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## Generalized Quadrupeds, Committed Bipedes, and the Shift to Open Habitats: An Evolutionary Model of Hominid Divergence

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### ABSTRACT

Proposed models of hominid divergence and the currently accepted hominoid phylogeny fail to account for the distinguishing human characters that led anatomists to hypothesize a prepongid or prehominoid divergence of hominids. Because humans share a cautious climbing ancestry with other hominoids, similarities in the anatomy and proportions of the human musculoskeletal structure with those of gorillas and cursorial cercopithecids suggest that hominids underwent selection for terrestrial quadrupedality after their divergence from a common semiarboreal hominoid ancestor. Selection for terrestrial quadrupedality explains generalized monkeylike characters in humans, reconciling anatomical evidence with the currently accepted hominoid phylogeny. By emphasizing limb movements in the sagittal plane and limb elongation, terrestrial quadrupedalism preadapts an arboreal cautious climber to habitual bipedality. Ecological models based on cercopithecine analogies indicate that at least two adaptive stages prior to the elaboration of human material culture

must have occurred if hominid divergence progressed from a semiarboreal life-style in a forest or woodland habitat to a committed terrestrial life-style in an open-country habitat. Based on a baboon model, the initial stage consisted of a generalized, widely distributed woodland ape. Predominantly quadrupedal, this ancestor utilized a wide range of behaviors to exploit a wide range of habitats and food resources. Analogous to gelada baboons, the second-stage hominids exhibited a commitment to open habitats while sacrificing generalized behaviors. The fossil evidence for hominid evolution closely fits this postulated model of hominid divergence. With decreasing geologic age, hominid fossils show an increasingly specialized structure and commitment to open habitats. The presence of (1) more than one hominid lineage committed to open habitats, (2) the likelihood of hybrids between different lineages, and (3) a discontinuous and fragmentary fossil record confound fossil phylogenies and the identification of ancestral hominids.

## INTRODUCTION

Before overwhelming biochemical evidence conclusively established the close relationship between African apes and humans, evidence from comparative anatomy supported a variety of alternate hominoid phylogenies. The most widely accepted of these hypothesized a prepongid divergence of hominids, either from a catarrhine precursor of cercopithecoids and hominoids, or from the common hominoid stock before or after the divergence of hylobatids (Schultz, 1936; Straus, 1949, 1962; Tuttle, 1975a).

More detailed anatomical studies, however, also showed these early phylogenies to be improbable (Lewis, 1969; Sarmiento, 1985a, 1988, 1994; Washburn, 1972). Retention of primitive characters or reversals to the primitive condition in hominids, parallelisms between African apes and orang-utans, and parallelisms between cercopithecoids and hominids, have served to confound interpretations of hominoid relationships (Sarmiento, 1985a, 1987a, 1988, 1994, 1995). Although these early phylogenies no longer convincingly organize available facts, the facts that have been marshalled to support them must be accounted for in evolutionary models of hominoid and hominid divergence, and be accommodated for in the accepted phylogenies (i.e., explained either as retentions from a primitive condition or parallelisms due to similarities in environment and/or behavior). Unfortunately, it has been the tradition of hominoid evolutionary studies to discard facts together with the outdated theories they support, and to dig up new facts to support new theories. It is the object of this study to construct a model for hominid divergence that organizes and accounts for the available facts, including those from the fossil evidence. Considering the failure of current models or phylogenies to explain hominid characters (Cela-Conde, 1996; Gebo, 1996; Hunt, 1994, 1996), and lack of consensus as to the locomotor behavior of early hominid fossils (Lovejoy, 1981, 1988, 1993; Sarmiento, 1985b, 1995, 1996; Stern and Susman, 1983; Susman et al. 1984), such an undertaking is warranted.

### HOMINOID PHYLOGENIES AND HOMINID DIVERGENCE

#### PREHOMINOID

Past studies supporting a divergence of hominids from a prehominoid stock emphasized the "primitive nature" of human body proportions and the similarities in the hands and feet of humans and pronograde primates (Osborn, 1927a, 1927b, 1929, 1930; Straus 1940, 1949). As stated by Osborn (1927a: 85) "... the better we understand the human anatomy and mechanism of both the hand and foot, and the more we learn of the fossil ancestors of man, the less close appears our relationship to the great anthropoid apes. ..." The most outspoken proponents of a prehominoid divergence—Wood-Jones (1916, 1929, 1940, 1948), Osborn (1927a,b, 1928, 1929, 1930) and Straus (1940, 1949, 1962, 1968)—agreed that it was nonparsimonious to interpose a brachiating stage in hominid evolution. Because upright trunk postures, a low intermembral index, and a well-developed thumb are characters that humans share with monkeys and/or primitive haplorrhines, interposing a brachiating stage with its associated pollical reduction and upper limb elongation would have required humans to revert to the primitive condition. Wood-Jones (1929, 1948) took this reasoning farther than the others, excluding a pronograde monkey stage in hominid evolution and deriving hominids from primitive, truncally erect, tarsier-like haplorrhines.

#### PREPONGID

By emphasizing anatomical similarities between humans and anthropoid apes, Keith (1916, 1934, 1940), Le Gros Clark (1934, 1971), Morton (1924, 1926, 1927), Morton and Fuller (1952), Schultz (1936, 1950b), and Tuttle (1975a) postulated a divergence of hominids from the common hominoid stock prior to and separate from modern pongids, but after hylobatids. Keith (1911, 1916) dissected 80 higher primates and examined 1065 anatomical characters (some unique to *Homo* and others shared in varying degree with the nonhuman primates) to construct a phylogeny. Unfortunately, Keith never pub-

lished a full list of the characters he considered or the complete results of his dissections (Keith 1940). In this regard, Schultz (1936, 1950b, 1968, 1969) presented the most concrete evidence in favor of a prepongoid divergence. By stressing the primitive nature of human characters, he showed that many of the supposedly unique or shared derived characters used to support a human–African ape clade exist as a matter of variation in the other hominoids and are quantitative (not qualitative) differences. He interpreted those characters that set orang-utans apart and reinforce an exclusive human–African ape ancestry as derived, i.e., acquired after orang-utan divergence from the common great ape stock and of no consequence to great ape phylogeny (Keith, 1916, 1934; Schultz, 1968; Tuttle 1975a). Neither Keith (1911, 1916) nor Schultz (1936, 1968), however, supplied an explanation for their finding that humans share more characters with gorillas than they do with any other great ape. While agreeing to a varying extent with Osborn (1930), Straus (1962), and Wood-Jones (1940) the proponents of a prepongoid divergence believed the primitive upperlimb anatomy of humans and their more monkeylike body proportions far outweighed similarities exhibited by humans and African apes (Keith, 1940, Le Gros Clark 1971; Schultz 1968; Tuttle 1975a).

#### PONGID

Although the close relationship between African apes and humans was hinted at more than a century earlier (Darwin, 1871; Huxley, 1863, 1864; Lamarck, 1809), Gregory (1910, 1916) and Keith (1911) were the first to postulate a phylogeny in which hominids diverged from the pongid stock. Initially, they both derived hominids from the African ape clade (Gregory 1910, 1916; Keith, 1911, 1916), but in subsequent studies only Gregory (1922, 1927a, 1927b, 1930, 1934) still favored a pongid–hominid divergence, albeit one in which hominids, African apes, and orang-utans diverged simultaneously. In contrast to Keith's tabulation of anatomical characters, Gregory (1910, 1916, 1922, 1934, 1951) emphasized the similarities in localized areas of anatomy and a functional complex/character analysis approach to unravel-

ling phylogeny. Well versed in mammalian systematics, Gregory (1922, 1934, 1936) stressed that (1) parallelisms are common features of evolution, and (2) Dollo's law of irreversibility applies to total loss of a structures and not to evolutionary trends in the reduction of structures. In this manner he accounted for all characters common to either cercopithecoids and humans, or to humans and gibbons exclusive of great apes, thus countering arguments for either a prehominoid or prepongoid divergence of hominids, respectively. By subscribing to the axiom that the closer the relationship the closer the parallelisms, Gregory (1922) further justified a human–pongoid clade based on the detailed resemblances of humans and African apes.

At the time, Elliot-Smith (1924), Geisler (1936), Huber (1931), Schwalbe (1923), Sonntag (1924b), and Weinert (1932) argued for an African ape divergence of hominids. Notably, aside from anatomical characters, most of these studies also cited early evidence from immunology (Nuttall, 1904) to bolster their phylogeny (i.e., the much stronger reaction chimpanzee and/or gorilla blood serum exhibits relative to that of the non-hominoid primates, when introduced to antibodies produced in response to human antigens). The African ape divergence has since been convincingly supported by studies based on different criteria including; paleogeography and the modern distribution of great apes (Kortlandt, 1965, 1968, 1972, 1981), behavior (Washburn, 1950a, 1963, 1967, 1968a, 1972), comparative anatomy of the hands and feet (Lewis, 1969, 1974, 1977, 1980a, 1980b, 1980c; Marzke, 1971, Sarmiento, 1983, 1985a, 1988, 1994), and diverse molecular analyses (Goodman, 1963, 1982; Goodman and Moore, 1971; Goodman et al., 1983; Hasewaga et al., 1985; Holme et al., 1989; Horai et al., 1995; Kohne et al., 1972; Rogers 1993, 1994; Ruvolo et al., 1991; Sarich and Wilson, 1967; Sibley and Alquist, 1984, 1987). Because these studies are based on different criteria than the anatomical characters initially used to construct a human–African ape clade, support for an African ape origin of hominids is overwhelming and has thus been popularly accepted (Diamond, 1991; Morris, 1967).



#### PARALLELISMS, PRIMITIVE REVERSIONS, OR RETENTIONS

With the acceptance of a hominid–African ape divergence, characters supporting a catarrhine, hylobatid, or orang-utan divergence for hominids and/or a great ape clade exclusive of hominids must be interpreted as parallelisms, primitive reversions, or retentions (Sarmiento, 1983, 1985a, 1985b, 1987a, 1988, 1994, 1995). Because (1) characters in the forelimb and foot that associate humans with cercopithecoids are quantitative (i.e., differ in dimensions or frequency of characters) and are superimposed on the unique shared derived anatomical elements of hominoids, and (2) primate taxa belonging to the same family or superfamily may show marked differences in body proportions (Schultz, 1930, 1956), the parallel development of such characters in humans and cercopithecoids is possible (Sarmiento, 1983, 1985a, 1985b, 1987a, 1988, 1994). In support of Gregory (1928a), but contrary to Wood-Jones (1916, 1929) and Straus (1949, 1962), body proportions are labile enough at higher taxonomic levels so as to not present major barriers to a hominid–African ape clade.

Absence of the human–cercopithecoid characters in great apes indicates that humans must have developed these after their divergence from the common African ape stock, or that these characters are primitive retentions and the shared great ape condition results from parallelisms. The following points, however, render it highly unlikely that the shared great ape condition could have developed in parallel without leaving evidence in the anatomy: (1) great ape characters are numerous and parts of a larger functional complex exhibited throughout the hominoid anatomy that satisfies the mechanical requisites for cautious climbing and its limiting component, vertical climbing (Sarmiento, 1995); (2) the cautious climbing complex has been strongly selected for in the shared hominoid anatomy, resulting in the formation of novel anatomical elements (Lewis 1969, 1977, 1980a, 1980b, 1980c; Sarmiento, 1985a, 1987a, 1988, 1995) (3) the convergent or parallel development of the cautious climbing anatomy between other mammalian fam-

ilies or subfamilies (i.e., colobines, atelines, lorises, paleopropithecines and bradypodids) is well documented by detailed differences in anatomy (Cartmill and Milton, 1977; Sarmiento, 1985a, 1995); and (4) in mammalian families that have developed the cautious climbing anatomy, it is found in all family members to a varying degree depending on their commitment to cautious climbing, suggesting that cautious climbing is a specialization requiring marked anatomical commitment over a relatively long evolutionary timespan. The association of a high intermembral index; elongated hands, feet, and upper-limb segments; and relative reduction of the thumb or toe with cautious climbing (Cartmill and Milton, 1977; Sarmiento, 1985, 1995) in a diverse group of mammals indicates that the more monkeylike proportions in humans are secondarily derived.

#### EVOLUTIONARY MODELS ACCOUNTING FOR THE HUMAN CHARACTERS

##### PHYLOGENETIC MODELS

The first evolutionary models on human origins were based on the shared characters chosen to construct phylogenies, but without considering cause. The point of divergence hypothesized for the hominid lineage, the number of stages the ancestral hominids evolved through, and the number of settings envisioned as the catalyst for hominid specializations varied depending on the characters emphasized. An adherent of prehominoïd divergence, Straus (1949, 1962, 1968) reconstructed the early hominid as a pronograde catarrhine lacking the characteristic hominoid specializations, but made no mention of how the uniquely human characters subsequently developed. Wood-Jones (1929), who postulated a preanthropoid divergence, envisioned the earliest hominids as small, agile, diurnal animals with hindlimbs longer than forelimbs, small jaws, no sexual dimorphism in the dentition, and with habitually bipedal habits while arboreal. In this arboreal setting, preadaptation for terrestrial bipedality was so complete that the animal needed only to descend to the ground. At the time, Wood-Jones' (1918) model, was also strongly influenced by the belief that a late divergence had a morally degrading effect on hu-

manity. Ripe with creationist overtones, his model strives to push human ancestry as far back in time as possible to intangible, less readily identifiable animals, in an effort to reduce the magnitude of this "degrading effect."

Gregory (1934), Keith (1903), Washburn (1950a, 1967, 1972), and Weinert (1932) adherents of pongid divergence, envisioned large terrestrial, plantigrade, quadrupedal apes as the hominid precursors. Although they emphasized the bipedal preadaptations seen in great apes and noted that this precursor was derived from more arboreal forms, none of these theorists elaborated on how such a terrestrial form would become a biped, or if this form had developed other terrestrial characters.

More recently, Tuttle (1974, 1975a), following the work of Morton (1924), reconstructed the early hominid as a forelimb suspensory ape (i.e., a loosely defined brachiator) fully preadapted to terrestrial bipedality. In doing so, he bypassed the theoretical problems of explaining how a terrestrial quadruped would become a biped, and provided an attractive model, if only for its simplicity. Unfortunately, Tuttle's model fails to account for the shared terrestrial features in the upper limbs of humans and African apes (Sarmiento, 1985a, b, 1988, 1994). Moreover, considering an African ape-hominid clade, his model makes the unparsimonious assumption that humans descended to the ground independent of African apes, both evolving in parallel the shared terrestrial anatomy (Sarmiento 1983, 1985a, 1985b, 1988, 1994, 1995). Surprisingly, in view of its shortcomings, some anatomists (Stern, 1976; Lewis, 1969, 1980a, 1980b, 1980c) and most paleoanthropologists concur with Tuttle's model when interpreting the locomotor behavior of Plio-pleistocene fossils (Clarke and Tobias, 1995; McHenry and Temerin, 1979; Robinson, 1972; Stern and Susman, 1983; Washburn, 1983; Zihlman, 1969; Zihlman and Bunker, 1979).

#### CAUSAL MODELS

Most causal models of hominid origins have focused on bipedalism, creating links between it and the other most apparently unique human characters, i.e., increased

brain size, reduced canines, and tool use (Bartholomew and Birdsell, 1953; Dart, 1957; Darwin 1871; Washburn, 1967, 1968a). The most convincing models emphasize the links between locomotor behaviors, postures, and diet (Hunt, 1994; Rose, 1984, 1991). Because these links directly reflect energy intake vs. energy expenditure, it is expected that they exert considerable selection pressures on the entire musculoskeletal structure and gnathic complex. For this reason, attempts to explain the origin of bipedalism (itself a locomotor behavior) and its associated anatomical characters on the basis of other factors gain little support. It is unlikely that social behaviors, i.e., threat display (Jablonski and Chaplin, 1993; Livingstone, 1962; Westcott, 1967), aggression (Kortlandt, 1980), evasion (Reynolds, 1931), vigilance/sentinel behaviors (Day, 1977; Ravey, 1978), sexual display (Guthrie, 1970; Montgomery, 1988), provisioning/carrying (Bartholomew and Birdsell, 1953; Hewes, 1961; Iwamoto, 1985; Lovejoy, 1981; Marzke, 1986; Washburn, 1967), or throwing (Fifer, 1987), in themselves selected for the bipedal anatomy necessary for locomotion. Selection pressures for long-distance travel associated with shifting patterns of food acquisition may have been important for perfecting bipedalism (Rose 1991), but could not have selected for bipedalism unless the behavior was already practiced. Although thermoregulatory concerns must constrain behavioral shifts and any accompanying changes in structure (Wheeler, 1985, 1993), it is doubtful that locomotor behaviors or their associated structure would have developed solely as a result of these concerns. In response to adaptive behaviors, the most appropriate structure within the given thermoregulatory constraints would be selected for.

Currently two opposing models of hominoid origins are popularly entertained (Campbell, 1985; Johanson and Edgar, 1996; Johanson et al., 1994; Jolly and White, 1994). Although both models treat few of the distinguishing human characters, and one fails to consider the human upper-limb anatomy and cercopithecoid-like body proportions, exploration of their logic and theoretical underpinnings is instructive.

**JOLLY'S SEEDEATERS:** Jolly's (1970) model of hominid origins successfully incorporates the concept of paradaptation or preadaptation. According to Jolly (1970), interpretations of hominid origins that rely on a close and exclusive interrelationship of unique human behaviors to unique human structures are tautological, and can never account for the origin of what they set out to explain. By noting that the characters distinguishing *Theropithecus* from *Papio* are similar to those distinguishing early hominids from great apes, Jolly's model focuses on the links between diet, behavior, and an open country habitat in gelada baboons to arrive at alternative behaviors to associate to unique human structures. Through this analogy, the model constructs an ecological scenario for the origin of humans, one in accord with fossil evidence. The continuing popularity of Jolly's model (Hunt, 1994, 1996) attests to the power of systematic studies for drawing structure-function analogies. Closely related forms with a largely shared morphology and behavior are apt to encounter similar problems in the environment and arrive at similar solutions, providing a rich source of analogies for interpreting structure and function. Following Jolly, other workers also underscored the links between feeding behavior and posture to address the origin of bipedalism and its associated structure (Rose, 1976; Wrangham, 1980; Hunt, 1994, 1996).

**LOVEJOY'S PROVISIONING BIPEDS:** Inspired by new fossil evidence (Johanson et al. 1978; Lovejoy, 1979), which he interpreted to indicate that hominid divergence and striding bipedality predated brain enlargement and cultural development, Lovejoy (1981) rationalized the need for a new model of human origins. He (1981) dismissed Jolly's model on the basis that (1) gelada baboons never became bipedal, (2) Hadar and Laetoli australopithecines have dentitions too generalized to conform to small-object feeding, and (3) paleoecology of Miocene "hominid" fossil sites does not indicate open grassland environments. Following Hewes (1961), Lovejoy (1981, 1993) postulated carrying behavior as the impetus for bipedality, constructing

links between bipedality, provisioning, home base, material culture, human epigamic traits, suppression of external indicators of ovulation, K-r selection strategy, monogamy, and the nuclear family. Lovejoy's model (1981, 1993) is full of incorrect assumptions and interpretations concerning the fossil hominoid evidence (Pilbeam, et al. 1990; Sarmiento, 1987a; Stern and Sussman, 1983), human and primate social systems (Kinzey, 1987; Milton, 1985; Terborgh, 1983), sexual characters and behaviors (Addams et al. 1978; Burt, 1992; Dahl 1988; Dahl and Nadler 1992; Dahl et al. 1993; Matteo and Risan, 1984; Milton, 1985; Schurman, 1982; Short, 1981; Small, 1996; Udry and Morris 1968), K-r selection strategy (Tooby and DeVore, 1987), and past models of hominid divergence (Jolly, 1970). Inured to Jolly's (1970) arguments, Lovejoy (1981, 1993) endowed unique and mutual relationships to the elements in his model, failing to present arguments for their evolutionary origin.

These shortcomings, however, pale beside his assumption (Lovejoy, 1981) that early hominids were not under the same "common" selection pressures that are universal to the other anthropoids, but underwent totally novel selection as a result of unknown, unique preadaptations inherited from Miocene hominoids.<sup>2</sup> Considering the existence of such a hominoid forbearer, it is perplexing why Lovejoy (1981) drew analogies to birds and canids, and searched in Miocene fossil hominoids for novel adaptations. If the preadaptive characters are present in an ancestral hominoid, then surely some traces of these behaviors and associated characters must still be present in the living hominoids. Setting hominids and their hominoid ancestors in a pristine habitat impervious to the same natural laws governing the nonhominid primates

<sup>2</sup> "It is more probable that significant preadaptations were present in early hominids that served as a behavioral base from which the breakthrough adaptations of later hominids could progressively develop. We are therefore in search of a novel behavioral pattern in Miocene hominoids that could evolve from typical primate strategies, but that might also include important elements of other mammalian strategies, that is, a behavioral pattern that arose by a recombination of common mammalian behavioral elements and the increased survivorship and birthrate." (Lovejoy, 1981: 344)

imparts a teleological dimension to Lovejoy's model that precludes scientific testing. The need to harken back to more distally related mammals for ancestral hominid features paints a Wood-Jonesian vision of hominid divergence and demonstrates a surprising irreverence for modern systematics.

### THE DISTINGUISHING HUMAN CHARACTERS

Table 1 summarizes the characters that distinguish humans from either chimpanzees or gorillas, and lists the primates most closely related to humans that exhibit or approximate each character. Figure 1 summarizes how these characters relate to the human-African ape divergence. The summary is based largely on the author's studies (Sarmiento, 1983, 1985a, 1985b, 1987a, 1987b, 1988, 1994, 1995), and on a review of the literature, taking care to include characters used to arrive at alternate phylogenies (Duckworth, 1915; Keith, 1894, 1902, 1903, 1916, 1923, 1929, 1934, 1940; Le Gros Clark 1934, 1971; Schultz 1930, 1936, 1937, 1950b, 1956, 1968; Sonntag 1923, 1924a, 1924b; Stern 1971, 1976; Straus 1940, 1941, 1942, 1949; Tuttle, 1969, 1972, 1974, 1975a, 1975b; Wood-Jones, 1929, 1948).

To test and further refine the proposed model, fossil Plio-pleistocene hominids housed in the following institutions were examined for the distinguishing human characters: University of the Witwatersrand Medical School, Johannesburg; Transvaal Museum, Pretoria; National Museum of Kenya, Nairobi; National Museum of Tanzania, Dar es Salaam; and National Museum of Ethiopia, Addis Ababa. Distinguishing characters considered (table 1) were verified by the author for both fossil and living taxa. The study focuses on the least variable anatomical characters and is not meant as an exhaustive summary of all distinguishing characters.

### DISTRIBUTION

Humans are distinguished from hominoids by a worldwide distribution both north and south of the tropics at elevations from below sealevel to above 5000 m. With a consider-

able distribution outside tropical zones, cercopithecoids are the primates that most closely approximate humans in this respect. *Papio* and *Cercopithecus* range from 15° to 20° north of the equator into the temperate zones of Subsaharan Africa south to the Cape of Africa (34°50'S) (Brain and Gartlan, 1968; Jolly, 1993; Nowack, 1991). *Macaca*, *Presbytis* and *Rhinopithecus* range into northern temperate areas with seasonally heavy snowfall (Bishop, 1979; Bleisch et al., 1993; Mehlman, 1988; Nakagawa, 1997; Wu, 1993). The Afro-Eurasian distribution of *Macaca* most closely approximates the worldwide distribution of modern humans (Nowack, 1991).

Gorillas and langurs most closely approximate humans in altitudinal range (Groves, 1970; Sarmiento et al. 1996; Vogel and Winkler, 1988), inhabiting areas from sea level to above 4000 m. Due to seasonal food availability in temperate forests and the absence of trees at high altitudes, all nonhuman primates approximating the human distribution patterns are terrestrial quadrupeds relying on terrestrial food sources (Nowack, 1991; Wu, 1993). Compared to their closest arboreal relatives, all such primates inhabit a wide range of elevations (i.e., from sea level to 3000 m) and are relatively large-bodied (Fedigan, 1994; Fleagle, 1988; Tenaza et al., 1988; Watanuki and Nakayama, 1993).

