathematical formulas are necessary to include in order to reduce the interference of other tissues and fluids that would be present in the cranial cavity of living organisms. It is necessary to account for these differences when converting ECV to brain size. It is also necessary to use regression formulas that relate volume to mass when converting ECV to brain mass. (Lieberman 2011). ECV is expressed in cubic centimeters ($cm^3$), and brain mass is expressed in grams (g). Another term, cranial capacity, also refers to the volume of an organism's skull cavity and is expressed in terms of cubic centimeters (Holloway et al. 2004). In the case of virtual or "3D" endocasts, the number of voxels (digitally represented pixels taken from CT scans of the endocast) are calculated to estimate endocranial volume for a specimen, which is typically expressed in cubic centimeters or milliliters (Bruner 2015).

### *2.4.1 Endocast Data*

Different methods of creating endocasts yield different results, which is problematic when researchers rely on the data provided by the casts to make assumptions about important moments in human brain evolution. Using the different materials available to fill the skull contributes to the unreliability of endocast data (Neubauer 2014). Original publications where a fossil hominin's cranial dimensions are described often lack information on how the endocast was made and which dimensions were measured to gather that data (Holloway et al. 2004). In some instances, researchers did not make any cast of the brain. Instead, they calculated the volume of the cranial vault by filling the skull with a substance and then, in turn, measured the volume of that substance to get a value for estimated cranial capacity (Holloway et al. 2004). Historically, the different substances used to do this included millet and mustard seeds, gunshot powder, and water (Holloway 2008). However, this is also problematic as different substances provide different results, as mentioned earlier.

Currently, most researchers have switched to creating virtual endocasts, as they are more reliable in measurement and do not require the fossil to be handled as much as creating physical endocasts do (Dumoncel et al. 2020). Preserving hominin fossil specimens is crucial for the state of paleoanthropology, as they are scarce and fragile. Virtual endocasts also allow scientists to reconstruct aspects of the skull when presented with a fragmentary specimen (Bruner 2017). Due to geological processes which occur during fossilization, most specimens are fragmentary upon discovery (Tobias 1971). Reconstructing a fossil specimen is an incredibly intricate process, and the use of computer technology has provided researchers with a more reliable way to piece together a fossil with less room for human error (Falk, 1987; 1992; 2009; Ponce de León and Zollikofer 1999). Once reconstructed, a virtual endocast of the fossil can be rendered for further analysis.

Although endocasts are a vital resource in paleoneurology, the data one can retrieve from them is limited in comparison to physical brains (Neubauer 2014). Gathering endocranial volume is one of the more accessible data points retrieved from endocasts (Falk 1987; Holloway et al. 2004). Therefore, brain size is one of the most relied on measurements in paleoneurology (Neubauer et al. 2012). Throughout the past few decades, CT and MRI technology have made recreating virtual endocasts much more reliable, contributing valuable information about the brains of paleospecies (Bräuer et al. 2020; Bruner 2007; Neubauer et al. 2018a, b). With these advancements, endocasts have also been able to provide some information regarding the shape and, on occasion, convolutional patterns of the brain that was once inside (Neubauer et al. 2009).

Depending on the state of a fossil skull, details about shape and size can be extrapolated using geometric morphometric principles by analyzing homologous landmarks of the brain to project differences or similarities across hominin and primate taxon (Bruner 2015). The models of other specimens are superimposed onto the one primed for analysis, and the actual measurements regarding size are factored out as a means to scale the models to the same size, allowing researchers to compare the size and shape of the brain as separate variables (Bruner 2007; Neubauer et al. 2009; Ponce de León et al. 2021). This technique employs multivariate statistics to determine how the endocasts relate or vary from one another in anatomical structure (Coqueugniot and Hublin 2012; Reardon et al. 2018).

Endocasts can reveal crucial information about the reorganization and increase in brain size throughout the evolution of the human brain. Utilizing comparative examples from living apes, humans, and hominin fossil skulls, endocasts are interpreted by researchers to provide inferences of how the brain has changed in shape and size throughout time. However, the interpretation of endocast data by different observers yields varying conclusions. Dean Falk outlines their limitations with the following excerpt (2014, 1),

> Although endocasts may yield information about the sulci that delimit the gyri and larger convolutions of the cerebral cortex, the degree to which sulcal patterns are reproduced on primate (including hominin) endocasts varies with species (smaller-brained species produce clearer endocasts than larger brained closely related species), age of the individual (infants and mature individuals produce less detailed endocasts than individuals of other ages), geological conditions (e.g., “natural endocasts” that occur in limeworks sites in South Africa are relatively detailed compared to artificially or electronically prepared ones), and luck.

Despite the caveats associated with endocasts, they have shown us two things for certain; that hominin brains have changed in overall structure through time, and that hominin brains have significantly increased in size over the course of millions of years (Falk 1987; 2014; Holloway et al. 2004; Neubauer 2014; Preuss 2017).

Fortunately, paleoneurology in the 21st century has seen notable advancements in imaging and computing technology that have provided insight into, as well as increasing, the reliability of endocasts (Dumoncel et al. 2020). Initial studies into the reliability of endocasts have yielded crucial findings into how a brain and its respective endocast compare in detail (Zollikofer and Ponce de León 2013). Although there have only been a handful of studies that address the subject of brain-to-endocast correlation, the research that has been done has proven helpful in understanding what we can confidently assess from endocasts. Fournier and colleagues conducted a study analyzing brain-to-endocast distance for almost 40 individuals and ascertained that the respective endocast does demonstrate the same asymmetry patterns as the brain itself (2011). A more recent study looking at the shape, size, and convolutional patterns represented on the brains (and endocasts) of 5 individuals has found that when using an integrated imaging approach (both MRI and CT scans), the location of sulci is apparent on the endocast (Dumoncel et al. 2020). Additionally, the study reported a close correlation of size and shape when comparing each pair of brains and endocasts, with the exception of the superior region of the endocast relative to the actual brain. Despite the superior region discrepancy of the study, this study, and others, have demonstrated that endocasts are a valuable asset for investigating and exploring hominin brains (Bruner 2017).

### *2.4.2 Assessing Cranial Capacity Variation in Hominins and Humans*

To efficiently assess the degree of cranial capacity variation in the genus *Homo*, it is important to review the current observed values for this trait in modern populations and ranges represented in the fossil record. Brain size can be influenced by an array of factors, including genetic and environmental ones (Beals et al. 1984; Hrvoj-Mihic et al. 2013). Despite the possible circumstances responsible for brain size variation in humans, the expected cranial capacity values for our species have been established based on a cumulation of studies that have measured skull (or brain) size in living populations (Acer et al. 2007; Henneberg 1988, 1990; Nooranipour and Farahani 2008; Olivier et al. 1978; Reardon et al. 2018). Individuals with brain size values on either extreme of the spectrum usually exhibit pathologies resulting in conditions such as microcephaly or macrocephaly (Stiles and Jernigan 2010). However, most populations report an average range for cranial capacity that represents the majority of individuals. Recent studies have found that modern human brain size variation can differ almost two-fold in non-pathological individuals of the same age (Giedd et al. 2015; Reardon et al. 2018).

Fossil specimens attributed to *Homo habilis* range in cranial capacity from 500 to 681 $cm^3$, while specimens belonging to early Pleistocene *Homo* prior to 1.5 million years ago range from 546 to 875 $cm^3$ (De Miguel and Henneberg 2001; Lieberman 2011). Early to Middle Pleistocene *Homo* specimens have reported cranial capacity values that range from 780 to 1356 $cm^3$ (Melchionna et al. 2020; Ponce de León et al. 2021). Later specimens belonging to Neandertal and archaic *Homo sapiens* populations range from 1013 to 1813 $cm^3$ (Holloway et al. 2004; Neubauer et al. 2018a).

Modern cranial capacity variation for human populations has been calculated by various researchers (Beals et al. 1984; Hawks 2011; Henneberg 1988; 1990). When looked at as a whole, modern human cranial capacity averaged at 1349.3 $cm^3$, with a standard deviation of 157 $cm^3$. Using data from modern human populations from various geographic regions, Henneberg (1990) established confidence intervals for cranial capacity in adult *Homo sapiens*. At 95%, cranial capacity ranges for the species are 1042 to 1658 $cm^3$, and at 99%, cranial capacity ranges are 946 to 1754 $cm^3$. These figures point to an overlap of cranial capacity values throughout time for the genus *Homo* and further support that cranial capacity can act as a valuable measure of morphological variation and species recognition.

Cranial capacity may seem to be an inadequate parameter to assess morphological variation and speciation events in human evolution. However, cranial capacity is correlated with other craniodental measurements of fossil hominins (Shepherd 2017) and is one of the most available measurements existing throughout paleoanthropological studies of the past centuries (Tobias 1971; Holloway et al. 2004). Measurements of cranial capacity are tied to other evolutionary trends apparent in the fossil record, such as encephalization and gracilization of the craniodental skeleton in human evolution (Bruner 2007; Foley 1990). Therefore, changes in cranial capacity throughout the fossil record correlate to changes in cranial shape and is another important factor of hominin brain evolution (Antón et al. 2007). Analyzing cranial capacity variation existing within past human and hominin populations can provide insight into how morphologically different or similar we are across other primate taxa.

# Chapter 3: Research Questions

This study utilizes the cranial capacity and age data of 156 hominins to explore the following questions:

1) Does cranial capacity variation in the genus *Homo* increase during time periods where there are suggested speciation events throughout the Pleistocene?
2) How does cranial capacity variation of hominins throughout the Pleistocene compare to modern humans, other living apes, and between time periods?

# Chapter 4: Materials

The dataset used in this study includes metric information for 156 hominin specimens, dated between 2.03 Ma to 12 Ka. The entire dataset includes information on each specimen's name, relative date, cranial capacity, latitudinal and longitudinal coordinates, and geographic region belonging to Europe, Asia, or Africa where the specimen was discovered, as well as its taxonomic designation. If there are various taxa that a specimen is attributed to, each known designation is also included. The dataset used in this study was established by reviewing publications from the past centuries featuring nonmetric and metric cranial information for each specimen, beginning with the original Neandertal specimens and Trinil from Java. Most specimens can be found within the HOMDAT file, created in 1984 by Beals and colleagues. Some revisions were made to the HOMDAT file by De Miguel and Henneberg (2001) with updated information for some hominin specimens. However, the current dataset was pieced together using various literary sources, with some specimens having been discovered after 2001.

The past 20 years have seen new hominin discoveries, better dating methods for fossils, as well as virtual reconstruction techniques for fossilized skeletal material (Morley et al. 2020; Ogihara et al. 2018; Semal et al. 2009; Soficaru et al. 2007; Vialet et al. 2010; Wu and Yan 2020; Wu and Zhang 2019). The current dataset includes new specimens attributed to the genus Homo, as well as revised ages and revised cranial capacity estimates where available in the literature. The dataset only includes specimens with identifiable sources for age and cranial capacity estimations, including the method from which the estimations derive. For these reasons, the new dataset has dwindled in size from the original HOMDAT file and De Miguel and Henneberg's data (2001), featuring hundreds of specimens. In the course of preparing the raw data, some duplicates for fossil specimens were found, and some specimens were removed on the basis that their actual age is relatively recent and not pre-Holocene. Sources for each fossil can be found within the supplementary excel spreadsheet and in the bibliography.

The updated dataset has been formatted into an excel file containing the respective source for each fossil specimen featured and other relevant information mentioned above. The dataset is sorted from oldest to most recent in geologic age. The dataset includes each fossil's known species designation. All hominins included in the dataset are deemed members of the genus *Homo* (Asfaw et al. 2002; Berger et al. 2015; De Miguel and Henneberg 2001; Falk et al. 2005; Kaifu et al. 2009; Li et al. 2017; Semaw et al. 2020; Tobias 1971; Vekua et al. 2002; Wu et al. 2019). The current dataset comprises hominin fossils with the following species designations, *Homo habilis*, *Homo rudolfensis*, *Homo ergaster*, *Homo erectus*, *Homo heidelbergensis*, *Homo neanderthalensis*, *Homo antecessor*, *Homo georgicus*, and *Homo sapiens*.

There were instances where specimens were excluded from the current dataset based on the associated age, preservation, and other criteria which may introduce error into the study. These criteria are discussed below, along with which estimates for date and cranial capacity were used in this analysis if multiples were identified.

