The Morphology of Oreopithecus bambolii
Pollical Distal Phalanx

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ABSTRACT Oreopithecus bambolii is a Late Miocene ape from Italy, first described in the late 19th century. Its interpretation is still highly controversial, especially in reference to its hand proportions and thumb morphology. In this study, the authors provide detailed descriptions of the available Oreopithecus pollical distal phalanx (PDP) specimens, as well as bivariate and multivariate morphometric analyses in comparison with humans, extant apes, selected anthropoid monkeys, and available Miocene PDP specimens. The multivariate results reveal two opposite poles on the hominoid PDP shape spectrum: on one side, a mediolaterally broad and dorsopalmarly short human PDP, and on the other side, the narrow and “conical” PDP of chimpanzees and orangutans. The authors contend that Oreopithecus exhibits intermediate PDP proportions that are largely primitive for hominoids because it shares morphological similarities with Proconsul. Furthermore, Oreopithecus displays a mediolaterally wide tuft for a hominoid, as well as a palmarly elevated attachment for a long tendon of a flexor muscle that is associated at its proximal edge with a proximal fossa and at its distal edge with an ungual fossa. These nonmetrical traits have been associated in humans with their capability to oppose and contact the proximal pads of the thumb and fingers, that is, pad-to-pad precision grasping. These traits reinforce previous studies that indicate a human-like thumb-to-hand length ratio compatible with pad-to-pad precision grasping in Oreopithecus. Although specific hand use is still unresolved in Oreopithecus, the results suggest enhanced manipulative skills (unrelated to stone tool-making) in this taxon relative to other (extant or fossil) hominoids. Am J Phys Anthropol 153:582–597, 2014. © 2014 Wiley Periodicals, Inc.

Oreopithecus bambolii is a Late Miocene ape (ca. 8.2–6.7 Ma; Rook et al., 2000; Casanovas-Vilar et al., 2011; Rook et al., 2011; Matson et al., 2012) first discovered by Cechi in 1862 in the lignite mines of the Monte Bamboli (Tuscany, Italy), from which the fossil was named (Gervais, 1872; Hürzeler, 1958; Berzi, 1973). Since then, more remains have been found in several localities of the paleoisland of Tuscany-Sardinia (Rook et al., 2006; Abbazzi et al., 2008). The most complete specimen is a partial skeleton, nicknamed “Sandrone” found in a coalmine in Baccinello (Grosseto) in 1958 by Hürzeler (Straus, 1958). Over the years, the interpretation of Oreopithecus has been highly controversial, being alternatively interpreted as a separate anthropoid lineage belonging to its own family (Oreopithecidae) or fitting in with cercopithecoids (Schlosser, 1887; Szalay and Delson, 1979), hominoids (Schwalbe, 1915; Straus, 1963; Harrison, 1986; Sarmiento, 1987), or even within early hominins (Hürzeler, 1954; Straus, 1957). For a historical review of Oreopithecus taxonomy, see the work of Delson (1986). One of the most controversial aspects of Oreopithecus has been its hand, especially the thumb, to which several studies have been devoted. Moyá-Sola et al. (1999, 2005b) proposed that Oreopithecus possessed a short hand relative to its body mass, with a thumb-to-finger length ratio similar to modern humans and baboons. Its pollical distal phalanx (PDP) showed a well-developed fossa on the proximal palmar surface for an inferred insertion of the flexor pollicis longus (FPL) tendon. This was interpreted by these authors as indicative of specific adaptations for a “human-like pad-to-pad precision grasping” (see below) in this taxon, which evolved convergently with later hominins as a result of relaxed forelimb-dominated locomotor behaviors as well as for efficient harvesting and feeding (Köhler


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and Moyà-Solà, 1997; Moyà-Solà et al., 1999; Rook et al., 1999).

Susman (2004, 2005) replied to both the above-mentioned communications, proposing that Oreopithecus displayed a basic modern-ape hand morphology and that the results of Moyà-Solà and coauthors were based on wrongly identified phalangeal specimens. Susman further stated that a FPL insertion (i.e., the palmar fossa described by Moyà-Solà and coauthors) was not identified before by previous studies of the IGF 11778 specimen. Moyà-Solà et al. (2005b) clarified that the fossa was not visible until more recently when both specimens were properly prepared and cleaned. A later communication by Marzke and Shrewsbury (2006) pointed out that the presence of a proximal fossa in the PDP of Oreopithecus as well as in any other primate is not directly related to a FPL insertion. Instead, Shrewsbury et al. (2003) found that the FPL attachment is reflected in a gable-shaped ridge, elevated palmarly, which is at the distal border of the fossa itself [Shrewsbury's proximal volar fossa (PVF)]. Although some of these features can be present in extant primates (Susman, 1998; Shrewsbury et al., 2003), only humans display a complex set of characters on their PDPs (a broad base, sesamoid facet, PVF, gable FPL attachment, ungual fossa, ungual spines, and a mediolaterally wide apical tuft). This complex is related to the use of the thumb and the other digits in specific types of precision gripping during refined manipulation and handling (i.e., pad-to-pad precision grasping; see the next section).

**WHAT IS HUMAN-LIKE PAD-TO-PAD PRECISION GRASPING?**

The term “precision grasping” is often used in the primate hand literature with different connotations between primatologists and anthropologists *sensu stricto*, and this has led to confusion and unnecessary arguments. However, “disagreement, as is so often the case, is largely attributable to a semantic difficulty” (Napier, 1960, p 654). Most primates can contact the tip of their thumb and index finger during different kinds of precision grasping in a broad sense. This implies an interaction between both hand rays (e.g., Christel, 1993; Pouydebat et al., 2008), especially in opposition to “power grasping” where the thumb plays a secondary role by securing the grip against the palm and directing the force being applied (Napier, 1960, 1993). Thus, in the general sense of precision grasping, even chimpanzees and orangutans (the great apes that exhibit more disproportionate thumb-to-hand length proportions; Schultz, 1930), are capable of manipulating objects by means of different kinds of hand and index finger “precision grip” interactions (e.g., thumb and index finger tip-to-tip and pad-to-side; Fig. 1). Relevantly, this is not the specific precision grasping we are addressing in our study.

As discussed by Marzke et al. (2009) and in previous studies by some of us (Alba et al., 2003; Moyà-Solà et al., 2008; Almécija et al., 2009a, 2010), it is important to recall that what Napier originally meant by a human “advanced precision grip” (Napier, 1960) was an unique capability for holding objects between the thumb and the index finger, “delicately yet securely between the opposed pulp surfaces” (Napier, 1960, p 652). Among extant hominoids, however, a pad-to-pad precision grasping (i.e., contact of the proximal portion of the thumb and index pulps) is restricted to humans. This type of grasping is largely precluded in the other taxa (and especially *Pan* and *Pongo*) due to the disproportionate length of their Digits II–V relative to the thumb (Fig. 1a,b; Napier, 1960; Tuttle, 1967, 1969, 1970; Napier, 1993), as well as by restricted passive hyperextension of the distal phalanges caused by relatively short flexor
proximal base just prior to the epiphysis (Fig. 3). Thus, BA#130 is slightly smaller than IGF 11778 and lacks the damage in the radial side of the base and tuft) and was assigned to a young adult (with some tendons (Tuttle, 1967; Christel, 1993). As a clarification to Pouydebat et al. (2008), Marzke et al. (2009) noted that Napier considered only the pad-to-pad contact (Fig. 1c) to be the “acme” of human precision grasping (Napier, 1960, p 652), involving “perfect” opposition of pulp surfaces of the thumb and index finger (Napier, 1993, p 55–56). This type of precision grip with its related morphological features for precision grasping displayed by humans. Furthermore, this study provides a complete morphometric analysis of the Oreopithecus PDP from the IGF 11778 partial skeleton and available Miocene fossil specimens.

