

ANIMALIA, *HOMO*, AND THE KINGDOM OF GOD

by *Russell H. Tuttle*

Abstract. I selectively and critically review the state of knowledge about human evolution and the place of humans vis-à-vis living apes, with emphasis on bipedal posture and locomotion, expansion of the brain and associated cognitive capacities, speech, tool behavior, culture, and society. I end with a personal perspective on God and Heaven.

Keywords: ancient footprints; ape rights; apes; art; brain and behavior; conservation; culture; ethics; evolutionary scenarios; fossils; God; Heaven; human evolution; language; numerical competence; phylogenetic models; society; speech mechanisms; symbol.

Scientists have established concretely that anatomically, physiologically, genetically, and behaviorally we are animals, that is to say, members of the Linnaean Kingdom Animalia. Although membership in the Kingdom of God is outside the province of modern science, at the end of this essay I venture personal thoughts on the subject. Between these widely separated realms, the place of humans and our ancestral species is often debated, sometimes hotly—though, mercifully, no one has gone to the stake over the issue in many decades.

Apes are focal in many arguments over the human career and condition, and they are commonly cited in attempts to highlight our special features or, contrarily, to show how close we are to other animals. When assessing the various arguments, it is important to distinguish between reconstructions, models, and scenarios.

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RECONSTRUCTIONS, MODELS, AND SCENARIOS

One commonly encounters the term *reconstruction* in evolutionary biological literature, particularly in regard to phylogenetic schemes. Accordingly, one is presented with “phylogeny reconstructions” based on various fossil, genetic, or comparative morphological analyses. In fact, it is misleading to imply that reconstruction has occurred. Instead, I propose that we devise models, because one rarely has enough bits to conduct a reconstruction. Experts can reassemble fossil skulls and other bones and artifacts if enough pieces are recovered, but even in fossil restorations a good deal of modeling may be required in lieu of missing pieces.

In the speculative realms of behavioral and ecological modeling, it often is the case that one proposes *scenarios* instead of models, particularly in the sense that physical scientists employ the term. Indeed, paleoanthropologists almost always are reduced to writing scientifically informed stories, because behavior and habitats are transitory and leave only tantalizing traces. Here the key phrase is *scientifically informed*. Persuasive paleoanthropological scenarios differ from science fiction in that the former constructs are bounded by facts. The extant apes and other animals, including humans, provide us with a wealth of suggestive anatomical, behavioral, and ecological data that complement patchy information from archaeology and paleontology.

Just as the salt in our cells attests to primeval origins in the sea, our gross anatomy and special senses bear abundant witness to extensive arboreal heritage in the human lineage. Our genetic code, blood proteins, bodily structure, and fragmentary fossil record evidence closest similarity with apes, all species of which are arboreal in current practice or recent heritage.

Our lineage is solidly rooted in the Primates, which is basically an arboreal order. For many decades, experts struggled for a precise definition of the Primates. Finally they reached a quasisensus whereby, instead of discrete features, our order was defined according to evolutionary trends, which arrogantly led to the human condition (Clark 1959). However, during the past decade, Robert Martin (1990) enumerated the primate characteristics, most of which are adaptations to arboreal habitats.

Typically, primates live in tropical and subtropical forests. Their extremities are designed for securely grasping arboreal supports: the hallux (first toe) is widely divergent; the hand is prehensile; most digits (and always the hallux) bear flat nails instead of claws; and the palms, soles, and sometimes the tail bear ridged pads of friction skin that reduce slippage and enhance tactile sensitivity.

Unlike most other mammalian orders, in Primates, locomotion is hind-limb dominated, which frees the hands to collect arboreal prey and to manipulate food and other objects without unduly compromising security during climbing, feeding, and rest.

The visual sense is emphasized in the Primates, which must judge distances in order to navigate complex, highly variable patterns of boughs, branches, twigs, and vines. The small litters, usually singletons, and the precocity of neonates are probably also adaptations to the demands of arboreal life.

Classically, the suite of postcranial characteristics that unite apes (families Hylobatidae and Pongidae) and humans (family Hominidae) in the superfamily Hominoidea was believed to adapt apes and our prebipedal ancestors for a peculiar form of arboreal locomotion—brachiation, or arm swinging—that is most dramatically exhibited by gibbons (Tuttle 1969). The upper limbs and torso figure prominently in arguments for a brachiating ape ancestry of the Hominidae. The following features are cited to support the brachiationist hypothesis: long upper limbs relative to trunk length; especially long forearms; long fingers, except the thumb; notable development of the thumb; broad flat chest; broad, single-unit breastbone; shoulder blades on the back wall of the chest; long collar bones; laterally directed shoulders; mobile shoulders and elbows; large arm-raising and scapular muscles; short trunk, particularly the lower back; reduced lower-back muscles; sacrum with >3 segments; no external tail; domed diaphragm; attachments of abdominal organs to the diaphragm and posterior abdominal wall; and a muscular pelvic diaphragm in the pelvic outlet (Tuttle 1974).

Arthur Keith (1923) proposed that some arm-swinging apes became too large for the trees. When they came to the ground, they adopted bipedal postures. Contrarily, Dudley Morton (1926) argued that because big brachiators are top-heavy, if they came to the ground they would revert to quadrupedal postures. Consequently, the ancestral hominids must have been small-bodied creatures with many resemblances to gibbons, except that they did not engage in acrobatic arm swinging.

The brachiationist theory was popular until about 1940. Thereafter, it fell into disfavor because *Proconsul heseloni*, a Miocene dental ape, did not show many features that were associated with brachiation. Nevertheless, from 1950 onward, Sherwood Washburn fought for the brachiationist cause and especially for a chimpanzeelike ancestral hominid (Tuttle 1974).

During the 1960s, field studies on great apes revealed that they do not engage extensively in arm-swinging locomotion. Further, chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and gorillas (*Pan gorilla*) prefer to travel between trees by terrestrial routes. Concurrently, I discovered that major features of African ape hands could be explained as adaptations to knuckle-walking instead of brachiation. Close observations of orangutans, which are more arboreal than the African apes, showed that they lacked the following features that characterize the knuckle-walking African apes: knuckle pads; shortened extrinsic flexor tendons to the fingers; restrictions on wrist extension and side-to-side movements; and tori (ridges) on the weight-bearing metacarpal bones in the distal palm (Tuttle 1969).

Humans sport no trace of the knuckle-walkers' features. Still, Washburn (1967) claimed that our ancestors were knuckle-walkers. I looked to the trees and proposed instead that, because all apes are climbers, climbing must have predisposed our ancestors for bipedalism (Tuttle 1975). Climbing vertically on tree trunks and vines and running bipedally atop branches probably were imperative in the evolution of hominid bipedalism. Because our ancestors were used to running bipedally on branches and had lower centers of gravity, they moved bipedally on the ground and never resorted to terrestrial quadrupedal locomotion. They probably also foraged bipedally more than apes do. These ancestral hominids were probably small-bodied, like the siamang (Tuttle 1975).

The ancestral great apes advanced more in the direction of general arboreal climbing and engaged in more suspensory behavior than our ancestors did. Their forelimbs and chests enlarged, and their centers of gravity were high in the trunk. So, when they came to the ground, they tipped over and walked quadrupedally. Because their arboreal fingers were long, they flexed them, which gave rise to knuckle-walking (Tuttle 1969).

I designated our hypothetical vertically climbing/arboreally bipedal ancestors *hylobatians* to signal modest body size, long lower limbs, barrel-shaped chests, and other similarities with gibbons versus great apes. The *hylobatians* were probably quite distinct from *hylobatid* apes, however, especially in forelimb and craniodental morphology. Although they engaged in some suspensory foraging, the *hylobatians* did not brachiate extensively, and they probably executed more hindlimb-propelled leaps than gibbons do (Tuttle 1975, 1994a).

