Functional signals and covariation in triquetrum and hamate shape of extant primates using 3D Geometric Morphometrics.

Marie J. M. Vanhoof[1], Lorenzo Galletta[2], Isabelle De Groote[3,4], Evie E. Vereecke[1]

[1]Department of Development & Regeneration, Biomedical Sciences Group, KU Leuven Campus Kulak, Kortrijk, Belgium

[2]School of Life and Environmental Sciences, Deakin University, Waurn Pounds, Victoria, Australia

[3]Department of Archaeology, Ghent University, Belgium

[4]Research Centre in Evolutionary Anthropology and Paleoecology, Liverpool John Moores University, UK

Short title: functional signals in primate triquetrum and hamate shape

Abstract

In this study, we want to investigate the covariation in the shape of two carpal bones, the triquetrum and hamate, and the possible association with locomotor behavior in a broad range of primate taxa. We applied 3D Geometric Morphometrics on a large dataset comprising 309 anthropoid primates of 12 different genera. Principal component analyses were performed on the covariance matrix of 18 (triquetrum) and 23 (hamate) Procrustes-aligned surface landmarks. A two-block partial least square analysis was done to test the covariance between triquetrum and hamate shape, without relying on the predictive models implicit in regression analyses. The results show that the carpal shape of quadrupedal anthropoids, which mainly use their wrist under compressive conditions, differs from that of suspensory primates as their wrist is possibly subjected to tensile and torsional forces. Within the hominids, differences in shape also distinguish more terrestrial from more arboreal species. Even within the great apes, we are able to capture shape differences between species of the same genus. In combination with behavioral and biomechanical studies, the results of this research can be used to establish form-function relationships of the primate hand which will aid the functional interpretation of primate fossil remains.

Keywords: carpal – wrist – morphology – locomotion – hand

Research highlights

Primates with distinct locomotor modes show differences in triquetrum and hamate shape. A clear separation is found between monkeys and hominoids. Even within hominids, we can distinguish between more terrestrial and more arboreal species.

1 INTRODUCTION

The primate hand displays a large variety of phenotypes which reflects an equally diverse functional repertoire (Liu, Xiong, and Hu 2016; Marzke 2009; Horn 1972; Almécija, Smaers, and Jungers 2015; Williams 2010; Thompson et al. 2018). The direct interaction between the primate hand and the surrounding environment during locomotion, and the variety of irregular and discontinuous supports, increase the evolvability of the hand bones compared to the bones of the proximal limb (e.g. Hallgrimsson et al., 2002; Hamrick, 2007; Shubin et al., 1997). As the primate hand needs to accommodate a large variety of superstrate/substrate size and orientation, it is expected that the morphology of the primate hand will reflect differences in functional demands placed on the hand (Kikuchi, Takemoto, and Kuraoka 2012; Kivell, Lemelin, Richmond, and Schmitt 2016; Lewis 1989; Daver, Berillon, and Grimaud-Hervé 2012).

Adaptive signals in the morphology of primate hand bones to specific hand use have been studied extensively (e.g. Daver et al., 2012; Hayama et al., 1994; Lemelin & Schmitt, 1998; Mcmahon et al., 2015; Prime & Ford, 2016; Rein, 2019; Richmond, 2001), and have provided valuable insight into the evolutionary history of the primate hand (e.g. Almécija et al., 2015; Kivell, 2011; Lewis, 1977; Marzke & Marzke, 2000; Ricklan, 1987; Stern, Jungers, & Susman, 1995; Susman, 1979; Tocheri, Orr, Jacofsky, & Marzke, 2008). Individual features of carpal and radioulnar morphology have been associated either with wrist mobility or stability and are used to deduce hand and wrist function in fossil primate taxa (Orr, 2017; Richmond, 2001; Richmond & Strait, 2000).

Most Old and New World monkeys display the generalized mammalian condition in which the ulna articulates with the triquetrum via the ulnar styloid process (Lewis, 1972). In extant

hominoids, there is a reduction in the ulnar styloid process leading to a reduced or even absent ulnocarpal articulation (Lewis, 1989; Sarmiento, 1988a). Moreover, a triangular articular disc and semilunar meniscus partially (hylobatids and *Pan*) or fully (*Pongo*, *Gorilla*, *Homo*) block contact between the ulna and the proximal row of carpal bones (Lewis 1965; Palmer and Werner 1981; Kivell 2016). Interestingly, a reduced ulnocarpal articulation is also observed in some suspensory non-hominoid primates (e.g., spider monkeys) and even in the highly suspensory two-toed sloths (Kivell et al. 2016; Cartmill and Milton 1977; Mendel 1979). Therefore, it has been suggested that a wrist with a reduced or absent ulnocarpal articulation might be functionally linked to climbing, bridging, and suspensory behaviors as it allows greater overall wrist mobility, specifically forearm supination (Cartmill & Milton, 1977; Lewis, 1969; O'Connor, 1975; Sarmiento, 1988a). Further, it has been advocated that an increased wrist mobility might allow the power grips needed during throwing and when using tools, as seen in humans (Marzke and Marzke 2000; Marzke, Wullstein, and Viegas 1992; Wolfe, Crisco, Orr, and Marzke 2006b; Young 2003). In addition to this separation of the ulna from the proximal carpal joint (Kivell 2016; Cartmill and Milton 1977; Lewis 1989), and to avoid joint collapse and preserve stability of the proximal carpal row, the reduction of the ulnocarpal articulation likely leads to changes in the morphology of the carpal bones as well.

We expect that the ulnar reduction observed in hominoid primates has led to a reorganization of the carpus and that this signal will be most pronounced at the ulnar side. Therefore, in this study, we focus on the shape of the triquetrum and hamate, two articulating carpal bones of the ulnar column of the wrist (**Figure 1**). Although ulnar reduction is most relevant for triquetrum morphology, hamate morphology has been linked to differences in locomotor behavior in previous research, and both carpal bones have not been studied in unison. In (semi-)terrestrial cercopithecoids, the morphology of the hamate, for example the oblique orientation of the

proximodistal axis within the carpus and the relatively small hamulus (Almécija et al., 2015; Hayama et al., 1994; Thompson, 2020), allows for dorsiflexion at the carpometacarpal joints and weight transfer through the ulnar side of the wrist, which is probably linked to the frequent use of palmigrade/digitigrade hand postures during locomotion (Patel, 2009; Schmitt, 2003). In hylobatids and *Pongo*, the distally protruding hamulus facilitates ulnar deviation and flexion of the wrist, movements that are important during arboreal locomotion (Sarmiento 1988b; Almécija et al. 2015; Lewis 1977). The hamate morphology of African apes seems to reflect knuckle-walking and weight-support functions. The proximodistal axis of their hamate has a rather vertical orientation within the carpus and the triquetrum-hamate joint is spiral shaped, which has been linked to greater compressive loading and stability (Jenkins and Fleagle 1975; Kivell, Barros, and Smaers 2013). Humans do not use their hands during habitual locomotion, and the shape of their hamate is probably linked to enhanced manipulation skills and the use of different grip types to construct and manipulate tools (Marzke 2013; Young 2003; Wolfe, Crisco, Orr, and Marzke 2006a).

The irregular shapes of the carpal bones, the complex articulations within the wrist, and the intraspecific variation within carpal shape make it, however, challenging to quantify carpal shape between different primate taxa using conventional 2D linear analyses (Adams, Rohlf, and Slice 2013; Adams, Rohlf, and Slice 2004; Kivell 2011; Yazaki et al. 2008; Joshi, Leahy, Badawi, and Chaudhari 2016; Rohlf and Marcus 1993). A powerful 3D quantification of carpal shape can be done using three-dimensional geometric morphometrics (3D GM), a state-of-the-art approach in quantitative morphological studies (Mitteroecker, Gunz, Windhager, and Schaefer 2013; Adams et al. 2013; Almécija, Orr, Tocheri, Patel, and Jungers 2015; Galletta, Stephens, Bardo, Kivell, and Marchi 2019; Lockwood, Lynch, and Kimbel 2002; van Heteren, MacLarnon, Soligo, and Rae 2016).

In this study, we use 3D shape data from the triquetrum and hamate to test the following hypotheses: We hypothesize 1) that shape variation in the triquetrum and hamate will allow us to distinguish between different anthropoid primate genera and that both carpal bones will show a similar separation of the different genera given that both bones are tightly connected in the carpus. 2) We expect that triquetrum shape will covary with hamate shape and that, within this covariation, we will be able to distinguish between the different primate genera based on locomotor behavior. Finally, as 3D GM allows for a detailed quantification of the complex and variable triquetrum and hamate shape, we expect 3) to identify previously unrecognized differences in bone shape between monkey, hylobatid, and hominid genera and that some of these morphological traits can be associated with differences in locomotor behavior.

2 METHODS

2.1 Specimen collection

The sample used in this study includes the triquetrum and hamate of 309 extant anthropoid primate specimens representing 12 different genera of four taxonomic clades, including plathyrrhines *(*genus *Ateles)*, cercopithecoids *(*genera: *Macaca, Mandrillus, Papio)*, hylobatids *(*genera: *Hoolock, Hylobates, Nomascus, Symphalangus)*, and hominids *(*genera: *Gorilla, Homo, Pan, Pongo)*. For each specimen, 3D surface meshes of the left triquetrum and hamate were used and, when not available, the right triquetrum and hamate were mirrored. Only adult specimens were included and specimens with signs of pathological alterations in the postcranial skeleton were excluded from this study. Details of the sample are provided in **Table 1.**

The 3D meshes used in this study were collected from different sources (see **online supplementary material, Table S12**). The largest part of the 3D surface meshes (86% of the total sample) were obtained via collaboration with Craig Wuthrich (East Carolina University, Anatomy and Cell Biology) and Sergio Almécija (AMNH, Division of Anthropology) and were acquired using laser scanning (Nextengine, Scanstudio HD Pro). Another set of 3D meshes (10% of the total sample) was collected using medical CT-scanning of cadaver and museum specimens (with a 64 slice Discovery HD 750 CT scanner, GE Healthcare, Little Chalfont, UK; Display Field of View [DFOV]: 250 mm, slice thickness: 0.625 mm, pixel spacing: 0.293/0.293 mm, voxel size: 0.054 mm^3, 100 kV, 180 mA, 512x512). Finally, we also downloaded 3D bone meshes from online image repositories such as KUPRI and Morphosource (4% of the total sample). All raw CT-scans were edited with Mimics software (Materialise, Leuven, Belgium) to clean the meshes and fill the holes, and 3-matic software (Materialise, Leuven, Belgium) was used to standardize all triquetrum and hamate models to a similar number of vertices.

