Knuckle Walking Signal in the Manual Digits of *Pan* and *Gorilla*

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ABSTRACT   This article examines the curvature of the manual proximal and middle phalanges of species belonging to *Pan, Gorilla, Ateles, Macaca, Pongo, Hylobates,* and *Cebus* to determine whether middle phalangeal curvature, when considered in conjunction with proximal phalangeal curvature, yields a locomotor signal. Prior studies have demonstrated the discriminatory power of proximal phalanges for separating suspensory species (including knuckle walkers) from pronograde quadrupedal species, but less emphasis has been placed on the distinguishing phalangeal characteristics of taxa within the suspensory category. This study demonstrates, first, that middle phalanges discriminate suspensory from nonsuspensory species, although not as cleanly as proximal phalanges. Finer discrimination of locomotor signals, including subtle differences among animals employing different modes of suspension, is possible through a comparison of the curvatures of the proximal phalanges and corresponding middle phalanges. Their relative curvature differs in quadrupeds, brachiators, and knuckle walkers. Knuckle walkers (*Pan* and *Gorilla*) have relatively little curvature of the middle phalanges coupled with marked curvature of the proximal phalanges, whereas brachiators (*Ateles* and *Hylobates*) display marked curvature of both proximal and middle phalanges, and pronograde quadrupeds (*Cebus* and *Macaca*) have relatively straight proximal and moderately curved middle phalanges. Quadrumanous climbers (*Pongo*) have a unique combination of traits, whereby curvature is high in both proximal and middle phalanges, but less so in the latter than the former. These differences, predictable on the basis of the biomechanical forces to which digits are subjected, may open a new venue for future research on the locomotor repertoire of prebipedal ancestors of hominins. Am J Phys Anthropol 135:27–33, 2008.   © 2007 Wiley-Liss, Inc.

The nature of the hominoid transition from quadrupedalism to bipedalism has been the subject of considerable debate (Begun, 1993; Shea and Inouye, 1993; Dainton and Macho, 1999; Richmond and Strait, 2000, 2001a,b; Corruccini and McHenry, 2001; Dainton, 2001; Kelly, 2001; Lovejoy et al., 2001; Richmond et al., 2001). Was the prebipedal ancestor of humans a knuckle walker or more suspensory? Past research on the morphology of the proximal phalanges and wrists of extant primates and early hominins has not resolved this debate (see review by Richmond et al., 2001). This article explores the extent to which the curvature of the middle phalanges may yield an alternative source of information. While curvature of the proximal phalanges has been linked biomechanically to suspensory behaviors, middle phalangeal curvature has yet to be examined. Phalangeal curvature is particularly attractive as a tool for paleontological inference because it has been shown to be epigenetically sensitive to variation in behavior (Richmond, 1998) and thus to confer evidence of lifetime activity patterns.

The curvature of the proximal phalanges of the manus of primates varies in conjunction with levels of suspension (Susman, 1979; Jungers et al., 1997, 2002; Richmond, 1998). Using computer modeling, Richmond (1998) showed that strain magnitudes experienced by curved manual proximal phalanges of siamangs under suspension are considerably lower that they would be, under similar loading conditions, if those phalanges were straight. This implies that the high forces and stresses generated during gripping and manual flexing in arboreal settings are resisted by some measure of phalangeal curvature (Jungers et al., 2002). Ontogenetic studies of proximal phalangeal curvature reveal that phalanges change as the positional behavior of individuals change, most probably via bone modeling and remodeling in response to mechanical stresses (Richmond, 1998). Although the extent of curvature may be genetically limited, it is clear that a biomechanical signal is preserved within the proximal phalanges. However, studies of the manual middle phalanges have not been conducted. Thus, we do not know the extent to which they also display a locomotor signal.