## 4.1 Cranial Capacity Data

Where available, the cranial capacity estimates using virtual endocast (or 3D endocast) data were chosen as the accepted value for that specimen. If multiple virtual endocasts were created and analyzed, and they yielded different cranial capacity estimations, then the average of the estimations was taken as the accepted value for that specimen. However, virtual endocast data were not available for all specimens as the use of CT imaging in paleoanthropology is a more recent endeavor (Kranioti et al. 2011; Kubo et al. 2008; Zollikofer and Ponce de León 2013). When there was no virtual endocast available, the cranial capacity estimate using partial endocast data made from substances such as plaster or rubber was taken. There are other methods of cranial capacity estimations utilizing formulas that were included for some specimens. In the case of multiple published cranial capacity estimations for a specimen with identifiable methods used, then the average value of estimates was calculated and taken as the acceptable value for that specimen. In past publications using cranial capacity data for fossil specimens, the method for the estimate was not recorded or mentioned. Because the value could not be traced or reproduced with no identifiable information available, some specimens were not included in the current dataset.

## 4.2 Age Estimations

The past few decades have also seen immense improvements in the relative and absolute dating of fossil material (Matsu'ura et al. 2020; Morley et al. 2020; Mounier et al. 2020; Semal et al. 2009; Sutikna et al. 2016). Considering some specimens, such as those found in France in the late 1800s, were dated solely using surrounding stratigraphy, some fossil ages have been revised (Guérin 2015). The accepted age associated with each fossil was determined by the following criteria; if the age estimate is corroborated with multiple dating methods employed at the fossil site; and if recent literature has accepted new dates for these fossils. These instances include the fossil known as Yunxian, dated initially to 400 Ka using one method, and then revised years later after employing various dating methods to around 800 Ka (Guo et al. 2013). Additionally, some fossils were bracketed with wide age margins, with gaps of 100,000 years or more, and new dating employed either directly on the skeleton or from the site allowed for better and more accurate bracketing.

## 4.3 Other Exclusions

Although some fossils have accompanying cranial capacity estimations and met other criteria for this study, some specimens were still excluded on the based on approximate age at death. This included specimens such as Mojokerto 1 and La Quina 18 to be discarded from the current dataset, as they are thought to belong to individuals that had not reached the age of at least 6 years prior to fossilization (Cartmill and Smith 2009; Coqueugniot et al. 2004). The age of an individual (especially those belonging to *Homo*) affects the size of the brain. For these reasons, infants were excluded in this study as the cranial capacity estimations for these individuals run much lower than adult specimens. Including infants and younger juveniles would then introduce possible errors into the study. However, specimens estimated to have been about the age of 7 or older, were included in this study as brain size does not significantly increase after this age and reaches around 90% of its adult size by this time in modern humans (Stiles and Jernigan 2010). There is still uncertainty regarding the specific ontogenetic processes affecting brain size in extinct hominins, but there is evidence that earlier *Homo* species, such as *H. erectus*, reached total cranial capacity at a younger age than modern humans (Coqueugniot et al. 2004; Hrvoj-Mihic et al. 2013). Therefore, the modern human range was used as the qualifying parameter in this case.

In some cases, there were cranial capacity estimations for specimens but no verifiable method for obtaining these estimations. As discussed previously, the methods for estimating cranial capacity vary in accuracy depending on the state of the skeletal material, along with other variables. Therefore, these specimens were excluded from this analysis as well as a way to reduce error for these values. There are additional fossils belonging to *Homo* that were not included in this study as well, on the basis of extremely fragmentary or nonexistent cranial material for a specimen. The specimen known as SK 847, belonging to early *Homo*, is one example as the remains are mostly from the facial skeleton, resulting in wide-ranging estimations for cranial capacity accompanied with large margins of error for the estimations (De Miguel and Henneberg 2001).

Although the dataset includes specimens from the genus *Homo*, the specimens belonging to *Homo naledi* and *Homo floresiensis* have been excluded as the purpose of this study is to analyze cranial capacity variation in the context of speciation throughout the Pleistocene. In the case of these discoveries, both exhibiting a small cranial capacity and associated with a relatively recent date (Berger et al. 2015; Dirks et al. 2017; Falk et al. 2005; Roberts et al. 2009; Sutikna et al. 2016), it was not helpful to include the values for these specimens, as both *Homo naledi* and *Homo floresiensis* are known to be extremely metrically different from other *Homo* living at the same time. Therefore, their separate species designation is appropriate, and when included, their extreme cranial capacity values heavily increase the amount of variation observed throughout a large portion of the Pleistocene, especially considering that this study applies the moving window method for assessing variation. Including these specimens inflates the amount of variation demonstrated by high CV values for the moving windows they are captured in. In this case, it is not appropriate to include these specimens in the context of analyzing suggested speciation events, as they already demonstrate their uniqueness in morphology compared to other *Homo* specimens.

The dataset used in this study featuring information for each hominin specimen is displayed in appendix A of this work. A more comprehensive version of this dataset, including geographic and additional cranial capacity descriptions, is included in the supplementary material accompanying this text.

## Chapter 5: Methods

In this study, I use the compiled dataset of 156 specimens to assess cranial capacity variation for the genus *Homo*, beginning with 2.03 Ma (representing the earliest verifiable crania of Early Pleistocene *Homo* used in this study) until the more recent date of 12 Ka (representing the early Holocene). This study aims to gauge the variation of cranial capacity present in hominins throughout the Pleistocene era. Rather than assessing if cranial capacity increased or decreased throughout time for Pleistocene hominins, this study assesses whether variation for cranial capacity has increased or decreased throughout time in conjunction with suggested speciation events for Pleistocene *Homo*. The coefficient of variation (CV) of cranial capacity for hominin fossil crania is the measure of variation analyzed in this study.

### 5.1 Coefficient of Variation

The coefficient of variation is calculated by taking the standard deviation of a sample (or population) and dividing it by the mean, then multiplying that by 100, resulting in a percentage value. In this formula, $s$ represents the standard deviation of a sample, and $\bar{x}$ represents the mean of that sample.

$$CV = \frac{s}{\bar{x}} \cdot 100$$

The coefficient of variation is a measure of relative variation. Measures of relative variation are necessary to include when utilizing datasets that feature specimens of various sizes. When using absolute measures of variation, such as standard deviation, the strength of that analysis may be fundamentally weakened because the data has not been transformed into comparable terms (Fricker 2013). This is most important when comparing specimens with a wide range in body size (Plavcan and Cope 2001). Therefore, when assessing variation in terms of species recognition for a highly variable sample, it is essential to use relative measures of variation. For these reasons, and in this context, it is appropriate to use the coefficient of variation (CV) to assess cranial capacity variation in Pleistocene *Homo* throughout time. All CV values discussed in this study are expressed as percentages but may not have a percentage sign directly after.

## 5.2 Rolling Window Method

This research utilizes the statistical technique of establishing rolling windows throughout the dataset. Once the rolling windows are captured, the samples can have various functions applied to them. In this study, the coefficient of variation for cranial capacity is calculated for each window. The rolling window samples were coded, calculated, and analyzed using R statistical software, an open-source program that allows users to create customized formulas for statistical analysis (Crawley 2013). The R package “zoo” was used in the statistical code for this study to utilize rolling window commands within the program. This analysis utilizes an overlapping rolling window, where the sample is divided into specified window sizes (in this case 20), and the rolling CV is calculated for each window, sliding by each data point to incorporate the next 20 points, computing the CV for that window, and so on. Figure 1 below illustrates the rolling window process used in this study. Because the window size is set to 20, the number of output CV values obtained in this study is 137. However, in total, there are 156 separate data points in this study.

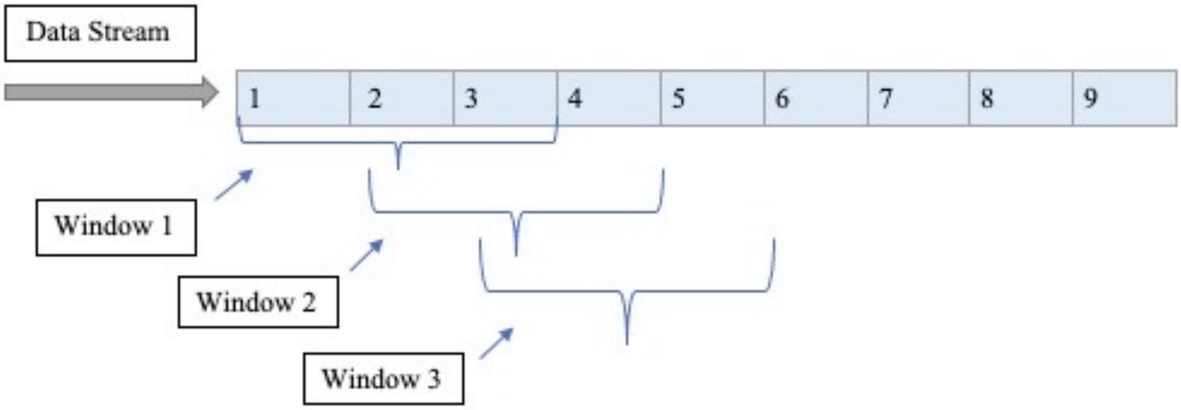

Figure 1. Rolling Window Process. Image created using Microsoft Word 2016.

When utilizing rolling averages and other measures using this technique, the window size should represent around 10 – 50% of the data points for an entire dataset (Hastie and Tibshirani 1987). To establish the rolling CV values of this dataset, a window size of 20 was used. Using the custom code created in R, the CV values for each rolling window were calculated. In addition to having the actual values available for analysis, the data was also plotted using R for a more robust interpretation and visual aid, with the coefficient of variation on the y-axis and relative date associated with each fossil on the x-axis (Crawley 2013). When plotting the data, the rolling average of fossil ages was computed using the window size of 20, which is the same size applied to the cranial capacity data.

Altering the window size does not significantly change the results. However, the nature of how the data is plotted when using large window sizes has a tendency to muddle or hide important breaks in the distribution of points on a graph (Fricker 2013). With more specimens, the first rolling window encompasses specimens ranging in age from 2.03 Ma to 800 Ka. With such a wide range in time, the temporal trends in the CV values are less noticeable, and this also makes it more challenging to analyze when decreases or increases in variation occurred

(Takezawa 2006). Using a smaller window allows for better visualization of the data, as well as a more robust interpretation. Utilizing rolling window functions can account for possible errors in dates and cranial capacity estimates embedded within datasets comprised of fossil material (Lee and Wolpoff 2003). The method is used as a data smoother for time series data to identify changes throughout a given dataset (Fricker 2013). As the purpose of this study is to search for possible speciation events, it is necessary to view the data with the added context of time, pinpointing when any changes occurred, and comparing these changes in the data to other evidence of speciation in the fossil record.

### 5.3 Data Analysis

In the context of merging statistical analysis and the fossil record, data visualization is an essential tool used by researchers in determining evidence for speciation (Baab 2008; Lee and Wolpoff 2003; Lee 2005; Plavcan and Cope 2001; Rightmire 2013; Scott 2014; Van Arsdale and Wolpoff 2013). The taxonomic argument relies on evidence of continuity or discontinuity made visible by graphing morphological data. If there is a break or noticeable difference in the distribution of data points on a graph, an assumption of discontinuity can be made. This is relevant when analyzing the distribution of data points to assess possible speciation throughout the fossil record, as evidence of a break in the data may offer further support for multiple species present in the dataset.

In addition to utilizing data visualization for this study, I also compare published CV values for cranial capacity for groups including modern humans, other living apes, and extinct hominins. By comparing the CV values of living primates and fossil groups with the values obtained in this study, a clearer parameter is set for how much variation is too much for one species. Instead of only comparing CV values of cranial capacity for modern humans with my dataset, utilizing multiple samples for comparison will establish more accurate criteria for expected CV values that represent more than one species. The CV values, along with the graphed data, allow for an interpretation of possible speciation events occurring throughout Pleistocene *Homo* by assessing cranial capacity variation in the entire sample.

The calculated values and graphs were analyzed and compared in the context of speciation events relevant to the validity for the taxonomic species of *H. rudolfensis*, *H. ergaster*, *H. heidelbergensis*, and *H. georgicus*. Other useful comparisons were made as well, such as the CV values of cranial capacity exhibited within chimpanzees, gorillas, orangutans, and modern humans, compared to this study's dataset.