Nobutoshi Yamazaki and Hidemi Ishida (1984) demonstrated that the energy loads on gibbon hind limbs are less when they run on the ground than when they run on branches or climb vertically. Thus, an arboreal biped comes to the ground with an advantage toward adapting to terrestrial bipedalism (Tuttle 1994a).

The *hylobatian* model has few active champions. Instead, there is renewed support for knuckle-walkers in our lineage, largely because of molecular data that imply closer affinity among humans, chimpanzees, and bonobos than among the African apes versus humans (Ruvolo et al. 1994; Horai et al. 1995; Adachi and Hasegawa 1995). If knuckle-walking were the basal condition of ancestral African apes, ancestral hominids also must have been knuckle-walkers. Otherwise, one must posit parallel evolution of knuckle-walking in the lineages of gorillas and of chimpanzees and bonobos. Until the functional meanings of the genetic data are shown to support a knuckle-walking model, I stand by the *hylobatian* model.

FOSSILS

Fossil evidence could require replacement of the *hylobatian* model by another, but this is unlikely. Nature seldom discloses its secrets fully and

never easily. Even if bones alone could inform us definitively about muscular actions, positional behavior, and phylogeny, the truth is that full documentation probably has not been preserved. Myriad telltale bits of evidence have been smashed and pulverized beyond recognition by natural and anthropogenic processes. Moreover, for a variety of practical and political reasons, we may never salvage enough of that which is buried in Africa and Eurasia. We are much better prepared to say what we do not know from the fossil evidence than to describe ancient apes in action and to argue dogmatically for specific transitional sequences that culminated in extant apes and people.

The problem of knuckle-walking is exemplary here. There is no clear indication of knuckle-walking in Miocene, Pliocene, and Pleistocene hand bones that are ascribed to the Hominoidea. Further, the fossil record for ancestry of extant African apes is unknown. Some salient features of obligate knuckle-walkers—knuckle pads and shortened digital flexor muscles—cannot be discerned from fossils, because they leave no trace on the finger bones. Unless fossil wrist bones were very similar to those of adult gorillas or chimpanzees, one could not infer reliably that their owners were obligate knuckle-walkers. The same is true for metacarpal tori, which are variably expressed ontogenetically in and interspecifically among gorillas, chimpanzees, and bonobos (Tuttle 1992). The postcranial remains of anthropoid primates that may have had a role in hominoid evolution over the past 35 million years basically underscore our arboreal heritage without yielding information on the specific postural and locomotor repertoire that immediately preceded obligate bipedalism.

The patchy fossil evidence of Oligocene and Miocene anthropoid postcranial anatomy offers no basis to argue a detailed model of morphological and positional behavioral developments, particularly of dramatic arm swinging, pongid versatile climbing, and knuckle-walking, which characterize gibbons, orangutans, and the African apes, respectively.

Remains of *Oreopithecus bambolii* indicate that by 7-Ma (million years), one hominoid species had achieved many of the postcranial hallmarks of the Hominoidea (Sarmiento 1987). Interestingly, its lower back is not as reduced as those of extant Pongidae (great apes: chimpanzees, bonobos, gorillas and orangutans) are. Instead, it is more like those of the Hylobatidae (lesser apes or gibbons) and the Hominidae.

Bits of other Eurasian Middle and Late Miocene Hominoidea suggest some development of postcranial features like those of modern apes (Moyà-Solà and Köhler 1996; Köhler, Moyà-Solà, and Alba 2001; Moyà-Solà et al. 1994; 2005), but no species is well enough represented to make overall comparisons with *Oreopithecus* and extant species.

The Pliocene and Early Pleistocene hominid records indicate that our ancestors retained arboreal features during the heydays of *Australopithecus*, *Paranthropus*, and perhaps even earliest *Homo*. There is notable controversy

over whether they are simply evolutionary baggage or truly attest to habitual arboreal activity (Tuttle 1988). After examining the trove of foot, hand, and other postcranial bones of 3 million-year-old *Australopithecus afarensis* from Hadar, Ethiopia, I concluded that some Pliocene *Australopithecus* were not fully emancipated from the trees (Tuttle 1981).

The second to fifth toes of *Australopithecus afarensis* are particularly ape-like: they are longish and curve downward like those of accomplished arboreal climbers. Even if their halluces were not markedly prehensile, these features would facilitate tree climbing and bipedal foraging and squatting on stout branches (Tuttle et al. 1991).

“Lucy” (A.L. 288-1) and other fossil hominids from Hadar sport additional features that may be linked to tree climbing, though traits that signal bipedalism are present also. The apish arboreal features include laterally flared hip bones, curved finger bones, and a long pisiform bone (Tuttle 1981). Peter Schmid’s (1983) model of Lucy’s skeleton is remarkably pongid in the chest and shoulders, which is more consistent with tree climbing than with humanoid bipedal running.

In known parts, South African australopithecine postcranial morphology does not differ markedly from that of *Australopithecus afarensis* (McHenry 1986). Ronald Clarke and Phillip Tobias (1995) argue that four foot bones of *Australopithecus* from the most ancient deposits at Sterkfontein indicate a prehensile hallux. John Robinson (1972) concluded that South African *Paranthropus* are more apish than *Australopithecus africanus* and that they probably climbed trees for food and shelter.

I focused attention on pongid features of the 1.8-Ma proximal and middle finger bones of *Homo habilis* from Olduvai Gorge, which indicate strong development of the flexor muscles of the fingers (Tuttle 1967). Subsequent studies have reinforced the inference that, though bipedal, *Homo habilis* regularly climbed trees (Tuttle 1988). Arboreal features are not manifest in specimens of *Homo erectus*, *Homo rudolfensis*, *Homo ergaster*, and later species of our genus. We therefore may assume that hominids were fully adapted to life on the ground by 1.5 Ma.

TREES, TOOLS, AND LODGING

On the basis of anatomical evidence and information on tool behavior of wild chimpanzees, I proposed that some Pliocene and perhaps early Pleistocene hominids may have engaged in arboreal stone tool use to process nuts, hard fruits, and possibly animal prey and to defend themselves against predators and rivals. Hand-held rocks, clubs, and long stabbing sticks, augmented by stone and vegetal missiles, would constitute a formidable defense when employed or launched from a tree platform. The early hominids probably stored raw materials, subsistence hammers, cutting tools, and defensive weapons in arboreal nests and cavities for use on foods growing in base trees, foods carried to them, and intruders (Tuttle 1992).

Secure lodge sites are a premier need of primates if they are to avoid nocturnal predators, parasites, pests, and inclement weather. Pongid apes spend a lot of time in their nests, presumably sleeping. We do not know why, though it must conserve energy (Tuttle 1986). We may expect that until hominids gained control of fire and learned to secure sturdy terrestrial shelters they bedded at night and during day rests in trees. Further, until they became accomplished runners they probably stayed near trees into which they could escape from predators (Tuttle 1994a).

When did our ancestors leave the nest? Obviously, once they quit the trees and spread into open country, true nesting would cease. Indeed, we have evidence that caves, rock shelters, and other structures replaced trees as lodge sites during the Middle Pleistocene. But during the Pliocene and perhaps Early Pleistocene, a reliance on arboreal nesting might have affected the sizes, compositions, and relations of early hominid groups as well as their choice of habitats.

FIRST STEPS AND LASTING IMPRESSIONS

The most impressive early evidence for bipedal Hominidae is the 3.5-Ma Laetoli G footprint trails (Leakey and Hay 1979). The Laetoli Footprint Tuff was deposited over a period of a few weeks at the end of the dry season and onset of the rainy season. Ash ejected from a nearby volcano became moist with rain; many animals, including three hominid individuals, walked in it; and it baked in the sun. A layer of volcanic ash buried the Footprint Tuff before the prints could erode. Chemical changes hardened the tuff to rocklike consistency. The Footprint Tuff itself provides a K/Ar (potassium/argon) date of 3.5 Ma, which certainly dates the creatures that walked in it (Hay 1987; Drake and Curtis 1987).

