21 November 1969, Volume 166, Number 3908 SCIENCE

Knuckle-Walking and the Problem of Human Origins

Studies on the hands of great apes and man lead to reevaluation of theories on hominoid evolution.

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While the taxonomic affinity of man and the African apes is generally undisputed, anthropologists have widely disparate opinions on the extent to which the common ancestors of man, chimpanzee, and gorilla resembled living pongids. Many authors proffer sketches of hominid evolution that include apelike stages (*1*), but few of these include details of the mechanisms whereby apelike forms evolved into more manlike apes which, in turn, culminated in man. Similarly, authors who suggest alternative theories that emphasize non-apelike precursors (*2*) have difficulty in delimiting the biomechanical and environmental changes involved in the transition from preman to man.

Several theories that have received special notice in discussions on human origins accentuate a "troglodytian" or great-ape stage immediately preceding the emergence of man, the plantigrade biped (*1*). In this article I assess the possibility of a troglodytian stage in human phylogeny in the light of recent behavioral and morphological studies on the hands of the great apes and man.

Brachiationist Theory

In his initial formulation of an evolutionary pathway that possibly culminated in man, Sir Arthur Keith proposed three "stages": hylobatian, troglodytian, and plantigrade (*3*). Arboreal quadrupedal monkey-like primates evolved into "brachiating" gibbon-like apes that had a predilection for suspending themselves in orthograde postures beneath branches; these were Keith's hypothetical hylobatians.

Keith also emphasized brachiation in the second stage of his theory; the major difference between "hylobatians" and "troglodytians" was the greater size of the latter.

Man also is orthograde in posture, but instead of hanging ape-wise from a superstratum he stands bipedally on a substratum.

Keith and later brachiationists could point to many features, particularly in the forelimb (upper limb) and trunk, that are shared by men and apes. For example, the "brachiators," like man, have long arms relative to trunk length, and long forearms in particular; long second to fifth fingers; thumbs of notable absolute size (but short relative to total hand length in apes); broad, anteroposteriorly flattened chests; strongly angled ribs; protrusion of the vertebral column into the chest cavity; a broad sternum, with progressive fusion of the sternal elements in adults; long collarbones; shoulder blades located on the posterior aspects of the chest wall; large acromial processes on the shoulder blades; laterally directed shoulder joints; considerable mobility of the shoulder and elbow joints; a relatively short truncal segment of the vertebral column—in particular, a short lumbar region; no tail; and a smaller coccyx and more sacral vertebrae than other anthropoid primates have (*4*).

In addition to the general bodily proportions and skeletal features listed above, the "brachiators" have in common certain characteristics of soft parts that may be related to their semierect and orthograde posturing. These include large muscles that raise the arm and rotate the shoulder blade (*5*); a characteristic arrangement of muscle fibers in the diaphragm; characteristic positions of the heart, lungs, and other organs in the body cavity; the close attachment of some abdominal organs to the diaphragm and posterior abdominal wall; a muscular pelvic diaphragm in the pelvic outlet; and lumbar back muscles that are smaller and show less fasciculation than those of other anthropoid primates (*3*).

Of the three great apes (chimpanzee, gorilla, and orangutan), the chimpanzee is generally considered by brachiationists the form that most closely resembles the prototypic large-bodied ape near the base of hominid phylogeny. Gorillas generally are considered too large to serve as hypothetical ancestral apes. Orangutans are too highly specialized in a unique mode of arboreal habitation to represent a phase in the human lineage.

Terrestriality in Apes

The terrestrial habits of the African apes (chimpanzees and gorillas) have been noted by nearly all authors who have discussed their relevance to an understanding of human evolution, but the evolutionary significance of their terrestriality has been obscured by oversimplified concepts of the apes as "brachiators." Until recently this problem was further obfuscated by an insufficiency of naturalistic behavioral

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studies of the great apes. As recently as 1967, the locomotion of chimpanzees and gorillas was classified as "modified brachiation" in an authoritative handbook of living primates (*6*); accordingly, "modification" in the locomotor activities of great apes primarily referred to a "chimpanzee and orangutan type of brachiation" (*6*). This classification does not adequately consider the unique terrestrial locomotive patterns of the African apes, which distinguish them from all other living primates.

Success in elucidating the problem of a troglodytian phase in human evolution depends upon refinement of our understanding of the evolutionary biology of the African apes. Thus we may ask, what are the adaptive modes of chimpanzees and gorillas and what features of their locomotive behavior and morphology may be accentuated in discussions on the role of "troglodytians" in human phylogeny?

Fig. 1. Juvenile gorilla in knuckle-walking locomotor posture. Note the fully pronated posture of the left hand and the hyperextended position of the metacarpophalangeal joints of the left-hand fingers. (Inset) Knuckle pads on the backs of the middle phalanges of a gorilla hand. [Photographs from Yerkes Regional Primate Research Center]

Chimpanzees and gorillas are basically forest dwellers, though chimpanzees have been observed to venture sporadically into sparsely wooded areas (*7*). Mountain gorillas in eastern Africa are predominantly terrestrial in foraging, feeding, nesting, and locomotive activities (*8*). Little is known about the activity patterns of western and eastern lowland gorillas, but there is evidence that they are somewhat more arboreal, especially in feeding and nesting behavior, than mountain gorillas (*8*). Chimpanzees are usually arboreal in feeding and nesting, although they have been observed to eat grasses and other ground plants during the dry season in Tanzania (*9*).