# Chapter 6: Results

The CV values including the oldest specimens remains around 17% and peak sometime after 1.77 Ma at 21%, with this time period representing the most observed variation throughout the entire study. This time period includes the specimens from Dmanisi, Gona, Sangiran, ER 3733, and ER 1805. The average CV value between 1.77 – 1.25 Ma is 20, dropping to around 16 afterward. The rolling window periods for fossil specimens dated to 1.25 - 1 Ma show a steady decline in variation compared to earlier periods, with CVs starting at around 16, then moving to about 12.5 by 1 Ma. Between the period of 850 – 600 Ka, CVs peak at around 15.5, a 3-point difference from the period before. After this period, there is again a trend of decreasing variation in cranial capacity, with an average CV of 13.5 around 700 – 500 Ka. This decrease continues in the time series, with CV values of about 10 – 11.5 calculated for the periods of 500 – 250 Ka.

The decreasing trend in variation continues, reaching the lowest point with an average CV of 8, sometime between 250 – 130 Ka. After 130 Ka, CV values increase and average around 13 for the period of 150 – 100 Ka. Around 120 – 70 Ka, CV values reach an average of 15 for a short interval but then decrease shortly after and continue to do so. The least amount of variation present in the sample occurs between 60 – 40 Ka, with an average CV of 7 for that period. Around 40 Ka, and after, the CV values begin to increase very slightly, with an average of 8.5. Between 45 – 35 Ka, CV values remain stagnant for the most part, with values between 8 and 9. After 35 Ka, the CV values show a marked increase, reaching an average of 12 for the remainder of the periods, demonstrating more variation in cranial capacity (between 35 Ka and the youngest specimens dated to 12 Ka) than there was 20,000 years prior.

Table 1 provides all CV values calculated for the rolling window samples of hominin cranial capacity and age throughout the Pleistocene, taken from appendix A. The rolling window sample number is listed on the left, with the CV on the right. Readers should remember that because this study uses the rolling window method with a window size of 20, there are 137 calculated CV values for the entire dataset of 156 specimens. Additionally, the CV values have been plotted against time and are displayed in Figure 2 below. An analysis for the meaning of the fluctuating cranial variation present through time is offered in the section below as well.

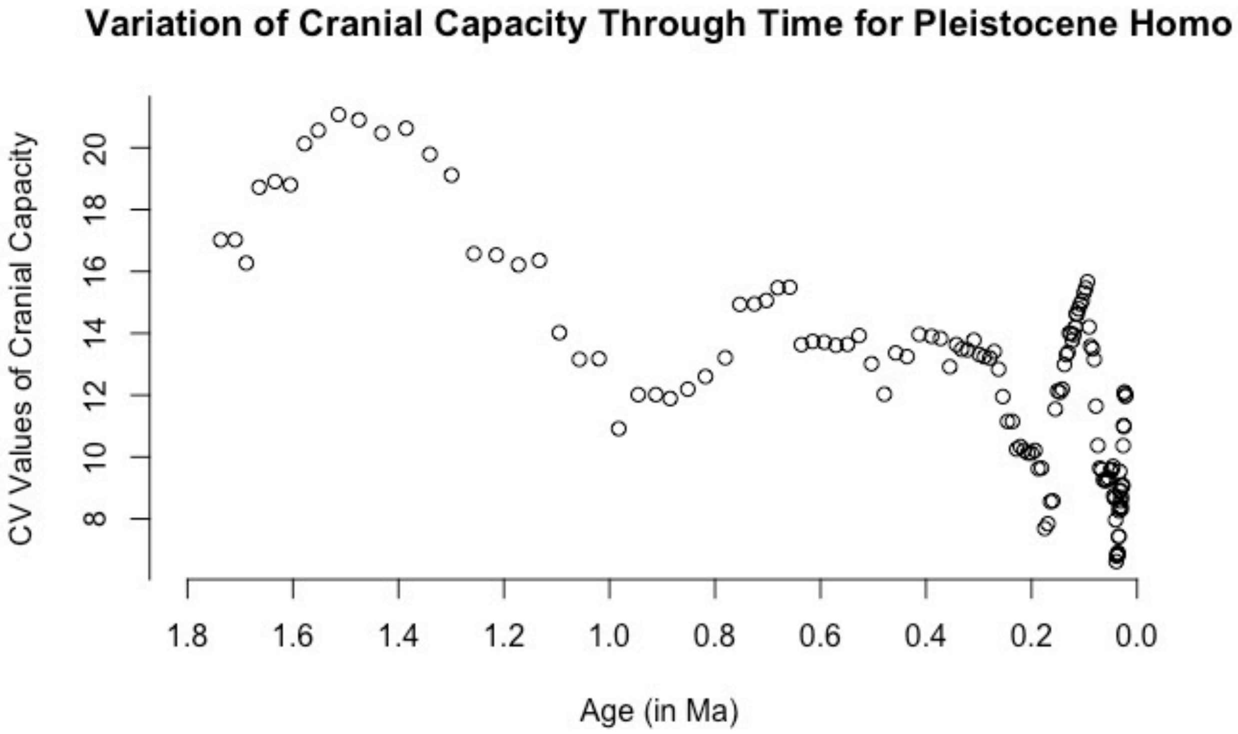

Figure 2. Scatterplot of calculated CV values of cranial capacity for rolling window samples of Pleistocene *Homo* specimens against time. Created using R Software for Mac 4.0.5 (https://www.r-project.org/). Original source code used in this study is listed in appendix B.

Table 1. Calculated CV values of cranial capacity for rolling window samples of Pleistocene *Homo* specimens.

| Sample | CV |
|---|---|
| | |
| 1 | 17.0170 |
| 2 | 17.0217 |
| 3 | 16.2703 |
| 4 | 18.7219 |
| 5 | 18.9052 |
| 6 | 18.8031 |
| 7 | 20.1312 |
| 8 | 20.5605 |
| 9 | 21.0731 |
| 10 | 20.9005 |
| 11 | 20.4759 |
| 12 | 20.6285 |
| 13 | 19.7913 |
| 14 | 19.1147 |
| 15 | 16.5756 |
| 16 | 16.5321 |
| 17 | 16.2130 |
| 18 | 16.3572 |
| 19 | 14.0191 |
| 20 | 13.1579 |
| 21 | 13.1763 |
| 22 | 10.9169 |
| 23 | 12.0153 |
| 24 | 12.0176 |
| 25 | 11.8903 |
| 26 | 12.1931 |
| 27 | 12.6018 |
| 28 | 13.2091 |
| 29 | 14.9343 |
| 30 | 14.9480 |
| 31 | 15.0608 |
| 32 | 15.4712 |
| 33 | 15.4889 |
| 34 | 13.6326 |
| 35 | 13.7381 |
| 36 | 13.7099 |
| 37 | 13.6104 |
| 38 | 13.6416 |
| 39 | 13.9275 |
| 40 | 13.0143 |
| 41 | 12.0307 |
| 42 | 13.3667 |
| 43 | 13.2469 |
| 44 | 13.9644 |
| 45 | 13.9031 |
| 46 | 13.8329 |
| 47 | 12.9180 |
| 48 | 13.6377 |
| 49 | 13.4835 |
| 50 | 13.4632 |
| 51 | 13.7796 |
| 52 | 13.3138 |
| 53 | 13.2452 |
| 54 | 13.2042 |
| 55 | 13.4107 |
| 56 | 12.8382 |
| 57 | 11.9519 |
| 58 | 11.1516 |
| 59 | 11.1508 |
| 60 | 10.2538 |
| 61 | 10.3381 |
| 62 | 10.2181 |
| 63 | 10.1287 |
| 64 | 10.1287 |
| 65 | 10.2123 |
| 66 | 9.6227 |
| 67 | 9.6419 |
| 68 | 7.6902 |
| 69 | 7.8411 |
| 70 | 8.5572 |
| 71 | 8.5828 |
| 72 | 11.5486 |
| 73 | 12.1371 |
| 74 | 12.0931 |
| 75 | 12.1943 |
| 76 | 12.9887 |
| 77 | 13.3081 |
| 78 | 13.3826 |
| 79 | 14.0098 |
| 80 | 13.9878 |
| 81 | 13.7723 |
| 82 | 13.9527 |
| 83 | 14.1970 |
| 84 | 14.6337 |
| 85 | 14.6100 |
| 86 | 14.7917 |
| 87 | 14.9481 |
| 88 | 15.0581 |
| 89 | 15.3136 |
| 90 | 15.4630 |
| 91 | 15.6669 |
| 92 | 14.2038 |
| 93 | 13.5844 |
| 94 | 13.4947 |
| 95 | 13.1547 |
| 96 | 11.6443 |
| 97 | 10.3702 |
| 98 | 9.6408 |
| 99 | 9.5833 |
| 100 | 9.2597 |
| 101 | 9.2376 |
| 102 | 9.2463 |
| 103 | 9.3162 |
| 104 | 9.5617 |
| 105 | 9.5923 |
| 106 | 9.6990 |
| 107 | 8.7517 |
| 108 | 8.6674 |
| 109 | 8.6828 |
| 110 | 7.9654 |
| 111 | 6.6192 |
| 112 | 6.7924 |
| 113 | 6.8487 |
| 114 | 6.9125 |
| 115 | 6.8375 |
| 116 | 7.4221 |
| 117 | 7.4411 |
| 118 | 8.2597 |
| 119 | 8.3542 |
| 120 | 9.5343 |
| 121 | 8.9189 |
| 122 | 8.9185 |
| 123 | 8.8876 |
| 124 | 8.5731 |
| 125 | 8.4090 |
| 126 | 8.3103 |
| 127 | 8.6880 |
| 128 | 9.0937 |
| 129 | 9.0572 |
| 130 | 9.0847 |
| 131 | 10.3663 |
| 132 | 11.0207 |
| 133 | 10.9814 |
| 134 | 12.0862 |
| 135 | 12.0846 |
| 136 | 11.9636 |
| 137 | 11.9924 |

# Chapter 7: Discussion

The nature of this study (implementing the rolling window method) does not permit one to identify exact dates when variation of cranial capacity changes occurred compared to previous periods, but instead offers estimations of when these changes occurred made apparent by the computed CV for each window. The fluctuations of variation for this morphological trait are then compared to the timing of suggested speciation events. The variation is also interpreted with the added context of what specimens are included in each window sample and how this might affect the amount of variation displayed.

Table 2 represents other published CV values for fossil hominin groups, living apes, and modern humans for comparison with this study's results. The fluctuations, either noticeable decreases or increases in variation occurring throughout the sample, provide insight into how the changes relate to time and speciation events in *Homo*. By comparing CV values from rolling window samples of the current study, and with previously published CV values for fossil hominins and apes from other studies, a robust interpretation of cranial capacity variation throughout our genus is discussed in the following sections and paragraphs.

In search of conservative parameters for comparison, other published CV values for cranial capacity which separate the various suggested species designations of Pleistocene *Homo* were used. For example, the CV for just *H. habilis* cranial capacity is 10.3, and the CV for *H. habilis* and *H. rudolfensis* combined is 14.7 (Booth 2010). In addition, CV values of cranial capacity for *H. erectus* (including only Asian specimens) is 13.1, and the CV values for *H. erectus* and *H. ergaster* combined is 14.9 (Guimaraes and Merino 2015). For these reasons, I interpret this study’s findings using the maximum CV value of 15 as a threshold of acceptable cranial capacity variation exhibited within a single species of *Homo*.

Table 2. Published CV values of cranial capacity for hominins and living apes for comparison.

| Group/ Species | CV of CC | Source |
|---|---|---|
| | | |
| Hominins | | |
| *Australopithecus africanus* | 7.7 | Henneberg and Thackeray 1995 |
| *Australopithecus africanus + Australopithecus afarensis* | 8.4 | Henneberg and Thackeray 1995 |
| *Paranthropus boisei* | 5.4 | Guimaraes and Merino 2015 |
| All australopiths (gracile and robust) | 11.6 | Henneberg and Thackeray 1995 |
| *Homo habilis (*with *H. rudolfensis)* | 14.7 | Booth 2010 |
| *Homo habilis (*without *H. rudolfensis)* | 10.3 | Booth 2010 |
| *Homo rudolfensis* | 5.5 | Booth 2010 |
| *Homo ergaster* | 15 | Guimaraes and Merino 2015 |
| *Homo georgicus* | 13.1 | Guimaraes and Merino 2015 |
| *Homo erectus* (Asia only) | 13.1 | Guimaraes and Merino 2015 |
| *Homo erectus + Homo ergaster* | 14.9 | Guimaraes and Merino 2015 |
| *Homo neanderthalensis* | 12.8 | Guimaraes and Merino 2015 |
| | | |
| Living Primates | | |
| | | |
| *Pan troglodytes* | 10.5 | Booth 2010 (Powell-Cotton & Rothchild Museums Collections) |
| *Gorilla gorilla* | 13 | Booth 2010 |
| *Pongo pygmaeus* | 11 | Booth 2010 |
| *Homo sapiens* (global) | 11.6 | Henneberg and Thackeray 1995 |
| | | |
| *Paranthropus boisei + Homo habilis sensu lato + Homo ergaster + Homo georgicus* | 20 | Guimaraes and Merino 2015 |

The CV values for cranial capacity reported in this study never get as low as the values reported for australopiths, which average around 5% (Lieberman 2011). For example, the CV of cranial capacity for *Paranthropus boisei* is 5.4% (Table 2; Guimaraes and Merino 2015). The combined CV for cranial capacity of all australopiths calculated by Henneberg and Thackeray (1995) is 11.6, the same as the global modern human value. The combined CV for all specimens used in this study is 25.1. Therefore, Pleistocene *Homo* is more morphologically variable in cranial capacity than gracile and robust australopiths combined, with a CV value that is more than doubled comparatively. This provides evidence of high cranial capacity variation among Pleistocene *Homo* as an entire genus compared to *Australopithecus*, which is the most probable ancestral genus to *Homo*.

