Exploring Phylogenetic and Functional Signals in Complex Morphologies: The Hamate of Extant Anthropoids as a Test-Case Study

SERGIO ALMÉCİJA,1,2,3* CALEY M. ORR,4 MATTHEW W. TOCHERI,5,6 BIREN A. PATEL,7,8 AND WILLIAM L. JUNGER1

1Department of Anatomical Sciences, Stony Brook University School of Medicine, Stony Brook, New York
2Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici Z (ICTA-ICP), campus de la UAB, c/ de les Columnes, s/n., 08193 Cerdanyola del Vallès, Barcelona, Spain
3NYCEP Morphometrics Group
4Department of Anatomy, Midwestern University, Downers Grove, Illinois
5Human Origins Program, Department of Anthropology, National Museum of Natural History, Smithsonian Institution, 10th and Constitution Avenue NW, Washington, DC
6Department of Anthropology, Center for the Advanced Study of Hominid Paleobiology, The George Washington University, Washington, DC
7Cell and Neurobiology, Keck School of Medicine, University of Southern California, Los Angeles, California
8Human and Evolutionary Biology Section, Department of Biological Sciences, University of Southern California, Los Angeles, California

ABSTRACT

Three-dimensional geometric morphometrics (3DGM) is a powerful tool for capturing and visualizing the “pure” shape of complex structures. However, these shape differences are sometimes difficult to interpret from a functional viewpoint, unless specific approaches (mostly based on biomechanical modeling) are employed. Here, we use 3DGM to explore the complex shape variation of the hamate, the disto-ulnar wrist bone, in anthropoid primates. Major trends of shape variation are explored using principal components analysis along with analyses of shape and size covariation. We also evaluate the phylogenetic patterning of hamate shape by plotting an anthropoid phylogenetic tree onto the shape space (i.e., phylo-morphospace) and test against complete absence of phylogenetic signal using posterior permutation. Finally, the covariation of hamate shape and locomotor categories is explored by means of 2-block partial least squares (PLS) using shape coordinates and a matrix of data on arboreal locomotor behavior. Our results show that 3DGM is a valuable and versatile tool for characterizing the shape of complex structures such as wrist bones in anthropoids. For the hamate, a significant phylogenetic pattern is found in both hamate shape and size, indicating that closely related taxa are typically the most similar in hamate form. Our allometric analyses show that major differences in hamate shape among taxa are not a direct con-

Grant sponsors: Fulbright Commission and the Generalitat de Catalunya (S.A.), the Spanish Ministerio de Economía y Competitividad (S.A.), the AAPA Professional Development Grant (S.A.); the Smithsonian Scholarly Studies Grant Program (M.W.T.); Leakey Foundation (B.A.P.); Wenner-Gren Foundation (C.M.O.); National Science Foundation; Grant numbers: 2009 BFUL 00049, 2009 BP-A 00226, CGL2011-27343, NSF-BCS 1316947, NSF-BCS-1317047, NSF-BCS 1317029.

*Correspondence to: Sergio Almécija; Department of Anatomical Sciences, Stony Brook University School of Medicine, Stony Brook, NY 11794-8081. E-mail: sergio.almecija@stonybrook.edu

Received 3 October 2014; Accepted 11 October 2014.
DOI 10.1002/ar.23079
Published online in Wiley Online Library (wileyonlinelibrary.com).
In primates, the hamate forms the distal ulnar aspect of the carpus (Fig. 1). It articulates proximally with the triquetrum (sometimes with the lunate as well), radically with the capitate, and distally with the fourth and fifth metacarpal bases. It has a hook-shaped projection, the hamulus, on its distopalmar side, which is the attachment site for two intrinsic muscles of the fifth digit (flexor digiti minimi and opponens digiti minimi). Variation in hamate shape has been used in studies of the evolution of modern human manipulative capabilities because human hamate morphology appears to favor the ability to form a variety of grips that are employed to construct and manipulate tools (Marzke et al., 1992, 1998; Marzke and Marzke, 2000; Marzke, 2013; Orr et al., 2013). The functional differentiation of monkey and ape wrists has also been a topic of particular interest for primate morphologists (Lewis, 1965, 1969, 1972; McHenry and Corrucini, 1975; O’Connor, 1975; Cartmill and Milton, 1977; Sarmiento, 1988; Lewis, 1989; Richmond, 2006). Specifically, hamate morphology has been important in discussions of hominoid locomotor evolution because of its role in wrist mobility (i.e., ranges of motion), which is necessary for behaviors such as vertical climbing and below-branch suspension used by extant apes (e.g., Tuttle, 1967; Lewis, 1972; Jenkins and Fleagle, 1975; O’Connor, 1975; Lewis, 1977; Beard et al., 1986; Sarmiento, 1988; Spoer et al., 1991; Sarmiento, 1994; Fleagle, 1999).

Monkeys and extant hominoid primates differ considerably in terms of ulnar wrist morphology. Most of these differentiating features are related to the derived complex in crown hominoids in which the ulnar styloid process is retracted from the proximal carpal row (Lewis, 1989; Sarmiento, 1988). Although the expression varies across apes, the imposition of fibrocartilage between the ulnar styloid process and the triquetropisiform complex (and reduction of the triquetrum) is thought to dramatically alter the load transmission regime through the wrist. This reorganization has been traditionally related to the capacity for increased supination at the distal radioulnar joint necessary for below-branch locomotion (Lewis, 1972; Sarmiento, 1985, 1988; Lewis, 1989). However, the loss of ulnocarpal articulation in the 12 million-year-old fossil great ape Pierolapithecus catalaunicus, in combination with its inferred orthograde body plan (Moya-Sola et al., 2004) but moderate hand length (Moya-Sola et al., 2005; Almécija et al., 2009; Alba et al., 2010), suggests that changes in the ulnar side of the wrist might have been initially related to extant great-ape-like vertical climbing and not specifically suspension. It is likely that differences in hamate shape between apes and monkeys at least in part reflect that reorganization of the ulnar side of the carpus.

Lewis (1972) described the wrist morphology of cercopithecoids as being largely similar across major taxonomic groups with colobines and cercopithecines exhibiting little variation in hamate form. He described both groups as exhibiting a wedge-shaped body set obliquely within the wrist, with a proximally oriented triquetral facet that forms a stable platform. The orientation of the articular facets and the corresponding blocky triquetrum and well-developed styloid process of the ulna probably facilitate load transfer on the ulnar side of the wrist while restricting ulnar deviation (Lewis, 1989; Sarmiento, 1988). O’Connor (1975) explained the relative uniformity of hamate morphology among cercopithecoid monkeys as resulting from their use of quadrupedal locomotion involving dorsiflexion of the wrist either in palmigrade or digitigrade postures (irrespective of habitat/substrate differences; see also Patel, 2009). Hypertension on the fifth carpometacarpal joint (and the fourth to a lesser degree) appears to facilitate such hand postures in pronograde quadrupeds. This is permitted by the lack of a developed “hook” on the hamate (i.e., hamulus) together with a proximal articular surface on the fourth and fifth metacarpals that extends onto the dorsal surface of the shaft (Corrucini, 1975; O’Connor, 1975).