### LOCOMOTOR CHARACTERS

UNIQUE CHARACTERS ASSOCIATED WITH BIPEDAL BEHAVIORS: Many of the distinguishing characters unique to humans are in the trunk and lower limbs. Associated to habitual and striding bipedality, these characters satisfy the following mechanical demands of modern human bipedalism:

(1) *support of additional weight on the lower limbs and lower half of the trunk*, i.e., a last lumbar vertebra with a large x-sectional body area, a large sacroiliac joint, a relatively large femoral and tibial shaft diameter, a large femoral head and correspondingly large acetabulum, a strong and well-developed sacrotuberous ligament, and a strongly developed sacrospinous ligament associated with a robust and invariably present ischial spine;

TABLE 1  
The Divergent Human-African Ape Characters and Their Presence in Other Primates

Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character	Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character
<b>External</b>		21) Heavily inflated, multi-chambered ethmoid sinus	Approximated by African apes
1) Short, slender, and poorly pigmented body hairs	Unique	22) Open orbit with large superior and inferior orbital fissures	Hylobatids, orang-utans, and cercopithecoids have superior fissure
2) Low hair density on trunk	Unique	23) Retention of sizable ethmolacrimal contact on the medial orbital wall	Pygmy chimpanzees and orang-utans; variable in African apes
3) Absence of tactile or sinus hairs	Unique?	24) Adult glabella situated fully on frontal, considerably above the horizontally aligned frontonasal and frontomaxillary sutures	Unique
4) Long scalp hair	Rivalled by hair length on back and shoulders of orang-utans	25) Nasal bones broad with late obliteration of nasal sutures	Unique? (some cercopithecoids)
5) Alignment of hair tracts	Unique	26) Absence of nasolacrimal bulla	Chimpanzees
6) Alopecia in older adults	Chimpanzees	27) Vertical plate of vomer inserts high on nasal crest	Unique
7) Subcutaneous fat layer with abundant vascularization	Unique	28) Strong nasal spine set perpendicular to vertically oriented incisive clivus	Unique
8) High density of cutaneous sweat (eccrine) glands on trunk, with apocrine glands enlarged and restricted to localized areas	Unique? (approximated by African apes)	29) Early obliteration of anterior alveolar premaxillary-maxillary sutures	Obliterated in newborn chimpanzees
9) High density of glycogen-containing sebaceous glands on back, shoulders, chest, head, and urogenital region associated with acne	Unique	30) Premaxillary processes flanking piriform aperture overgrown by maxilla	Approximated by some western lowland gorillas
10) Low and wide nipple position	Unique (marked nipple width seen in orang-utans)	31) Small nasally divided incisive foramen variably presents a small single palatal opening	Small foramen seen in orang-utans
11) Female epigamic pectoral features	<i>Theropithecus</i>	32) Short temporal process of zygomatic bone	Cercopithecoids?
12) Epigamic hair on face and body	Gorillas, orang-utans, and cercopithecoids	33) Malar tubercle positioned mainly on zygomatic bone	Unique?
13) Strong sexual dimorphism in body size; 1.35:1 male to female ratio	Gorillas and orang-utans exhibit greater dimorphism in size	34) Absence of simian shelf	Asian colobines
14) Ear relatively small with lobule	Approximated by gorillas	35) Absence of maxillary-premaxillary palatal sinus inflation	Gorillas
15) Primitive dermatoglyphics pattern	Some cercopithecids	36) Protruding chin	Unique
16) Absence of pigmentation on palms and soles	Some cercopithecids	37) Marked differentiation of facial muscles	Unique (approximated by African apes)
17) Nasal morphology; nasal septal cartilage protrudes strongly anterior to the piriform aperture, and the alar cartilages are well developed	Approximated by gorillas	38) Small conical filiform papillae on tongue, anterior lingual glands (Nuhn), and profuse circumvallate papillae	Orang-utans
18) Well-exposed eye sclera	Approximated by gorillas	<b>Cranium</b>	
<b>Face</b>		39) Ethmosphenoid contact within anterior cranial fossa (absence of frontobasilar contact)	Orang-utans (variable) and hylobatids
19) Relatively small face and jaw with small gape	Approximated by gibbons		
20) Relatively broad interorbital region	Gorillas		

TABLE 1  
(Continued)

Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character	Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character
40) Sphenoparietal contact at pterion	Hylobatids and orang-utans; variable in African apes	58) Head balanced on spine with inferior orientation and anterior displacement of foramen magnum and occipital condyles	<i>Rhinopithecus</i> (approximated by pygmy chimpanzees)
41) Flexed basicranium	Unique (approximated by pygmy chimpanzees)	59) Marked elevation of cranial roof above supraorbital margin	Unique (approximated by pygmy chimpanzees)
42) Crista galli with wide cribriform plate above mid-orbital level	Unique	60) High temporoparietal suture	Unique (approximated by pygmy chimpanzees)
43) Deep pituitary fossa	<i>Rhinopithecus</i> (approximated by pygmy chimpanzees)	61) Inferiorly disposed nuchal crest	Approximated by pygmy chimpanzees
44) Laterally expanded lesser wing of sphenoid forming crested upper border of superior orbital fissure	Unique	62) Relatively small lateral semicircular canal	Unique?
45) Short basisphenoccipital with body of vomer overriding basisphenoid	Unique	63) Wide pterygo-maxillary cleft or fissure	Mountain gorillas and hylobatids
46) Small and deep glenoid fossa with raised articular planum and a vertical tympanic plate	Unique	<b>Dental</b>	
47) Large tympanic vagina enveloping large ossified styloid process	Approximated by <i>Rhinopithecus</i> , <i>Presbytis</i> , and <i>Pygathrix</i>	64) Cheek tooth surface area and incisal edge length reduced relative to body weight	Unique?
48) Presence of foramen lacerum	Orang-utans and hylobatids	65) Reduction of premolar to molar surface area	Cercopithecoids and chimpanzees
49) Mediolaterally short auditory tube and tympanic plate	Unique	66) Vertically implanted incisors that are small relative to molars	<i>Brachyteles</i>
50) Long axes of petrous bone and auditory tube, nearly aligned and set diagonal to sagittal plane	Unique?	67) Small, spatulate, bluntly pointed canines	<i>Brachyteles</i>
51) Large and consistent mid-meningeal branch of maxillary artery travelling through foramen spinosum	Variable in African apes	68) Slight or absent sexual differentiation of canines	Hylobatids, <i>Brachyteles</i> , and <i>Callicebus</i>
52) Sphenoid spine forming entoglenoid	Unique? (seen rarely in gorillas)	69) Single-rooted premolars	Occasionally seen in both gorillas and chimpanzees
53) Foramen spinosum and ovale fully within alisphenoid	Occasionally seen in gorillas	70) Bicuspid p3	<i>Brachyteles</i> ?; variable in chimpanzees and orang-utans
54) Large pterygoid (vidian) canal carrying autonomic nerves to lacrimal gland and nasal mucosa	Canal smaller in African apes, absent in orang-utans and hylobatids	71) Thick molar enamel	Orang-utans
55) Strong development of mastoid with mammillary process and medially adjacent digastric fossa	Approximated by gorillas and <i>Theropithecus</i>	72) Flat molar wear	Orang-utans and chimpanzees
56) Large brain and cranial capacity	Unique	73) Low cusped molars	Chimpanzees and orang-utans
57) Large cerebellum	Unique	74) Reduction or absence of hypoconulid most marked on m1	Orang-utans and cercopithecoids
		75) Reduction and/or loss of M3 and m3	Callithricids
		76) Early eruption of permanent canine and central incisor	Cercopithecines and atelines
		77) Small, spatulate milk canine	Atelines
		78) Multicusped molariform dp3	Cercopithecines

TABLE 1  
(Continued)

Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character	Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character
79) Eruption of milk canines before 2nd milk molar	Cercopithecines	100) Thoracolumbar region forming a large percentage of trunk length, associated with short sacrum	Hylobatids (approximated by cercopithecoids)
80) Parabolic dental arcade and short palate	<i>Brachyteles</i> ; <i>Rhinopithecus</i> females	101) Marked ventral displacement of vertebral column into thorax	Unique
<b>Neck</b>		102) Single articular surface on head of 1st rib with 7th cervical vertebra lacking rib articulation	<i>Theropithecus</i>
81) Absence of laryngeal pouches or air sacs	<i>Hylobates lar</i> and cercopithecoids	103) Twelve ribs	Orang-utans and hylobatids
82) Sharp angle of nasopharynx to oropharynx with an inferiorly situated larynx	Unique	104) Narrow sternum	Gibbons
83) Specialized vocal cords of larynx	Unique	105) Conservative chest girth	Gibbons
84) Cervical lordosis	Cercopithecoids	106) Seventeen thoracolumbar vertebrae	Hylobatids (variable in African apes)
85) Relatively long neck	Cercopithecoids	107) Barrel-shaped chest	Hylobatids
86) Bifid and short spinous processes of upper cervical vertebrae	Cercopithecoids (approximated by <i>Hylobates</i> )	108) Five lumbar vertebrae	Hylobatids and atelids
87) Presence of transverse foramina on C7	Unique?	109) Relatively long lumbar region and space between pelvis and thorax	Cercopithecoids
88) Fusion of sternomastoid and sternocleidom. m.	Orang-utans	110) Marked lumbar lordosis	Approximated by cercopithecoids
<b>Trunk</b>		111) Superoinferiorly wide and posteriorly directed spinous processes on lumbar vertebrae	Unique? ( <i>Brachyteles</i> ; approximated by some cercopithecoids)
89) Relatively well-differentiated scalene musculature inserting on more than one rib	Cercopithecoids and pygmy chimpanzees	112) Large x-sectional area and marked wedging of last lumbar vertebral body	Unique
90) Reduced number of tendinous inscriptions on rectus abdominus	Approximated by chimpanzees and orang-utans	113) Marked width between spinal articulations of last lumbar vertebra and progressive caudal increase in the interfacet diameter of last four lumbar vertebrae	Unique (approximated by cursorial cercopithecines)
91) External oblique m. attaching on iliac crest and lacking acetabular attachment	Approximated by gorillas and pygmy chimpanzees	114) Progressive caudal increase in the x-sectional area of the pedicles of lumbar vertebrae	Unique
92) Presence of pyramidalis m.	Cercopithecoids	115) Broad sacrum	Unique
93) Differentiation of erector spinae and intrinsic back musculature	Cercopithecoids have better differentiated muscles	116) Ventral concavity of sacrum	Unique
94) Separate deep transversus perinei m. with strong development of the urogenital fascia	Unique	117) Center of gravity of body close to hip joint	Unique? (indrids, galangines, and tarsiers)
95) Relatively poorly developed and restricted sphincter ani externus	Gibbons	118) Reduced number of sacral vertebrae	Approximated by cercopithecoids
96) True inguinal ligament	Unique	119) High number of coccygeal vertebrae	Approximated by chimpanzees
97) Early obliteration of inguinal canals at birth	Unique	120) Sacroiliac joint large, with wide alae and lateral angles	Unique
98) No trace of ischial callosities, associated with a gluteus maximus wrapping around the ischium	Unique? (atelines; some trace variably seen in all great apes)	121) Short ilium, reduced vertical height from acetabulum to sacroiliac joint	Cercopithecoids
99) Strong sacrotuberous ligament	Atelines and gorillas		

TABLE 1  
(Continued)

Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character	Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character
122) Wide iliac blades	Gorillas	142) Palmaris longus and brevis m. usually present	Approximated by gorillas
123) Laterally facing iliac blade and parasagittal orientation of iliac fossa	Cercopithecoids (approximated by gorillas)	143) Well-developed forearm wrist extensors	Cercopithecoids
124) Posterior expansion of ilium and iliac crest forming a large postauricular area	Unique (approximated by cercopithecines)	144) Large, separate long flexor tendon and muscle belly for pollex	Unique (approximated by <i>Theropithecus</i> and gibbons)
125) Short ischium decreasing ischio-acetabular distance	Unique? (cercopithecoids?)	145) Extensor pollicis brevis m.	Approximated by gorillas and <i>Presbytis</i>
126) Short pubis	Unique?	146) Presence of 1st palmar interossei and well-developed thenar musculature	Cercopithecoids and hylobatids
127) Pelvic aspect of acetabulum with well-developed iliopsoas groove	Unique?	147) Absence of manual contrahentes	Gorillas
128) Large inflated anterior inferior iliac spine for large iliofemoral ligament and reflected head of rectus femoris	Unique?	148) Palmar lumbricals may variably show basal phalanx insertion	Gorillas, baboons, and <i>Theropithecus</i>
129) Invariably present and strong ischial spine (anteacetabular spine) associated with sacrospinous ligament	Unique? (approximated by orang-utans)	149) Abductor pollicis longus m. sends main tendon to base of 1st metacarpal	Cercopithecoids
130) Strong iliac tuberosity and pillar	Unique	150) S-shaped clavicle	Cercopithecoids
131) Iliac long axis perpendicular to sacral articulation; rotation of iliac alae and sacral articulation such that pelvic canal approximates horizontal	Unique	151) Large inferior scapular angle and small barglenoid angle	Gorillas and cercopithecoids
132) Deep, angulated sciatic notch	Unique (approximated by gorillas)	152) Short scapula with vertical vertebral border and small supraspinous fossa	Orang-utans
<b>Upper Limbs</b>		153) Upper limbs short relative to lower limbs (low intermembral index) and to trunk length	Indrids, galagines, and tarsiers
133) Poorly divided pectoralis major m., absence of separate pectoralis abdominus m.	Chimpanzees	154) Low brachial index	Gorillas
134) Pectoralis minor m. inserting on coracoid with 2-5 rib origin	Variable in gorillas and orang-utans	155) High humeral torsion	Unique (approximated by African apes)
135) Trapezius m. aponeurotic at midline with distal origin from all thoracic vertebrae	Approximated by orang-utans and gorillas	156) Relatively short and broad hand with generalized proportions	Gorillas and cursorial cercopithecoids
136) Absence of omocervicalis (atlantoscapularis) m.	Unique?	157) Distal branching of thumb relative to the palm; cleft between thumb and index finger distally disposed	Cercopithecoids
137) Latissimus dorsi attaching on scapula with T6-T12 origin	Unique? (approximated by cercopithecoids)	158) Absence of interdigital manual webbing	Orang-utans
138) Absence of dorsoepitrochlearis	Approximated by gorillas	159) Relatively large and long thumb and high opposability index	<i>Theropithecus</i> (approximated by mountain gorillas)
139) Serratus anterior origin restricted to first eight ribs	Unique (approximated by cercopithecoids)	160) Short fingers	Gorillas, <i>Theropithecus</i> , and baboons
140) Separation of rhomboids with restricted cervical origin	Unique	161) Full omission of ulnar head and styloid from proximal carpal joint by triangular articular disc, associated with a short ulnar styloid process	Gorillas
141) Coronoid head of pronator teres m.	Chimpanzees		



TABLE 1  
(Continued)

Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character	Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character
162) Pisiform and hamulus palmarly oriented	Gorillas and cursorial cercopithecoids	182) Gastrocnemius m. large relative to soleus m., all with a relatively long triceps surae tendon	Cercopithecoids
163) Reduced pisiform length	Orang-utans	183) Soleus m. with tibial origin	Lorisines and atelines; variably seen in African apes
164) Superoinferiorly broad and palmarly elongated hamulus	Gorillas	184) Plantaris m. usually present, but attaches on calcaneus as typical in hominoids	Approximates cercopithecoids
165) Large inferior angle of hamate	Gorillas and cercopithecoids	185) Expansive insertion of tibialis posterior	Gorillas
166) Trapezium crest well formed	Unique?	186) Segregation of flexor fibularis and flexor tibialis tendons to hallux and lateral toes, respectively	Unique
167) Styloid process on 3rd metacarpal	Variable in gorillas	187) Peroneus tertius	Always present in eastern gorillas, variable in lowland gorillas; occasional in baboons
168) Expanded apical tufts and spines (variably) on distal manual phalanges	Gorillas and baboons	188) Strongly formed plantar aponeurosis	Gorillas and cercopithecoids
169) Long and robust 2nd metacarpal associated with an index finger that is long relative to the ring finger	Approximated by <i>Theropithecus</i>	189) Absence of deep head of flexor digitorum brevis m.	Unique
170) Straight phalanges with poorly developed flexor sheaths	Cercopithecines	190) Well-developed two-headed quadratus plantae m.	Unique (well-developed lateral head in cercopithecoids)
<b>Lower Limbs</b>		191) Ossi metatarsi quinti m. replaced by lateral plantar ligament	Variably replaced in orang-utans
171) Large fascial insertion for gluteus maximus m.	Cercopithecoids	192) Adductor hallucis transversus with origin from 2nd–5th metatarsal heads	Approximated by gorillas
172) Relatively large gluteus maximus m., limited to and encompassing proximal third of thigh	Atelines	193) Pedal interossei axis through second digit	Variable in gorillas
173) Sacrotuberous ligament on deep surface of superficial gluteal (gluteus maximus) m.	Atelines (approximated by orang-utans and gorillas)	194) Pedal lumbrical and interossei insertion on base of proximal phalanges, with limited extensor expansion insertion	Gorillas and cercopithecoids
174) Superficial gluteal m. larger than gluteus medius and minimus m.	Orang-utans and gibbons	195) Full absence of pedal contrahentes	Gorillas
175) Scansorius m. fully fused to gluteus minimus m.	Cercopithecoids	196) Posteriorly projected and proximally expanded ischial tuberosity	Unique
176) Iliotrochantericus m. absent	Lorisines; variably absent in cercopithecoids	197) Marked anterior and inferior acetabular orientation	Unique?
177) Strongly developed and separate tensor fascia femoris	Cercopithecoids and <i>Alouatta</i>	198) Comparatively large femoral head and acetabulum	Unique
178) Origin of gracilis m. on ischiopubic ramus	Orang-utans and atelines	199) High femoral neck angle	Orang-utans, atelines, and lorisines
179) Adductor magnus and ischiocondylarus (presemimembranosus) m. fused	Cercopithecoids	200) Relatively short femoral neck	Approximated by orang-utans
180) Insertion of semimembranosus into knee capsule	33% of gorillas; occasional in orang-utans, macaques, and atelines	201) High femoral torsion	Cercopithecoids
181) Short head of biceps femoris m. inserted mainly on the tendon of the long head of biceps	Pygmy chimpanzees, gibbons, and atelines; variable in common chimpanzees		

TABLE 1  
(Continued)

Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character	Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character
202) High bicondylar or femoral carrying angle	Orang-utans, atelines, and lorises	221) Big toe long relative to foot length, more distally projected than lateral digits	Unique (approximated by mountain gorillas)
203) Relative large femoral and tibial shaft x-sectional areas	Unique? (approximated by indrids, galagines, and tarsiers)	222) Distally extended sole with web between hallux and second metatarsal	Approximated most closely by mountain gorillas
204) Narrow and anteriorly extended intercondylar notch	Cercopithecoids	223) Lateral plantar process of tuber calcanei (associated with lateral plantar ligament) replaces large peroneal trochlea	Unique
205) Deep patellar groove with a more anteriorly projecting lateral lip	Cursorial cercopithecines	224) Transverse tarsal arch	Gorillas and cursorial cercopithecines
206) Lateral femoral condyle larger than medial	Cercopithecoids	225) High longitudinal pedal arch	Unique
207) Anterior transverse ligament of the knee joint	Unique?	226) Strong, well-defined spring ligament with a cartilaginous articular area and a correspondingly well-defined surface on the talar head	Approximated by chimpanzees
208) C-shaped lateral meniscus in knee joint	Orang-utans	227) Well-developed two-banded bifurcated ligament	Unique
209) Tibial plateau surface concave to planar	Orang-utans?	228) Large and elongated tarsals especially cuboid	Unique (approximated by cercopithecoids)
210) Nearly perpendicular set of proximal articular surface to tibial long axis in both sagittal and frontal plane	Lorises (approximated by orang-utans and atelines)	229) Large and expanded long plantar ligament	Unique
211) Posteriorly disposed and reduced proximal tibiofibular facet	Cursorial cercopithecines	230) Fusion of distal phalanx of 5th digit with occasional absence of middle phalanx	Approximated by mountain gorillas
212) High positive tibial torsion	Approximated by cercopithecoids	231) Nearly planar first tarsometatarsal joint	Callithricids (approximated by mountain gorillas and <i>Theropithecus</i> )
213) Absent or reduced distal tibiofibular facet	Cercopithecoids	232) Massive plantar process of tuber calcanei (heel process)	Gorillas
214) Mediolaterally compressed distal fibula with mediolaterally narrow and restricted peroneal groove and laterally facing subcutaneous malleolar surface	Cursorial cercopithecines	233) High talar torsion	Approximated by mountain gorillas
215) Tibial long axis set at right angles to talar articular surface in frontal plane	Cercopithecoids (mainly cursors)	234) External rotation of calcaneal body and talar articulations relative to heel process	Cursorial cercopithecoids
216) Dorsiflexed set of talar articulation relative to tibial long axis	Unique? (approximated by cercopithecoids)	235) Relatively strong plantar flexion of calcaneal neck	Unique
217) Foot short relative to body weight	Approximated by gorillas	236) Absence of weight-bearing tubercles on distal tarsus	Platyrrhines and strepsirrhines
218) Reduction in length of pedal phalanges emphasizes reduction of middle phalanges	Gorillas and cursorial cercopithecines	237) Dorsal expansion of articular surfaces on metatarsal heads	Unique (approximated by cursorial cercopithecines)
219) Relatively narrow foot	Orang-utans and <i>Theropithecus</i>	238) Straight metatarsal shafts	Cercopithecines
220) Nonopposable adducted hallux; long axis, and dorsal and plantar surfaces of big toe oriented as for other digits	Callithricines (approximated by <i>Theropithecus</i> and gorillas)	<b>Viscera</b>	
		239) Striated musculature restricted to upper third of esophagus	Lemurs

TABLE 1  
(Continued)

Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character	Characters That Distinguish Humans from Chimpanzees and/or Gorillas	Most Closely Related Primate Exhibiting the Human Character
240) Kidney with multiple calyces	Unique (calyx number approximated by chimpanzees)	259) Long life	Unique
241) Multilobulated liver	Human lobule number approximated by chimpanzees	260) Marked postnatal changes in cranial capacity	Unique
242) Relatively large uterus	Unique?	261) Primitive sequence of epiphyseal union	Cercopithecoids
<b>Genital</b>		262) Delayed ossification of distal radius and proximal humeral epiphyses	Orang-utans
243) Morphology of sperm	Approximated by gorillas	263) Delayed ossification of cranial suture	Cercopithecoids
244) Large penis with large glans	Glans present in gorillas and hylobatids; chimpanzee penis relatively longer	<b>Distribution and Behaviors</b>	
245) No os penis	Platyrrhines; variably absent in great apes	264) Worldwide distribution both north and south of the tropics	Approximated by <i>Papio</i> , <i>Macaca</i> , <i>Cercopithecus</i> , and <i>Presbytis</i>
246) No external signs of ovulation	Orang-utans and platyrrhines (approximated by gorillas)	265) Large altitudinal range from below sea level to above 5000 m	Approximated by gorillas and cercopithecids
247) Labia majora and mons pubis persist into adulthood	Unique?	266) Fully terrestrial; trees rarely climbed for feeding	Some eastern gorillas and <i>Theropithecus</i>
248) Glabrous petal-like labia minora	Unique	267) Full striding bipedality, walking and running with extended knee and thigh	Unique
249) Early descent of testicles	Unique?	268) Palmigrade hand postures	Cercopithecoids; postures variably seen in orang-utans, chimpanzees, and hylobatids
250) Relatively small testicles	Smaller in gorillas and orang-utans	269) Language	Unique
<b>Life History and Development</b>		270) Tool use	Chimpanzees and orang-utans
251) Relatively short ovulatory cycle	Cercopithecoids	271) Most sensitive to 2000–3000 Hz sounds, with an adult range between 20 and 25,000 Hz	Unique?
252) Nine-month gestation period	Orang-utans	272) Hunting and/or herding significant component of food acquisition in most human societies	Approximated by chimpanzees
253) Relatively heavy newborn	Approximated by hylobatids	273) Large repertoire of learned behaviors	Unique?
254) Long postnatal development and long infant-dependency periods	Unique	274) Marked capacity for dissipating heat through perspiration	<i>Erythrocebus</i>
255) Short intrauterine development period compared to postnatal life	Unique	275) Weeping	Unique
256) High rate of prenatal growth compared to postnatal growth	Unique	276) Social systems based on polygyny and serial monogamy; matrilineal and patrilineal communities	Gorillas and orang-utans
257) Myelination of pyramidal tract does not occur until 1st year of life	Unique?		
258) Relatively long quadrupedal infant stage preceding bipedality	Unique		

**Notes:**

- 1) Montagna, 1985; Schultz, 1931, 1936.  
2) Montagna, 1985; Schultz, 1936; Straus, 1950.  
3) Friedenthal, 1908; Van Horn, 1970.  
4) Montagna, 1985; Schultz, 1936, 1968.  
5) Friedenthal, 1908; Schwalbe, 1923; Wheeler, 1991c, 1992b; Wood-Jones, 1916, 1929.  
6) Allen, 1925; Elliott, 1912; Montagna, 1985; Montagna and Uno, 1968.

