Universitat Autònoma de Barcelona
Facultat de Ciències
Departament de Biologia Animal, Biologia Vegetal i d'Ecologia
Unitat d'Antropologia Biològica

PhD Thesis

Evolution of the hand in Miocene apes: implications for the appearance of the human hand

Sergio Almécija
2009

Institut Català de Paleontologia

Paleoprimatology and
Human Paleontology

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Memòria presentada per Sergio Almécija per optar al títol de Doctor per la Universitat Autònoma de Barcelona, programa de doctorat en Biologia (opció Antropologia) del Departament de Biologia Animal, Biologia Vegetal i d'Ecologia. Recerca dirigida pel Professor Salvador Moyà-Solà, ICREA a l'Institut Català de Paleontologia i a la Unitat d'Antropologia Biològica del Departament de Biologia Animal, Biologia Vegetal i d'Ecologia, Universitat Autònoma de Barcelona.

Doctorand:
Sergio Almécija

Director:
Prof. Salvador Moyà-Solà

To the Big Bang, for everything

Contents

Pròleg [Prologue, in Catalan]

Aquesta treball de tesi és el resultat de la investigació duta terme des de gener de 2006, quan vaig començar a gaudir d'una beca de Formació d'Investigadors de la Generalitat de Catalunya. Anteriorment ja em dedicava a la 'paleo', però no estrictament a la recerca. Recordo que estava acabant la carrera de Biologia i l'única cosa que tenia al cap era que volia dedicar-me a l'evolució humana. En aquell temps passava la meitat de les hores de la meva vida excavant a l'Abocador de Can Mata (els Hostalets de Pierola, l'Anoia). Vaig començar la meva 'aventura canmatiana' l'1 de desembre de 2004; el mateix any havia estat descrit *Pierolapithecus catalaunicus*—trobat en aquell mateix indret gairebé dos anys abans. Doncs bé, el primer dia de feina a l'abocador, un dels paleontòlegs crida al meu bon col·lega Jose Robles (co-director de la intervenció paleontològica a la zona) i li diu via *walkie*: "escolta Jose, he trobat un fòssil molt *xulo*". I tant *xulo*, es tractava d'un fragment de la mandíbula d'un nou gènere d'homínid miocè, *Anoiapithecus brevirostris*, en l'estudi del qual he tingut el plaer d'involucrar-me. En aquell moment vaig pensar: "això és al·lucinant", però la idea de treballar allà com a investigador no era encara al meu cap.

Sembla ser que dedicar-se a la paleoantropologia en aquest país és força difícil (més encara quan el material d'estudi són fòssils d'humans en sentit estricte, dels quals hi ha poques restes). El cas és que durant un esmorzar a la feina, el meu col·lega David Alba (llavors també co-director a Can Mata) se'm va apropar i em va dir: "escolta nen, i tu ja tens clar què faràs quan acabis la carrera?" Jo estava convençut que em dedicaria a l'evolució humana, tot i que he de reconèixer que no tenia NI IDEA de com m'ho faria. El David em va convèncer que estudiar els 'monos' del Miocè era bona idea, ja que constituïen el primer pas de l'evolució dels homínids (en sentit ampli), des dels seus ancestres més semblants a les actuals mones fins als actuals grans antropomorfs (*great apes*) i humans; de fet, només es tractava d'ampliar els horitzons d'estudi. Per saber com varen aparèixer els primers hominінis bípedes en el trànsit Miocè-Pliocè (a l'entorn de 6 Ma) és imprescindible conèixer els seus antecedents del Miocè. I precisament d'això tracta la primera meitat de la tesi. Resumiré la història dient que en David, sense que jo ho sabés, ja havia parlat amb en Salvador Moyà-Solà (cap general del projecte dels Hostalets i actual director de l'Institut Català de Paleontologia), i que aquest s'havia mostrat interessat a dirigir-me la tesi gairebé sense coneixe'm... s'ha de ser temerari!

A excepció dels metacarpians i falanges, els ossos de la mà i el peu són d'aquells que la majoria de paleontòlegs no especialitzats posen dins el gran sac del mateix nom: ‘os de mà o peu’, sense fer-ne distincions. Això, juntament amb el fet que tots ells articulin mútuament d'una manera molt específica, ha fet que des de sempre m'hagin atret d'una manera molt especial, en tant que puzles d'entreteniment. En Salvador portava interessat en el tema de l'evolució de la mà en els homínids des que va trobar-se amb l'estrany cas d'*Oreopithecus bambolii* als anys noranta. També havia realitzat amb en David i la Meike Köhler un estudi sobre la mà d'*Australopithecus afarensis* i en tenia encetat des de feia uns anys un altre sobre la mà de l'Homínid 7 d'Olduvai (OH 7) atribuïda a *Homo habilis*. Més endavant jo mateix m'incorporaria a l'estudi d'aquesta mà, que constitueix el capítol 5 d'aquesta tesi. Des de llavors vaig quedar captivat per aquest fòssil, que és part essencial també dels Capítols 6 i 7.

Així, sense saber-ho, vaig heretar la responsabilitat de tirar endavant un tema especialment interessant per al meu director; i més tenint en compte que s'estava acumulant la feina amb la mà d'*Hispanopithecus laietanus* de Can Llobateres (Sabadell) i les més recent troballa de *Pierolapithecus* (amb dues mans parcials d'un mateix individu). No puc queixar-me: aquell mateix any vaig demanar una beca predoctoral i me la van concedir; i a partir del gener de 2006 vaig poder dedicar-me a temps complet a fer recerca. Recordo que no em va costar gaire posar-m'hi; en Salvador tenia sobre la seva taula de feina una muntanya (literalment) d'articles sobre el tema. Recordo que vaig passar-me gairebé un any llegint i escanejant pàgina a pàgina aquests articles (més temps amb això segon, ja que molts d'ells eren molt antics i no existien en versió PDF), abans de poder fer el primer cop d'ull a un dels meus fòssils d'estudi. A dia d'avui la majoria d'aquests articles ja estan disponibles en versió electrònica, i a més l'institut disposa d'un escàner que digitalitza de forma automàtica...

Respecte al treball presentat en aquesta tesi, per tal de poder incloure tota la feina realitzada en aquests quatre anys, s'ha optat per donar-li un format com si d'una tesi clàssica es tractés. No obstant, aquesta tesi ha de ser vista com un compendi de publicacions. Cada capítol, a excepció de la introducció, constitueix un article independent, amb la seva metodologia, apartats i nomenclatura propis. Així s'ha indicat al principi de cadascun d'ells, on apareix la seva referència original, així com el seu estatus actual (en el cas de tractar-se de manuscrits no publicats). Així doncs, tot el present treball resulta de la col·laboració de varis autors, i hauria d'avaluar-se també en funció d'això. Els diferents estudis independents (capítols/articles) corresponen a uns objectius inicials específics, que són indicats a l'apartat *Objectives of this work* del Capítol 1.

L'objectiu era comprendre l'evolució de la mà en els grans antropomorfs fòssils i actuals, així com trobar les seves implicacions per a l'origen de la mà humana, estructura de la qual, crec, no fa falta esmentar la gran importància que té en les nostres vides. Així doncs, la primera part de la recerca (Capítols 2 a 4) se centra en l'estudi dels homínids miocens, especialment *Pierolapithecus* i *Hispanopithecus,* mentre que la segona (Capítols 5-7) està dedicada a la posterior evolució d'aquesta estructura en els homininis (=homínids bípedes) plio-pleistocens africans. Aquesta darrera part presta especial atenció als orígens de la 'cultura lítica' i la seva relació amb l'evolució de la mà humana moderna.

L'abast inicial consistia a treballar en l'evolució de tots els ossos dels quals està formada la mà; no obstant, els resultats d'aquesta tesi corresponen només a l'anàlisi dels 'ossos llargs' (metacarpians i falanges). Això és degut al fet que en un principi només disposava de les dades numèriques d'aquests ossos (mesurades per en Salvador i el David), que jo he anat ampliant a mesura que he pogut visitar diferents col·leccions osteològiques. També he anat compilant dades dels ossos del canell i del peu, però la base de dades és encara massa minsa per poder-ne fer anàlisis estadístiques—deixant de banda la falta de temps. No obstant, espero tenir resultats també de les parts no estudiades en el futur pròxim. Especialment interessants seran els resultats referents a la coevolució de la mà i el peu en les primeres formes bípedes.

Ja per acabar, un altre fet curiós és que quatre anys després d'haver començat a fer el doctorat peso 10 kg més, tinc molt menys cabell i necessito ulleres per reconèixer la gent pel carrer... La pregunta que em faig tot sovint és quina part de tot 'això' és deguda als anys (*nature*) i quina a la tesi (*nurture*)?

Sergio Almécija
Bellaterra, setembre de 2009.

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Mereixen especial esment els coautors dels articles que formen part del present treball: els doctors Salvador Moyà-Solà, David M. Alba i Meike Köhler. El Salvador ha estat, a més, el meu director de tesi (i director de l'ICP) i li he d'agrair que sempre

m'hagi tractat com un col·lega, i no pas com un alumne; i sobretot que mantingués 'viu' el meu intel·lecte enviant-me *mails* de feina els diumenges a les 9 del matí. El David és una de les persones més pràctiques que conec i un *freak* sense mesura: estudia cargols actuals per 'relaxar-se' en el seu 'temps lliure'(?). A ell i a en Salvador els vull agrair el suport i assessorament continu en la lluita contra alguns vells paradigmes científics. La Meike fa un temps que ha abandonat els primats com a àrea primària d'estudi, però el coneixement produït quedarà per sempre. Sense ells tres hagués estat impossible realitzar la tasca, i això ho dic en el sentit més estricte de les paraules. Van ser ells qui van trobar els esquelets parcials d'*Hispanopithecus* i *Pierolapithecus*, que constitueixen la primera meitat d'aquesta tesi. També van ser ells els primers a dir obertament que la mà de l'*Homo habilis* probablement NO pertanyia al gènere *Homo*!

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Chapter 1

A brief introduction to the hands of the primates

HAND ANATOMY

It is well know that all primates share a more or less plesiomorphic hand, in the sense that it is a pentadactyl structure (Figure 1.1), inherited from the first amniotes (Tuttle 1992). Its main anatomical regions are the following:

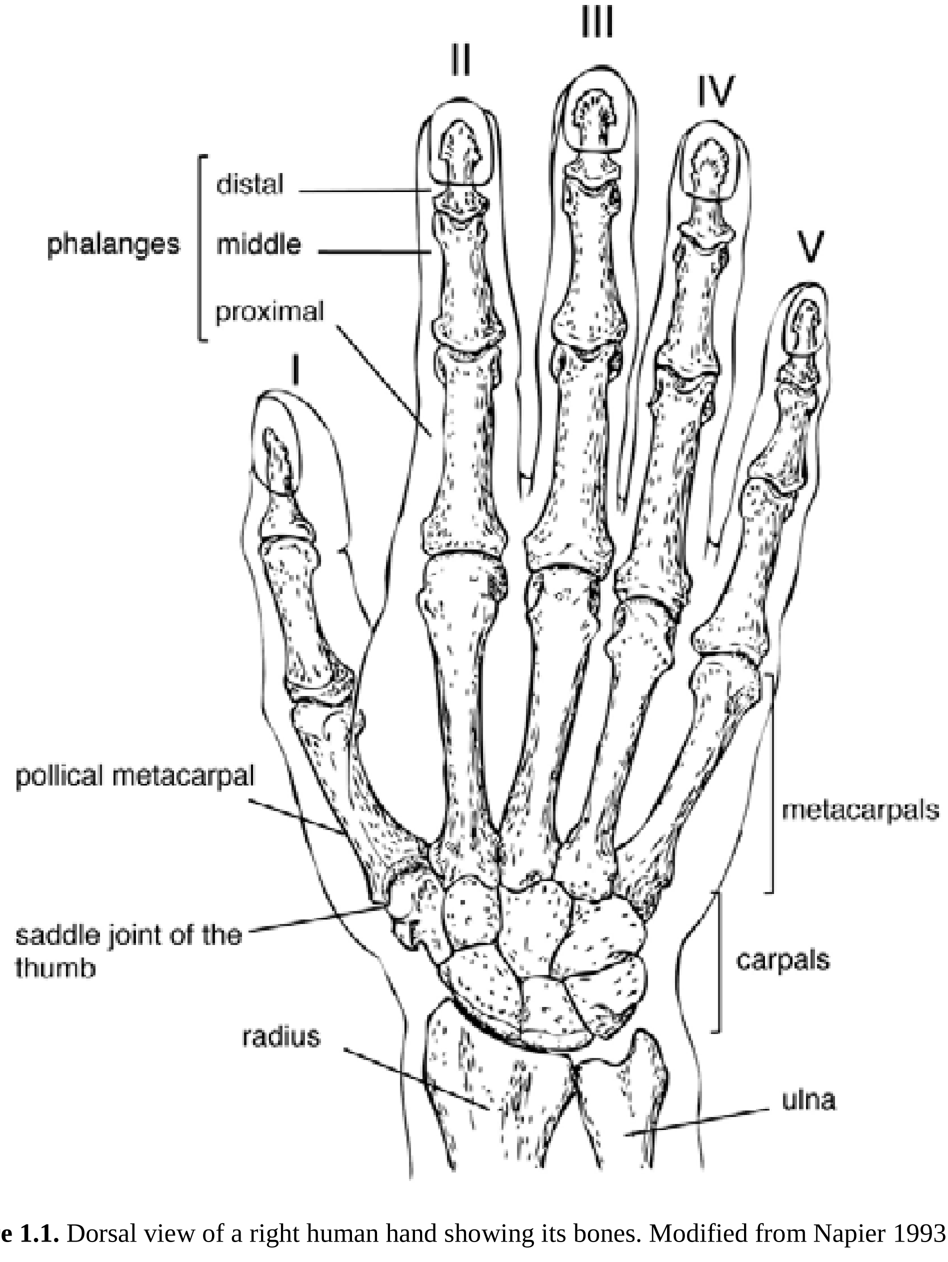


Figure 1.1. Dorsal view of a right human hand showing its bones. Modified from Napier 1993.

Wrist: a derived feature of the primate hand would be the fusion of some carpals or wrist bones (Tuttle 1992). The wrist joint connects the forelimb (i.e. radius + ulna) with the rest of the hand by through articulation with the metacarpals. It is composed by 8 bones in humans; these are, from the proximal to the distal row, and from the radial to the ulnar side: scaphoid, lunate, triquetrum, pisiform, trapezium, trapezoid, capitate and hamate. Most primates have an extra bone, the centrale, which is commonly fused with the scaphoid in African apes and humans; this is interpreted as a synapomorphy of this clade, although its functional interpretation has been highly debated (e.g. Tuttle 1967, 1992; Schultz 1969; Napier 1993; Gebo 1996; Kivell and Begun 2007).

Metacarpals: the metacarpals are the bones of the 'palm'. There are five, one for each ray (=metacarpal + respective phalanges). Although it can vary among different primate families, all apes and humans follow a general metacarpal length sequence (Susman 1979): ray II > ray III > ray IV > ray V > ray I.

Phalanges: they are the most distal elements of the hand. Each digit (sum of phalanges in each ray) is numbered as follows: ray I (thumb/pollex), ray II (index finger), ray III (middle finger), ray IV (ring finger) and ray V (little finger). Primates display a modified manual digital formula (=number of phalanges on each ray I-V), from the more primitive 2-3-4-5-3 to the current 2-3-3-3-3 (Tuttle 1992). This means that the hand of primates (including humans) displays three phalanges in each digit, with the exception of the thumb, which only has two (the same applies to the foot). They are named according to its relative position: proximal phalanges, middle (or intermediate) phalanges, and distal phalanges (Figure 1.1). An important derived feature of primates would be the development of nails (instead of claws) in the distal phalanges. There are however some exceptions to this respect, such as marmosets, tamarins and the aye-aye (Tuttle 1992; Napier 1993).

Joints, muscles and movements: as a whole, the human hand is composed by 27 bony elements (8 wrist bones + 5 metacarpals + 14 phalanges). Each bone articulates, at least, with another one by means of a synovial joint, which is the most common type of joint in the body (Napier 1993). The are several kinds of synovial joints, but one that deserves particular attention is the saddle-shaped (concavo-convex) joint between the trapezium and the pollical metacarpal (see Figure 1.1). Its saddle shape enables a wide range of movements: flexion, extension, adduction, abduction and the combination of the former (Napier 1960, 1993; Gray 1977). This is probably the most important joint of the hand, because most of thumb movements occur at this joint, and not at the metacarpophalangeal or interphalangeal ones (Aiello and Dean 1990).

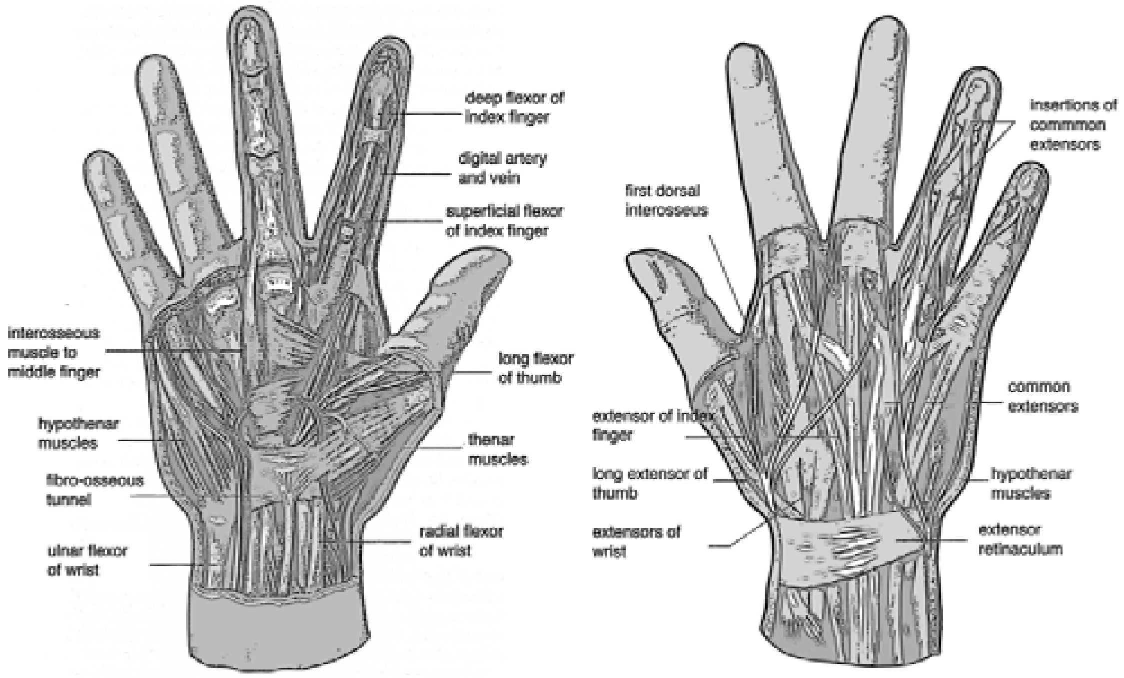


Figure 1.2. Palmar (left) and dorsal (right) view of a right human hand showing the main muscles and tendons. Modified from Napier 1993.

The movements of the hand are due to many different muscles (see Figure 1.2), which we can roughly classify as extrinsic or intrinsic. Extrinsic muscles originate outside the hand; in fact, the bulk of the musculature implied in hand movement is physically located in the forearm. These include, among others, the long flexors and extensors of the fingers and wrist. The instrinsic muscles, on the contrary, are physically located inside the hand. These include, among others, the thenar and hypothenar muscles, the interossei and the lumbricals. The thenar and hypothenar muscles are devoted, respectively, to the movements of the thumb and little finger. The interossei, in turn, are mainly devoted to the lateral movements of the digits: while the dorsal interossei *abduct* the fingers away from the midline of the hand (i.e. separate), the palmar interossei *adduct* the fingers (i.e. move the fingers towards the midline of the hand). Finally, the lumbricals, assisted by the interossei, are responsible for the flexion at the metacarpophalangeal and extension at the interphalangeal joints, respectively (Gray 1977).

The ulnar deviation of the whole hand is also called adduction, because of the classical human anatomical depictions (e.g. the ‘Vitruvian Man’ of da Vinci), in which the hands are positioned so that the palms are frontally directed; as a result, ulnar deviation of the hand results in an approximation towards the body (White and Folkens 2005). In the same way, the deviation of the hand towards the side of the radius (= radial deviation) is called abduction. We can also put the palms of the hand turned downwards (i.e. we *pronate* our hands) or upwards (i.e. we *supinate* our hands). In both cases, the rotational movement take place at the radioulnar joint of the forearm (Gray 1977).

PREHENSION

This capability is of utmost significance in the hands of primates. Although all primates share a hand with a relatively primitive overall structure, it is further distinctive among all pentadactyl creatures because of its prehensile capabilities. This attribute alone may potentially have unlimited possibilities, involving both locomotion and manipulation. Because of that, prehensile capabilities have important implications for primate evolution (Cartmill 1985), most of which still awaiting to be evaluated. The presence of claws is incompatible with prehensility, because the claws grow spreading over the distal phalanges, thus impeding any kind of effective manipulation. So, while the rest of mammals, especially the ‘small-handed creatures’ such as squirrels, must to use both hands in order to manipulate objects (mainly during feeding), most primates can manipulate using just one hand (Napier 1993).

The intrinsic manual anatomy that enables prehensile capabilities is the possession of relatively short metacarpals and long phalanges (Lemelin 1999). This trait is attained in primates thanks to their relatively long proximal phalanges. The reverse condition in the human foot (i.e. long metatarsals and short phalanges) disables it for effective prehensile capabilities. The Dermoptera (flying lemurs) and Megachiroptera (fruit bats and flying foxes) also display prehensile hands with grasping capabilities, but theirs result from elongated middle phalanges. The early Cenozoic (around 65 Ma) origin of primates seems to have involved a revolutionary change in the formation of the digital ray pattern, leading to primates with grasping hands (Hamrick 2001).

HAND FUNCTION AND CAPABILITIES

The hands of primates are complex structures, the evolution of which has been driven mainly by two different kinds of selective pressures: locomotor ones, and manipulatory ones (Tuttle 1967, 1969). As a result, different taxa can significantly differ in their intrinsic proportions, humans having relatively short hands with long thumbs, and apes showing the opposite condition (Figure 1.3). This would simply reflect differences in the degree of commitment to manipulation and locomotion in the hands of humans and great apes (Napier 1960, 1993; Tuttle 1967, 1969).

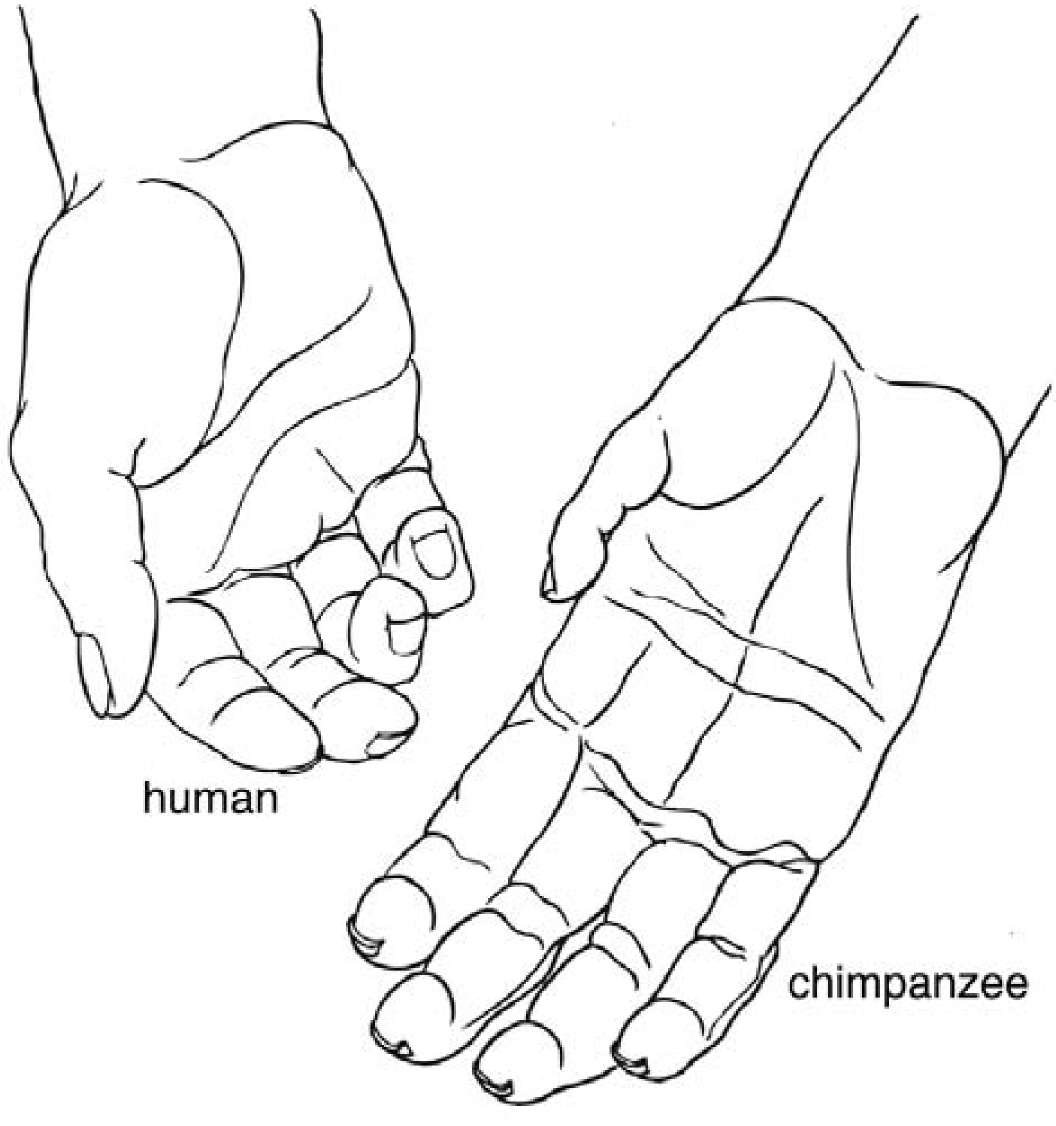


Figure 1.3. Right hand of a human compared to that of a chimpanzee in palmar view. Note the disproportionately short thumb in the chimp. Modified from Napier 1993.

Hand and manipulation

During manipulation, the human thumb plays a central role thanks to its long relative length, which allows to manipulate objects with precision between the pulp of the pollical distal phalanx and the distal phalanges from the other digits, and also because of the reciprocal morphology of the articular surfaces on the trapezium and first metacarpal (Napier 1956, 1960, 1993). There are many different classifications of the many different grips that human hands are capable of (e.g. Marzke 1986, 1997; Shrewsbury and Sonek 1986). However, John Napier, who pioneered the study of this subject, distinguish two basic types of grip (Napier 1956, 1960, 1993):

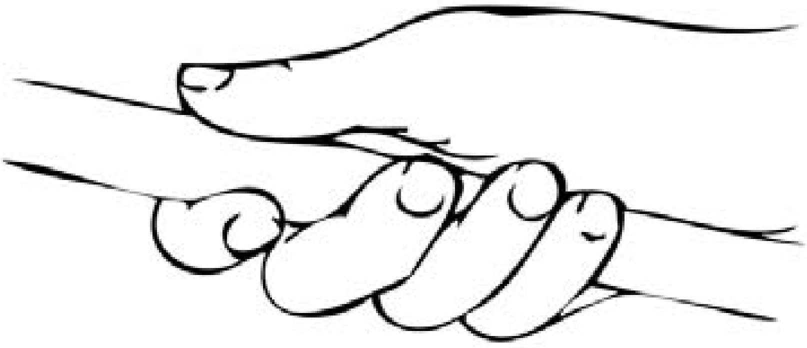
Power grip: executed between the surface of the fingers and the palm. In some instances, the thumb can collaborate by supplying directional control. Power predominates over control (although there is always an element of control, too, e.g. as during hammer manipulation). See Figure 1.4.

Precision grip: executed between the distal phalanges of the thumb and those of other digits. There are many subtle modifications depending of how 'precise' must be the control, such as the contact between the proximal pulps (i.e. pad-to-pad) or the distal pulps (i.e. tip-to-tip), among others. See Figure 1.4.

Tool behavior (Tool using + Tool making): tool behavior can be employed to refer simultaneously to both tool use and tool making on any type of raw material (Beck 1980). Tool use, in turn, can be defined as "the external deployment of an unattached environmental object to alter more efficiently the form, position, or condition of another object", whereas tool making can be defined as "any modification of an object by the user or conspecific so that the object serves more effectively as a tool" (Beck 1980, pp. 10-11). Tool use has been documented in a wide spectrum of animal species (Beck 1980), including primates such as baboons (Beck 1974) and apes both in captivity and in the wild (see review in McGrew 1993). It seems, however, that important cognitive differences exist with tool using between monkeys and apes. Amongst apes, only chimpanzees show frequent and diverse tool use in wild environments uninfluenced by humans (McGrew 1993). Chimpanzee tool behavior not only involves tool use of natural objects, but in many instances modification of them also (e.g. Teleki 1974;

Boesch and Boesch 1990), i.e. tool making. In the wild, however, chimpanzee tool-making behavior is limited to organic raw materials, whereas tool making with lithic raw materials (= stone-tool making) has only been documented for humans. Moreover, unlike humans, chimpanzees manufacture all their tools with their teeth and hands, and do not use secondary tools (i.e. tools to make tools), at least in the wild (McGrew 1993).

precision grip



power grip

Figure 1.4. Precision grip and power grip in humans. The maximum refinement of the human manipulation is reached during the pad-to-pad precision. Modified from Aiello and Dean 1990.

The origin of the proportions of the human hand is still being debated: while the most common view postulates that it appeared as an ‘adaptation’ for tool using and tool making (Susman 1988a, b, 1989, 1994, 1998), more recent studies based on the hand of *Australopithecus*—which antedates the first lithic industries by nearly one million years—postulate that the basic human hand proportions, enabling pad-to-pad precision grasping, were already present in this taxon (Alba *et al.* 2003; Green and Gordon 2008). These results would suggest that the origin of human-like proportions was unrelated to stone-tool making, and probably associated with the freeing of the hands from their locomotor function thanks to the advent of bipedalism (Alba *et al.* 2003). This point of view would vindicate the classical views of Oakley (1949), Napier (1962a, b), and Washburn (1967), according to which the size and organization of the brain would be essential for the conception and manufacture of lithic tools, while hand morphology would be rather subsidiary.

Hand and locomotion

The hand participates in the locomotion of all primates except humans. There is a huge diversity of locomotor types, the most important ones practiced to some extent by all extant or fossil apes:

Palmigrady: during palmigrady, progression takes place above mostly horizontal or slightly inclined arboreal supports by sustaining the weight of the body on the whole palmar region of the hand. The proximal region strikes first, and the weight is then transferred to the more distal elements (i.e. the phalanges; Whitehead 1993).

Digitigrady: it is similar to palmigrady, but the weight is supported on the head of the metacarpals and the palmar surface of the phalanges, but there is no sequence of weight transmission (Whitehead 1993). The touchdown normally involves only digits II-V, and the tip of the thumb merely contacts the substrate intermittently (Etter 1973). This locomotor behavior is reserved to committed terrestrial quadrupedal monkeys (such as baboons), in which, among others, it increases the length of the forearms (Whitehead 1993).

Vertical climbing: it implies a progression along vertical or markedly inclined arboreal supports by employing the propulsive force of the limbs. The trunk is held approximately vertical, with the hands and feet grasping one or more supports. Several features of hominoids (including orthogrady-related features) can be essentially considered adaptations to vertical climbing (Sarmiento 1988, 1995).

Suspension: all extant apes show adaptations for below-branch suspensory behaviors in the hand, which mainly involve elongation and curvature (especially of the phalanges) and a highly developed flexor apparatus (muscles + tendons + bone insertions). Suspension is helpful in large arboreal animals (such as extant great apes), when they exploit the feeding niche of slender terminal branches (Cartmill 1985). While great apes practice a slow type of suspension that may be termed arm-swinging, a particular type known as ricochetal brachiation is practiced by gibbons, differing from the former by its fast pendulous movements and by the existence of a phase of free flight (Gebo 1996). Suspension can imply forelimbs only, and forelimbs plus hindlimbs. Furthermore it is compatible with both pronograde and orthograde dominated behaviors (Thorpe and Crompton 2006).

Clambering: orangutans are the most arboreal extant great apes, and although they employ a huge diversity of positional modes, they employ a characteristic positional behavior termed clambering, in which their four extremities are used to hang from or to grasp several arboreal supports simultaneously, thus distributing their body mass without collapsing slender branches due to its large weight (Thorpe and Crompton 2006). Their ‘hook grip’ is made without the intervention of their pollices and halluces, which are very reduced, especially marked in the case of the latter (Tuttle and Rogers 1966). Clambering is also compatible with orthograde and pronograde positional behaviors.

Knuckle-walking: the hands of the African apes (chimpanzees and gorillas), in turn, reflect another compromise between two opposite locomotor behaviors. They have to perform both arboreal behaviors (including suspension) and quadrupedal traveling when on the ground (Tuttle 1967, 1969). In the arboreal milieu, the possession of long hands is beneficial, because it increases the covered surface of the trunk circumference (and so the friction resistance; Preuschoft 1973). However, the possession of long digits would be incompatible with an efficient terrestrial standard digitigrade quadrupedal locomotion; this problem has been circumvented by African apes thanks to the acquisition of knuckle-walking (Tuttle 1967, 1969). During knuckle-walking, the digits of fingers II-V are flexed, with the dorsal surface of the middle phalanges contacting the substrate. The metacarpals are held off of the substrate and almost in line with the forearm. This position is produced by hyperextension of the proximal phalanges at the metacarpophalangeal joints, flexion of the proximal interphalangeal joints, and flexion at the distal interphalangeal joints. The thumb does not touch the substrate.

OBJECTIVES OF THIS WORK

The work reported here has been devoted to understanding the evolution of the modern-human hand, including its proportions, morphology and adaptations, particularly in relation to precision grasping capabilities. To do so, it is necessary to reconstruct the main evolutionary changes in the postcranial skeleton of hominins (*Australopithecus, Paranthropus* and early *Homo*) during the Plio-Pleistocene, which are tightly related to their lifestyle and locomotion. Although there is a general agreement that these forms were mainly terrestrial bipeds, some degree of arboreality has been inferred for australopiths. However, the amount and type of arboreal locomotion remains to be tested. Most interesting would be to elucidate the origin, morphotype and positional behavior of the last common ancestor of African apes and humans. However, the lack of putative fossils of this ancestor precludes doing so at the moment being.

Molecular and paleontological data suggest that the earliest hominins evolved somewhere around 8-6 Ma, towards the end of the Miocene epoch (e.g. Stauffer *et al.* 2001; Haile-Selassie 2001; Senut *et al*. 2001; Brunet *et al.* 2002). Thus, it is absolutely essential to understand the main postcranial changes involved during the evolution of Miocene apes. Particularly important is the acquisition of the modern orthograde bodyplan and the coevolution of hand and foot morphology. The latter anatomical regions are directly connected to the locomotor substrate and hence ‘shaped’ to it. Changes in the hand may be immediately reflected in the foot, and vice versa.

Fortunately, the Catalan fossil record has provided several of the most important Miocene apes, including a considerable amount of isolated hand bones, as well as two partial skeletons: the skeleton of *Hispanopithecus laietanus* from Can Llobateres (Sabadell); and that of *Pierolapithecus catalaunicus* from Barranc de Can Vila 1 (els Hostalets de Pierola). The information provided by these remains will enable to answer some interesting questions, bringing some light into the evolution of the first great apes and the posterior origin of the earliest bipedal hominins.

To sum up, this thesis can be subdivided into several objectives (or questions to be answered), which are covered by the several chapters:

1- Which was the morphotype and positional behavior of the last common ancestor of great apes and humans? Did all the European Miocene apes share similar locomotor repertoires, or they were diverse to this respect?
This topic is especially discussed in the Chapters 2 and 4.

2- When did the first suspensory behaviors displayed by extant great apes appear? Do they have a common origin in hylobatids and great apes? Or they evolved more than once? Are extant apes a good model for making evolutionary inferences?
All these questions are dealt in Chapter 3.

3- Did the human hand morphology evolve as an adaptation for tool making? Or, on the contrary, it was merely an exaptation of a pre-existing morphology that initially emerged for a different reason (as it has been pointed out by other recent studies)?
This subject is treated in depth in Chapter 5, but the discussion is extended in Chapters 6 and 7.

4- When did the original human-like morphology of the hand evolve? It is a recent acquisition or an ancient symplesiomorphy of hominins?
This issue, one of the main points of this work, is dealt in Chapter 7.

Chapter 2

Pierolapithecus catalaunicus: Insights from the hand phalanges of a stem great ape

based on:

Almécija S, Alba DM, Moyà-Solà S (2009). *Pierolapithecus* and the functional morphology of Miocene ape hand phalanges: Paleobiological and evolutionary implications. *Journal of Human Evolution* 57: 284-297.

Chapter 2

Pierolapithecus catalaunicus: Insights from the hand phalanges of a stem great ape

INTRODUCTION

The first orthograde-related features from the hominoid fossil record are documented by the Moroto vertebrae (Walker and Rose 1968; Ward 1993; Sanders and Bodenbender 1994; Filler 2008). These vertebral remains, which are attributed to the early Miocene taxon *Morotopithecus* by Gebo *et al.* (1997), display a remarkably modern ape morphology, which is interpreted as being related to an increased stiffness of the lumbar region (Sanders and Bodenbender 1994) and indicative of an orthograde bodyplan (MacLatchy *et al.* 2000). Unfortunately, the lack of anatomical evidence from other key anatomical regions, such as ribs, wrist, phalanges, etc., precludes making a secure assessment on the locomotor repertoire of this taxon. This is precluded not only by the mosaic nature of evolution (Alba 2008), but also by the pervasive occurrence of homoplasy in vertebral morphology among primates (Nakatsukasa *et al.* 2007a). Unlike *Morotopithecus*, the partial skeleton of the middle Miocene stem great ape *Pierolapithecus catalaunicus* provides an unequivocal evidence of an orthograde bodyplan, as indicated by torso morphology, a short lumbar vertebral region and the loss of ulnocarpal articulation (Moyà-Solà *et al.* 2004, 2005).

As such, *Pierolapithecus* represents a unique opportunity to understand the transition from a pronograde to an orthograde bodyplan. On the basis of phalangeal morphology and proportions, it has been previously argued that this taxon still lacked adaptations to below-branch suspension (Moyà-Solà *et al.* 2004, 2005). Available evidence from the roughly coetaneous *Dryopithecus fontani* is much more scanty, including a humeral diaphysis of modern appearance (Pilbeam and Simons 1971; Begun 1992), as well as a proximal partial femur that suggests a quadrupedal bodyplan (Moyà-Solà *et al.* 2009), with no specific suspensory adaptations. The latter are not recorded until the late Miocene by the great ape *Hispanopithecus laietanus* (formerly *Dryopithecus laietanus*, see Moyà-Solà *et al.* 2009), which nevertheless still retain, like

Pierolapithecus, some palmigrady-related features (Moyà-Solà and Köhler 1996; see also Chapter 3). This shows that Miocene apes displayed locomotor repertoires unlike those currently found among living taxa. In particular, they shared to some degree a generalized bodyplan related to generalized arboreal quadrupedalism (Rose 1983), being "primarily 'Miocene hominoid-like' rather than like any contemporary group" (Rose 1983, p. 416). As such, this strongly suggests that locomotor evolution in this group cannot be reconstructed on the basis of extant taxa alone.

In this chapter, we provide a detailed description and morphometric analysis of the manual phalanges of *Pierolapithecus*, by further comparing them to other Miocene hominoids. The recently described phalanges from Paşalar (Turkey), attributed to *Griphopithecus* by Ersoy *et al.* (2008), are of particular interest. This is due to their older age, as well as the pronograde locomotor repertoire inferred for this taxon on the basis of other postcranial material, indicating generalized above-branch arboreal quadrupedalism (Begun 1992, 2007) with no suspensory adaptations (Begun 2002, p. 345). On the basis of morphofunctional analyses and intrinsic phalangeal proportions, we make paleobiological inferences on the evolution of the hominoid locomotor repertoire during the Miocene. In particular, we test the hypothesis of whether the acquisition of vertical climbing and suspension was decoupled during evolution, or whether, on the contrary, these behaviors are inextricably linked to one another, as living hominoids would suggest.

MATERIALS AND METHODS

Measurements

In order to numerically evaluate differences in intermediate and proximal phalangeal proportions between the different taxa, we measured the following seven standard variables to the nearest 0.1 mm in the available fossil specimens and in the comparative extant sample: maximum length; and transverse (mediolateral and dorsopalmar) diameters at the base, midshaft and trochlea (see also Appendix 3.1). Curvature (in degrees) was also measured by means of the included-angle method (Susman *et al.* 1984; Stern *et al.* 1995; Jungers *et al.* 1997; Richmond and Whalen

2001). Length and basal mediolateral breadth were also measured for distal phalanges I and III (pollical and middle finger respectively).

The comparative fossil sample

Measurements taken by the authors on the original specimens were employed for *Pierolapithecus catalaunicus* IPS21350 (see Moyà-Solà *et al.* 2004) and *Hispanopithecus laietanus* IPS18800 (Moyà-Solà and Köhler 1996). Measurements taken on casts were employed for the *Sivapithecus parvada* proximal phalanx GSP19700 (Rose 1986) and also for the specimens of *Proconsul heseloni* KNM-RU2036AA/AC and KNM-RU2036Y, identified respectively as proximal phalanx IV and intermediate phalanx III in Napier and Davis (1959, their Figure 26). In the latter case, measurements were corrected in order to compensate for the lack of epiphyses in the intermediate phalanx, following the same method as in Chapter 5. Additional data were taken from the literature for the Paşalar specimens K1421, G1004 and R1667 (Ersoy *et al.* 2008), the *Sivapithecus* specimen GSP45782 (Madar *et al.* 2002), and *Australopithecus afarensis* specimens AL333x-19 and AL333-88 (Bush *et al.* 1982). Phalanges of *Nacholapithecus kerioi* (Nakatsukasa *et al.* 2003) were not included in the numerical analysis due to the lack of complete specimens preserving phalangeal length. Curvature was measured on the original specimens or good-quality casts, except in the case of Paşalar, for which values were taken from Ersoy *et al.* (2008).

The comparative extant sample

The comparative sample of extant primates employed in this study for morphometric comparisons includes adult individuals from all living ape genera, humans and two pronograde monkeys (macaques and baboons). *Pan* includes both bonobos (*P. paniscus*) and common chimpanzees (*P. troglodytes*); *Gorilla* includes both eastern (*G. beringei*) and western (*G. gorilla*) gorillas; *Pongo* includes the two subspecies of orangutans (*P. pygmaeus*); *Hylobates* includes both siamangs (*H. syndactylus*) and two species of gibbons (*H. agilis* and *H. muelleri*); *Homo* includes only modern humans (*H. sapiens*); *Papio* includes two baboon species (*P. cynocephalus* and *P. ursinus*); and *Macaca*, finally, includes several macaque species (*M. fascicularis*, *M. fuscata*, *M. nemestrina*, *M. nigra*, *M. silenus* and *M. sylvanus*). Total sample size for each variable is reported in Appendix 2.2. For multivariate analyses of proximal and intermediate (= middle) phalanges (see below), however, only those individuals recording the seven measured variables were included: for the fourth proximal phalanx, 74 *Pan*, 90 *Gorilla*, 39 *Pongo*, 43 *Homo*, 13 *Hylobates*, 33 *Papio* and 19 *Macaca*; for the third intermediate phalanx, 69 *Pan*, 75 *Gorilla*, 37 *Pongo*, 37 *Homo*, 11 *Hylobates*, 31 *Papio* and 18 *Macaca*. Length of distal phalanges I and III was measured in 13 *Pan*, 14 *Gorilla*, 15 *Pongo*, 21 *Homo*, 16 *Hylobates* and 15 *Macaca*, while basal breadth of these bones was measured in 6 *Pan*, 5 *Gorilla*, 7 *Pongo*, 6 *Homo*, 8 *Hylobates* and 14 *Macaca*.

Statistical methods

Statistical computations and morphometric analyses were performed, separately for proximal, intermediate and distal phalanges, by means of the statistical package SPSS v. 15.0. In the case of proximal phalanges, measurements from the fourth manual ray were employed because the available fossil specimens are attributed to this ray. In the case of intermediate phalanges, measurements from the third manual ray were employed, in spite of the fact that most of the fossil specimens investigated might be attributed to either the third or the fourth manual ray. Be that as it may, similar results were obtained for both proximal and intermediate phalanges by employing measurements from third instead of fourth manual ray and vice versa (results not shown). Raw data for the seven measured variables were log-transformed by using natural logarithms (ln). A principal components analysis (PCA) was performed by using the covariance matrix, separately for proximal and intermediate phalanges.

In order to be able to compare the intrinsic phalangeal proportions among the several extant and fossil taxa, we employed allometric methods to derive measurements of intrinsic relative phalangeal length. There is a controversy on whether ratios or allometric residuals are more suitable for making morphometric comparisons (see discussion in Alba *et al.* 2003, p. 232). Most prominently, Jungers *et al.* (1995) have criticized the use of residuals by arguing that they should not be employed when the aim of the study “is to identify individuals … of the same *shape* after accounting for overall size differences” (Jungers *et al.* 1995, p. 137; emphasis added). On the contrary, the use of residuals should be favored when making functional inferences, given the fact that allometry (i.e. the change in size with shape) is an ubiquitous phenomenon in nature (e.g. Corruccini 1987). As such, simple bivariate ratios can only control for size differences under very particular conditions (isometry), which are rarely encountered in morphometrics (Albrecht *et al.* 1993). Allometric residuals, on the contrary, remove scaling effects by measuring only those portions of shape that are uncorrelated with size (Albrecht *et al.* 1995). Thus, the criticism that within this allometric “size-free framework, shape information is discarded simple because it is correlated with size” (Jungers *et al.* 1995, p. 153) simply does not apply here. This is due to the fact that our aim is precisely to remove size-scaling effects within each taxon, in order to ensure that the reported differences between them are due to functional requirements (related to different locomotor repertoires), instead of merely resulting from their different body size ranges.

Allometric residuals can be understood as the deviation of a particular individual (an actual measurement) from the value expected for an ‘average’ specimen of that particular size (e.g. Klingenberg 1998, p. 35). These residuals were computed by fitting the linearized version of the allometric equation (Gould 1966, 1975; Klingenberg 1998): $\ln y = b \cdot \ln x + a$. Least-squares linear regression—which has been favored for predictive purposes (Smith 1994)—was employed as the line-fitting method. This is because the aim of the study was not to make functional interpretations from the computed allometric slopes—something that would be unwarranted given the use of static adult allometry. Instead, our aim was to correlate allometric grade shift departures among the several extant taxa with their differences in locomotor behaviors, as well as to compute allometric residuals for particular fossil taxa.

Phalangeal length, which displayed a disproportionate loading on PC2 (see below), was used as the dependent (y) variable. An overall measure of phalangeal size was employed as the independent (x) variable. In particular, the first principal component (PC1) was taken as a proxy for overall phalangeal size. This is warranted given the fact that all variables had similar loadings approaching unity on this component (Hammer and Harper 2006; see ‘Morphometric comparisons’ for further details). The PC1 was not ln-transformed, because the PCA was already based on logged measurements. The robusticity of this approach was also tested by repeating the analyses with the geometric mean (GM) of the several linear measurements (including length) as the overall phalangeal size variable (see Jungers *et al.* 1995, for further details). Given the fact that the GM mean was ln-transformed, the resulting variable is equivalent to the arithmetic mean of the ln-transformed linear measurements.

Allometric residuals of ln phalangeal length vs. PC1 (or ln GM) were thus employed as a size-corrected variable of intrinsic relative phalangeal length. In order to compute allometric residuals, instead of employing evolutionary allometry (a single regression for all the taxa together, on the basis of their mean species values), we derived separate static, mixed-sex allometric regressions for each genus by using adult individual data. Allometric grade differences between the several taxa were investigated by means of analysis of covariance (ANCOVA), in order to test for equality of slopes and intercepts. For computing the allometric residuals of all individuals, we selected the chimpanzee regression as the reference baseline. Accordingly, the mean of the chimpanzee allometric residuals is, by definition, zero; other taxa will show on average positive or negative residuals, depending on whether they display relatively longer or shorter phalanges, respectively. Differences between mean values for the allometric residuals among the several extant taxa were investigated by means of analysis of variance (ANOVA) and post-hoc multiple comparisons (Bonferroni); residuals derived for fossil specimens were compared with the 95% confidence interval for the several extant taxa. Equivalent results would have been obtained by employing the regression line of any other taxon studied, given the fact that ANCOVA could not discard equality of slopes, but only equality of intercepts (see ‘Morphometric comparisons’ below).

The allometric residuals of intrinsic relative phalangeal length employed here can be also interpreted as the inverse of robusticity. Nevertheless, the measures of intrinsic relative length, as computed here for proximal and intermediate phalanges, differ from traditional measures of robusticity because our metric compares length to all the other phalangeal dimensions simultaneously. Moreover, bivariate ratios such as robusticity indices, in principle, do not correct for size-scaling effects, whereas the residuals employed here are size-corrected. For comparative purposes, following Harrison (1989), we also computed midshaft robusticity (midshaft breadth / length x 100) for both proximal phalanx IV and intermediate phalanx III. The mean values of the indices of robusticity among extant taxa were compared by means of ANOVA and post-hoc multiple comparisons (Bonferroni), whereas the values computed for fossil specimens were compared with the 95% confidence interval for the mean of the several extant taxa.

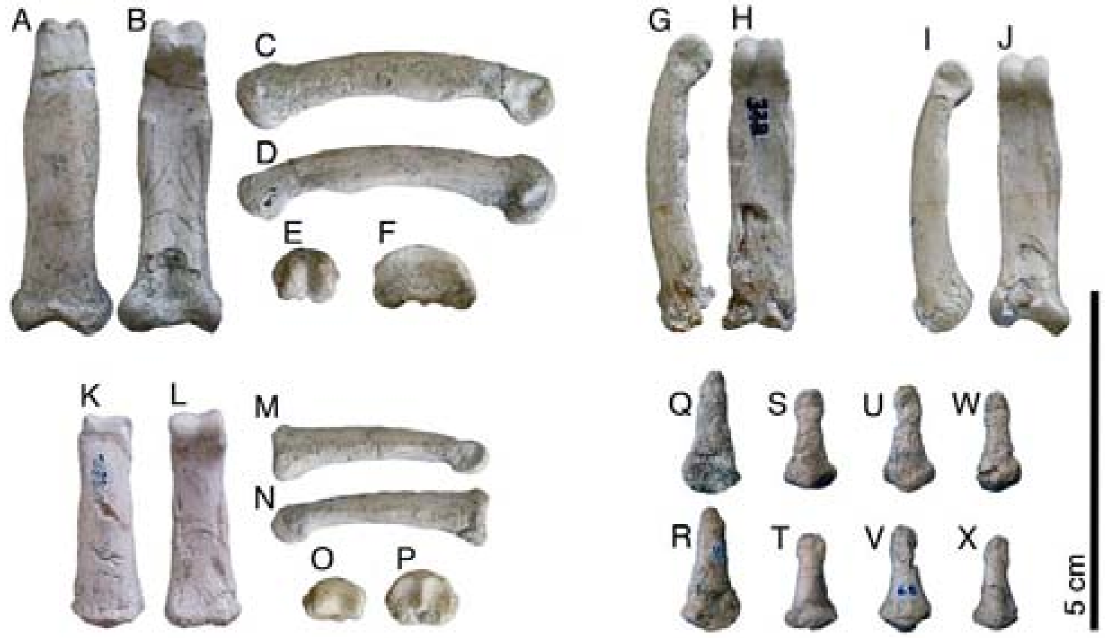


Figure 2.1. Manual phalanges of *Pierolapithecus catalaunicus* from BCV1: (**A**-**F**) Right fourth proximal phalanx IPS21350.14 in dorsal (**A**), palmar (**B**), ulnar (**C**), radial (**D**), distal (**E**) and proximal (**F**) views; (**G**-**H**) Left second proximal phalanx IPS21350.12 in radial (**G**) and palmar (**H**) views; (**I**-**J**) Left fifth proximal phalanx IPS21350.15 in radial (**I**) and palmar (**J**) views; (**K**-**P**) Third or fourth intermediate phalanx IPS21350.13 in dorsal (**K**), palmar (**L**), ulnar (**M**), radial (**N**), distal (**O**) and proximal (**P**) views; (**Q**-**R**) Right pollical distal phalanx IPS21350.16 in palmar (**Q**) and dorsal (**R**) views; (**S**-**T**) Distal phalanx IPS21350.18 in palmar (**S**) and dorsal (**T**) views; (**U**-**V**) Distal phalanx IPS21350.19 in palmar (**U**) and dorsal (**V**) views; and (**W**-**X**) Distal phalanx IPS21350.20 in palmar (**W**) and dorsal (**X**) views.

In the case of distal phalanges, it should be taken into account that it is difficult to find ray-associated distal phalanges in the fossil record, and even in the skeletal collections of extant taxa. As a result, the available extant comparative sample of distal phalanges is very restricted in comparison to proximal and intermediate ones. Nevertheless, in order to compare the proportions between the pollical and the remaining phalanges in *Pierolapithecus*, we computed the ratios between distal phalanges I / III for both length and basal breadth.

DESCRIPTION OF THE MANUAL PHALANGES OF PIEROLAPITHECUS

The eight phalanges of *Pierolapithecus* described in this paper are depicted in Figure 2.1 (see also Table 2.1 for measurements).

Proximal phalanges

The three available proximal phalanges are morphologically very similar to one another. The largest one (IPS21350.14; see also Figure 2.2), which is complete except for minimal damage on the dorsodistal and proximopalmar portions of the shaft, is identified as a right fourth proximal phalanx, due to its overall dimensions and its marked basal asymmetry—with an ulnarly protruding tubercle for the insertion of the fourth dorsal interosseous (see Susman 1979). The slightly smaller specimen IPS21350.12, which displays a somewhat damaged basal portion, is very similar to the one mentioned above, but displays fainter muscular impressions. This specimen is identified as a left second proximal phalanx, on the basis of the apparently more protruding right tubercle (in dorsal view) for insertion of the first dorsal interosseous and of the narrower and more palmarly-protruding trochlear condyle on the same side (see Susman 1979). The other proximal phalanx, IPS21350.15, is also very similar on morphological grounds. On the basis of its smaller dimensions, the ulnar bowing of the flexor sheath ridge and the very protruding palmar tubercle (for insertion of the hypothenar muscles), this specimen can be identified as a left fifth proximal phalanx (see Susman 1979). Moreover, the ulnar trochlear condyle of this phalanx shows the opposite condition than the second proximal one, by being narrower and more palmarly protruding than on the radial side. This is a typical feature of apes (Susman 1979), which display paramedian proximal phalanges with the trochleae tilted towards the main axis of the hand (normally the third ray).

All these proximal phalanges display a moderate degree of curvature (included angle of 53º in IPS21350.14, 45º in IPS21350.12 and 56º in IPS21350.15). The base is wide, with huge palmar tubercles that define a conspicuous palmar channel (very wide in IPS21350.14), and with the proximal articular surface for the metacarpal extending dorsally onto the shaft. In palmar view, the shaft is mediolaterally flat, but displays conspicuous flexor sheath ridges that protrude palmarly, attaining their maximum development on the distal third of the shaft. These ridges disappear before reaching the trochlea, thus causing a marked narrowing on the distal end of the shaft. The trochlea is small as compared to the diaphysis and, especially, to the huge base. It displays a narrow trochlear groove and, in dorsal or palmar view, it is not parallel-sided, but distally convergent.

Table 2.1. Measurements of the phalanges of *Pierolapithecus catalaunicus* from BCV1 reported in this paper; specimens IPS21350.13 and IPS21350.14 were included in the numerical analyses. All measurements in mm except for the included angle (in degrees).

Variable	IPS21350.12	IPS21350.13	IPS21350.14	IPS21350.15	IPS21350.16	IPS21350.18	IPS21350.19	IPS21350.20
L	43.6	32.1	48.0	41.8	18.8	14.9	16.1	14.8
MLB	--	11.4	15.8	12.0	8.8	7.9	7.9	6.7
DPB	--	8.4	10.0	9.4	--	5.7	5.9	5.0
MLMS	9.7	8.3	11.3	9.2	5.3	4.2	4.0	3.7
DPMS	6.2	4.9	6.4	5.3	4.6	4.3	4.6	4.0
MLT	7.8	8.0	8.6	7.3	4.4	4.4	4.3	3.8
DPT	6.4	5.1	7.6	6.1	3.9	3.1	3.9	3.3
IA	45	--	53	56	--	--	--	--

Abbreviations: L = maximum length; ML = mediolateral width; DP = dorsopalmar height; B = base; MS = midshaft; T = trochlea/tuft; IA = included angle.

Intermediate phalanx

A single intermediate manual phalanx of *Pierolapithecus*, IPS21350.13, is available (see measurements in Table 2.1). We attribute this phalanx to one of the central manual rays (III or IV) because, among others, it lacks the pronounced trochlear deviation towards the central axis of the hand (Susman 1979) as well as the pronounced basal asymmetry (S.A. personal observation) that is characteristic of lateral intermediate phalanges. On dorsal view, the trochlea of IPS21350.13 is slightly deviated towards the right, so that it must correspond to the third manual ray if it comes from the right hand, or to the fourth if it comes from the left one. The shaft is quite straight, and displays deep insertions for the *flexor digitorium superficialis* on the proximal third of the palmar side. Both proximal and distal articular surfaces are small, so that in dorsal or palmar view they do not mediolaterally protrude from the shaft. The trochlea displays a broad and shallow groove, as well as deep pits for the insertion of the collateral ligaments. The base of the phalanx is symmetrical, but in palmar view the left condyle of the trochlea is broader and less distally protruding than the right one.

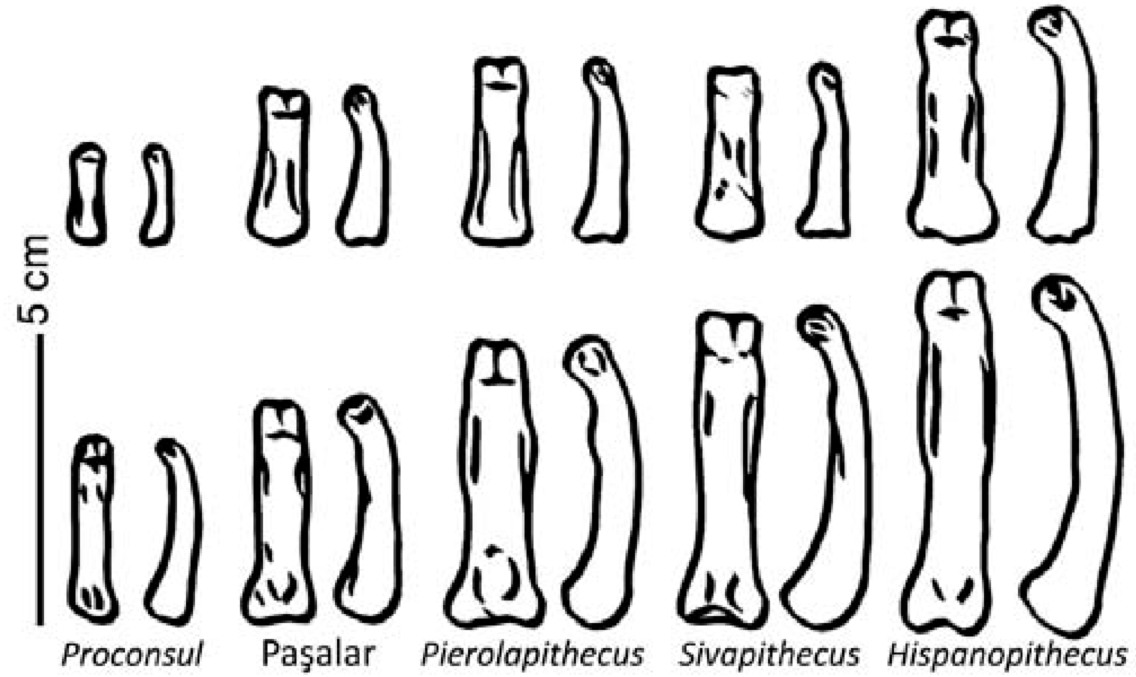


Figure 2.2. Schematic depiction of intermediate (top) and proximal (bottom) manual phalanges of selected Miocene apes included in the morphometric analyses, in palmar (left) and lateral (right) views. All proximal phalanges are from the fourth ray, whereas intermediate ones correspond to either the third or the fourth ray; except for *Proconsul,* there is no unequivocal correspondence between each pair of proximal and intermediate phalanges. Note the remarkable overall similarity between the several specimens and the sequential increase in length of proximal phalanges from early (*Proconsul*) to late (*Hispanopithecus*) Miocene; regarding intermediate phalanges, only *Hispanopithecus* displays a significant degree of curvature, due to a palmarly-bent trochlea.

Distal phalanges

Finally, four distal manual phalanges of *Pierolapithecus* are available. The largest one (IPS21350.16) is a pollical distal phalanx. This specimen is almost complete except for the basal portion, which is eroded on its dorsal and palmar surfaces. This phalanx is tentatively attributed to the right side, because its ulnar articular surface and basal tubercle are more distally situated than the corresponding radial ones. This further agrees with the ulnar condyle of the pollical proximal phalanx, which also extends more distally than the radial one, while the latter is more convex and extends more palmarly. This is a typical anthropoid feature (S.A. personal observation), extensively studied in humans by Shrewsbury *et al.* (2003). In dorsal view, the shaft of IPS21350.16 is broad at the base and tapers distally in both mediolateral and dorsopalmar dimensions. The tip is almost conical (slightly more convex dorsally), with a barely perceptible tuft on the dorsoulnar side.