## 7.1 Early Pleistocene

As mentioned earlier, the highest variation exhibited throughout the sample occurs sometime between 1.77 – 1.25 Ma, where CV values reach a peak of 21%. The earlier samples also show high variation with CV values around 17 – 18.5%. Interestingly, the period with the highest CV includes specimens with various species designations such as *H. georgicus*, *H. erectus*, *H. ergaster*, and *H. habilis*. The specimens listed in this period were found in various geographic locations, covering western Eurasia, southeast Asia, and Africa. Specimens featured in this period are those from Koobi Fora, Gongwangling, Georgia, and the Olduvai Gorge (Antón 2003; Zhu et al. 2015). The amount of variation demonstrated for this period makes sense under the pretense that these specimens truly do belong to at least more than one species, as the CV values for this period are the highest observed in this study. However, further analysis will have to be performed in order to ascertain just how many species are present.

The most probable explanation is that if there are multiple species present, there is more evidence for those multiple species to be *H. georgicus* and/ or *H. ergaster*, rather than *H. rudolfensis*. As the specimens associated with *H. georgicus* and *H. ergaster* have multiple attributable crania included in this study. This is in contrast to *H. rudolfensis*, which is only represented by one skull, ER-1470, and dated to 2.03 Ma (McDougall et al. 2012; Ponce de León et al. 2021). The timing of the peak CV value, which occurs after *H. rudolfensis* is phased out of the rolling window samples, coincides with this interpretation. It is also possible that *H. rudolfensis* is a valid species, separate from *Homo habilis*, and is responsible for contributing to the CV values of 17 early on in this study, which is still higher than CV values reported for any living ape or modern humans. However, because the CV values peak sometime after 1.77 Ma, once the fossil specimens from Dmanisi and those deemed *H. ergaster* are included, the case for *H. georgicus* and *H. ergaster* is stronger. At the very least, this analysis provides further evidence of speciation at this time, instead of the alternative explanation that the specimens of this period all belong to a single lineage.

## 7.2 Early to Middle Pleistocene

This period also includes a high amount of variation, reaching a peak CV of about 15.5 sometime around 850 – 600 Ka, followed by a slight decrease in CV values afterward with an average of 13.5 by 600 Ka. This is higher than values reported for other living apes, with gorillas the most variable with a CV of 13 for cranial capacity. The amount of variation for this period also provides further evidence that more than one *Homo* species may have been present during this period. This time period coincides with the appearance of *Homo heidelbergensis*, which some paleoanthropologists believe to be a transitional species between *H. erectus* and *H. sapiens*, as well as the possible ancestral species to *H. neanderthalensis*. More information about *Homo heidelbergensis* is provided earlier in the text. Towards the end of this period, CV values remain around 13.5% and continue to drop with CV values around 500 Ka averaging at 12%, eventually reaching values of around 8% by 250 Ka.

The specimens included in this sample are the Ceprano cranium from Italy, which had a separate taxonomic status suggested by Mallegni and colleagues (2003), and the recently discovered specimen known as Gombore 2 from Ethiopia (Profico et al. 2016). This period also features *H. erectus* specimens from both the Sangiran dome and Zhoukoudian cave. Although the Sangiran and Zhoukoudian *H. erectus* samples are all from Asia and are similar in age, the crania from Java are smaller and slightly morphologically different than those from China (Antón 2003; Indriati et al. 2011). As the results demonstrate moderate variation of cranial capacity, it is possible that the taxonomic status of *H. heidelbergensis*, separate from *H. erectus*, is valid.

Further evidence is provided by the timing of the observed CV values increasing to 15.5%, as this occurs earlier on in this period when a mixture of *H. erectus* fossils and possible *H. heidelbergensis* fossils are included for analysis. The CV values of this period are slightly above 15%, compared to the CV value of 14.9% for samples comprised of *H. erectus* and *H. ergaster*, and *Homo ergaster* at 15% (Guimaraes and Merino 2015). This could imply that there is more than one species present in this period. However, because this period also matches variation seen in specific fossil groups, it could simply mean that there are high amounts of cranial capacity variation for Pleistocene *Homo* regardless of species designation.

## 7.3 Middle to Late Pleistocene

The period between 500 – 250 Ka saw a stasis of CV values ranging from around 10 to 11.5 until steadily decreasing sometime after 250 Ka. A majority of the specimens included during this period are *H. erectus*, with the exception of the Atapuerca sample from Spain, which has had its own species designation proposed by researchers who initially studied the remains, known as *Homo antecessor* (Bermúdez de Castro et al. 1997). The cranial morphology from fossils found at Atapuerca was thought to be more primitive than other archaic hominins from the same period, but the cranial capacity for the skulls was larger than other contemporary hominins. Although there may be more than one species present in this sample, if one were to accept *H. antecessor* as a species, there is still less variation in cranial capacity than in modern humans and gorillas. This period also includes *H. heidelbergensis* specimens. Earlier periods show much higher variation when still including *H. heidelbergensis* fossils; however, sometime after 500 Ka, variation decreases. This may weaken evidence for *H. heidelbergensis* as a separate species considering the values are not consistently high throughout the existence of this group. This period mirrors CV values reported for a chimpanzee sample of cranial capacity data, at 10.5%, as well as the orangutan CV of cranial capacity at 11%. Results from this period do not provide sufficient evidence to invoke a multiple species explanation for the *Homo* fossils of this time.

With an average CV value of about 8, the low amount of variation occurring around 250 – 130 Ka is interesting, as this time period includes specimens from both *H. neanderthalensis* and the oldest known *H. sapiens*, as well as specimens belonging to “archaic” *H. sapiens* and *H. heidelbergensis* (Athreya and Wu 2017; Harvati et al. 2019; Martinón-Torres et al. 2017;

Mounier et al. 2016). It also includes some *Homo erectus* specimens. Some specimens from this period have had their taxonomic place in the lineage consistently questioned and analyzed. For example, the Narmada cranium from India, the Biache specimen from France, and the almost complete skeleton from China known as Jinniushan 1 are included in this period. These fossils, among others such as Maba 1 (also included in this period), have been subjected to various morphometric and cladistic analyses in attempts of securing a solid designation within our genus (Athreya 2007; Cameron et al. 2004; Kaifu 2017; Rougier 2003; Wu and Bruner 2016; Xiao et al. 2014). Researchers still have reached a consensus for the placement of these fossils despite various analyses using different methodologies.

The results demonstrate that the sample shows less variation of cranial capacity than the global modern human sample. The CV value of 8 is also lower than the CV values recorded for distinct samples of *H. habilis*, *H. ergaster*, *H. erectus*, and *H. georgicus*. The CV values of this period are lower than those reported for single populations of chimpanzees, gorillas, orangutans, and modern humans despite the geographic dispersal of the fossils accounted for in this time frame. This possibly lends evidence to the argument that Neandertals and humans should be considered one species, represented by subspecies designations instead. This interpretation is corroborated by recent studies comparing ancient genomes of both groups, leading to the revelation that these groups did produce offspring with one another on more than one occasion (Curnoe and Thorne 2003; Dannemann and Racimo 2018). Other recent research provides additional evidence of genetic admixture between “archaic” humans and modern humans in Africa (Wall et al. 2019).

These revelations contradict the very classical concept of what constitutes a species, lending further evidence into the complex processes and history of human evolution (Marks

2005). Additionally, other hominin species known from very few fossil remains also existed during this time, such as the Denisovans. It is possible that the specimens with uncertain species designations from this time are hybrids, or descendants of hybrids from these groups, or even belong to a subspecies not yet described in scientific publications (Glantz et al. 2009; Kaifu 2017). This might be the reason that the specimens from this period appear to have less cranial capacity variation than other periods and in modern times, especially considering the geographic range that these specimens once inhabited.

## 7.4 Late Pleistocene

In contrast with the previous period, featuring *H. sapiens*, *H. neanderthalensis*, and those attributed to *H. heidelbergensis* or "archaic" *H. sapiens*, the CV values are higher for the specimens dated to 120 – 70 Ka. However, the variation exhibited throughout this period is not as high as other periods, with CV values reaching 15. This could be explained by the presence of multiple taxa as well. This period includes specimens such as those from Ngandong, which are among the most recent *Homo erectus* specimens in the fossil record, living around ~113 Ka (Baab 2011; Kaifu et al. 2011; Rizal et al. 2019). Other specimens within this group include mostly Neandertals and a few *H. sapiens*. The cranial capacity variation present in this sample is higher than modern values for living apes and humans, reinforcing the concept of multiple species present throughout this time. The cranial capacity variation exhibited within this period could be due to the late presence of *H. erectus* combined with the larger values reported for Neandertals. This scenario provides further evidence that the genus *Homo* is not comprised of one single evolving lineage in the Late Pleistocene.

The period of around 60 – 40 Ka, reporting an average CV of about 7, displays the least amount of variation for cranial capacity of the genus *Homo* reported in this study. The variation of cranial capacity in this period is much lower than that for a global sample of modern humans, with an average CV of 11.6. This period also features primarily Neandertals, with just a few *H. sapiens* specimens. Even with the presence of multiple species in the sample, there is still less variation than all other periods. This can possibly be explained by the overlap in cranial capacity for specimens of this time, rather than understanding the lack of variation as evidence of only one species present. It is worth noting that Neandertals had, on average, large cranial capacities compared to their *H. sapiens* counterparts (Ogihara et al. 2018). Notably, humans living before 10 Ka, on average, had larger cranial capacities compared to their modern-day counterparts (Hawks 2011). Perhaps, for these reasons, the amount of variation remained low for this period, even if one considers Neandertals and *H. sapiens* separate species.

It is worth noting that the period of 250 – 130 Ka demonstrated similar variation with this period and featured both Neandertals and *H. sapiens* within the sample. This correlation could be tied to previous assumptions and efforts that assume these groups are related subspecies rather than entirely separate entities (Curnoe and Thorne 2003; Kaifu 2017; Mounier et al. 2016). A recent study has shown that Neandertal DNA contributed to modern human cranial and brain morphology (Gregory et al. 2017). Another study reports that an archaic *Homo* lineage passed down an adaptive allele for brain size to modern human populations (Evans et al. 2006). With the evidence of low variation occurring in both samples, it is possible that genetic admixture between groups contributed to similar cranial capacity values. Considering that a previous study obtained a CV of 12.8 for the cranial capacity of Neandertals (Guimaraes and Merino 2015), the current results of this study featuring primarily Neandertal specimens demonstrate even less variation, with an average of 7%. Regardless of these comparisons, it is appropriate to infer that Late Pleistocene *Homo* had relatively low cranial capacity variation despite geography and the possibility of multiple taxa throughout the sample.

## 7.5 Late Pleistocene and Into the Holocene

For the duration of the sample, the CV values resemble modern human CV values for cranial capacity, with an average of about 12% by 35 Ka, which continues until the last rolling windows featuring the most recent specimens dated to 12 Ka. As mentioned earlier, the modern human CV value for a global sample of cranial capacity is 11.6 (Henneberg and Thackeray 1995). The period of 35 – 12 Ka analyzed in this study includes primarily *H. sapiens* fossils, featuring specimens from Europe, Africa, and Asia. Some researchers have noticed a trend of decreasing cranial capacity in modern humans beginning around the onset of the Holocene, aligning with the arrival of agricultural practices (Henneberg 1988; Hawks 2011). Even with a decrease in average cranial capacity for modern humans occurring sometime around the onset of the Holocene, this study demonstrates that the amount of variation exhibited within our species of recent times remained virtually the same as the amount of variation present within our species 30,000 years ago.