The smallest of the three bipedal individuals, "G-1," made one trail, and two larger individuals produced a second trail that is parallel to the first. The intermediate-sized hominid, "G-3," partially overprinted the footprints of the largest individual, "G-2." The two trails are designated G-1 and G-2/3 (Tuttle 1987).

In all observable features of foot shape and walking pattern, the three creatures that made the trails are indistinguishable from modern habitually barefoot human beings who are walking slowly. That they were accomplished bipeds is concrete, because the 69 footprints extend over 27 meters of open habitat with no hand impression anywhere along the trails. Laetoli hominid G foot indices, which indicate foot length versus foot breadth, fit comfortably within a global sample of human foot indices. The hallux is aligned with the lateral four toes, and the gap between it and the second toe is quite human, particularly when compared to undeformed feet of persons who have never worn constraining footwear (Tuttle et al. 1990). The lateral four toes are arrayed relative to the hallux and to each

other as in a modern human foot, and none extends notably beyond the tip of the hallux. The toes of Laetoli G hominids are approximately 30 percent of total foot length, which is not significantly different from mean relative toe length of never-shod Peruvian Indians and Tanzanian Hadzabe (Tuttle, Webb, and Baksh 1991; Musiba et al. 1997).

The Laetoli hominid G prints evidence a medial longitudinal arch. Apparently, the transfer of body weight during bipedal walking was quite human—from robust heel strike, more lightly along the lateral sole, then more heavily medially across the ball of the foot so that the brunt of toe-off was borne by the hallux, which, unlike the lateral toes, regularly left prominent impressions in the substrate. Contrarily, African pongid prints are flatfooted with the toes arrayed quite differently from those of human prints (Tuttle et al. 1992).

The Laetoli trackways provide important information not only on the pedal morphology of their makers but also about the way they walked. Because their step lengths are short compared with the statures inferred from foot length, we are confident that the Laetoli hominids walked slowly in the moist volcanic ash. We cannot measure their actual speeds or know how often they may have paused. Observed features of gait (foot angle, step length, stride length, stride width, relative stride width, foot lengths per stride) and inferred features of gait (relative stride, velocity, relative speed, cadence) based on studies of never-shod Peruvian Indians and captive bipedal apes fail to place the Laetoli G printmakers unequivocally with either humans or apes (Tuttle et al. 1992).

Moreover, inferences about the relative humanness of Laetoli G hominid gaits are confounded by our ignorance of their actual statures and bodily proportions. Because the morphology of their feet is so like that of *Homo sapiens*, we used the regression of human stature on foot length to predict the statures of G-1 and G-3 to be 122 cm (4 ft) and 141 cm (4 ft 8 in), respectively. Yet, it is unlikely that the Pliocene Laetoli hominids were built like modern humans. They may have had relatively shorter lower limbs and perhaps longer lumbar regions than we do, and surely their neurocranial heights were lower than ours because of smaller brains.

It is unlikely that G-1 walked snugly side by side with G-2 or G-3. Variations in the gaits that are exhibited by the two trackways are sufficient to argue that G-1 was not intimately in contact with either G-2 or G-3. The diorama at the American Museum of Natural History, New York City, which depicts two adult hominids walking side by side, with the male embracing the female's left shoulder, is fanciful. Because they were walking in an exotic substance, it is unremarkable that the two trails are quite close together.

It also is unsurprising that G-3 walked in the tracks of G-2. Acacia thorns are in the Laetoli footprint tuffs. Moreover, the novelty of the substrate may have induced one individual to tread where its predecessor

had walked uneventfully. G-3 might also have overprinted the tracks of G-2 as a pastime. Hunters commonly walk in one another's tracks.

The sexes and ages of the three Laetoli individuals cannot be inferred from the trails, so actual sexual dimorphism of the species is inaccessible. Assuming that G-1 is an adult female and G-3 is an adult male, their inferred statures suggest that, like modern humans and chimpanzees, the species was moderately dimorphic (86 per cent) in body size. However, if Louise Robbins's (1987) guesstimate of 176 cm (5 ft 9 in) for the stature of G-2 is correct, one could speculate that G-3 and G-2 are an adult male and an adult female, respectively, and that G-1 is a subadult. Accordingly, the species remains moderately dimorphic (82–87 per cent) (Tuttle 1996).

Optionally, if we assume that G-1 represents an adult female, G-2 an adult male, and G-3 a subadult male, the species was quite dimorphic (70 per cent), though falling short of conditions exhibited by gorillas and orangutans (Tuttle et al. in press). Only this scenario approaches Henry McHenry's (1994) estimate of sexual dimorphism (64 percent) for *Australopithecus afarensis*, which is based on predicted average weights.

The preeminent contribution of the Laetoli Site G footprints to hominid evolutionary biology is their demonstration that bipedal locomotion over a notable span of relatively open habitat was possible for at least one species of the Hominidae 3.5 million years ago. This milestone precedes the first evidence of lithic artifacts by approximately one million years.

In order to place the Laetoli G footprints in hominid phylogeny, we must know who made them. Regrettably, data are insufficient to determine the species that left the prints. In an earlier era, one might assign them descriptively to a unique species—*Ichnanthropus bipes*—until additional fossils indicated that they should be sunk into another species. Today, however, prudence dictates that they be classified as Hominidae *genus et species indeterminata* (Tuttle 1996). If the Laetoli hominid G prints were undated or were dated at least 1 Ma younger, they probably would be acceptable in a species of *Homo* because of their striking humanness. I cannot recommend this, because genus *Homo* is based primarily on craniodental traits (Tuttle 2005).

It is reasonable to expect that open-country hominids would have evolved feet like ours before they achieved craniodental traits that define our species or even our genus. My studies of the 3-Ma foot bones from Hadar (Tuttle 1981) indicate that, if they belong to *Australopithecus afarensis*, the Laetoli G hominids should not be referred to *Australopithecus afarensis*, which are distinguished by apish curved toes that are unlikely to produce virtually human footprints.

Given that, like other Late Miocene-Early Pleistocene mammals, both *Australopithecus* and *Homo* are characterized by adaptive radiation, it is imprudent to expect that a single species of *Australopithecus* was the only hominid in eastern Africa 3.5 million years ago (Tuttle 1988). Indeed,

discoveries in Kenya (Leakey et al. 1995), Chad (Brunet et al. 1995) and Ethiopia (*A. garhi* in Ethiopia [Asfaw et al. 1999; Kimbel, Johanson, and Rak 1994; White et al. 1993; 1994; 1995; Haile-Selassie, Suwa, and White 2003]) indicate that during the Pliocene Epoch, Africa hosted several hominid species.

In 1995, Meave Leakey and coworkers described a new species of *Australopithecus* based on specimens from Kanapoi and Allia Bay, Kenya. At 3.5–4 Ma, *Australopithecus anamensis* is a half million years older than the Laetoli specimens that are assigned to *Australopithecus afarensis* (Johanson, White, and Coppens 1978). A partial leg bone from Kanapoi indicates that *Australopithecus anamensis* was bipedal. Interestingly, Leakey and colleagues (1995) note that dentally *Australopithecus anamensis* more closely resembles Laetoli specimens that are assigned to *Australopithecus afarensis* than specimens of *Australopithecus afarensis* from Hadar, Ethiopia. One might therefore argue that the Laetoli and Hadar samples are from different species. I also suspect that some Kenyan and Tanzanian Pliocene hominids were more advanced in pedal morphology and perhaps other features of the lower limb that are related to bipedalism than the Ethiopian hominids were. During the Pliocene, both Kanapoi and Laetoli were relatively open habitats, while Hadar had more closed wooded areas.