The remaining three distal phalanges belong to some of rays II to V. IPS21350.18 is an entirely complete specimen, while IPS21350.19, the largest one of these three phalanges, is only slightly eroded at the base, further lacking small fragments of the shaft just proximal to the tuft. Finally, IPS21350.20, the smallest one, lacks a small bone portion on the palmar side of the base; in dorsal view, the apical tuft of the latter is deviated towards the right side, so that it must belong to a paramedian ray (either II or V). Since both IPS21350.18 and IPS21350.19 lack the tuft deviation displayed by IPS21350.20, it can be inferred that the two former most likely correspond to the median rays (III and IV). Moreover, given the fact that the third distal ray is usually longer than the remaining ones (S.A. personal observation), IPS21350.19 and IPS21350.18 can be tentatively attributed to rays III and IV, respectively. All these distal phalanges, in any case, display a relatively wide base surrounded by strong muscular insertions. The palmar lips are more protruding than the dorsal ones, and a median keel links both. The shafts are roughly conical, although the dorsopalmar diameters are slightly larger than the mediolateral ones. The dorsal surfaces of these phalanges are more convex than the palmar ones, which are nearly flat. Finally, the tufts do not protrude beyond the shaft distally, but flare laterally.

MORPHOLOGICAL COMPARISONS

In the descriptions below, we will refer to Figure 2.1, in order to show the structures being described in *Pierolapithecus*. A schematic depiction of the main features mentioned below for both proximal and intermediate phalanges of *Pierolapithecus* and other Miocene apes can be found in Figure 2.2 (see also Table 2.2 for a list of the similarities and differences displayed by these taxa).

Proximal phalanges

The proximal phalanges of the several Miocene apes included in this study are quite similar to one another (Figure 2.2). In these taxa, the proximal phalanges (Figures 2.1A-J) display several primitive (monkey-like) features at the base, such as large palmar tubercles (Figures 2.1B,J) and a proximal articular surface that extends onto the dorsal aspect of the shaft (Figures 2.1A,F). In most of these taxa, the variably developed flexor sheath ridges are clearly situated on the distal third of the shaft (Figures

2.1B,H,J); only in *Hispanopithecus*, these ridges are more proximally positioned, by extending from the first until the second third of the shaft, as in living great apes. In all instances, the palmar aspect of the shaft is rather flat (Figures 2.1B,H,J)—or concave, when the flexor sheath ridges protrude palmarly. Phalangeal curvature (Figures 2.1C,D,G,I; Figure 2.2) in these Miocene apes ranges from slight in *Proconsul* (45º), to moderate in Paşalar, *Pierolapithecus* and *Sivapithecus* (around 50-60º), and to very marked in *Hispanopithecus* (>70º). All these taxa display developed pits for the attachment of the collateral ligaments on the trochlea (Figures 2.1C,D,G,I). The latter tapers distally (Figure 2.1A) and displays a narrow trochlear groove (Figure 2.1E) in most of them—the only exception being *Sivapithecus*, whose phalanx GSP19700 has a parallel-shaped trochlea with a broad trochlear groove (also see Rose 1986).

Intermediate phalanges

The intermediate phalanges are even more similar than the proximal ones between the several Miocene apes (Figure 2.2). All of them display strong muscular impressions, with deep insertions for the superficial flexors, which can produce distinct ridges along the proximal half of the shaft (Figure 2.1L). The shaft is only slightly curved (Figures 2.1M,N) and the trochleae are relatively small (Figure 2.1O), with conspicuous insertions for the collateral ligaments (Figures 2.1M,N). Only *Hispanopithecus* clearly departs from this pattern, by displaying stronger muscular impressions (especially at the base), as well as a pronounced curvature of the distal portion of the shaft, which results in a palmarly-bent trochlea (see also Chapter 3). The middle phalanx GSP47582 of *Sivapithecus* further displays a somewhat different lateral profile, resulting from its flat shaft with palmarly very protruding flexor sheath ridges (also see Madar *et al.* 2002).

Distal phalanges

There are not many pollical distal phalanges of fossil apes for comparison, except for those of *Proconsul*, which belong to subadult specimens and are incomplete (Begun *et al.* 1994). Be that as it may, on the basis of the description published by Begun *et al.* (1994), these pollical distal phalanges closely resemble that of *Pierolapithecus* (Figures 2.1Q,R). Unfortunately, due to palmar erosion, we cannot evaluate the insertion for the tendon of the flexor muscle in IPS21350.16 (Figure 2.1Q), which is strong in the distal phalanges of *Proconsul* thumbs. On the contrary, extant apes display a relatively narrow pollical distal phalanx with only very faint muscular impressions. A feature shared by *Pierolapithecus* and *Proconsul* (see Begun *et al.* 1994) is the flat to slightly convex morphology of the two portions of the articular surface of the pollical distal phalanx (Figures 2.1Q,R), whereas extant apes and humans display a biconcave articular surface more similar to the remaining distal phalanges. The non-pollical distal phalanges (Figures 2.1S-X) also differ from those of extant hominoids, particularly by having palmar lips larger than the dorsal ones, so that this articular surface in *Pierolapithecus* does not face palmarly. This primitive feature is also retained in *Proconsul* (Begun *et al.* 1994), *Sivapithecus* (Madar *et al.* 2002, their Figure 15) and *Hispanopithecus* (see Chapter 3).

Table 2.2. Main morphological features of the manual proximal phalanges of Miocene apes discussed in this paper.

		Base	
Taxon	**Shape**	**Palmar tubercles**	**Articular surface**
Proconsul	Width >> height	Define a narrow channel	Extends dorsally onto the shaft
Paşalar	Width >> height	Define a narrow channel	Extends dorsally onto the shaft
Pierolapithecus	Width >> height	Define a wide channel	Extends dorsally onto the shaft
Sivapithecus	Width > height	Define a narrow channel	Extends dorsally onto the shaft
Hispanopithecus	Width ≈ height	Define a narrow channel	Laterally restricted, slightly extends dorsally onto the shaft

		Shaft	
Taxon	**Curvature**	**Position of sheath ridges**	**Development of sheath ridges**
Proconsul	Slight	Distal third of the shaft	Do not protrude palmarly
Paşalar	Moderate	Distal third of the shaft	Protrude palmarly
Pierolapithecus	Moderate	Distal third of the shaft	Protrude palmarly
Sivapithecus	Moderate	Distal third of the shaft	Protrude palmarly
Hispanopithecus	High	More proximal (first to second third of the shaft)	Protrude palmarly but are less conspicuous

		Trochleae	
Taxon	**Shape**	**Trochlear groove**	**Pits for the collateral ligaments**
Proconsul	Distally convergent	Narrow	Large
Paşalar	Distally convergent	Narrow	Very large
Pierolapithecus	Distally convergent	Narrow	Very large
Sivapithecus	Parallel	Broad	Very large
Hispanopithecus	Distally convergent	Narrow	Very large

MORPHOMETRIC COMPARISONS

The descriptive statistics of the extant comparative sample for the several linear measurements included in this study is reported in Table 2.3, including sample size, mean, standard deviation, 95% confidence interval and maximum-minimum range. The 95% confidence intervals of extant taxa for each variable are compared to the measurements for individual fossil specimens in Table 2.3.

Table 2.3. Measurements, allometric residuals and indices for the proximal and intermediate phalanges of *Pierolapithecus*, as compared to other fossil taxa included in the morphometric analyses. All measurements in mm except for the included angle (in degrees), and residuals and indices (dimensionless).

Proximal phalanges

Taxon	***Pierolapithecus***	***Hispanopithecus***	***Australopithecus***	**Paşalar**	***Sivapithecus***	***Proconsul***
No.	**IPS21350.14**	**IPS18800**	**AL333x-19**	**K1421**	**GSP19700**	**KNM-RU2036AA/AC**
Ray	**IV**	**IV**	**IV**	**IV**	**IV**	**IV**
L	48.0	62.7	38.3	40.0	51.5	29.9
MLB	15.8	14.1	13.0	12.3	14.4	7.5
DPB	10.0	12.0	11.0	9.8	12.4	6.3
MLMS	11.3	11.5	8.30	8.7	9.5	4.9
DPMS	6.4	7.3	5.90	5.4	6.3	4.3
MLT	8.6	9.8	9.10	7.8	10.5	5.1
DPT	7.6	8.2	6.50	6.30	7.1	4.0
IA	53	71	40	52	57	45
RIRPL	-0.031	0.173	-0.179	-0.102	0.031	-0.112
IMR	23.54	18.34	21.67	21.75	18.45	16.39

Intermediate phalanges

Taxon	***Pierolapithecus***	***Hispanopithecus***		***Australopithecus***	**Paşalar**		***Sivapithecus***	***Proconsul***
Variable	**IPS21350.13**	**IPS18800**		**AL333-88**	**G1004**	**R1667**	**GSP47582**	**KNM-RU2036Y**
Ray	**III/IV**	**III?**	**IV**	**III**	**III/IV**	**III/IV**	**IV?**	**III**
L	32.1	40.0	41.3	25.7	27.8	28.7	29.5	18.2
MLB	11.4	14.3	13.1	11.2	10.1	11.2	11.3	6.1
DPB	8.4	9.3	10.9	9.2	8.2	8.8	8.4	4.6
MLMS	8.3	9.6	9.7	8.5	7.8	8.3	8.4	4.9
DPMS	4.9	5.7	7.0	5.2	5.3	5.1	4.2	2.9
MLT	8.0	(9.3)	9.2	8.1	8.0	8.6	8.1	5.6
DPT	5.1	6.3	6.0	5.2	5.4	6.1	5.4	3.2
RIRPL	-0.086	-0.003	-0.001	-0.306	-0.204	-0.221	-0.152	-0.231

Abbreviations: L = maximum length; ML = mediolateral width; DP = dorsopalmar height; B = base; MS = midshaft; T = trochlea/tuft; IA = included angle; RIRPL = residual of intrinsic relative phalangeal length; IMR = index of midshaft robusticity; (estimated measurement).

The results of the PCA have been plotted in Figures 2.3A (for proximal phalanges) and 2.3C (for intermediate phalanges) and further reported in Table 2.4. For both proximal and intermediate phalanges, the first principal component (PC1) explains most of the variance (94% and 93%, respectively), with all the loadings on the original variables closely approaching unity. Accordingly, the PC1 can be taken to represent an overall phalangeal size (Hammer and Harper 2006), which can be employed for computing intrinsic phalangeal proportions (see below). The PC1 mainly separates monkeys, hylobatids and *Proconsul*, on the one hand, from living and fossil great apes, on the other. On the basis of proximal phalanges, Paşalar displays a PC1 score intermediate between *Proconsul* and other Miocene apes, whereas for intermediate phalanges, Paşalar most closely resembles *Pierolapithecus* and *Sivapithecus*. For both types of phalanges, *Hispanopithecus* displays the highest scores along PC1, well within the range of chimpanzees and orangs.

High scores on the second principal component (PC2), which explains nearly 4% of variance in both cases, permit to distinguish chimpanzees and, especially, hylobatids and orangutans, from the remaining living simians included in the analysis. The former taxa are characterized by a significant contribution of arboreal behaviors (vertical climbing and suspension) to their locomotor repertoires. Interestingly, among fossil taxa, only *Hispanopithecus* approaches this condition. On the contrary, the remaining fossil taxa display lower scores along PC2, most closely approaching the condition of quadrupedal monkeys, except for the proximal phalanx of *Sivapithecus*, which displays an intermediate condition. A close inspection of the PCA results regarding the PC2 shows that several variables display un-negligible loadings. For proximal phalanges, in particular, the larger the PC2, the longer the phalanx and the higher the trochlea, while the shaft and the base become progressively narrower. However, for both proximal and intermediate phalanges, length displays an outstanding positive loading as compared to the remaining variables in the PC2 (see Table 2.4). As such, the differences reported above for this component basically results from the relative length of the phalanges.

Allometric regressions of ln phalangeal length vs. PC1, reflecting intrinsic relative phalangeal length, are reported in Figures 2.3B and 2.3D for proximal and intermediate phalanges, respectively (see regressions in Table 2.5). A visual examination already shows the existence of allometric grade shifts between different taxa, which is confirmed by ANCOVA comparisons. Thus, equality of slopes between the several taxa cannot be discarded ($F=0.924$, $p=0.478$ for proximal phalanges, and $F=0.456$, $p=0.840$ for intermediate ones). On the contrary, ANCOVA results indicate that there are significant differences in the intercept at $p<0.001$ ($F=118.4$ for proximal phalanges, and $F=114.2$ for intermediate ones). Even though at different size ranges, both humans and the several more terrestrial taxa (macaques, baboons and gorillas) display very similar phalangeal proportions; the two more arboreal taxa (hylobatids and orangutans), on the contrary, differ by displaying relatively elongated phalanges, whereas the more generalized chimpanzees displays an intermediate condition. The regressions obtained by employing ln GM (Appendix 2.1) instead of PC1 as the variable of overall phalangeal size are virtually identical to those reported above, showing the same allometric grade differences. This stems from the fact that all the original logged variables show similar loadings on the PC1, so that the latter is directly proportional to ln GM, which is the arithmetic mean of the logged variables. Nevertheless, ANCOVA comparisons show that equality of slopes among the different taxa can be discarded with $p<0.001$ ($F=10.623$ for proximal phalanges and $F=7.682$ for intermediate ones), which precludes computing residuals for all individuals on the basis of a single regression line (see below).

The residuals of intrinsic relative phalangeal length (Figure 2.4; Tables 2.3 and 2.6), computed by taking the chimpanzee allometric regression of ln length vs. PC1 as the reference baseline, allow us to more clearly evaluate the allometric grade differences between several extant taxa. In the case of the fourth proximal phalanx, ANOVA results show that there are significant differences at $p<0.001$ ($F=412.1$), whereas post-hoc multiple comparisons indicate that there are significant differences in all cases except between *Homo* and *Gorilla*, on the one hand, and *Papio* and *Macaca*, on the other. With regard to the third middle phalanx, ANOVA results confirm that there are significant differences at $p<0.001$ ($F=343.7$), while post-hoc multiple comparisons indicate that all species-pair comparisons show significant differences except for *Macaca* as compared either *Gorilla* or *Homo*, and neither between *Pongo* and hylobatids.

When the residuals of fossil specimens are compared with the confidence intervals for the extant taxa, the following results are obtained. *Proconsul* and Paşalar, like *Australopithecus*, most closely resemble quadrupedal monkeys, gorillas and modern humans for both proximal and intermediate phalangeal proportions. The remaining fossil apes, on the contrary, show some degree of intrinsic phalangeal elongation (more accentuated in the proximal than in the intermediate phalanges), thus more closely approaching the condition displayed by living arboreal apes. The condition displayed by *Pierolapithecus* and *Sivapithecus* is somewhat intermediate, albeit matching the chimpanzee condition regarding the proximal phalanges. *Hispanopithecus* differs from the remaining fossil apes by more closely approaching the hylobatid and orangutan condition, although the proximal phalanx is again relatively longer than the intermediate ones.

Ratios of midshaft robusticity for the proximal phalanges (Tables 2.3 and 2.7) show similar results, if it is taken into account that robusticity is inversely proportional to relative length. ANOVA comparisons indicate that there are differences among the extant taxa at $p<0.001$ ($F=269.4$). Post-hoc multiple comparisons indicate that all comparison between pairs of taxa also show significant differences, except for *Pan* as compared to either *Papio* or *Macaca*. When fossil specimens are compared to them, it emerges that *Hispanopithecus* and *Sivapithecus* are most comparable to chimpanzees and baboons, whereas Paşalar and *Pierolapithecus* are somewhat stouter, more closely matching, like australopiths, the condition of macaques and humans (no fossil taxon even approaches the high robusticity displayed by gorillas). *Proconsul* is the most gracile among the fossil taxa included in the study, although less so than orangutans and, especially, hylobatids, which display very gracile proximal phalanges at the midshaft.

Table 2.4. Results of the principal components analyses (PCA) with the covariance matrices based on ln-transformed phalangeal measurements for proximal and intermediate phalanges separately.

	Proximal phalanges		**Intermediate phalanges**	
	PC1	**PC2**	**PC1**	**PC2**
Eigenvalue	0.813	0.033	6.527	0.259
% variance	93.6	3.8	93.3	3.7
% cumulative variance	93.6	97.4	93.3	97.0
	Rescaled component loadings			
	Proximal phalanges		**Intermediate phalanges**	
Variable	**PC1**	**PC2**	**PC1**	**PC2**
ln L	0.862	0.493	0.903	0.421
ln DPT	0.975	0.154	0.983	0.036
ln MLT	0.982	-0.064	0.958	-0.208
ln DPMS	0.979	-0.102	0.971	-0.080
ln MLMS	0.977	-0.136	0.966	-0.144
ln DPB	0.991	0.058	0.989	0.069
ln MLB	0.966	-0.176	0.988	-0.069
	Coefficient matrix for computing component scores			
	Proximal phalanges		**Intermediate phalanges**	
Variable	**PC1**	**PC2**	**PC1**	**PC2**
ln L	0.092	1.307	0.138	1.627
ln DPT	0.147	0.573	0.151	0.139
ln MLT	0.131	-0.211	0.147	-0.804
ln DPMS	0.180	-0.464	0.149	-0.307
ln MLMS	0.220	-0.756	0.148	-0.557
ln DPB	0.148	0.216	0.151	0.268
ln MLB	0.115	-0.517	0.151	-0.267

Abbreviations: ln=natural logarithm; other abbreviations as in Table 2.1.

Finally, with regard to distal phalanges, due to the lack of fossil material for other fossil taxa, the morphometrical approximation used with proximal and intermediate phalanges cannot be employed. Nevertheless, a qualitative assessment indicates that, as compared to the remaining distal phalanges, the pollical distal phalanx of *Pierolapithecus* is much larger than in extant apes. Quantitative comparisons based on the ratios of pollical vs. third distal phalanx for both length and base breadth (Table 2.8 and Figure 2.5) confirm this assertion, indicating that, as compared to the remaining distal phalanges, the pollical distal phalanx of *Pierolapithecus* is much larger than in extant apes. This is most evident regarding length, for which the ratio for *Pierolapithecus* is well above 1 and higher than the upper limit of the 95% confidence interval for all living apes and macaques, thus most closely approaching the condition displayed by *Homo*.

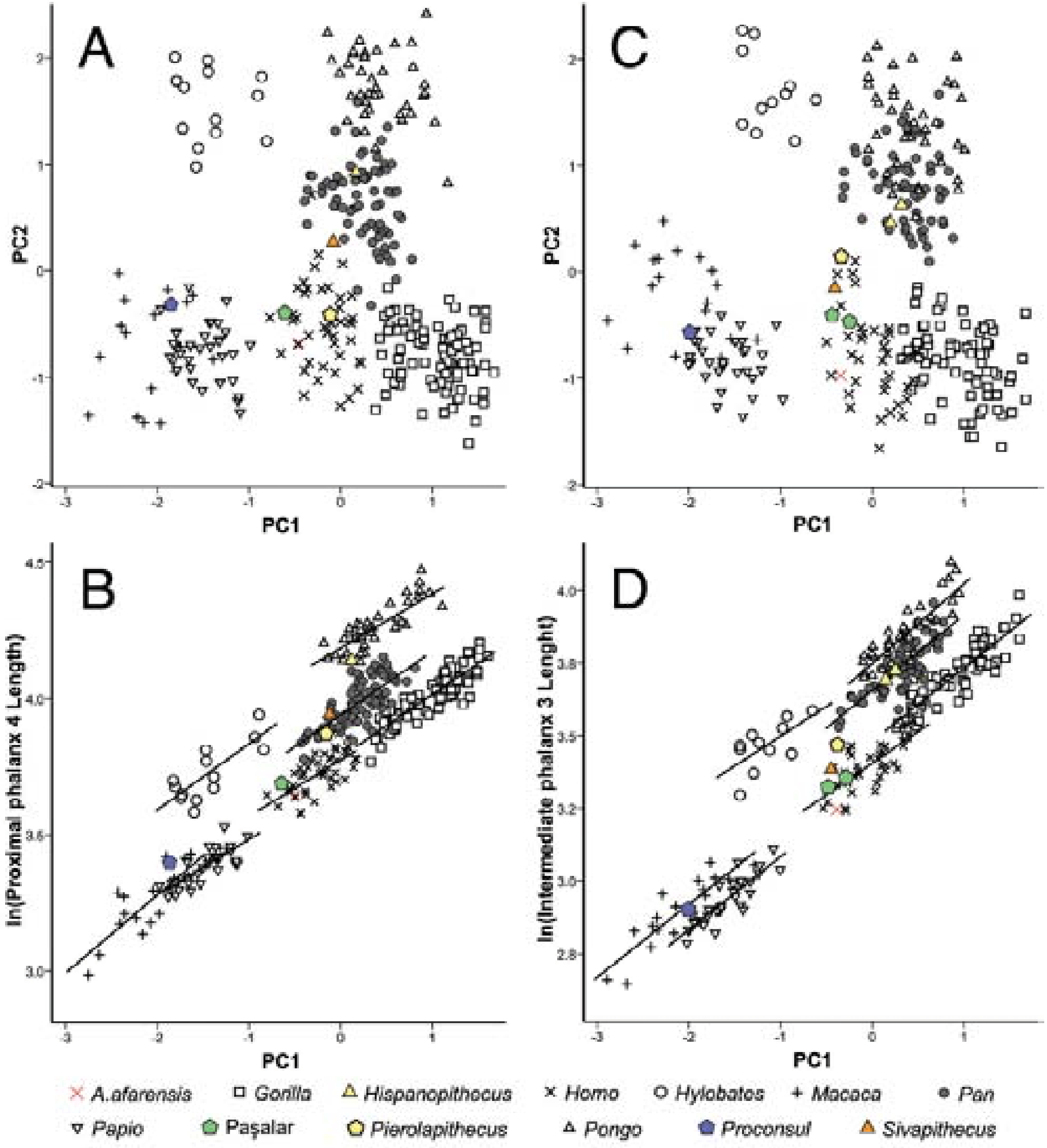


Figure 2.3. Bivariate plots of the second vs. first principal components for proximal (**A**) and intermediate (**C**) phalanges, and linear regressions of ln-transformed phalangeal length vs. the first principal component (taken as a measure of overall phalangeal size) for proximal (**B**) and intermediate (**D**) phalanges. The linear regressions (reported in Table 2.5) were derived separately for each taxon. Note that there are allometric grade shifts between several taxa (see text for further explanations).

DISCUSSION

Phalangeal morphology in Miocene apes

The overall morphology of the manual phalanges of *Pierolapithecus* is very similar to that of other Miocene apes. As previously noted by other authors (Ersoy *et al.* 2008), the phalanges of these taxa are much more similar to one another than as compared to living apes—a pattern that is also found for most other anatomical regions (Rose 1983). These similarities in phalangeal morphology extend to several taxa not included in the morphometric analysis due to the lack of complete specimens, such as *Nacholapithecus*; particularly striking are the resemblances between IPS21350.14 and the *Nacholapithecus* specimen KNM-BG17811 (see Nakatsukasa *et al.* 2003).

Thus, Miocene apes primitively retain monkey-like, palmigrady-related features on the basal portion of the proximal phalanges, such as strong palmar tubercles and a proximal articular surface extending onto the dorsal aspect of the shaft—i.e. the proximal articular surface is more dorsally oriented (see Figure 3.4 for *Hispanopithecus* and Duncan *et al.* 1994, for a discussion of this feature at the metatarsophalangeal joint). These taxa further share the presence of marked flexor sheath ridges along the shaft of both proximal and intermediate phalanges, which are indicative of powerful-grasping capabilities. This is consistent with the narrow trochlear grooves present in the proximal phalanges of most of these taxa (except *Sivapithecus*). This feature, already present in the stem catarrhine *Aegyptopithecus* (Hamrick *et al.* 1995), is interpreted as a way to stabilize the interphalangeal join in a close-packed position around arboreal supports of large diameter (see discussion in Nakatsukasa *et al.* 2003). This is consistent with the evidence provided by the pollical distal phalanx of *Pierolapithecus*, which is longer and broader than in extant apes. As such, the thumb probably played an important role in assisting the rest of the fingers during power grasping, as inferred for *Proconsul* (Begun *et al.* 1994), *Nacholapithecus* (Nakatsukasa *et al.* 2003) and *Sivapithecus* (Madar *et al.* 2002).

The above-mentioned morphological similarities in phalangeal morphology between the several Miocene hominoids indicate that pronograde behaviors such as above-branch, powerful-grasping palmigrady (assisted with the thumb), already present in stem apes (*Proconsul*), constituted a significant component of the locomotor repertories of different hominoid lineages at least until the late Miocene. This does not preclude the possibility that the relative frequency of the several locomotor modes might have changed through time. Indeed, a greater frequency of orthograde behaviors, as compared to *Proconsul*, has been previously inferred for younger, presumably pronograde taxa, such as *Nacholapithecus* (Nakatsukasa *et al.* 2003, 2007a) and *Sivapithecus* (Madar *et al.* 2002; see below for further discussion).

Table 2.5. Linear regressions of ln phalangeal length vs. first principal component (PC1, taken as an overall measurement of phalangeal size), computed in order to test for differences in relative phalangeal length among the several extant taxa included in the morphometric comparisons.

Proximal phalanges										
Taxon	**N**	**r**	**SEE**	**p**	**slope**	**95% CI**		**intercept**	**95% CI**	
Pan	74	0.747	0.057	$p<0.001$	0.230	0.182	0.277	3.938	3.922	3.955
Gorilla	90	0.888	0.041	$p<0.001$	0.231	0.206	0.257	3.781	3.754	3.807
Pongo	39	0.779	0.053	$p<0.001$	0.199	0.145	0.252	4.183	4.156	4.210
Homo	43	0.692	0.053	$p<0.001$	0.206	0.138	0.274	3.776	3.754	3.798
Hylobates	13	0.796	0.066	$p<0.01$	0.241	0.119	0.363	4.073	3.893	4.253
Papio	33	0.828	0.038	$p<0.001$	0.210	0.158	0.262	3.692	3.6136	3.772
Macaca	19	0.844	0.069	$p<0.001$	0.288	0.194	0.381	3.856	3.661	4.051
Intermediate phalanges										
Taxon	**N**	**r**	**SEE**	**p**	**slope**	**95% CI**		**intercept**	**95% CI**	
Pan	66	0.823	0.052	$p<0.001$	0.260	0.215	0.305	3.654	3.634	3.673
Gorilla	75	0.885	0.048	$p<0.001$	0.252	0.221	0.283	3.479	3.449	3.510
Pongo	37	0.857	0.055	$p<0.001$	0.273	0.217	0.330	3.746	3.718	3.774
Homo	37	0.726	0.056	$p<0.001$	0.216	0.146	0.286	3.403	3.385	3.422
Hylobates	11	0.653	0.066	$p<0.05$	0.203	0.026	0.381	3.702	3.491	3.913
Papio	31	0.877	0.040	$p<0.001$	0.254	0.201	0.307	3.339	3.253	3.425
Macaca	18	0.880	0.060	$p<0.001$	0.250	0.178	0.321	3.421	3.267	3.574

Abbreviations: N=sample size; r=correlation coefficient; SEE=standard error of estimate; p=significance; CI=confidence interval.

Phalangeal curvature

Despite phalangeal similarities between the orthograde *Pierolapithecus* and other, presumably more pronograde, middle Miocene apes, phalangeal morphology did not remain completely unchanged during evolution. Thus, even though most of the taxa discussed in this paper display striking morphological similarities, some of them do significantly differ regarding phalangeal curvature and/or elongation. Thus, the highly curved proximal phalanges of *Hispanopithecus* uniquely depart from those of the remaining taxa by falling well into the range of orangutans (see measurements for extant taxa in Richmond and Whalen 2001); moreover, the former taxon further differs by displaying markedly curved intermediate phalanges. On the contrary, middle Miocene taxa display a more moderate degree of curvature (50-60º) only slightly higher than in *Proconsul*, the latter fully overlapping with the range of quadrupedal monkeys.

A recent work by Deane and Begun (2008), based on a discriminant analysis of phalangeal curvature, classifies both *Hispanopithecus* and *Pierolapithecus* as suspensory taxa. Leaving aside the considerable differences in phalangeal curvature between these taxa, Deane and Begun's (2008) approach also overlooks many of the morphological and proportional differences between the phalanges of the two above-mentioned taxa. As such, merely classifying both taxa as ‘suspensory’ is an oversimplification, because it does not take into account that the locomotor repertoire of each particular taxon is a combination of several locomotor modes, which are practiced in different frequencies and which have a different significant from an adaptive viewpoint in each particular taxon (see for example Thorpe and Crompton 2006, regarding orangutans).

As noted by Richmond (2007, p. 689), it has been long recognized by many authors that “phalangeal shaft curvature is related to the strains associated with arboreal and especially suspensory activity” (e.g. Susman 1979; Stern *et al.* 1995). In part, curvature is genetically determined, although to some extent it is also an ecophenotypic feature that change throughout ontogeny by bone remodeling as a response to changing mechanical stresses (e.g. Richmond and Whalen 2001). Sarmiento (1988, his Figure 1) argues, on the basis of a biomechanical model, that during the typical hominoid hook grasp, the force applied by the long flexor tendon is only a small fraction of weight, and that if the curvature of the proximal phalanx is great enough, the animal can hang without applying an active muscular force. A recent biomechanical examination of phalangeal curvature by Richmond (2007) has further confirmed the previously-recognized association between increased arboreality and more pronounced curvature, by concluding that “phalangeal curvature reduces the strains associated with arboreal, and especially suspensory, activity involving flexed digits” (Richmond 2007, p. 678). Accordingly, despite their similar classification in Deane and Begun's (2008) analysis, the differences in phalangeal curvature between *Pierolapithecus* and *Hispanopithecus* (around 20º) are highly suggestive that the locomotor repertoires of these taxa emphasized different kinds of arboreal behaviors.

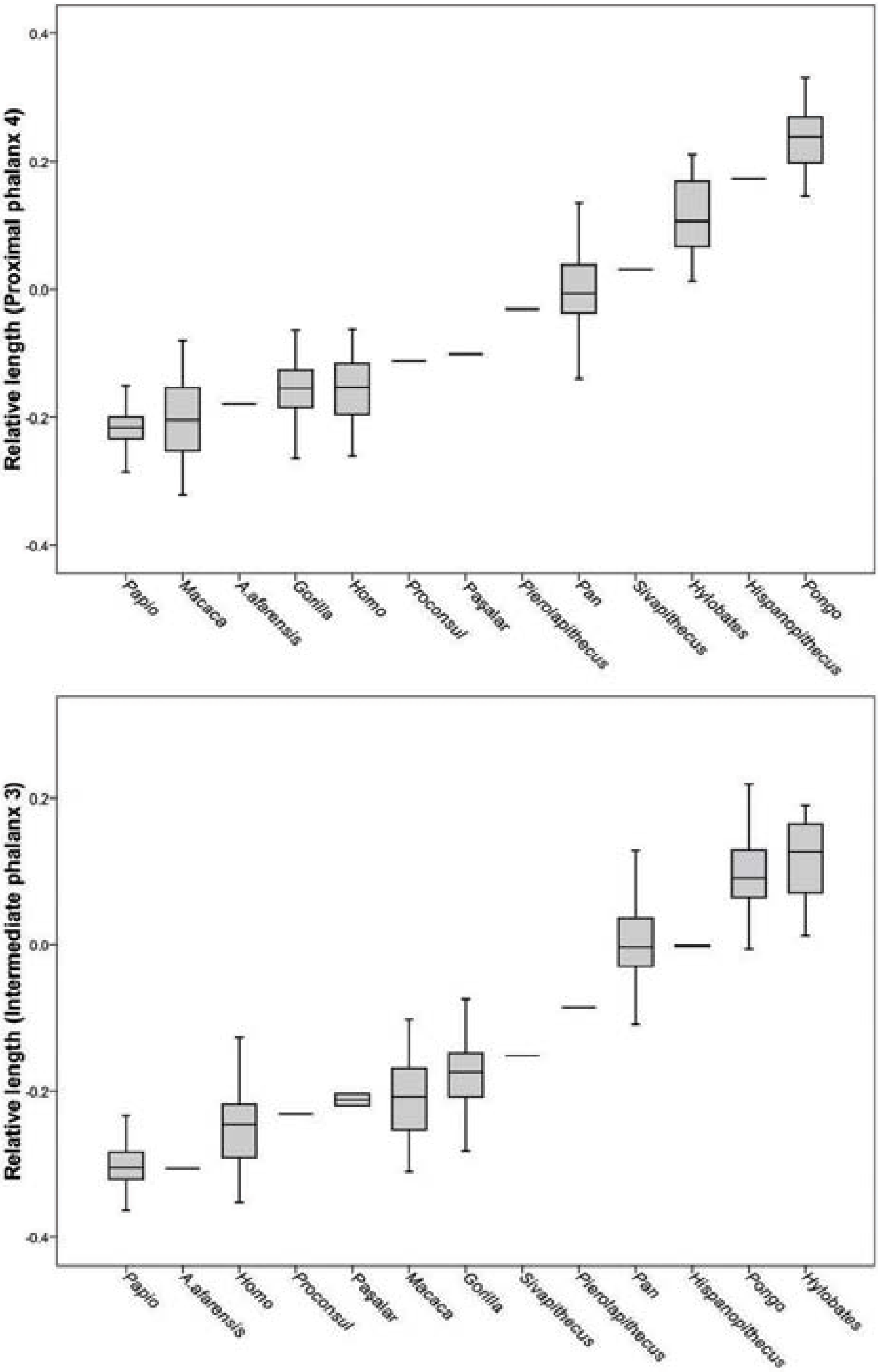


Figure 2.4. Boxplots of residuals of relative phalangeal length computed as observed phalangeal length minus expected phalangeal length for *Pan*. The chimpanzee linear regression employed as the baseline for computing residuals is reported in Table 2.5. Horizontal lines represent the median values, whereas the boxes represent the 25% and 75% percentiles, and the whiskers the maximum-minimum ranges (by excluding outliers).

Table 2.6. Descriptive statistics of the residuals of intrinsic relative phalangeal length for extant taxa, computed from the linear regression of phalangeal length vs. PC1, by taking chimpanzees as the reference (i.e. mean chimpanzee residual equals zero).

Proximal phalanges

Taxon	N	Mean	SD	95% CI		Range	
Pan	74	0.000	0.056	-0.013	0.013	-0.139	0.136
Gorilla	90	-0.156	0.041	-0.164	-0.147	-0.264	-0.065
Pongo	39	0.233	0.054	0.215	0.250	0.056	0.330
Homo	43	-0.157	0.053	-0.173	-0.141	-0.260	-0.063
Hylobates	13	0.118	0.063	0.079	0.156	0.012	0.210
Papio	33	-0.216	0.038	-0.229	-0.202	-0.285	-0.117
Macaca	19	-0.202	0.070	-0.236	-0.169	-0.321	-0.080

Intermediate phalanges

Taxon	N	Mean	SD	95% CI		Range	
Pan	66	0.000	0.051	-0.013	0.013	-0.138	0.128
Gorilla	75	-0.181	0.047	-0.192	-0.170	-0.283	-0.075
Pongo	37	0.098	0.055	0.079	0.116	-0.007	0.220
Homo	37	-0.249	0.056	-0.268	-0.231	-0.352	-0.128
Hylobates	11	0.114	0.065	0.070	0.157	0.012	0.191
Papio	31	-0.305	0.039	-0.319	-0.291	-0.387	-0.210
Macaca	18	-0.212	0.058	-0.241	-0.183	-0.311	-0.103

Abbreviations: N=sample size; SD=standard deviation; CI=confidence interval.

Table 2.7. Descriptive statistics of the indices of midshaft robusticity for the fourth proximal phalanx of extant taxa, computed as mediolateral midshaft breadth / phalanx length (in %).

Taxon	N	Mean	SD	95% CI		Range	
Pan	75	19.21	2.24	18.69	19.72	14.02	25.34
Gorilla	92	30.10	3.07	29.47	30.74	24.20	38.14
Pongo	39	15.85	1.90	15.23	16.46	13.65	23.73
Homo	45	21.46	2.40	20.73	22.18	17.36	27.41
Hylobates	13	13.29	1.39	12.45	14.13	11.65	15.89
Papio	33	18.81	1.78	18.18	19.45	15.61	23.13
Macaca	19	18.18	2.48	16.99	19.38	14.55	22.98

Abbreviations: N=sample size; SD=standard deviation; CI=confidence interval.

Table 2.8. Descriptive statistics of the pollical to third distal phalanx ratios showed in Figure 2.5.

Distal phalanx I length/Distal phalanx III length

Taxon	N	Mean	SD	95% CI		Range	
Pan	6	0.912	0.111	0.795	1.028	0.790	1.106
Gorilla	5	0.951	0.095	0.833	1.069	0.825	1.088
Pongo	6	0.712	0.063	0.645	0.778	0.627	0.772
Homo	5	1.243	0.048	1.184	1.302	1.190	1.311
Hylobates	8	0.845	0.077	0.781	0.909	0.710	0.914
Macaca	14	0.718	0.091	0.665	0.770	0.616	0.902
Pierolapithecus	1	1.168					

Distal phalanx I MLB/Distal phalanx III MLB

Taxon	N	Mean	SD	95% CI		Range	
Pan	6	0.832	0.152	0.673	0.992	0.677	1.093
Gorilla	5	0.808	0.166	0.601	1.014	0.645	1.064
Pongo	6	0.843	0.054	0.786	0.899	0.768	0.934
Homo	5	1.335	0.116	1.191	1.478	1.182	1.464
Hylobates	8	0.967	0.204	0.796	1.137	0.646	1.262
Macaca	14	1.106	0.111	1.042	1.170	0.971	1.359
Pierolapithecus	1	1.114					

Abbreviations: MLB=mediolateral width of the base; N=sample size; SD=standard deviation; CI=confidence interval.

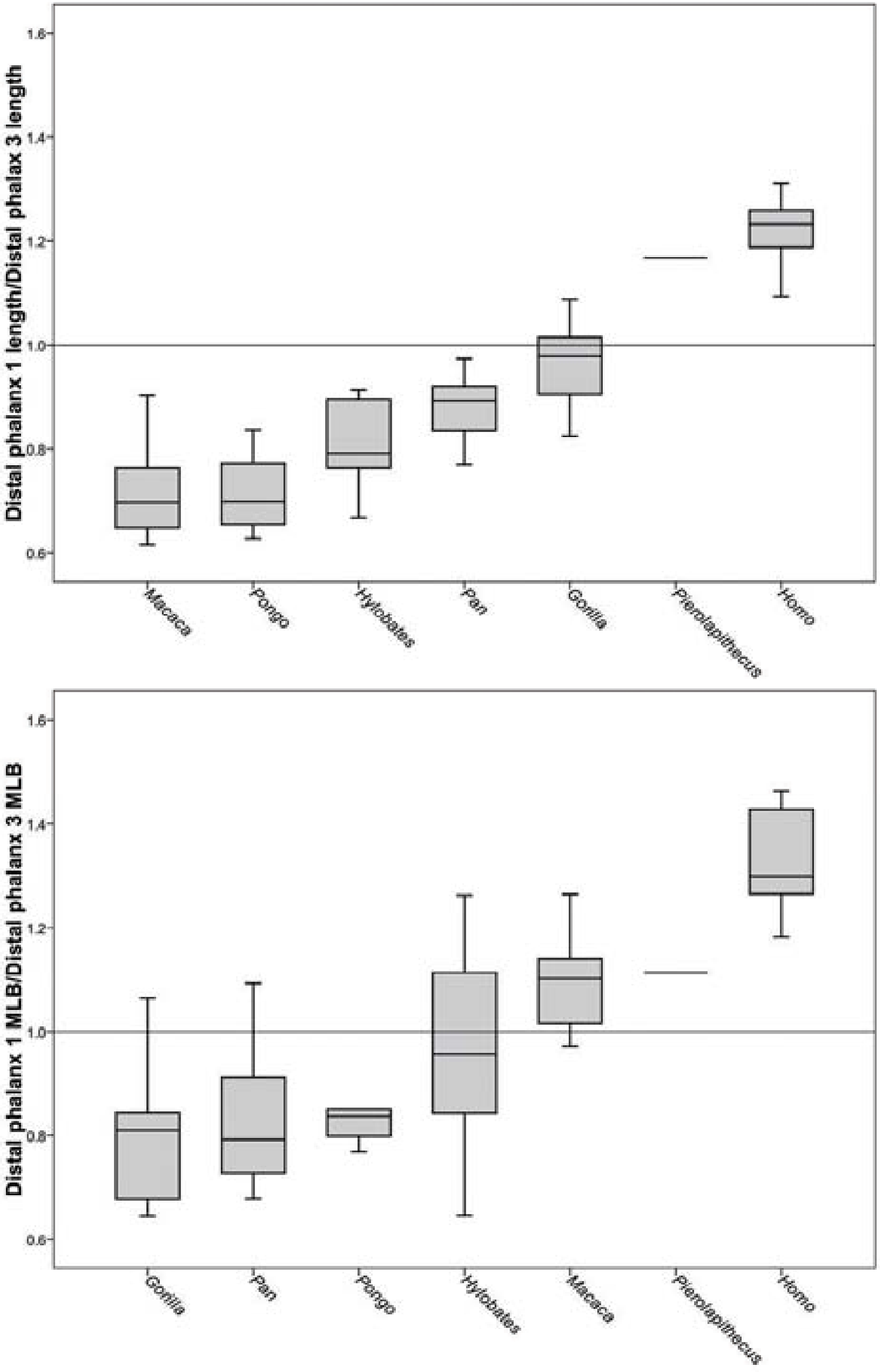


Figure 2.5. Boxplots showing ratios of the pollical distal phalanx dimensions relative to distal phalanx III: proximodistal length (top) and mediolateral base breadth (MLB, bottom). Horizontal lines represent the median values, whereas the boxes represent the 25% and 75% percentiles, and the whiskers the maximum-minimum ranges (by excluding outliers).

Robusticity and intrinsic relative phalangeal length

The robusticity indices reported in this paper for proximal phalanges must be interpreted carefully, given the fact that they do not control for size-scaling effects. The latter might explain the low phalangeal robusticity displayed by *Proconsul*. All the middle and late Miocene apes, however, display similar values of robusticity, which are most comparable, or even slightly greater, than in chimpanzees, macaques and baboons, clearly departing from the much more gracile condition displayed by orangutans and hylobatids. The moderately high midshaft robusticity of the proximal phalanges of these Miocene apes, including *Pierolapithecus* and *Hispanopithecus*, might be related to the mechanical requirements of primitively-retained, quadrupedal behaviors.

Be that as it may, somewhat different locomotor repertoires can be also inferred for *Pierolapithecus* and *Hispanopithecus* on the basis of differences of intrinsic relative length of their phalanges (Figure 2.4). *Hispanopithecus* displays the highest degree of intrinsic elongation, while Paşalar most closely resembles *Proconsul*, and both *Sivapithecus* and *Pierolapithecus* display somewhat intermediate values. As far as extant primates from the comparative sample are concerned, intrinsic relative length of the proximal and intermediate phalanx apparently reflects a gradient of terrestriality-arboreality, progressively increasing from terrestrial cercopithecids to humans, gorillas, chimpanzees and, finally, hylobatids and orangutans. The results for *Hispanopithecus* are very close to hylobatids and orangutans, the most arboreal and suspensory taxa among extant apes. The same results are reported in Chapter 3 for *Hispanopithecus*—and most of the extant comparative sample—on the basis of the relative length of the proximal phalanges relative to body mass (Figure 3.9B), thus indicating that the intrinsic measure of phalangeal relative length employed here shows the same correlation to the degree of arboreality than phalangeal length relative to body size.

From a functional viewpoint, the long hands of extant apes, characterized by their elongated long bones and relatively short thumbs, have been customarily interpreted as an arboreal adaptation that enables the hand for functioning as a grasping hook (Sarmiento 1988, his Figure 1) during below-branch suspension (Straus 1940; Napier 1967; Preuschoft 1973; Susman 1979; Inouye 1992). The long-handed extant apes can grasp very thick arboreal supports by pressing the fingers against one side of the branch or stem; the reaction force is transmitted to the opposite side onto the thumb or the thenar and hypothenar areas of the hand. A large compressive force must be exerted between the fingers and the carpal part of the palm, in order to provide enough frictional resistance and prevent the hand from slipping off, and this is only possible if a large portion of the stem's circumference is covered by the hand (Preuschoft 1973). This provides a biomechanical explanation for empirical relationship found between several measurements of hand and phalangeal length and the degree of arboreal commitment. In fact, the degree of manual elongation of chimpanzees, intermediate between the more terrestrial gorillas and the more arboreal orangutans and hylobatids, has been interpreted as a biomechanical compromise between knuckle-walking and arboreal grasping behaviors (Susman 1979). The shorter proximal phalanges of African apes, especially gorillas, would help to prevent the integrity of the metacarpophalangeal joint during knuckle-walking (Susman 1979; Inouye 1992; see Figure 2.6C,D). In the case of *Pierolapithecus,* differences in intrinsic phalangeal relative length as compared to *Hispanopithecus* are highly suggestive of underlying differences in their respective locomotor repertoires, with the former being less adapted to the arboreal behaviors, such as suspension, displayed by extant apes.

Interestingly, given the fact that *Pierolapithecus* already possesses an orthograde bodyplan (Moyà-Solà *et al.* 2004), the roughly comparable phalangeal proportions of *Sivapithecus* cannot be interpreted as necessarily excluding the possession of an orthograde bodyplan in the latter taxon. Reconstructing the postcranial bodyplan and inferring the locomotor repertoire of *Sivapithecus* have proved very contentious, due to the implications for interpreting its phylogenetic status as a member of the Ponginae. The many craniofacial features shared by *Sivapithecus* and *Pongo* (see review in Kelley 2002) have led most authors to conclude that both taxa are closely related. However, the recognition of pronograde-related features in two humeral diaphyses attributed to this taxon (Pilbeam *et al.* 1990; Richmond and Whalen 2001) have led to the so-called "*Sivapithecus* dilemma" (Pilbeam and Young 2001): if *Sivapithecus* is considered a member of the *Pongo*-clade, then either (a) most of the postcranial features shared by orangutans and African apes must be homoplastic; or (b) *Sivapithecus* must have secondarily lost them. Pilbeam (1996, 1997) has favored the view that *Sivapithecus* and most other Eurasian Miocene hominoids might be members of an archaic hominoid radiation. However, as recently noted by Begun (2007, p. 943), the primitive postcranial features of *Sivapithecus* most likely “reflect mosaic evolution of the hominid skeleton, uniquely derived features of the anatomy of *Sivapithecus*, as well as some parallelism in extant hominoids.” Although the humeral morphology of this taxon is quite monkey-like, this might merely indicate that below-branch suspension was rarely practiced by this taxon (Richmond and Whalen 2001; Madar *et al.* 2002)—instead of necessarily reflecting a pronograde bodyplan or securely excluding other orthograde behaviors. The presence of robust and well-developed pollices and halluces in this taxon, like in *Nacholapithecus* (Nakatsukasa *et al.* 2003) and, presumably, *Pierolapithecus* (on the basis of the pollical distal phalanx reported in this paper), suggest that these taxa displayed pollex/hallux-assisted, powerful-grasping capabilities, instead of the hook grasp of extant apes. As noted by Madar *et al.* (2002), the powerful grasping of these Miocene apes might have been employed during above-branch palmigrade quadrupedalism, as well as vertical climbing and orthograde clambering. On the contrary, it is inconsistent with the suspensory adaptations displayed by extant anthropoids, especially great apes, which tend to favor the reduction of the first manual ray in both hands and feet (Straus 1941; Tuttle and Rogers 1966).

Thus, the phalangeal proportions and morphology of *Sivapithecus* are compatible with the possession of a pronograde-dominated locomotor repertoire with some orthograde behaviors, as inferred by Madar *et al.* (2002). At the same time, however, they do not necessarily exclude an essentially orthograde bodyplan, given the phalangeal similarities with *Pierolapithecus* shown in this paper. Unfortunately, the key anatomical regions that indicate orthograde in *Pierolapithecus* (see Moyà-Solà *et al.* 2004) are still unknown for *Sivapithecus*. As such, it is not possible to test to what extent its postcranial bodyplan was orthograde, although it seems clear that, like *Pierolapithecus* and other Miocene apes, it shows a unique combination of locomotor behaviors that lacks a modern analogue among hominoids (Madar *et al.* 2002). Be that as it may, a considerable increase in intrinsic phalangeal relative length, like that found in committed arboreal and suspensory living apes (hylobatids and orangutans), is not recorded until *Hispanopithecus*, where it is associated with both an orthograde bodyplan (Moyà-Solà and Köhler 1996) and orang-like suspensory adaptations (see Chapter 3).

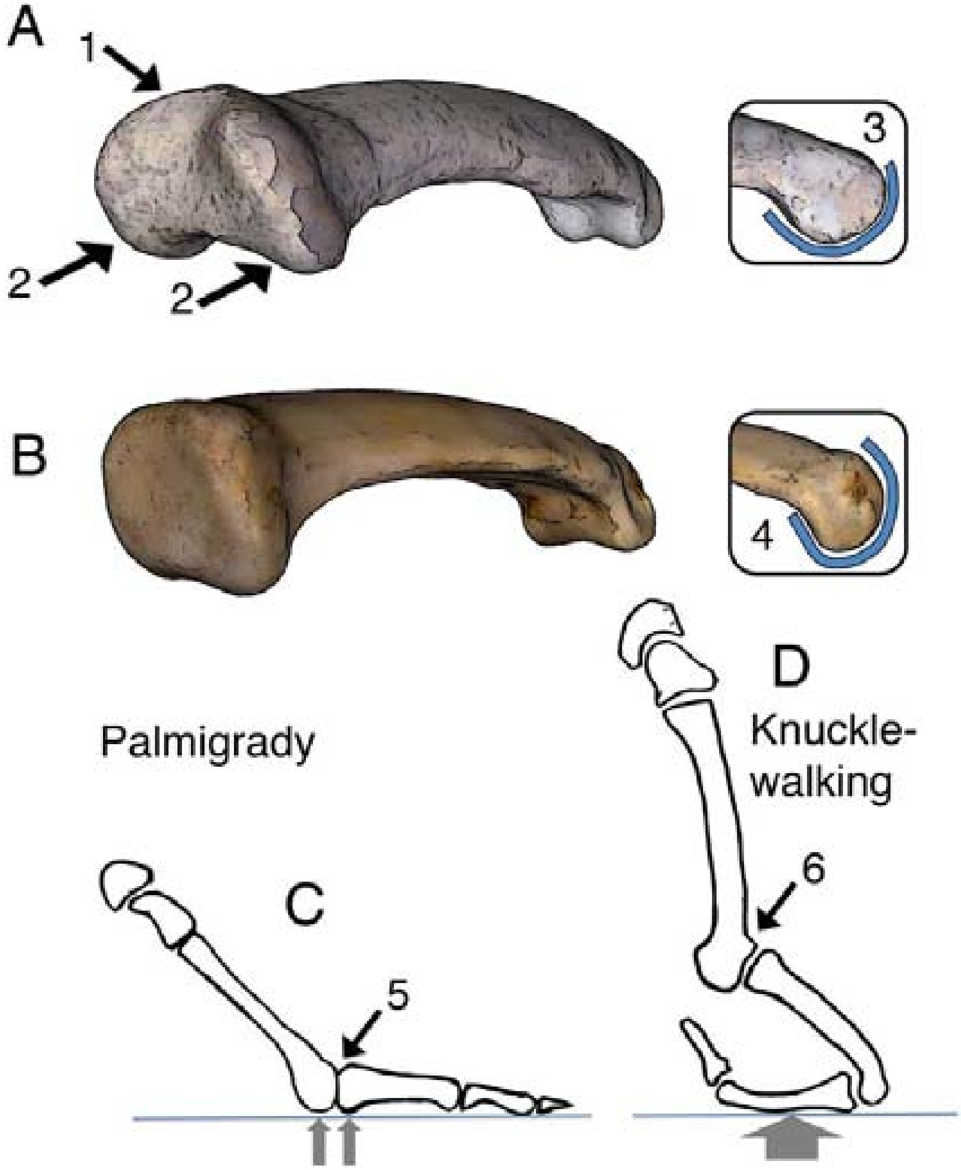


Figure 2.6. (**A**-**B**) Oblique rear view and lateral detail of the trochlea of a virtual model of the right fourth proximal phalanx of *Pierolapithecus catalaunicus* IPS21350.14 (**A**), as compared to the same bone in a chimpanzee (**B**); (**C**-**D**) Schematic depiction of different hand postures in palmigrady (**C**) and knuckle-walking (**D**). Note that *Pierolapithecus* differs from chimpanzees by basal dimensions and morphology, including a dorsally-oriented proximal articular facet (**1**) as well as large and laterally protruding palmar tubercles (**2**). *Pierolapithecus* further differs by the shape of the trochlea (**3**), which is proximodistally longer and not palmarly-bent, unlike in chimpanzees (**4**). Among extant primates, these differences relate to different hand postures. In chimps and other suspensory taxa, the morphology of the trochlear profile (**4**) contributes to the overall curvature of the phalanx, allowing them to hang efficiently during the hook grasp. With regard to the metacarpophalangeal joint, during palmigrady (**C**) ground reaction force acts upon the palmar side of the hand (double arrows). As a result, proximal phalanges show well-developed palmar tubercles associated to large sesamoid bones, in order to channel the long flexor tendons during hyperextension of this joint (**5**); this is further reflected in the dorsally-directed proximal articular facets (**1**). In knuckle-walking (**D**), ground reaction force acts instead against the dorsal aspect of the intermediate phalanges (single arrow); as a result, mechanical stresses on the proximal phalanges are very different, and there is no need for well-developed palmar tubercles or large sesamoids; moreover, there are dorsal ridges on the metacarpal heads, in order to prevent the collapse of the metacarpophalangeal joint during hyperextension (**6**), so that the proximal articular surface of the proximal phalanges is not dorsally-oriented.

Suspensory behaviors in *Pierolapithecus*

On the basis of the degree of phalangeal curvature and intrinsic relative length reported for *Pierolapithecus* in this paper, roughly comparable to those of chimpanzees, suspensory behaviors cannot be completely discarded for the former taxon. It should be taken into account, however, that African apes are largely terrestrial, and display a derived and specialized type of digitigrady (knuckle-walking; see Figure 2.6D) that can be understood as a kind of locomotor compromise (Tuttle 1975), enabling them to travel efficiently when on the ground while, at the same time, allowing them to retain a long hand suitable for arboreal behaviors (including suspension) for feeding and nesting. Accordingly, the figures of intrinsic phalangeal length derived for *Pierolapithecus* must indicate at the very least that this taxon was less committed to below-branch suspensory behaviors than hylobatids, orangutans and *Hispanopithecus*. Moreover, while chimpanzees share several suspensory-related features with the above mentioned taxa, *Pierolapithecus* displays a more primitive phalangeal morphology (Figure 2.6) suggesting that suspension in this taxon must have been much more rare and less adaptively significant. The morphology of the proximal phalanges of chimpanzees (Figure 2.6B), including the lack of large basal palmar tubercles, the non-dorsally-directed proximal articular facet, and the proximodistally-short and palmarly-bent trochlea, fits the morphological pattern of the most suspensory extant apes, thus contrasting with the morphology of *Pierolapithecus* and other early to middle Miocene apes, which resembles instead that of quadrupedal extant taxa.

The orthograde bodyplan documented by the partial skeleton of *Pierolapithecus*, combined with phalangeal morphology, also has profound implications for the evolution of the hominoid locomotor repertoire during the Miocene. Considering the information provided by *Pierolapithecus*, our results indicate that only a moderate lengthening of the proximal and the intermediate phalanges (Figure 2.4) was associated with the acquisition of an orthograde bodyplan. This fact is evident when the homologous hand elements from Paşalar, interpreted as belonging to a pronograde form—tentatively identified as *Griphopithecus* by Ersoy *et al.* (2008)—are taken into account (Figure 2.4). This taxon shows a phalangeal shape similar to that of the pronograde genus *Proconsul*. Given the lack in *Pierolapithecus* of the elongated hand and phalangeal morphology typical of modern arboreal apes, it is reasonable to infer that the orthograde bodyplan, first documented by this taxon, was originally an adaptation to vertical climbing and perhaps other orthograde behaviors with the exclusion of below-branch suspension (Moyà-Solà *et al.* 2004, 2005).

Traditionally, most of the apendicular and axial features shared by living hominoids have been related to forelimb-dominated, below-branch suspension (e.g. Keith 1923). This, however, is far from clear, because in living hominoids these features are also functionally related to other orthograde behaviors, such as vertical climbing and clambering (Crompton *et al.* 2008). On the basis of extant taxa alone, it is not possible to discern between climbing and suspensory adaptations, because living apes simultaneously display both types of behavior. This has led to diverging interpretations of the orthograde adaptations shared by these taxa. For example, Ward (1993) attributed it to forelimb-dominated, arboreal locomotion, including both vertical climbing and below-branch suspension. Gebo (1996), on the contrary, suggested that suspension would be the main adaptive reason explaining the morphological design of the hominoid thorax and forelimb, while Sarmiento (1995) suggested instead that orthogrady-related features were mainly related to cautious and vertical climbing. Current function, however, must not be automatically equated with the original target of selection (Gould and Vrba 1982); in other words, fossil evidence is required in order to distinguish between exaptations and true adaptations.

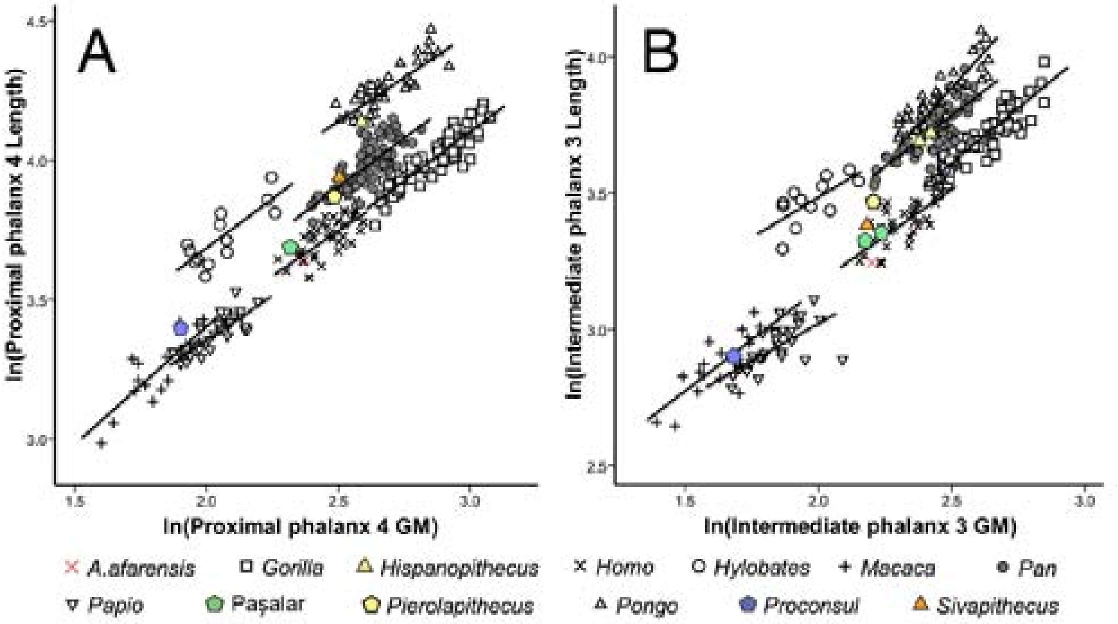
Hunt (1991) considered that the possession of a shallow and wide thorax to be a suspensory adaptation, while the lack of ulnocarpal articulation would be an adaptation to them both. The latter author similarly interprets the possession of long and curved manual phalanges as an adaptation to grasping vertical weight-bearing structures during vertical climbing and arm-hanging (Hunt 1991). *Pierolapithecus*, however, shows that orthograde features related to thorax shape and lack of ulnocarpal articulation are most likely to be original adaptations exclusively to vertical climbing. As noted by Nakatsukasa *et al.* (2003), features originally useful for climbing would have been probably useful for suspension latter. This view is supported by our results, according to which, with regard to suspension, most orthogrady-related features would be “preadaptive” with regard to brachiation (Cartmill, 1985, p. 88), i.e. exaptations instead of adaptations. We therefore concur with Crompton *et al.* (2008) that the acquisition of the crown-hominoid bodyplan was probably much more related to generalized orthogrady than specifically to suspensory behaviors, which could have been later independently developed to some extent by several hominoid lineages (Moyà-Solà *et al.* 2004, 2005; see also Chapter 3).

CONCLUSIONS

The evidence discussed in this paper confirms the view that locomotor evolution in hominoids, including the acquisition of climbing and suspensory adaptations, took place in a stepwise, mosaic fashion (Ward 2007; Alba and Moyà-Solà 2008). *Proconsul* shows that taillessness preceded the emergence of an orthograde bodyplan (Nakatsukasa *et al.* 2004), being merely associated with the development of the powerful-grasping capabilities (Begun *et al.* 1994), the latter required in order to compensate for the loss of balancing function (Ward 2007). Similarly, *Pierolapithecus* shows that the evolution of very long and curved phalanges, not recorded until *Hispanopithecus*, was decoupled from the acquisition of orthograde features that are functionally related to vertical climbing. The short phalanges with a moderate degree of curvature of Paşalar are entirely compatible with the retention of a pronograde bodyplan, as already argued by Ersoy *et al.* (2008). As far as phalanges are concerned, the orthograde bodyplan of *Pierolapithecus*, clearly documented by several other anatomical regions (lumbar vertebrae, ribs and carpal morphology; see Moyà-Solà *et al.* 2004), is merely reflected in a somewhat higher degree of phalangeal elongation.

The lack of pronounced phalangeal curvature and elongation in *Pierolapithecus*, together with its moderate intrinsic phalangeal length and its primitive (monkey-like) morphology of proximal phalanges—particularly at the metacarpophalangeal joint—, strongly suggest that this taxon, like other middle Miocene apes, lacked specific adaptations to below-branch suspension. The latter are not recorded until the late Miocene by *Hispanopithecus* (see Chapter 3). This does not mean that *Pierolapithecus* never practiced suspensory behaviors, but suggests that the latter had not become adaptively significant yet. According to this interpretation, the evolutionary transition from a pronograde towards an orthograde bodyplan would have been decoupled from the acquisition of suspensory behaviors, being mainly related to the acquisition of enhanced vertical-climbing capabilities (Moyà-Solà *et al.* 2004, 2005; Crompton *et al.* 2008).