### MATERIALS AND METHODS

Anatomical descriptions are primarily informed by the well-preserved PDP belonging to the left hand of the IGF 11778 skeleton, supplemented by observations of the more partial BA#130 specimen. Most of the anatomical terms used here are described and analyzed elsewhere (Shrewsbury et al., 2003). Apart from anatomical descriptions, the main proportions of the Oreopithecus more complete PDP specimen (IGF 11778) were compared with a modern sample of primates, including

| TABLE 1. Pollical distal phalanx measurements and summary statistics (in mm) |
|-----------------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
|                             | L              | DPT            | MLT            | DPMS           | MLMS           | DPB            | MLB            |
| Alouatta (n = 4)            | Mean           | 13.18          | 2.13           | 2.35           | 2.15           | 2.23           | 2.23           | 3.05           | 4.65       |
|                             | SD             | 0.87           | 0.29           | 0.17           | 0.19           | 0.19           | 0.10           | 0.44           | 0.26       |
|                             | Range          | 12.5–14.4      | 1.7–2.3        | 2.2–2.5        | 1.9–2.3        | 2.1–2.3        | 2.5–2.5        | 4.4–5         |
| Nasalis (n = 9)             | Mean           | 8.07           | 2.26           | 2.91           | 2.12           | 2.51           | 3.13           | 5.51           |
|                             | SD             | 1.08           | 0.27           | 0.40           | 0.38           | 0.38           | 0.40           | 0.40           | 0.77       |
|                             | Range          | 6.7–9.6        | 1.9–2.7        | 2.3–3.5        | 1.6–2.6        | 2.0–3.0        | 2.5–3.6        | 4.5–6.4        |
| Macaca (n = 5)              | Mean           | 7.66           | 1.72           | 3.10           | 1.64           | 2.98           | 2.84           | 5.94           |
|                             | SD             | 0.73           | 0.18           | 0.50           | 0.22           | 0.37           | 0.25           | 0.83           |
|                             | Range          | 7–8.9          | 1.5–1.9        | 2.6–3.9        | 1.3–1.9        | 2.5–3.5        | 2.5–3.2        | 5–7.1          |
| Papio (n = 29)              | Mean           | 9.42           | 2.31           | 4.49           | 2.23           | 3.32           | 4.32           | 7.09           |
|                             | SD             | 1.03           | 0.37           | 0.62           | 0.26           | 0.44           | 0.51           | 0.72           |
|                             | Range          | 6.7–11.2       | 1.8–3.3        | 3.2–6          | 2.8–2.8        | 2.5–4.2        | 3.4–5.4        | 5.9–8.5        |
| Hylobates (n = 11)          | Mean           | 9.67           | 1.96           | 2.93           | 1.77           | 3.06           | 2.90           | 5.64           |
|                             | SD             | 0.66           | 0.14           | 0.27           | 0.27           | 0.40           | 0.19           | 0.48           |
|                             | Range          | 8.6–10.5       | 1.7–2.2        | 2.6–3.5        | 1.5–2.4        | 2.4–3.7        | 2.6–3.2        | 4.9–6.5        |
| Pongo (n = 18)              | Mean           | 15.21          | 3.24           | 4.34           | 3.50           | 3.31           | 6.00           | 8.68           |
|                             | SD             | 2.20           | 0.49           | 0.95           | 0.33           | 0.58           | 0.88           | 1.37           |
|                             | Range          | 12.1–19.2      | 2.5–4.2        | 3.1–6.7        | 2.9–4.1        | 2.2–4.5        | 4.5–8          | 7–12.1         |
| Gorilla (n = 18)            | Mean           | 20.86          | 4.81           | 7.18           | 4.20           | 5.69           | 7.80           | 12.94          |
|                             | SD             | 2.62           | 0.73           | 0.88           | 0.50           | 0.77           | 0.86           | 1.58           |
|                             | Range          | 16.5–25.5      | 3.3–6.1        | 5.3–9.1        | 3.2–5.1        | 4.6–8          | 6.1–9.2        | 9.3–15.3       |
| Pan (n = 33)                | Mean           | 18.06          | 3.69           | 4.78           | 3.71           | 3.54           | 5.80           | 8.53           |
|                             | SD             | 1.81           | 0.56           | 0.90           | 0.51           | 0.48           | 0.70           | 0.84           |
|                             | Range          | 15.3–21        | 2.8–5.6        | 2.8–6.7        | 2.85–3         | 2.7–4.6        | 4.6–7.3        | 7–10.2         |
| H. sapiens (n = 25)         | Mean           | 22.32          | 3.43           | 9.28           | 4.47           | 7.44           | 8.22           | 14.03          |
|                             | SD             | 1.74           | 0.43           | 1.12           | 0.56           | 0.79           | 0.68           | 1.09           |
|                             | Range          | 19.1–26        | 2.54–2         | 7.1–11.1       | 3.4–5.3        | 6–8.7          | 7–9.7          | 12–16.3        |
| Proconsul                   | Mean           | 11.4           | 2.5            | 3.5            | 2.4            | 3.6            | 3.3            | 5.4            |
|                             | SD             | 4.1            | 0.2            | 0.4            | 0.4            | 0.5            | 0.4            | 0.8            |
|                             | Range          | 9.8–13         | 2.2–3.4        | 3.3–6.8        | 2.9–5.1        | 3.8–7          | 5–9.1          | 13–19.4        |

The extant sample includes the following species: Alouatta seniculus, Macaca nemestrina, Papio cynocephalus, Nasalis larvatus, Pongo pygmaeus and P. abelii, Pan troglodytes and G. beringei, Homo sapiens, and Hylobates lar. Parentheses in the actual IGF 11778 specimen represent the preserved measurements. They are marked in bold font to easily compare with the inferred measurements from the reconstructed digital model. Midshaft was estimated in BA#130 to take the measurements. All measurements are given in maximum lengths. Abbreviations: L, proximodistal length; DPT, dorsopalmar tuft; MLT, maximediolateral tuft; DPMS, dorsopalmar midshaft; MLMS, mediolateral midshaft; DPB, dorsopalmar base; MLB, mediolateral base.
modern humans, all extant great ape genera, *Hylobates*, as well as selected platyrrhine and cercopithecoid monkeys (see Table 1 for sample details). A single *Theropithecus gelada* specimen available was inspected for comparison but not included in the analyses. The fossil comparative sample includes the most complete available PDP specimens from the Miocene. The complete phalanx (PH 96) associated with the juvenile *Proconsul heseloni* individual I from the Kaswanga Primate Site (Early Miocene of Rusinga Island, Kenya; Begun et al., 1994), IPS 21350.16, with a slightly damaged base and eroded palmar surface, is attributed to the skeleton of the fossil Middle Miocene great ape from Spain *Pierolapithecus catalaunicus* (Moyà-Solà et al., 2004; Alméija et al., 2009b). Another complete phalanx is attributed to the early hominin *Orrorin tugenensis* from the Late Miocene of Kenya (Gomery and Senut, 2006; Alméija et al., 2010). A PDP attributed to *Afropithecus* (KNM-WK 17032) from the early Miocene of Kenya has been reported (Leakey et al., 1988), although it is actually a non-PDP, probably belonging to one of the lateral rays of the foot (Sergio Alméija, personal observation). All fossils were measured from the original specimens with the exception of *Orrorin*, which was measured from a high-quality research cast. Although both *Oreopithecus* PDP specimens are incomplete, the main proportions of the actual IGF 11778 can be confidently estimated (i.e., incompletely preserved maximum length and mediolateral width of the base) from a “corrected” digital model. We copied, mirror-imaged, and pasted the ulnar tubercle and tuft onto the radial side and filled in the distal end following the tuft curvature in *Geomagic* software (ver. 2012).