In any case, Ethiopian specimens of *Australopithecus afarensis* span nearly one million years (Kimbel, Johanson, and Rak 1994), and it is likely that other hominid species lived contemporaneously in the more open habitats of eastern and perhaps southern, northern, and western Africa.

On the basis of habitats, the most arboreally adapted Pliocene hominid may prove to be *Ardipithecus ramidus*, from <6-Ma deposits at Aramis, Ethiopia. Aramis appears to have been closed woodland during the Pliocene (WoldeGabriel et al. 1994). The few cranial bits of *Ardipithecus* are chimpanzeelike, and the dentition also sports chimpanzeelike features, though on balance it seems to be hominid. The extent to which *Ardipithecus* was bipedal cannot be determined from the postcranial remains reported by T. D. White, G. Suwa, and B. Asfaw (1994), because they do not include bones from the lower limb. Anterior placement of the foramen magnum hints that *Ardipithecus* may have been more bipedally disposed than chimpanzees are (White et al. 1994).

Postcranial elements are much more plentiful for *Australopithecus afarensis*, which lived between 3.8 and 3.0 Ma. Nonetheless, the nature and extent of their bipedality is hotly debated. In the United States, polar views are argued by a group at SUNY, Stony Brook, who maintain that *Australopithecus afarensis* is a highly arboreally adapted missing link between apes and us (Stern and Susman 1983), versus C. Owen Lovejoy (1988) and Bruce Latimer (1991), who believe that *Australopithecus afarensis* were as capable bipeds as we are.

In keeping with the adage “if it looks like a duck, it walks like a duck,” if Lucy doesn’t look like Lucille Ball, surely she did not walk like her. Although arboreal features are less compelling in the lower limbs of *Australopithecus afarensis* than the SUNY claims thereof, they are more manifest than is admissible to Lovejoy and Latimer. Strong cases have been made for pronounced adaptation to bipedality in the ankle joint, proximal foot, knee joint, and pelvis of *Australopithecus afarensis* (Tuttle 1994a).

Function, Models, and Scenarios. Some of the confusion surrounding interpretation of lower-limb morphology in *Australopithecus afarensis* may be the result of our inability to link specific features to bipedal standing and squatting versus walking or running in *Homo sapiens* (Tuttle 1994a).

Our feet must bear our entire body weight; they are on the front line against ground reaction forces when we stand, squat, and move. Their peculiar morphology reflects the special demands that are placed upon them. As we stand, our total weight is evenly balanced between the feet. Within each foot, approximately half of each pedal load falls on the heel, and the other half is distributed among six contact points under the metatarsal heads (Morton 1935). Squatting can shift notable weight from the pedal balls to the heels, thereby eccentrically loading them.

Running is the supreme mechanical challenge to the ball and toes, particularly the great toe, especially when we sprint quasi-digitigrade. Long curved toes would not fare well during humanoid bipedal running. Because the Laetoli toe prints are utterly humanoid, there is no reason *prima facie* to deny them the ability to run in a human fashion. I would not set them on this course without a series of forefoot impressions that indicate stride lengths that are longer than those now exposed or skeletal remains that document humanoid pelvis and lower limbs in the Laetoli Beds.

The large human heel serves as a powerful lever for the triceps surae (calf) muscle, which plantarflexes the foot at the ankle joint during bipedal walking and running. But the robust heel probably also evolved to serve the postural functions of standing and squatting. African apes, particularly gorillas, also have robust heels, yet they rarely engage in bipedal locomotion. However, they squat for long periods of time to forage and to rest. Squatting and bipedalism increase the height that foragers can reach overhead, and squatters are better prepared for locomotion than were they to sit or to recline. Therefore, we should consider the possibility that robustness of the heel evolved in our lineage in response to squatting, bipedal foraging, and short-distance bipedal travel before early hominids were fully adapted to obligate bipedalism and long-distance travel. In this scenario, the toes may have retained arboreal features while the heel and ankle joint were more truly humanoid (Tuttle, Hallgrímsson, and Stein 1998).

Accordingly, I endorse the following scenario, which builds on Kevin Hunt’s (1994) model and which is reasonably derived from a Miocene hylobatian model (Tuttle 1994a).

Ethiopian *Australopithecus afarensis* commonly stood bipedally on the ground in order to forage on overhanging branches in forest edge and other low-canopied areas. Their lower backs were lordotic, and they could align the thigh and leg bones into straight columns, which saved muscular energy during sustained stances on fully extended lower limbs. While consuming their harvests, the Pliocene hominids squatted often (instead of sitting), thereby further selecting for robust heels and balance between the heel and the forefoot as well as between their feet. Alternate rising and squatting enhanced development of the anterior thigh, hamstring, and gluteal muscles as knee and hip extensors, which also continued to serve them well for climbing trees to forage arboreally, to evade terrestrial enemies, and to nest. As Hunt (1994) observed in Gombe chimpanzees, shifts to nearby foraging sites were made bipedally, though via walking instead of shuffling. Rising onto the ball of the foot to reach overhead may have contributed to reduction of the lateral four toes and would have enhanced development of the calf muscles.

Extensive ventures into open country probably were not characteristic of Ethiopian *Australopithecus afarensis*. The long-distance walking foot, and especially the running foot, developed in other hominid species, which had adapted to more extensively open habitats.

Language, Culture, and Society. As difficult as it is to document and to explain the evolution of human bipedality and tool behavior, such projects shine empirical vis-à-vis elusive topics like the origins of human language, nonmaterial culture, and society, which left few traces for paleoanthropologists to decipher.

Consequently, we resort to extant creatures for ideas. This exercise intrigues sociobiologists and laypersons but perturbs some sociocultural anthropologists and other social scientists. Cognitive neuroscientists and psycholinguists have joined physical anthropologists, archaeologists, primatologists, and comparative psychologists as innovative contributors to human evolutionary puzzles.

However one apportions factors of nature and nurture, all must admit that the brain is basic to human social and maintenance behavior. Human brains are about three times larger than those of apes of comparable body weight. Much of the increase in human brain size is achieved postnatally. A newborn monkey has about 60 percent and a newborn chimpanzee about 46 percent of adult brain weight; a human neonate has only about 25 percent of adult brain weight. Although the human brain continues to grow into the late teens, most of its size is achieved by the sixth year (Tuttle 1986).

Hominid brain evolution evidences a threefold increase in size over the past 3 million years. Brain size doubled between *Australopithecus* (3 Ma) and *Homo erectus* (1.5 Ma). Stone-tool technology was rather simple dur-

ing the heyday of *Australopithecus* and *Homo habilis*, became more elaborate during the time of *Homo erectus*, and really burgeoned during the Late Pleistocene (125–10 Ka). *Homo erectus* used fire from about 500,000 years ago (Tuttle 1986; Klein 1989).

Human brains are notable for hemispheric dominance, as reflected in the localization of linguistic functions, usually on the left side, and handedness. The relationship between laterality of hand preference and hemispheric dominance for speech is not clear-cut; some left-handers, for example, are right-brain dominant for speech (Tuttle 1986).

In humans, two cerebral areas are particularly interesting, as they seem to be related to our capacities for language. An area of parietal and temporal cortex, containing Wernicke's area, is commonly larger in the left cerebral hemisphere, and the frontal cortex, containing Broca's area, is also usually larger on the left side. Classically, Broca's area was basic to verbal articulation, and Wernicke's area was related to understanding speech (Passingham 1982). Experts have challenged the classic view of simple linguistic roles for Broca's area and Wernicke's area. It appears that Broca's area is involved in general grammatical processing instead of articulation per se. Writing and manual signing can be as disrupted as speech is by injury to Broca's area. Moreover, deeper areas of the brain also are implicated in disturbance of grammar. Their specific interactions with Broca's cap are unclear (Pinker 1994). Wernicke's area appears to house the dictionary, which selects words to be sent to Broca's area, where they are assembled syntactically (Pinker 1994).