Appendix 2.1. Linear regressions of ln-transformed phalangeal length vs. ln-transformed geometric mean (taken as a measure of overall phalangeal size) for proximal (**A**) and intermediate (**B**) phalanges. The linear regressions. Note that these figures are virtually identical to those derived employing PC1 instead of ln GM (Figures 2.3B and 2.3D).



Appendix 2.2. Descriptive statistics for the seven metrical variables measured (in mm) in the comparative extant sample.

Proximal Phalanx IV Length

Taxon	N	Mean	SD	95% CI		Range	
Pan	84	54.31	4.43	53.35	55.28	43.76	63.57
Gorilla	105	54.90	4.95	53.94	55.86	43.27	66.93
Pongo	48	71.06	5.79	69.38	72.74	62.34	87.38
Homo	58	41.91	2.89	41.15	42.67	35.83	47.96
Hylobates	13	41.75	4.49	39.04	44.47	36.00	51.40
Papio	33	29.30	1.98	28.60	30.01	26.35	34.12
Macaca	19	26.32	3.19	24.78	27.85	19.80	30.90

Proximal Phalanx IV Dorsopalmar Trochlear Height

Taxon	N	Mean	SD	95% CI		Range	
Pan	1	75	9.85	0.95	9.63	10.07	7.47
Gorilla	2	91	11.31	1.35	11.03	11.59	8.60
Pongo	3	39	9.92	1.20	9.53	10.31	8.07
Homo	4	46	7.57	0.80	7.33	7.81	5.58
Hylobates	5	13	5.85	0.73	5.41	6.30	5.10
Papio	6	33	4.81	0.47	4.65	4.98	4.03
Macaca	7	19	3.96	0.53	3.70	4.21	2.90

Proximal Phalanx IV Mediolateral Trochlear Breadth

Taxon	N	Mean	SD	95% CI		Range	
Pan	75	11.53	1.26	11.24	11.82	7.49	13.70
Gorilla	91	15.00	1.86	14.61	15.38	11.83	19.25
Pongo	39	11.74	1.41	11.28	12.20	9.15	14.50
Homo	46	10.77	1.14	10.43	11.11	7.58	13.20
Hylobates	13	6.45	0.69	6.04	6.87	5.20	7.70
Papio	33	6.71	0.60	6.49	6.92	5.78	8.00
Macaca	19	5.58	0.77	5.21	5.96	4.50	7.40

Proximal Phalanx IV Dorsopalmar Midshaft Height

Taxon	N	Mean	SD	95% CI		Range	
Pan	75	7.59	0.98	7.37	7.82	5.19	9.67
Gorilla	92	10.63	1.57	10.31	10.96	7.63	14.20
Pongo	39	7.47	1.26	7.07	7.88	5.34	11.02
Homo	47	6.42	0.56	6.26	6.59	4.89	7.75
Hylobates	13	4.02	0.47	3.73	4.30	3.20	4.80
Papio	33	4.10	0.50	3.92	4.27	3.21	4.90
Macaca	19	3.28	0.57	3.01	3.56	2.30	4.30

Proximal Phalanx IV Mediolateral Midshaft Breadth

Taxon	N	Mean	SD	95% CI		Range	
Pan	75	10.39	1.49	10.05	10.73	7.74	14.73
Gorilla	92	16.68	2.44	16.17	17.19	12.91	22.21
Pongo	39	11.28	1.69	10.73	11.83	8.72	15.45
Homo	47	8.94	1.08	8.62	9.25	7.11	11.12
Hylobates	13	5.56	0.93	5.00	6.13	4.50	7.20
Papio	33	5.51	0.64	5.29	5.74	4.29	6.90
Macaca	19	4.76	0.72	4.41	5.11	3.60	5.80

Proximal Phalanx IV Dorsopalmar Basal Height

Taxon	N	Mean	SD	95% CI		Range	
Pan	74	13.35	1.15	13.08	13.61	10.92	16.56
Gorilla	90	16.78	2.06	16.35	17.21	12.43	21.51
Pongo	39	14.50	1.61	13.98	15.02	11.46	18.05
Homo	44	11.40	0.92	11.12	11.68	9.65	13.02
Hylobates	13	7.22	1.05	6.59	7.86	5.90	9.10
Papio	33	7.22	0.65	6.99	7.46	6.21	8.57
Macaca	19	5.76	0.82	5.36	6.15	4.60	7.60

Proximal Phalanx IV Mediolateral Basal Breadth

Taxon	N	Mean	SD	95% CI		Range	
Pan	74	14.28	1.39	13.95	14.60	11.46	17.76
Gorilla	91	19.64	2.46	19.13	20.15	15.08	24.29
Pongo	39	15.13	1.95	14.50	15.76	12.02	19.40
Homo	45	14.47	1.29	14.08	14.85	11.70	17.00
Hylobates	13	7.64	1.24	6.89	8.39	6.00	9.60
Papio	33	9.63	0.98	9.29	9.98	8.34	11.36
Macaca	19	7.94	0.96	7.48	8.40	6.40	9.40

Intermediate Phalanx III Length

Taxon	N	Mean	SD	95% CI		Range	
Pan	80	42.07	3.79	41.23	42.92	34.08	52.57
Gorilla	89	40.74	4.18	39.86	41.62	33.04	53.65
Pongo	49	46.31	7.14	44.26	48.36	13.70	60.13
Homo	52	30.08	2.36	29.43	30.74	25.59	34.95
Hylobates	12	32.33	2.59	30.68	33.97	27.00	36.10
Papio	34	18.64	1.73	18.04	19.24	13.60	22.43
Macaca	19	18.09	2.15	17.05	19.13	14.10	21.40

Intermediate Phalanx III Dorsopalmar Trochlear Height

Taxon	N	Mean	SD	95% CI		Range	
Pan	69	6.95	0.79	6.76	7.14	5.14	8.76
Gorilla	75	7.91	1.06	7.67	8.16	6.05	11.42
Pongo	40	6.87	1.12	6.51	7.23	2.50	9.10
Homo	37	6.15	0.71	5.91	6.38	4.86	8.06
Hylobates	12	4.38	0.47	4.08	4.67	3.60	5.30
Papio	34	3.85	0.55	3.66	4.05	3.00	5.50
Macaca	19	3.08	0.52	2.83	3.34	2.10	4.10

Intermediate Phalanx III Mediolateral Trochlear Breadth

Taxon	N	Mean	SD	95% CI		Range	
Pan	69	9.60	0.98	9.37	9.84	7.40	11.73
Gorilla	75	13.19	1.56	12.83	13.55	10.43	16.91
Pongo	40	10.05	1.50	9.57	10.53	4.90	12.57
Homo	37	10.06	1.02	9.72	10.39	8.10	12.51
Hylobates	12	6.17	0.51	5.84	6.49	5.60	7.50
Papio	34	6.16	0.77	5.89	6.42	3.40	7.63
Macaca	19	5.37	0.78	5.00	5.75	4.30	6.80

Intermediate Phalanx III Dorsopalmar Midshaft Height

Taxon	N	Mean	SD	95% CI		Range	
Pan	71	5.74	0.75	5.56	5.92	3.55	8.70
Gorilla	75	6.98	0.90	6.77	7.19	4.98	9.58
Pongo	40	5.68	1.17	5.31	6.05	2.20	9.67
Homo	37	5.48	0.60	5.29	5.68	4.45	6.47
Hylobates	12	3.47	0.47	3.17	3.76	2.80	4.40
Papio	34	3.37	0.58	3.17	3.57	2.59	5.20
Macaca	19	2.63	0.46	2.41	2.85	2.00	3.80

Intermediate Phalanx III Mediolateral Midshaft Breadth

Taxon	N	Mean	SD	95% CI		Range	
Pan	71	9.81	1.17	9.54	10.09	7.65	12.97
Gorilla	76	13.74	2.18	13.24	14.24	9.95	17.63
Pongo	40	9.53	1.62	9.01	10.05	5.80	13.55
Homo	37	8.75	1.01	8.41	9.08	7.28	11.12
Hylobates	12	6.33	1.11	5.63	7.04	4.80	8.30
Papio	34	5.49	0.76	5.23	5.76	4.25	7.50
Macaca	19	4.49	0.74	4.13	4.85	3.40	5.90

Intermediate Phalanx III Dorsopalmar Basal Height

Taxon	N	Mean	SD	95% CI		Range	
Pan	69	11.35	1.26	11.04	11.65	8.59	14.19
Gorilla	75	13.25	1.64	12.87	13.63	10.41	17.38
Pongo	40	11.71	1.89	11.11	12.32	4.20	17.64
Homo	37	9.82	0.74	9.57	10.07	8.33	10.93
Hylobates	12	6.70	0.72	6.25	7.16	5.60	7.70
Papio	34	5.66	0.68	5.42	5.90	4.82	8.10
Macaca	19	4.88	0.71	4.54	5.22	3.60	6.70

Intermediate Phalanx III Mediolateral Basal Breadth

Taxon	N	Mean	SD	95% CI		Range	
Pan	69	14.85	1.28	14.54	15.16	11.81	17.19
Gorilla	75	18.71	2.40	18.16	19.26	14.81	24.82
Pongo	40	14.62	2.33	13.88	15.37	5.30	18.50
Homo	37	13.68	1.21	13.28	14.08	11.56	15.92
Hylobates	12	8.19	1.13	7.48	8.91	6.80	10.10
Papio	34	8.05	0.91	7.73	8.36	6.93	11.50
Macaca	19	6.62	0.75	6.25	6.98	5.30	7.90

Distal Phalanx I Length

Taxon	N	Mean	SD	95% CI		Range	
Pan	13	18.14	1.76	17.08	19.20	14.70	21.51
Gorilla	14	19.29	1.67	18.33	20.25	16.35	22.48
Pongo	15	15.13	2.17	13.93	16.34	12.10	18.80
Homo	36	22.81	3.08	21.77	23.85	10.39	26.90
Hylobates	16	10.61	1.20	9.97	11.26	8.43	13.10
Papio	18	7.45	1.05	6.93	7.97	5.70	9.10
Macaca	13	18.14	1.76	17.08	19.20	14.70	21.51

Distal Phalanx I Mediolateral Basal Breadth

Taxon	N	Mean	SD	95% CI		Range	
Pan	6	8.26	1.06	7.15	9.38	6.50	9.40
Gorilla	6	10.94	3.11	7.68	14.21	7.26	15.29
Pongo	9	9.39	1.43	8.29	10.49	7.42	11.60
Homo	21	14.46	1.18	13.93	15.00	12.57	16.98
Hylobates	8	5.29	0.63	4.76	5.81	4.20	5.90
Papio	18	6.01	0.65	5.68	6.33	4.90	6.90
Macaca	6	8.26	1.06	7.15	9.38	6.50	9.40

Distal Phalanx III Length

Taxon	N	Mean	SD	95% CI		Range	
Pan	13	20.51	1.89	19.37	21.65	17.30	23.98
Gorilla	12	19.95	1.95	18.72	21.19	15.64	22.97
Pongo	16	21.30	2.90	19.75	22.84	16.02	26.30
Homo	21	19.10	1.78	18.29	19.92	16.90	23.75
Hylobates	16	13.19	1.73	12.26	14.11	10.00	16.00
Papio	14	10.28	1.61	9.35	11.21	8.60	13.70
Macaca	13	20.51	1.89	19.37	21.65	17.30	23.98

Distal Phalanx III Mediolateral Basal Breadth

Taxon	N	Mean	SD	95% CI		Range	
Pan	6	10.03	1.03	8.95	11.11	8.60	11.19
Gorilla	5	12.41	1.09	11.06	13.76	11.25	13.60
Pongo	7	10.82	1.40	9.53	12.12	8.87	12.60
Homo	6	11.33	1.03	10.25	12.41	10.13	12.31
Hylobates	8	5.60	0.82	4.92	6.28	4.20	6.50
Papio	14	5.40	0.92	4.87	5.93	3.90	7.00
Macaca	46	8.40	3.06	7.49	9.31	3.90	13.60

Chapter 3

Hispanopithecus laietanus: The first steps towards the orangutan suspensory behaviors

based on:

Almécija S, Alba DM, Moyà-Solà S, Köhler M (2007). Orang-like manual adaptations in the fossil hominoid *Hispanopithecus laietanus*: First steps towards great ape suspensory behaviours. *Proceedings of the Royal Society B* 274: 2375-2384.

Chapter 3

Hispanopithecus laietanus: The first steps towards the orangutan suspensory behaviors

INTRODUCTION

Ape hands reflect a compromise between manipulative and locomotor selection pressures, albeit more closely resembling the 'true hands' of humans than the 'foot-hands' of other primates (Napier 1993). Besides differences in carpal, metacarpal and phalangeal morphology, the hands of extant apes and humans significantly differ in proportions. Human hands are shorter and display relatively longer thumbs, presumably due to the removal of locomotor selection pressures with the advent of bipedalism (Alba *et al*. 2003). The morphology and proportions of the fossil hand bones from the stem ape *Proconsul* (Napier and Davis 1959; Begun *et al.* 1994), interpreted as a palmigrade quadruped with powerful grasping abilities (Ward 1993), indicate that a short hand with a relatively long thumb is the primitive condition from which the elongated hands of the orthograde living apes must have evolved. Postcranial remains of *Pierolapithecus* (Moyà-Solà *et al.* 2004, 2005), which already lacks ulnocarpal articulation, permit to infer an orthograde bodyplan in spite of the lack of suspensory adaptations (Moyà-Solà *et al.* 2005). This taxon, interpreted as a stem great ape on the basis of cranial anatomy (it combines a derived great-ape facial pattern with a primitive, more prognathic profile with low and posterior glabella; Moyà-Solà *et al.* 2004), therefore indicates that a combination of orthograde climbing and pronograde palmigrady is likely to be ancestral for hominoids as a whole. While this suggests that suspensory adaptations are homoplastic between hylobatids and hominids (Moyà-Solà *et al.* 2004, 2005), the question remains as to whether they are homologous at least between orangutans and African apes.

The postcranial remains of the fossil great ape *Hispanopithecus laietanus* Villalta and Crusafont, 1944 (Primates, Hominidae) from Can Llobateres (late Miocene, MN10, ca. 9.5 Ma, Moyà-Solà and Köhler 1996; Köhler *et al.* 2001) permit testing of this hypothesis. This taxon, variously interpreted as an early pongine (Köhler *et al.* 2001;

Moyà-Solà and Köhler 1993, 1995) or hominine (Begun *et al.* 1997), represents the first evidence of an orthograde bodyplan with suspensory adaptations in the hominoid fossil record. Here we focus on morphological and morphometric analyses of the *H. laietanus* partial hand from Can Llobateres, in order to infer the positional repertoire of this taxon. This is the first time that *Hispanopithecus* (or *Dryopithecus* s.l.) metacarpals and complete proximal phalanges are described in detail and interpreted from a functional and evolutionary viewpoint.

Figure 3.1. Reconstruction of the *H. laietanus* partial hand IPS18800 from Can Llobateres 2, in dorsal (**A**) and palmar (**B**) view.

MATERIALS AND METHODS

Measurements and comparative sample

Maximum length and transverse (mediolateral and dorsopalmar) diameters of both metacarpals and phalanges (proximal and intermediate or middle) were measured at the base, midshaft and head/trochlea to the nearest 0.1 mm in both *Hispanopithecus* and the extant comparative sample. Other investigators have employed all these measurements previously (e.g. Inouye 1992; see also Appendix 3.1 for a detailed explanation). Curvature (in degrees) was computed using the included angle method (Jungers *et al.* 1997). Adult body mass (in kg) for individual specimens, taken from museum records, was also employed for the comparative sample. This sample included individuals from the following genera: *Pan* (both *Pan paniscus* and *Pan troglodytes*); *Gorilla* (both *Gorilla gorilla* and *Gorilla beringei*); *Pongo* (including the two extant subspecies); *Homo* (i.e. *Homo sapiens*); and *Papio* (*Papio cynocephalus*).

Statistical techniques

When comparing the relationship between two given metrical variables (y and x) across a broad sample of taxa differing in size, size-scaling effects must be taken into account by computing variables of relative size. In many instances, simple shape ratios (y/x) or bivariate comparisons (y versus x) do not adequately reflect relative size, because in many instances different variables tend to vary allometrically (according to a nonlinear relationship) instead of isometrically (in a directly proportional way). Allometric variation can be depicted using the so-called allometric equation $y = b \cdot x^k$ (Gould 1966; Klingenberg 1998), which is often logarithmically transformed ($\ln y = \ln b + k \cdot \ln x$), in order to linearize the relationship between the two variables being compared. In this paper, allometric regressions, computed by means of linear regression with ln-transformed data, were employed for removing size-scaling effects when comparing different taxa. The term ‘allometric regression’ is hence employed throughout the paper to refer to ‘linear regression on the basis of ln-transformed data’. Natural logarithms (ln) were used for transforming the raw measurements, whereas least-squares linear regression was employed as the line-fitting method. Static, mixed-sex adult allometry was employed in all instances for each living genus separately.

Manual proportions and robusticity of the long bones of the hand were assessed by means of bivariate allometric comparisons and multivariate discriminant (canonical) analyses. Multivariate analyses included measurements from all the manual rays for which *Hispanopithecus* measurements or reliable estimations are available (Table 3.1) except for distal phalanges (which are of uncertain attribution). Bivariate comparisons were restricted to manual ray IV, although similar results would be obtained for other rays. Intrinsic manual ray proportions were assessed by means of an allometric regression of phalangeal length (proximal + intermediate phalanges) versus metacarpal length. Robusticity of metacarpal and proximal phalanx was evaluated by means of separate allometric regressions of base and head/trochlea area (computed as the product between the mediolateral width and the dorsopalmar height) versus bone length. Finally, relative lengths of metacarpal and proximal phalanx were calculated by means of separate allometric regressions of bone length versus body mass.

With regard to multivariate analyses, manual overall proportions were assessed by means of a discriminant analysis of bone lengths, whereas metacarpal and phalangeal robusticity was evaluated on the basis of two different analyses including bone length as well as transverse diameters. *Hispanopithecus* was classified on the basis of Mahalanobis distances to group centroids, whereas cluster diagrams were plotted using Euclidean distances on the basis of group centroids and the *Hispanopithecus* discriminant scores for all four available discriminant functions. Statistical computations were made by means of the statistical package SPSS v. 14.0, and graphics were plotted using EXCEL 2000 and PAST v. 1.54.

RESULTS

Reconstruction and morphological description

The reconstruction of the partial hand IPS18800 from Can Llobateres 2 is depicted in Figure 3.1 (see Table 3.1 for measurements), except for five associated sesamoids (not figured). The morphology of the fourth proximal phalanx, as compared to *Sivapithecus*, *Pongo*, among other taxa, is further depicted in greater detail in Figure 3.2, whereas the morphology of the fourth metacarpal is depicted in Figure 3.3. All the manual remains of IPS18800 were found associated but non-articulated with one another in a very restricted space of ca. 0.02 m^2, with no repeated elements, so that we can be confident that the remains belong to the right hand of a single individual. There is more scatter with regard to the cranium IPS18000 and the other postcranial bones of IPS18800 due to carnivore activity. However, given the lack of repeated postcranial elements, it is reasonable to assume that all these remains belong to the same adult male individual.

Figure 3.2. Proximal and ulnar views of the fourth proximal phalanx in selected fossil and extant taxa: (**A**) *Papio* sp.; (**B**) *Sivapithecus*; (**C**) *Hispanopithecus*; (**D**) *Pongo*; (**E**) *Pan*; (**F**) *Gorilla*. All the depicted specimens come from the right side (the *Sivapithecus* one being a mirror-image of a cast from the left side).

Table 3.1. Measurements of the several hand bones (metacarpals and phalanges) of the *H. laietanus* IPS18800 partial hand from Can Llobateres. All measurements are given in millimeters (mm). Values between parentheses are estimates.

	MC2	**MC3**[1]	**MC4**	**MC5**[1]	**PP2**[2]	**PP3**	**PP4**	**PP5**[3]	**MP2**	**MP3**[4]	**MP4**[5]	**MP5**	**DP2**	**DP4**	**DP5**[6]
L	75.2	(72.7)	65.5	--	(53.2)	59.6	62.7	(49.6)	31.4	40.0	(41.3)	33.6	16.0	19.1	16.6
BML	12.6	11.4	10.8	11.0	(13.0)	13.3	14.1	12.4	11.3	14.3	13.1	12.1	8.4	9.3	8.1
BDP	14.9	13.4	13.0	11.0	(10.1)	11.9	12.0	10.3	8.3	9.3	10.9	9.0	6.1	6.6	(5.9)
MSML	7.3	(8.6)	7.8	(7.4)	(11.0)	11.7	11.5	(10.4)	8.5	9.6	9.7	9.4	3.5	4.5	3.6
MSDP	6.6	(8.5)	(7.5)	(6.5)	(6.3)	7.3	7.3	(5.9)	4.8	5.7	7.0	5.3	3.8	3.9	3.5
HML	12.5	--	12.1	--	9.0	9.6	9.8	--	7.8	(9.3)	9.2	8.4	4.1	5.5	4.6
HDP	13.5	--	15.3	--	7.6	7.8	8.2	--	5.7	6.3	6.0	5.5	3.7	3.8	3.5

[1]Metacarpal head lacking; [2]Lacking a small fraction of the proximal articular facet; [3]Trochlear area missing; [4]Lacking most of the ulnar part of the trochlea; [5]Some fragments of the central diaphysis missing; [6]Lacking a fragment of the base at the palmar side. Abbreviations: MC=metacarpal, PP=proximal phalanx, MP=middle phalanx, L=length, B=base, MS=midshaft, H=head (in metacarpals)/trochlea (in phalanges), ML=mediolateral breadth, DP=dorsopalmar height.)

In this partial hand, all manual digits but the first one are more or less completely preserved. The fourth metacarpal is broken into two fragments (Figures 3.1 and 3.3), which cannot be glued together due to sediment infilling and minimal distortion. However, no fragment of diaphysis is lacking, so that metacarpal length can be readily measured. The reconstruction employed here differs from the previous one (Moyà-Solà and Köhler 1996; Moyà-Solà *et al.* 1999) by discarding putative thumb fragments and by the new ray assignment of the third and fourth proximal phalanges. In the new reconstruction, the fourth proximal phalanx is longer than the third one, as is common among extant orangutans (especially males, Susman 1979). As noted by the latter author, "when proximal phalanx IV exceeds III in length, the former bone is also more asymmetrical. In this case the third phalanx takes on a pattern normally seen in II", although "the overall robusticity of proximal phalanx III is still greater than that of IV" (Susman 1979, p. 225). Accordingly, the manual ray attributions of the third and fourth proximal phalanges employed here are justified by several lines of evidence, including: (1) the congruence between articular facets of fourth metacarpal and fourth proximal phalanx; (2) by the greater shaft robusticity of third vs. fourth proximal phalanx (143% vs. 133%), according to Susman's criterion (Susman 1979, footnote 2); and (3) the greater development of the radial side of the base in the third proximal phalanx (where the second dorsal interosseous insert) and the ulnarly-favored basal asymmetry in the fourth one (displaying a more protruding ulnar tubercle for insertion of the fourth interosseous; Figures 3.1, 3.2 and 3.4). In spite of these compelling anatomical arguments, in order to avoid any potential bias due to manual ray assignment of proximal phalanges III and IV, statistical comparisons were carried out by taking into account the two possible assignments.

Table 3.2. Main results from the three discriminant analyses, including centroids of extant taxa and discriminant scores for *Hispanopithecus*. Sample size is N=72, 88 and 72 (*Pan*), N=81, 140 and 56 (*Gorilla*), N=39, 34 and 29 (*Pongo*), N=35, 49 and 24 (*Homo*), and N=29 (*Papio*). Abbreviations: CA=Canonical axis (discriminant function).

	overall proportions				**metacarpal robusticity**				**phalangeal robusticity**			
	CA1	**CA2**	**CA3**	**CA4**	**CA1**	**CA2**	**CA3**	**CA4**	**CA1**	**CA2**	**CA3**	**CA4**
eigenvalue	8.447	5.302	3.008	0.523	8.655	6.351	1.929	1.618	17.65	11.542	4.752	3.8
% of Variance	48.9	30.7	17.4	3.0	46.7	34.2	10.4	8.7	46.8	30.6	12.6	10.1
cumulative %	48.9	79.6	97.0	100.0	46.7	80.9	91.3	100.0	46.8	77.3	89.9	100.0
canonical corr.	0.946	0.917	0.866	0.586	0.947	0.929	0.812	0.786	0.973	0.959	0.909	0.890
Pan	-0.906	2.351	1.562	-0.539	1.768	-1.349	0.310	-1.854	-1.025	2.699	-1.577	1.580
Gorilla	0.285	-0.682	0.706	0.985	1.068	2.529	-0.444	0.519	0.022	2.469	1.524	-2.517
Pongo	5.769	-1.709	-0.566	-0.670	3.013	-4.704	1.149	2.430	9.649	-2.950	-0.384	0.353
Human	-1.117	2.367	-3.858	0.142	-5.671	0.403	2.017	0.057	-3.049	-3.181	4.537	2.637
Papio	-4.959	-4.492	-0.432	-0.684	-4.473	-3.281	-3.552	0.172	-4.622	-5.886	-2.398	-1.597
Hispanopithecus	4.080	0.047	-3.945	-1.254	-1.718	-2.334	-1.281	-0.245	5.681	-5.041	-3.249	1.991

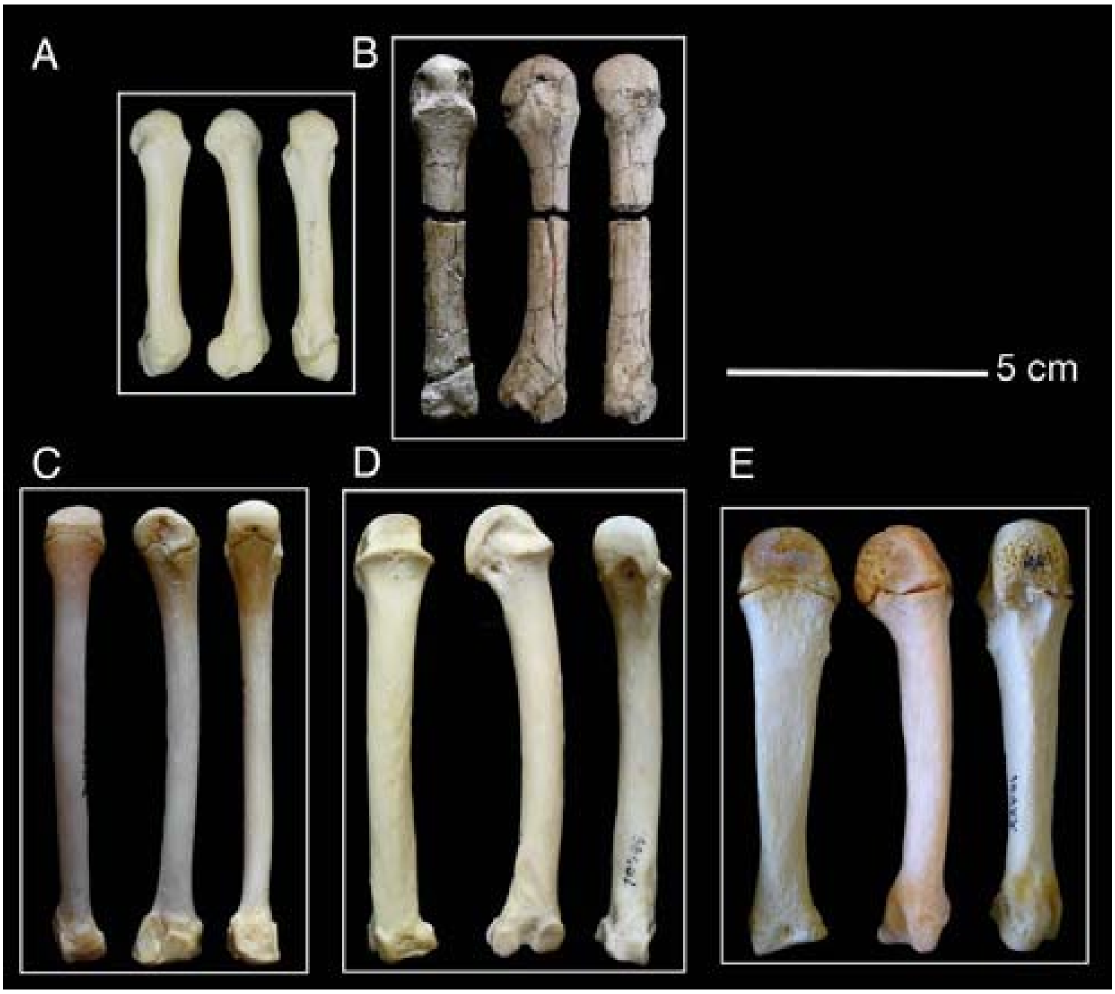


Figure 3.3. Dorsal, radial and palmar views of the fourth metacarpal in selected fossil and extant taxa: (**A**) *Papio* sp.; (**B**) *Hispanopithecus*; (**C**) *Pongo*; (**D**) *Pan*; (**E**) *Gorilla*.

The functionally most relevant morphological features of the *Hispanopithecus* partial hand are described below. The metacarpals are short and stout (Figures 3.1 and 3.3), with subcircular (nearly circular) diaphyseal cross-sections and without strong muscular impressions. The pits for the attachment of the collateral ligaments are well-developed and very dorsally-placed, causing a marked dorsal constriction of the metacarpal head unlike that of any extant great ape (Lewis 1977; Susman 1979). In contrast, metacarpal heads do resemble extant great apes in being smooth (non-fluted), i.e. with no trace of palmar grooves (Lewis 1977). Unlike the metacarpals, the proximal phalanges are long, slender and very curved (Figures 3.1 and 3.2), with an average included angle of 73º (69º the second, 78º the third, and 71º the fourth), which is higher than in *Hylobates* and *Ateles* (around 50-60º), but fully comparable to *Pongo* (around 75º) (Jungers *et al.* 1997; Richmond and Whalen 2001). Moreover, articular surfaces on the bases of the proximal phalanges are laterally restricted and almost circular (Figure 3.2), more closely resembling those of orangutans, albeit extending slightly at the midline onto the dorsal aspect of the shaft (Figures 3.2 and 3.4). In contrast, these articular facets are laterally- and palmarly-surrounded by well-defined ridges (Figure 3.2), with expanded areas for the insertion of the collateral ligaments and interossei muscles. The proximal phalanges further display strongly developed palmar tubercles, and distally positioned, strong flexor sheath ridges that are laterally and even palmarly expanded (causing a palmar concavity; Figures 3.1 and 3.4). Distally, articular surfaces of proximal phalanges are relatively small, albeit with well-developed pits for the collateral ligaments of the proximal interphalangeal joint (Figures 3.2 and 3.4). The trochleae are high and palmarly-bent (Figures 3.2 and 3.4), with a deep and narrow trochlear groove. Intermediate phalanges also display strong muscular impressions, with deep insertions for the superficial flexors (producing developed ridges at the proximal half of the shaft), and laterally and palmarly voluminous areas for the attachment of collateral ligaments and other interphalangeal joint structures (Figure 3.4). Trochleae, on the other side, are relatively small, with conspicuous muscular insertions at the distal part of the shaft on the palmar side only (Figure 3.4). The curvature of the intermediate phalanges is particularly marked at the distal shaft, causing a palmarly-bent trochlea (Figure 3.4). Finally, distal phalanges are different from those of extant hominoids by several features, including larger palmar lips as compared with dorsal ones (Figure 3.4), so that the articular surface does not face palmarly as in living forms (Begun *et al.* 1994).

Morphometric comparisons

Descriptive statistics for the extant comparative sample have been reported in Appendix 3.2. Three different discriminant (canonical) analyses were performed with extant hominid genera and baboons (Table 3.2 and Figures 3.5 and 3.6; see also Appendix 3.3), in order to evaluate, on the basis of the long bones of the hand, overall manual proportions (only length measurements included), as well as hand robusticity (separately for metacarpals and phalanges, and including both length and transverse diameters). These analyses discriminate very well among the extant genera (98% of original cases correctly classified). On the basis of overall manual proportions, *Hispanopithecus* is classified as an orangutan, irrespective of ray assignment of third and fourth proximal phalanges. When metacarpal robusticity is taken into account, *Hispanopithecus* fails to cluster with orangutans, showing instead a greater similarity with baboons. In contrast, as far as phalangeal robusticity is concerned, *Hispanopithecus* is classified again with orangutans. This holds even when third and fourth proximal phalanges are taken for one another, and indicates that, in spite of overall manual proportions resembling orangutans, the long bones of the hand of *Hispanopithecus* are not completely orang-like. Its greatest similarities with *Pongo* lie on the phalangeal region, whereas the metacarpals still retain primitive proportions.

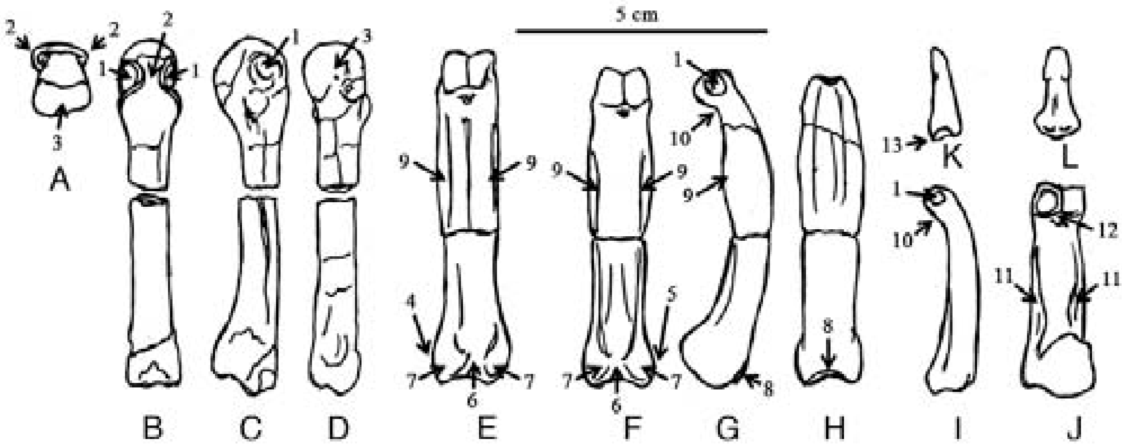


Figure 3.4. Line drawing of selected bones from the *H. laietanus* partial hand IPS18800 from Can Llobateres, showing the main anatomical features discussed in the text: (**A**) fourth metacarpal in distal, (**B**) dorsal, (**C**) radial and (**D**) palmar views, (**E**) fourth proximal phalanx in palmar view, (**F**) third proximal phalanx in palmar, (**G**) radial and (**H**) dorsal views, third intermediate phalanx in (**I**) radial and (**J**) palmar views, possible fourth distal phalanx in (**K**) radial and (**L**) palmar views. Characters: 1, enlarged pits for the collateral ligaments; 2, marked dorsal constriction of metacarpal heads; 3, smooth palmar surface of metacarpal heads; 4, enlarged ulnar tubercle; 5, protruding radial tubercle; 6, deep groove for channeling the long flexor tendons; 7, well-developed palmar tubercles; 8, dorsal extension of the proximal articular surface; 9, strong and distally positioned flexor sheath ridges; 10, palmarly bent trochlea; 11, well-developed insertions for the superficial flexors; 12, conspicuous muscular insertions at the palmar side only; 13, larger palmar lips.

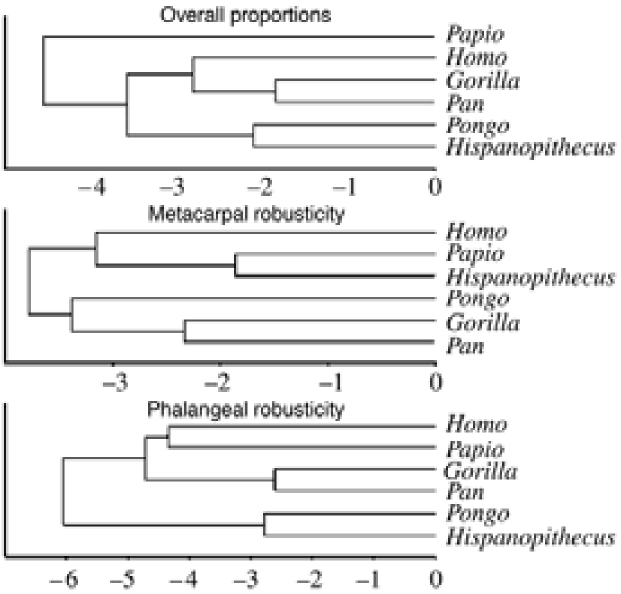


Figure 3.5. Results of the three discriminant analyses, displayed by means of UPGMA clusters based on Euclidean distances computed from group centroids (extant genera) and discriminant scores (*Hispanopithecus*) for the four canonical axes (see Table 3.2).

With regard to allometric bivariate comparisons (regressions reported in Appendix 3.4), when the intrinsic manual ray proportions are taken into account (Figure 3.7), baboons display shorter phalanges relative to metacarpals than hominids, but orangutans differ from African apes (and humans) by displaying even longer phalanges, not only on absolute terms, but also at equal metacarpal lengths. *Hispanopithecus* clearly departs from the hominine regression, but displays a position that would be expected for an orangutan with absolutely shorter metacarpals, irrespective of the attribution of third and fourth proximal phalanges. This indicates that the former taxon also displays long phalanges relative to the metacarpals. With regard to metacarpal and phalangeal robusticity (Figure 3.8), gorillas are always the most robust great apes and orangutans the least. Interestingly, *Hispanopithecus* displays a different pattern for metacarpals and phalanges, with the former being considerably robust (similar to African apes), but phalanges being comparatively very slender (fully comparable to those of orangutans, which holds irrespective of manual ray attribution of third and fourth proximal phalanges). Finally, when bone length relative to body mass is evaluated (Figure 3.9), the same patterns are obtained for metacarpals and phalanges: humans display the relatively shortest manual rays and orangutans the longest, with African apes displaying intermediate values. Relative metacarpal and phalangeal length in *Hispanopithecus* can be evaluated by taking into account published estimates of body mass in this taxon (Moyà-Solà and Köhler, 1996, their Table 1). Four different estimates, ranging from 30 to 37 kg (mean value, 34 kg) were derived by Moyà-Solà and Köhler (1996) on the basis of postcranial measurements of the femur, tibia and lumbar vertebrae, which are directly related to weight-bearing and therefore display a high correlation with body mass. Interestingly, *Hispanopithecus* displays a remarkably different pattern in metacarpals as compared to phalanges: whereas relative metacarpal length is very low (lower than in all extant great apes, gorillas included), proximal phalanx length relative to body mass is very high (almost in the range of female orangutans in both relative and absolute grounds). These results do not significantly vary when uncertainty in body mass estimation is taken into account (Figure 3.9), and hold irrespective of manual ray assignment of third and fourth proximal phalanges.

DISCUSSION

Functional interpretation

Several morphological features of the *Hispanopithecus* long bones of the hand indicate powerful grasping capabilities. Thus, the strong flexor sheath ridges along the shafts of proximal and intermediate phalanges result from the presence of powerful flexors, which is further confirmed by the presence of strongly developed tubercles at the base of proximal phalanges. These tubercles would have reinforced the deep groove of the figrocartilaginous glenoid plate that channels the long flexor tendons along the base of the proximal phalanges, in their course from the metacarpophalangeal joint to the flexor sheaths (Susman 1979), thus preventing them from dislocation (Rose 1986; Nakatsukasa *et al.* 2003). This contrasts with the smooth palmar surface of the metacarpal heads, which indicates that, if present at all, periarticular sesamoids would have only minimally contributed to the thickening of the lateral margins of the glenoid plate for providing additional channeling of the powerful flexors during extreme extension (Lewis 1977). This permits to infer that dorsiflexed postures at the metacarpophalangeal joint would not have been so hyperextended as in committed palmigrade and digitigrade terrestrial forms, where large sesamoids are regularly present, in association with a well-developed fluting of the metacarpal heads. In contrast to the smooth palmar surface, the metacarpal heads of *Hispanopithecus* displays a marked dorsal constriction. A similar constriction is present, albeit to a lesser extent, in *Nacholapithecus*, *Proconsul* and some cebids such as *Alouatta* (Rose *et al.* 1996), in which the general morphology of the metacarpal head has been related to “grasping hand use during predominantly pronograde quadrupedal activities” (Rose *et al*. 1996, p. 10). The latter authors interpret the dorsal origin of the collateral ligaments as permitting an increased range of abduction-adduction and/or axial rotation at the metacarpophalangeal joint, albeit without compromising stability by becoming taut at flexed postures. The pronounced dorsal constriction of the *Hispanopithecus* metacarpal heads, however, probably results, at least in part, from the great development of the pits for insertion of the collateral ligaments of the metacarpophalangeal joint. According to Begun *et al.* (1994), well-developed insertion areas for the collateral ligaments at the metacarpophalangeal and interphalangeal joints would reflect the great significance of transversely-oriented (mediolateral) bending stresses. These stresses might have been huge in a form such as *Hispanopithecus,* with relatively short metacarpals but very long phalanges, due to the unique combination of palmigrady and suspension (see later). Moreover, since the collateral ligaments of the metacarpophalangeal joints become taut at flexed postures, the large and dorsally-positioned pits for their insertion at the metacarpal heads would have ensured enhanced resistance against lateral stresses during climbing and/or suspension, further providing a secure and powerful grasp during palmigrade quadrupedalism.

The significance of palmigrady in *Hispanopithecus* is confirmed by the dorsal extension of the proximal articular facets of the proximal phalanges and by the length and robusticity of the metacarpals, which unlike phalanges are quite robust and relatively shorter than in extant great apes. The robusticity of metacarpals depends to a large extent on their length relative to body mass, those of orangutans being the longest and the least robust, since they do not habitually support weight-bearing compressive stresses. On the contrary, the short and stout metacarpals of *Hispanopithecus* are indicative of palmigrade quadrupedalism, most closely resembling those of stem hominoids such as *Proconsul*. The proximal articular facets on the proximal phalanges of *Hispanopithecus*, albeit somewhat elliptical (broader than higher), display a more circular contour than those of middle-sized *Sivapithecus* (Rose 1986), thus more closely resembling orangutans (Figure 3.2). The relatively wider proximal articular facet, together with its greater dorsal extension, suggest a higher significance of palmigrady at the expense of suspensory behaviors in *Sivapithecus*. In the cluster analysis of overall manual proportions on the basis of discriminant functions, *Hispanopithecus* clusters with orangutans, and these two taxa further resemble each other by the great degree of phalangeal elongation relative to metacarpals. When body mass is taken into account, *Hispanopithecus* only resemble orangutans by the relative length of the phalanges, whereas the metacarpals are remarkably short, which explains why the length of phalanges relative to metacarpals is even greater in *Hispanopithecus*. This further explains the different patterns of metacarpal and phalangeal robusticity displayed by *Hispanopithecus* in both multivariate and bivariate comparisons. The pronounced orang-like slenderness of the *Hispanopithecus* phalanges is thus attributable to the high degree of phalangeal elongation, most similar to that of orangutans when allometric comparisons are taken into account. This must be interpreted as a feature functionally related to orthograde suspensory behaviors such as arm-hanging and swinging, which can be also inferred from the palmar concavity on the shafts and tall trochleae of proximal phalanges (Begun 1993).

Suspension is further indicated by a degree of phalangeal curvature that is higher than in *Sivapithecus* (around 50º: Richmond and Whalen 2001), but fully comparable to extant orangutans. If our ray attribution of the phalanges if correct, *Hispanopithecus* also displays a fourth proximal phalanx longer than the third one, indicating an orang-like ulnar shift of the main axis of the hand, which has been related to grasping vertical supports during climbing (Susman 1979), and might merely reflect a high commitment to arboreality in this relatively large-bodied taxon. Strong muscular insertions on the intermediate phalanges just proximal to the trochlea are restricted to the palmar side of the shaft, unlike in *Nacholapithecus*, where both palmar and dorsal insertions are present (Nakatsukasa *et al*. 2003), suggesting a higher emphasis on flexion over extension in *Hispanopithecus*. This, combined with the considerable length and curvature of the phalanges, and the relatively small but palmarly-bent trochleae of the intermediate phalanges, suggests that this taxon would have displayed an orang-like double-locking mechanism. When the hand is held in a double-locked position in orangutans, the tips of the fingers are tucked into the skin-fold present where the finger meets the palm, so that with further flexion, the locked fingers are rolling into the palm, thus permitting to securely grasp slender vertical supports (Napier 1993, p. 27 and his Figures 10 and 11; see also Napier, 1960, p. 651 and his Figure 3b and his Figure 3 in Plate I).

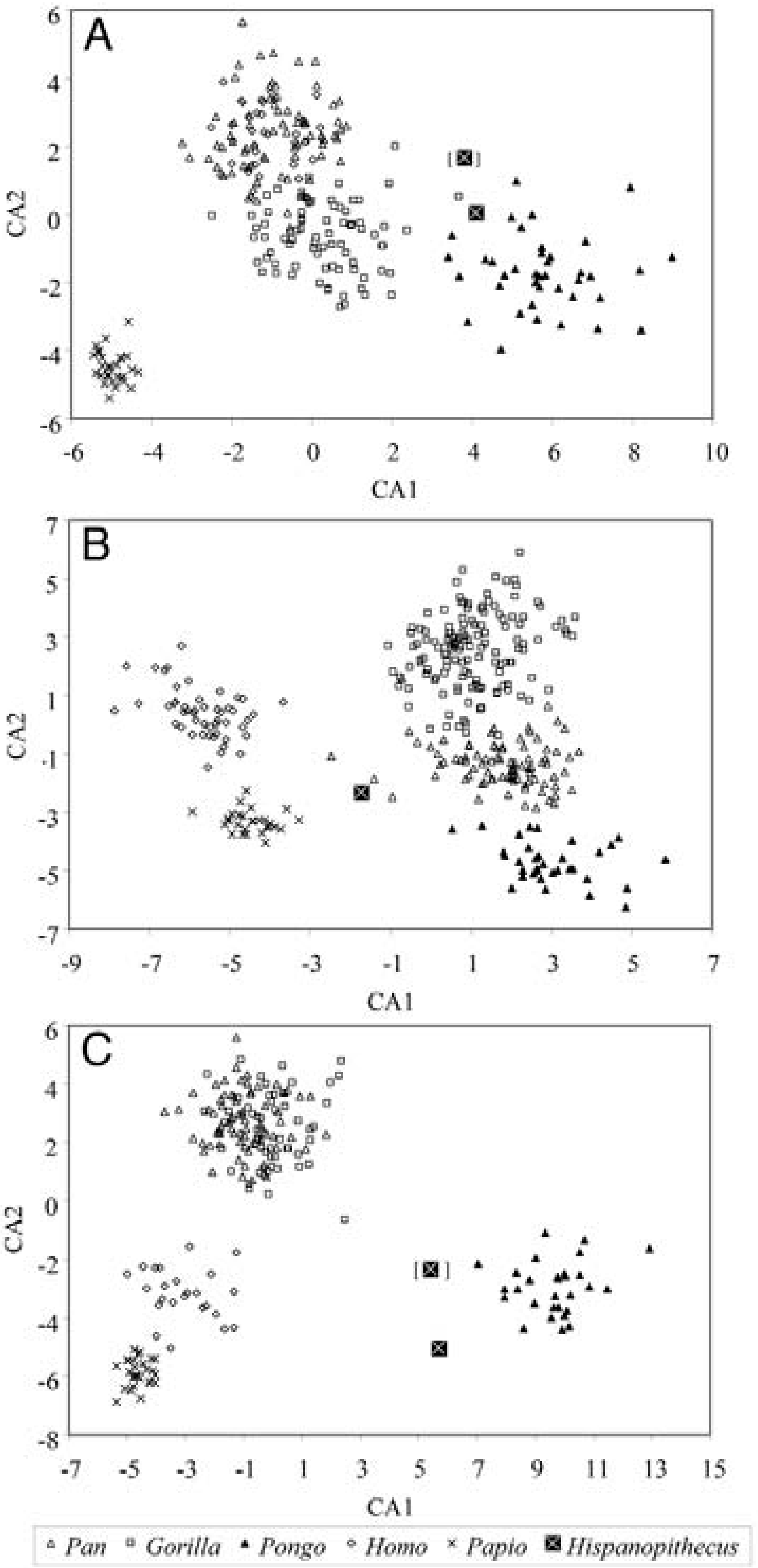


Figure 3.6. Bivariate plot of second vs. first canonical axes (discriminant functions) for the three discriminant analyses: (**A**) Overall manual proportions; (**B**) Metacarpal robusticity; and (**C**) Phalangeal robusticity. The results for *Hispanopithecus* by interchanging third and fourth proximal phalanges are displayed within brackets.

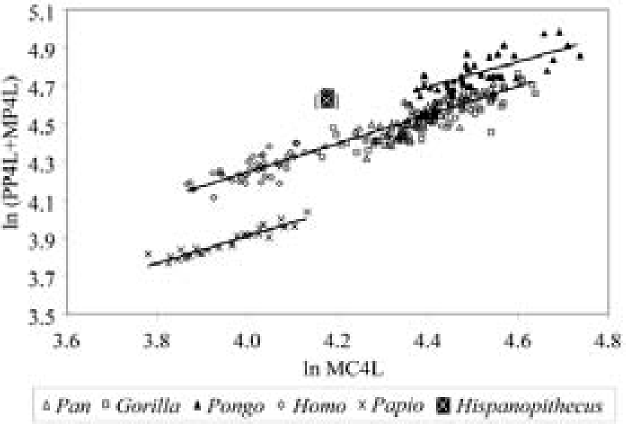


Figure 3.7. Intrinsic manual ray IV proportions displayed as an allometric bivariate plot of phalangeal vs. metacarpal length in hominines, orangutans and baboons. The results for Hispanopithecus by interchanging third and fourth proximal phalanges are displayed within brackets. Abbreviations: MC=Metacarpal; PP=Proximal phalanx; MP=Intermediate phalanx; L=Length.

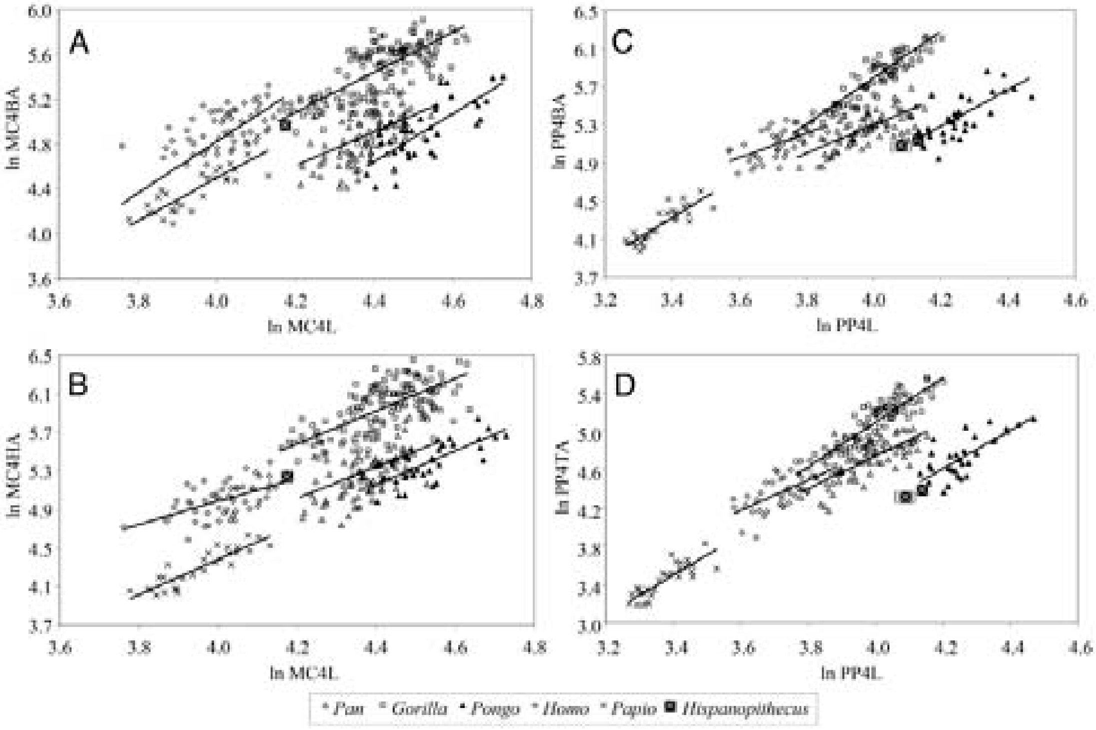


Figure 3.8. Robusticity of metacarpal and proximal phalanx IV displayed as allometric bivariate plots of articular area vs. bone length in extant hominids and baboons: (**A**) Robusticity of metacarpal base; (**B**) Robusticity of metacarpal head; (**C**) Robusticity of proximal phalanx base; (**D**) Robusticity of proximal phalanx trochlea. The results for *Hispanopithecus* by interchanging third and fourth proximal phalanges are displayed within brackets. Abbreviations: MC=Metacarpal; PP=Proximal phalanx; B=Base; H=Head; T=Trochlea; L=Length; A=Area.

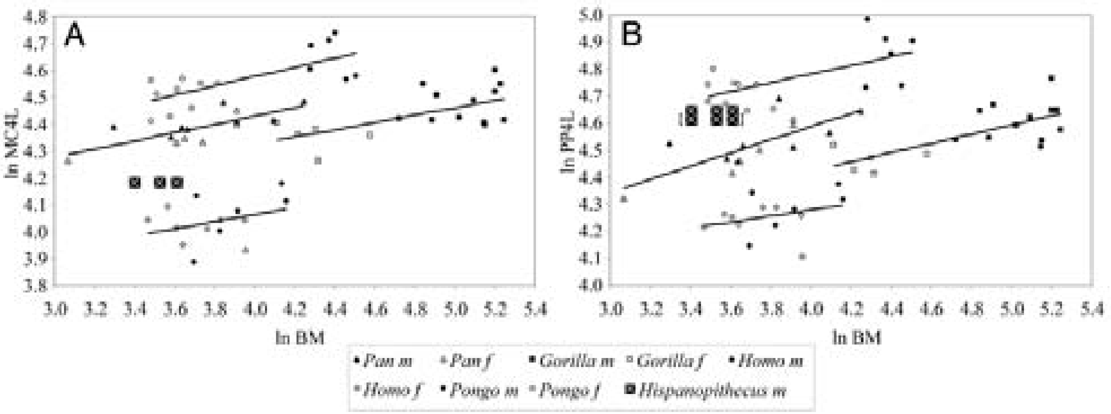


Figure 3.9. Relative metacarpal and phalangeal length in manual ray IV, displayed as allometric bivariate plots of bone length vs. body mass in extant hominids and baboons: (**A**) Relative metacarpal length; and (**B**) Relative proximal phalanx length. The several points corresponding to *Hispanopithecus* do not represent different individuals, but different size estimates. The results for *Hispanopithecus* by interchanging third and fourth proximal phalanges are displayed within brackets. Black symbols: males; open symbols: females. Abbreviations: MC=Metacarpal; PP=Proximal phalanx; BM = Body mass.

Paleobiological reconstruction and evolutionary inferences

The partial hand of *H. laietanus* displays a combination of two sets of features that cannot be found in any living or known fossil catarrhine: (1) the short and stout metacarpals, with a generalized catarrhine morphology, which are indicative of palmigrady on horizontal supports; and (2) the elongated, curved and slender phalanges, which together with other characters indicate suspensory behaviors. Our results hence allow us to infer that *Hispanopithecus* displayed a unique locomotor repertoire, combining vertical climbing with both suspensory orthograde behaviors and some kind of pronograde palmigrady with powerful-grasping capabilities. Orangutans employ an enormous diversity of different positional modes: vertical climbing and suspensory orthograde behaviors are most frequent, but they also occasionally use above-branch quadrupedalism (as do *Pan* spp.) and, uniquely among extant apes, pronograde suspensory positional behavior (in particular, torso-pronograde suspensory locomotion) (Thorpe and Crompton 2006; see their Appendices A and B for further details on pronograde suspensory behaviors in orangutans). *Hispanopithecus* would presumably have displayed a similarly diverse positional repertoire, already employing suspensory behaviors (such as clambering) for travelling and feeding on slender branches, but with a much greater emphasis on above-branch pronograde quadrupedalism (at the expense of arm-swinging) when moving through horizontal or slightly inclined arboreal supports. Powerful-grasping palmigrady would have been employed in the case of moderately large branches, whereas a more standard palmigrady (with no assistance from the thumb, albeit with markedly ulnarly-deviated hand postures) would have been performed on larger ones.

While the elongated and slender phalanges of *Hispanopithecus* are best interpreted as derived characters, the short and stout metacarpals are most probably a primitive retention. A priori, phalangeal lengthening seems most important for suspensory behaviors (being essential for the hook grasp and the double-locking mechanism), but metacarpal lengthening would be further advantageous. This indicates that the retention of short and stout metacarpals in *Hispanopithecus* must be also functionally interpreted, resulting from the action of some additional selection pressure, related to palmigrady, that would be acting against the lengthening of the palm. The hand anatomy of *Hispanopithecus* thus reflects a functional compromise between the biomechanical demands of suspensory and quadrupedal behaviors, which are the two dominant locomotor modes that can be inferred for this taxon.

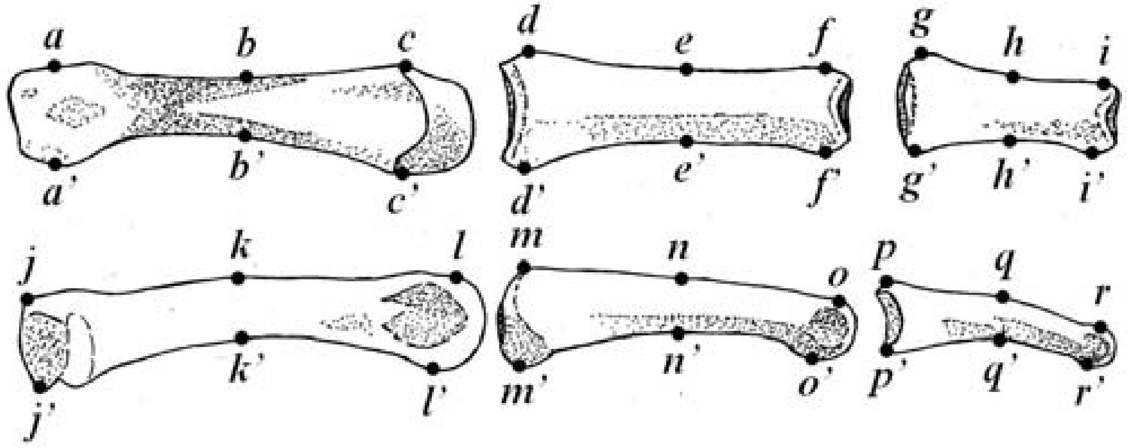
Whether the reported phalangeal similarities to orangutans are synapomorphic or homoplastic is difficult to determine, given current uncertainties on the phylogenetic position of *Hispanopithecus* and the scarcity of fossil hominoid postcranial remains. Several workers have previously stressed the preponderant role of homoplasy in hominoid evolution (Larson 1998; Young 2003), with most similarities found between the brachiating atelines and hylobatids with the exclusion of great apes (Young 2003). The documented manual similarities of *Hispanopithecus* with extant orangutans, even including an ulnar shift of the main axis of the hand, support previous proposals that this taxon is an early member of the *Pongo*-clade (Moyà-Solà and Köhler 1993, 1995, 1996; Köhler *et al.* 2001). However, even if *Hispanopithecus* is alternatively interpreted as an early hominine (Begun *et al.* 1997), its hand morphology indicates that the last common ancestor of living great apes and humans must have been more primitive than inferred on the basis of extant taxa, by retaining palmigrade adaptations subsequently lost in several subclades independently. Thus, while the short manual rays of the stem hominid *Pierolapithecus* confirms that the long-handed pattern of hylobatids and living great apes is the homoplastic result of parallel evolution from orthograde but non-suspensory ancestors (Moyà-Solà *et al*. 2004, 2005), *Hispanopithecus* further suggests that suspensory adaptations, to some degree, also evolved independently between pongines and hominines.

The uniqueness of the *Hispanopithecus* locomotor repertoire further suggests that the evolution of positional behaviors in hominoids has occurred in a mosaic fashion. *Proconsul* would illustrate the initial stage, characterized by tail loss (Nakatsukasa *et al.* 2004), which probably occurred once grasping was sufficiently powerful to entirely support the balancing function. *Pierolapithecus* documents a more derived pattern, in which ulnocarpal articulation had been lost as an adaptation to vertical climbing (Moyà-Solà *et al.* 2004) in spite of the retention of palmigrady (see Chapter 2). *Hispanopithecus* reflects an even more derived pattern, in which palmigrade behaviors remain significant, but suspensory adaptations have been already selected. The adaptive reasons underlying the evolution of suspensory behaviors in hominoids has been related to their large body size, permitting them to have access to food resources located in the periphery of the canopy (Hunt 1992). Powerful-grasping palmigrady would have permitted to maintain balance in a relatively large-bodied tailless primate such as *Proconsul* during above-branch quadrupedalism (Kelley 1997), but not to exploit the feeding niche that includes the slenderest branches at the crown's periphery, due to its relatively large body mass. Amongst extant great apes, the almost strictly arboreal orangutans have circumvented these limitations by more heavily relying on below-branch arm-hanging and swinging, whereas chimpanzees and gorillas have become secondarily adapted to terrestrial travel between feeding sites (although they still employ suspensory behaviors when on the trees). These considerations, together with the mosaic nature of the *Hispanopithecus* locomotor repertoire, suggest that suspensory behaviors progressively replaced palmigrady during great ape evolution, until the latter behavior was definitely abandoned as a significant component of their positional behavior in the ancestors of the surviving lineages. Anatomically, this abandonment would have implied the selection for longer palms relative to body mass (with a concomitant reduction of thumb length relative to the rest of the hand), due to suspensory-related selection pressures.

