



Pierolapithecus and the functional morphology of Miocene ape hand phalanges: paleobiological and evolutionary implications

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ABSTRACT

The partial skeleton of *Pierolapithecus*, which provides the oldest unequivocal evidence of orthogrady, together with the recently described phalanges from Paşalar most likely attributable to *Griphopithecus*, provide a unique opportunity for understanding the changes in hand anatomy during the pronogrady/orthogrady transition in hominoid evolution. In this paper, we describe the *Pierolapithecus* hand phalanges and compare their morphology and proportions with those of other Miocene apes in order to make paleobiological inferences about locomotor evolution. In particular, we investigate the orthograde/pronograde evolutionary transition in order to test whether the acquisition of vertical climbing and suspension were decoupled during evolution. Our results indicate that the manual phalanges of Miocene apes are much more similar to one another than to living apes. In particular, Miocene apes retain primitive 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 repertoires of different hominoid lineages at least until the late Miocene. Nonetheless, despite their striking morphological similarities, several Miocene apes do significantly differ in phalangeal curvature and/or elongation. *Hispanopithecus* most clearly departs by displaying markedly-curved and elongated phalanges, similar to those in the most suspensory of the extant apes (hylobatids and orangutans). This feature agrees with several others that indicate orang-like suspensory capabilities. The remaining Miocene apes, on the contrary, display 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 body plan, as far as this particular anatomical region is concerned, is reflected only 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 as taillessness antedated the acquisition of an orthograde body plan, 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.

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Introduction

The first orthograde-related features from the hominoid fossil record are seen in the Moroto vertebrae (Walker and Rose, 1968; Ward, 1993; Sanders and Bodenbender, 1994; Filler, 2007). These vertebral remains, 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 increased

stiffness of the lumbar region (Sanders and Bodenbender, 1994) and indicative of an orthograde body plan (MacLatchy et al., 2000). Unfortunately, the lack of evidence from other key anatomical regions, such as ribs, wrist, phalanges, etc., precludes making a secure assessment of 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., 2007). Unlike *Morotopithecus*, the partial skeleton of the middle Miocene stem great ape *Pierolapithecus catalaunicus* provides unequivocal evidence of an orthograde body plan, as indicated by torso

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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 body plan. On the basis of phalangeal morphology and proportions, it has been previously argued that this taxon lacked adaptations to below-branch suspension (Moyà-Solà et al., 2004, 2005). Available evidence from the roughly contemporaneous *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 body plan (Moyà-Solà et al., 2009), with no specific suspensory adaptations. The latter adaptations are not recorded until the late Miocene in the great ape *Hispanopithecus laietanus* (formerly *Dryopithecus laietanus*, see Moyà-Solà et al., 2009), which nevertheless still retains, as does *Pierolapithecus*, some palmigrady-related features (Moyà-Solà and Köhler, 1996; Almécija et al., 2007). Thus, Miocene apes displayed locomotor repertoires unlike those of living apes. In particular, they shared to some degree a generalized body plan related to generalized arboreal quadrupedalism (Rose, 1983), being primarily “Miocene hominoid-like” rather than like any contemporary group “(Rose, 1983: 416). As such, this strongly suggests that locomotor evolution in this group cannot be reconstructed on the basis of extant taxa alone.

In this paper, we provide a detailed description and morphometric analysis of the manual phalanges of *Pierolapithecus* by 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 because of their greater age, as well as the pronograde locomotor repertoire indicating generalized above-branch arboreal quadrupedalism (Begun, 1992, 2007: 938) with no suspensory adaptations (Begun, 2002: 345) which has been inferred for this taxon on the basis of other postcranial material. On the basis of morphofunctional analyses and intrinsic phalangeal proportions, we make paleobiological inferences about the evolution of the hominoid locomotor repertoire during the Miocene. In particular, we test whether the acquisition of vertical climbing and suspension were decoupled during evolution, or whether 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 (Almécija et al., 2007: their Supplementary Fig. 10) to the nearest 0.1 mm: maximum length; and transverse (mediolateral and dorsopalmar) diameters at the base, midshaft and trochlea. 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. Measurements were taken by two of the authors of this paper (S.A. and D.M.A.) or kindly provided by E. Sarmiento; interobserver error for these kinds of measurements was previously found to be low (Alba et al., 2003).

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 (see

Moyà-Solà and Köhler, 1996; and Almécija et al., 2007). 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 as proximal phalanx IV and intermediate phalanx III, respectively (Napier and Davis, 1959: Fig. 26). In the latter case, measurements were corrected in order to compensate for the lack of epiphyses in the intermediate phalanx, following Moyà-Solà et al. (2008). 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 A.L.333x-19 and A.L.333-88 (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 includes adults of all the hominoid genera including humans, as well as two genera of 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*) species; *Pongo* includes the two subspecies of *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* includes five macaque species (*M. fascicularis*, *M. fuscata*, *M. nemestrina*, *M. nigra*, *M. silenus*, and *M. sylvanus*). Total sample size for each variable is reported in the Supplementary Online Material (SOM) Table 1. For multivariate analyses of proximal and intermediate phalanges (see below), however, only those individuals preserving all 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 using natural logarithms (ln). A principal component analysis (PCA) was performed by using the covariance matrix separately for proximal and intermediate phalanges.

