Phalangeal curvature in a chimpanzee raised like a human: Implications for inferring arboreality in fossil hominins

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Arboreal primates such as chimpanzees exhibit pronounced curvature in their hand and foot phalanges, which is assumed to develop throughout life in response to mechanical loads produced by grasping and hanging from branches. Intriguingly, ancient fossil hominins also exhibit substantial phalangeal curvature, which, too, has been interpreted as a direct result of habitual arboreality during life. Here, we describe the phalangeal curvature of a chimpanzee who was raised during the 1930s in New York City to live much like a human, including by having very few opportunities to engage in arboreal activities. We show that the degree of hand and foot phalangeal curvature in this individual is indistinguishable from that of wild chimpanzees and distinct from humans. Thus, rather than being a direct effect of mechanical loads produced by lifetime arboreal activities, phalangeal curvature appears to be shaped largely by genetic factors. An important implication of this finding is that phalangeal curvature among fossil hominins is evidently best interpreted as a primitive trait inherited from an arboreal ancestral species rather than proof of engagement in arboreal activities during life.

human evolution | locomotion | suspension | climbing | bone curvature

Among the most hotly debated anatomical features of ancient hominin fossils is the marked degree of longitudinal curvature seen in the proximal phalanges of the hands and feet of *Australopithecus*, *Paranthropus*, and certain early *Homo* species (1–6). Across living primates, pronounced phalangeal curvature is found only among taxa that spend substantial amounts of time living and moving in trees, with the greatest curvature among chimpanzees and other species that frequently suspend their bodies below branches (7, 8). This begs an obvious yet contentious question: Does the phalangeal curvature of fossil hominins indicate a significant degree of arboreality, and maybe even frequent suspensory locomotion? At the crux of debates are sharply differing assumptions about the mechanistic causes of phalangeal curvature. Most researchers believe that phalangeal curvature is a phenotypically plastic trait that develops throughout life in response to mechanical loads experienced by hands and feet during arboreal locomotion (9–12). According to this view, hominin phalangeal curvature can be interpreted as direct evidence of routine engagement in arboreal activities during life (13, 14). Other researchers, however, have suggested that phalangeal curvature is probably largely genetically determined, and its presence among fossil hominins may be functionally unimportant and simply a primitive retention from an earlier arboreal primate ancestor (15, 16).

Here, we report a unique piece of evidence that helps clarify the extent to which phalangeal curvature is shaped by arboreal locomotion during life relative to genetic factors. Specifically, we describe the curvature of the hand and foot proximal phalanges of a female chimpanzee named Suzy who was raised to live like a human in New York City during the 1930s (Fig. 1*A*). Suzy was captured in the wild in Africa as a young infant and shipped by freighter in 1931 to Gertrude Lintz, a wealthy socialite and collector of exotic animals. From about 1 y of age, Suzy lived on Lintz's 2-acre estate in Brooklyn, along with hundreds of other animals in Lintz's collection, including more than a dozen other young chimpanzees. As Lintz recounts in her autobiography (17), all of her chimpanzees were deliberately raised to live as similarly as possible to human children. Suzy died in 1941 from a kidney disorder, when she was a young adolescent and roughly 11 y old (18). After her death, Suzy's skeleton was donated to the Peabody Museum of Harvard University.

In Lintz's autobiography (17), she describes the process of raising her chimpanzees to live like humans, which involved training them to wear clothes and shoes, sit in chairs, eat with cutlery and drink from cups, bathe and brush their teeth, use toilets, and sleep on mattress beds with blankets. Most importantly, Lintz raised her chimpanzees to develop human-like patterns of locomotion, by training them to habitually walk bipedally and restricting their chances to engage in arboreal climbing and suspension. Lintz's chimpanzees were kept indoors most of the time, due, in part, to the often cold temperatures of New York. But, even during warm periods, the chimpanzees were only ever allowed a few hours outdoors in the yard per day, during which time they would reportedly play much like human children do, including on swings, teeter-totters, and horizontal bars, as well as occasionally climbing trees. Without a doubt, however, Lintz's chimpanzees participated in very little arboreal locomotion compared to wild chimpanzees, who, as infants (≤5 y old) and juveniles (>5 y to 10 y old), spend, respectively, up to ∼70% and 45% of their time moving in trees (19, 20). During this early ontogenetic period, when wild chimpanzees are highly arboreal, is also when their phalanges become markedly curved (12).