Recognizing the mosaic nature of locomotor evolution in hominoids further provides new insights into the interpretation of other fossil great apes such as *Sivapithecus*. Reported pronograde features in the postcranial skeleton of this taxon

(Richmond and Whalen 2001) have proved difficult to reconcile with its orang-like cranial morphology, leading to the so-called “*Sivapithecus* dilemma” (Pilbeam and Young 2001). Available postcranial evidence for the latter taxon suggests a combination of palmigrady and powerful grasping with some amount of vertical climbing and minimal orthograde clambering (Madar *et al*. 2002). The morphology of the proximal phalanges and the metacarpophalangeal joint certainly indicate a higher emphasis of suspensory behaviors in *Hispanopithecus* than in *Sivapithecus*. Also, the morphology of several other anatomical regions in *Hispanopithecus*, including lumbar vertebrae and femur (Moyà-Solà and Köhler 1996; Köhler *et al*. 2001), indicates that palmigrade adaptations do not necessarily preclude the existence of an orthograde bodyplan with suspensory adaptations, by implication also in other Miocene hominoids, even though this combination is unknown among extant members of this group.

Appendix 3.1. Schematic depiction of right fourth manual ray of *Homo sapiens* in palmar and lateral views, indicating the points employed for taking the measurements. Measurements: *a–a’*: metacarpal mediolateral base width (MCBML); *b–b’*: metacarpal mediolateral midshaft width (MCSML); *c–c’*: metacarpal mediolateral head width (MCHML); *d–d’*: proximal phalanx mediolateral base width (PPBML); *e–e’*: proximal phalanx mediolateral midshaft width (PPSML); *f–f’*: proximal phalanx mediolateral trochlear width (PPTML); *g–g’*: intermediate phalanx mediolateral base width (MPBML); *h–h’*: intermediate phalanx mediolateral midshaft width (MPSML); *i–i’*: intermediate phalanx mediolateral trochlear width (MPTML); *j–j’*: metacarpal dorsopalmar base height (MCBDP); *k–k’*: metacarpal dorsopalmar midshaft height (MCSDP); *l–l’*: metacarpal dorsopalmar head height (MCHDP); *m–m’*: proximal phalanx dorsopalmar base height (PPBDP); *n–n’*: proximal phalanx dorsopalmar midshaft height (PPSDP); *o–o’*: proximal phalanx dorsopalmar trochlear height (PPTDP); *p–p’*:: intermediate phalanx dorsopalmar base height (MPBDP); *q–q’*: intermediate phalanx dorsopalmar midshaft height (MPSDP); *r–r’*: intermediate phalanx dorsopalmar trochlear width (MPBDP).



Appendix 3.2. Descriptive statistics of the several long bones of the hand in the extant comparative primate sample, including *Pan* spp. (*P. troglodytes* and *P. paniscus*), *Gorilla* spp. (including *G. gorilla* and *G. beringei*), *Pongo pygmaeus* (*P. p. pygmaeus* and *P. p. abelli*), *Homo sapiens* and *Papio cynocephalus*. (Abbreviations: MC=metacarpal, PP=proximal phalanx, MP=intermediate phalanx, L=length, B=base, MS=midshaft, H=head (in metacarpals)/trochlea (in phalanges), ML=mediolateral breadth, DP=dorsopalmar height, N=sample size, SD=standard deviation, SE=standard error, CI=confidence interval.)

BM

	N	Mean	SD	SE	CI		Range	
Pan	21	42.51	12.08	2.64	37.01	48.01	21.50	70.00
Gorilla	18	135.78	44.59	10.51	113.60	157.95	61.23	190.00
Pongo	16	53.52	22.18	5.54	41.71	65.34	32.66	90.72
Homo	28	46.23	9.97	1.88	42.36	50.10	31.20	68.50

MC1L

	N	Mean	SD	SE	CI		Range	
Pan	104	39.66	3.54	0.35	38.97	40.35	30.80	48.50
Gorilla	164	46.84	5.65	0.44	45.97	47.71	34.04	59.48
Pongo	47	44.93	4.33	0.63	43.66	46.20	38.50	57.19
Homo	74	43.87	4.89	0.57	42.74	45.00	16.12	55.17
Papio	29	32.23	2.78	0.52	31.17	33.28	28.15	37.22

MC1BML

	N	Mean	SD	SE	CI		Range	
Pan	92	11.07	1.23	0.13	10.82	11.32	7.55	13.38
Gorilla	147	16.21	2.33	0.19	15.83	16.59	11.20	24.70
Pongo	34	12.32	1.78	0.30	11.70	12.94	8.84	17.45
Homo	56	15.09	1.57	0.21	14.67	15.51	10.53	19.49
Papio	29	9.50	0.96	0.18	9.14	9.86	8.04	11.41

MC1BDP

	N	Mean	SD	SE	CI		Range	
Pan	92	11.92	1.29	0.13	11.65	12.19	7.05	16.47
Gorilla	147	16.90	2.50	0.21	16.49	17.31	10.92	23.18
Pongo	34	13.35	1.93	0.33	12.67	14.02	10.48	18.61
Homo	57	14.88	1.48	0.20	14.48	15.27	12.38	19.78
Papio	29	7.63	0.85	0.16	7.30	7.95	6.26	9.27

MC1MSML

	N	Mean	SD	SE	CI		Range	
Pan	88	8.08	1.06	0.11	7.86	8.31	5.50	11.99
Gorilla	147	12.23	2.15	0.18	11.88	12.58	7.33	19.20
Pongo	34	7.70	1.43	0.24	7.20	8.20	5.07	11.49
Homo	58	11.55	1.58	0.21	11.14	11.97	8.77	18.63
Papio	29	4.78	0.64	0.12	4.54	5.03	3.86	6.17

MC1MSDP

	N	Mean	SD	SE	CI		Range	
Pan	89	6.60	0.97	0.10	6.39	6.80	5.00	11.87
Gorilla	147	8.77	1.42	0.12	8.54	9.00	5.91	12.29
Pongo	34	6.22	0.99	0.17	5.88	6.57	4.39	8.66
Homo	58	8.45	0.96	0.13	8.19	8.70	6.34	10.62
Papio	29	3.77	0.48	0.09	3.59	3.95	3.04	4.76

MC1HML

	N	Mean	SD	SE	CI		Range	
Pan	87	9.43	0.97	0.10	9.22	9.64	6.90	12.00
Gorilla	145	15.04	2.36	0.20	14.65	15.42	10.70	21.92
Pongo	34	11.27	1.95	0.33	10.60	11.95	8.28	17.63
Homo	58	14.66	1.62	0.21	14.23	15.09	10.74	19.18
Papio	29	6.89	0.88	0.16	6.55	7.22	5.63	8.71

MC1HDP

	N	Mean	SD	SE	CI		Range	
Pan	87	10.80	8.16	0.88	9.06	12.53	5.29	84.75
Gorilla	145	12.88	1.56	0.13	12.62	13.13	9.54	15.60
Pongo	34	10.37	1.69	0.29	9.78	10.96	8.03	14.36
Homo	57	12.77	1.18	0.16	12.45	13.08	9.76	15.34
Papio	29	6.78	0.77	0.14	6.49	7.08	5.47	8.49

MC2L

	N	Mean	SD	SE	CI		Range	
Pan	103	87.08	7.11	0.70	85.69	88.47	69.54	106.20
Gorilla	165	88.49	9.95	0.77	86.97	90.02	67.95	110.80
Pongo	47	97.62	8.95	1.30	94.99	100.24	83.60	119.27
Homo	73	67.07	5.70	0.67	65.74	68.40	52.05	83.39
Papio	29	53.41	4.86	0.90	51.56	55.25	45.54	61.48

MC2BML

	N	**Mean**	**SD**	**SE**	**CI**		**Range**	
Pan	92	13.17	1.33	0.14	12.89	13.44	10.49	15.84
Gorilla	147	18.09	2.29	0.19	17.72	18.47	13.50	24.72
Pongo	34	12.85	1.45	0.25	12.35	13.36	9.69	16.41
Homo	59	16.26	1.64	0.21	15.83	16.68	13.05	20.64
Papio	29	8.59	0.99	0.18	8.21	8.97	7.27	10.57

MC2BDP

	N	**Mean**	**SD**	**SE**	**CI**		**Range**	
Pan	92	16.25	1.72	0.18	15.90	16.61	11.00	20.91
Gorilla	147	22.49	2.94	0.24	22.01	22.97	14.70	28.85
Pongo	34	16.43	2.10	0.36	15.70	17.16	13.05	20.74
Homo	58	16.68	1.54	0.20	16.27	17.08	13.53	19.71
Papio	29	12.21	1.23	0.23	11.74	12.68	10.38	14.24

MC2MSML

	N	**Mean**	**SD**	**SE**	**CI**		**Range**	
Pan	92	7.85	0.81	0.08	7.68	8.02	6.09	10.50
Gorilla	150	12.22	1.90	0.16	11.91	12.52	8.55	16.88
Pongo	35	7.19	1.09	0.18	6.82	7.57	5.98	10.46
Homo	62	7.94	0.82	0.10	7.73	8.15	6.41	9.81
Papio	29	5.33	0.61	0.11	5.10	5.57	4.04	6.71

MC2MSDP

	N	**Mean**	**SD**	**SE**	**CI**		**Range**	
Pan	92	8.08	0.99	0.10	7.87	8.28	5.80	12.01
Gorilla	150	10.21	1.67	0.14	9.94	10.48	6.97	19.30
Pongo	35	8.04	1.33	0.22	7.58	8.50	6.08	12.20
Homo	62	8.81	0.92	0.12	8.58	9.05	6.94	10.69
Papio	29	5.27	0.68	0.13	5.01	5.53	4.30	6.81

MC2HML

	N	**Mean**	**SD**	**SE**	**CI**		**Range**	
Pan	91	12.25	1.47	0.15	11.95	12.56	9.14	17.12
Gorilla	147	17.23	2.69	0.22	16.79	17.67	11.94	23.43
Pongo	35	13.76	1.69	0.29	13.18	14.34	11.22	18.86
Homo	55	14.13	1.59	0.21	13.70	14.56	11.53	17.86
Papio	29	8.03	0.82	0.15	7.72	8.35	6.67	9.72

MC2HDP

	N	**Mean**	**SD**	**SE**	**CI**		**Range**	
Pan	90	15.53	1.64	0.17	15.18	15.87	9.70	19.49
Gorilla	147	20.18	2.70	0.22	19.74	20.62	14.79	27.80
Pongo	35	15.64	2.15	0.36	14.91	16.38	13.28	23.72
Homo	56	13.45	1.12	0.15	13.15	13.75	10.88	16.59
Papio	29	8.37	0.81	0.15	8.06	8.68	7.06	9.99

MC3L

	N	**Mean**	**SD**	**SE**	**CI**		**Range**	
Pan	103	86.46	6.27	0.62	85.24	87.69	71.00	103.30
Gorilla	166	86.71	9.63	0.75	85.23	88.18	64.51	109.30
Pongo	48	96.03	8.47	1.22	93.57	98.49	82.50	117.43
Homo	76	64.80	5.66	0.65	63.51	66.10	49.39	77.24
Papio	29	52.63	4.99	0.93	50.73	54.53	43.67	62.00

MC3BML

	N	**Mean**	**SD**	**SE**	**CI**		**Range**	
Pan	91	13.44	1.06	0.11	13.22	13.66	10.85	16.05
Gorilla	148	18.44	16.23	1.33	15.80	21.08	12.17	202.40
Pongo	34	13.15	1.95	0.33	12.47	13.83	9.81	18.83
Homo	61	13.30	1.11	0.14	13.01	13.58	10.99	16.55
Papio	29	9.14	1.11	0.21	8.72	9.56	7.39	11.21

MC3BDP

	N	**Mean**	**SD**	**SE**	**CI**		**Range**	
Pan	91	16.62	1.62	0.17	16.29	16.96	12.50	20.10
Gorilla	147	21.74	2.60	0.21	21.32	22.17	15.10	27.52
Pongo	34	16.72	1.76	0.30	16.11	17.34	13.53	20.41
Homo	61	16.27	1.64	0.21	15.85	16.69	13.28	19.69
Papio	29	10.72	1.07	0.20	10.31	11.12	9.13	12.63

MC3MSML

	N	**Mean**	**SD**	**SE**	**CI**		**Range**	
Pan	91	8.23	0.97	0.10	8.03	8.43	6.26	10.60
Gorilla	149	10.86	1.38	0.11	10.64	11.09	8.15	14.56
Pongo	35	7.21	0.95	0.16	6.88	7.53	5.56	10.01
Homo	62	8.03	0.67	0.09	7.86	8.20	6.34	9.36
Papio	29	6.26	0.74	0.14	5.98	6.54	5.18	7.58

MC3MSDP

	N	Mean	SD	SE	CI		Range	
Pan	91	8.77	1.03	0.11	8.55	8.99	6.00	11.83
Gorilla	150	12.38	1.81	0.15	12.08	12.67	8.45	17.17
Pongo	35	8.56	1.34	0.23	8.10	9.02	6.45	12.29
Homo	62	9.04	0.77	0.10	8.85	9.24	7.44	11.10
Papio	29	5.07	0.66	0.12	4.82	5.31	4.00	6.41

MC3HML

	N	Mean	SD	SE	CI		Range	
Pan	90	13.67	1.91	0.20	13.27	14.07	9.25	18.97
Gorilla	148	18.83	3.04	0.25	18.34	19.32	10.80	27.27
Pongo	35	14.46	1.71	0.29	13.87	15.04	11.44	17.51
Homo	58	13.80	1.43	0.19	13.42	14.17	11.17	17.06
Papio	29	8.60	0.87	0.16	8.27	8.93	7.26	10.74

MC3HDP

	N	Mean	SD	SE	CI		Range	
Pan	89	17.23	1.95	0.21	16.81	17.64	9.60	21.50
Gorilla	147	21.61	2.83	0.23	21.15	22.07	15.31	28.84
Pongo	35	16.51	1.67	0.28	15.93	17.08	13.90	19.83
Homo	59	13.56	1.11	0.14	13.27	13.84	11.52	15.97
Papio	29	9.04	1.02	0.19	8.65	9.43	7.60	11.68

MC4L

	N	Mean	SD	SE	CI		Range	
Pan	101	79.93	7.19	0.72	78.51	81.35	40.00	96.50
Gorilla	166	82.96	8.83	0.69	81.60	84.31	64.28	103.30
Pongo	46	92.33	8.51	1.25	89.80	94.86	79.50	113.90
Homo	71	56.40	4.43	0.53	55.35	57.45	43.32	65.30
Papio	29	52.68	5.01	0.93	50.77	54.59	44.05	62.71

MC4BML

	N	Mean	SD	SE	CI		Range	
Pan	90	10.29	1.34	0.14	10.01	10.57	7.07	14.20
Gorilla	149	15.01	2.01	0.16	14.69	15.34	10.48	18.61
Pongo	31	9.89	1.45	0.26	9.35	10.42	7.30	12.47
Homo	55	11.61	1.20	0.16	11.28	11.93	9.20	14.13
Papio	29	8.05	1.00	0.19	7.67	8.43	6.75	10.82

MC4BDP

	N	Mean	SD	SE	CI		Range	
Pan	90	12.45	1.45	0.15	12.15	12.75	7.26	15.60
Gorilla	148	15.63	1.93	0.16	15.31	15.94	11.31	19.94
Pongo	34	13.93	1.77	0.30	13.31	14.55	11.01	17.47
Homo	55	11.93	1.11	0.15	11.63	12.23	9.59	14.20
Papio	29	10.03	1.02	0.19	9.64	10.42	8.38	11.75

MC4MSML

	N	Mean	SD	SE	CI		Range	
Pan	90	7.19	1.11	0.12	6.96	7.43	4.97	10.20
Gorilla	150	10.45	1.71	0.14	10.17	10.73	6.76	14.48
Pongo	35	6.90	1.09	0.18	6.52	7.27	5.24	9.81
Homo	59	6.60	0.79	0.10	6.39	6.80	5.25	9.23
Papio	29	5.62	0.73	0.14	5.34	5.90	4.72	7.14

MC4MSDP

	N	Mean	SD	SE	CI		Range	
Pan	90	7.82	0.93	0.10	7.63	8.02	5.00	12.53
Gorilla	150	10.58	1.62	0.13	10.32	10.84	7.22	15.30
Pongo	35	7.80	1.28	0.22	7.36	8.24	5.85	11.12
Homo	59	7.39	0.69	0.09	7.21	7.57	6.12	8.95
Papio	29	4.50	0.63	0.12	4.26	4.74	3.39	5.62

MC4HML

	N	Mean	SD	SE	CI		Range	
Pan	89	12.24	1.63	0.17	11.90	12.58	8.46	17.30
Gorilla	148	18.42	2.88	0.24	17.95	18.89	12.00	26.00
Pongo	33	13.84	1.69	0.29	13.24	14.44	10.85	17.85
Homo	56	11.97	1.23	0.16	11.64	12.30	9.56	14.89
Papio	29	8.24	0.83	0.15	7.93	8.56	7.16	9.71

MC4HDP

	N	Mean	SD	SE	CI		Range	
Pan	88	15.78	1.78	0.19	15.40	16.15	9.50	20.84
Gorilla	147	20.62	2.78	0.23	20.17	21.08	13.60	25.40
Pongo	35	15.71	1.84	0.31	15.07	16.34	12.54	19.71
Homo	55	12.23	1.01	0.14	11.95	12.50	10.05	14.42
Papio	29	8.74	0.86	0.16	8.41	9.07	7.45	10.34

MC5L

	N	Mean	SD	SE	CI		Range	
Pan	102	72.76	5.85	0.58	71.61	73.91	59.55	87.50
Gorilla	163	80.38	9.08	0.71	78.98	81.78	61.26	104.40
Pongo	44	84.33	7.41	1.12	82.08	86.58	71.24	104.36
Homo	74	52.69	3.89	0.45	51.78	53.59	41.34	60.41
Papio	29	53.41	5.02	0.93	51.50	55.32	46.03	64.13

MC5BML

	N	Mean	SD	SE	CI		Range	
Pan	92	9.05	1.40	0.15	8.76	9.34	6.44	12.65
Gorilla	145	15.64	2.57	0.21	15.22	16.06	10.00	20.50
Pongo	33	10.14	1.24	0.22	9.70	10.58	8.05	13.09
Homo	59	12.75	1.47	0.19	12.37	13.13	10.00	16.11
Papio	29	8.82	1.16	0.22	8.38	9.27	6.86	12.20

MC5BDP

	N	Mean	SD	SE	CI		Range	
Pan	92	9.96	1.37	0.14	9.68	10.24	6.40	13.10
Gorilla	146	14.63	2.16	0.18	14.28	14.98	10.40	21.22
Pongo	33	12.80	1.77	0.31	12.17	13.43	9.22	15.42
Homo	59	10.91	0.88	0.11	10.68	11.14	8.92	12.53
Papio	29	7.88	0.84	0.16	7.56	8.20	6.63	9.66

MC5MSML

	N	Mean	SD	SE	CI		Range	
Pan	92	6.99	0.95	0.10	6.79	7.19	4.63	9.71
Gorilla	146	11.39	2.39	0.20	11.00	11.78	7.50	16.93
Pongo	35	7.97	1.29	0.22	7.53	8.42	5.74	10.95
Homo	60	7.10	0.89	0.12	6.87	7.33	5.50	9.28
Papio	29	4.11	0.60	0.11	3.88	4.34	3.24	5.88

MC5MSDP

	N	Mean	SD	SE	CI		Range	
Pan	92	6.25	0.77	0.08	6.09	6.41	4.49	8.86
Gorilla	145	8.87	1.38	0.11	8.65	9.10	6.20	13.10
Pongo	34	6.72	1.18	0.20	6.31	7.13	4.96	10.52
Homo	60	7.23	1.02	0.13	6.96	7.49	5.54	9.78
Papio	29	5.23	0.93	0.17	4.87	5.58	4.04	7.04

MC5HML

	N	Mean	SD	SE	CI		Range	
Pan	91	9.53	1.58	0.17	9.20	9.86	6.84	19.00
Gorilla	145	14.72	2.19	0.18	14.36	15.08	8.74	19.81
Pongo	35	12.64	1.69	0.28	12.06	13.22	9.52	16.48
Homo	61	11.62	1.08	0.14	11.34	11.90	9.10	14.30
Papio	29	7.90	0.95	0.18	7.54	8.26	6.56	10.03

MC5HDP

	N	Mean	SD	SE	CI		Range	
Pan	90	13.04	1.41	0.15	12.75	13.34	6.50	17.11
Gorilla	145	18.91	2.96	0.25	18.42	19.40	12.68	25.87
Pongo	35	14.00	1.71	0.29	13.41	14.58	11.23	17.73
Homo	61	11.27	1.05	0.13	11.00	11.53	8.81	13.83
Papio	29	8.13	0.91	0.17	7.78	8.47	6.81	10.59

PP1L

	N	Mean	SD	SE	CI		Range	
Pan	78	26.40	2.68	0.30	25.80	27.01	20.00	34.01
Gorilla	91	28.17	3.65	0.38	27.41	28.93	19.47	35.52
Pongo	37	25.75	3.66	0.60	24.53	26.97	17.84	32.22
Homo	57	30.95	2.98	0.39	30.16	31.74	24.05	40.67
Papio	29	16.38	1.18	0.22	15.93	16.84	13.61	18.96

PP1BML

	N	Mean	SD	SE	CI		Range	
Pan	67	10.70	1.07	0.13	10.44	10.97	7.57	13.47
Gorilla	78	15.49	1.97	0.22	15.04	15.93	11.64	18.91
Pongo	32	10.88	1.37	0.24	10.38	11.37	8.37	13.72
Homo	40	15.31	1.20	0.19	14.93	15.69	12.66	17.49
Papio	29	7.65	0.73	0.14	7.37	7.93	6.48	9.42

PP1BDP

	N	Mean	SD	SE	CI		Range	
Pan	67	9.24	0.85	0.10	9.04	9.45	7.46	11.01
Gorilla	78	12.33	1.52	0.17	11.99	12.67	9.57	15.25
Pongo	33	9.12	1.21	0.21	8.69	9.55	6.98	11.97
Homo	40	11.09	1.09	0.17	10.74	11.43	9.05	13.96
Papio	29	5.69	0.55	0.10	5.48	5.90	4.67	6.81

PP1MSML

	N	Mean	SD	SE	CI		Range	
Pan	68	6.01	0.66	0.08	5.85	6.17	4.55	8.04
Gorilla	78	9.10	1.21	0.14	8.82	9.37	6.89	12.28
Pongo	31	5.89	0.97	0.17	5.53	6.24	4.09	7.95
Homo	40	8.98	0.93	0.15	8.69	9.28	7.02	11.34
Papio	29	4.44	0.96	0.18	4.07	4.80	3.55	8.82

PP1MSDP

	N	Mean	SD	SE	CI		Range	
Pan	62	5.47	0.66	0.08	5.30	5.64	3.97	7.11
Gorilla	78	7.11	1.50	0.17	6.77	7.45	5.24	17.00
Pongo	30	4.47	0.93	0.17	4.13	4.82	3.09	6.40
Homo	40	6.45	0.79	0.12	6.20	6.70	4.88	8.09
Papio	29	3.36	0.38	0.07	3.21	3.50	2.60	4.19

PP1TML

	N	Mean	SD	SE	CI		Range	
Pan	67	18.98	89.18	10.89	-2.77	40.73	6.04	738.00
Gorilla	78	11.29	1.42	0.16	10.97	11.61	7.97	13.92
Pongo	34	8.90	1.40	0.24	8.41	9.39	6.73	12.26
Homo	41	11.65	2.28	0.36	10.93	12.37	0.01	13.72
Papio	29	5.98	0.55	0.10	5.77	6.19	5.04	7.02

PP1TDP

	N	Mean	SD	SE	CI		Range	
Pan	67	5.63	0.65	0.08	5.48	5.79	3.70	6.75
Gorilla	78	6.98	0.98	0.11	6.76	7.20	4.96	9.50
Pongo	33	5.51	0.96	0.17	5.17	5.85	4.01	7.27
Homo	41	8.45	1.12	0.18	8.09	8.80	6.61	11.69
Papio	29	3.87	0.46	0.08	3.70	4.05	3.08	4.69

PP2L

	N	Mean	SD	SE	CI		Range	
Pan	82	49.77	4.10	0.45	48.87	50.67	42.27	59.61
Gorilla	103	51.18	5.06	0.50	50.19	52.17	41.10	64.63
Pongo	40	64.85	5.24	0.83	63.17	66.52	56.40	77.61
Homo	58	40.75	3.32	0.44	39.88	41.62	28.62	48.62
Papio	29	25.11	1.75	0.33	24.45	25.78	22.45	28.52

PP2BML

	N	Mean	SD	SE	CI		Range	
Pan	72	14.10	1.22	0.14	13.81	14.39	11.59	16.62
Gorilla	89	19.43	2.58	0.27	18.89	19.98	14.37	24.96
Pongo	34	14.57	1.85	0.32	13.92	15.21	11.65	18.98
Homo	43	15.69	1.60	0.24	15.19	16.18	10.89	18.89
Papio	29	9.03	0.83	0.15	8.71	9.34	7.69	10.82

PP2BDP

	N	Mean	SD	SE	CI		Range	
Pan	72	12.45	1.18	0.14	12.18	12.73	10.42	15.53
Gorilla	89	15.69	1.99	0.21	15.27	16.11	11.79	20.01
Pongo	33	13.83	1.56	0.27	13.27	14.38	11.72	17.64
Homo	41	11.57	0.90	0.14	11.29	11.86	9.77	13.49
Papio	29	6.95	0.68	0.13	6.69	7.21	5.87	8.07

PP2MSML

	N	Mean	SD	SE	CI		Range	
Pan	73	10.10	1.33	0.16	9.79	10.41	7.79	13.71
Gorilla	90	15.87	2.25	0.24	15.40	16.34	11.40	20.85
Pongo	33	10.99	1.48	0.26	10.47	11.51	8.74	14.45
Homo	44	9.14	1.04	0.16	8.82	9.46	6.59	11.27
Papio	29	5.67	0.70	0.13	5.41	5.94	4.33	7.16

PP2MSDP

	N	Mean	SD	SE	CI		Range	
Pan	73	6.83	1.00	0.12	6.60	7.07	4.73	9.42
Gorilla	90	9.85	1.51	0.16	9.53	10.16	6.46	13.39
Pongo	33	6.96	1.22	0.21	6.53	7.39	5.04	9.55
Homo	44	6.40	0.55	0.08	6.23	6.57	5.14	7.29
Papio	29	4.05	0.47	0.09	3.87	4.23	3.25	4.83

PP2TML

	N	Mean	SD	SE	CI		Range	
Pan	72	10.51	1.23	0.14	10.22	10.80	5.93	12.56
Gorilla	89	14.10	1.78	0.19	13.73	14.48	10.32	18.28
Pongo	34	11.40	1.23	0.21	10.97	11.83	9.11	14.01
Homo	44	10.92	1.09	0.16	10.59	11.25	8.51	13.10
Papio	29	6.25	0.59	0.11	6.03	6.48	5.51	7.44

PP2TDP

	N	Mean	SD	SE	CI		Range	
Pan	72	8.82	0.89	0.11	8.61	9.03	6.51	10.89
Gorilla	89	10.77	1.30	0.14	10.50	11.05	8.01	14.13
Pongo	34	9.29	1.27	0.22	8.85	9.74	7.04	12.17
Homo	44	7.46	0.82	0.12	7.21	7.71	5.66	9.05
Papio	29	4.63	0.49	0.09	4.44	4.81	3.95	5.50

PP3L

	N	Mean	SD	SE	CI		Range	
Pan	83	58.33	4.53	0.50	57.34	59.32	49.08	68.46
Gorilla	105	57.56	5.28	0.52	56.54	58.58	47.62	70.99
Pongo	43	71.82	5.96	0.91	69.98	73.65	62.60	88.06
Homo	60	44.81	2.81	0.36	44.08	45.54	40.00	51.95
Papio	29	28.93	2.24	0.42	28.08	29.78	25.87	35.55

PP3BML

	N	Mean	SD	SE	CI		Range	
Pan	72	16.51	5.83	0.69	15.14	17.88	12.50	63.68
Gorilla	91	21.17	2.61	0.27	20.63	21.71	14.97	25.96
Pongo	34	15.84	1.95	0.33	15.16	16.52	12.84	21.18
Homo	43	15.86	1.48	0.23	15.41	16.32	13.02	18.74
Papio	29	9.84	0.87	0.16	9.51	10.18	8.61	11.82

PP3BDP

	N	Mean	SD	SE	CI		Range	
Pan	72	14.66	1.28	0.15	14.36	14.96	11.68	17.78
Gorilla	91	17.45	2.34	0.25	16.97	17.94	13.63	23.34
Pongo	34	15.22	1.72	0.29	14.62	15.82	12.96	18.87
Homo	44	12.33	0.90	0.14	12.06	12.61	10.76	14.06
Papio	29	7.56	0.71	0.13	7.28	7.83	6.53	9.05

PP3MSML

	N	Mean	SD	SE	CI		Range	
Pan	73	11.90	1.75	0.20	11.50	12.31	8.93	16.61
Gorilla	92	18.14	2.63	0.27	17.60	18.69	12.16	24.99
Pongo	34	11.72	1.67	0.29	11.14	12.31	9.36	15.98
Homo	47	9.56	0.96	0.14	9.28	9.85	7.83	11.95
Papio	29	6.16	0.71	0.13	5.89	6.43	5.04	7.67

PP3MSDP

	N	Mean	SD	SE	CI		Range	
Pan	73	8.18	1.10	0.13	7.93	8.44	5.60	10.29
Gorilla	92	11.46	1.60	0.17	11.13	11.79	7.31	16.22
Pongo	34	7.84	1.38	0.24	7.36	8.32	6.08	12.12
Homo	47	6.99	0.66	0.10	6.79	7.18	5.61	8.38
Papio	29	4.21	0.49	0.09	4.03	4.40	3.44	5.42

PP3TML

	N	Mean	SD	SE	CI		Range	
Pan	72	12.61	1.35	0.16	12.30	12.93	8.78	15.60
Gorilla	91	15.73	2.02	0.21	15.31	16.15	11.03	20.09
Pongo	34	12.50	1.77	0.30	11.88	13.12	9.97	17.60
Homo	45	11.61	1.19	0.18	11.25	11.97	9.54	14.16
Papio	29	6.76	0.66	0.12	6.51	7.01	5.61	8.27

PP3TDP

	N	Mean	SD	SE	CI		Range	
Pan	72	10.47	1.01	0.12	10.24	10.71	7.85	13.53
Gorilla	91	12.03	1.60	0.17	11.70	12.36	8.69	17.70
Pongo	34	10.20	1.28	0.22	9.75	10.64	8.18	12.82
Homo	46	7.87	0.74	0.11	7.65	8.09	6.42	9.27
Papio	29	5.01	0.56	0.10	4.80	5.23	4.18	6.59

PP4L

	N	Mean	SD	SE	CI		Range	
Pan	82	54.35	4.48	0.50	53.36	55.33	43.76	63.57
Gorilla	103	54.89	5.00	0.49	53.91	55.87	43.27	66.93
Pongo	41	70.78	5.87	0.92	68.93	72.63	62.34	87.38
Homo	57	41.88	2.90	0.38	41.11	42.65	35.83	47.97
Papio	29	29.29	2.08	0.39	28.50	30.08	26.35	34.12

PP4BML

	N	Mean	SD	SE	CI		Range	
Pan	72	14.31	1.40	0.17	13.98	14.64	11.46	17.76
Gorilla	89	19.66	2.48	0.26	19.13	20.18	15.08	24.29
Pongo	32	14.98	1.89	0.33	14.30	15.66	12.02	19.40
Homo	44	14.41	1.24	0.19	14.03	14.79	11.71	16.47
Papio	29	9.57	0.91	0.17	9.23	9.92	8.34	11.36

PP4BDP

	N	Mean	SD	SE	CI		Range	
Pan	72	13.36	1.16	0.14	13.09	13.63	10.92	16.56
Gorilla	88	16.77	2.08	0.22	16.33	17.21	12.43	21.51
Pongo	32	14.36	1.68	0.30	13.75	14.96	11.46	18.05
Homo	43	11.38	0.92	0.14	11.10	11.66	9.65	13.02
Papio	29	7.22	0.64	0.12	6.98	7.47	6.21	8.57

PP4MSML

	N	Mean	SD	SE	CI		Range	
Pan	73	10.42	1.49	0.17	10.07	10.76	7.74	14.73
Gorilla	90	16.69	2.47	0.26	16.17	17.20	12.91	22.21
Pongo	32	11.23	1.73	0.31	10.61	11.86	8.72	15.45
Homo	46	8.90	1.06	0.16	8.58	9.21	7.11	11.12
Papio	29	5.45	0.61	0.11	5.22	5.69	4.29	6.90

PP4MSDP

	N	Mean	SD	SE	CI		Range	
Pan	73	7.60	0.99	0.12	7.37	7.84	5.19	9.67
Gorilla	90	10.62	1.54	0.16	10.30	10.95	7.63	14.20
Pongo	32	7.39	1.30	0.23	6.93	7.86	5.34	11.02
Homo	46	6.41	0.56	0.08	6.24	6.58	4.89	7.75
Papio	29	4.08	0.48	0.09	3.90	4.26	3.21	4.89

PP4TML

	N	Mean	SD	SE	CI		Range	
Pan	73	11.52	1.25	0.15	11.23	11.82	7.49	13.69
Gorilla	89	15.02	1.88	0.20	14.63	15.42	11.83	19.25
Pongo	32	11.63	1.40	0.25	11.13	12.14	9.15	14.33
Homo	45	10.73	1.12	0.17	10.39	11.06	7.58	13.20
Papio	29	6.59	0.54	0.10	6.39	6.80	5.78	7.87

PP4TDP

	N	Mean	SD	SE	CI		Range	
Pan	73	9.83	0.92	0.11	9.62	10.05	7.47	11.57
Gorilla	89	11.29	1.34	0.14	11.01	11.57	8.60	14.17
Pongo	32	9.78	1.20	0.21	9.35	10.22	8.07	12.71
Homo	45	7.55	0.79	0.12	7.31	7.78	5.58	10.26
Papio	29	4.77	0.47	0.09	4.59	4.95	4.03	5.85

PP5L

	N	Mean	SD	SE	CI		Range	
Pan	81	42.22	3.45	0.38	41.46	42.99	32.53	51.59
Gorilla	101	45.94	4.47	0.44	45.06	46.83	38.17	56.06
Pongo	40	60.71	5.16	0.82	59.05	62.36	52.24	74.11
Homo	57	33.26	2.48	0.33	32.60	33.92	28.34	38.33
Papio	29	25.33	1.80	0.33	24.65	26.02	22.55	29.30

PP5BML

	N	Mean	SD	SE	CI		Range	
Pan	70	11.30	1.08	0.13	11.04	11.56	9.06	13.86
Gorilla	87	17.09	3.65	0.39	16.31	17.87	12.18	44.14
Pongo	32	13.31	1.65	0.29	12.71	13.90	11.20	16.56
Homo	43	13.61	1.37	0.21	13.19	14.04	10.59	16.08
Papio	29	8.53	0.90	0.17	8.19	8.88	6.98	10.87

PP5BDP

	N	Mean	SD	SE	CI		Range	
Pan	70	10.70	1.03	0.12	10.45	10.94	8.84	13.23
Gorilla	87	14.49	1.88	0.20	14.09	14.89	10.89	18.78
Pongo	32	12.64	1.48	0.26	12.10	13.17	10.41	15.58
Homo	44	9.90	0.79	0.12	9.66	10.14	8.37	11.10
Papio	29	6.57	0.65	0.12	6.32	6.82	5.41	7.74

PP5MSML

	N	Mean	SD	SE	CI		Range	
Pan	72	7.60	1.16	0.14	7.32	7.87	5.29	10.31
Gorilla	88	14.02	2.25	0.24	13.54	14.50	9.15	19.21
Pongo	32	9.88	1.48	0.26	9.35	10.42	7.96	13.23
Homo	45	8.16	0.97	0.14	7.86	8.45	6.41	9.93
Papio	29	4.79	0.60	0.11	4.57	5.02	3.56	6.09

PP5MSDP

	N	Mean	SD	SE	CI		Range	
Pan	72	6.20	0.83	0.10	6.01	6.40	4.49	9.20
Gorilla	88	8.77	1.65	0.18	8.42	9.12	4.70	16.60
Pongo	32	6.33	1.13	0.20	5.92	6.74	4.60	8.39
Homo	45	5.62	0.54	0.08	5.46	5.79	4.24	6.61
Papio	29	3.67	0.46	0.09	3.49	3.84	2.86	4.60

PP5TML

	N	Mean	SD	SE	CI		Range	
Pan	71	8.78	0.95	0.11	8.56	9.01	6.87	11.28
Gorilla	86	12.96	1.52	0.16	12.64	13.29	9.63	16.76
Pongo	32	10.55	1.29	0.23	10.09	11.02	8.60	12.97
Homo	44	9.00	0.93	0.14	8.72	9.29	6.83	11.34
Papio	29	5.96	0.55	0.10	5.75	6.17	4.96	7.17

PP5TDP

	N	Mean	SD	SE	CI		Range	
Pan	71	7.51	0.98	0.12	7.27	7.74	5.86	12.05
Gorilla	86	9.72	1.37	0.15	9.43	10.01	6.93	13.17
Pongo	32	8.81	1.15	0.20	8.40	9.23	7.29	11.47
Homo	44	6.24	0.60	0.09	6.06	6.42	4.54	7.48
Papio	29	4.43	0.43	0.08	4.26	4.59	3.77	5.41

MP2L

	N	Mean	SD	SE	CI		Range	
Pan	77	32.34	3.35	0.38	31.57	33.10	24.12	42.55
Gorilla	87	34.13	6.41	0.69	32.76	35.49	26.40	80.00
Pongo	40	38.66	5.59	0.88	36.87	40.45	23.70	54.64
Homo	47	25.05	2.49	0.36	24.32	25.78	19.97	31.94
Papio	29	15.47	1.29	0.24	14.98	15.96	13.39	18.14

MP2BML

	N	Mean	SD	SE	CI		Range	
Pan	67	12.37	1.07	0.13	12.11	12.63	9.96	14.51
Gorilla	72	16.61	2.21	0.26	16.09	17.13	12.85	22.79
Pongo	31	13.16	1.70	0.31	12.54	13.79	9.42	16.27
Homo	35	12.55	1.04	0.18	12.20	12.91	10.22	14.58
Papio	29	7.12	0.62	0.11	6.89	7.36	6.10	8.36

MP2BDP

	N	Mean	SD	SE	CI		Range	
Pan	67	9.80	0.97	0.12	9.56	10.03	7.73	11.63
Gorilla	72	12.06	1.64	0.19	11.68	12.44	8.98	18.18
Pongo	31	10.81	1.22	0.22	10.36	11.26	8.37	13.08
Homo	34	8.80	0.67	0.11	8.56	9.03	7.49	9.75
Papio	29	5.22	0.43	0.08	5.06	5.38	4.51	5.95

MP2MSML

	N	Mean	SD	SE	CI		Range	
Pan	68	8.18	1.06	0.13	7.92	8.43	6.14	11.28
Gorilla	73	11.48	1.81	0.21	11.06	11.91	8.33	15.63
Pongo	31	8.55	1.66	0.30	7.94	9.16	4.42	12.53
Homo	35	7.72	0.78	0.13	7.45	7.99	6.13	9.40
Papio	29	4.83	0.56	0.10	4.62	5.04	3.92	6.01

MP2MSDP

	N	Mean	SD	SE	CI		Range	
Pan	68	4.94	0.58	0.07	4.80	5.08	3.73	7.12
Gorilla	72	6.09	0.89	0.11	5.88	6.30	4.33	9.89
Pongo	31	5.34	1.09	0.20	4.94	5.74	3.16	8.27
Homo	35	4.83	0.38	0.06	4.70	4.96	3.87	5.51
Papio	29	3.00	0.34	0.06	2.87	3.14	2.40	3.63

MP2TML

	N	Mean	SD	SE	CI		Range	
Pan	68	8.36	0.84	0.10	8.16	8.56	6.32	10.89
Gorilla	71	11.57	1.29	0.15	11.26	11.87	8.92	14.27
Pongo	31	9.49	1.34	0.24	9.00	9.98	6.89	12.83
Homo	35	9.21	0.90	0.15	8.90	9.52	7.45	11.23
Papio	29	5.69	0.49	0.09	5.51	5.88	4.96	6.79

MP2TDP

	N	Mean	SD	SE	CI		Range	
Pan	68	5.83	0.68	0.08	5.66	5.99	3.99	7.59
Gorilla	71	6.75	0.77	0.09	6.57	6.94	5.09	8.27
Pongo	31	6.55	1.03	0.18	6.17	6.93	5.02	9.73
Homo	34	5.52	0.59	0.10	5.31	5.73	4.71	7.75
Papio	29	3.54	0.38	0.07	3.40	3.69	3.00	4.52

MP3L

	N	Mean	SD	SE	CI		Range	
Pan	77	42.04	3.81	0.43	41.17	42.90	34.08	52.57
Gorilla	87	40.70	4.22	0.45	39.80	41.60	33.04	53.65
Pongo	41	46.77	5.64	0.88	44.99	48.55	34.00	60.13
Homo	51	30.00	2.31	0.32	29.35	30.65	25.59	34.95
Papio	29	18.83	1.58	0.29	18.23	19.43	16.22	22.43

MP3BML

	N	Mean	SD	SE	CI		Range	
Pan	66	14.84	1.30	0.16	14.52	15.16	11.81	17.19
Gorilla	73	18.70	2.43	0.28	18.14	19.27	14.81	24.82
Pongo	32	14.74	1.76	0.31	14.10	15.37	12.43	18.50
Homo	36	13.64	1.20	0.20	13.24	14.05	11.57	15.92
Papio	29	7.94	0.69	0.13	7.68	8.20	6.93	9.51

MP3BDP

	N	Mean	SD	SE	CI		Range	
Pan	66	11.34	1.29	0.16	11.03	11.66	8.59	14.19
Gorilla	73	13.26	1.66	0.19	12.88	13.65	10.41	17.38
Pongo	32	11.88	1.52	0.27	11.33	12.42	9.92	17.64
Homo	36	9.81	0.75	0.12	9.55	10.06	8.33	10.93
Papio	29	5.52	0.48	0.09	5.34	5.71	4.82	6.61

MP3MSML

	N	Mean	SD	SE	CI		Range	
Pan	68	9.81	1.18	0.14	9.52	10.09	7.65	12.97
Gorilla	74	13.73	2.19	0.25	13.22	14.23	9.95	17.63
Pongo	32	9.50	1.58	0.28	8.93	10.07	6.89	13.55
Homo	36	8.70	0.97	0.16	8.37	9.02	7.29	11.12
Papio	29	5.30	0.54	0.10	5.10	5.51	4.25	6.28

MP3MSDP

	N	Mean	SD	SE	CI		Range	
Pan	68	5.72	0.76	0.09	5.53	5.90	3.55	8.70
Gorilla	73	6.99	0.91	0.11	6.77	7.20	4.98	9.58
Pongo	32	5.76	1.09	0.19	5.37	6.15	4.55	9.67
Homo	36	5.47	0.60	0.10	5.27	5.67	4.45	6.47
Papio	29	3.23	0.41	0.08	3.07	3.38	2.59	4.33

MP3TML

	N	Mean	SD	SE	CI		Range	
Pan	66	9.61	1.00	0.12	9.37	9.86	7.40	11.73
Gorilla	73	13.21	1.57	0.18	12.85	13.58	10.43	16.91
Pongo	32	10.07	1.27	0.22	9.61	10.53	8.13	12.57
Homo	36	10.03	1.02	0.17	9.69	10.38	8.10	12.51
Papio	29	6.19	0.60	0.11	5.97	6.42	5.38	7.63

MP3TDP

	N	Mean	SD	SE	CI		Range	
Pan	66	6.95	0.80	0.10	6.76	7.15	5.14	8.76
Gorilla	73	7.89	1.06	0.12	7.64	8.14	6.05	11.42
Pongo	32	6.89	0.80	0.14	6.60	7.18	5.33	8.30
Homo	36	6.13	0.70	0.12	5.89	6.37	4.86	8.06
Papio	29	3.81	0.50	0.09	3.62	4.00	3.00	5.28

MP4L

	N	Mean	SD	SE	CI		Range	
Pan	77	38.94	3.91	0.45	38.05	39.83	29.50	49.13
Gorilla	87	39.10	4.50	0.48	38.14	40.06	27.44	50.20
Pongo	40	46.48	5.20	0.82	44.82	48.15	39.30	59.93
Homo	48	28.45	2.50	0.36	27.73	29.18	23.93	33.70
Papio	29	18.64	1.49	0.28	18.08	19.21	16.50	22.17

MP4BML

	N	Mean	SD	SE	CI		Range	
Pan	68	13.77	1.21	0.15	13.48	14.06	10.60	16.03
Gorilla	73	17.84	2.36	0.28	17.29	18.39	13.37	23.78
Pongo	32	14.19	1.66	0.29	13.59	14.79	11.62	17.48
Homo	35	12.64	1.08	0.18	12.27	13.02	10.36	14.80
Papio	29	7.74	0.69	0.13	7.48	8.01	6.68	9.18

MP4BDP

	N	Mean	SD	SE	CI		Range	
Pan	68	10.67	1.07	0.13	10.41	10.93	7.88	13.10
Gorilla	73	12.62	1.55	0.18	12.26	12.98	9.80	16.47
Pongo	32	11.55	1.30	0.23	11.08	12.02	9.58	14.17
Homo	36	9.18	0.81	0.14	8.91	9.46	7.76	11.20
Papio	29	5.41	0.45	0.08	5.24	5.58	4.71	6.23

MP4MSML

	N	Mean	SD	SE	CI		Range	
Pan	67	8.82	1.19	0.14	8.53	9.11	6.62	11.82
Gorilla	74	12.75	2.15	0.25	12.25	13.25	9.28	16.75
Pongo	32	9.27	1.54	0.27	8.72	9.82	6.65	12.55
Homo	36	8.10	0.94	0.16	7.78	8.42	6.69	10.00
Papio	29	5.19	0.54	0.10	4.99	5.40	4.39	6.51

MP4MSDP

	N	Mean	SD	SE	CI		Range	
Pan	67	5.35	0.69	0.08	5.18	5.51	3.85	7.99
Gorilla	74	6.65	0.91	0.11	6.44	6.86	4.89	9.18
Pongo	32	5.63	1.04	0.18	5.25	6.00	4.12	8.95
Homo	36	4.96	0.56	0.09	4.77	5.15	4.08	6.09
Papio	29	3.13	0.36	0.07	2.99	3.27	2.51	3.97

MP4TML

	N	Mean	SD	SE	CI		Range	
Pan	68	8.97	1.06	0.13	8.71	9.23	6.21	11.20
Gorilla	73	12.57	1.46	0.17	12.23	12.91	10.17	17.10
Pongo	32	10.00	1.45	0.26	9.48	10.53	7.98	13.34
Homo	36	9.57	0.84	0.14	9.29	9.86	7.55	11.70
Papio	29	6.03	0.48	0.09	5.85	6.22	5.34	7.05

MP4TDP

	N	Mean	SD	SE	CI		Range	
Pan	68	6.38	0.76	0.09	6.20	6.57	4.45	8.03
Gorilla	73	7.32	0.94	0.11	7.10	7.54	5.27	9.91
Pongo	32	6.81	1.01	0.18	6.45	7.18	5.23	9.70
Homo	35	5.42	0.57	0.10	5.22	5.61	4.39	6.55
Papio	29	3.70	0.42	0.08	3.53	3.86	3.04	5.01

MP5L

	N	Mean	SD	SE	CI		Range	
Pan	77	27.27	2.82	0.32	26.64	27.91	22.00	36.85
Gorilla	85	31.40	3.86	0.42	30.57	32.24	24.72	42.49
Pongo	40	38.04	4.98	0.79	36.45	39.63	30.46	50.88
Homo	41	20.49	2.09	0.33	19.83	21.15	16.25	27.56
Papio	29	14.88	1.72	0.32	14.22	15.53	9.18	18.22

MP5BML

	N	Mean	SD	SE	CI		Range	
Pan	67	10.16	1.00	0.12	9.91	10.40	8.14	12.80
Gorilla	69	15.10	2.16	0.26	14.58	15.62	11.33	20.50
Pongo	31	12.41	1.74	0.31	11.77	13.05	10.13	16.36
Homo	30	10.82	0.94	0.17	10.47	11.17	8.43	12.85
Papio	29	6.84	0.58	0.11	6.61	7.06	5.69	7.96

MP5BDP

	N	Mean	SD	SE	CI		Range	
Pan	67	8.29	0.78	0.10	8.10	8.48	6.37	10.11
Gorilla	70	11.30	1.54	0.18	10.94	11.67	7.68	15.46
Pongo	31	10.40	1.36	0.24	9.90	10.90	8.68	13.79
Homo	31	7.79	0.62	0.11	7.57	8.02	6.19	8.83
Papio	29	5.05	0.46	0.08	4.88	5.22	4.09	5.98

MP5MSML

	N	Mean	SD	SE	CI		Range	
Pan	67	6.18	0.87	0.11	5.97	6.39	4.45	8.33
Gorilla	72	10.08	1.88	0.22	9.64	10.52	6.77	14.66
Pongo	32	8.03	1.37	0.24	7.54	8.52	6.25	11.46
Homo	31	6.95	0.80	0.14	6.66	7.24	5.61	8.64
Papio	29	4.36	0.48	0.09	4.17	4.54	3.38	5.16

MP5MSDP

	N	Mean	SD	SE	CI		Range	
Pan	67	4.42	0.56	0.07	4.29	4.56	3.02	6.16
Gorilla	71	5.81	0.90	0.11	5.60	6.02	3.96	8.32
Pongo	32	5.02	1.01	0.18	4.65	5.38	3.69	8.24
Homo	31	4.40	0.40	0.07	4.25	4.54	3.65	5.16
Papio	29	2.85	0.35	0.07	2.72	2.99	2.26	3.56

MP5TML

	N	Mean	SD	SE	CI		Range	
Pan	67	7.33	0.81	0.10	7.13	7.52	5.56	9.01
Gorilla	71	10.73	1.29	0.15	10.43	11.04	7.97	13.95
Pongo	32	9.08	1.15	0.20	8.66	9.49	7.34	11.55
Homo	29	8.31	0.68	0.13	8.06	8.57	6.47	9.68
Papio	29	5.49	0.45	0.08	5.32	5.66	4.92	6.52

MP5TDP

	N	Mean	SD	SE	CI		Range	
Pan	67	5.01	0.65	0.08	4.85	5.17	3.21	6.37
Gorilla	71	6.25	0.81	0.10	6.06	6.44	4.79	8.41
Pongo	32	6.22	0.86	0.15	5.91	6.53	4.63	8.18
Homo	29	4.60	0.54	0.10	4.40	4.81	3.05	5.48
Papio	29	3.32	0.42	0.08	3.16	3.48	2.65	4.35

Appendix 3.3. Numerical results of the multivariate analyses. (Unstandardized coefficients for the canonical discriminant functions obtained from the three discriminant analyses. Abbreviations: CA=Canonical axis (discriminant function); MC=Metacarpal; PP=Proximal phalanx; MP=Intermediate phalanx; B=Base; MS=Midshaft; H=Head (for metacarpals); T=Trochlea (for phalanges); L=Length; ML=Mediolateral (width); DP=Dorsopalmar (height); numbers refer to manual ray.)

Overall Proportions

variable	CA1	CA2	CA3	CA4
MC2L	-0.029	0.077	-0.169	0.127
MC3L	0.009	0.258	-0.040	0.011
MC4L	-0.072	-0.422	0.369	-0.078
PP2L	0.262	0.061	-0.450	0.225
PP3L	0.028	0.362	0.122	-0.068
PP4L	0.120	-0.167	0.023	-0.332
PP5L	0.145	-0.253	-0.038	-0.094
MP2L	-0.055	0.006	0.094	0.017
MP3L	-0.200	0.259	0.224	-0.071
MP4L	-0.050	-0.042	0.027	0.035
MP5L	0.047	-0.143	-0.082	0.374
(Constant)	-9.862	-2.785	-5.598	-0.685

Metacarpal Robusticity

variable	CA1	CA2	CA3	CA4
MC2L	0.010	-0.029	-0.017	0.035
MC2BML	-0.200	0.155	0.447	0.035
MC2BDP	-0.078	0.031	-0.306	0.038
MC2MSML	0.223	0.411	-0.085	0.015
MC2MSDP	-0.144	-0.127	0.250	-0.205
MC2HML	-0.292	-0.210	0.388	-0.028
MC2HDP	0.251	0.066	-0.005	0.045
MC3L	0.019	0.034	0.184	-0.081
MC3BML	0.009	-0.007	-0.007	-0.005
MC3BDP	0.111	0.370	0.206	-0.295
MC3MSML	-0.383	0.083	-0.204	-0.698
MC3MSDP	0.164	0.281	0.067	0.283
MC4L	0.079	-0.084	-0.127	0.105
MC4BML	-0.193	0.289	-0.166	-0.191
MC4BDP	-0.207	-0.431	-0.286	-0.059
MC4MSML	0.060	0.007	-0.286	0.151
MC4MSDP	-0.013	-0.057	0.046	-0.210
MC4HML	0.343	0.220	-0.172	0.133
MC4HDP	0.330	0.068	-0.157	-0.390
MC5BML	-0.393	0.008	-0.144	0.341
MC5BDP	-0.008	-0.329	0.284	0.702
MC5MSML	0.265	-0.162	0.154	0.086
MC5MSDP	-0.390	-0.011	-0.118	0.228
(Constant)	-5.292	-3.960	-3.477	-2.291

Phalangeal Robusticity				
variable	CA1	CA2	CA3	CA4
PP2L	0.259	-0.056	0.342	0.100
PP2BML	-0.443	-0.145	0.818	0.708
PP2BDP	0.509	-0.454	0.375	-0.363
PP2MSML	0.294	0.418	-0.210	0.012
PP2MSDP	-0.016	0.075	-0.274	-0.124
PP2TML	0.171	-0.055	0.366	0.049
PP2TDP	-0.540	0.037	-0.486	0.111
PP3L	-0.033	0.400	0.160	0.271
PP3BML	-0.012	-0.047	0.047	0.057
PP3BDP	-0.093	-0.341	-0.039	-0.654
PP3MSML	-0.199	0.463	-0.355	-0.330
PP3MSDP	-0.096	0.029	0.362	-0.100
PP3TML	-0.404	0.082	-0.336	0.259
PP3TDP	-0.060	0.903	-0.639	-0.427
PP4L	0.093	-0.377	-0.222	-0.150
PP4BML	-0.346	-0.421	-0.216	-0.490
PP4BDP	0.150	0.602	0.414	0.605
PP4MSML	0.271	-0.297	-0.066	-0.229
PP4MSDP	0.163	-0.067	-0.274	0.222
PP4TML	0.152	-0.015	-0.029	-0.523
PP4TDP	0.222	0.328	-0.024	0.101
PP5L	0.281	-0.175	-0.199	-0.088
PP5BML	0.007	-0.003	0.051	0.025
PP5BDP	-0.200	0.392	0.172	-0.270
PP5MSML	0.168	0.067	0.563	-0.056
PP5MSDP	-0.377	0.136	-0.150	0.197
MP2L	-0.069	0.003	0.086	0.140
MP2BML	0.436	-0.106	0.625	-0.126
MP2BDP	-0.407	0.192	-0.583	-0.554
MP2MSML	-0.351	-0.135	-0.565	0.075
MP2MSDP	0.222	-0.385	-0.212	-0.402
MP2TML	0.072	0.544	0.540	0.182
MP2TDP	0.662	-0.434	-0.364	0.883
MP3L	-0.293	0.095	-0.022	0.255
MP3BML	0.455	-0.079	-0.378	-0.308
MP3BDP	0.025	-0.212	0.246	0.676
MP3MSML	0.224	0.314	0.246	0.171
MP3MSDP	-0.550	0.512	0.281	-0.279
MP3TML	-0.095	-0.246	0.049	0.003
MP3TDP	0.222	-0.171	-0.200	0.102
MP4L	-0.037	0.056	-0.089	-0.229
MP4BML	-0.223	0.467	-0.344	-0.205
MP4BDP	0.107	0.214	0.508	0.988
MP4MSML	-0.332	-0.416	-0.080	0.076
MP4MSDP	0.457	0.322	-0.054	0.056
MP4TML	-0.491	0.107	-0.138	-0.087
MP4TDP	-0.555	-0.233	0.372	-0.187
MP5L	0.104	0.085	-0.149	-0.261
MP5BML	-0.243	-0.190	-0.176	0.357
MP5BDP	0.640	-0.278	-0.081	-0.749
MP5MSML	-0.003	-0.525	0.222	0.558
MP5MSDP	-0.844	0.145	-0.121	1.148
MP5TML	0.430	-0.216	0.121	-0.361
MP5TDP	-0.027	-0.616	-0.194	-0.309
(Constant)	-9.743	-6.007	-4.713	-2.116

Appendix 3.4. Allometric regressions. (Least-squares, mixed-sex, static-adult allometric regressions of phalangeal vs. metacarpal length for manual ray IV, and of basal and head/trochlear area vs. length for both metacarpals and proximal phalanges of manual ray IV. Abbreviations: A=Area (computed as the product of mediolateral width and dorsopalmar height); MC=Metacarpal; PP=Proximal phalanx; MP=Intermediate phalanx; B=Base; MS=Midshaft; H=Head (for metacarpals); T=Trochlea (for phalanges); L=Length; ML=Mediolateral (width); DP=Dorsopalmar (height); numbers refer to manual ray.)

Intrinsic Proportions of Manual Ray IV

Taxa	x	y	N	R	Slope	Intercept
Pan	ln(MC4L)	ln(PP4L+MP4L)	74	0.812	1.028	0.025
Gorilla	ln(MC4L)	ln(PP4L+MP4L)	87	0.860	0.786	1.062
Pongo	ln(MC4L)	ln(PP4L+MP4L)	40	0.705	0.674	1.712
Homo	ln(MC4L)	ln(PP4L+MP4L)	43	0.750	0.708	1.409
Papio	ln(MC4L)	ln(PP4L+MP4L)	29	0.941	0.718	1.023
Homininae	ln(MC4L)	ln(PP4L+MP4L)	204	0.933	0.752	1.223

Robusticity of Metacarpal IV Base Area

Taxa	x	y	N	R	Slope	Intercept
Pan	ln(MC4L)	ln(MC4BA)	88	0.523	1.504	-1.743
Gorilla	ln(MC4L)	ln(MC4BA)	148	0.736	1.793	-2.489
Pongo	ln(MC4L)	ln(MC4BA)	34	0.755	2.145	-4.836
Homo	ln(MC4L)	ln(MC4BA)	56	0.551	1.154	0.276
Papio	ln(MC4L)	ln(MC4BA)	29	0.849	1.881	-3.068

Robusticity of Metacarpal IV Head Area

Taxa	x	y	N	R	Slope	Intercept
Pan	ln(MC4L)	ln(MC4HA)	86	0.385	1.628	-1.859
Gorilla	ln(MC4L)	ln(MC4HA)	147	0.657	1.704	-1.617
Pongo	ln(MC4L)	ln(MC4HA)	34	0.741	1.756	-2.612
Homo	ln(MC4L)	ln(MC4HA)	56	0.571	1.190	0.190
Papio	ln(MC4L)	ln(MC4HA)	29	0.895	1.828	-2.970

Robusticity of Proximal Phalanx IV Base Area

Taxa	x	y	N	R	Slope	Intercept
Pan	ln(PP4L)	ln(PP4BA)	71	0.714	1.479	-0.651
Gorilla	ln(PP4L)	ln(PP4BA)	87	0.895	2.445	-4.025
Pongo	ln(PP4L)	ln(PP4BA)	32	0.720	1.907	-2.759
Homo	ln(PP4L)	ln(PP4BA)	44	0.617	1.282	0.306
Papio	ln(PP4L)	ln(PP4BA)	29	0.865	2.179	-3.126

Robusticity of Proximal Phalanx IV Trochlear Area

Taxa	x	y	N	R	Slope	Intercept
Pan	ln(PP4L)	ln(PP4TA)	72	0.728	1.694	-2.035
Gorilla	ln(PP4L)	ln(PP4TA)	88	0.884	2.331	-4.233
Pongo	ln(PP4L)	ln(PP4TA)	32	0.761	1.997	-3.780
Homo	ln(PP4L)	ln(PP4TA)	46	0.655	1.585	-1.533
Papio	ln(PP4L)	ln(PP4TA)	29	0.833	2.090	-3.611

Chapter 4

Locomotor inferences from *Pierolapithecus* and *Hispanopithecus* phalanges

based on:

Alba DM, Almécija S, Moyà-Solà S (under review). Locomotor inferences in *Pierolapithecus* and *Hispanopithecus*: Reply to Deane and Begun (2008). *Journal of Human Evolution*.

Chapter 4

Locomotor inferences from *Pierolapithecus* and *Hispanopithecus* phalanges

INTRODUCTION

Deane and Begun (2008) recently used a high-resolution polynomial curve fitting (HR-PCF) methodology (Deane *et al.* 2005) for measuring hominoid phalangeal curvature. Polynomial curvature measurements can be taken from fragmentary specimens, and generally yield results congruent with those computed by other methodologies, such as the included angle (IA; Stern *et al.* 1995). Deane and Begun's (2008) approach is therefore promising for making locomotor inferences in fossil taxa. These authors found their results for extinct hominoids, such as *Dryopithecus* (here referred to *Hispanopithecus*[1]), to be broadly consistent with pre-existing locomotor hypotheses, with the exception of *Pierolapithecus*, which appeared most similar to suspensory hominoids (contra Moyà-Solà *et al.* 2004). While we applaud such methodological advances in paleobiology, we disagree with Deane and Begun's (2008, p. 699) conclusion that "it is likely that the positional behavior and locomotor adaptations of *Pierolapithecus* included a significant suspensory component." As explained below, both phalangeal morphometry and morphology indicate that the positional behavior of *Pierolapithecus*, unlike that of *Hispanopithecus*, did not include a significant suspensory component.