Preuschoft (1973) presented an extensive array of force diagrams of manual digits of chimpanzees subjected to loading in a variety of locomotor postures. During knuckle walking, the metacarpophalangeal (MCP) joints are hyperextended and weight is borne primarily on the dorsal aspects of the middle phalanges (Tuttle, 1969; Preuschoft, 1973; Marzke and Wullstein, 1996; Wunderlich and Jungers, 1998). At each phase of a knuckle-walking bout in chimpanzees, pressure is highest at the third digit (Matarazzo, unpublished data; Fig. 1). The tensile forces placed on the metacarpals and proximal phalanges during knuckle walking are largely

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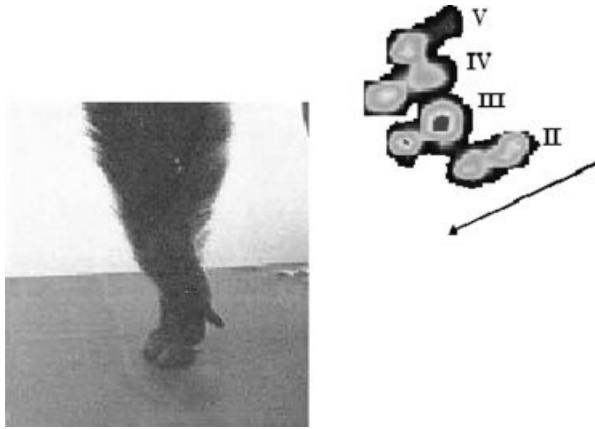
Fig. 1. Adult male chimpanzee right hand contacting pressure mat and resultant pressure distribution output. Pressure is highest on the middle phalanx of the third digit. Arrow points in the direction of movement.

TABLE 1. Locomotor classification of species examined

Taxon	N	Degree of suspension	Primary mode of locomotion
Hylobates lar	97 (M 49; F 47; U 1)	High	Brachiation
Pongo pygmaeus	19 (M 5; F 11; U 3)	High	Quadrumanous climbing
Ateles spp.	14 (M 4; F 6; U 4)	High	Brachiation
Pan troglodytes	25 (M 12; F 13)	Low	Knuckle walking
Gorilla g. gorilla	23 (M 12; F 9; U 2)	Low	Knuckle walking
Gorilla g. beringei	11 (M 8; F3)	Low	Knuckle walking
Cebus apella	15 (M 7; F 8)	Very Low	Quadrupedalism
Macaca fascicularis	20 (M 12; F 5; U 3)	Very Low	Quadrupedalism
Macaca nemestrina	16 (M 6; F 8; U 2)	Very Low	Quadrupedalism

M = males; F = females; U = unknown.

ameliorated by tendons which are strengthened when the hand is in the knuckle-walking position (Tuttle, 1969, p 955; Preuschoft, 1973, p 65). African apes possess deeper and more flexed metacarpal heads than do orangutans resulting in increased moment arms of the long digital flexors which work to resist the torque of the ground reaction force that tends to hyperextend the proximal phalanges (Susman, 1979). This tendon support leaves compression as the main force acting upon the digits. However, given the position of the digital elements during knuckle walking, the middle phalanges are subjected to dorsoventral compression, whereas the proximal phalanges experience compression along their proximodistal axes (Preuschoft, 1973, see p 47 and 53). One would predict that the middle phalanges will be straighter than the proximal phalanges to allow for increased ground-to-digit surface contact and greater dissipation of the compressive force along these elements (Richmond et al., 2001). In suspensory postures, the proximal and middle phalanges are subjected to similar bending moments when the hand is maintained in a hook-like position (Preuschoft, 1973).

In the case of nonknuckle-walking digitigrade quadrupeds such as macaques, flattened middle phalanges are expected for entirely different reasons. Typically in digitigrade quadrupedalism, the MCP joints of Digits II–V are hyperextended with the metacarpals held in a vertical position (Hayama et al, 1994). It is primarily the palmar aspects of the distal phalanges that contact the substrate, and the manual rays are held at an acute angle to the ground surface. Using finite element analyses of the proximal phalanges of patas monkeys and macaques, Richmond (1998, p 208) showed that straighter phalanges withstand loading situations with high compressive joint reaction forces better than do curved phalanges under increased bending strains such as those experienced in terrestrial walking. He also postulated, on the basis of observed kinematic data, that patas-like manual postures would be nearly impossible with highly curved phalanges, as they would require "an improbable degree of hyperextension" at the MCP joint (1998, p 208).