The African apes normally move from one feeding or nesting site to another on terrestrial pathways. They are fundamentally semierect quadrupeds, assuming knuckle-walking postures both on the ground and on stout horizontal branches, even high in trees (*8, 9*). In the knuckle-walking posture the distal and middle segments of the fingers are flexed and the proximal segments are hyperextended. The palm is elevated and aligned with the wrist and forearm (Figs. 1 and 2). Thus, in knuckle-walkers only the backs of the middle segments of the fingers come in contact with the substratum (*10, 11*). These areas of the fingers are covered by "knuckle pads" that exhibit all features of typical frictional skin—namely, absence of pilosebaceous systems and the development of dermatoglyphic patterns, with eccrine sweat glands opening on the peaks of the epidermal ridges [(*12*) and Fig. 1].

Biomechanics of Knuckle-Walking

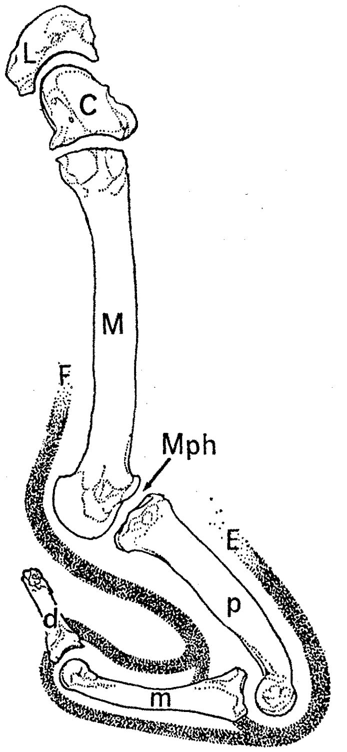
Many unique features of the bones, ligaments, and muscles in the hands of African apes are correlated with the biomechanical demands of knuckle-walking (*11*). In the knuckle-walking posture, the hand of a large-bodied ape is subjected to considerable compressive force, which tends to produce collapse downward at the wrist and metacarpophalangeal joints. The associated configurations of the articular surfaces in these joints increase their integrity in close-packed positions. Furthermore, the ligaments and tendons in the hand are so strengthened and so positioned that they absorb the tensile components of stresses incurred in knuckle-walking.

For instance, the carpal bones in the wrist articulate snugly with one another. Special bony ridges are present on the dorsal aspect of the distal articular surface of the radius and the scaphoid bone. In the close-packed position these ridges are apposed, thereby increasing the stability of the wrist when it is extended. The palmar portion of the wrist joint capsule is extremely thick, due to the development of oblique and horizontally directed ligaments that bind the carpal bones to the radius and ulna, to metacarpal bones II to V, and to each other (*11, 13*).

The hyperextended posture (Fig. 2) of the proximal segments of the fingers makes the metacarpophalangeal joints even more susceptible than the wrist to downward collapse. Considerable hyperextension at these joints occurs where the articular surfaces of the metacarpal head extend onto their dorsal aspects [(*11*) and Fig. 3]. A prominent transverse ridge is located at the base of the dorsal articular surface of each metacarpal head (Fig. 3). As in the wrist, these ridges are important for maintaining the integrity of the metacarpophalangeal joints in the close-packed position of hyperextension.

Although the bone-ligament mechanisms of the wrist are probably sufficient to maintain its integrity in static knuckle-walking postures, the flexor muscles may provide important supplementary supporting forces during knuckle-walking progression. These muscles are prominently developed in chimpanzees and gorillas [(*11*) and Fig. 4a].

The metacarpophalangeal joints of the second to fifth fingers are supported by the powerful long digital flexor tendons that are closely apposed to their palmar surfaces. In chimpanzees and gorillas, these tendons are shortened; the distal segments of the fingers cannot be fully extended when the proximal segments of the fingers or the wrist are bent backward (*11*). The hyperextended position of the proximal segments of the fingers probably places the long flexor muscles in a state of passive stretch. This not only assists in supporting the metacarpophalangeal joints during the knuckle-walking stance but also provides some propulsive force at the distal extremity of the forelimb as the hand clears the ground during knuckle-walking strides.



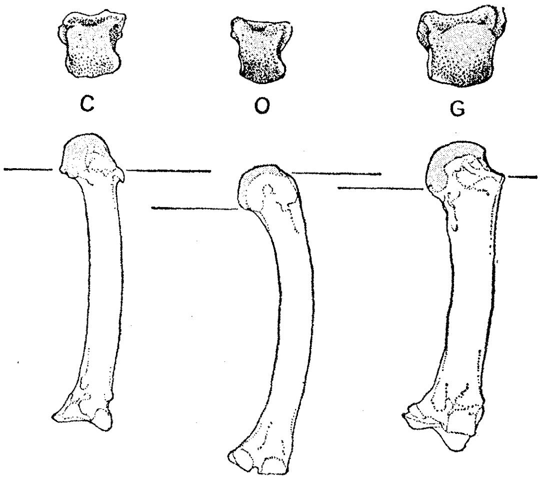
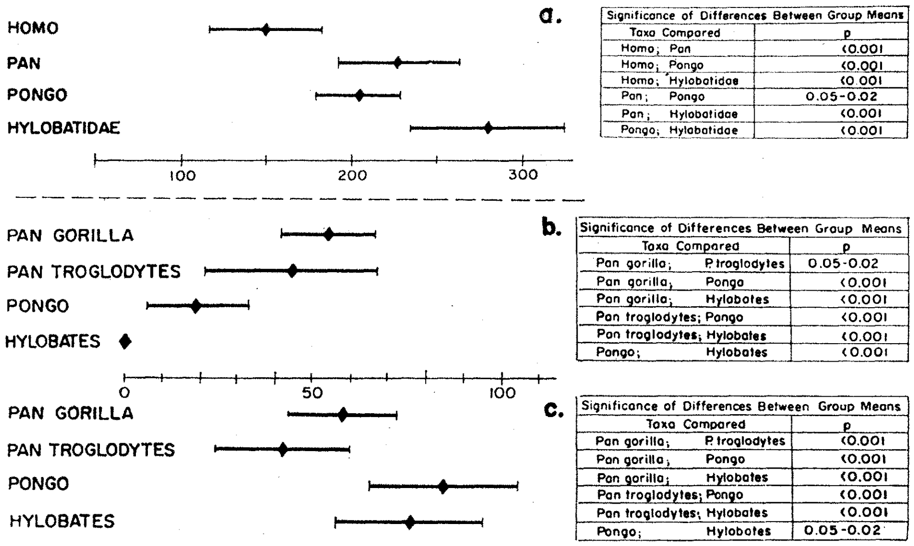


