Characterizing the body morphology of the first metacarpal in the Homininae using 3D geometric morphometrics

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Running title: Characterizing MC1's morphology in the Homininae

Abstract

Objectives: Extinct hominins can provide key insights into the development of tool use, with the morphological characteristics of the thumb of particular interest due to its fundamental role in enhanced manipulation. This study quantifies the shape of the first metacarpal's body in the extant Hominidae and some fossil hominins to provide insights about the possible anatomical correlates of manipulative capabilities.

Materials and methods: The extant sample includes MC1s of modern humans (n=42), gorillas (n=27) and chimpanzees (n=30), whilst the fossil sample included *Homo neanderthalensis*, *Homo naledi* and *Australopithecus sediba*. 3D geometric morphometrics were used to characterize the overall shape of MC1's body.

Results: Humans differ significantly from extant great apes when comparing overall shape. *H. neanderthalensis* mostly falls within the modern human range of variation although also showing a more robust morphology. *H. naledi* varies from modern human slightly, whereas *A. sediba* varies from humans to an even greater extent. When classified using a linear discriminant analysis, the three fossils are categorized within the *Homo* group.

Discussion: The results are in general agreement with previous studies on the morphology of the MC1. This study found that the modern human MC1 is characterized by a distinct suite of traits, not present to the same extent in the great apes, that are consistent with an ability to use forceful precision grip. This morphology was also found to align very closely with that of *H. neanderthalensis*. *H. naledi* shows a number of human-like adaptations consistent with an ability to employ enhanced manipulation, whilst *A. sediba* apparently presents a mix of both derived and more primitive traits.

Keywords: MC1; 3D geometric morphometrics; Semi-landmarks; Hominins; African apes

1 Introduction

There is no doubt that the extremely dexterous human hand is unmatched among animals. As a result, the human hand has been the subject of considerable paleoanthropological research over the years in order to provide a better understanding of the processes that led to its evolution (Almécija, Smaers, & Jungers, 2015a; Key, 2016; Lewis, 1977; Marzke & Marzke, 2000; Susman, 1998). Much of this has been directed at how the hand morphology of higher primates correlates to their manipulative capabilities, and how fossil morphology can be used to infer tool use in extinct hominin species (Almécija & Alba, 2014; Kivell, Kibii, Churchill, Schmid, & Berger, 2011; Marchi, Proctor, Huston, Nicholas, & Fischer, 2017; Napier, 1955). The thumb and its components, most notably the first metacarpal (MC1), plays a fundamental role in object manipulation and the study of its anatomy has therefore been at the center of research in this field (Galletta, Stephens, Bardo, Kivell, & Marchi, 2019; Marchi et al., 2017). However, the constant discovery of new fossils (e.g. *Homo Naledi;* Berger et al., 2015) and the development of new morpho-functional analysis tools mean that there is still much about the tool use behaviors and manipulative capabilities of extinct hominins that is yet to be uncovered.

Amongst the extant great apes, humans possess the superior manipulative capabilities, with the ability not only to adeptly utilize the objects in their environment, but also to manufacture complex tools in ways that require high levels of dexterity. These advanced skills are facilitated in part by a unique thumb morphology: the human thumb is long relative to the length of the fingers compared to other less dexterous

apes, with powerful thenar musculature and robust thumb bones (Almécija, Moyà-Solà, & Alba, 2010; Almécija et al., 2015; Feix, Kivell, Pouydebat, & Dollar, 2015; Tuttle, 1969).

In comparison to human hands, non-human great apes, especially chimpanzees and orangutans, have longer, robust fingers relative to their shorter, more gracile thumbs, which is probably the result of selective pressures associated with locomotor behaviors such as suspension and knuckle-walking (Almécija et al., 2015; Püschel, Marcé-Nogué, Chamberlain, Yoxall, & Sellers, 2020; Richmond & Strait, 2000). Both gorillas and chimpanzees have been observed using tools in the wild, to varying degrees; however, their manipulative capabilities are limited due to the constraints imposed by their hand morphology. Chimpanzees are prolific tool users, known to use tools both in nature and captivity (Boesch & Boesch, 1990). Examples of chimp tool use include termite fishing with specially crafted sticks (Sanz, Call, & Morgan, 2009), hunting bush babies with sharp spears and nut-cracking with stones (Sanz & Morgan, 2007). Gorillas are less reliant on tool use due the fact that they exploit food resources differently from chimpanzees (e.g., crack nuts with their teeth), but they have been observed using sticks to test the depth of water and to support themselves when crossing deep water (Breuer, Ndoundou-Hockemba, & Fishlock, 2005). However, whilst non-human great apes do regularly use their thumbs to manipulate objects, they are not as efficient as humans in using forceful precision grips (Marzke, Marchant, McGrew, & Reece, 2015; Marzke & Wullstein, 1996).

Traditionally it was believed that extinct hominin species also fell into this category, lacking the manual dexterity of modern humans (Lewis, 1977; Niewoehner, 2001, 2006; Rightmire, 1972). However, there is a growing body of evidence that many

hominins as early as *O. tugenensis* (Gommery & Senut, 2006) show the capacity to efficiently use tools, with the ability to use forceful precision grips as dexterously as humans (Alba, Moyà-Solà, & Köhler, 2003; Feix et al., 2015; Karakostis, Hotz, Scherf, Wahl, & Harvati, 2017; Kivell et al., 2011; Tocheri, Orr, Jacofsky, & Marzke, 2008). Human-like features would have been present along with traits suitable for arboreal locomotion, which lead to the suggestion that the hominin hand evolved in a mosaic fashion showing a manual morphology adapted to these two functional demands (i.e., manipulation and locomotion) (Kivell et al., 2011; Kivell, 2015). This mixed morphology is apparent in the hand of *A. sediba* and *H. naledi* (Kivell et al., 2011; 2015) whereas the hand of Neanderthals would be fully derived (Tocheri et al., 2008).