Whereas certain occipital and frontal asymmetries can be related to handedness in humans, they cannot be so linked in great apes, because there is insufficient evidence that apes possess comparable degrees of laterality for hand preference (Tuttle 1986). All patterns of cerebral asymmetry in apes are different from that which is shared by all species of *Australopithecus* and *Homo*. Nevertheless, because fossil hominid specimens do not allow detailed consideration of which cerebral areas expanded relative to others, behaviors such as handedness and especially language remain elusive to paleoanthropologists (Holloway and Coste-Lareymondie 1982).

SPEECH IN HUMAN EVOLUTION

Some paleoanthropologists have inferred speech from endocranial features in fossil hominid specimens. Others have denied speech to many fossil hominids on the basis of basicranial and mandibular morphology. Still others have claimed that human speech was not developed fully in early members of anatomically modern *Homo sapiens* because of the simplicity of tool kits and art before the Upper Paleolithic Period, which began only 40,000 years ago.

Endocranial Morphology. P. V. Tobias (1991) claimed that *Homo habilis*, which lived ca. 2.3–1.6 Ma at Olduvai, Tanzania, probably possessed some capacity for speech, because there is evidence of Broca's area in the left frontal lobe, which impressed the inner surface of the braincase in Olduvai Hominid 24, a nearly adult female specimen with an endocranial capacity of 594 cc. Tobias also claimed that he could detect well-developed speech areas on the endocasts of KNM-ER 1470, which he classified as *Homo habilis* but which now is *Homo rudolfensis*. The specimen is from East Turkana, Kenya, and is contemporaneous with *Homo habilis*. Its cranial capacity is 752 cc.

Ralph Holloway (1983) noted that, almost without exception, the interior surface of the neurocranium is poorly preserved in early hominids from Olduvai Gorge and East Turkana, so no cerebral surface detail is present, especially in regions that might evidence Wernicke's area. Nonetheless, he reported the presence of left Broca's caps in two specimens of *Homo rudolfensis*. Three specimens of African *Homo erectus* from East and West Turkana imply Broca's caps that are more discrete on the right side. Tobias found only a hint of Broca's area and no trace of Wernicke's area in *Australopithecus*. Contrarily, Holloway speculated that the type specimen of *Australopithecus africanus*—the Taung child—and an adult specimen of *Australopithecus afarensis* show that Wernicke's area had emerged by 3 Ma, but he found no Broca's area on their endocasts.

Among Plio-Pleistocene hominids, the mean values of cranial capacity are larger for *Homo habilis* and *Homo rudolfensis* than those of all species of *Australopithecus* and extant Pongidae but notably less than the mean cranial capacities of *Homo erectus* and especially of later Pleistocene and Recent Hominidae.

Mere increase in brain size, particularly of little more than 250 cc, and changes in gross shape of the brain, are insufficient to claim verbal abilities for *Homo habilis* and *Homo rudolfensis*. Moreover, the evidence for particular speech areas is suspect. The partial crania of OH-24 and KNM-ER 1470 were reassembled from many small pieces. OH-24 was severely crushed and remains deformed despite clever reassembly (Tobias 1991). The meticulously patched braincase of KNM-ER 1470 also is distorted (Holloway 1983).

If cerebral expansion is functionally important in *Homo habilis* and *Homo rudolfensis*, this may imply general increase in cognitive abilities, manipulatory skill, or other factors important to survival in the Early Pleistocene instead of rudimentary articulate speech. Indeed, prominent Broca's caps occur on some chimpanzee endocasts (Holloway 1983), yet no ape has uttered a word despite laborious attempts to get them to speak.

Two classic experiments were conducted in the United States. The Kelloggs (1933) and the Hayeses (1951) fostered infant female chimpanzees in order to document the extent to which their bourgeois homes could

humanize them. “Gua” did not even babble, let alone recite nursery rhymes. After much human tuition, including molding her lips, “Viki” produced only four hoarse, breathy utterances, imaginatively glossed as *mama*, *papa*, *cup*, and *up*. Viki’s vocalizations would decay if her trainers did not drill her regularly (Tuttle 1986). Gua’s vocalizations were predominantly emotional responses to provocations that were readily apparent. Viki was also mum between emotional calls. This is in keeping with the observation that naturalistically apes appear to express only affect vocally and manifest no ability to control the vocal tract to communicate ideas versus emotions (Tuttle 1986).

It is equally difficult to link hints of Wernicke’s area to linguistic ability in early hominids. Monkeys have laterality in the receipt of salient communicative features of their specific vocal signals (Heffner and Heffner 1995). If the discernment of specific communicative features is located in the left temporal region of monkey brains, laterality to comprehend communicative utterances should not be considered unique to humans (Tuttle 1986).

Morphology of the Vocal Tract. Although human speech in myriad varieties is reasonably linked to our relatively spacious pharynx and mobile tongue, there is no compelling anatomical reason to deny some form of vocal language in ancestral hominids. Several authors argue that without a lowered larynx and expanded supralaryngeal region, articulate human speech is fairly excluded (Lieberman 1994; Laitman, Heimbuch, and Crelin 1979). Consequently they reason that even Neanderthals, who lived ca. 250,000–25,000 years ago, were inept vocally and probably also quite primitive cognitively vis-à-vis *Homo sapiens* of the Upper Paleolithic.

It is simplistic to expect that, were its brain and cognitive capacity developed, and were its vocal cords, pharynx, and mouth innervated so that concepts as well as emotions could be expressed voluntarily, an ape or an *Australopithecus* could not express itself verbally. Decades ago, Frederic Wood Jones (1940) and E. Lloyd DuBrul (1958) noted that gibbons and great apes have lowered larynges and concomitant gaps between the epiglottis and soft palate, albeit less than the human condition (Wind 1992; Nishimura 2004). The calls of gibbons are wonderfully varied in pitch and pattern. If their air columns were broken into discrete bits by consonantal sounds, they could emulate words. The same may be said for great apes. The calls of bonobos are quite different from those of chimpanzees (Tuttle 1986). Orangutans, chimpanzees, and bonobos have notoriously mobile lips and tongues, surely transcending the human condition. All that they lack is wiring to recruit them for speech.

I am not convinced that one can veridically model the vocal tracts of fossil hominids based on degree of basicranial flexion or inferred mandibular mechanisms. There simply are too few bony landmarks related to

the lips, tongue, and soft structures of the throat to anchor models of phonemic production in our macerated ancestors.

Tools, Art, and Talk. The stunning Upper Paleolithic efflorescence of artifacts, characterized by remarkable spatiotemporal stylistic variability in tools, bodily ornaments, and visual arts (Lewin 1993), probably signals a major cognitive enhancement of symbolic capabilities in our lineage. But whether or how this phenomenon relates to the evolution of speech in modern *Homo sapiens* is moot. If one subscribes to Howard Gardner's (1983) theory of multiple intelligences in *Homo sapiens*, much of tool behavior and artistic ability are premised on neurological substrates fundamentally different from those that support human verbal ability. Accordingly, the awesome array of polished bone, antler, and stone artifacts and beautiful cave art do not inform us directly about when speech became a regular, indeed essential, component of the human condition.

Human tool behavior is an expression of Gardner's (1983) bodily-kinesthetic intelligence, which depends upon representation of movements in the basal ganglia and cerebellum and relatively direct connections between the motor cortex and the spinal cord. Gardner notes that human children begin to use language notably before they become sophisticated tool users. This raises the possibility that a form of speech may have preceded forms of tool behavior that are symbolic.