We studied Suzy's hand and foot bones based on the reasoning that, if arboreal locomotion during life is required to develop the marked proximal phalangeal curvature seen in fossil hominins and extant arboreal primates, then the phalanges of a chimpanzee who lived as Suzy did should resemble more closely those of a human than a wild chimpanzee.

Results

The degree of curvature in Suzy's hand and foot proximal phalanges (digits II to V) was assessed by measuring their included angles (Fig. 1*B*). Included angle calculations assume that the

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Data deposition: The data reported in this paper have been deposited in the MorphoSource database, https://www.morphosource.org/.

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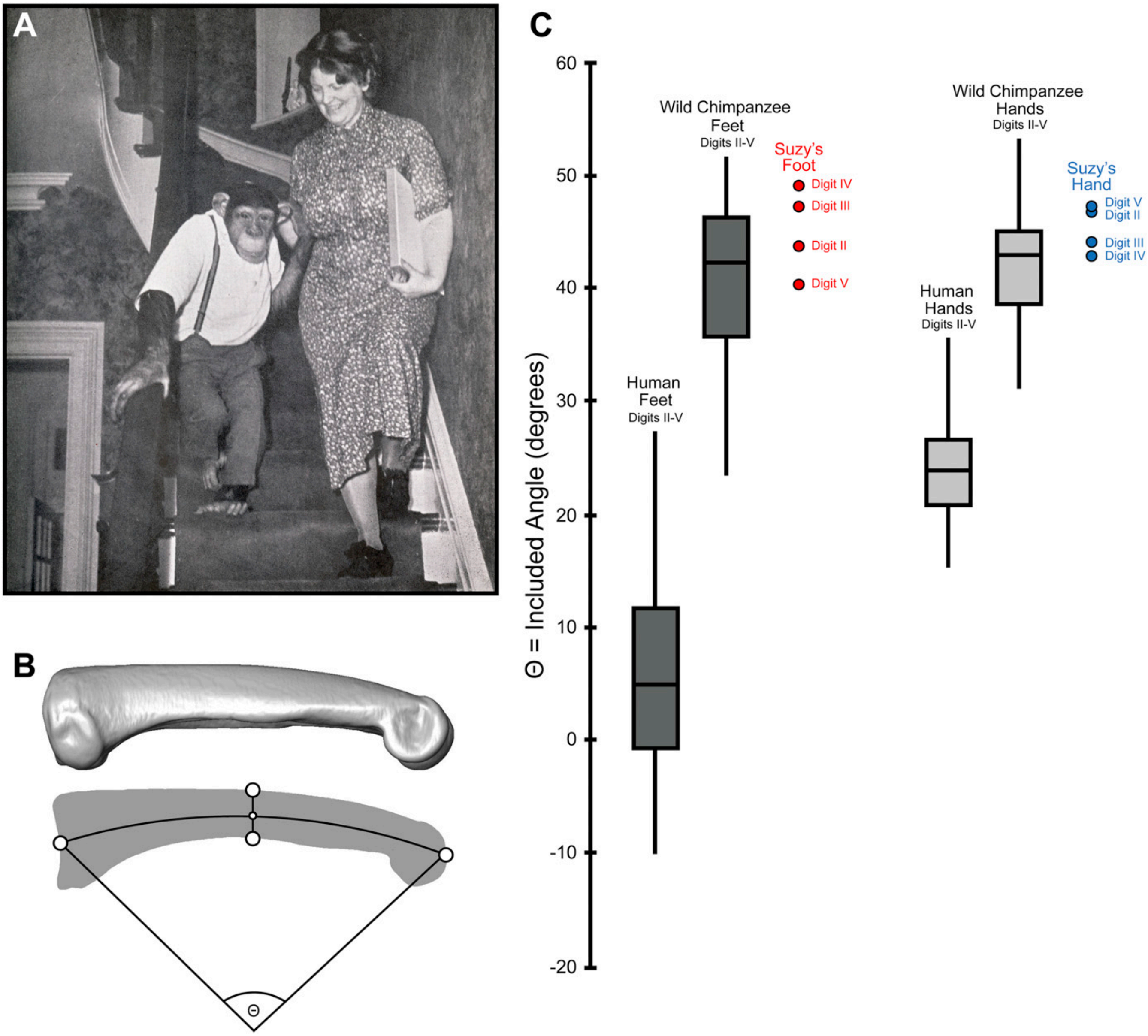