In order 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 controversy as to whether ratios or allometric residuals are more suitable for making morphometric comparisons (see discussion in Alba et al., 2003: 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: 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 (Albretsch et al., 1993). Allometric residuals, on the other hand, remove scaling effects by measuring only those portions of shape that are uncorrelated with size (Albretsch 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: 153) is not relevant 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: 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 ‘Morphometric comparisons’), 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). 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 (e.g., Almécija et al., 2007). 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).

The allometric residuals of intrinsic relative phalangeal length employed in this paper can be 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-adjusted. For comparative purposes, following Harrison (1989), we also computed midshaft robusticity (midshaft breadth/length \times 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.

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 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 1 (see also Table 1 for measurements).

Proximal phalanges

The three available proximal phalanges are morphologically very similar to one another. The largest one (IPS21350.14; see also Fig. 2), which is complete except for minimal damage on the dorso-distal 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 interosseus (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 interosseus 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

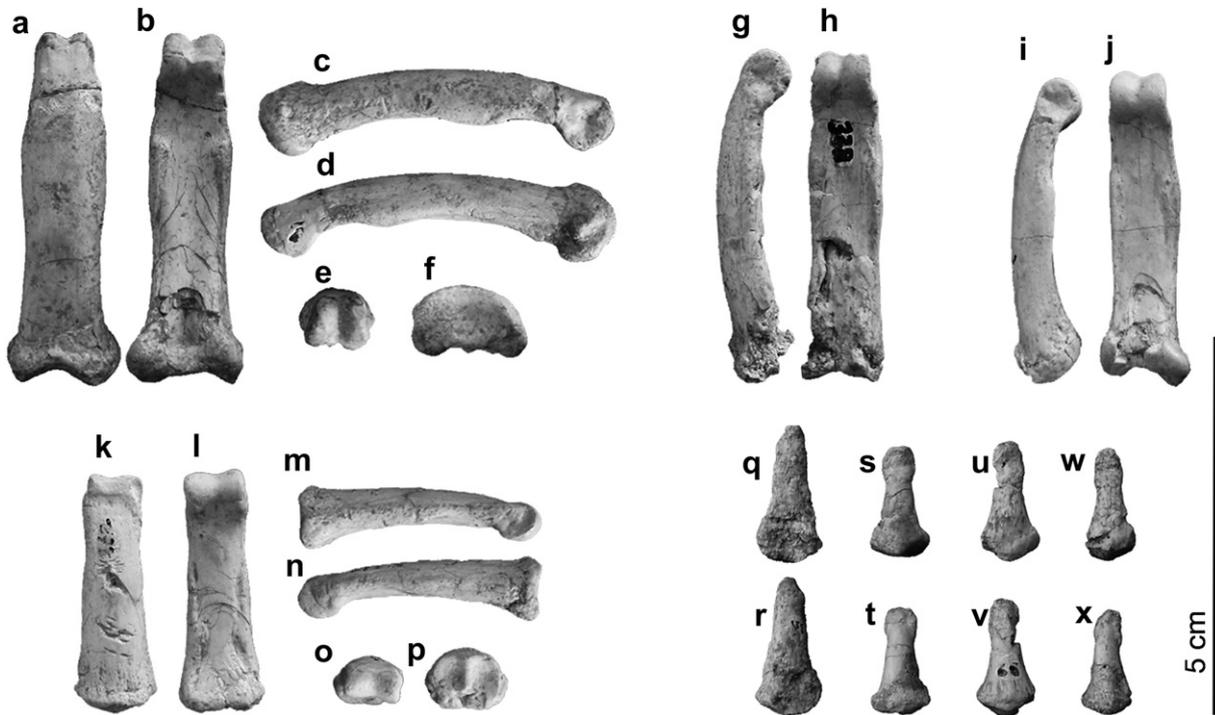


Figure 1. Manual phalanges of *Pierolapithecus catalaunicus* from BCV1: (a–f) Right fourth proximal phalanx IPS21350.14 in dorsal (a), palmar (b), ulnar (c), radial (d), distal (e), and proximal (f) views; (g–h) Left second proximal phalanx IPS21350.12 in radial (g) and palmar (h) views; (i–j) Left fifth 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.

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 does the second proximal phalanx, by being narrower and more palmarly protruding than on the radial side. Such asymmetry 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 of these proximal phalanges display a moderate degree of curvature (included angle of 53° in IPS21350.14, 45° in IPS21350.12, and 56° 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. The trochlea displays a narrow trochlear groove and, in dorsal or palmar view, it is not parallel-sided but rather distally convergent.

