

Fossil hominins, quadrupedal primates and the origin of human bipedalism: a 3D geometric morphometric analysis of the Primate hamate

Homininés fossiles, primates quadrupèdes et l'origine de la bipédie : une analyse morphométrique géométrique 3D de l'hamatum chez les primates

G. Daver · F. Déroit · G. Berillon · S. Prat · D. Grimaud-Hervé

Received: 24 March 2014; Accepted: 27 May 2014
© Société d'anthropologie de Paris et Springer-Verlag France 2014

Abstract This note illustrates the value of studying non-human primates, especially quadrupedal primates, in order to investigate the origins of human bipedalism. Two distinct hypotheses postulate that hominins and African great apes share a common ancestor predominantly engaged in specialized forms of locomotion, i.e., arboreal orthograde (climbing or arboreal bipedalism) on the one hand and semiterrestrial locomotion (which includes climbing and quadrupedalism) on the other. Both hypotheses are supported by analysis of the wrist morphology of Pliocene hominins, and both have recently been challenged by a third hypothesis based on the study of *Ardipithecus ramidus* wrist morphology, which has shown general affinities between the latter hominin and quadrupedal primates. However, all three interpretations rely on rather limited knowledge of the variability of wrist bones in quadrupedal primates. Here, we propose to address the question of the origins of human bipedalism by means of a three-dimensional analysis of a carpal bone, the hamate, whose morphology appears to vary according to the locomotor

behaviour of primates. We compared the original specimens of Pliocene hominins (*Australopithecus*) with a large sample of non-human primates, including various quadrupedal anthropoids. Our results confirm that, on the one hand, the shape of the hamate in primates varies significantly according to their locomotor behaviour and, on the other hand, that the hypothesis of the semiterrestrial origin of human bipedalism can be rejected. The affinities between Pliocene hominins and most of extant quadrupedal primates indicate that the hands of early hominins partly retained a morphology inherited from a generalist quadrupedal ancestor, which concurs with the hypothesis recently proposed from the hand bones of *Ar. ramidus*.

Keywords Carpals · Evolution · Quadrupedalism · Bipedalism · 3D geometric morphometrics

Résumé Cette note vise à illustrer l'intérêt d'étudier les primates non-humains, notamment quadrupèdes, pour mieux caractériser l'origine de la bipédie humaine. Deux hypothèses stipulent que les homininés partageraient avec les grands singes africains un ancêtre commun impliqué majoritairement dans une forme de locomotion spécialisée, à savoir : l'hypothèse d'une orthograde arboricole (grimper ou bipédie arboricole) et l'hypothèse d'une semi-terrestrialité (qui inclue quadrupédie et grimper). Ces deux propositions sont notamment supportées par l'analyse morphologique du poignet des homininés pliocènes. Ces propositions ont été récemment remises en cause par une troisième interprétation fondée sur l'étude morphologique des os du poignet d'*Ardipithecus ramidus*, et qui a mis en évidence des affinités globales entre ce dernier homininé et des singes quadrupèdes. Cependant, ces trois propositions reposent sur une connaissance limitée de la variabilité de ces os chez les primates quadrupèdes. Nous proposons donc d'aborder la question de l'origine de la bipédie humaine par l'analyse

G. Daver (✉)
IPHEP : Institut de Paléoprimatologie
et de Paléontologie Humaine : évolution et paléoenvironnements,
UMR (CNRS) 7262, Université de Poitiers,
Bât. B35 – TSA 51106, 6, rue Michel Brunet,
86073, cedex 9, France
e-mail : guillaume.daver@univ-poitiers.fr

F. Déroit · D. Grimaud-Hervé
Département de Préhistoire,
UMR (CNRS) 7194, Muséum national d'Histoire naturelle,
43, rue Buffon, 75005 Paris, France

G. Berillon · S. Prat
UPR (CNRS) 2147, Dynamique de l'Evolution Humaine,
44, rue de l'Amiral Mouchez,
75014 Paris, France

tri-dimensionnelle d'un os carpien, l'hamatum, dont la morphologie varierait selon les modes locomoteurs des primates, en considérant des fossiles originaux d'homininés (*Australopithecus*) ainsi qu'un large échantillon d'anthropoïdes actuels, incluant une grande variété de primates quadrupèdes. Nos résultats confirment d'une part, que la forme de l'hamatum des primates varie selon les comportements locomoteurs, et d'autre part, que l'hypothèse d'une origine semiterrestre de la bipédie humaine peut être rejetée. Les affinités entre les hominins pliocènes et la plupart des primates quadrupèdes actuels soutiennent que les mains des hominins anciens ont en partie retenu une morphologie héritée d'un primate quadrupède généraliste. Ce résultat est en accord avec l'hypothèse récemment proposée à partir des os de la main d'*Ar. ramidus*.