Fig. 2 (left). "Exploded" third digital ray and associated carpal bones and tendons in the hand of an adult female chimpanzee in the knuckle-walking posture. Note that considerable hyperextension is possible at the metacarpophalangeal joint (*Mph*) due to the backward extension of the articular surface of the metacarpal head (*M*). (*L*) Lunate; (*C*) capitate; (*p*) proximal phalanx; (*m*) middle phalanx; (*d*) distal phalanx; (*E*) extensor tendon complex; (*F*) flexor tendon complex. Fig. 3 (right). Medial aspect (bottom row) and distal end (upper row) of the third metacarpal bone of the chimpanzee (*C*), orangutan (*O*), and gorilla (*G*). The distal articular surfaces are indicated by shading. Horizontal lines indicate the extent of the anterior and posterior articular areas. Note the limited posterior extension of the distal articular surface and the greater curvature of the metacarpal in the orangutan.



Significance of Differences Between Group Means	
Taxa Compared	p
Homo; Pan	<0.001
Homo; Pongo	<0.001
Homo; Hylobatidae	<0.001
Pan; Pongo	0.05-0.02
Pan; Hylobatidae	<0.001
Pongo; Hylobatidae	<0.001

Significance of Differences Between Group Means	
Taxa Compared	p
Pan gorilla; P. troglodytes	0.05-0.02
Pan gorilla; Pongo	<0.001
Pan gorilla; Hylobates	<0.001
Pan troglodytes; Pongo	<0.001
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Pan gorilla; Hylobates	<0.001
Pan troglodytes; Pongo	<0.001
Pan troglodytes; Hylobates	<0.001
Pongo; Hylobates	0.05-0.02

Fig. 4. (a) The relative weights of total flexor muscles in the forearms of man (*Homo*), chimpanzees and gorillas (*Pan*), orangutans (*Pongo*), and gibbons and siamangs (Hylobatidae), expressed as percentages of the weights of total extensor muscles in the forearm: (total flexors × 100)/(total extensors). (b) Degrees of backward extension (dorsiflexion) of the metacarpophalangeal joints in digits II to V of gorillas (*Pan gorilla*), chimpanzees (*Pan troglodytes*), orangutans (*Pongo*), and gibbons (*Hylobates*). (c) Degree of backward extension (dorsiflexion) of the wrist in gorillas (*Pan gorilla*), chimpanzees (*Pan troglodytes*), orangutans (*Pongo*), and gibbons (*Hylobates*). Means and 90 percent fiducial limits are indicated by diamonds and horizontal bars, respectively. The significance of the differences between group means were determined by *t*-tests.

Patterns of Knuckle-Walking

In the foregoing discussion the common features related to knuckle-walking in the African apes are outlined. Now let us note some ways in which the knuckle-walking habitus of gorillas differs from that of chimpanzees—a situation not unexpected in view of the greater size and the advanced terrestriality of gorillas.

First, the bony and ligamentous structures that are prominently developed in knuckle-walkers have their most notable expression in gorillas (*11*).

Second, while gorillas are indistinguishable from chimpanzees with respect to the relative development of major muscle groups in the forearm and hand, they are notably distinct from chimpanzees in possessing nearly equal development of total hand and total foot musculature. Chimpanzees, by contrast, possess a greater mass of total foot muscles than of total hand muscles [(*11*) and Fig. 5]. This may be related to the fact that chimpanzees climb trees more often than gorillas do.

Third, studies of captive chimpanzees and gorillas indicate that the gorillas consistently place all four fingers of a hand on the ground when knuckle-walking. In chimpanzees, the third and fourth fingers always make contact with the ground during each forelimb stride but the second and fifth digits are sometimes flexed and clear of the ground, with no apparent impairment of gait (*11*). I have not observed gorillas knuckle-walking with the second or fifth digit clear of the ground.

Finally, there are certain differences in the positioning of the hand. Individual chimpanzees assume a wide variety of knuckle-walking postures. They may fully pronate the hand, to a position approximately perpendicular to the line of travel; more frequently, however, they partially pronate it, to a position oblique or nearly parallel to the line of travel. By contrast, gorillas (even at an early age) are likely to fully pronate the hand during knuckle-walking (Fig. 1). This gives gorillas a characteristic square-shouldered appearance, with shoulders jutting forward and elbows projecting laterally (*11*).

