

**THE ARTICULAR WRIST COMPLEX IN MIOCENE AND PLIO-PLEISTOCENE
AFRICAN HOMINOIDS: ANATOMOFUNCTIONAL
AND MORPHOMETRIC COMPARATIVE APPROACH**

**LE COMPLEXE ARTICULAIRE DU POIGNET DES HOMINOÏDES MIOCÈNES ET
PLIO-PLÉISTOCÈNES AFRICAINS : APPROCHE COMPARATIVE
ANATOMO-FONCTIONNELLE ET MORPHOMÉTRIQUE**

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RÉSUMÉ

Cette thèse avait pour objectif d'étudier la mise en place des spécialisations fonctionnelles de la main des hominidés pliocènes et de tester l'hypothèse de la terrestrialité à l'origine de la lignée hominidé. 115 os du poignet mio-pliocènes originaux, parmi lesquels 27 restaient à décrire, ont été comparés à 392 spécimens ostéologiques de poignets d'anthropoïdes actuels. 14 poignets de cadavres d'anthropoïdes non humains ont été également analysés. Une approche transdisciplinaire a été conduite d'abord à l'aide de radiographies (n = 10), de dissections (n = 14) et d'observations morphologiques (n = 392) puis à l'aide de la morphométrie géométrique 3D appliquée à l'étude des os du complexe fonctionnel capitatum-hamatum (n[capitatum] = 245 ; n[hamatum] = 222 ; n[capitatum fossiles] = 10 ; n[hamatum fossiles] = 6). Ainsi, j'ai montré que pour les mouvements de flexion-extension du poignet, les hominoïdes actuels, à l'image des autres anthropoïdes, présentaient une plus grande mobilité médio-carpienne qu'antébrachio-carpienne. Toutefois, pour les mouvements de déviation radio-ulnaire, *Homo*, *Gorilla* et *Pongo* présentent plus de mobilité antébrachio-carpienne que les autres anthropoïdes en raison de leur processus styloïde ulnaire atrophié. Par ailleurs, les tissus mous stabilisateurs de la mécanique carpienne (ligaments et tendons) sont associés à des marqueurs ostéologiques liés aux postures des mains (quadrupédie et suspension). L'analyse morphométrique géométrique tridimensionnelle a mis en évidence que la conformation de chacun des os était liée i) soit aux différents types de saisie de force pratiquées par les anthropoïdes, ii) soit à leur comportement de suspension et de quadrupédie. D'un point de vue paléobiologique, j'ai proposé de nouvelles interprétations fonctionnelles des os du poignet, replacées dans le cadre fonctionnel de l'ensemble du squelette locomoteur des hominoïdes mio-plio-pléistocènes africains. Au moins quatre types de palmigradie arboricole ont probablement coexisté au Miocène. Une tendance à la terrestrialité se confirme au Miocène moyen chez *Equatorius* qui aurait pu pratiquer une forme de digitigradie ou de knuckle-walking. La main des hominidés pliocènes devait être utilisée dans une saisie de force intégrant une opposition du pouce comme chez *Homo*, exploitée soit dans un grimper, soit dans la manipulation et la fabrication d'outils. D'un point de vue évolutif, ce travail a notamment mis en évidence : i) une mise en place précoce (Miocène ancien) des spécialisations morpho-fonctionnelles propres aux hominoïdes actuels, ii) des caractères communs partagés par les hominidés pliocènes et miocènes, iii) une émergence tardive des spécialisations fonctionnelles du poignet *Homo*, probablement héritées d'un ancêtre arboricole.

Mots-clés : poignet, locomotion, hominoïdes, Néogène, anatomie fonctionnelle, morphométrie géométrique.

Keywords: wrist, locomotion, hominoids, Neogene, functional anatomy, geometric morphometrics.