Most species' middle phalanges are subjected to forces similar to those experienced by the proximal
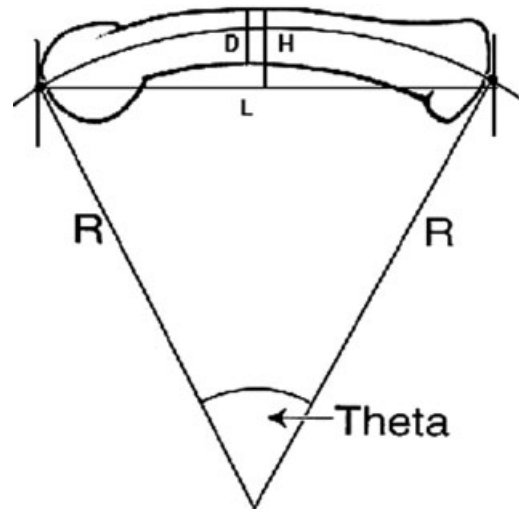

Fig. 2. Curvature measurements: *D* depth, *H* height, *L* length, *R* radius of curvature. (Image adapted from Jungers et al., 1997).

phalanges and would be expected therefore to show similar degrees of curvature. This is true of more suspensory primates for which one might expect high phalangeal curvature, and of nonknuckle-walking quadrupeds for which lower degrees of curvature are expected for both proximal and middle phalanges. In the case of the knuckle walkers, however, markedly different force regimes are applied to proximal and middle phalanges. Thus, different degrees of curvature should characterize the proximal and middle phalanges. The purpose of this article is to determine whether or not a locomotor signal can be found within the manual middle phalanges of primates, when considered in conjunction with proximal phalangeal curvature. Specifically the hypothesis being tested is that the relative curvature of the middle to proximal phalanges will distinguish knuckle walkers from more highly suspensory primates, even when their values for proximal phalangeal curvature, taken alone, fail to do so.

TABLE 2. ANOVAs and descriptive statistics for curvature values

Taxon	Proximal phalangeal curvature (Px3)		Middle phalangeal curvature (Md3)		Index of relative (Md3/Px3) curvature	
	Mean	SD	Mean	SD	Mean	SD
Hylobates lar	52°	4.8	55°	5	1.06	0.11
Pongo pygmaeus	65°	5.8	54°	6	0.84	0.12
Ateles spp.	51°	5.9	53°	8.8	1.04	0.12
Pan troglodytes	55°	4.4	46°	6.4	0.84	0.12
Gorilla g. gorilla	54°	5.6	45°	4.6	0.85	0.11
Gorilla g. beringei	55°	4.9	48°	4.1	0.88	0.07
Cebus apella	36°	3.9	47°	5.1	1.33	0.17
Macaca fascicularis	45°	6.6	53°	5.8	1.18	0.17
Macaca nemestrina	39°	4.9	47°	6.9	1.24	0.13
ANOVA	$F = 45.51$	$F = 13.07$	$F = 38.85$			
	$P < 0.01$	$P < 0.01$	$P < 0.01$			

