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Knuckle-Walking Anteater: A Convergence Test of Adaptation for Purported Knuckle-Walking Features of African Hominidae

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ABSTRACT Appeals to synapomorphic features of the wrist and hand in African apes, early hominins, and modern humans as evidence of knuckle-walking ancestry for the hominin lineage rely on accurate interpretations of those features as adaptations to knuckle-walking locomotion. Because *Gorilla*, *Pan*, and *Homo* share a relatively close common ancestor, the interpretation of such features is confounded somewhat by phylogeny. The study presented here examines the evolution of a similar locomotor regime in New World anteaters (order Xenarthra, family Myrmecophagidae) and uses the terrestrial giant anteater (*Myrmecophaga tridactyla*) as a convergence test of adaptation for purported knuckle-walking features of the Hominidae. During the stance phase of locomotion, *Myrmecophaga* transmits loads through flexed digits and a vertical manus, with hyperextension occurring at the metacarpophalangeal joints of the weight-bearing rays. This differs from the locomotion of smaller, arboreal anteaters of outgroup genera *Tamandua* and *Cyclopes* that employ extended wrist postures during above-branch quadrupedality. A number of features shared by *Myrmecophaga* and *Pan* and *Gorilla* facilitate load transmission or limit extension, thereby stabilizing the wrist and hand during knuckle-walking, and distinguish these taxa from their respective outgroups. These traits are a distally extended dorsal ridge of the distal radius, proximal expansion of the nonarticular surface of the dorsal capitate, a pronounced articular ridge on the dorsal aspects of the load-bearing metacarpal heads, and metacarpal heads that are wider dorsally than volarly. Only the proximal expansion of the nonarticular area of the dorsal capitate distinguishes knuckle-walkers from digitigrade cercopithecids, but features shared with digitigrade primates might be adaptive to the use of a vertical manus of some sort in the stance phase of terrestrial locomotion. The appearance of capitate nonarticular expansion and the dorsal ridge of the distal radius in the hominin lineage might be indicative of a knuckle-walking ancestry for bipedal hominins if interpreted within the biomechanical and phylogenetic context of hominid locomotor evolution. Am J Phys Anthropol 128:639–658, 2005. © 2005 Wiley-Liss, Inc.

Knuckle-walking is a form of locomotion utilized by chimpanzees and gorillas in which weight is borne on flexed middle phalanges, with hyperextension occurring at the metacarpophalangeal joint. Recently, there has been renewed interest in the hypothesis that bipedal hominins evolved from a knuckle-walking ancestor (reviewed in Richmond et al., 2001). The study presented here tests hypotheses of adaptation for features thought to be associated with knuckle-walking in the African apes (*Pan* and *Gorilla*) by examining the evolution of a similar locomotor regime in New World anteaters.

Given the strength of molecular data suggesting that *Homo* and *Pan* share a more recent common ancestor than either does with *Gorilla* (Ruvolo, 1994, 1995, 1997; Satta et al., 2000), one of the most parsimonious scenarios involves a knuckle-walking last common ancestor of the clade [*Gorilla*, (*Homo*, *Pan*)] (Fig. 1, node A). Other alternatives involve the parallel evolution of knuckle-walking: once in the *Gorilla* clade, and a second time either in the last common ancestor of *Pan* and *Homo* (Fig. 1, node B) or in the chimpanzee lineage following its split from the lineage leading to hominins (Fig. 1, point C). The first two scenarios imply that bipedal hominins evolved from a knuckle-walking ancestor. A number of researchers pointed to possible retained knuckle-walking features in modern humans (Marzke, 1971; Corrucini, 1978; Sarmiento, 1988; Begun, 1994; Gebo, 1996), and recent morphometric analyses of fossil hominin distal radii suggest the possibility of vestigial features related to knuckle-walking in the wrists of *Australopithecus anamensis* and *Australopithecus afarensis* (Richmond and Strait, 2000; Corruccinni and McHenry, 2001; Richmond et al., 2001). These studies provide morphological evidence of adaptation to knuckle-walking at node A (Fig. 1).

It is usually presumed that forelimb characters shared by gorillas and chimpanzees, to the exclusion of the more arboreal and suspensory orangutans and hylobatids, reflect adaptations for knuckle-walking. Such characters are argued to constitute a complex by which loads are distributed more effectively, extension is limited, and shearing stresses are minimized at the antebrachiocarpal (proximal carpal), midcarpal, carpometacarpal, and meta-

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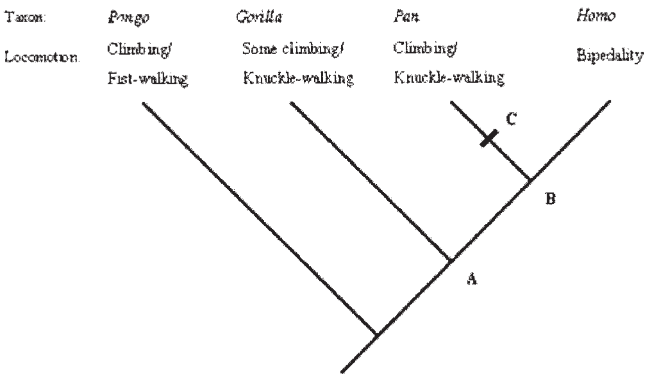

Fig. 1. Phylogeny of knuckle-walking in Hominidae. See text for discussion.

carpophalangeal joints. The current functional significance of some of the characters assessed in these studies (discussed in detail below) is supported by comparative and experimental data. Tuttle (1967) emphasized that the osteological morphology of *Pan* and *Gorilla* significantly limited extension at the wrist relative to the morphology seen in *Pongo* and *Hylobates*. Subsequently, Jenkins and Fleagle (1975) confirmed joint kinematic mechanisms contributing to limited motion by examining radiographs and cineradiographic films of chimpanzee knuckle-walking. These detailed studies of hand and wrist kinematics and morphology of the knuckle-walking African apes provide an incipient understanding of the form and function of the morphology associated with knuckle-walking. However, the interpretation of anatomical features of the African apes as *adaptations* for knuckle-walking (such that they evolved *specifically* for the behavior of knuckle-walking) is confounded to a degree by phylogeny.

It is presumed that the primitive habitus for all extant hominoids is a mostly arboreal and suspensory lifestyle, but this is not secure, and as such the polarities for supposed knuckle-walking features are not known with certainty. Given fossil evidence that *Sivapithecus*, probably sister taxon to *Pongo*, may have been a generalized, large-bodied quadruped (Pilbeam et al., 1990), there remains the possibility of a high degree of parallel evolution in the relatively closely related members of the hominoid clade (Larson, 1998). If such parallelism can occur, it is possible that given similarly structured wrists and hands due to close ancestry, chimpanzees and gorillas could have evolved knuckle-walking independently (Dainton and Macho, 1999). In such a scenario, primitive wrist and hand structures could have been *exapted* (or "preadapted," i.e., used by the organism for a function other than its original purpose; see Gould and Vrba, 1982) for function in knuckle-walking, or at least these structures do not act as impediments to knuckle-walking, i.e., so-called *nonaptations* (Gould and Vrba, 1982). If true, evidence from so-called vestigial features in the wrists and hands of early hominins and modern humans would be equivocal with regard to the evolution of knuckle-walking and its status as the locomotor pattern that preceded bipedality. Furthermore, the appearances of features that seem to stabilize the wrist provide evidence of knuckle-walking ancestry insofar as those features are clearly distinct from features associated with other locomotor styles (such as generalized, cercopithecid-like terrestrial digitigrady) with possibly similar requirements of stabilization (Richmond et al., 2001). Establishing a trait-function correlation, in which phylogeny is controlled to distinguish the features that constitute the true knuckle-walking *adaptation*, would strengthen claims that supposed vestigial features in early hominin and modern human wrists are remnants of a knuckle-walking ancestry.

One method of examining the adaptive correlation of morphology with a particular behavior is by studying the convergent evolution of that behavior in taxa that do not share a close common ancestor. This "convergence approach" (Coddington, 1994) holds that if a morphological character is associated with the behavior in each of the compared taxa, then the argument that the character evolved specifically for the behavior is strengthened in a statistical sense by controlling for phylogeny. Convergence study has been used frequently in the study of primate evolution. For example, it is central to the visual predation hypothesis for primate origins (Cartmill, 1974), the study of hominoid wrist adaptation by analogy to the lorises (Cartmill and Milton, 1977), and understanding the adaptive significance of primate gait patterns by analogy to the woolly possum (Schmitt and Lemelin, 2002). Cartmill (1990) even suggested studying adaptations to bipedality by a comparative analysis of humans and bipedal flightless birds and dinosaurs. Presumably, such a convergence test was the impetus for Richmond et al. (2001) to compare African apes with the chalicothere, an extinct perissodactyl thought to have loaded its forelimb in a flexed digitigrade ("knuckle-walking") posture. Although the fossil hand of the chalicothere, *Chalicotherium grande*, shows some convergences on the African ape condition (Zapfe, 1979; Richmond et al., 2001), an adaptive trait-function correlation cannot be tested by directly examining the hand postures and joint kinematics of this animal. In addition, there is an insufficient phylogenetic framework within which to examine the evolution of a "knuckle-walking" complex in the chalicothere clade. However, a study of an *extant* species that does not share a close common ancestor with the African apes, but walks in a similar manner, and for which there exist strong morphological and molecular phylogenetic data, might provide insight into the adaptive trait-function relationship between features of the wrist and hand and knuckle-walking locomotion.

The giant anteater (*Myrmecophaga tridactyla*) provides such a convergence model. *Myrmecophaga* is a terrestrial (Montgomery, 1985; Shaw et al., 1985) member of the family Myrmecophagidae (New World anteaters) in the order Xenarthra, which also includes sloths and armadillos (Nowack, 1999). Due to their relatively primitive osteology and locomotor diversity, xenarthrans have been compared to primates by others interested in examining the adaptation and function of the locomotor skeleton (e.g., Jenkins, 1970; Yalden, 1972; White, 1993; Hamrick et al., 2000). The giant anteater's locomotor mode has been described as walking with flexed digits on "the sides and knuckles of the hands" (Nowack, 1999, p. 155). All xenarthrans exhibit large claws, and it is probable that "knuckle-walking" in *Myrmecophaga* evolved out of the need to tuck these claws out of the way during terrestrial quadrupedalism, which is functionally similar to the hypothesized reason for knuckle-walking in the African apes, who retain long digits for climbing and suspension while living a largely terrestrial lifestyle (Tuttle, 1967, 1975; Whitehead, 1993). The use of the forelimbs in locomotion by the giant anteater might be similar enough to knuckle-walking in the African great apes to provide a convergence test of adapta-

TABLE 1. Osteological traits of wrist and hand thought to be associated with terrestriality or knuckle- walking specifically[1]

Primate traits	Description	Presumed functional significance
Wrist		
KW, T?	Distal projection of dorsal radius	Limits extension of proximal carpal joint
T	Coplanar scaphoid-lunate surfaces	Distributes load
KW*	Intermediate to large, dorsally oriented scaphoid notch	Distributes load
T	Elongate, rod-like, and palmarly oriented pisiform	Increases flexor carpi ulnaris moment arm?
KW*	Fused os centrale	Resists transverse shear across wrist?
KW	Enlarged trapezoid	Distributes load
KW	Trapezoid facet of scaphoid oriented normal to second metacarpal long axis	Reduces shearing stress at joint
T	Broad antebrachiocarpal and midcarpal joints	Distributes load
KW	Dorsal ridges on capitate, hamate	Limits extension at midcarpal joint
KW	Waisted capitate neck	Facilitates close-pack with scaphoid, thereby limiting extension at midcarpal joint
KW? T?	Long proximodistal ridge on capitate head separating lunate and scaphoid facets	?
KW	Large hamate spiral facet	Allows conjunct rotation with triquetrum, resulting in close-packing and stabilizing midcarpal joint?
KW	"Keeled" carpometacarpal joints (e.g., with trapezoid)	Stability at CMC joints, limiting transverse shear
Metacarpals and Phalanges		
T	Transverse ridges on dorsal aspects of weight-bearing metacarpal heads	Stabilizes MP joints
T	Dorsal expansion of metacarpal head	Facilitates load bearing
KW? T?	Metacarpal head wider dorsally than palmarly	Tightens collateral ligaments during extension

[1] T, terrestrial trait; KW, knuckle-walking trait; KW, knuckle-walking in context of other features (modified from Richmond et al., 2001).

tion for purported knuckle-walking morphology in the African apes, early hominins, and humans. Evidence for specific adaptation to knuckle-walking would be indicated by the functionally relevant morphology shared by *Myrmecophaga* and the African apes that also distinguished each from their respective outgroups as well as from digitigrade cercopithecids. Features shared by *Myrmecophaga*, *Pan*, and *Gorilla*, along with terrestrially digitigrade primate taxa, might represent adaptations to terrestriality, but considered alone may not be indicative of knuckle-walking.