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INTRODUCTION

My doctoral research aimed to evaluate wrist functions in Mio-Pliocene human ancestors in order to precise first hominids hands specializations and to further test current hypothesis of emergence of bipedalism (Daver 2007). Recent hypotheses have stated that the African apes/*Homo* Last Common Ancestor (LCA) might be a knuckle-walker² as suggested by hand morphology of Middle Miocene hominoid (McCrossin *et al.* 1998) and wrist morphology of Pliocene hominids (Gebo 1996; Sarmiento 1998; Richmond, Strait 2000; Richmond *et al.* 2001; Begun 2004; Richmond 2006). Alternatively, an arboreal (climbing and/or hand-assisted bipedalism) hypothesis has recently been championed (Thorpe *et al.* 2007; Crompton *et al.* 2008). This latter hypothesis is based on arboreal-like hand morphologies in oldest hominids (Haile-Selassie 2001; Semaw *et al.* 2005) possibly exploited in a power grip³ (Gommery, Senut 2006) and not exclusively in a hook grip⁴ typical of suspensory Asian apes. Because the wrist allows the precise orientation of the hand and because this joint could retained in bipedal hominids plesiomorphic traits inherited from the LCA (Lewis 1977; Corruccini 1978; Heinrich *et al.* 1993; Richmond, Strait 2000; Richmond *et al.* 2001; Richmond 2006), the study of the wrist is of first importance in paleoanthropological studies. So far, functional interpretations of these plesiomorphic traits have been limited because of the low congruence of the wrist complex and of the difficulty of quantifying carpal bones shape. Thus, I conducted a transdisciplinary approach. First, a morphofunctional and experimental analysis of living anthropoids aimed to identify new osteological traits on fossils associated with hand postures. Second, a three-dimensional osteometric (3D) analysis focused on the capitate-hamate functional complex of living and fossil hominids. Integrating conclusions of both approaches allowed a better understanding of the postural roles of the wrist in fossil hominoids and assessing terrestrial quadrupedalism in hominid ancestors.

MATERIAL AND METHODS

I analyzed 115 original wrist bones attributed to both Miocene (*Proconsul*, *Turkanapithecus*, *Afropithecus*, *Kalepithecus*, *Limnopithecus?*, *Rangwapithecus?*, *Dendropithecus?*, *Equatorius*, *Nacholapithecus*), and Pliocene genera (*Australopithecus*, *Paranthropus*), including 27 undescribed specimens. These fossils are representative of the taxonomic diversity currently recognized for these periods and were compared with 88 modern humans, and 314 living non-human anthropoids (including 23 genera). In addition, 14 (4 non-*Homo* hominoids; 3 ceboids, 7 cercopithecoids) wrist specimens from non-human anthropoids cadavers were analyzed.

A transdisciplinary approach was carried out through two complementary axes. First, radiographs and dissections of 10 wrists removed from cadavers allowed characterizing carpal kinematics in anthropoids. I also identified the osteological traits associated with entheses on carpal bones of living anthropoids (n = 392) in order to assess the role played by ligaments and tendons into carpal motions. Second, the 3D geometric morphometric analyses focused on both bones of the capitate-hamate functional complex (245 capitates; 222 hamates; 10 partial capitate-hamate complexes from Miocene (*Proconsul*, *Equatorius*, *Limnopithecus?*), Pliocene (*Australopithecus*) and Pleistocene (*Homo*).

THE WRIST OF LIVING HOMINOIDS

Carpal kinematics analyses of ten living quadrupedal non-hominoid anthropoids revealed that flexion-extension results more from midcarpal mobility than from radiocarpal mobility, as it has been observed in hominoids (Jenkins, Fleagle 1975; Sarmiento 1988). In radioulnar deviation, non-hominoid anthropoids display also a higher midcarpal mobility. This condition was observed in only two hominoids, *Pan* and *Hylobates* (Jouffroy, Medina 2002), while *Homo*, *Pongo* and *Gorilla* are characterized by a more mobile antebrachiocarpal joint. These results support that *Pan* and *Hylobates* may best described as retaining a plesiomorphic anthropoid wrist function. Dissections of 14 living anthropoids and morphological observations of 392 osteological specimens showed that terrestrial non-hominoid anthropoids display osteological traits associated with stabilization for flexion-extension and radioulnar deviation. By comparison, hominoids morphofunctional