Similarly, visual arts—painting and sculpture—are expressions of Gardner's spatial intelligence, which is centered principally in posterior regions of the right cerebral hemisphere. Therefore, I agree with Alexander Marshack: "The problem of language origins or language competence is not clarified . . . by Upper Paleolithic symbol and imagery" (1992, 444).

APE ART, NUMBERS, TOOLS, CULTURE, AND SOCIETY

Pace brisk sales of colorful chimpanzee smearings in London (Morris 1962), apes are not artists. Because chimpanzees failed to draw, paint, or sculpt representational figures, David and Ann Premack (1983) concluded that they are unable to analyze complex objects into their parts and to understand the relations among them. Accordingly, apes currently offer few clues to the evolution of symbolically mediated visual arts.

The cognitive mapping skills of chimpanzees also are devoid of symbolic overtones. They quickly learn the locations, distances, directions, relative quantities, and other features of desired and fearful objects; can approach series of them by economical routes of their own design; and can remember them over considerable spans. Moreover, they can find objects that were hidden while they viewed the act via television. But some chimpanzees could not orient themselves toward incentives in a distant room on the basis of simple small-scale models, that is, symbolic maps, like ones

comprehensible to five-year-old humans (Premack and Premack 1983).

Chimpanzee control of numbers is somewhat more advanced than their artistic skill (Boysen 1993), but their level of accomplishment is not robust enough to assist theory on the evolution of Gardner's logical-mathematical intelligence in humans. Chimpanzees can match low numbers of objects even when samples are dissimilar in shape, color, mass, area, and length, but if the number of objects exceeds seven, they flag (Tuttle 1986).

Apes excel in problems that require the use of tools and exhibit insight during problem solving (Tuttle 1986). Nonetheless, there is no evidence that ape tool use is symbolically mediated. Consequently, one should not refer to the tool-behavioral and other variations among chimpanzee populations as cultural. Symbolically mediated behavior has not been documented in naturalistic groups of apes, even though there is strong evidence that bonobos and chimpanzees can manipulate artifactual signs and objects in ways that imply remarkable command of the symbols that were invented and proffered them by inquisitive people (Savage-Rumbaugh 1986; Savage-Rumbaugh et al. 1993).

The invention and habitual naturalistic use of symbols is quintessentially human. Therefore, I join the chorus of sociocultural anthropologists and urge that culture be defined restrictively as symbolically mediated behavior and shared ideas. It is hyperbolic to speak of chimpanzee culture (Wrangham et al. 1994) unless they evidence naturalistic symbolic mediation of an activity. For instance, I contest claims that chimpanzee tools and tool behavior exemplify culture (Goodall 1986; McGrew 1992; Boesch 1995). Instead, I would term them local or demic behavioral variations.

Comparisons between chimpanzee tool kits and the artifacts of particular human groups in order to deign the former cultural does no credit to the rich natural histories of any of these hominoids. We no longer deny remarkable symbolic capacity to human groups that lack systems of writing, monuments, and other hallmarks of technical sophistication. Historically, all human groups manifest rich symbolically mediated language, religion, and social, political and economic systems, even in the absence of elaborate material culture. The demands on the Gardnerian intrapersonal and interpersonal intelligences of people who live in vicissitudinous environments with relatively few artifacts are mind-boggling to people who are privileged with many comforting gadgets and shelters. Their social, linguistic, mental, and spiritual inventions are even more awesome.

Mere presence of innovation, dissemination, standardization, durability, diffusion, and tradition in chimpanzee tool or other behaviors does not tip the scales in favor of culture in the absence of symbols. I stress the importance of symbols in the definition of culture not out of an aversion for communion with apes but in the hope that researchers will continue to press them for evidence of symbolic invention (Boesch 1991) or at least to identify cognitive substrates that they may have for it.

Apes, monkeys, and other brainy mammals are a rich resource for persons brave enough to speculate on the origins of human society. Except orangutans, which are often solitary, each major kind of ape proffers something for theorists who emphasize a particular variety of human social behavior and for persons who see features of their own society reflected in those of apes.

Gibbons are noteworthy for their monogamy, the constancy of which may transcend the human condition (Tuttle 1986). Recent field studies show that some gibbons occasionally cheat on their mates (Palombit 1994; Reichard 1995), which is reminiscent of the human condition. Unlike humans, there is no extension of the nuclear family.

Gorillas appeal to persons who stress male dominance and patriarchy. A characteristic group has one silverback, one or more blackjacked males, adult females outnumbering males, and several youngsters of various ages. The silverback is the hub of the cohesive group. Females and youngsters cluster about him, while other males are peripheral. The proximity of females to one another is attributed to their common attraction to the silverback instead of mutuality. On Mt. Visoke, four youngsters survived loss of their mothers because a silverback parented them (Tuttle 1986).

Chimpanzees and bonobos exhibit complex sociality, some of which remains to be clarified by field studies on nonprovisioned groups. Both species live in unit-groups, numbering up to 120 individuals, which forage, travel, and nest in much smaller bands that vary daily in number and composition. Like gorillas, nubile female chimpanzees and bonobos emigrate from their unit-groups, but unlike gorillas, males generally remain in their natal groups. Otherwise, bonobos and chimpanzees are quite distinct (Tuttle 1986).

Chimpanzee society is dominated by males, which form the stable core of the unit-group. There is a top male, followed by several others whose ranks depend upon which other males are present. High-ranking males spend a lot of time grooming reciprocally. Some individuals tend to assist one another preferentially if one of them is threatened (Tuttle 1986).

Among female chimpanzees, lasting alliances are rare, and they can have relatively clear dominance ordering. Their boldness seems to depend upon the presence of an adolescent son and perhaps by their estrous condition. The status of youngsters depends upon the presence and status of their mothers. Mutual grooming reinforces the bonds between mothers and their offspring, which intensifies as they mature (Tuttle 1986).

Despite the occurrence of promiscuity and sexual orgies during band reunions, many Gombe chimpanzee females were impregnated during restrictive associations with single males. Consortship requires notable female cooperation (Tuttle 1986).

Bonobos have stronger affiliations between males and females than chimpanzees do, and the core of the group is bisexual. The organizational hub

of bonobo social groups may be based on intimate relations among adult females, particularly mothers, which often retain strong bonds with their sons. Adult male bonobos appear to be less strongly bonded with one another than chimpanzee males are (Kano 1992).

The facts that bonobos are more pacific and tolerant in intergroup, intersexual, and intrasexual relationships and are highly sexual place them first among apes with modelers who would view our heritage free of killer apes (Tuttle 1993).

Takayoshi Kano (1992) concluded that, like bonobos and chimpanzees, people are fundamentally promiscuous. Emergence of the human nuclear family has been a particularly knotty problem for Western evolutionary theorists. Instead of the nuclear family, Kano advocates a matricentric extended family as the pristine hominid social unit, which recalls nineteenth-century arguments (Bachofen 1948), though differently premised. Accordingly, after continuous female sexual receptivity had developed in safe, fruitful forests, our pongoid female forebears seduced males to remain with their reproductive units as they adapted to harsher savanna conditions. In this scenario, an initial male-female pair forms, expands with the births of their sons and immigrant females, and then breaks into new pairs and lone individuals upon the matriarch's death. The love attachment of males for their mothers is transferred to their mates and eventually transcends the sexual bond (Kano 1992).

Modelers of emergent hominid societies on the basis of extant ape societies seldom tackle the overriding fact that humans have a wide variety of kinship, social, sexual, and political arrangements, all of which are maintained and expressed symbolically as well as practically (Schneider 1968; Schusky 1974). Again, I would stress the need to search for the cognitive and neural bases of symbolic representation, manipulation, and invention in apes instead of citing forms of behavior that appear to haringer specific human conditions. It may be that the capacity to represent feelings, situations, objects, and ideas symbolically arose *sui generis* before being commandeered, probably with modifications, by the various Gardnerian intelligences. It will take all of our combined mental faculties and much sophisticated technology, probably over many years, to discover the nature of this innovation, its neurological substrates, and its temporal development. Apes can play important roles in this enterprise only if they are studied and viewed in their own right instead of as steps toward the human condition.