METHODS

Phalangeal curvature was assessed for 240 individuals belonging to three superfamilies (the Hominoidea, Ceboidea, and Cercopithecoidea). All osteological samples were housed in collections at the National Museum of Natural History, Washington, DC and the Museum of Comparative Zoology, Cambridge, MA. Each superfamily was represented by at least two species (Table 1). Samples of *Gorilla gorilla gorilla,* and *G. g. beringei* were separated and treated as independent taxa because of slight differences in their locomotor propensities; *G. g. gorilla* populations use arboreal settings in higher frequencies (Remis, 1995, 1998). Individuals were included in the sample only if both the proximal and corresponding middle phalanges of the third digit were present and the epiphyses on all phalanges were fully fused. Phalangeal curvature was measured using the procedure outlined in Jungers et al. (1997; Fig. 2). This method of calculating curvature is based on three measures: projected height (H), dorso-palmar midshaft diameter (D), and interarticular length (L). These values are used to calculate the radius of curvature (R) using the following equation:

$$R = [(H - D/2)^2 + (L/2)^2]/[2(H - D/2)].$$

The angle of curvature, theta (θ), is calculated as follows:

$$\theta = 2 \cdot \arcsin(L/2R).$$

The resulting curvature value was converted from radians to degrees by multiplying by 57.295. This method was also chosen to facilitate comparisons with published data, as it has been widely used to examine phalangeal curvature in a variety of fossil primates (Susman et al., 1984; Rose, 1986; Jungers et al., 1994, 1997; Hamrick et al., 1995). Stern et al. (1995) found it to be usually independent of length. The third digit was chosen for analysis because it is the central axis of the hands of most of the species studied here, and because both chimpanzees and gorillas consistently use their third manual digits when knuckle walking (Inouye, 1994). To capture the relationship between curvatures of the proximal and middle phalanges of the third manual digit (Px3 and Md3, respectively), an Index of Relative Curvature (Md3 curvature/Px3 curvature) was calculated. Because no significant differences in curvature or
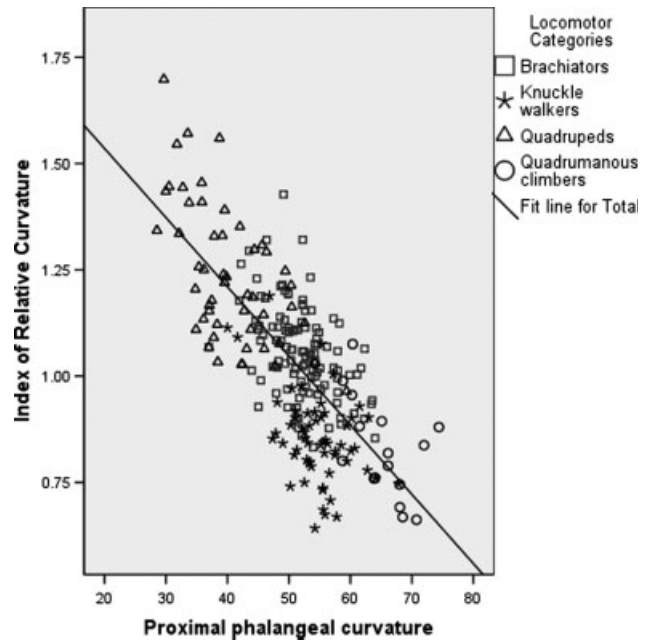

Fig. 3. Scatterplot of the index of relative curvature vs. proximal phalangeal curvature.

index values for males and females belonging to individual taxa were found, with the exception of *Gorilla gorilla beringei* for whom female sample size was low, all analyses were based on pooled sexes.

Degrees of curvature for both the proximal and middle phalanges were analyzed using SPSS statistical software Version 14.0. Analysis of variance (ANOVA) with Tukey's posthoc test of honestly significant differences (HSD) was used to check the significance of differences in proximal and middle phalangeal curvature, as well as the index of relative curvature, across taxa, and across locomotor groups. Regression analysis was used to compare the relationship between proximal phalangeal curvature and the index of relative curvature for members of different locomotor groups.