# Chapter 8: Conclusion

The results of this study are not equipped to identify exactly which species and how many were present at any given time, but with the context of previous work done in the subject and identifying trends in the CV values throughout time, some interpretations can be made. The most convincing evidence for speciation provided in this study coincides with suggested speciation events for Pleistocene *Homo* made by other researchers, sometime between 2 – 1 Ma (Kidder and Durband 2000; 2004; Stringer 1984; Rightmire 2008; Wood 1984). This interpretation would support the existence of multiple species of early *Homo* and based on the timing of when changes in variation occurred, there is evidence to support the validity of either *H. georgicus* or *H. ergaster* as separate from *H. erectus*. It is also possible that both groups may be distinct species in their own right. Other evidence of speciation is offered later in the time series at around 850 Ka, aligning with the appearance of fossils deemed *H. heidelbergensis*, although not as compelling as earlier periods analyzed in this work. Middle Pleistocene *Homo* demonstrated low amounts of cranial capacity variation, with CV values for mixed samples of *H. sapiens* and Neandertals much lower than modern human or ape values. This study has also offered insight into how past populations of humans compare to modern humans and apes regarding cranial capacity variation.

Because the scope of this study is limited to making definitive claims for multiple species, the most conservative takeaway is that the amount of cranial capacity variation exhibited within the first million years of our genus is higher than any known variation represented in living apes or modern humans. The cranial capacity variation within the first million years of our genus is also higher than CV values computed for distinct species of *Homo*, such as *Homo* *ergaster* with a CV of 15. The entire dataset yields a CV of 25.1, providing evidence that *Homo* is a highly variable genus compared to other hominin groups, such as *Australopithecus*.

Perhaps some variation of cranial capacity in *Homo* can be explained by the wide geographical range of specimens, as australopiths are only known from Africa. Geography and climate can account for some degree of variation for this trait (as discussed earlier in this paper). Still, it is very unlikely that it accounts for more than a two-fold difference in variation. For modern humans, cranial capacity variation deriving from geography and climate only accounted for less than 30% of the observed variation (Henneberg 1990), so a CV of 25.1 for *Homo*, compared to a CV of 11.6 for gracile and robust australopiths, cannot be explained solely by environmental differences of geography and climate. Figure 3 featured below is a map demonstrating the dispersal of hominin fossil finds attributed to *Homo* used in this study.

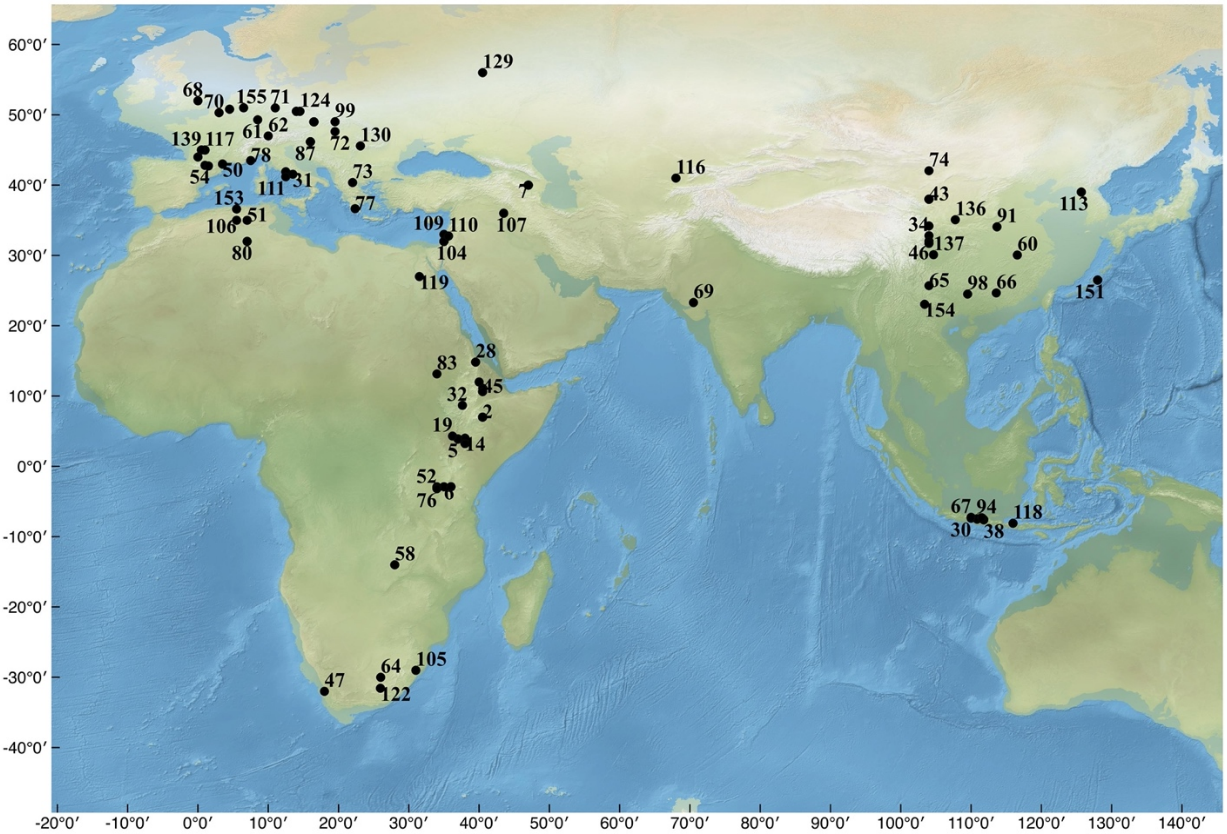

Figure 3. Map of Pleistocene *Homo* fossil sites used in this study. The fossil sites are numbered the same as those that appear in appendix A of this work. The pigmented shade around the current coastline reflects land coverage during the Last Glacial Maximum when sea levels were about 120 meters lower compared to modern levels (Khan et al. 2019). Hominin dispersals and habitation may have occurred in areas that are now covered by water. This map was created using QGIS Software 3.16.4 (https://qgis.org).

The initial CV values of 17 – 18.5% demonstrate that there is significant variation in cranial capacity among the earliest members of the genus. The peak CV value of 21 appearing a little later in the sample may indicate when and with what specimens the highest variation can be attributed. Because the highest variation occurs within samples comprised of the Dmanisi fossils and those designated to *H. ergaster* and then decreases when these specimens are no longer included within rolling window samples, either one may be a valid species distinct from *H. erectus*. Alternatively, it could also mean that both are valid species of Pleistocene *Homo*.

Therefore, the best evidence for multiple species using CV values of cranial capacity exists within this time period. This interpretation coincides with the multiple species' designations attributed to the specimens of this time period as well. They include *H. habilis*, *H. georgicus*, *H. ergaster*, and *H. erectus*. However, it is difficult to ascertain just how many possible species there are for this period.

Other possible evidence of speciation from this analysis occurs sometime around 850 – 600 Ka, and the increased variation of cranial capacity compared to other periods may offer further support to the distinct taxonomic designation of *H. heidelbergensis*. As the sample includes fossils from both *H. erectus* and *H. heidelbergensis*, the rise in variation could be explained by the presence of multiple species. Because the observed CV values begin to steadily decrease after this period, as the oldest *H. heidelbergensis* fossils are phased out with each new rolling window, it could be possible that the increase of this period correlates to the speciation event associated with *H. heidelbergensis*. Although, the decrease in variation continues after 500 Ka, when some of the more recent *H. heidelbergensis* fossils are still included. However, because the CV values of the Middle Pleistocene are only slightly higher than those reported for strict taxonomic fossil groups of *Homo*, this period does not provide the most convincing evidence of speciation studied in this analysis.

Around 500 – 250 Ka, CV values remain stagnant for the most part, around 10 – 11.5. This is still an interesting observation as the sample included specimens from *H. erectus* and another proposed species, *Homo antecessor*. However, the variation of this period is less than that of modern humans and is within the CV values for chimpanzees and orangutans, possibly providing evidence that there was only one species present at this time. This period also weakens earlier evidence regarding *H. heidelbergensis* speciation, with variation high initially and decreasing by 500 Ka. The period of 250 – 130 Ka featuring the least amount of variation for cranial capacity could mean the sample is comprised of subspecies rather than separate and distinct categories. With CV values closer to those recorded for a sample of modern humans from Europe, with a CV of 10.2 for cranial capacity (Booth 2010; Macdonell 1906), as opposed to a geographically diverse sample, it is apparent that specimens of this time had significant overlap in cranial size, despite belonging to various regions and possibly different taxa.

The cranial capacity variation for *Homo* of the Late Pleistocene maintained relatively similar CV values compared to the Middle Pleistocene, with the exception of an observed increase sometime around 120 Ka. During that time, there was a population of *H. erectus* in Java with smaller cranial capacities compared to other specimens from that time, such as Qafzeh 9 and Xuchang 1. Xuchang 1 has one of the largest cranial capacity estimates in the sample, at 1800 $cm^3$ (Li et al. 2017). The fossil also exhibits a mosaic cranial morphological pattern, with similarities and differences compared to Neandertals and *H. sapiens* (Trinkaus and Wu 2017). The variation observed from specimens dated to 120 – 70 Ka may come from combining *H. erectus* cranial capacities with Neandertal and *H. sapiens* cranial capacities. For these reasons, there is not substantial evidence to claim further speciation within this time period, as *H. erectus* as a distinct species separate from *H. sapiens* and Neandertals has been substantiated by numerous other studies (Antón et al. 2007; Baab 2015; Bokelmann et al. 2019; Bräuer et al. 1997; Martinón-Torres et al. 2017). The Ngandong *Homo erectus* fossils from Java most likely represent a late surviving population of hominins, which are an unlikely group to have contributed to the origins of modern human populations (Bräuer 2008; Frayer et al. 1993; Kaifu et al. 2008; 2015).

Another interesting discovery from this study also lies with the revelation that variation of cranial capacity for samples comprised of Neandertals and humans is less than the variation exhibited in modern humans of recent date. This occurred twice within the periods of about 250 – 130 Ka (which included *Homo erectus* specimens as well) and again around 60 – 40 Ka. For the period of 60 – 40 Ka, featuring mostly Neandertals, the variation of this period is still significantly lower than previously published CV values for a strictly Neandertal sample despite the possibility of multiple taxa present. The last rolling window samples from 35 – 12 Ka demonstrated almost identical CV values of cranial capacity for modern humans globally, with an average of around 12 compared to the modern value of 11.6. This period included all *Homo sapiens* specimens, which provides a basis to make comparisons between archaic and modern human cranial capacity variation.

## 8.1 Limitations

As mentioned earlier, this study also yields some limitations on eliminating cranial capacity variation introduced by variables other than speciation. The fossil record is extremely fragmented, both in theory and in physical reality. The fossilization process often does not preserve entire skeletons, making it difficult to ascertain sex for fossil hominins in most cases. Postcranial material is rare for hominin fossils, and even with these materials available for analysis, researchers still experience uncertainty for assigning sex to remains (Bello et al., 2006; Rosenberg et al. 2006). One explanation for a highly variable cranial sample of Pleistocene *Homo* is that there is a high degree of sexual dimorphism within the genus, especially amongst early members. Assigning sex to fossil remains may allow for comparison among probable male and probable female skulls in terms of cranial capacity variation. However, this avenue of research is problematic for a variety of reasons.

One reason is that researchers have not reached a consensus on exactly how dimorphic extinct *Homo* groups were (Bilsborough 2005; Kidder and Durband 2004; Rightmire et al. 2006; Ruff 2002). Another reason is that there is no ability on the researcher's part to remedy an uncertain sex assessment when the material simply does not exist unless they were to increase excavations in hopes of finding more fossil material to match a specimen. For these reasons, it is impossible to definitively determine the amount of variation for cranial capacity due to sexual dimorphism within our genus. However, the most appropriate choice for comparison would be modern measurements of *H. sapiens* separated by sex. But even then, it still does not address the uncertainty that comprises the hominin fossil record.

Another limitation of this study is based on the widespread geographic range that fossils belonging to our genus exist on. Modern humans are able to live and do live in all kinds of extreme and temperate environments around the world. Other *Homo* did too, ranging in habitats that span Europe, Asia, and Africa. Geography and climate do have some effect on body size, and therefore brain size (Ruff et al. 1997). For these reasons, it is challenging to gauge how much cranial capacity variation can be accounted for due to climate rather than speciation. The only comparable sample to assess cranial capacity variation in terms of geography is found in studies measuring modern human groups across various regions. However, no other living ape has such a range in environment, limiting the number of comparisons researchers can make.