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[1] *Hispanopithecus* Villalta and Crusafont 1944 has long been considered a junior subjective synonym of *Dryopithecus* Lartet 1856. However, on the basis of a lower face attributed to *D. fontani* (the type species of the genus), Moyà-Solà *et al.* (2009) have recently resurrected the genus *Hispanopithecus* (type species: *H. laietanus*), to which these authors further attribute other Vallesian species previously classified into *Dryopithecus*, such as *H. crusafonti* and *H. hungaricus*; the latter had been previously referred to *D. brancoi* by Begun and Kordos (1993), but most recently the same authors (Begun and Kordos 2008) reassigned it to *Rudapithecus hungaricus*.

LOCOMOTOR INFERENCES BASED ON MANUAL PHALANGES

On locomotor categories

Based on polynomial curvature measurements, Deane and Begun (2008) perform a discriminant function analysis that classifies extinct taxa into predefined locomotor categories: knuckle-walking, suspensory, terrestrial quadruped, arboreal quadruped, and biped. They conclude that "While all other fossil taxa are most similar to extant quadrupeds, *Pierolapithecus* and *Dryopithecus* [=*Hispanopithecus*] are more closely aligned with extant suspensory hominoids" (Deane and Begun 2008, p. 695). The number of extant cases correctly classified by the analysis is low (57%), suggesting that additional information (other than curvature) would be required. Nevertheless, Deane and Begun (2008) note that the proportion of correctly-identified suspensory taxa is higher than for other categories, thus concluding that the classification of *Pierolapithecus* into this category is reliable.

Some degree of simplification is certainly required when defining functional groups, but the inclusion of hylobatids and orangutans into a single category may be unwarranted, due to extensive differences in their locomotor repertoires. While hylobatids perform an agile, ricochetal brachiation most similar to that of atelines (Turnquist *et al.* 1999; Young 2003), orangutans display a much wider repertoire of locomotor behaviors (Cant 1987; Hunt 1991; Thorpe and Crompton 2006); the latter include, besides vertical climbing and arm-swinging, a large amount of orthograde clambering, and even pronograde quadrupedalism and suspension to some degree. Conflating hylobatids and orangutans into a single suspensory category is therefore unlikely to permit accurate locomotor inferences in fossil taxa. Other categorizations are possible, such as distinguishing small-bodied brachiators (hylobatids and spider monkeys) from quadrumanous climbers (orangutans), even though both groups are highly suspensory (Matarazzo 2008). Moreover, it should not be forgotten that locomotor repertoires inferred for extinct hominoids must not be restricted to those displayed by extant apes; just the reverse is expected, given the mosaic nature of evolution (Stern and Susman 1991). This is clearly illustrated by several fossil apes, such as *Proconsul* (Rose 1983; Ward 1993, 2007; Walker 1997; Begun 2007; Crompton *et al.* 2008). Unfortunately, Deane and Begun (2008) did not report discriminant scores, group centroids, or Mahalanobis distances, which would have been useful for evaluating to what extent *Pierolapithecus* resembles suspensory hominoids more than quadrupedal monkeys, or whether *Hispanopithecus* fits better than *Pierolapithecus* into the suspensory category.

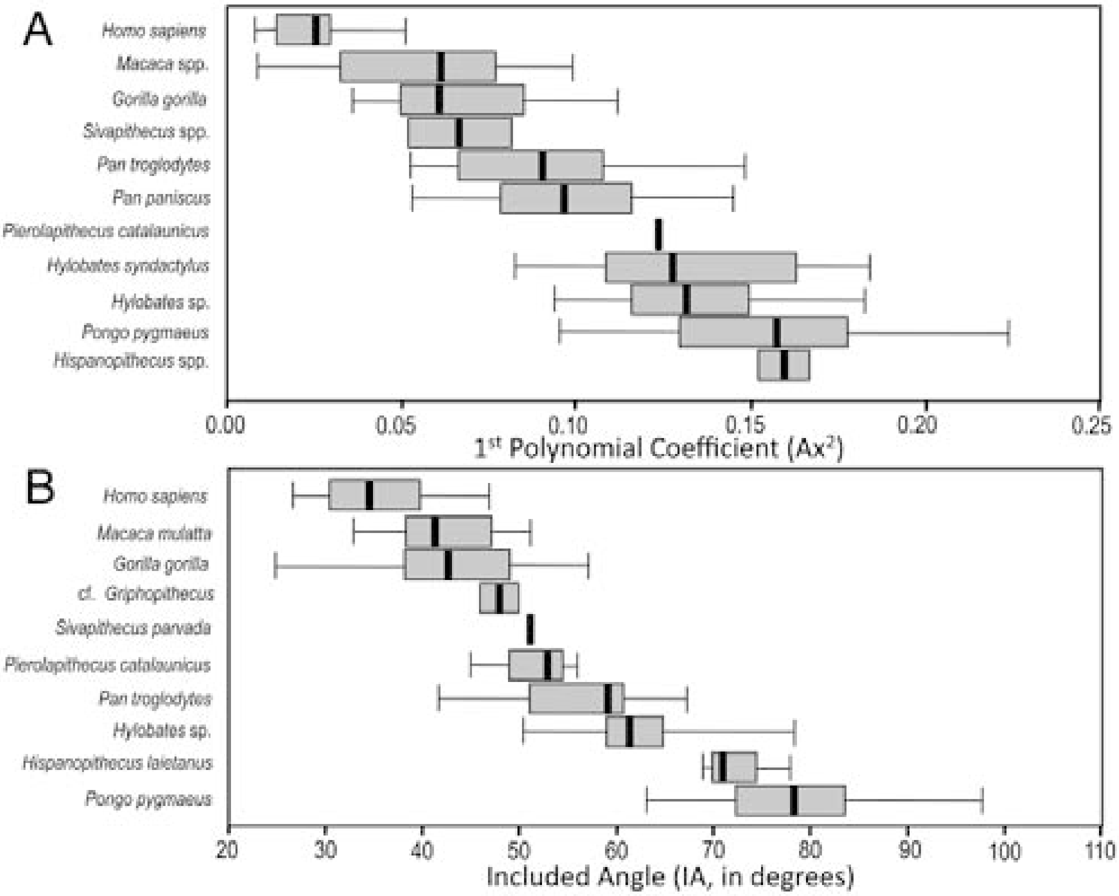


Figure 4.1. Boxplots comparing curvature of proximal phalanges as computed on the basis of the first polynomial component (**A**, after Deane and Begun, 2008: Fig. 3) and included angle (**B**, data taken from Richmond and Jungers 2008: Fig. S5, except for fossil taxa reported in Table 4.1). Black vertical lines represent the median, boxes the 50% of the values, and whiskers the maximum-minimum range.

Phalangeal curvature based on included angle (IA) measurements

The main advantage of Deane and Begun's (2008) approach, namely, its applicability to fragmentary specimens, is not required for either *P. catalaunicus* or *H. laietanus*, because several complete phalanges are available (see Chapters 2 and 3). Moreover, the merits of polynomial measurements notwithstanding, IA remains as the most widely employed and repeatable methodology for measuring phalangeal curvature (Stern *et al.* 1995; Jungers *et al.* 1997; Richmond and Whalen 2001; Ersoy *et al.* 2008; Matarazzo 2008; Richmond and Jungers 2008). On the basis of the first polynomial coefficient computed by Deane and Begun (2008), *Hispanopithecus* resembles orangutans, while *Pierolapithecus* most closely resembles hylobatids and displays phalanges more curved than chimpanzees (Figure 4.1A). IA measurements (Figure 4.1B; Table 4.1 and Appendix 4.3) similarly show an orang-like degree of proximal phalanx curvature for *Hispanopithecus* (see Chapter 3); *Pierolapithecus*, on the contrary, displays a much lower curvature (see Chapter 2), being more comparable to (in fact, displaying less curved phalanges than) the knuckle-walking chimpanzees, and further most closely resembling the fossil apes *Griphopithecus* and *Sivapithecus* (Figure 4.1B; Table 4.1 and Appendix 4.3), for which a non-suspensory locomotor repertoire has been inferred (Begun 1992, 2007; Madar *et al.* 2002). Regarding chimps, hylobatids and *Pierolapithecus*, polynomial and IA measurements clearly do not yield the same results, which deserves further investigation and emphasizes our contention that other sources of evidence must be sought.

Index of relative curvature (IRC)

A finer discrimination between locomotor categories is possible when both proximal and middle phalangeal curvature is considered simultaneously by computing an index of relative curvature (IRC; Matarazzo 2008; see Appendix 4.3); thus, even though small brachiators and African apes display similarly-curved proximal phalanges they can be distinguished on this basis. The IRC for *Pierolapithecus* and *Hispanopithecus*, much lower than one, resembles the great-ape pattern, which differs from small brachiators by displaying proximal phalanges more curved than middle ones. *Hispanopithecus* most closely resembles orangutans by the extremely high curvature values, in agreement with previous inferences of highly suspensory behaviors for this taxon (Moyà-Solà and Köhler 1996; Moyà-Solà *et al.* 2005; Deane and Begun 2008; see also Chapters 2 and 3). On the contrary, *Pierolapithecus* most closely resembles African apes, given their more moderate proximal phalangeal curvature and lower middle phalanx curvature. This does not rule out suspensory behaviors in *Pierolapithecus*, but clearly indicates that it resembles neither orangs nor hylobatids (the most suspensory living taxa), so that a much lower commitment to suspension must be inferred. Although African apes are suspensory to some degree, they are also largely terrestrial. As such, interpreting the *Pierolapithecus* chimp-like pattern as indicative of suspension would be as unwarranted as interpreting it as indicative of knuckle-walking. Further evidence is thus clearly required.

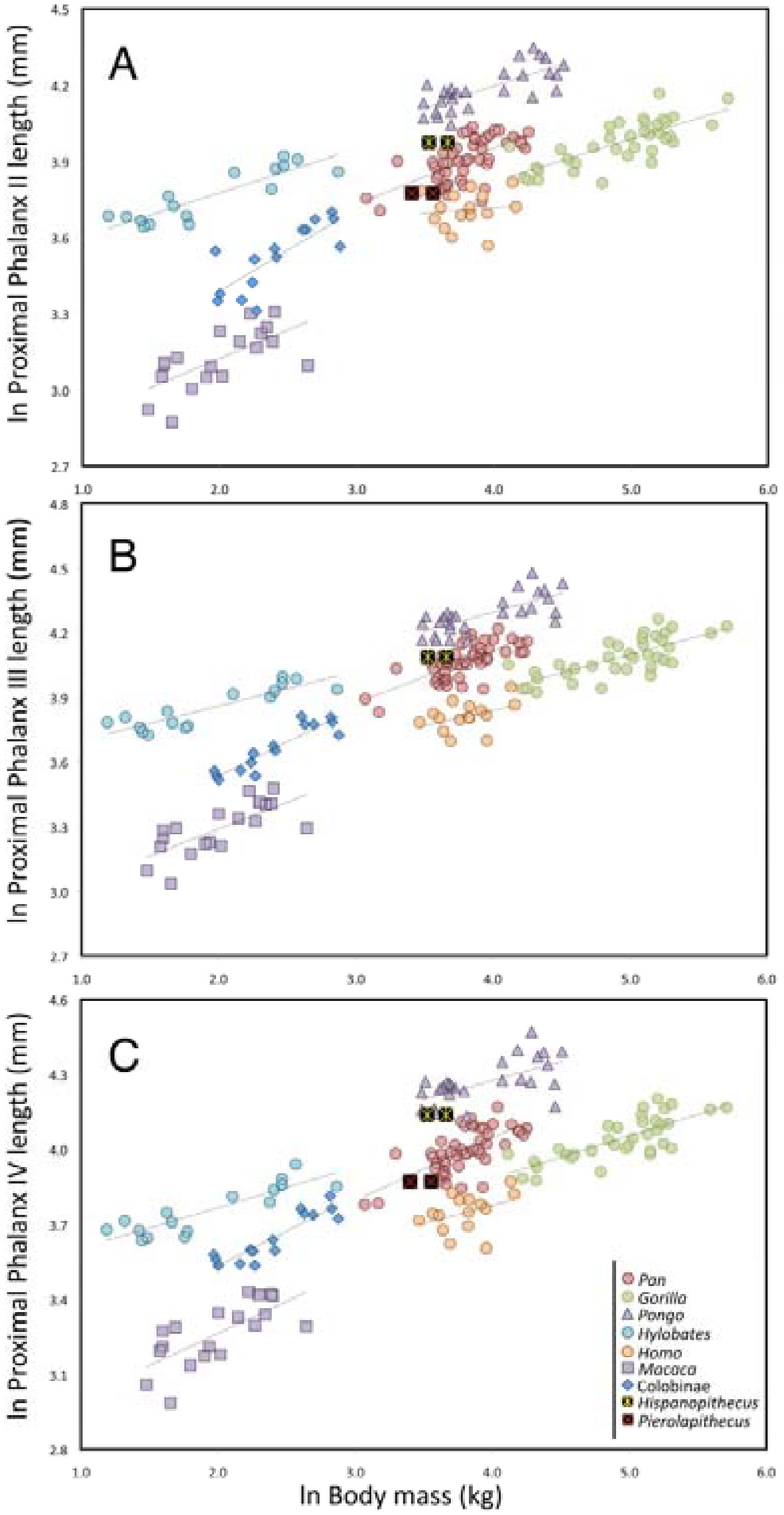


Figure 4.2. Relative phalangeal length (RPL) displayed as allometric bivariate plots of bone length versus body mass in extant hominoids, macaques and colobines, separately for manual rays II (**A**), III (**B**) and IV (**C**).

Table 4.1. Included angle (IA) measurements of phalangeal curvature (in degrees) of the proximal and middle phalanges of *Pierolapithecus*, *Hispanopithecus* and other fossil taxa.

Taxon	Specimen	Phalanx	Manual ray	IA
Pierolapithecus catalaunicus	IPS21350.12	PP	II	45[1]
Pierolapithecus catalaunicus	IPS21350.14	PP	IV	53[1]
Pierolapithecus catalaunicus	IPS21350.15	PP	V	56[1]
Pierolapithecus catalaunicus	IPS21350.13	MP	III/IV	37[2]
Hispanopithecus laietanus	IPS18800	PP	II	69[3]
Hispanopithecus laietanus	IPS18800	PP	III	78[3]
Hispanopithecus laietanus	IPS18800	PP	IV	71[3]
Hispanopithecus laietanus	IPS18800	MP	II	52[2]
Hispanopithecus laietanus	IPS18800	MP	III	48[2]
Hispanopithecus laietanus	IPS18800	MP	IV	(42)[2]
Hispanopithecus laietanus	IPS18800	MP	V	53[2]
cf. *Griphopithecus*	K1420	PP	III	51[4], 50[2]
cf. *Griphopithecus*	K1421	PP	IV	52[4], 46[2]
Sivapithecus parvada	GSP 19700	PP	IV	51[5]

Literature sources: 1 = Chapter 2; 2 = This study; 3 = Chapter 3; 4 = Ersoy *et al.* (2008); 5 = Richmond and Whalen (2001: Fig. 15.7). Abbreviations: PP = proximal phalanges; MP = middle phalanges.
Note: Estimated values due to some bone damage between parentheses. IA measurements for cf. *Griphopithecus* were repeated for this study from *Ersoy et al.* (2008: Fig. 3) by S.A., who also took the IA measurements for *P. catalaunicus* and *H. laietanus*.

Relative phalangeal length (RPL)

The relative length of digits or manual phalanges further permits to discriminate highly from less suspensory taxa (Alba *et al.* 2003; Moyà-Solà *et al.* 2005; see also Chapters 2 and 3). On the basis of multivariate analyses of standard phalangeal measurements we computed an intrinsic index of relative phalangeal length (RPL; see Chapter 2), which reflects the degree of arboreality. This index shows that, as compared to middle Miocene hominoids, *Hispanopithecus* displays elongated phalanges, thus resembling orangutans and hylobatids; *Pierolapithecus*, on the contrary, shows relatively shorter phalanges, thus being more similar to chimpanzees and *Sivapithecus* (see Chapter 2 Figures 2.3B,D and 2.4, and Tables 2.3 and 2.6).

Here we show that equivalent results are obtained when the RPL is computed in relation to body mass (Figures 4.2 and 4.3; see Appendix 4.1 for further details on methods and results). All hominoids display relatively longer phalanges than terrestrial monkeys such as macaques. However, as noted by Susman (1979), chimpanzees display a phalangeal length intermediate between orangutans and gorillas; moreover, only the most committed arboreal, suspensory apes (hylobatids and orangutans) significantly depart from the colobine condition, the latter being arboreal quadrupedal monkeys with only limited suspensory capabilities. Among hominoids, a higher RPL is correlated to increasing arboreality, from humans + gorillas, to chimpanzees, to hylobatids + orangs (the latter further departing regarding the fourth manual ray). *Hispanopithecus* displays a higher RPL than *Pierolapithecus*, being intermediate between chimps and suspensory taxa, and even overlapping with the latter regarding the fourth phalanx; *Pierolapithecus*, on the contrary, much more closely matches the colobine and chimpanzee conditions. Again, this agrees with inferences of orang-like suspensory capabilities in *Hispanopithecus* (see Chapter 3), and further confirms previous accounts of *Pierolapithecus* displaying shorter phalanges (Moyà-Solà *et al.* 2004, 2005; see also Chapter 2), most closely resembling taxa with a significant quadrupedal component.

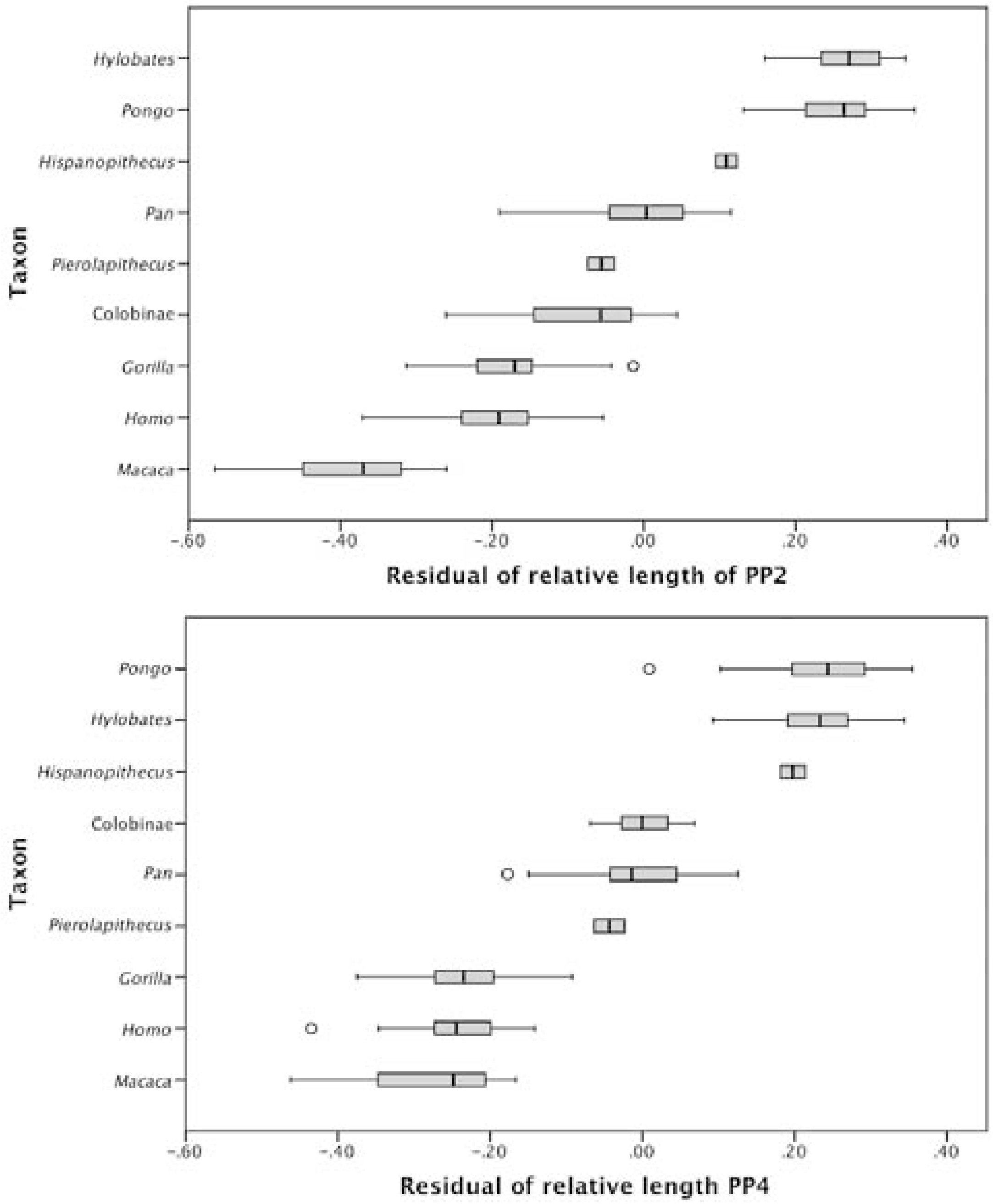


Figure 4.3. Boxplots of residuals of relative length for the second (PP2) and fourth (PP4) proximal phalanges (see descriptive statistics in Appendix 4.5), by taking chimpanzee regressions (reported in Appendix 4.4) as a criterion of subtraction.

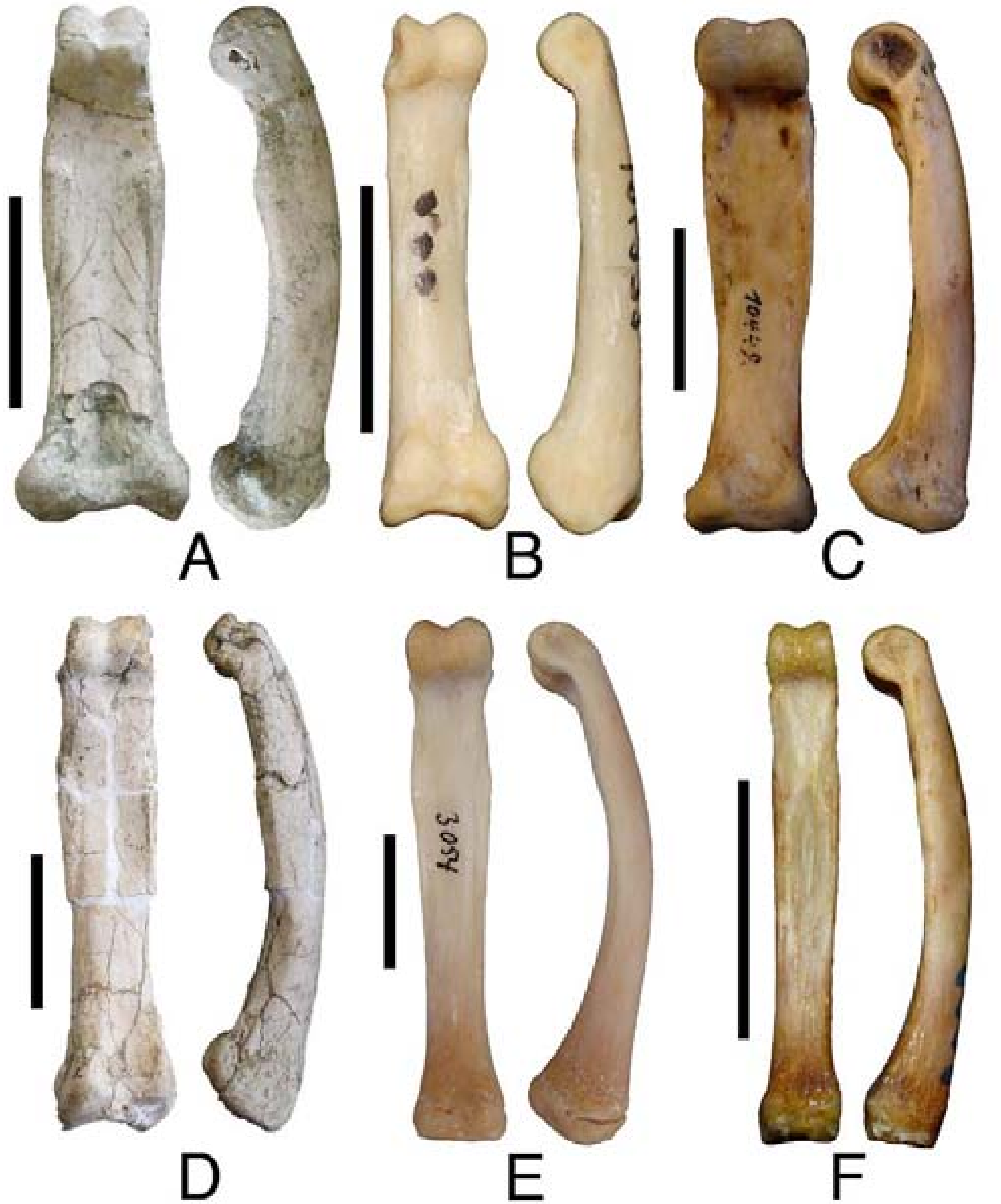


Figure 4.4. Fourth proximal phalanges of *Pierolapithecus catalaunicus* (**A**) and *Hispanopithecus laietanus* (**D**), as compared to colobines (*Nasalis larvatus*, **B**), chimpanzees (*Pan troglodytes*, **C**), orangutans (*Pongo pygmaeus*, **E**) and gibbons (*Hylobates moloch*, **F**), in palmar and lateral views. All phalanges are scaled to the same length; scale bars represent 2 cm. Note that both Miocene apes and colobines differ from living hominoids by displaying larger palmar tubercles as compared to the trochlea, with a distinct groove for channeling the flexors during palmigrady. *Hispanopithecus*, however, differs from *Pierolapithecus* (and more closely resemble extant suspensory forms) by displaying, among others, a longer and more curved proximal phalanx, with smaller palmar tubercles, a narrower channel and a more beaked trochlea.

Phalangeal morphology

Besides morphometric variables, phalanges provide a considerable amount of morphological evidence. Early to middle Miocene apes are quite similar in phalangeal morphology, by displaying many features functionally related to palmigrady and powerful-grasping capabilities (see Chapter 2). Despite morphometric similarities with chimpanzees regarding curvature and relative length, *Pierolapithecus* considerably differs regarding phalangeal morphological details. The latter indicate a lack of the suspensory-related features shared between chimpanzees, orangutans and hylobatids, and indicate instead the retention of primitive, palmigrady-related features (large basal palmar tubercles, dorsally-directed proximal articular facet, non-palmarly-bent trochlea; see Figure 4.4 and Chapter 2, for further details). This indicates that, despite displaying chimp-like, intermediate phalangeal curvature and relative length, the *Pierolapithecus* phalanges display a morphological pattern that does not resemble any extant suspensory ape, even when the African apes are included amongst the latter.

DISCUSSION

Moyà-Solà *et al.* (2004) inferred an orthograde bodyplan for *Pierolapithecus* on the basis of ribs, clavicle, lumbar vertebrae and wrist anatomy, but argued that this taxon lacks specific suspensory adaptations (see also Moyà-Solà *et al.* 2005). This has been disputed by Begun and co-workers (Begun and Ward 2005; Begun *et al.* 2006; Begun 2007; Deane and Begun 2008), who argue that similarities with hylobatids are indicative of "a considerable suspensory capability" for this taxon (Deane and Begun 2008, p. 699). To a large extent, Begun, Ward and co-authors (Ward 1993, 2007; Begun and Ward 2005; Deane and Begun 2008) follow Keith's (1923) interpretation that the set of forelimb and trunk features shared by living apes (orthogrady) would have been originally related to brachiation: e.g. "Living apes all share a suit of *adaptations* to below-branch, forelimb-dominated arboreality" (Ward 2007, p. 1013, italics added). This must not be necessarily so, because orthograde features are also functionally related to other behaviors displayed by living hominoids (Crompton *et al.* 2008), including climbing, clambering and even facultative bipedalism. Current function must not be equated with the original target of selection, especially given previous assertions that original climbing adaptations could have been later coopted for suspensory behaviors (Cartmill 1985; Nakatsukasa *et al.* 2003; Moyà-Solà *et al.* 2004, 2005; see also Chapter 2).

The relationship between phalangeal curvature and arboreal behaviors, particularly suspensory ones (Stern *et al.* 1995), is grounded on sound biomechanical models (Richmond 2007). Phalangeal curvature is particularly appealing for inferring behavior because it is largely ecophenotypical, i.e. largely results from mechanical stresses experienced during ontogeny (Richmond and Whalen 2001; Richmond 2007; Matarazzo 2008). Nevertheless, for inferring the positional behavior of extinct taxa, insights from phalangeal curvature are too limited and should not be used alone. This is recognized by Deane and Begun (2008, p. 699), who warn us that "caution should be exercised when analyzing phalangeal curvature independent of other postcranial characters." A 'total morphological pattern' approach (Stern and Susman 1991), by taking all the available evidence into account, is therefore required. It is beyond the scope of this paper to discuss other anatomical regions in further detail, but phalangeal morphology and proportions are revealing enough regarding the possession of suspensory adaptations. Orangutans and hylobatids are characterized not only by curved phalanges, but also by longer manual rays than other apes (e.g. Susman 1979), and therefore both aspects deserve consideration.

The fact that *Pierolapithecus* displays a lower phalangeal curvature cannot be simply attributed to shorter phalanges, since IA values are expected, everything else being equal, to *increase* at lower lengths (Susman *et al.* 1984; Ohman and Latimer 1986). As such, the lower IA and RPL values of *Pierolapithecus* as compared to *Hispanopithecus* strongly indicate significant locomotor differences (see below). Both taxa display locomotor repertoires with no modern analogue amongst hominoids, by retaining morphological primitive features indicative of a significant amount of above-branch, powerful palmigrady, despite their orthograde bodyplan (Moyà-Solà and Köhler 1996; Moyà-Solà *et al.* 2004; see also Chapters 2 and 3). The retention of pronograde quadrupedalism in middle and late Miocene hominoids should not be surprising, given that orangutans still employ pronograde quadrupedalism to some degree (Cant 1987; Thorpe and Crompton 2006; Crompton *et al.* 2008), and given other fossil evidence highlighting the mosaic nature of hominoid evolution (Rose 1983, 1994; Rae 1999;

Ward 2007; Alba and Moyà-Solà 2008), with newer adaptations being progressively superimposed upon more ancient ones.

Palmigrady would have been gradually abandoned as suspensory behaviors became progressively more adaptively significant (Begun and Ward 2005; see Chapters 2 and 3), and hence the retention of palmigrady-related features does not rule out the possession of suspensory capabilities. This is clearly illustrated by *Hispanopithecus* (see below); however, the considerable differences in phalangeal elongation, curvature and morphology between this taxon and *Pierolapithecus* certainly point out to significant locomotor differences, most likely related to suspensory behaviors. The high degree of phalangeal curvature and elongation in *Hispanopithecus*, closely resembling the orangutan condition, permits to infer a significant amount of suspensory behaviors despite palmigrade retentions (Moyà-Solà and Köhler 1996; Moyà-Solà *et al.* 2005; see Chapter 3). On the contrary, the lower degree of phalangeal curvature and elongation of *Pierolapithecus*, as shown here and in Chapter 2, is indicative, at the very least, of a much less significant suspensory component. Given similarities with chimpanzees, suspensory behaviors cannot be completely discarded on morphometric grounds, but the similar condition displayed by colobines clearly indicates that these similarities cannot be taken as specific suspensory adaptations. Moreover, extensive differences in phalangeal morphology between *Pierolapithecus* and chimpanzees (see Chapter 2) further indicate that the former lacks the suspensory-related features that characterize all living great apes.

CONCLUSIONS

Phalangeal morphology is a rich source of anatomical information for making locomotor inferences in extinct hominoids, but there is no reason to rely on curvature alone, given additional sources of anatomical evidence even from the same anatomical region. *Pierolapithecus* and *Hispanopithecus* are both classified as suspensory by Deane and Begun's (2008) discriminant analysis, but the latter is difficult to interpret because: (1) they conflate the brachiating hylobatids with the clambering orangutans into a single "suspensory" category; and (2) they do not report the discriminant scores and group centroids that would be required to see to what extant *Pierolapithecus* fits into the suspensory category into which it is classified. On the basis of IA measurements for both proximal and middle phalanges, we show that *Pierolapithecus* phalanges are much less curved than those of both *Hispanopithecus* and orangutans, further displaying a curvature pattern that does neither fit that of small brachiators. The lower degree of RPL in *Pierolapithecus* further indicates a much lower significance of suspensory behaviors than in *Hispanopithecus*. Finally, phalangeal morphology shows that *Pierolapithecus*, unlike the largely terrestrial and less suspensory chimpanzees, lacks specific suspensory adaptations, most closely resembling the condition of other early to middle Miocene apes and extant quadrupedal taxa. Overall, the evidence provided by *Pierolapithecus* falsifies the hypothesis that suspensory behaviors were the main original target of selection underlying the acquisition of orthogrady (see also Moyà-Solà *et al.* 2004, 2005; Crompton *et al.* 2008). Nothing precludes suspension having been sporadically employed by the orthograde *Pierolapithecus*, but available evidence clearly indicates that it would not have been practiced to the same degree as in hylobatids, orangutans, *Hispanopithecus*, or even in the less suspensory African apes. As concluded by us in Chapter 2, *Pierolapithecus* “lacked specific adaptations to below-branch suspension”, and cataloguing it as an extinct suspensory ape is not warranted when all the available phalangeal evidence is taken into account.

Appendix 4.1. Relative phalangeal length (RPL)

Materials and methods

The allometric relationship between proximal phalangeal length and body mass was computed on the basis of phalangeal length (in mm) from the second (PP2L), third (PP3L) and fourth (PP4L) manual rays and body mass (BM, in kg); natural logarithms (ln) were employed. Only adult individuals were included in mixed-sex samples. Allometric regressions were plotted separately for the following groups: *Pan* (both chimpanzees and bonobos); *Gorilla* (gorillas); *Pongo* (orangutans); *Homo* (modern humans); *Hylobates* s.l. (both gibbons and siamangs); *Macaca* (macaques, including *M. fascicularis*, *M. nigra*, *M. silenus*, *M. sinica* and *M. sylvanus*); and Colobinae (including *Procolobus badius* and *Nasalis larvatus*). Also, two fossil taxa were included: *Hispanopithecus laietanus* and *Pierolapithecus catalaunicus*. For extant specimens, actual BM was employed when available when museum records; otherwise, predicted body mass, as computed on the basis of Ruff's (2003) equations, was employed. In these cases, femoral head superoinferior diameter was used as the BM estimator; Ruff's (2003) hominoid regression was employed for apes and humans, whereas the total sample regression was employed for cercopithecoids. Two BM estimates of 30 and 35 kg, derived from lumbar vertebral measurements, were employed for *Pierolapithecus* following Moyà-Solà *et al.* (2004). In the case of *Hispanopithecus*, two BM estimates were employed: 34 kg, computed on the basis of several postcranial estimators (Moyà-Solà and Köhler 1996); and a somewhat higher estimate of 39 kg, based on measurements from the femoral head (Moyà-Solà *et al.* 2009).

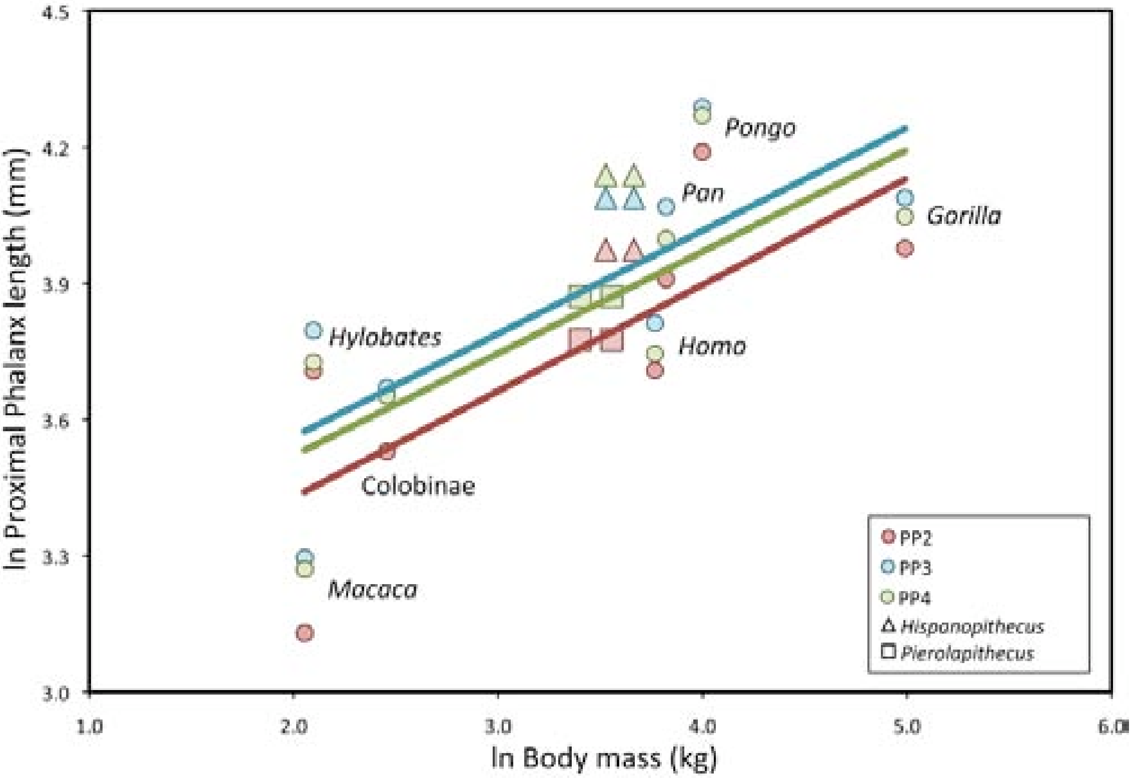
Two different allometric approaches were followed, one based in individual values (Approach 1) and the other one based on mean values for each group (Approach 2). For Approach 1, allometric regressions derived separately for each taxon were compared with one another by means of analysis of covariance (ANCOVA). Also, regressions derived separately for each manual ray in the genus *Pan* were employed as a criterion of substraction for computing allometric residuals for living and fossil individuals, following an approach already employed in Chapter 2. This is warranted because ANCOVA results (see below) showed that differences between allometric slope were not significant between groups. The residuals of relative phalangeal length were computed across the several extant taxa by means of analysis of variance (ANOVA) and post-hoc multiple comparisons (Bonferroni), whereas comparisons between extinct and living taxa were carried out by taking into account the 95% confidence interval for the mean of the several extant groups. With regard to Approach 2, a single regression line was computed on the basis of the mean values of phalangeal length and body mass for each taxonomic group. The resulting best-fist line was not interpreted as reflecting functional equivalence, but as depicting an ‘average’ condition from which the several taxa can differ to some degree. Allometric residuals were computed for each group mean, thus reflecting to what degree the several taxa depart from each other. Residuals were also computed for each individual, and treated statistically as in Approach 1. Statistical computations were made by means of the SPSS v. 16.0 statistical package.

Results

All the allometric regressions of proximal phalanx length vs. body mass (Figure 4.2 and Appendix 4.4) were found to be statistically significant, except for those of *Homo*, which were not. The 95% confidence intervals for the allometric slopes overlap to a considerable degree among the several taxa, and ANCOVA results confirm that the null hypothesis of slope homogeneity cannot be discarded at $p<0.05$ ($p=0.144$, $p=0.078$ and $p=1.59$ for the second, third and fourth manual rays, respectively). Intercepts also overlap to some degree, but ANCOVA results indicate that significant differences exist among several groups at $p<0.001$.

In order to compare the degree of phalangeal elongation between the several groups, in Approach 1, allometric residuals were computed on the basis of the chimpanzee regression line (see Figure 4.3), which is warranted given that homogeneity of slopes cannot be discarded. ANOVA comparisons of the allometric residuals (Figure 4.3; see descriptive statistics in Appendix 4.5) indicate that differences between taxa are statistically significant at $p<0.001$ for the three manual rays studied ($F=248.3$ for PP2L, $F=261.1$ for PP3L, and $F=220.4$ for PP4L). The individual residuals obtained on the basis of Approach 2 (see descriptive statistics in Appendix 4.6) are compatible with those obtained by using Approach 1, and significant differences at $p<0.001$ are also found for the three manual rays ($F=244.1$ for PP3L; $F=263.7$ for PP3L, and $F=223.6$ for PP4L). This coincidence of the results of the two approaches strengthens the view that observed pattern of relative phalangeal length is not an artifact resulting from the use of the chimp regression as the baseline for computing residuals. Post-hoc multiple comparisons (Appendix 4.7) indicate that most pairs of taxa being compared display significant differences regarding relative phalangeal length, except *Gorilla* as compared to *Homo*, and *Pongo* as compared to *Hylobates*, in all instances, as well as in *Macaca* as compared to *Gorilla* and *Homo*, or colobines as compared to *Pan*, in some cases. Overall, these results indicate that there is a gradient of relative phalangeal length that can be correlated with increased arboreality. This gradient is best summarized by the residuals of relative length computed on the basis of mean values for the several taxa (Appendix 4.8), running from macaques to humans + gorillas (-0.13 to -0.17), to colobines (-0.01 to 0.03), to chimpanzees (0.05 to 0.09), to hylobatids (0.18 to 0.26) + orangutans (0.27 to 0.30); see also Figures 4.2 and 4.3, as well as the figure from Appendix 4.2. When the fossil forms are included, *Hispanopithecus* falls between chimpanzees and suspensory taxa regarding manual rays II and III (0.15 to 0.18), whereas regarding the IV manual ray (0.25 to 0.28) it falls very near to the suspensory taxa. *Pierolapithecus* (-0.01 to 0.00), on the contrary, most closely matches the colobine condition, displaying a lower relative length than chimpanzees.

Appendix 4.2. Relative phalangeal length on the basis of mean values for each group, displayed as allometric bivariate plots of bone length versus body mass in extant hominoids, macaques and colobines, separately for manual rays II, III and IV. Note that all the manual rays follow the same allometric trend, although manual ray III is on average the longest and the manual II the shortest, for each taxon. Note also that macaques and, to a lesser degree, humans and gorillas display relatively shorter phalanges than average, whereas there is progressive trend towards larger phalanges than average from chimpanzees to hylobatids to orangutans. This plot clearly shows that *Pierolapithecus* has an average phalangeal length for its body mass (most comparable to colobines), whereas *Hispanopithecus* displays much longer phalanges than average (most comparable to hylobatids and orangutans), irrespective of the body mass estimate employed; the latter also holds irrespective of manual rays III and IV are interchanged with one another. Best-fist lines have been reported in Appendix 4.4.



Appendix 4.3. Included angle (IA) values of phalangeal curvature (in degrees) and index of relative curvature (IRC) for the third manual ray in extant catarrhines (taken from Matarazzo 2008), as compared to the values computed for *Hispanopithecus* and *Pierolapithecus* (from Table 4.1).

	IA PP		**IA MP**		**IRC**	
Taxon	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Hylobates lar	52	0.49	55	0.51	1.06	0.01
Pongo pygmaeus	65	1.33	54	1.38	0.84	0.03
***Ateles* spp.**	51	1.58	53	2.35	1.04	0.03
Pan troglodytes	55	0.88	46	1.28	0.84	0.02
Gorilla g. gorilla	54	1.17	45	0.96	0.85	0.02
Gorilla g. beringei	55	1.48	48	1.24	0.88	0.02
Cebus apella	36	1.01	47	1.32	1.33	0.04
Macaca fascicularis	45	1.48	53	1.30	1.18	0.04
Macaca nemestrina	39	1.23	47	1.73	1.24	0.03
Pierolapithecus catalaunicus	53	—	37	—	0.70	—
Hispanopithecus laietanus	74.5	—	45	—	0.60	—

Abbreviations: SE = standard error; PP = proximal phalanges; MP = middle phalanges.
Notes: IRC = IA MP / IA PP. Data for *Pierolapithecus* based on a fourth PP and third or fourth MP; data for *Hispanopithecus* based on average values for the third and fourth manual rays. SE computed on the basis of standard deviations (SD) and sample sizes (N) reported by Matarazzo (2008: Tables 1 and 2), as SE = SD / √N; the 95% confidence interval for the mean can be computed as ±1.96·SE.

Appendix 4.4. Allometric regressions of proximal phalanx length vs. body size.

			ln BM vs. ln PP2L			
Taxon	**N**	**r**	**SEE**	**p**	**slope**	**intercept**
Pan	47	0.628	0.068	0.000	0.219	3.075
Gorilla	36	0.740	0.061	0.000	0.166	3.157
Pongo	27	0.733	0.058	0.000	0.173	3.505
Homo	15	0.135	0.073	0.631	0.048	3.525
Hylobates	16	0.883	0.051	0.000	0.175	3.424
Macaca	19	0.671	0.090	0.002	0.232	2.661
Colobinae	15	0.777	0.085	0.001	0.320	2.751
All means	7	0.766	0.242	0.045	0.234	2.960

			ln BM vs. ln PP3L			
Taxon	**N**	**r**	**SEE**	**p**	**slope**	**intercept**
Pan	47	0.719	0.058	0.000	0.243	3.144
Gorilla	36	0.738	0.063	0.000	0.170	3.247
Pongo	27	0.716	0.062	0.000	0.177	3.589
Homo	15	0.425	0.063	0.114	0.144	3.267
Hylobates	16	0.884	0.046	0.000	0.161	3.540
Macaca	19	0.717	0.086	0.001	0.252	2.786
Colobinae	15	0.916	0.046	0.000	0.317	2.902
All means	7	0.779	0.224	0.039	0.227	3.108

			ln BM vs. ln PP4L			
Taxon	**N**	**r**	**SEE**	**p**	**slope**	**intercept**
Pan	47	0.681	0.068	0.000	0.252	3.036
Gorilla	35	0.760	0.058	0.000	0.170	3.203
Pongo	27	0.611	0.071	0.001	0.153	3.665
Homo	15	0.369	0.073	0.176	0.141	3.212
Hylobates	16	0.874	0.049	0.000	0.162	3.443
Macaca	19	0.712	0.090	0.001	0.258	2.747
Colobinae	15	0.903	0.043	0.000	0.275	2.986
All means	7	0.777	0.223	0.040	0.225	3.072

Abbreviations: N=sample size; r=correlation coefficient; SEE=standard error of estimate; p=significance; BM=body mass (actual or estimated); PP2L, PP3L, PP4L=length of proximal phalanges from the second, third and fourth manual rays (respectively).

Appendix 4.5. Descriptive statistics for allometric residuals of relative phalangeal length, computed on the basis of the *Pan* allometric regressions reported in Appendix 4.4. The two figures provided for each fossil taxon correspond to the two BM estimates employed in each case.

			Allometric residual of PP2L vs. BM				
Taxon	**N**	**Mean**	**SD**	**95% CI**		**Range**	
Pan	47	0.00	0.07	-0.02	0.02	-0.19	0.11
Gorilla	36	-0.18	0.06	-0.20	-0.16	-0.31	-0.01
Pongo	27	0.25	0.06	0.23	0.27	0.13	0.36
Homo	15	-0.20	0.08	-0.24	-0.15	-0.37	-0.05
Hylobates	16	0.27	0.05	0.24	0.29	0.16	0.34
Macaca	19	-0.39	0.09	-0.43	-0.35	-0.57	-0.26
Colobinae	15	-0.08	0.09	-0.13	-0.03	-0.26	0.04
Hispanopithecus	1	0.12					
Hispanopithecus	1	0.09					
Pierolapithecus	1	-0.04					
Pierolapithecus	1	-0.07					

			Allometric residual of PP3L vs. BM				
Taxon	**N**	**Mean**	**SD**	**95% CI**		**Range**	
Pan	47	0.00	0.06	-0.02	0.02	-0.16	0.11
Gorilla	36	-0.25	0.07	-0.28	-0.23	-0.39	-0.09
Pongo	27	0.18	0.07	0.16	0.21	0.03	0.30
Homo	15	-0.25	0.06	-0.29	-0.22	-0.40	-0.15
Hylobates	16	0.24	0.06	0.20	0.27	0.10	0.35
Macaca	19	-0.34	0.08	-0.38	-0.30	-0.51	-0.21
Colobinae	15	-0.06	0.05	-0.09	-0.04	-0.15	0.04
Hispanopithecus	1	0.09					
Hispanopithecus	1	0.06					

			Allometric residual of PP4L vs. BM				
Taxon	**N**	**Mean**	**SD**	**95% CI**		**Range**	
Pan	47	0.00	0.07	-0.02	0.02	-0.18	0.13
Gorilla	35	-0.24	0.07	-0.26	-0.22	-0.38	-0.09
Pongo	27	0.24	0.08	0.21	0.27	0.01	0.35
Homo	15	-0.25	0.07	-0.29	-0.21	-0.43	-0.14
Hylobates	16	0.23	0.07	0.20	0.27	0.09	0.34
Macaca	19	-0.28	0.09	-0.32	-0.23	-0.46	-0.17
Colobinae	15	0.00	0.04	-0.02	0.03	-0.07	0.07
Hispanopithecus	1	0.21					
Hispanopithecus	1	0.18					
Pierolapithecus	1	-0.02					
Pierolapithecus	1	-0.06					

Abbreviations: SD=standard deviation; CI=confidence interval; other abbreviations as in Appendix 4.4.

Appendix 4.6. Descriptive statistics for allometric residuals of relative phalangeal length, computed on the basis of the 'all means' allometric regressions reported in Appendix 4.4. The two figures provided for each fossil taxon correspond to the two BM estimates employed in each case.

			Allometric residual of PP2L vs. BM				
Taxon	**N**	**Mean**	**SD**	**95% CI**		**Range**	
Pan	47	0.06	0.07	0.04	0.08	-0.14	0.17
Gorilla	36	-0.14	0.07	-0.16	-0.12	-0.27	0.04
Pongo	27	0.31	0.06	0.28	0.33	0.18	0.42
Homo	15	-0.14	0.08	-0.19	-0.10	-0.32	0.01
Hylobates	16	0.35	0.06	0.32	0.38	0.23	0.44
Macaca	19	-0.30	0.09	-0.35	-0.26	-0.48	-0.18
Colobinae	15	0.00	0.09	-0.05	0.04	-0.18	0.13
Hispanopithecus	1	0.18					
Hispanopithecus	1	0.15					
Pierolapithecus	1	0.02					
Pierolapithecus	1	-0.01					

			Allometric residual of PP3L vs. BM				
Taxon	**N**	**Mean**	**SD**	**95% CI**		**Range**	
Pan	47	0.10	0.06	0.08	0.11	-0.06	0.21
Gorilla	36	-0.14	0.07	-0.16	-0.12	-0.28	0.01
Pongo	27	0.28	0.06	0.26	0.31	0.13	0.40
Homo	15	-0.16	0.06	-0.19	-0.12	-0.31	-0.06
Hylobates	16	0.30	0.06	0.27	0.33	0.18	0.40
Macaca	19	-0.27	0.08	-0.31	-0.23	-0.45	-0.14
Colobinae	15	0.01	0.05	-0.02	0.04	-0.08	0.11
Hispanopithecus	1	0.18					
Hispanopithecus	1	0.15					

			Allometric residual of PP4L vs. BM				
Taxon	**N**	**Mean**	**SD**	**95% CI**		**Range**	
Pan	47	0.07	0.07	0.05	0.09	-0.10	0.20
Gorilla	35	-0.14	0.06	-0.16	-0.12	-0.26	-0.01
Pongo	27	0.31	0.07	0.28	0.34	0.10	0.44
Homo	15	-0.18	0.07	-0.22	-0.14	-0.36	-0.07
Hylobates	16	0.25	0.06	0.22	0.28	0.14	0.34
Macaca	19	-0.26	0.09	-0.30	-0.21	-0.45	-0.14
Colobinae	15	0.03	0.04	0.01	0.06	-0.04	0.11
Hispanopithecus	1	0.28					
Hispanopithecus	1	0.25					
Pierolapithecus	1	0.04					
Pierolapithecus	1	0.00					

Abbreviations: SD=standard deviation; CI=confidence interval; other abbreviations as in Appendix 4.4.

Appendix 4.7. Post-hoc multiple comparisons (Bonferroni) for allometric residuals of relative phalangeal length (see descriptive statistics in Appendixes 4.5 and 4.6, for Approaches 1 and 2, respectively).

	Allometric residual of PP2L vs. BM (Approach 1)						**Allometric residual of PP2L vs. BM (Approach 2)**					
	Pan	*Gorilla*	*Pongo*	*Homo*	*Hylobates*	*Macaca*	*Pan*	*Gorilla*	*Pongo*	*Homo*	*Hylobates*	*Macaca*
Gorilla	***						***					
Pongo	***	***					***	***				
Homo	***	NS	***				***	NS	***			
Hylobates	***	***	NS	***			***	***	NS	***		
Macaca	***	***	***	***	***		***	***	***	***	***	
Colobinae	**	***	***	***	***	***	NS	***	***	***	***	***

	Allometric residual of PP3L vs. BM (Approach 1)						**Allometric residual of PP3L vs. BM (Approach 2)**					
	Pan	*Gorilla*	*Pongo*	*Homo*	*Hylobates*	*Macaca*	*Pan*	*Gorilla*	*Pongo*	*Homo*	*Hylobates*	*Macaca*
Gorilla	***						***					
Pongo	***	***					***	***				
Homo	***	NS	***				***	NS	***			
Hylobates	***	***	NS	***			***	***	NS	***		
Macaca	***	***	***	**	***		***	***	***	**	***	
Colobinae	*	***	***	***	***	***	***	***	***	***	***	***

	Allometric residual of PP4L vs. BM (Approach 1)						**Allometric residual of PP4L vs. BM (Approach 2)**					
	Pan	*Gorilla*	*Pongo*	*Homo*	*Hylobates*	*Macaca*	*Pan*	*Gorilla*	*Pongo*	*Homo*	*Hylobates*	*Macaca*
Gorilla	***						***					
Pongo	***	***					***	***				
Homo	***	NS	***				***	NS	***			
Hylobates	***	***	NS	***			***	***	NS	***		
Macaca	***	NS	***	NS	***		***	***	***	*	***	
Colobinae	NS	***	***	***	***	***	NS	***	***	***	***	***

Abbreviations: ***=p<0.001; **=p<0.01; *=p<0.05; NS=non-significant.

Appendix 4.8. Allometric residuals of relative phalangeal length, computed on the basis of mean values for each extant taxon and the ‘all means’ equations reported in Appendix 4.4. The two figures provided for each fossil taxon correspond to the two BM estimates employed in each case.

	Allometric residual		
Taxon	**PP2**	**PP3**	**PP3**
Pan	0.05	0.09	0.07
Gorilla	-0.15	-0.15	-0.15
Pongo	0.29	0.27	0.30
Homo	-0.13	-0.15	-0.17
Hylobates	0.26	0.21	0.18
Macaca	-0.31	-0.28	-0.26
Colobinae	-0.01	0.00	0.03
Hispanopithecus	0.18	0.18	0.28
Hispanopithecus	0.15	0.15	0.25
Pierolapithecus	0.02	—	0.04
Pierolapithecus	-0.01	—	0.00

Abbreviations as in Appendix 4.4.

Chapter 5

Homo habilis or *Paranthropus*?

based on:

Moyà-Solà S, Köhler M, Alba DM, Almécija S (2008). Taxonomic attribution of the Olduvai Hominid 7 manual remains and the functional interpretation of hand morphology in robust australopithecines. *Folia Primatologica* 79: 215-250.

Chapter 5

Homo habilis or *Paranthropus*?

INTRODUCTION

“I am not attempting to urge here that the Olduvai hands forthwith be accepted as belonging to *Paranthropus.* This interpretation seems to me to be at least as good as the other and in some respects even better. What I am suggesting is that we should be open-minded about their affinities until sounder and more complete evidence is available. It seems to me clear that the grounds for assuming them to be associated taxonomically with the cranial material from the same site are wholly inadequate.”
Robinson (1972, pp. 196-197)

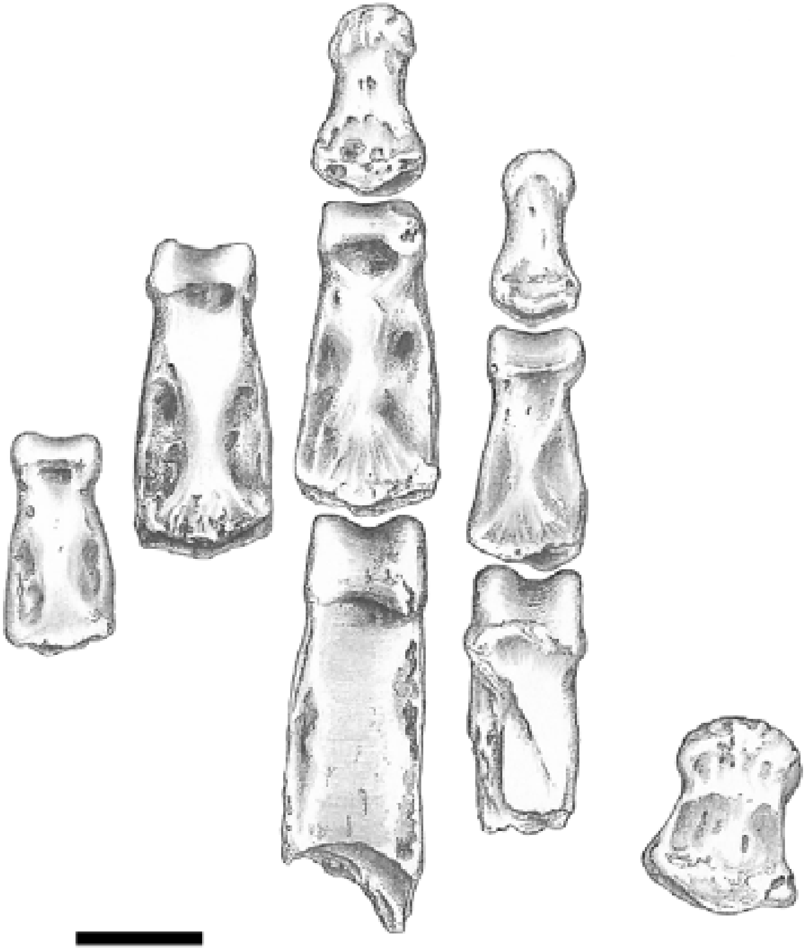


Figure 5.1. Reconstruction of the OH 7 partial hand from Olduvai Bed I, locality FLK NN, in palmar view; only phalanges are included. Scale bar = 1 cm.

The species *Homo habilis* Leakey, Tobias and Napier, 1964 was originally described on the basis of fossil remains discovered at Olduvai Gorge (Tanzania) by Louis and Mary Leakey, including some manual (Leakey 1960) and craniodental (Leakey 1961) remains. Before the formal description of the species, Napier (1962a) already described the fifteen recovered hand bones from Olduvai Bed I locality FLK NN (level 3, ca. 1.75 Ma), corresponding at least to two different individuals, an adult one, and a "juvenile" (subadult) one. Later on, in the original description of the species, Leakey *et al.* (1964) formally designated a holotype (named Olduvai Hominid 7, or OH 7) and several paratypes. The OH 7 holotype was intended to comprise many different bones from the type locality, including not only the craniodental remains (most of a mandibular body, an isolated upper molar, and two parietals), but also most of the available hand bones, which were attributed to a "single juvenile individual" (Leakey *et al.* 1964, p. 8). According to this, the manual remains of OH 7 included (see Figure 1): two fragmentary proximal phalanges (specimens H and I), four middle phalanges without epiphyses (specimens D, E, F and G), a pollical distal phalanx (A) and two additional distal phalanges (B and C) with fused epiphyses, the base of a second metacarpal (O), a trapezium (Q), a scaphoid (P), and a partial capitate (R). Only the two more complete proximal phalanges (specimens J and K), considered to belong to a second, fully adult individual (Napier 1962a), were excluded from the holotype. Instead, they were included by Leakey *et al.* (1964) in the paratype OH 8, which further comprised a quite complete foot and some other postcranial remains. To sum up, ever since the original description of *H. habilis*, the OH 7 manual remains have been generally considered to belong to the right hand of a single subadult individual (Day 1976; Susman 1982). Only the specimen R, interpreted as a capitate (Napier 1962a), has been sometimes excluded from consideration (e.g. Susman and Creel 1979), since it must correspond to the left side (Lewis 1973, 1977; Day 1976).

Nowadays, *H. habilis* is generally accepted as a well-established species. The original definition of the species, however, was problematic from the beginning (Robinson 1965a), so that "For 15 years after the species was created, probably a majority of competent scholars in the field did not accept that *H. habilis* was a valid species" (Tobias 1989, pp. 141-142). Leakey *et al.* (1964) considered that the newly erected species, *H. habilis*, was sufficiently different from *Paranthropus boisei* and other australopithecines on the basis of tooth size and morphology, with the larger brain size and somewhat advanced hand morphology of the former suggesting a closer affinity with the genus *Homo*. The classification of *H. habilis* into the genus *Homo* was based almost exclusively on the craniodental evidence (both endocranial capacity and dental measurements), not on the postcranial one (Tobias 1965, 1989). However, the original describers designated the new species *habilis* (‘handy’), in order to emphasize the tool-making abilities attributed to the new species (Tobias 1965), which further reinforced their taxonomical argument. The OH 7 cranial remains yielded an estimated endocranial capacity of about 650-700 cm^3 (Tobias 1964, 1968, 1971; Vaišnys *et al.* 1984; but see Wolpoff 1981 for a lower estimate). In relative terms, this indicates a degree of encephalization beyond the australopithecine level, thus suggesting that *H. habilis*, and not *Paranthropus boisei*, was the responsible for the Oldowan industry from Olduvai Gorge. In this light, it was certainly a natural assumption that the OH 7 hand, which comes from the same locality as the craniodental remains, and had been previously considered compatible with tool making (Napier 1962b), could not only belong to the same species, but even to the same individual.