Several studies have focused on different anatomical features of the hand in an effort to understand the extent to which the hand of early hominins is adapted to manipulative abilities (e.g., Almécija et al., 2010; Galletta et al., 2019; Green & Gordon, 2008; Skinner et al., 2015), in particular regarding the joint areas of the MC1, as this bone plays a crucial role in complex manipulative behaviors. However, whilst there is now a greater understanding of the manipulative capabilities of hominins, much of the research on the MC1 dates back to the past century and often contained only qualitative assessments (Aubriot & Tubiana, 1981; Barmakian, 1992; Imaeda, An, & Cooney, 1992; Napier, 1956, 1960; Tuttle, 1969). Even the most recent quantitative research that has been conducted using three-dimensional geometric morphometric (3DGM) techniques have focused only on those certain areas of the MC1 deemed to be most important in controlling manipulation, such as the trapeziometacarpal joint connecting the thumb to the wrist (i.e., proximal articular surface; Marchi et al., 2017) and the first metacarpal distal articular surface (Galletta et al., 2019). As a result, most of MC1's morphology (i.e., its body) has yet to be fully quantitatively analyzed to

assess its possible importance when assessing possible correlates with manipulative abilities.

Consequently, in this study body morphology of the MC1 was quantified using 3DGM in order help in the identification of structures in extant species that may be correlated with human-like manipulative capabilities and determining if similar morphologies are present in fossil hominins. The sample investigated in this study included three extant African ape genera (*Homo, Gorilla, Pan*) and three fossil hominins (*Homo neanderthalensis*, *Homo naledi* and *Australopithecus sediba*). Based on previous literature about thumb morphology and function, the following hypotheses were tested:

Hypothesis 1: MC1 morphology significantly differs between humans and extant great ape species

Though great apes use their hand for manipulative activities, their specialisation is more a consequence of their locomotion (i.e., knuckle-walking and arborealism) (Almécija, Moyà-Solà, & Alba, 2010). It is therefore expected that the selective pressures associated with locomotor behaviour in chimpanzees and gorillas will result in an MC1 morphology that varies significantly from that of bipedal humans. Furthermore, different use of the human thumb during manipulation and human adaptations to precise and forceful tool use are expected to lead to an MC1 morphology that differs from other extant apes.

Hypothesis 2: All fossil hominin specimens exhibit an MC1 morphology more similar to humans than other great apes

H. neanderthalensis, A. sediba and *H. naledi* have overall hand morphologies that appear to align with human hands to a greater extent than those of non-human great

apes. They possess adaptations, such a long thumb and short fingers, that are associated with advanced manipulative capabilities in modern humans (Holliday et al., 2018; Kivell et al., 2011). Given these morphological characteristics and the inferred tool using abilities of *H. naledi, A. sediba* and *H. neanderthalensis* in previous studies, they would be expected to have an MC1 morphology more closely aligned with humans than gorillas or chimpanzees.

2 Material and methods

2.1 Sample

The extant sample used in this study includes MC1s of modern humans (*Homo sapiens*; n=42), chimpanzees (*Pan troglodytes*; n=30), and gorillas (*Gorilla gorilla* and *Gorilla beringei*; n=27) (Table S1). The human MC1s came from a medieval cemetery in Burgos, Spain (Casillas Garcia & Alvarez, 2005) and the surface models were obtained using a Breuckmann SmartSCAN structured light scanner. The non-human sample came from museum collections and they came from different origins (i.e., wild-shot, captivity and unknown origin). Their surface models were collected using photogrammetry as described in Bucchi et al., (2020). Both scanned and photogrammetry models are high resolution, therefore providing a good representation of the original anatomy. The resolution of the models generated using surface scanner and photogrammetry have been previously tested and found to be comparable (Giacomini et al., 2019), thus allowing us to combine these data types in our analyses. Only adult individuals were included in the study and right MC1s were preferred (although left MC1s were reflected when their antimere was not present).

The fossil sample includes the right metacarpal from a *Homo neanderthalensis*, the right metacarpal from a *Homo naledi* and the left metacarpal from an *Australopithecus*

sediba. The *H. neanderthalensis* sample was found in La Ferrassie archaeological site in Savignac-de-Miremont, France. The skeleton was discovered in 1909 and is estimated to be 70–50,000 years old (Guérin et al., 2015). The *Homo naledi* sample (Morphosource identifier: S2110) was recovered in 2013 from the Rising Star cave system in South Africa and has been dated to around 250,000 years ago (Dirks et al., 2017). The *A. sediba* sample (Morphosource identifier: S2490) was taken from the near complete wrist and hand of an adult female [Malapa Hominin 2 (MH2)] discovered in Malapa, South Africa (Berger et al., 2010). The latter fossils were downloaded from Morphosource https://www.morphosource.org/, whereas the Neanderthal was obtained from a cast housed at the Catalan Institute of Human Paleoecology and Social Evolution (IPHES).

2.2. 3DGM

3D coordinates were collected using the software Landmark Editor 3.6 (Wiley et al., 2005) to quantify the MC1's morphology. Eight curves comprising 20 equidistant coordinates each were placed at pre-defined points on the MC1 (Figure 1). These coordinates were chosen to provide a good representation of the overall shape of the shaft of the bone. The first and last coordinates from each one of the eight curves were treated as fixed landmarks, whereas all the rest of the coordinates (i.e., 144 coordinates) were considered as semi-landmarks. A generalized Procrustes superimposition was performed on the coordinate data to remove differences due to scale, translation, and rotation, thus obtaining shape variables (Bookstein, 1991). The semi-landmarks were slid on the MC1's surface by minimizing bending energy (Bookstein, 1997; Gunz, Mitteroecker, & Bookstein, 2005).