Although immense efforts were made to reduce any possible error associated with fossil specimen data, the dataset is still not perfect. For example, the reliability of virtual reconstructions of endocasts has proven to yield more accurate measurements compared to various seed and gunshot techniques (Dumoncel et al. 2020; Neubauer et al. 2012; Ogihara et al. 2018; Ponce de León et al. 2021). However, only some virtual endocasts exist for the hominin fossil record. This led to using cranial capacity data obtained from other methods such as millet seeds and water displacement. If I were to exclude specimens without an accompanying virtual endocast, the dataset of this study would dwindle from 156 specimens to about half that. With a smaller dataset, it becomes even more challenging to make informed interpretations regarding the morphological variation of paleospecies.

Despite these limitations, this study has offered valuable information regarding paleospecies cranial variation across time. Lacking a basis to make informed interpretations regarding expected cranial variation within paleospecies has been one drawback to this field of study (Plavcan and Cope 2001; Rightmire 2008; Smaers et al. 2021; Tattersall 1986). The current study provides a starting point for more detailed and robust applications assessing variation in Pleistocene *Homo* by establishing an updated database with descriptive information for fossil hominins included within our genus.

## 8.2 Future Directions

Future work into this subject holds the possibility of providing researchers with stronger criteria to assess morphological variation within paleospecies. One avenue to do this would be to perform CT scans of fossil skulls that have not yet had the chance to undergo such imaging techniques. The implementation of MRI and CT imaging techniques has allowed paleoanthropologists to reconstruct fossil skulls virtually, allowing for more accurate measurements of brain size, brain shape, and ontogenetic processes of hominin brains (Bruner

2007; Grimaud-Hervé et al. 2020; Indriati and Antón 2010; Kubo et al. 2008; Melchionna et al. 2020). Earlier reports from paleoanthropologists of the 19th century and going into the 20th century featured some metric descriptions of fossil material but often did not follow a standardized methodology (Hrdlička 1930; Wolpoff et al. 2006; Wu and Poirier 1995). This leads to uncertainty for how such measurements were obtained, and in the case of cranial capacity, the methodology is important. For this study, many fossil specimens were excluded from the database as the measurements associated with the specimen were unable to be verified in past publications.

By incorporating CT imaging and creating virtual endocasts, fossil material can be assessed in standardized terms, reducing room for error (Dumoncel et al. 2020). This technology also allows for more precise measurements of cranial landmarks for morphometric comparisons (Bruner 2017). The field of geometric morphometrics has enabled researchers to compare fossil skulls, among many other parts of the body, to one another in a more meaningful manner (Bruner 2015). Cranial landmarks are calculated using various software and 3D imaging technology, and skulls can be compared based on shape and layout, with the problem of scaling accounted for. The past few decades have seen a concerted effort to create virtual endocasts of fossil skulls in the field of anthropology (Falk et al. 2005; Gunz et al. 2009; Neubauer et al. 2018a; Ogihara et al. 2018; Wu and Yan 2020; Zhang et al. 2015). Hopefully, along with continued efforts to provide fossil sites with reliable dates, future revisions to the hominin fossil record will provide more accurate parameters to assess and analyze variation within paleospecies.

Assessing cranial variation within living primates can also aid researchers in studying expected amounts of variation for paleospecies. Although there has been work done which calculated CV values for cranial capacity for chimpanzees, gorillas, and orangutans, other primate cranial diversity should be investigated as well (Falk 2015; Preuss 2017; Strait and Grine 2004). Obtaining CV values for other primate species will establish a larger database for comparison against the fossil record overall. However, this also has fundamental problems as other living primates around the world are not our closest living ancestors like chimpanzees are. However, orangutans and gorillas are closer to us genetically than other primates (Cartmill and Smith 2009). Therefore, trying to compare primate cranial variation against hominin variation may not yield any new information for the hominin fossil record but may offer insight into the present variation of biological species in general.

Regardless of this, the problem of methodology again rears its head with the comparable datasets that are available for other living ape species. Just as the case for fossil skulls, efforts to establish a virtual endocast database for living primates may prove to be more accurate in obtaining standardized measurements than previous methods. I also hope to see revised research featuring the HOMDAT file or those using De Miguel and Henneberg's dataset of hominin cranial capacity from their 2001 study. As mentioned previously, the validity of some ages and cranial capacity estimations for specimens have been challenged, altering the accuracy of these datasets, along with the accuracy of their results. Some examples include the studies done by Ash and Gallup (2007) and Bailey and Geary (2009), adapted from De Miguel and Henneberg's data. Within both datasets, the researchers included duplicates of fossil specimens, and age estimates that were inaccurate (in one case by 1 million years), and cranial capacity estimations taken from fragmented and unrestored skulls, contributing to a possible inaccuracy of results.

In the near future, I hope to publish this study in an academic journal so that other researchers may access the database of cranial capacity for Pleistocene *Homo* specimens established in this study. If nothing else, having a repository of fossil hominin information with attributable bibliographical sources is a useful resource for the scientific community and those interested in the morphological variation of hominins.

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# Appendix A: Pleistocene *Homo* Cranial Capacity and Age Dataset

| # | Fossil Name | Age (Ma) | CC ($cm^3$) | Taxon | Dating Method | Date Source | Cranial Capacity Estimation Method | Estimation Source |
|---|---|---|---|---|---|---|---|---|
| 1 | ER 1470 | 2.03 | 752 | hh, hrud | Combined radiometric dating | McDougall et al. 2012 | Virtual endocast by CT | Ponce de León et al. 2021 |
| 2 | Omo L894-1 | 1.89 | 500 | hh | Combined radiometric dating | Cartmill and Smith 2009 | Preliminary estimation using outer measurements | Boaz and Howell 1977 |
| 3 | ER 3732 | 1.89 | 775 | hh | Combined radiometric dating | Cartmill and Smith 2009 | Endocast and water displacement | Holloway et al. 2004 |
| 4 | OH 24 | 1.87 | 597 | hh | Combined radiometric dating | Cartmill and Smith 2009 | Endocast and water displacement | Holloway et al. 2004 |
| 5 | ER 1590 | 1.85 | 825 | hh | Combined radiometric dating | Cartmill and Smith 2009 | Endocast and water displacement | Holloway et al. 2004 |
| 6 | OH 7 | 1.81 | 681 | hh | Combined radiometric dating | Cartmill and Smith 2009 | Partial endocast and water displacement | Holloway et al. 2004 |
| 7 | Dmansi D2280 | 1.77 | 730 | he, hg | Argon-Argon and paleomagnetism | Ferring et al. 2011 | Virtual endocast by CT | Ponce de León et al. 2021 |
| 8 | Dmansi D2282 | 1.77 | 650 | he, hg | Argon-Argon and paleomagnetism | Ferring et al. 2011 | Outer measurements | Lordkipanidze et al. 2007 |
| 9 | Dmansi D2700 | 1.77 | 601 | he, hg | Argon-Argon and paleomagnetism | Ferring et al. 2011 | Virtual endocast by CT | Ponce de León et al. 2021 |
| 10 | Dmansi D3444 | 1.77 | 641 | he, hg | Argon-Argon and paleomagnetism | Ferring et al. 2011 | Virtual endocast by CT | Ponce de León et al. 2021 |
| 11 | Dmansi D4500 | 1.77 | 546 | he, hg | Argon-Argon and | Ferring et al. 2011 | Virtual endocast by CT | Ponce de León et al. 2021 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | paleomagnetism | | | |
| 12 | ER 1805 | 1.75 | 582 | hh | Revised stratigraphy and combined radiometric dating | McDougall et al. 2012 | Endocast and water displacement | Holloway et al. 2004 |
| 13 | OH 16 | 1.66 | 638 | hh | Combined radiometric dating | Cartmill and Smith 2009 | Partial endocast and water displacement | Holloway et al. 2004 |
| 14 | ER 1813 | 1.65 | 509 | hh | Revised stratigraphy and combined radiometric dating | McDougall and Brown 2006 | Endocast and water displacement | Holloway et al. 2004 |
| 15 | ER 3733 | 1.65 | 866 | he, herg | Revised stratigraphy and combined radiometric dating | McDougall et al. 2012 | Combined virtual endocast estimations by CT | Melchionna et al. 2020; Neubauer et al. 2018a |
| 16 | Gongwangling 1 | 1.63 | 780 | he | Paleomagnetism | Zhu et al. 2015 | Partial endocast and Lee-Pearson formula | De Miguel and Henneberg 2001 |
| 17 | ER 3883 | 1.58 | 831 | he, herg | Biostratigraphy, paleomagnetism, and radioisotopic dating | Cartmill and Smith 2009 | Combined virtual endocast estimations by CT | Melchionna et al. 2020; Neubauer et al. 2018a |
| 18 | DAN5/P1 - Gona | 1.55 | 598 | early h | Magneto-stratigraphic dating | Semaw et al. 2020 | Endocast and water displacement | Semaw et al. 2020 |
| 19 | KNM-ER 42700 | 1.55 | 732 | he | Argon-Argon dating | McDougall and Brown 2006 | Virtual endocast by CT | Neubauer et al. 2018b |
| 20 | Sangiran 38 | 1.53 | 875 | he | Argon-Argon dating | Idriati and Antón 2010 | Average of estimates from endocast and water displacement | Idriati and Antón 2010 |
| 21 | OH 13 | 1.48 | 650 | hh | Combined | Cartmill and | Endocast and water displacement | Holloway et al. 2004 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | radiometric dating | Smith 2009 | | |
| 22 | KNM-WT 15000 | 1.47 | 850 | he, herg | Paleomagnetism and radioisotopic dating | McDougall et al. 2012 | Virtual endocast by CT | Neubauer et al. 2018a |
| 23 | OH 9 | 1.4 | 1013 | he | Biostratigraphy, paleomagnetism, and radioisotopic dating | Cartmill and Smith 2009 | Virtual endocast by CT | Neubauer et al. 2018a |
| 24 | Sangiran 4 | 1.27 | 908 | he, pe | FT and U-series | Matsu'ura et al 2020 | Endocast and water displacement | Holloway et al. 2004 |
| 25 | Sangiran 2 | 1.27 | 793 | he, pe | FT and U-series | Matsu'ura et al 2020 | Virtual endocast by CT | Neubauer et al. 2018a |
| 26 | Sangiran 31 | 1.27 | 1000 | he, pe | FT and U-series | Matsu'ura et al. 2020 | Outer measurements taken from endocast | Kaifu et al. 2011b |
| 27 | Bukuran | 1.25 | 916 | he | Average of Argon-Argon, stratigraphy, and volcanic tuff dates | Grimaud-Hervé et al. 2012 | Average of estimates using Olivier et al. 1978 formula | Grimaud-Hervé et al. 2012 |
| 28 | Buia | 1 | 995 | he, herg | Radiometric and palemagnetism | Cartmill and Smith 2009 | Teff seeds | Bruner et al. 2016 |
| 29 | Daka | 1 | 995 | he | Paleomagnetism | Cartmill and Smith 2009 | Teff seeds | Asfaw et al. 2002 |
| 30 | Trinil 2 | 0.9 | 940 | he, pe | Magneto-stratigraphic and volcanic tuff dating | Cartmill and Smith 2009 | Endocast and water displacement | Holloway et al. 2004 |
| 31 | Ceprano | 0.85 | 1165 | he, ahs, hhei | Radiopotassium dating, and stratigraphy | Cartmill and Smith 2009 | Endocast and water displacement | Holloway et al. 2004 |