To evaluate the main proportions of IGF 11778 in comparison with our PDP sample, seven standard measurements (Fig. 2) were collected to the nearest 0.1 mm. For IGF 11778, both measurements are given for the actual bone (with preserved dimensions) as well as the estimated length and base widths. To facilitate shape comparisons, all PDP specimens were size-adjusted by dividing each original length by the overall PDP size, approximated by the geometric mean (GM) of the available original measurements. Thus, each one of these ratios provides a dimensionless “Mosimann shape variable” of the respective original dimension (Mosimann, 1970; Jungers et al., 1995). The mediolateral expansion of the apical or ungual tuft (referred as tuft, from now on) relative to the PDP base (expansion index: mediolateral tuft width/mediolateral base width × 100) was found to be correlated in humans with pulp development (Mittra et al., 2007). Thus, to inspect the degree of pulp development in the *Oreopithecus* thumb relative to other anthropoid primates, Mittra’s expansion index was further examined in IGF 11778. The significance of differences in mean values for this index was tested by means of analysis of variance and *post hoc* multiple comparisons (Bonferroni method). Allometric scaling of the tuft was also considered to know if tuft width development covaries predictably with overall PDP size. Least squares regressions of log-transformed (using natural logarithms) mediolateral tuft width versus PDP size (approximated again by the GM) were computed independently for each taxon. Homogeneity of slopes was tested by means of analysis of covariance (ANCOVA), and *post hoc* multiple comparisons (Bonferroni method) were performed on estimated marginal means (generic means adjusted for covariate effects) to check for differences in the elevation between the different taxa examined.

Major trends of shape variation between species in our primate PDP sample were summarized by means of a principal components analysis (PCA) computed on the covariance matrix of extant species shape ratios means and fossil specimens. In addition to the full set of seven shape variables, this analysis was repeated with the six available lengths in the *Pierolapithecus* as a means of including the latter specimen in the morphometric comparisons. All analyses were performed using *SPSS* ver. 17 and *PAST* (Hammer et al., 2001). As a sensitivity test, all analyses include the actual available measurements from the specimen (thus, including incomplete lengths), as well as the maximum estimated measurements (total length and mediolateral base breadth) from the corrected IGF 11778. Both specimens are analyzed as different operational taxonomic units. Detailed close ups to the *Oreopithecus* PDP specimens are provided in Figure 3, and Figure 4 provides morphological comparisons with representative specimens of the comparative sample.

**RESULTS**

**Anatomical descriptions**

One of the main points that Marzke and Shrewsbury (2006) stressed regarding the *Oreopithecus* PDP morphology was that the attachment for the FPL just distal to the proximal fossa (PVF of Shrewsbury et al., 2003) would be functionally important for inferring precision grasping in *Oreopithecus* rather than the fossa *per se*. It is worth mentioning that it is not possible to know whether or not the flexor tendon insertion found in fossil PDPs really belongs to an independent FPL or from the radial portion of the *flexor digitorium profundus* (FDP)
**Fig. 3.** Pollical distal phalanges of *Oreopithecus bambolii*. Both individuals have been previously depicted and figured elsewhere (Moya-Sola et al., 1999, 2005b). In this figure, we represent them by means of high-resolution surface laser scans to show the surface detail anatomy discussed in the text. BA#130 is depicted in palmar (a) and oblique lateropalmar (b) views. IGF 11778 is depicted in palmar (c), oblique ulnopalmar (d), dorsal (e), and proximal (f) views. A digitally corrected version of IGF 17788 shows its main proportions in palmar (g), ulnar (h), and proximal (i) views. Color code is as follows: orange = proximal volar fossa; red = *flexor pollicis longus* attachment; green = ungual fossa; blue = tuft; purple = *extensor pollicis longus* insertion.

**Fig. 4.** Morphological comparisons. Pollical distal phalanges of the taxa examined are compared with an overall similar size. Color code is as follows orange = proximal palmar fossa (PVF of Shrewsbury et al., 2003), referred here as palmar fossa in taxa extending over the whole palmar surface; red = flexor tendon attachment; green = ungual fossa; blue = palmarly protruding distal tuft. Among extant taxa, only humans and *Hylobates* have a proper *flexor pollicis longus* (FPL) muscle with a palmarly protruding insertion attachment for its tendon (marked in bold red). Only hominins and *Oreopithecus* exhibit an ungual fossa (green) in between the attachment for the FPL (bold red) and a palmarly protruding tuft (blue).
as observed in other primates (Susman, 1998; Diogo et al., 2012) or even to another anomalous muscle tendon. Thus, in this article, when describing fossils, we will only denote the presence or absence of a flexor muscle tendon.

In palmar view, BA#130 (of uncertain side attribution) shows two elevated tubercles connected by a nonelevated isthmus (Fig. 3a). The left one is poorly developed, whereas the right one, which is situated slightly distally, is more palmarly raised. By contrast, the proximal base of IGF 11778 (from the left hand) displays very distinct ulnar and radial tubercles on the palmar surface at the distal margin of the PVF. These two elevated markings strongly suggest radial and ulnar attachments of a flexor muscle’s tendinous band. The two sides of the flexor band are connected by a proximodistally narrow and slightly elevated isthmus between the two tubercles for possible attachment of central slips of the flexor tendon (Fig. 3c). In palmar view, the radial tubercle of IGF 11778 is slightly larger than the ulnar, which is situated slightly more distally than the radial. These tubercles were discernible in previously published figures of these specimens (Maya-Solé et al., 1999, 2005b); however, they received little deliberation. In both specimens, the two distinct tubercles on the proximal palmar surface of the PDP delineate a proximal region as a PVF and a distal depressed area as the ungual fossa over the entire diaphysis of the PDP. IGF 11778 displays a more proximally constricted PVF (Fig. 3c,d), whereas BA#130 shows a larger proximodistally extending PVF (Fig. 3a,b). IGF 11778 shows no noticeable sesamoid facet at the palmar midline base of the PDP for an articulation with a sesamoid bone or cartilage within the palmar plate (Fig. 3c). The base is too incomplete in BA#130 to make such an observation, regarding the presence or absence of any sesamoid facet. From the palmar surface markings on these two PDPs, it is not possible to suggest if any satellite slips of the flexor tendon attachments were present, as can be observed during dissections for humans or for baboons (Shrewsbury et al., 2003). There are no noticeable ungual spines in either specimen for which satellite slips of the flexor tendon can be attached. What can be inferred is that a pollical flexor tendon has attachments to the two proximal palmar tubercles on the palmar surface of the PDP.

Distal to the two tubercles, the diaphysis of these two PDPs contains an ungual fossa (Fig. 3a–d), which extends distally to the base of a slightly palmarly protruding tuft at the PDP distal end. Even though its radial section has been broken off, the tuft of IGF 11778 (Fig. 3c) is more flaring bilaterally relative to the shaft than in BA#130 (Fig. 3a). The functional significance of the ungual fossa and tuft is that the surface area for the distal ungual pulp overlies and attaches palmarly to the tuft, whereas the proximal ungual pulp overlies and attaches palmarly to the area over the ungual fossa (Shrewsbury and Johnson, 1975; Shrewsbury et al., 2003). The dorsal side of the base in IGF 11778 shows a marked proximal rim for the attachment of the extensor pollicis longus (Fig. 3e,f). The radial lateral basal tubercle of IGF 11778 is broken off (Fig. 3c,d,f), and the proximal portion of the base in BA#130 is absent (Fig. 3a). Our impression is, however, that the base of the Oreopithecus PDP specimens was wide and dorsopalmarly flat (see corrected IGF 11778 specimens in Fig. 5g–i).