2.2 3D Geometric Morphometrics

To capture the overall shape of the triquetrum and hamate, we used fixed landmarks. On the surfaces of the 3D triquetrum and hamate models we positioned 18 and 23 landmarks, respectively, based on definitions of Sergio Almécija (Almécija et al. 2015). Full details of the landmark definitions and positioning are provided in **Figure 2** and **Table 2** and **3**. All landmark positioning was done in *Landmark Editor* software (version 3.0) (Wiley et al., 2005).

A generalized Procrustes analysis (GPA) (Dryden & Mardia, 1998; Gower, 1975) was carried out on all fixed landmark coordinates to remove the effects of variation in location, orientation, and scale from the coordinates, and superimpose the objects into a common coordinate system. These aligned shape coordinates were then subjected to a principal component analysis (PCA) to explore major patterns of shape variations (see also Polly, Lawing, Fabre, and Goswami 2013; Polly 2008; Almécija et al. 2015).

We tested for an allometric signal in the data (i.e. covariation of shape and size) by performing a procrustes ANOVA on genera using log-transformed centroid size (logCS) using the Geomorph v 3.3.1 package (Adams and Otárola-Castillo 2013). Centroid size of the 3D bone model was used as a proxy of body size as body size was unknown for most specimens. Analyses of covariance (ANCOVA) on scores along principal components (PCs), using the genera as categorical variable and size as a covariate, were used to test for significant differences across the different genera and Tukey HSD tests were used for pairwise post hoc comparisons. A Hotelling's T^2 test for the multivariate difference of means on PC1-PC4 was used to evaluate potential significant differences between species within the same genus (*Gorilla*: *G. gorilla* and *G. beringei*; *Pongo*: *P. abelii* and *P. pygmaeus*; *Pan*: *P. paniscus* and *P. troglodytes*; *Macaca*: *M. fascicularis* and *M. mulatta*; hylobatids: gibbons (*Hylobates*,

Hoolock, *Nomascus*) and siamangs (*Symphalangus*)). To correct for multiple testing, the significance level was set to $p<0.01$ for this test (Andrade, 2019).

We performed a two-block partial least squares (2B-PLS) analysis to test for covariation between triquetral and hamate shape (Marugán-Lobón, 2010; Rohlf & Corti, 2000; van Heteren et al., 2016). In 2B-PLS, in contrast to a multivariate regression, both 'blocks' are treated symmetrically rather than as one set of variables (X-axis) being used to predict variation in the other set of variables (Y-axis). The new pairs of variables represent linear combinations of variables within the original two sets ('blocks'), so that these new variables account for as much of the covariation as possible to find relationships between the two original 'blocks' without assuming that one is the cause for the variation in the other. In our study, one block represents the hamate shape (X-axis) and the other block represents the triquetral shape (Y-axis). The RV coefficient, a multivariate analogue of the squared correlation, was used as an overall measure of association between the two blocks (Escoufier, 1973), and a permutation test (10,000 alterations) was employed against the null hypothesis of complete independence.

To evaluate repeatability and accuracy of landmark placement, one individual of each extant genus (or significantly different species) was randomly selected and landmarked six times by the same researcher (MV), with at least three days between each landmarking procedure (Proctor 2010; Galletta et al. 2019). The different sets of repeated measures were subsequently subjected to a GPA and PCA, as described above. The relative clustering of these repeated measures was compared to the clustering of the whole genus, and a significant difference between both clusters (i.e. low variance between the different repeated measures) verifies the repeatability of the landmarks (Lockwood et al. 2002; Proctor, Broadfield, and Proctor 2008; Fernández et al. 2015). This was done by assessing heteroscedasticity between the repeated

measures of one individual and the rest of the genus using a multivariate correspondent of the Levene test along the first three PCs (Anderson, 2006; Galletta et al., 2019).

All statistical analyses were performed in the R environment using the Geomorph v 3.3.1 package (Adams and Otárola-Castillo 2013). R was also used to create the graphical output to interpret the results and for visualization, using the package rgl v 0.100.54 (Adler et al., 2017). The significance value was set at 0.05.

3 RESULTS

3.1 Allometric analysis and repeatability

The allometric analysis on the scores along PC1–PC4, using the genera as independent categorical variables and the log-transformed centroid size as a covariate, shows a significant effect of size on triquetrum shape (p=0.001, cor=0.60) and hamate shape (p=0.001, cor=0.80) (**supplementary online material, Figure S1**). For the triquetrum, 6.8% of the total variance is explained by size, while for the hamate this is 14.5%. Given this result, size is taken into account for the subsequent analyses and used as a covariate in the ANCOVAs. As the repeated measures are easily distinguished from the rest of the sample for all taxa and clustered in the morphospace (i.e. repeated measures are significantly different from the whole genus; p<0.001), the landmark placement is repeatable for the purposes of this study. The graphical output and statistical results of the repeatability test can be found in the supplementary online material (**Figure S1a-c, Figure S2a-c** and **Table S1**).

3.2 Significant differences between species

As no significant differences are found between *P. abelii*/*P. pygmaeus* and *M. fascicularis/M. mulatta,* the single species are pooled and all the subsequent analyses for the shape of the triquetrum (p>0.05) and hamate (p>0.05) use the *Pongo* and *Macaca* genus as groups. Both *P. paniscus* and *P. troglodytes*, as well as both species of *Gorilla* (*G. beringei* and *G. gorilla*), are treated as separate groups due to significant differences in the shape of their triquetrum (*Gorilla*: p=0.002; *Pan*: p<0.001) and hamate (*Gorilla*: p=0.02; *Pan*: p<0.001). Significant differences are also found between gibbons (*Hylobates*, *Hoolock*, *Nomascus*) and siamangs (*Symphalangus*) (triquetrum: p<0.001; hamate: p=0.04), but these are already treated as separate groups. All Hotelling's T^2 test results are provided in supplementary online material (**Table S2**).

3.3 Principal components and shapes

For the triquetrum (t), the first four PCs in the PCA account for 70% of the total variance, while for the hamate (h) this is just over 50%. When looking at the different principal components, PC1 explains 45.0% (t) and 26.5% (h) of the total variance, PC2 15.5% (t) and 13.0% (h), PC3 5.9% (t) and 7.4% (h), and PC4 4.0% (t) and 6.1% (h). The other PCs only account for a small proportion of the remaining variance and will not be discussed. For the triquetrum, assumption four about the homogeneity of variances is violated for PC1 and PC3 and is therefore adjusted according to Long and Ervin (Long & Ervin, 2000). The ANCOVAs show that for the triquetrum and hamate the different primate taxa are significantly separated along PC1-PC4 ($p < 0.001$).

A bivariate scatterplot of PC1 against PC2 for the triquetrum (**Figure 3A**) separates *Ateles* and the cercopithecoids from the other clades. Hylobatids and hominids overlap in the morphospace. The different hominid genera partially overlap in the morphospace and show the following pattern: *Pongo* and *Homo* occupy the left part, *Gorilla* and *P. troglodytes* are situated in the central part of the morphospace, while *P. paniscus* occupies the upper right quadrant. For the hamate (**Figure 3B**), the hylobatids are separated from the other groups, and monkeys partially overlap with *Ateles* and the hominids.

A bivariate scatterplot of PC1 against PC3, for both the triquetrum and hamate (**Figure 4A-B**), does not separate any of the clades in the morphospace although the hylobatids only partially overlap with the other anthropoid primates in case of the hamate. For the triquetrum, hylobatids overlap with *Pongo* and *Homo*, while the cercopithecoids overlap with *P. paniscus*. For the hamate, cercopithecoids overlap with *Pan* and *Ateles*.

A bivariate scatterplot of PC1 against PC4 shows (high) overlap between the different clades, only separating the hylobatids from the other clades for the hamate, and is therefore not

discussed in the main text (**supplementary online material, Figures S2-S3 and Tables S6 and S10**).

When looking at the boxplots of PC1 (**Figure 5A**), the shape variations of the triquetrum allow us to visually distinguish four groups: 1) cercopithecoids; 2) *Ateles* and *P. paniscus*; 3) *Gorilla* and *P. troglodytes*; 4) *Homo*, *Pongo*, and the hylobatids. *Homo* is significantly different from every other genus, with the exception of *Symphalangus*, and *Hoolock* (**supplementary online material, Table S3**). Group 1, 2, and 3, with little overlap between these groups, occupy the positive side of the PC1 axis which describes a triquetrum shape that is proximodistally long and mediolaterally narrow, and the facet for the ulna has a deeper cup-like structure. The pisiform facet is proximopalmarly oriented. The negative side of PC1 is occupied by *Homo*, *Pongo* and the hylobatids, and the latter two overlap in the morphospace and are not significantly different. Their triquetrum is proximodistally short, mediolaterally wide, and has a flatter articular facet for the ulna. The facet for the pisiform is located more distally. *Pongo* is further distinguished from the hylobatids by a larger hamate facet. Among the African apes (*Gorilla* and *Pan*), *P. paniscus* is significantly different from *G. beringei* ($p<0.001$) and *G. gorilla* ($p<0.001$), a result also found for PC3 (**supplementary online material, Table S5**).