In contrast to the minimal morphological variation in the hamate documented thus far in quadrupedal monkeys, considerable diversity in hamate shape has been reported for extant apes and humans. In both Pongo and the hylobatids (that highly rely heavily on below-branch suspension), the hamate is described as composing a larger proportion of the midcarpal articular surface and contributing to a quasi-ball-and-socket joint that allows considerable mobility (Jenkins and Fleagle, 1975; Jenkins, 1981; Richmond et al., 2001). Lewis (1972, 1989) also described hylobatid hamates as retaining a somewhat oblique-set within the overall carpus (similar to monkeys). However, the hylobatid hamate has an unlarly facing triquetral facet and a rounded proximal “head” that articulates with the lunate and nearly excludes this latter bone from articulating with the capitale. The proximal aspects of the hamate and capitate together contribute to a globular distal midcarpal row that is engulfed by the lunate, scaphoid, and centrale (e.g., Jenkins and Fleagle, 1975; Lewis, 1989). Consequently, it does not present a large, flat, platform-like articulation. Thus, the hylobatid configuration is in stark contrast to the stable weight-bearing platform for the triquetrum in monkeys. Lewis (1972, 1989) considered the hylobatid midcarpus to be a less well-developed version of the great ape wrist, which he viewed as ideally adapted to suspensory locomotion. However, the hylobatid geometry is better considered as a uniquely...
derived modification that facilitates midcarpal rotation during their highly specialized style of ricochetal brachiation (e.g., Jenkins, 1981; Kivell et al., 2013).

Wrist morphometric analyses, such as individual shape ratios based on traditional linear measurements and angles have been used in the past to describe differences amongst different locomotor categories in primates (e.g., Sarmiento, 1988; Spoor et al., 1991). Other studies have employed multivariate statistical analyses to explore morphometric variation in the wrist in comparison to a priori assigned locomotor groups (Begun and Kivell, 2011). However, the hamate, like other wrist
bones with complex shapes and multiple articular surfaces for surrounding bones, has proved difficult to characterize numerically at the species and even genus level. Alternative approaches based on three-dimensional (3D) quantification of carpal and tarsal anatomy have been particularly useful at discriminating among closely related taxa (Tocheri et al., 2003, 2005, 2007; Marzke et al., 2010; Tocheri et al., 2011; Dunn et al., 2014). For example, this approach was used to compare the hamates of fossil hominin taxa within the context of modern great ape-human variation (Orr et al., 2013).

Since the 1990s, the ongoing development of three-dimensional geometric morphometrics (3DGM) has enabled the simultaneous analysis and visualization of complex morphology (Bookstein, 1991; Rohlf and Marcus, 1993; Dryden and Mardia, 1998; Hammer and Harper, 2006). This method quantifies shape more comprehensively than two-dimensional geometric morphometrics (2DGM) and other methods, and may often capture subtle shape differences between specimens within a species or among different taxa. Subsequently, the shape differences can be intuitively visualized as “warpings” of 3D surfaces generated from thin-plate spline algorithms (Wiley et al., 2005). Several recent examples exist in anthropology using 3DGM to characterize human and primate postcranial elements (e.g., Turley et al., 2011; Almécia et al., 2013; Bastir et al., 2013; Sylvester, 2013; Tallman et al., 2013; Turley and Frost, 2013; Knigge et al., this volume).

Geometric morphometric analyses characterize complex shapes and reveal overall phenetic affinities effectively. However, the functional significance of shape differences captured by 3DGM is often difficult to interpret. For instance, the observed shape differences often lack the explicitly biomechanical foundation that typically underlies studies based on linear or other 3D measurements taken to represent specific elements of a particular mechanical model (e.g., load and lever arms, torques, etc.) (Terhune, 2013; Knigge et al., this volume). Nevertheless, 3DGM analyses can use coordinate data that contain biomechanically relevant dimensions to help interpret the visual results from a functional point of view (e.g., Almécia et al. 2013; Figueirido et al., 2013). A common procedure is to rely on multivariate statistical analyses (e.g., discriminant function analysis, MANOVA, etc.) to test for differences among “functional” groups defined a priori (e.g., Polly, 2008). This is similar to the way that multivariate analyses are conducted using more traditional measurements. Another approach is to perform a multivariate regression or multivariate multiple regression of shape coordinate data and, for example, locomotor categories, taxonomic groups, substrate use, body masses, etc. and inspect how dependent variables of interest relate to each other and to the shape coordinates. Degree and pattern of covariation can be assessed by comparing angles between the projected vectors of different regression analyses (e.g., Turley et al., 2011; Rein and Harvati, 2013; Turley and Frost, 2013). However, results of regression approaches are still difficult to interpret when different locomotor categories (or covariates) are correlated with each other. For example, hypothetical shape changes correlated with “terrestriality” may not be clearly separated from those correlated with general “quadrupedalism” (whether it is arboreal or terrestrial).

In this study, we use 3D coordinate shape data derived from 3D surface scans to accomplish four main objectives:

1. Characterize the complex shape morphology of the hamate among extant anthropoid primates in an effort to distinguish among taxa relying solely on their major patterns of shape variation. Based on previous studies, we hypothesize that hominoids will show a larger degree of shape diversity in comparison to platyrhines and cercopithecoids. In comparison to hominoids, platyrhine and cercopithecoid monkeys are expected to share larger metacarpal articular surfaces extending onto smaller hamuli facilitating dorsiflexion at the carpometacarpal joints.

2. Test for the presence of phylogenetic structure in hamate shape and size (i.e., are closely related taxa being more similar to one another than more distantly related taxa?). We expect hamate form (i.e., shape plus size) in hominoids to be different from catarrhine and platyrrhine monkeys, with hyllobatids being the most divergent of all apes in terms of shape.

3. Explore the predictable covariation of hamate shape and size among taxa to assess if shape differences across taxa are related to size differences. Although we expect hyllobatids and monkeys to differ in both shape and size relative to great apes, it is unlikely that differences in overall hamate shape will be caused by differences in size alone. To our knowledge, predictability of that covariation has not been inspected in a comparable dataset of anthropoid primates (but see Orr et al., 2013 for an analysis of specific univariate features and hamate size in great apes and humans).

4. Test if (and how) hamate shape covaries with a matrix of known locomotor behaviors to examine whether shape differences (overall) can be reasonably interpreted in a functional context. We hypothesize that shape differences between monkey, hyllobatid and great ape taxa are related to both phylogenetic divergence and associated differences in locomotor behaviors. Hence, we expect a significant portion of total shape variation to significantly covary with predominant locomotor behaviors. For example, given previous observations in the specialized type of locomotion and wrist morphology of hyllobatids, we expect a large amount of the total anthropoid hamate shape variance to significantly covary with locomotor behaviors (i.e., due at least to brachiation in hyllobatids).