Shape ratios

Table 1 provides the summary statistics for the seven measurements taken in our sample. The GM and the seven shape variables are represented in Figure 5 as boxplots. Oreopithecus, like Pierolapithecus, has an absolutely larger PDP than Pan and Pongo, whereas Orrorin, like Gorilla and especially humans, display larger PDPs (Fig. 5a). The Proconsul specimen is considerably smaller, being in the upper size range of monkeys (as KPS1 is a subadult specimen, a larger size is expected for an adult of this taxon). In terms of relative proximodistal length, Oreopithecus and Proconsul are in the range of humans and Gorilla, whereas Pierolapithecus is in the low range of Pongo and Pan, which display long PDPs relative to the other dimensions. The latter condition is extreme for Alouatta, an obvious outlier in this analysis. The catarrhine monkeys and Orrorin display relative shorter PDPs (Fig. 5b). In terms of the dorsopalmar height of the tuft (Fig. 5c), all the fossils examined display very similar values, in the low range of extant apes and Alouatta and the upper range of Hylobates. Cercopithecines have slightly lower values; Nasalis is slightly higher. Modern humans stand out by having relatively shorter dorsopalmar tuft heights. For values of relative tuft mediolateral width (Fig. 5d), humans display the better-developed tufts, followed closely by Papio, Pan, Pongo, and Nasalis display lower values, like Proconsul, whereas Macaca, Gorilla, Oreopithecus, and Orrorin are intermediate. Alouatta displays the shortest values, with similarities to Pierolapithecus. Among extant taxa, there is a clear separation between PDPs with a longer dorsopalmar height at the midshaft (Alouatta, Nasalis, Pongo, and Pan) and taxa with shorter dorsopalmar midshafts, which are relatively wider (Macaca, Papio, Gorilla, H. sapiens, and Hylobates). Oreopithecus, Proconsul, and Orrorin are in an intermediate position between both groups, whereas Pierolapithecus is in the upper range of Pan and Pongo (Fig. 5e). For the mediolateral width of the midshaft (Fig. 5f), H. sapiens, Hylobates, and Macaca show high values, whereas Alouatta and especially Pongo and Pan show very low degrees of midshaft expansion. Papio, Nasalis, and Gorilla are in a more intermediate range. Oreopithecus is in between the mid and low ranges, Orrorin and Pierolapithecus are in the middle to high ranges, and Proconsul is in the upper range. The analysis of the mediolateral width of the base (Fig. 5h) shows that Macaca has the relatively widest base, whereas Pan and especially Alouatta have the narrowest base. The remaining extant taxa show intermediate values between these extremes. Proconsul, Pierolapithecus, and Orrorin are in the range of Alouatta (and lower range of Pan); however, there are differences in Oreopithecus depending on the actual and corrected IGF 11778 specimens. The former is between Pan and Alouatta, but a much higher value emerges from the corrected version, which overlaps with most of the taxa. From the internal shape analysis of the dorsopalmar height of the base (based on the seven-variable GM and thus not including Pierolapithecus; Fig. 5g) shows that Pongo has the tallest base. Nasalis, Macaca, Alouatta, and especially Hylobates all have a shorter base. Papio, Gorilla, Pan, and H. sapiens have intermediate values between Pongo and the remaining taxa. All the Miocene fossil taxa display similar values, which among the taxa analyzed.
Tuft expansion

The expansion index (Mittra et al., 2007) shows that when the mediolateral expansion of the tuft is examined in relation to the base (Fig. 6), *Papio* and especially *H. sapiens* exhibit more expanded tufts than the remaining extant taxa (*P* < 0.008). There are no statistical differences between the remaining extant genera; however, *Gorilla* on one side and *Alouatta* and especially *Pongo* on the other side show a tendency to have slightly more and less expanded tufts, respectively. *Proconsul* is between the midranges of *Papio* and modern humans, whereas *Orrorin* is on the upper human range and *Pierolapithecus* on the low interquartile range of *Pan* and midrange of *Pongo*. More evident differences exist between the actual *Oreopithecus* specimen (in the upper human range) and the corrected version (intermediate between humans-*Papio* and the remaining taxa).

When covariation of mediolateral tuft expansion and PDP size is inspected through ANCOVA (Fig. 7), homogeneity of slopes cannot be discarded (*F* = 1.64; *P* = 0.143) for all extant taxa with the exception of *Pan*, which shows a significantly higher slope. Results of the allometric regression analyses are reported in Table 2, showing that isometry cannot be discarded for any extant genus with the exception of *Pan* (positive allometry). Regression of *Alouatta* was nonstatistically significant, probably due to its small sample size and was therefore not reported. Post hoc Bonferroni comparisons on estimated marginal means of genera with similar slopes (i.e., excluding *Pan* and *Alouatta*; comparisons evaluated at lnGM = 1.66) show that modern humans,
Fig. 6. Boxplot showing the tuft expansion index. Fossils and boxplots are as in Figure 5. The vertical line facilitates the visual comparison of IGF 11778c to the remaining taxa. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Fig. 7. Allometric relationship of mediolateral tuft width and PDP size. Size was approached by the geometric mean of six measurements (as in Fig. 5a). Regression lines for every extant taxa (except Alouatta) are indicated (dashed lines are Pan and Hylobates).

### TABLE 2. Results of regression analyses reported in Figure 7

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>R</th>
<th>SEE</th>
<th>P</th>
<th>Slope</th>
<th>95% CI</th>
<th>Intercept</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nasalis</td>
<td>9</td>
<td>0.945</td>
<td>0.127</td>
<td>0.000</td>
<td>0.967</td>
<td>0.668–1.267</td>
<td>−0.116</td>
<td>−0.482–0.251</td>
</tr>
<tr>
<td>Macaca</td>
<td>5</td>
<td>0.982</td>
<td>0.139</td>
<td>0.003</td>
<td>1.260</td>
<td>0.819–1.701</td>
<td>−0.357</td>
<td>−0.876–0.163</td>
</tr>
<tr>
<td>Papio</td>
<td>29</td>
<td>0.906</td>
<td>0.104</td>
<td>0.000</td>
<td>1.151</td>
<td>0.939–1.363</td>
<td>−0.137</td>
<td>−0.438–0.165</td>
</tr>
<tr>
<td>Hylobates</td>
<td>11</td>
<td>0.786</td>
<td>0.280</td>
<td>0.003</td>
<td>1.107</td>
<td>0.473–1.741</td>
<td>−0.297</td>
<td>−1.081–0.487</td>
</tr>
<tr>
<td>Pongo</td>
<td>18</td>
<td>0.883</td>
<td>0.194</td>
<td>0.000</td>
<td>1.464</td>
<td>1.052–1.876</td>
<td>−0.971</td>
<td>−1.652–0.289</td>
</tr>
<tr>
<td>Gorilla</td>
<td>17</td>
<td>0.659</td>
<td>0.233</td>
<td>0.004</td>
<td>0.790</td>
<td>0.294–1.286</td>
<td>0.354</td>
<td>−0.669–1.377</td>
</tr>
<tr>
<td>Pan</td>
<td>31</td>
<td>0.914</td>
<td>0.141</td>
<td>0.000</td>
<td>1.710</td>
<td>1.421–2.000</td>
<td>−1.433</td>
<td>−1.933–−0.933</td>
</tr>
<tr>
<td>H. sapiens</td>
<td>25</td>
<td>0.888</td>
<td>0.130</td>
<td>0.000</td>
<td>1.205</td>
<td>0.936–1.473</td>
<td>−0.534</td>
<td>−0.892–0.244</td>
</tr>
</tbody>
</table>

All regressions show slopes significantly different from zero ($P < 0.004$).