These obtained shape variables were then used in a principal component analysis (PCA) to quantify overall shape variation. The data set of extant hominoids was then grouped by genus and the Procrustes variance of observations in each group (i.e., the mean squared Procrustes distance of each specimen from the mean shape of the respective group) was computed as a simple measure to assess morphological disparity within each one (Klingenberg & McIntyre, 1998; Zelditch, Sheets, & Fink, 2003). Procrustes variance was applied here as way to evaluate intra-genus variation, and absolute differences in Procrustes variances were computed to test differences in morphological disparity among groups (these differences statistically evaluated through permutation). Then, a multi-group linear discriminant analysis (LDA) (also known as canonical variate analysis) was run to maximize separation between groups using the principal components (PCs) that accounted for 90% of the sample variance. Performance was calculated using the confusion matrix from which the overall classification accuracy was computed, as well as the Cohen's Kappa statistic (Püschel, Marcé-Nogué, Gladman, et al., 2020; Püschel, Marcé-Nogué, Gladman, Bobe, & Sellers, 2018). The complete dataset was resampled using a 'leave-one-subject-out' cross-validation, as a way to asses classification performance (Kuhn & Johnson, 2013). Pairwise PERMANOVA tests with Bonferroni corrections for multiple comparisons were performed to assess for shape differences between the three extant genera using the again PCs that accounted for 90% of the sample variance. Euclidean distances were selected as similarity index.

All these analyses were carried out in R 3.5.1 (R Core Team, 2019), using the 'geomorph' 3.1.2 (Adams, Collyer, & Kaliontzopoulou, 2019) and 'MASS' 7.3-51.5 packages (Venables & Ripley, 2002).

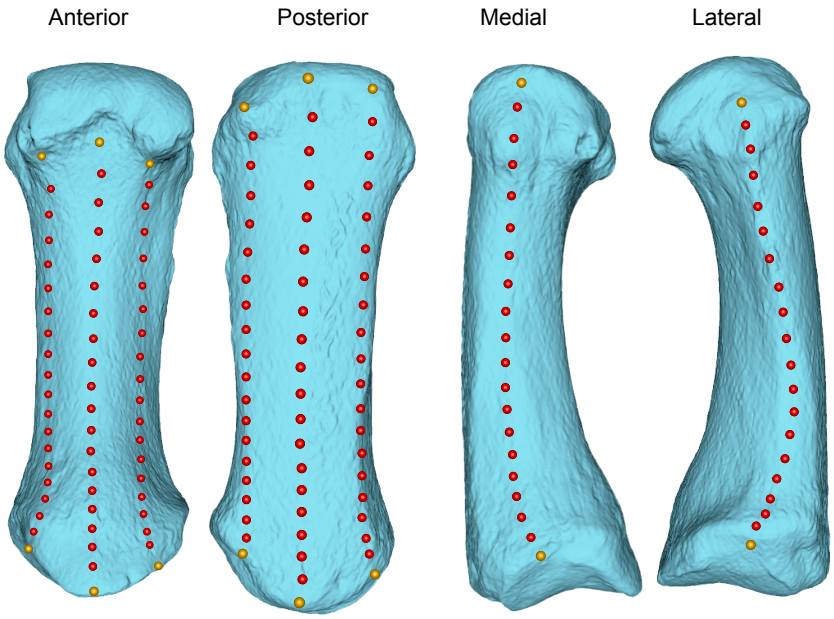


Figure 1. Illustration of the 16 landmarks (black spheres) and 144 semi-landmarks (red spheres) used to quantify MC1's body morphology.

3 Results

3.1 Principal component analysis

The PCA performed using the shape variables returned 102 PCs. The first 22 PCs accounted for ~ 90% of the total variance of the sample, hence offering a reasonable estimate of the total amount of MC1's shape variation, which were then used in the LDA and pairwise PERMANOVA tests. The first three PCs in the PCA account for ~ 57% of the total variance and display a relatively clear separation between the extant African ape genera (Fig. 2a). PC1 explains 40.8 %, PC2 10.44% and PC3 5.43% of total variance, respectively (Fig. 1a-d).

Violin plots of PC1 (Fig. 2b) show a notable difference between gorillas and humans vs. chimpanzees. Humans and gorillas exhibit the highest PC1 scores, representing a wider distal articular surface, a larger proximal articular surface, a significantly more

240 robust shaft. Chimpanzees show the lowest PC1 scores, representing a narrower
241 proximal articular surface, a smaller distal head, smaller radial and ulnar epicondyles
242 and a more gracile shaft. *H. neanderthalensis* falls within the human and gorilla
243 distributions and is distinct completely from the chimpanzees. *H. naledi* falls within the
244 human distribution, whilst *A. sediba* is characterized by a lower PC1 score and aligns
245 closer to the *Pan* distribution. None of the analyzed fossils fall within any of
246 interquartile ranges (IQR) (i.e., black bars in Fig. 1b-d) of any of the extant genera.
247
248 Violin plots of PC2 (Fig. 2c) shows distinct variation between the extant genera, with
249 a morphological continuum ranging from *Gorilla* (higher PC2 values), *Pan* (central PC2
250 values) and *H. sapiens* (lower PC2 scores). Interestingly, due to the presence of a
251 couple of outliers, the morphological variation in *Gorilla* encompasses the whole range
252 of observed morphological variation. The *Gorilla* sample has the highest PC2 scores,
253 representing an extended palmar lip, a more curved shaft and more rounded ends.
254 The modern human distribution shows the lowest PC2 scores, representing flatter
255 distal and proximal articular ends, as well as larger radial palmar condyles at the distal
256 end. The chimpanzee sample lies in between the gorilla and modern human samples
257 displaying an intermediate morphology. In a similar fashion as chimpanzees, the three
258 fossils are located at intermediate positions in PC2 distribution. *H. neanderthalensis*
259 and *H. naledi* display PC2 scores that are within the *Pan* IQR, whilst *A. sediba* has
260 lower values.
261
262 Violin plots of PC3 (Fig. 2d) show a similar distribution of PC scores for the three extant
263 genera. From a morphological perspective, higher scores are associated with more
264 robust morphologies displaying more marked muscular attachments (for the opponens

pollicis, first dorsal interosseous and abductor pollicis longus muscles), while lower values correspond to more gracile MC1s. *H. naledi* and *A. sediba* show values which are within the *Pan* or *H. sapiens* distribution, but outside their IQR and at opposite extremes of the axis. *H. neanderthalensis* lies outside the distribution of any of the extant genera, probably due to its particularly robust morphology and associated marked muscular insertion areas.