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2. Quadrupedalism used by African apes where body weight is supported on dorsum of fingers middle phalanges.
 3. Prehensile hand function where the palm contacts the substrate. In *Homo*, the power grip can be associated with the opposition of the thumb (Marzke *et al.* 1992).
 4. Prehensile hand function where the palm does not contact the substrate (Marzke *et al.* 1992).

specializations of the carpus were precised. Great apes are characterized by stabilization systems of the supination and the ulnar deviation involved in the hook grip. Specific carpal kinematics of *Homo*, *Gorilla* and *Pongo* are clearly related with ulnar head morphology. *Pongo* and *Homo* display a better stabilization of thumb extension while *Homo* is distinguished by a unique thumb flexion-extension stabilization.

Geometric morphometrics of each bone of the capitate-hamate complexes showed that living hominoids exhibit a greater morphological variability than all other anthropoid, reflecting their contrasting positional repertoires. These results confirm previous analyses based on traditional methods (Corruccini *et al.* 1975). Although our main results reflect hand postures utilized by living anthropoids, they also emphasize osteological traits peculiar to each bone of the capitate-hamate complex. For the capitate, our main results highlight the different utilization of a power grip: i) human differs clearly from other anthropoids by the morphologies of the facets for the trapezoid and the lunate, this illustrates major compressive loads linked to thumb opposition; ii) all great apes share a less projected trapezoid contact. Influenced by size, this feature illustrates the compressive loads associated to a power grip devoid of thumb opposition. Our results also highlighted differences between suspensory and terrestrial anthropoids, as well as between African hominoids specializations. Results of the shape analysis of the hamate show some clear morphological differences between quadrupedal anthropoids who utilize the wrist in compression and suspensory anthropoids who utilize their wrist in tension: i) Asian apes and *Pan* exhibit a proximodistally elongated hamate due to tension loads applied during the hook grip; ii) great apes are characterized by their dorsopalmarly enlarged hamates and their better stabilization of carpometacarpal IV-V joints. Influenced by size, this trait is associated to an optimized absorption of compressive forces during flexion-extension movements involved in traction behaviours or knuckle-walking. Other results also highlighted features that distinguish terrestrial and arboreal anthropoids, as well as ceboid specializations.

THE WRIST OF FOSSIL HOMINIDS

For *Proconsul*, 67 antebrachiocarpal fossils were studied and 21 described for the first time. Like arboreal quadruped anthropoids, *Proconsul heseloni* displays

a weakly stabilized radioulnar deviation and flexion-extension. Both antebrachiocarpal and midcarpal congruence are optimized in extension and ulnar deviation, associated to a more mobile intermetacarpal II-III joint. Interestingly, this anthropoid resembles living hominoids (*e.g.* antebrachial pronosupination abilities, thumb mobility, carpal architecture, hamate-capitate complex congruence). *Proconsul nyanzae* wrist differs from *Proconsul heseloni* by both lower stabilized ulnocarpal and carpometacarpal II joints and, as *Afropithecus*, a more congruent midcarpal joint. *Turkanapithecus* differs from *Proconsul* because it lacks the stabilization of the hominoid-like supination and exhibits a better stabilization for flexion-extension. By contrast to what has been previously described, small-sized Miocene anthropoids are unique when compared with their contemporaries. These primates exhibit some ceboid-like wrist functions such as the lowest radioulnar pronosupination ability (*Limnopithecus?*), the highest degree of midcarpal supination (*Rangwapithecus?*), a better stabilization of the radial midcarpal joints (*Dendropithecus?*) and the weakest midcarpal extension stabilization (*Kalepithecus?*). The first description of Middle Miocene hominoids wrists highlighted two functional trends. On the one hand, *Nacholapithecus* wrist shares with *Proconsul* and living hominoids an efficient supination stabilization as well as a better load transmission in the radial compartment of the antebrachiocarpal joint. On the other hand, *Equatorius* differs from *Nacholapithecus* by higher level of wrist stability for both radioulnar deviation and flexion-extension, a stabilized thumb extension as in *Pongo* and *Homo*.