Abbreviations: SEE, standard error of estimate; CI, confident interval.

**Principal components analyses**

When all the shape ratios provided in Figure 5 are summarized by means of a PCA (see Fig. 8a and Table 3, Iteration 1), major extant taxonomic groups can be identified with the first two PCs. The major axis of shape variation (i.e., PC1, explaining 55.2% of total variance) is positively correlated with overall proximodistal length and negatively correlated with mediolateral tuft and midshaft width. The two species of Pan and Pongo, and especially Alouatta show high values along this axis, reflecting their overall mediolaterally narrow PDPs with a predominant proximodistal length dimension, resulting in an overall “conical” shape. On the other extreme of PC1, modern humans, followed by Macaca and Papio are characterized by PDPs with a broader appearance. Gorilla, Nasalis, Proconsul, and Oreopithecus show intermediate values on this axis, with Hylobates and Orrorin being intermediate between Miocene hominoids and cercopithecoid terrestrial monkeys. PC2 (19.1% of variance) is positively correlated with dorso-palmar height of the base and negatively with mediolateral shaft width. This axis clearly separates great apes, modern humans, and cercopithecoid monkeys by their positive values from Alouatta, Miocene hominoids, Orrorin, and Hylobates, all of which are restricted to the negative side of the axis.

A second iteration of this same analysis excludes the dorso-palmar height of the base—the variable most highly correlated with PC2 in iteration 1—to include Pierolapithecus (Fig. 8b and Table 3). PC1 (59.8% of
**TABLE 3. Results of the principal components analyses reported in Figure 8**

<table>
<thead>
<tr>
<th>Variables</th>
<th>Iteration 1</th>
<th>Iteration 2</th>
<th>Iteration 1</th>
<th>Iteration 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proximodistal length</td>
<td>0.45</td>
<td>−0.27</td>
<td>0.46</td>
<td>0.32</td>
</tr>
<tr>
<td>Dorsopalmar tuft</td>
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<td>−0.26</td>
<td>0.35</td>
<td>−0.29</td>
</tr>
<tr>
<td>Mediolateral tuft</td>
<td>−0.45</td>
<td>0.06</td>
<td>−0.49</td>
<td>−0.42</td>
</tr>
<tr>
<td>Dorsopalmar midshaft</td>
<td>0.34</td>
<td>−0.10</td>
<td>0.39</td>
<td>0.00</td>
</tr>
<tr>
<td>Mediolateral midshaft</td>
<td>−0.55</td>
<td>−0.48</td>
<td>−0.46</td>
<td>0.73</td>
</tr>
<tr>
<td>Dorsopalmar base</td>
<td>0.11</td>
<td>0.70</td>
<td>−0.25</td>
<td>−0.34</td>
</tr>
<tr>
<td>Mediolateral base</td>
<td>−0.22</td>
<td>0.34</td>
<td>−</td>
<td>−</td>
</tr>
</tbody>
</table>

Variables are shape variables, as each original measurement was divided by the geometric mean (GM) of seven (Iteration 1) or six (Iteration 2) variables. Loadings > 0.40 or < −0.40 are marked in bold. Remaining axes explain less than 12% and 10% of the variance, respectively, and do not provide meaningful discrimination.

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total variance) is driven by the same shape variables as in the first iteration, but now PC2 is driven positively by mediolateral midshaft and negatively with mediolateral tuft. This more restrictive shape analysis yields a cluttered morphospace configuration (i.e., more overlap between major taxonomic groups) than in the first iteration. *Pierolapithecus* occupies an intermediate position between orangutans and chimpanzees in PC1 and is extreme in PC2 (positive values), resulting from a combination of an overall long PDP with a very narrow tuft. When the dorsopalmar height of the base is excluded, PC2 separates *Pierolapithecus*, *Proconsul*, *Hylobates*, *Alouatta* and *H. sapiens* from the remaining taxa. *Oreopithecus* in this iteration is most similar to gorillas and *Nasalis*.

**DISCUSSION**

**PDP proportions and “pad-to-pad” features in *Oreopithecus***

In this study, we reevaluated the PDP morphology of *Oreopithecus* (based in IGF 11778 and BA#130) in comparison with other selected anthropoid primates and with currently available Miocene hominoid fossils. The presence of features that have been related to pad-to-pad precision grasping in modern humans (Shrewsbury et al., 2003) is evaluated (Figs. 3 and 4), and morphometric affinities of IGF 11778 relative to our comparative sample are assessed by means of bivariate (Figs. 5–7) and multivariate (Fig. 8) analyses. A summary of the main metric and nonmetric features of the *Oreopithecus* PDP and our comparative sample is available in Table 4. Our PCA on the covariance matrix of specific means (Fig. 8a) shows that some major taxonomic groups can be separated by means of the major trends in PDP shape variation: platyrrhines and catarrhines; cercopithecoids, great apes, and hyllobatids. Modern humans are not arranged by phylogenetic proximity to African apes; instead, their overall flat and wide PDPs are more similar to that of terrestrial cercopithecoid monkeys. All Miocene taxa considered occupy a similar position in the morphospace, similar to *Hylobates*, which suggests that PDP proportions characterized by moderate tuft and midshaft width and by a dorsopalmarly short base are likely plesiomorphic for Hominoidea. On the other hand, the species of *Pan* and *Pongo* are more similar to each other in terms of their overall cylindrical shape (i.e., less mediolaterally expanded at the midshaft and tuft (Fig. 5d,f); and their more dorsopalmarly expansion at the midshaft than other hominoids (Fig. 5e)). Although *Oreopithecus* shows a PDP with primitive proportions (Fig. 8a), it has a mediolaterally well-developed tuft for an ape, similar to the early hominin *Orrorin* (Figs. 5d and 7), although less so when the corrected version of IGF 11778 is analyzed by means of the expansion index (Fig. 6). The tuft seems to be variable in this taxon, at least from a qualitative inspection to BA#130 (Fig. 3a). A mediolaterally expanded tuft is functionally relevant, because in humans, it is also correlated with an expanded digital pulp in pollical (Shrewsbury et al., 1988) and in nonpollical (Mittra et al., 2007) distal phalanges.

A suite of features in the PDP of humans was extensively described in relation to a “pad-to-pad” interaction of the thumb and one or more of the remaining digits (Shrewsbury et al., 2003). This suite of characters was visually reconstructed in relation to the soft tissue by Almécija et al. (2010, their Fig. 1). Essentially, this morphology is reflected by a proximal palmar fossa (PVF of Shrewsbury et al., 2003) associated with a palmarly protruding ridge at the distal border of the PVF for attachment of the FPL tendon. The digital pulp distal to the flexor tendon attachment functions to accommodate the shape of the object being manipulated or held. The functions of the digital pulp are reflected in the presence of an ungual fossa, associated with an overlying mobile proximal pulp. The ungual fossa is defined proximally by the FPL tendon attachment and distally by a relatively wide and palmarly elevated tuft. The tuft itself is associated with a more stable distal ungual pulp (Shrewsbury and Johnson, 1975; Shrewsbury et al., 2003). Finally, ungual spines project proximally from the radial and ulnar borders of the tuft. Laterals *intraosseous* ligaments are attached to the spines, which sustain the lateral nail bed and support the lateral borders of the proximal ungual pulp. These individual morphological features can be found in selected specimens of different extant primates (Susman, 1998); however, among extant taxa, the entire complement of features described can only be consistently found in modern humans (see Fig. 4; Shrewsbury et al., 2003).