Fig. 1. Suzy and the degree of curvature in her proximal hand and foot phalanges. (*A*) Suzy and Gertrude Lintz at their home in New York City. Reprinted from ref. 17. (*B*) Phalangeal landmarks used to calculate included angle (Θ), a measure of longitudinal bone curvature (7, 9). The surface rendering is from a microcomputed tomography scan of Suzy's right proximal digit II manual phalanx. (*C*) Included angle values for the proximal phalanges of digits II to V in the hands and feet of Suzy, wild chimpanzees, and humans. Values for Suzy are from the right hand and foot. Data from wild chimpanzees (n = 63 and 37 hand and foot bones, respectively) and humans (n = 146 and 71 hand and foot bones, respectively) are from the literature (9).

longitudinal curvature of a given phalanx (i.e., in the dorsopalmar or dorsoplantar direction of the hand and foot, respectively) represents an arc length on the perimeter of a circle (9). For comparison to Suzy, included angle values of hand and foot proximal phalanges (digits II to V) from a sample of wild chimpanzees and humans were obtained from the literature (9).

As shown in Fig. 1*C*, Suzy's hand and foot proximal phalanges exhibit a degree of curvature that is equivalent to the phalanges of wild chimpanzees. Moreover, Suzy's phalangeal curvature levels are outside the range of the human sample.

Discussion

Despite having been raised in New York City to live much like a human, with very few opportunities to engage in arboreal locomotion, Suzy developed a degree of phalangeal curvature in her hands and feet that is indistinguishable from that of wild chimpanzees and distinct from humans. This finding is inconsistent with the hypothesis that routine arboreal locomotion during life is necessary to develop the pronounced phalangeal curvature observed in fossil hominins and extant arboreal primates, including chimpanzees (9–14). Although mechanical loads produced by locomotion may have some influence on curvature development (21), the striking resemblance of Suzy's finger and toe bones to those of wild chimpanzees indicates that genetic factors likely play a much greater role in determining phalangeal curvature than environmental factors. Consequently, the results of this study provide support for the idea that the marked phalangeal curvature of fossil hominins is best interpreted as a primitive trait inherited from an arboreal ancestral species (15,

16) rather than a direct sign of engagement in arboreal activities during life (13, 14).

Evidence that phalangeal curvature is determined mainly by genetic factors does not refute the hypothesis that the locomotion of extinct hominins included frequent arboreality. Such evidence only indicates that phalangeal curvature alone does not prove the importance of arboreal activities within the locomotor repertoire of a hominin species. Assessing the behavioral significance of any single primitive retention in a fossil species is inevitably challenging, since the trait may have been actively maintained by stabilizing selection because it was still functionally important, or the trait may have become functionless and been retained simply because it was not selected against (16). If arboreality was common among extinct hominins, then phalangeal curvature would have been useful for minimizing diaphyseal bending strains produced by grasping and hanging from branches (11, 22). Yet, if phalangeal curvature was no longer functionally important to a hominin species, it might not have compromised bipedal locomotion or manual dexterity enough to have been under strong negative selection (16). It is thus impossible to resolve whether phalangeal curvature was functionally important or unimportant to ancient hominins without taking into account additional anatomical traits relevant to locomotor performance (23).

Suzy is obviously only a sample size of one, so some prudence is warranted when considering the results of this study. To our knowledge, none of the skeletons of Lintz's other chimpanzees were preserved for research after their death. Moreover, in hindsight, Lintz's goal of raising her chimpanzees to live like humans was ethically very problematic, and it is thus unlikely that such an endeavor will ever be repeated. Nevertheless, future research is needed to confirm the important role that genetic factors play in shaping phalangeal curvature relative to mechanical loading and other environmental factors. Until then, we hope this unusual case study from Suzy will help caution interpretations of arboreality among fossil hominins from relying on phalangeal curvature alone.

Materials and Methods

The Peabody Museum catalog number for Suzy's skeleton is 42-35-50/N3942.0. Included angle values for Suzy's phalanges were calculated using an established set of three-dimensional landmark coordinates (7) based on surface renderings obtained from high-resolution microcomputed tomography scanning (voxel resolution: 0.1044 and 0.1025 mm for hand and foot bones, respectively) at Harvard University's Center for Nanoscale Systems.

Data Availability. Microcomputed tomography images of Suzy's phalanges are available at https://www.morphosource.org/Detail/SpecimenDetail/Show/specimen_id/30385.