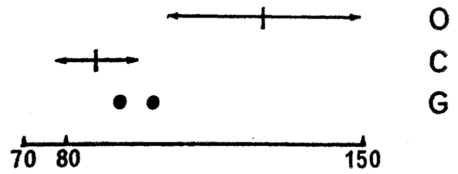

Fig. 5. The relative weights of total forearm and hand muscles in orangutans (*O*), chimpanzees (*C*), and gorillas (*G*), expressed as percentages of total leg and foot musculature: (total forearm and hand muscles × 100)/(total leg and foot muscles). Means (vertical bars) and 90-percent fiducial limits (horizontal arrows) are indicated for samples of orangutan and chimpanzee. The dots represent individual specimens of gorilla. The weights for orangutans are significantly different from those for the African apes.

In the gorilla, pronation of the hand is effected by medial rotation of the shoulder and radioulnar joints. Differences in shoulder morphology between chimpanzees and gorillas (*14*) may partially explain the different knuckle-walking postures of the two forms. In addition, preliminary studies on the radioulnar joints of gorillas indicate that gorillas cannot supinate the hand to the extent that chimpanzees can (*11*). Thus care must be taken to avoid overgeneralization in considering hand posturing in the knuckle-walking apes (*15*).

Evolution of Knuckle-Walking

Numerous anatomical details in chimpanzees and gorillas attest to the fact that they evolved from ancestors that were adapted for arboreal climbing and probably also for suspensory posturing (*3–5*). Furthermore, chimpanzees and, to a lesser extent, gorillas are active climbers today. Chimpanzees and young gorillas occasionally hang beneath, and arm-swing along, branches while foraging, playing, and engaging in agonistic displays (*8, 9*).

The question thus arises, In what manner did the arboreal ancestry of the African apes predispose them to knuckle-walking? Keith and other brachiationists believed that the large size of the "troglodytians" may have inclined them toward terrestriality (*3*).

The hands of great apes were commonly portrayed as inflexible anatomical hooks adapted for brachiation (*4, 10, 16*). Hence it was supposed that, when on the ground, pongids would have little choice but to walk on the back surfaces of their hooked hands.

But orangutans, gibbons, spider monkeys, and other highly arboreal primates can flatten out their hands and assume palmigrade postures when forced to the ground [(*11*) and Fig. 6]. In natural habitats these primates engage in arm-swinging more frequently than African apes do. Furthermore, studies on anesthetized orangutans and gibbons reveal that, unlike African apes, they have flexible wrists (Fig. 4c) and that they lack the general permanent shortness of the long digital flexor tendons that is characteristic of chimpanzees and gorillas (*11*). Thus, the hands of orangutans and gibbons are *not* inflexible anatomical hooks and are poorly designed for knuckle-walking.

During the adaptive shift to terrestriality, the long-fingered troglodytian ancestors of the African apes were probably faced with the following alternative: they could either adopt flexed-finger postures or undergo progressive shortening of the fingers. Long fingers are biomechanically inefficient and generally maladaptive in terrestrial primates. If the position of the fingers is such that they act effectively as propulsive levers—that is, if the extended fingers are parallel to the line of travel when the hand is pronated and medially rotated—they will be subjected to considerable shear stress owing to their length. Thus, terrestrial monkeys, for instance, have fingers that are short by comparison with those of arboreal monkeys (*17*).

When orangutans, gibbons, and spider monkeys assume full palmigrade postures during terrestrial locomotion, they rotate their hands laterally so that the extended fingers are markedly angled or perpendicular to the line of travel [(*11*) and Fig. 6]. This permits them to use the forelimbs as supporting props without the extended fingers' sustaining the injurious stresses that would otherwise be inevitable.

But in long-handed troglodytians, outwardly projecting fingers would be inefficient on the forest floor because they would snag on vegetation and other protrusions. Fully palmigrade locomotive postures may be observed in captive orangutans because cage floors offer little obstruction to their projecting hands. But orangutans generally flex their fingers during locomotion even in situations where they need not do so (*11*).

In summary, on the basis of biomechanical considerations and the behavior of living long-handed primates, it may be inferred that the troglodytian ancestors of the African apes probably assumed flexed-finger postures during the initial shift to terrestriality.

The flexed-finger postures of early troglodytians may have been similar to the "fist-walking" or "modified palmigrade" postures of living orangutans (Fig. 7). During fist-walking, orangutans flex their long fingers so that the backs of the *proximal* segments make contact with the ground (*11*). In captive animals, fist-walking is observed much more frequently than palmigrade posturing. Free-ranging orangutans fist-walk along large horizontal branches (*18*) and use their fists to pack down nesting materials (*19*).

In some phases of the fist-walking locomotive cycle, the palm and wrist are aligned with the forearm. But in young orangutans, the wrist bends backward to a notable extent when the load shifts onto the supporting hand [(*11*) and Fig. 8]. In some adult fist-walkers, the powerfully developed flexor muscles of the wrist may limit this backward extension.

If the early terrestrial troglodytians were initially fist-walkers, one of the first changes that probably occurred as they advanced toward knuckle-walking was the development of intrinsic supporting mechanisms in the wrist. These features would permit alignment of the forearm, wrist, and palm with minimum exertion by the flexor muscles.