TABLE 1  
(Continued)

- 7) Montagna, 1972, 1985; Wood-Jones, 1916, 1929.
- 8) Elizondo, 1988; Montagna, 1985; Straus, 1950.
- 9) Harrison and Montagna, 1973; Montagna, 1972, 1985.
- 10) Schultz, 1936; Schwartz, 1984.
- 11) Alvarez, 1973; Cant, 1981; Dunbar, 1984; Gallup, 1982; Jolly, 1970, 1972.
- 12) Darwin, 1871; Harrison and Montagna, 1973; Jolly, 1970; Montagna, 1985; Pocock, 1925; Schultz, 1968.
- 13) Lyon, 1908, 1911; Jungers and Susman, 1984; Sarmiento, 1985a; Schultz, 1950a, 1953.
- 14) Schultz, 1936, 1968; Wood-Jones, 1916, 1929.
- 15) Biegert, 1963; Cummins and Midlo, 1943; Fiedler, 1956; Schlaginhaufen, 1905; Straus, 1949.
- 16) Hewes, 1983.
- 17) Author's notes; Deniker, 1885; Gregory, 1922; Hofer, 1972; Raven, 1950; Schultz, 1935.
- 18) Author's notes; Schultz, 1940.
- 19) Biegert, 1963; Picq, 1990a, 1990b; Schultz, 1936; Weidenreich, 1943.
- 20) Author's notes; Schultz, 1936, 1968.
- 21) Cave and Haines, 1940; Weinert, 1926.
- 22) Owen, 1868; Rak et al., 1996; Sonntag, 1923, 1924a, 1924b; author's notes.
- 23) Cramer, 1977; Schultz, 1968; Wood-Jones, 1916, 1929.
- 24) Weinert, 1926; Olson, 1978, 1981, 1985.
- 25) Schultz, 1936; Wood-Jones, 1916, 1929; author's notes.
- 26) Cave and Haines, 1940; Keith, 1902; author's notes.
- 27-28) Clarke, 1977; Robinson, 1953; Ward and Kimbel, 1983; McCollum et al., 1993; McCollum and Ward, 1997.
- 29) Ashley-Montague, 1935; Bolk, 1913; Remane, 1927; Schultz, 1936; Woo, 1944; Wood-Jones, 1947.
- 30) Clarke, 1977; Wood-Jones, 1929, 1947.
- 31) Schwartz, 1984; McCollum et al., 1993; McCollum and Ward, 1997.
- 32) Wood-Jones, 1916, 1929.
- 33) Author's notes.
- 34) Weidenreich, 1936; Wood-Jones, 1916, 1929.
- 35) Caves and Haines, 1940; McCollum et al., 1993; Ward and Kimbel, 1983.
- 36) Straus, 1949; Weidenreich, 1936; Wood-Jones, 1916, 1929.
- 37) Ruge, 1887; Huber, 1931.
- 38) Sonntag, 1924b.
- 39) Gregory, 1927a, 1928b; Schultz, 1968; Wood-Jones, 1916, 1929.
- 40) Ashley-Montagu, 1933; Cramer, 1977; Schultz, 1968; Sonntag, 1924b; Wood-Jones, 1929.
- 41) Biegert, 1963; Cramer, 1977; DuBrul and Laskin, 1977; Fenart and DeBlock, 1973; LeGros Clark, 1970; Weidenreich, 1941.
- 42) Sonntag, 1924b; Wood-Jones, 1929; author's notes.
- 43) Wood-Jones, 1929.
- 44) Rak et al., 1996; Sonntag, 1924b; author's notes.
- 45) Dean and Wood, 1981, 1982; Sarmiento, in prep. b.
- 46) DuBrul, 1977; Le Gros Clark, 1955b; Picq, 1990a, 1990b; Sonntag, 1924b; Wood-Jones, 1929.
- 47) Sarmiento, 1993, 1995, in prep. b; Weidenreich, 1943; Zuckerman et al., 1962.
- 48) Schwartz, 1984; Wood-Jones, 1929.
- 49) Clarke, 1977; Dean, 1984; Sarmiento, 1993, in prep. b; Weidenreich, 1951.
- 50) Tobias, 1967; Dean and Wood, 1981, 1982.
- 51) Sarmiento, in prep. b; Sonntag, 1923, 1924a, 1924b.
- 52) Dean, 1984, 1985; Picq, 1990a, 1990b; Sarmiento, in prep. b; Tobias, 1967; Weidenreich, 1941, 1943, 1951.
- 53) Sarmiento, in prep. b; Sutton, 1884; Tobias, 1967; Wood-Jones, 1916, 1929.
- 54) Gardner et al., 1975; author's notes.
- 55) Jolly, 1970, 1972; Le Gros Clark, 1955a; Schultz, 1950a, 1968; Tobias, 1967; Walensky, 1964.
- 56) Schultz, 1936, 1968.
- 57) Aiello and Dean, 1990; author's notes.
- 58) Dean and Wood, 1981, 1982; Le Gros Clark, 1971; Schultz, 1942, 1955.
- 59) Clarke, 1977; Coolidge, 1933; Le Gros Clark, 1955b.
- 60) Le Gros Clark, 1955b; Tobias, 1967.
- 61) Fenart and Deblock, 1973; Le Gros Clark, 1947, 1955b; Schultz, 1950a, 1955.
- 62) Spoor et al., 1994, 1996.
- 63) Duckworth, 1915; Sonntag, 1924b; Wood-Jones, 1916, 1929.
- 64) Sarmiento, in prep. b; Wood, 1995; author's notes.
- 65) Andrews and Martin, 1987; Sarmiento, in prep. b; author's notes.
- 66) Jolly, 1970; Sarmiento, 1987a, 1995; Rosenberger, 1992; Zingesser, 1973.
- 67) Le Gros Clark, 1955b; Milton, 1985; Sarmiento, 1987a, 1995; Straus, 1949; Zingesser, 1973.
- 68) Le Gros Clark, 1955b; Milton, 1985; Wood-Jones, 1916, 1929.
- 69) Sarmiento, 1987a; Turner, 1981; Wood, 1991; Wood et al., 1988; Wood-Jones, 1916, 1929.
- 70) Le Gros Clark, 1955b; Sarmiento, 1987a, 1995.
- 71) Gannt, 1983; Le Gros Clark, 1955b; Schwartz, 1984; von Koenigswald, 1952; Weidenreich, 1943.
- 72-73) Le Gros Clark, 1955b; Sarmiento, 1987a; Weidenreich, 1937.
- 74) Cadien, 1972; Sarmiento, 1987a.
- 75) Cadien, 1972; Hershkovitz, 1977; Hill, 1960; Le Gros Clark, 1955b.
- 76) Anemone, 1995; Hartman and Straus, 1961; Hill, 1962; Le Gros Clark, 1955b; Wood-Jones, 1916, 1929.
- 77) Le Gros Clark, 1955b, 1971; Straus, 1949; Wood-Jones, 1916, 1929; author's notes.
- 78) Broom, 1929; Grine, 1984; Le Gros Clark, 1955b; Virchow, 1919; Weidenreich, 1937.
- 79) Hartman and Straus, 1961; Straus, 1949.
- 80) Le Gros Clark, 1955b; Robinson, 1953; Straus, 1949; author's notes.
- 81) Brandes, 1931; Stark and Schneider, 1960; Schultz, 1936, 1968.
- 82) Lieberman, 1994; Lieberman et al., 1972.
- 83) Kelemen, 1969; Stark and Schneider, 1960.
- 84) Schultz, 1961; author's notes.
- 85) Schultz, 1936, 1968.
- 86) Ankel, 1967; Duckworth, 1915; Sonntag, 1924b; Schultz, 1961; author's notes.
- 87) Schultz, 1961; author's notes.
- 88) Primrose, 1899; Raven, 1950; Stewart, 1936.
- 89) Forster, 1916; Miller, 1952; Stewart, 1936.
- 90) Loth, 1931.
- 91) Miller, 1952; Pira, 1913; Raven, 1950; Sommer, 1907; Stewart, 1936.
- 92) Loth, 1931; Straus, 1949.
- 93) Donisch, 1973; Hartman and Straus, 1961; Stewart, 1936.
- 94-95) Eggeling, 1896; Elftman, 1932.
- 96) Keith, 1894; Schultz, 1936; Stewart, 1936.
- 97) Eggeling, 1896; Elftman, 1932; Schultz, 1936.

TABLE 1  
(Continued)

- 98) Hill, 1962; Schultz, 1936, 1968; Straus, 1949; Schwartz, 1984.
- 99) Keith, 1894; Raven, 1950; Stern, 1971, 1972, 1976.
- 100–101) Schultz, 1936, 1961.
- 102) Schultz, 1961; Ohman, 1986; author's notes.
- 103–108) Schultz, 1930, 1936, 1961.
- 109) Schultz, 1930, 1936, 1960; Straus, 1949; Wood-Jones, 1916, 1929.
- 110) Abitbol, 1987a; Schultz, 1961; author's notes.
- 111) Ankel, 1967; Schultz, 1961; author's notes.
- 112) Abitbol, 1987a; Koritke et al., 1957; Robinson and Grimm, 1925; Sarmiento, 1985b, 1996.
- 113) Latimer and Ward, 1993; Robinson, 1972; author's notes.
- 114) Shapiro, 1993.
- 115) Robinson, 1972; Schultz, 1930, 1961; author's notes.
- 116) Abitbol, 1987b; Stern and Susman, 1983.
- 117) Kimura, 1996; Palmer, 1944; Sarmiento, 1985a; author's notes.
- 118–119) Schultz, 1961.
- 120) Straus, 1929; Schultz, 1936, 1953; Stern and Susman, 1983.
- 121) Biegert and Mauer, 1972; Le Gros Clark, 1955a; Schultz, 1936; Straus, 1929.
- 122) Biegert and Mauer, 1972; Reynolds, 1931; Schultz, 1930, 1936, 1961; Straus, 1929; Waterman, 1927; Weidenreich, 1913.
- 123) Reynolds, 1931; Sarmiento, 1985a; Schultz, 1930, 1936; Straus, 1929; Waterman, 1927.
- 124) Le Gros Clark, 1955a, 1955b; Schultz, 1936; Straus, 1929.
- 125–126) Jungers, 1991a; LeGros Clark, 1955a; Straus, 1929; Waterman, 1927.
- 127) LeGros Clark, 1955a, 1955b; Reynolds, 1931; Stern and Susman, 1983; Straus, 1929; Waterman, 1927.
- 128) Straus, 1929; Schultz, 1936.
- 129) LeGros Clark, 1955a, 1955b; Mednick, 1955.
- 130) LeGros Clark, 1955a, 1955b; Straus, 1929.
- 131) Straus, 1929.
- 132) Reynolds, 1931; Straus, 1929; Waterman, 1927.
- 133) Ashton and Oxnard, 1963; Stewart, 1936.
- 134) Ashton and Oxnard, 1963; Loth, 1931; Preuschoft, 1965.
- 135–137) Ashton and Oxnard, 1963; Stewart, 1936.
- 138) Loth, 1931; Preuschoft, 1965.
- 139–140) Ashton and Oxnard, 1963; Loth, 1931; Stewart, 1936.
- 141) Raven, 1950; Pira, 1914; Sommer, 1907; Straus, 1949.
- 142) Preuschoft, 1965; Sarmiento, 1994.
- 143) Day and Napier, 1963; Straus, 1941; Tuttle, 1969.
- 144) Jolly, 1965, 1970, 1972; Maier, 1971, 1993; Sarmiento, 1994; Straus, 1949; Wood-Jones, 1916, 1929.
- 145) Straus, 1941; Sarmiento, 1994.
- 146) Day and Napier, 1961, 1963; Lessertisseur, 1958; Lewis, 1965; Napier, 1961; Sarmiento, 1994.
- 147) Forster, 1917; Jouffroy and Lessertisseur, 1959; Marzke, 1971; Sarmiento, 1994.
- 148) Maier, 1971; Mehta and Gardner, 1961; Raven, 1950; Sarmiento, 1994; author's notes.
- 149) Hartman and Straus, 1961; Marzke, 1971; Straus, 1941, 1942; Sarmiento, 1994.
- 150) Author's notes.
- 151) Ashton and Oxnard, 1964; Schultz, 1930; Stern and Susman, 1983.
- 152) Ashton and Oxnard, 1964; Roberts, 1974; Schultz, 1930, 1936; Schwartz, 1984.
- 153–154) Napier and Napier, 1967; Schultz, 1936, 1956, 1968; Straus, 1949; Wood-Jones, 1916, 1929.
- 155) Sarmiento, 1985a.
- 156) Sarmiento, 1994; Straus, 1949; Schultz, 1930, 1936; Wood-Jones, 1942.
- 157–158) Wood-Jones, 1942.
- 159) Ashley-Montagu, 1931; Jolly, 1970, 1972; Maier, 1971, 1993; Sarmiento, 1994, in prep. a; Wood-Jones, 1942.
- 160) Etter, 1973; Jolly, 1965, 1972; Sarmiento, 1985a, 1994; Susman, 1976, 1979.
- 161) Lewis, 1969, 1974; Sarmiento, 1985a, 1988, 1994.
- 162–164) Jouffroy, 1991; Sarmiento, 1985a, 1987a, 1994.
- 165) Sarmiento, 1985a, 1988.
- 166) Lewis, 1977.
- 167) Marzke, 1983, 1986; Marzke and Marzke, 1987; Sarmiento, 1994.
- 168) Susman, 1976, 1979; Sarmiento, in prep. a; author's notes.
- 169) Jolly, 1972; Maier, 1993; Sarmiento, in prep. a; Wood-Jones, 1942.
- 170) Stern et al., 1995; Susman, 1976, 1979; Susman et al., 1984; Tuttle, 1969, 1970; author's notes.
- 171) Sigmon, 1974; Stern, 1971, 1972.
- 172–173) Stern, 1971, 1972; Uhlman, 1968.
- 174) Sigmon, 1974, 1975.
- 175–176) Ayer, 1948; Sigmon, 1969, 1974; Satoh, 1965; Uhlman, 1968.
- 177) Stern, 1971, 1972, 1976; Sigmon, 1974; Uhlman, 1968.
- 178) Stern, 1971, 1976.
- 179) Stern, 1971, 1976; Uhlman, 1968.
- 180) Forster, 1903; Pira, 1914; Sommer, 1907; Preuschoft, 1961; Raven, 1950; Uhlman, 1968.
- 181) Uhlman, 1968.
- 182–183) Urbanowicz and Prejzner-Morawska, 1972.
- 184) Loth, 1908, 1931; Sarmiento, 1994; Straus, 1949; Urbanowicz and Prejzner-Morawska, 1972.
- 185–189) Straus, 1930; Sarmiento, 1994; Sarmiento and Butynski, in prep.; Wells, 1935.
- 190) Lewis, 1962; Sarmiento, 1994; Straus, 1930, 1949.
- 191) Sarmiento, 1994; Weidenreich, 1922, 1940.
- 192) Straus, 1930; Sarmiento, 1994; Sarmiento and Butynski, in prep.
- 193–194) Manter, 1945; Sarmiento, 1994; Sarmiento and Butynski, in prep.; Straus, 1930.
- 195) Jouffroy and Lessertisseur, 1959; Sarmiento, 1994; Straus, 1930.
- 196) Lovejoy et al., 1973; Stern and Susman, 1983; Weidenreich, 1913; author's notes.
- 197) Gardner et al., 1975; Sarmiento, 1985.
- 198) Jungers, 1988b, 1991b; Schultz, 1936, 1953.
- 199–200) Lovejoy and Heiple, 1970; Martin and Saller, 1957; Walker, 1973.
- 201) Elfman, 1945; Fabry et al., 1973; Sarmiento, 1985a.
- 202) Sarmiento, 1985a; Tardieu and Preuschoft, 1996.
- 203) Schultz, 1953; Sarmiento, 1985a; this study.
- 204–206) Kern and Straus, 1949; Stern and Susman, 1983; Tardieu, 1979, 1981, 1986.
- 207) Gardner et al., 1975.
- 208–209) Heller and Langman, 1964; Kaplan, 1957; Ross et al., 1958; Tardieu, 1979, 1981, 1983, 1986.
- 210–211) Author's notes.
- 212) Elfman, 1945; Sarmiento, 1985a, 1987b.
- 213) Stern and Susman, 1983; author's notes.
- 214) Stern and Susman, 1983; author's notes.
- 215) Carrano, 1997; Davis, 1964; Inman, 1976; Latimer et al., 1987; Rose, 1994; author's notes.

TABLE 1  
(Continued)

216) Davis, 1964; Inman, 1976; Sarmiento, 1994; Stern and Susman, 1983; Susman et al., 1984; author's notes.	1968; Wood-Jones, 1944.	249) Elftman, 1932; Schultz, 1936; Wood-Jones, 1929.
217) Sarmiento, 1994.	232) Latimer and Lovejoy, 1989; Sarmiento, 1983, 1994; Weidenreich, 1922, 1940.	250) Dahl, 1985, 1988; Dahl et al., 1993; Moller, 1988.
218) Schultz, 1934, 1963a; Strasser, 1989; Straus, 1942; Wood-Jones, 1944; author's notes.	233) Day and Wood, 1968; Sarmiento, 1994.	251) Dahl et al., 1991; Graham, 1981; Nadler, 1977, 1981; Schultz, 1936; Watts, 1991.
219) Jolly, 1965, 1972; Sarmiento, 1994; Schultz, 1956, 1963a, 1968.	234) Gebo, 1992; author's notes.	252–256) Schultz, 1936.
220) Forster, 1927; Jolly, 1965, 1972; Hill, 1960, 1970; Sarmiento, 1994; Schultz, 1934, 1936, 1963a; Weidenreich, 1922; Wood-Jones, 1916, 1929, 1944.	235) Gebo, 1992; Sarmiento, 1994; author's notes.	257) Carpenter, 1979.
221) Jolly, 1965, 1970; Hill, 1966, 1970; Sarmiento, 1994; Schultz, 1936, 1963a; Wood-Jones, 1944.	236) Elftman and Manter, 1935b; Sarmiento, 1985a, 1994; Weidenreich, 1922, 1940.	258) Hrdlicka, 1931; Schultz, 1936; Straus, 1940.
222) Sarmiento, 1994; Schultz, 1934; Wood-Jones, 1929, 1944.	237) Latimer and Lovejoy, 1990a, 1990b; Sarmiento, 1994; Susman et al., 1984.	259–263) Schultz, 1936, 1968.
223) Weidenreich, 1922, 1940.	238) Jolly, 1965, 1972; author's notes.	264) Napier and Napier, 1967; Nowack, 1991.
224–225) Elftman, 1960; Elftman and Manter, 1935a, 1935b; Jones, 1941; MacConnail, 1945; Inman, 1976; Inman and Mann, 1964; Morton, 1922, 1924; Rose, 1994; Sarmiento, 1994; Weidenreich, 1922.	239) Bartlakowski, 1930; Washburn, 1950b.	265) Groves, 1970; Sarmiento et al., 1996.
226) Lewis, 1980b; Sarmiento, 1994.	240) Straus, 1934.	266) Dunbar, 1984; Jolly, 1972; Sarmiento et al., 1996; Schaller, 1963.
227) Gomberg, 1985.	241) Straus, 1936.	267) Inman et al., 1981; Wood-Jones, 1929.
228) Morton, 1924; Sarmiento, 1994; Schultz, 1936, 1963a; Straus, 1949.	242) Atkinson and Elftman, 1950; Wislocki, 1932.	268) Hrdlicka, 1931; Sarmiento, 1988; Schultz, 1936; Straus, 1940.
229) Gomberg, 1985; Lewis, 1980b; Sonntag, 1923, 1924a, 1924b.	243) Retzius, 1914–16.	269) Keleman, 1969; Lieberman, 1973; Ploog, 1989.
230) Schultz, 1936; Straus, 1942; author's notes.	244) Dahl, 1994; Dahl and Nadler, 1990.	270) McGrew, 1994; van Shaik et al., 1996.
231) Hill, 1960, 1966, 1970; Jolly, 1972; Morton, 1924; Schultz, 1936,	245) Schultz, 1936, 1968; Hill, 1958, 1962.	271) Fay, 1988; Stebbins, 1983.
	246) Burt, 1992; Dahl, 1988; Dahl and Nadler, 1992; Graham, 1981; Short, 1981; Schurman, 1982; Watts, 1991.	272) Butynski, 1982; Teleki, 1973.
	247–248) Atkinson and Elftman, 1950; Dahl, 1985, 1988; Dahl and Nadler, 1992; Montagna, 1985, Schultz, 1968; Wislocki, 1936.	273) Oakley, 1972.
		274) Elizondo, 1988; Montagna, 1985; Porter, 1993.
		275) Ashley-Monatgu, 1960.
		276) Kinzey, 1987; author's field notes from Virungas, Bwindi, and Mt. Tshiaberimu.

(2) *maintenance of an erect trunk during shifts in the center of gravity*, i.e., marked ventral displacement of the vertebral column relative to the trunk, lumbar vertebrae with superoinferiorly wide and posteriorly directed spinous processes, strong lumbar lordosis, marked wedging of last lumbar vertebra, acute sacral promontory angle, lumbar vertebrae with mediolaterally wide pedicles and a wide interfacet diameter (both dimensions progressively increasing caudally), a relatively broad sacrum, strong posterior projection of iliac crest with large postauricular area, a strong iliac pillar and tuberosity, a stout and prominent anterior inferior iliac spine for attachment of a strong iliofemoral ligament, and a markedly short ilia with a closed sciatic notch;

(3) *prevention of herniation and/or prolapsus of the abdominal and pelvic contents*, i.e., inguinal ligament, early descent of testes and complete obliteration of inguinal canals, ventrally concave sacrum, pelvic canal approximating the horizontal, and a separate deep transversus perinei muscle and associated strong development of the urogenital fascia;

(4) *propulsion with a semidigitigrade foot, and an extended hip and knee joint*, i.e., pelvic aspect of acetabulum with a well-developed iliopsoas groove, marked anterior and inferior acetabular orientation, a posteriorly projected and proximally expanded ischial tuberosity, an anterior transverse ligament of the knee joint, a capsular insertion of semimembranosus m., high positive tibial torsion,

segregation of the long digital flexor tendons, a large tibial origin for soleus m., and a well-developed two headed quadratus plantae m.;

(5) *maintenance of the plantar arches for effectively supporting and accelerating entire body weight on a single foot*, i.e., absence of the deep head of the flexor digitorum brevis m. (FDB), strongly aponeurotic superficial head of FDB sending short tendons to all five digits, spring ligament with fibrocartilage or sesamoid reinforced by the underlying tendon of tibialis posterior m., lateral plantar process and associated lateral plantar ligament, absence of weight-bearing tubercles on the distal tarsal bones, a proximal expansion of the long plantar ligament, a well-developed bifurcated ligament, proximodistally elongated tarsals (especially the cuboid), a plantar-flexed calcaneal neck, high talar torsion, a distally extended sole, and a relatively long big toe.

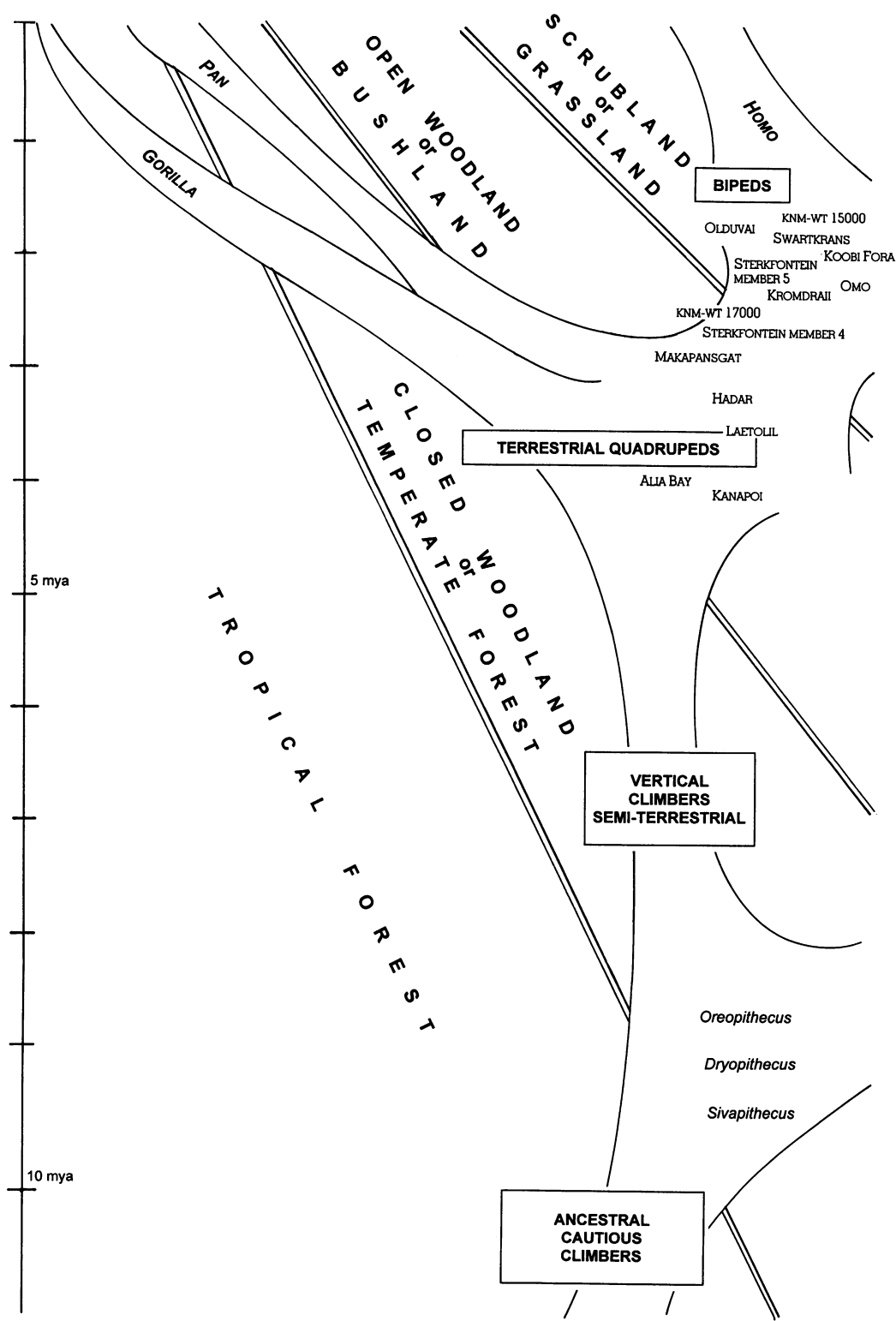
Most of the unique postcranial characters are osteoligamentous as opposed to muscular specializations. As such, they minimize the muscular energy necessary for maintaining bipedal joint postures and visceral integrity, thus reflecting the habitual nature of human bipedalism. Because no other primate has developed habitual terrestrial bipedality or these unique morphological characters, their association in a structure-function complex is further reinforced.