**MATERIALS AND METHODS**

**Sample and Data Collection**

We sampled 253 hamates representing 18 extant genera, including platyrrhines, cercopithecoids, hyllobatids, and hominids (great apes and humans) (Fig. 2; Table 1). Hominoid taxa (i.e., hyllobatids and hominids) were sampled more extensively to capture their patterns of variation, whereas monkey taxa (especially platyrrhines) were included as comparisons to help better contextualize the hominoid groups. To capture the overall form (i.e., shape plus size) of the anthropoid hamate, we collected 23 landmarks (Fig. 3; Table 2) from the surfaces of 3D digital hamate models using Landmark Editor software (ver. 3.6) (Wiley et al., 2005). The 3D models were obtained using laser scanning (Nextengine, Scanstudio HD Pro), with the exception of three small
platyrrhine hamates (*Aotus, Saguinus, Saimiri*) that were acquired using micro-CT imaging with surfaces extracted using the segmentation tool of Avizo software (ver. 7.0). All raw scans were edited with Geomagic (vers. 12–2013) to clean the meshes, fill holes, and standardize all hamate models to a similar number of vertices. It has been shown that scale-free data collected from 3D surface models obtained from different sources are reasonably compatible (Tocheri et al., 2011). All final 3D models were opened in Landmark Editor for data collection.

The phylogenetic relationships of the taxa examined (Fig. 2) were recovered from a chronometric consensus tree based on molecular data and downloaded from “The 10KTrees Project” (ver. 3; http://www.10ktrees.fas.harvard.edu) (Arnold et al., 2010). Some nomenclature, such as the new generic name (*Hoolock*) for hoolock gibbons (Mootnick and Groves, 2005), was updated to reflect recent taxonomic revisions.

**Analyses**

Shape data were obtained from raw coordinates through a full (generalized) Procrustes fit analysis—which rotates, translates and size-scales the landmark configurations to unit of centroid size—and posterior orthogonal projection on to the tangent space (Dryden and Mardia, 1998). Major patterns of hamate shape variation were explored through a principal components analysis (PCA). The original coordinate system of the shape space was transformed to the principal components of the covariance matrix of the original variables, such that the new shape space was centered on the average shape configuration. Thus, the first principal component axis runs through the major axis of variation in the data with subsequent axes running at orthogonal angles through the minor axes of variation, implying a rigid rotation of the original variables (Polly, 2008; Polly et al., 2013). Shape differences among our extant sample of anthropoid primates were tested by means of multivariate analysis of variance (MANOVA) of the first three principal components (which concentrate 53.4% of the variance). Post hoc significant differences among platyrrhines, cercopithecoids, hylobatids, the three great ape genera and modern humans was assessed through Hotelling’s *P* values (Bonferroni’s corrected).

To assess the phylogenetic patterning in the shape space, we mapped a phylogenetic tree onto the shape space defined by the two first axes of a PCA of the covariance matrix of extant taxa means. Hypothetical ancestral states (internal nodes in the tree) were reconstructed using squared-change parsimony (Maddison, 1991) with a method developed for geometric data in which shape is treated as a single multidimensional character and weighed by branch length (Klingenberg and Gidaszewski, 2010). Subsequently, the estimated ancestral node configurations were plotted on the original shape space, and the branches of the tree were connected to obtain a phylomorphospace (Rohlf, 2002; Sidlauskas, 2008; Monteiro, 2013). The previous steps were necessary to subsequently test for the presence of a phylogenetic signal in hamate shape space by means of
a permutation test approach (Laurin, 2004) extended for multivariate analysis of coordinate data (Klingenberg and Gidaszewski, 2010). This technique simulates the null hypothesis of complete absence of phylogenetic structure among hamate shapes in extant anthropoids. The species mean shape configurations were randomly distributed as the TIPS of the phylogeny in 10,000 permutations. For each permutation, tree length (i.e., the sum of the squared Procrustes distances between ancestral and descendant shapes for all branches) was computed. If more than 5% of the resulting tree lengths computed in the permutation test were greater than the one obtained with the original data, the null hypothesis of absence of phylogenetic structure in the data was rejected.

Covariation of hamate shape and size (i.e., allometry) was explored using multivariate regression of all the Procrustes coordinates on log-transformed centroid size (logCS), using both species mean configurations (i.e., TIPS of the phylogeny) and phylogenetic independent contrasts (PICs; Felsenstein, 1985). To assess the reliability of these multivariate regressions, a permutation test (10,000 iterations) against the null hypothesis of independence between the dependent (hamate shape) and independent (logCS) variables was performed.

We also performed a two-block partial least squares (PLS) analysis to test for covariation between hamate shape and locomotor categories in selected taxa (Rohlf and Corti, 2000). This method differs from multivariate regression in that both the shape and covariate 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). These new pairs of variables (the different PLSes) represent linear combinations of variables within the original two sets (the blocks). These linear combinations are constructed so that the new variables account for as much of the covariation as possible between the two original sets with the goal to find relationships between them without assuming that one is the cause of the variation in the other. In our case, one block was constituted by hamate shape (Procrustes coordinates) and the other by a matrix of the frequencies of use for several types of arboreal locomotion by extant hominoid and selected anthropoid species (Table 3). Data on arboreal locomotion was used because it is available for more taxa (Thorpe and Crompton, 2006; their Table 7 and references therein). The RV coefficient, a multivariate analogue of the squared correlation (Escoufier, 1973), was used as an overall measure of association between the two blocks, and a permutation test (10,000 iterations) was employed against the null hypothesis of complete independence. In addition, a second PLS analysis was carried out on the PICs for both blocks of variables to test if covariation between