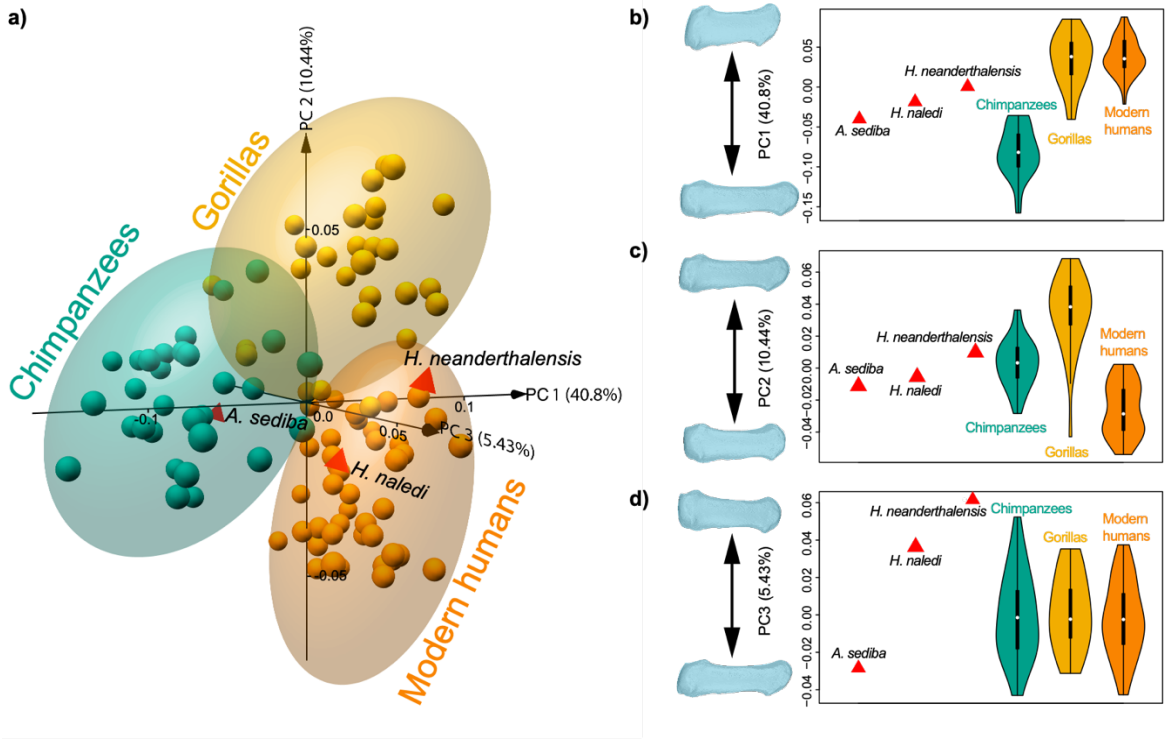


Figure 2. Principal component analysis of the shape data: the a) three main axes of morphological variation are displayed (ellipses represent 95% confidence intervals, whilst fossils are shown as red tetrahedrons); Violin plots of the PCs scores of the analyzed sample are shown for b) PC1, c) PC2 and d) PC3 (fossil values are displayed as red triangles). The models closest to the mean shape was warped to match the multivariate mean using the thin plate spline method. The obtained average model was then warped to represent the variation along the three plotted PC axes (mag = 1).

3.2 Morphological disparity

281 To compare the amounts of shape variation between the extant genera, we used
282 Procrustes variance as a way to assess intra-genus variation. The obtained results
283 show that three extant genera show a similar magnitude of disparity. Nevertheless,
284 gorillas exhibit a higher Procrustes variance as compared to modern humans and
285 chimpanzees (Table 1a). Gorillas are significantly different to modern humans, and
286 chimpanzees when comparing absolute variance differences, whilst modern human
287 do not significantly differ from chimpanzees (Table 1b).
288

Table 1. Morphological disparity results

a) Procrustes variance			
Chimpanzees	0.004840776		
Gorillas	0.006378662		
Modern humans	0.004423507		
b) Pairwise differences			
	Chimpanzees	Gorillas	Modern humans
Chimpanzees		**0.009**	0.393
Gorillas	0.001537886		**0.001**
Modern humans	0.000417269	0.001955155	

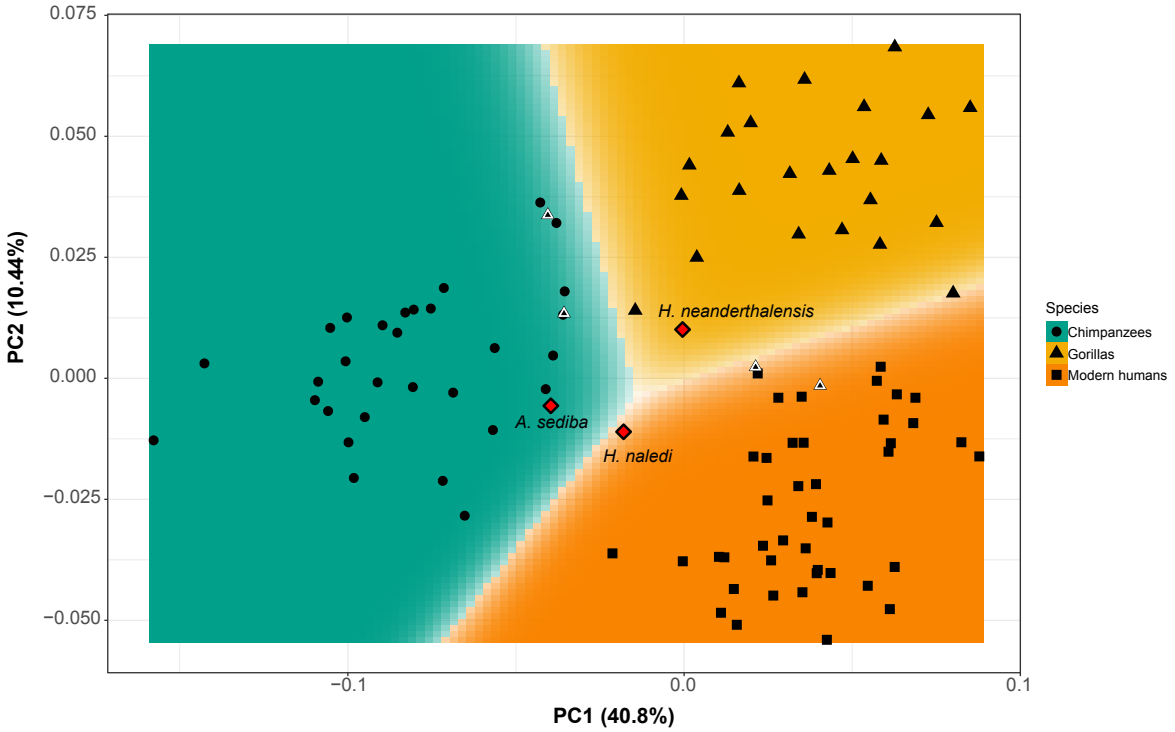
Above the diagonal: p-values (significant in bold); below the diagonal: absolute differences.