PROXIMITY

Despite our dramatic similarities to apes, scientists never have agreed upon the place of our species in the Linnaean classificatory system, largely because of our peculiar mode of locomotion and unusual constellation of behaviors based on symbolic communication, thought, and artifacts. In

the eighteenth century, Johann Blumenbach and Georges Cuvier placed us in a separate Order, the Bimanes (Spencer 1995), while James Monboddo, Jean-Jacques Rousseau, and Charles Bonnet argued that great apes share our species (Barnard 1995; Stoczkowski 1995). Whereas the mid-nineteenth-century genius Thomas Huxley (1863) humbled *Homo sapiens* by close placement with the apes, nearly a century later his gifted grandson, Julian Huxley, arrogantly proposed that we constitute a new evolutionary grade—the Psychozoa—that is “at least equivalent in magnitude to all the rest of the animal Kingdom” (1958, 36). Jared Diamond (1992) declared us to be a third chimpanzee, congeneric with bonobos and chimpanzees, while Merlin Donald (1991) concluded that because of our marvelous minds we deserve our own Order. Altogether, the boundary of *Homo sapiens* has been—as is typical of the species when such classificatory matters arise—intensely contested by the splitters and the lumpers who are always with us.

Four decades ago, Morris Goodman (1963) boldly recommended that the African apes join us in the Hominidae, because two-dimensional starch-gel electrophoretic patterns of their blood proteins were more similar to human ones than to orangutan and gibbon proteins. He left orangutans hanging alone in the Pongidae and gibbons in the Hylobatidae. Like other unorthodox suggestions that are based on novel scientific methods, Goodman’s idea was vigorously attacked. With the efflorescence of cladistics and after many more proteins and DNAs were studied, experts became increasingly comfortable about our cofamilial status with chimpanzees, gorillas, and bonobos.

Today, cladists argue for even more radical supraspecific reclassification of *Homo sapiens* to the extent that it could be nearly impossible to teach hominoid evolution articulately. For example, in Goodman’s (1992) latest scheme, vernacularly people are nonchimpanzee; nonbonobo hominins and the great apes are nonhylobatine, nonhuman hominids. It is faddish in English scientific and lay publications to refer to people as other apes, presumably reflecting acceptance of the genetically premised cladistic taxonomies. Note that if Diamond’s (1992) joining chimpanzees and bonobos with us in genus *Homo* is correct, they should be called the second and third humans instead of humans being the third or wise chimpanzee.

During the past twenty years, a variety of biomolecular studies indicated that there might be a chimpanzee-human clade to the exclusion of gorilla. The most widely cited study is that of Charles Sibley and Jon Ahlquist (1984; 1987), who conducted DNA hybridization tests that imply that 98.4 percent of chimpanzee and human genomes are the same. However, armed with fresh analyses of data from hominoid DNA hybridization experiments, Jonathan Marks and coworkers (1988) incisively challenged the existence of a special chimpanzee-human clade. In addition, data from DNA sequences have failed to resolve the branching order of

chimpanzees, gorillas, and humans. Marks (1995a, b) called attention to several studies that suggest that chimpanzees and gorillas are closer to one another than either is to humans (Dangel et al. 1995; Livak, Rogers, and Lichter 1995; Meyer et al. 1995). Maryann Ruvolo (1995) rebutted some arguments for a tritomy of lineages leading to gorilla, chimpanzee-bonobo, and humans and reasserted the case for a chimpanzee-bonobo-human clade.

Because there is no magic molecule to resolve the controversy, it probably will continue to flare and rage even as new DNA segments are sequenced from larger samples of primates. In the interim, I will continue to teach and to write on the assumption that we are not apes and apes are not people. Indeed, given some of our so-called animal behavior, apes probably are blessed by distance from humanity. I adhere to the classic three-family scheme, in which Hominidae is reserved gradistically for culturally dependent, ecologically specialized humans and their bipedal ancestors, Pongidae embraces all of the great apes, and the Hylobatidae accommodates the gibbons.

PARITY

The remarkable genetic closeness of apes to people sparks questions about how we are to interact with them. Moreover, because of modern transportation, sophisticated means to nurture captives, numerous zoological parks, and prolific coverage by mass media, globally people from all walks of life can observe apes in a variety of contexts ranging from natural to cruelly bizarre. In revulsion to the latter and in response to the former, many scientists and nonscientists are lobbying vigorously for better treatment of apes and other nonhuman animals. Chimpanzees, gorillas, orangutans, and bonobos are highly persuasive poster mammals in the general animal-rights movement.

Paola Cavalieri and Peter Singer (1993) codified the case for bonobos, chimpanzees, gorillas, and orangutans in a Declaration on Great Apes, which is supported by an impressive roster of 36 scientists and humanists in a thirty-chapter book titled *The Great Ape Project*. The oft-cited figure of 98.4 percent overall similarity between chimpanzee and human DNAs is an important datum in the call for equal rights of apes with people. Subscribers to the Great Ape Project also cite the performance of apes in artifactual language studies to support their claims of equal rights of apes to life, liberty, and nonpersecution. In brief, they demand expansion of the anthropocentric community of equals to include not only all people—as great apes—but also chimpanzees, bonobos, gorillas, and orangutans. Accordingly, (1) no member of the community may kill another, except in self-defense or similar extremity; (2) no member should be imprisoned without due legal process, and current captives should be released; and (3) no great ape should be subjected to severe pain, either wantonly or for an alleged benefit to others. Captives are to be liberated to lead their different

lives as equals in their own special territories in captor nations or in their native forests (Cavaliere and Singer 1993).

Before I resume patrol on the boundary of *Homo sapiens*, I must declare deep sympathy with the plight of apes and myriad other creatures on our planet. Of course, we should conserve the great apes and their remnant habitats. All nations that have indigenous populations of apes should respond vigorously to the international call for their conservation via hands-off approaches to their habitats and bodies. Wealthier nations should assist the host nations to establish community-based conservation programs (Tuttle 1994b). We should eschew extreme notions of human transcendence over biology and try to learn as much as we can about the human career and condition by observing the behavior of captives and natural populations of apes. We should stop their dyseducational use as Calibans in drag by entertainers, pet owners, and advertisers (Tuttle 1994b).

The proposition upon which I cannot be dogmatic and confess uneasy ambiguity concerns whether we should eliminate the use of apes as subjects in medical and basic biological research via painful invasive and highly restrictive procedures. I do think that in most cases we should stop, but I cannot declare arrogantly that all such usage should cease. Certainly, it is reasonable to urge that the biomedical community provide detailed reasons why other means, such as tissue culture, genetic manipulation, computer models, and observations of human patients and naturally afflicted nonhuman subjects cannot serve instead during quests for information, treatments, and cures.

It may be imprudent for advocates of the Great Ape Project to premise their case on current genetic information. Although chimpanzees and humans may express approximately 98.4 percent overall similarity in their nuclear DNAs, this still leaves numerous individual genes that differ. Critically, we do not know the functional meaning of the genetic data or how it is expressed developmentally via interactions with complex environmental factors (Tuttle 1994b).

Interestingly, despite frequent mention of the genetic closeness of humans, chimpanzees, bonobos, and gorillas, the topic of possible hybridization between people and African apes is largely ignored in *The Great Ape Project*. Bonobos and chimpanzees, which have the same diploid number of chromosomes ($2n=48$), can produce hybrids, and siabons have been produced via interbreeding siamang ($2n=50$) with lar gibbons ($2n=44$). We cannot deny the possibility that humans ($2n=46$) and chimpanzees could birth hupanzees. Of course, such radical experiments should be unnecessary to establish universal humane treatment of apes (Tuttle 1994b).