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species/subspecies</th>
<th>Female</th>
<th>Male</th>
<th>Unknown</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Homo</td>
<td>Homo sapiens</td>
<td>8</td>
<td>33</td>
<td>14</td>
<td>55</td>
</tr>
<tr>
<td>Pan</td>
<td>Pan paniscus</td>
<td>10</td>
<td>11</td>
<td>1</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>P. troglodytes troglodytes</td>
<td>5</td>
<td>5</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>P. troglodytes schweinfurthii</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>P. troglodytes verus</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>P. troglodytes ssp.</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Gorilla</td>
<td>Gorilla gorilla</td>
<td>7</td>
<td>15</td>
<td>1</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>G. beringei beringei</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>G. beringei graueri</td>
<td>6</td>
<td>11</td>
<td>3</td>
<td>20</td>
</tr>
<tr>
<td>Pongo</td>
<td>Pongo pygmaeus</td>
<td>7</td>
<td>7</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Pongo abelii</td>
<td>1</td>
<td>4</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Pongo sp.</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Symphalangus</td>
<td>Symphalangus syndactylus</td>
<td>4</td>
<td>6</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td>Hooock</td>
<td>Hooock hooock</td>
<td>2</td>
<td>3</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Hylodates</td>
<td>Hylobates klossi</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Hylobates lar</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Nomascus</td>
<td>Nomascus leucogenys</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Papio</td>
<td>Papio anubis</td>
<td>4</td>
<td>5</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Papio cynocephalus</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Macaca</td>
<td>Macaca mulatta</td>
<td>5</td>
<td>5</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td>Nasalis</td>
<td>Nasalis larvatus</td>
<td>3</td>
<td>5</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>A louatta</td>
<td>Alouatta seniculus</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>12</td>
</tr>
<tr>
<td>Ateles</td>
<td>Ateles belzebath</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Ateles fusciceps</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Ateles Geoffroyi</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Ateles paniscus</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Ateles sp.</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Brachyteles</td>
<td>Brachyteles arachnoides</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Lagothrix</td>
<td>Lagothrix lagotricha</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Aotus</td>
<td>Aotus trivirgatus</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Saginus</td>
<td>Saginus oedipus</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Saimiri</td>
<td>Saimiri sciureus</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total sample</td>
<td></td>
<td>253</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
hamate shape and arboreal locomotion was detected when considering phylogenetic structure. The amount of shape variance explained by each PLS axis was computed by dividing the “singular value” (or “singular warp”) of each PLS by total variance within the shape block (sum of eigenvalues, computed after a PCA of the shape data).

To visualize morphological variation associated with each axis in each analysis, coordinates of shape change along the axes were imported into Landmark Editor and used to warp (using thin-plate splines) a 3D hamate model of *Pan troglodytes* (shown in Fig. 3) into desired score values. All the statistical analyses were carried out using *MorphoJ* (ver. 1.05; Klingenberg, 2011), *PAST*
Overall, humans, gorillas, hylobatids, and monkeys (and to a lesser degree chimps and orangutans) can be differentiated from one another based on their hamate shapes when the three first PC axes (accounting for 53.4% of the variance, Fig. 4D) are inspected together (Fig. 4A). Post hoc comparisons reveal that monkeys, hylobatids, *Pongo*, *Gorilla*, *Pan*, and *H. sapiens* are statistically different from each other based on the variation along the three first axes (*P* < 0.0001).

Our analyses also show significant differences between hamate shape in platyrrhines and cercopithecoids (*P* < 0.05).

PC1 (25.8% of total variance) is related to overall proportions of the hamate body and hamulus, as well as to the relative depth of the fourth and fifth metacarpal articulations. This axis generates four relatively distinct clusters of hylobatids, monkeys, *Pan/Pongo*, and *Gorilla/Homo* from left (negative) to right (positive) (Fig. 4B,C). Most *Ateles* specimens are near the negative extreme of the monkey cluster, overlapping with hylobatids. Hylobatids have hamate bodies and hamuli that are proximodistally long, and radioulnarly and dorsopalmarly narrow (Fig. 4D). The fifth metacarpal facet projects distally over that of the fourth metacarpal while the medial side of the hamate is oriented obliquely. Conversely, human and gorilla hamates are proximodistally short, and radioulnarly and dorsopalmarly wide, with a sigmoid medial side and a more vertical overall orientation of the bone.

PC2 (15.3% of variance) is also related to the radioulnar width of the hamate body, along with the size and orientation of the hamulus and the articular surfaces for the triquetrum and metacarpals. Along this axis, hylobatids are maximally separated from monkeys, with hominid taxa falling in between these two extremes, although humans overlap more with monkeys than do the other hominids (Fig. 4B). Negative values correspond to radioulnarly narrow hamulates with large hamuli that project distally, triquetal facets that are dorsopalmarly wide proximally and dorsopalmarly narrow distally, and fifth metacarpal facets that are radioulnarly narrow relative to those of the fourth metacarpal. In contrast, positive values on this axis describe hamates with a radioulnarly wide body, a small and less distally projecting hamulus, a triquetal facet that is dorsopalmarly narrow proximally and distally but widest at its midpoint, and a fifth metacarpal facet that is larger than that of the fourth metacarpal and extends onto the hamulus. Together, PC1 and PC2 separate hominids from both hylobatids and anthropoid monkeys (Fig. 4B).

PC3 (12.3% of variance) is related to hamate body proportions, the shape and distal projection of the hamulus, and the outline shape of the metacarpal articulations. This axis clearly separates gorillas from modern humans (negative and positive values respectively), while also acting to separate *Pan* and monkeys (negative values) from *Pongo* and hylobatids (positive values). Negative values correspond to radioulnarily wider and proximodistally shorter hamates (but to a smaller extent than seen in PC 1 and 2), distally projecting hamuli and a trapezoidal outline for the metacarpal facets with its larger dimension located dorsally. In addition, the fifth metacarpal facet extends distally onto the hamulus. Positive values correspond with hamate bodies that are slightly longer proximodistally and slightly narrower radioulnarily, hamuli that extend palmarly and a square-shaped articular outline for the metacarpals. The fifth metacarpal facet does not extend on to the hamulus. Overall, the combination of PC1 and PC3 (Fig. 4C) separates humans, hylobatids and gorillas (with the exception of two specimens) from the remaining taxa.
Phylogenetic Structure in the Extant Anthropoid Hamate Shape and Size

Shape space patterns based on species means reasonably display a phylogenetic structure (Fig. 5). This is confirmed by the results of our permutation test \((P < 0.0001)\), allowing us to reject the null hypothesis of complete lack of phylogenetic signal. However, the maximum axis of variance in shape space (i.e., PC1) is defined by monkeys (especially some platyrrhine species) and hylobatids, respectively, with great apes in an intermediate position. Branch lengths indicate that, not only within hominoids but also within the whole sample of anthropoid species examined here, most of the shape changes occurred in the branch (Fig. 5, marked in red) connecting the hypothetical ancestor of all hominoids (LCAH) and that of hylobatids. Modern hominoids exhibit fewer shape differences in their hamates than do hylobatids (i.e., they have changed less) since their divergence from the LCAH. This phylomorphospace (reconstructed based solely on the extant taxa included) suggests that since the LCAH, the hamates of modern humans and gorillas have “evolved more” than that of chimps (i.e., common chimpanzees and bonobos), which are reconstructed by this analysis as having secondarily evolved into a morphology similar to that of orangutans (thus indicating homoplasy). Orangutan hamate shape appears more conservative among great apes. Similarly as with hamate shape, when hamate centroid size is mapped onto our anthropoid phylogeny (Fig. 6), differences in size are evident among taxa and phylogenetic signal is further detected \((P < 0.0001)\).