Intermediate phalanx

A single intermediate manual phalanx of *Pierolapithecus*, IPS21350.13, is available (see measurements in *Table 1*). We attribute this phalanx to one of the central manual rays (III or IV) because, among other things, it lacks the pronounced trochlear deviation towards the central axis of the hand (*Susman, 1979*) as well as the pronounced basal asymmetry (S.A., pers. obs.) that is characteristic of lateral intermediate phalanges. In 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

Table 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).^a

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	–	–	–	–

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

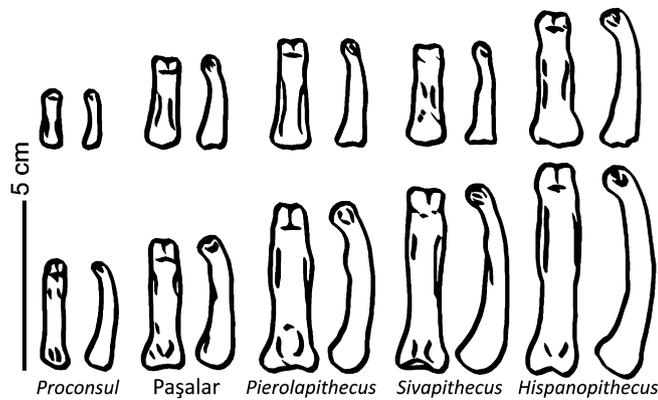


Figure 2. Schematic depiction of intermediate (top) and proximal (bottom) manual phalanges of selected Miocene apes included in the morphometric analyses, in palmar (left) and lateral (right) views. All proximal phalanges are from the fourth ray, whereas intermediate phalanges correspond to either the 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.

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 digitorum superficialis muscle on the proximal third of the palmar surface. 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 is the right.

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 on the radial side, while the latter is more convex and extends more palmarly. Such extension is a typical anthropoid feature (S.A., pers. obs.), 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 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 of the three, lacks a small bone portion on the palmar side of the base; in dorsal view, the apical tuft of the latter deviates 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 these two most likely correspond to the median rays (III and IV). Moreover, given the fact that the third distal ray is usually longer than the others (S.A., pers. obs.), IPS21350.19 and IPS21350.18 can be attributed tentatively to rays III

and IV, respectively. All of these distal phalanges, in any case, display a relatively wide base surrounded by strong muscular insertions. The palmar lips are more protruding than are the dorsal, and a median keel links both lips. The shafts are roughly conical, although the dorsopalmar diameters are slightly larger than are the mediolateral. The dorsal surfaces of these phalanges are more convex than the palmar, 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 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 (see also Table 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 similar to one another (Fig. 2). In these taxa, the proximal phalanges (Fig. 1a–j) display several primitive (monkey-like) features at the base, such as large palmar tubercles (Fig. 1b, j) and a proximal articular surface that extends onto the dorsal aspect of the shaft (Fig. 1a, f). In most of these taxa, the variably developed flexor sheath ridges are situated on the distal third of the shaft (Fig. 1b, h, j); only in *Hispanopithecus* are these ridges more proximally positioned, extending from the first to the second third of the shaft, as in living great apes. In all instances, the palmar aspect of the shaft is flat (Fig. 1b, h, j)—or concave, when the flexor sheath ridges protrude palmarly. Phalangeal curvature (Figs. 1c, d, g, i and 2) in these Miocene apes ranges from slight in *Proconsul* (45°), to moderate in *Paşalar*, *Pierolapithecus*, and *Sivapithecus* (around $50\text{--}60^\circ$), to very marked in *Hispanopithecus* ($>70^\circ$). All of these taxa display developed pits for the attachment of the collateral ligaments on the trochlea (Fig. 1c, d, g, i). The latter tapers distally (Fig. 1a) and displays a narrow trochlear groove (Fig. 1e) in most taxa—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 among taxa than are the proximal (Fig. 2). All of the intermediate phalanges display strong muscular impressions, with deep insertions for the superficial flexors, which can produce distinct ridges along the proximal half of the shaft (Fig. 1l). The shaft is only slightly curved (Fig. 1m, n) and the trochleae are relatively small (Fig. 1o), with conspicuous insertions for the collateral ligaments (Fig. 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 (Almécija et al., 2007). The middle phalanx GSP47582 of *Sivapithecus* further displays a somewhat different lateral profile, resulting from its flat shaft with strongly protruding flexor sheath ridges on the palmar surface (also see Madar et al., 2002).

Distal phalanges

There are not many pollical distal phalanx phalanges of fossil apes for comparison, except for the incomplete and subadult specimens of *Proconsul* (Begun et al., 1994). Be that as it may, on the