Mots clés Carpiens · Évolution · Quadrupédie · Bipédie · Morphométrie géométrique 3D

Introduction

Three competing evolutionary hypotheses are currently attempting to describe the locomotor habits that led to the emergence of human bipedalism, each strongly supported by the interpretations of the hand morphology of early hominins¹ [1]). The first hypothesis maintains that hominin ancestors probably engaged in arboreal orthogrady, either for climbing on vertical substrates or for hand-assisted bipedalism suited to moving on flexible branches. This assumption is mainly supported by the proportions of the hand and the morphology of hominin phalanges from c.a. 7 to c.a. 1.5 Ma (for a detailed discussion, see [2]). The second hypothesis favours semiterrestrial locomotion, including climbing on vertical supports and quadrupedalism on the ground, such as knuckle-walking² the latter hypothesis being supported especially by an enlarged midcarpal complex (capitate + hamate) in the oldest species of the genus *Australopithecus* [3-6]. More recently, a third hypothesis has been put forward, based on the skeleton of *Ar. ramidus* (c.a. 4.4 Ma) [7]. Among other morphological features, the anatomy of the hands of *Ar. ramidus*, and particularly of the midcarpal complex, supports closer affinities with palmigrade³ monkeys than with extant apes, which tends to chal-

lenge the scenarios for the semiterrestrial and orthograde origins of human bipedalism [7]. Therefore, comparing the morphology of the midcarpal bones of early hominins and of various quadrupedal non-human primates is essential to a better characterisation of the emergence of human bipedalism.

In primates, the morphology of the midcarpal complex is particularly influenced by locomotor constraints during the stance phases. In terrestrial quadrupedal primates, the wrist adopts a posture with a slight extension and ulnar deviation, during which the joint and particularly the hamate are subject to high compressive forces [8,9] that are mainly exerted proximodistally [10]. In comparison, arboreal palmigrade primates [11,12] achieve more extension and ulnar deviation associated with mediolaterally oriented vertical ground reaction forces [9]. The midcarpal complex of suspensory primates, however, is subject to tensile forces [13]. As a result, all the above-mentioned studies strongly suggest that the morphology of the midcarpal joint should provide a particularly good indicator of locomotor habits in extant and extinct primates. Previous morphometric analyses of carpal bones have shown patterns of morphological variation associated with locomotor behaviour in primates [5,11,14-18]. Some of these studies, based on angular and metrical data, have clearly shown that the hamates of extant and extinct hominins are morphologically closer to those of terrestrial quadrupedal primates (e.g. gorillas, chimpanzees and olive baboons) than to those of arboreal apes (gibbons, siamangs and orangutans) [e.g. 5,6,15-18]. Terrestrial quadrupedal primates are characterized by the proximodistally compressed shape of the hamate with a triquetral facet facing proximally, while arboreal apes share a proximodistally elongated hamate and a triquetral facet facing medially. However, the above-mentioned studies included rather small comparative samples in terms of both overall size and representation of quadrupedal monkeys (e.g. n=43, with 8 monkeys [5], n=79 with 43 monkeys [15,17], n=78 with 25 monkeys [16] and n=106 with 16 monkeys [18]), and did not always apply appropriate methodologies for studying small-sized bones. Therefore, a reappraisal of the morphological affinities of the hamates of fossil hominins still requires detailed consideration of the exact nature of the variations in shape of this bone, using a large sample of quadrupedal primates and more appropriate methodologies.

The aim of this study was to test whether the hamates of Pliocene hominins and modern humans share morphological traits with semiterrestrial anthropoids. Two hypotheses were tested: i) the shape of the hamate of terrestrial and semiterrestrial quadrupedal anthropoids differs from that of more arboreal and suspensory primates; ii) the shape of hominin hamates has more affinities with that of semiterrestrial primates than any other anthropoids. To test these two hypotheses, we compared the hamates of *Au. afarensis* with those

¹Hand posture typical of African apes where body weight is anteriorly supported on dorsum of middle phalanges of the fingers during the stance phase.

²Hand posture typical of African apes where body weight is anteriorly supported on dorsum of middle phalanges of the fingers during the stance phase.

³Hand posture especially used by most quadrupedal primates, where the palm and the palmar faces of fingers contact the support during stance phase.

of non-human primates exhibiting various types of locomotor behaviour by applying a three-dimensional geometric morphometric approach.

Materials and Method

This study covered 222 hamates of different anthropoids, including 60 monkeys, with various locomotor habits. Only adult individuals with epiphyseal unions of antebra-chial bones, with no obvious pathologies were considered. A particular effort was made to include hamates of wild-caught individuals. The analyses were based on pooled-sexes samples, since the morphology of the carpus in primates is thought to be mainly constrained by high locomotor loads, so that sexual dimorphism seems to have relatively little impact on carpal morphology [19]. Eight locomotor groups were defined according to their habitual substrates and hand postures [20,21]: terrestrial bipedalism, hands with no locomotor functions (noted TNLF, i.e. *Homo sapiens*, n=51); semiterrestrial knuckle-walking (noted STKW, i.e. *Pan*, n=40); terrestrial knuckle-walking (noted TKW, i.e. *Gorilla*, n=30); suspension and hook grip⁴ (noted SHG, i.e. *Pongo*, n=13); brachiation and hook grip (noted BHG, i.e. *Hylobates* and *Symphalangus*, n=28); terrestrial and semiterrestrial digitigrady⁴ (noted T/STD, i.e. *Papio* and *Macaca*, n=33); cercopithecoïd arboreal palmigrady (=CAP, i.e. *Rhinopithecus*, *Trachypithecus*, *Presbytis*, *Nasalis*, *Colobus*, *Ptilocolobus*, *Procolobus*, n=17); ateline arboreal palmigrady and hook grip (=AAP/AHG, i.e. *Ateles*, n=10)⁵.