Predicable Covariation of Hamate Shape and Size

The multivariate regression of shape and log-transformed centroid size \((\log \text{CS})\) based on species means \((\text{TIPS})\) shows a significant relationship \((P < 0.05)\), although accounting only for minimal portion \((8.4\%)\) of total shape variation (Fig. 7A). An inspection of the plot suggests that the relationship is mostly artifactual, being caused by the presence of three platyrrhine species that are comparatively small \((\text{Saimiri, Saguinus, Aotus})\). This is confirmed by the regression of the phylogenetically independent contrasts \((\text{PICs})\) of hamate shape and \(\log \text{CS}\), revealing no significant relationship \((P = 0.8; \text{Fig. 7B})\). This result indicates that differences in hamate shape among extant hominoids and other anthropoids are not merely “explained” or predicted by their differences in size.

Locomotor Signatures in the Hamate

The results of PLS show that there is a strong and significant overall association between hamate shape and the types of arboreal locomotion \((\text{RV} = 0.73; \ P < 0.0001)\). The relationship stands (although not as strongly) when considering phylogenetic structure through the use of PICs \((\text{RV} = 0.57; \ P < 0.05)\). Figure 8 shows the results for the first two PLS that account for 98% of the total covariance.

Along PLS1 \((79.5\% \text{ of total covariation and } 99\% \text{ of the total shape variation})\), negative values in the arboreal locomotion block are related to brachiation and arm-swinging, and covary most with proximodistally long and radioulnarly narrow hamate bodies, as well as with large and distally extending hamuli and convex triquetral facets. Conversely, positive values in the locomotor block are mostly related to “quadrupedal/tripedal walk” behaviors and to a lesser degree to “vertical climbing and descent” modes of locomotion. These latter arboreal locomotor types covary most in the hamate shape block with proximodistally shorter and radioulnarly broader hamates, with less distally protruding hamuli and “spiral” shaped triquetral facets.

Along PLS2 \((18.2\% \text{ of total covariation and } 47.3\% \text{ of the total shape variation})\), negative values covary most with “orthograde clamber and transfer” behaviors and to a lesser extent with “quadrupedal/tripedal walk”, whereas in the hamate shape block they relate to proximodistally short and radioulnarly wide hamates, with

---

**TABLE 3. Proportion of arboreal locomotion used in the two-block partial least squares (PLS) analysis**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>QTW</th>
<th>VCD</th>
<th>BW</th>
<th>OCT</th>
<th>BFS</th>
<th>DL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pan paniscus</td>
<td>0.32</td>
<td>0.53</td>
<td>0.01</td>
<td>0.255</td>
<td>0.09</td>
<td>0.04</td>
</tr>
<tr>
<td>Pan troglodytes schweinfurthii</td>
<td>0.36</td>
<td>0.49</td>
<td>0.07</td>
<td>0.05</td>
<td>0.05</td>
<td>0.00</td>
</tr>
<tr>
<td>Pan troglodytes verus</td>
<td>0.22</td>
<td>0.68</td>
<td>0.03</td>
<td>0.08</td>
<td>0.07</td>
<td>0.01</td>
</tr>
<tr>
<td>Gorilla beringei beringei</td>
<td>0.53</td>
<td>0.4</td>
<td>0.02</td>
<td>0.06</td>
<td>0.05</td>
<td>0.00</td>
</tr>
<tr>
<td>Gorilla gorilla gorilla</td>
<td>0.19</td>
<td>0.48</td>
<td>0.05</td>
<td>0.17</td>
<td>0.02</td>
<td>0.00</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>0.18</td>
<td>0.26</td>
<td>0.07</td>
<td>0.22</td>
<td>0.13</td>
<td>0.01</td>
</tr>
<tr>
<td>Symphalangus syndactylus</td>
<td>0.00</td>
<td>0.32</td>
<td>0.08</td>
<td>0.00</td>
<td>0.59</td>
<td>0.02</td>
</tr>
<tr>
<td>Hylabates lar</td>
<td>0.01</td>
<td>0.16</td>
<td>0.02</td>
<td>0.00</td>
<td>0.67</td>
<td>0.14</td>
</tr>
<tr>
<td>Papio Anubis</td>
<td>0.68</td>
<td>0.21</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.10</td>
</tr>
<tr>
<td>Ateles belzebuth</td>
<td>0.21</td>
<td>0.13</td>
<td>0.01</td>
<td>0.28</td>
<td>0.22</td>
<td>0.02</td>
</tr>
<tr>
<td>Lagothrichis lagotricha</td>
<td>0.29</td>
<td>0.14</td>
<td>0.00</td>
<td>0.30</td>
<td>0.09</td>
<td>0.04</td>
</tr>
</tbody>
</table>

QTW, quadrupedal and tripod walk; VCD, vertical climb and descent; BW, bipedal walk; OCT, orthograde clamber and transfer; BFS, brachiation and forelimb swing; DL, drop and leap. Data were obtained from Table 7 in Thorpe and Crompton (2006). Their percentages are presented here as a proportion.

\(a\)Average data for males and females, obtained from Carlson (2005).

\(b\)Unknown, but because drop and leap probably constitute a very small component of western gorillas locomotor repertoire, it was approximated at 1%.

\(c\)Thorpe and Crompton (2006) study, omitting juveniles.

\(d\)Data reported in Thorpe and Crompton (2006) for gibbons corresponds to pooled data for \(H. \text{agilis, H. lar and H. pileatus}\) from different sources. Because data come from different sources, and not all arboreal behaviors reported in the original studies were included, percentages often do not add to 100%.
Fig. 4. Hamate shape variation among extant anthropoid primates. A: Major taxonomic groups are differentiated along the first three principal components (PCs). B: Plot showing PC1 vs. PC2 (25.8% and 15.3% of variance explained, respectively). C: Plot showing PC1 vs. PC3 (12.3% of variance explained). D: Percentages of the total variance accounted for each PC and warped surfaces (based on a thin-plate spline) representing shape changes associated with each axis (in ulnar, dorsal, and distal views, respectively). PC1 represents values of $-0.20$ and $+0.20$; PC2 represents values of $-0.20$ and $+0.20$; PC3 represents values of $-0.15$ and $+0.15$. 
large facets for the metacarpals (especially the fifth), small and nonprojecting hamuli and dorsopalmarly short triquetral facets on the proximal portion. In contrast, positive values that mostly covary in the arboreal locomotor block are related to "vertical climb and descent" behavior. In the hamate shape block, this corresponds to slightly proximodistally longer and radioulnarily narrower hamates, with larger and distally projecting hamuli, and larger and more globular proximal portions of the triquetral facets (thus forming a true spiral facet).

When the distribution of taxa in the PLS bivariate plots is inspected (Fig. 8), overall, closely related taxa occupy a similar position in the scatter, similarly to the anthropoid hamate shape space (Figs. 4, 5). Extant species average configurations (in dorsoulnar view) were plotted. Phylogenetic structure is detected in this shape space (tree length: 0.22; $P < 0.0001$). LCAH indicates the reconstructed position for the last common ancestor of all modern hominoids. The longest branch (red marked) is leading from the LCAH to the hylobatids. B: Percentages of the total variance accounted for each PC.