Table 2

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

Base			
Taxon	Shape	Palmar tubercles	Articular surface
<i>Proconsul</i>	Width >> height	Define a narrow channel	Extends dorsally onto the shaft
Paşalar	Width >> height	Define a narrow channel	Extends dorsally onto the shaft
<i>Pierolapithecus</i>	Width >> height	Define a wide channel	Extends dorsally onto the shaft
<i>Sivapithecus</i>	Width > height	Define a narrow channel	Extends dorsally onto the shaft
<i>Hispanopithecus</i>	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
<i>Proconsul</i>	Slight	Distal third of the shaft	Do not protrude palmarly
Paşalar	Moderate	Distal third of the shaft	Protrude palmarly
<i>Pierolapithecus</i>	Moderate	Distal third of the shaft	Protrude palmarly
<i>Sivapithecus</i>	Moderate	Distal third of the shaft	Protrude palmarly
<i>Hispanopithecus</i>	High	More proximal (first to second third of the shaft)	Protrude palmarly but are less conspicuous
Trochlea			
Taxon	Shape	Trochlear groove	Pits for the collateral ligaments
<i>Proconsul</i>	Distally convergent	Narrow	Large
Paşalar	Distally convergent	Narrow	Very large
<i>Pierolapithecus</i>	Distally convergent	Narrow	Very large
<i>Sivapithecus</i>	Parallel	Broad	Very large
<i>Hispanopithecus</i>	Distally convergent	Narrow	Very large

basis of the description published by Begun et al. (1994), these pollical distal phalanx phalanges closely resemble that of *Pierolapithecus* (Fig. 1q, r). Unfortunately, due to palmar erosion, we cannot evaluate the insertion for the tendon of the flexor muscle in IPS21350.16 (Fig. 1q). This insertion is strong in the distal phalanges of *Proconsul* thumbs, whereas 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 (Fig. 1q, r), whereas extant apes and humans display a biconcave articular surface more similar to the remaining distal phalanges. The non-pollical distal phalanges (Fig. 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 Fig. 15), and *Hispanopithecus* (Almécija et al., 2007).

Morphometric comparisons

The descriptive statistics of the extant comparative sample for the several linear measurements included in this study, including sample size, mean, standard deviation, 95% confidence interval, and maximum–minimum range, are reported in Table 3. For each variable, the 95% confidence intervals of extant taxa are compared to the measurements for individual fossil specimens in Table 3.

The results of the PCA have been plotted in Figure 3a (for proximal phalanges) and 3c (for intermediate phalanges) and further reported in Table 4. For both proximal and intermediate phalanges, the first principal component (PC1) explains most of the variance (94% and 93%, respectively), with all of the loadings on the original variables closely approaching unity. Accordingly, 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). 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 the 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 orangutans.

High scores on the second principal component (PC2), which explains nearly 4% of the variance in both cases, 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 PC2 shows that several variables display non-negligible loadings. For proximal phalanges, in particular, the larger the PC2 score, 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 a strongly positive loading compared to the remaining variables on PC2 (see Table 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 Figure 3b, d for proximal and intermediate phalanges, respectively (see regressions in Table 5). Visual examination shows the existence of allometric grade shifts between different taxa, which are 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 phalanges). Alternatively, 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 phalanges). Even though in different size ranges, both humans and the several more terrestrial taxa (macaques, baboons, and gorillas) display very similar phalangeal proportions. On the other hand, the two more arboreal taxa (hylobatids and orangutans) differ by displaying relatively elongated phalanges, and the more generalized

Table 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).^a

Proximal phalanges							
Taxon	<i>Pierolapithecus</i>	<i>Hispanopithecus</i>	<i>Australopithecus</i>	Paşalar	<i>Sivapithecus</i>	<i>Proconsul</i>	
No.	IPS21350.14	IPS18800	A.L.333x-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	<i>Pierolapithecus</i>	<i>Hispanopithecus</i>	<i>Australopithecus</i>	Paşalar	<i>Sivapithecus</i>	<i>Proconsul</i>	
Variable	IPS21350.13	IPS18800	AL333-88	G1004	R1667	GSP47582	KNM-RU2036Y
Ray	III/IV	III?	IV	III	III/IV	III/IV	IV?
L	32.1	40.0	41.3	25.7	27.8	28.7	29.5
MLB	11.4	14.3	13.1	11.2	10.1	11.2	11.3
DPB	8.4	9.3	10.9	9.2	8.2	8.8	8.4
MLMS	8.3	9.6	9.7	8.5	7.8	8.3	8.4
DPMS	4.9	5.7	7.0	5.2	5.3	5.1	4.2
MLT	8.0	9.3	9.2	8.1	8.0	8.6	8.1
DPT	5.1	6.3	6.0	5.2	5.4	6.1	5.4
RIRPL	-0.086	-0.003	-0.001	-0.306	-0.204	-0.221	-0.152
							-0.231

^a 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.

chimpanzees display an intermediate condition. The regressions obtained by employing ln GM (SOM Fig. 1a, b) instead of PC1 as the variable of overall phalangeal size are virtually identical to those reported above, showing the same allometric grade differences. This result stems from the fact that all of 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 (Fig. 4; Tables 3 and 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 yield 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 to 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*, Paşalar, and *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 in 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 3 and 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 comparisons 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, *Hispanopithecus* and *Sivapithecus* are most comparable to chimpanzees and baboons, whereas Paşalar, *Pierolapithecus*, and *Australopithecus* are somewhat stouter, more closely matching the condition of macaques and humans. No fossil taxon even approaches the high robusticity levels of gorillas. *Proconsul* is the most gracile among the fossil taxa included in the study, although less gracile than orangutans and, especially, hylobatids, which display very gracile proximal phalanges at the midshaft.