In the PDPs of *Oreopithecus*, the morphology and spatial location of the tubercles just distal to a PVF, projecting palmarly, suggest the presence of a strong attachment for the long tendon of a pollical flexor muscle. The locations and size for these tendon attachments (i.e., the tubercles) suggest that, as in humans, its function at the interphalangeal joint is for flexion with conjunct rotation, the latter motion reducing the forces of flexion across the joint. Unlike in Plio-Pleistocene and modern hominin PDPs, there is no noticeable sesamoid facet in *Oreopithecus* at the palmar midline base of the PDP for a sesamoid bone or cartilage within the palmar plate to ride up on the facet during flexion and to increase the torque of the flexor tendon. Furthermore, as in modern humans and fossil hominins (Susman, 1998; Shrewsbury et al., 2003; Almécija et al., 2010), both *Oreopithecus* PDP specimens display both a PVF and an ungual fossa delineated proximally and distally, respectively, by the protruding flexor tendon insertion and the tuft (Figs. 3 and 4). The flexor attachment appears distinctive in *Oreopithecus* by being slightly separated wide and palmarly elevated tuft. Nevertheless, there is an isthmus ridge connecting the two tubercles, which could account tendon attachment continuity. In brief, many of the features present in the hominins PDP that are related to pad-to-pad precision grasping are also present in the *Oreopithecus* specimens, except for the presence of ungual spines and sesamoid facets. It is noteworthy that ungual spines seem to be only moderately developed or absent in some later Miocene, Pliocene, and Pleistocene hominins (Gommer and Senut, 2006; Lovjoy et al., 2009; Almécija et al., 2010; Ward et al., 2012), whereas a sesamoid facet is not present in the six-million-year-old BAR 190191 (*Orrorin tugenensis*), even though all the remaining features are already present (Almécija et al., 2010). In that previous analysis, focusing on available hominins, the dorsopalmar height of the tuft was not available in our comparative sample and thus not measured. The combination of the prior and the current analyses offers an interesting picture: by excluding that single diameter (dorsopalmar height of tuft), *Orrorin* falls within the modern human PDP morphometric variation (Fig. 3 in Almécija et al., 2010), whereas its proportions look less human and...
more similar to hylobatids, Proconsul, and Oreopithecus when that variable is included in this study. A dorsopalmarly high tuft is most probably plesiomorphic for hominoids, as it was already pointed out in that previous work (Almécia et al., 2010). Similarly, and in contrast to modern humans, high dorsopalmar tuft dimensions have also been reported for Australopithecus afarensis (Ward et al., 2012) and Australopithecus sediba (Kivell et al., 2011) reinforcing the plesiomorphic status of this character in these hominins as well. Overall, the presence of pad-to-pad traits in Oreopithecus and Orrorin, with only moderate mediolateral development suggests that these traits can evolve prior to modern human PDP proportions.

**Relationship between PDP morphology and intrinsic hand length proportions**

The implicit assumption of this and previous studies that analyze the presence of pad-to-pad precision grasping features in the PDP is that the intrinsic hand proportions allow for such precision grasps to be present (Shrewsbury et al., 2003; Almécia et al., 2010), that is, the thumb is long enough so that the proximal pads of the thumb and one or more of the remaining digits can oppose each other. However, this argument does not necessarily imply that a long thumb relative to digits can be related only to enhanced precision grasping. For example, terrestrial digitigrade monkeys exhibit thumb-to-digit length proportions approaching those of humans (Schultz, 1930; Napier, 1960, 1993), coupled with wide PDP tufts (especially Papio; Figs. 4–8). However, the mechanism responsible for these hand proportions and thumb morphology in these digitigrade monkeys probably has nothing to do with enhanced manipulation. Conversely, the specific locomotor adaptations are linked to a high degree of terrestriality, such as Digita II–V length reduction (Etter, 1973) and use of tip of the thumb in weight support (e.g., Tuttle, 1967, 1993). Explicit analyses of thumb morphology and intrinsic hand length proportions are necessary to test the former assumption. Therefore, the following discussion is intended only to summarize the results in PDP anatomy and proportions in our primate sample taking into account the available data on hand proportions and hand use in extant primates to evaluate how our implicit functional assumption stands.

Cercopithecoid monkeys show PDP proportions similar to those of humans (Fig. 8). Instead of a human-like PVP (limited to the proximal palmar portion of the phalanx by a marked FPL attachment), cercopithecoids (with the exception of Theropithecus) display a more extensive fossa, occupying most of the palmar basal and diaphyseal surface of the PDP while reaching distally to the proximal edge of the tuft (Fig. 4). A flexor tendon from the radial component of the FDP (e.g., Whitehead, 1993; Susman, 1998; Diogo et al., 2012) traverses distally to attach to the base or surface of the tuft (Fig. 9 in Shrewsbury et al., 2003). Consequently, the complex of the PVF, distal protruding flexor muscular attachment, and ungual fossa appears limited to modern and fossil hominins (Susman, 1998; Shrewsbury et al., 2003; Almécia et al., 2010) and Oreopithecus (Fig. 4). Gorilla, Alouatta, and Proconsul exhibit a portion of shaft between the flexor insertion and the tuft; however, neither the tendon attachment nor the tuft protrude palmarly. Thus, a proper ungual fossa is lacking (Fig. 4). Theropithecus gelada presents a complex similar to that of hominins: presence of PVF with a conspicuously protruding gabled insertion for a long flexor; however, no clear ungual fossa is present (Fig. 4). Etter (1973) described the particular case of the gelada baboons, which displays an especially elongated pollical metacarpal (but not phalanges) and shortened second ray, as the result of an extreme reduction of the intermediate phalanx, thereby conferring the geladas with a human-like pad-to-pad “precision handling” capability as evaluated in terms of thumb to index length proportions (Etter, 1973, p 343). The special adaptation of the hands of geladas is also evident in a special differentiation of the FDP, as well as other thumb muscles (Maier, 1971), thus being analogous to a proper FPL. This is explained as specific feeding adaptations in monkeys that spend 70% of their daily activity collecting grass blades, seeds, and rhizomes (Jolly, 1970). Therefore, other than humans, Theropithecus is the only modern species with reported pad-to-pad precision grip behaviors, which are further accompanied by intrinsic hand length proportions allowing for such a grip, as well as a PDP with a flexor attachment configuration similar to that of hominins and Oreopithecus (Fig. 4). We hypothesized that subtle PDP differences in geladas could be related to the use of the thumb for weight bearing and/or the evolution of specifically manipulatory-related features in an already specialized terrestrial digitigrade monkey. This evidence highlights the complexity of the PDP anatomy and how the evolutionary history of a taxon should be taken into account when analyzing the evolutionary process, especially considering the raw materials originally available for natural selection to operate (Gould and Lewontin, 1979). Future studies including a more complete sample of Theropithecus specimens are necessary to properly characterize and interpret the PDP of the gelada baboons.