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1. R. L. Susman, N. Creel, Functional and morphological affinities of the subadult hand (O.H. 7) from Olduvai Gorge. *Am. J. Phys. Anthropol.* **51**, 311–332 (1979).
2. J. T. Stern Jr., R. L. Susman, The locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* **60**, 279–317 (1983).
3. B. G. Richmond, W. L. Jungers, *Orrorin tugenensis* femoral morphology and the evolution of hominin bipedalism. *Science* **319**, 1662–1665 (2008).
4. T. L. Kivell, J. M. Kibii, S. E. Churchill, P. Schmid, L. R. Berger, *Australopithecus sediba* hand demonstrates mosaic evolution of locomotor and manipulative abilities. *Science* **333**, 1411–1417 (2011).
5. T. L. Kivell *et al*., The hand of *Homo naledi*. *Nat. Commun.* **6**, 8431 (2015).
6. B. G. Richmond *et al*., The upper limb of *Paranthropus boisei* from Ileret, Kenya. *J. Hum. Evol.* **141**, 102727 (2020).
7. T. R. Rein, The correspondence between proximal phalanx morphology and locomotion: Implications for inferring the locomotor behavior of fossil catarrhines. *Am. J. Phys. Anthropol.* **146**, 435–445 (2011).
8. B. A. Patel, S. A. Maiolino, "Morphological diversity in the digital rays of primate hands" in *The Evolution of the Primate Hand*, T. L. Kivell *et al*., Eds.(Springer, New York, NY, 2016), pp. 55–100.
9. J. T. Stern Jr., W. L. Jungers, R. L. Susman, Quantifying phalangeal curvature: An empirical comparison of alternative methods. *Am. J. Phys. Anthropol.* **97**, 1–10 (1995).
10. W. L. Jungers *et al*., "Ecomorphology and behavior of giant extinct lemurs from Madagascar" in *Reconstructing Behavior in the Primate Fossil Record*, J. M. Plavcan *et al*., Eds. (Kluwer, New York, NY, 2002), pp. 371–411.
11. B. G. Richmond, Biomechanics of phalangeal curvature. *J. Hum. Evol.* **53**, 678–690 (2007).
12. K. A. Congdon, Interspecific and ontogenetic variation in proximal pedal phalangeal curvature of great apes (*Gorilla gorilla, Pan troglodytes*, and *Pongo pygmaeus*). *Int. J. Primatol.* **33**, 418–427 (2012).
13. E. Harmon, "Age and sex differences in the locomotor skeleton of *Australopithecus*" in *The Paleobiology of Australopithecus*, K. E. Reed, J. G. Fleagle, R. E. Leakey, Eds. (Springer, Dordrecht, The Netherlands, 2013), pp. 263–272.
14. T. L. Kivell, Evidence in hand: Recent discoveries and the early evolution of human manual manipulation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **370**, 20150105 (2015).
15. B. M. Latimer, "Locomotor adaptations in *Australopithecus afarensis*: The issue of arboreality" in *Origine(s) de la Bipédie chez les Hominidés*, Y. Coppens, B. Senut, Eds. (Centre National de la Recherche Scientifique, Paris, France, 1991), pp. 169–176.
16. C. V. Ward, Interpreting the posture and locomotion of *Australopithecus afarensis*: Where do we stand? *Am. J. Phys. Anthropol.* **45** (suppl. 35), 185–215 (2002).
17. G. D. Lintz, *Animals Are My Hobby*, (McBride & Co., New York, NY, 1942).
18. E. A. Hooton, H. W. Nissen, "Correspondence between EA Hooton and HW Nissen dated 11/26/1941" (Peabody Museum archives 995-1, box 19, Harvard University, Cambridge, MA, 1941).
19. D. M. Doran, The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: A case study of paedomorphism and its behavioral correlates. *J. Hum. Evol.* **23**, 139–157 (1992).
20. L. A. Sarringhaus, L. M. MacLatchy, J. C. Mitani, Locomotor and postural development of wild chimpanzees. *J. Hum. Evol.* **66**, 29–38 (2014).
21. L. E. Lanyon, The influence of function on the development of bone curvature: An experimental study on the rat tibia. *J. Zool.* **192**, 457–466 (1980).
22. N. H. Nguyen, D. H. Pahr, T. Gross, M. M. Skinner, T. L. Kivell, Micro-finite element (μFE) modeling of the siamang (*Symphalangus syndactylus*) third proximal phalanx: The functional role of curvature and the flexor sheath ridge. *J. Hum. Evol.* **67**, 60–75 (2014).
23. J. T. Stern Jr., R. L. Susman, ""Total morphological pattern" versus the "magic trait": Conflicting approaches to the study of early hominid bipedalism" in *Origine(s) de la Bipédie chez les Hominidés*, Y. Coppens, B. Senut, Eds. (Centre National de la Recherche Scientifique, Paris, France, 1991), pp. 99–111.