Biomechanically, the most challenging aspect of the adaptive shift by incipient knuckle-walkers probably involved elevation and hyperextension of the proximal digital segments, so that the load rested exclusively on the middle segments of the flexed fingers.

If early troglodytians had markedly curved fingers, resembling those of orangutans or gibbons, major modifications in the configuration of the bones and joints must have occurred before knuckle-walking could be implemented in their terrestrial descendants. Although Asian apes can fully extend their fingers, the fingers generally remain curved. In passive orangutans and gibbons, the proximal segments of the fingers cannot be bent backward very far beyond the normal extended position wherein the palm and fingers form a continuous concave curve at the metacarpophalangeal joints (Fig. 4b). This curvature is determined not only by the shape of the bones themselves but also by the permanent flexion set of their articular surfaces in the joints (*11*).

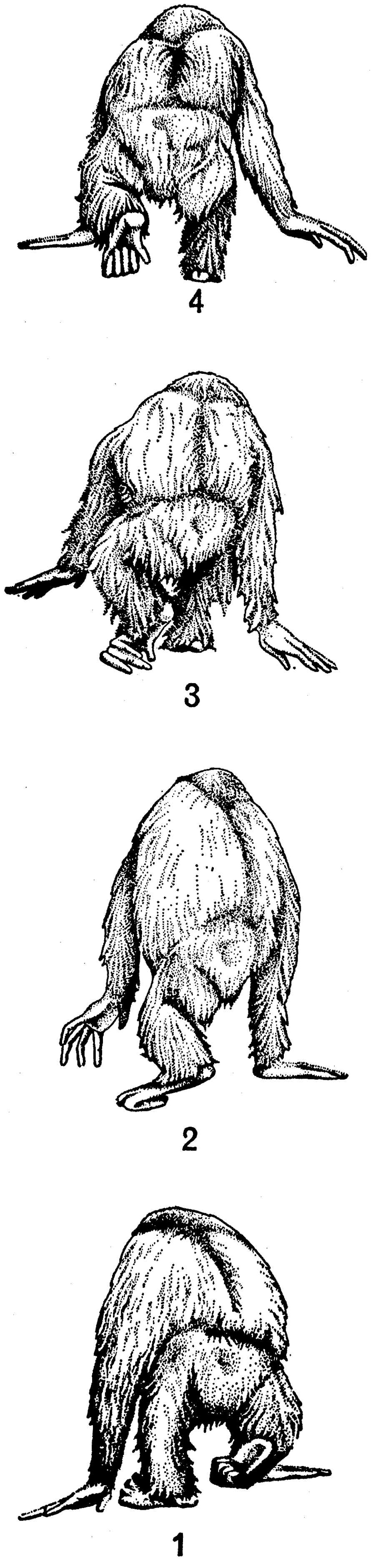

Fig. 6. Posterior view of orangutan engaged in rapid palmigrade locomotion. (1) Right forelimb and left hindlimb serve as supports while left hand is elevated and right foot is swung forward. (2) Right forelimb serves as chief supporting prop just prior to contact by right foot. Left forelimb is swung forward and left hindlimb is elevated. (3) Right hindlimb serves as major supporting prop as left forelimb and left hindlimb are swung forward. Right forelimb is elevated. (4) Left hand contacts the ground. Left forelimb and right hindlimb are principal supports. Right hand and left foot are clear of the ground.

The assumption of modified palmigrade postures may have provided the selective complex whereby the bones and joints of the fingers in early terrestrial troglodytians became prospectively adapted for knuckle-walking. In the modified palmigrade posture the palm rests on the ground with the proximal segments of the fingers extended (or slightly hyperextended) and the middle and distal segments of the fingers flexed [(*11*) and Fig. 7]. If the early troglodytians initially assumed modified palmigrade postures, changes in the wrist to restrict extension probably followed changes in the digits, because the wrist must be bent backward markedly in order for the animal to assume these postures.

In summary, two theoretical pathways are suggested for the evolution of knuckle-walking: (i) fist-walking → incipient knuckle-walking → consistent knuckle-walking, and (ii) modified palmigrade locomotion → incipient knuckle-walking → consistent knuckle-walking. Perhaps future discoveries of fossil hands and biomechanical studies of the sort now in progress at the University of Chicago (*20*) will indicate which, if either, of these models approximates the actual evolutionary pathway.

The Pongid Radiation

The extent to which the common ancestors of the three great apes were adapted for suspensory posturing and locomotion cannot be determined with certainty. The fossil record contains little evidence that is of assistance in the reconstruction of postcranial anatomy in ancestral pongids. Available remains of pongids from Miocene and early Pliocene deposits generally do not exhibit advanced anatomical features related to suspensory posturing (*11, 21*). Postcranial remains of pongids from subsequent periods are completely lacking.

Many features that are commonly associated with brachiation have evolved in parallel at least three and possibly more than five times in the Primates. Gibbons and siamangs are uniquely adapted for ricochetal armswinging (*11*). Zoogeographical and anatomical evidence clearly documents independent evolution of adaptations for suspensory posturing in South American ateline monkeys (*4*). Substantial anatomical evidence also supports the inference that features related to suspensory posturing developed independently in *Oreopithecus* (*22*).

In contrast with these primate lineages, determining the expression of parallel evolution in the great apes is extremely problematical due to the paucity of paleontological and paleozoogeographical data. The most parsimonious hypothesis, based on comparative studies of living pongids, portrays the common ancestors of the great apes as possessing notable prospective adaptations for suspensory posturing and locomotion.