With the exception of the hamates of *Ar. ramidus* [7] and *Au. sediba* [22], which are currently under study, the two hamates of early hominins with sufficiently well-preserved articular borders were included in this study. These two hamates have been attributed to *Australopithecus afarensis* (A.L. 333-50, Hadar (Ethiopia), ca. 3.2 Ma [23]), and to cf. *Au. afarensis* (KNM-WT 22944 I, South Turkwel (Kenya), c.a. 3.5 Ma [22,24]). The functional morphology of these *Australopithecus* hamates has been deemed generally similar despite several morphological differences [24].

Seven 3D landmarks were defined at the maximum curvature of the articular contours of the hamate (Fig. 1, Table 1) Due to the small size of the specimens, the use of binocular glasses was necessary (Zeiss, x1.5). The landmarks were digitized with Microscribe 3DX with safety stabilization. The left hamates were digitized and when they were not available, the right hamates were digitized and mirrored.

⁴Hand posture used during forelimb dominated behaviours - climbing, suspension, brachiation - where only the palmar faces of the flexed digits contact the substrate.

⁵Hand posture during the quadrupedal stance phase, where only the palmar faces of the digits contact the support.

A generalized Procrustes analysis (GPA) of the Cartesian coordinates of the landmarks was performed. As an exploratory approach, Procrustes aligned coordinates were analysed using principal component analysis (PCA). The discrimination between the eight locomotor groups was then tested with a canonical variate analysis (CVA). To reduce the dimensionality of the data, the scores for the first ten PCs that accounted for more than 90% of the total variance were used as variables for the CVA [25]. Means equality between each pair of locomotor groups was tested with a pairwise Hotelling's test followed by a permutation test. The morphological affinities of the fossil specimens were assessed by adding them *a posteriori* in the CVA [25], to exclude any *a priori* assumption as to their locomotion. Procrustes superimpositions were performed with Morphologika [26] and statistical analyses with R [27,28].

Results

While the 10 first principal components account for more than 90% of the total variance, only PC1 vs. PC2 (36.7% of the total variance) exhibit variations in shape linked with locomotor groups (Fig. 2). The scatterplot for PC1 vs. PC2 clearly shows that the range of shape variation in apes (SHG, BHG, STKW, TKW) largely exceeds the range in quadrupedal monkeys (i.e. T/STD, CAP, AAP/AHG). Increasing values along the PC1 are associated with i) proximodorsal orientation and medial extension of the plane of the articular surfaces for the triquetrum and lunate, ii) medial extensions of the dorsal border of the metacarpal IV facet, iii) the palmar junction point of the metacarpal facets, which is proximal on the hamulus. PC1 shows a clear grouping of brachiating apes (BHG) at the lowest values while quadrupedal monkeys (i.e. T/STD, CAP, AAP/AHG) and humans (TNLF) mainly scatter at the highest scores. The great apes are intermediate: terrestrial knuckle-walkers (TKW) are closer to quadrupedal monkeys and humans, while suspensory great apes (SHG) and semiterrestrial knuckle-walkers (STKW) are intermediate between brachiating apes and quadrupedal primates and humans. Increasing values along PC2 correspond to i) a dorsopalmar enlargement of the articular facet of metacarpal IV and of the proximal contact areas ii) proximal and distal articular planes that are oriented orthogonally to the longer axis of the bone, iii) the palmar junction point of the metacarpal facets located more distally on the hamulus. PC2 shows a clear pattern where quadrupedal monkeys and brachiating apes tend towards the lowest values and great apes towards the highest values. Humans scatter all along PC2. Fossil hamates scatter in the range of variation of hominoids (Fig. 2): KNM-WT-22944 I falls within the variation of semiterrestrial knuckle-walkers (STKW, i.e. *Pan*) and suspensory apes (SHG, i.e. *Pongo*),

Table 1 Definition of landmarks on the hamate of anthropoids / Définition des points-repères sur l'hamatum des anthropoïdes.	
Landmark abbreviations	Definitions
HPd	Dorsal point between the facets of the capitate (noted C in Figure 1) and the lunate (noted L in Figure 1)
HPp	Palmar point between the facets of the capitate and the lunate
HDd	Dorsal point between the facets of metacarpals IV (MCIV in Figure 1) and V (MCV in Figure 1)
HDp	Palmar point between the facets of the metacarpals IV and V
HDpl	Point at the maximum curvature, located latero-palmarly, on the facet of metacarpals IV
HDdl	Point at the maximum curvature, located dorso-laterally, on the facet of metacarpals IV
Hdm	Distal-most point located on the proximal articular contour of the triquetral facet (T in Figure 1)