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 8 and Fig. 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

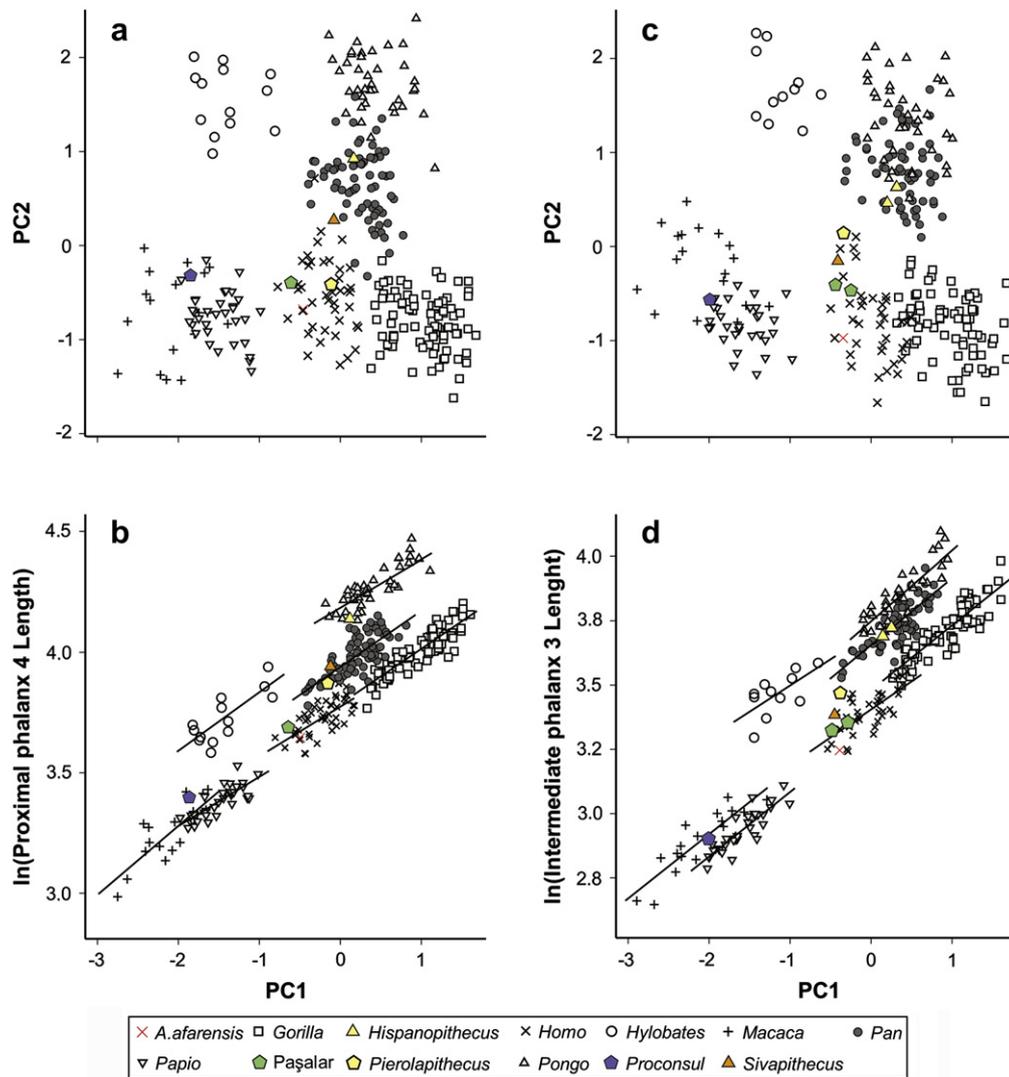


Figure 3. Bivariate plots of the second vs. first principal components for proximal (a) and intermediate (c) phalanges, and linear regressions of ln-transformed phalangeal length vs. the first principal component (taken as a measure of overall phalangeal size) for proximal (b) and intermediate (d) phalanges. The linear regressions (reported in Table 5) were derived separately for each taxon. Note that there are allometric grade shifts between several taxa (see text for further explanations).

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*.

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 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, such as *Nacholapithecus*, not included in the morphometric analysis due to the lack of complete specimens; particularly striking are the resemblances between IPS21350.14 and the *Nacholapithecus* specimen KNM-BG17811 (see Nakatsukasa et al., 2003).

Thus, Miocene apes 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, as previously described for *Hispanopithecus* [Almécija et al., 2007: 5, Fig. 4; see also 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 joint in a close-packed position around arboreal supports of large diameter (see discussion in Nakatsukasa et al., 2003). Such an interpretation 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*

Table 4

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

	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
Variable	Proximal phalanges		Intermediate phalanges	
	PC1	PC2	PC1	PC2
Rescaled component loadings				
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				
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

^a Abbreviations: ln = natural logarithm; other abbreviations as in Table 1.

(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 repertoires of different hominoid lineages at least until the late Miocene. This does not preclude the possibility that the relative frequency of 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, 2007) and *Sivapithecus* (Madar et al., 2002; see below for further discussion).