The divergence of orangutans and the African apes probably evinces a *dichotomous* pattern of evolution (*23*), wherein no living species closely resembles the common ancestral species. Whereas ancestral chimpanzees and gorillas experienced an adaptive shift to terrestriality, ancestral orangutans advanced, and specialized in, a unique mode of four-digit prehension and suspensory posturing (*11*).

Fig. 7. Juvenile orangutan progressing with right hand in fist-walking posture and left hand in modified palmigrade posture.

Orangutans are easily the heaviest of strictly arboreal mammals. They prefer swamp-forest habitats in which the forest floor is seasonally or permanently flooded and thereby rendered unsuitable as a substratum for locomotion (*18*). The culmination of trends toward advanced ability to climb and cling in the forest canopy may have occurred during late Tertiary and Pleistocene times in response to periodic flooding of the Sunda Shelf region of Southeast Asia (*11, 24*).

The shortest, most parsimonious pathway for evolution of the African apes would be the derivation of gorillas, through increasingly advanced adaptation to terrestriality, from smaller apes not unlike living chimpanzees. Thus, the African apes evince an *excurrent* pattern of evolution (*23*) wherein the ancestral form of a species is represented among its closest living relatives.

The times of emergence of the three pongid lineages cannot be determined with certainty on the basis of available paleontological evidence. However, numerous teeth and associated cranial remains of *Dryopithecus* from Miocene and early Pliocene deposits in East Africa, South Asia, and Europe demonstrate remarkable similarities to corresponding parts of living apes, especially the African forms (*25*).

Simons and Pilbeam suggest that the ancestry of chimpanzees and gorillas may be discerned in *different* species of *Dryopithecus* (*25*). These workers believe that the separation of the two main lines of African apes occurred in middle or even early Miocene times, some 18 to 25 million years ago (*25*). Since available postcranial remains of *Dryopithecus* possess few features related to advanced suspensory posturing, it follows (i) that gorillas and chimpanzees evolved many features related to "brachiation" in parallel and (ii) that their adaptations to knuckle-walking are also parallelisms.

This interpretation of the fossil evidence is not consistent with the parsimonious evolutionary pathway that is inferred on the basis of comparative studies of living pongids. Final resolution of this problem depends upon further discoveries and studies on postcranial remains of *Dryopithecus*, especially the large species, and of later fossil pongids. In addition, more detailed studies on variability in the dentitions and skulls of living and fossil pongids should be made, to provide broader bases for inference on possible evolutionary pathways.

Thus, until more convincing evidence is brought forward to support extreme parallelisms in the closely related species of African apes, it seems distinctly possible that only one species of *Dryopithecus* gave rise to the common ancestor of these forms. Despite the frequent occurrence of parallel evolution in the locomotive systems of primates, the similarities between chimpanzees and gorillas are so particular that I now favor the parsimonious view of evolution in the African apes.

Were Man's Ancestors Knuckle-Walkers?

If elucidating the evolution of extant apes presents many problems, elucidating the derivation of man from hypothetical apes presents far more. Several schools of thought have arisen in response to the fascinating challenge of man's theoretical origins. For convenience their adherents may be loosely grouped and termed brachiationists, antibrachiationists, and prebrachiationists.

The brachiationists (*26*) hold the view that man evolved from ancestral apes that were notably advanced with respect to suspensory posturing and arm-swinging. The antibrachiationists (*27*), on the other hand, suggest that the features of upper limb and trunk that man shares with the "brachiating apes" are parallelisms that evolved (through undetermined mechanisms) in direct response to orthograde bipedalism.

The prebrachiationists (*28*) occupy more or less conservative positions between these two poles. They suggest that, although the common ancestor of man and the troglodytian apes was not an advanced brachiator, it possessed notable evolutionary tendencies toward this pattern of movement and toward the associated morphology. Accordingly, the prebrachiationists also must grant a certain degree of parallel evolution in the upper limb and trunk of man and apes.

The diversity of locomotive patterning in living apes and the observation that arm-swinging is an infrequent component in the behavioral repertoires of African apes indicate that reexamination of the chimpanzee model of human ancestry might be profitable. In particular, recognition of knuckle-