**DISCUSSION**

**Characterization of Hamate Morphology Among Extant Anthropoids**

Our 3DGM results largely agree with previous observations on the relative uniformity of hamate shape within cercopithecoids, as well as the extensive overlap with platyrrhine taxa (Fig. 4). At the same time, when compared at the species level, platyrrhines exhibit consistent shape differences vis-à-vis cercopithecoids (Fig. 5), although more species and specimens per taxa are necessary to formally confirm this observation. However, overall, major anthropoid taxonomic groups can be characterized by means of their major trends of hamate shape variation (Fig. 4A). By relying on the two major axes of variation (Fig. 4B), extant hominoid hamates are readily distinguishable from those of extant monkeys, and in turn, those of hylobatids can be distinguished from those of great apes and humans. Within hominidae, human and gorilla hamates are more easily differentiated compared with those of chimps and orangutans (Fig. 4A,C). This observation might be explained by sympleisomorphy of the latter two in comparison to the more derived morphologies of humans and gorillas (Fig. 5) as similarly observed by others (Kivell et al., 2013).

**Inspection of the Phylogenetic Structure in Anthropoid Hamate Shape**

As explained above, major shape differences exist among major taxonomic groups, and thus a significant phylogenetic pattern is detected (Fig. 5). Not only is the colobine *Nasalis* similar to the papionin taxa, in accord with prior work (Lewis, 1972; O’Connor, 1975), but platyrrhines also overlap almost completely in shape space with cercopithecoids despite their early divergence time (Fig. 2). In contrast, extant hominoids—which are more closely related to each other than to platyrrhines or cercopithecoids—occupy a larger portion of the shape space (i.e., higher shape disparity). This is remarkable considering that this analysis incorporates fewer terminal taxa from the hominoids than from monkeys (12 vs. 14
respectively). These results suggest that hominoids, as a group, have experienced increased selective pressures on wrist morphology in comparison to other anthropoids. The hominoid’s larger hamate shape disparity is in large part due to the highly distinctive hylobatids; the longest branch in the hominoid part of the tree occurs between the last common ancestor of all hominoids (LCAH) and that of all hylobatids (Fig. 5, marked in red), suggesting a large amount of evolutionary change in the lineage leading to gibbons and siamangs. Similar results have been found recently when relying on a Mosimann shape space and a phylogenetic PCA (Kivell et al., 2013). These results support the hypothesis that hylobatids are highly autapomorphic in their hamate morphology (more so than great apes relative to monkeys). Derived wrist morphology in hylobatids is probably related to their very specialized ricochetal brachiation (e.g., Jenkins, 1981), which could be considered part of an early hominoid radiation in a new adaptive zone.

Fossil evidence also strengthens the view that hylobatids are too derived in their wrist joints to be considered good ancestral models for hominoids. Based on the study of the wrist bones of *Proconsul*, Lewis (1972) observed morphological traits enhanced for greater mobility in comparison to monkeys and hypothesized that an early feature defining hominoids in their new ecological niche different from other catarrhine primates was related to “brachiation”. However, he admitted that the term brachiation, with the connotations of a highly derived gibbon-like behavior, was probably not the most adequate term to describe the entire repertoire of arboreal activities displayed by early hominoids. In fact, latter studies have found that, on the basis of their total morphological patterns, early and middle Miocene apes relied heavily on arboreal palmigrade quadrupedalism and some type of climbing, but not below-branch suspension (e.g., Ward et al., 1993; Madar et al., 2002; Ishida et al., 2004; Moyà-Solà et al., 2004; Ward, 2007), although some workers have inferred knuckle-walking for *Sivapithecus* (Begun and Kivell, 2011).

The shape space defined by anthropoid primate means (Fig. 5) is similar to that of individual specimens (Fig. 4B) although it shows an inversion of the two major axes of variance (i.e., PC1 in the first analysis is PC2 in the second and vice versa). There is a shape shift in modern hominoids relative to monkeys. This shift involves an enlargement of the hamulus with a concomitant reduction of the relative size of the metacarpal facets, as well as a dorsopalmar enlargement of the proximal portion of the triquetral facet, which also happens to be more globular (see changes in PC2 of Fig. 4). This latter morphology may be related to the “concavo-convex spiral complex” described in extant great apes by Lewis (1972; see discussion below). As for the enlargement of the hamulus in hominoids, the small (and likely plesiomorphic) hamulus described for *Proconsul* (Beard et al., 1986) and *Sivapithecus* (Spoor et al., 1991) suggests that its size increased independently in hylobatids and extant great apes. The results of our PLS (Fig. 8) reinforce the idea that the small hamuli of fossil apes are related to quadrupedalism (PLS1) and/or even orthograde clambering (PLS2).

Extant great apes (especially gorillas) and humans occupy a region of the hamate shape space that is characterized by dorsopalmarly extended hamates (and hamuli) that are also less obliquely oriented. This is also evidenced by the more nearly coplanar positioning of the metacarpal facets (i.e., the fifth metacarpal facet does not extends as far distally beyond the fourth when the
Fig. 7. Predictable covariance of anthropoid hamate shape and size. **A**: Anthropoid species average shapes regressed on log-transformed centroid size (TIPS) reveals a significant relationship ($P < 0.05$) although only accounting for 8.4% of the total shape variation. **B**: Regression of phylogenetic independent contrasts (PICs) of shape and log-transformed centroid size reveals no significant relationship ($P = 0.8$).
radial side of the bone is aligned vertically as it does in monkeys and hylobatids; see PC1 in Fig. 4).

Since the reconstructed LCAH, orangutans (followed by chimps) seem to possess the most plesiomorphic hamate shape, while gorillas and humans with stockier hamate bodies and palmarly extending hamuli display the most derived hamates within extant Hominidae, in agreement with recent findings using similar methods (Kivell et al., 2013). While the hamate morphology of gorillas can be intuitively associated with weight bearing in these large-bodied terrestrial hominoids (Sarmiento, 1994), the morphology of the human hamate (freed from selective locomotor pressures) should be explored under the scope of enhanced manipulation. Future analyses including fossil species near major evolutionary splitting events (e.g., Almécija et al., 2013) and employing phylogenetically weighted PCA (e.g., Kivell et al., 2013; Polly et al., 2013) may allow a better determination of the polarity and degree of shape change within each lineage, and thus properly allow us to assess and resolve the patterns and tempo of hominoid hamate evolution.

Is There Predictable Covariation between Hamate Shape and Size?

Although significant phylogenetic patterning exists in both hamate shape and size (Figs. 5, 6), a very weak correlation of hamate shape and size exists when species means are compared to each other (Fig. 7A), and even becomes statistically nonsignificant when studying their phylogenetic independent contrasts (Fig. 7B). This indicates that the observed shape differences between big taxonomic groups are not simply correlated with overall size. However, it could be argued that some of the locomotor behaviors displayed by different anthropoid taxa analyzed here are more or less compatible with a certain body mass. For example, among other factors, brachiation is facilitated in hylobatids because they are small (e.g., Preuschoft and Demes, 1985; Swartz, 1989). In that sense, certain behaviors could show some amount of significant covariation with size (predictable or not) and in turn with specific aspects of shape (see following section). Future analyses (Almécija et al., in preparation) will inspect if and how patterns of hamate shape variation within hominoid species are predictably correlated with size.