Table 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.^a

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

^a 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 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 (50–60°) only slightly higher than in *Proconsul*, the latter fully overlapping with the range of quadrupedal monkeys.

A recent paper 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 adaptive significance in each taxon (see for example Thorpe and Crompton, [2006], regarding orangutans).

As noted by Richmond (2007: 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 changes throughout ontogeny by bone remodeling as a response to changing mechanical stresses (e.g., Richmond and Whalen, 2001). Sarmiento (1988: his Fig. 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 active muscular force. A recent biomechanical examination of phalangeal curvature by Richmond (2007) has further

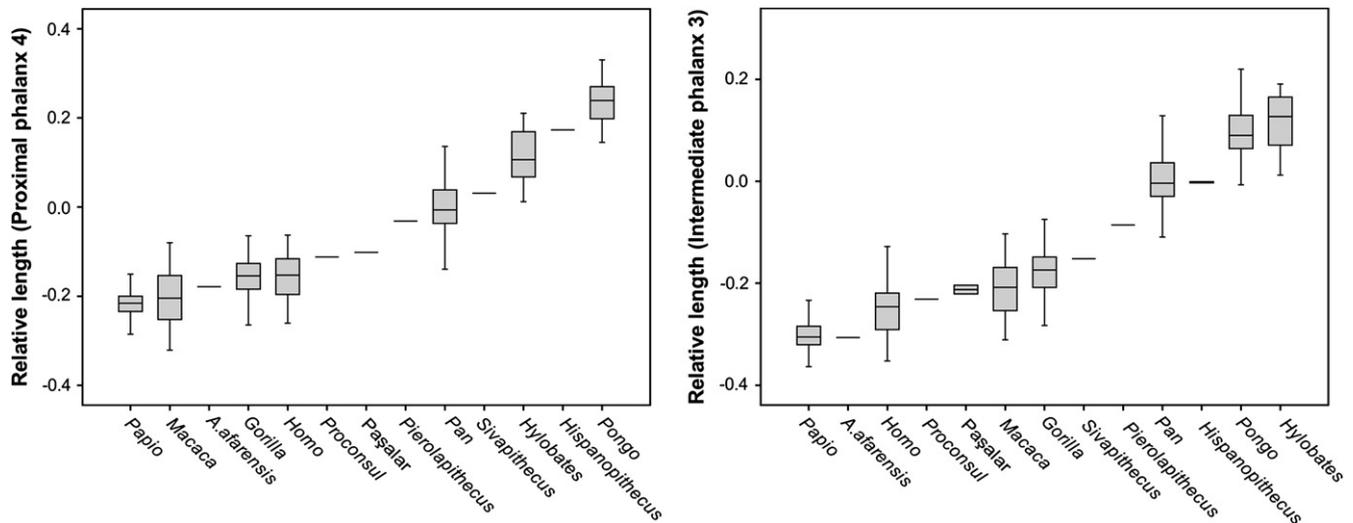


Figure 4. Boxplots of residuals of relative phalangeal length computed as observed phalangeal length minus expected phalangeal length for *Pan*. The chimpanzee linear regression employed as the baseline for computing residuals is reported in Table 5. Horizontal lines represent the median values, whereas the boxes represent the 25% and 75% percentiles, and the whiskers the maximum–minimum ranges (by excluding outliers).

Table 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).^a

Taxon	n	Mean	SD	95% CI	Range
Proximal phalanges					
<i>Pan</i>	74	0.000	0.056	−0.013 0.013	−0.139 0.136
<i>Gorilla</i>	90	−0.156	0.041	−0.164 −0.147	−0.264 −0.065
<i>Pongo</i>	39	0.233	0.054	0.215 0.250	0.056 0.330
<i>Homo</i>	43	−0.157	0.053	−0.173 −0.141	−0.260 −0.063
<i>Hylobates</i>	13	0.118	0.063	0.079 0.156	0.012 0.210
<i>Papio</i>	33	−0.216	0.038	−0.229 −0.202	−0.285 −0.117
<i>Macaca</i>	19	−0.202	0.070	−0.236 −0.169	−0.321 −0.080
Intermediate phalanges					
<i>Pan</i>	66	0.000	0.051	−0.013 0.013	−0.138 0.128
<i>Gorilla</i>	75	−0.181	0.047	−0.192 −0.170	−0.283 −0.075
<i>Pongo</i>	37	0.098	0.055	0.079 0.116	−0.007 0.220
<i>Homo</i>	37	−0.249	0.056	−0.268 −0.231	−0.352 −0.128
<i>Hylobates</i>	11	0.114	0.065	0.070 0.157	0.012 0.191
<i>Papio</i>	31	−0.305	0.039	−0.319 −0.291	−0.387 −0.210
<i>Macaca</i>	18	−0.212	0.058	−0.241 −0.183	−0.311 −0.103

^a Abbreviations: n = sample size; SD = standard deviation; CI = confidence interval.

Table 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 %).^a

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

^a Abbreviations: n = sample size; SD = standard deviation; CI = confidence interval.