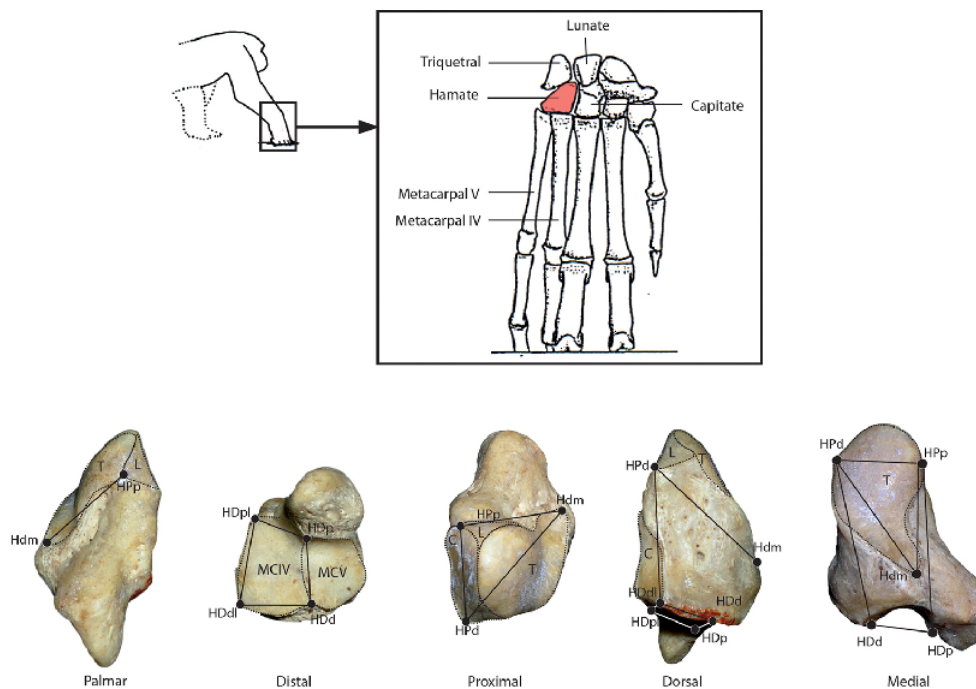


Fig. 1 Landmarks used for this study, example from the common chimpanzee (*Pan troglodytes*). Top left, lateral view of the forelimb during knuckle-walking. Top right, the knuckle-walking hand (the hamate is coloured) in the dorsal view (modified from [38]). Bottom, anatomical landmarks selected on the hamate. Dotted line, contours of the articular surfaces. For the abbreviations, see Table 1) / *Points-repères utilisés pour cette étude ; exemple à partir du chimpanzé commun (Pan troglodytes)*. En haut à gauche, vue latérale du membre antérieur au cours du knuckle-walking. En haut à droite, la main au cours du knuckle-walking en vue dorsale (modifié d'après [38]). En bas, sélection des points-repères anatomiques de l'hamatum (Lignes tiretées ; contours des surfaces articulaires. Pour les abréviations voir Tableau 1

while A.L. 333-50 falls within the variation of the suspensory apes (SHG, i.e. *Pongo*), brachiating apes (BHG, i.e. *Hylobates* and *Symphalangus*) and at the limit of variation of semiterrestrial knuckle-walkers (STKW, i.e. *Pan*) and semiterrestrial and terrestrial digitigrade primates (T/STD, i.e. cercopithecines).

The combination of CV1 and CV2 accounts for the greater part of the discrimination (70.6%) between the eight locomotor groups (Fig. 3). Despite rather large overlaps, the results from the pair-wise Hotelling's test show sig-

nificant discrimination between all locomotor groups. Overall, three locomotor groups are clearly distinguished, their distinctiveness being influenced by PC1 and 2: i) BHG exhibit a dorsopalmarly brief and proximodistally elongated shape, restricted and medially oriented surfaces for the proximal carpals, metacarpal facets extending distally on the dorsum of the hamulus; ii) quadrupedal monkeys including palmigrade and digitigrade species (T/STD, CAP and AAP/AHG), which largely overlap with TNLF; these are characterized by mediolaterally enlarged shapes, facets on