Exploring Covariation of Hamate Shape and Locomotion

Most of the hamate functional morphology discussion has focused on the shape of the triquetral articular surface and the length and orientation of the hamulus. In this section, we discuss how previous observations on the anthropoid hamate morphology relate to our results. Lewis (1972) considered African apes to share a common hamate morphology: a narrower version of the wedge-shaped monkey hamate that is oriented with the
long axis of the body directed proximodistally instead of obliquely as in monkeys and hylabatids. This morphology reduces the articulation with the lunate (increasing articulation with the capitate) and causes the triquetral facet to be aligned more obliquely. This arrangement causes the triquetral facet to be more ulnarly oriented overall, but distally “inflected” toward the hamulus, resulting in the so-called “spirally concavo-convex” facet. Lewis (1972) contended that the “spiral” character of the triquetral facet contributed to the “screw mechanism” of the midcarpal complex, working as a “close-packing” system limiting extension, which he argued is an adaptation to resisting the tensile forces associated with regular suspension. Such screw-clamp kinematics of the carpus has been found in humans and chimpanzees (MacConaill, 1941; Orr et al., 2010), but the exact role of triquetrohamate facet contributed to the “close-packing” system limiting extension, which he argued is an adaptation to resisting the tensile forces associated with regular suspension. Such screw-clamp kinematics of the carpus has been found in humans and chimpanzees (MacConaill, 1941; Orr et al., 2010), but the exact role of triquetrohamate form in that mechanism is not clear (Orr, 2010). Furthermore, Jenkins and Fleagle (1975) argued that the presence of the spiral concavo-convex complex is common in quadrupeds such as Macaca, thus falsifying the connection between this trait and below-branch suspension. Sarmiento (1994) pointed out that the spiral complex effectively increases the radius of curvature of the carpal row proximally and increases the surface area of the distal triquetrohamate joint that is directed orthogonal transarticular loads when the midcarpus is extended. As such, he suggests that this character is related to quadrupedalism rather than suspension.

It has been hypothesized that the overall degree of convexity of the hamate triquetral facet reflects the potential range of flexion-extension at the midcarpus (Spoor et al., 1991). This facet is more curved (or globular) in apes and flatter proximally in terrestrial monkeys, with the latter ostensibly preventing extension during terrestrial locomotion in nonprimate mammals (Yalden, 1971). However, cadaver-based experiments indicate that although Papio has limited mobility at the triquetrohamate joint during dorsiflexion, palmigrade-capable monkeys exhibit much larger ranges of motion at this articulation than do chimpanzees or orangutans (Orr, 2010). Sarmiento (1988) provided the first quantitative study relating the orientation of the triquetral facet (computing angles between the capitate, triquetral and metacarpal facets) with the capacity of weight transfer through the triquetrohamate joint. As with Lewis, Sarmiento related the more ulnarily oriented triquetral facets of hominoids such as Pan and Pongo to less effective weight transmission and wider range of movement at the midcarpal joint (in comparison to that of monkeys). However, he noted that the triquetral facet in gorillas is nearly parallel to the articular surfaces for the metacarpals, thus favoring weight support (Sarmiento, 1988, 1994). Other studies using traditional goniometric measurements (Richmond, 2001) and least-squares planes fit to segmented joint surfaces of 3D polygon models of the hamate (Orr et al., 2013) had similar results with gorillas displaying the most proximally oriented triquetral surfaces.

Our PLS results based on arboreal locomotor behaviors and with PLS1 accounting for 79.5% of shape-arboreal locomotion covariance (and up to 99% of the total hamate shape variation) also indicate that quadrupedal primates exhibit wider hamate bodies with less globular and more proximally oriented triquetral facets and smaller hamuli than do suspensory taxa (Fig. 8). In terms of the “spiral” complex on the triquetral facet—assuming that its morphology is related to the long axis of the hamate body being more proximodistally aligned, with a globular (more convex) proximal end and a more concave distal portion—our PC1 of the entire anthropoid sample (Fig. 4) captures a gradient (negative to positive) from hylabatids to monkeys, followed by Pongo/Pan and finally Gorilla/Homo. Therefore, our results agree with those of Lewis (1972, 1989) in indicating better development of this complex in extant great apes (and humans) than in monkeys. However, hylabatids show the most disparate (autapomorphic) morphology, with no trace of “spiralization”. Instead, they exhibit an oblique proximodistal axis of the hamate with a large and very globular triquetral facet that lacks the distal concavity. This shape is most likely related to the “ball-and-socket” midcarpal morphology that has been widely interpreted as an adaptation for their very specialized ricochetal brachiation (e.g., Tuttle, 1969; Lewis, 1972; Usherwood et al., 2003). Hylabatids also exhibit relatively proximodistal long hamates, which Kivell et al. (2013) hypothesize is related to their overall long forelimbs (Drapeau and Ward, 2007) in relation to enhanced suspension. Hylabatids are also the smallest of the modern hominoids (Smith and Jungers, 1997), which is probably tightly related to their unique capability among hominoids to perform a true “ricochetal brachiation” involving a period of free flight (e.g., Conroy and Fleagle, 1972; Preuschoft and Demes, 1985; Swartz, 1989; Hunt, 1991). Hylabatids therefore define the shape that is related to brachiation along the first axis of the PLS analysis (Fig. 8A,C).

Although there is some overlap, Pan and Gorilla display a more globular proximal triquetral facet (i.e., concavoconvex) than does Pongo (PC3 in Fig. 4C). This may reflect a wider weight-bearing midcarpal surface in the African apes. The complex morphology of the spiral concavoconvex morphology found in some monkeys (Jenkins and Fleagle, 1975), Proconsul (Lewis, 1972), orangutans, and especially some African ape taxa might be explained in terms of the functional demands of arboreal locomotion in these forms. These locomotor behaviors require both enhanced mobility (i.e., rotation and ulnar deviation) and stability. The close-packing mechanism provided by the spiral facet has been hypothesized to be advantageous during knuckle-walking (e.g., Richmond et al., 2001), but the distribution of this feature may instead indicate its importance during use of the hand in arboreal settings. High positive loadings of vertical climbing associated with a highly convex proximal triquetral facet in PLS2 further suggest that this is the case (Fig. 8).