Yalden (1972) and Taylor (1978) studied the forelimb anatomy of the lesser anteater (*Tamandua tetradactyla* and *T. mexicana*) and its functional relation to arboreality and digging for ants and termites. Taylor (1985) further examined the forelimb of *Myrmecophaga* and the pygmy anteater (*Cyclopes didactylus*). However, detailed studies of the giant anteater's use of the hand and wrist during locomotor behavior and corresponding anatomy are lacking. Thus, the goals of this study were as follows:

1. To determine if the locomotion and hand postures of the giant anteater are appropriately analogous to the knuckle-walking of African apes;
2. To identify features of the *Myrmecophaga* hand and wrist that converge functionally with *Pan* and *Gorilla*, and that distinguish these taxa from their non-knuckle-walking outgroups and terrestrially digitigrade primates; and
3. Through the above analyses, to help determine the traits most likely to be *adaptive* to knuckle-walking, thereby suggesting which features of the early hominin and modern human wrists might be reliably indicative of a knuckle-walking ancestry.

In addition, the use of features shared by *Myrmecophaga*, *Pan*, *Gorilla*, and cercopithecid-like, terrestrially digitigrade primates for reconstructing the locomotor evolution of hominins is discussed in light of the biomechanical and phylogenetic context.

METHODS

Examination of kinematics of hand/wrist use during locomotion in *Myrmecophaga*

A pilot study was conducted to determine whether *Myrmecophaga* could be appropriately labeled a "knuckle-walker" in a manner similar to chimpanzees and gorillas. Video footage of giant anteaters was shot at the Phoenix Zoo, using a Cannon ES-190 8-mm Video Camcorder at 30 frames per second. An adult male, adult female, and infant (~6 months) were observed and filmed, and standard 35-mm photographs were taken. The animals were observed walking on both flattened dirt and grass in the enclosure as well as on concrete, with no apparent differences in locomotion observed between these substrates. Frame-by-frame observations of the video footage were made using the slow-motion function on a VHS videocassette recorder and television. Video footage of chimpanzee knuckle-walking was used for comparison.

Wrist joint kinematics and articulations were examined by manipulating the hands and using standard radiographs of anesthetized giant anteaters taken during veterinary examinations at the Phoenix Zoo, as well as by manipulation of dry skeletal specimens. Three live animals were observed and manipulated: an adult male, adult female, and juvenile female (the same animal filmed, but at ~15 months old), although only the adult male and juvenile female were radiographed. To simulate weight-bearing, the animals' forearms were placed in mock locomotor stance phase, based on the position of the hand as observed from the video footage. In addition, it became clear upon observation of the hands of the animals prior to taking the radiographs that the weight-bearing area of the hand was distinctly marked by callus development and fresh mud from the enclosure. A similar method of passive manipulation and radiography of the wrist was utilized by others interested in carpal joint kinematics (Yalden, 1972; Jenkins and Fleagle, 1975; Richmond et al., 2001). Finally, range-of-motion measurements of the antebrachiocarpal joint (flexion, extension, abduction, and adduction) were taken from all three animals by measuring the angle between the antebrachium and the approximate long axis of the third metacarpal, using a goniometer.

Morphology

The study of morphology in the anteaters involved a descriptive and quantitatitive analysis of stabilizing osteological features of the *Myrmecophaga* wrist and hand that may be convergent with traits distinctive of knuckle-walking African apes. While the shapes of some of the myrmecophagid hand bones differ from those of the apes, both groups share the primitive mammalian state of pentadactyly and eight separate, identifiably homologous carpals (Yalden, 1966, 1972), making comparisons relatively straightforward. The morphometric analysis included features identified during the descriptive data collection that might be analogous to features seen in *Pan* and *Gorilla*. Osteological traits thought to be associated with either general terrestriality or knuckle-walking specifically are listed in Table 1, along with their purported functional significances (from data in primary sources compiled by Richmond et al., 2001). "Knuckle-walking traits" are considered those characters that are distinctive of knuckle-walking African apes (and in some cases shared with early hominins and humans), whereas "terrestrial traits" are also shared by terrestrially digitigrade monkeys. Features analogous to the African apes that appear in *Myrmecophaga* were then compared to *Myrmecophaga*'s arboreal outgroup taxa *Tamandua* and *Cyclopes*, to determine if such features are derived traits correlated with the adoption of knuckle-walking in a terrestrial habitus within the Myrmecophagidae.

Tamandua is the closest living relative of the giant anteater (Engelmann, 1985; Sarich, 1985; Gaudin and Branham, 1998; Reiss, 2001; Barros et al., 2003). The tamandua has been described as scansorial, spending time in the trees and on the ground (Montgomery, 1985), although "[its] movements on the ground appear rather clumsy, and unlike *Myrmecophaga*, they do not seem able to gallop" (Nowack, 1999, p. 156). In addition, the tamandua walks on the side of its hands rather than its knuckles, exhibits more extended hand postures (Fig. 2a), and is capable of more extension at the wrist than is *Myrmecophaga* (Yalden, 1966). These descriptions of forelimb use in locomotion were confirmed by observing video footage of a tamandua on the ground and in an arboreal setting at the Woodland Park Zoo (Seattle, WA).

Arboreality is reconstructed as the primitive habitus for the myrmecophagids (Gaudin and Branham, 1998; Taylor, 1985), as shown in Figure 2b. The pygmy anteater (*Cyclopes didactylus*) is exclusively arboreal (Montgomery, 1985), and is the outgroup to the clade that includes *Tamandua* and *Myrmecophaga*. *Cyclopes* shares with *Tamandua*, and the fossil taxon *Protamandua*, features related to arboreality such as a prehensile tail and laterally displaced deltoid tubercles of the humerus (Gaudin and Branham, 1998). In this study, it was predicted that these arboreal anteaters would show wrist/hand morphologies emphasizing mobility in extension (the presumed primitive state related to pronograde hand positions in above-branch quadrupedality), while the giant anteater wrist would show derived features promoting stability, limiting extension, and facilitating load-bearing at the antebrachiocarpal, midcarpal, carpometacarpal, and metacarpophalanageal joints.

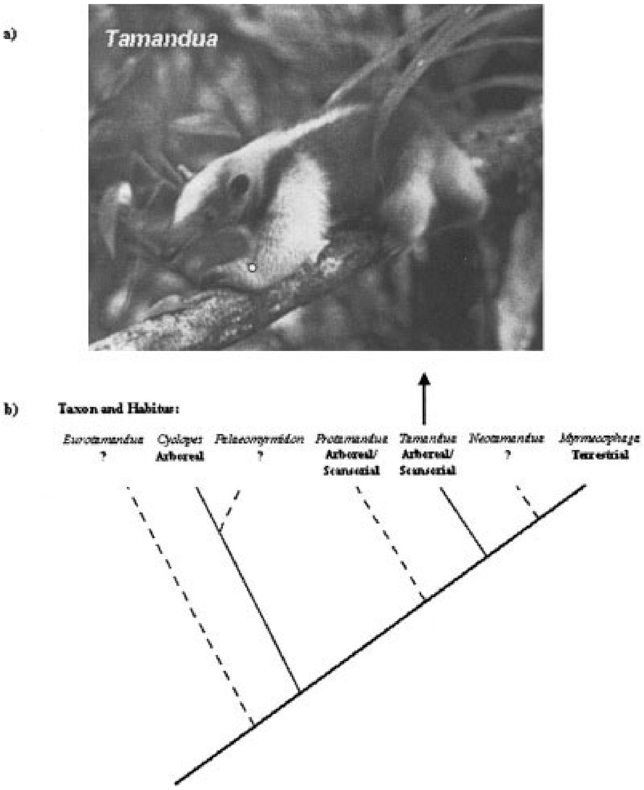

Fig. 2. **a:** *Tamandua* on arboreal support. Note extended wrist posture. Captive specimens filmed at Woodland Park Zoo (Seattle, WA) also used this hand posture when terrestrial. White dot marks approximate location of antebrachiocarpal joint. Photo used with permission of Phil Myers (animaldiversity.ummz.umich.edu). **b:** Phylogeny of Myrmecophagidae. Dashed lines indicate fossil taxa. This morphology-based cladogram (Gaudin and Branham, 1998) is consistent with molecular data of extant taxa (Engelmann, 1985; Sarich, 1985; Barros et al., 2003). Arboreality is reconstructed as primitive habitus.

Specimens from the American Museum of Natural History, the Smithsonian National Museum of Natural History, and the Denver Museum of Nature and Science were utilized and are listed along with sample sizes in Table 2. In addition, primate material housed in the above institutions was used for comparative purposes, along with descriptions of primate morphology from the literature.

Morphometrics

The following measurements were taken to the nearest 0.1 mm, using Mitutoyo digital calipers. A diagram of measurements taken is shown in Figure 3. Effective radius

TABLE 2. Myrmecophagid sample used in this study

Taxon	Mass[1]	No. of #radii	No. of capitates	No. of pisiforms[2]	No. of #MC4[2]
C. didactylus	0.35	13	10	5	0
M. tridactyla	22.0	21	10	14	8
T. mexicana	4.2	20	10	11	7
T. tetradactyla	4.7	18	9	9	9

[1] Species mean body weight data (kg) from Silva and Downing (1995).
[2] Total number of pisiforms and fourth metacarpals (MC4) associated with radii (for size correction).

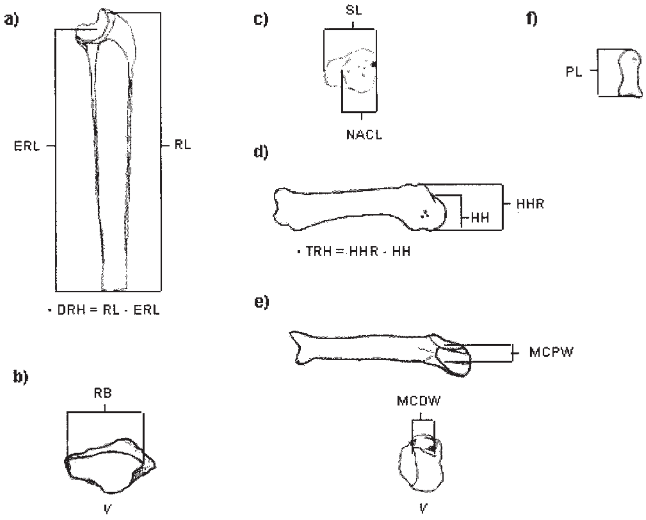

Fig. 3. Schematics of measurements taken. Metrics derived from primary measurements (DRH and TRH) are shown below relevant diagram. See text for explanation of indices calculated from these metrics. **a:** Ulnar view of radius. ERL, effective radius length (distance between proximal and distal articular surfaces); RL, radius length with dorsal ridge; DRH, dorsal ridge height. **b:** Distal view of radius articular surface. RB, radio-ulnar breadth of articular surface of distal radius. **c:** Dorsal view of capitate. SL, capitate length in dorsal view; NACL, length of nonarticular surface. **d:** Ulnar view of fourth metacarpal. HH, height of MC4 head; HHR, MC4 head height with transverse ridge; TRH, height of transverse ridge. **e:** Volar view of MC4. MCPW, palmar width of head; MCDW, dorsal width of head. **f:** Pisiform. PL, pisiform length; V, volar.

length (ERL), radio-ulnar breadth of the distal radius articular surface (RB), and the geometric mean of ERL and RB were used as size proxies, and the results using each were compared. Further discussion of statistical treatment and size correction follows the list of indices.

Size-standardized indices. From the metrics demonstrated in Figure 3, the following indices were calculated to standardize the variables by size.

1. Dorsal-ridge index (DRI): DRI = (DRH/size proxy) × 100; quantifies the distal projection of the dorsal ridge.
2. Dorsal-capitate index (DCI): DCI = (NACL/CL) × 100; quantifies the length of the nonarticular surface of the dorsal capitate as a percentage of overall capitate length (with the remainder being the percentage of *articular* length).
3. Fourth-metacarpal-transverse-ridge index (TRI): TRI = (TRH/ERL) × 100; quantifies height of dorsal transverse ridge of metacarpal 4 (MC4).
4. Fourth-metacarpal-head-width index (MCW): MCW = (MCDW/MCPW) × 100; quantifies the relative width of the dorsal vs. volar aspects of MC4.
5. Pisiform-size index (PI): PI = (MPL/ERL) × 100; quantifies the length of the pisiform.

Size correction and statistical analysis. Size adjustment in morphometrics is a persistent and difficult problem (reviewed in Jungers et al., 1995). Size is an important issue in this study because large body size in *Myrmecophaga* was probably selected for as predator defense in a terrestrial habitus (Taylor, 1985). Thus, given the likely selective primacy of overall body size, if features covary with body size across taxa, then the interpretation of those features as adaptations to locomotion is complicated by the possibility that interspecific differences are artifacts of scaling. On the other hand, those features that differentiate *Myrmecophaga* from *Tamandua* and *Cyclopes* that cannot be explained primarily as effects of scaling, and have functional consequences, may be supported as adaptations to the giant anteater's form of knuckle-walking.