For the hamate (**Figure 5B**), the shape variations separate five groups: 1) *Gorilla*; 2) *Homo*; 3) *Pan* and the cercopithecoids; 4) *Ateles* and *Pongo*; 5) hylobatids. Among the African apes, all genera are significantly different from each other ($p<0.001$), with the exception of *G. beringei* and *G. gorilla* (**supplementary online material, Table S7**). *Gorilla* is situated on the positive side of the PC1 axis, with *Homo* situated near this positive extreme. *Homo* is significantly different from every other genus, with the exception of *Macaca* and *Mandrillus*. The proximodistal axis of the hamate of *Gorilla* and *Homo* shows a more vertical orientation in the carpus compared to that of the other primates. The hamate is proximodistally short,

mediolaterally and dorsopalmarly wide, and shows an S-shape on the medial side (i.e. spiral triquetrum-hamate articulation). The negative side of PC1 is occupied by the hylobatids, while the *Ateles* specimens are near the negative extreme and slightly overlap with the hylobatids. The hamate of *Ateles* and the hylobatids is proximodistally long, and mediolaterally and dorsopalmarly more narrow compared to the hamate of *Gorilla*. The medial side is oriented obliquely in the carpus, and the facet for the fifth metacarpal projects more distally compared to that of the fourth metacarpal.

The boxplots of PC2 of the triquetrum (**Figure 6A**) distinguish four groups: 1) *Pan*; 2) *Gorilla*, *Homo*, and *Nomascus*; 3) *Hoolock*, *Hyobates*, *Symphalangus*, cercopithecoids, and *Pongo*; 4) *Ateles*. All African apes are significantly different from each other ($p<0.05$; **supplementary online material, Table S4**). *Pongo* is significantly different from *Hylobates* ($p<0.001$), and within hylobatids, *Nomascus* is significantly different from *Hylobates* and *Hoolock* ($p<0.001$). Group 3 and 4, with no overlap between both groups, occupy the negative side of the PC2 axis and have a triquetrum that is proximodistally longer with a more concave ulnar facet. The facet for the pisiform is located more proximopalmarly in *Ateles* compared to that of cercopithecoids and hominoids. The triquetrum of the genus *Pan* is characterized by positive PC2 values which correspond to a triquetrum that is proximodistally short and dorsopalmarly narrow. The pisiform facet is located more distally, and the ulnar facet is flatter than in the other studied genera.

For the hamate, the shape variations distinguish three groups: 1) *Ateles* and cercopithecoids; 2) *Homo*; 3) hylobatids, *Pongo*, and great apes. *Pongo* is significantly different from the hylobatids ($p<0.05$), with the exception of *Nomascus* (**supplementary online material, Table S8**). The third group, characterized by negative PC2 values, corresponds to a mediolaterally narrow hamate with a large hamulus that projects distally. The facet for the fifth metacarpal is

mediolaterally narrow relative to the facet for the fourth metacarpal. The triquetral facet is dorsopalmarly wide proximally, but narrows distally. The hamate of the first group is characterized by positive PC2 values, and overlaps with the PC2 values of *Homo*, which correspond to a hamate with a mediolaterally wide body and a smaller hamulus. The facet for the fifth metacarpal is larger compared to that of the fourth metacarpal, and it extends onto the hamulus. The triquetral facet is wide at its midpoint, and dorsopalmarly more narrow at the proximal and distal side than that of the hominoid triquetrum.

When looking at the boxplots of PC3, no clearly distinct groups can be identified (**Figure 7A**). *Ateles* is significantly different from all other genera ($p<0.001$), except *Gorilla* and *Symphalangus* (**supplementary online material, Table S5**). These genera, together with *Hylobates*, *Hoolock*, and *P. troglodytes*, are characterized by negative PC3 values. This corresponds to a proximodistally short triquetrum with a convex palmar side. The other genera (cercopithecoids, *Homo*, *P. paniscus*, *Pongo*, and *Nomascus*) are characterized by positive PC3 values, which corresponds to a triquetrum that is proximodistally long. The pisiform facet is rotated to the medial side, which results in a more concave facet for the ulna. For the hominids, *Homo* is significantly different from *Gorilla* and *P. troglodytes* ($p<0.001$), but not from *Pongo* and *P. paniscus*. Within the hylobatids, *Symphalangus* is significantly different from *Hoolock* and *Nomascus*.

For the hamate (**Figure 7B**), *Homo* and *Pongo* are significantly separated from the other taxa (**supplementary online material, Table S9**) and are characterized by positive PC3 values, together with *Hoolock*, which correspond to a hamate that is slightly longer proximodistally. The hamulus is also shorter, and the facet for the fourth and fifth metacarpal is more square-shaped than that of the hamate of the other groups. The other genera (cercopithecoids, *Gorilla*, *Pan*, *Hylobates*, *Nomascus*, *Symphalangus*, and *Ateles*) are characterized by negative PC3

values, which corresponds to a hamate that is slightly shorter proximodistally. The hamulus, as well as the facet for the fifth metacarpal, projects distally. Within the hylobatids, *Hylobates* is significantly different from *Hoolock* ($p<0.001$) and *Symphalangus* ($p<0.001$).

3.4 Covariation between triquetrum and hamate shape

The results of the 2B-PLS analysis show that there is a strong and significant overall association between triquetrum shape and hamate shape (RV=0.74; p=0.001). The results for the three PLS axes, which account for 90.1% of the total covariation, can be found in **Figure 8** and **supplementary online material, Figure S11 Table S7**. Cercopithecoids, *Pan*, and *Gorilla* are grouped on the lower left quadrant (negative values) of PLS1, which explains 63.8% of the total covariation. These negative values correspond to a 'blocky' triquetrum (proximodistally long and mediolaterally narrow), a proximally situated pisiform facet, and a concave facet for the ulna, in combination with a proximodistally short and mediolaterally wide hamate with a short hamulus and distally projecting facet for the fifth metacarpal. In contrast, hylobatids and *Pongo* fall in the upper right quadrant (positive values) and are characterized by a cylindrically-shaped triquetrum (proximodistally short and mediolaterally wide) with a more distally projecting pisiform facet and a proximodistally long and mediolaterally narrow hamate with a distally projecting hamulus.

Along PLS2, which explains 26.4% of the total covariation, African great apes and *Homo* fall in the lower left quadrant (negative values) and are characterized by a dorsopalmarly wide triquetrum with a distally located pisiform facet. The hamate is proximodistally short with a distally projecting hamulus, and the medial border of the hamate body is S-shaped. The fifth metacarpal facet is smaller compared to that for the fourth metacarpal, and both facets project as far distally. Cercopithecoids and *Ateles* fall in the upper right quadrant (positive values), which correspond to a proximodistally long triquetrum with a small facet for the lunate, a more

proximally projecting pisiform facet, and a concave facet for the ulna. The hamate is proximodistally long with a short hamulus, and a C-shaped medial border. Both metacarpal facets are comparable in size, but the facet for the fifth metacarpal projects more distally. PLS3 explains only 3.8% of the total covariation and will not be discussed in the main text (**supplementary online material, Figure S4**).

4 DISCUSSION

In this study, the shape variability of the triquetrum and hamate of 12 different primate genera (309 specimens) is quantified using 3DGM. A summary of the differences of triquetrum and hamate shape can be found in **Table 4**. The eigenvalues and factor loadings can be found in the **online supplementary material, Tables S13-15**.

4.1 Major patterns of triquetrum and hamate shape

We hypothesized that is it possible to distinguish between the different primate genera relying solely on major differences of triquetrum and hamate shape, and that both carpal bones will show a similar separation. While triquetrum and hamate shape does allow us to distinguish between some primate genera, other genera within the same clade as well as genera of different clades, show some overlap in the morphospace (**Figures 3** and **4**). Moreover, this overlap is different for both carpal bones. Looking at the two major axes of variation (**Figure 3**), the triquetrum of the hominids is separated from that of monkeys (cercopithecoids and *Ateles*) but overlaps with that of the hylobatids. In contrast, the hamate of hominids is easily distinguished from that of the hylobatids, and only slightly overlaps with the cercopithecoids. Comparing shape variation between the bones is hampered, however, by the different coordinate system of the principal components and the different number of fixed landmarks.

For both the triquetrum and hamate there is a significant effect of size on shape. It could be argued that some differences in locomotor behavior between the different primate genera are associated with body mass. For example, in hylobatids, brachiation is not only facilitated by their long arms, slender hook-like hands, and a ball-and-socket wrist joint, but also because they are relatively small primates (Schwartz and Yamada 1998; Preuschoft and Demes 1985; Bartlett, Light, and Brockelman 2016; Michilsens, Vereecke, D'août, and Aerts 2009; Marzke 2009). However, only a small part of the total variance is explained by size, so the observed

shape differences between the different primate genera are not simply explained by size alone but will also show influence of locomotion and/or phylogeny and/or manipulation/grip types.

4.2 Covariation between triquetrum and hamate shape and locomotor signal

We hypothesized that triquetrum shape would covary with hamate shape and that within this covariation we would be able to distinguish between the different primate genera based on locomotor behavior. Indeed, when looking at the results of the 2B-PLS analysis, we find clear support for our second hypothesis as there is a strong covariation between triquetrum and hamate shape.

Ateles and the cercopithecoids are characterized by negative PLS1 values (cercopithecoids are the negative extreme) and positive PLS2 values (*Ateles* are the positive extreme). This corresponds to a blocky triquetrum (mediolaterally narrow and proximodistally long) with a concave ulnar facet. The pisiform facet is most proximally located in cercopithecoids, compared to the other studied primates, and slightly more distally in *Ateles*. The corresponding hamate shape shows a hamate with a short hamulus, a wide body (proximodistally short and mediolaterally wide), and a distally projecting facet for the fifth metacarpal, although it projects slightly less distally in *Ateles*.

Pongo and hylobatids are characterized by positive PLS1 and PLS2 values. They have a cylindrically shaped triquetrum (mediolaterally wide and proximodistally short) with a relatively flat ulnar facet and distally located pisiform facet. The hamate that corresponds with this triquetral shape is mediolaterally narrow and proximodistally long and the hamulus projects distally, but the facet for the fifth metacarpal does not extend as far distally, relative to the fourth metacarpal, as it does in cercopithecoids and *Ateles*.