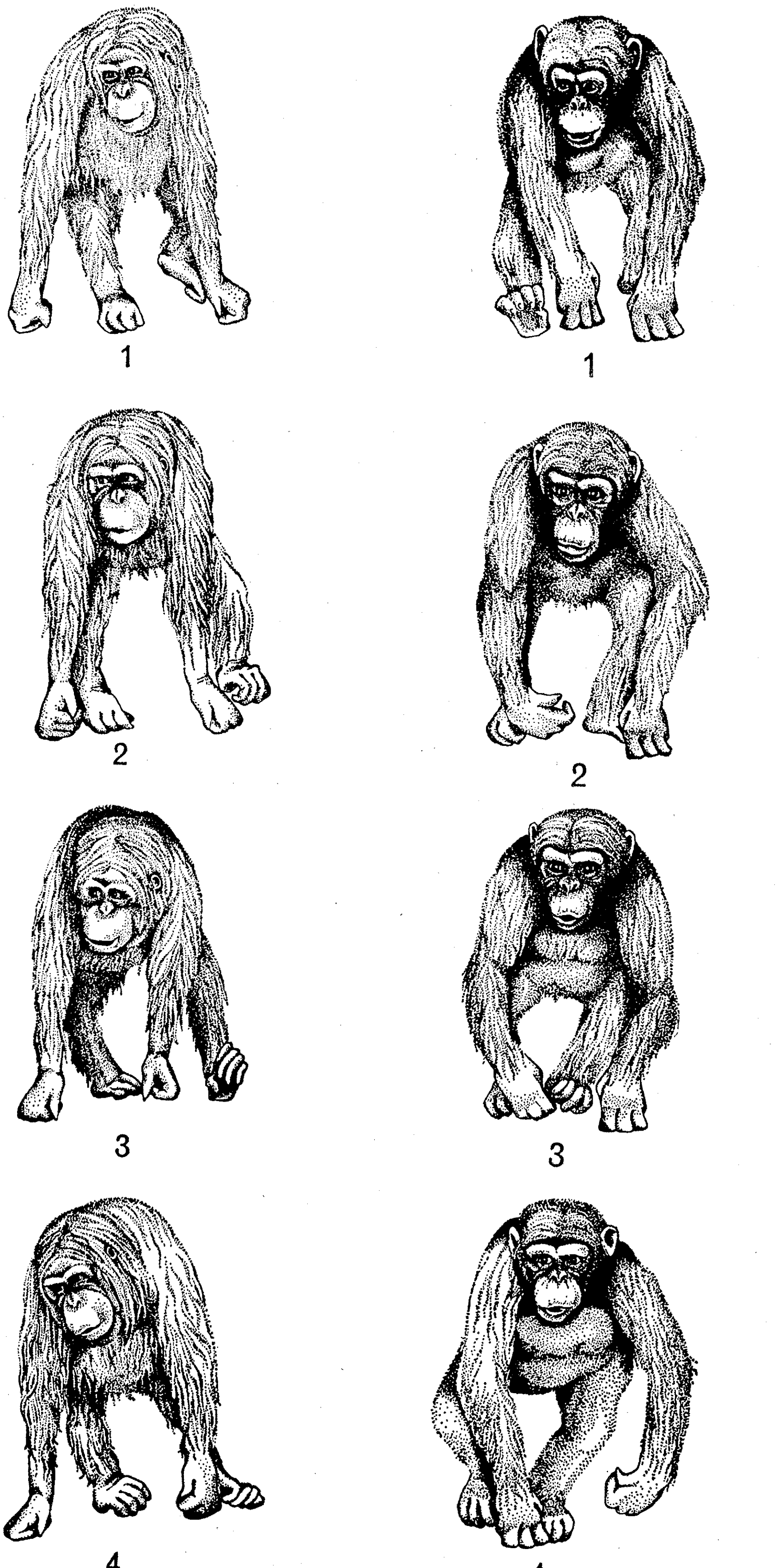

Fig. 8. Fist-walking locomotion in young orangutan compared with knuckle-walking locomotion in young chimpanzee. (1) Right hand just prior to elevation from the ground. (2) Right hand during swing phase of forelimb stride. (3) Right hand of orangutan in contact with the ground. Right hand of chimpanzee just prior to contact with the ground. (4) Support phase of right forelimb. Note the marked backward extension of the wrist in the orangutan. In the orangutan the proximal phalanges make contact with the ground, whereas in the chimpanzee the load rests on the middle phalanges of the right hand.

walking as a unique terrestrial locomotive pattern in the African apes poses the following question for troglophilic brachiationists: Were man's ancestors knuckle-walkers before they were bipeds?

Washburn, an anthropologist who has persistently postulated a remarkably chimpanzee-like ancestor for man, recently responded to this question by interpolating a knuckle-walking stage between stages of brachiation and bipedalism (*15, 29*). He suggests that "the general ape anatomy" of the human hand and "the general reduction of hair on the dorsal surfaces of the fingers and toes" support the inference that man and chimpanzee evolved from a common knuckle-walking ancestor (*15*). This evolutionary model implies an excurrent pathway in human evolution.

Insofar as I can discern from dissections of numerous ape and human hands, there are no features in the bones, ligaments, or muscles of the latter that give evidence for a history of knuckle-walking (*11*). With the exception of "evidence" from the distribution of midphalangeal hair, all the features cited by Washburn may be considered parallelisms or common adaptations to a past history of suspensory posturing. Furthermore, there are notable differences between chimpanzee and man in "form of wrist," "development of flexion," and other features that Washburn lists as "general ape" characteristics in the hand. In fact there are considerable differences between the hands of African and of Asian apes, which should preclude overgeneralization on the manual anatomy of apes (*11*).

At first glance, the absence of midphalangeal hair on the fingers of African apes and man suggests a common knuckle-walking heritage. But more detailed genetic and histological studies are needed before this observation may be incorporated reliably into an evolutionary model. While depilation of the fingers in man may result from relatively simple genetic influence (*30*), the genetic mechanisms underlying the development of knuckle pads are probably different. Furthermore, in man, depilation of the toes is more usual than depilation of the fingers (*30*). Are we to conclude therefrom that man's feet once possessed knuckle-pads that were used for a unique pattern of "pedal knuckle-walking"?

Finally, in man, midphalangeal hair occurs with *greatest* frequency on the ring and middle fingers (*30*). These are precisely the digits that the chimpanzee must use in knuckle-walking (*11*).