RESULTS

Mean values for phalangeal curvature and for indices of relative curvature of taxonomic groups are displayed in Table 2. These values differ significantly by taxon. The correlation ($r = -0.91$) between mean values for

TABLE 3. Tukey's posthoc test of honestly significant differences (HSD) among taxa for proximal phalangeal curvature

Taxon	Pongo pygmaeus	Pan troglodytes	Gorilla g. gorilla	Gorilla g. beringei	Cebus apella	Macaca nemestrina	Macaca fascicularis	Ateles spp.
Hylobates lar	**	NS	NS	NS	**	**	**	NS
Pongo pygmaeus		**	**	**	**	**	**	**
Pan troglodytes			NS	NS	**	**	**	*
Gorilla g. gorilla				NS	**	**	**	NS
Gorilla g. beringei					**	**	**	NS
Cebus apella						NS	**	**
Macaca nemestrina							**	**
Macaca. fascicularis								NS

* $P < 0.05$.
** $P < 0.01$.

TABLE 4. Tukey's posthoc test of honestly significant differences (HSD) among taxa for middle phalangeal curvature

Taxon	Pongo pygmaeus	Pan troglodytes	Gorilla g. gorilla	Gorilla g. beringei	Cebus apella	Macaca nemestrina	Macaca fascicularis	Ateles spp.
Hylobates lar	NS	**	**	**	**	**	NS	NS
Pongo pygmaeus		**	**	*	*	*	NS	NS
Pan troglodytes			NS	NS	NS	NS	**	*
Gorilla g. gorilla				NS	NS	NS	**	*
Gorilla g. beringei					NS	NS	NS	NS
Cebus apella						NS	NS	NS
Macaca nemestrina							NS	NS
Macaca fascicularis								NS

* $P < 0.05$.
** $P < 0.01$

TABLE 5. Tukey's posthoc test of honestly significant differences (HSD) among taxa for the index of relative curvature

Taxon	Pongo pygmaeus	Pan troglodytes	Gorilla g. gorilla	Gorilla g. beringei	Cebus apella	Macaca nemestrina	Macaca fascicularis	Ateles spp.
Hylobates lar	**	**	**	**	**	**	**	NS
Pongo pygmaeus		NS	NS	NS	**	**	**	**
Pan troglodytes			NS	NS	**	**	**	**
Gorilla g. gorilla				NS	**	**	**	**
Gorila g. beringei					**	**	**	**
Cebus apella						NS	*	**
Macaca nemestrina							NS	**
Macaca fascicularis								*

* $P < 0.05$.
** $P < 0.01$.

proximal phalangeal curvature and the corresponding index of relative curvature is significant at the 0.001 level for all included taxa ($N = 9$). Species with high proximal phalangeal curvature tend to have relatively low indices of relative curvature (i.e., their middle phalanges tend to be less curved than their proximal).

A linear regression fitted to all individuals in the analysis shows that the index of relative curvature decreases as proximal phalangeal curvature increases (Fig. 3). The slope (-0.016) is significantly lower than zero ($P < 0.001$) and the y-intercept is also significantly different from zero ($P < 0.001$). In general, knuckle walkers (with indices of relative curvature lower than "expected" given their high proximal phalangeal curvature) fall below the regression line. ANOVA (with Tukey's post-hoc tests of HSD) reveals no significant differences between *Hylobates lar* and *Ateles* spp. in proximal phalangeal curvature (Table 3), middle phalangeal curvature (Table 4), or the index of relative curvature (Table 5). However, each of these small-bodied brachiators does differ significantly from members of other locomotor groups in a variety of measures.

Proximal phalangeal curvature values fall as expected from earlier studies (Jungers et al. 1997, 2002; Table 3). *Pongo pygmaeus* has significantly higher proximal phalanx curvature values than do any of the other species in the sample. The proximal phalangeal curvature values for the various species of knuckle walkers are not significantly different from each other, *Hylobates lar*, or *Ateles* spp., but they are significantly higher than those of the quadrupeds, *Macaca* and *Cebus* (Table 3). *Macaca fascicularis* and *M. nemestrina* show differences in the curvature of their proximal phalanges ($P < 0.01$; Table 3), with the more arboreal *M. fascicularis* exhibiting greater curvature (though lower than all suspensory taxa) than the heavier and more terrestrial *M. nemestrina*.