After the generalized acceptance of *H. habilis*, however, several problems still remain, particularly regarding the attribution of the postcranial material to *H. habilis*. Thus, while the attribution of the OH 7 hand bones to *H. habilis* has not been questioned by most authors (including recent reviewers, e.g. Wood and Richmond 2000), there have been some significant exceptions. Robinson (1972), who did not even accept the taxonomic validity of *H. habilis* (Robinson 1965a, b), most severely criticized the attribution of the manual specimens to this taxon, and especially the failure of Leakey *et al.* (1964) to take other plausible alternatives into account. The attribution of the OH 7 hand bones to *H. habilis*, as previously noted by Robinson (1972), is almost exclusively grounded on the subadult age of the specimens. Given the inherent weakness of this criterion, and the lack of a sound taphonomical association between the specimens, this taxonomic attribution should not be automatically accepted without further consideration. Rather, it is our contention that morphological criteria must be investigated, in order to test the alternative taxonomic attribution of the postcranial material to *P. boisei*. Robinson (1972) already attempted to solve this question by taking into account the few australopithecine hand specimens known at that time. The number of available fossil hominin hand bones, however, has considerably increased during the last decades, including the *Australopithecus afarensis* remains from Hadar (Bush *et al.* 1982; Alba *et al.* 2003), the *A. africanus* remains from Sterkfontein (Ricklan 1987), and the additional material of *P. robustus* recovered from Swartkrans (Susman 1988a, b, 1989).

Here, we test, on morphological grounds, the currently accepted taxonomic hypothesis that the OH 7 hand specimens can be unambiguously assigned to *H. habilis*. Our morphometric and morphological comparisons with both extant humans and fossil hominins indicate that the alternative hypothesis, that the OH 7 hand bones belong to *Paranthropus*, is by far much more likely than the traditionally accepted one. This has dramatic implications for several hypotheses discussed during the last decades, and particularly for the contention that *Paranthropus* from Sterkfontein was also a toolmaker (Susman 1988a, b, 1989, 1994). On the light of the new taxonomic attribution favored here, we further re-evaluate the morphological adaptations of the *Paranthropus* hand from an evolutionary perspective.

MATERIALS AND METHODS

Methodology and variables employed

In order to test the currently accepted hypothesis that the OH 7 hand remains must be attributed to *Homo* instead of *Paranthropus*, we compared these manual specimens with humans (*H. sapiens*, *H. neanderthalensis* and *H. erectus* s.l.) as well as australopithecines (*A. afarensis*, *A. africanus* and *P. robustus)*. Our aim is to evaluate the taxonomic affinities of the OH 7 hand exclusively on the basis of morphometric and morphological comparisons, independently from the rather circumstantial evidence employed *a priori* by Leakey *et al.* (1964) for attributing the OH 7 hand to *Homo*. The taxonomic attribution of the fossil comparative material employed in this paper is not problematical, except for the isolated hand bones from Swartkrans (South Africa), where both *Homo* and *Paranthropus* have been recorded. Accordingly, the attribution of this material will be discussed with greater detail in the next pages.

We focused our analysis mainly on the OH 7 phalanges (see Figure 5.1) for the following reasons: (1) These are the best-preserved specimens; and (2) These elements can be compared with the corresponding ones in the *P. robustus* collection from

Swartkrans. Numerical analyses were based on both distal and middle phalanges of the OH 7 hand, whereas the two fragmentary proximal phalanges were evaluated on morphological grounds, but where excluded from numerical comparisons. The following measurements were taken in OH 7 and/or in the comparative sample:

(a) Pollical distal phalanx (DP1): Mediolateral shaft width (MLS), mediolateral width of the apical tuft (MLT), and maximum length (L).
(b) Middle phalanges (MP): proximodistal trochlear length (PDA; in palmar view, from the intertrochlear groove to its proximalmost extension), mediolateral trochlear width (MLT), and mediolateral width at midshaft (MLS).
(c) Middle phalanges (MP), proximal phalanges (PP) and metacarpals I (MC1), IV (MC4) and V (MC5): mediolateral width at midshaft (MLS), dorsopalmar height at midshaft (DPS), mediolateral width at head/trochlear region (MLH/MLT), dorsopalmar height at head/trochlear region (DPH/DPT), and maximum length (L).
(d) Middle phalanges of second (MP2) and third (MP3) manual rays: length (L).

Most of the variables employed are standard measurements (e.g. Inouye 1992). In some instances, midshaft area (AS, for metacarpals and phalanges), head area (AH, for metacarpals only) and trochlear area (AT, for phalanges only), was computed as the product between mediolateral and dorsopalmar diameters of these anatomical regions.

The comparative sample only included adult specimens, except in the case of the phalanx from the ‘Turkana boy’ (KNM-WT 15.000-BO), attributed to *H. erectus* s.l. or *H. ergaster*. The presence of fused epiphyses in the distal phalanges of OH 7 indicates that hand growth was nearly completion. The lack of epiphyses in the case of OH 7 middle phalanges, however, precludes an unambiguous comparison when length measurements are involved, since an artifactually shortened diaphysis could potentially increase the perceived robusticity. This is however partially compensated by the bottle-shaped morphology of the OH 7 middle phalanges, with mediolateral width tending to increase when the point of midshaft is displaced towards the base when epiphyses are taken into account. Moreover, results were replicated by taking into account an increase in length based on extant great ape phalanges with non-fused epiphyses.

Statistical comparisons

Several of the measurements above were used in bivariate allometric comparisons, in order to evaluate phalangeal shape (including robusticity): MLS vs. L as well as MLT vs. L in pollical distal phalanges (DP1); PDA vs. MLT in middle phalanges (MP); and MLT vs. MLS, also in middle phalanges. For the purposes of this paper, we define robusticity as a size-corrected shape variable reflecting the relationship between a transverse (mediolateral or dorsopalmar) diameter and length for a particular long bone of the hand. In all instances, allometric techniques were employed by using ln-transformation of individual values and linear regression between two variables (least-squares method), in order to remove size-related scaling effects (see also Alba *et al.* 2003 and Chapters 2 and 3, for more details on this methodology). Indices are not advisable because, in most cases, size variation between two given variables is not linear, and hence the former fail to adequately remove size-related variation. Allometric residuals (the deviations of observed measurements from expected values for an 'average' specimen of that particular size; see Klingenberg 1998) were computed by fitting the allometric equation ($\log y = b \cdot \log x + a$) to logarithmically transformed data (natural logarithms) by means of linear regression. Allometric regressions were therefore employed as a criterion of substraction (e.g. Gould 1975), in order to test for "biomechanical scaling", in which "interspecific proportion differences are required in order to maintain functional equivalence at different body sizes" (Shea 1983, p. 35). Allometric residuals for fossil taxa were computed from the modern human regression line, and then compared with the human residuals. Accordingly, these allometric residuals must be interpreted as size-independent shape variables, reflecting morphological differences with regard to the condition displayed by modern humans. Furthermore, residuals of midshaft area robusticity and head/trochlear area robusticity were computed on the basis of the chimpanzee regression, separately for metacarpals I, IV and V (manual rays separated), as well as proximal phalanges (mixed manual rays II to V) and middle phalanges (mixed manual rays). The resulting allometric residuals reflect differences with regard to the chimpanzee condition, which is currently the best available proxy for an ancestral condition for both humans and australopithecines; comparable results would have been obtained by employing human-derived instead of chimp-derived residuals. Finally, an index of phalangeal length between second and third middle phalanges was computed as a shape ratio for both humans and baboons, in order to evaluate this relationship in fossil hominins and geladas. In this particular case, the allometric regression between the two variables was found to be isometric; accordingly, allometric residuals were not required for removing size-scaling effects. When possible, residuals (and indices) were compared by means of analysis of variance (ANOVA) and post-hoc multiple comparisons (Bonferroni method), although this was not possible in the case of fossil taxa when only a single specimen was available; in those cases, the residual for the fossil taxon was compared with the 95% confidence interval for the mean and with the maximum-minimum range of other taxa. Statistical comparisons were carried out with SPSS v. 14.0.

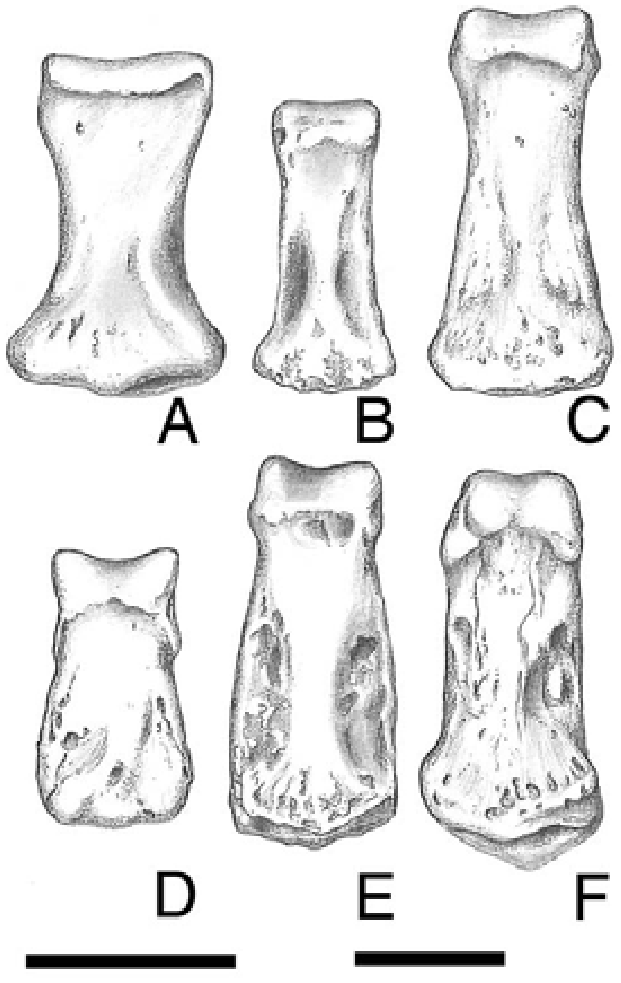


Figure 5.2. Comparison of middle phalanges of hominin and selected non-hominin taxa, in palmar view: (**A**) *H. neanderthalensis*; (**B**) *H. erectus* s.l. KNM-WT 15.000-BO from Nariokotome; (**C**) *H. sapiens*; (**D**) *Theropithecus gelada*; (**E**) OH 7 (specimen E) from Olduvai Gorge Bed 1, locality FLK NN; (**F**) *P. robustus* SKX 5021 from Swartkrans Member 1. Scale bars = 1 cm; left scale bar for (**D**), right bar for the rest.

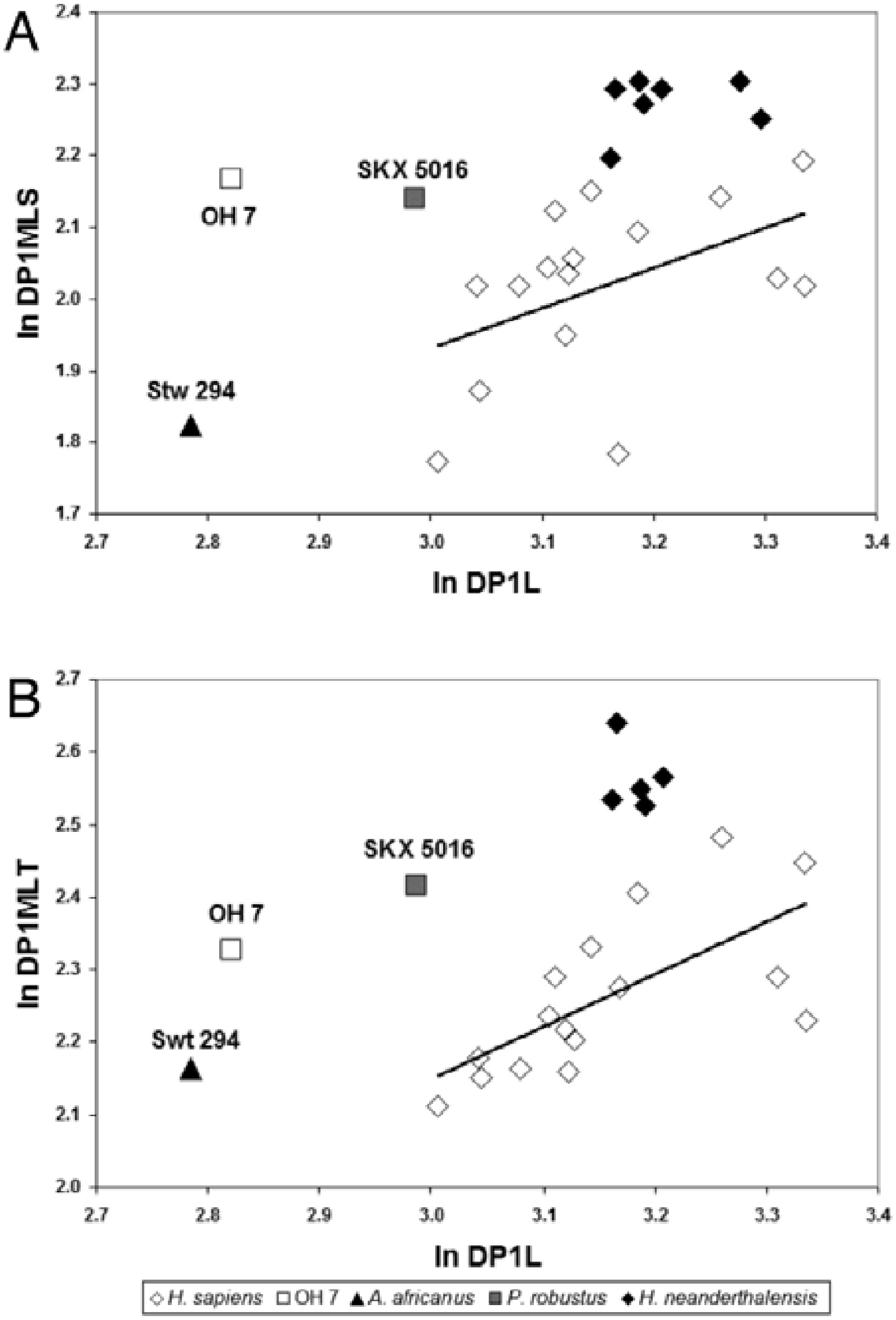


Figure 5.3. Allometric bivariate plot of ln-transformed data in order to evaluate the mediolateral robusticity of the pollical distal phalanx: (**A**) Robusticity of the shaft; and (**B**) Robusticity of the distal tuft. Abbreviations: DP1 = pollical distal phalanx; MLS = mediolateral width of the shaft; MLT = mediolateral width of the apical tuft; L = length. The continuous line corresponds to *H. sapiens*. Note the similar position of SKX 5016 (attributed to *Paranthropus robustus*) and OH 7 (attributed here to *P.* cf. *boisei*), which display a considerable robusticity as compared to modern humans, Neandertals, and the australopithecine *A. africanus* (Stw 294). Human allometric regression equations: (**A**) ln DP1MLS = 0.563 ln DP1L + 0.242, r = 0.480, p=0.060, N=16; (**B**) ln DP1MLT = 0.722 ln DP1L – 0.018, r = 0.684, p< 0.001, N=16.

Comparative sample

With regard to the fossil material included in the comparisons, besides OH 7, it includes: phalanges of *P. robustus* from Swartkrans (South Africa; Susman 1988a, b, 1989), including SKX 5021, 36712, 9449, 35439 and 5019; *A. afarensis* from Hadar AL 333 (Ethiopia; Bush *et al.* 1982); *A. africanus* from Sterkfontein (South Africa), including Stw 28 and Stw 293 (Ricklan 1987); *H. erectus* s.l. from Nariokotome (Kenya; KNM-WT 15.000-BO; Walker and Leakey 1993); and *H. neanderthalensis* from Shanidar and Kebara (Israel; Trinkaus 1983; Vandermeersch 1991). Measurements of the above-mentioned fossils specimens where taken from casts when not available from the literature. The extant comparative sample included modern humans (*H. sapiens*) in all instances, as well as chimpanzees (*Pan troglodytes*) for computing midshaft robusticity, and humans (*H. sapiens*) and baboons (*Papio* sp.) for computing relative length of middle phalanges between manual rays II and III. Measurements where partially taken by the authors, but in the case of *Theropithecus*, mean data for extant geladas (*Theropithecus gelada*) were taken from Etter (1973), whereas data for the extinct *T. brumpti* were taken from Jablonski (1986) and Jablonski *et al.* (2002). Manual ray assignment in the case of *A. afarensis* followed Alba *et al.* (2003).

RESULTS

The reconstruction of the OH 7 hand has been depicted in Figure 5.1, while in Figure 5.2 one of its middle phalanges (the fourth one) is compared with phalanges of other hominin and selected non-hominin taxa. Regressions for evaluating shaft and tuft robusticity of the pollical distal phalanx (Figure 5.3 and Table 5.1) suggest negative allometry for shaft and tuft width vs. total length. Although there is a considerable scatter of extant human specimens, Neandertals significantly display stouter pollical distal phalanges with regard to midshaft (F=27.636, p<0.001) and tuft (F=54.318, p<0.001). In the case of australopithecines, no post-hoc multiple comparisons can be carried out. However, while *A. africanus* (Stw 294) only displays higher robusticity than modern humans in the case of the distal tuft, both *P. robustus* (as represented by SKX 5016) and OH 7 display much higher residuals for both the tuft and the midshaft. The higher residuals of *P. robustus* and OH 7 are quite similar and roughly comparable to those of Neandertals, although OH 7 even exceeds the latter with regard to shaft robusticity.

Regressions for assessing the relative proximodistal extension of the distal trochlea in middle phalanges (Figure 5.4 and Table 5.1) suggest slightly negative allometry for proximodistal extension of the distal trochlea vs. mediolateral trochlear width. ANOVA comparisons with the allometric residuals on the basis of the human regression indicate that there are significant differences (F=18.466, p<0.001), al least in some cases. The middle phalanx of the 'Turkana boy', in fact, does not show significant differences with regard to modern humans, whereas the Swartkrans phalanx SKX 13476, like the Neandertal specimen investigated, tend to display smaller values than extant humans, although within their maximum-minimum range. However, in the case of australopithecines, both gracile and robust ones display much larger values than modern humans. When more than a single specimen is included in the comparisons, either their confidence intervals or their maximum-minimum ranges overlap with the corresponding values in humans, indicating that these differences are statistically significant. The same is true for the OH 7 middle phalanges. When taxa represented by a single specimen are excluded, in order to carry on post-hoc multiple comparisons, the overall ANOVA results remain significant (F=32.470, p<0.001). The pairwise comparisons on the basis of the Bonferroni method indicate that the allometric residuals of *A. afarensis, P. robustus* and OH 7 differ from modern humans at p<0.001, whereas no statistically significant differences can be found to this regard between robust and gracile australopithecines, or between OH 7 and either of them (p=1.000 in the case of *P. robustus* as well as *A. africanus*).

Regressions for investigating relative trochlear width in middle phalanges (Figure 5.5 and Table 5.1) indicate considerable negative allometry for trochlear width vs. midshaft width. ANOVA comparisons with the allometric residuals on the basis of the human regression indicate that there are significant differences (F=34.874, p<0.001) among the several taxa. SKX 13476 from Swartkrans, like *H. erectus* s.l from Nariokotome, fall slightly below the human regression line, outside the confidence interval, but still within the maximum-minimum range. Neandertal specimens, on the contrary, are placed considerably above the human regression line, although the ranges between these two human species overlap to some degree. Just the contrary occurs in australopithecines, both gracile and robust, and especially in OH 7. When the taxa represented by a single specimen are excluded from the comparisons, in order to perform post-hoc multiple comparisons, differences are even more significant (F=58.352, $p<0.001$). Pairwise comparisons among the several taxa indicate that modern humans significantly differ from all the other species considered at $p<0.001$, by displaying trochlear areas relatively wider than australopithecines, but relatively narrower than Neandertals (which autapomorphically display considerably wider trochleae than all the remaining taxa). No significant differences, on the contrary, can be found between gracile and robust australopithecines ($p=0.609$), or between OH 7 and australopithecines, either gracile or robust ($p=1.000$ in the case of *P. robustus*, and $p=0.325$ in the case of *A. afarensis*).

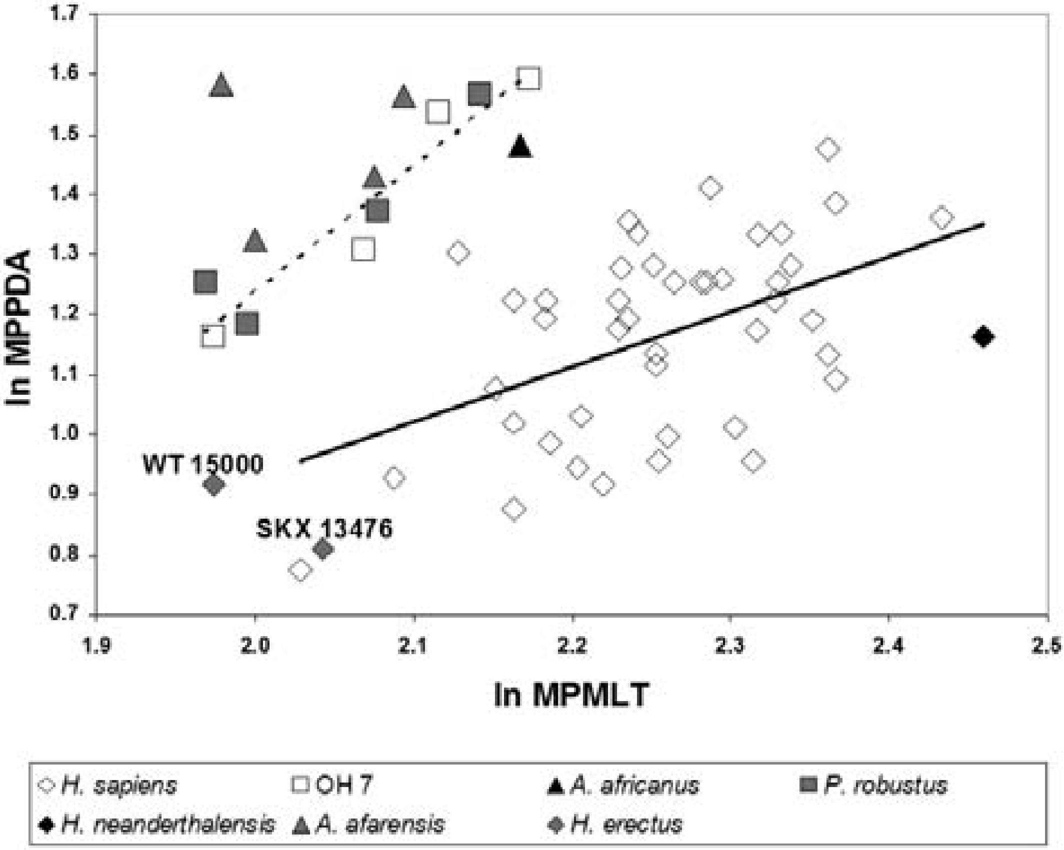


Figure 5.4. Allometric bivariate plot of ln-transformed data in order to evaluate the proximodistal extension of the distal trochlea of middle phalanges relative to mediolateral width. Abbreviations: MP = middle phalanges; PDA = proximodistal length of the distal trochlea in palmar view; MLT = mediolateral trochlear width. The continuous line corresponds to *H. sapiens*, while the discontinuous one corresponds to *Paranthropus* spp. (*P. robustus* as well as OH 7, which we attribute to *P.* cf. *boisei*). Note the position of Swartkrans middle phalanx SKX 13476, which we attribute to *Homo* due to similarities with human phalanges, and particularly the *H. erectus* s.l. specimen WT 15000 from Nariokotome. Note also the greater robusticity of australopithecine phalanges, i.e. *Australopithecus* spp. as well as *Paranthropus* spp. (including the OH 7 phalanges). Human allometric regression equation: $\ln \mathrm{MPPDA} = 0.911 \ln \mathrm{MPMLT} - 0.892$, $r = 0.495$, $p< 0.001$, $N = 46$.

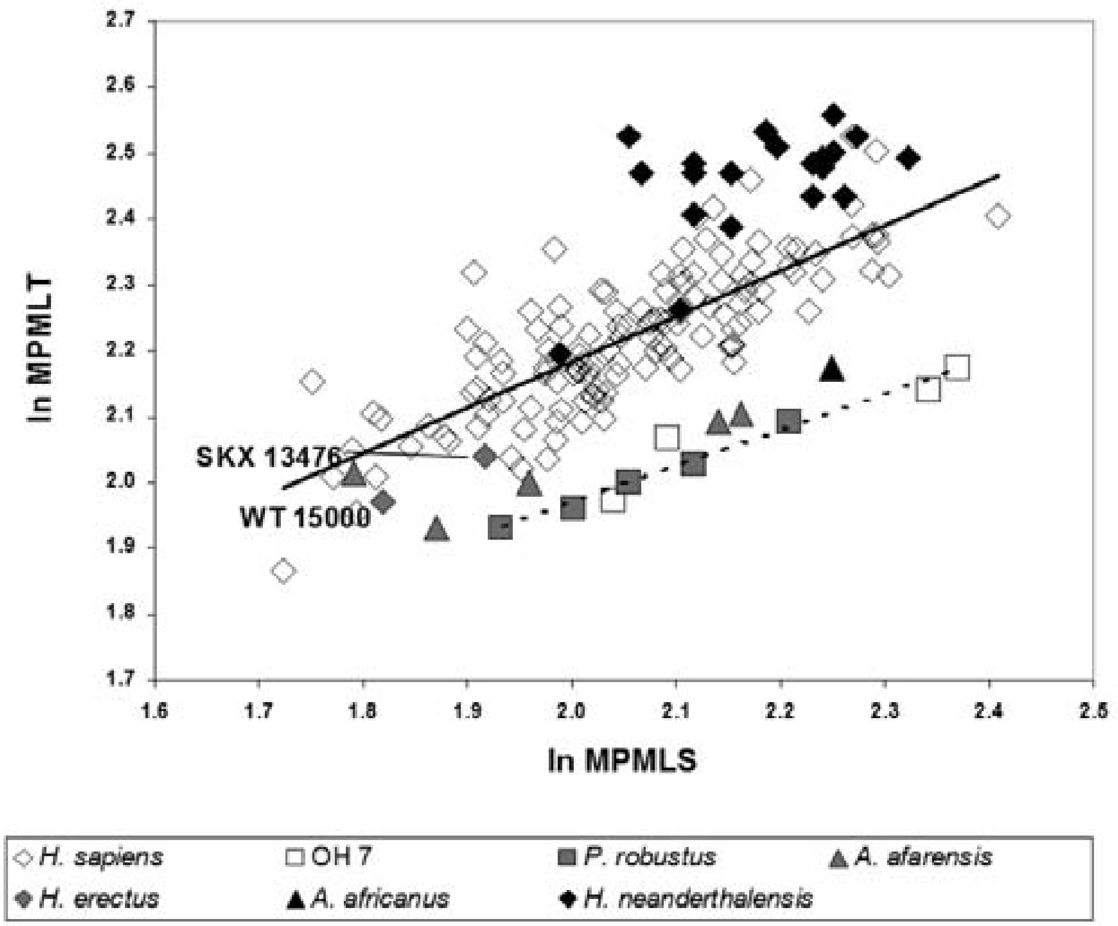


Figure 5.5. Allometric bivariate plot of ln-transformed data in order to evaluate trochlear width relative to midshaft width in middle phalanges (mixed manual rays). Abbreviations: MP = middle phalanges; MLT = mediolateral trochlear width; MLS = mediolateral midshaft width. The continuous line corresponds to *H. sapiens*, while the discontinuous one corresponds to *Paranthropus* spp. (*P. robustus* as well as OH 7, attributed here to *P.* cf. *boisei*). Note that while Neandertals tend to display relatively broader trochleae than modern humans, australopithecines display the opposite condition. This is particularly accentuated in *Paranthropus* spp. (including the OH 7 phalanges), whereas *Australopithecus* spp. display a less extreme condition. Human allometric regression equation: ln MPMLT = 0.693 ln MPMLS + 0.797, r = 0.804, <0.001, p= N = 131.

Table 5.1. Descriptive statistics of allometric residuals computed on the basis of human allometric equations reported in Figures 5.3 to 5.5.

Allometric residual of shaft mediolateral robusticity of the pollical distal phalanx (DP1MLS vs. DP1L) (Figure 5.3)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	16	0.00	0.11	-0.06	0.06	-0.24	0.14
OH 7	1	0.34	--	--	--	--	--
***P. robustus* (SKX5016)**	1	0.22	--	--	--	--	--
***A. africanus* (Stw 294)**	1	0.01	--	--	--	--	--
H. neanderthalensis	7	0.22	0.04	0.18	0.26	0.15	0.27

Allometric residual of tuft mediolateral robusticity of the pollical distal phalanx (DP1MLT vs. DP1L) (Figure 5.3)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	16	0.00	0.08	-0.04	0.04	-0.16	0.15
OH 7	1	0.31	--	--	--	--	--
***P. robustus* (SKX5016)**	1	0.28	--	--	--	--	--
***A. africanus* (Stw 294)**	1	0.17	--	--	--	--	--
H. neanderthalensis	5	0.28	0.05	0.22	0.35	0.24	0.37

Allometric residual of relative proximodistal extension of the distal trochlea in middle phalanges (MPPDA vs. MPMLT) (Figure 5.4)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	46	0.00	0.14	-0.04	0.04	-0.26	0.26
OH 7	4	0.39	0.13	0.19	0.60	0.26	0.50
P. robustus	4	0.37	0.10	0.21	0.53	0.26	0.51
A. afarensis	4	0.51	0.13	0.31	0.71	0.39	0.67
A. africanus **(Stw 331)**	1	0.40	--	--	--	--	--
Homo **sp. (SKX 13476)**	1	-0.16	--	--	--	--	--
H. erectus **(KNM-WT 15000)**	1	0.01	--	--	--	--	--
H. neanderthalensis	1	-0.19	--	--	--	--	--

Allometric residual of relative trochlear mediolateral width in middle phalanges (MPMLT vs. MPMLS) (Figure 5.5)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	131	0.00	0.07	-0.01	0.01	-0.13	0.20
OH 7	4	-0.24	0.04	-0.31	-0.17	-0.28	-0.18
P. robustus	5	-0.22	0.01	-0.24	-0.21	-0.23	-0.20
A. afarensis	5	-0.14	0.07	-0.23	-0.06	-0.19	-0.02
A. africanus **(Stw 331)**	1	-0.18	--	--	--	--	--
Homo **sp. (SKX 13476)**	1	-0.08	--	--	--	--	--
H. erectus **(KNM-WT 15000)**	1	-0.09	--	--	--	--	--
H. neanderthalensis	20	0.15	0.07	0.12	0.18	0.01	0.31

Abbreviations: DP1MLS = mediolateral width of the shaft of distal pollical phalanx; DP1MLT = mediolateral width of the apical tuft of distal pollical phalanx; DP1L = length of distal pollical phalanx; MPPDA = proximodistal length of the distal trochlea in middle phalanges; MPMLT = mediolateral trochlear width in middle phalanges; MPMLS = mediolateral midshaft width in middle phalanges; N = sample size; SD = standard deviation; CI = confidence interval.

With regard to residuals indicating robusticity at midshaft (Figures 5.6A and 5.7, and Table 5.2), the results for OH 7 are restricted to middle phalanges, and even in this case, caution should be taken when interpreting the results, since the OH 7 middle phalanges lack the epiphyses. Relative robusticity was also investigated for some metacarpals as well as proximal phalanges in other selected taxa, including humans, but also *P. robustus*, *A. afarensis* and *H. neanderthalensis*. In all these instances, the chimpanzee regression was taken as the standardization criterion, by computing the residuals on the basis of the chimpanzee regression line. ANOVA comparisons on the basis of these residuals between humans and chimpanzees indicate that significant differences can be found regarding midshaft robusticity in middle phalanges (F=277.795, p<0.001), proximal phalanges (F=95.447, p<0.001), and metacarpals I (F=157.941, p<0.001), IV (F=141.769, p<0.001) and V (F=132.537, p<0.001). In all instances, humans display a greater robusticity than chimps, this difference being the greater in pollical metacarpals, and the lesser in proximal phalanges (see mean allometric residuals for humans in Table 5.2). When fossil taxa are taken into account, post-hoc multiple comparisons can be only carried out in the case of phalanges, not metacarpals (with the exception of *H. neanderthalensis* and the fifth metacarpal in *A. afarensis*). The comparison of single australopithecine values with the human confidence interval, however, suggest that *A. afarensis* display values of midshaft robusticity in metacarpals somewhat lower than humans, approximately intermediate between them and chimps, although within the human confidence interval except in the case of the fifth metacarpal. In the latter case, *A. afarensis* is still intermediate between humans and chimpanzees, with the two available values falling outside the confidence intervals of both. However, *A. afarensis* cannot be shown to statistically differ from either of them to this regard (p=0.542 and p=0.383, respectively), due to small sample size. *P. robustus*, on the contrary, displays residual values above the human confidence intervals, thus indicating significantly greater degrees of metacarpal robusticity, although these differences cannot be tested by using post-hoc multiple comparisons. Like *Paranthropus*, Neandertals display a greater degree of first metacarpal robusticity at midshaft than *H. sapiens* (although differences are not statistically significant, probably due to small sample size); unlike *Paranthropus*, however, robusticity of fourth of fifth metacarpals in Neandertals is most comparable to extant humans.

Table 5.2. Descriptive statistics of allometric residuals of midshaft robusticity computed on the basis of the chimpanzee allometric equations reported in Figure 5.6.

Allometric residual of midshaft robusticity of metacarpal I (MC1AS vs. MC1L)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	59	0.45	0.19	0.40	0.50	0.06	0.98
H. neanderthalensis	2	0.68	0.08	-0.05	1.41	0.62	0.74
P. troglodytes	64	0.00	0.21	-0.05	0.05	-0.53	0.83
A. afarensis	1	0.35	--	--	--	--	--
P. robustus	1	0.58	--	--	--	--	--

Allometric residual of midshaft robusticity of metacarpal IV (MC4AS vs. MC4L)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	57	0.34	0.18	0.29	0.39	-0.04	0.96
H. neanderthalensis	3	0.40	0.08	0.19	0.61	0.31	0.47
P. troglodytes	63	0.00	0.13	-0.03	0.03	-0.28	0.24
A. afarensis	1	0.29	--	--	--	--	--
P. robustus	1	0.77	--	--	--	--	--

Allometric residual of midshaft robusticity of metacarpal V (MC5AS vs. MC5L)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	60	0.38	0.19	0.33	0.43	-0.10	0.76
H. neanderthalensis	2	0.37	0.21	-1.52	2.27	0.22	0.52
P. troglodytes	65	0.00	0.17	-0.04	0.04	-0.41	0.64
A. afarensis	2	0.20	0.03	-0.08	0.48	0.18	0.22
P. robustus	1	0.62	--	--	--	--	--

Allometric residual of midshaft robusticity of proximal phalanges (PPAS vs. PPL)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	188	0.19	0.18	0.17	0.22	-0.22	0.63
H. neanderthalensis	15	0.48	0.12	0.41	0.55	0.29	0.68
P. troglodytes	212	0.00	0.21	-0.03	0.03	-0.53	0.53
A. afarensis	8	0.16	0.17	0.01	0.30	-0.08	0.51
P. robustus	3	0.56	0.11	0.29	0.83	0.43	0.62

Allometric residual of midshaft robusticity of middle phalanges (MPAS vs. MPL)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	148	0.35	0.19	0.31	0.38	-0.21	0.85
H. neanderthalensis	20	0.80	0.24	0.68	0.91	0.34	1.22
P. troglodytes	199	0.00	0.19	-0.03	0.03	-0.56	0.63
A. afarensis	5	0.39	0.08	0.29	0.49	0.26	0.48
P. robustus	5	0.71	0.09	0.60	0.82	0.58	0.82
OH 7	4	0.68	0.10	0.52	0.83	0.55	0.78
OH 7 (corrected)	4	0.62	0.09	0.48	0.76	0.53	0.71

Abbreviations: N = sample size; SD = standard deviation; CI = confidence interval.

When fossil taxa are taken into account with regard to phalangeal robusticity at midshaft, ANOVA results remain significant for both proximal (F=43.024, $p<0.001$) and middle (F=112.091, $p<0.001$) phalanges. In the case of proximal phalanges, post-hoc comparisons fail to find significant differences between *A. afarensis* and either chimpanzees (p=0.240) and humans (p=1.000), thus confirming the somewhat intermediate degree of robusticity of this taxon. On the contrary, *P. robustus* displays significant differences not only from chimpanzees ($p<0.001$), but also with regard to humans ($p<0.05$) and *A. afarensis* ($p<0.05$), thus indicating that the hand of this taxon is extraordinarily robust not only with regard to metacarpals, but also proximal phalanges. The middle phalanges of Neandertals are more robust than chimpanzees ($p<0.001$), *A. afarensis* ($p<0.01$) and humans ($p<0.001$), but they cannot be shown to statistically differ from *P. robustus* (p=1.000). Finally, when middle phalanges are taken into account, humans and gracile australopithecines are totally comparable (p=1.000), being both significantly more robust than chimpanzees at $p<0.001$. Again, *P. robustus* is more robust than chimpanzees and humans ($p<0.001$), but differences with regard to *A. afarensis* cannot be statistically demonstrated (p=0.147), probably due to small sample size, since neither their respective confidence intervals nor ranges overlap. Again, Neandertals significantly differ from chimps, extant humans and gracile australopiths ($p<0.001$), but cannot be shown to differ from *P. robustus* (p=1.000). Similarly, the OH 7 middle phalanges can be shown to be more robust than either chimpanzees ($p<0.001$) and humans ($p<0.01$), but they fail to significantly differ from *A. afarensis* (p=0.417), again probably due to small sample sizes, since the mean robusticity value of the OH 7 phalanges is about 75% higher than the *A. afarensis* one. No statistical differences can be found between OH 7 and *P. robustus* with regard to the midshaft robusticity of middle phalanges (p=1.000), although Neandertals neither differ from any of these taxa (p=1.000). When the total length of the OH 7 middle phalanges is estimated by taking into account a 7% length increase (this factor being computed on the basis of extant great ape phalanges), and the point of midshaft measurements is displaced accordingly, significant results are obtained only with regard to chimps ($p<0.001$), do not showing differences with either modern humans (p=0.068) or the remaining taxa (p=1.000).

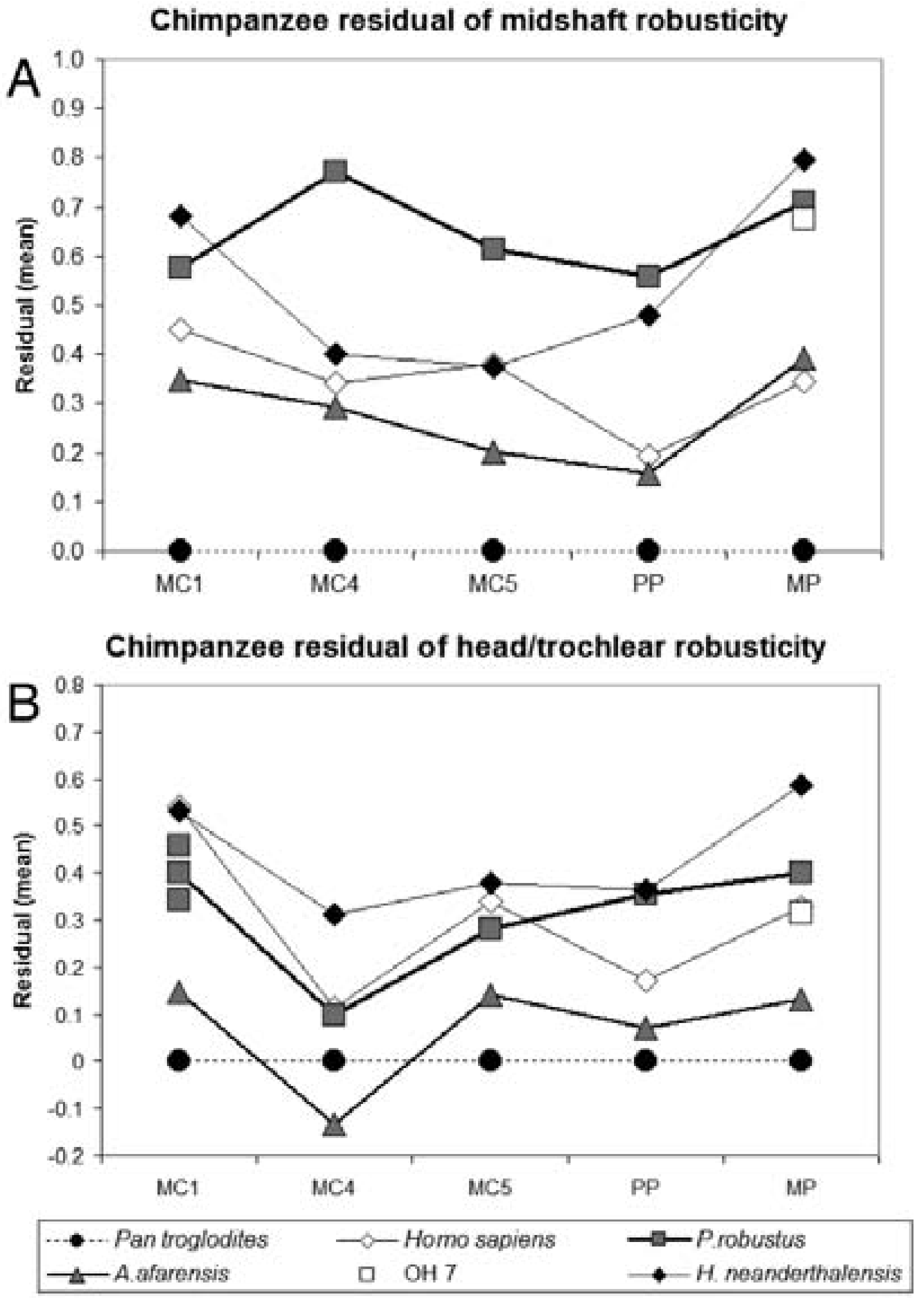


Figure 5.6. Allometric residuals of midshaft robusticity (**A**) and head/trochlear robusticity (**B**), computed on the basis of the allometric regressions of midshaft area and head/trochlear area (respectively) vs. bone length in chimpanzees. Regressions computed separately for metacarpals I, IV and V (separately), as well as proximal phalanges and middle phalanges (rays II to V together). The position of OH 7 should be interpreted cautiously: given the lack of epiphyses, the actual residuals should be somewhat lower. Chimpanzee allometric equations: ln MC1AS = 1.108 ln MC1L – 0.069, r = 0.428, p< 0,001, N = 64; ln MC4AS = 1.445 ln MC4L – 2.270, r = 0.658, p< 0.001,N = 63; ln MC5AS = 0.842 ln MC5L + 0.213, r = 0.359, p< 0.01, N = 65; ln PPAS = 1.885 ln PPL – 3.108, r = 0.789, < 0.001, N = 212; ln MPAS = 1.421 ln MPL – 1.307, r = 0.819, p< 0.001, N = 199; ln MC1AH = 1.065 ln MC1L + 0.656, r = 0.557, p< 0.001, N = 63; ln MC4AH = 1.229 ln MC4L – 0.081, r = 0.503, p< 0.001, N = 61; ln MC5AH = 1.065 ln MC5L + 0.312, r = 0.455, p< 0.001, N = 63; ln PPAT = 1.866 ln PPL – 2.718, r = 0.862, p< 0.001, N = 209; ln MPAT = 1.276 ln MPL – 0.563, r = 0.859, p< 0.001, N = 198. Abbreviations: MC1 = pollical metacarpal; MC4 = fourth metacarpal; MC5 = fifth metacarpal; PP = proximal phalanges (II to V); MP = middle phalanges (II to V); AS = midshaft area (computed as the product between mediolateral width and dorsopalmar height); AH/AT = head/trochlear area (for metacarpals and phalanges, respectively; computed as the product between mediolateral width and dorsopalmar height); L = length.

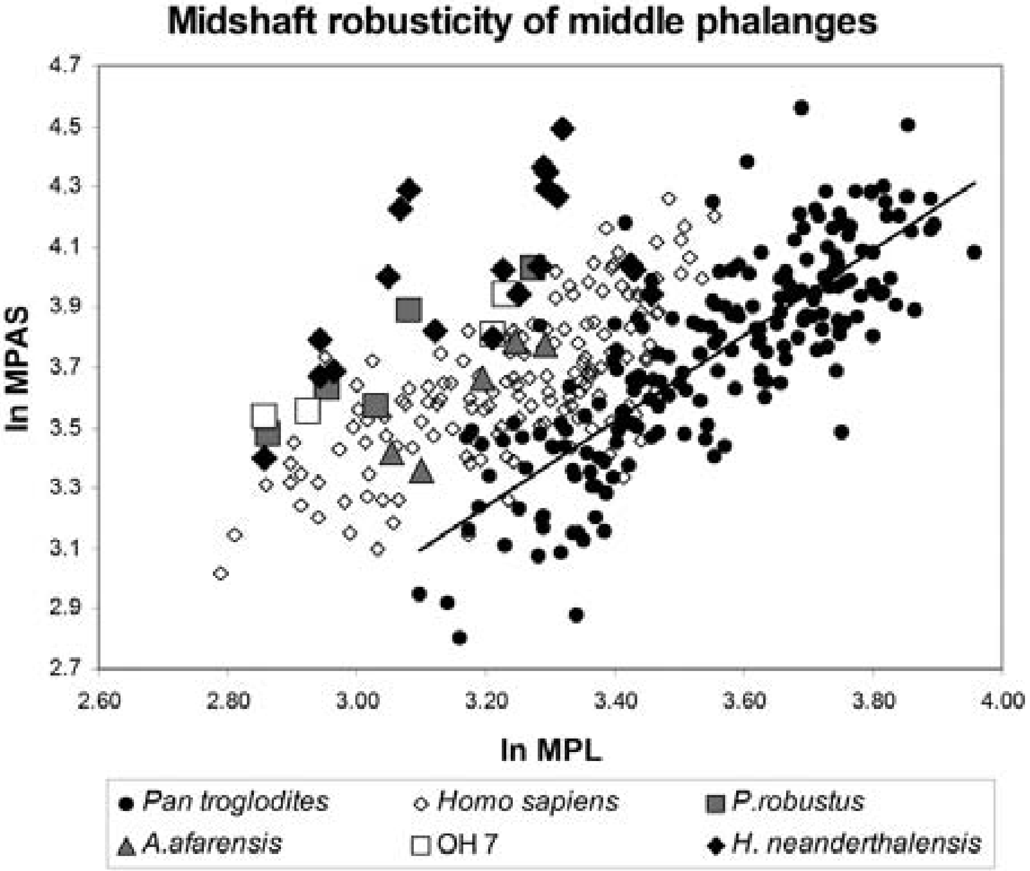


Figure 5.7. Allometric bivariate plot of ln-transformed data in order to evaluate midshaft robusticity, i.e. area relative to bone length in middle phalanges (mixed manual rays II to V). Abbreviations as in Figure 5.6. The regression line is derived for chimpanzees, and is reported in the legend of Figure 5.6. The position of OH 7 should be interpreted cautiously, given the lack of epiphyses (see text for further details).

When the same analysis of robusticity is repeated for head/trochlear area (Figure 5.6B and Table 5.3) ANOVA comparisons between humans and chimpanzees indicate that significant differences can be found in all instances, with the former being always more robust: middle phalanges (F=378.322, $p<0.001$), proximal phalanges (F=124.795, $p<0.001$), and metacarpals I (F=382.889, $p<0.001$), IV (F=15.578, $p<0.001$) and V (F=140.635, $p<0.001$). All australopithecines display a degree of metacarpal head robusticity more or less intermediate between humans and chimpanzees, except the fourth metacarpal of *A. afarensis*, where robusticity is lower than in chimps. *P. robustus* displays higher values than *A. afarensis* but lower than in humans, even when the degree of uncertainty for the pollical metacarpal is taken into account. Neandertals tend to display a higher robusticity only in the case of the fourth metacarpal, but differences cannot be shown to be statistically significant in any instance. With regard to trochlear robusticity in phalanges, ANOVA results for humans and chimps indicate that differences remain significant for both proximal (F=42.662, p<0.001) and middle (F=100.551, p<0.001) phalanges. In gracile australopithecines, residuals of trochlear robusticity for proximal phalanges are only slightly higher than in chimpanzees, and no differences can be found as compared to either humans (p=0.728) or chimps (p=1.000). Robust australopithecines and Neandertals, on the contrary, display much higher residuals. Neandertals differ from all the remaining taxa (p<0.001) except robust australopiths (p=1.000), whereas the latter can be shown to differ from chimps (p<0.001), but neither from extant humans (p=0.392) or gracile australopiths (p=0.064). Finally, when middle phalanges are taken into account, *A. afarensis* displays again a somewhat intermediate condition, although it cannot be shown to differ from either humans (p=0.067) or chimps (p=0.842). *P. robustus* and especially Neandertals, on the contrary, display much higher residuals. Robust australopiths are thus significantly more robust than chimps (p<0.001), and more comparable with Neandertals (p=0.216) and especially extant humans (p=1.000), whereas differences with regard to *A. afarensis* are not statistically significant (p=0.078), possibly due to small sample sizes. Neandertals are even more robust, differing from all the remaining taxa, except *P. robustus*, at p<0.001. OH7 also displays high trochlear robusticity residuals, thus being stouter than chimps (p<0.001), but comparable to *A. afarensis* and, especially, *P. robustus* and modern humans (p=1.000). Interestingly, OH 7 significantly differs from Neandertals (p<0.05) by displaying a less extreme degree of robusticity to this regard.

When the overall patterns or robusticity for metacarpals and phalanges is compared simultaneously, either for midshaft (Figure 5.6A) or head/trochlear (Figure 5.6B) values, some interesting patterns become clearer. Both at midshaft and at the distal region, extant humans and, especially, Neandertals are always more robust than chimpanzees, although the amount of the difference depends on both the particular variable and the particular bone that are being considered. Differences between humans and chimpanzees are most evident at the pollical metacarpal, with regard to both midshaft and, especially, head robusticity. As compared to chimps, the fourth metacarpal is only slightly more robust in modern humans, whereas the fifth one is also markedly more robust, although not as much as the first one. Similarly, both proximal and middle phalanges are more robust (especially in Neandertals, but also in modern humans), with robusticity being greater in middle than in proximal phalanges. Gracile australopiths, as represented by *A. afarensis*, resemble modern humans in the pattern of midshaft robusticity (albeit being somewhat less robust in the case of the first and fifth metacarpals), whereas with regard to head/trochlear robusticity, they display a human-like pattern but at lower robusticity values, intermediate between modern humans and chimpanzees (except in the case of the fourth metacarpal, which is comparatively less robust). Robust australopithecines, as represented by *P. robustus*, display a pattern similar to gracile australopithecines, but at higher values of robusticity. Thus, in the case of midshaft robusticity, *P. robustus* is more robust than modern humans and *A. afarensis*, although the former taxon further differs from humans by the low degree of first metacarpal robusticity as compared to the rest of the hand. Only Neandertals display high levels of midshaft robusticity comparable to *P. robustus* in some instances, particularly the first metacarpal and the phalanges. Regarding head/trochlear robusticity, *P. robustus* more closely resembles humans than any other taxon, although differing from modern humans (but not Neandertals) by the higher degree of phalangeal robusticity, especially at the proximal ones. The OH 7 middle phalanges display high degrees of robusticity, closely resembling *P. robustus* and Neandertals in the case of midshaft robusticity, and further resembling *P. robustus* and modern humans (but not Neandertals, which display higher values) in the case of trochlear robusticity. As such, the OH 7 middle phalanges only fit the robust australopithecine model, when midshaft and trochlear robusticity values are taken into account simultaneously.

Finally, with regard to the relationship between the length of middle phalanges of manual rays II and III, an allometric plot has been reported in Figure 5.8. In spite of the fact that modern humans and baboons display non-overlapping size ranges for the length of these middle phalanges, a single allometric regression was employed (Figure 8), since the two separate regressions (not reported) were virtually identical. This indicates that humans and baboons, despite many differences in hand use, display very similar proportions at different size ranges. Interestingly, the 95% confidence interval for the slope does not permit to exclude isometry, whereas the confidence interval for the intercept indicates that the latter is significantly different from zero. This reflects the fact that, in this particular case, shape is proportionally maintained in spite of size increase, not only within taxa, but also between them, even though one of the variables (MP2L) is smaller than the other (MP3L). Since the length ratio between the second and the third middle phalanges is not affected by allometry, there is no need to employ residuals, so that a simple shape index MP2L / MP3L was employed instead (Figure 5.8 and Table 5.4). ANOVA comparisons between humans and baboons did not find significant differences to this regard (F=0.049, p=0.825), and both the mean values and the 95% confidence intervals for the mean were the same in both. On the contrary, the OH 7 phalangeal index, like those of extant as well as fossil geladas, was significantly lower, indicating relatively shorter index middle phalanges. Since the OH 7 and gelada indices fell outside the 99.9% confidence intervals for the human and baboon mean, it can be asserted that these differences are significant at the p<0.001 level. Just the opposite condition is displayed by *A. afarensis*, where the value of the index exceeds the upper limit of the human confidence interval (although not the maximum value registered among extant humans).

Table 5.3. Descriptive statistics of allometric residuals of metacarpal head and phalangeal trochlear robusticity computed on the basis of the chimpanzee allometric equations reported in Figure 5.6.

Allometric residual of head robusticity of metacarpal I (MC1AH vs. MC1L)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	58	0.54	0.16	0.50	0.58	0.08	0.91
H. neanderthalensis	2	0.53	0.01	0.41	0.66	0.52	0.54
P. troglodytes	63	0.00	0.15	-0.04	0.04	-0.28	0.41
A. afarensis	1	0.15	--	--	--	--	--
***P. robustus* (estimated)**	1	0.15	--	--	--	--	--

Allometric residual of head robusticity of metacarpal IV (MC4AH vs. MC4L)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	56	0.11	0.14	0.07	0.15	-0.19	0.38
H. neanderthalensis	3	0.31	0.06	0.16	0.47	0.24	0.36
P. troglodytes	61	0.00	0.16	-0.04	0.04	-0.32	0.43
A. afarensis	1	-0.13	--	--	--	--	--
P. robustus	1	0.10	--	--	--	--	--

Allometric residual of head robusticity of metacarpal V (MC5AH vs. MC5L)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	60	0.34	0.15	0.30	0.38	-0.04	0.60
H. neanderthalensis	3	0.38	0.19	-0.10	0.86	0.16	0.54
P. troglodytes	63	0.00	0.17	-0.04	0.04	-0.33	0.54
A. afarensis	2	0.14	0.08	-0.59	0.87	0.08	0.20
P. robustus	1	0.28	--	--	--	--	--

Allometric residual of trochlear robusticity of proximal phalanges (PPAT vs. PPL)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	182	0.17	0.14	0.15	0.19	-0.19	0.54
H. neanderthalensis	15	0.37	0.10	0.31	0.42	0.24	0.59
P. troglodytes	209	0.00	0.16	-0.02	0.02	-0.39	0.46
A. afarensis	8	0.07	0.30	-0.18	0.33	-0.25	0.78
P. robustus	3	0.36	0.13	0.03	0.68	0.21	0.46

Allometric residual of midshaft robusticity of middle phalanges (MPAS vs. MPL)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	140	0.33	0.16	0.30	0.35	-0.02	0.98
H. neanderthalensis	19	0.59	0.13	0.52	0.65	0.38	0.83
P. troglodytes	198	0.00	0.15	-0.02	0.02	-0.47	0.59
A. afarensis	5	0.13	0.07	0.05	0.22	0.03	0.21
P. robustus	5	0.40	0.16	0.20	0.60	0.17	0.59
OH 7	4	0.31	0.13	0.11	0.52	0.23	0.51

Abbreviations: N = sample size; SD = standard deviation; CI = confidence interval.

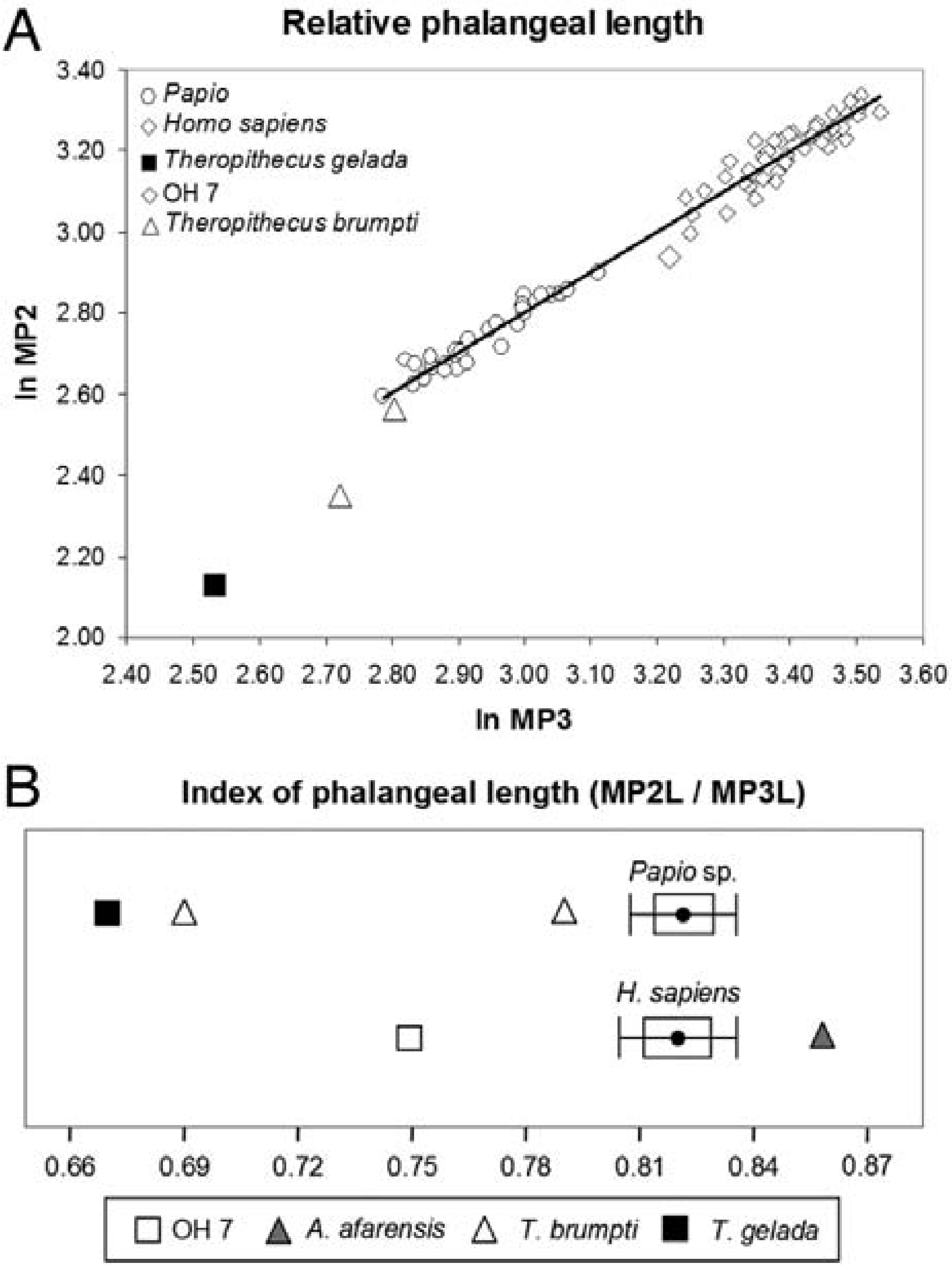


Figure 5.8. (**A**) Allometric bivariate plot of ln-transformed data in order to evaluate the relative length of middle phalanges between manual rays II and III in humans and baboons. Note the departure from the regression line in both OH7 and geladas. Allometric equation: ln MP2L = 0.989 ln MP3L – 0.162, r = 0.991, $p < 0.001$, N = 73 (44 *H. sapiens* + 29 *Papio* sp.). (**B**) Index of relative phalangeal length (MP2L / MP3L). Mean values, as well as 95% and 99.9% confidence intervals, are depicted for humans and baboons. Taxa in the legend are represented by individual data (in the case of extinct ones) or mean data (in the case of extant geladas). Abbreviations: MP = middle phalanges; L = length.

Table 5.4. Descriptive statistics of the index of relative length for middle phalanges II and III (MP2L vs. MP3L)

Taxon	N	Mean	SD	95% CI		Range	
H. sapiens	44	0.82	0.03	0.81	0.83	0.77	0.89
***Papio* sp.**	29	0.82	0.02	0.81	0.83	0.78	0.87
OH 7	1	0.75	--	--	--	--	--
A. afarensis	1	0.86	--	--	--	--	--
***T. gelada* (mean)**	1	0.67	--	--	--	--	--
T. brumpti	2	0.74	0.07	0.10	1.38	0.69	0.79

DISCUSSION

Taxonomic attribution of the Swartkrans hominin phalanges

Before evaluating the taxonomic attribution of the OH 7 hand, it is necessary to briefly review the assignment of the hominin manual remains from Swartkrans. Robinson (1972) already compared the Olduvai hand material with that of Swartkrans, especially with the thumb metacarpal SK 84 (Napier 1959), which he attributed to *P. robustus*. Attribution of this material is not straightforward, however, since Swartkrans Members 1 and 2 have both provided well-preserved craniodental remains of *H. erectus* and *P. robustus* (Brain 1981; Brain *et al.* 1988; Grine 1989). Hence, it is quite difficult to securely attribute the isolated hand bones (and other postcranial material) from this locality to one taxon or another (Trinkaus and Long 1990). However, given the fact that more than 95% of the hominin craniodental remains from Swartkrans Member 1 are attributable to *P. robustus*, Susman (1988a, b, 1989, 1991, 1994) has argued that most hand remains are also likely to belong to this taxon. This taphonomical argument was criticized by Trinkaus and Long (1990), on the basis of lack of knowledge of the differential preservation rates between craniodental and postcranial remains. However, there seems to be no reason *a priori* for assuming that they should not be at least correlated (Susman 1991).