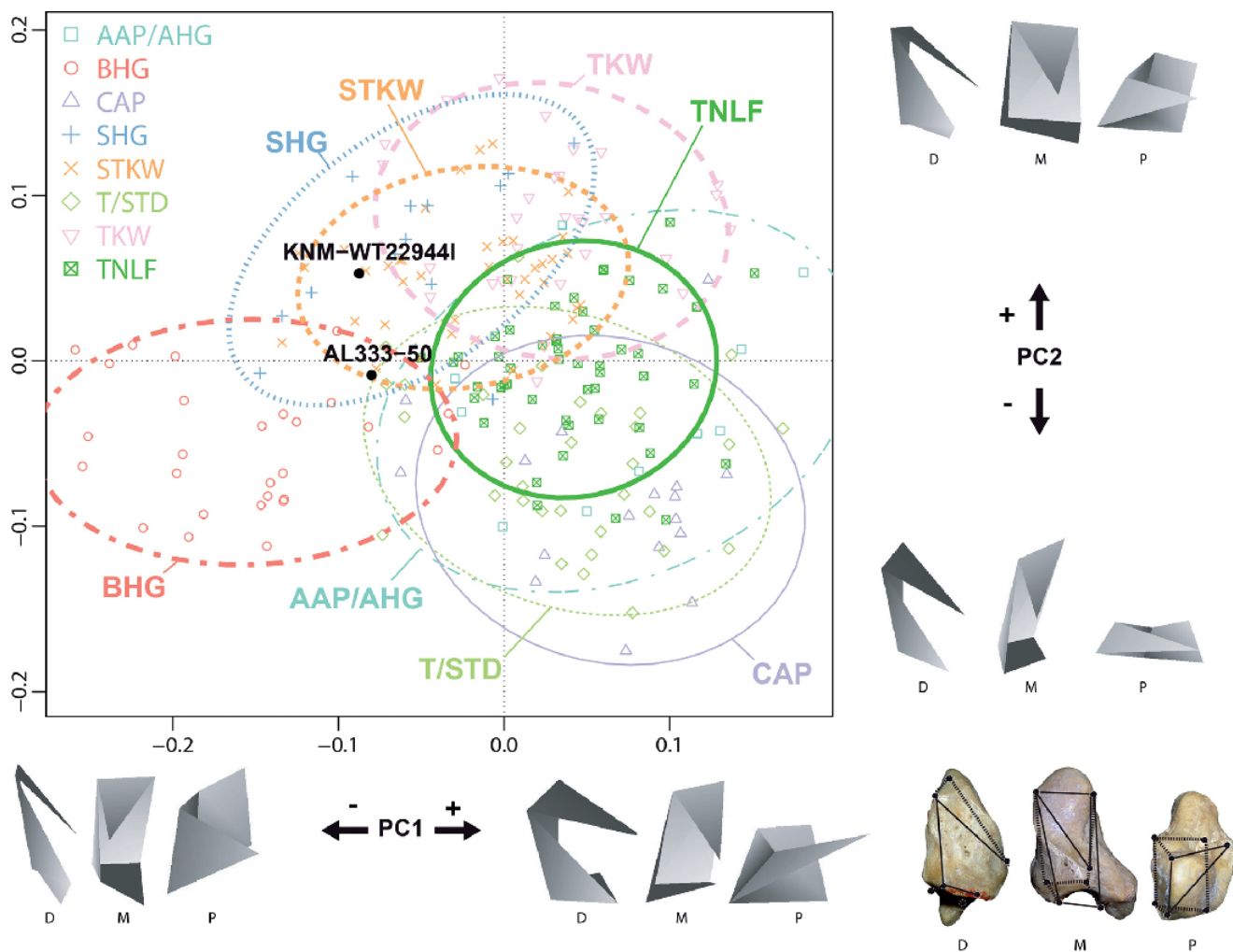


Fig. 2 Principal component analysis on Procrustes coordinates of 7 landmarks of the hamate (PC1 vs. PC2) (with 95% ellipses). For each axis, maximum warping is shown in the distal (D), medial (M) and proximal views (P). A hamate (*Pan troglodytes*) is shown as an example for visualizing the landmarks. Abbreviations: TNLF, terrestrial, hand with no locomotor function; STKW, semiterrestrial knuckle-walking; TKW, terrestrial knuckle-walking; SHG, suspension and hook grip; BHG, brachiating and hook grip; T/STD, terrestrial and semiterrestrial digitigrady; CAP, cercopithecoid-like arboreal palmigrady; AAP/AHG, arboreal ateline-like palmigrady and hook grip / *Analyses en composantes principales des résidus Procrustes de 7 points-repères de l'hamatum (PC1 vs PC2) (avec ellipses à 95%). Pour chaque axe, les déformations maximales des conformations sont indiquées en vues distale (D), médiale (M) et proximale (P). Un hamatum (*Pan troglodytes*) est présenté en exemple afin de visualiser les points-repères. Abréviations : TNLF, terrestre, mains sans fonctions locomotrices ; STKW, knuckle-walking semi terrestre ; TKW, knuckle-walking terrestre ; SHG, suspension et crochet anatomique ; BHG, brachiation et crochet anatomique ; T/STD, digitigradie terrestre et semi-terrestre ; CAP, palmigradie arboricole de type cerco-pithecoïde ; AAP/AHG, palmigradie arboricole de type ateliné et crochet anatomique.*

the proximal carpals that are extended and more proximally oriented and metacarpal facets restricted to the base of the dorsum of the hamulus; iii) great apes (TKW; STKW, SHG), which all have an intermediate morphology with dorsopalmally enlarged shapes and metacarpal facets extending distally on the dorsum of the hamulus. Within the locomotor groups of apes, the most suspensory (SHG) resemble brachiating apes and the most terrestrial and quadrupedal (gorillas) resemble quadrupedal monkeys. Chimpanzees (STKW)

overlap the SHG range of variation more broadly than the TKW range. With regard to the fossil specimens, KNM-WT-22944 I falls within the range of variation of terrestrial knuckle-walkers (TKW, i.e. *Gorilla*) while A.L. 333-50 falls within the overlapping area of terrestrial bipeds (TNLF, i.e. *Homo sapiens*), semiterrestrial knuckle-walkers (STKW, i.e. *Pan*), terrestrial and semiterrestrial digitigrade monkeys (T/STD, i.e. *Papio* and *Macaca*) and arboreal palmigrade atelines using a hook grip (AAP/AHG, *Ateles*). The