The uniquely high humeral torsion finds no ready explanation in human locomotor behaviors. Because long-bone torsion has a strong environmental component, the high human value probably reflects upper limb use and forces applied to an arm that is not habitually loaded, as opposed to any specific ancestral behavior (Sarmiento, 1985a).

**HINDLIMB-DOMINATED LOCOMOTOR BEHAVIORS:** Two characters distinguishing humans from African apes are seen only in prosimians i.e., a low intermembral index, and a low center of gravity (close to the hip joint). Both characters are correlates of hindlimb-dominated locomotor behaviors and erect trunk postures (Gunther et al., 1992; Schultz, 1956, 1968), and reflect exceptionally hypertrophied and elongated hindlimbs. Given the disproportionate size of the hindlimbs, living indrines, galagines, and tarsiers are all bipeds when traveling either on the ground or on

relatively large horizontal supports (Gunther et al., 1992; Fleagle, 1988; Napier and Napier, 1967; Richards, 1978). In contrast to the striding bipedal gait of humans, all of these forms use saltatory bipedalism (Gunther et al., 1992; Fleagle, 1988; Napier and Napier, 1967; Richards, 1978). The relatively greater mass and length of the hindlimbs and the inability of the forelimbs to reach the substrate without assuming inverted trunk postures or excessive flexion of the hindlimb joints leads to preferential weighing of the hindlimbs. The need to keep the trunk and forelimbs directly centered above the springing action of the hindlimbs leads to erect trunk postures. Most terrestrial mammals in which the hindlimbs reach such a disproportionate size (intermembral indices below 70) are bipeds (Sarmiento, 1985a). Notably, all terrestrial primates with intermembral index values above 79 are predominantly quadrupeds, no matter how close their phylogenetic relationship may be to a biped (Fleagle, 1988; Sarmiento, 1985a; Schultz, 1937; 1953; 1956).

**TERRESTRIAL QUADRUPEDAL BEHAVIORS:** Many characters that distinguish humans from chimpanzees either fail to distinguish humans from gorillas, or they show a cline in which gorillas most closely approximate humans. These characters, found mainly in the limbs, satisfy the mechanical demands of weight support and propulsion in quadrupedal behaviors (Sarmiento, 1985a, 1985b, 1988, 1994), i.e., the proportions of the hand and foot, a weight bearing triangular articular disc omitting the ulna from the radiocarpal joint, the relative length of thumb and big toe, the low brachial index, the scapular angles, the hamate's facet angles, a palmarly oriented and robust hamulus, the palmarly oriented pisiform, a styloid process on the base of the 3rd metacarpal, an expansive insertion of tibialis posterior m., a well-developed plantar aponeurosis, the disposition of the foot's sole, the development of the tuber calcanei, palmar interossei with a basal phalanx insertion, the full loss of manual and pedal contrahentes, the high incidence of a palmaris longus and brevis m., a pedal interossei axis through the second digit, the origin of the adductor hallucis transversus m., fusion of the distal and middle phalanx of the 5th pedal digit with occasional absence of the





middle phalanx, restricted hallucial abduction, and the presence of a peroneus tertius m. (Sarmiento, 1983, 1985a, 1985b, 1987a, 1988, 1994). Although in modern humans the above-listed lower limb characters satisfy the mechanical demands of terrestrial bipedality, the presence of quadrupedal characters in the human upper limb suggests the lower limb characters initially arose in response to quadrupedal behaviors (Sarmiento, 1994). The more humanlike development of some of these characters in the more terrestrial mountain gorilla (*G. g. beringei*) relative to western lowland gorillas (*G. g. gorilla*) (i.e., the robusticity of the tuber calcaneum, the degree of phalangeal curvature, the high incidence of a peroneus tertius m., a pedal interossei axis through the 2nd digit, the development of the transverse head of adductor hallucis m., a relatively large hallux and pollex, a distally extended sole, hand and foot proportions, big toe abductability, the transverse arch, and high talar torsion) further supports a terrestrial quadrupedal origin for these characters in humans. Because with increasing terrestriality the quadrupedal African apes increasingly approximate the human lower limb anatomy (Sarmiento, 1994), ter-

restrial quadrupedality best explains how these characters could have evolved in an early semiterrestrial hominid that had not yet developed the committed anatomy necessary for full-time bipedality.

Many of the hand and foot proportions that are mechanical requisites of terrestrial quadrupedalism in humans and gorillas are also seen in cercopithecoids. Additionally, cercopithecoids share terrestrial quadrupedal characters with humans not seen in either African ape. These characters, which are generally better developed in cursorial cercopithecoids, satisfy the following mechanical requisites of quadrupedal behaviors:

(1) *forelimb propulsion and weight bearing with palmigrade or semidigitigrade postures* i.e., a cercopithecoid-like palmar dermatoglyphics pattern, well-developed forearm wrist extensors relative to flexors, abductor pollicis longus m. with a large insertion on the base of the 1st metacarpal, straight phalanges with poorly developed flexor sheaths, relatively robust 5th metacarpal with a large base, palmar lumbricals with basal phalanx insertions, S-shaped clavicle, distal prolongation of the web between the

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Fig. 1 Diagram of the human-African ape divergence as interpreted in this study. Of the characters in table 1 distinguishing humans from either African ape, 6(?), 10(?), 12-14, 26, 35, 38(?), 39(?), 40, 48, 70, 71, 74, 90, 103-108, 113(?), 115, 118, 119, 122(?), 129(?), 133(?), 134(?), 137(?), 138, 142, 158, 173(?), 180(?), 181(?), 184, 199(?), 202(?), 209(?), 210(?), 241(?), 243(?), 246, 250, 251(?), 252(?), 261(?), 270, 276 are hypothesized or verified by fossil evidence to be present in the most recent human-African ape ancestor; 73, 78, 81, 91, 92, 100, 102, 109, 130, 147, 161, 162, 171, 215, 216, 268 are hypothesized to approximate the human condition during or at the end of stage I; 1-5, 7-9, 11, 15, 16, 18, 20, 29-31, 33, 37, 43, 45-47, 50, 52-55, 58, 61, 66-68, 72, 76, 80, 82, 84-89, 93, 96, 99, 111, 114, 116, 117, 120, 121, 123-127, 128, 129(?), 131, 132, 136, 140, 141, 143-146, 148-154, 156-160, 163-170, 172, 174, 175-179, 182, 183, 185-196, 204, 205, 207, 208, 211-214, 217-224, 226-234, 236, 237, 239, 240, 247, 249, 262, 263, 265-267, 271, 272, 274, 275 are hypothesized to approximate the human condition during or at the end of stage II; 17, 19, 23, 25, 28, 32, 34, 36, 41, 42, 44, 49, 51, 63-65, 69, 75, 83, 94, 95, 97, 98, 101, 110, 112, 135, 155, 197-201, 203, 207, 225, 235, 242, 244, 248, 253-260, 264, 269, 273 probably developed with the elaboration of material culture. Ancestral characters followed by a question mark, may have been modified during human divergence, but reverted back to the ancestral condition in response to practiced behaviors. Quantitative characters may be expected to show a cline which over time increasingly approximates the human condition. Starting from the hypothesized cautious climbing ancestor of humans and African apes (Sarmiento, 1995), two evolutionary stages prior to the elaboration of material culture are necessary to evolve the human characters: (1) a long-ranging generalized quadrupedal woodland ape that would have occupied a variety of habitats, making the transition from forest to open habitat through increases in frequency of terrestrial behaviors (stage I); and (2) a committed open habitat ape that sacrificed generalized behaviors and no longer ranged into forests (stage II).

1st and 2nd metacarpal, and a short upper limb relative to trunk length;

(2) *hindlimb propulsion with semidigitgrade foot postures* i.e., large fascial insertion for gluteus maximus m., consistent absence of scansorius m., strongly developed and separate tensor fascia femoris m., a fused adductor magnus and ischiocondylar m., a large gastrocnemius m. relative to soleus m., a relatively long triceps surae tendon, lateral femoral condyle larger than medial, a narrow and anteriorly extended intercondyloid notch, deep patellar groove with an anteriorly projected lateral lip, absent or reduced distal tibiofibular facet, mediolaterally compressed distal fibula, tibial long axis set at right angles (in the frontal plane) to the talar trochlea, anterior inclination of tibia's talar articulation, lumbricals and interossei with basal phalanx insertions, straight metatarsal shafts and dorsal expansion of articular surfaces on metatarsal heads;

(3) *control of trunk movement during upper and lower limb movement*, i.e., presence of pyramidalis m., latissimus dorsi with an attachment on the scapula and restricted origin from T6-T12, restricted serratus anterior origin, marked differentiation of the erector spinae and the intrinsic back musculature, comparatively long thoracolumbar and lumbar vertebral regions, a slight sacrolumbar lordosis, progressive caudal increase in the interfacet diameter of the last four lumbar vertebrae, reduced number of sacral vertebrae, sacral articular surface with its long axis perpendicular to that of the ilium, large postauricular area, and a short ilium and ischium relative to trunk length;

(4) *alignment of the major planes of hindlimb segment movement to forward motion*, i.e., lateral orientation of the iliac blades, posteriorly disposed and reduced proximal tibio-fibular facet, relatively high femoral and tibial torsion, and external rotation of calcaneal body and talar articulation relative to the heel process.

Notably, many of the muscular specializations humans share with cercopithecoids are cursorial in nature, emphasizing the actions of muscles across more than one joint and the coordinated and conjunct movement of the propulsive segments in the plane of forward motion (Sarmiento, 1983, 1985a). Be-

cause humans share these terrestrial quadrupedal characters with cercopithecoids exclusive of African apes (their closest relatives), humans must have independently undergone selection for terrestrial quadrupedality more marked than that seen in either African ape. That many of the trunk and lower limb characters are also mechanical requisites of modern human bipedality serves to further emphasize the preadaptive role of quadrupedalism (Sarmiento, 1994).

**CAUTIOUS CLIMBING:** Reaffirming their shared cautious climbing ancestry (Sarmiento 1995), humans and African apes are distinguished by very few cautious climbing characters. Notably those cautious climbing trunk characters that do distinguish them (i.e., 17 thoracolumbar vertebrae, 12 pairs of ribs, and 5 lumbar vertebrae; length of lumbar region; and trunk length relative to body weight, chest girth, and sternal breadth) show a less derived condition in humans and one that is less committed to cautious climbing behaviors (Sarmiento, 1985a, 1995). A small body size in the arboreal ancestors of humans (Morton, 1924) would have alleviated selection pressure for the cautious climbing anatomy (Cartmill and Milton, 1977; Sarmiento, 1983, 1985a, 1995) and may explain the less derived human condition. However, because all of these characters are quantitative, they may fail to leave evidence of parallelisms or reversals and are thus unable to resolve whether humans reverted to their less derived condition or whether African apes gained their more derived condition independent of humans.

The palmarly projected triquetral facet, the large and palmarly oriented hamulus, and the palmar orientation of the pisiform itself—all characters associated with the elongated pisiform of African apes, specifically gorillas—indicate that the length of the human pisiform has probably reverted to the primitive cautious climbing condition, a certain result of the loss of the hand's role in quadrupedal propulsion and weight bearing (Jouffroy, 1991; Sarmiento 1985a, 1988). Reversion to a less derived, more monkeylike condition as a result of selection for terrestrial quadrupedal behaviors may also explain the human trunk characters.

Compatible with human bipedalism, but

not with African ape behaviors, a number of distinguishing characters in the human lower limb satisfy the following mechanical demands of cautious climbing behaviors (Sarmiento, 1985a; 1995): (1) use of lower limb with an extended thigh and knee joint i.e., relationships and development of the sacrotuberous ligament, relatively large superficial gluteal m., gracilis m. origin on ischiopubic ramus, and an approximately perpendicular set (in the frontal plane) of the tibial long axis to the proximal tibial articular plane; (2) maximization of total volume of space that can be covered by lower limbs, i.e., high femoral neck angle; and (3) maintenance of leg parallel to support during vertical climbing with laterally rotated thigh, i.e., femoral bicondylar angle. The presence of these characters in orang-utans and the cautious climbing atelines and/or lorisines associates them to cautious climbing behaviors.

Some musculoskeletal characters present in atelines and/or lorisines, and more pronounced or unique to humans from among the hominoids, can also be associated to cautious climbing behaviors i.e., a gluteus superficialis m. encompassing the proximal third of the thigh, a semimembranosus insertion into the knee capsule, and a high femoral bicondylar angle. All of these characters provide a mechanical advantage when the thigh and knee joint are used in extended postures (Stern, 1971; Sarmiento, 1985a). Because human bipedalism also emphasizes extended knee and thigh postures, all of the lower limb cautious climbing characters distinguishing humans from African apes could have been lost in the common human African ape ancestor and regained independently in humans in response to bipedalism, further obfuscating their polarity.

#### MANIPULATIVE CHARACTERS

Some distinguishing characters in the human hand can be interpreted as specializations for manipulation and are approximated by gorillas and gelada baboons (*Theropithecus gelada*). By enabling independent and powerful movement of the thumb in humans, the large and well-differentiated thenar musculature, the extensor pollicis brevis m., and the large and fully separate long pollical flexor tendon and muscle belly, have functional

analogues in the *Theropithecus* hand (Maier, 1971, 1993). In *Theropithecus* a high opposability index, relatively large thenar musculature, and relatively long and robust thumb with a correspondingly well-formed long flexor tendon and muscle belly (albeit not separate from the common deep flexor muscle; Maier, 1971, 1993) enhances the ability of the thumb and index finger to individually pluck small food items, accumulating them in the palm before bringing a handful up to the mouth (Jolly, 1965, 1970). By emphasizing independent movements of the thumb, such dexterity enables the efficient exploitation of large numbers of relatively small food items (i.e., corms, seeds and grass blades; Dunbar and Dunbar, 1974; Jolly, 1970, 1972), which would otherwise prove too costly to bring to the mouth individually.

The uniquely human trapezoid crest, which provides a buttress for the enlarged and ventrally expanded metacarpal articular surface and an attachment site for the corresponding joint capsule and ligaments, can be associated to a large thumb, a long and robust 2nd metacarpal, a high opposability index, and thus manipulation. The same applies to the separate and well-differentiated extensor indices of humans, which further contributes to the independent movement and control of the index finger against the thumb in the human pinch grip. Both of these characters which are unique to humans from among primates, may be used to further argue that the human hand has undergone strong selection for thumb/index manipulation.

The large apical tufts on the distal phalanges of humans, which are approximated by gorillas (Sarmiento, in prep. a.), have also been associated with manipulation (Marzke, 1997). Because the degree of digital pad deformation associated with an increase in applied force causes a logarithmic decrease in the friction coefficient (Cartmill, 1979; Sarmiento, 1985a, 1988), large apical tufts preventing marked deformation and reduction of the friction coefficient are more precisely associated with a greater applied force on the pads, and correlate well with a large body size (Cartmill, 1979). Presence of, or approximation to, the distinguishing human manual characters in gorillas and geladas (both ter-

restrial quadrupeds) suggests that terrestriality may be a requisite for developing the human structures and the associated manipulative behaviors (Napier, 1970). The presence of a separate long flexor tendon and muscle belly for the big toe, and a relatively long and robust big toe and 2nd metatarsal in humans and in some gorillas (Sarmiento, 1994; Sarmiento and Butynski, in prep.) suggest that weight support and propulsion are as important for the development of these characters as is manipulation. In this regard, the alleged human manipulative characters may be largely opportunistic and can trace their evolutionary origin to quadrupedalism (Sarmiento, 1994).

#### CRANIAL, FACIAL, AND DENTAL CHARACTERS

The distinguishing craniofacial and dental characters of humans are related mainly to a large brain size, a small face, and a reduced masticatory complex with restricted gape (i.e., relatively small dentition with reduction and/or loss of the M3 and m3, protruding bony chin, large superior and inferior orbital fissures, strongly flexed basicranium with an anteriorly set and inferiorly oriented foramen magnum, a deep pituitary fossa, mediolaterally narrow glenoid articulation with a short external auditory meatus, a raised articular planum and deep glenoid fossa, a vertically disposed tympanic plate acting as a posterior buttress for the jaw joint, a tympanic vagina enveloping a robust and ossified styloid process, a crista galli, and a marked elevation of the cranial roof above the supraorbital margin with a glabella positioned fully on the frontal; see Biegert, 1963; Clarke, 1977; Cramer, 1977; Dean, 1984, 1985; Fenart and DeBlock, 1973; Sarmiento, in prep. b; Weidenreich, 1941, 1943; Wood-Jones, 1916, 1929, 1948). Many of the nasal specializations (i.e., the elaborated and heavily inflated ethmoid sinuses, a vertically oriented incisive clivus with anteriorly protruding nasal spine, a maxillary-premaxillary suture internalized on the lateral wall of the nasal cavity, well-developed nasal cartilages protruding anterior to the piriform aperture, broad nasal bones with late obliteration of nasal sutures, a vertical plate of vomer inserting posterior to an anteriorly protruding nasal spine) reflect the need to maintain a minimum nasal

mucosa area with decrease in face size (Ashley-Montagu, 1935; Cave and Haines, 1940; McCollum and Ward, 1993, 1997; Wood Jones, 1916, 1929).

The large human brain and cerebellum has been associated to culture and a large capacity for learned behaviors (Aiello and Dean, 1990; Elliot Smith, 1924; Krantz, 1968). In turn, culture and the ability of modern humans to prepare foods through the use of tools and fire have been associated with the reduction of the face and masticatory complex (Bartholomew and Birdsell, 1953; Pilbeam, 1972; Washburn, 1968b).

**MOLAR CRUSHING AND OCCLUSAL SURFACE AREA:** The presence of a well-developed crushing surface on p4, an obliquely set p3 with a lingual cusp, a relatively small canine, and the absence of a diastema are all distinguishing human dental characters. Reflecting the ancestral folivorous-cautious climbing complex, they are best developed in humans but variably expressed in great apes and generalized folivorous anthropoids (Sarmiento, 1987a, 1995).

By sacrificing canine honing to maximize cheektooth occlusal surface area, the human canine and premolar characters are seemingly at odds with other distinguishing human characters (i.e., small cheekteeth occlusal area relative to body size, small premolars relative to molar or cheek teeth occlusal area, and their correlates, variable loss of upper and lower third molars, and single-rooted premolars, respectively). Also exhibited by chimpanzees, relatively small cheekteeth reflect foods that (1) require very little dental processing, and (2) are rich relative to the animals energetic needs, and thus need not be processed in bulk. With decreasing food quality and/or increasing (1) bulk of ingested food, (2) energy demands, and (3) amount of dental processing, increases in cheekteeth occlusal area save both time and energy in reducing the total number of mandibular strokes necessary per volume of food processed (Sarmiento, 1995; in prep. b). Large occlusal areas also distribute wear over a larger surface, thereby prolonging the lifetime of the teeth. The reduced human dentition can therefore be associated to an energy-rich diet (i.e., meat; Butynski, 1982) and tool use in food preparation (Picq,

1990a, 1980b, Washburn, 1968b), both of which relax selection pressures for maximizing occlusal area. Because the overall reduction in molar and premolar surface area is superimposed on the human dental characters designed to maximize premolar area, the latter must have predated overall dental reduction in hominid evolution.

Dental characters that distinguish humans from either African ape (but not from orangutans) probably represent the shared human great ape condition (i.e., thick molar enamel, low cusped molars, flat molar wear, and reduction or absence of hypoconulids). In association with the folivorous cautious climbing complex (Sarmiento, 1995), molars with these characters process foodstuff by crushing and grinding as opposed to shearing or slicing. Their morphology reflects the ingestion of objects with varied physical properties that no one specialized dentition can effectively handle and a diet that is not strictly folivorous (Sarmiento, 1995).

**HORIZONTAL LENGTH OF THE DENTAL ROW:** A number of gnathic characters unique to humans (from among hominoids) can be associated with an anterior dentition that is set close (horizontally) to the jaw joint and is reduced relative to total occlusal surface area (i.e., small vertically implanted incisors, reduced premaxilla and a parabolic dental arcade, see Sarmiento, 1987a, 1995). As exhibited in both folivores (i.e., *Brachyteles arachnoides*) and small tough object feeders (i.e., *Rhinopithecus* and *T. gelada*; Jolly, 1970; Sarmiento, 1995), these characters reflect an emphasis on molar occlusion at the cost of varied incisal function (Jolly, 1972; Smith, 1983). Bringing the incisors closer (horizontally) to the jaw joint sacrifices the gape, and hence the size of objects that can be processed, but increases the occlusal force the incisors can apply for nipping and shearing food items (Sarmiento, 1995), and the magnitude of unilateral chewing forces that the symphysis can withstand (Hylander, 1988). The parabolic dental arcade crowds the cheektooth row, reducing the difference in sagittal plane moment arms between the cheekteeth farthest and closest to the jaw joint, resulting in a more even distribution of occlusal force along the length of the row (Sarmiento in prep. b; Ward and Molnar,

1980). Moreover, because the cheekteeth farther (horizontally) from the jaw joint are closer to the midline, the reduction of occlusal forces resulting from a relatively reduced muscular moment arm in the sagittal plane are compensated for by increased muscular moment arms in the frontal plane (Sarmiento in prep. b). Finally, with rotation of the mandible around a vertical axis and alternating antero-posterior displacements at the glenoid joint, the geometry of a parabolic dental arcade ensures maximum occlusal contact during side-to-side chewing (Sarmiento in prep. b).

**DENTAL DEVELOPMENT:** Humans are distinguished from all other hominoids by a multicusped molariform dp3 and by spatulate milk canines that erupt early relative to the other teeth. These characters emphasize early in development the need to maximize the functional length of the incisor row, and the occlusal cheektooth area, and are no doubt associated with marked differences in the diets of human and great ape infants. A multicusped dp3 is common to baboons and macaques and probably reflects (1) the ingestion of foods that necessitate considerable dental processing, (2) early weaning, and (3) precocious infants, all correlates of an r-selection strategy. The early eruption of the human permanent canine can also be related to an early need to increase the functional length of the incisor row, and an emphasis on permanent teeth for nipping and shearing.

As noted by Jolly (1970), the distinguishing human dental characters are all part of a complex in the human jaw and basicranium associated to small tough-object feeding. A correlate of maximizing occlusal force, reducing the horizontal distance from the molar row to the jaw joint decreases the basicranial length, thus crowding basicranial structures and their attachment sites, and resulting in many of the distinguishing human basicranial characters (i.e., short basisphenoccipital, diagonal orientation of the petrous temporal, a tympanic vagina and crest, a sphenoid spine, a vomer which overrides the basisphenoid, and vertically set pterygoid plates; Dean, 1984, 1985; Dean and Wood, 1981, 1982; Sarmiento in prep. b; Weidenreich, 1941).

The wide interorbital and biglenoid di-

ameters of humans are in part corollaries of space constraints on an orthognathic face with a compromised anteroposterior length (Weidenreich, 1941, 1943), and thus are related to bringing the dentition horizontally closer to the jaw joint. Maximizing the biglenoid and bizygomatic width relative to the width of the dental arcade, however, also maximizes occlusal forces, increasing the moment arms of the masticatory muscles in the frontal plane (Sarmiento, in prep. b).

Associated with a vertically set tympanic plate, the anteroposteriorly narrow and deep glenoid joint (a narrow but raised articular planum) sacrifices anteroposterior movements associated with varied incisal action (Jolly, 1970; Smith, et al. 1983). By making possible superoinferior displacements of the mandible, however, a deep glenoid joint enables simultaneous occlusion along the length of the molar row (Sarmiento, in press b). Simultaneous occlusion is also enhanced by a jaw joint that is offset at a considerable perpendicular distance from the molar row (Biegert, 1963; Marcus and Sarmiento, 1996; Sarmiento, in prep. b). Reflecting a restricted gape and the small size of ingested foods, a vertically set ascending ramus with an offset jaw joint sacrifices the lever arms of the muscles of mastication in the parasagittal plane with increasing angular displacements at the jaw joint (Picq, 1990a, 1990b; Sarmiento in prep. b). Although the small human glenoid indicates that very little of the resultant forces of mastication occur across the jaw joint (with most of the muscular force being applied at the molar occlusal area), its small size also reflects the reduced occlusal molar area of modern humans (Picq, 1990a, 1990b; Sarmiento, in prep. b).