Beyond the above-mentioned taphonomical argument, Susman further advocated for the use of “morphological criteria ... to distinguish the two hominids (=hominins) at Swartkrans” (Susman 1988a, p. 782; see also Susman 1989, p. 470). Thus, on the basis of similarities with the partial *H. erectus* skeleton KNM-WT 15000, Susman (1988a, 1991, 1994) attributed the SK 84 pollical metacarpal to *H.* cf. *erectus*, while he considered the other pollical metacarpal, SKX 5020, to belong to *P. robustus*. On the contrary, Trinkaus and Long (1990) argued that no significant morphological differences could be found between the two metacarpal specimens, further trying to show, on statistical grounds, that size differences—SK 84 is smaller than SKX 5020—did not permit to reject the hypothesis that these bones belong to the same species (but see Susman 1991). Leaving aside the particular merits of the arguments put forward by the above-mentioned investigators, it must be stressed that they all agreed that morphological criteria must be employed in order to assign isolated hand specimens when *Paranthropus* and *Homo* coexist in a particular site. In fact, Susman (1988a, 1989, 1991) clearly considered the morphological criterion more significant than the taphonomical one, given his assignment of SK 84 to *Homo* in spite of a 95% craniodental prevalence of *Paranthropus* at this Swartkrans member.

Besides the above-mentioned pollical metacarpals, the other specimen from Swartkrans that has received much attention is the distal phalanx of the thumb SKX 5016 (Susman 1988a, b, 1989, 1998), given the significance of this particular bone for making paleobiological inferences on tool making. Susman (1988a, b, 1989) attributed this specimen to *P. robustus* on the basis of his taphonomical argument for Swartkrans Member 1, and also on the basis of allometric size congruence with thumb metacarpal SKX 5020 but not SK 84 (Susman 1988a, footnote 11; see also Susman 1989). Two particular morphological features of this distal phalanx (the mediolaterally broad apical tuft and the well-developed pit for the insertion of the *flexor pollicis longus*) have been stressed by Susman (1988a, b, 1989), since they reflect strong similarities with modern humans (see also discussion in Marzke 1997). Our results on relative robusticity of pollical distal phalanges (Figure 5.3) indicate that SKX 5016 is very robust, suggesting that this specimen was correctly attributed to *Paranthropus* by Susman (1988a, b, 1989).

With regard to the relative proximodistal extension of the trochlea in palmar view in middle phalanges (Figure 5.4), our results indicate that both in gracile and robust australopithecines, this articular facet is longer as compared to humans. These differences confirm the utility of this trait for discriminating between *Homo* and *Paranthropus* middle phalanges at Swartkrans. To this regard, the middle phalanx SKX 13476 from Swartkrans Member 1, like the Neandertal specimen included in the analysis and the Nariokotome WT-15000 specimen, but unlike australopithecines, has a short trochlea, suggesting that this specimen does not belong to *Paranthropus* (contra Susman 1988b), but rather to *Homo*.

Regarding the relative width of the trochlear area in middle phalanges (Figure 5.5), our results confirm that further significant differences exist to this regard between australopithecines (both gracile and robust), on the one hand, and humans, on the other, with Neandertals further differing from modern humans in the opposite direction than australopithecines. Gracile as well as robust australopithecines, thus, display relatively narrower trochlear regions than humans, or in other words, the middle phalanges of the former are wider at midshaft as compared to the trochlea. *Australopithecus* tends to be somewhat less extreme than *Paranthropus* to this regard, but no significant differences can be found, and in any case both australopithecine genera resemble one another much more closely than either the human condition. All the Swartkrans middle phalanges included in the analysis as *P. robustus* do significantly differ from the human pattern, except the above-mentioned specimen SKX 13476. In the latter specimen, like in the middle phalanx of *H. erectus* from Nariokotome, the trochlear region is relatively narrower than in modern humans, but not to such an extreme degree as in australopithecines. This confirms that this phalanx is best attributed to *Homo*, as already concluded on the basis of the preceding criterion.

To sum up, our allometric analyses confirm that most of the postcranial remains from Swartkrans Member 1 can be morphometrically discriminated from *Homo*, thus being attributable to *Paranthropus*, as previously argued by Susman (1988a, b, 1989, 1991, 1994) on the basis of the relative abundance of craniodental remains. At the same time, our analyses reinforce the contention that Susman's taphonomic criterion is not sufficient in itself, because it does not permit to discard the presence of some specimens of the genus *Homo*, even though minority. More precisely, our results not only confirm that the pollical distal phalanx SKX 5016 must be attributed to *Paranthropus* (Susman 1988a, b, 1989), but further indicate that the middle phalanx SKX 13476 must be attributed to *Homo* instead of *Paranthropus* (contra Susman 1988b). An allometric assessment of midshaft robusticity in *Homo*, *Australopithecus* and *Paranthropus*, as compared to chimpanzees, further permits to realize that robust australopithecines are indeed robust not only regarding the cranium, but also the postcranium as well, at least as far as metacarpals and phalanges are concerned. Thus, while gracile australopithecines generally resemble modern humans with regard to overall hand robusticity, except for some details of the metacarpals, robust australopithecines outstand by a generalized and extremely robust pattern, which is only matched by the degree of midshaft robusticity displayed by the OH 7 middle phalanges.

Taxonomic attribution of the OH 7 phalanges

The inclusion of the OH 7 hand in the type series of *H. habilis* as part of the holotype by Leakey *et al.* (1964) was based on several lines of evidence, which are however much less reliable than generally assumed. On taphonomical grounds, the OH 7 hand bones come from the same site as the craniodental remains, on which the diagnosis of *H. habilis* was mainly based (Leakey *et al.* 1964). However, the spatial association of the *H. habilis* craniodental remains with the postcranial ones is far from determinant. Most of the hand material was attributed to a single individual OH 7, except for the two adult proximal phalanges, attributed to the paratype OH 8 that also includes a partial foot and some other remains (Leakey *et al.* 1964). The OH 7 hand and the OH 8 foot were separated by about 4.5 m on level 3 (Susman and Creel 1979, after Leakey 1971), but there was a considerable dispersion of the bones due to extensive evidence of carnivore activity (M.D. Leakey in Susman and Creel 1979, p. 325), thus complicating the determination of how several individuals were present at the site. While there is agreement that the two adult proximal phalanges of OH 8 do not belong to the same subadult individual than the OH 7 hand (Napier 1962a; Susman and Creel 1979), it has been suggested by some authors that the OH 8 foot (and the OH 35 tibia and fibula as well) could indeed belong to the same individual than OH 7 (Susman and Creel 1979; Susman and Stern 1982). As noted by Wood *et al.* (1998), however, both taphonomic data and anatomical comparisons indicate instead that OH 8 and OH 35 most likely belong to different individuals, if not species. This argument as recently stressed by Gebo and Schwartz (2006) who considered that the OH 8 foot shows greatest morphological similarity with a talus from Kromdraai (TM-1517) suggesting that the best taxonomic allocation of the OH 8 foot specimen is with *P. boisei*.

Although the latter authors do not dispute the attribution of the OH 7 hand to *H. habilis*, one might ask why these remains should be necessarily attributed to the same individual and species as the OH 7 craniodental specimens. Tuttle (1967, pp. 198-199) first suggested that “the (OH 7) hand bones might belong to *Paranthropus*”, since they “possess many features which resemble those of living great apes”. The attribution to

Homo of the OH 7 hand depends on their association with the OH 7 craniodental material as a single individual. However, without a close spatial association between the manual and the craniodental remains, the proposal that them all belong to a single individual merely relies on the subadult ontogenetic age of these specimens. As noted by Robinson (1972, p. 195), however, this evidence is not conclusive enough since "the type mandible and the parietals belong to a juvenile and so do some of the hand bones, it is a natural assumption that all belonged to the same individual. While this is a natural assumption, it, of course, does not follow that it is a correct assumption, especially since it is clear that more than one individual occurred in the site". This question is further complicated by the presence of a second hominin taxon, *Paranthropus boisei*, at Olduvai Gorge by this time. Some of the cranial and dental remains of *H. habilis* included in the paratype OH 6 come from Olduvai Bed I locality FLK, which also yielded a cranium of *P. boisei*. Therefore, we know for certain that the two species coexisted not only in time, but also in space. For this reason, soon after the original description of *H. habilis*, Howell (1965) already criticized the use of the postcranial evidence in the diagnosis. Given the state of knowledge at that time, Howell (1965, p. 401) argued that it would not be "inconceivable that the structure found in the NN I hominid will prove also to have been characteristic of (*Australopithecus*)". This was explicitly recognized by Tobias, according to which, "although the hand and foot reveal a remarkably hominine (=hominin) pattern, we do not know whether a similar degree of hominization characterized the hand and the foot of the australopithecines themselves" (Tobias 1965, p. 392). In other words, given the lack of australopithecine and early human fossil material for comparison, it cannot be discarded that some of the *H. habilis* postcranial paratypes actually belong to another taxon, as already suggested for the OH 8 foot, which was attributed to an australopith by Wood (1974)—an issue far from being settled, since Kidd *et al.* (1996) recently left this specimens unassigned.

To sum up, given the lack of a sound spatial association between the several remains, and the presence of two hominin taxa at Olduvai by this time, the taxonomic assignment of the OH 7 hand to *H. habilis* almost exclusively relies on the subadult age of the postcranial and the craniodental specimens. While this ontogenetic criterion certainly fails to falsify the single individual/species hypothesis, the taxonomic attribution of OH 7 hand specimens merely remains a reasonable hypothesis that should be further tested with all the other available evidence, particularly the morphological one. Lewis (1977, p. 185) already complained that the Olduvai hand and other fossils of early hominins are in some cases “attributed on rather dubious grounds to *Homo*”, with the taxonomic attribution being apparently “determined more by site of recovery than by morphological insights”. In fact, on the basis of morphological evidence alone, Robinson (1972) had explicitly argued that the OH 7 hand material appeared too primitive as compared to *H. sapiens*, further noting that the Olduvai phalanges were “remarkably robust” and “quite strongly curved”, which was “a little incongruous in relation to a creature that appears to have been appreciably smaller and more lightly built than even a small form of modern man such as Bush people“ (Robinson 1972, p. 196). Robinson (1972 pp. 196-197) felt the attribution the OH 7 hand to *Paranthropus* seemed “reasonable” or “at least as good as the other and in some respects even better”, so that he concluded that “we should be open-minded about their affinities until sounder and more complete evidence is available”.

Indeed, the taxonomic assignment of the OH 7 phalanges from Olduvai can be evaluated on the basis of the same morphometric criteria utilized with the Swartkrans specimens. Thus, while the pollical distal phalanx Stw 294 from Sterkfontein is only somewhat stouter than those of modern humans regarding the tuft, the pollical distal phalanx of OH 7 most closely resembles the *P. robustus* specimen SKX 5016 by displaying a degree of robusticity at both midshaft and tuft, which is much greater than in modern humans (Figure 5.3). The Stw 294 specimen is usually attributed to *Australopithecus africanus* (Ricklan 1987), although Susman (1998, pp. 38-39) suggested that it might be equally attributed to early *Homo*, an issue that cannot be unambiguously resolved with the present analyses. On the contrary, the high robusticity values of both SKX 5016 indicate that the latter is much more likely to belong to *Paranthropus* than to *Homo*. Only the pollical distal phalanges of Neandertals, generally characterized by a high degree of postcranial robusticity, are also comparatively stouter to these regards, although at least OH 7 appears more robust regarding robusticity at the shaft.

The attribution of the OH 7 manual specimens to *Paranthropus* is further strengthened by the results for the relative extension of the trochlea (Figure 5.4), as well as relative trochlear width (Figure 5.5) and midshaft robusticity (Figures 5.6 and 5.7) in the middle phalanges. To all these regards, the OH 7 phalanges significantly depart from the human condition, but do not significantly differ from the australopithecine one. Certainly, the OH 7 middle phalanges resemble Neandertals with regard to the high degree of midshaft robusticity (Figure 5.6A), but regarding trochlear robusticity the former display much lower values (Figure 5.6B), suggesting a different (non-human) pattern of robusticity. On the contrary, the OH 7 middle phalanges cannot be shown to differ from the australopithecine condition regarding either midshaft or trochlear robusticity, most closely resembling the *Paranthropus* condition. In modern humans, the middle phalanges display wider trochleae relative to the midshaft as compared to australopiths, and this relationship is even more exaggerated in the robust middle phalanges of Neandertals (Figure 5.5). As a result, the OH 7 middle phalanges fit the *Paranthropus* model of robusticity, but fail to resemble either *H. sapiens* or *H. neanderthalensis* regarding both midshaft and trochlear robusticity simultaneously. With regard to morphological comparisons, in the middle phalanges of both OH 7 and *Paranthropus*, the shafts flare laterally, providing large and deeply excavated insertion areas for the flexors, while the trochlear region is relatively slender (mediolaterally narrow and proximodistally long), thus emphasizing the robust aspect of the shaft. Moreover, the pollical distal pollical phalanx is mediolaterally extremely robust at midshaft (Susman 1988a, b, 1989), thus clearly differing from the *Homo* condition. Taken together, all these morphometric and morphological similarities of the OH 7 phalanges with those of australopithecines (but not humans, extant and fossil), together with the lack of direct evidence regarding the association of the manual specimens with the OH 7 craniodental material to the same individual, strongly advocate for an alternative taxonomic attribution of the OH 7 partial hand to *Paranthropus boisei*, which is the only other hominin species thus far recorded at Olduvai Bed I.

An alternative interpretation of the similarities of the OH 7 and *Paranthropus* hand specimens is that *H. habilis* had *Paranthropus*-like hand. This interpretation might appear to be congruent with the claims suggesting that *H. habilis* has an australopithecine-like postcranium (Johanson *et al.* 1987; Johanson 1989; Leakey *et al.* 1989; Hartwig-Scherer and Martin 1991). Different opinions have been put forward on the postcranial proportions of *H. habilis*, but these inferences are based on relatively scanty and fragmentary postcranial material object of divers interpretations. On the basis of the fragmentary skeleton OH 62, Johanson *et al.* (1987; see also Johanson 1989) and Hartwig-Scherer and Martin (1991) concluded that the postcranial remains of

H. habilis are remarkably primitive. Partly on this basis, both *H. habilis* and *H. rudolfensis* have been suggested to be best included in the genus *Australopithecus* (Wood and Collard 1999, 2001; Wood 2000), since a modern human bodyplan (or ‘adaptive pattern’) does not appear until *H. erectus* s.l. in spite of the obvious differences in craniodental morphology (reduced masticatory apparatus and expanded brain, McHenry and Coffing 2000). Recent studies, however, rather suggest less primitive postcranial proportions for *H. habilis* (Korey 1990; Richmond *et al.* 2002; Haeusler and McHenry 2004; Reno *et al.* 2005). Considering these evidences, no reason exists to accept without discussion that the peculiar anatomy of the OH 7 hand is a single consequence of the more australopithecine character of the *H. habilis* postcranial skeleton. The fact that the OH 7 hand bones more closely resembles that of *P. robustus* than *A. afarensis*/*africanus* indicates that the OH 7 hand case is of incorrect attribution rather than of retention of primitive australopithecine features.

This attribution of the OH 7 manual remains to *Paranthropus boisei* does not mean that the phalanges of the former are morphologically identical to the previously reported phalanges from Swartkrans (Susman 1988a, b, 1989), which belong to a different species, *P. robustus*. Among others, the four middle phalanges of OH 7 apparently display a greater degree of curvature on the dorsal aspect of the diaphysis, as well as a parallel (instead of distally convergent) trochleae, with a much wider intertrochlear groove. These middle phalanges further display morphological differences at the trochlea, with OH 7 lacking the sharp notch present in *P. robustus* at the proximopalmar area of the intertrochlear region (Susman 1989). In addition, the OH 7 middle phalanges are clearly bottle-shaped, unlike those of *P. robustus* from Swartkrans, as previously noted by Susman (1989). In both taxa, however, not only the base, but also most of the diaphysis of the middle phalanges are clearly wider than the trochlear region. The bottle-shaped morphology of OH 7 is essentially attributable to differences in the extent of the insertions of the *flexor digitorium superficialis*. In both taxa, these insertions form marked scars that extend distally from the base of the phalanx. In OH 7, however, they do not form well-developed ridges individualized from the diaphysis, unlike in some specimens of *P. robustus* from Swartkrans. Moreover, in the latter taxon, the insertions for the finger flexors almost extend until the trochlear region, whereas in OH7 they end at about the distal two thirds of the diaphysis, forming a evident constriction below the trochlear region that defines the distinct bottle-shape morphology. It is currently difficult to evaluate the significance of the above-mentioned differences, especially given the subadult ontogenetic stage of OH 7. They might be partly attributable to inter-individual variation, or partly indicative of differences in the locomotor repertoire of these taxa (some degree of arboreality has been suggested for OH 7 by Susman and Stern 1979; Tuttle 1981 and Susman 1982). In any case, these differences are consistent with the two samples representing different species of the same australopithecine genus.

Two adult and complete proximal phalanges from Olduvai Gorge have been traditionally excluded from the holotype of *H. habilis*. It has been generally accepted that these adult phalanges belong to a different individual than OH 7 hand, but different opinions have been put forward regarding its taxonomical attribution. Napier (1962a) considered that these phalanges were attributable to the same taxon than OH 7, and Leakey *et al.* (1964) did indeed include them in the *H. habilis* paratype OH 8. However, given the size and shape differences, Susman and Creel (1979, p. 312) latter concluded that these two phalanges "almost certainly do not represent the same species as the subadult remains" (see also Day 1976). It is unlikely that these specimens belong to *Homo*, so that an attribution to a smaller individual (female?) of *Paranthropus boisei* is reasonable, together with the possibility that these specimens belong to a non-hominin primate (e.g. Day 1976). If our alternative attribution of the OH 7 hand to *Paranthropus* is correct, then it follows that the actual hand morphology of *H. habilis* is virtually unknown, except for the proximal fragments of two proximal phalanges from the KNM-ER 3735 skeleton, briefly described by Leakey and Walker, (1985, p. 152) and (Haeusler and McHenry 2007, p. 403). Unfortunately, these phalanges cannot be compared with those of OH 7 because of their fragmentary nature (proximal fragments in KNM-ER 3735 versus distal fragments in OH 7).

Hand function in *Paranthropus*

H. habilis has been considered by most authors as the most likely responsible of the Oldowan industry (Oakley 1949; Napier 1962a, p. 411; Washburn 1967), to the exclusion of *Paranthropus*. Susman (1988a, b, 1989, 1994) however, has repeatedly disputed this idea, forcefully arguing that *Paranthropus* was also a toolmaker. By comparing *Paranthropus* hand remains with OH 7, Susman (1989, p. 472) concludes that, “There is every morphological reason to impute tool behavior to *Paranthropus* that there is to assign tool behavior to *H. habilis* or any other early hominid”. Put simply, Susman's (1989) conclusion is derived, by using a syllogistic argument, from the following two arguments: (1) The OH 7 hand bones are attributable to *H. habilis*, which is a toolmaker; and (2) The morphology of *Paranthropus* hand remains closely resembles the morphology of the OH 7 hand. Combined, these propositions allow Susman to conclude that *Paranthropus* was also a toolmaker. On logical grounds, this argument appears to be correct, but it does not stand a closer scrutiny. In particular, we are faced to the paradox that, in order to conclude that *Paranthropus* from Swartkrans was a toolmaker, we must first accept that the Olduvai hand is from a toolmaker; but this, in its turn, depends on the assignment of the Olduvai hand to *Homo*, on the basis that this taxon is a more probable toolmaker than *Paranthropus* at this site! One might rather alternatively suggest that the similarities previously noted by Susman between *P. robustus* and OH 7 rather argue in favor of attributing the latter specimens to *Paranthropus* instead of *Homo*. *Per se*, our alternative taxonomic attribution of the OH 7 hand remains to *Paranthropus* neither contradicts nor supports the traditional assumption that the larger-brained hominin at Olduvai (i.e. *Homo*) was the toolmaker. However, it strongly suggests that the tool-making abilities previously inferred for *Paranthropus* at Swartkrans should be re-evaluated on the light of the new taxonomic hypothesis.

A correct approach to the hand function of *Paranthropus* should include manipulative activities, other than tool behavior, which form important part of the primate hand activities. The exclusive discussion of hand function in the realm of tool behavior would inevitably lead to circular reasoning, making inevitable reach the conclusion that the derived features of the *Paranthropus* (or other taxa) hand are adaptations related to tools (Alba *et al.* 2003). Therefore, under this perspective, in the following section we will revise those hand features that are relevant to or have been used to infer hand function in *Paranthropus*, from a broader angle, taking account primate manipulative behaviors, including food-gathering and processing.

One of the characteristics of the *Paranthropus* hand phalanges is the relative small size of the distal joint surfaces in relation to the cross-sectional area of the diaphysis. Humans, extant and fossil, show an opposite pattern (Figure 5.6). It should be taken into account that, in contrast to other manipulative behaviors such as small object-feeding, stone flaking requires the application of short, glancing blows with hard objects. The toughness of these objects provides very short times of deceleration, and thus very high forces (Preuschoft and Fritz 1977), the hand structure of the toolmaker must be able to withstand. The work of powerful muscles renders the forces across the joints much larger than the forces in the shaft (Currey 2002). Accordingly, joint surfaces must be large compared with the cross-sectional area of the bone, which has the additional advantage that lateral stability of the joint increases. This is most likely to be the case in *Homo*, especially in the robust Neandertals, but not in *Paranthropus*. This strongly suggests differences in hand function between both taxa.

Because the thumb is considered to play a central role in refined, human-like precision grasping (Napier 1962b; Susman 1994), in its turn highly related to tool behaviors, earlier inferences about hand function in *Paranthropus* were drawn particularly from thumb morphology (Susman 1994). Humans show an expanded metacarpal head of the pollex relative to metacarpal length (see Figure 5.6B), which reflects increased transarticular forces from added thumb musculature (Susman 1994). This character is considered to be diagnostic of tool making and asserted to be present in *Paranthropus* (Susman 1994). Our analyses of hand robusticity confirm that, with regard to metacarpal head robusticity, *P. robustus* closely resembles humans by a degree of robusticity higher than in chimps and gracile australopithecines. However, when robusticity at midshaft is further taken into account, it emerges that robust australopithecines metacarpals and phalanges are extraordinarily robust. Though higher than in humans and gracile australopithecines, midshaft robusticity of the pollical metacarpal is rather moderate as compared to other metacarpals and phalanges, contrasting with the human pattern, which is characterized by a disproportionately high robusticity in the pollical metacarpal as compared to other hand bones. The pattern of relative hand bone robusticity, thus, is quite different between *Homo* and *Paranthropus*, with the latter taxon rather resembling *A. afarensis*, albeit being much more robust overall. In other words, *Paranthropus* lacks the disproportionately hypertrophied first metacarpal, which characterizes the genus *Homo* (Figure 5.6). This strongly suggests that hand function was different between *Homo* and *Paranthropus*, because their hands were exposed to different stresses.

Another characteristic of the OH 7 hand is the short intermediate phalanx of the index finger as compared to the third one (Figure 5.8). These peculiar proportions of the intermediate phalanx of the second digit of the OH 7 hand only have a parallel in primates, the gelada baboon *Theropithecus*. In fact, bipedal hominids share a series of features related to manipulative activities such as pad-to-pad precision grasping, which are also present in the manual grazer *Theropithecus*. These include thumb-finger proportions that permit a precision grip with pulp-to-pulp contact (Napier and Napier 1967; Jolly 1970; Etter 1973; Jablonski 1986; Maier 1993; Alba *et al.* 2003). Significantly, there are further features shared exclusively by *Theropithecus* and *Paranthropus*. Their short and robust medial phalanges are expanded at midshaft, and the distal phalanx of the thumb is extraordinarily robust in both taxa. Moreover, exclusively in both, *Theropithecus* and *Paranthropus* (OH 7), the middle phalanx of the index finger is much reduced as compared to the third one (Figure 5.8), even when compared to modern humans and baboons. The fact that *A. afarensis* rather displays a relatively much longer index middle phalanx further supports that *Paranthropus* is derived to this regard, thus having converged toward the *Theropithecus*-like condition, resembling both the extant *T. gelada* and the extinct *T. brumpti*.

In *Theropithecus*, the very short index finger, combined with the long thumb, results in a high opposability-index (even exceeding that of modern humans), which has been related to specialized precision grasping (Napier and Napier 1967; Jolly 1970; Jablonski 1986; Maier 1993). *T. gelada* importantly differs from its close relative, *Papio* spp., by utilizing a distinct harvesting technique that conditions the peculiar hand morphology of this genus. Geladas are manual grazers (Napier and Napier 1967; Jolly 1970; Maier 1993; Dunbar 1977) that, by alternate rotary motions of the hands, continually snip off grass blades (as well as seeds and rhizomes) with the thumb and index finger, gathering them into the palm of the hand, and, when a handful is collected, transferring them to the mouth (Dunbar 1977). These manipulative behaviors (harvesting and foot processing), though weaker, might still severely condition the mechanical design of the hand if practiced with sufficient frequency. They are thus likely a powerful determinant of hand anatomy. Several authors have considered the potential role of continuously repeated, though less vigorous activities, on skeletal morphology, such as in mastication (Hylander 1979, 1988) or in other loading regimes such as simple standing (Rubin *et al.* 2001). However, no attempt has been made hitherto to study this in hominin hands, in spite of the fact that weak, but cyclically repeated manipulative activities, often related to professional tasks such as in the case of musicians (e.g. piano playing), are well known to cause painful osteomuscular pathologies (tendinitis or synovitis, washing woman syndrome) that might even lead to necrosis of the bones involved (Gray 1977; Brandfonbrener 1990, 2003; Wilson 1998; Parry 2003). Therefore, in primates devoting much of the day to continuously repeated manipulative activities, such as specialized harvesting techniques, the ability of the hand to withstand these cyclical small loads is likely to condition fitness. Hence, one would expect their hand structure to be subject to important selection pressures related to manipulation, even though these activities are unrelated with tools.

On the basis of analogies with papionin monkeys, Jolly (1970) proposed a graminivorous feeding niche for australopithecines. Jolly's (1970) hypothesis, is consistent with inferences on masticatory stresses drawn from jaw (Hylander 1979, 1988), facial buttresses (Hylander 1979), and estimations of the rate of food breakdown from tooth morphology (Lucas *et al.* 1986). Lucas *et al.* (1986), in particular, favored Jolly's (1970) proposal for *Paranthropus,* arguing that “the peculiar ... dentition of the robust australopithecines suggests a diet in which small, hard, brittle objects were a major component”, further concluding that “robust australopithecines were basically specialized seed-eaters with perhaps a fairly large component of roots, storage organs and young leaves in their diet” (Lucas *et al.* 1986, p. 200). Dental microwear studies (Grine 1981, 1986; Grine and Kay 1988; Scott *et al.* 2005) indicate that, despite some trophic overlap, *Paranthropus* consumed more hard and brittle items than *Australopithecus* (Scott *et al.* 2005). Isotopic analyses (Lee-Thorp *et al.* 1994, 2000; Sponheimer and Lee-Thorp 1999, 2003; van der Merwe *et al.* 2003; Peters and Vogel 2005; Lee-Thorp and Sponheimer 2006; Sponheimer *et al.* 2005, 2006a, b) further indicate that both *Australopithecus* and *Paranthropus* consumed considerable quantities of C_4 resources, which must have consisted of grasses, sedges, and/or animals that ate these plants. Despite the uncertainties regarding the particular type of C_4 food items consumed, this represents an important ecological difference with respect to extant apes (Lee-Thorp and Sponheimer 2006), which consume typical resources of forested habitats even when inhabiting relatively open environments (Sponheimer and Lee-Thorp 2003). As noted by Sponheimer *et al.* (2006a, p. 980), the isotopic data indicate that, although “*Paranthropus* was not a dietary specialist”, “savanna-based foods such as grasses or sedges or animals eating these foods made up an important but highly variable part of its diet". As such, baboons seem better dietary analogs of these hominins, since they "exhibit a flexibility and willingness to use ^{13}C-enriched savanna resources that appears to be absent in chimpanzees yet characteristic of australopithecines" (Sponheimer *et al.* 2006b, p. 132).

The important morphological differences between the hand of *Paranthropus* and *Homo* (fossil and extant) indicate that both hands are submitted to different loading regimens and that the *Paranthropus* pattern probably reflects an adaptation to manual activities other than tool making. The traits *Paranthropus* and *Theropithecus* share suggest the possibility that *Paranthropus* regularly exploited savannah resources, which may have consisted in small vegetal food items, and probably requiring a continuous feeding in order to ingest the daily ration necessary for sustenance. Though remarkable, these similarities between *Paranthropus* and *Theropithecus* do not necessarily imply a similar, gelada-like diet, but strongly suggest that the hands of both taxa were subject to similar loading regimes during manual harvesting and manipulation of food items. The lateral flaring of the *Paranthropus* phalanges might reflect continuous though weak, rather than powerful but less frequent, activities of the finger flexors. This interpretation agrees with our inferences about forces across the finger joints, the relatively slender thumb (as compared to the rest of the hand), and the australopithecine pattern (opposed to the human-like) of robusticity in the hand bones of *Paranthropus*.

In the light of these considerations, we propose the hypothesis that the particular morphometric features of the *Paranthropus* hand are structural adaptations to counter fatigue failure generated by cyclical small loads through day-long, sequential motions of hands and fingers in manipulation and harvesting of small food items. This is in agreement with paleodietary inferences from dental evidence, and also with the inferred significant masticatory abilities in *Paranthropus*, regarded as indicative of little if any extra-oral processing (Hylander 1979, 1988; Grine 1981; Lucas *et al.* 1986; Sponheimer and Lee-Thorp 1999). This new hypothesis on the adaptations of the *Paranthropus* hand supports previous assumptions that *Homo* was the unique author of the Oldowan culture. The evidence presented in this paper rather suggests that tool making was not part of the manual activities of *Paranthropus*, being instead related to feeding manipulative behaviors. In this way, the new hypothesis proposed here vindicates the older views of Oakley (1949), Napier (1962a, b), and Washburn (1967), and the more recent views of van Schaik *et al.* (1999), that size and organization of the brain are fundamental for the conception and manufacture of lithic tools, with hand morphology being rather subsidiary.

Implications for the study of the origin of the hominid hand and culture

Among the most interesting conceptual corollaries of the reanalysis of the OH 7 hand, is the realization that discussing hominid hand function only in the realm of tool behavior leads to the circular reasoning that the derived hominid traits of the are necessarily adaptations associated to tools. This point is particularly important because, besides increased brain size and stone tools, the only evidence for the origin of human technology is considered to come from the morphology of early hominin hand bones (Napier 1962a, b; Susman 1988a, b, 1989, 1994, 1998; Marzke 1997).

The conceptual basis that supports such notion arises from the work of Napier (1956, 1960, 1962a, b), with the description and classification of the basic movements that the human hand performs while using and manufacturing tools: the precision grip and the power grip. The anatomical correlates of these grips, as described by Napier (1962a, b), are considered to be diagnostic criteria (in different degrees, depending on the author) for inferring tool use or tool making in fossil hominins. There is however different approaches, depending on the author, on what specific basis the different types of tool behavior, and particularly tool making, should be inferred from the morphology of hominin fossil hand bones.

The original approach of Napier (1962a, b), on which all the posterior work is based, suggests that hand anatomy criteria alone do not suffice to infer tool making. In Napier's (1956, p. 913) words: “it is in the elaboration of the central nervous system and not in the specialization of the hand that we find the basis of human skill”. Accordingly, regarding the OH 7 hand, Napier considered that “On anatomical grounds there is no doubt that the Olduvai hand was sufficiently advanced in terms of the basic power and precision grips to have used naturally occurring objects as tools ... There is less certainty about toolmaking, which involves not only a peripheral but also a central intellectual factor” (Napier 1962a, p. 411). This author, hence, clearly requires that anatomical criteria from the hand must be further supported by external criteria, based on cognitive capabilities, in order to be able to confidently infer tool making for a fossil hand. According to this author, "the Olduvai hand activated by a brain and a neuromuscular mechanism of commensurate development would have little difficulty in making the tools that were found with it" (Napier 1962b, p. 8), so that "Given the intellectual ability", the construction of the Oldowan stone tools was "well within the physical capacity of the Olduvai hand" (Napier 1962a, p. 411). It is therefore clear that, according to this view, hand anatomy by itself is insufficient to infer tool making. A similar argument is held by Washburn (1967, p. 25): "The reason that tool making evolved so slowly was that the brain had to evolve before the skills of *Homo erectus* were anatomically possible. According to this view, the explanation of human evolution is to be sought in the feedback relation between successful behavior and the biology that makes the behavior possible. And the most important changes are in the brain". This traditional view is reinforced by the recent work of van Schaik *et al.* (1999, p. 737), who conclude that "experiments suggest that great apes cannot attain the level of sophistication reached by Oldowan tool makers", so that "it is likely that these new skills do indeed reflect increased cognitive abilities" (contra Wynn and McGrew 1989, who attributed an "ape adaptive grade" to the Oldowan tools). These authors suggest that "the most likely elements differentiating the stone-tool-making hominids (=hominins) from great apes would be increased intelligence or a higher degree of tolerance accompanied by increased opportunities for strong reliance on tools", further remarking that "Increased intelligence is likely to be expressed in increased relative brain size" (van Schaik *et al.* 1999, p. 737). The assumption that inferences on the cognitive abilities of fossil humans can be drawn from the study of lithic industry ('cognitive archaeology', see Wynn 2002, and commentaries therein) points out the link between cognition/intelligence and tool making, further stressing the contention that the latter cannot be evaluated solely on the grounds of hand morphology.

The latter approach is however the one followed by Susman (1988a, b, 1989, 1994, 1998). This approach is more straightforward and simplistic than the preceding one, since it is based on the untested (and unquestioned) assumption that tool behavior leaves unequivocal anatomical traces on hand morphology. In particular, it is assumed that precision-grip-related features, as defined by Napier (1962a, b), are diagnostic of tool making in fossil hominins, leading to the conclusion that "Tool behavior (precision grasping or handling) does become evident in the hominid (=hominin) hand around 2.0 million years ago, 500,000 years after the appearance of stone tools" (Susman 1995, p. 589). Susman's approach is therefore grounded on the equation between precision grasping and tool making (Susman 1994, 1995, 1998). In order to work, this inferential methodology must assume, on *a priori* grounds, that the anatomical features defining human-like (i.e. pad-to-pad) precision grasping originally evolved as a tool-making adaptation (see discussion below, and Alba *et al.* 2003, for further details). It must be stressed that even though Susman (1998) claims to be applying the original approach of Napier, this is not actually the case. Unlike Napier's (1962a, b), Susman's approach does not consider necessary the use of any external test based on cognitive capabilities. Indeed, the equation between precision grasping and tool making leads Susman to conclude instead that, since *Paranthropus* was a toolmaker, high cognitive capabilities did not play a crucial role in the origin of tool making, so that "the acquisition of tool behavior (=making) does not account for the emergence and success of early *Homo*" (Susman 1988a, p. 781).

Marzke (1986, 1997) takes a somewhat different approach for inferring different types of tool behaviors in fossil hominines. Thus, despite accepting essentially the same criteria for recognizing tool making in the fossil record, Marzke proposes a gradual appearance of these behaviors through time, leading from opportunistic flake production towards habitual, widespread and systematic Oldowan tool making. Marzke admits that many of the features related with tool behavior probably evolved well before the advent of stone-tool making, reflecting a growing dependence upon the use of unmodified stone, bone, and wood tools. To sum up, Marzke (1997) infers the presence in early hominins, before the advent of stone-tool making, of some tool behaviors more refined than those displayed by extant great apes. As a result, however, this author does not consider the appearance of one of these features in isolation to be diagnostic of tool making. Rather, only the appearance of all these features altogether could be taken as indicative of tool making in the fossil record. In fact, caution is urged by Marzke (1997) when attempting to distinguish an advanced stage of tool using from an early stage of tool making. Marzke (1986, 1997) considers that the hand of *Australopithecus afarensis* would already display some human-like features, although probably incapable of human-like precision grasping. On the contrary, regarding the OH 7 hand, Marzke (1997, p. 108) concludes that, as compared to australopithecines (both *Australopithecus* and *Paranthropus*), “There is more compelling evidence for tool-making capacity in the Olduvai hand”.

Despite the obvious methodological and epistemological differences between the above-discussed different approaches to hominin hand evolution, they have all a factor in common: their analysis is restricted to the domain of tool behavior. This is however an unwarranted starting point, since it inevitably leads to circular reasoning, i.e. to the unavoidable conclusion that the origin of the human hand was triggered by adaptation to tool using and/or making, without even taking alternative hypotheses into consideration. An alternative view, however, was put forward by Alba *et al.* (2003, 2005), which tested Susman's equation between tool-making and human-like precision grasping on the basis of manual remains of *A. afarensis* from locality AL 333/333w in Ethiopia. On the basis of morphometric comparisons, these authors concluded that “*A. afarensis* possessed overall manual proportions, including an increased thumb/hand relationship that, contrary to previous reports, is fully human and would have permitted pad-to-pad human-like precision grip capability” (Alba *et al.* 2003, p. 225). Given the fact that this australopithecine species predates the appearance of stone tools in the archaeological record, the latter authors further concluded that their conclusions “permit a confident refutation of the null hypothesis that human-like manual proportions are an adaptation to stone tool-making” (Alba *et al.* 2003, p. 225).

Although several alternatives were discussed by Alba *et al.* (2003, 2005), they proposed that the selection pressures posed by complex manipulative behaviors in non-human primates would have been enough to trigger the evolution of human-like manual proportions (including a thumb/hand index permitting pad-to-pad precision grasping), once locomotor selection pressures imposed by forelimb-dominated behaviors were relaxed with the adoption of habitual terrestrial bipedalism. These advantageous human-like manual proportions, more similar to those of terrestrial cercopithecoid monkeys (Napier and Napier 1967; Jolly 1970; Etter 1973; Maier 1993) than to those of extant great apes, could have been merely later coopted for stone-tool making, but in that case, they could not be employed to infer stone-tool making in the fossil record (Alba *et al.* 2003, 2005). This hypothesis is in agreement with the alternative functional explanation proposed in this paper to account for the morphology of the robust australopithecine hands. Under this view, many of the features previously considered to be indicative of stone-tool using and/or making in the fossil record would not be truly diagnostic, most likely resulting from the adaptation to a variety of complex manipulative activities essentially related to food gathering and processing.

SUMMARY AND CONCLUSIONS

We summarize below the main contributions of this chapter:

1) The OH 7 partial hand from locality FLK NN at Olduvai Bed I, which is part of the *Homo habilis* holotype, is investigated on morphometric and morphological grounds, with particular emphasis on the four middle phalanges and pollical distal phalanx.
2) Allometric comparisons with fossil and modern humans (*Homo*), as well as robust and gracile australopithecines (*Paranthropus* and *Australopithecus*, respectively), indicate that *Paranthropus* differs from humans by the greater robusticity of the pollical distal phalanx, the greater proximodistal extension of the distal trochlea, the narrower trochlear region as compared to the midshaft in middle phalanges, and a generalized pattern of increased robusticity in both middle phalanges, proximal phalanges, and metacarpals (but not particularly the pollical one).
3) Given the lack of a sound spatial association between the OH 7 manual and craniodental remains, and the presence of two hominin taxa (*H. habilis* and *P. boisei*) at Olduvai by this time, the taxonomic assignment of the OH 7 hand to *H. habilis* almost exclusively relies on the subadult age of the postcranial and cranial specimens. On the basis of the above-mentioned morphometric criteria, however, OH 7 is most likely attributed to the genus *Paranthropus*.
4) The new taxonomic assignment of the OH 7 hand forces to re-examine hand function in *Paranthropus*, which had been previously interpreted as a toolmaker on the basis of similarities with the supposedly *H. habilis* OH 7 remains. It is argued that manipulative selection pressures, other than tool making, should be also taken into account. We conclude that *Paranthropus* hand morphology (including OH 7) is not consistent with stone-tool making, but could be rather related to continuously-repeated manipulative activities during specialized food gathering and processing. This agrees with the similar degree of index shortening in *Paranthropus* and

Theropithecus, and recent paleodietary evidence indicating that the former consumed considerable amounts of C_4-rich food items.

5) The new hypothesis proposed for hand function in *Paranthropus* has important implications for understanding the evolution of the human hand. While some authors have noted that, besides hand morphology, cognitive abilities should be also taken into account for inferring tool making, other investigators have previously inferred tool making in *Paranthropus* on the basis of the simple equation between precision-grip-related features and tool making. The latter assumption was already refuted by Alba *et al.* (2003) on the basis of *A. afarensis* manual remains, which predate the appearance of stone tools in the archaeological record. On the basis of the currently available evidence, we therefore conclude that it is highly unlikely that *Paranthropus* regularly engaged in tool-making behaviors.

Chapter 6

OH 7: The original handy man?

based on:

Almécija S, Alba DM, Moyà-Solà S (2009). OH 7, the curious case of the original handy man? *Paleolusitana* 1: 85-92.

Chapter 6

OH 7: The original handy man?

INTRODUCTION

The hands of humans differ from those of apes by being considerably shorter relative to body mass, so that the former display relatively longer thumbs (Alba *et al.* 2003). From a functional viewpoint, this can be easily explained by to the striking differences in locomotor behaviors between apes and humans: while the former need long hands for arboreal behaviors, such as vertical climbing and below-branch suspension, the acquisition of habitual terrestrial bipedalism in the human lineage (and the concomitant loss of locomotor function by the hands) permitted the optimization of manual proportions for manipulative purposes (Alba *et al.* 2003, 2005). As such, australopiths (*Australopithecus* and *Paranthropus*) already display human-like manual proportions, i.e. short hands with a relatively long thumb (Alba *et al.* 2003, 2005; Green and Gordon 2008). In this sense, human hands are more similar to the hands of stem hominoids such as *Proconsul* (Begun *et al.* 1994), which were essentially generalized arboreal primates with powerful-grasping capabilities with no suspensory adaptations. Whether the short hands of humans evolved from a long-handed condition similar to that of chimpanzees (our living closest relative, according to molecular studies) remains to be tested by fossil evidence. Nonetheless, given the short-handed condition of australopithecines, there seems to be no doubt that this is a plesiomorphic condition for the genus *Homo*. Given the fact that the manual remains of *A. anamensis* predate by about one million years the first stone tools, it has been concluded that human-like hand proportions are not an adaptation to tool making (Alba *et al.* 2003, 2005).

Many other morphological features of the hand of modern humans have been identified as tool-making adaptations. Ideally, these functional hypotheses must be contrasted with the evidence provided by the fossil record. Unfortunately, however, the evidence of manual remains of fossil *Homo* species is very scarce; Neandertals (*H. neanderthalensis*) are an exception, but given their recent chronology, they cannot provide many insights on the hand of early *Homo*. Some remains are available for *H.*

ergaster from Nariokotome (or *H. erectus* s.l., see Walker and Leakey 1993), and also from *Homo* sp. from Swartkrans (Susman 1988a, 1989). Albeit with some differences, these remains can be identified as belonging to *Homo*, a situation that strikingly contrasts with the OH 7 partial hand from bed I locality FLK NN (Napier 1962), which in the past has been attributed to *H. habilis* ('handy man') by most researchers. This hand is of topmost significance, not only because its chronology (ca. 1.75 Ma) postdates the appearance of lithic remains in the record, but especially because it has been attributed to one of the earliest *Homo* species (the other being *H. rudolfensis*). In the original description of *H. habilis*, Leakey *et al.* (1964) included the manual remains, together with craniodental remains from the same locality, into the holotype of the species (OH 7)—mainly on the basis that they all belonged to a subadult individual and with no clear taphonomic association. Most researchers have subsequently accepted the attribution of all these remains to a single individual, albeit with some notorious exceptions (Robinson 1972). In Chapter 5 this taxonomic attribution was evaluated, and noted that, on morphological and morphometrical grounds, the phalanges of OH 7 most closely resemble those of robust australopiths (*Paranthropus*), thereby concluding that an attribution to *P. boisei*, also documented at the same site, seemed more likely. Interestingly, a similar conclusion was recently reached regarding the foot OH 8 (Gebo and Schwartz 2006), also included by Leakey *et al.* (1964) into the hypodigm of *H. habilis* as a paratype.

Chapter 5 mainly focused on middle phalanges, founding that the OH 7 middle phalanges displayed trochleae with primitive (australopith-like) proportions, while at the same being derived by displaying mediolaterally expanded shafts. To sum up, the proportions of these phalanges do not fit a human-like pattern (either fossil or extant), most closely resembling the phalanges of the South-African robust australopith, *P. robustus*. Relatively little attention was devoted to the OH 7 distal phalanges, concentrating only on the pollical one. The mediolateral robusticity at the tuft and the shaft was investigated, showing that, like *P. robustus* and Neandertals, the OH 7 pollical distal phalanx departed from the modern human condition by displaying a stouter phalanx both at the tuft and at midshaft. In this chapter, we review the morphological evidence provided by the OH 7 manual phalanges, and provide further morphometrical evidence regarding the robusticity of the distal phalanges by comparing the first with the third manual ray.

MATERIALS AND METHODS

Regarding the morphometric comparisons, phalangeal robusticity was computed by means of a logarithmically transformed bivariate index, following the formula: DPR = ln (MLT/L), where DPR means ‘distal phalanx robusticity’, MLT ‘mediolateral tuft width’ and L ‘maximum phalanx length’. The use of ratios has been criticized by some morphometricians, with statistical difficulties arising because a quotient of two variables (X/Y) is not a linear function of the variables X and Y. However, as noted by Hills (1978) these difficulties disappear by applying logarithms, because the log (X/Y) = log X - log Y, i.e. the log-transformed ratio is a linear function of log X and log Y (see also Smith 1999), so that the assumption that the variable analyzed displays a normal distribution is much more rarely disturbed. The resulting log-transformed index, DPR, was then investigated by means of analysis of variance (ANOVA). The mean values of extant taxa were compared with one another by means of post-hoc multiple comparisons (Bonferroni method), whereas the values for individual fossil specimens were compared with extant taxa on the basis of their respectives 95% confidence intervals. Statistical calculations were carried out by means of the statistical package SPSS 16.0. Besides the OH 7 distal phalanges I and III (specimens A and B, respectively), the fossil sample included the pollical and middle finger distal phalanges of *P. robustus* from Swartkrans (respectively, SKX 5016 and SKX 27504) and *H. neanderthalensis* from La Ferrassie I and Shanidar 3, 4 and 5; measurements were taken from good quality casts or from the literature (Trinkaus 1983; Susman 1989). The comparative extant sample includes the extant ape genera, i.e. chimpanzees and bonobos (*Pan*), gorillas (*Gorilla*) and orangutans (*Pongo*), as well as pronograde monkeys such as baboons (*Papio*, *Mandrillus* and *Theropithecus*) and macaques (*Macaca*), and modern humans (*H. sapiens*). All measurements were made to the nearest 0.1 mm.

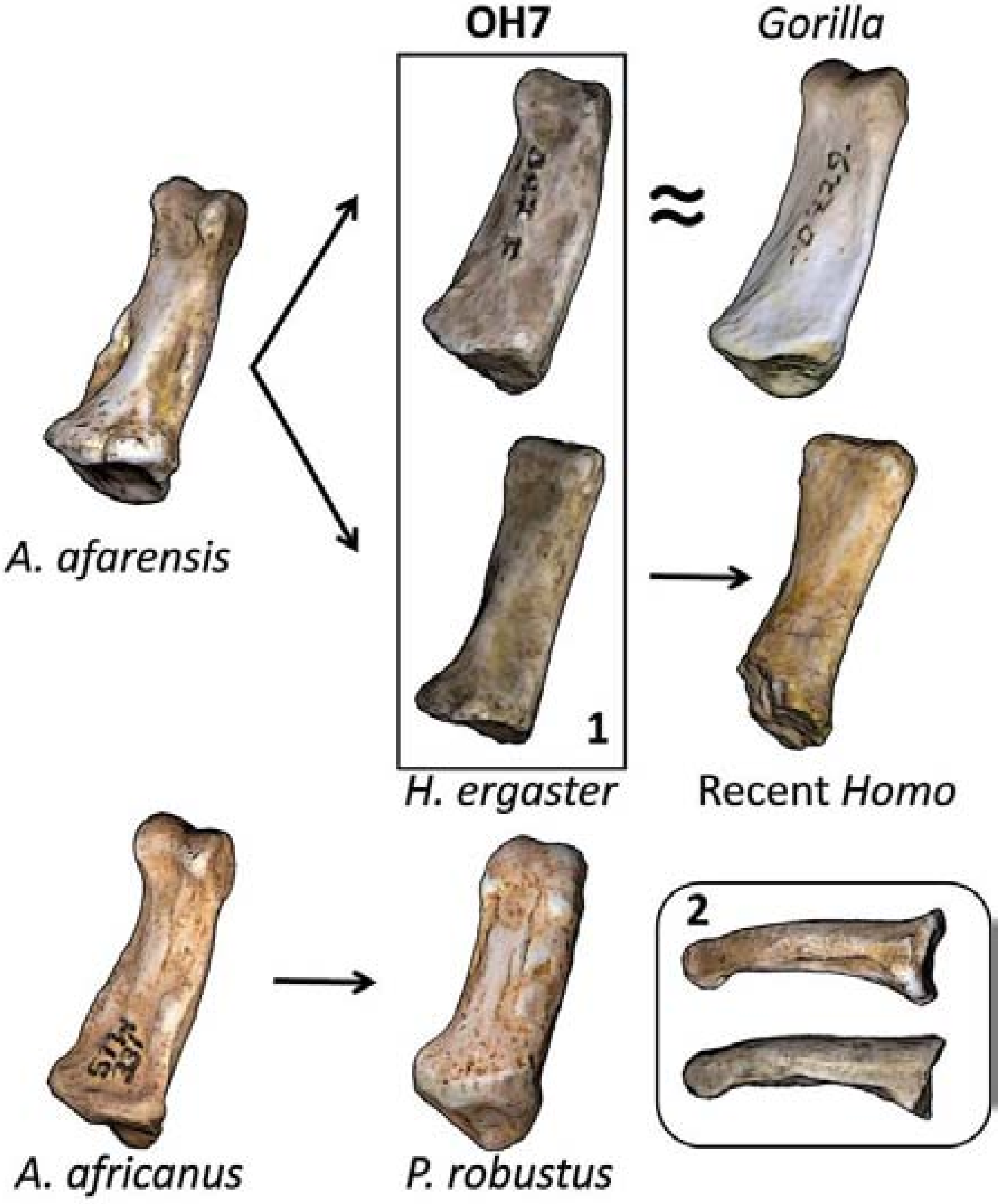


Figure 6.1. Composition showing a virtual model of the middle phalanx in different fossil and extant hominid taxa: *Australopithecus afarensis* (AL 333-88), *A. africanus* (Stw 331), *Paranthropus* cf. *boisei* (OH 7 F; subadult specimen with unfused epiphysis), *Homo erectus* s.l. (or *H. ergaster*, KNM-WT 15000-BO; subadult specimen with unfused epiphysis), *P. robustus* (SKX 5021), *Gorilla gorilla* (subadult specimen with unfused epiphysis) and recent *Homo* (Hortus XXV; subadult specimen with unfused epiphysis). All them are represented in oblique-palmar view and scaled to the same size in order to easily visualize the morphological differences. Even though both OH 7 and *H. ergaster* are nearly contemporaneous and are represented by subadult individuals, they differ considerably in morphology (Box 1). Note that, in *Homo*, the trochlear region is especially characteristic in subadult specimens. Interestingly, *A. afarensis* and OH 7 display a very similar lateral profile in middle phalanges (Box 2). See text for further details.

RESULTS

Morphological comparisons

A comparison of middle phalanx morphology between OH 7 and selected hominid taxa can be seen in Figure 6.1. The OH 7 middle phalanges display mediolaterally-expanded shafts, especially in the proximal two thirds. Distally, the margins of the shaft converge abruptly just before the trochlea, giving them their characteristic 'bottle-shaped' appearance. Furthermore, these phalanges show a slightly curved shaft and relatively small trochleae (see also Chapter 5). These latter features of the OH 7 middle phalanges closely resemble those of *Australopithecus*, and must be thus interpreted as symplesiomorphic (see Figure 6.1, Box 2); only the increased shaft robusticity would be a derived condition as compared to *Australopithecus*. On the contrary, the dorsopalmar diameter of these phalanges is relatively small, giving them a roughly flat appearance, most similar to the morphology found among living gorillas, which display robust hand bones due to their huge body mass. The middle phalanges of *P. robustus* display an overall stouter appearance due to their shorter and wider shafts (both dorsopalmarly and mediolaterally), lacking any trace of curvature. The morphology of the OH 7 middle phalanges thus strikingly differs from that of the phalanges of *H. ergaster* (or *H. erectus* s.l. KNM-WT 15000-BO; Walker and Leakey 1993; see Figure 6.1, Box 1), which is only slightly younger than OH 7, and which similarly correspond to a subadult individual (as shown by the lack of epiphyses). The basal morphology of the phalanges cannot be evaluated due to the unfused epiphyses, but the shaft of KNM-WT 15000-BO is already straight, as in modern humans, further resembling the latter by the lack of the very deep fossae that are associated with a prominent palmar keel and protruding ridges, and which would be indicative of powerful flexor muscles. Further resemblances with modern humans can be found at the trochlear region; thus, although the trochlea in KNM-WT 15000-BO is not completely developed (due to its subadult ontogenetic status), unlike the OH 7 specimens, it most closely resembles the trochlear region of a subadult *H. sapiens*.

Like the middle phalanges, the distal phalanges of OH 7 further depart from the human condition by being exceptionally robust, especially at the level of the shaft, which is mediolaterally expanded (see Figure 6.2), as in the middle phalanges. The OH 7 pollical distal phalanx is exceptionally wide, which gives to it an overall flat appearance. In palmar view, it shows a huge fossa, which is even larger (in absolute and relative terms) than in extant humans. A remarkable difference with respect to the human pollical distal phalanx is the lack of ungual spines on the lateral borders of the apical tuft. The overall morphology is very similar to that of the pollical distal phalanx SKX 5016, attributed to *P. robustus* (see Susman 1989: his Figure 1).

Morphometric comparisons

The descriptive statistics for DPR has been reported in Table 6.1; see Figure 6.2 for a comparison of the numerical results between OH 7 and the other taxa included in the morphometric analysis. With regard to the extant taxa, ANOVA comparisons indicate that significant differences exist for both the pollical ($F=34.7$, $p<0.001$) and the third ($F=14.7$, $p<0.001$) distal phalanges. Post-hoc multiple comparisons further show that there are more differences between the several pairs of groups regarding the pollical than the third distal phalanx. In particular, with regard to the pollical distal phalanx, all pair comparisons display significant differences (at least $p<0.05$), except for chimpanzees as compared to gorillas and orangutans, and for humans as compared to macaques and baboons. In other words, extant apes differ from humans and quadrupedal monkeys by displaying low (chimpanzees and orangutans) to moderate (gorillas) degrees of pollical distal phalanx robusticity, whereas humans and monkeys display, respectively, high to very high degrees (see Figure 6.2). The degree of pollical distal phalanx robusticity displayed by Neandertals overlaps with that of modern humans, although being more similar (even higher) on average to that of macaques and baboons. The degree of robusticity displayed by OH 7 is clearly above the 95% confidence interval of all these taxa and only minimally overlaps with the maximum range displayed by macaques, being most comparable (albeit higher) to the figure displayed by *P. robustus*. When the robusticity of the third distal phalanx is taken into account, it emerges that Neandertals, despite their higher robusticity, resemble modern humans and extant great apes by displaying a similar degree of robusticity for both distal phalanges. OH 7 and *P. robustus*, on the contrary, appear more similar to the condition displayed by monkeys, in which there is a great disparity in the degree of robusticity displayed by both phalanges, with the pollical one being much more robust than that from the third manual ray.

Table 1. Descriptive statistics for distal phalanx robusticity (DPR); see text for more details.

			DPR (manual ray I)				
Taxon	**N**	**Mean**	**SD**	**95% CI**		**Range**	
Orangutans	12	-1.33	0.10	-1.39	-1.26	-1.53	-1.14
Chimpanzees	23	-1.29	0.12	-1.34	-1.24	-1.57	-1.09
Gorillas	16	-1.12	0.26	-1.26	-0.98	-1.83	-0.77
Modern humans	20	-0.87	0.20	-0.97	-0.78	-1.15	-0.19
Neandertals	4	-0.65	0.11	-0.82	-0.48	-0.79	-0.53
Macaques	18	-0.72	0.17	-0.80	-0.63	-1.04	-0.48
Baboons	5	-0.72	0.07	-0.81	-0.64	-0.77	-0.61
OH 7	1	-0.49				-0.49	-0.49
P. robustus	1	-0.57				-0.57	-0.57
			DPR (manual ray III)				
Taxon	**N**	**Mean**	**SD**	**95% CI**		**Range**	
Orangutans	11	-1.46	0.10	-1.53	-1.40	-1.68	-1.36
Chimpanzees	23	-1.13	0.15	-1.20	-1.07	-1.57	-0.84
Gorillas	15	-1.00	0.12	-1.07	-0.93	-1.31	-0.86
Modern humans	6	-0.94	0.17	-1.12	-0.76	-1.21	-0.77
Neandertals	4	-0.64	0.16	-0.89	-0.39	-0.85	-0.49
Macaques	14	-1.25	0.22	-1.38	-1.12	-1.52	-0.86
Baboons	4	-1.20	0.16	-1.45	-0.96	-1.37	-1.00
OH 7	1	-0.83				-0.83	-0.83
P. robustus	1	-0.94				-0.94	-0.94

DISCUSSION

According to Shrewsbury *et al.* (2003), there is a set of features that characterize the human pollical distal phalanx, and which are functionally related to the human ability of holding objects with precision between the pads of the thumb and the others fingers: (a) A compartmentalized pulp, with a more or less static distal pulp, as well as a large, fatty and mobile, proximal one, which would assure an adequate friction and accommodation of the pulp of the thumb and the that of the other fingers to the shape of the surface of the object during precision grip; (b) The presence of ungual spines, with a prominent ulnar one; and (c) The marked asymmetry of the *flexor pollicis longus* attachment towards the radial side. These asymmetries are the osteological correlates of the interphalangeal joint of the human thumb, in which the flexion is accompanied by pronation, so that the pulp of the thumb faces that of the rest of the fingers during flexion. This brings the maximum contact surface with the objects manipulated during tool use and tool making. Shrewsbury *et al.* (2003) found that some of the features that characterize the human pollical distal phalanx could also be found in nonhuman primates, especially baboons. These primates, like humans, show developed ungual spines, with a more prominent ulnar one. However, only modern humans show a high frequency of asymmetry in the radial side of the *flexor pollicis longus* insertion (Shrewsbury *et al.* 2003), so that the latter feature alone might be a good indicator of manipulative behavior in fossil species.

It is noteworthy that the *flexor pollicis longus* of OH 7 pollical distal phalanx does not even display ungual spines, as previously noted by Shrewsbury and Sonek (1986), and that its insertion for the *flexor pollicis longus* neither shows any evidence of asymmetry. The latter authors concurred with the generalized view that OH 7 would have been capable of human-like precision grasping, albeit noting that the lack of ungual spines in the pollical distal phalanx would be indicative of limited compartmentalization and, as such, indicative of a restricted precision grip capability. Our results further indicate that, in spite of the high (Neandertal-like) degree of tuft robusticity in the pollical distal phalanx, when non-pollical manual rays are taken into account, the pattern of robusticity of OH 7, like that of *Paranthropus*, is monkey-like and does not fit neither the great-ape nor the human pattern. In great apes, the pollical distal phalanx is only slightly more robust than the third distal one in orangutans, whereas in African apes the reserve condition is found. In both modern humans and Neandertals, the degree of distal phalanx tuft robusticity for the first and third manual rays is very similar, thus more closely resembling the great-ape condition. In monkeys, on the contrary, the pollical distal phalanx is much more robust than the third distal phalanx; the same condition is also found, albeit to some lower degree, in both OH 7 and *Paranthropus*. These differences in the pattern of distal phalangeal robusticity deserve further investigation from a functional viewpoint. It is important to note that terrestrial cercopithecines display relatively short hands like humans, even though their hand morphology reflects a main compromise between quadrupedal locomotion in hard substrates and manipulation—in fact, baboons display a high opposability index, i.e. the relationship between the first and the second ray, which in *Theropithecus gelada* is even higher than in humans (Etter 1973)—. Since *Paranthropus* was a habitual biped when on the ground, strong locomotor selection pressures upon hand morphology can be discarded. As such, its morphology must be regarded in the context of manipulative adaptations. OH 7 and *P. robustus* do not show exactly the same morphology for the middle phalanges, being the former roughly flatter and slightly more curved, while in the latter they are stouter and straighter. Anyway, these subtle differences might be just attributable to specific adaptations in different species of the same genera, i.e. *P. boisei* and *P. robustus*. In any case, the similarities between OH 7 and *Paranthropus* confirm the previous conclusions reached in Chapter 5 that the former most likely does not belong to genus *Homo*, further reinforcing the functional hypothesis that the manual proportions of the robust australopiths, instead of being indicative of tool making, could be related to particular feeding adaptations such as those displayed by gelada baboons.