289

290 3.3 Linear discriminant analysis

291 The LDA model using the first 22 PCs clearly distinguishes between the three extant
292 genera, displaying an outstanding performance with almost perfect classification

293 results after cross-validation (Accuracy: 0.98; Cohen's Kappa: 0.97; Figure 3). When
294 using the obtained discriminant function to classify the fossils into the extant categories
295 (as way of assessing morphological affinities) (Table 2), the three of them were
296 robustly classified into the *Homo* category (all posterior probabilities were extremely
297 close to 1), hence indicating that, in spite of their differences, their morphology is closer
298 to that of modern humans. There were significant differences between all extant
299 genera when analyzing 22 PCs from the PCA carried out using the shape variables
300 (Table 3).



301

302 Figure 3. Decision boundary plot for the first 22 PCs the PCA carried out using the shape variables.
303 The two variables that contributed the most to each LDA models are displayed (i.e., PC1 and PC2).
304 The space is colored depending on what substrate preference the (LDA model predict that region
305 belongs to, whereas the lines between colored areas represent the decision boundaries. Color intensity
306 indicates the certainty of the prediction in a particular graph area (i.e., darker colors mean a higher
307 probability of belonging to a certain category). Symbols surrounded by a white rim correspond to
308 misclassified specimens for the plotted variables, whilst fossil are in red.

309

Table 2. Prediction results for the fossil sample.

	LDA model		
	Posterior probabilities		
Species	Chimpanzees	Gorillas	Modern humans
Australopithecus sediba	0.09	0.00	0.91
Homo naledi	0.00	0.00	1.00
Homo neanderthalensis	0.00	0.00	1.00

Table 3. Pairwise PERMANOVA results

	F-model	Bonferroni-corrected p-value
Modern humans vs. gorillas	15.84	**0.0003**
Modern humans vs. chimpanzees	68.87	**0.0003**
Chimpanzees vs. gorillas	42.03	**0.0003**

4 Discussion

The first hypothesis was that the shape of the human MC1 would differ significantly from that of *Pan* and *Gorilla*, due to the variation in their manipulative capabilities and locomotive behaviors. Results from the analyses provide strong support for this hypothesis, confirming that there is indeed significant morphological variation between the extant great apes. Interestingly, we also found clear differences between chimpanzees and gorillas, with gorillas closer (i.e., more similar) to humans than to chimpanzees (PC1). The second hypothesis was that all fossil hominin species would exhibit an MC1 morphology more similar to humans than other great apes. The results also support this hypothesis. However, it is important to notice that even though the

three fossils are more similar to the modern humans, they also display some distinct features, different from those which would be typically expected in modern *H. sapiens*.

5.1 Humans and great apes MC1 shape

The 3DGM data indicate that modern human MC1 morphology is significantly different from the rest of the extant hominids, therefore allowing us to accept the first hypothesis. The human distal head is characterized by a flatter, larger distal articular surface and larger radial and ulnar epicondyles. The proximal base of the human MC1 is also larger and flatter in both the radioulnar and dorsovolar aspects, with less pronounced curvature than that seen in other hominid species. These are all morphologies that are consistent with previous 3DGM analysis of the proximal (Marchi et al., 2017) and distal (Galletta et al. 2019) surfaces of the human MC1. The shaft, an area that has not previously been analyzed using 3DGM, is characterized by being significantly more robust, with a greater curvature and a larger ridge on its lateral side, corresponding to the insertion of the opponens pollicis muscle.

The flatter and larger distal articular surface in humans has been interpreted as an adaptation that limits dorso-palmar motion whilst preventing radioulnar motion (Barmakian, 1992), thereby stabilizing the MC1 and facilitating forceful power and precision grasping. In apes that distal articular surface has a more pronounced curvature, rendering the metacarpophalangeal joint (MCPJ) less stable and unable to sustain high loads (Galletta et al., 2019). The pronounced radial and ulnar epicondyles found at the distal head of the human MC1 (as described by PC1) serve a similar purpose, reducing the range of motion and stabilizing the MCPJ. These epicondyles act as anchor points for collateral ligaments, which insert at the base of the proximal

phalanx. When the thumb is flexed these ligaments tighten and limit the radioulnar motion of the proximal phalanx (Imaeda et al., 1992). Larger epicondyles are therefore thought to act as stronger anchors by providing a greater area for the collateral ligaments to attach to, helping stabilize the MCPJ during the high forces that are experienced by the thumb during manipulation (Galletta et al., 2019). The proximal articular surface in humans is also flatter (as described by PC2), but in contrast this is correlated with a higher range of motion at the trapeziometacarpal joint (TMCJ), rather than a lower one (Marzke et al., 2010). It is this combination in humans of high mobility at the TMCJ and low mobility at the MCPJ that facilitates a high level of manual dexterity, whilst also allowing the thumb to sustain high loads during forceful tool use. High mobility at the TMCJ plays a key role in the pad-to-pad opposition abilities of the human hand, in which the thumb is able to rotate and touch the apical tip of each phalanx. In many human manipulative activities like precision grips the thumb needs to be highly abducted, which means that the load is radially shifted on the joint surface (Lewis, 1977; Marchi et al., 2017). The observed larger radially extended proximal surface is therefore important because, whilst it allows for a greater radial extension, it also helps the joint resist high levels of radial displacement by providing a greater surface area for the abducted MC1 (Hamrick, 1996).