The 3D geometric morphometric analysis confirm that Miocene capitates (*Proconsul heseloni* and *Limnopithecus?*) show morphological affinities for arboreal anthropoids and suspensory hominoids (*e.g.* orangutan). This results support that these two fossil primates probably utilized a power grip with no thumb opposition. *Proconsul* hamates are morphologically close to that of quadrupedal non-hominoid anthropoids and *Homo* while *Equatorius* show more morphological affinities for cercopithecoids.

In Pliocene hominids, *Australopithecus* shares with *Proconsul* common morphological features (pronosupination abilities; capitate-hamate complexes congruence; carpometacarpal II-III joint morphologies). From a functional point of view, *Australopithecus*, differs from Miocene anthropoids (less stabilization for supination, better stabilization for midcarpal supination

and extension, antebrachio-carpal ulnar deviation and flexion abilities closer to that of *Pan* and *Pongo*, better transmission of compressive loads on the lunate-capitate joint). Carpal morphology of Pliocene hominids show also an important functional diversity: *Australopithecus afarensis* hamate exhibits a lower carpometacarpal IV-V joint stabilization and a lower degree of midcarpal pronation and ulnar deviation than the South Turkwell hominid. *Australopithecus anamensis* shows more stability for carpometacarpal II-III joints as do so non-human hominoids, as well as a *Homo*-like stabilization for thumb flexion-extension. *Paranthropus* differs from *Australopithecus* because of a better stabilization of flexion-extension and because of a *Pan/Pongo*-like pronosupination ability. This conclusion illustrates that two Pliocene hominids with different radioulnar pronosupination and/or radioulnar deviation strategies coexisted.

The 3D morphometrics analyses showed that Pliocene capitates exhibit some clear morphological affinities for human capitates typical of the utilization of a *Homo-like* power grip. Both Pliocene hamates are included in the great apes variability. The south Turkwell hamate (3,5 My) does not fall within *Homo* variability and differs from *Australopithecus afarensis* because of its radioulnarly enlarged shape typical of that of living African great apes. The morphological descriptions also highlighted the close morphological affinities shared by the South Turkwell hamate and that of African great apes (ex: a better stabilization of hamatometacarpal IV-V,

presence of an elongated triquetral facet). Regarding hamate morphologies, this results suggest that between 3,5 and 3 Ma, two morphotypes are represented, an older one which recalls the hamate of African great apes and a younger one closer to *Homo* (*contra* Ward *et al.* 1999).

CONCLUSION

During the Miocene, at least four types of arboreal palmigrady may have coexisted; a palmigrady with hominoid-like wrist specializations (*Proconsul heseloni*, *Nacholapithecus*), a cercopithecoid-like palmigrady (*Turkanapithecus*), a ceboid-like palmigrady (*Limnopithecus?*, *Dendropithecus?*, *Rangwapithecus?*; *Kalepithecus?*) and a semi-terrestrial palmigrady (*Afropithecus*, *Proconsul nyanzae*). A terrestrial trend is especially supported by *Equatorius* wrist morphology, potentially used in a digitigrade/knuckle-walker hand posture. Pliocene hominid hands were involved in a power grip with thumb opposition, either utilized in climbing or in manipulation/tool-making (Marzke *et al.* in press). Although their wrist share morphological features with Miocene anthropoids (*fig. 1*), no persistent knuckle-walking traits have been identified. This conclusion challenges the knuckle-walking hypothesis of bipedalism emergence (Richmond, Strait 2000; Richmond *et al.* 2001; Begun 2004; Richmond 2006).