It is noteworthy that, in general and in striking contrast to the situation for proximal phalanges, middle phalangeal curvature values do not distinguish the knuckle walkers from all of quadrupedal taxa (Table 4).
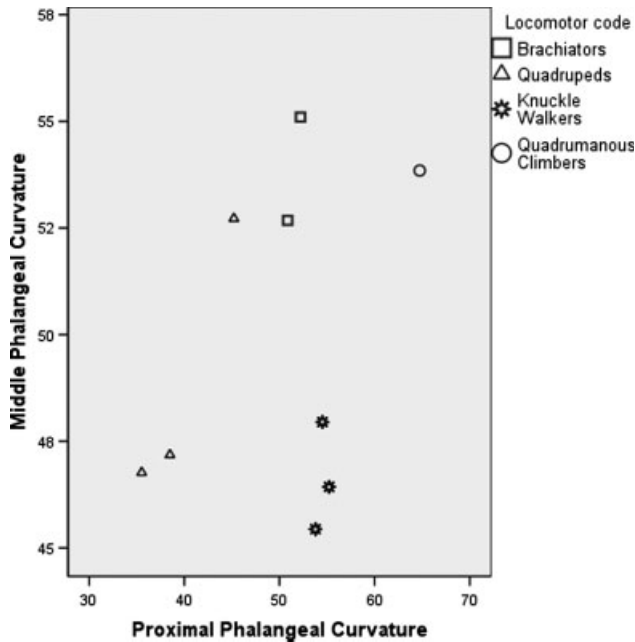
Fig. 4. Scatterplot of middle vs. proximal phalangeal curvature (species means).

Middle phalangeal curvature values are high in *Pongo pygmaeus*, *Hylobates lar*, and *Ateles* spp. and low in *Pan troglodytes*, *Gorilla gorilla gorilla*, *G. g. berigei*, *Cebus apella*, and *Macaca nemestrina*; they are higher than expected in the quadrupedal *M. fascicularis* which were predicted to have curvature values closer to those of the other quadrupedal taxa (Table 2). *M. fascicularis* and *M. nemestrina* do not differ significantly in the curvature of their middle phalanges although values for *M. fascicularis* tend to be higher than those of *M. nemestrina*, and they overlap to a greater degree with *Ateles* spp. (at the low end of the range for highly suspensory taxa). In a pairwise comparison with *Ateles* spp., *M. fascicularis* do not differ in middle phalangeal curvature taken alone.

When considered in combination with the curvature of the proximal phalanx, an interesting pattern emerges (Table 5). Knuckle walkers (*Pan troglodytes*, *Gorilla gorilla gorilla* and *G. g. beringei*) have relatively little curvature of the middle phalanges coupled with marked curvature of the proximal phalanges, whereas agile, small-bodied brachiators (*Ateles* spp. and *Hylobates lar*) display marked curvature of both the proximal and middle phalanges, and quadrupeds that do not engage in knuckle walking (*Cebus apella*, *Macaca fascicularis* and *M. nemestrina*) have relatively straight proximal and moderately curved middle phalanges (Fig. 4). *Pongo pygmaeus* has a unique combination of traits, whereby curvature is high in both proximal and middle phalanges, but less so in the latter than the former.

The result is significantly higher values for the index of relative curvature (>1.0) in the quadrupeds (with relatively flat proximal phalanges), values near 1.0 for agile, small-bodied brachiators (but nevertheless significantly higher than quadrumanous climbers and knuckle walkers), and low values (<1.0) for *Pongo pygmaeus*, *Pan troglodytes*, *Gorilla gorilla gorilla*, and *G. g. beringei*, whose middle phalanges are flatter than the proximal phalanges (Table 5). Taken alone, proximal phalangeal curvature fails to distinguish knuckle walkers from bra-

chiators while the index of relative curvature fails to distinguish knuckle walkers from quadrumanous climbers. The combination of low values for the index of relative curvature and relatively low absolute values for the curvature of the middle phalanx distinguishes knuckle walkers from all other primates in the sample, including *Pongo pygmaeus* (Table 6). *P. pygmaeus* can be distinguished by the combination of very high values for proximal phalanx curvature, high values for middle phalangeal curvature, and low values for the index of relative curvature.