In reference to the greater development of the hamulus in extant hominoids in comparison to monkeys, it has been related to the action of the flexor carpi ulnaris (which primarily inserts on the pisiform) but acts on the hamulus by means of the pisohamate ligament (Schön and Ziemer, 1973; O’Connor, 1975; Lewis, 1977). A palmarly protruding hamulus favors powerful flexion of a fully extended wrist (Sarmiento, 1988). Conversely, the hamulus is more distally oriented in hominoid taxa that regularly use arboreal supports. A distally oriented hamulus improves the lever arm of the flexor carpi ulnaris for ulnar deviation, flexion of an already flexed wrist, or preventing dorsiflexion (Sarmiento, 1988, 1994; Patel
et al., 2012); thus, it is probably related to increasing wrist torque potential during climbing or suspension. Sarmiento (1994) pointed out that the hamulus of gorillas is better developed than in chimpanzees, with a more palmar extension similar to that of modern humans. He argued that this provides an advantageous lever arm for flexion of an extended wrist and prevents extension at the hamate-metacarpal fifth joint. Such an arrangement may be related to use of the hand for propulsion during terrestrial quadrupedalism (Sarmiento, 1994; see also Patel et al., 2012).

As for the palmar extension of the modern human hamate, it should probably be interpreted as a modification for enhanced manipulation (Orr et al., 2013). Two intrinsic hypothenar muscles (flexor digiti minimi and opponens digiti minimi) originate on the hamulus and insert on the ulnar side of the fifth metacarpal shaft and the base of the fifth proximal phalanx. In humans, these muscles act in flexion and opposition of the fifth digit to the lateral fingers, thus facilitating the palmar cupping and cylindrical grips important for a variety of human grips (Marzke et al., 1992, 1998; Reece, 2005; Niewoehner, 2006; Marzke, 2013). Our PLS results using the whole hamate landmark configuration as a multidimensional shape variable (Fig. 8) indicate that a distally protruding hamulus is associated with both suspension (negative values along PLS1) and vertical climbing (positive values along PLS2), thus reinforcing the previously stated arguments. However, the hominoid suspensory traits are not observed in Ateles, as previously reported (e.g., Lewis, 1989; Kivell et al., 2013) which has been explained by the use of a prehensile tail during suspensory behaviors and their substantial amount of time engaging in quadrupedal locomotion (Cant et al., 2001; see Table 3). Other studies have shown convergences between Ateles and hylobatids concentrated in the shoulder, humeral shaft, and elbow (e.g., Rose, 1996; Larson, 1998; Young, 2003; Patel et al., 2013).

Although a PLS based on the PICs of shape and arboreal locomotor behaviors may be related to use of the hand for propulsion during terrestrial quadrupedalism and vertical climbing. Future work incorporating fossils will focus on further elucidating the evolutionary histories of hamate phenotypic evolution and functional morphology.


to the following researchers and curators for granting access to collections under their care: Emmanuel Gilissen and Wim Wendelen, Royal Museum of Central Africa; Patrick Semal and Georges Lenglet, Royal Belgian Institute of Natural Sciences; Judy Chu-pasko, Museum of Comparative Zoology; Eileen Westwig and Neil Duncan, American Museum of Natural History; Richard Thorington and Linda Gordon, United States National Museum (Smithsonian). Ashley Hammond generously provided most of the Symphalangus hamate scans used in this study from the Bavarian State Zoological Collections. Soledad de Esteban-Trivigno offered insightful methodological discussion. Paul O’Higgins and Kristi Lewton educated one of us (S.A.) in the application and use of PLS to coordinate shape data and matrices of locomotor behaviors. A “Transmitting Science” course on GM and phylogenetics imparted by Chris Klingenaar during September 2013 near Barcelona inspired part of the analyses performed in this work. We are especially grateful to Siobhán Cooke and Claire Terveer for inviting us to provide a manuscript to this special issue of The Anatomical Record. This is NYCEP morphometrics contribution number 86.

SUMMARY AND CONCLUSIONS

In this work, and with a deep exploratory spirit, we sought to quantitatively characterize a biologically complex morphology, such is the case of the anthropoid hamate, using three-dimensional geometric morphometrics. Major trends of shape variation were inspected in 253 anthropoid primates using principal components analysis on the covariance matrix of 23 Procrustes-aligned surface landmarks. This approach allowed us to characterize and distinguish the hamate of hominoids from those of platyrrhine and cercopithecoid monkeys. Furthermore, differences between hylobatids and great apes and even among great ape genera were captured without relying on a priori grouping methods like canonical discriminant functions. This indicates that 3DGM is a reliable tool for accurately capturing subtle shape differences in complex biological structures.

The anthropoid primate phylogenetic tree was mapped onto hamate shape and size spaces by reconstructing internal nodes using squared-change parsimony. This allowed us to perform permutation tests that identified the presence of phylogenetic structure in both hamate shape and size. This indicates that, overall, more closely related taxa tend to exhibit more similar hamates (probably also due to phylogenetic clustering of similar locomotor behaviors). Although different anthropoid taxonomic groups exhibit both different hamate shape and size, allometric regressions reveal very small to non-significant (TIPS vs. PICs respectively) predictable covariance between hamate shape and size. Thus, our results show that differences in hamate size alone do not explain differences in hamate shape among taxa. We further hypothesized about the functional evolution of the hominoid wrist on the basis of the hamate.

We also used two-block partial least squares of shape data and a matrix of arboreal locomotor behaviors to test the covariance of hamate shape and observed locomotion without relying on the predictive models implicit in regression analyses. This analysis revealed that, among anthropoids, some aspects of hamate shape covary significantly with the frequency of brachiation, arboreal quadrupedalism and vertical climbing. Future work incorporating fossils will focus on further elucidating the evolutionary histories of hamate phenotypic evolution and functional morphology.

ACKNOWLEDGEMENTS

We are indebted to the following researchers and curators for granting access to collections under their care: Emmanuel Gilissen and Wim Wendelen, Royal Museum of Central Africa; Patrick Semal and Georges Lenglet, Royal Belgian Institute of Natural Sciences; Judy Chupasko, Museum of Comparative Zoology; Eileen Westwig and Neil Duncan, American Museum of Natural History; Richard Thorington and Linda Gordon, United States National Museum (Smithsonian). Ashley Hammond generously provided most of the Symphalangus hamate scans used in this study from the Bavarian State Zoological Collections. Soledad de Esteban-Trivigno offered insightful methodological discussion. Paul O’Higgins and Kristi Lewton educated one of us (S.A.) in the application and use of PLS to coordinate shape data and matrices of locomotor behaviors. A “Transmitting Science” course on GM and phylogenetics imparted by Chris Klingenaar during September 2013 near Barcelona inspired part of the analyses performed in this work. We are especially grateful to Siobhán Cooke and Claire Terveer for inviting us to provide a manuscript to this special issue of The Anatomical Record. This is NYCEP morphometrics contribution number 86.
LITERATURE CITED


Orr CM. 2010. Adaptations to knuckle-walking and digitigrady: a three-dimensional kinematic and morphometric analysis of the anthropoid wrist. Doctoral dissertation, Arizona State University, Tempe, AZ.