The analysis follows Jungers et al. (1995), who urged the use of ratios for size standardization over empirically determined regression equations used as lines of subtraction. Effective radius length (ERL; radius length minus dorsal ridge height) was used to standardize the measurements of the height of the dorsal ridge of the distal radius, the height of the transverse dorsal ridge of metacarpal 4, and maximum pisiform length. An allometric relationship between the size proxy and a measure of overall body size (e.g., mass) can bias the results. Negative allometry of the proxy (in the index denominator) with overall body size will tend to bias the magnitude of the index toward larger subjects, while positive allometry will bias the magnitude of the index toward smaller subjects. Allometry will only be a major problem for this study if the size proxy is negatively allometric with overall body size, because all indices are predicted to be higher in the largest taxon (*Myrmecophaga*). Positive allometry of the size proxy would result in lower index values for *Myrmecophaga* and would thus be conservative. Because the scaling relationships of the linear dimensions of the limbs with body mass are unknown in myrmecophagids, the analysis was also conducted using the radial-ulnar breadth of the articular surface of the distal radius (RB) and the geometric mean of ERL and RB (as a measure of overall radius size), and the results were compared. Although the possibility that arboreal anteaters might have relatively longer forelimbs than *Myrmecophaga* to facilitate bridging activities cannot be discounted, there is no a priori functional reason to suspect them to have relatively broader articular surfaces of the distal radii (ranges of motion in radial and ulnar deviation at the antebrachiocarpal joint are equivalent in the large and small taxa; see Yalden, 1966). As discussed in Results and Discussion, equivalent results between the

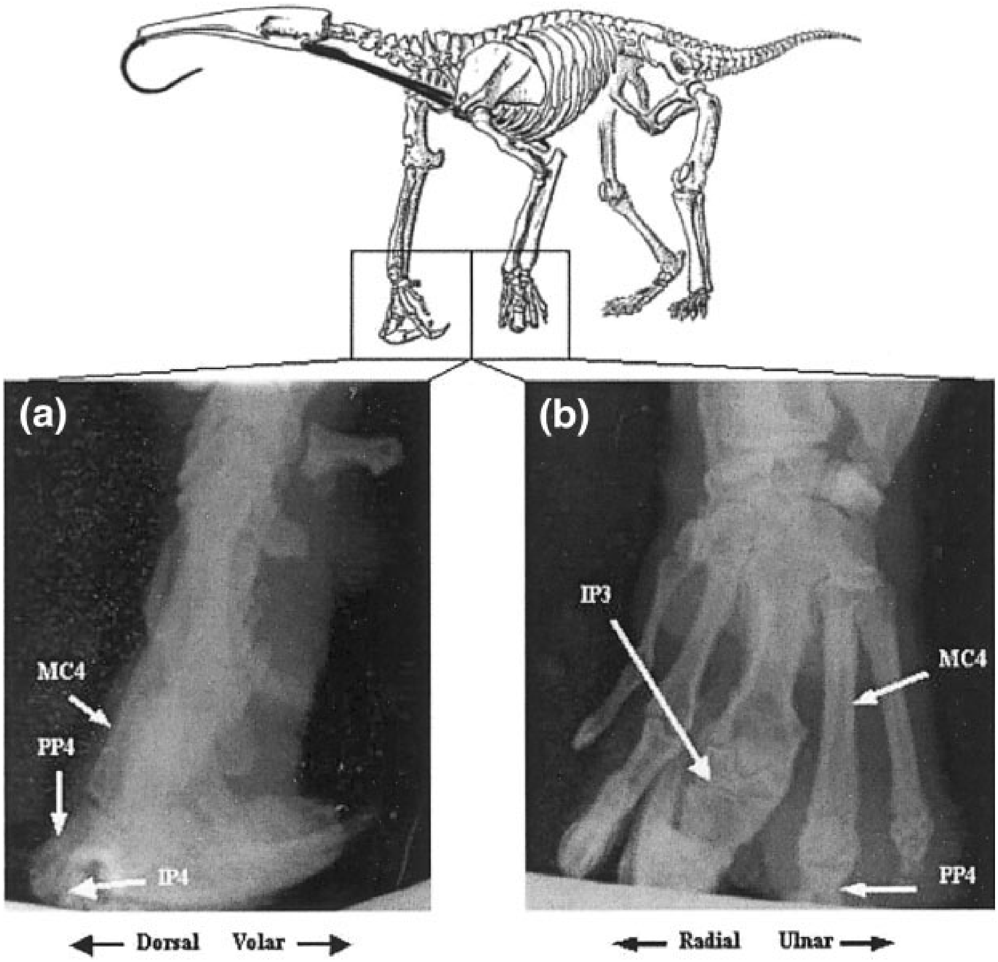

Fig. 4. Radiographs in (**a**) dorsovolar plane and (**b**) radio-ulnar plane. MC4, fourth metacarpal; IP4, proximal interphalangeal joint of fourth ray; PP4, fourth proximal phalanx. In a, note hyperextension at fourth metacarpophalangeal joint. In b, note slight angle between phalanges and long axis of metacarpals. Drawing of *Myrmecophaga* skeleton modified from Vaughan et al. (2000).

three size proxies, as well as the clear functional consequences of the morphological differences in question, support the validity of ERL as a size proxy.

The dorsal capitate index and fourth metacarpal head width index differ from the other indices because they are not corrected for size by ERL. A simple index between the length of the nonarticular surface of the dorsal capitate (NACL) and overall capitate length (CL) captures the proportion of dorsal surface covered by rough, nonarticular surface more intuitively than does the index NACL/ERL, because the feature of interest is how this proximal expansion of the nonarticular surface shortens the articular path of the scaphoid on the capitate in midcarpal extension. The remainder of CL − NACL is effectively the length of the *articular* surface of the dorsal capitate. Even if CL itself does not scale with isometry in myrmecophagids, interest in this feature is not related to scaling vs. body size, but with defining the length of the articular path in a localized anatomical region. It does not matter whether overall scaphoid length has increased or if the nonarticular surface has expanded, because the same functional relationship results. If there is no difference between the two smaller taxa (who are themselves of different body sizes) for this index, then there is no reason to suspect that differences between arboreal anteaters and *Myrmecophaga* are simply scaling artifacts. Similarly, with the width of the metacarpal head articular surfaces, the interest lies in whether or not the dorsal aspect is wider than the volar aspect.

Univariate statistical techniques were used to analyze the morphometric data, because the focus was on differences in specific features. Nonparametric Mann-Whitney U-tests and Kruskal-Wallace ANOVA with post hoc nonparametric “Tukey-type” multiple comparisons (Zar, 1996) were used to test for statistically significant differences in more than one pairwise comparison. These nonparametric techniques were used to control for deviations from normality and low sample sizes, and the multiple-comparison tests were used to control for the accumulation of type I errors. In all cases, it was predicted that if the quantified trait is related to knuckle-walking locomotion in *Myrmecophaga*, the index would be higher in *Myrmecophaga* than in either of the two smaller, arboreal anteaters. Measurements for the two species of tamandua listed in Table 2 (*T. mexicana* and *T. tetradactyla*) do not differ significantly between taxa (Mann-Whitney U, *p*-values between 0.2–0.9 for all cases); thus, they are pooled as a single taxonomic unit. Unfortunately, an adequate sample of *Cyclopes* metacarpals was not available to compare the TRI and MCW of this taxon to the other two.

RESULTS AND DISCUSSION

Kinematics of hand use during locomotion in *Myrmecophaga*

Figure 4 shows the hand position of *Myrmecophaga* during locomotion. The drawing included in Figure 4 from

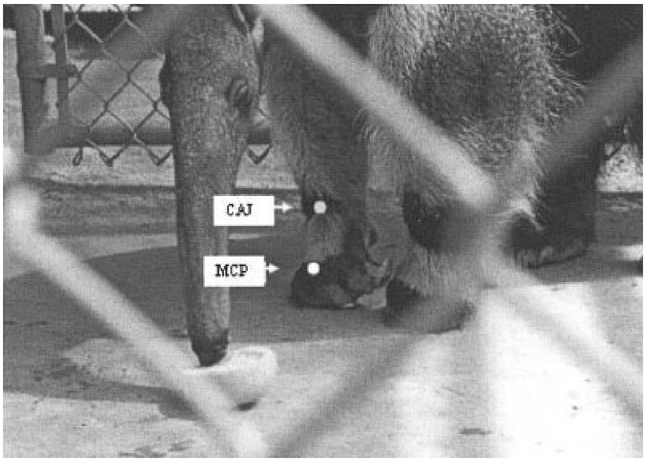

Fig. 5. *Myrmecophaga* male standing. Position of forelimb approximates stance phase of locomotion, although during higher walking speeds, third digit appears to roll onto substrate. CAJ, antebrachiocarpal joint, MCP, metacarpophalangeal joint. Note hyperextension at MCP.

Vaughan et al. (2000) is corroborated by the video footage collected for this study (Fig. 5). Contra the assertion of Yalden (1966) that the giant anteater walks by rolling its hands onto the metacarpal heads, the video shows that *Myrmecophaga* bears weight primarily through the flexed fourth digit. Upon initial observation, it appears that *Myrmecophaga* bears weight on its metacarpal heads, but this is misleading because of the morphology of the manual rays. Most significant are the shortened and specialized proximal and middle phalanges of the anteater, which may give the appearance of a "fist-walking" locomotion similar to orangutans. Also, as shown by manipulation of skeletal material and the radiographic data, the orientation of the metacarpal articular facet on the proximal phalanx, and the topography of the metacarpal head, are such that a slight angle is formed between the phalanges and the long axis of the metacarpal (i.e., radial deviation of the phalanges), rather than the phalanges being directly in line with the metacarpal. This results in the dorsolateral aspect of the phalanx as a weight-bearing surface as much as the dorsum for some rays (see below). In addition, MC4 is significantly longer than MC3, making it impossible for weight to be borne directly on the distal ends of the metacarpal heads and proximal phalanges. Consequently, as shown by the radiographs, weight must be borne on the more distal phalanges during stance phase (Fig. 4b). In the African great apes, weight is borne entirely by middle phalanges 2–5, with the proximal phalanges hyperextended on the metacarpal heads (Tuttle, 1967).

The video shows that forelimb stance phase is initiated by the contact of a fatty pad uniting digits 4 and 5 onto the substrate, with the radio-ulnar axis of the hand held perpendicular to the line of motion. Like those of the African apes (Wunderlich and Jungers, 1998), the ulnar-side digits initiate contact with the substrate. The fourth and fifth metacarpals are approximately the same length, but the fifth digit is substantially reduced, has lost the distal phalanx, and is fully subsumed within the pad. The metacarpal heads are slightly radially torqued, and the orientations of the articular facets are such that the phalanges are oriented in a slight radial direction relative to the long axis of the metacarpals (Fig. 4b). This configuration results in weight being borne on the dorsum and ulnar side of the middle phalanx of the fourth digit and the second phalanx (or "middle" phalanx, although the true distal phalanx has been lost) of the fifth digit, which is fully embedded in the pad. The video footage shows that the fourth and possibly fifth metacarpophalangeal joints are hyperextended (Fig. 5). This is confirmed by the radiograph (Fig. 4a) of mock stance phase, again showing that weight is passed directly through flexed phalanges hyperextended at the metacarpophalangeal joint. When the pad and dorsal aspect of the fourth middle phalanx (both marked by calluses and mud) are manipulated and compressed, the fourth and fifth proximal phalanges are hyperextended at the metacarpophalangeal joint. In fact, for compression to occur on the callused portion of the hand, it is impossible for flexion at that joint to occur, which further rules out the use of true fist-walking postures in which weight is borne on the dorsum of the proximal phalanx.

Wunderlich and Jungers (1998) reported that chimpanzees initiate stance phase by striking the substrate with the middle phalanges of the fourth and fifth digits, but typically walk with the palm facing medially. Thus, contra the orientation in *Myrmecophaga*, in *Pan* the radio-ulnar axis tends to be in line with the direction of motion. However, Inouye (1994a,b) found that gorillas more frequently emphasize the ulnar aspect of the hand, utilizing all four digits (2–5), with the palm facing posteriorly. These authors also found that chimpanzees and bonobos more frequently exclude the fifth digit from weight-bearing.

In midstance phase, as the fatty pad compresses, the distal phalanx of the third digit appears to contact the substrate, although it might not bear much weight at this point. As the body is brought forward, slight extension occurs at the antebrachiocarpal joint. Prior to midstance, the long axis of the metacarpus is held at a fairly constant angle to the substrate (approximately 70°). This angle does not change appreciably until the forearm approaches 90° to the substrate. Presumably at this point, the extension-limiting mechanisms of the wrist (discussed below) come into effect. From the video, the forearm appears to act as a rigid lever throughout the propulsive phase, with motion occurring primarily at the glenohumeral joint as in *Pan* and *Gorilla* (Tuttle, 1967; Jenkins and Fleagle, 1975), a situation probably resulting from the hand and wrist being locked in limited extension. Concomitant with this motion of the metacarpus, the hand necessarily rolls such that more weight is borne onto the distal phalanx of the third digit, which appears to play a more prominent role in late stance phase and push-off at moderate to higher walking speeds. Weight is borne on the middle phalanges in *Pan* and *Gorilla*, and this is the case for the fourth (and maybe fifth) ray of *Myrmecophaga*. However, as discussed below, when weight is transferred to the third ray in the giant anteater, the load must be borne on the distal phalanx, because the middle phalanx is locked in extension with the proximal phalanx.

In mid- to late stance phase, the video sequence shows that the metacarpus is in line with the forearm as the manus is held approximately vertical to the substrate, and the third digit is rolled onto the ground and appears to bear weight momentarily (Fig. 5). The skin over the dorsum of the third distal phalanx was callused and marked by mud in the specimens examined, which further suggests that the third digit plays some role in weight-bearing (although it is possible that digging activities contribute to the formation of the callus as well). During this time, the fourth metacarpophalangeal joint reaches its highest degree of hyperextension, and the dorsal transverse ridges on the metacarpal heads (discussed below) are presumably called into effect for stabilization and to limit further motion at this joint. Push-off begins shortly after the forearm passes 90° to the substrate. The wrist comes into flexion, followed shortly after by the lifting of the phalanges from the ground.