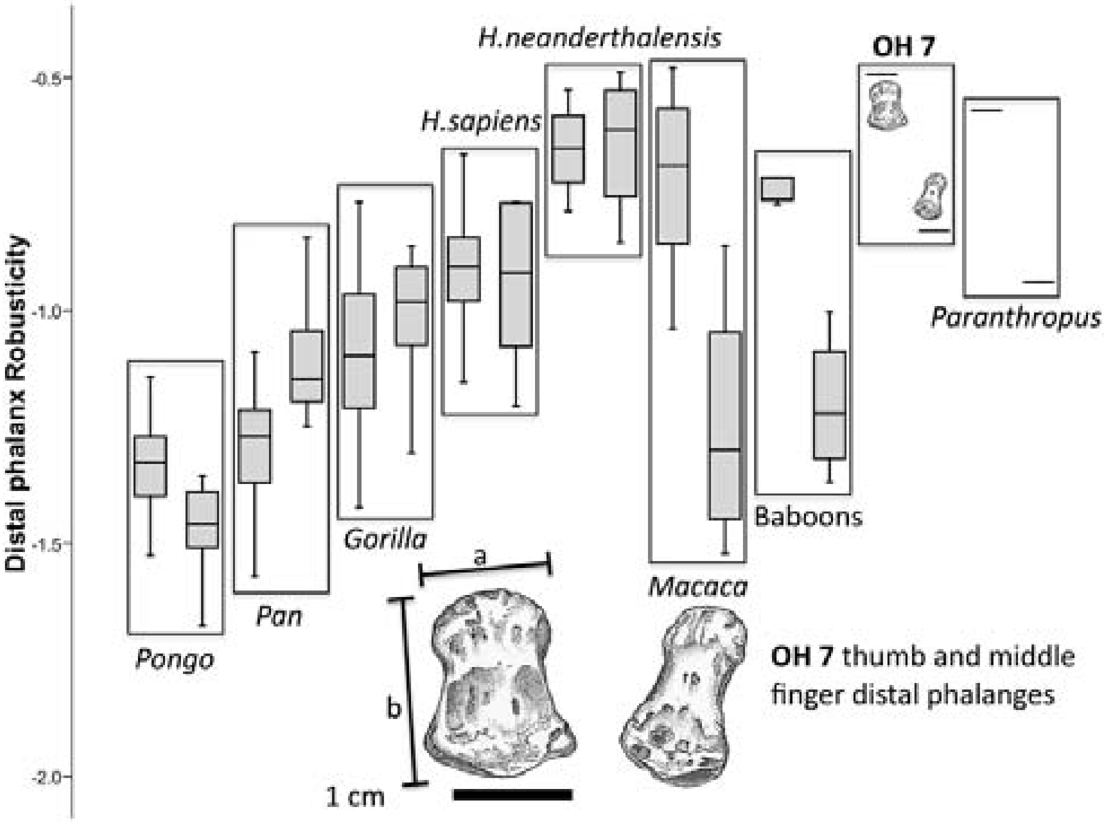


Figure 6.2. Boxplot showing the robusticity of the distal phalanges in selected extant taxa, Neandertals, OH 7 and *Paranthropus robustus*. The robusticity refers to the distal end (a) in relation to the maximum length of the phalanx (b). In each taxa, the robusticity for the pollical and middle finger distal phalanges is represented (left/right respectively). Horizontal lines represent the median values, whereas the boxes represent the 25% and 75% percentiles, and the whiskers the maximum-minimum ranges.

CONCLUSIONS

The morphological and morphometric comparisons reported in this chapter further reinforce previous conclusions, according to which the OH 7 hand remains do not fit the morphological pattern found among the several species of the genus *Homo*, including its nearly contemporary species *H. ergaster* that is similarly represented by subadult remains. Our results regarding the robusticity of distal phalangeal proportions further indicate that OH 7 neither fits a great-ape pattern to this regard: both humans and great apes display a similar robusticity on the pollical and non-pollical distal phalanges; on the contrary, OH 7 displays a monkey-like pattern, in which the pollical distal phalanx shows an exceptional robusticity at the tuft, as compared to the distal phalanges from other rays. Among fossil hominins, this pattern of robusticity is only displayed by the genus *Paranthropus*, thus favoring the view that the OH 7 hand remains most likely belongs to a robust australopith.

Chapter 7

Orrorin tugenensis: Early origins of refined manipulation

based on:

Almécija S, Moyà-Solà S, Alba DM (unsubmitted manuscript). *Orrorin tugenensis* reveals a common origin for human-like precision grasping and bipedalism.

Chapter 7

Orrorin tugenensis: Early origins of refined manipulation

INTRODUCTION

One of the hallmarks of humankind is the possession of a complex repertoire of manual grips (Napier 1993). In humans, the thumb plays a central role, being involved in almost all possible prehensile typologies (Shrewsbury and Sonek 1986; Napier 1993). This is possible thanks to human intrinsic manual proportions, i.e. a long thumb relative to the rest of the hand. The maximum expression of refined manipulation is reached during pad-to-pad precision grasping, which facilitates the opposition between the palmar aspect of the proximal pulp of the thumb with that of one or more fingers (Shrewsbury and Sonek, 1986). This capability is reflected in the morphology of the distal phalanges, especially that of the thumb, which shows specific features related to the soft tissues involved in precision holding (Shrewsbury *et al.* 2003). The traditional view postulates that tool use and tool making were the original selective pressures that prompted the emergence of these manual skills (Susman 1988a, b, 1994). However, it has previously argued that human-like manual proportions appeared too early in hominin evolution, significantly before the advent of stone-tool making, which would contradict the former hypothesis (Alba *et al.* 2003). Under this alternative view, manual proportions would have been selectively optimized for manipulation once the hands became freed from its ancestral locomotor function (Alba *et al.* 2003). *Orrorin tugenensis*, from the Lukeino Formation (Kenya, ca. 6 Ma), is the earliest unequivocal hominin displaying bipedal adaptations (Senut *et al.* 2001; Pickford *et al.* 2002; Galik *et al.* 2004; Richmond and Jungers 2008). Here we provide a morphometric and morphofunctional analysis of the available pollical distal phalanx BAR 1901'01 attributed to this taxon (Gommery and Senut 2006), in order to test the hypothesis that human-like precision grasping coevolved with bipedal locomotion.

MATERIALS AND METHODS

The *Orrorin* pollical distal phalanx BAR 1901’01 was compared on morphometric grounds with a selected sample of living and fossil catarrhine primates, including humans. The comparative extant sample includes the following taxa: extant ape genera, i.e. chimpanzees and bonobos (*Pan*; N=35), gorillas (*Gorilla*; N=19) and orangutans (*Pongo*; N=23); pronograde monkeys, such as baboons (*Papio*, *Mandrillus* and *Theropithecus*; N=31) and macaques (*Macaca*; N=18); and modern humans (*H. sapiens*; N=19). Besides the *Orrorin* phalanx, the comparative fossil sample includes the distal phalanges from the thumb of: *Australopithecus africanus* from Sterkfontein (Stw 294), *P. robustus* from Swartkrans (SKX 5016), *Paranthropus* cf. *boisei* from Olduvai (OH 7-A) and *H. neanderthalensis* from La Ferrassie I and Kebara 2. Measurements for fossil specimens were taken from the originals, good quality casts or from the literature (Ricklan 1988; Susman 1989; Vandermeersch 1991).

A principal components analysis (PCA), derived on the basis of the covariance matrix, was employed in order to undertake morphometric comparisons between the *Orrorin* pollical distal phalanx and that of other hominins and extant primates, including humans. This analysis, which does not assume group membership on *a priori* grounds, was based on the following seven variables (made to the nearest 0.1 mm) from the pollical distal phalanx: length (L); mediolateral width at the apical tuft (MLT), midshaft (MLS) and the base (MLB); and dorsopalmar height at the midshaft (DPS) and the base (DPB). These variables were logged by using natural logarithms (ln) before employing them in the analysis. A canonical variate analysis (CA), which defines groups *a priori*, was also undertaken on the basis of the same variables; fossil taxa were left ungrouped, but classified on the basis of this discriminant analysis. In order to visualize group membership, a cluster analysis was performed on the basis of Euclidean square distances between group centroids (for extant taxa) and discriminant scores (for fossils), by using the centroid linkage (unweighted pair-group centroid) method, which minimizes the dissimilarity between cluster centroids.

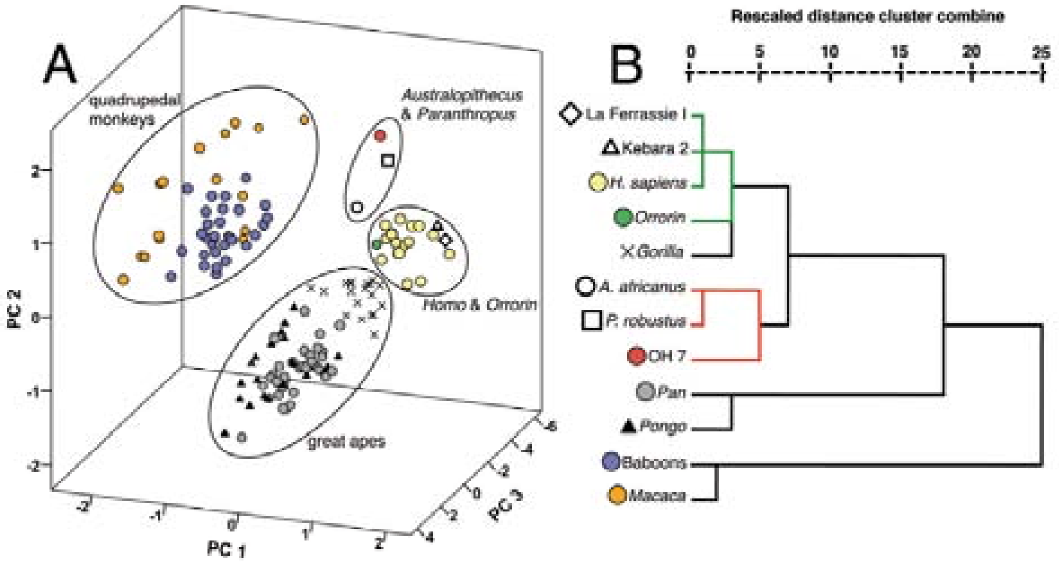


Figure 7.1. Morphometric analyses of the pollical distal phalanx. (**A**) Principal components analysis (PCA) based on pollical distal phalanx measurements, which clearly distinguishes quadrupedal monkeys, great apes, humans and australopiths (*Australopithecus* and *Paranthropus*); *Orrorin* (BAR 1901'01) most closely resembles modern humans. (**B**) Cluster analysis based on rescaled Euclidean squared distances derived from a canonical variate analysis; this analysis identifies a cluster of australopiths (robust forms), while *Orrorin* is the first early hominin that clusters with modern and fossil *Homo* (gorillas also cluster with humans due to its large absolute size).

RESULTS

The principal components analysis (PCA, Figure 7.1A) shows that the *Orrorin* pollical distal phalanx most closely resembles that of extant humans than that of other Plio-Pleistocene hominins, great apes or quadrupedal monkeys. The first component (PC1) largely reflects phalangeal size (Table 7.1), ranging from monkeys, to great apes, to *Homo*. To this regard, chimps and orangs somewhat overlap with monkeys, whereas gorillas slightly overlap with humans; fossil hominins are close to the gorilla/human overlap, although *Paranthropus* phalanges (including OH 7; see ‘Discussion’ below) are somewhat larger. The second component (PC2), on the contrary, mostly reflects shape (Table 7.1): positive values mainly result from larger mediolateral tufts and shafts (i.e. mediolaterally robust and flattened phalanges), whereas negative ones are mainly due to larger dorsopalmar diameters at the base and, especially, to higher lengths (i.e. slender and conical-shaped phalanges). Great apes show the latter pattern (although gorillas slightly overlap with modern humans), while the remaining taxa display some degree of apical (tuft) and midshaft expansion, and are hence relatively short. Among fossil hominins, Neandertals and *Orrorin* fall within the PC2 range of modern humans, and *A. africanus* displays only slightly higher values; *Paranthropus*, on the contrary, due to its extremely mediolateral robust phalanges, displays much higher PC2 values close to the upper limit of monkeys, which show a combination of relatively short pollical distal phalanx with mediolaterally expanded shafts and tufts. The third component (PC3), finally, is basically driven by dorsopalmar midshaft height (Table 7.1); although it only explains a small proportion of the variance, it enables to separate *Orrorin* from gorillas due to the higher phalanx of the former.

The canonical variate analysis (CA; Tables 7.2 and 7.3), which correctly classifies 90% of the original cases (100% in the case of humans), yields similar results to the PCA. All hominins are classified as humans; however, both *A. africanus* and *Paranthropus* spp. fail outside the modern-human range with $p<0.05$, whereas both Neandertals ($p=0.312$ and $p=0.604$) and *Orrorin* ($p=0.217$) fall within the human range of variation. In fact, *Orrorin* is the fossil taxon (other than fossil *Homo*) closest to the modern-human centroid (Table 7.4). This is further reflected by a cluster analysis (Figure 7.1B), which separates *Australopithecus* and *Paranthropus* in a 'large and robust' cluster for this phalanx of the thumb, while *Orrorin* clusters with humans. Although gorillas also cluster with humans, this is interpreted as an artifact attributable to its similar overall dimensions in spite of extensive morphological differences (Figure 7.2). Thus, regarding pollical distal phalanx proportions, *Orrorin* resembles humans by showing a flatter and larger phalanx than gorillas, both in absolute and especially relative terms, given that the gorilla body mass is approximately thrice that of humans, while that of *Orrorin* has been estimated to be around 35-50 kg (Nakatsukasa *et al.* 2007b). These phalanges of the thumb in *Paranthropus*, although displaying features similar to modern humans, depart from the human condition by being exceptionally short and robust, especially at the level of the shaft and tuft, which are mediolaterally expanded. They resemble, in terms of robusticity, enlarged versions of quadrupedal monkeys (Figure 7.1A).

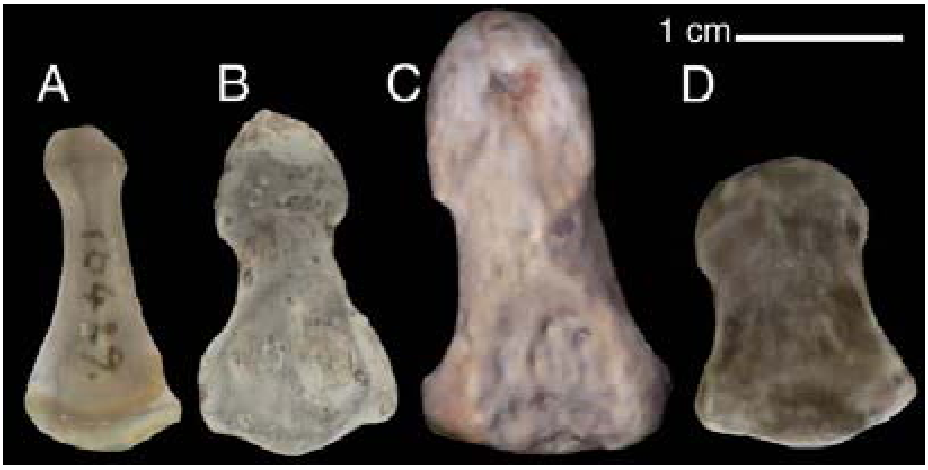


Figure 7.2. Pollical distal phalanges of (**A**) *Gorilla*, (**B**) *Orrorin* (BAR 1901'01), (**C**) *H. sapiens*, and (**D**) *Paranthropus* cf. *boisei* (OH 7-A), in palmar view. Although the gorilla phalanx (A) appears to display similar proportions to *Orrorin* (B) and humans (C) in multivariate analyses, this artifactually results from its huge body mass (even surpassing 200 kg in males), so that the pollical distal phalanx is in fact relatively much smaller than in the other taxa. A close morphological inspection of these phalanges of the thumb readily shows that neither gorillas (A) nor *Paranthropus* (D) display the set of morphological features related to precision holding that are shared by *Orrorin* (B) and humans (C). See text and Figure 7.3 for further details.

DISCUSSION

Besides morphometric similarities, the pollical distal phalanx of *Orrorin* displays a typically-human set of morphological features that are interpreted to be functionally related to human pad-to-pad precision grasping abilities (Shrewsbury *et al.* 2003). Particularly significant are the pronounced *flexor pollicis longus* insertion with marked asymmetry towards the radial side; the occurrence of dissymmetric ungual spines, with a prominent ulnar one; and the presence of an ungual fossa (Figures 7.2B and 7.3). The radial asymmetries present on the *flexor pollicis longus* insertion and ungual spines are the osteological correlates of the interphalangeal joint of the human thumb, in which flexion is accompanied by pronation, so that the pulp of the thumb faces that of the remaining fingers. This provides the maximum contact surface with the objects being manipulated. The presence of ungual spines itself is an indicator, together with the presence of an ungual fossa, of a fully compartmentalized digital pulp, with a more or less static distal part, as well as a large, fatty and mobile, proximal one (Shrewsbury *et al.* 2003). This would ensure an adequate friction and accommodation of the shape of the object between the pulp of the thumb and those of the fingers during precision holding. Some of these features can be also found in nonhuman primates (Shrewsbury *et al.* 2003), but only modern humans display them all; in particular, the asymmetry in the radial side of the *flexor pollicis longus* gabled insertion is exclusive of humans, so that the latter feature alone might be a good indicator of manipulative behavior in fossil species (Shrewsbury *et al.* 2003). Furthermore, uniquely among fossil hominins, the *Orrorin* pollical distal phalanx displays strongly developed lateral tubercles (Figure 7.3C), involved in the support of the nail bed (Shrewsbury and Johnson 1975) and the proximal ungual pulp (Shrewsbury and Sonek 1986).

The presence of the above-mentioned features in *Orrorin* permits us to infer human-like manual intrinsic proportions for this taxon, its distal phalanx being fully prepared to accommodate objects between the palmar aspect of its pulp and that of the fingers. Some of these precision-grasping features in this pollical phalanx of *Orrorin* had been previously noticed, although they were interpreted as an adaptation to arboreal locomotion reflecting “the precision grip essential for climbing and balancing, different from that of apes” (Gommery and Senut 2006, p. 372). However, given the fact that no arboreal primate displays this set of features, we favor the hypothesis linking the marked and detailed similarities between the pollical distal phalanx of *Orrorin* and extant humans as being functionally related only with refined object manipulation.

By the way, the *Orrorin* phalanx retains some primitive features shared with australopiths (e.g. small ungual fossa and proximally protruding median eminence of the articular surface). However, it is most remarkable that although the Plio-Pleistocene australopiths also show some morphological features related to precision grip (Gommery and Senut 2006), the 6-million-years-old pollical distal phalanx of *Orrorin* is more human-like in overall proportions and morphology than these later hominins. This is consistent with the previously described femoral morphology, in which among early hominin taxa, *Orrorin* has the smallest distance from the modern human centroid (Richmond and Jungers 2008). These facts suggest that australopiths—and especially *Paranthropus*—are autapomorphic, by displaying a robusticity pattern on the distal phalanges that is convergent with that of quadrupedal monkeys, as previously suggested for these taxa on the basis of the middle and non-pollical distal phalanges (see Chapters 5 and 6).

The highest resemblance between *Orrorin* and modern humans, with the exclusion of australopiths, is an unexpected result that bears important implications for the understanding of the selective pressures originally involved in the evolution of human manual skills. The latter were traditionally interpreted as adaptations to tool use and tool making (Susman 1988a, b, 1994), but this has been refuted on several grounds (Alba *et al.* 2003; see also Chapter 5). The presence of human-like manual proportions in the hand of *A. afarensis,* significantly predating the appearance of lithic tools in the record, enabled to falsify the traditional hypothesis (Susman 1988a, b, 1994) that the possession of a relatively long thumb was an adaptation to stone-tool making (Alba *et al.* 2003). This led to the alternative proposal that the selective pressures posed by complex manipulative behaviors, already present in non-human primates, would have been enough to drive the evolution of human-like manual proportions enabling pad-to-pad precision grasping, once the locomotor selection pressures posed by forelimb-dominated behaviors were relaxed with the adoption of habitual terrestrial bipedalism (Hartwig and Doneski 1998; Alba *et al.* 2003).

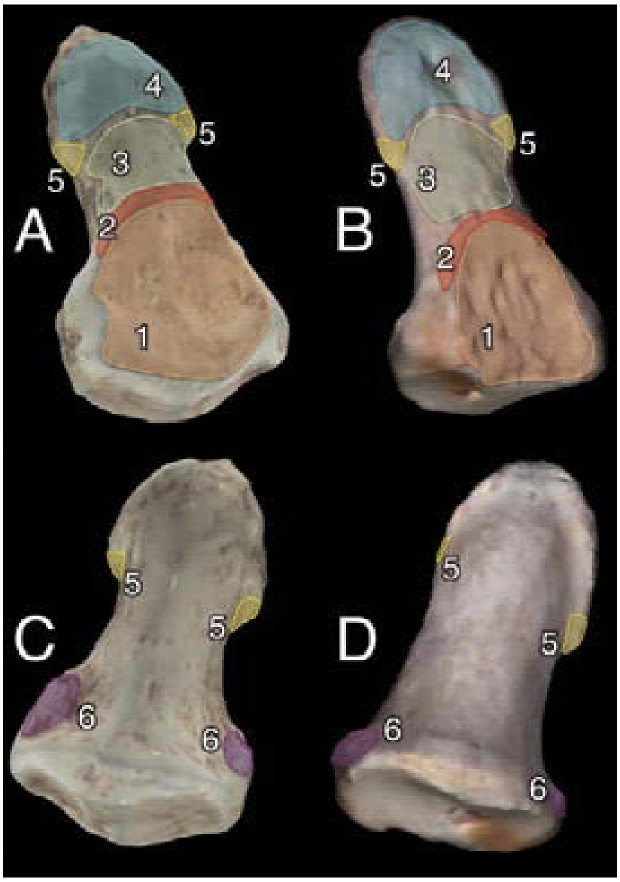


Figure 7.3. Morphological features of the pollical distal phalanx shared by *Orrorin* (BAR 1901'01; **A**, **C**) and modern humans (**B**, **D**), in oblique proximopalmar (**A**, **B**) and oblique proximodorsal (**C**, **D**) views: a huge proximopalmar fossa (1); a gabled insertion for the *flexor pollicis longus* with radial asymmetry (2); a compartmentalized digital pulp, differentiated into two (proximal and distal regions), which is further correlated with the presence of an ungual fossa (3), a wide tuft (4) and ungual spines (5) with ulnar emphasis; and developed lateral tubercles (6). Specimens scaled to the same size.

Regarding the taxonomic and anatomic attribution of the OH 7 hand remains

The original attribution of the OH 7 partial hand from Olduvai Bed I to *H. habilis* (Leakey *et al.* 1964) has been subsequently accepted by most authors (Susman and Creel 1979; Shrewsbury and Sonek 1986; Napier 1993). However, here we follow the ascription to *Paranthropus* based on morphological and morphometric grounds (see Chapter 5 and 6). The OH 7 pollical distal phalanx (OH 7-A) markedly differs from that of extant apes and humans, which led some authors to consider the alternative identification as a hallucial distal phalanx (Susman and Creel 1979). This would be supported by the strong muscular attachments and, especially, the slight axial torsion at the apical tuft (functionally related to bipedalism). This hypothesis was however discarded by its very same proposers, after a discriminant analysis indicating “that the fossil is closer to human distal phalanges than to those of any other hominoid and is somewhat more like a pollical than a hallucial phalanx” (Susman and Creel 1979, p. 325). We concur with this attribution, especially given that no differences in axial torsion can be noticed as compared to modern humans or even extant apes (Figure 7.2), in which the apical tuft is slightly twisted, so that it faces the rest of the fingers. It is also noteworthy that OH 7-A does not even display ungual spines (Shrewsbury and Sonek 1986), and that its *flexor pollicis longus* insertion neither shows any evidence of asymmetry (Figure 7.2). In the past, it has been accepted that the OH 7 hand would have been capable of human-like precision grasping, although the lack ungual spines in its distal phalanges would be indicative of limited compartmentalization and, as such, of a restricted precision-grip capability (Shrewsbury and Sonek 1986). Be that as it may, the similarities between OH 7 and *Paranthropus robustus* further confirm that the former should not be attributed to *Homo*, further reinforcing the functional hypothesis relating the manual proportions of robust australopiths with feeding adaptations instead of tool making (see Chapters 5 and 6).

CONCLUSIONS

The pollical distal phalanx of the *Orrorin* thumb unequivocally shows precision grasping capabilities in spite of its ancient chronology, most closely resembling modern humans than the later Plio-Pleistocene australopiths—including OH 7, which show a derived robusticity pattern. This indicates that refined manipulation is an ancient acquisition already present by the late Miocene. This is consistent with the hypothesis that habitual terrestrial bipedalism and the possession of skillful hands do constitute a single adaptive complex. Both types of behaviors might have been simultaneously selected, by synergistically favoring each other. These hand capabilities would have not been coopted until much later for tool making, coinciding with the encephalization increase that took place ca. 2.5 Ma.

Table 7.1. Main results of the principal components analysis (PCA) based on pollical distal phalangeal measurements, including the rescaled component matrix for the first three principal components used in this study.

Variables	PC1	PC2	PC3
% variance	84.9	9.8	2.0
% cumulative variance	84.9	94.7	96.7
Eigenvalue	0.649	0.075	0.015
ln L	0.924	-0.335	0.043
ln MLT	0.904	0.371	0.110
ln DPS	0.923	-0.260	-0.243
ln MLS	0.884	0.422	-0.146
ln DPB	0.947	-0.196	0.130
ln MLB	0.966	0.042	0.130

Abbreviations: PC = principal component; L = length; MLT = mediolateral width at the tuft; DPS = dorsopalmar height at midshaft; MLS = mediolateral width at midshaft; DPB = dorsopalmar height at the base; MLB = mediolateral width at the base.

Table 7.2. Main results of the canonical variate analysis (CA) based on distal phalangeal measurements, including standardized coefficients of discriminant functions.

Variables	CA1	CA2	CA3	CA4	CA5
% variance	72.1	23.2	3.6	1.0	0.1
% cumulative variance	72.1	95.3	98.9	99.9	100.0
Eigenvalue	15.108	4.865	0.747	0.211	0.018
Canonical correlation	0.968	0.911	0.654	0.418	0.134
ln L	1.035	-0.393	0.745	-0.089	-0.535
ln MLT	-0.435	0.362	0.866	-0.582	0.551
ln DPS	0.512	-0.460	-0.332	0.820	0.631
ln MLS	-0.558	0.787	0.242	0.627	-0.271
ln DPB	0.180	-0.011	-0.200	-0.614	0.594
ln MLB	0.072	0.559	-1.222	-0.025	-0.534

Abbreviations: CA = canonical axis; other abbreviations as in Table 7.1.

Table 7.3. Extant group centroids and fossil discriminant scores derived by the canonical variate analysis.

Taxa	CA1	CA2	CA3	CA4	CA5
Orrorin	1.648	1.961	0.890	1.796	0.426
A. africanus	-0.595	2.983	1.365	0.186	1.685
OH 7	-2.144	6.447	0.766	-0.002	0.539
P. robustus	-0.519	5.732	1.728	0.073	-0.045
La Ferrassie I	3.458	5.095	0.398	-0.311	2.004
Kebara 2	3.146	5.635	0.731	-0.202	0.537
Pan	3.155	-2.237	0.966	0.000	-0.037
Gorilla	2.693	2.453	-0.694	-0.381	-0.246
Pongo	1.995	-1.900	-1.561	0.159	0.113
H. sapiens	2.595	3.980	0.512	0.429	0.162
Baboons	-4.482	0.174	0.183	-0.605	0.087
Macaca	-6.547	-0.312	-0.005	0.788	-0.132

Table 7.4. Euclidean square distances of the *Orrorin* pollical distal phalanx BAR 1901'01 with respect to extant group centroids and other fossil individuals.

Taxa	Distance from BAR 1901'01
H. sapiens	7.053
Gorilla	9.033
OH 7	10.475
Kebara 2	19.764
La Ferrassie I	20.270
P. robustus	22.801
Pan	23.339
Pongo	23.814
A. africanus	37.759
Baboons	47.149
Macaca	74.453

Summary

Chapter 1

The hand of primates is a more or less primitive structure inherited from the first amniotes. However it shows subtle innovations; the most important of them is the possession of a unique intrinsic organization in which the proximal phalanges are relatively long as compared to the metacarpals. This ultimately allowed primates to have a hand with prehensile capabilities. With the exception of humans, the hand of primates participates in both locomotion and manipulation, its morphology thus reflecting some kind of compromise between both selective pressures. The study of the hand in fossil and extant apes and humans would permit to make functional and evolutionary inferences regarding the main changes occurred in this particular structure, as well as its role in human evolution.

Chapter 2

The partial skeleton of *Pierolapithecus*, which provides the oldest unequivocal evidence of orthogrady, together with the phalanges from Paşalar most likely attributable to *Griphopithecus* (a pronograde taxon), provide a unique opportunity for understanding the changes in hand anatomy during the pronogrady/orthogrady transition in hominoid evolution. In this chapter, we describe the *Pierolapithecus* hand phalanges and compare their morphology and proportions with those of other Miocene apes, in order to make paleobiological inferences on locomotor evolution. In particular, we investigate the orthograde/pronograde evolutionary transition, in order to test whether the acquisition of vertical climbing and suspension was decoupled during evolution. Our results indicate that the manual phalanges of Miocene apes are much more similar to one another than as compared to living apes. In particular, Miocene apes primitively retain features related to powerful-grasping palmigrady on the basal portion, the shaft and the trochlea of the proximal phalanges. These features suggest that above-branch quadrupedalism, inherited from stem hominoids, constituted a significant component of the locomotor repertories of different hominoid lineages at least until the late Miocene. Nonetheless, despite their striking morphological similarities, several Miocene apes do significantly differ regarding phalangeal curvature and/or elongation. *Hispanopithecus* most clearly departs by displaying markedly-curved and elongated phalanges, like the most suspensory of the extant apes (hylobatids and orangutans). The remaining Miocene apes, on the contrary, display a low to moderate phalangeal curvature, and short to moderately-elongated phalanges, which are indicative of the lack of suspensory adaptations. As such, the transition from a pronograde towards an orthograde bodyplan, as far as this particular anatomical region is concerned, is merely reflected in somewhat more elongated phalanges, which may be functionally related to enhanced vertical-climbing capabilities. Our results therefore agree with the view that hominoid locomotor evolution largely took place in a mosaic fashion: just like taillessness antedated the acquisition of an orthograde bodyplan, the emergence of the latter—being apparently related only to vertical climbing—also preceded the acquisition of suspensory adaptations, as well as the loss of primitively-retained, palmigrady-related features.

Chapter 3

Morphological and biometrical analyses of the partial hand IPS18800 of the fossil great ape *Hispanopithecus laietanus* (= *Dryopithecus laietanus*), from the late Miocene (ca. 9.5 Ma) of Can Llobateres (Catalonia, Spain), reveal many similarities with extant orangutans (*Pongo*). These similarities are interpreted as adaptations to below-branch suspensory behaviors, including arm-swinging and clambering/postural feeding on slender arboreal supports, thanks to the possession of an orang-like ‘double-locking mechanism’. This is confirmed by the long and highly curved phalanges of *Hispanopithecus*. The short and stout metacarpals with dorsally constricted heads, together with the dorsally extended articular facets on proximal phalanges, indicate the persistence of significant degrees of palmigrady. A powerful grasping capability is indicated by the great development of basal phalangeal tubercles, the marked insertions for the flexors on phalangeal shafts and the large pits for the collateral ligaments. The morphology of the *Hispanopithecus* long bones of the hand indicates a unique positional repertoire, combining orthogrady with suspensory behaviors and palmigrade quadrupedalism. The retention of powerful grasping and palmigrady suggests that the last common ancestor of hominids might have been more primitive than what can be inferred on the basis of extant taxa, suggesting that pronograde behaviors are compatible with an orthograde bodyplan suitable for climbing and suspension.

Chapter 4

Phalangeal morphology is a rich source of anatomical information for making locomotor inferences in extinct hominoids, but there is no reason to rely just on one of its traits. However, Deane and Begun's (2008) do so after a discriminant analysis that merely relies in phalangeal curvature, classifying both *Pierolapithecus* and *Hispanopithecus* as suspensory apes. In Chapter 4 we show that on the basis of included angle measurements for both proximal and middle phalanges, *Pierolapithecus* phalanges are much less curved than those of both *Hispanopithecus* and orangutans, further displaying a curvature pattern that does neither fit that of small brachiators. The lower degree of relative phalangeal length in *Pierolapithecus* further indicates a much lower significance of suspensory behaviors than in *Hispanopithecus*. Finally, phalangeal morphology shows that *Pierolapithecus*, unlike the largely terrestrial and less suspensory chimpanzees, lacks specific suspensory adaptations, most closely resembling the condition of other early to middle Miocene apes and extant quadrupedal taxa. Overall, the evidence provided by *Pierolapithecus* falsifies the hypothesis that suspensory behaviors were the main original target of selection underlying the acquisition of orthogrady. Nothing precludes suspension having been sporadically employed by the orthograde *Pierolapithecus*, but available evidence clearly indicates that it would not have been practiced to the same degree as in hylobatids, orangutans, *Hispanopithecus*, or even in the less suspensory African apes.

Chapter 5

In this chapter we test the currently accepted taxonomic hypothesis that the hand of the *Homo habilis* holotype Olduvai Hominid 7 (OH 7) from Olduvai Gorge can be unambiguously assigned to *Homo*. Morphometric and morphological comparison with humans and australopiths (*Australopithecus* and *Paranthropus*) indicate that the OH 7 hand most likely belongs to *Paranthropus*. The morphological adaptations of *Paranthropus* are thus further evaluated in the light of the alternative taxonomic hypothesis for OH 7. Functional analyses suggest that morphological features related to human-like precision grasping, previously considered diagnostic of tool making by some, may be alternatively attributed to specialized manual feeding techniques in robust australopiths.

Chapter 6

The phalanges from the Olduvai Hominid 7 (OH 7) partial hand are evaluated from a morphological and morphometric viewpoint, with special emphasis on the distal phalanges. These remains have been traditionally attributed to the holotype of *Homo habilis*. However, in Chapter 5 we conclude that, given their similarities with the remains of *Paranthropus robustus*, an attribution to the robust australopith *Paranthropus* appears much more likely. The results of this chapter confirm this conclusion, further indicating that the pattern of robusticity of the pollical and middle finger distal phalanges in OH 7 differs from the pattern displayed by modern and fossil humans, as well as by the great apes, much more closely resembling the pattern displayed by quadrupedal monkeys and the genus *Paranthropus*.

Chapter 7

Ever since Darwin it has been hypothesized that the origin of bipedalism was related to the freeing of the hands for manipulative purposes. Fossil remains of *Orrorin tugenensis* (Kenya, ca. 6 Ma) enable to test this hypothesis, since it is the earliest hominin unequivocally displaying bipedalism-related features. In this chapter we provide a morphometric analysis of the *Orrorin* pollical distal phalanx in order to test whether bipedalism coevolved with enhanced manipulative behaviors. Our results reveal typical human-like features related to precision grasping, indicating bipedalism and human manipulation originally evolved as part of the same adaptive complex. This confirms previous hypotheses relating the origin of refined manipulation, unrelated to tool making, with the relaxation of locomotor selection pressures on the forelimbs. Our analyses not only show that human-like precision grasping is an ancient acquisition already present by the late Miocene, but remarkably indicate that the thumb morphology of *Orrorin* is more human-like than that of australopiths. These results suggest that, starting from a human-like thumb pattern, some later Plio-Pleistocene hominin lineages became specialized in terms of hand robusticity. These conclusions suggest that we should be very cautious when making functional inferences from supposedly intermediate hominin forms, such as the Olduvai Hominid 7 hand.

Discussion and conclusions

The results reported in this work represent a significant contribution regarding the origin of hominids, the morphology and positional behavior of the first hominins, and ultimately the origin of the human hand:

Most early Miocene hominoids (e.g. *Proconsul*, ca. 20 Ma) were mainly arboreal palmigrade primates (Begun *et al.* 1994), still retaining a pronograde bodyplan (Ward 1993). They had already lost the external tail (formerly employed as a balancing organ), once they begun to increase in body mass. Instead, they developed enhanced manual grasping capabilities to perform this function (Kelley 1997). The hands of these stem hominoids were relatively short, and very similar to those of extant monkeys (Napier 1993; see also Chapter 2).

Our results on the phalangeal morphology of the already orthograde *Pierolapithecus* (ca. 12 Ma; Moyà-Solà *et al.* 2004, see Chapters 2 and 4) show that this stem great ape—and most other Miocene apes—still retained a relatively short hand, with an overall monkey-like phalangeal morphology, and which still lacked adaptations to suspensory behaviors. However, *Pierolapithecus*, which already had lost the ulnocarpal articulation (Moyà-Solà *et al.* 2004), shows a slight degree of elongation in the proximal phalanges (these Chapters 2 and 4). This, together with the possession of an orthograde bodyplan must be seen as an adaptation to vertical climbing in such relatively large arboreal forms (Moyà-Solà *et al.* 2004; Chapter 2). The small amount of phalangeal elongation would increase the surface of friction with vertical supports (Preuschoft 1973) and the loss of the articulation between the ulna and the carpals would enhance the degree of ulnar deviation of the hand (O'Connor 1975). Furthermore, the thumb of *Pierolapithecus*—as inferred from its pollical distal phalanx—, contrary to that of extant apes, was long, and probably assisted powerful grasping during vertical climbing and above-branch palmigrady. We do not discard sporadic suspensory behaviors in *Pierolapithecus*, although the lack of specific adaptations preclude us against interpret it as a suspensory ape. Under this point of view, suspension would appeared just as an exaptation of an already present orthograde bodyplan—and locomotor repertoire—together with somewhat elongated hands.

The relatively short hand of *Pierolapithecus*, with a relative long thumb, still retaining palmigrade features in its proximal phalanges, and lacking specific adaptations for suspension, is seen here as close to the original hand morphotype from which the elongated hands of extant great apes and the shortened hands of humans evolved.

Hispanopithecus (ca. 9 Ma) is the earliest known fossil great ape showing suspensory adaptations (Moyà-Solà and Köhler 1996, this Chapter 3). Its hand displays an unusual configuration—completely unknown among extant and extinct primates—which combines an orang-like pattern of phalangeal elongation and morphology on the proximal and middle phalanges with and a palmigrade, monkey-like pattern in the metacarpals (Chapters 2 and 3). We must be careful when making any evolutionary interpretation, because the hands of fossil primates are the result of their own locomotor and manipulatory history, and not necessarily a precursor of extant primate hands (Tuttle 1967; Lovejoy 2007). However, in this case, the very specific suspensory adaptations of *Hispanopithecus,* such as the ulnar shift of the main axis of the hand that is only documented in extant orangutans (specifically males; see Susman 1979), are too suspicious not to be interpreted as stem pongine features. Be that as it may, the unknown morphology of *Pierolapithecus* and *Hispanopithecus* among extant primates, led us to stress that evolutionary inferences should not be based on extant taxa alone. Morphological evolution of the ape hand apparently occurred in a mosaic fashion: first elongation in the phalangeal region and then in the metacarpals. Furthermore, since the stem great ape *Pierolapithecus* does not show suspensory adaptations, 'suspension' must be homoplastic, at least, between lesser apes and great apes. The questions that remains to be answered is whether suspension is homoplastic between African apes and orangutans, and even in African apes between gorillas and chimps.

With respect to the earliest bipedal hominins, several hominin genera have been reported more or less during the same period (late Miocene to early Pliocene): *Sahelanthropus* from Chad (ca. 7 Ma; Brunet *et al.* 2002), *Orrorin* from Kenya (ca. 6 Ma; Senut *et al.* 2001) and *Ardipithecus* from Ethiopia (ca. 5.5 Ma; Haile-Selassie 2001). The possibility has been discussed that these three early hominins might belong to the same genus (Haile-Selassie *et al.* 2004), and even that *Sahelanthropus* might not be a Hominini at all, but a Gorillini (Wolpoff *et al*. 2002). Be that as it may, the case is that no postcranial remains have been published yet for *Sahelanthropus* and the postcranial remains of *Ardipithecus* are very scarce. Moreover, their supposed bipedal capabilities only rely in the position of the foramen magnum (Brunet *et al.* 2002) and on the basal morphology of one pedal proximal phalanx (Haile-Selassie 2001), respectively.

Fortunately, bipedalism in *Orrorin* is reasonably well-supported in several ways by its femoral anatomy (Senut *et al.* 2001; Pickford *et al.* 2002; Galik *et al.* 2004; Richmond and Jungers 2008). Their discoverers, however, suggest that this taxon would combine terrestrial bipedalism with some degree of arboreal locomotion (Senut *et al.* 2001; Gommery and Senut 2006). The material recovered from the hand of *Orrorin* is very scarce—just one partial proximal phalanx and a complete pollical distal phalanx. However, the set of features described for the phalanx of the thumb—including a fully compartmentalized pulp region—are indicative of a fully opposable pollex with pulp to pulp precision grasping capabilities (this Chapter 7). Furthermore, morphological analyses reveal that, contrary to some later Plio-Pleistocene australopiths, these phalanges are similar to that of modern humans (this Chapter 7). The combination, in this early hominin, of human-like precision grasping capabilities with bipedalism suggests that both functional abilities share a common origin (or, at least, are evolutionarily very related to one another). The evolution of features related to precise manipulation (i.e. human-like hand proportions, where the thumb is long relative to the rest of the fingers and fully opposable, as well as the presence of digital pulp compartmentalization) would have been driven by the already present manipulative selection pressures in the hands—also present in the hands of non-human primates—such as feeding, nesting, etc. (Tuttle 1967, 1969). This was possible once the hand was largely freed from its locomotor demands, thanks to the advent of bipedalism (Hartwig and Doneski 1998; Alba *et al.* 2003).

Tuttle (1967, p. 204) asserted that “the hands of early Hominidae [=Hominini] probably had proportions more like those of modern *Homo sapiens* than to modern great apes”. However, he proposed that a modern human configuration would be prompted by the combination of object manipulation plus some degree of *terrestrial* palmigrady. Selection for tool making would merely shaped the human hand to its final modern shape.

To this respect, a significant question that remains to be tested by future finds from the fossil record is whether bipedalism initially evolved on the ground or in trees. From the lines above, it is clear that Tuttle was an advocate of the ‘ground origin’. However, there is still an open debate between the advocates of the terrestrial and the arboreal origins of bipedalism. The latter generally postulate a knuckle-walking stage in human evolution. This point of view has a long tradition, ever since Keith's (1923) brachiationist theory, which distinguished three main stages during human evolution: hylobatian, troglodytian, and plantigrade. This model stated that arboreal pronograde primates evolved into long-handed, hylobatid-like apes that practiced orthograde suspension. The ‘troglodytian stage’ was represented by a larger form than the previous one—most similar to extant chimps—whose hands were seen as inflexible ‘brachiating-hooks’. So it was supposed that when on the ground these forms MUST use the back of their ‘hook-hands’ to walk. This was a nice story about the origins of knuckle-walking and about how humans passed across this stage during the transition of the arboreal milieu and the terrestrial bipedalism.

More recently, Richmond and colleagues (Richmond and Strait 2000; Richmond *et al.* 2001) have identified putative knuckle-walking features in the wrist region of *Australopithecus anamensis* and *A. afarensis*. However, other features traditionally considered indicative of knuckle-walking (see for instance Tuttle 1967, 1969) are not present in these or in earlier hominin forms. These authors interpreted this fact as revealing that bipedal hominins did not practice knuckle-walking anymore, but had retained some of its related features from a knuckle-walker ancestor. After their proposal, their study has been refuted by several authors (Corruccini and McHenry 2001; Dainton 2001; Lovejoy *et al.* 2001), who found that the former results most probably demonstrate ape-like affinities instead of knuckle-walking adaptations. Furthermore, in a recent paper, Kivell and Schmitt (2009) interestingly show that the classic features, traditionally interpreted to be diagnostic of knuckle-walking in African apes, can be seen, instead, as adaptations—different in *Pan* and *Gorilla*—to habitual extended postures of the wrist in the arboreal substrate. This, in turn, would indicate that knuckle-walking appeared independently in chimps and gorillas and that the presence of some putative knuckle-walking features in the wrist of some hominins would indicate that “human bipedalism evolved from a more arboreal ancestor occupying the ecological niche common to all living apes” (Kivell and Schmitt 2009, p. 1).

It is also noteworthy that recent studies based on the positional behavior of extant orangutans show that bipedalism—assisted by the hand—is commonly used to access the fine terminal branches of trees (Thorpe *et al.* 2007; Crompton *et al.* 2008; Thorpe 2009). Then, terrestrial bipedalism would not be but an exaptation of an already existing behavior, most frequently seen in orangutans but also employed by other apes (Thorpe *et al.* 2007). Although with some differences, this is similar to the older view of Tuttle (1969, p. 960): "when arboreal populations shifted to terrestrial habitats, chimpanzees became semierect quadrupeds, while man was predisposed toward orthograde bipedality". If bipedalism appeared in an arboreal context, this would explain why almost all bipedal hominins still retain arboreal-related features in its forelimbs (Filler 2007; Thorpe *et al.* 2007; Crompton *et al.* 2008; Thorpe 2009). It would be nice, however, to be able to discern whether these arboreal features were merely non-functional, plesiomorphic retentions, or instead still-functional adaptations. Some largely ecophenotypical features, such as phalangeal curvature (e.g. Preuschoft 1973; Richmond 2007), might offer in the future some hope to be able to these between these competing hypotheses.

Reconstructing the original locomotor repertoire of the last common ancestor between hominins and African apes is an interesting topic, outside the scope of this work. However, our results on hand morphology of Miocene apes can bring some light to this respect: Richmond and Jungers (2008) reported that the *partial* proximal phalanx available for *Orrorin* shows an included angle of 52º, thus resembling chimps, and hence presumably being fully compatible with a knuckle-walking locomotion. Interestingly, *Orrorin* shows exactly the same degree of curvature that we found in *Pierolapithecus* and other middle Miocene apes, which is therefore the plesiomorphic condition for non-suspensory, arboreal apes (these Chapters 2 and 4). Furthermore, knuckle-walking must be seen as a compromise in African apes between the possession of very long hands for the arboreal locomotion (including suspension) and a modified type of digitigrade terrestrial quadrupedalism (see Tuttle 1967, 1969). Since the relative length of the *partial* proximal phalanx of *Orrorin* remains to be evaluated, and knuckle-walking can be identified in African apes using relative curvature of proximal and middle phalanges, it is not possible to infer knuckle-walking just in the basis of the curvature of its proximal phalanx. To sum up, if *Orrorin* is not interpreted as a suspensory ape (and there is no reason to do so at the moment being), then it follows that humans must not necessarily pass through a knuckle-walking stage before the acquisition of terrestrial bipedalism.

The fossil record suggests that during the Pliocene (around 5-2 Ma) human evolution was restricted to the African continent. This was the time of the genus *Australopithecus* (and *Ardipithecus* at the earliest Pliocene). The most complete set of hand bones—attributed to *A. afarensis*—comes from the AL 333/333w locality from Hadar, Ethiopia (Bush *et al.* 1982). Interestingly, the intrinsic hand proportions of this taxon, especially the relationship between the thumb and the rest of the hand, was found to be modern-human-like, in spite of the fact that these remains predate the earliest stone tools by nearly 1 million years (Alba *et al.* 2003). Similar results were subsequently found in *A. africanus* from South Africa (Green and Gordon 2008). In both australopiths, the thumb was found to be relatively long, promoting a high degree of manipulative dexterity (i.e. precision grasping capabilities), although its ape-like slenderness would indicate different mechanical demands than in later, stone-tool making hominins (Alba *et al.* 2003; Green and Gordon 2008).

The later Plio-Pleistocene hominins include the earliest members of the genus *Homo,* together with the genus *Paranthropus* (or robust australopiths). Both hominins are generally supposed to be derived from an *Australopithecus* ancestor, although it is far from clear from which one. The debate on the origin of *Homo* and “what is *Homo* and what is not” is considerable and outside the scope of this work (see reviews in Wood 2000; Wood and Collar 1999, 2001; Wood and Richmond 2000; Wood and Lonergan 2008). What it is relevant here is the origin of the modern-human hand, and its relationship with stone-tool making.

One of the main problems is the coexistence in time and space (even in the same site) of both *Homo* and *Paranthropus*. In the South African site of Swartkrans, there are levels with both hominins plus the presence of stone tools. Randall Susman (Susman 1988a, b, 1989, 1994, 1998) postulated, based on the similarities between the hand remains of South African *Paranthropus* (i.e. *P. robustus*) and those of the earliest putative toolmaker (i.e. *H. habilis*) from Olduvai Gorge (Tanzania; Leakey *et al*. 1964), that there was no reason not to impute tool-making capabilities to *Paranthropus* too. Under this point of view, one must accept that increased cognitive capabilities (attributed to increased encephalization in *Homo*) did not play a crucial role in the systematic use of lithic technology. However, as we pointed out on morphological grounds in Chapters 5 and 6 (see also Tuttle 1967; Robinson 1972; Tocheri *et al.* 2008), the manual remains from Olduvai most probably belong to *Paranthropus*. As such, Susman's paradigm cannot be sustained anymore.

Another problem of Susman's hypothesis is his equation between tool using and tool making. It seems more likely that *all* bipedal hominins already possessed enhanced manipulative capabilities long before the regular advent of stone-tool making, once they freed their hands thanks to the acquisition of committed bipedalism (Alba *et al.* 2003; Green and Gordon 2008; these Chapters 5, 6 and 7). We completely agree that *Paranthropus* (including OH 7) had advanced manipulative capabilities (i.e. pad-to-pad precision grasping), even though the overall morphology of the hand bones of *P. robustus* and OH 7 (*P.* cf. *boisei*) is not human-like at all. In Tuttle words, "only the configuration of the terminal phalanges prevent the Olduvai hands from being assigned to another hominoid family. And even the terminal thumb phalanx is not closely similar to *Homo*" (Tuttle 1967, p. 199). In Chapters 6 and 7, we show that OH 7 neither shows a human-like morphology or robusticity pattern in the distal phalanges. This condition—like that in *Paranthropus robustus*—is probably derived, being convergent with quadrupedal monkeys. The latter, in turn, display also enhanced manipulative capabilities, which are directly related to their committed terrestrial digitigrady (Etter 1973).

Probably stone-tool making did play an important role in determining many of the morphological adaptations of the human hand into its current shape (such as increase in thumb and joints robusticity as a response to the stresses caused by regular stone-tool making). It does not follow, however, that all the human-like features of the hand are an adaptation to tool making, this new function having merely coopted more ancient acquisitions as exaptations to tool making.

Finally, we summarize below the **main conclusions of this doctoral thesis:**

(1) The several fossil apes investigated suggest that the evolution of the hand proceeded in a mosaic fashion and to a some degree independently in several lineages. Accordingly, inferences should not be based on extant taxa alone, since fossil apes often display a more primitive condition than expected on the basis of their hypothetical last common ancestor as reconstructed on the basis of living taxa. This is an unexpected and interesting result that would deserve further research in the framework of more specific hypotheses.

(2) *Pierolapithecus* indicates that a relatively short hand with arboreal-palmigrade, monkey-like features, including a relatively long thumb for assisted grasping, is the original hand pattern from which the elongated hands of extant apes and the shortened ones of humans evolved. This answers part of the first objective of this doctoral thesis, i.e. elucidating a plausible ancestral hand morphotype for all hominids.

(3) From this original hand pattern, and on the basis of the *Hispanopithecus* hand, it follows that the evolution of ape hand morphology towards suspensory behaviors probably occurred in a mosaic fashion: first the elongation of the phalanges, and later on that of the metacarpals. Furthermore, if *Pierolapithecus* is considered a stem great ape *without* suspensory adaptations, the latter must be homoplastic, at least, between lesser apes and great apes. The question that remains to be answered is whether suspension is homoplastic between African apes and orangutans. These conclusions cover the rest of the first aim and also answers the second question of this work, relative to the origins of suspensory behaviors.

(4) From the morphological study of the *Orrorin* thumb, we propose that precision grasping capabilities appeared early in human evolution, probably more or less simultaneously with bipedalism. This was possible thanks to the relaxation of locomotor selection pressures in hands, thus being functionally unrelated to stone-tool making. It is most plausible that lithic industry is exclusive of the genus *Homo*, being originally linked to an increase in encephalization in this genus. By the time of the establishment of a stone culture on a regular basis, hominins already possessed modern-human-like hand proportions. Stone-tool making would have driven only the latest portion of human evolution, by increasing the robusticity of the joints and of the thumb. This elucidates the third and fourth initial questions relative to the when and why did the human-like hand morphology evolved.

(5) The hand remains of the Olduvai Hominid 7 (OH 7), traditionally interpreted as an ‘intermediate form’ and an early member of the genus *Homo*—even belonging to the holotype of “*Homo*” *habilis*—should be ascribed into the genus *Paranthropus*. In turn, the hand of *Paranthropus* shows specific adaptations that are convergent with those displayed by quadrupedal monkeys. These may be attributable to specific manual feeding adaptations in bipedal hominins. This outcome further clarifies the third and four aims of this research, being in consonance with the hypothesis of an early origin of manipulation, related to bipedalism instead of tool making.

Epilogue

We are very lucky for the existence of fossils. These are like ‘magic windows’, allowing us to take a look to the past. Unfortunately, these windows are not completely open... usually we can just take a glance and see a small portion of what it was. Then we can infer what and how it must or might have been. It is nice to see how new techniques appear every day, how we can quantify more and more precisely, and how we can test new hypotheses in a more ‘refined’ way. However, what I most wonder about is that ideas that come from the new approaches often agree with what had been said long before.

I completely marvel at the new possibilities that CT scanning, 3D laser scanners and so offer to us. We can now observe structures that were there before, but hidden to the eye, some of them with phylogenetic or functional relevance, such as the cranial sinuses or the cortical bone or the trabecular orientation in long bones... Moreover, it is possible to virtually reconstruct our ancestors and other fossils fast and easily, without even touching them! Could be this a problem instead?

However, I feel frustrated when some of the ‘new revolutionary findings’ in paleontology (and especially paleoanthropology) ultimately rely on having blind faith in the *already* existent conclusions/attributions (i.e. working in the same paradigm) and then follow them. Any work presenting revolutionary ideas must necessarily go against pre-established paradigms, which are substantiated by a huge amount of papers that support them. As such, the new hypotheses will find an enormous opposition by many scholars and researchers that do not want their work to be refuted. What I am just trying to stress is that mainstream paleontological research should also consist in the production of new and innovatory ideas, apart from using new techniques to verify what was already said long before.

Glossary

Below there is the definition of some unexplained terms that appear along the text:

- Ape: any member of the superfamily Hominoidea, excluding humans and their closest fossil relatives. Extant Hominoidea = apes + humans. See 'Hominoid'. Apes comprise:

- **- Great apes:** including the extant gorillas and chimpanzees (African apes) + orangutans. See also 'Hominid'.
- **- Lesser apes:** only including the extant gibbons and siamangs, family Hylobatidae. There is no clear evidence of any gibbon ancestor in the fossil record, except perhaps for the dentognathic remains of the Chinese *Yuanmoupithecus* (Harrison *et al.* 2008).

- Australopith (or australopithecine): informal term employed here to refer to members of the genera *Australopithecus* and *Paranthropus*; the latter are usually referred to as 'robust australopiths'.

- *Australopithecus*: (*australis* 'southern' + *pithēkos* 'ape'), is a hominin genus that mainly inhabited the east and south of Africa during the Pliocene (around 5-2 Ma). All of them were habitual terrestrial bipeds, but some degree of arboreality has been inferred for some. This genus includes at least five different species, and it is broadly accepted that one of them eventually gave origin to the first members of the genus *Homo*. The same or another species would have given rise to the robust, derived forms that coexisted in the time and space with early members of the genus *Homo*, being classified into the genus *Paranthropus*.

Bodyplan: two different anatomical bodyplans can be distinguished among anthropoid primates (e.g. Ward 1993; Moyà-Solà and Köhler 1996):

- **- Orthograde bodyplan:** it is characterized by the following features: a short, wide and shallow thorax; large clavicles and dorsally placed scapulae with more laterally-facing glenoid fossae; expanded and dorsally-rotated iliac blades; shorter and stiffer vertebral column, especially in the lumbar region. This pattern is derived for extant apes and humans, being suitable for forelimb-dominated climbing and below-branch suspension, as well as hindlimb-dominated terrestrial bipedalism, permitting among others a greater limb mobility.

- **Pronograde bodyplan: it is characterized by the following features:** craniocaudally longer, mediolaterally narrow and dorsoventrally deep thorax; small clavicles and laterally-positioned scapulae with ventrally-facing glenoid fossae; narrow and laterally facing iliac blades; long and flexible spinal column; and arms shorter than legs. This pattern represents the primitive anthropoid condition, and is most suitable for pronograde quadrupedalism, both on trees and on the ground, with the limbs moving along the parasagittal plane.

- *Dryopithecus*: (*drus* ‘tree’ + *pithēkos* ‘ape’), fossil great ape from the middle Miocene of Europe (ca. 12 Ma). Most of the specimens consist on mandibles and other fragmentary dentognathic remains, so little is know about its postcranial bodyplan, apart from a humerus from France (Pilbeam and Simons 1971) and a partial femora from Spain (Moyà-Solà *et al.* 2009), indicating a more primitive bodyplan than in later great apes.

- Exaptation: structure that did not originally evolve to perform their current utility, but were later coopted in order to do so. True adaptations instead originally evolved for performing their current function. The are then two different evolutionary processes: adaptation, leading to true adaptations; and cooptation, producing exaptations (Gould and Vrba 1982).

- *Griphopithecus*: (*gryphos* ‘lion-eagle’ [mythological creature with the body of a lion and the head and wings of an eagle]+ *pithēkos* ‘ape’), this is one of the first fossil great apes documented outside Africa (ca. 15 Ma; Begun 2002). From their scarce postcranial remains, it seems that it still possessed a pronograde bodyplan with short, monkey-like manual phalanges (Ersoy *et al.* 2008).

- *Hispanopithecus*: (*Hispania* ‘Spain’ + *pithēkos* ‘ape’), is a fossil great ape from the late Miocene of Europe (ca. 9-10 Ma). It has long been considered a junior subjective synonym of *Dryopithecus*. However, on the basis of a lower face attributed to *D. fontani* (the type species of the genus), Moyà-Solà *et al.* (2009) have recently resurrected the genus *Hispanopithecus* (type species: *H. laietanus*), to which these authors further attribute other Vallesian species previously classified into *Dryopithecus*, such as *H. crusafonti* and *H. hungaricus*; the latter had been previously referred to *D. brancoi* by Begun and Kordos (1993), but most recently the same authors (Begun and Kordos 2008) reassigned it to *Rudapithecus hungaricus*. Moyà-Solà and Köhler (1996) considered *Hispanopithecus* to be a stem pongine.

- **Hominoid:** any member of the Hominoidea superfamily, humans + apes. They can be distinguished from monkeys (Cercopithecoidea and Ceboidea), among others, by the absence of an external tail, the medial torsion of the humeral head, a low position of the maxillopremaxillary suture/nasal contact and a wide anteroposterior palate. Especially characteristic is the presence of an orthograde bodyplan. The superfamily Hominoidea includes the extant families Hominidae and Hylobatidae.
    - **Hominid:** hominoid member of the family Hominidae, humans + great apes (+ fossil relatives). Traditionally, only the forms more closely related to extant humans than to great apes were considered hominids (great apes being classified into the Pongidae), but currently a wider conception of this family is usually employed. See ‘*Pierolapithecus*’.
        - **Hominine:** hominid member of the subfamily Homininae. It includes humans + African apes (+ fossil relatives).
            - **Gorillin:** hominine member of the tribe Gorillini: extant gorillas.
            - **Hominin:** hominine member of the tribe Hominini, which includes taxa more closely related to extant humans than to great apes. A simple definition would include all the bipedal Plio-Pleistocene hominids (+ the earliest hominins from the very late Miocene).
            - **Panin:** hominine member of the tribe Panini: extant chimpanzees.
        - **Pongine:** hominid member of the subfamily Ponginae. It only includes extant orangutans (+ fossil relatives).
    - **Hylobatid:** hominoid member of the family Hylobatidae. See ‘Lesser apes’.

- ***Orrorin*:** (‘original man’), an early hominin from the late Miocene of Kenya (ca. 6 Ma). Despite its ancient age, *Orrorin* shows close affinities with extant humans in femoral morphology and in the pollical distal phalanx, even closer than in the case of the later australopiths. This combination of bipedalism- and precision-grasping-related features suggests that both adaptations share a common origin.

- *Paranthropus*: (*para*- [expressing relationship] + *anthrōpos* ‘man’), a hominin genus that coexisted during the early Pleistocene in the east and south of Africa, simultaneously with the genus *Homo* (between around 3 to 1 Ma). Although bipedal and displaying precision-grip capabilities in its hand, its degree of encephalization was not significantly higher than that of earlier australopiths.

- *Pierolapithecus*: (‘from Pierola’ + *pithēkos* ‘ape’), a fossil great ape from the middle Miocene of els Hostalets de Pierola (ca. 12 Ma, Catalonia). *Pierolapithecus* already possessed an orthograde bodyplan, although it is considered a stem hominid because of is facial anatomy, which combines a short face with the frontal processes of the maxillae, the flat nasals, and the orbits in the same plane, with high zygomatic roots, a high nasoalveolar clivus and a broad nasal aperture widest at the base. Moreover, it has lost the contact between the ulna and the wrist. The latter is seen as an adaptation to improve ulnar deviation for enhancing vertical climbing capabilities in larger-bodied great apes.

- *Proconsul*: (‘before Consul’ the African *Proconsul* (ca. 20 Ma) is one of the oldest known members of the superfamily Hominoidea. This stem hominoid includes several species, still displaying a pronograde bodyplan. The generic name comes from that time ‘Consul’, the name that was being used as a circus name for performing chimpanzees.

- *Sivapithecus*: (*Siva* ‘the auspicious one’ [which is an Indian deity] + *pithēkos* ‘ape’). A genus from the Siwalik Hills of India and Pakistan (around 12.5-8.5 Ma) that shares many facial features with extant orangs. However, some postcranial remains (especially the humerus) suggest a somewhat pronograde bodyplan. This apparent contradiction has been termed the ‘*Sivapithecus* dilemma’ (Pilbeam and Young 2001).

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