We hypothesize that the morphological characteristics of the human MC1 shaft presented here, such as a significantly more robust build, are likely adaptations that further serve to facilitate forceful tool use. Indeed, a thicker MC1 shaft would be able to better withstand the high levels of stress placed upon the thumb by sustained power and precision grasping (Key & Dunmore, 2015; Marzke, Wullstein, & Viegas, 1992; Rolian, Lieberman, & Zermeno, 2011). It has been also related to a greater

373 development of the thenar musculature attaching into the shaft that is highly active
374 during hard hammer percussion and that would favor thumb opposition (Marzke, 2013;
375 Marzke, Toth, Schick, & Reece, 1998).
376
377 5.1 Fossil hominin MC1 shape
378 The general scientific consensus in recent years is that *H. neanderthalensis* had a
379 hand morphology and manipulative capabilities that were very similar to those of
380 humans, challenging the previously held beliefs that *H. neanderthalensis* lacked the
381 derived adaptations for advanced and precise human-like tool use (Karakostis et al.,
382 2017; Karakostis, Hotz, Tourloukis, & Harvati, 2018; Niewoehner, 2001, 2006; Tocheri
383 et al., 2008; Trinkaus & Villemeur, 1991). The results align well with this consensus,
384 with the *H. neanderthalensis* specimen showing several similarities with the modern
385 humans. The described morphology is one of a flatter (PC2) and larger (PC1) distal
386 articular surface, bigger epicondyles at the distal head (PC1) and a flatter proximal
387 articular surface (PC2). However, *H. neanderthalensis* also differs in exhibiting a
388 particularly robust MC1 with strongly marked muscular insertions.
389
390 Previous analysis on the thumb morphology of *Homo naledi* fossils has indicated that
391 it has derived characteristics compatible with forceful precision grip and human-like
392 manipulative abilities (Berger et al., 2015; Kivell, 2015). Such characteristics include
393 a well-developed crest for the opponens pollicis insertion and flat distal/proximal
394 articular surfaces (Kivell et al., 2015; Galletta et al. 2019). The results generally agree
395 with these observations and conclusions, whilst also presenting some potentially new
396 insights. The morphology of the *H. naledi* sample had a human-like robustness of the
397 shaft (PC1), suggesting that the MC1 was adapted to sustain high loads, such as those

experienced during forceful tool use. This suggests that *H. naledi* was potentially capable of a degree of advanced manipulation, such as forceful precision and power grasping. These findings are therefore consistent with previous functional interpretations of *H. naledi* thumb morphology (Galletta et al. 2019). Whilst the evidence suggests that *H. naledi* was almost certainly able to perform an certain degree of advanced manipulation, and was likely a tool-user, it also suggests that it had not yet showed the full repertoire of manipulative adaptations exhibited by humans and *H. neanderthalensis* (Berger et al., 2015; Kivell et al., 2015; Galletta et al., 2019).

Previous analysis of *A. sediba* hand morphology has found that it possessed a number of advanced *Homo*-like features, such as a longer thumb relative to shorter fingers, that potentially indicate advanced manipulative capabilities, while retaining primitive traits as a gracile MC1, similar to those of other australopithecines (Kivell et al., 2011). Recent 3DGM studies that have analyzed the MC1 in particular have come to the conclusion that if *A. sediba* was indeed utilizing tools, as some hand proportion and trabecular evidence suggests (Kivell et al., 2011; Skinner et al., 2015), then it was doing so in a way that differed from that of early *Homo* and modern humans (Marchi et al., 2017; Galletta et al., 2019). This conclusion was reached due to aspects of their MC1 morphology that were deemed inconsistent with the ability to employ forceful precision grips, namely a gracile MC1 shaft, more curved proximal articular surface and smaller radial and ulnar epicondyles. These morphologies suggest that the range of motion would not have been great enough at the TMCJ to facilitate the necessary abduction-adduction for thumb opposition and pad-pad precision grips. The results agree with this consensus, with the *A. sediba* sample presenting a gracile shaft (PC1), and smaller epicondyles at the distal head. These morphologies suggest that the *A.*

sediba MC1 did not have the strength or stability to withstand the forces involved with precision grips, nor the range of motion at the TMCJ to facilitate them. Overall the results therefore align with previous research, in the sense that they present *A. sediba* as having a patchwork of primitive and derived characteristics, a few of which are indicators of an ability to use tools, but most of which suggest that this ability was incipient and certainly not comparable to the forceful precision grip abilities of humans and *H. neanderthalensis*.

6. Conclusion

The aim of this study was to quantify the 3D morphology of the first metacarpal in extant African hominoids, in order to facilitate a more informed functional interpretation of fossil hominin morphology. The results are in general agreement with previous studies on the morphology of the MC1 in extant and extinct hominids and the inferences made by them. This study found that the human MC1 is characterized by a distinct suite of traits, not present to the same extent in non-human great apes, that are consistent with an ability to use forceful precision and power grips; namely flatter proximal and distal ends, larger epicondyles at the distal head and a more robust shaft. This morphology was also found to align very closely with that of the *H. neanderthalensis* sample, supporting all the evidence that indicates that Neanderthals were functionally capable of utilizing tools in the same way as modern humans. Analysis of the *H. naledi* specimen suggested that it had a number of human-like adaptations consistent with an ability to employ advanced manipulation and was therefore likely able to use stone tools in a similar way to humans. The *A. sediba* fossil presented a number of derived MC1 features that indicate a degree of dexterity, but

448 also several traits which were more similar to the African apes (i.e., probably primitive
449 traits). Overall the results obtained both aligned with and added to past functional
450 interpretations of hominin morphology, thereby reinforcing the validity of 3DGM as a
451 method of quantifying MC1 morphology and providing a deeper insight into the
452 function and structure of the thumb in both extant hominids and fossil hominins.
453

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464 **Author contributions**

465 TAP and AB designed the study. AB and CL generated the 3D models. JM and TAP
466 analyzed the data. TAP carried out the data visualizations. All authors interpreted the
467 data and wrote the manuscript.
468