DISCUSSION

The analyses reported here reveal that the knuckle walkers do indeed possess relatively straight middle phalanges as compared with their corresponding proximal phalanges. The knuckle walkers included in this study (*Pan troglodytes*, *Gorilla gorilla gorilla*, and *G. g. beringei*) frequently travel terrestrially via knuckle walking, but also spend varying amounts of time using suspensory postures (Tuttle, 1969; Inouye, 1994; Doran, 1997). During knuckle walking, the ground surface is contacted by the dorsal surfaces of the middle phalanges placing a considerable amount of compressive force onto the middle phalanges. Thus it was expected that these elements will be relatively straight allowing weight to be distributed across the middle phalanges during locomotion.

Gorillas display a different pattern of weight distribution than chimpanzees when knuckle walking. Digits II–V all contact the surface when gorillas knuckle walk. However, weight appears to be placed primarily on the dorsal surfaces of the II and III middle phalanges (Tuttle, 1969; Inouye, 1994). In contrast, common chimpanzees emphasize Digits III and IV, and keep Digit II flexed so that it may only lightly contact the substrate (Tuttle, 1969; Inouye, 1994). It has also been noted that chimpanzees vary considerably in hand and digit posture when knuckle walking, whereas gorillas consistently contact the ground surface with Digits II–V and maintain their hands in a fully pronated position while knuckle walking (Inouye, 1994). Whether noncorresponding elements should or should not give parallel signals will depend on the homogeneity of pressures across the digits. An analysis of differences in weight distribution across the digits is currently being conducted, and should shed light on this issue.

Like the knuckle walkers, *Cebus apella*, *Macaca fascicularis*, and *M. nemestrina* do not display comparable proximal and middle curvature values. They possess relatively straight proximal phalanges and moderately curved middle phalanges, and therefore indices of relative curvature greater than 1. This phalangeal pattern was not initially expected for these quadrupedal primates. It was predicted that their middle and proximal phalanges would experience similar forces during locomotion and thus show similarly low curvature values. As these taxa use arboreal substrates at least some of the time (Rodman, 1979; Cant, 1988; Burr et al., 1989; Garber and Rehg, 1999) their relatively high middle phalangeal curvature values must reflect the biomechanical constraints of gripping those substrates. It is interesting that the absolute values are slightly higher in the more arboreal (*Macaca fascicularis*) than terrestrial (*M. nemestrina*) macaques, and that *M. fascicularis* stand alone among these species in not differing significantly in middle pha-

TABLE 6. *Comparison of phalangeal curvature and relative curvature values by locomotor groups*

Locomotor group	Middle phalangeal curvature (range of species means)[a]	Proximal phalangeal curvature (range of species means)	Index of relative curvature
Brachiators	High (53°–55°)	High (51°–52°)	~1.0
Quadrumanous climbers	High (54°)	Very high (65°)	<1.0
Pronograde quadrupeds	Moderate to high (47°–53°)	Low (36°–45°)	>1.0
Knuckle walkers	Low to moderate (45°–48°)	High (54°–55°)	<1.0

[a] Very high: above 55, High: 51–55, Moderate: 46–50, Low: below 46.

langeal curvature from *Hylobates lar* and *Pongo pygmaeus*.