Finally, another forearm component to the gait cycle is initiated by the swing phase. The hand is brought further into flexion ($\sim 90^\circ$ to the forearm), allowing it to clear the ground. After the forelimb has swung far enough anteriorly to allow clearance, the wrist is extended and the hand is prepared for contact. Just prior to contact, the phalanges are extended at the metacarpophalangeal joints, so that the middle phalanges of digits 4 and probably 5 meet the ground. A similar extension at the metacarpophalangeal joints prior to substrate contact occurs in the chimpanzee forelimb swing phase (Tuttle, 1967; personal observation of chimpanzee video footage). If *Myrmecophaga* was a fist-walker similar to the orangutan, then there would be no need to extend the digits prior to touching down the hand.

The kinematics of knuckle-walking in the giant anteater are distinctive from the apes in a few ways, thus limiting to some degree the inferences that can be drawn between groups. Some differences such as gait sequence are obvious, with anteaters utilizing a lateral sequence gait, while African apes use a diagonal sequence. However, gait differences are unlikely to influence differences in stabilizing mechanisms of the wrist. Other distinctions, such as the greater emphasis on the ulnar aspect of the hand in anteaters vs. the employment of all digits 2–5 at various times in apes, might have a greater effect in shaping morphology. This is underscored by the primitive retention of contact between the (relatively large) ulnar styloid with the proximal carpal row in giant anteaters, in contrast with the intervention of a meniscus between the styloid and carpals in the great apes (Lewis, 1969). That extensive contact occurs between the ulnar styloid and the triquetrum in *Myrmecophaga* suggests that the giant anteater is more capable of passing weight through the ulnar aspect of the hand than are the African apes. This may have resulted in different adaptations to weight-bearing and stabilization, since the load is primarily passed through the central part of the hand in the apes.

Another possibly important difference from the apes is that the proximal and middle phalanges are shortened in all anteaters (Taylor, 1978, 1985; personal observation), and appear to be oriented slightly obliquely to the long axis of the metacarpals (Fig. 4b). The oblique orientation is due to a slight radial deviation to the metacarpal heads. Thus, it is likely that weight is borne on the radial aspect of the phalanges of the fourth and maybe the third and fifth digits as much as on the dorsal aspects. This might produce a force vector (from the ground reaction force) in the ulnar direction that tends to collapse the wrist into abduction (radial deviation). It is possible that, because the ground reaction force is shared by both radial (collapsing the hand into abduction) and palmar (collapsing hand into extension) vector components, the tendency for the wrist to collapse into extension might be somewhat less than in African apes.

Despite the noted differences, the locomotion of *Myrmecophaga* is crucially similar to African apes, in that weight is borne through a vertical manus with flexed digits hyperextended at the metacarpophalangeal joints. Thus, the overall pattern of load-bearing in the hand and wrist is quite similar, and wrist and hand function during locomotion may be considered appropriately analogous between the two groups. Indeed, simply given that the manus is held approximately vertical to the substrate (vs. the primitive extended wrist postures of *Tamandua* and *Cyclopes*, in which the manus is held approximately horizontal to the substrate), it is reasonable to suspect that natural selection may have acted on the *Myrmecophaga* wrist and hand to produce extension-limiting and stabilization mechanisms of the wrist, similar to those seen in African apes (and possibly the terrestrially digitigrade cercopithecids). The implications of the vertical manus posture during the stance phase of locomotion are discussed further (below) in assessing knuckle-walking adaptations in the Hominidae. In addition, the kinematics of particular joints of the carpus will be discussed, with the description of morphological features.

Morphology

Myrmecophaga shows a number of features of the hand and wrist that are derived relative to arboreal anteaters, and are functionally similar to those seen in African apes (and in some cases, digitigrade cercopithecids) that act to stabilize the wrist in knuckle-walking terrestrial locomotion. These features are summarized in Table 3, and are discussed below. The giant anteater is distinctive metrically from *Tamandua* and *Cyclopes* in all features quantified (Fig 6), and these are statistically significant (Table 4), although Cyclopes has a relatively longer pisiform than *Myrmecophaga* (the opposite of what was predicted).

Size effects. The results of Kruskal-Wallace and multiple-comparison tests are 100% equivalent for each of the three size-proxies used. Also, in the case of DRI and DCI, there is no statistically significant difference between *Tamandua* and *Cyclopes* (Table 4), but there are pairwise differences between each of these taxa and *Myrmecophaga*. This suggests that there is no simple scaling relationship in these indices, such that the indices get larger with increasing body size (because *Tamandua* is intermediate in size between *Cyclopes* and *Myrmecophaga*). Furthermore, as discussed in detail below, each of the differences in measured morphology between *Myrmecophaga* and the arboreal taxa has significant functional consequences with regard to joint ranges of motion, as evidenced by radiography and the manipulation of dry bones. For example, in *Myrmecophaga*, the dorsal ridge of the distal radius clearly inhibits the animal from extending its wrist beyond a certain degree, whereas this is not the case in smaller anteaters. Thus, differences in index values between taxa are unlikely to be purely artifacts of allometric scaling. In the interest of conserving space, only the results using ERL are reported in Table 4 and Figure 6. What follows is a descriptive analysis of myrmecophagid hand and wrist morphology.

Claws and soft tissues. The overall appearance of the myrmecophagid hand is quite different from the primate hand, although the underlying skeleton has impor-

TABLE 3. Features of myrmecophagid wrist and hand

Anatomical region	*Myrmecophaga*	*Tamandua*	*Cyclopes*
Antebrachiocarpal joint	Broad[1]	As in *Myrmecophaga*	As in *Myrmecophaga*
	Volar tilt of distal radius resulting in distally projecting dorsal ridge that articulates with ridge on dorsal scaphoid[1–3]	Articular surface of distal radius oriented perpendicularly to long axis of shaft with little or no dorsal ridge	As in *Tamandua*
	Scaphoid and lunate articular facets on distal radius are coplanar[1]	As in *Myrmecophaga*	As in *Myrmecophaga*
	Dorsal ridge is continuous, with no deep scaphoid notch, unlike *Pan* and *Gorilla*, although there is distinct extension of articular facet for scaphoid onto ridge[2]	NA	NA
Midcarpal joint	Broad[1,2]	As in *Myrmecophaga*	As in *Myrmecophaga*
	Os centrale fused to scaphoid[1,2]	As in *Myrmecophaga*	As in *Myrmecophaga*
	Trapezoid facet of scaphoid oriented perpendicular to long axis of hand,[1,2] but trapezoid not enlarged[2]	As in *Myrmecophaga*	As in *Myrmecophaga*
	Dorsal ridges on capitate and hamate[1,2]	As in *Myrmecophaga*	As in *Myrmecophaga*
	Capitate is notched, but proximal "head" is not bulbous as in apes, such that there is no prominent "waisted" appearance[2]	As in *Myrmecophaga*	As in *Myrmecophaga*
	Nonarticular surface of dorsal capitate is extended proximally[1,3]	Capitate head has more articular surface exposed dorsally relative to *Myrmecophaga*, allowing for more rotation of scaphoid onto dorsal capitate and thus greater midcarpal extension	Similar to *Tamandua*; even greater articular area is exposed dorsally, and in some specimens extends completely to MCP joint, such that entire dorsal surface is articular
	There is a ridge along capitate head, as in *Pan* and *Gorilla*, although head articulates only with scaphoid	As in *Myrmecophaga*	As in *Myrmecophaga*
	Large hamate spiral facet[1]	As in *Myrmecophaga*	As in *Myrmecophaga*
Carpometacarpal joints	Jagged and keeled joint surfaces (including trapezoid)[1]	As in *Myrmecophaga*	As in *Myrmecophaga*
Metacarpophalangeal joints	Extension of dorsal articular surface into a pronounced dorsal ridge on weight-bearing ray (MC4)[1,3]	Little to no dorsal ridge on any of metacarpals	As in *Tamandua*?
	Dorsal MC articular surface wider than palmar surface[1,3]	Dorsal MC articular surface approximately same width as palmar surface	As in *Tamandua*?
	Short middle phalanges, with third middle phalanx highly reduced and specialized due to large claw	As in *Myrmecophaga*	As in *Myrmecophaga*
Pisiform	Elongate and palmarly oriented[1–3]	As in *Myrmecophaga*	Extremely long

[1–3] Similar to morphology of *Pan* and *Gorilla*.
[2] See Discussion.
[3] See Results for quantitative analysis.

tant similarities. Of primary importance are the large claws, of which the third ray claw is the largest. Although the claws are of fundamental adaptive significance for anteaters, *Myrmecophaga* has not been observed to use its claws as frequently for digging for termites as is seen in *Tamandua* (Montgomery and Lubin, 1977; Montgomery, 1985; Shaw et al., 1985), although they probably play a role in defense (Taylor, 1985). Thus, it is unlikely that any apomorphic features of the hand and wrist of *Myrmecophaga* (vis-à-vis *Tamandua* and *Cyclopes*) would be related to increasing digging efficiency.

As noted in the discussion of kinematics (above), a pad consisting primarily of fat and connective tissue unites digits 4 and 5 in the Myrmecophagidae (Taylor, 1978, 1985), and the first digit is greatly reduced; thus, anteaters appear superficially to have just three manual rays. This pad contacts the ground first and appears to provide a broader base of support for the hand in locomotion. In addition to the osteological features that stabilize the hand, there are almost certainly ligamentous structures that offer support as well. Unfortunately, without a cadaver specimen, such structures could not be assessed in this study. Forelimb musculature might also support the wrist in locomotion, although it is possible that just as in chimpanzees, osteoligamentous structures are sufficient to provide support (Tuttle, 1967; Jenkins and Fleagle, 1975; Richmond and Strait, 2000), such that the wrist and digital flexors remain mostly quiescent or only variably active in forelimb stance phase (Tuttle et al., 1972; Susman and Stern, 1979). Taylor (1978, 1985) described the musculature of the myrmecophagid forelimb and its specializations for powerful flexion of the third digit claw for rending and tearing of

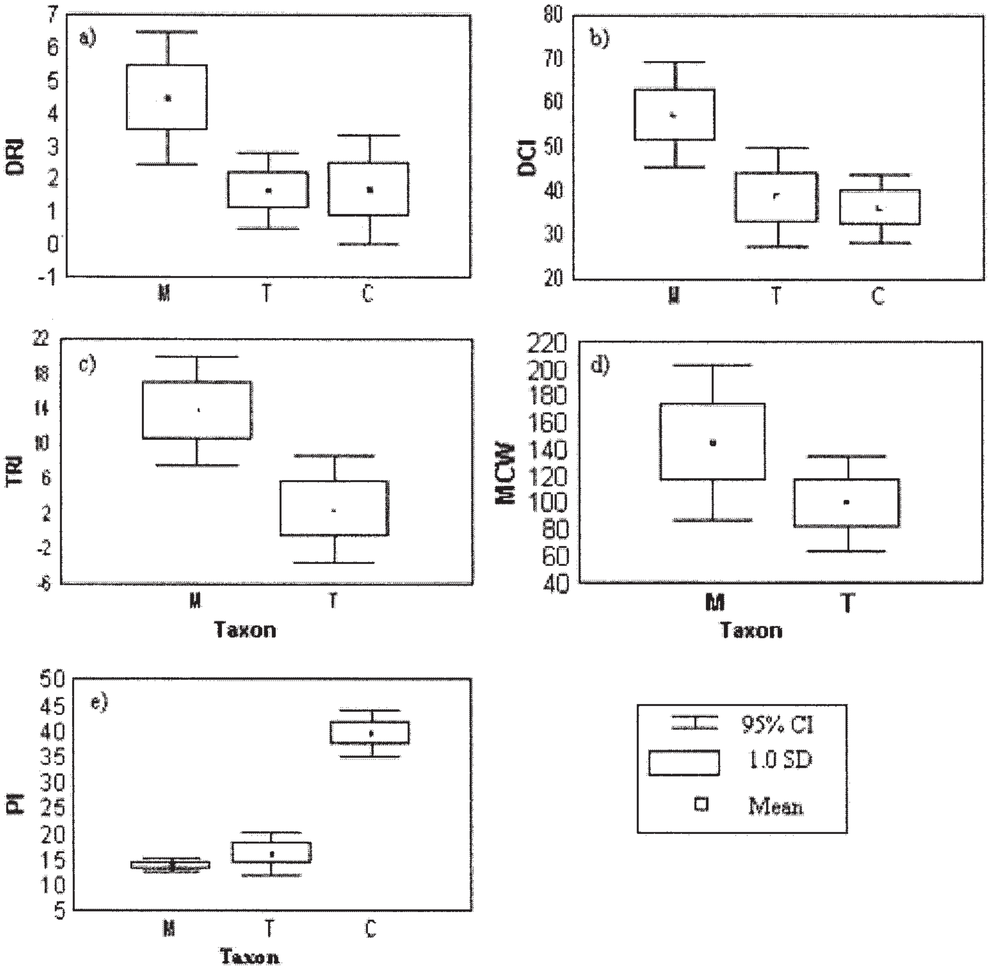

Fig. 6. Metric comparisons between myrmecophagid taxa for calculated indices. a: DRI, dorsal-ridge index; b: DCI, dorsal-capitate index; c: TRI, fourth metacarpal-triceps-ridge index; d: MCW, fourth metacarpal-head-width index; e: PI, pisiform-size index.

ant and termite nests and for defense. It is uncertain how such modifications affect locomotion, but given that the forelimb musculature is virtually identical in all three taxa (Taylor, 1985), it does not appear that myological specializations play a significant role in *Myrmecophaga*'s mode of locomotion.