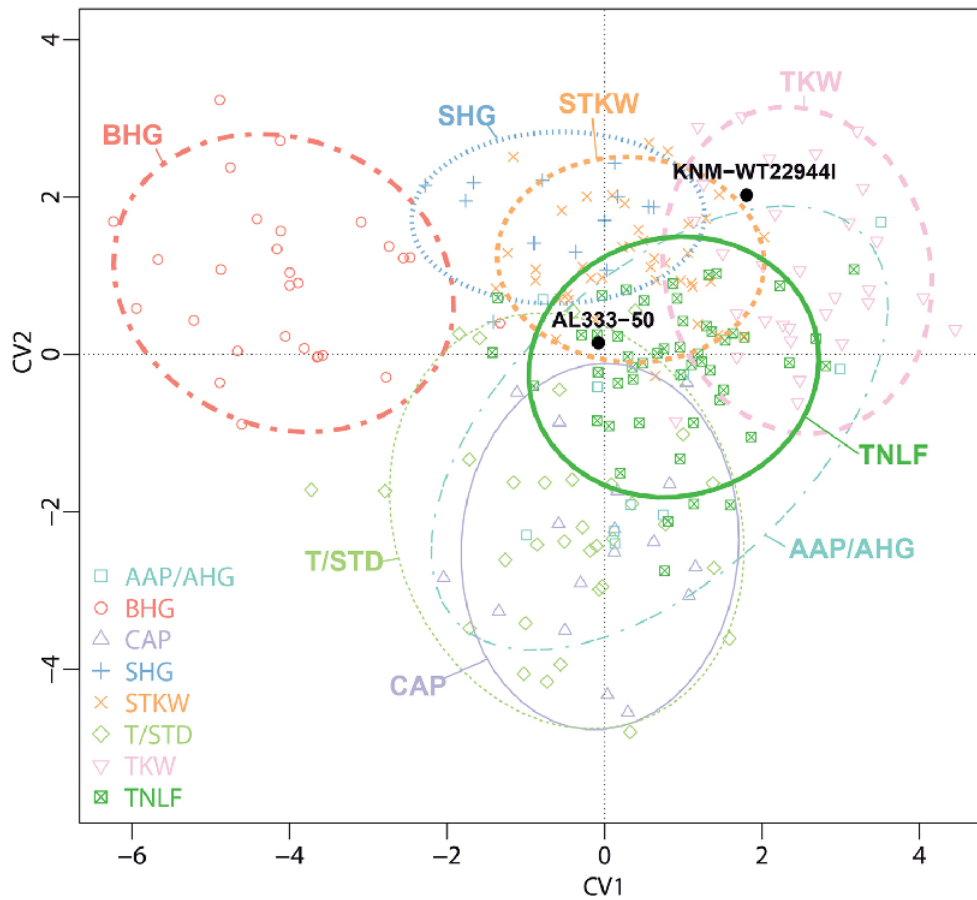


Fig. 3 Canonical variate analysis on the 10 first principal components (CV1 vs. CV2) (with 95% ellipses). Abbreviations: TNLF terrestrial, hand with no locomotor function; STKW, semiterrestrial knuckle-walking; TKW, terrestrial knuckle-walking; SHG, suspensory hook grip; BHG, Brachiating hook grip; T/STD, terrestrial and semiterrestrial digitigrady; CAP, cercopithecoid-like arboreal palmigrady; AAP/AHG, arboreal ateline-like palmigrady and hook grip / *Analyse canonique des 10 premières composantes principales (CV1-CV2) (avec ellipses à 95 %)*. Abbreviations : TNLF, terrestre, mains sans fonctions locomotrices ; STKW, knuckle-walking semiterrestre ; TKW, knuckle-walking terrestre ; SHG, suspension et crochet anatomique ; BHG, brachiation et crochet anatomique ; T/STD, digitigradie terrestre et semiterrestre ; CAP, palmigradie arboricole de type cercopithecoïde ; AAP/AHG, palmigradie arboricole de type ateliné et crochet anatomique.

difference between the two fossils is mainly due to i) the distal extension of the metacarpal facets on the hamulus and ii) the elongated triquetral facet in the South Turkwel specimen.

Discussion and conclusion

Relationships between hamate shape variations and locomotor hand postures in non-human primates

Our first aim was to test whether the hamate bones of terrestrial and semiterrestrial quadrupedal anthropoids differ from those of suspensory primates. The present study does not support this hypothesis, contrary to previous studies [5-6, 15-18]. By including a wide diversity of quadrupedal mon-

keys, the results show that there are no clear-cut differences in shape between terrestrial/semiterrestrial primates and arboreal quadrupedal primates, or between digitigrade and palmigrade monkeys when considering the 3D configurations of articular surfaces. Instead, this study shows that quadrupedal anthropoids, which mainly use their wrist under highly compressive conditions, differ from brachiating and suspensory primates, which mostly use their wrist under tensile conditions, in the mediolaterally enlarged hamate shape with a distally-extended proximal articular plane that is also more proximally oriented. In this enlarged comparative framework, the hamate morphologies of great apes are intermediate, reflecting a mechanical compromise between use of the wrist under tensile and compressive conditions. While the more suspensory great apes (orangutans and some chimpanzees) show more affinities with hylobatids, the more