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|---|---|---|---|---|---|---|---|---|
| 32 | Gombore 2 | 0.85 | 1080 | he, hhei | Paleomagnetism and biostratigraphy | Profico et al. 2016 | Virtual endocast by CT | Profico et al. 2016 |
| 33 | OH 12 | 0.84 | 727 | he | Average of paleomagnetism dates | Cartmill and Smith 2009 | Endocast and water displacement | Holloway et al. 2004 |
| 34 | Yunxian | 0.8 | 1050 | he | Paleomagnetism, stratigraphy, and paleosol dating | Guo et al. 2013 | Virtual endocast by CT | Vialet et al. 2010 |
| 35 | Zhoukoudian E (III) | 0.8 | 915 | pe, he | U-series | Shen et al. 2001 | Endocast and linear measurements | Wu et al. 2010 |
| 36 | Sangiran 3 | 0.79 | 975 | pe, he | FT and U-series | Matsu'ura et al 2020 | Partial endocast and formula for estimation | Holloway et al. 2004 |
| 37 | Sangiran 12 | 0.79 | 1059 | pe, he | FT and U-series | Matsu'ura et al 2020 | Endocast and water displacement | Holloway et al. 2004 |
| 38 | Sangiran 17 | 0.79 | 1004 | pe, he | FT and U-series | Matsu'ura et al 2020 | Endocast and water displacement | Holloway et al. 2004 |
| 39 | Sangiran 10 | 0.79 | 855 | pe, he | FT and U-series | Matsu'ura et al 2020 | Endocast and water displacement | Holloway et al. 2004 |
| 40 | Sangiran IX | 0.79 | 870 | pe, he | FT and U-series | Matsu'ura et al 2020 | Virtual endocast by CT | Kaifu et al. 2011a |
| 41 | Zhoukoudian D1 (II) | 0.73 | 1020 | sp, he | Radioisotopic dating | Shen et al. 2009 | Endocast and linear measurements | Wu et al. 2010 |
| 42 | Zhoukoudian L1 (X) | 0.73 | 1225 | sp, he | Radioisotopic dating | Shen et al. 2009 | Endocast and linear measurements | Wu et al. 2010 |
| 43 | Zhoukoudian L2 (XI) | 0.73 | 1015 | sp, he | Radioisotopic dating | Shen et al. 2009 | Endocast and linear measurements | Wu et al. 2010 |
| 44 | Zhoukoudian L3 (XII) | 0.73 | 1030 | sp, he | Radioisotopic dating | Shen et al. 2009 | Endocast and linear measurements | Wu et al. 2010 |
| 45 | Bodo | 0.6 | 1250 | ahs, hhei | Argon-Argon and biostratigraphy | Cartmill and Smith 2009 | Virtual endocast by CT | Holloway et al. 2004 |
| 46 | Nanjing | 0.6 | 876 | he | ESR and U-series dating | Zhao et al. 2001 | Endocast and water displacement | Wu et al. 2011 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 47 | Saldanha 1 | 0.5 | 1225 | he, ahs | Stratigraphy | Schwartz and Tattersall 2003 | Endocast and water displacement | De Miguel and Henneberg 2001 |
| 48 | Atapuerca 4 | 0.448 | 1356 | ahs, hhei, h ant | TT-OSL | Demuro et al 2019 | Virtual endocast by CT | Melchionna et al. 2020 |
| 49 | Atapuerca 5 | 0.448 | 1125 | ahs, hhei, h ant | TT-OSL | Demuro et al 2019 | Millet seeds | De Miguel and Henneberg 2001 |
| 50 | Atapuerca 6 | 0.448 | 1220 | ahs, hhei, h ant | TT-OSL | Demuro et al 2019 | Millet seeds | De Miguel and Henneberg 2001 |
| 51 | Salé 1 | 0.412 | 880 | he | ESR | Cartmill and Smith 2009 | Endocast and water displacement | Holloway et al. 2004 |
| 52 | Ndutu 1 | 0.4 | 1100 | he, n, ahs | Biostratigraphy and volcanic tuff dating | Cartmill and Smith 2009 | Regression formula using outer measurements | De Miguel and Henneberg 2001 |
| 53 | Zhoukoudian H3 (V) | 0.4 | 1140 | sp, he | U-series | Shen et al. 2001 | Endocast and linear measurements | Wu et al. 2010 |
| 54 | Arago 21 | 0.37 | 1166 | ahs, hs, hhei | Biostratigraphy and morphological comparisons | Cartmill and Smith 2009 | Endocast and water displacement | Holloway et al. 2004 |
| 55 | Sambungmacan 3 | 0.36 | 920 | he | Argon-Argon, ESR and U-series dating | Indriati et al. 2011 | Combined virtual endocast estimations by CT | Melchionna et al. 2020; Neubauer et al. 2018a |
| 56 | Sambungmacan 4 | 0.35 | 1006 | he | Argon-Argon, ESR and U-series dating | Indriati et al. 2011 | Virtual endocast by CT | Baba et al. 2003 |
| 57 | Sambungmacan 1 | 0.35 | 1035 | he | Argon-Argon, ESR and U-series dating | Indriati et al. 2011 | Virtual endocast by CT | Baba et al. 2003 |
| 58 | Broken Hill 1 | 0.35 | 1249 | he, ahs, hs, hhei, h rhod | Biostratigraphy | Cartmill and Smith 2009 | Virtual endocast by CT | Neubauer et al. 2018a |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 59 | Hexian | 0.32 | 1025 | he | ESR, TL, and U-series | Schwartz and Tattersall 2003 | Endocast and water displacement | Wu and Zhang 2019 |
| 60 | Hualongdong 6 | 0.303 | 1150 | ahs, h | U-Th series | Wu et al. 2019 | Virtual endocast by CT | Wu et al. 2019 |
| 61 | Reilingn | 0.3 | 1430 | ahs | Biostratigraphy and morphological comparisons | Cartmill and Smith 2009 | Endocast and water displacement | Holloway et al. 2004 |
| 62 | Steinheim 1 | 0.3 | 1140 | n, ahs, hhei | Biostratigraphy | Cartmill and Smith 2009 | Virtual endocast by CT | Prossinger et al. 2003 |
| 63 | KNM-ER 3884 | 0.27 | 1400 | ahs | U-series | Bräuer et al. 1997 | Outer measurements | Bräuer et al. 1997 |
| 64 | Florisbad 1 | 0.259 | 1280 | ahs, n, hhei | ESR and OSL | Cartmill and Smith 2009 | Linear measurements | Kappelmann 1996 |
| 65 | Dali 1 | 0.259 | 1120 | he, n, ahs, hs | TT-OSL | Sun et al. 2017 | Millet seeds | Wu and Athreya 2013 |
| 66 | Maba 1 | 0.253 | 1336 | ahs | Average of U-series dates | Shen et al. 2014 | Virtual endocast by CT | Wu and Bruner 2016 |
| 67 | Ngawi 1 | 0.25 | 952 | he | Combined FT dates, ESR, U-series, and biostratigaphy | Cartmill and Smith 2009 | Virtual endocast by CT | Neubauer et al. 2018a |
| 68 | Swanscombe 1 | 0.25 | 1325 | n | TL and U-series | Cartmill and Smith 2009 | Partial endocast, using arc and chord measurements | Holloway et al. 2004 |
| 69 | Narmada 1 | 0.22 | 1200 | ahs, hhei, hs | Stratigraphy | Cartmill and Smith 2009 | Outer measurements using Buxton 1925 formula | Sonakia and Kennedy 1985 |
| 70 | Biache | 0.21 | 1331 | n, hhei | TL | Cartmill and Smith 2009 | Average of regression equations | Rougier 2003 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 71 | Ehringsdorf 9 | 0.205 | 1450 | n | ESR and U-series | Cartmill and Smith 2009 | Reconstruction and water displacement performed by Weidenreich; cited in Hrdlička 1930 | Hrdlička 1930 |
| 72 | Vértesszöllös 2 | 0.205 | 1301 | ahs, n, hs | U-series | Cartmill and Smith 2009 | Average of 4 formulas; linear regression, polynomial, power curve, and exponential curve | Wolpoff 1977 |
| 73 | Petralona 1 | 0.2 | 1162 | n, ahs, hhei | ESR | Cartmill and Smith 2009 | Virtual endocast by CT | Neubauer et al. 2018a |
| 74 | Jinniushan | 0.2 | 1360 | ahs, hs | ESR and U-series | Cartmill and Smith 2009 | Endocast and water displacement | Wu and Zhang 2019 |
| 75 | Omo 2 | 0.195 | 1491 | ahs, hs | Volcanic tuff dating | Brown et al. 2012 | Virtual endocast by CT | Neubauer et al. 2018a |
| 76 | Laetoli 18 | 0.19 | 1237 | ahs, hs | Combined U-Th series, amino acid racemization on associated finds, and radiometric dating | Cartmill and Smith 2009 | Virtual endocast by CT | Neubauer et al. 2018a |
| 77 | Apidima 2 | 0.17 | 1290 | hs | U-series | Harvati et al. 2019 | Virtual endocast by CT | Bräuer et al. 2020 |
| 78 | Lazaret | 0.165 | 1250 | hhei, n | Stratigraphy | Cartmill and Smith 2009 | Outer measurements | Holloway et al. 2004 |
| 79 | Jebel Irhoud 1 | 0.16 | 1375 | n, hs | ESR and U-series | Cartmill and Smith 2009 | Virtual endocast by CT | Neubauer et al. 2018a |
| 80 | Jebel Irhoud 2 | 0.16 | 1467 | n, hs | ESR and U-series | Cartmill and Smith 2009 | Virtual endocast by CT | Neubauer et al. 2018a |
| 81 | KNM-ES-11693 | 0.16 | 1210 | ahs | Biostratigraphy | Cartmill and Smith 2009 | Virtual endocast by CT | Bräuer et al. 2004 |

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|---|---|---|---|---|---|---|---|---|
| 82 | Herto 1/16 | 0.157 | 1450 | hs, hs idaltu | Radioisotopic dating | Cartmill and Smith 2009 | Teff seeds | White et al. 2003 |
| 83 | Singa 1 | 0.133 | 1400 | hs | ESR and U-Th series | Cartmill and Smith 2009 | Outer measurements taken from endocast | Stringer 2016 |
| 84 | Krapina 5 | 0.13 | 1397 | n | ESR | Rink et al. 1995 | Virtual endocast by CT | Cofran et al. 2020 |
| 85 | Krapina 3 | 0.13 | 1272 | n | ESR | Rink et al. 1995 | Virtual endocast by CT | Cofran et al. 2020 |
| 86 | Krapina 2 | 0.13 | 1286 | n | ESR | Rink et al. 1995 | Virtual endocast by CT | Cofran et al. 2020 |
| 87 | Krapina 6 | 0.13 | 1158 | n | ESR | Rink et al. 1995 | Virtual endocast by CT | Cofran et al. 2020 |
| 88 | Krapina 1 | 0.13 | 1419 | n | ESR | Rink et al. 1995 | Virtual endocast by CT | Cofran et al. 2020 |
| 89 | Saccopastore 1 | 0.12 | 1094 | n | Stratigraphy | Bruner and Manzi 2008 | Virtual endocast by CT | Bruner and Manzi 2008 |
| 90 | Saccopastore 2 | 0.12 | 1290 | n | Stratigraphy | Bruner and Manzi 2008 | Outer measurements and formula | Bruner and Manzi 2008 |
| 91 | Xuchang 1 | 0.115 | 1800 | ahs, hs, n | OSL | Li et al. 2017 | Virtual endocast by CT | Li et al. 2017 |
| 92 | Ngandong 14 | 0.113 | 1127 | h solo, he | ESR and U-series | Rizal et al. 2019 | Virtual endocast by CT | Neubauer et al. 2018a |
| 93 | Ngandong 1 | 0.113 | 1172 | h solo, he | ESR and U-series | Rizal et al. 2019 | Endocast and water displacement | Holloway et al. 2004 |
| 94 | Ngandong 6 | 0.113 | 1251 | h solo, he | ESR and U-series | Rizal et al. 2019 | Endocast and water displacement | Holloway et al. 2004 |
| 95 | Ngandong 7 | 0.113 | 1028 | h solo, he | ESR and U-series | Rizal et al. 2019 | Virtual endocast by CT | Melchionna et al. 2020 |
| 96 | Ngandong 9 | 0.113 | 1135 | h solo, he | ESR and U-series | Rizal et al. 2019 | Endocast and water displacement | Holloway et al. 2004 |
| 97 | Ngandong 13 | 0.113 | 1231 | h solo, he | ESR and U-series | Rizal et al. 2019 | Endocast and water displacement | Holloway et al. 2004 |
| 98 | Liujiang | 0.11 | 1567 | hs | U-series | Cartmill and Smith 2009 | Virtual endocast by CT | Wu et al. 2008 |
| 99 | Gánovce 1 | 0.105 | 1320 | n | Stratigraphy | Ahern et al. 2013 | Partial endocast and linear measurements | Vlček 1955 |