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

Table 8

Descriptive statistics of the pollical to third distal phalanx ratios showed in Figure 5.^a

Taxon	n	Mean	SD	95% CI	Range
Distal phalanx I length/Distal phalanx III length					
<i>Pan</i>	6	0.912	0.111	0.795 1.028	0.790 1.106
<i>Gorilla</i>	5	0.951	0.095	0.833 1.069	0.825 1.088
<i>Pongo</i>	6	0.712	0.063	0.645 0.778	0.627 0.772
<i>Homo</i>	5	1.243	0.048	1.184 1.302	1.190 1.311
<i>Hylobates</i>	8	0.845	0.077	0.781 0.909	0.710 0.914
<i>Macaca</i>	14	0.718	0.091	0.665 0.770	0.616 0.902
<i>Pierolapithecus</i>	1	1.168			
Distal phalanx I MLB/Distal phalanx III MLB					
<i>Pan</i>	6	0.832	0.152	0.673 0.992	0.677 1.093
<i>Gorilla</i>	5	0.808	0.166	0.601 1.014	0.645 1.064
<i>Pongo</i>	6	0.843	0.054	0.786 0.899	0.768 0.934
<i>Homo</i>	5	1.335	0.116	1.191 1.478	1.182 1.464
<i>Hylobates</i>	8	0.967	0.204	0.796 1.137	0.646 1.262
<i>Macaca</i>	14	1.106	0.111	1.042 1.170	0.971 1.359
<i>Pierolapithecus</i>	1	1.114			

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

flexed digits” (Richmond, 2007: 678). Accordingly, despite their similar classification in Deane and Begun’s (2008) analysis, the differences in phalangeal curvature between *Pierolapithecus* and *Hispanopithecus* (around 20°) are highly suggestive that the locomotor repertoires of these taxa emphasized different kinds of arboreal behaviors.

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 of 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

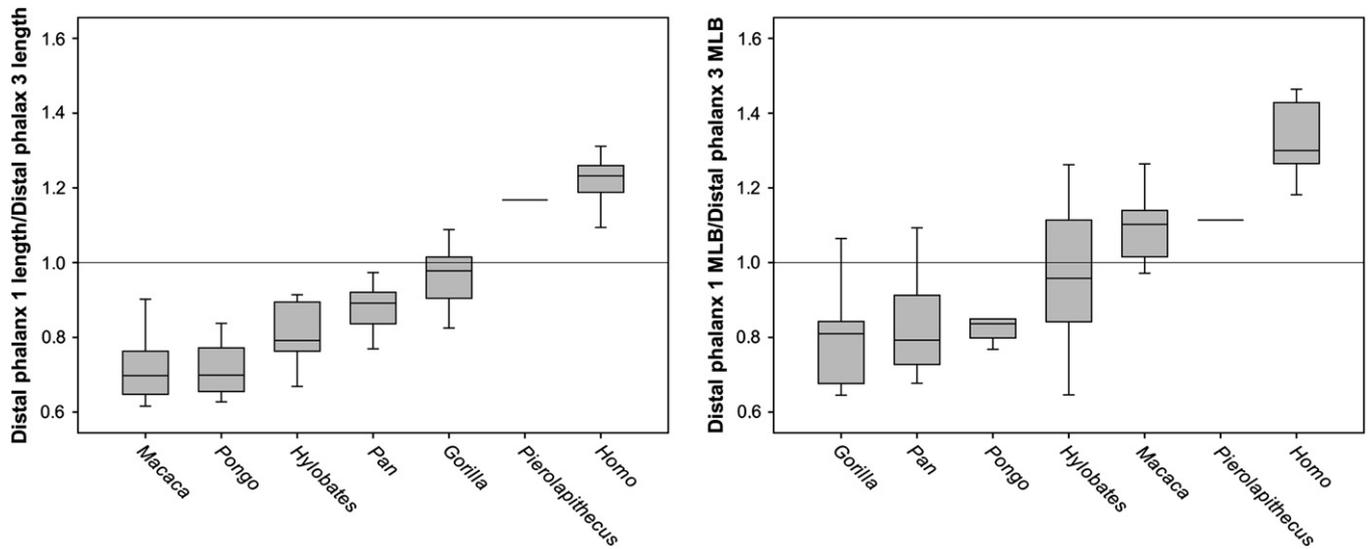


Figure 5. Boxplots showing ratios of the pollical distal phalanx dimensions relative to distal phalanx III: proximodistal length (left) and mediolateral base breadth (MLB) (right). Horizontal lines represent the median values, whereas the boxes represent the 25% and 75% percentiles, and the whiskers the maximum–minimum ranges (by excluding outliers).

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 (Fig. 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 have been previously reported for *Hispanopithecus*—and most of the extant comparative sample—on the basis of the relative length of the proximal phalanges relative to body mass (Almécija et al., 2007: Fig. 9b), thus indicating that the intrinsic measure of phalangeal relative length employed in this paper shows the same correlation to the degree of arboreality as 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 to function as a grasping hook (Sarmiento, 1988: his Fig. 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 the 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 preserve the integrity of the metacarpophalangeal joint during knuckle-walking (Susman, 1979; Inouye, 1992; see Fig. 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 arboreal behaviors, such as suspension, that are displayed by extant apes.