terrestrial and quadrupedal great apes (gorillas) display closer affinities with quadrupedal monkeys. Knuckle-walking has been proven to represent a mechanical compromise that enables a primate which is osteologically adapted to arboreal life to be secondarily adapted to locomotion on the ground [29]. However, the discrimination observed between chimpanzees and gorillas can be linked to their distinct locomotor behaviour patterns. While adult and subadult chimpanzees mainly support their anterior body weight on the dorsum of digits II to III only when on the ground, thus partly freeing the hamate from compressive constraints (Fig. 1), gorillas support their body weight on the four medial digits (II to V), thus fully loading the hamate [30]. Ontogenic analyses of carpal traits classically associated with knuckle-walking also suggest that knuckle-walking is different between chimpanzees and gorillas [20,30]. Therefore, this study shows that comparing isolated carpal bones of anthropoids allows crucial functional signals of primate locomotion to be identified, even if we are aware that the study of the entire midcarpal complex would be more suitable (e.g. [30]). Allometry has been proven to explain part of the morphological variation of this carpal complex in Strepsirrhine primates, African apes and humans (e.g. [7,11,19,32], but this relationship still needs to be investigated at the anthropoid scale [33]) and is currently under study [34]. For instance, this study (as illustrated by the PC2) shows that great apes differ from other anthropoids in the following characters: the hamate shapes are enlarged dorsopalmarly and the proximal and distal articular plans are oriented orthogonally to the longer axis of the bone and not obliquely as in other anthropoids. These characters may help to withstand surface reaction forces due to repeated flexion-extension movements of the wrist in great apes during climbing activities [15].

Morphological affinities of hominin hamates: implications for the origin of hominin bipedalism

Our second hypothesis was that the hamate of extant humans and archaic hominins (here corresponding to *Au. afarensis*, $n=2$) share more morphological affinities with semiterrestrial primates than with other primates. This study, which includes a large spectrum of quadrupedal primates, does not support this hypothesis. Indeed, *Australopithecus afarensis* shares a common morphological pattern with terrestrial bipeds (humans) but no specimen of *Au. afarensis* shares exclusive affinities with semiterrestrial anthropoids (*Macaca*, *Papio*, *Gorilla* and *Pan*) as assumed [5,6,15–18]. Rather, *Au. afarensis* shows general affinities with all quadrupedal primates, including semiterrestrial, terrestrial and highly arboreal quadrupedal monkeys. Therefore, this study supports the hypothesis that the *Au. afarensis* hamate shape is probably inherited from a generalist quadrupedal

primate that would have been able to use a hook grip similar to that of New World monkeys (e.g. here, atelines). Such a result is compatible with a scenario whereby hominins originate from a palmigrade primate, as proposed from the hand bones of *Ar. ramidus* [7]. Indeed, palmigrady is thought to represent the ancestral condition among primates, and the locomotor hand posture the most frequently used by primates whether terrestrial or arboreal [7]. Quadrupedalism was probably predominant in the locomotor repertoires of Miocene hominoids either on arboreal or terrestrial substrates (for a summary on this topic see [35]). Most Miocene apes would have been able to use palmigrade postures, even if more specialized locomotor hand postures such as knuckle-walking [22; 36] or digitigrady [37] have been also proposed. While evidence from the fossil record is obviously still too scarce to validate such claims definitively, accurately identifying the osteological correlates of locomotor functions in extant (comparative morphology, experimental approaches) and extinct quadrupedal primates could bring innovative answers to the question of the origin of hominin locomotor abilities.

Acknowledgments We are grateful to the curatorial staff in the following institutions: *Musée Royal d'Afrique Central*, Tervuren; *Natuurhistorisch Museum Naturalis*, Leiden; *Anthropologische Institut und Museum*, Zurich-Irchel University; *Zoologische Museum, Universiteit van Amsterdam*; *Collection d'anatomie comparée* and *Collection d'anthropologie du Musée de l'Homme, Muséum national d'Histoire naturelle*, Paris. This study was supported by a “Louis Forest” grant from the *Chancellerie des Universités de Paris* and the *Société des Amis du Muséum National d'Histoire Naturelle et du Jardin des Plantes*.

References

1. Wood B, Lonergan N (2008) The hominin fossil record: taxa, grades and clades. *J Anat* 12:354–76
2. Crompton RH, Vereecke EE, Thorpe SKS (2009) Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. *J Anat* 212:501–43
3. Richmond BG, Begun DR, Strait DS (2001) Origin of human bipedalism: The knuckle-walking hypothesis revisited. *Am J Phys Anthropol Suppl* 33:70–105
4. Begun DR (2004) Knuckle-walking and the origin of human bipedalism. In: Meldrum DJ, Hilton CE (eds) *From biped to strider: The emergence of modern human walking, running, resource transport*. Kluwer Academic/Plenum Publishers, New York, pp 9–33
5. Richmond BG (2006) Functional morphology of the midcarpal joint in knuckle-walkers and terrestrial quadrupeds. In: Ishida H, Tuttle R, Pickford M, Ogihara N, Nakatsukasa M (eds) *Human origins and environmental backgrounds*, Springer, New York, pp 105–22