Antebrachiocarpal joint. The proximal carpal joint of all three myrmecophagid taxa involves the primitive mammalian inclusion of both the radius articulating with the scaphoid laterally and the lunate medially, and articulation of the ulnar styloid with the triquetrum (Fig. 4). This differs from the derived state of extant hominoids, involved with increasing the range of ulnar deviation, in which the ulnar styloid is reduced and excluded from articulation with the proximal carpal row by the intervention of an intra-articular meniscus (Lewis, 1969; Sarmiento, 1988). In *Myrmecophaga*, the articular surfaces of both the scaphoid and lunate exhibit low dorsopalmar and radio-ulnar radii of curvature (although both bones are much more curved in the dorsopalmar direction), and together form a continuous convex arc that articulates with the deep concavity of the distal radius. As in African apes (Jenkins and Fleagle, 1975; Corruccini, 1978), the scaphoid is relatively large compared to the lunate. The articular surface of the distal radius in *Tamandua* and *Cyclopes* is much less concave, and the proximal articular surfaces of the scaphoid

TABLE 4. Results of quantitative comparisons of myrmecophagid morphology

Variable	Pairwise comparison[1]	Test statistic[2]	*P*-value[3]
DRI	*Myrmecophaga* vs. *Tamandua*	Q = 6.18	<0.001
	Myrmecophaga vs. *Cyclopes*	Q = 5.02	<0.001
	Tamandua vs. *Cyclopes*	Q = 0.35	ns
DCI	*Myrmecophaga* vs. *Tamandua*	Q = 4.43	<0.001
	Myrmecophaga vs. *Cyclopes*	Q = 3.06	<0.001
	Tamandua vs. *Cyclopes*	Q = 0.55	ns
TRI	*Myrmecophaga* vs. *Tamandua*	U′ = 128.0	<0.001
MCW	*Myrmecophaga* vs. *Tamandua*	U′ = 12.0	<0.01
PI	*Myrmecophaga* vs. *Tamandua*	Q = 2.83	<0.01
	Myrmecophaga vs. *Cyclopes*	Q = 4.69	<0.01
	Tamandua vs. *Cyclopes*	Q = 2.82	<0.01

[1] See Figure 7a–e for index means and visual comparisons.

[2] Q, "Tukey-type" *post hoc* multiple comparison test following a significant Kruskal-Wallace H-statistic that rejected null hypothesis of equal means for three taxa. U′, one-tailed Mann-Whitney test statistic for a two-taxon pairwise comparison.

[3] ns, nonsignificant ($P > 0.05$).

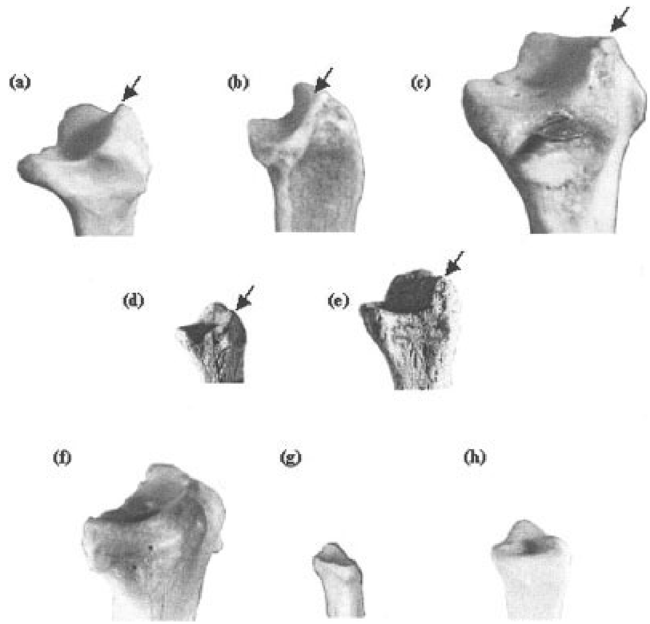

Fig. 7. Distal radii in ulnar view. **a:** *Pan*. **b:** *Myrmecophaga*. **c:** *Gorilla*. **d:** *A. afarensis* (cast). **e:** *A. anamensis* (cast). **f:** *Pongo*. **g:** *Tamandua*. **h:** *Homo*. Note deep concavity of African apes, fossil hominin species, and *Myrmecophaga*, and how dorsal ridge (indicated by arrows) extends distally in these taxa, but also note that unlike African apes, a notch does not interrupt dorsal ridge of *Myrmecophaga*. Morphology of *Cyclopes* (not shown) is similar to *Tamandua*, being relatively flat, with no prominent ridge.

and lunate extend farther onto the dorsal aspects of the bones in arboreal anteaters, an observation that corroborates Yalden (1966). Tuttle (1967) and Sarmiento (1988) found that a deeply concave distal radius distinguishes *Pan* and *Gorilla* from *Pongo* and *Hylobates*. However, this deep concavity is largely the result of the volar tilt of the distal radius and distally extending dorsal ridge (discussed below), and thus does not constitute a character independent of those traits.

Similar to the radius of *Pan* and *Gorilla*, there is an overall volar tilt to the distal radius of *Myrmecophaga*, such that along the ulnar border, at the ulnar notch, the palmar surface makes an angle of approximately 30°, with the long axis defined by the interosseus crest (Fig. 7). The dorsal margin of the distal radius is defined by a sharp ridge that runs obliquely from the ulnar side to the radial side, such that the radial aspect of the ridge that articulates with the scaphoid extends farther distally than the ulnar aspect. As in *Pan* and *Gorilla* (Tuttle, 1967), the distally extended ridge of *Myrmecophaga* seems to be a consequence of the volarly "tilted" distal epiphysis of the radius, which in turn contributes to the deep concavity of the joint in all three of these species.

The distal radii of *Tamandua* (Fig. 7g) and *Cyclopes* are not tilted as in *Myrmecophaga* (Fig. 7b), and do not show the high dorsal ridge (demonstrated metrically in Fig. 6a) or deep concavity, being similar in many respects to the state of an arboreally palmigrade, quadrupedal primate such as *Alouatta* (Richmond et al., 2001; personal observation). This observation is in agreement with Yalden (1966, p. 131), who noted that in *Tamandua*, "The distal surface of the radius is rather flatter in FES [the flexor-extensor section], and lacks the prominent distally projecting extensor lip [seen in *Myrmecophaga*]". Yalden (1972) found that the tamandua wrist can achieve up to 80° of hyperextension, with 60° occurring at the antebrachiocarpal joint, and can employ this greater wrist mobility in arboreal quadrupedality (Fig. 2). Specific values are not available for *Cyclopes*, but given that its wrist morphology is nearly identical to that of *Tamandua*, it presumably has a similarly high range of motion. According to Yalden (1966), the manus of *Myrmecophaga* is capable of only 10–15° of total extension, all occurring at the antebrachiocarpal joint. Range-of-motion measurements of the anesthetized giant anteaters at the Phoenix Zoo (Table 5) corroborate the data of Yalden (1966), although the juvenile female was capable of up to 27° of total extension (still substantially less than the tamandua). Extension is limited to the degree that *Myrmecophaga* would be *incapable* of utilizing the palmigrade hand postures used by the arboreal taxa in above-branch quadrupedality. Osteologically, this limited mobility is primarily effected by the following mechanism.

TABLE 5. Antebrachiocarpal joint ranges of motion in anesthetized Myrmecophaga[1]

Specimen	Extension	Flexion	Adduction	Abduction
Adult male	10°	85°	30°	30°
Adult female	10°	84°	12°	48°
Juvenile female	27°	85°	33°	28°
Mean	16°	85°	25°	35°

[1] Total range of motion (antebrachiocarpal + midcarpal motion).

Along the dorsal ridge of *Myrmecophaga* there is an extension of the distal radial articular surface onto the ridge, taking the form of a flattened facet typically bordered dorsally by bone of ruffled, "remodeled" appearance. A corresponding facet appears on a dorsal beak of the scaphoid/os centrale, and is continuous with the convex articular surface. As evidenced by radiography and manipulation of dry bones, when the carpus is extended, the ridge appears to "roll" onto the beak, such that weight might be transmitted to the scaphoid, and further extension of the wrist would be prohibited (Figs. 8, 9). Comparative and experimental radiographic and cineradiographic data (Tuttle, 1967; Jenkins and Fleagle, 1975) showed a similar close-packing (or "locking") mechanism to be a key limitation of wrist extension during the support phase of chimpanzee knuckle-walking (and presumably for gorillas, given that they have a similar antebrachiocarpal morphology). See Figure 8 for a comparison of this mechanism in *Myrmecophaga* and *Pan* vs. *Tamandua*. Extension at the antebrachiocarpal joint is limited to 8° in *Pan troglodytes* (Jenkins and Fleagle, 1975) and 12° in *Gorilla gorilla* (Sarmiento, 1985, 1988). In contrast, *Pongo pygmaeus* is capable of 33° of extension at this joint (Sarmiento, 1985, 1988). Modern humans also lack a prominent radial dorsal ridge, and are capable of 36° of antebrachiocarpal extension.

Although the radial dorsal ridge in *Myrmecophaga* does drastically limit extension of the antebrachiocarpal joint as in *Pan* and *Gorilla* (Tuttle, 1967), a possibly significant difference from the African ape state is the lack of a large, dorsally placed scaphoid notch that interrupts the ridge. The clear, dorsally oriented articular facet on the radial dorsal ridge in *Myrmecophaga* described above is not as large or as deep as the "scaphoid notch" of the radius of African apes and terrestrially digitigrade cercopithecids, as described by Richmond and Strait (2000).

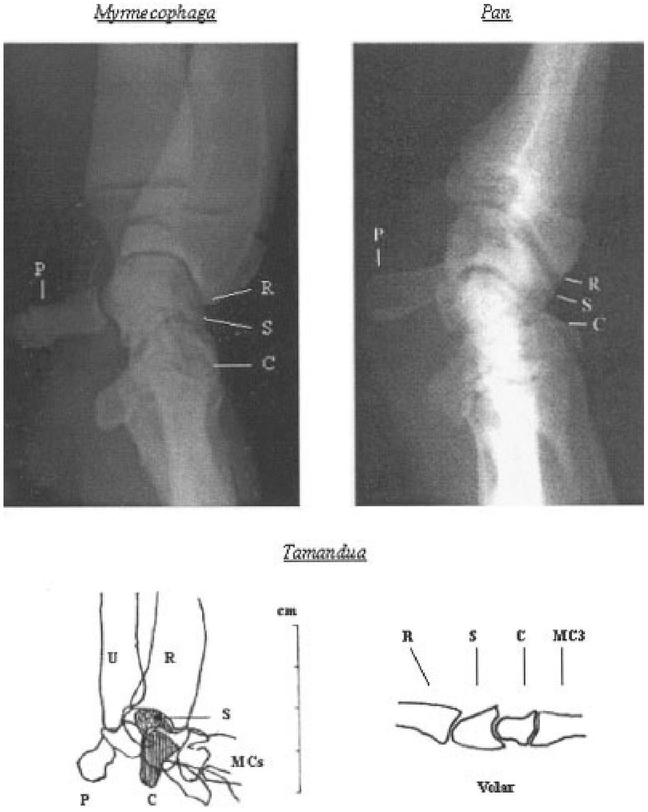

Fig. 8. Comparative kinematics of antebrachiocarpal joint in *Pan*, *Myrmecophaga*, and *Tamandua* (ulnar view and schematic dorsovolar section). Note deep concavity of distal radius in *Pan* and *Myrmecophaga*. Dorsal ridge contacts scaphoid, effectively limiting extension at this joint. Contrast this with substantially flatter distal radius and high range of motion of *Tamandua*. C, capitate; MC, metacarpal; P, pisiform; R, radius; S, scaphoid; U, ulna;. Radiograph of chimpanzee reproduced from Richmond et al. (2001), and tracing of *Tamandua* radiographs modified from Yalden (1972).

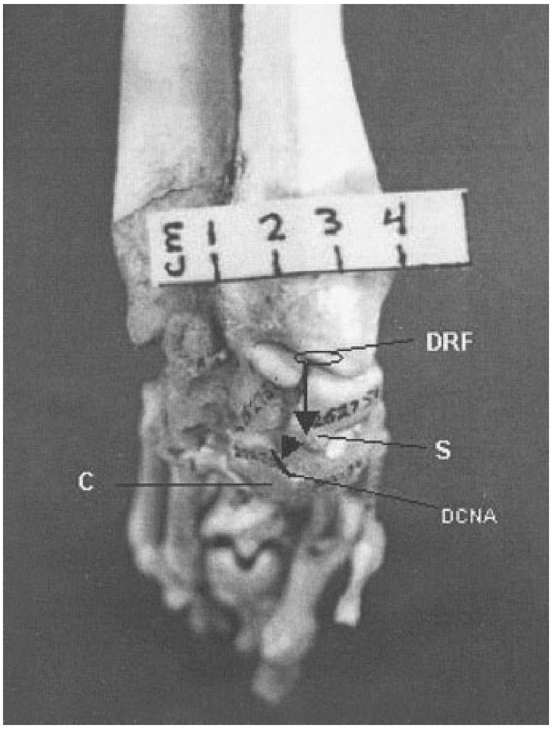

Fig. 9. Kinematics of joint stabilization in *Myrmecophaga*. This photo of ligamentous specimen in dorsal view is shown with wrist in flexion. During wrist extension (indicated by arrows), dorsal ridge facet of distal radius (DRF) contacts dorsal beak of scaphoid (S). Scaphoid in turn slides dorsally onto capitate (C), and is stopped at edge of dorsal capitate nonarticular surface (DCNA). DCNA is expanded proximally in *Myrmecophaga* relative to arboreal anteaters, thereby shortening articular path of scaphoid on capitate, and limiting extension at midcarpal joint.