Fossil evidence relevant to the possible use of hands for locomotion is more complete for man than for the African apes. Hand bones, belonging to more than one individual, have been recovered from Bed I of Olduvai Gorge, Tanzania. These bones are associated with cranial and other postcranial fragments that have been assigned to the taxon *Homo habilis*, a form evincing affinities with both the gracile form of *Australopithecus* and with later, more advanced hominids (*31*). Preliminary studies on the original remains and published illustrations indicate that there are no features in the specimens that document unequivocally a knuckle-walking habitus or heritage (*11, 31*). Unfortunately, there are no distal radii or metacarpal bones. From these bones the occurrence or nonoccurrence of knuckle-walking might be discerned more readily.

The proximal and middle phalanges are notably curved, indicating either that these animals used their hands for suspensory posturing or that their ancestors used their hands for this purpose.

This inference is supported also by evidence from fragmentary shoulder girdles of early Pleistocene hominids. Oxnard measured available fragments of a fossil shoulder blade and collarbone and compared these with an extensive series of measurements on comparable parts in living primates. The fossils compare most closely with the highly arboreal Asian apes (*32*).

Furthermore, in a series of sophisticated biometrical and mathematical studies, Oxnard demonstrated that it is more likely that the human shoulder evolved from the shoulder of a large-bodied arboreal ape than from those of arboreal and terrestrial monkeys, ricochetal arm-swinging apes, or knuckle-walkers (*33*). The minimum pathway for evolution of the human shoulder from a shoulder represented by living forms may have been a single step—"*loss* by the human shoulder of the single function of raising the arm above the head for purposes of suspension . . . during foraging and locomotion" (*33*). A selective complex for achieving integrity of the shoulder joint in positions of rest and manipulative activities may have acted to further modify the human shoulder in the direction of its modern configuration.

In summary, evidence from hominid upper limbs generally indicates that the ancestors of man probably engaged in some form of suspensory posturing, and that they assumed bipedal postures very soon after venturing to the ground. Accordingly, man probably did not pass through a knuckle-walking stage; the phylogeny of man and apes probably represents a dichotomous pattern of evolution.

If this pathway proves to be a correct assessment of human phylogeny, we must consider arboreal habitats as the environmental context in which the fundamental divergence of ancestral man and the troglodytians occurred. This divergence may have resulted from differential usage of the hindlimbs by populations of troglodytians such that the center of gravity shifted more toward the pelvis in man's ancestors. By contrast, ancestral chimpanzees probably made more use of the forelimbs in foraging and locomotion. Thus their centers of gravity remained in, or perhaps moved even higher into, the chest.

Subsequently, when arboreal populations shifted to terrestrial habitats, chimpanzees became semierect quadrupeds, while man was predisposed toward orthograde bipedality.

Adaptation to bipedal plantigrade locomotion has so altered the structure of the human lower limb, especially the foot, that it is difficult to discern precisely the arboreal usage of these organs in ancestral forms. Therefore, the mechanisms whereby ancestral hominids diverged from ancestral pongids are highly elusive. Studies on the use of the hindlimb as part of locomotor, foraging, and feeding behaviors in arboreal monkeys and apes, particularly in Asian langurs, orangutans, gibbons, siamangs, and advanced South American monkeys, may provide more basis for inferring possible evolutionary pathways of man and apes.

Summary

In chimpanzees and gorillas many features once thought to be characteristic of brachiating hands are in fact unique products of adaptation for terrestrial knuckle-walking.

The African apes can maintain static knuckle-walking postures with a mini-

mum of muscular effort because of special bone-ligament-muscle mechanisms in their wrists and metacarpophalangeal joints. The powerfully developed wrist and digital flexor muscles are called into action during knuckle-walking strides. The knuckle-walking posture allows these muscles not only to serve supporting functions but also to provide propulsive forces at the distal extremity of the forelimb in various phases of the locomotive cycle.

Comparative anatomical and behavioral evidence indicates that, in early troglodytians, the shift from arboreal foraging and locomotion to terrestrial knuckle-walking entailed adaptations in hand posture and structure that were more complex than mere placement of an inflexible brachiating hook topsy-turvy on the ground. The terrestrial troglodytians probably evolved first through a fist-walking or modified palmigrade phase wherein the hand was used as a supporting prop but not as an effectual propulsive lever. This stage was probably followed by a phase of incipient knuckle-walking in which the wrist and finger bones and joints were further modified to effect a characteristic knuckle-walking habitus. In this posture, not only does the hand serve as a supporting prop but the fingers act as propulsive levers.

Gorillas probably evolved from chimpanzee-like knuckle-walking troglodytians through advanced adaptation for terrestrial foraging and feeding.

Divergence of the hominid lineage from the lineage of the African apes probably occurred before the evolution of knuckle-walking. Recent fossil discoveries and comparative anatomical studies support the hypothesis that man evolved from a large-bodied arboreal ape that was adapted for some degree of suspensory posturing and locomotion. It is suggested that the initial divergence between man and ape may have occurred in arboreal habitats through differential use of the forelimbs and the hindlimbs.

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34. I thank Drs. F. C. Howell, C. E. Oxnard, R. Singer, and L. VanValen, of the University of Chicago, for their helpful suggestions and improvements of the text. The drawings were made by Mr. P. Murray, University of Chicago. This research was supported by National Science Foundation grants GS-834 and GS-1888 and by Public Health Service research career development award No. 1-K04-GM16347-01 from the National Institutes of Health. Supplementary support was provided by U.S. Public Health Service general research support grant No. FR-5367 to the University of Chicago; by NIH grant No. FR-00165 to the Yerkes Regional Primate Research Center, Atlanta, Georgia; and by the Wenner-Gren Foundation for Anthropological Research.