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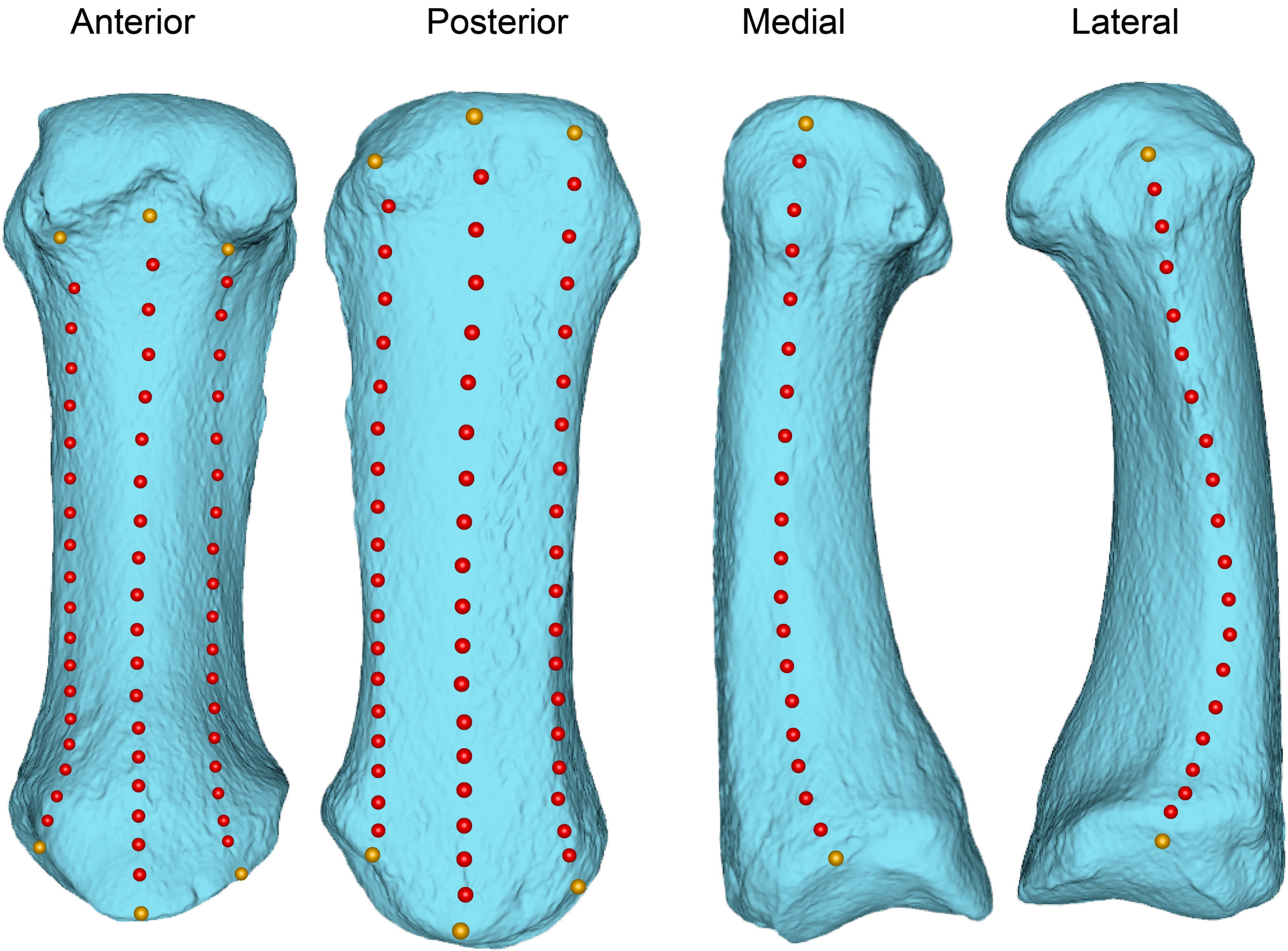