Thus, these features do not seem to be functionally analogous beyond the fact that in both groups, they mark the bony locale at which the scaphoid articulates with the dorsal edge of the distal radius in extension. Richmond and Strait (2000) found that the ridge and dorsal orientation and relatively larger size of the notch discriminate knuckle-walking apes from other extant hominoids, and presumably lodging of the scaphoid within this notch provides greater stability in extended wrist postures. However, digitigrade monkeys, such as *Papio*, which also walk with the manus held relatively vertical to the substrate, show a similar dorsal extension and a (deeper and broader) notch, although the “ridge” appears more as a knob-like process than an actual ridge in many cases (Richmond and Strait, 2000; personal observation). The radius of curvature of the distal radial articular surface in *Papio* also appears to be higher than in *Myrmecophaga*, *Pan*, or *Gorilla*, with no significant volar tilt to the epiphysis. In digitigrade cercopithecids, Richmond et al. (2001) noted that the scaphoid rotates farther prior to contact between the scaphoid ridge and dorsal ridge of the radius than occurs in African apes. This is in agreement with observations of cercopithecid behavior. For example, patas monkeys (*Erythrocebus patas*) employ more extended hand positions in terrestrial locomotion than do African apes (Richmond, 1998). Likewise, *Papio* employs palmigrade hand positioning (~50° of wrist extension) on arboreal supports (Schmitt, 1994).

The observation and measurement of a dorsal ridge on the distal radii of australopithecines (*A. anamensis* and *A. afarensis*) played a prominent role in the argument by Richmond and Strait (2000) for a knuckle-walking ancestry for hominins. The presence of a ridge as a knuckle-walking adaptation might be strengthened by its prominent development in *Myrmecophaga*, as this feature does indeed distinguish the giant anteater from its arboreal outgroups. Unfortunately, distinguishing knuckle-walking from digitigrady might remain difficult, given that digitigrade monkeys also show some development of a similar radial dorsal ridge. However, such monkeys do not show the volar tilt and deep concavity of the distal radius. Although the functional significance of the volar tilt itself is not immediately apparent, it does not seem to be a matter of body size, for larger baboons overlap in body mass with *Myrmecophaga* (Silva and Downing, 1995; Smith and Jungers, 1997). In any case, the development of a distally projecting dorsal ridge of the distal radial epiphysis could be a hallmark of a locomotor style that involves the manus being held vertical to the substrate (the implications of this morphology for reconstructing the locomotor evolution of the Hominidae are discussed further below).

Midcarpal joints. As in African apes (Richmond et al., 2001), the midcarpal joint is broad, spanning the breadth of the hand in all three myrmecophagid taxa. Given similar morphology in arboreal and terrestrial anteaters, a broad midcarpal joint is not supported as a specific adaptation for stability during the knuckle-walking locomotion of *Myrmecophaga*. Stability at the midcarpal joint might be important in both the terrestrial and arboreal habitus of anteaters; alternatively, a broad midcarpal joint provides increased surface area for bearing large joint reaction forces in powerful flexion of the claw (Taylor, 1978, 1985).

Frequent and developmentally early fusion of the os centrale to the scaphoid, a possible synapomorphy of *Gorilla*, *Pan*, and *Homo*, was discussed by numerous authors (Schultz, 1936; Marzke, 1971; Jenkins and Fleagle, 1975; Lewis, 1974, 1985; Sarmiento, 1988; Begun, 1994; Gebo, 1996; Richmond and Strait, 2000; Richmond et al., 2001). Scaphoid-centrale fusion might stabilize the midcarpal joint when it is loaded in compression, and might be a vestigial knuckle-walking feature in humans. However, the os centrale is similarly fused to the scaphoid in all three myrmecophagid taxa, and Yalden (1972, p. 393) reported that "a separate centrale is unrecorded among the *Edentata* [Xenarthra]". Given that the Xenarthra comprise a mammalian group with a diversity of locomotor modes (from the exclusively suspensory sloths to the terrestrial and fossorial armadillos), scaphoid-centrale fusion in this group cannot be linked specifically to knuckle-walking. Furthermore, as in rare cases when scaphoid-centrale fusion occurs in orangutans (discussion in Richmond et al., 2001), in the xenarthrans, the os centrale forms a dorsal beak off of the scaphoid that contacts the capitate. This is contra the condition in African apes, in which the os centrale portion of the scaphoid is wedged between the capitate and trapezoid, thereby reinforcing the radial aspect of the midcarpal joint. Thus, scaphoid-centrale fusion in *Myrmecophaga* provides no evidence of this feature's role as an adaptation to knuckle-walking. Although it might still constitute a knuckle-walking adaptation in African apes, and a possible exaptation in *Myrmecophaga*, these hypotheses can be neither supported nor rejected. However, even within primates, the functional/adaptive interpretation of scaphoid-centrale fusion is confounded, because extant and fossil indriids of varying locomotor regimes also regularly fuse the os centrale to the scaphoid (Jouffroy, 1975; Schwartz and Yamada, 1998; Hamrick et al., 2000). Furthermore, some authors questioned the hypothesis of homology for scaphoid-centrale fusion between African apes and humans, due to possible differences in how this trait develops during ontogeny between *Pan* and *Gorilla* on the one hand and *Homo* on the other (Schwartz and Yamada, 1998).

The capitate and hamate of the myrmecophagids together constitute a broad convex articular surface that is received by a radio-ulnar trough formed by a deep concavity in the scaphoid and a U-shaped concavity defined by palmar and dorsal horns of the lunate. Extension is limited significantly at this joint by two primary mechanisms. Firstly, the insertion of the os centrale beak of the scaphoid into a concave dimple on the dorsal aspect of the capitate limits rotation of the capitate head in the scaphoid concavity, probably upon loading of the beak by the dorsal ridge of the radius. This forms a linked chain between the dorsal ridge of the radius with the scaphoid beak and finally the beak with the capitate, resulting in a close-packed position with extension being progressively more limited at each articulation (Fig. 9). Secondly, the dorsal horn of the lunate articulates with a triangular notch on the dorsal hamate. The "dimple" in the dorsal capitate and the triangular notch of the dorsal hamate are both bordered distally by a slight ridge. Although these features may correspond functionally to the "dorsal ridge" on the capitate and hamate in the African apes, *Tamandua* and *Cyclopes* also show this ridged morphology.

Pan and *Gorilla* both display a "waisted" capitate neck (Lewis, 1969; Jenkins and Fleagle, 1975), and this feature was observed in early hominin hands by a number of authors (Bush et al., 1982; McHenry, 1983; Ward et al., 1999), but this study provides no evidence either way for its role as an adaptation to knuckle-walking. The neck of the capitate in *Myrmecophaga* is somewhat restricted and notched, although not to the extent seen in African apes, and the head is shorter and less bulbous than in primates in general, such that a direct comparison of this feature with the apes is untenable. Lewis (1972) suggested that the waisted appearance of the capitate facilitates a configuration in which the os centrale-portion of the scaphoid wedges into the notch between the capitate and trapezoid, producing a close-packed relationship that is related to suspensory behavior. This suspensory-adaptation hypothesis was refuted by other authors (Jenkins and Fleagle, 1975; Corruccini et al., 1978), who pointed out that such a configuration is common in semiterrestrial primates such as *Macaca*, and that *Pongo* and *Hylobates* practice arm-swinging behaviors with more frequency than do *Pan* and *Gorilla*, and have capitate heads that are not waisted to the same degree.

In *Tamandua* and *Cyclopes*, the capitate head is slightly more bulbous in the dorsopalmar plane, such that the scaphoid rotates farther dorsally in extension before contacting the ridges on the capitate dimple (mentioned previously) than is seen in *Myrmecophaga*. In addition, the nonarticular surface of the dorsal capitate extends farther proximally over the capitate head of *Myrmecophaga* (Fig. 6b), thereby shortening the articular path of the scaphoid on the capitate (Fig. 9) relative to its outgroups. The slightly more bulbous capitate heads of *Tamandua* and *Cyclopes* and their larger percentage of articular surface area on the dorsal capitate account in part for the observations by Yalden (1966, 1972) that the tamandua is capable of 20° of hyperextension at the midcarpal joint, while no motion occurs at this joint in the giant anteater. Greater ligamentous restraint in *Myrmecophaga* might also play a role in limiting motion, but no cadaver specimens of this species were available to test this hypothesis. The nonarticular surface of the dorsal capitate also appears to be expanded in *Pan*, *Gorilla*, and *Homo* relative to *Pongo*, *Hylobates*, and digitigrade primates such as *Papio* (Richmond et al., 2001; Begun, 2004; personal observation), although there are no published quantitative data to report. Relative to the reported 52° of extension at the midcarpal joint of *Pongo* and 53° in *Hylobates* (Sarmiento, 1988), maximum extension of the midcarpal joint is limited in African apes, with 26° of motion in *Pan* (Jenkins and Fleagle, 1975) and 35° in *Gorilla* (Sarmiento, 1988). Motion at the human midcarpal joint is similarly limited at 39° (Sun et al., 2000).

On the dorsal aspect of the capitate head of *Myrmecophaga*, a slight keel runs proximodistally (and actually forms a short ridge at its distal extent), dividing the capitate head into scaphoid and lunate surfaces. Corruccini (1978) noted a similar proximodistal ridge as distinctive of African apes, although the functional significance of this feature is not obvious (Richmond et al., 2001). A very slight keel occurs variably in *Papio*, but does not form a sharp ridge at any point along its length (personal observation). A similar feature distinguishes *Myrmecophaga* from its arboreal outgroups, but once again, a functional significance is not immediately apparent. Due to the shorter and less bulbous head of *Myrmecophaga* vs. primates in general, it is difficult to assess whether this feature is analogous between the groups.

A long spiral facet appears on the proximal aspect of the hamate of all myrmecophagid taxa for articulation with the triquetral, which might produce a conjunct rotation via a screw-like effect in which the concavo-convex articular surface of the triquetrum spirals around to lock into a supinated close-packed position in a deep concavity at the end of the hamate's facet. Lewis (1972) discussed the same morphology in chimpanzees and humans, and suggested that the conjunct rotation co-occurs with other close-packing mechanisms, such as the rotation of the scaphoid onto the waisted capitate neck. Jenkins and Fleagle (1975) could not verify a conjunct rotation in the midcarpal joint during chimpanzee wrist extension by examining radiographic images, and showed that the triquetral-hamate configuration is related to pronation and supination at the midcarpal joint, rather than functioning as an extension-limiting mechanism. Furthermore, because the large hamate spiral facet does not distinguish *Myrmecophaga* from its outgroups, and because of the functional ambiguities, it is not clear that this feature represents an adaptation to knuckle-walking.

Carpometacarpal joints. The myrmecophagid carpometacarpal joint is characterized by a complex jagged appearance, especially in dorsal view, functionally similar to the "keeled" (Richmond et al., 2001) pattern seen in African great apes. This is especially evident in the joints between the capitate and the specialized and enlarged third metacarpal, and between the hamate and third and fourth metacarpals (Fig. 4b). The triangular-shaped distal capitate fits into a correspondingly shaped notch in the dorsal aspect of proximal MC3. The hamate is quite broad, and a deep trough on the distal side receives an extended convex ridge on the palmar aspect of the proximal MC 3, while a rounded projection connects the hamate transversely with the lateral aspect of the capitate head. Medial to the trough on the hamate, a knob-like process projects from the dorsal half of the distal articular surface, and a bony keel extends palmarly from the knob; both are received by the deeply excavated notch of the proximal MC 4. Carpometacarpal joints 3 and 4 are likely to bear the majority of the load passed through the hand in locomotion and posture of *Myrmecophaga*, and this complex interlocking probably limits shearing stress at these joints, thereby increasing stability. However, because the carpometacarpal joint morphology of *Tamandua* and *Cyclopes* is almost identical to that of *Myrmecophaga*, its origin as an adaptation is probably related to stabilizing the rays during the use of the large claws, although it may be exaptive for knuckle-walking terrestriality. Also, a configuration similar to the type III fourth metacarpal arrangement of Marzke et al. (1994), common in African apes, in which there is no contact between the fourth metacarpal and the capitate, resulting in a more jagged carpometacarpal joint, is observed in the giant anteater, but also in *Tamandua* and *Cyclopes*. This configuration is probably related to the expansion of the specialized clawed third ray in all myrmecophagids (Taylor, 1985), rather than to any aspect of locomotion. As such, it is unlikely that the metacarpal articular arrangement of *Myrmecophaga* has converged on an African ape-like type III metacarpal articular condition.