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|---|---|---|---|---|---|---|---|---|
| 100 | Qafzeh 11 | 0.103 | 1283 | hs | ESR and TL | Cartmill and Smith 2009 | Virtual endocast by CT | Coqueugniot et al. 2014 |
| 101 | Qafzeh 9 | 0.103 | 1497 | hs | ESR and TL | Cartmill and Smith 2009 | Virtual endocast by CT | Ogihara et al. 2018 |
| 102 | Qafzeh 6 | 0.103 | 1524 | hs | ESR and TL | Cartmill and Smith 2009 | Virtual endocast by CT | Neubauer et al. 2018a |
| 103 | Skhul 4 | 0.1 | 1554 | n, hs | ESR and TL | Cartmill and Smith 2009 | Lee-Pearson formula using unrestored skull | De Miguel and Henneberg 2001 |
| 104 | Skhul 5 | 0.1 | 1363 | n, hs | ESR and TL | Cartmill and Smith 2009 | Virtual endocast by CT | Ogihara et al. 2018 |
| 105 | Border Cave | 0.07 | 1507 | hs | ESR and isolucine epimerization of ostrich shells | Cartmill and Smith 2009 | Lee-Pearson formula | De Miguel and Henneberg 2001 |
| 106 | Gibraltar 1 | 0.06 | 1213 | n | aDNA analysis and stratigraphy | Bokelmann et al. 2019 | Virtual endocast by CT | Ogihara et al. 2018 |
| 107 | Shanidar 1 | 0.06 | 1600 | n | Radiocarbon dating and stratigraphy | Schwartz and Tattersall 2003 | Endocast and water displacement | Holloway et al. 2004 |
| 108 | Shanidar 5 | 0.06 | 1550 | n | Radiocarbon dating and stratigraphy | Schwartz and Tattersall 2003 | Endocast and water displacement | Holloway et al. 2004 |
| 109 | Amud 1 | 0.057 | 1736 | n | ESR | Cartmill and Smith 2009 | Virtual endocast by CT | Amano et al. 2015 |
| 110 | Manot 1 | 0.055 | 1219 | hs | U-Th series | Grimaud-Hervé et al. 2020 | Virtual endocast by CT | Grimaud-Hervé et al. 2020 |
| 111 | Monte Circeo I | 0.054 | 1421 | n, hs | ESR and U-series | Schwarcz et al. 1991 | Virtual endocast by CT | Neubauer et al. 2018a |

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|---|---|---|---|---|---|---|---|---|
| 112 | La Chapelle-aux-Saints | 0.05 | 1512 | n | Stratigraphy | Rendu et al. 2014 | Virtual endocast by CT | Ogihara et al. 2018 |
| 113 | Ryonggok 3 | 0.0475 | 1650 | hs | U-series | Bae and Guyomarc'h 2015 | Linear measurements from casts of skull | Bae and Guyomarc'h 2015 |
| 114 | Ryonggok 7 | 0.0475 | 1450 | hs | U-series | Bae and Guyomarc'h 2015 | Linear measurements from casts of skull | Bae and Guyomarc'h 2015 |
| 115 | La Ferrassie 1 | 0.047 | 1643 | n | OSL | Guérin et al. 2015 | Virtual endocast by CT | Ogihara et al. 2018 |
| 116 | Teshik-Tash | 0.04 | 1525 | n, hs | Stratigraphy | Glantz et al. 2009 | Endocast and water displacement | Hollway et al. 2004 |
| 117 | Le Moustier 1 | 0.04 | 1575 | n | TL | Cartmill and Smith 2009 | Virtual endocast by CT | Ponce de León and Zollikofer 1999 |
| 118 | Wajak 1 | 0.039 | 1513 | hs | U-series | Storm et al. 2013 | Average of estimations using von Bonin's formula and outer measurements from Dubois | Storm et al. 1992 |
| 119 | Nazlet Khater 2 | 0.038 | 1420 | hs | AMS Radiocarbon dating and ESR | Crevecoeur et al. 2009 | Virtual endocast by CT | Mounier et al. 2016 |
| 120 | Spy 1 | 0.036 | 1287 | n | Radiocarbon dating | Semal et al. 2009 | Virtual endocast by CT | Neubauer et al. 2018a |
| 121 | Spy 2 | 0.036 | 1527 | n | Radiocarbon dating | Semal et al. 2009 | Virtual endocast by CT | Cofran et al. 2020 |
| 122 | Hofmeyr | 0.036 | 1580 | hs | OSL and U-series | Grine et al. 2010 | Virtual endocast by CT | Grine et al. 2010 |
| 123 | La Quina 5 | 0.035 | 1350 | n | Radiocarbon dating | Cartmill and Smith 2009 | Virtual endocast by CT | Melchionna et al. 2020 |
| 124 | Mladeč 5 | 0.035 | 1650 | hs | Radiocarbon dating | Mounier et al. 2020 | Regression formula using cast | Wolpoff et al. 2006 |
| 125 | Mladeč 1 | 0.035 | 1606 | hs | Radiocarbon dating | Mounier et al. 2020 | Virtual endocast by CT | Ogihara et al. 2018 |
| 126 | Zhoukoudian - Upper Cave 103 | 0.035 | 1385 | hs | AMS Radiocarbon dating | Li et al 2018 | Average of estimations using Lee-Pearson | Wu and Zhang 2019 |

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|---|---|---|---|---|---|---|---|---|
| | | | | | | | Formula and Woo Formula | |
| 127 | Zhoukoudian - Upper Cave 102 | 0.035 | 1500 | hs | AMS Radiocarbon dating | Li et al 2018 | Average of estimations using Lee-Pearson Formula and Woo Formula | Wu and Zhang 2019 |
| 128 | Zhoukoudian - Upper Cave 101 | 0.035 | 1564 | hs | AMS Radiocarbon dating | Li et al 2018 | Average of estimations using Lee-Pearson Formula and Woo Formula | Wu and Zhang 2019 |
| 129 | Sunghir 1 | 0.034 | 1514 | hs | AMS Radiocarbon dating | Nalawade-Chavan et al. 2014 | Average of estimations using Lee-Pearson Formula, Millet seeds, and Olivier et al. 1978 Formula | Trinkaus et al. 2014 |
| 130 | Cioclovina 1 | 0.033 | 1499 | hs | Radiocarbon dating | Soficaru et al. 2007 | Virtual endocast by CT | Kranioti et al. 2011 |
| 131 | Dolní Věstonice 14 | 0.031 | 1663 | hs | Radiocarbon dating | Mounier et al. 2020 | Virtual endocast by CT | Neubauer et al. 2018a |
| 132 | Dolní Věstonice 13 | 0.031 | 1590 | hs | Radiocarbon dating | Mounier et al. 2020 | Virtual endocast by CT | Neubauer et al. 2018a |
| 133 | Dolní Věstonice 15 | 0.031 | 1385 | hs | Radiocarbon dating | Mounier et al. 2020 | Virtual endocast by CT | Neubauer et al. 2018a |
| 134 | Dolní Věstonice 16 | 0.031 | 1542 | hs | Radiocarbon dating | Mounier et al. 2020 | Virtual endocast by CT | Neubauer et al. 2018a |
| 135 | Dolní Věstonice 3 | 0.031 | 1285 | hs | Radiocarbon dating | Mounier et al. 2020 | Endocast and water displacement | Holloway et al. 2004 |
| 136 | Jingchuan 1 | 0.031 | 1464 | hs | OSL and associated tools and fauna | Li et al. 2010 | Virtual endocast by CT | Zhang et al. 2015 |
| 137 | Ziyang | 0.03 | 1250 | hs | Average of radiocarbon dates | Wu and Yan 2020 | Virtual endocast by CT | Wu and Yan 2020 |
| 138 | Cro-Magnon 1 | 0.0276 | 1574 | hs | Radiocarbon dating | Cartmill and Smith 2009 | Virtual endocast by CT | Ogihara et al. 2018 |
| 139 | Cro Magnon 3 | 0.0276 | 1813 | hs | Radiocarbon dating | Cartmill and | Virtual endocast by CT | Neubauer et al. 2018a |

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|---|---|---|---|---|---|---|---|---|
| | | | | | | Smith 2009 | | |
| 140 | Předmostí 10 | 0.0265 | 1452 | hs | Radiocarbon dating | Cartmill and Smith 2009 | Linear measurements performed by Matiegka 1934; cited in Wolpoff et al. 2006 | Wolpoff et al. 2006 |
| 141 | Předmostí 4 | 0.0265 | 1518 | hs | Radiocarbon dating | Cartmill and Smith 2009 | Linear measurements performed by Matiegka 1934; cited in Wolpoff et al. 2006 | Wolpoff et al. 2006 |
| 142 | Předmostí 9 | 0.0265 | 1555 | hs | Radiocarbon dating | Cartmill and Smith 2009 | Linear measurements performed by Matiegka 1934; cited in Wolpoff et al. 2006 | Wolpoff et al. 2006 |
| 143 | Předmostí 3 | 0.0265 | 1608 | hs | Radiocarbon dating | Cartmill and Smith 2009 | Linear measurements performed by Matiegka 1934; cited in Wolpoff et al. 2006 | Wolpoff et al. 2006 |
| 144 | Pavlov 1 | 0.0262 | 1472 | hs | Radiocarbon dating | Cartmill and Smith 2009 | Linear measurements performed by Vlček 1991; cited in Wolpoff et al. 2006 | Wolpoff et al. 2006 |
| 145 | Brno II | 0.0237 | 1500 | hs | Radiocarbon dating | Cartmill and Smith 2009 | Endocast and water displacement | Holloway et al. 2004 |
| 146 | Brno III | 0.0237 | 1304 | hs | Radiocarbon dating | Cartmill and Smith 2009 | Endocast and water displacement | Holloway et al. 2004 |
| 147 | Abri Pataud 1 | 0.02 | 1334 | hs | AMS Radiocarbon dating | Chiotti et al. 2015 | Combined virtual endocast estimations by CT | Melchionna et al. 2020; Neubauer et al. 2018a |
| 148 | Ohalo 2 | 0.019 | 1475 | hs | Radiocarbon dating | Nadel et al. 1995 | Virtual endocast by CT | Neubauer et al. 2018a |
| 149 | Chancelade 1 | 0.0182 | 1452 | hs | Radiocarbon dating | Mounier et al. 2020 | Virtual endocast by CT | Melchionna et al. 2020 |
| 150 | Minatogawa 4 | 0.018 | 1170 | hs | Radiocarbon dating | Kaifu et al. 2009 | Virtual endocast by CT | Kubo and Kono 2011 |

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|---|---|---|---|---|---|---|---|---|
| 151 | Minatogawa 2 | 0.018 | 1170 | hs | Radiocarbon dating | Kaifu et al. 2009 | Millet seeds | De Miguel and Henneberg 2001 |
| 152 | Minatogawa 1 | 0.018 | 1335 | hs | Radiocarbon dating | Kaifu et al. 2009 | Virtual endocast by CT | Kubo et al. 2008 |
| 153 | Taza 1 | 0.016 | 1125 | hs | Radiocarbon dating | Meier et al. 2003 | Endocast and mustard seeds | Meier et al. 2003 |
| 154 | Maludong | 0.013 | 1327 | hs | AMS and U-series | Curnoe et al. 2012 | Virtual endocast by CT | Curnoe et al. 2012 |
| 155 | Oberkassel 2 | 0.012 | 1330 | hs | AMS Radiocarbon dating | Street et al. 2006 | Virtual endocast by CT | Neubauer et al. 2018a |
| 156 | Oberkassel 1 | 0.012 | 1492 | hs | AMS Radiocarbon dating | Street et al. 2006 | Virtual endocast by CT | Neubauer et al. 2018a |

# Appendix B: Original Source Code for R Software

R Statistical Software for Mac 4.0.5: https://www.r-project.org/

Zoo package for R Statistical Software: https://cran.r-project.org/web/packages/zoo/index.html

Some abbreviations used in source code:

CC: Cranial Capacity

NoFloresNaledi: Data spreadsheet uploaded to R (Appendix D)

Rollapply: Function in R for rolling window formulas

SD: Standard deviation

Zoo: Supplemental package for R Software to perform rolling window functions

To create CV Value Scatterplot (Figure 3):

```
> library(zoo)
> plot.default(x = rollapply(NoFloresNaledi$Age, 20, mean), y = rollapply(NoFloresNaledi$CC,
20, sd)/ rollapply(NoFloresNaledi$CC, 20, mean) * 100, xlab = "Age (in Ma)", ylab = "CV
Values of Cranial Capacity", main = "Variation of Cranial Capacity Through Time for
Pleistocene Homo", ylim=range(rollapply(NoFloresNaledi$CC, 20, sd)/
rollapply(NoFloresNaledi$CC, 20, mean) * 100), xlim=rev(c(.01, 1.8)), axes = FALSE)

> par(new=TRUE)

> axis(1, at = seq(.0, 1.8, by = .2))

> par(new=TRUE)

> axis(2, at = seq(6, 22, by = 2))
```

To Calculate Rolling Window CV Values from Dataset (Table 1):

```
> rollapply(NoFloresNaledi$CC, 20, sd)/ rollapply(NoFloresNaledi$CC, 20, mean) * 100
```