The African apes are located at the negative side of PLS1 and PLS2 (negative extreme). These values correspond to a blocky triquetrum similar to that of the cercopithecoids, but with a pisiform facet that is located slightly more distally, a less concave ulnar facet and a

dorsopalmarly wide hamate facet. The African ape hamate is similar to that of *Ateles*, but it is proximodistally shorter, the hamulus projects more distally, and the facet for the fifth metacarpal is smaller compared to that of the fourth metacarpal.

Homo is characterized by positive PLS1 values and negative PLS2 values, and their triquetrum and hamate shape is situated in between the African apes and *Pongo* on both PLS axes.

In the following paragraphs, the differences in triquetrum and hamate shape that distinguish the different primate genera are discussed in detail within the context of locomotor behavior.

4.3 Locomotor groups and carpal shapes

For the (semi-)terrestrial cercopithecoids, our findings are in line with the results of previous research (Kivell, Barros, and Smaers 2013; Sarmiento 1988). The oblique orientation of the hamate within the carpus, and the proximally-oriented facet for the triquetrum forms a stable platform which enables weight transfer through the ulnar side of the wrist in combination with the blocky triquetrum and fully elaborated ulnocarpal articulation (reflected by a concave ulnar facet; Corruccini, 1978; Lewis, 1972, 1989; Sarmiento, 1988a). The smaller hamulus and the extension of the fourth and fifth metacarpal facets onto the hamulus facilitate dorsiflexion at the carpometacarpal joints (Almécija et al. 2015), while the distally projecting facet for the fifth metacarpal allows for hyperextension at the metacarpophalangeal joint (Hayama et al., 1994; Thompson, 2020). When the triquetrum and pisiform are fully articulated, the proximopalmarly oriented pisiform facet gives the *m. flexor carpi ulnaris* (FCU), the most important muscle during wrist flexion and ulnar deviation, an optimal lever arm to counteract the stress on the ulnar side of the wrist during quadrupedal locomotion (Sarmiento 1988; Vanhoof, van Leeuwen, Galletta, and Vereecke 2020). These morphological features are most likely linked to the use of palmigrade/digitigrade hand postures during quadrupedal locomotion as seen in the cercopithecoid taxa (Hayama et al., 1994; Higurashi et al., 2018; Patel, 2009; Patel & Polk, 2010; Schmitt, 2003). Although *M. mulatta* is more terrestrial compared to *M. fascicularis*

(Cant, 1988; Dunbar, 1989; Fleagle, 1980; Rawlins, 1982; Rodman, 1979), no significant differences in shape were found between both species within the cercopithecoids.

For the highly arboreal hylobatids and *Pongo*, we find a similar shape of the triquetrum and hamate, as illustrated by the PCA results, which is consistent with previous studies (Almécija et al., 2015; Kivell et al., 2013; Sarmiento, 1988). The distal migration of the pisiform, in combination with the distally protruding hamulus of the hamate in hylobatids and *Pongo* increases the lever arm of the FCU, facilitating ulnar deviation and flexion of the wrist (Sarmiento 1988; Vanhoof, van Leeuwen, and Vereecke 2020). The cylindrical shape and a relatively flat ulnar articular surface of the triquetrum, increases the amount of 'gliding' possible between the ulnar styloid and the carpus. These changes in wrist morphology allow for a large amount of forearm pro-supination and ulnar deviation of the wrist, which are both important during arboreal locomotion (Lewis 1977; Sarmiento 1988; Almécija et al. 2015). However, hylobatids and *Pongo* also show some previously unrecognized differences in triquetrum and hamate shape that can be linked to their differences in locomotor behavior. The proximal facet of the triquetrum of *Pongo*, who do not display gibbon-like brachiation, has a more concave shape, and this shape is significantly different compared to that of *Hylobates* and *Symphalangus*. The hamate of *Pongo* is dorsopalmarly wider and has a slightly longer hamulus compared to the hylobatids. In addition, a semilunar meniscus fully blocks contact between the ulna and the carpus in *Pongo* and aids in weight transfer through the ulnar side of the wrist (Kivell et al. 2016). All these morphological characteristics could be important during the use of a fist-walking position, in which hand is loaded through the ulnar side as it is held in an ulnarly deviated and dorsiflexed position. The distal position of the triquetrum in the *Pongo* carpus also contributes to the high range of motion of the wrist (Isler & Thorpe, 2003). As it is

fully cupped by the lunate, the triquetrum glides on the proximal carpal row rather than rotating alongside it when the wrist dorsiflexes (Orr, 2017).

Unique among the primates, is the ball-and-socket midcarpal joint of the hylobatids, which accommodates for the large wrist mobility that is used in ricochetal brachiation, a highly specialized form of brachiation that includes a true flight phase between each contact with a handhold (Fleagle, 1976b; Tuttle, 1969). While this ball-and-socket morphology has since long been acknowledged (Lewis, 1977), we were able to identify differences in carpal shape between hylobatid genera that have not been reported before. For example, we found shape differences in the triquetrum of *Symphalangus* compared to that of *Hoolock* and *Nomascus*. The latter show a deeper cup-like articulation surface for the ulna, probably important to protect the wrist against hypermobility during their frequent use of ricochetal brachiation, while *Symphalangus* have a triquetrum that is dorsopalmarly wider, which forms a stable platform for weight transfer through the ulnar side of the wrist more like that of the great apes. *Symphalangus* do not use ricochetal brachiation and their locomotor repertoire includes more climbing than observed in other hylobatid genera (Fleagle, 1976a), which seems to correlate to the more hominid-like shape of their triquetrum. The higher body weight of *Symphalangus* compared to the other gibbons (on average 12kg versus 6kg) also has an influence on the forces exerted on the wrist during climbing and brachiation. Given the small sample size of the different hylobatid genera we should, however, be cautious when interpreting these results.

Ateles show a convergent forelimb morphology to the hylobatids, which has been related to their frequent use of suspensory locomotion (Schmidt, 2011), and this is also observed in their triquetrum and hamate shape. They show a distopalmarly position of the pisiform facet on the triquetrum, and a proximodistally long and more narrow hamate with an obliquely oriented medial side, traits that allow for a high wrist mobility – especially forearm rotation – that is

used in suspensory locomotion, climbing, and clambering (Cant, 1986; Rosenberger et al., 2008; Youlatos, 1996). However, unlike hylobatids, the ulnar facet on the triquetrum is concave, the distal ulna directly articulates with the triquetrum, the hamulus of the hamate is smaller, and the facet for the fifth metacarpal projects distally over that of the fourth metacarpal. These morphological traits are similar to those of the cercopithecoids, and might be important for providing stability on the ulnar carpus during palmigrade quadrupedal walking and running (Mittermeier, 1978; Mittermeier & Fleagle, 1976; Vilensky & Larson, 1989).

The hand morphology of African great apes is linked to knuckle-walking and weight-support functions, and this is reflected in the shape of the triquetrum. Like the cercopithecoids, African great apes are characterized by a robust triquetrum, but their pisiform facet is located more distally (although less distally compared to the hylobatids and *Pongo*). Their hamate is proximodistally short and dorsopalmarly wide, with a distally projecting hamulus which protrudes palmarly, and shows a more vertical orientation within the overall carpus compared to cercopithecoids, but also compared to hylobatids and *Ateles* (Almécija et al. 2015). The facet for the fifth metacarpal is smaller compared to the facet for the fourth metacarpal, and does not extend as far distally beyond the fourth as it does in monkeys and hylobatids, which creates a more complex and stable articulation that limits sliding and rotation at these joints (Kivell et al. 2016). The more pyramidal shape of the triquetrum and the spiral triquetrum-hamate articulation are probably linked to greater compressive loading and stability (Jenkins and Fleagle 1975; Kivell et al. 2013), while the palmarly protruding hamulus enables palmar flexion. The proximal facet is flatter compared to cercopithecoids and, in combination with the retraction of the ulnar styloid process, possibly enables a larger degree of ulnar deviation, although macaques also appear to have a large degree of ulnar deviation (Jouffroy & Medina, 2002). All these morphological traits can be linked to their frequent use of knuckle-walking

behavior. Within the African apes, differences in triquetrum and hamate shape are observed between *Pan* and *Gorilla*, which might be related to differences in hand positioning during knuckle-walking. Chimpanzees and bonobos mainly load the dorsum of digits 2 and 3, thus partially freeing the hamate from compressive constraints, while gorillas support their body weight on digits 2 to 5 which fully loads the hamate (Matarazzo, 2013; Wunderlich & Jungers, 2009). The substantially higher body weight of *Gorilla* compared to Pan will further increase the loading of the hamate. To enable load transmission through the ulnar side of the wrist, *Gorilla* have a more robust hamate with a triquetral facet that is nearly parallel to the articular surfaces of the metacarpals. The ulnar facet of the triquetrum is more concave in *Pan* compared to *Gorilla*, which might explain why *Gorilla* tend to use more dorsiflexed wrist postures throughout the stance phase of knuckle-walking (Finestone et al., 2018). For the genus *Pan*, bonobos (*P. paniscus*) and chimpanzees (*P. troglodytes*) are significantly different for both triquetrum and hamate shape which might be associated with differences in locomotor behavior, given their close phylogenetic relationship and similar body size. Bonobos travel substantial distances arboreally, while chimpanzees mostly travel terrestrially between feeding and resting sites (Doran, 1993). Triquetrum and hamate shape of bonobos is also more similar to that of the more arboreal western gorillas (*Gorilla gorilla*) who use significant amounts of vertical climbing (Remis, 1995; Doran and McNeilage, 1998). In contrast, the triquetrum and hamate of chimpanzees, which can vary substantially in their frequency of terrestriality versus arboreality depending on the population, subspecies, or developmental stage (Pontzer & Wrangham, 2004; Sarringhaus et al., 2014), are more similar to that of the eastern gorillas (*Gorilla beringei*), which comprises the Grauer gorillas (*Gorilla beringei graueri*), with both highland and lowland populations, and the more terrestrial mountain gorillas (*Gorilla beringei beringei*) (Neufuss, Robbins, Baeumer, Humle, and Kivell 2018; Knigge, Tocheri, Orr, and Mcnulty 2015; Tocheri et al. 2011; Doran 1997; Doran and McNeilage 1998).