Finally, the orientation of the trapezoid facet on the scaphoid is normal to the long axis of the second metacarpal, and the second metacarpal surface on the trapezoid is keeled, similar to the condition seen in African apes and variably in humans (Richmond et al., 2001). Such a configuration is argued to facilitate load transmission in knuckle-walking apes and to limit shearing stresses across the second carpometacarpal joint. However, having observed that weight does not appear to be borne at all by the second digit in *Myrmecophaga*, features associated with the second ray are probably not linked to knuckle-walking, unless shearing stresses are propagated transversely beyond the weight-bearing rays. Furthermore, this morphology is also found in *Tamandua* and *Cyclopes*, suggesting that this feature is not related to knuckle-walking in myrmecophagids.

Metacarpophalangeal joint and phalanges. As interpreted by other authors (Taylor, 1978, 1985), the myrmecophagid metacarpals are constructed to facilitate the long claws of the distal phalanges, used primarily in digging and tearing into vegetation to access insect colonies. The third manual ray wields the largest claw, and is consequently the most specialized, such that the third metacarpal is robust and greatly enlarged relative to the other rays. The distal joint surface of MC3 is characterized by a central keel and medial and lateral condyles, with the central keel extending farthest distally. These keels articulate with deep, dorsopalmarly arced concavities in the short proximal phalanx, and provide significant lateral stability while allowing for a wide range of flexion and extension (Taylor, 1978, 1985). Any comparison of the myrmecophagid hand to that of hominoids must take into account the highly specialized claws. One consequence of morphology related to the large clawed third ray is that while weight is borne on the dorsal aspects of the middle phalanges of all rays in *Pan* and *Gorilla* (and the fourth and probably fifth rays in *Myrmecophaga*), when weight is transferred to the third ray of *Myrmecophaga*, it is the distal phalanx that bears the load. This is because the proximal and middle phalanges of the third digit in all myrmecophagid taxa are interlocking to the degree that almost no motion can occur at the proximal interphalangeal joint (Fig. 4b), although flexion and extension are possible at the metacarpophalangeal joint and distal interphalangeal joint. Consequently, the proximal and middle phalanges of the third ray can be thought of as a single digital segment, such that the third distal phalanx of *Myrmecophaga* is functionally analogous to the third *middle* phalanx in the apes.

The most obvious feature of the giant anteater metacarpophalangeal joints related to knuckle-walking is the presence of a prominent dorsal transverse ridge on the head of MC4. Unlike MC3, the fourth metacarpal of the myrmecophagids resembles the morphology of hominoids, being slender and relatively unspecialized. The

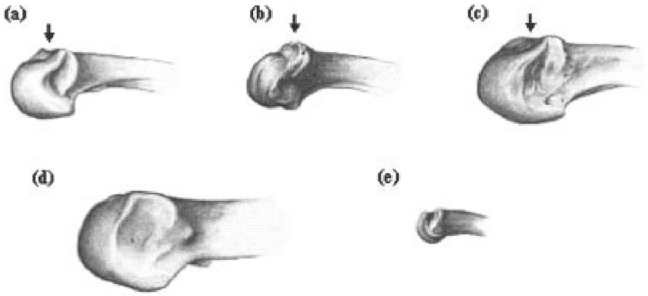

Fig. 10. Morphology of fourth metacarpal head in (**a**) *Pan*, (**b**) *Myrmecophaga*, (**c**) *Gorilla*, (**d**) *Pongo*, and (**e**) *Tamandua*. Arrow denotes pronounced ridge on dorsal aspect of head in *Myrmecophaga*, *Gorilla*, and *Pan*. In *Myrmecophaga*, fourth proximal phalanx (PP4) can be clearly seen to contact this ridge in Figure 4a (with radiotranslucent articular material intervening).

articular surface of the MC4 head is expanded to the crest of the high dorsal transverse ridge, and the prominent development of this ridge distinguishes *Myrmecophaga* from *Tamandua* (Figs. 6c, 10). The one specimen of a *Cyclopes* MC4 examined revealed no ridge, but was not included in the metric analysis. A corresponding facet appears on the dorsomedial aspect of the fourth proximal phalanx in *Myrmecophaga*, and it is likely that, as in African great apes (Tuttle, 1967), these features stabilize the metacarpophalangeal joints in hyperextension, and facilitate efficient weight-bearing during the forelimb stance and push-off phases of locomotion. The orientation of the facet on the phalanx, and the topography of the metacarpal head, result in a slight angle between the phalanges and the long axis of the metacarpal, rather than the phalanges being directly in line with the metacarpal, as in apes. In addition, MC4 is significantly longer than MC3, and the implications of this arrangement were discussed above, in terms of kinematics.

Stabilization in extension is also provided at myrmecophagid MC3, due primarily to the presence of medial and lateral "horns" at the proximal edge of the dorsal articular surface. These horns can be seen most easily in lateral or medial view, and each rises above the primary articular surface, similar to the ridge on MC4 of *Myrmecophaga*. Although this MC3 "ridge" may play some role in *Myrmecophaga*'s mode of locomotion, especially when the hand rolls over onto the third digit, the morphology of the third metacarpal is indistinguishable between the three anteater taxa. Thus, this feature in *Myrmecophaga* is not supported as an adaptation for knuckle-walking. It is the dorsal transverse ridge of MC4 that separates *Myrmecophaga* from its outgroups, highlighting the kinematic data suggesting that the fourth ray is the primary weight-bearing ray in stance phase.

Susman (1979) argued that the greater dorsal width vs. palmar width of the metacarpal heads in African great apes acts to tighten the collateral ligaments during extension of the proximal phalanx. All myrmecophagids have well-developed collateral ligaments at the metacarpophalangeal joints (Taylor, 1978), and *Myrmecophaga* is distinguished from *Tamandua* in that the fourth metacarpal head is wider dorsally than palmarly (Fig. 6d). The articular surface of *Tamandua* narrows considerably at the proximal edges of both the palmar and dorsal aspects, while the head in *Myrmecophaga* narrows only palmarly and maintains its width dorsally. More detailed anatomical work using myrmecophagid cadaver specimens is necessary to determine whether this affects the function of the collateral ligaments as it does in *Pan* and *Gorilla*, but if so, it may further support the hypothesis that this constitutes a knuckle-walking adaptation. In any case, it provides a larger area for weight transmission in an extended joint posture.

Pisiform morphology. The pisiform of the knuckle-walking African apes is long and palmarly oriented. This was argued to be a knuckle-walking adaptation because it increases the moment arm of the flexor carpi ulnaris by being longer, and due to the palmar orientation, specifically increases the moment arm when the carpus is slightly extended (Sarmiento, 1988). In addition, Sarmiento (1988) noted that a palmarly directed pisiform is characteristic of all terrestrial mammals that he examined. Although the myrmecophagid pisiform is long and palmarly oriented in all three taxa, *Cyclopes* has the longest pisiform (Fig. 6e). This was reported by others (Taylor, 1985), and seems to function as an extra, nonmobile "digit" that extends from the palm and aids in grasping small vines, similar in a superficial way to the famed "thumb" of the giant panda (Endo et al., 1999). The relative length of the pisiform is significantly lower in *Myrmecophaga* compared to *Tamandua* as well (Table 4 and Fig. 6e); therefore, a long pisiform is not supported as an adaptation to terrestrial knuckle-walking in the Myrmecophagidae. Furthermore, given the inactivity of the flexor carpi ulnaris during knuckle-walking in *Gorilla* (Tuttle et al., 1972), and unpublished data suggesting that a lengthened pisiform does not significantly increase the actual moment arm of this muscle measured via tendon excursion (Marzke, personal communication), an elongated pisiform might not represent a knuckle-walking adaptation in African apes.

Implications for assessing adaptations to knuckle-walking in the Hominidae

A convergence study can only provide *positive* or equivocal evidence in testing hypotheses of adaptation for purported knuckle-walking features of the African Hominidae (or any other such study). That is, because all taxonomic groups have unique evolutionary histories, a convergence test cannot truly *falsify* a hypothesis of adaptation for a particular lineage. However, convergence study can provide *positive* support for the hypothesis that structure X is an adaptation to function F, if X distinguishes F-performing taxa from their respective non-F-performing outgroups. To provide a *hard* test of the hypothesis of a knuckle-walking hominin ancestor, feature X should also distinguish knuckle-walkers (the African apes and *Myrmecophaga*) from terrestrially digitigrade primates who might have similar requirements of wrist stabilization. However, features shared by knuckle-walking and digitigrade taxa might still provide a *softer* test of the hypothesis of a knuckle-walking ancestor for bipedal hominins. This "soft test" couples evidence for adaptation to a vertical manus form of terrestrial locomotion, with the phylogenetic context and our current understanding of the biomechanics of knuckle-walking.

By the above logic, there are two features of *Myrmecophaga* for which this study provides hard positive evidence for adaptation to knuckle-walking specifically. These are features shared by *Myrmecophaga*, *Pan*, and *Gorilla*, to the exclusion of their respective outgroups and digitigrade primates: 1) proximal expansion of the nonarticular surface of the dorsal capitate; and 2) wider dorsal surface (relative to palmar surface) of the primary weight-bearing ray(s). Two other features are shared between knuckle-walkers and digitigrade primates, and are supported as adaptations to a vertical manus form of terrestrial progression (discussed in detail below): 1) the distally extending dorsal ridge of the distal radius; and 2) the dorsal transverse ridge of the weight-bearing ray(s). A number of other features were suggested to constitute knuckle-walking adaptations in African apes (Table 1) that either are not seen in an analogous form in *Myrmecophaga* (e.g., the waisted capitate neck and dorsally oriented scaphoid "notch" of the distal radius) or are present but cannot be tied specifically to knuckle-walking in *Myrmecophaga* because they appear in that taxon's non-knuckle-walking outgroups, *Tamandua* and *Cyclopes* (e.g., the fused os centrale and hamate and capitate dorsal ridges). Such features may still represent adaptations in apes and perhaps exaptations or nonaptations (Gould and Vrba, 1982) in *Myrmecophaga*. However, this study can only provide equivocal results in such cases, and cannot support or reject these post hoc hypotheses.

A specific problem in studying the evolution of knuckle-walking and recognizing knuckle-walking in fossil primates (McCrossin and Benefit, 1997; McCrossin et al., 1998; Richmond and Strait, 2000; Richmond et al., 2001) is distinguishing features that may be related to knuckle-walking from features related to generalized terrestrial digitgrady. General (cercopithecid-like) digitigrady is a form of locomotion in which the manus is also held relatively vertical to the substrate, and might also require some restraint to extension and load distribution mechanisms at the joints of the hand and the wrist. As discussed, digitigrade monkeys also frequently show a distally extending dorsal ridge of the distal radius as well as transverse ridges on their metacarpal heads (Richmond et al., 2001). The inability of some features to distinguish knuckle-walking from other forms of digitigrady poses some difficulty to recognizing knuckle-walking *specifically* in the fossil record and tracing its evolutionary origin.

Another complicating factor for this study concerns biomechanical differences between the knuckle-walking of *Myrmecophaga* and *Pan* and *Gorilla*. As discussed regarding kinematics, although weight is borne on flexed digits extended at the metacarpophalangeal joint, these digits are oriented just slightly obliquely to the long axis of the metacarpals, and the proximal phalanges are substantially shorter than those of apes. Such differences may have some biomechanical ramifications. For example, shorter proximal phalanges of the weight-bearing rays result in a shorter moment arm of the ground reaction force acting to flex and collapse the first interphalangeal joint, and as a consequence of the kinematic chain, extend the metacarpophalangeal joint. However, no matter what the interpretation, two important points remain: 1) during the stance phase of locomotion, the manus of *Myrmecophaga* is held relatively vertical to the substrate, with flexed digits hyperextended at the metacarpophalangeal joint such that a premium is placed on limiting extension at all of the joints of the hand and wrist (excluding the interphalangeal joints); and 2) as in digitigrade primate taxa, this kinematic regime is almost certainly an adaptation to increasing locomotor efficiency in a terrestrial habitus, given that digitigrady is a common phenomenon among terrestrial animals of many lineages (Whitehead, 1993; Hildebrand and Goslow, 2001). The functional significance of such vertical manus postures is that they increase the overall length of the forelimb such that a greater distance is traveled per muscle contraction (Whitehead, 1993) as well as the number of limb elements, thereby increasing the summation of velocities for a limb in motion (Hildebrand and Goslow, 2001). The knuckle-walking of *Pan*, *Gorilla*, and *Myrmecophaga* and the generalized digitigrade locomotion of the terrestrial cercopithecids can be viewed as different forms of a vertical manus[1] form of locomotor progression.

Two traits do distinguish knuckle-walkers from digitigrade cercopithecids: the *volarly tilted* distal radius in combination with the dorsal ridge, and the proximally expanded nonarticular surface of the dorsal capitate. However, the functional significance of a tilted radius is not immediately obvious, other than that it seems to result in the development of the dorsal ridge in knuckle-walkers. Digitigrade cercopithecids often show a similar ridge *without* the volar tilt, such that most of the distal radial articular surface is approximately perpendicular to the long axis of the shaft (Jenkins and Fleagle, 1975; Corruccini, 1978; Richmond and Strait, 2000; Richmond et al., 2001). The tilt in knuckle-walkers may have some functional significance independent of the ridge, or may simply be another architectural approach to producing a ridge, different from the approach found in digitigrade cercopithecids. If a functional explanation can be found for having a tilted distal radius, then this feature might be useful for differentiating between knuckle-walkers and generalized digitigrade primates. Furthermore, in digitigrade cercopithecids, the ridge appears more "knob-like" and is ulnarly adjacent to a much wider and deeper notch than appears in the apes (see Fig. 5 in Richmond et al., 2001). As already discussed, digitigrade cercopithecids apparently have more mobility in extension than do African apes and *Myrmecophaga*. It is possible that, rather than acting to limit extension in these digitigrade taxa, the "ridge" acts to restrict adduction/abduction in extended joint positions. Although there is a notch in *Pan* and *Gorilla*, it is narrower and more "filled-in." If so, then the radius dorsal ridge of cercopithecids might not be functionally analogous with those of knuckle-walkers. A topography of the distal radial articular surface that *drastically* limits extension (as it does in African apes and *Myrmecophaga*) might be considered truly adaptive to knuckle-walking vs. generalized digitigrady. More work is needed to compare the structure and function of the radiocarpal joint in African apes and digitigrade taxa.