Hand manipulation and locomotion are two main (and sometimes opposite) selective pressures shaping the hands of primates (Napier, 1960, 1993). Extant great apes provide a good example of this: Pan and Pongo show the shortest thumbs in relation to their elongated hand, presumably for an efficient below-branch “hook grasp” during below-branch suspension (Schultz, 1930; Sarmiento, 1994) as well as Pan and Pongo (Fig. 4). Both taxa also share a similar PDP morphology with poorly developed tendon insertions on the palmar aspect and with a narrow tuft (Figs. 4–8 and Table 4). However, the presence or absence of any insertion on the palmar aspect of the PDP seems to be widely variable in great apes, Pongo being the extreme case, where roughly 95% of the specimens do not exhibit a functional tendon (Straus, 1942; Diogo et al., 2012). We argue that similar PDP morphology and intrinsic hand proportions in Pan and Pongo could be explained by suspensory-related homoplasy in great apes (e.g., Almécia et al., 2013b). This argument is reinforced by the more moderate thumb-to-digit length proportions in gorillas (more terrestrial than Pan and Pongo), and especially the highly terrestrial mountain gorillas (Schultz, 1930; Tuttle, 1967; Sarmiento, 1994) as well as their more moderate PDP proportions (Figs. 4 and 8). Even with the short thumb relative to digits and the lack of a proper FPL, extant great apes exhibit well-developed thenar muscles (but not to the degree of humans) and use their hands for a variety of power and precision grips (Napier, 1960; Tuttle, 1967, 1969, 1970;
### TABLE 4. Main morphological features of the pollical distal phalanges analyzed in this work

<table>
<thead>
<tr>
<th>Species</th>
<th>Base</th>
<th>Midshaft</th>
<th>Tuft</th>
<th>Flexor insertion</th>
<th>Ungual</th>
<th>Ungual</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dorsopalmar</td>
<td>Mediolateral</td>
<td>Dorsopalmar</td>
<td>Mediolateral</td>
<td>Dorsopalmar</td>
<td>Mediolateral</td>
</tr>
<tr>
<td>Alouatta</td>
<td>Short</td>
<td>Very narrow</td>
<td>Tall</td>
<td>Narrow</td>
<td>Tall</td>
<td>Very narrow</td>
</tr>
<tr>
<td>Nasalis</td>
<td>Short</td>
<td>Intermediate</td>
<td>Tall</td>
<td>Intermediate</td>
<td>Tall</td>
<td>Narrow</td>
</tr>
<tr>
<td>Macaca</td>
<td>Short</td>
<td>Very wide</td>
<td>Short</td>
<td>Wide</td>
<td>Short</td>
<td>Intermediate</td>
</tr>
<tr>
<td>Papio</td>
<td>Tall</td>
<td>Wide</td>
<td>Short</td>
<td>Intermediate/ wide</td>
<td>Short</td>
<td>Wide</td>
</tr>
<tr>
<td>Hylobates</td>
<td>Short</td>
<td>Intermediate</td>
<td>Short</td>
<td>Wide</td>
<td>Short</td>
<td>Narrow</td>
</tr>
<tr>
<td>Pongo</td>
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<td>Wide</td>
<td>Tall</td>
<td>Narrow</td>
<td>Tall</td>
<td>Narrow</td>
</tr>
<tr>
<td>Gorilla</td>
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<td>Wide</td>
<td>Short</td>
<td>Intermediate</td>
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<td>Intermediate</td>
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<td>H. sapiens</td>
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<td>Short</td>
<td>Wide</td>
<td>Very short</td>
<td>Wide</td>
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<tr>
<td>Proconsul</td>
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<td>Very narrow</td>
<td>Intermediate</td>
<td>Wide</td>
<td>Tall</td>
<td>Intermediate</td>
</tr>
<tr>
<td>Pierolapithecus</td>
<td>?</td>
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<td>Wide</td>
<td>Tall</td>
<td>Very narrow</td>
</tr>
<tr>
<td>BAR 1801'01</td>
<td>Short</td>
<td>Narrow</td>
<td>Intermediate</td>
<td>Wide</td>
<td>Tall</td>
<td>Intermediate</td>
</tr>
</tbody>
</table>

Abbreviations: PVF, proximal volar (= palmar) fossa; FDP, flexor digitorium profundus; FPL, flexor pollicis longus.
Christel, 1993; Napier, 1993; Pouydebat et al., 2008). However, a human-like pad-to-pad contact is precluded by the disproportionate length of their Digits II–V relative to the thumb (see Discussion section in Alba et al., 2003; Almécija et al., 2009a; Marzke et al., 2009; Almécija et al., 2010), as well as the shortness of the common flexor tendons (Christel, 1993).

Hylobatids provide an alternative anatomical solution, reconciling highly specialized suspensory behaviors and well-developed thumbs. Even though they are the most suspensory of the modern hominoids, hylobatids still exhibit moderate thumb-to-hand length proportions (Schultz, 1930), moderate PDP proportions (Fig. 8), and an insertion marking on the palmar side (Fig. 4) for a proper FPL (Straus, 1942; Diogo et al., 2012). Furthermore, hylobatids exhibit a deep cleft that separates the thumb from the palm at the metacarpal level (Fig. 10 in Straus, 1942) to enable the hand for secure grips—assisted by the thumb—during arboreal locomotion as well as to allow the thumb to be “bent across the proximal palm, where it is of no hindrance in brachiation” (Straus, 1942, p. 229). Hylobatids suggest that a proper FPL can be present in some Miocene apes due to evolutionary history but unrelated to enhance manipulative behaviors. If this suggestion holds true, then the possession of a FPL would not be a hominoid synapomorphy, but rather the plesiomorphic status for Hominoida. Extant great apes might have lost a proper FPL in relation to thumb shortening relative to hand length (Straus, 1942; Lovejoy et al., 2009; Almécija et al., 2012). Until more specific analyses relating to PDP morphology and intrinsic hand proportions are available, the observations discussed above support the hypothesis that the presence of pad-to-pad traits on the PDP palmar side can only evolve in hands with long thumbs relative to digit(s). We argue that this was the case of Oreopithecus.

Oreopithecus as part of the bigger picture

The complete, although juvenile, PDP specimen of Proconsul (KPS1-PH96) has been described as possessing a “deep pit” on its palmar side, indicating the insertion for a long flexor tendon (Begun et al., 1994). A shallow PVF is present in this specimen, followed dis- tally by a rugose surface, suggesting an insertion for the long pollical flexor tendon (Fig. 4). However, this insertion does not protrude palmarly as in hominins or in Oreopithecus (Table 4), although its subadult status should caution our speculations. The KPS1 specimen shows similar overall PDP proportions with Oreopithecus (Fig. 8a), although with less-developed mediolateral tuft (Figs. 5d and 7; although uncertain for expansion index, Fig. 6), which has been related to distal pulp development (Mittra et al., 2007). As previously observed (Almécija et al., 2009b), the Pierolapithecus PDP specimen appears to have a faint proximal depression on its palmar side (slight abrasion of the palmar side hinders any detailed anatomical description; Fig. 4) and a weakly developed tuft (Figs. 5d–8). The case is similar for the more partial IPS 4333 specimen from Castell de Barberà where the base is absent (Almécija et al., 2012). This might suggest similar thumb morphology in Spanish Miocene apes (i.e., long PDP with reduced tuft). There is a general agreement that most Miocene apes would have better developed thumbs than their extant relatives, which were used to assist in power grasping during above-brachium quadrupedalism and, possibly, in climbing (Pilbeam et al., 1980; Begun et al., 1994; Madar et al., 2002; Nakatsukasa et al., 2003; Ward, 2007; Almécija et al., 2009b, 2012). Thus, a moderately long thumb could actually be the plesiomorphic state for great apes, as suggested by these previous analyses on proximal pollical phalanx length relative to body mass (Almécija et al., 2012). Furthermore, with the exception of the European Late Miocene Hispanopithecus/Rudapithecus suspensory group (Begun, 1993; Moyà-Solà and Köhler, 1996; Almécija et al., 2007), with disputed phy- letic affinities (e.g., Alba, 2012; Begun et al., 2012), stem hominoids and great apes have been discussed as exhibiting only moderate hand lengths, certainly shorter than modern suspensory forms (e.g., Napier and Davis, 1959; Moyà-Solà et al., 2005a; Almécija et al., 2009b). Accord- ingly, moderate thumb-to-hand length proportions allowing (although not necessarily selected) for a better pad- to-pad contact than that observed on extant apes could actually be plesiomorphic for hominoids and originally related to above-branch palmigrady assisted by the thumb (Almécija et al., 2007, 2009b, 2012). Hence, humes (hand length proportions i.e., long thumb rela- tive to hand) could have evolved without the drastic changes that starting from a “chimp-like” ancestor would imply (Ashley-Montagu, 1931; Harrison, 1991; Lovejoy et al., 2009).