Some of the human characters associated with the small tough-object feeding complex are also common to folivorous primates and probably originated in the cautious climbing, common hominoid ancestor (Sarmiento, 1987a, 1995). By exploiting small terrestrial food objects, *Theropithecus* and *Rhinopithecus* are the primates which have most closely converged on the human character complex (Jolly, 1970, 1972; Sarmiento, 1995). A folivorous heritage in *Rhinopithecus*, however, results in a closer approximation to humans (Sarmiento, 1995). Because many of the

characters associated with folivory are common to the living and fossil hominoids (Sarmiento, 1987a, 1995), whereas most of those associated with small tough-object feeding are unique to humans, the latter must have developed after the African ape-hominid divergence. Folivory probably predapted hominids to small tough-object feeding (Sarmiento, 1995). In this regard, three stages of selection, can be recognized in the human basicranial and gnathic characters: (1) a shared hominoid stage associated to cautious climbing and folivory; (2) a stage of small tough-object feeding unique to humans, but approximated by some terrestrial cercopithecids; and (3) a more recent stage that emphasizes overall dental reduction and is associated to a diet (probably meat) that is high in energy relative to the cost of dental processing.

#### CERVICAL CHARACTERS

The distinguishing human cervical characters are strongly bound to the distinguishing human craniofacial characters. The small face to large cranium ratio, basicranial flexion, and the disposition of the foramen magnum results in a head with a more posteriorly placed center of gravity which is nearly balanced on the spine (Schultz, 1942). A vertically oriented cervical spine with a lordosis for balancing the head is possible because of cervical vertebrae with short and bifid spinous processes (Schultz, 1961).

The cervical lordosis and basicranial flexion, in turn, compromise the suprahoid volume and result in the sharp angle between the nasopharynx and oropharynx (Lieberman, 1994). Compensations for a compromised suprahoid include: (1) a reduced masticatory complex and submandibular musculature; (2) the more inferior position of the human larynx, hyoid, and root of the tongue; and (3) an associated, long ossified styloid process. As such, all these characters are also correlates of basicranial flexion and the cervical lordosis.

A better balanced head and a vertically disposed cervical column with a lordosis facilitate neck mobility by reducing the total amount of force across the cervical joints. With less force needed to balance the head, cervical muscles can dedicate proportionate-

ly less energy for maintaining postures and more for movement. In this regard, the inferiorly disposed nuchal crest, the projecting mastoid, the absence of a rib articulation on C7, the presence of a transverse cervical foramen on C7, the more inferior position of the shoulder blades relative to the thorax, and some of the distinguishing characters of the human dorsoscapular musculature (i.e., absence of omocervicalis, restricted cervical origin of rhomboids) are also correlates of increased neck mobility. By enhancing sound localization and increasing the range of the visual field, head and neck mobility is advantageous in social interactions, interspecies competition, feeding, and predator avoidance.

Notably, a cervical lordosis and the associated short, but cranioflexed, spinous processes are characters found in quadrupedal cercopithecids (Schultz, 1961), many of which dorsiflex the neck, so that the upper segments of the cervical column are vertically disposed and perpendicular to those of the thorax (Schultz, 1961). Because the atlantoaxial joint provides as much or more rotatory movement than do all of the other cervical vertebrae combined, vertical postures of its rotatory axis maximizes head-turning ability (Hall, 1965). This ability improves behind the back range of vision, which in primates is otherwise compromised by forward-facing orbits (Le Gros Clark, 1971). In monkeys, the lordosis also enables dorsoventral neck mobility for face-forward and head-up postures in varying orientations of the trunk, thus increasing the level of vision (Schultz, 1961).

With a protruding mastoid process, an inferiorly disposed nuchal crest, and no costal articulation on C7, gelada baboons further parallel humans. Habitually erect trunk postures, rotation and mediolateral neck flexion, and tandem upperlimb mobility during feeding (Dunbar, 1984) are behaviors exhibited by geladas bearing on these characters. Because all nonhuman hominoids have limited neck mobility (Schultz, 1961), the human condition is best interpreted as derived. In accordance with other human musculoskeletal characters common to cercopithecoids, especially geladas, the human cervical lordosis and associated morphology can prob-

ably trace its origin to quadrupedal behaviors and erect-trunk feeding postures.

#### VISCERAL CHARACTERS

A multilobated kidney with multiple pyramids and calyces is the only unique visceral character that distinguishes humans from all other primates. Because there is an upper limit to the length (resistance to flow) and diameter (absorption) of a nephron's tubes for efficient function, large mammals that produce more urine must increase the number of nephrons and the number of lobes (renal units) that the kidney is divided into, or compromise functional tube length and/or diameter (Danzler, 1989). Considering that great apes solve this problem by dividing their kidney into many subpyramids, but usually exhibit a single pyramid and calyx (Straus, 1934; Elftman and Atkinson, 1950), the human condition cannot be simply explained by a greater amount of urine production and/or a large body size. Dividing and partitioning the areas of urine collection reduces the size of any single calculus (kidney stone) and thus increases the chance that it could lodge in the kidney or ureter, block kidney drainage, and lead to full loss of kidney function. Human dependency on perspiration (and thus water loss) for heat dissipation could at times increase urine concentration close to the point of saturation. As such, the unique kidney morphology may be related to the unique external human thermoregulatory specializations. The ability of humans to release high concentrations of bone calcium into the blood stream and the associated high risk of calculi such a release of calcium can bring about, however, may also select for multiple pyramids and calyces, thus associating them to high blood calcium levels. Unfortunately, very little comparative physiological data exists to test either of these hypotheses.

Humans share with lemurids, and are distinguished from great apes, in having striated musculature on only the upper one-third of the esophagus. Because in erect trunk postures, gravity assists in moving ingested food to the stomach and preventing regurgitation, an apelike esophagus with striated muscles along three-fourths or more of its length may not be necessary.

## EXTERNAL CHARACTERS

Most of the distinguishing external characters of humans can be interpreted as thermoregulatory specializations, helping to maintain a constant body temperature with marked fluctuations in ambient temperatures, i.e., short and poorly pigmented body hairs, relatively low hair density, alignment of hair tracts, long scalp hair (in non-Africans and some Africans; Ebling, 1985), thick subcutaneous fat layer, high density of cutaneous sweat glands (eccrine), and abundant skin vascularization (Elizondo, 1988; Wheeler, 1984, 1985, 1991a, 1991b, 1991c, 1993). According to Wheeler (1984, 1985, 1991a, 1992a) these characters are directly related to open environments and to the different orientation a bipedal body presents to environmental cooling and radiation sources. The presence of some of the distinguishing human characters in the patas monkeys, an open-country primate, further supports this argument (Elizondo, 1988). The high density of sebaceous glands on the back, shoulder, chest and head of humans are probably also part of this complex. Without thick body hair, sebaceous secretions in these areas can provide an adult biped's skin better protection from the degrading effect of solar radiation.

Alternatively, differences in the distribution patterns of subcutaneous fat and body hair between human males and females also associates these characters with sexual selection. Because the more hirsute nature of males relative to females and prepubescents contradicts what thermoregulatory models predict for the larger sized male, it is clear that sexual selection has had more than a secondary effect on these characters. The association of pheromones with skin gland secretions (Montanga 1985; Mykytowycz, 1970) suggests that sexual selection probably also influences the distribution and size of these glands. In this regard, although the uniquely human external characters reflect thermoregulatory concerns, they have no doubt also undergone strong sexual selection (Darwin, 1871).

## SEXUAL CHARACTERS

A large glans with a long penis (pars distalis) in males and a glabrous petal-like labia

minora with a subcutaneously fatty labia majora and mons pubis in adult females are genital characters unique to humans. In contrast, the pronounced estrus swellings of females associated with the long glans-less penis of males are unique to chimpanzees, as are the associated morphologies of the gorilla and orang-utan genitalia (Hill, 1958). Such species-specific character distribution is expected for structures that serve as external signs of mate recognition, and are up to the whims of sexual selection (Darwin, 1871; Mayr, 1982; Patterson, 1985).

The enlarged nonlactating breasts of women are also sexual characters unique to humans. The development of analogous structures in *T. gelada*, associates breasts with concealment of the perineum in erect trunk postures (due to either sitting or bipedal standing) and the need to provide an effective substitute for sexual attraction (Jolly, 1970; Short, 1981). Unlike the epigamic pectoral characters of *T. gelada* (Alvarez, 1973), however, women's breast do not signal the time of ovulation, variably becoming tender and swollen just prior to menstruation. Because women need a minimum percentage of body fat to initiate and maintain ovulation (Frisch, 1975, 1978), and the nulliparous breast is composed mainly of fat, its development and fullness provides a signal to the male that a female is reproductively fit (Cant, 1981; Gallup, 1982), without divulging the time of ovulation and sacrificing the ability to illicit the prolonged attention of males. The enlarged nonlactating breasts of nulliparous women probably find their origin in the enlarged breasts common to pregnant or lactating great apes. By mimicking a sign of fertility and fitness, nulliparous females could gain access to the social benefits otherwise reserved for matriarchs and proven ovulators. Notably, in both humans and *T. gelada*, the pectoral epigamic characters are best developed in nulliparous females, losing their characteristic shape and/or symmetry with repeated pregnancy (Dunbar, 1984; Gallup 1982) at an age when fertility is proven, group membership is a given, and their attractive function is no longer needed. When considering which sign of reproductive fitness to mimic, it is significant that in humans 4 months of lactation requires more than



twice the energy of bringing a pregnancy to term (Frisch, 1975).

Most of the remaining sexual characters fail to distinguish humans from gorillas and/or orang-utans (i.e., considerable sexual dimorphism in body size, relatively small testicles, and no external signs of ovulation). As noted, external signs of ovulation are absent in both the human breast and vulva. Although on close inspection, genital swellings can be seen in captive western lowland gorillas around the time of ovulation, and slight swellings may be variably seen in Virunga gorillas (Watts, 1991; H. Steklis, personal commun.), their visibility is dependent on females presenting themselves. In gorillas and orang-utans the shared characters may therefore be associated with female choice and male monopolization of estrus females (Dahl, 1994; Dahl et al. 1993; Moller, 1988; Nadler, 1982; Short, 1981). Epigamic characters in adult male orang-utans (the cheekpads and light haired beard and mustache; Schultz, 1968), gorillas (the beard, bare chest, and silver-haired back; Matschie, 1914; Sarmiento et al., 1996; Schwarz, 1927), and human males (beard, mustache, and body hair distribution; Harrison and Montagna, 1973), are also part of this complex related to female choice. Functionally analogous to the human breast, the plump and subcutaneously fatty labia majora of subadult nulliparous orang-utan and gorilla females, which are later lost in adulthood, probably also serve to attract males and establish social bonds. Generally, in nonhuman primates the social system corresponding to the shared human gorilla and orang-utan characters are serial monogamy and/or polygyny (Kinzey, 1987; Moller, 1988; Short, 1981), systems that are also common to most human societies (Ford and Beach, 1952; Murdock, 1949). Because, with the exception of chimpanzees, this complex of characters is largely common to humans and great apes, it is best interpreted as the ancestral human-great ape condition.

#### DEVELOPMENT

Although great apes are distinguished from the nonhominoid primates in having greater longevity and a longer postnatal development period, humans have taken this

trend further and are unique among primates in showing the greatest longevity and the absolutely longest postnatal development period. Additionally, humans exhibit (1) the absolutely longest gestation period of any primate, (2) the longest infant dependency period, (3) the highest rate of prenatal growth relative to postnatal growth, (4) the most marked postnatal changes in cranial capacity, and (5) brain and neural motor pathways that are not fully developed until after the first year of life. Because the human gestation period is about the same duration as that of orang-utans, and is relatively short when compared to a much prolonged postnatal life, human gestation length is best interpreted as a shared, ancestral great ape character.

In the skeleton, the long human development period is manifested as a delayed ossification of epiphyses and cranial sutures. Most similar to that of cercopithecoids, the sequence of epiphyseal union can be associated in part to the more monkeylike human proportions (Sarmiento, MS on file).

Long infant dependency and postnatal developmental periods are associated with learned human behaviors. These periods are marked by a span of 20 months or more in which the infant is unable to speak. During this time, the infant communicates via facial expressions, hand gestures, nonspecific stereotypical cries, and weeping. The latter is a unique human character thought to prevent drying of the nasal mucosa (Ashley-Montagu, 1960). Postulated as essential for modern human speech, the cervical lordosis, basicranial flexion, and descent of the larynx develop after infants reach 6 months of age (Lieberman, 1973; Ploog, 1989). Full myelination of the pyramidal track necessary for coordinated muscular control does not occur until 1 year of age (Carpenter, 1979).

Prior to adopting full-time bipedality, human infants undergo a quadrupedal stage of variable duration in which the body weight may be fully propped up on extended limbs with palmigrade and plantigrade hand and foot postures (Hrdlicka, 1931). With the attainment of bipedal postures, human infants develop the lumbar lordosis characteristic of adults (Inman et al., 1981) and subsequently progress from walking to running. Due mainly to proportionately shorter limbs, a higher

center of gravity (Palmer, 1944), and different lower-limb long-bone torsions (Hutter and Scott, 1949), infants under 4 or 5 years of age have a bipedal kinematic pattern that differs markedly from adults (Grieve and Gear, 1966; Foley et al., 1979). This pattern continues to be modified (albeit slightly) until humans reach a nearly adult stature, and into old age. The significance of a learning component in bipedality is underscored by the failure of congenitally blind infants to stand up bipedally without external stimuli (Inman et al., 1981).

Generally, the human developmental characters are in accord with a K-selected strategy and may have originated in common with great apes in stable, predictable environments (i.e. the tropics; Sarmiento, 1995). Human and great ape body size also associates the common human-great ape developmental characters with bet-hedging strategies in temperate areas (Richard, 1985). Some human developmental characters, however, are common to cercopithecoids and show a tendency for r-selection when compared to African apes (i.e. shorter ovulatory cycles, high prenatal growth rate, and relatively heavy newborns). Because modern human neonates are just as helpless as those of African apes despite their body weight and high prenatal growth rate, such r-selected characters, if real, probably reflect a past heritage.

#### CULTURE

**LANGUAGE:** Although all higher primates use vocalizations to communicate, and hominoids as a group have characteristic laryngeal specializations (Stark and Schneider, 1960), spoken language is a character that distinguishes humans from all other primates. Expired air passing through the laryngeal vocal cords, which are made to vary in tension and length by movements of the laryngeal cartilages, produce the raw sounds of human speech (Gardner et al., 1975). Resonance in the nasal, pharyngeal, and oral cavities and contraction of lingual, labial, and palatal muscles, however, all contribute to producing the final spoken word (Oldfield, 1947; Ploog, 1989).

Considering that humans can still speak after removal of the larynx (Gardner et al., 1975; Oldfield, 1947), dependent and direct

associations of human speech to laryngeal specializations are tenuous. Requiring coordination between the muscles of the pharynx, larynx, tongue, facial expression and expiration, and sensory feedback from the auditory centers, speech reflects neuronal control and cognitive abilities more than any specific somatic specialization (Penfield and Roberts, 1959; Ploog, 1989). Additionally, speech reflects a nearly limitless capacity for humans to learn, remember and coordinate complex motor behaviors in various localized areas of the anatomy (Carpenter, 1979; Ploog, 1989).

Although differences between the human and ape larynx are quantitative as opposed to qualitative (Kelemen, 1969; Stark and Schneider, 1960), apes cannot be taught to speak and allegedly lack the morphological structures necessary to produce human speech (Lieberman et al., 1972; Ploog, 1989), including a direct cortical pathway to the medulla (Jurgens, 1976). Principally, superior suspension of the larynx relative to humans results in an inability of the nonhuman hominoids to keep the epiglottis and soft palate apart and produce the long drawn-out sounds characteristic of human speech (Kelemen, 1969; Lieberman, 1973, 1994; Lieberman et al., 1972; Ploog, 1989). As noted, the more inferior position of the larynx and hyoid, the inferior origin of the tongue, and a supero-inferiorly long pharynx—all correlates of modern human speech—can be associated with basicranial flexion and the marked cervical lordosis.

Marked differentiation of facial muscles (Huber, 1931; Rugge, 1887), the well-exposed eye sclera, and possibly the absence of pigmentation on the palms and soles (Hewes, 1983) are characters that add to the repertoire of signals associated with human speech. Approximated in African apes, these characters underscore the significance of communication in early hominids and probably originated independently of speech as different parts of a communication system. Because many of the anatomical structures recruited for human speech may serve other primary functions, their recruitment in speech is largely opportunistic and need not reflect a heritage of strong selection for speech or be uniquely specialized for speech.

The marked auditory sensitivity of humans

to differences in low-frequency sounds (2000–3000 Hz) can be associated to the range of frequencies of human speech (Fay, 1988; Stebbins, 1983). Correlated to open habitats, this sensitivity may have predisposed the frequency of human vocalizations.

**TOOLS:** The ability to make and use tools is a character humans share with chimpanzees and orang-utans (Hall, 1968; McGrew, 1994; van Shaik et al. 1996), suggesting that tool use or its tendency was present in the human–great ape ancestor. Modern humans, however, are unique in having further developed their commonly shared ancestral abilities by producing a complex tool culture in which tools are used to make tools. Associated with a wide repertoire of learned behaviors, all relying on joint and muscle coordination and its memory, human tool use is not restricted to manipulative behaviors, but explores the totipotentiality of the human musculoskeletal structure (Oakley, 1972). As such, it makes innovative and opportunistic use of the existing anatomical structures and is analogous to human speech. Although capabilities for toolmaking were present in the common human–African ape ancestor, labor-intensive food resources requiring extensive manipulation may have further preadapted humans to tool use (Jolly, 1970). The cognitive and conceptual process of tool making has been associated with the symbols of language, and also with hunting (Krantz, 1968; Oakley, 1972) and the high intake of meat in the human diet (Butynski, 1982). In support of this correlation, common chimpanzees exhibit the most developed tool culture among the nonhuman primates (McGrew, 1994) and often engage in cooperative hunting (Teleki, 1973).

#### DERIVED VS. PRIMITIVE OR GENERALIZED CHARACTERS

Characters distinguishing humans from either or both genera of African apes, but not from orang-utans and/or hylobatids, are best interpreted as primitive for hominoids, with African apes exhibiting the derived condition. Some of these characters are widely seen in various primate groups and cannot be directly related to any behavior, but may represent a generalized condition (i.e., sphenoparietal contact, ethmolacrimar contact on the

medial orbital wall, absence of frontobasilar contact, presence of foramen lacerum, presence of 1st palmar interossei m., attachments of pectoralis minor m., attachments of trapezius m. and the extent of its aponeurosis, short scapula with vertical border, relatively small supraspinous fossa, barrel-shaped chest, absence of interdigital webbing, high frequency of plantaris tendon despite its lack of continuity with plantar aponeurosis, absence of ossi-metatarsi quinti m., c-shaped lateral meniscus in the knee joint, concave to planar tibial plateau surface, relatively short femoral neck and large femoral head, and poorly developed and restricted sphincter ani externus m.). Although these characters may be referred to as primitive, their wide distribution among various primate groups indicates they are compatible with a wide range of behaviors and generalized in function. Because many of these characters exist at low frequencies within African apes, reversion in humans to the primitive or generalized condition as a result of selection for generalized behaviors is always a possibility, thereby confusing polarity. As such, the ancestral human–African ape condition is uncertain.

Characters that humans share with chimpanzees and/or orang-utans to the exclusion of gorillas (i.e., absence of a nasolacrimar bulla, less extensive lobation of the liver, lower number of coccygeal vertebrae, strong development of the coronoid head of pronator teres, rectus abdominus with reduced number of tendinous inscriptions, poorly divided pectoralis major m., the absence of a separate pectoralis abdominus m., and short head of biceps femoris m. inserting on the long head) are best interpreted as derived characters in gorillas, with orang-utans, chimpanzees, and humans exhibiting the ancestral human–great ape condition. Likewise, some of the characters that humans share with gorillas and/or orang-utans exclusive of chimpanzees (i.e., relatively small ear with a lobule, premaxillary nasal process overgrown by maxilla, wide pterygomaxillary cleft, wide ilia relative to trunk length, and an external oblique m. attaching on the iliac crest) are best interpreted as the derived condition in chimpanzees. Because these characters exhibit variability within the hominoid

taxa, and character polarity must be decided on the condition of only a few taxa without direct or clear association to a functional complex, there is considerable ambiguity as to their condition in the most recent human–African ape ancestor.

### PHYLOGENY

The greater number of characters humans have in common with gorillas suggests a closer relationship between them than either shares with chimpanzees. Among closely related taxa, however, it is often difficult to separate shared–derived characters from parallelisms. A close relationship confirms that many of the distinguishing characters will be relatively labile (otherwise they could never be fixed over relatively short evolutionary periods) and quantitative as opposed to qualitative in nature (Schultz, 1936).

Common ancestry and recent evolutionary origin also guarantee that parallel structures will lack the differences in detail necessary to divulge evidence of their independent acquisition. For instance, the low frequency of the peroneus tertius m. in lowland gorillas and its virtual absence in chimpanzees, Asian apes, and the nonhominoid primates support an independent origin for the high incidence of this muscle in humans and mountain gorillas; however, nothing in the detailed anatomy of the muscle vouches that this is the case (Sarmiento and Butynski, in prep.). The same applies to the shift in the functional axis of the interossei muscles from the 3rd to the 2nd digit, a shift that is also more prevalent in humans and mountain gorillas, but has probably occurred independently.

Because humans and gorillas are closely related and many of the characters they share can be associated to terrestriality, the independent acquisition of these shared characters is a real possibility that confounds phylogenetic analysis. When characters related to increased terrestriality are excluded, the uniquely shared and derived chimpanzee–human characters (i.e., the early obliteration [prenatal] of the premaxillary-maxillary suture on the anterior alveolus) more or less offset the uniquely shared and derived human–gorilla characters (i.e., external nasal morphology, premaxillary-maxillary suture

variably internalized in the lateral wall of the nasal cavity, facial musculature and sperm morphology) and provide conflicting evidence as to which ape is more closely related to humans.

With a more distant relationship and fewer morphological similarities, cercopithecids fail to exhibit the detailed anatomical characters that are mechanical requisites of gorilla and human terrestriality (i.e., the intrinsic anatomy of the hands and feet, low brachial index, and loss or marked attenuation of the dorsoepitrochlearis m.). In cases where cercopithecines show complex structures similar to those of humans, these can be shown to be convergent. Although both have a well-developed flexor accessorius m. with an analogous function, the human muscle is two-headed and not fully homologous with the single-headed cercopithecoid muscle (Lewis, 1962; Sarmiento, 1983). Likewise, differences in humans and cercopithecids in the insertion of the functionally analogous fascial or anterior portion of the gluteus maximus m. reveals a nonhomology (Stern, 1972). The presence of these nonhomologies (homoplasies) underscores the independent development of terrestrial behaviors in humans and cercopithecids and refutes the likelihood that any of their other common terrestrial characters that lack the complexity needed to test for parallelisms are shared–derived or primitive retentions.

### HOMINID ANCESTORS

Considering its cautious climbing ancestry (Sarmiento, 1995), the last common human–African ape ancestor probably exhibited (1) all characters of the cautious climbing folivorous complex common to humans and African apes (Sarmiento, 1995), and (2) primitive characters that distinguish humans from either African ape, but not from Asian apes or cercopithecines. This ancestor may also have shown other cautious climbing characters that are not uniformly well developed in all living great apes, but are present in humans and/or nonhominoid cautious climbers (i.e., femoral bicondylar angle, long pubis, high femoral neck angle, and the complex of anatomical characters related to extension of the hip and knee joint; Sarmiento, 1995). As

noted, the ancestral condition for cautious climbing characters that are derived in humans in terms of the nonhominoid primates, but are more conservative than those seen in great apes (i.e., narrower, barrel-shaped chest with 12 pairs of ribs, five lumbar vertebrae, and a much shorter pelvis relative to trunk length than that of great apes), cannot be resolved based solely on the comparative anatomy of living taxa.

In view of the ancestral human–African ape condition, all distinguishing human characters indicate that hominid divergence progressed from a semiarboreal life-style in a forest or woodland habitat to a committed terrestrial life-style in an open-country habitat. Common to humans and African apes, terrestrial behaviors must also have been common to the most recent human–African ape ancestor. Because hominoids as a group do not show as strong a commitment to the cautious climbing complex as do other arboreal nonhominoids (Sarmiento, 1995), it is possible that this complex evolved in common with partial terrestriality. The presence of shared characters in the hands and feet of African apes, which satisfy mechanical requisites of terrestriality (Sarmiento, 1985a, 1988, 1994), supports this assumption. The numerous terrestrial characters that humans share with gorillas exclusive of chimpanzees indicate that humans and gorillas underwent further terrestrial selection exclusive of chimpanzees or that chimpanzees have lost these terrestrial specializations since their divergence. The cercopithecoid-like musculo-skeletal anatomy in humans attests to an additional stage of selection pressures for terrestriality independent of African apes. Selection for terrestriality at this stage sacrificed arboreal behaviors in humans and was much stronger than that undergone by gorillas.