Richmond et al. (2001) described the dorsal nonarticular surface of the capitate in the African apes as proximally expanded relative to the Asian apes and digitigrade monkeys, and my own qualitative observations corroborate this description (although I do not have quantitative data for primates, and more data should be collected to examine variation in this feature). Thus, for this study, proximal expansion of the nonarticular surface of the dorsal capitate is the feature that most clearly distinguishes knuckle-walkers from generally digitigrade primates.

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[1] Properly this should be referred to as "approximately vertical manus," because the hands of African apes and digitigrade cercopithecids are actually slightly extended during stance phase, but I have chosen *vertical manus* for brevity.

However, this proximal expansion is also relative to the outgroup condition. It is possible that digitigrade primates could have a proximally expanded nonarticular surface relative to more arboreal outgroups. Kinematic and range-of-motion data are needed on differences in hand function during locomotion between arboreal cercopithecid taxa that almost exclusively use palmigrade hand postures and the digitigrade taxa.

Morphological features that appear in the hominin lineage shared by *Myrmecophaga*, *Pan*, and *Gorilla*, to the exclusion of their respective outgroups and digitigrade primates, are supported as adaptations to knuckle-walking and provide strong inference of a knuckle-walking last common ancestor (LCA) of *Gorilla*, *Pan*, and hominins (Fig. 1, node A). Only one such feature (proximal expansion of the nonarticular surface of the dorsal capitate) appears in the hominin lineage. Human capitates show the African ape state of proximal expansion (Richmond et al., 2001; my personal observation), and the *A. afarensis* capitate (AL 333-40) shares the morphology of *Gorilla*, *Pan*, and *Homo* (personal observation).

Features that appear in the hominin lineage that are shared by African apes, *Myrmecophaga*, and terrestrially digitigrade primates suggest that hominins may have had an ancestor adapted to using some sort of vertical manus posture for more efficient terrestrial locomotion. The dorsal ridge of the distal radius was described and analyzed quantitatively in the fossil hominin species *Australopithecus anamensis* and *A. afarensis* (see Fig. 7d,e, following Richmond and Strait, 2000; Richmond et al., 2001). The distally projecting ridge, representing half of the close-packing (or locking) mechanism of the antebrachiocarpal joint, formed by contact of the ridge with the dorsal scaphoid (Richmond and Strait, 2000), might constitute evidence of a hominin ancestor that practiced a locomotor mode involving vertical manus during the forelimb stance phase.

Distinguishing between digitigrady and knuckle-walking in fossil taxa might be a particularly difficult problem given only metacarpals (e.g., McCrossin and Benefit, 1997; McCrossin et al., 1998), although some preliminary data suggest that there are differences in the relative sizes of the metacarpal ridge between knuckle-walkers and digitigrade primates (McCrossin, 2002). In any event, the metacarpal traits examined in this study do not appear in known fossil hominins or modern humans. Some authors (Susman, 1979; Shea and Inouye, 1993; Inouye, 1994a,b) pointed out that the absence of the dorsal transverse ridges of the metacarpal heads in fossil hominins may not refute the knuckle-walking ancestor hypothesis, because these ridges sometimes do not appear in knuckle-walking bonobos (*Pan paniscus*). Furthermore, the ridges might represent a bone remodeling response to weight-bearing, rather than being under tight genetic control: something akin to the "squatting" facets of the talar neck. The dorsal aspect of the metacarpal head is not wider dorsally than palmarly in fossil hominins or modern humans (Richmond et al., 2001), although it is possible that this feature results from a bone-remodeling response as well. More research is needed to examine the development of these metacarpal features.

The vertical manus hypothesis for the last common ancestor of *Gorilla*, *Pan*, and hominins

Knuckle-walking and cercopithecid-like digitigrady (what I am calling *generalized* digitigrady) are "vertical manus" forms of locomotion which constitute similar adaptations to terrestrial life. In the case of knuckle-walking apes, generalized digitigrady, with the volar aspects of the fingers contacting the ground, would be difficult and inefficient due to the retention of long digits for climbing that would result in large bending moments at the metacarpophalangeal joints during push-off. Knuckle-walking provides a compromise solution to the problem of increasing stride length and number of limb elements to facilitate terrestrial progression while retaining those long digits (Tuttle, 1967, 1975). The convergent case of *Myrmecophaga* corroborates this notion: the giant anteater retains long, curved digital claws and powerful digital flexors (Taylor, 1985) in a terrestrial milieu that likely selected for similar adaptations to increase locomotor efficiency. The biomechanical problem of practicing digitigrady with long digits was solved as in the African apes by flexing the digits in an analogous knuckle-walking position. Because there is some overlap in features of the hand and wrist of knuckle-walkers and generalized digitigrade primates, the current resolution afforded by the comparative anatomical data may not always distinguish between these locomotor modes in fossil specimens. However, if the "vertical manus hypothesis" holds, the phylogenetic context and biomechanics of knuckle-walking (as currently understood) support the hypothesis that the ancestors of bipedal hominins were knuckle-walkers rather than cercopithecid-like digitigrade primates for the following reasons.

It is unlikely that the last common ancestor (LCA) of *Gorilla*, *Pan*, and hominins itself was a terrestrial, cercopithecid-like digitigrade primate. All nonhuman hominoids practice some degree of arboreal suspensory or vertical climbing behavior, and display a shoulder morphology allowing mobility of the arm above the head and digital anatomy related to powerful grasping to facilitate this lifestyle (Fleagle, 1999). Humans retain a mobile shoulder joint, and the fossil hominin genus *Australopithecus* is also characterized by the retention of a mobile shoulder and somewhat long, curved digits with strong flexor insertion markings (Stern and Susman, 1983; Susman et al., 1984). Such morphology is probably homologous in *Pan* and early hominins; otherwise, it would have had to evolve separately in both, and a third time in *Gorilla*. Assuming that long and powerfully grasping digits are biomechanically incompatible with generalized digitigrady (Tuttle, 1967; Richmond et al., 2001), there are two possibilities for the retention in the hominin clade of features related to a vertical manus form of locomotor progression:

1. They are retained from a terrestrially digitigrade ancestor preceding the LCA which then became adapted to a completely suspensory life (*Pongo*-like), and gave up terrestrial life while evolving suspensory adaptations, but never lost the stabilization features of the wrist absent in extant Asian apes. Later, *Pan* and *Gorilla* evolved knuckle-walking independently as a compromise for secondary terrestriality and hominins evolved bipedality, but retained some of the primitive vertical manus features without having had a knuckle-walking ancestor.
2. The LCA of *Pan*, *Gorilla*, and *Homo* was a knuckle-walker evolved from a primarily suspensory/vertical climbing ancestor. Presumably in this case, the suspensory ancestor was derived further back from a more generalized arboreal quadruped, such as many

of the Miocene hominoid fossil taxa appear to have been (surveyed in Fleagle, 1999).[2]

A scenario such as number 2, in which the LCA evolved from an arboreal to a terrestrial animal, is more parsimonious than number 1, where it evolved from terrestriality to arboreality and back to terrestriality (via knuckle-walking in African apes and bipedality in hominins). Alternatively, future work might show that long, curved digits are not actually incompatible with generalized digitigrady. In this case, we might imagine an LCA that was in transition to being a partially suspensory primate and practiced generalized terrestrial digitigrady with long fingers and strong digital flexors. This "transitional hypothesis" would assume a combination of morphology and behavior for which we have no modern analogue, and would beg the question of why *Pan*, *Gorilla*, and *Myrmecophaga* are knuckle-walkers rather than generally digitigrade. In any case, the transitional hypothesis and the knuckle-walking LCA hypothesis have similar implications for reconstructing scenarios for the evolution of bipedality, because both hold that bipedality evolved from an already semiterrestrial primate.

The only other plausible option for a vertical manus form of progression is that the earliest hominin ancestors were fist-walkers when terrestrial, similar to modern *Pongo*, but there are no known anatomical specializations needed to practice such a locomotor mode (Tuttle, 1967). *Pongo* is capable of a much greater degree of extension at the wrist than *Pan* or *Gorilla*, and utilizes a variety of hand postures such as palmigrady and modified fist-walking (in which the thumb is recruited for support) in addition to standard fist-walking during terrestrial progression (Tuttle, 1967). During palmigrady, the hand is extended almost 90° by the combined motion of the antebrachiocarpal and midcarpal joints (Tuttle, 1967; Sarmiento, 1988), and *Pongo* is capable of a much greater degree of extension at both the antebrachiocarpal and midcarpal joints than are African apes (Tuttle, 1967; Jenkins and Fleagle, 1975; Sarmiento, 1988). This fact suggested to Tuttle (1967) that fist-walking does not represent a specialized locomotor mode, but a behavioral modification of an almost exclusively arboreal primate that has maintained a wrist with a greater range of motion to facilitate life in the trees. Indeed, male orangutans (more terrestrial than females) are reported to spend only 11% of their daily activity time on the ground (Rodman, 1973). It is probable that the larger base of support afforded by using the entire dorsum of proximal phalanges 2–5, and the buttressing effect of the flexed digits acting to support the carpus and metacarpus as the thenar and hypothenar pads are pressed to them during weight-bearing, are sufficient to maintain the verticality of the manus during fist-walking locomotion, such that no extension-limiting osteological specializations are necessary. Thus, fist-walking is an unlikely candidate for a vertical manus form of locomotion, although a similar form of hand positioning might have been used in lieu of generalized digitigrady if the "transitional" LCA hypothesis discussed previously is viable.

If early hominins did indeed retain adaptations to maintaining a vertical manus during terrestrial locomotion (vestigially or by stabilizing selection for practiced knuckle-walking[3]), then based on our current understanding of the biomechanics of these forms of locomotion, the simplest hypothesis is that their ancestors were knuckle-walkers rather than generally digitigrade. However, more research on the biomechanical differences between knuckle-walking and generalized, cercopithecid-like digitigrady is warranted.

CONCLUSIONS

The giant anteater, *Myrmecophaga tridactyla*, uses its hand and wrist in a way similar to the knuckle-walking African apes, *Pan* and *Gorilla*, such that the manus is held in a vertical position to the substrate, and the weight-bearing digits are hyperextended at the metacarpophalangeal joint and flexed at the interphalangeal joints. These similarities allow for a convergence test of purported osteological adaptations to knuckle-walking in African apes. Features shared between groups, to the exclusion of their respective outgroups and digitigrade primates, are supported as adaptations to terrestrial knuckle-walking by limiting extension and facilitating weight-bearing at the antebrachiocarpal, midcarpal, and metacarpophalangeal joints. These features include proximal expansion of the nonarticular surface of the dorsal capitate, and weight-bearing metacarpal heads that are wider dorsally than palmarly. The distally projecting dorsal ridge of the distal radial epiphysis and dorsal transverse ridge of the weight-bearing metacarpal heads are shared by *Gorilla*, *Pan*, and *Myrmecophaga* to the exclusion of their outgroups, but similar features appear in terrestrially digitigrade primates; they are thus supported as adaptations to a vertical manus form of terrestrial locomotion, but are not tied specifically to knuckle-walking by this study. Conclusions regarding other key features purported to be related to knuckle-walking, such as early scaphoid-centrale fusion, are equivocal. That the dorsal ridge of the distal radius and expanded nonarticular surface of the dorsal capitate are reported for some hominin taxa suggests that hominins are descended from an ancestor with a wrist adapted to support a vertical manus during locomotion in a terrestrial habitus. If evidence for vertical manus features in early hominin taxa withstands further scrutiny, then the current state of knowledge regarding phylogenetic context and biomechanics favors a knuckle-walking last common ancestor of *Gorilla*, *Pan*, and hominins over an ancestry of generalized digitigrady.

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[2] One of the earliest Miocene hominoid taxa, *Proconsul*, shows no dorsal ridge development of its distal radius (KNM-RU 2036) and is most similar to a generalized arboreal quadruped such as *Alouatta* (Richmond et al., 2001; my personal observations), consistent with the rest of the skeleton (Ward et al., 1993; Ward, 1993). Kappelman et al. (2003) suggested that *Ankarapithecus* (~9.8 ma) might lie near the stem of the great ape clade and was a generalized arboreal quadruped based on phalangeal and radial morphology (although the distal radius articular surface is unfortunately missing).

[3] This study does not aim to contribute to the long-standing dispute over how to interpret plesiomorphic characters in locomotor reconstruction of fossil taxa (e.g., see review of debate on *A. afarensis* locomotion in Ward, 2002). For the purposes of reconstructing the phylogeny of knuckle-walking, it should make no difference whether such traits are phylogenetic, *nonaptive* "baggage" in a specific taxon (although once adaptive), or sustained adaptations to practiced knuckle-walking.

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