Analyses also reveal that the relatively small-bodied, highly suspensory taxa (*Ateles* spp. and *Hylobates lar*) share a suite of phalangeal characteristics, including similar values for proximal phalangeal curvature, middle phalangeal curvature, and the index of relative curvature. Both groups display relatively high values for proximal (second only to those of *Pongo pygmaeus*) and middle phalangeal curvature, giving them relative curvature values that approximate 1. Both practice a form of fluid brachiation and possess long curved Digits II–V and a reduced pollex (Garber and Rehg, 1999; Chang et al., 2000; Cant et al., 2001; 2003; Tague, 2002; Youlatos, 2002; Usherwood et al., 2003). Both inhabit tropical rain forests with diverse vegetation, and in any given brachiation bout they may need to adjust to different superstrate diameters, shapes, slopes, and heights (Bertram, 2004). Differences in forest structure may explain a wide range of observed variation in the phalangeal curvature values within this group, but more research is needed to test such hypotheses.

Pongo pygmaeus displays high degrees of both proximal and middle phalangeal curvature which are significantly greater than those seen in the knuckle walkers. Because of the extremely high curvature of their proximal phalanges relative to the marked curvature of their middle phalanges, their values for the index of relative curvature are comparable with those of knuckle walkers, and significantly different from the small-bodied agile brachiators (*Ateles* spp. and *Hylobates lar*) with whom they were expected to group on the basis of their high degree of suspension. However, although they are highly suspensory, *Pongo pygmaeus* do not practice locomotor patterns similar to those of the agile brachiators. Their primary mode of locomotion has been described as quadrumanous climbing which is characterized by usage of both hands and feet to grip branches as they move deliberately throughout the canopy (Tuttle and Cortright, 1988). What must be emphasized here is that *Pongo pygmaeus* can be distinguished from knuckle walkers when both the index of relative curvature and absolute proximal phalangeal curvature values are taken into consideration.

The existence of a clear knuckle walking "signal" in the skeletal anatomy of the hand may prove to be useful given the ongoing debate concerning knuckle walking in hominin evolution (Begun, 1993; Shea and Inouye, 1993; Dainton and Macho, 1999; Richmond and Strait, 2000, 2001a, 2001b; Corruccini and McHenry, 2001; Dainton, 2001; Kelly, 2001; Lovejoy et al., 2001; Richmond et al., 2001). If corresponding elements of the hands of the earliest hominins (or other fossil hominoids) can be found, then the relative curvatures of the proximal and middle phalanges can be assessed. This might open a new venue

for understanding the evolution of hominoid locomotion—one that centers appropriately on those very elements of the hand that can be expected to have supported body mass during ground locomotion in knuckle walkers.

CONCLUSIONS

Past studies of the proximal phalanges have revealed a relationship between degree of suspension and phalangeal curvature, with highly suspensory animals possessing the most curved proximal phalanges. This study confirmed this relationship and determined that a weaker but significant correlation exists between suspensory propensity and manual middle phalangeal curvature. In addition it was determined that the index of relative curvature, taken together with the absolute degree of curvature of the proximal phalanx, provides a functional signal not accessible from either the proximal or middle phalanges alone, that distinguishes knuckle walkers from other quadrupeds as well as from highly suspensory species. Knuckle walkers (*Pan troglodytes*, *Gorilla gorilla gorilla*, and *G. g. beringei*) have relatively little curvature of the middle phalanges coupled with marked curvature of the proximal phalanges (but not as marked as in *Pongo pygmaeus*).

In summary, the highly suspensory *Hylobates lar*, *Ateles* spp., and *Pongo pygmaeus* show considerable curvature of both proximal and middle manual phalanges, knuckle walkers possess relatively straight middle phalanges and curved corresponding proximal phalanges, and nonknuckle walking quadrupeds have relatively curved middle phalanges and straighter proximal phalanges. These differences are consistent with expectations based on the locomotor repertoires of these primates. Knuckle walkers, in particular, place a considerable amount of compressive force onto their manual middle phalanges while knuckle walking and straighter middle phalanges allow for greater phalangeal surface contact with the ground and more even distribution of weight throughout these elements.

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