#### NEW MODEL OF HOMINID DIVERGENCE

##### CERCOPITHECINES

Although no living nonhuman hominoid has made a transition to open habitats, several cercopithecine lineages, to varying degrees have; these provide a range of ecological analogies for reconstructing the hominid

shift (Jolly, 1970).<sup>3</sup> Considering that African catarrhines are commonly found in sympatric associations exploiting overlapping resources and have probably evolved together to do so (Crook and Aldrich-Blake, 1968; Dunbar and Dunbar, 1974; Gautier-Hion, 1978; Hall, 1965b; Hunt, 1996; Jolly, 1972, 1993; Richards, 1985; Struhsaker, 1978), the existence of an African ape that would have made the transition to open habitats together and in competition with the various lineages of cercopithecines is expected.

**WOODLANDS AND SAVANNAS:** Widely distributed throughout subsaharan Africa in riverine woodland or savanna woodland mosaics (bushland), savanna baboons (*Papio cynocephalus*)<sup>4</sup> and vervets (*Cercopithecus aethiops*) are preferentially frugivorous (Crook and Aldrich-Blake, 1968; Dunbar and Dunbar 1974; Fedigan and Fedigan, 1988; Gartlan and Brain, 1968; Hamilton et al., 1978; Nakagawa, 1989; Struhsaker, 1967a, 1967b). Smaller in body size, vervets usually aug-

<sup>3</sup> Because the closest relatives of humans are presently found in Africa, African primates were chosen as analogies for reconstructing the hominoid shift. Outside of Africa, *Macaca*, *Rhinopithecus*, and *Presbytis* have all made the shift to more open habitats. Although New World monkeys are largely arboreal, prolonged incursions into open habitats are common in *Alouatta* and *Cebus*, the two most generalized forms. Many of the behavioral and ecological variables that apply to this shift in African monkeys, also apply to the Eurasian and South American monkeys, which in the case of some Asian monkeys may even show closer structural convergence with hominids (Sarmiento, 1995). Regardless on which continent human divergence occurred, the hominoid structure may be expected to respond in similar ways to open habitats.

<sup>4</sup> In this work, the yellow (*P. c. cynocephalus*), anubis (*P. c. anubis*), and chacma (*P. c. ursinus*) baboons are considered the same species and separate from hamadryas baboons (*P. hamadryas*). Although it may be convincingly argued that hamadryas and savanna baboons should be placed in the same species given a naturally occurring hybrid zone (Jolly, 1993), a specific distinction for hamadryas baboons is supported by; ecological and behavioral differences between hamadryas and savanna baboons, the presence of a mechanism that seems to limit gene flow between male anubis and female hamadryas baboons, no clear correspondence between subspecies and species designations and the degree of genetic differences (i.e., relatedness), and natural production of viable hybrids between different genera of cercopithecines (Jolly et al., 1997; Yalden et al., 1977). Further study of the hybrid zones between the different populations of *Papio* are necessary to clarify which taxonomy is appropriate.

ment a larger proportion of their diet with insects and small vertebrates (Fedigan and Fedigan, 1988; Gartlan and Brain, 1968; Struhsaker, 1967a,b), whereas baboons augment their diet with grasses, leaves, and/or herbs (Dunbar and Dunbar, 1974; Hamilton et al. 1978; Harding, 1976; Post, 1978, 1982). Considered omnivores by some (Altmann and Altmann, 1970; Fedigan and Fedigan, 1988; Hamilton et al., 1978), both cercopithecines have an opportunistic and varied diet that includes leaves, herbs, flowers, seeds, grass, roots (bulbs, rhizomes, and tubers), tree gum, invertebrates, small vertebrates, and in the case of baboons, vervets, hares, and small antelopes (Butynski, 1982; Dunbar and Dunbar, 1974; Gartlan and Brain, 1968; Fedigan and Fedigan, 1988; Harding 1973, 1975; Hausfater, 1976; Hausfater and Bearce, 1976; Post, 1978, 1982; Rose, 1977; Struhsaker, 1967a, 1967b; personal obs.). In areas where fruit is not abundant, baboons may consume largely grasses and herbs (Harding, 1976; Post, 1982) and seem better able than the smaller size vervets to tolerate seasonal fluctuations in food quality (Struhsaker, 1976). Nevertheless, both vervets and baboons deal effectively with scarce resources, readily changing their preferred diet and adjusting their ranging pattern, foraging behavior, and group size and composition to best cope with the given situation (Byrne et al., 1990, 1993; Dunbar and Dunbar, 1974; Galat and Galat-Luong, 1977; Gartlan and Brain, 1968; Harding, 1976; Harrison, 1983; Kavanagh, 1981; Post, 1982).

Baboons and vervets are terrestrial quadrupeds that range into open habitats and move (between feeding sites) terrestrially to feed on the secondary growth flanking streams, lakes, or rivers at the edge of forests or open habitats (Hall, 1962, 1965b; Hamilton, et al. 1978; Rose, 1977, 1979; personal obs.). Despite their terrestrial nature, however, both primates can usually be found in proximity to trees, climbing and leaping in trees to feed, shelter, and avoid predators.

Baboons are not as restricted to woodland habitats as are vervets (Fedigan and Fedigan, 1988; Hall, 1965b; Rose 1979), and are found in a wide range of habitats from arid semidesert areas to closed forests and gallery

forests (Jolly, 1993; Post, 1982; Rowell, 1966; personal obs. in the Harts River valley, South Africa, and in Bwindi, Kalinzu and Budongo forests, Uganda). The presence of baboons in equatorial forests east of the bend in the Congo River, however, may be due to the absence of forest-specialized, sympatric papionins (Jolly, 1993). Without specialized arboreal competitors, vervets range into temperate or high-elevation forests (personal obs. in riparian forest in the Transvaal and Natal; T. Butynski, personal obs. in Eritrea), and inhabit the tropical forests of the Caribbean Islands where they were introduced (Fedigan and Fedigan, 1988).

Baboons and vervets may have overlapping ranges with chimpanzees, blue monkeys (*C. mitis*), and other forest-based primates (Brain and Gartlan, 1968; Hunt, 1996; Jolly, 1993; Rose, 1979; Rowell, 1966). Relative to their forest congeners, vervets have long day ranges and large home ranges, which, as in baboons, increase with decreasing food density (Barton et al. 1992; Fedigan and Fedigan, 1988; Gartlan and Brain, 1968; Harding, 1976; Post, 1978; Struhsaker, 1967b). Correlated to their larger body size and greater affinity for open habitats, baboons have much longer day ranges, larger home ranges, and devote a much greater proportion of time to locomotor behaviors than do vervets (Hall, 1965b; Rose, 1979).

Owing to a varied food supply and habitat, baboons and vervets have varied locomotor behaviors and feeding postures, and a generalized musculoskeletal structure (Brain and Gartlan, 1968; Jolly, 1965; Rose, 1976, 1977, 1979). Although unable to directly compete with more specialized primates in any one habitat (Crook and Aldrich-Blake, 1968; Dunbar and Dunbar, 1974; Gartlan and Brain, 1968; Fedigan and Fedigan, 1988; Hall, 1965b; Jolly, 1970, 1993), baboons and vervets have a dietary and behavioral plasticity that enables them to exploit marginal habitats and colonize new areas (Galat and Galat-Luong, 1977; Hall, 1965b; Struhsaker, 1967b).

With high energy demands and a relatively low-quality diet (Leonard and Robertson, 1997), baboons have relatively large molars. Their large spatulate incisors provide a varied and important role in food processing,

especially for husking and peeling fruit (Jolly, 1965, 1970).

**OPEN COUNTRY:** Confined mainly to semi-desert scrublands, grasslands or high-altitude meadows in subsaharan Africa north of the equator (in areas characterized by a prolonged, severe dry season), geladas, hamadryas baboons (*P. h. hamadryas*), and patas monkeys (*Erythrocebus patas*) are cursorial quadrupeds committed to open country (Dunbar, 1984; Hall, 1965a; Kummer, 1995; Yalden *et al.*, 1977). Patas monkeys may preferentially inhabit open acacia woodlands and are not as restricted to open habitats as are geladas and hamadryas baboons, (Chism and Rowell, 1988; Hall, 1965a).

The diet of open-country cercopithecines includes many of the same food items common to baboons and vervets (Chism and Rowell, 1988; Dunbar, 1977; Nakawaga, 1989), but emphasizes foods that are more abundant in open country. Geladas and hamadryas baboons emphasize seeds, roots, grasses, and herbs (Dunbar, 1977; Iwamoto, 1993; Kummer, 1995). Smaller in body size and with correspondingly higher nutritional needs, patas monkey emphasize herbaceous buds, gums, and invertebrates (Chism and Rowell, 1988; Hall, 1965a; Nakawaga, 1989). Both patas monkeys and hamadryas baboons also rely on acacia trees for many food items, and seasonally venture into woodlands, when fruits are abundant (Chism and Rowell, 1988; Hall, 1965a; Kummer, 1995). Because many of the food items consumed by the open-country cercopithecines are small objects collected at ground level, manipulation with an opposable thumb and index finger is an important stage of food processing (Bishop, 1963; Dunbar and Dunbar, 1974; Hall, 1965a; Jolly, 1970). As in savanna baboons, terrestrial collection of food from trees or shrubs often elicits bipedal behaviors (Chism and Rowell, 1988; Hall, 1965a; Kummer, 1995; Rose, 1976, 1977; Wrangham, 1980).

Associated with behavioral and morphological specializations for exploiting densely distributed grasses in high-altitude meadows, geladas have on average much shorter day ranges, smaller home ranges, and exist at much greater densities (77 per km<sup>2</sup>) than do patas monkeys or hamadryas baboons (1.8–

9.7 animals per km<sup>2</sup>; Chism and Rowell, 1988; Dunbar, 1984; Dunbar and Dunbar 1974; Hall, 1965a, 1965b; Kummer, 1995). With a less specialized gnathic complex and manual proportions, and a more varied and widely scattered diet, hamadryas baboons and patas monkeys must cover larger areas to satisfy their nutritional needs. Their proportionately long hindlimbs relative to those of geladas (Jolly, 1965, 1972) are specializations for ranging long distances, saving energy by reducing the total number of strides per distance travelled.

All the open-habitat cercopithecines have a one male–multifemale mating unit (Dunbar, 1984; Hall, 1965a; Kawai *et al.* 1983; Kummer, 1995), a system common to savanna baboons and vervets when ranging in impoverished habitats (Byrne *et al.*, 1990; Gartlan and Brain, 1968). Geladas or hamadryas baboon units further associate into bands forming large groupings around water sources, and sleeping and feeding sites, where the range of more than one group overlaps (Crook and Aldrich-Blake, 1968; Kawai *et al.*, 1983; Kummer, 1995). Adult patas monkey males usually do not tolerate adult males from other groups, and prevent the fusion of units (Hall, 1965a). However, there seems to be variability in patas monkey social systems and large groups, with multimale–multifemale mating have been observed (Harding and Olson, 1986).

Geladas and hamadryas baboons are restricted to treeless habitats where opportunities for tree use are not common (Crook and Aldrich-Blake, 1968; Dunbar, 1984; Kummer, 1995). Even when trees are available, geladas are rarely arboreal (Dunbar, 1984). Both geladas and hamadryas baboons usually sleep or shelter on the ground in cliffs and/or rocky outcrops (Crook and Aldrich-Blake, 1964; Dunbar, 1984; but see Iwamoto, 1996), a behavior variably seen in savanna baboons (Crook and Aldrich-Blake, 1968; personal obs. in the Transvaal, Harts River valley, and in Natal, South Africa) and less frequently in patas monkeys (Chism and Rowell, 1988). In woodlands, patas monkey can be observed feeding and preferentially sleeping and resting in trees (Chism and Rowell, 1988; Hall 1965a; personal obs.). They may also leap between trees to avoid terrestrial descents

(Chism and Rowell, 1988; Hall, 1965a), a behavior facilitated by their relatively small body size.

All the open-country cercopithecines may coexist with baboons and/or vervets, overlapping in range and food resources (Chism and Rowell, 1988; Crook and Aldrich-Blake, 1968; Dunbar, 1984; Hall, 1965a, 1965b; Kummer, 1995). Their sympatry with baboons and/or vervets is characterized by a preference for open habitats over woodlands and a commitment to terrestrial locomotion and food gathering. Sacrificing more generalized behaviors, the specialized gnathic complex and musculoskeletal structure of geladas can outcompete that of the more generalized savanna baboon in open habitats (Dunbar, 1977; Dunbar and Dunbar, 1974; Jolly, 1970, 1972). Similarly, the larger body size, longer limbs, and more elongate but compact hands and feet of patas monkeys (Etter, 1973; Strasser, 1989; author's notes) sacrifice arboreal behaviors, but are better suited than those of vervets for ground travel and for exploiting terrestrial food sources (Chism and Rowell, 1988; Hall, 1965b). Relative to vervets, the greater amount of time that patas monkeys devote to moving and feeding terrestrially vs. arboreally (Hall, 1965b; Isbell et al., in press; Nakagawa, 1989; Rose 1979) attests to a greater commitment to open habitats. The close morphological similarities between savanna and hamadryas baboons (Jolly, 1965, 1993) indicate that their divergent specializations are largely behavioral.

Due to a greater morphological and/or behavioral commitment to open habitats at the expense of generalized behaviors, and a distribution bounded by the more generalized savanna baboon, geladas and hamadryas baboons have a localized distribution. Patas monkeys are less localized in distribution than are the other open-country cercopithecines, probably because they are less committed to open habitats and there are no competing guenons as adept in open woodlands.

In times of drought, the quantity and quality of available food sources in savanna and open habitats may be drastically reduced causing mass death of baboons, vervets, and patas monkeys (Galat and Galat-Luong 1977; Kummer, 1995; Nakagawa, 1989;

Struhsaker, 1976). Correlates of unpredictable environments, the numerous r-selected characters found in vervets and patas monkeys (Rowell and Richards 1979) are absent in papionins (given their larger body size).

#### STAGE I

Based on a cercopithecine model, the development of distinguishing human characters in the most recent common ancestor of humans and African apes can be best conceived in two adaptive stages. In analogy to savanna baboons, the initial stage of hominid divergence would have involved a wide-ranging, generalized open-woodland ape with the ability to exploit diverse habitats. Based in woodlands, but ranging into adjacent grasslands or gallery forests, the hominid ancestor at this stage had a varied diet, coming from both arboreal and terrestrial food sources. Forests and woodlands would have provided leaves and fruits while grasslands provided seeds, rhizomes, grasses, and herbs.

Moving terrestrially between arboreal food sources, this human ancestor would have retained or conceivably emphasized some climbing ability, especially on vertical supports (Prost, 1981; Sarmiento 1985a, 1995b). Climbing would have also been important for shelter and security. Because mediolateral movements of the hindlimb segments necessary for climbing are not compatible with an efficient cursorial bipedalism, which restricts the hindlimb segments to movements in the plane of forward motion (Sarmiento, 1985a), it is unlikely bipedalism was used when speed was emphasized or when moving long distances. In these cases and when the animal was moving through the thick underbrush characteristic of many woodlands, quadrupedalism would have been preferred. Considering this ape's cautious climbing ancestry, however, bipedal standing or short-distance walking during feeding (Rose, 1991), wading in flooded or muddy areas, and/or walking along lake shores or river banks, all circumstances eliciting bipedality in great apes (Ellis, 1991; Hornaday, 1910; Hunt, 1994; Kohler, 1959; Kortlandt 1995; personal obs.), would have been much more common than reported in baboons (Rose, 1976). As in baboons, a large home range,



long day range, and the ability to exploit varied habitats would have enabled this ape to colonize mosaic woodlands outside of the tropics and range into high altitudes (above 2000 m). Structurally, this taxon would have exhibited the generalized body segment proportions of baboons and other noncommitted, generalized primates, making possible a wide repertoire of locomotor behaviors and postures. As a generalized ape, it would probably have retained, albeit with some modification, most of the characters common to the human-African ape ancestor.

## STAGE II

As noted by Jolly (1970), *Theropithecus*, a highly terrestrial graminivore, serves as a model for the next stage of hominid divergence. Restricted to grasslands and scrublands near water, the hominid ancestor at this stage would have exploited mainly terrestrial food sources. Because of the dry habitat, its diet probably consisted of tough and abrasive foods similar to those consumed by geladas or hamadryas baboons. Relative to the food of geladas, however, the diet probably included a greater diversity of food sources and differed in the proportion of food types consumed (both factors of a hominoid ancestry; Kortlandt, 1983). Rhizomes and seeds, probably collected in erect sitting postures, would have been emphasized (Hatley and Kappelman, 1981; Jolly 1970; Peters, 1987). Due to the low water content of the diet, drinking water from nearby sources was necessary. Collection of terrestrial food items and the associated emphasis on a thumb-index finger grip would have developed the humanlike thumb. Relaxation of selection pressures for incisal use in food processing and an emphasis on molar crushing and grinding were factors in the relative reduction of the anterior dentition and development of the humanlike jaw and basicranial characters (Jolly, 1970). Sporadically exhibited by open-habitat cercopithecines (Butynski, 1982; Galat and Galat-Luong, 1977; Harding, 1975; Kummer 1995; Struhsaker, 1967a, 1967b), especially in times of food shortages, opportunistic capture of small vertebrates would have persisted from the common human-African ape ancestor. Seasonal forays into woodlands would have provided some fruit and leaves, but

these would have been collected mainly in terrestrial bipedal postures rather than by climbing (Rose, 1984; Wrangham, 1980; see below).

Climbing abilities at this stage would have been sacrificed as a result of a terrestrial commitment. Increases in relative lower-limb length and size, a response to increased terrestrial quadrupedality in most cercopithecines, but not in geladas (Jolly 1965, 1972), and pedal and manual compactness would have resulted in body-segment proportions closer to those of modern humans. An emphasis on maintaining the limbs in the plane of forward motion for efficient cursorial quadrupedality, would have opened the way for developing a lateral stabilizing mechanism at the hip joint and striding bipedality (Sarmiento, 1985a, 1985b, 1996). Whether this taxon can be considered a biped or a terrestrial quadruped depends on the frequency of each behavior, the individual concerned, and the habitat and resources exploited at any time. Differences relative to modern humans in the duration of the learning and/or developmental stages leading to bipedalism, however, would be expected.

Analogous to open-habitat cercopithecines, group size, day range, home range, and density would have varied depending on food resources. Congregation of hominid ancestors at sleeping, feeding, and drinking sites, however, would be expected. The high density of animals occurring at times, and strong social cohesion in seasonally impoverished environments, would have placed a premium on enhancing symbolic communication and cooperation to minimize fighting and avoid predation.

The close association of female body fat with fertility and the role of fat distribution in sexual attraction are both correlates of seasonal fluctuations in food quality and availability, and provide evidence that food shortages of the magnitude experienced in open habitats had a greater selective impact on humans than on great apes. The overall strong commitment of the distinguishing external, visceral, developmental, acoustic, and sexual human characters to open habitats at the expense of a generalized structure suggests that this stage had strong limiting selection pressures.

## FULL DEVELOPMENT OF DISTINGUISHING HOMINID CHARACTERS AND AFRICAN APE DIVERGENCE

Although most of the distinguishing human characters may find their origin in a *Theropithecus*-like stage of human evolution (exhibiting a commitment to open country), the complete development of many of these characters probably occurred concurrently with elaboration of material culture (Jolly, 1970), a prolonged postnatal development period, and an increase in brain size. This applies especially to those behaviors with a marked learning component that emphasize neuronal control and an opportunistic use of the existing musculoskeletal structure (i.e., bipedalism, language and a complex tool culture, and the neural and musculoskeletal characters that develop ontogenetically as a result of these behaviors). Once established in open country, positive feedback loops between scavenging, meat eating, tool use, cooperative hunting and communication must have had a considerable impact on the final development of the human characters (Butynski, 1982; Krantz, 1968; Oakley, 1972; Shipman, 1986). Elaboration of material culture, however, would have increasingly freed the musculoskeletal structure from selective pressures, precluding marked modifications, especially to the postcranial anatomy.

According to a cercopithecine analogy, the marked commitment to terrestriality exhibited by the distinguishing human characters indicates that at least two adaptive stages prior to the advent of material culture are necessary to derive the human characters from the ancestral human-African ape condition. Each of these stages structurally and behaviorally preadapts the hominid ancestor to its subsequent habitat. In a stage II ancestor fully preadapted to bipedalism, changing patterns of food acquisition could have served to further select for modern human bipedality, i.e., from bipedal feeding at arboreal sources (Jolly and White, 1994) to hunting or scavenging associated with carrying behaviors (Rose, 1991).

The semiterrestrial/terrestrial nature of African apes, especially gorillas, suggests the human-African ape split may not have oc-

curred until a woodland stage of hominid evolution was under way. As noted by Kortlandt (1975), the strong competitive pressures that culture-bearing hominids may have exerted could have pushed African apes away from the shared ancestral habitat and resources. Kortlandt's argument gains further support from the dental specializations of gorillas and chimpanzees and from the habitats and food resources presently exploited by them, both of which are derived away from the hypothesized ancestral condition (Sarmiento, 1995; this study).

Additional evidence bearing on (1) the stage at which African apes diverged; and (2) the sequence of appearance of the human characters, their degree of development, and their association to each other at each adaptive stage, is provided by the fossil record, which may be used to test the proposed model.

## FOSSIL RECORD

### OREOPITHECUS

Predating the last human-African ape ancestor, *Oreopithecus* is the best known and most complete of the late Miocene hominoid fossils (Sarmiento, 1987a). Exhibiting the cautious climbing folivorous complex expected in a stem hominoid (Sarmiento, 1987a, 1995; Schultz, 1960; Straus, 1963), *Oreopithecus* was probably a vertical climbing arboreal biped that practiced bipedal wading on its descents to a swamp-covered forest floor, a behavior common to pygmy chimpanzees and orang-utans (Badrian and Badrian, 1977; Hornaday, 1910; Kortlandt, 1995). Its five lumbar vertebrae, relatively short pelvis, barrel-shaped thorax, femoral bicondylar angle and strong ischial spine (Biegert and Mauer, 1972; Kohler and Moya, 1997; Sarmiento, 1987a; Schultz, 1960; Straus, 1963), suggest that these characters are primitive for humans and African apes. Significantly, this fossil occurs in a late Miocene circum-Mediterranean swamp forest, considerably north of the tropics. Although *Oreopithecus* may ultimately prove that the common human-African ape ancestor evolved outside of the tropics and reentered as a semiterrestrial ape, much less complete fossil evidence shows that true hominoids

were relatively widespread at this time, occurring in Europe (Begun and Kordos, 1993; de Bonis et al. 1990; Kordos, 1988; Moya-Sola and Kohler 1993, 1996), Asia (Andrews and Tekkaya, 1980; Pilbeam et al., 1990; Wu, 1987; Wu et al. 1986), and tropical Africa (Hill, 1994; Hill and Ward, 1988).

#### HADAR

The earliest recognizable and relatively complete "hominid" fossils that provide evidence as to the sequence of appearance of hominid adaptations are the Hadar australopithecines. Notably, these australopithecines lack those unique skeletal characters that in modern humans are associated with habitual bipedality (i.e., a low intermembral index [ $<80$ ], a long hindlimb, a ventrally concave sacrum, a marked lumbar lordosis, markedly shortened and laterally facing iliac blades, a 1st sacral vertebra with a large x-sectional body area, a grooved iliopubic eminence, a large sacroiliac joint, a relatively large femoral and tibial shaft diameter, a large femoral head and correspondingly large acetabulum, a humanlike iliac pillar and tuberosity, a stout and prominent anterior inferior iliac spine for attachment of a strong iliofemoral ligament, a posteriorly projected and proximally expanded ischial tuberosity, and high positive tibial and femoral torsion; Kimbel et al., 1994; Lovejoy, 1979; Sarmiento, 1985a, 1985b, 1987b, 1996; Susman and Stern, 1983). They also lack some of the characters that modern humans share with cursorial cercopithecines (i.e., straight manual and pedal phalanges, a long axis of the auricular area set perpendicular to that of the ilium, a lateral femoral condyle invariably larger than the medial condyle, a narrow and anteriorly extended intercondyloid notch, deep patellar groove with an anteriorly projected lateral lip, consistently absent or reduced distal tibiofibular facet, a mediolaterally compressed distal fibula, lateral orientation of the iliac blades, and a posteriorly disposed and reduced proximal tibio-fibular facet (Stern and Susman, 1983; Susman et al., 1984; author's notes). The presence of weight-bearing tubercles on the distal tarsal bones, an apelike navicular morphology, the ectocuneiform's hamulus, proximodistally short cuneiforms, a groove for the abductor digiti minimi on the

plantar aspect of the base of the 5th metatarsal, and the absence of a large and distinct articular area for the spring ligament on the talar head (Gomberg and Latimer, 1984; Latimer et al., 1982; McHenry, 1991; Sarmiento, 1991, 1994) further indicate that Hadar australopithecines lacked the fixed transverse and longitudinal arches characteristic of modern humans. Because modern human bipedalism requires a commitment to terrestriality, but the Hadar australopithecines lack human pedal arches and also some of the committed terrestrial characters that humans share with cursorial cercopithecines, it is highly unlikely that these forms could have been committed bipeds.