For *Homo*, the shape of the triquetrum and hamate should be interpreted in the light of their enhanced manipulation skills since humans do not use their hands during habitual locomotion. The flat articular surface of the triquetrum for the ulna, in combination with a short ulnar styloid process and triangular fibrocartilage complex that fully blocks contact between the ulna and the rest of the carpus, enables a large amount of ulnar deviation and forearm supination which might allow for the power grips associated with, for example, tool making and use or throwing (Marzke et al. 1992; Wolfe, Crisco, Orr, and Marzke 2006a; Young 2003). For the hamate, the *m. flexor digiti minimi* and *m. opponens digiti minimi* originate from the palmarly extended hamulus and insert on the ulnar side of the fifth metacarpophalangeal joint. As these muscles act in flexion and opposition of the fifth digit towards the other fingers, a good lever arm (provided by the hamulus) facilitates the cupping of the hand, which on its turn improves the ability to form a variety of grips that are employed to construct and manipulate tools (Marzke 2013; Young 2003; Wolfe et al. 2006b). In addition, the articular surface for metacarpal four and five is much flatter compared to the African apes, and the fourth metacarpal facet is smaller compared to the fifth metacarpal facet. This is probably related to greater loading of the ulnar digits and allowing slight rotation of the fifth digit during flexion as it opposes the thumb during forceful power-squeeze grips (Marzke et al. 1992; Marzke 1997; Orr et al. 2013).

5 Conclusions

In this study, we quantified the triquetrum and hamate shape of different anthropoid primate taxa and demonstrated a significant covariation between the shape of these carpals as well as a clear link with locomotor behavior.

The shape analyses of the triquetrum and hamate show a clear separation between monkeys (*Ateles* and the cercopithecoids) and hominoids (hylobatids, great apes, and humans). Cercopithecoids are characterized by a 'block-shaped' triquetrum with a proximopalmarly orientation of the pisiform facet and concave articular surface for the ulna, and a hamate with a small hamulus and oblique orientation relative to the full carpus, as possible adaptation to quadrupedal palmigrade and/or digitigrade hand postures. Arboreal primates, like *Pongo* and hylobatids, have a cylindrically shaped triquetrum with a flatter ulnar facet and more narrow and proximodistally long hamate with a large and distally projecting hamulus, to enable the larger wrist mobility needed for suspensory behaviors. Within the hominids, we were even able to capture differences between the different genera. The triquetrum and hamate shape of bonobos (*Pan paniscus*) is similar to that of western gorillas (*Gorilla gorilla*), while chimpanzees (*Pan troglodytes*) show a similar triquetrum and hamate shape to eastern gorillas (*Gorilla beringei*). The difference between both species of *Pan*, and the similarities with the different *Gorilla* species, could be explained by differences in locomotor behavior and the proportion of arboreality versus terrestriality.

In contrast to nonhuman primates, where we observe a link with locomotor behavior, the shape of the human triquetrum and hamate is most likely linked to the enhanced manipulation skills.

Acknowledgements

The authors thank the different zoos and institutes which provided the primate specimens: Pieter Cornillie (Ghent University, campus Merelbeke), Koen Nelissen (KU Leuven, campus Gasthuisberg), François Druelle (Zoological and Botanical Park of Mulhouse, France), Robby Van der Velden (Pakawi Park, Belgium), Sergio Almécija (American Museum of Natural History, Division of Anthropology, New York), Emmanuel Gilissen (Royal Museum for Central Africa, Belgium), Pierre de Wit (Adventure Zoo Emmen, the Netherlands). Furthermore, we thank dr. Olivier Vanovermeire and Henk Lacaeyse from the Medical Imaging Department, AZ Groeninge (Kortrijk, Belgium) for CT-scanning of the specimens. Finally, we would like to thank the students who assisted during segmentation of the CT scan images. Funding for this project was obtained from KU Leuven (project C14/16/082).

Author contributions

EEV and MJMV conceived and designed the study; MJMV performed the data collection and landmarking; MJMV and LG performed the data analysis; MJMV, LG, ID, and EEV interpreted the data and wrote the manuscript; all authors reviewed and approved the final manuscript.

References

Adams, D. C., & Otárola-Castillo, E. (2013). Geomorph: An r package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution*, *4*(4), 393–399. https://doi.org/10.1111/2041-210X.12035

Adams, D. C., Rohlf, J. F., & Slice, D. E. (2004). Geometric morphometrics: Ten years of progress following the 'revolution.' *Italian Journal of Zoology*, *71*(1), 5–16. https://doi.org/10.1080/11250000409356545

Adams, D. C., Rohlf, J. F., & Slice, D. E. (2013). A field comes of age: geometric morphometrics in the 21 st century. *Hystrix, the Italian Journal of Mammalogy*, *24*(1), 7–14. https://doi.org/10.4404/hystrix-24.1-6283.

Adler, D., Murdoch, D., Nenadic, O., Urbanek, S., Chen, M., Beghardt, A., Bolker, B., Csardi, G., Strzelecki, A., Senger, A., & Eddelbuettel, D. (2017). *Rgl: 3D visualization using OpenGL, R package*. https://cran.r-project.org/package=rgl

Almécija, S., Orr, C. M., Tocheri, M. W., Patel, B. A., & Jungers, W. L. (2015). Exploring Phylogenetic and Functional Signals in Complex Morphologies: The Hamate of Extant Anthropoids as a Test-Case Study. *Anatomical Record*, *298*(1), 212–229. https://doi.org/10.1002/ar.23079

Almécija, S., Smaers, J. B., & Jungers, W. L. (2015). The evolution of human and ape hand proportions. *Nature Communications*, *6*(1), 1–11. https://doi.org/10.1038/ncomms8717

Anderson, M. J. (2006). Distance-Based Tests for Homogeneity of Multivariate Dispersions. *Biometrics*, *62*(1), 245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x

Andrade, C. (2019). Multiple Testing and Protection Against a Type 1 (False Positive) Error Using the Bonferroni and Hochberg Corrections. *Indian Journal of Psychological Medicine*, *41*, 99–100.

Bartlett, T. Q., Light, L. E. O., & Brockelman, W. Y. (2016). Long-term home range use in white-handed gibbons (Hylobates lar) in Khao Yai National Park, Thailand. *American Journal of Primatology*, *78*(2), 192–203. https://doi.org/10.1002/ajp.22492

Cant, J. G. H. (1986). Locomotion and Feeding Postures of Spider and Howling Monkeys: Field Study and Evolutionary Interpretation. *Folia Primatologica*, *46*(1), 1–14. https://doi.org/10.1159/000156232

Cant, J. G. H. (1988). Positional behavior of long-tailed Macaques (Macaca fascicularis) in Northern Sumatra. *American Journal of Physical Anthropology*, *76*(1), 29–37. https://doi.org/10.1002/ajpa.1330760104

Cartmill, M., & Milton, K. (1977). The lorisiform wrist joint and the evolution of "brachiating" adaptations in the hominoidea. *American Journal of Physical Anthropology*, *47*(2), 249–272. https://doi.org/10.1002/ajpa.1330470206

Corruccini, R. S. (1978). Comparative osteometrics of the hominoid wrist joint, with special reference to knuckle-walking. *Journal of Human Evolution*, *7*(4), 307–321. https://doi.org/10.1016/S0047-2484(78)80072-4

Daver, G., Berillon, G., & Grimaud-Hervé, D. (2012). Carpal kinematics in quadrupedal monkeys: Towards a better understanding of wrist morphology and function. *Journal of Anatomy*, *220*(1), 42–56. https://doi.org/10.1111/j.1469-7580.2011.01448.x

David Polly, P., Michelle Lawing, A., Fabre, A. C., & Goswami, A. (2013). Phylogenetic principal components analysis and geometric morphometrics. *Hystrix*, *24*(1). https://doi.org/10.4404/hystrix-24.1-6383

Doran, D.M. (1993). Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion. *American Journal of Physical Anthropology*, *91*(1), 83–98. https://doi.org/10.1002/ajpa.1330910106

Doran, D.M. (1997). Ontogeny of locomotion in mountain gorillas and chimpanzees. *Journal of Human Evolution*, *32*(4), 323–344. https://doi.org/10.1006/jhev.1996.0095

Doran, D.M., & McNeilage, A. (1998). Gorilla ecology and behavior. *Evolutionary Anthropology: Issues, News, and Reviews*, *6*(4), 120–131. https://doi.org/10.1002/(SICI)1520-6505(1998)6:4

Dryden, I., & Mardia, K. (1998). *Statistical Shape Analysis*. Wiley.