6. Gebo DL (1996) Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominid bipedalism. *Am J Phys Anthropol* 101:55–92
7. Lovejoy CO, Simpson SS et al (2009) Careful climbing in the Miocene: the forelimbs of *Ardipithecus ramidus* and humans are primitive. *Science* 326:70
8. Jenkins FA, Fleagle JG (1975) Knuckle-walking and the functional anatomy of the wrists in living apes. In: Tuttle RH (ed) *Primate functional morphology and evolution*. Mouton: The Hague, Paris, pp 213–27
9. Whitehead PF (1993) Aspects of the anthropoid wrist and hand. In: Gebo DL (ed) *Postcranial adaptations in nonhuman primates*. Northern Illinois University Press, Dekalb, pp 96–120
10. Schmitt D (1994) Forelimb mechanics as a function of substrate type during quadrupedalism in two anthropoid primates. *J Hum Evol* 26:441–457
11. Hamrick MW (1996) Functional morphology of the lemuriform wrist joints and the relationship between wrist morphology and positional behavior in arboreal primates. *Am J Phys Anthropol* 99:319–44
12. Lemelin P, Schmitt D (1998) The relation between hand morphology and quadrupedalism in primates. *Am J Phys Anthropol* 105:185–97
13. Jenkins FA (1981) Wrist rotation in primates: a critical adaptation for brachiators. *Symp Zool Soc Lond* 48:429–51
14. Corruccini RS, Ciochon RL, Mchenry HM (1975) Osteometric shape relationships in wrist joint of some anthropoids. *Folia Primatol* 24:250–74
15. Sarmiento EE (1988) Anatomy of the hominoid wrist joint - its evolutionary and functional implications. *Int J Primatol* 9:281–345
16. Spoor CF, Sondaar PY, Hussain ST (1991) A new hominoid hamate and first metacarpal from the late Miocene Nagri formation. *J Hum Evol* 21:413–24
17. Sarmiento EE (1994) Terrestrial traits in the hands and feet of gorillas. *Am Mus Novit* 3091:1–56
18. Corruccini RS (1978) Comparative osteometrics of hominoid wrist joint, with special reference to knuckle-walking. *J Hum Evol* 7:307–21
19. Kivell TL, Guimont I, Wall CE (2013) Sex-related shape dimorphism in the human radiocarpal and midcarpal joints. *Anat Rec* 296 (1):19–30
20. Kivell TL, Schmitt D (2009) Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. *Proc Natl Acad Sci (USA)* 106:14241–6
21. Fleagle JG (1999) *Primate adaptation and evolution*. New York: Academic Press.
22. Kivell TL, Kibii JM et al (2011) *Australopithecus sediba* hand demonstrates mosaic evolution of locomotor and manipulative abilities. *Science* 333:1411–7
23. Bush ME, Lovejoy CO et al (1982) Hominid carpal, metacarpal, and phalangeal bones recovered from the Hadar formation - 1974-1977 collections. *Am J Phys Anthropol* 57:651–77
24. Ward CV, Leakey MG et al (1999) South Turkwel: A new Pliocene hominid site in Kenya. *J Hum Evol* 36:69–95
25. Penin X, Baylac M (1999) Comparison of skulls of *Pan* and *Pongo* using tridimensional procruste superimpositions. *C R Acad Sci Paris Ser III*, 322:1099–1104
26. O'Higgins P, Jones N (2006) Tools for statistical shape analysis. Hull York medical school. <http://sites.google.com/site/hymsfme/resources>
27. R Development Core Team (2013) R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. URL <http://www.R-project.org/>
28. Claude J (2008) *Morphometrics with R*. Springer, Berlin, 315 pp
29. Tuttle RH (1970) Postural, propulsive and prehensile capabilities in the cheiridia of chimpanzees and other great apes. In: Bourne GH (ed) *The chimpanzee*, vol.2. Karger, Basel, New York, pp 167-253
30. Wunderlich RE, Jungers WL (2009) Manual digital pressures during knuckle-walking in chimpanzees (*Pan troglodytes*). *Am J Phys Anthropol* 139:394–403.
31. Daver G, Berillon G, Grimaud-Hervé D. (2012) Carpal kinematics in quadrupedal monkeys: towards a better understanding of wrist morphology and function. *J Anat* (220):42–56
32. Dainton M, Macho GA (1999) Did knuckle-walking evolve twice? *J Hum Evol* 36:171–94
33. Daver G (2009) The articular wrist complex in Miocene and Pliocene African hominoids: anatomofunctional and morphometric comparative approach. *Bull Mém Soc Anthropol Paris* 21:233–9
34. Daver G, Detroit F (2012) Forme et fonction du complexe médio-carpien des primates anthropoïdes actuels : implication pour l'émergence de la bipédie chez les hominins. Actes du 7^e symposium morphométrie et évolution des formes, pp 17-18
35. Ward CV (2007) Postural and locomotor adaptations of nonhuman hominoids. In: Henke, W, Tattersall I (eds) *Handbook of Palaeoanthropology*, Vol. 2: Primate evolution and human origins. Springer, Berlin, pp 1011-1030
36. McCrossin ML, Benefit BR et al (1998) Fossil evidence for the origins of terrestriality among Old World higher primates. In: Strasser E, Fleagle JG, Rosenberger A, McHenry H (eds) *Primate locomotion: recent advances*, Plenum Press: New York, pp 353-96
37. Patel BA, Susman RL et al (2009) Terrestrial adaptations in the hands of *Equatorius africanus* revisited. *J Hum Evol* 57:763–72
38. Inouye SE (1994) The ontogeny of knuckle-walking behavior and associated morphology in the African apes. Northwestern University, Evanston, Illinois, 513p