The absence of the full suite of human bipedal characters and the presence of several apelike postcranial characters (i.e., the elongated pisiform, the waisted capitate, the orientation of the glenoid [shoulder] joint, the contours and orientation of the articular surfaces of the knee and ankle joint, the relatively tight curvature of the first carpometacarpal joint, curved pedal and manual phalanges, and attenuated ungual phalangeal tufts), have led Stern and Susman (1983) to argue that Hadar australopithecines are partially arboreal. They tempered their conclusion by noting that the posteriorly displaced sacral articular surface, the short ilium, the iliac pillar and a strongly valgus knee (high femoral bicondylar angle) indicated Hadar australopithecines were bipedal when terrestrial.

The orientation of the glenoid and the relative length, width, and degree of curvature of the manual and pedal phalanges in Hadar australopithecines are intermediate between humans and gorillas (Susman et al., 1984), and closely approximate values for mountain gorillas (Sarmiento, 1994). Because mountain gorillas are terrestrial quadrupeds (Sarmiento et al., 1996; Schaller, 1963), such characters in the shoulder and hand are more correctly associated with terrestrial quadrupedality. The short styloid process, contours of the ulnar head, and the orientation of the hamate's articular surfaces (Bush et al., 1982; Johanson et al., 1982; Lovejoy et al., 1982) further indicate that the Hadar australopithecines had developed the derived weight-bearing triangular articular disc in the ulno-

carpal joint common to gorillas and humans. The waisted capitate, elongated pisiform, and large palmarly oriented hamulus of the Hadar hand (Bush et al., 1982; Johanson et al., 1982; Lovejoy et al., 1982) are in part terrestrial characters absent in the hands of the more arboreal Asian apes (Sarmiento, 1985a, 1988, 1994). The posteriorly facing iliac blades, lateral orientation of the acetabulum, and low femoral torsion indicate that the knee joint in AL 288-1 was laterally directed. The femoral bicondylar angle therefore contributed only partially to forming the carrying angle, in marked contrast to the condition in human bipeds (Sarmiento, 1985a, 1985b). With humero-femoral, brachial, femoro-coxae, and intermembral indices intermediate between those of humans and pygmy chimpanzees (Schultz 1930, 1936; Zihlman and Cramer, 1978), and within the range of generalized terrestrial monkeys (i.e., baboons and macaques), the proportions of the most complete Hadar australopithecine AL 288-1 (Jungers, 1982, 1988a, 1991a) also suggest terrestrial quadrupedality. The alleged bipedal characters in the foot and ankle joint cited by Latimer and Lovejoy (1989, 1990a, 1990b) and Latimer et al. (1987) also satisfy the mechanical requisites of quadrupedal cursors and are probably quadrupedal in origin (Carrano, 1997; Sarmiento, 1994; this study).

Plots of (1) humeral vs. femoral circumference, and (2) the log of the x-sectional area of the superior surface of the 1st sacral body relative to either humeral or femoral circumference show that AL 288-1 is fully out of the range of humans and is similar to baboons and chimpanzees (figs 2,4,6). Significantly, these plots distinguish free-ranging from captive-born-and-raised orang-utans based on ontogenetic differences in body weight (figs. 3, 5, 7; Sarmiento 1985a). With a humeral circumference approximating that of the femur, and a x-sectional area of the 1st sacral body that is small relative to either femoral or humeral circumference, AL 288-1 had a weight distribution in the limbs and lower back during its lifetime that was most like that of a quadruped. The orientation of the acetabular articular surface relative to the pelvis also indicates the hip joint was loaded in the flex postures characteristic of a quadruped (fig. 8).

Despite marked terrestrial adaptations in the hands and feet, the relatively small body size of AL 288-1 (Jungers, 1991a; McHenry, 1988, 1992) indicates that it was more adept in trees than are either adult gorillas or humans. In AL 288-1, the (1) relatively long pubis (reflecting a wide biacetabular distance), and (2) high femoral bicondylar angle associated with low femoral torsion and posteriorly facing iliac blades can be associated with vertical climbing ability on relatively large supports (Sarmiento, 1985a, 1985b, 1987b). By reducing the moment arms of the resultant force vectors at the foothold, the short hindlimbs of AL 288-1 (Jungers and Stern, 1983) would also have facilitated climbing (Sarmiento, 1985a, 1985b, 1989). The terrestrial hand and foot proportions indicate that the Hadar australopithecines, when arboreal, preferred using relatively large supports as substrates, relegating suspensory activities to the forelimbs.

Given its small body size (Jungers, 1982, 1988a, 1991a), the hand and foot characters, especially the short pedal phalanges of AL 288-1 (Latimer, 1991), attest to a heritage of strong selection pressures for terrestriality. Considering that African apes exhibit an increase in terrestrial behaviors and fuller development of the associated terrestrial characters in the hands and feet with an increase in body size (Sarmiento, 1994), selection for terrestriality in the Hadar australopithecines was much greater than is presently exhibited in either African ape. Alternatively, as in some cercopithecines (Strasser, 1989), the short digits of Hadar australopithecines may reflect ambient temperatures, indicating they evolved at high elevations or in temperate forests.

Common to all hominoids (Carpenter and Durham, 1969), bipedal behaviors were probably common to the Hadar australopithecines. Considering iliac orientation and hindlimb long-bone torsions effecting propulsive movements of the thigh, leg, and foot in different planes (Sarmiento, 1985a, 1987b), and relatively short hindlimbs, it is unlikely that such bipedal behaviors could have been used when speed was at a premium or when the animal was moving long distances. In these cases, and when moving through heavy underbrush, Hadar australo-

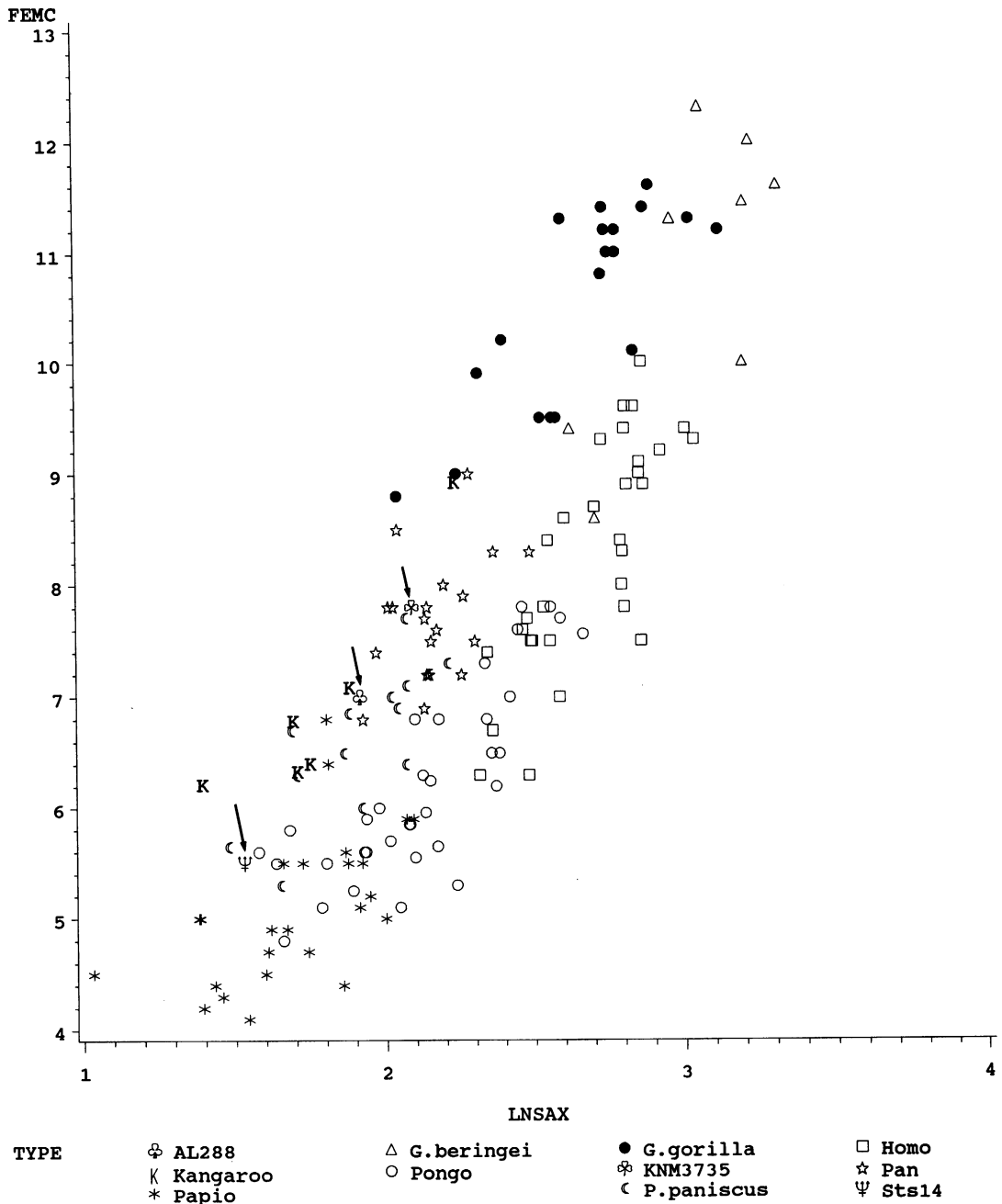


Fig. 2. The natural log of the x-sectional area of the superior articular surface of the body of the 1st sacral vertebra vs. the midshaft circumference of the femur in hominoids, baboons, and some Pliocene "hominid" fossils (AL288 = A.L. 288-1, KNM3735 = KNM-ER 3735,  $y = y\text{-intercept}$ ;  $r^2$  values adjusted). Humans (*Homo*), slope = 3.94,  $y = -2.39$ ,  $r^2 = 0.6117$ ; Virunga gorillas (*G. g. beringei*), slope = 3.84,  $y = -0.816$ ,  $r^2 = 0.455$ ; lowland gorilla (*G. g. gorilla*), slope = 2.71,  $y = 3.31$ ,  $r^2 = 0.6271$ ; pygmy chimpanzees (*P. paniscus*), slope = 2.17,  $y = 2.41$ ,  $r^2 = 0.562$ ; chimpanzees (*Pan*), slope = -0.0306,  $y = 8.01$ ,  $r^2 = 0.000$ ; orang-utans (*Pongo*), slope = 2.43,  $y = 0.983$ ,  $r^2 = 0.670$ ; baboons (*Papio*), slope = 1.55,  $y = 2.47$ ,  $r^2 = 0.303$ .

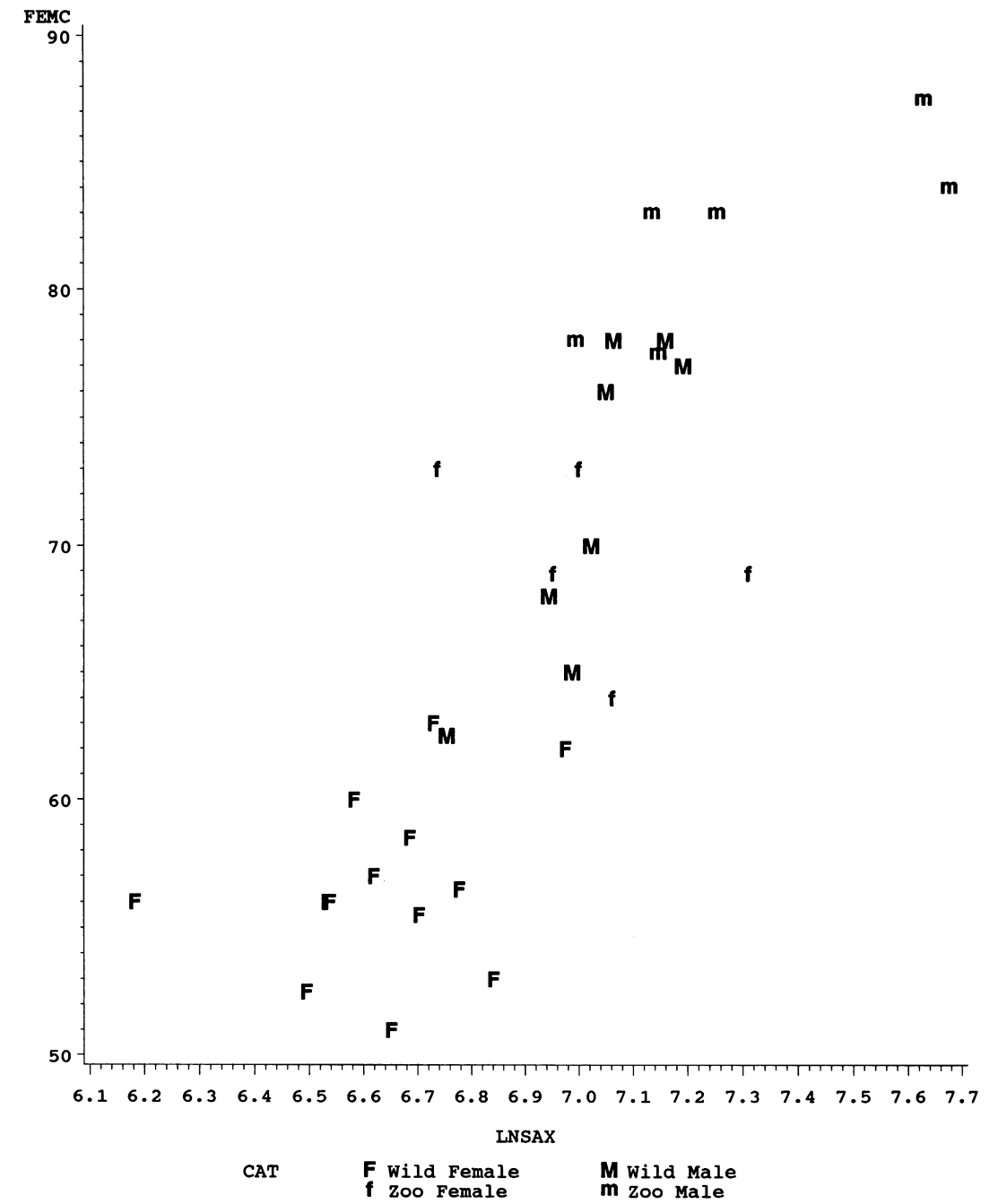


Fig. 3. The natural log of the x-sectional area of the superior articular surface of the body of the 1st sacral vertebra vs. the midshaft circumference of the femur in free-ranging and captive born and raised orang-utans (see fig. 2 caption). Free-ranging orang-utans (Wild male and Wild female), slope = 27.9,  $y = -127$ ,  $r^2 = 0.632$ ; captive orang-utans (Zoo male and Zoo female), slope = 16.14,  $y = -39.3$ ,  $r^2 = 0.303$ .

pitheciine would have preferred quadrupedalism. The Laetoli footprints provide evidence that a hominoid nearly contemporaneous with Hadar (Drake et al., 1987) engaged in bipedal behaviors with a peculiar orientation of the foot axis, and different kinematics than are seen in modern humans (Tuttle, 1987; Tuttle et al., 1990, 1991).

Dentally, the Hadar australopithecines show the large molars (Allen et al., 1982) expected in a wide-ranging, generalized ape, which consumed in bulk a varied diet of low quality relative to its energetic needs. As in baboons, a large molar surface area increased the amount of food that these australopithecines could crush per mandibular stroke, reflecting a lack of commitment to the specific physical attributes of any one food type. The relatively large anterior dentition and the anteroposteriorly broad but shallow glenoid joint indicate that the incisors had a varied role in food processing (i.e., peeling, stripping, nibbling, and tearing; Jolly, 1970; Sarmiento, in prep. b; Smith et al., 1983).

Cranially, the relatively narrow interorbital breadth of Hadar reflects a prognathic face and incisors, and more inferiorly and anteriorly disposed nasal cavity and paranasal sinuses. The supero-inferiorly broad zygomatic arch and large zygoma are correlates of large masticatory muscles necessary for crushing a large volume of food. The inferior orientation of the foramen magnum, the large and inferiorly disposed nuchal crest, and the anteroposteriorly short and inferiorly oriented suboccipital area all point to (1) relatively short, horizontally (transversely) disposed spinous processes of the upper cervical vertebrae, and (2) some degree of cervical lordosis. As noted, these characters emphasize neck mobility, enabling face-forward head postures with both horizontal and erect trunk postures.

All the AL 288-1 characters are consistent with a hominid that has reached the first adaptive stage of hominid divergence as described in this study. Lacking the suite of characters associated with a marked commitment to open habitats, this taxon could be best described as a generalized, quadrupedal savanna ape with a varied diet. The alleged presence of the same species (Boaz, 1983, 1988; Tobias, 1980, 1988; Azzarolli personal

commun.) or genus (Brunet et al., 1996) at various other localities, representing a wide range of habitats (Brunet et al., 1997; Rayner et al., 1993, 1996; White et al., 1993) and a distribution rivaling that of baboons and vervets, provides circumstantial evidence of its generalized behaviors and habits. Unless it represents more than one species (Senut and Tardieu, 1985), body size differences among locality 333/333w fossil hominids concur with a polygynous mating system as predicted by the model (Lockwood et al., 1996; McHenry, 1991; Richmond and Jungers, 1995; Sigmon, 1991).

#### STERKFONTAIN

Evidence as to the locomotor behavior of Sterkfontein australopithecines is not as abundant. Swayed by an *os coxa* with a broad and seemingly short ilia (Sts 14), a wide sacrum (Sts 14), and a large femoral bicondylar angle (Sts 34, TM 1513), researchers arrived at a general consensus that the Sterkfontein australopithecines were bipeds (Le Gros Clark, 1947, 1955a,b; Leutenegger, 1977; Lovejoy, 1978; Lovejoy et al., 1973; McHenry, 1975; Robinson, 1972; Zihlman, 1969, 1978). The alleged presence in Sts 14 of a humanlike lumbar lordosis (Robinson, 1972) is muted by a last lumbar vertebral body composed largely of plaster, a large sacral promontory angle, and a shallow sacral curvature (fig. 9; Sarmiento, 1996).

Recent discovery of the left talus, navicular, mesocuneiform, and 1st metatarsal from the same individual conclusively shows that these australopithecines lacked a fixed medial longitudinal arch and had some ability for hallucial abduction (Clarke and Tobias, 1995). Clarke and Tobias (1995) have taken this discovery as indicative of arboreal behaviors. A slightly closer approximation to humans than shown by the foot bones of Hadar australopithecines, and the overall similarities to gorillas, when interpreted together with the short and robust metacarpals and manual phalanges (Ricklan, 1987, 1988, 1990), suggest that this foot can be best associated to terrestrial quadrupedality. A distal femur (Sts 34) with a pronounced lateral lip and a relatively large medial condyle, which finds similarities with those of cercopithecoids (Kern and Straus, 1949) also indicates

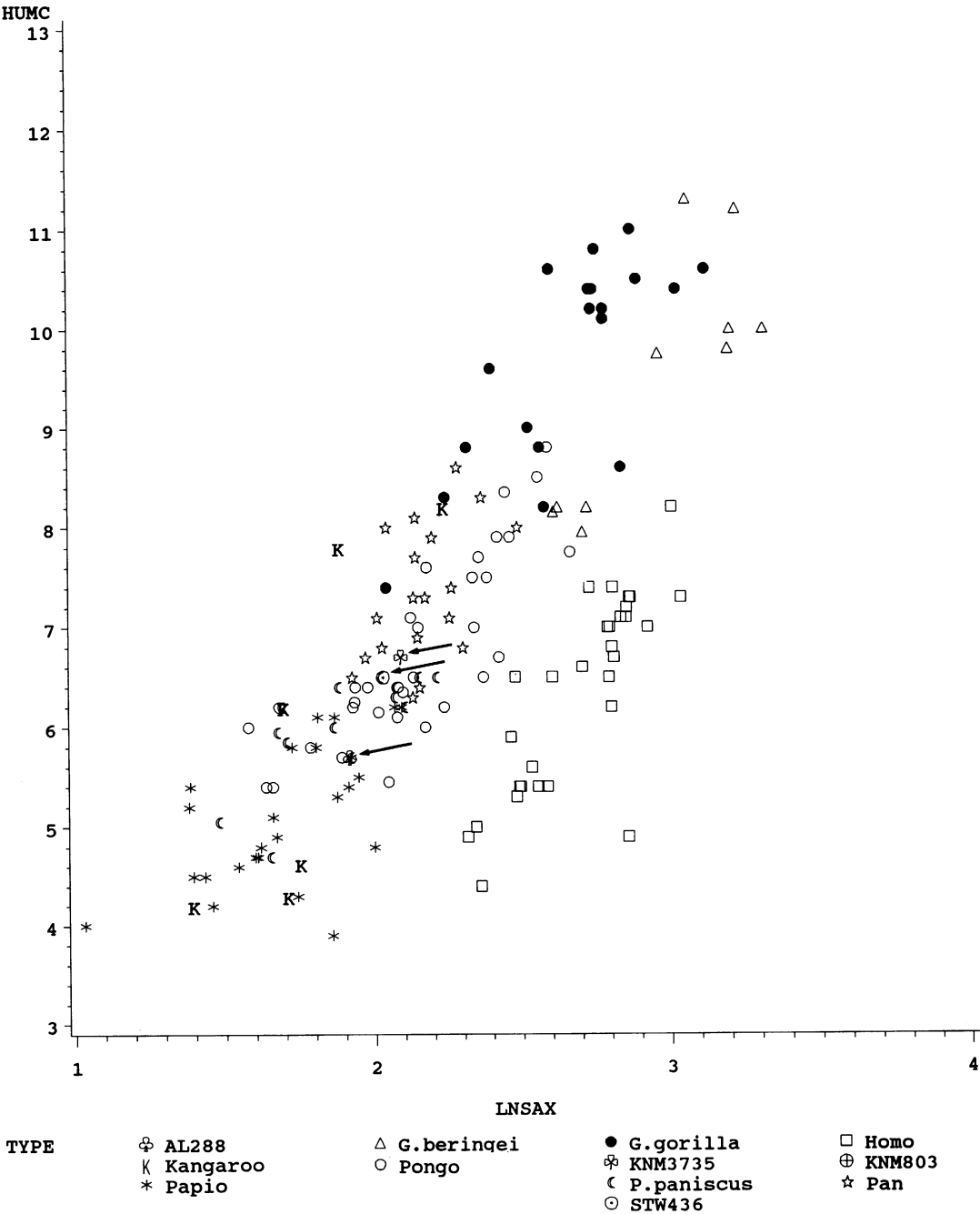


Fig. 4. The natural log of the x-sectional area of the superior articular surface of the body of the 1st sacral vertebra vs. the midshaft circumference of the humerus in hominoids, baboons, and some Plio-pleistocene "hominid" fossils (see fig. 2 caption). Humans, slope = 3.75,  $y = -3.84$ ,  $r^2 = 0.590$ ; Virunga gorillas, slope = 3.69,  $y = -1.413$ ,  $r^2 = 0.527$  gorillas, slope = 2.96,  $y = 1.80$ ,  $r^2 = 0.548$  pygmy chimpanzees, slope= 2.082,  $y = 2.071$ ,  $r^2 = 0.578$ ; chimpanzees, slope= 1.8619,  $y = 3.374$ ,  $r^2 = 0.0853$ ; orang-utans, slope= 2.74,  $y = 0.899$ ,  $r^2 = 0.691$ ; baboons, slope= 1.65,  $y = 2.32$ ,  $r^2 = 0.333$ .