The overall picture of our morphometric analyses shows that the PDP of Oreopithecus is not modern-human-like but rather primitive. However, it shows on its palmar side a combination of features present in fossil hominins (to the exception of OH 7; Fig. 4 and Table 4): a PVF, a palmarly-protruding flexor insertion marking, an ungual fossa, and a palmarly protruding and slightly wide tuft (Susman, 1988; Gommery and Senut, 2006; Almécija et al., 2010; Kivell et al., 2011; Ward et al., 2012). These traits suggest a better-developed flexor apparatus for the PDP of Oreopithecus than in extinct and in extant great apes. In Oreopithecus, these qualitative features are further accompanied with better-developed tufts than in previous Miocene apes, especially in comparison with Pierolapithecus. Some of these fossil PDPs are attributed to hominins species with inferred human-like intrinsic hand length proportions, prefiguring the establishment of a systematic stone-tool culture (Alba et al., 2003; Green and Alba, 2008). Recently, an insertion for the fully developed Austra- lopithecus fossil record, a virtually complete associated hand was found for Australopithecus sediba (ca. 2 Ma), indicating long thumb relative to third digit (slightly above humans) but unassociated with stone tools (Kivell et al., 2011). This evidence indicates that enhanced manipulative skills allowed by more efficient pad-to-pad contact could have evolved in early hominins from Miocene-ape- like (moderate) hand length proportions once selective pressures posed by forelimb locomotor behaviors became relaxed with the advent of terrestrial bipedalism (Alba et al., 2003; Almécija et al., 2010). Thus, among the vast array of traits characterizing the human hand (Napier, 1956, 1960, 1993), intrinsic length proportions would not have necessarily evolved originally in relation to stone tool-making specifically. They probably were exapted for the latter in hominins with advanced cognitive capabilities and, as a consequence, “purposive actions” (Napier, 1956, 1962; Alba et al., 2003).

Oreopithecus has been alternatively reconstructed as being a slow-moving (Schultz, 1960), an agile suspens-oryclimber (e.g., Szalay and Delson, 1979; Jungers, 1984; Harrison, 1986; Junger, 1987; Sarmiento, 1987;
Although the proportions of its postcranial long bones indicate the pattern of an extant ape-like forelimb (Jungers, 1987), neither its hand proportions are of a suspensory type of ape nor is their morphology compatible with a pronograde monkey-like creature (Moyà-Solà et al., 1999, 2005b), although different interpretations have been presented (Susman, 2004, 2005). The phalangeal curvature in *Oreopithecus* (36°, using the included angle technique) estimated by (Susman 2004) falls within the low range of African apes, but interestingly, also within range of early hominins (Susman, 1988; Stern et al., 1995; Richmond and Jungers, 2008) and well below the range of any other available Miocene ape (Alba et al., 2010). We believe that this low degree of manual phalangeal curvature in *Oreopithecus* is a compelling argument for low degree of suspensory locomotion.

The origins of *Oreopithecus* are still obscure (see introductory paragraph of this work and references therein); however, previous studies have established that *Oreopithecus* evolved and lived in the insular paleoecosystem of Tuscany and Sardinia (e.g., Moyà-Solà and Köhler, 2003; Rook et al., 2006; Abbazzi et al., 2008). A commonly observed thesis is that animals develop very particular adaptations under insular conditions, with several different physiological and morphological adaptive processes being described for mammals of the Mediterranean islands (e.g., Bover et al., 2008; Palombo et al., 2008; van der Meade, 2008; Köhler and Moyà-Solà, 2009; Quintana et al., 2011). Most of the insular adaptations involve enhanced energy processing that include improved harvesting and reduction of energy expensive locomotor behaviors (Moyà-Solà and Köhler, 2003; Köhler et al., 2007). In this resource-limited insular ecosystem, enhanced manipulative capabilities in *Oreopithecus* relative to modern apes would have improved its harvesting capabilities and, thus, its fitness (Köhler and Moyà-Solà, 1997; Moyà-Solà et al., 1999; Rook et al., 1999; Moyà-Solà and Köhler, 2003; Moyà-Solà et al., 2005b). This evolutionary scenario would explain why *Oreopithecus* displays a bizarre combination of features including modern ape-like limb long-bone proportions (Jungers, 1987) which we suggest is part of its needed evolutionary history, in combination with a short hand (Moyà-Solà et al., 1999, 2005b). Moderate hand length in *Oreopithecus* could, however, be interpreted largely as plesiomorphic (evolved from more moderate hand length proportions inferred for stem hominoids and stem great apes) or secondarily derived in this taxon from a long-handed suspensory ancestor (which would imply a larger amount of change). Only the finding of complete associated thumb and median digital bones in *Oreopithecus* will allow us to actually test its "real" intrinsic hand proportions and thus the functional significance of its PDP anatomy. Suspensory adaptations have evolved several times independently between some platyrrhines and hominoids (Erikson, 1963) and also within hominoids (Larson, 1998; Moyà-Solà et al., 2004; Almécija et al., 2007; Ward, 2007; Alba, 2012; Alba et al., 2012), probably by different means (Straus, 1942). We further propose that pad-to-pad precision grasping evolved independently at least three times in catarrhines; during the Late Miocene of Europe (*Oreopithecus*), of Africa (early hominins) and again in *Theropithecus* during the Pliocene (Jablonski, 1986).

**CONCLUSIONS**

Our morphometric analyses indicate that *Oreopithecus* displays a pollical distal phalanx (PDP) of intermediate proportions between the overall wide and flat PDP of humans and some cercopithecoid monkeys and the conical PDPs of *Pierolapithecus*, chimpanzees, orangutans, and especially *Australopithecus*. Thus, *Oreopithecus* shows a PDP with overall similar morphometric affinities to *Hylobates*, *Gorilla*, and *Nasalis*, as well as to *Proconsul* and the Late Miocene *Orrorin*, and are interpreted as plesiomorphic. In addition, the *Oreopithecus* PDP palmar surface exhibits protruding tubercles for insertion of a long pollical flexor tendon associated with proximal and distal (ungual) fossae, respectively. This arrangement has only been found in humans and fossil relatives and has been associated with the presence of a proper flexor pollicis longus (FPL) as well as differentiated pulp regions. These traits have been previously linked with enhanced pad-to-pad precision grasping in humans and are compatible with previous studies reporting human-like thumb-to-fingers length proportions in *Oreopithecus*. Moderate length relationships, however, have been inferred in the past for other more “generalized” Miocene apes. Our results support the interpretation that the intrinsic hand proportions of *Oreopithecus* are more similar to those of humans and other primates with a moderate thumb-to-hand length ratio (in opposition to the homoplastically derived proportions displayed by suspensory extant hominoids). We conclude that the total morphological pattern of the *Oreopithecus* hand and thumb is compatible with enhanced manipulative skills (unrelated to stone tool-making) in this species, relative to modern hominoids. Those adaptations are compatible with the insular ecosystem contextual background previously reported for this taxon, improving its harvesting feeding capabilities in a resource-limited environment. Only future finding of more complete and associated hand bones of *Oreopithecus* would allow testing the intrinsic hand proportions of this puzzling fossil taxon.

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