Naturalistic observations and intensive laboratory studies, most particularly artifactual language studies, leave little doubt that great apes have highly developed intellectual abilities, sensibility, and personalities. Indeed, of all the arrogant conceits in which humans have indulged, among

the greatest must be the claim that only we are aware of ourselves, have individual identities, and think about what we are doing, have done, and will do. It has been argued that consciousness and its concomitant, mind, are premised on human language. According to this dogma, thoughts are impossible in the absence of human language (Tuttle 1986). Scientists from diverse disciplines have challenged these beliefs vigorously (Griffin 1981; 1984; Byrne 1995; Byrne and Whiten 1988).

Gordon Gallup (1975) provided the best experimental evidence for self-awareness in apes via a study of the responses of chimpanzees to their reflections in mirrors. Healthy humans more than twenty months old show self-objectification and correctly identify their own reflections in mirrors. Most other animals react to their reflections as if they are viewing other individuals of their species, commonly in the form of aggressive or sexual displays. Like monkeys, apes initially react socially to their mirror images, but after several days young and adult chimpanzees begin to use the mirror to explore parts of their bodies that are normally out of view or difficult to position for direct viewing. They also use the mirror to inspect food wadges in their mouths, clean between their teeth, pick their noses, blow bubbles, and make faces. This led Gallup to conclude that they must recognize themselves in the mirror and that they may have a self-concept.

To test these hypotheses, he anesthetized subjects that had and that did not have prior experience with mirror-image testing and placed spots of red dye on the superior aspects of their brow ridges and ears. Once alert and introduced to a mirror, the experienced subjects directed many responses toward the spots, including touches that were followed by visual and olfactory inspection of their exploratory fingers. The mirror-naive subjects reacted socially to the mirror. Adult orangutans also have passed Gallup's dye test after exposure to mirrors.

We do not know whether self-recognition in mirrors truly reflects self-awareness of a human sort or that lack of evidence for mirror-image recognition demonstrates absence of self-consciousness. Carolyn Ristau and Donald Robbins (1982, 218) challenged that Gallup's data "do not require an interpretation that the chimpanzee has an awareness of self as a mind; an awareness of self as a body will suffice."

Donald Griffin (1981) resolved that the complex, versatile, and limited symbolic behavior of signing chimpanzees is especially compelling evidence that nonhuman animals have mental experiences and conscious intentions. He claimed that to the extent that human thinking is linked to language, we could use the complexity and versatility of animal communication to indicate mental experiences for them. Thus, the difference between humans and nonhumans is one of degree, not of kind.

Few could read Frans de Waal's (1989) elegant accounts of chimpanzee, bonobo, and macaque interactions without viewing them as socially intelligent, sometimes even sophisticated. They are highly sensitive, perceptive,

insightful, alert individuals. In short, they sport many earmarks of personality. Observers of both free-ranging and captive apes and other primates are soon struck by the variety of personalities within their study groups. It is moot whether the subjects themselves are aware of their own quirks and qualities and are actively involved mentally in shaping personalities that are homologous with human ones.

The consensual reaction to the first two decades of intensive nonhuman language research was that great apes had not mastered syntax of the kind that allows humans to produce sentences creatively. Embedding has barely been explored, and it is unlikely to occur until simpler sentencelike constructions are generated spontaneously by the subjects (Tuttle 1986).

As investigators of two-way communication with apes realized the elusiveness of syntax, they turned to problems of semantics, just as linguists shifted from a heavy concentration on syntax to questions of semantics in human speech. But it is much easier to demonstrate that great apes know how than that they know what. Clearly they can label objects with arbitrary and iconic symbols and remember a remarkable number of artifactual signs. However, skeptics argued, they had not exhibited comprehension of meaning such that the English glosses that are applied by investigators are the unequivocal equivalents of human words (Tuttle 1986). Thus, although apes can name and symbolize, we still do not know precisely what they know or that their use of symbols is homologous with our own symbolic capabilities.

A more productive protocol would emphasize symbolic communication in naturalistic social relations instead of focusing on food and bourgeois children's toys and activities (Tuttle 1986). E. Sue Savage-Rumbaugh and colleagues (1993) advanced the field in this direction with a star bonobo, "Kanzi." As an eight-year-old, he convincingly evidenced comprehension of spoken English (74 percent correct), comparable to that of a two-year-old human child (65 percent correct). He readily responds to novel verbal instructions, such as "Put the melon in the potty" and "Go outdoors and get the pine needles." His performance fell off dramatically (33 percent success) when asked to give two different objects collectively to an animate receiver.

I cannot predict the impact of the Great Ape Project on public policy. The best hope of its subscribers is to expand lobbies that protect the lives and dignity of these magnificent creatures and to extend the mandate to embrace all animals that evidence personalities. Like people, they can return great joy to those who love them and attempt to understand them on their own terms. The bottom branch is that policy makers must bend to a largely emotional appeal that deeply prods our moral, spiritual being—the essence of humanity—the impulse of which may, in fact, embrace more broadly our primate relatives (Tuttle 1994b). I am skeptical that the Great Ape Project holds the answer but am at a loss to suggest viable options.

The enlistment of analogies to injustices that men visit upon slaves (usually people of color), intellectually impaired persons, women, children, and gender extenders are unsettling in ways that deter me from supporting the declaration on great apes, were I not already intimately acquainted with them. Such comparisons neither promote the equal dignity of all humans nor lead to a full appreciation of the adaptive complexes and novel capabilities of apes (Tuttle 1994b).

We can be fairly confident that apes have more to say and that we have much more to learn about them and from them. I hope that Kanzi and his successors will share more of their feelings, thoughts, and ideas via an artificial and eventually a natural system of communication. Nonetheless, I conclude that, at best, there is an iota of chance that someday a bonobo or chimpanzee will address a human audience in a mutually intelligible language on the topic of “Animalia, *Pan*, and the Kingdom of God.”

DID FLO AND KING TUTANKHAMUN GO TO HEAVEN?

“Flo” (1929–1972), a deceased member of the Kasakela community in Gombe National Park, Tanzania, is arguably the world’s most famous chimpanzee. Jane Goodall (1986; 1990; van Lawick-Goodall 1971) guaranteed her card-catalogue immortality along with her own. Flo was a devoted, highly successful mother and popular member of the Gombe community. Far less renowned, “King Tutankhamun” was the Tuttle family’s Springer spaniel from 1977 until his death in 1992. He too was an endearing, loving member of a community: Hyde Park in Chicago, U.S.A. He made many friends, including our cat, “Jock,” and generated abundant tranquility and joy. I do not believe in Heaven as a specific place where good or faithful persons retire after death. Instead, I believe that God is Love, the most comprehensive form of which is the community of loving spirits that is ever growing with the love of past, extant, and future beings. The spirits of all loving animals—not just people and perhaps great apes—are easily accommodated within this concept. While it may unsettle the ego to realize that one cannot endure as an entity, such realization need not impede communion with God and concomitant constructive behavior toward all inhabitants of Earth.

NOTE

This essay is synthesized from a quartet of lessons, under the general title “Apes and Human Evolution,” that I presented at the Collège de France in November 1995. I am profoundly grateful to Professeur Yves Coppens for this challenge and for sponsoring me and to Professeurs Coppens, Pascal Picq, and James W. Fernandez for their good collegueship and generosity during the visit in Paris. I also happily recall the many critical, attentive undergraduate and graduate students who have helped to test ideas in this essay over the past twenty-eight years of teaching “Apes and Human Evolution” at the University of Chicago.

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