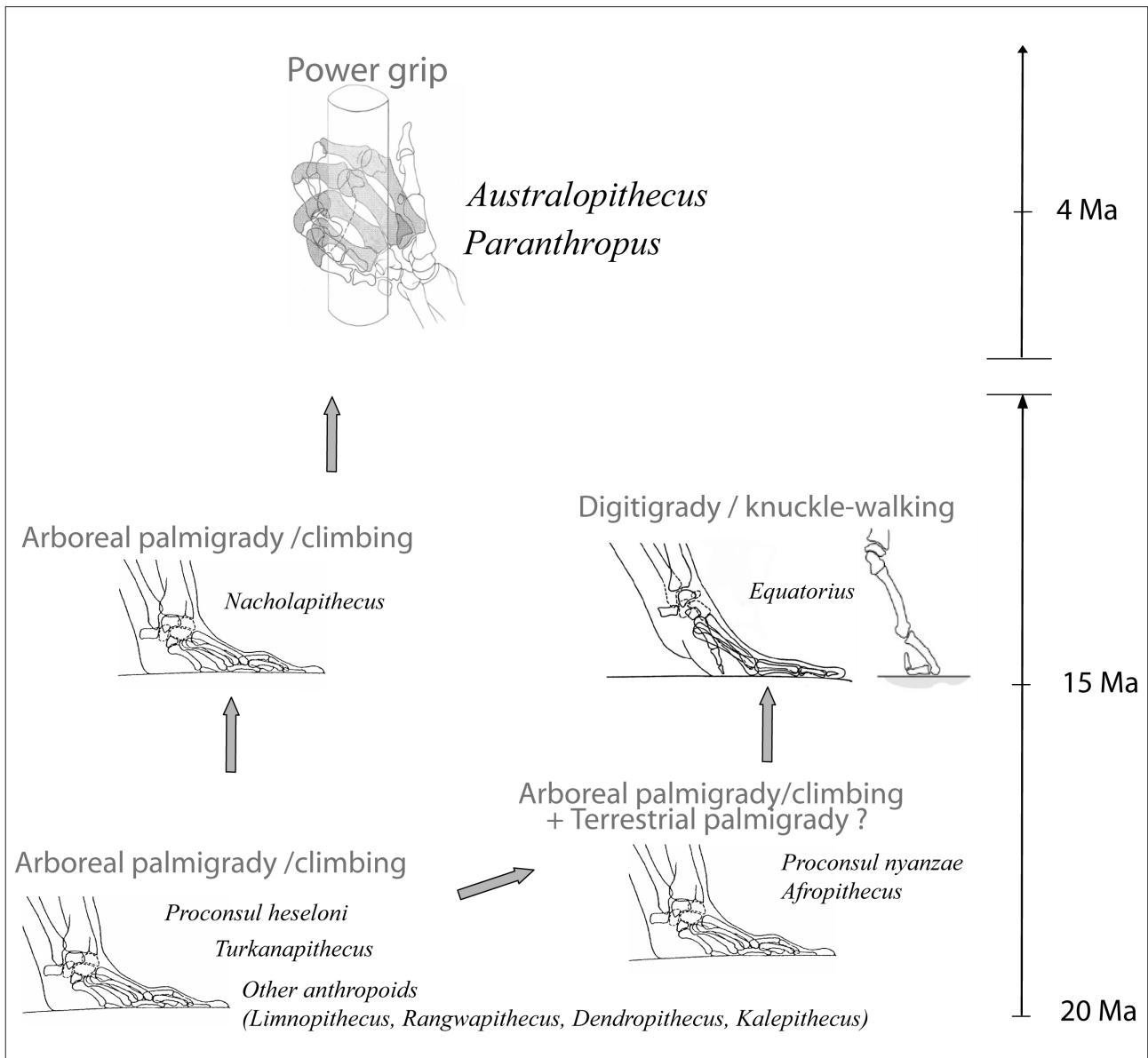


Fig. 1—Main hand postures used by Miocene and Pliocene hominoids: illustrations of the hand postures from Lewis (1977), Whitehead (1993), Richmond and Strait (2000).

Fig. 1 - Principales postures de mains employées par les hominoïdes miocènes et pliocènes : illustrations des posturaux de mains extraites de Lewis (1977), Whitehead (1993), Richmond et Strait (2000).

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