Dunbar, D. C. (1989). Locomotor behavior of rhesus macaques (Macaca mulatta) on Cayo Santiago. *Puerto Rico Health Sciences Journal*, *8*(1), 79–85. http://www.ncbi.nlm.nih.gov/pubmed/2780972

Escoufier, Y. (1973). Le Traitement des Variables Vectorielles. *Biometrics*, *29*(4), 751. https://doi.org/10.2307/2529140

Fernández, P. J., Almécija, S., Patel, B. A., Orr, C. M., Tocheri, M. W., & Jungers, W. L. (2015). Functional aspects of metatarsal head shape in humans, apes, and Old World monkeys. *Journal of Human Evolution*, *86*, 136–146. https://doi.org/10.1016/j.jhevol.2015.06.005

Finestone, E. M., Brown, M. H., Ross, S. R., & Pontzer, H. (2018). Great ape walking kinematics: Implications for hominoid evolution. *American Journal of Physical Anthropology*, *00*, 1–13. https://doi.org/10.1002/ajpa.23397

Fleagle, J. G. (1976a). Locomotion and posture of the malayan siamang and implications for hominoid evolution. *Folia Primatologica*, *26*(4), 245–269. https://doi.org/10.1159/000155756

Fleagle, J. G. (1976b). Locomotion and posture of the Malayan siamang and implications for hominoid evolution. *Folia Primatol (Basel)*, *26*(4), 245–269. https://doi.org/10.1159/000155756

Fleagle, J. G. (1980). Locomotion and Posture. In *Malayan Forest Primates* (pp. 191–208). Springer US. https://doi.org/10.1007/978-1-4757-0878-3_7

Galletta, L., Stephens, N. B., Bardo, A., Kivell, T. L., & Marchi, D. (2019). Three-dimensional geometric morphometric analysis of the first metacarpal distal articular surface in humans, great apes and fossil hominins. *Journal of Human Evolution*, *132*, 119–136. https://doi.org/10.1016/j.jhevol.2019.04.008

Gower, J. C. (1975). Generalized procrustes analysis. *Psychometrika*, *40*(1), 33–51. https://doi.org/10.1007/BF02291478

Hallgrimsson, B., Willmore, K., & Hall, B. K. (2002). Canalization, developmental stability, and morphological integration in primate limbs. *American Journal of Physical Anthropology*, *119*(S35), 131–158. https://doi.org/10.1002/ajpa.10182

Hamrick, M. (2007). Evolvability, limb morphology, and primate origins. In M. Ravosa & M. Dagosto (Eds.), *Primate Origins: Adaptations and Evolution* (pp. 381–396). Springer Science & Business Media.

Hayama, S., Chatani, K., & Nakatsukasa, M. (1994). The Digitigrade Hand and Terrestrial Adaptation in Japanese Macaques. *Anthropological Science*, *102*, 115–125.

Higurashi, Y., Goto, R., & Kumakura, H. (2018). Intra-individual variation in hand postures during terrestrial locomotion in Japanese macaques (Macaca fuscata). *Primates*, *59*(1), 61–68. https://doi.org/10.1007/s10329-017-0619-6

Horn, R. N. van. (1972). Structural Adaptations to Climbing in the Gibbon Hand. *American Anthropologist*, *74*(3), 326–334. https://doi.org/10.1525/aa.1972.74.3.02a00050

Isler, K., & Thorpe, S. K. S. (2003). Gait parameters in vertical climbing of captive, rehabilitant and wild Sumatran orang-utans (Pongo pygmaeus abelii). *Journal of Experimental Biology*, *206*(22), 4081–4096. https://doi.org/10.1242/jeb.00651

James Rohlf, F., & Marcus, L. F. (1993). A revolution morphometrics. *Trends in Ecology & Evolution*, *8*(4), 129–132. https://doi.org/10.1016/0169-5347(93)90024-J

Jenkins, F., & Fleagle, J. (1975). Knuckle-walking and the functional anatomy of the wrist in living apes. In R. Tuttle (Ed.), *Primate functional morphology and evolution* (pp. 213–227). Mouton & Co.

Joshi, A. A., Leahy, R. M., Badawi, R. D., & Chaudhari, A. J. (2016). Registration-based morphometry for shape analysis of the bones of the human wrist. *IEEE Transactions on Medical Imaging*, *35*(2), 416–426. https://doi.org/10.1109/TMI.2015.2476817

Jouffroy, F. K., & Medina, M. F. (2002). Radio-ulnar deviation of the primate carpus: an X-ray study. *Z Morphol Anthropol*, *83*, 275–289.

Kikuchi, Y., Takemoto, H., & Kuraoka, A. (2012). Relationship between humeral geometry and shoulder muscle power among suspensory, knuckle-walking, and digitigrade/palmigrade quadrupedal primates. *Journal of Anatomy*, *220*(1), 29–41. https://doi.org/10.1111/j.1469-7580.2011.01451.x

Kivell, T. L., Lemelin, P., Richmond, B. G., & Schmitt, D. (2016). *The Evolution of the Primate Hand* (Tracy L. Kivell, P. Lemelin, B. G. Richmond, & D. Schmitt (eds.)). Springer New York. https://doi.org/10.1007/978-1-4939-3646-5

Kivell, Tracy L. (2016). The Primate Wrist. In Tracy L. Kivell, P. Lemelin, B. G. Richmond, & D. Schmitt (Eds.), *The Evolution of the Primate Hand* (pp. 17–54). Springer Science & Business Media.

Kivell, Tracy L., Barros, A. P., & Smaers, J. B. (2013). Different evolutionary pathways underlie the morphology of wrist bones in hominoids. *BMC Evolutionary Biology*, *13*(1). https://doi.org/10.1186/1471-2148-13-229

Kivell, Tracy L. (2011). A comparative analysis of the hominin triquetrum (SKX 3498) from

Swartkrans, South Africa. *South African Journal of Science*, *107*(5–6), 1–10. https://doi.org/10.4102/sajs.v107i5/6.515

Knigge, R. P., Tocheri, M. W., Orr, C. M., & Mcnulty, K. P. (2015). Three-Dimensional Geometric Morphometric Analysis of Talar Morphology in Extant Gorilla Taxa from Highland and Lowland Habitats. *The Anatomical Record*, *298*(1), 277–290. https://doi.org/10.1002/ar.23069

Lemelin, P., & Schmitt, D. (1998). The relation between hand morphology and quadrupedalism in primates. *American Journal of Physical Anthropology*, *105*(2), 185–197. https://doi.org/10.1002/(SICI)1096-8644(199802)105:2<185::AID-AJPA6>3.0.CO;2-U

Lewis, O. J. (1965). Evolutionary change in the primate wrist and inferior radio-ulnar joints. *The Anatomical Record*, *151*(3), 275–285. https://doi.org/10.1002/ar.1091510309

Lewis, O. J. (1969). The hominoid wrist joint. *American Journal of Physical Anthropology*, *30*(2), 251–267. https://doi.org/10.1002/ajpa.1330300211

Lewis, O. J. (1972). Osteological features characterizing the wrists of monkeys and apes, with a reconsideration of this region inDryopithecus(Proconsul)africanus. *American Journal of Physical Anthropology*, *36*(1), 45–58. https://doi.org/10.1002/ajpa.1330360107

Lewis, O. J. (1977). Joint remodelling and the evolution of the human hand. *Journal of Anatomy*, *123*, 157–201.

Lewis, O. J. (1989). *Functional Morphology of the Evolving Hand and Foot*. Oxford University Press.

Liu, M.-J., Xiong, C.-H., & Hu, D. (2016). Assessing the manipulative potentials of monkeys, apes and humans from hand proportions: implications for hand evolution. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 1–9.

https://doi.org/10.1098/rspb.2016.1923

Lockwood, C. A., Lynch, J. M., & Kimbel, W. H. (2002). Quantifying temporal bone morphology of great apes and humans: an approach using geometric morphometrics. *Journal of Anatomy*, *201*(6), 447–464. https://doi.org/10.1046/j.1469-7580.2002.00122.x

Long, J. S., & Ervin, L. H. (2000). Using Heteroscedasticity Consistent Standard Errors in the Linear Regression Model. *The American Statistician*, *54*(3), 217–224. https://doi.org/10.1080/00031305.2000.10474549

Marugán-Lobón, J. (2010). Combining shape data and traditional measurements with the 2B-PLS: testing the covariation between avian brain size and cranial shape variation as an example. In J. Reitner, M. H. Trauth, K. Stüwe, & D. Yuen (Eds.), *Morphometrics for nonmorphometricians* (pp. 179–190). Springer.

Marzke, M. W., Wullstein, K. L., & Viegas, S. F. (1992). Evolution of the power (“squeeze”) grip and its morphological correlates in hominids. *American Journal of Physical Anthropology*, *89*(3), 283–298. https://doi.org/10.1002/ajpa.1330890303

Marzke, Mary W. (1997). Precision grips, hand morphology, and tools. *American Journal of Physical Anthropology*, *102*(1), 91–110. https://doi.org/10.1002/(SICI)1096-8644(199701)102:1<91::AID-AJPA8>3.0.CO;2-G

Marzke, Mary W. (2009). Upper-limb evolution and development. *Journal of Bone and Joint Surgery - Series A*, *91-A*, 26–30. https://doi.org/10.2106/JBJS.I.00102

Marzke, Mary W. (2013). Tool making, hand morphology and fossil hominins. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1630), 1–8. https://doi.org/10.1098/rstb.2012.0414

Marzke, Mary W., & Marzke, R. F. (2000). Evolution of the human hand: Approaches to acquiring, analysing and interpreting the anatomical evidence. *Journal of Anatomy*,

197(1), 121–140. https://doi.org/10.1017/S0021878299006342

Matarazzo, S. (2013). Manual pressure distribution patterns of knuckle-walking apes. *American Journal of Physical Anthropology*, *152*(1), 44–50. https://doi.org/10.1002/ajpa.22325

Mcmahon, T., Zijl, P. C. M. Van, & Gilad, A. A. (2015). The Advantage of Throwing the First Stone: How Understanding the Evolutionary Demands of Homo sapiens is Helping Us Understand Carpal Motion. *J Am Acad Orthop Surg*, *27*(3), 320–331. https://doi.org/10.1002/nbm.3066.Non-invasive

Mendel, F. C. (1979). The wrist joint of two-toed sloths and its relevance to brachiating adaptations in the hominoidea. *Journal of Morphology*, *162*(3), 413–424. https://doi.org/10.1002/jmor.1051620308

Michilsens, F., Vereecke, E. E., D'août, K., & Aerts, P. (2009). Functional anatomy of the gibbon forelimb: Adaptations to a brachiating lifestyle. *Journal of Anatomy*, *215*(3), 335–354. https://doi.org/10.1111/j.1469-7580.2009.01109.x