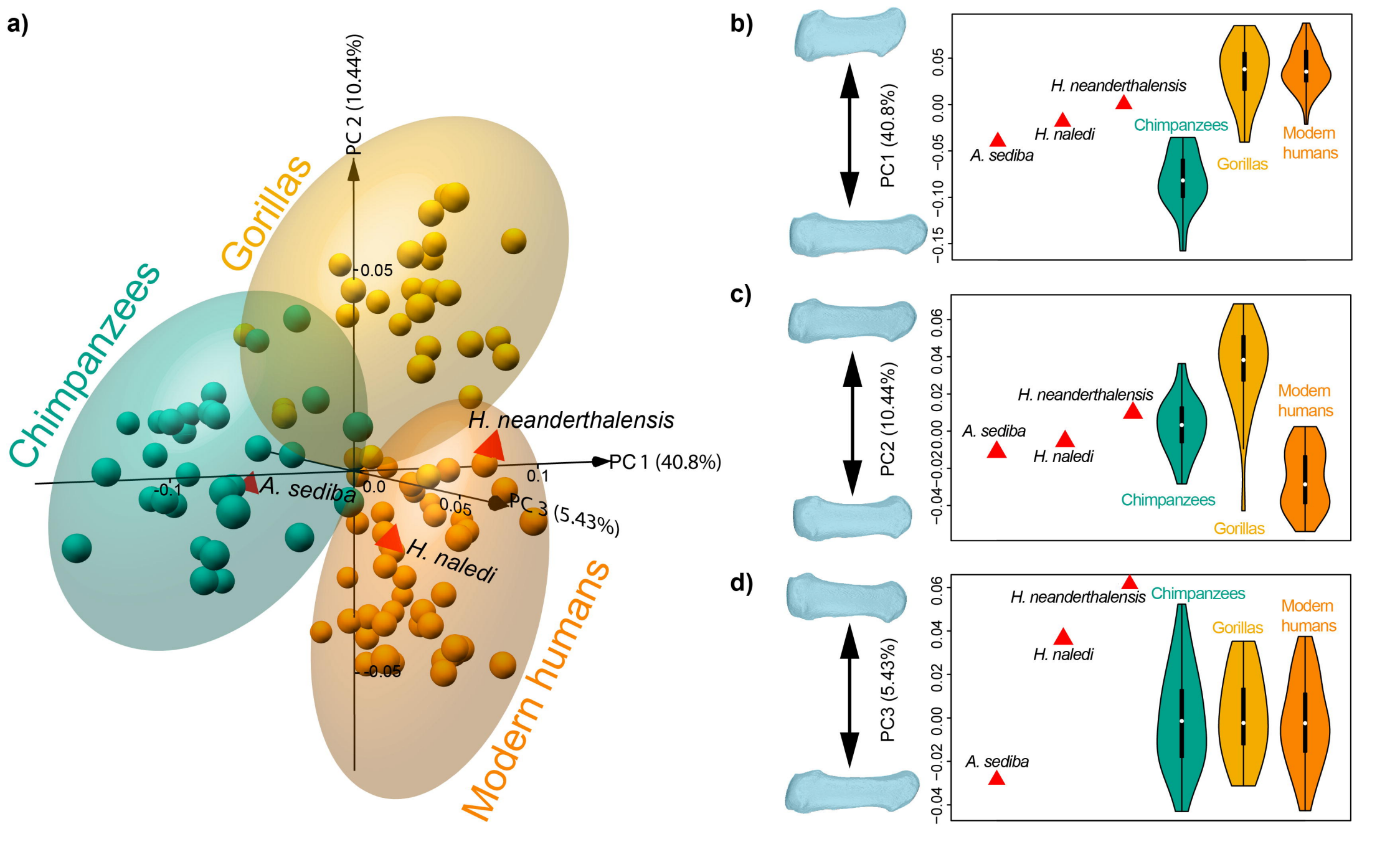
a)
PC 2 (10.44%)
PC 1 (40.8%)
PC 3 (5.43%)
Chimpanzees
Gorillas
Modern humans
H. neanderthalensis
H. naledi
A. sediba
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b)
PC1 (40.8%)
H. neanderthalensis
H. naledi
A. sediba
Chimpanzees
Gorillas
Modern humans
0.05
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−0.05
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−0.15
c)
PC2 (10.44%)
H. neanderthalensis
A. sediba
H. naledi
Chimpanzees
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Modern humans
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d)
PC3 (5.43%)
H. neanderthalensis
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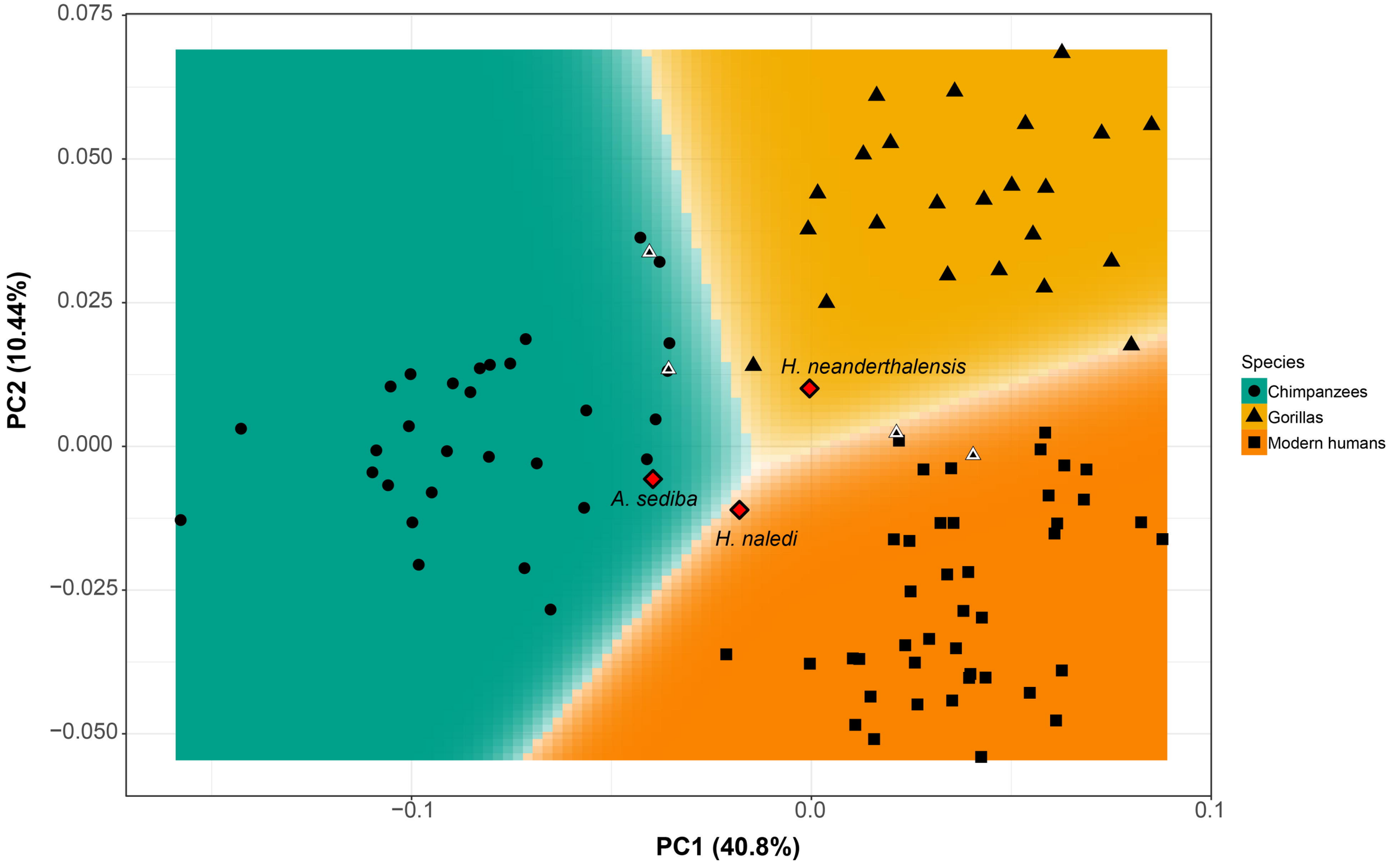
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PC2 (10.44%)
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H. neanderthalensis
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Species
Chimpanzees
Gorillas
Modern humans