Interestingly, given the fact that *Pierolapithecus* already possesses an orthograde body plan (Moyà-Solà et al., 2004), the roughly comparable phalangeal proportions of *Sivapithecus* cannot be interpreted as necessarily excluding the possibility of an orthograde body plan in the latter taxon. Reconstructing the postcranial body plan and inferring the locomotor repertoire of *Sivapithecus* has proven 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 these two 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: 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 body plan or securely excluding other orthograde behaviors. The presence of robust and well-developed

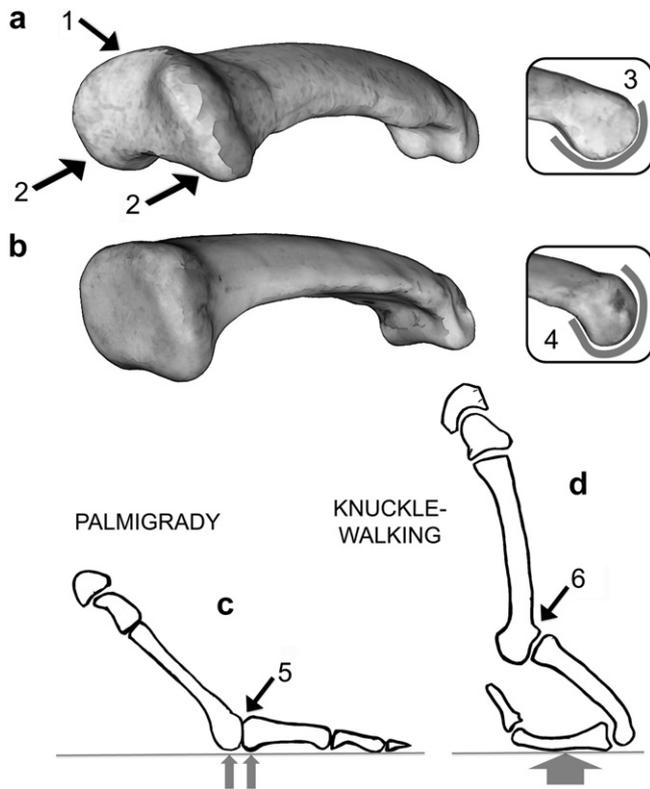


Figure 6. (a–b) Oblique rear view and lateral detail of the trochlea of a virtual model of the right fourth proximal phalanx of *Pierolapithecus catalaunicus* IPS21350.14 (a), as compared to the same bone in a chimpanzee (b); (c–d) Schematic depiction of different hand postures in palmigrady (c) and 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 with 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.

pollices and halluces in this taxon, as well as 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 quadrupelism, 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, 1942; 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 body plan, 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 the extent to which its postcranial body plan 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 analog 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 body plan (Moyà-Solà and Köhler, 1996) and orangutan-like suspensory adaptations (Almécija et al., 2007).

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 Fig. 6d) that can be understood as a kind of locomotor compromise (Tuttle, 1975), which enables 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 (Fig. 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 (Fig. 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 resemble instead quadrupedal extant taxa.

The orthograde body plan 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 (Fig. 4) was associated with the acquisition of an orthograde body plan. 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 (Fig. 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 body plan, 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 appendicular 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 orthograde-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 later. This view is supported by our results, according to which, with regard to suspension, most orthograde-related features would be “preadaptive” with regard to brachiation ([Cartmill, 1985: 88], i.e., exaptations instead of adaptations). We therefore concur with Crompton et al. (2008) that the acquisition of the crown-hominoid body plan was probably much more related to generalized orthograde than specifically to suspensory behaviors, which could have been developed independently later by several hominoid lineages (Moyà-Solà et al., 2004, 2005; Almécija et al., 2007).

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; Almécija et al., 2007; Alba and Moyà-Solà, 2008). *Proconsul* shows that taillessness preceded the emergence of an orthograde body plan (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 from Paşalar are entirely compatible with the retention of a pronograde body plan, as already argued by Ersoy et al. (2008). As far as phalanges are concerned, the orthograde body plan 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 retention of palmigrady-related features in *Hispanopithecus*, as reflected by the basal morphology of the proximal phalanges and

the morphology and proportions of the metacarpals (Almécija et al., 2007), suggests that, with the passing of time during hominoid evolution, new locomotor behaviors were progressively—and probably independently—incorporated into the ancestral ape morphotype. As a result, new adaptations became superimposed upon more primitive features; some of the latter became significantly modified, but others (such as palmigrady-related features) were retained for a considerable time span. 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 in *Hispanopithecus* (see also Almécija et al., 2007). This does not mean that *Pierolapithecus* never practiced suspensory behaviors but suggests that the latter had not become adaptively significant. According to this interpretation, the evolutionary transition from a pronograde towards an orthograde body plan 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).

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jhevol.2009.02.008.

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