Mittermeier, R. A. (1978). Locomotion and Posture in Ateles geoffroyi and Ateles paniscus. *Folia Primatologica*, *30*(3), 161–193. https://doi.org/10.1159/000155862

Mittermeier, R. A., & Fleagle, J. G. (1976). The locomotor and postural repertoires ofAteles geoffroyi andColobus guereza, and a reevaluation of the locomotor category semibrachiation. *American Journal of Physical Anthropology*, *45*(2), 235–255. https://doi.org/10.1002/ajpa.1330450210

Mitteroecker, P., Gunz, P., Windhager, S., & Schaefer, K. (2013). A brief review of shape, form, and allometry in geometric morphometrics, with applications to human facial morphology. *Hystrix*, *24*(1), 1–8. https://doi.org/10.4404/hystrix-24.1-6369

Neufuss, J., Robbins, M. M., Baeumer, J., Humle, T., & Kivell, T. L. (2018). Gait

characteristics of vertical climbing in mountain gorillas and chimpanzees. *Journal of Zoology*, *306*(2), 129–138. https://doi.org/10.1111/jzo.12577

O'Connor, B. L. (1975). The functional morphology of the cercopithecoid wrist and inferior radioulnar joints, and their bearing on some problems in the evolution of the Hominoidea. *American Journal of Physical Anthropology*, *43*(1), 113–121. https://doi.org/10.1002/ajpa.1330430115

Orr, C. M. (2017). Locomotor Hand Postures, Carpal Kinematics During Wrist Extension, and Associated Morphology in Anthropoid Primates. *Anatomical Record*, *300*(2), 382–401. https://doi.org/10.1002/ar.23507

Orr, C. M., Tocheri, M. W., Burnett, S. E., Awe, R. D., Saptomo, E. W., Sutikna, T., Jatmiko, Wasisto, S., Morwood, M. J., & Jungers, W. L. (2013). New wrist bones of Homo floresiensis from Liang Bua (Flores, Indonesia). *Journal of Human Evolution*, *64*(2), 109–129. https://doi.org/10.1016/j.jhevol.2012.10.003

Palmer, A. K., & Werner, F. W. (1981). The triangular fibrocartilage complex of the wrist—Anatomy and function. *Journal of Hand Surgery*, *6*(2), 153–162. https://doi.org/10.1016/S0363-5023(81)80170-0

Patel, B. A. (2009). The interplay between speed, kinetics, and hand postures during primate terrestrial locomotion. *American Journal of Physical Anthropology*, *234*(June 2009), 222–234. https://doi.org/10.1002/ajpa.21138

Patel, B. A., & Polk, J. D. (2010). Distal forelimb kinematics in erythrocebus patas and papio anubis during walking and galloping. *International Journal of Primatology*, *31*(2), 191–207. https://doi.org/10.1007/s10764-010-9394-6

Polly, P. D. (2008). Adaptive zones and the pinniped ankle: A three-dimensional quantitative analysis of carnivoran tarsal evolution. *Vertebrate Paleobiology and Paleoanthropology*,

9781402069963, 167–196. https://doi.org/10.1007/978-1-4020-6997-0_9

Pontzer, H., & Wrangham, R. W. (2004). Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. *Journal of Human Evolution*, *46*(3), 315–333. https://doi.org/10.1016/j.jhevol.2003.12.006

Preuschoft, H., & Demes, B. (1985). Influence of Size and Proportions on the Biomechanics of Brachiation. In *Size and Scaling in Primate Biology* (pp. 383–399). Springer US. https://doi.org/10.1007/978-1-4899-3647-9_17

Prime, J. M., & Ford, S. M. (2016). Hand Manipulation Skills in Hylobatids. In *Evolution of Gibbons and Siamang* (pp. 269–289). https://doi.org/10.1007/978-1-4939-5614-2

Proctor, Daniel J., Broadfield, D., & Proctor, K. (2008). Quantitative three-dimensional shape analysis of the proximal hallucial metatarsal articular surface inHomo,Pan,Gorilla, andHylobates. *American Journal of Physical Anthropology*, *135*(2), 216–224. https://doi.org/10.1002/ajpa.20723

Proctor, Daniel Jason. (2010). *Three-dimensional morphometrics of the proximal metatarsal articular surfaces of Gorilla, Pan, Hylobates, and shod and unshod humans* [University of Iowa]. https://doi.org/10.17077/etd.8nx9bkin

Rawlins, R. G. (1982). *Locomotor Ontogeny of the Cayo Santiago Macaques: A Behavioral and Morphological Analysis* (R. G. Rawlins (ed.)). Richard Rawlins, Ph.D HCLD.

Rein, T. R. (2019). A Geometric Morphometric Examination of Hominoid Third Metacarpal Shape and Its Implications for Inferring the Precursor to Terrestrial Bipedalism. *Anatomical Record*, *302*(6), 983–998. https://doi.org/10.1002/ar.23985

Remis, M. (1995). Effects of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. *American Journal of Physical Anthropology*, *97*(4), 413–433. https://doi.org/10.1002/ajpa.1330970408

Richmond, B. G. (2001). Functional Morphology of the Midcarpal Joint in Knuckle-Walkers and Terrestrial Quadrupeds. *Human Origins and Environmental Backgrounds*, 105–122. http://dx.doi.org/10.1007/0-387-29798-7_8

Richmond, B. G., & Strait, D. S. (2000). Evidence that humans evolved from a knuckle-walking ancestor. *Nature*, *404*(6776), 382–385. https://doi.org/10.1038/35006045

Ricklan, D. E. (1987). Functional anatomy of the hand of Australopithecus africanus. *Journal of Human Evolution*, *16*(7–8), 643–664. https://doi.org/10.1016/0047-2484(87)90018-2

Rodman, P. S. (1979). Skeletal differentiation of Macaca fascicularis and Macaca nemestrina in relation to arboreal and terrestrial quadrupedalism. *American Journal of Physical Anthropology*, *51*(1), 51–62. https://doi.org/10.1002/ajpa.1330510107

Rohlf, F. J., & Corti, M. (2000). Use of two-block partial least-squares to study covariation in shape. *Systematic Biology*, *49*(4), 740–753. http://apps.isiknowledge.com/full_record.do?product=WOS&search_mode=GeneralSearch&qid=106&SID=N1AMjKKKDN487ejm1B4&page=1&doc=1

Rosenberger, A. L., Halenar, L., Cooke, S. B., & Hartwig, W. C. (2008). Morphology and evolution of the spider monkey, genus Ateles. In C. J. Campbell (Ed.), *Spider Monkeys: Behavior, Ecology and Evolution of the Genus Ateles* (pp. 19–49). Cambridge University Press.

Sarmiento, E. E. (1988a). Anatomy of the hominoid wrist joint: Its evolutionary and functional implications. *International Journal of Primatology*, *14*(A), 1–345. https://doi.org/10.1007/BF02737381

Sarmiento, E. E. (1988b). Anatomy of the hominoid wrist joint: Its evolutionary and functional implications. *International Journal of Primatology*, *9*(4), 281–345. https://doi.org/10.1007/BF02737381

Sarringhaus, L. A., MacLatchy, L. M., & Mitani, J. C. (2014). Locomotor and postural development of wild chimpanzees. *Journal of Human Evolution*, *66*, 29–38. https://doi.org/10.1016/j.jhevol.2013.09.006

Schmidt, M. (2011). Locomotion and postural behavior. *Advances in Science and Research*, *5*(1), 23–39. https://doi.org/10.5194/asr-5-23-2010

Schmitt, D. (2003). Mediolateral reaction forces and forelimb anatomy in quadrupedal primates: Implications for interpreting locomotor behavior in fossil primates. *Journal of Human Evolution*, *44*(1), 47–58. https://doi.org/10.1016/S0047-2484(02)00165-3

Schwartz, J. H., & Yamada, T. K. (1998). Carpal anatomy and primate relationships. *Anthropological Science*, *106*(Supplement), 47–65.

Shubin, N., Tabin, C., & Carroll, S. (1997). Fossils, genes and the evolution of animal limbs. *Nature*, *388*(6643), 639–648. https://doi.org/10.1038/41710

Stern, J. T., Jungers, W. L., & Susman, R. L. (1995). Quantifying phalangeal curvature: An empirical comparison of alternative methods. *American Journal of Physical Anthropology*, *97*(1), 1–10. https://doi.org/10.1002/ajpa.1330970102

Susman, R. L. (1979). Comparative and functional morphology of hominoid fingers. *American Journal of Physical Anthropology*, *50*(2), 215–236. https://doi.org/10.1002/ajpa.1330500211

Thompson, N. E. (2020). The biomechanics of knuckle-walking: 3-D kinematics of the chimpanzee and macaque wrist, hand and fingers. *The Journal of Experimental Biology*, *223*(14), jeb224360. https://doi.org/10.1242/jeb.224360

Thompson, N. E., Ostrofsky, K. R., Mcfarlin, S. C., Robbins, M. M., Stoinski, T. S., & Almécija, S. (2018). Unexpected terrestrial hand posture diversity in wild mountain gorillas. *American Journal of Physical Anthropology*, *December 2017*, 1–11.

https://doi.org/10.1002/ajpa.23404

Tocheri, M. W., Orr, C. M., Jacofsky, M. C., & Marzke, M. W. (2008). The evolutionary history of the hominin hand since the last common ancestor of Pan and Homo. *Journal of Anatomy*, *212*(4), 544–562. https://doi.org/10.1111/j.1469-7580.2008.00865.x

Tocheri, M. W., Solhan, C. R., Orr, C. M., Femiani, J., Frohlich, B., Groves, C. P., Harcourt-Smith, W. E., Richmond, B. G., Shoelson, B., & Jungers, W. L. (2011). Ecological divergence and medial cuneiform morphology in gorillas. *Journal of Human Evolution*, *60*(2), 171–184. https://doi.org/10.1016/j.jhevol.2010.09.002

Tuttle, R. H. (1969). Quantitative and Functional Studies on the Hands of the Anthropoidea. I. The Hominoidea. *Journal of Morphology*, *128*(3), 309–363.

van Heteren, A. H., MacLarnon, A., Soligo, C., & Rae, T. C. (2016). Functional morphology of the cave bear (Ursus spelaeus) mandible: a 3D geometric morphometric analysis. *Organisms Diversity & Evolution*, *16*(1), 299–314. https://doi.org/10.1007/s13127-015-0238-2

Vanhoof, M.J.M., van Leeuwen, T., Galletta, L., & Vereecke, E. E. (2020). The forearm and hand musculature of semi-terrestrial rhesus macaques (Macaca mulatta) and arboreal gibbons (fam. Hylobatidae). Part II. Quantitative analysis. *Journal of Anatomy*. https://doi.org/10.1111/joa.13314

Vanhoof, Marie J. M., Leeuwen, T., & Vereecke, E. E. (2020). The forearm and hand musculature of semi-terrestrial rhesus macaques (Macaca mulatta) and arboreal gibbons (Fam . Hylobatidae). Part I. Description and comparison of the muscle configuration. *Journal of Anatomy*, joa.13222. https://doi.org/10.1111/joa.13222

Vilensky, J., & Larson, S. G. (1989). Primate Locomotion: Utilization And Control Of Symmetrical Gaits. *Annual Review of Anthropology*, *18*(1), 17–35.

https://doi.org/10.1146/annurev.anthro.18.1.17

Wiley, D., Amenta, N., Alcantara, D., Ghosh, D., Kil, Y., Delson, E., Harcourt-Smith, W., Rohlf, F., John, K., & Hamann, B. (2005). Evolurionary Morphing [Abstract]. *IEEE Visualization Conference*, 431–438.

Williams, S. A. (2010). Morphological integration and the evolution of knuckle-walking. *Journal of Human Evolution*, *58*(5), 432–440. https://doi.org/10.1016/j.jhevol.2010.03.005

Wolfe, S. W., Crisco, J. J., Orr, C. M., & Marzke, M. W. (2006a). The Dart-Throwing Motion of the Wrist: Is It Unique to Humans? *Journal of Hand Surgery*, *31*(9), 1429–1437. https://doi.org/10.1016/j.jhsa.2006.08.010

Wolfe, S. W., Crisco, J. J., Orr, C. M., & Marzke, M. W. (2006b). The dart-throwing motion of the wrist. Is it unique to humans? *The Journal of Hand Surgery*, *31A*(5), 1429–1437. https://doi.org/10.1016/j.jhsa.2007.02.012

Wunderlich, R. E., & Jungers, W. L. (2009). Manual digital pressures during knuckle-walking in chimpanzees (Pan troglodytes). *American Journal of Physical Anthropology*, *139*(3), 394–403. https://doi.org/10.1002/ajpa.20994

Yazaki, N., Burns, S. T., Morris, R. P., Andersen, C. R., Patterson, R. M., & Viegas, S. F. (2008). Variations of Capitate Morphology in the Wrist. *Journal of Hand Surgery*, *33*(5), 660–666. https://doi.org/10.1016/j.jhsa.2008.02.002

Youlatos, D. (1996). Atelines, Apes and Wrist Joints. *Folia Primatol*, *67*, 193–198.

Young, R. W. (2003). Evolution of the human hand: the role of throwing and clubbing. *Journal of Anatomy*, *202*(1), 165–174.

Tables

Table 1 – Total triquetrum and hamate sample analyzed in this study.

Table 2 – Definitions of the fixed landmarks to capture triquetrum external shape.

Table 3 – Definitions of the fixed landmarks to capture hamate external shape (see also (Almécija, Orr, et al., 2015).

Table 4 – Summary of the differences of triquetrum and hamate shape between the different primate genera.

Figure legends

Figure 1 – Palmar and dorsal view of the human hand. The hamate is highlighted in green, and the hamulus and facets for the triquetrum and fourth and fifth metacarpal are indicated. The triquetrum is highlighted in blue with indication of the ulnar and hamate facet.

Tm = trapezium, Td = trapezoid, C = capitate, S = scaphoid, L = lunate, P = pisiform, R = radius, U = ulna.

Figure 2 – Left triquetrum (blue) and hamate (green) of *Homo sapiens* illustrating the fixed surface landmarks used in this study, 18 for the triquetrum and 23 for the hamate (see also (Almécija, Orr, et al., 2015)). Definitions of the fixed landmarks can be found in Table 2 and 3.

Figure 3 – Scatterplot of the first (x-axis) and second (y-axis) principal component (PC1 vs. PC2) scores for (A) the triquetrum and (B) hamate: [PURPLE; Plathyrrhines] *Ateles*, [GREEN; Hominids] *Gorilla beringei* (circle), *Gorilla gorilla* (square), *Homo* (diamond), *Pan paniscus* (triangle), *Pan troglodytes* (inverted triangle), *Pongo* (asterisk), [BLUE; Hylobatids] *Hoolock* (circle), *Hylobates* (square), *Nomascus* (diamond), *Symphalangus* (triangle), [ORANGE; Cercopithecoids] *Macaca fascicularis* (circle), *Macaca mulatta* (square), *Mandrillus* (diamond), *Papio* (triangle). The grey shapes ('meshes') show extreme shapes for PC1 and PC2 in three different views (from top to bottom): (A) lateral view (facet for lunate), distal view (facet for hamate), palmar view (facet for pisiform (†) and ulna (arrow)); (B) medial view (facet for triquetrum), dorsal view, distal view (facet for metacarpal 4 and 5). To generate these shapes, the bone mesh that is closest to the general mean shape is selected and warped to the mean shape itself. This mean mesh is then warped to the landmark positions calculated for the different PCs (max. and min. values).

Figure 4 – Scatterplot of the first (x-axis) and third (y-axis) principal component (PC1 vs. PC3) scores for (A) the triquetrum and (B) hamate: [PURPLE; Plathyrrhines] *Ateles*, [GREEN; Hominids] *Gorilla beringei* (circle), *Gorilla gorilla* (square), *Homo* (diamond), *Pan paniscus* (triangle), *Pan troglodytes* (inverted triangle), *Pongo* (asterisk), [BLUE; Hylobatids] *Hoolock* (circle), *Hylobates* (square), *Nomascus* (diamond), *Symphalangus* (triangle), [ORANGE; Cercopithecoids] *Macaca fascicularis* (circle), *Macaca mulatta* (square), *Mandrillus* (diamond), *Papio* (triangle). The grey shapes ('meshes') show extreme shapes for PC1 and PC2 in three different views (from top to bottom): (A) lateral view (facet for lunate), distal view (facet for hamate), palmar view (facet for pisiform (†) and ulna (arrow)); (B) medial view (facet for triquetrum), dorsal view, distal view (facet for metacarpal 4 and 5).

Figure 5 – Boxplot of the first principal component scores (PC1) for the (A) triquetrum and (B) hamate. Black lines are the medians, boxes are the interquartile ranges, whiskers are the non-outlier ranges, and empty circles are outliers. The grey shapes ('meshes') show extreme shapes for PC1 (top: positive PC1 values, bottom: negative PC1 values) in three different views (from left to right): (A) lateral view (facet for lunate), distal view (facet for hamate), palmar view (facet for pisiform (†) and ulna (arrow)); (B) medial view (facet for triquetrum), dorsal view, distal view (facet for metacarpal 4 and 5).

Mac = *Macaca*, Man = *Mandrillus*, Pa = *Papio*, G-b = *Gorilla beringei*, G-g = *Gorilla gorilla*, Homo = *Homo*, Pan-p = *Pan paniscus*, Pan-t = *Pan troglodytes*, Pongo = *Pongo*, Hool = *Hoolock*, Hyl = *Hylobates*, Nom = *Nomascus*, Symph = *Symphalangus*, At = *Ateles*

Figure 6 – Boxplot of the second principal component scores (PC2) for the (A) triquetrum and (B) hamate. Black lines are the medians, boxes are the interquartile ranges, whiskers are the non-outlier ranges, and empty circles are outliers. The grey shapes ('meshes') show extreme shapes for PC2 (top: positive PC2 values, bottom: negative PC2 values) in three different views (from left to right): (A) lateral view (facet for lunate), distal view (facet for hamate), palmar

view (facet for pisiform (†) and ulna (arrow)); (B) medial view (facet for triquetrum), dorsal view, distal view (facet for metacarpal 4 and 5).

Figure 7 – Boxplot of the third principal component scores (PC3) for the (A) triquetrum and (B) hamate. Black lines are the medians, boxes are the interquartile ranges, whiskers are the non-outlier ranges, and empty circles are outliers. The grey shapes ('meshes') show extreme shapes for PC3 (top: positive PC3 values, bottom: negative PC3 values) in three different views (from left to right): (A) lateral view (facet for lunate), distal view (facet for hamate), palmar view (facet for pisiform (†) and ulna (arrow)); (B) medial view (facet for triquetrum), dorsal view, distal view (facet for metacarpal 4 and 5).

Figure 8 – PLS1 scores of a two-block partial least squares (2B-PLS) analysis of triquetrum and hamate shape that shows a significant association (RV = 0.75 ; p = 0.001). The grey shapes ('meshes') show extreme shapes for PLS1 in three different views (from left to right): [triquetrum] lateral view (facet for lunate), distal view (facet for hamate), palmar view (facet for pisiform (†) and ulna (arrow)); [hamate] medial view (facet for triquetrum), dorsal view, distal view (facet for metacarpal 4 and 5).

Figure 9 – PLS2 scores of a two-block partial least squares (2B-PLS) analysis of triquetrum and hamate shape that shows a significant association (RV = 0.75 ; p = 0.001). The grey shapes ('meshes') show extreme shapes for PLS2 in three different views (from left to right): [triquetrum] lateral view (facet for lunate), distal view (facet for hamate), palmar view (facet for pisiform (†) and ulna (arrow)); [hamate] medial view (facet for triquetrum), dorsal view, distal view (facet for metacarpal 4 and 5).