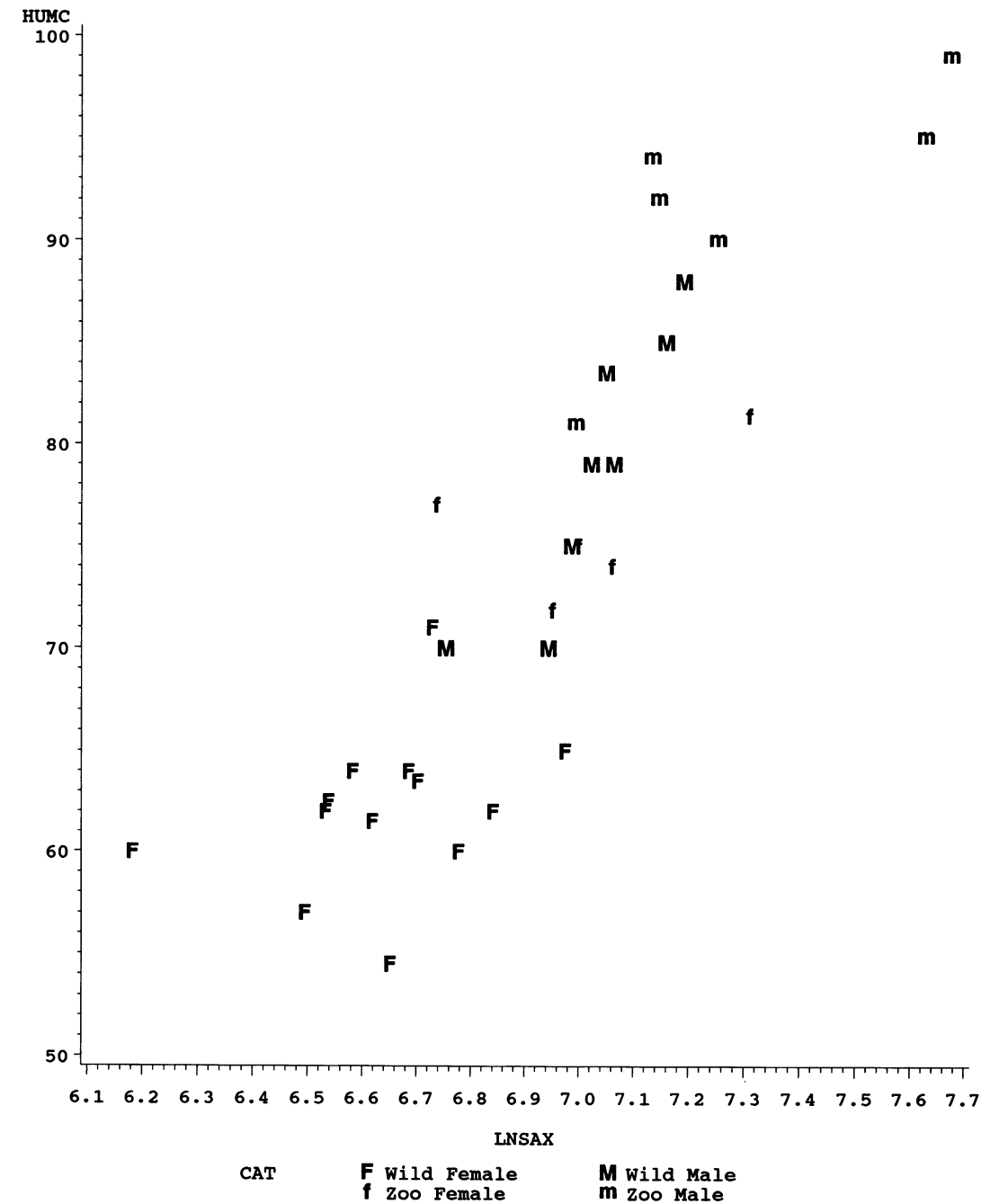


Fig. 5. The natural log of the x-sectional area of the superior articular surface of the body of the 1st sacral vertebra vs. the midshaft circumference of the humerus in free-ranging and captive born and raised orang-utans (see fig. 2 and fig. 3 caption). Free-ranging orang-utans, slope = 31.12,  $y = -142$ , Adj.  $r^2 = 0.653$ ; Captive orang-utans, slope = 25.25,  $y = -104$ ,  $r^2 = 0.546$ .

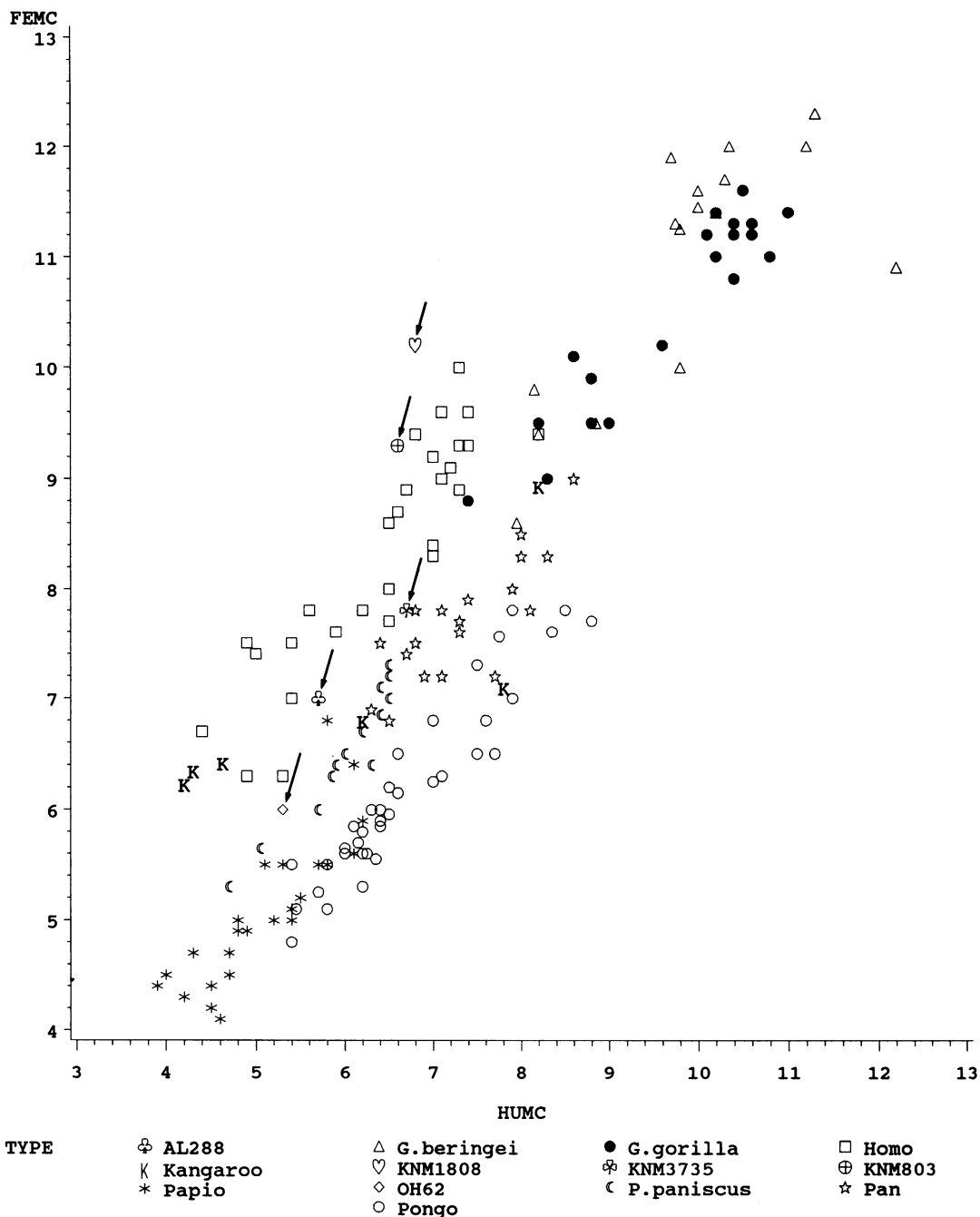


Fig. 6. Humeral vs. femoral midshaft circumference in hominoids, baboons, and some Plio-pleistocene "hominid" fossils (human and great ape regressions were used to calculate the humeral circumference of KNM-ER 803 from the sum of its radial and ulnar circumference values, KNM803 = KNM-ER 803, KNM1808 = KNM-ER 1808, see fig. 2 caption). Humans, slope = 0.921,  $y = -2.43$ ,  $r^2 = 0.7942$ ; Virunga gorillas, slope = 1.023,  $y = 0.827$ ,  $r^2 = 0.843$ ; gorillas, slope = 2.67,  $y = 0.811$ ,  $r^2 = .881$ ; pygmy chimpanzees, slope = 1.01,  $y$  intcpt. = 0.469, Adj.  $r^2 = 0.9012$ ; chimpanzees, slope = 1.089,  $y = -0.124$ ,  $r^2 = 0.379$ ; orang-utans, slope = 0.857,  $y = 0.397$ ,  $r^2 = 0.899$ ; baboons slope = 0.840,  $y = 0.808$ ,  $r^2 = 0.720$ .

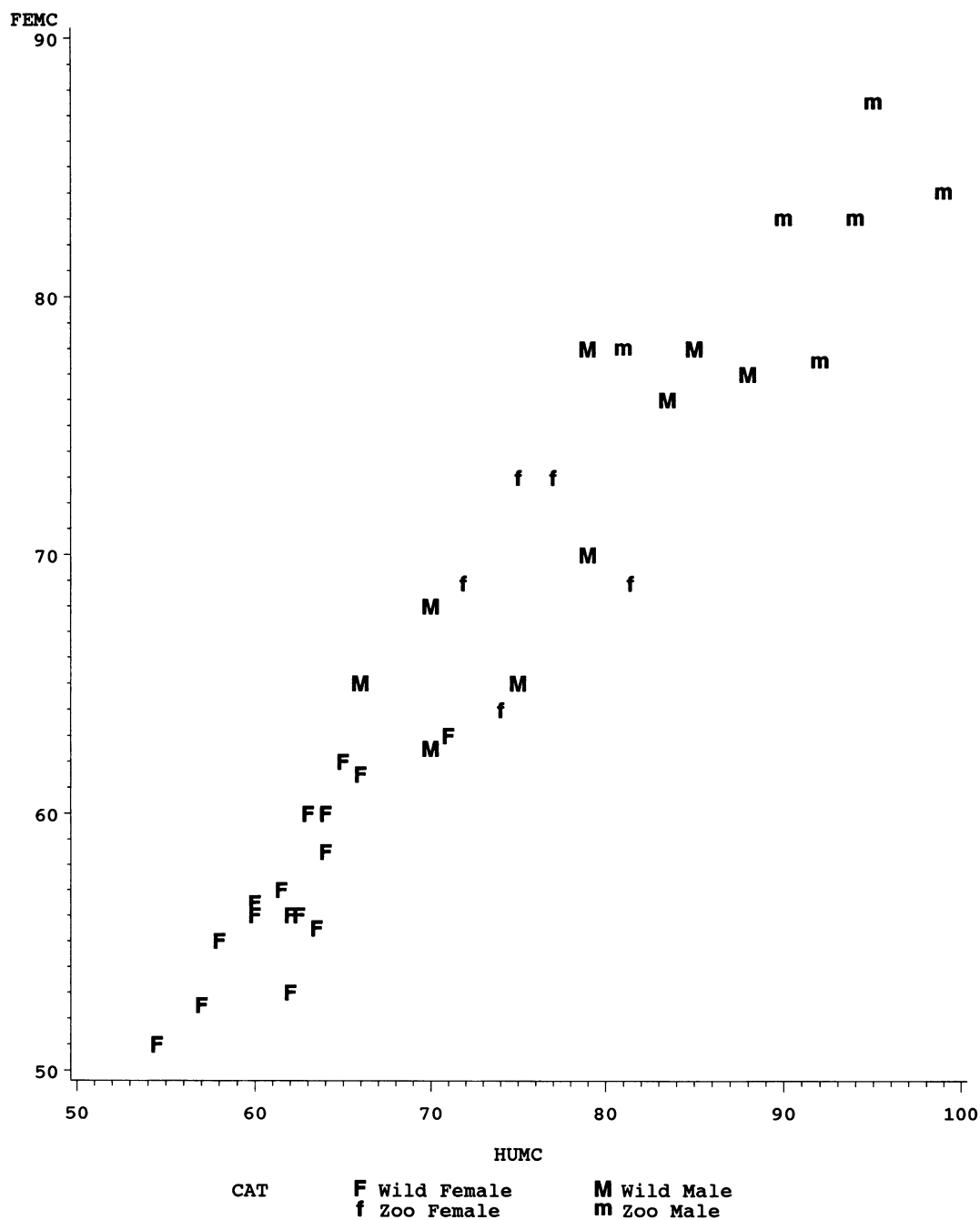
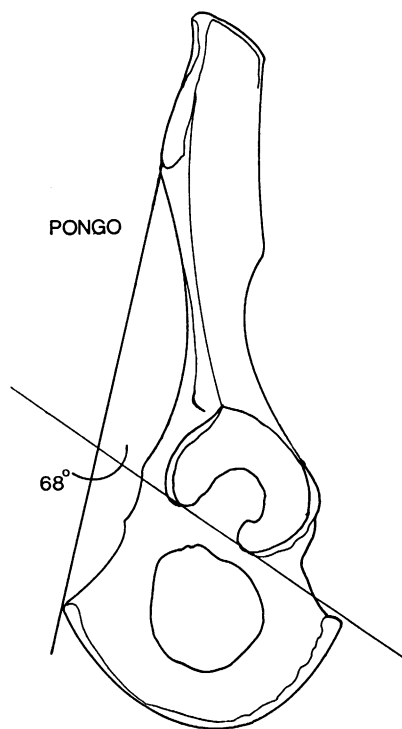
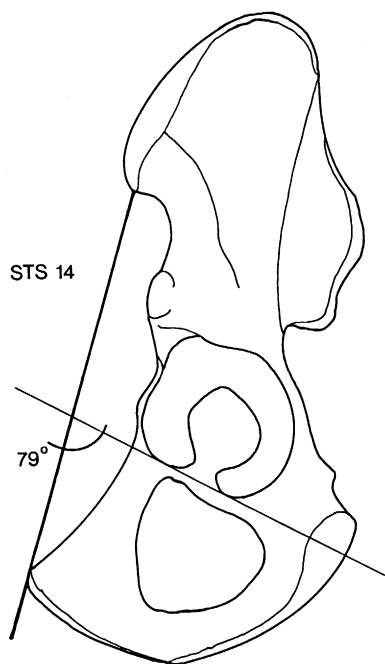
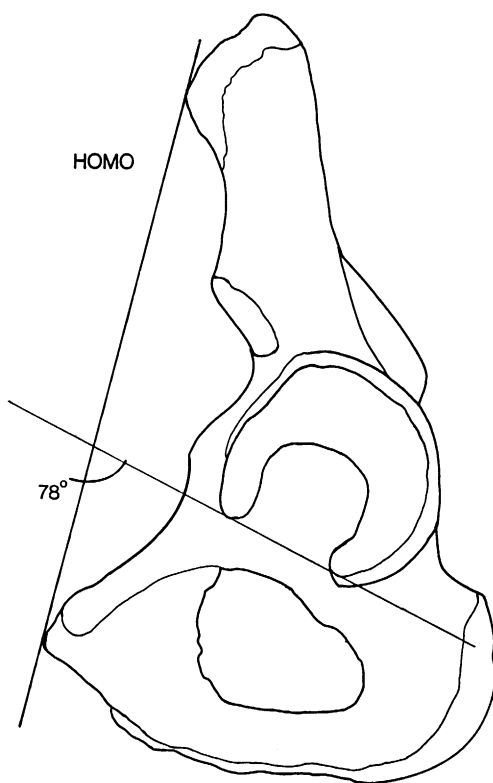
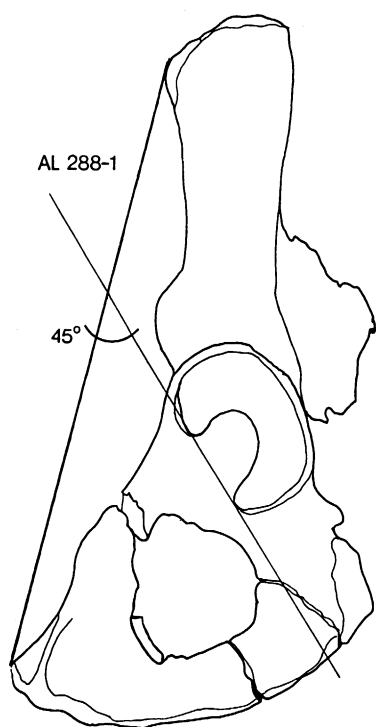


Fig. 7. Humeral vs. femoral midshaft circumference in free-ranging and captive born and raised orang-utans (see fig. 2 and fig. 3 caption). Free-ranging orang-utans, slope = 0.855,  $y = 4.40$ , Adj.  $r^2 = 0.911$ ; captive orang-utans, slope = 0.678,  $y = 19.1$ , Adj.  $r^2 = 0.741$ .



terrestrial quadrupedality, but not exclusive of bipedality.

Similar to that of AL 288-1, the x-sectional area of the superior surface of the 1st sacral body of Sts 14 relative to its femoral circumference also indicates quadrupedality (fig. 2). In support of this interpretation, the posteriorly facing iliac blades indicate the absence of a humanlike lateral-stabilizing mechanism at the hip joint. However, a much more expansive lunate articular area than seen in AL 288-1, with an orientation approximating that of humans, indicates a degree of thigh extension in Sts 14 not present in AL 288-1. The anteroposteriorly broad sacroiliac joint with its long axis perpendicular to the ilia further points to more humanlike sacroiliac loading and postures, which are not evident in AL 288-1. Both of these latter characters and the progressive caudal increase in the interfacet diameter of the lower lumbar vertebrae are correlates of bipedal postures and/or locomotion. Developed to some degree in cursorial cercopithecoids, these characters are not exclusively bipedal and can also be associated to quadrupedality.

Larger than the pelvis of Sts 14, the pelvis from Stw 430-463 approximates the human condition more closely. The x-sectional area of the superior surface of its 1st sacral body relative to humeral circumference, however, exhibits values similar to AL 288-1, also indicating quadrupedality (fig. 4). Notably, Sts 14 and Stw 430-463 have 5.5 and 6 lumbar vertebrae, respectively (author's notes), numbers that are higher than those usually found in humans. Unfortunately, most other postcrania at Sterkfontein are not associated, and there seems to be more than one morphotype represented by the postcranial remains. The strong probability that at least four species and three genera are known cranially (Clarke, 1988, 1990, 1996; Hughes and To-

bias, 1977; Kuman, 1994; Sarmiento, in prep. b), and the clear presence of more than one morphotype at the type site (Kimbel and Rak, 1993; Sarmiento, 1992; Sarmiento in prep. b), seriously confounds more detailed interpretations of their behaviors.

Both cranial and postcranial remains exhibit a mosaic of characters, reflecting a mixture of stage I and stage II hominids. More advanced toward the human direction than Hadar, some craniodental remains (e.g., Sts 19 and Sts 53) are surprisingly *Homo*-like (Kimbel and Rak, 1993; Sarmiento, in prep. b) whereas others (e.g., Stw 252) are more pongidlike (Clarke, 1988), representing stage II and stage I hominids, respectively. A diet of leaves as indicated by microwear analysis (Grine, 1981, 1987) is consistent with a stage I designation. In the more recent member 5 deposits, the presence of tools (Kuman, 1994, 1996; Robinson, 1961) and the remains of early *Homo* (Hughes and Tobias, 1977) suggest a stage II designation. An ape-like maturation length, as exhibited in the dentition (Benyon and Dean, 1988; Bromage, 1987; Bromage and Dean 1985) is in agreement with both stage I and II hominids that have not yet elaborated material culture. On the whole, Sterkfontein is best interpreted as a hominid lineage increasingly committed to open habitats with some individuals at or near the threshold of material culture.

#### SWARTKRANS

Relative to Sterkfontein or Hadar, the Swartkrans os coxae are much more humanlike, especially Sk 3155 (Brain et al., 1974; McHenry, 1975; McLatchy, 1996). Despite a damaged anterior ilia in Sk 3155, the approximation of the missing anterior superior iliac spine to the anterior inferior iliac spine is suggested by the contours of the iliac crest and anterior border of the ilia. The closed

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Fig. 8. Angle values for the relative orientation of the lunate articulation in A.L. 288-1, Sts 14, a female orang-utan (*Pongo*), and a human (*Homo*). The angle is defined by the intersection of the line passing through the anterior superior iliac spine and the most superior point of the pubic symphysis, with the line tangential to the most inferior points on the anterior and posterior horns of the lunate articular surface. Values for comparative sample: *Pongo*,  $N = 30$ ,  $X = 68^\circ$ , range =  $58^\circ$ – $88^\circ$ ,  $SD = 8.6$ ; *Pan*,  $N = 35$ ,  $X = 63^\circ$ , range =  $41^\circ$ – $83^\circ$ ,  $SD = 11.5$ ; *Gorilla*,  $N = 25$ ,  $X = 61^\circ$ , range =  $46^\circ$ – $75^\circ$ ,  $SD = 8.2$ ; *Homo*,  $N = 30$ ,  $X = 78^\circ$ , range  $65^\circ$ – $89^\circ$ ,  $SD = 6.3$ .

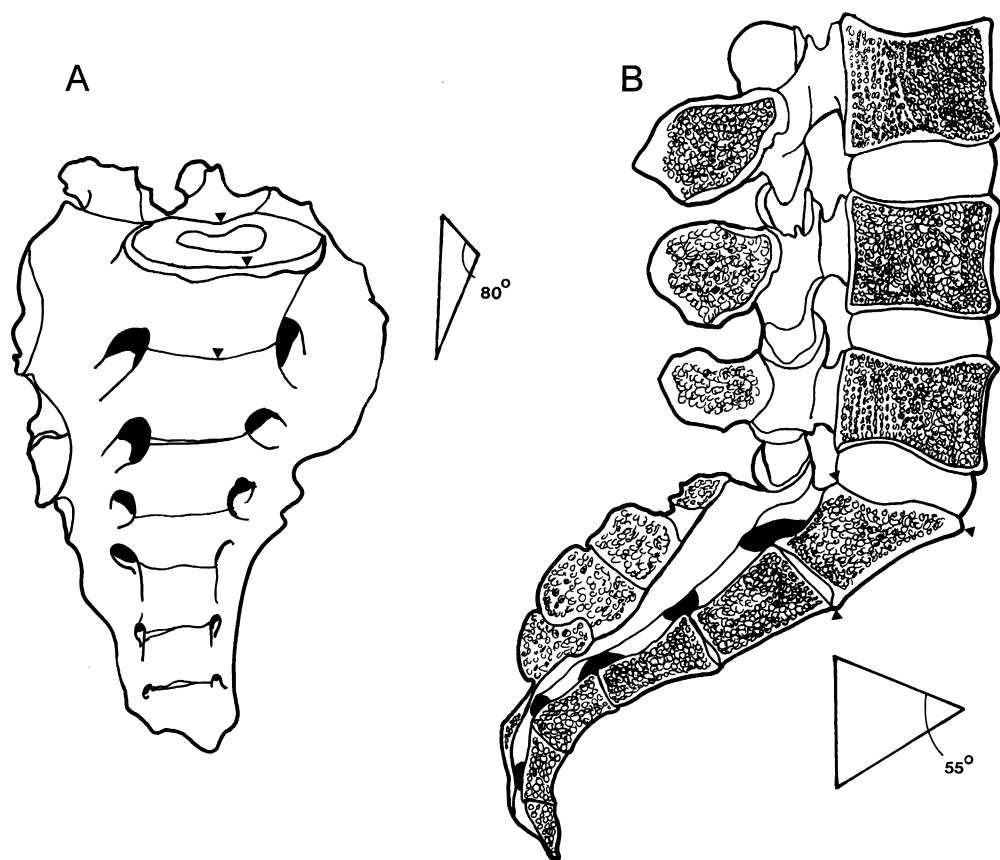


Fig. 9. The three points (marked by arrows) and corresponding lengths of the three sides of the triangle used to calculate the sacral promontory angle as illustrated on a gorilla sacrum (A) and a hemisected human sacrolumbar column (B). The acute sacral promontory angle in humans makes the transition from a lumbar lordosis to a sacral kyphosis. Fossil values: Sts 14 =  $84^\circ$ , Stw 439 =  $76^\circ$ , AL 288-1 =  $85^\circ$ , KNM-ER 3735 =  $84^\circ$  (damaged). Values for comparative sample: *Pongo*,  $N = 25$ ,  $X = 72^\circ$ , range =  $67^\circ$ – $81^\circ$ , SD = 4.8; *Pan*,  $N = 35$ ,  $X = 80.3^\circ$ , range =  $73^\circ$ – $94^\circ$ , SD = 5.8; *Gorilla*,  $N = 25$ ,  $X = 79^\circ$ , range =  $74^\circ$ – $85^\circ$ , SD = 2.7; *Homo*,  $N = 36$ ,  $X = 66.6^\circ$ , range =  $53^\circ$ – $79^\circ$ , SD = 7.6.

and deeply angulated sciatic notch, the orientation and contours of the auricular area, the greatly expanded postauricular area, and the development of the anterior inferior spine all approximate the human condition. The postauricular and auricular areas, and the sciatic notch, further suggest a shortened ilia, which relative to the orientation of the acetabulum is more laterally facing than those from Sterkfontein (author's notes). As noted by Susman (1988, 1989, 1994), the metacarpals, metatarsals, and pedal and manual phalanges closely approximate those of humans in length, robusticity, and curvatures. In contrast to stage I hominids, the distal pollical

phalanx is humanlike in its dimensions (Ricklan, 1990; Susman, 1989). The proximal articulation of the hallucial metatarsal (SKX 45690) suggests an adducted hallux. Additionally, the 5th metatarsal (SKX 33380) shows a roughened surface, presumably for attachment of the peroneus tertius m. (Susman and Stern, 1991). Although Susman (1994) and Susman and Stern (1991) have interpreted these pedal and manual characters as indicative of bipedality and tool making, they can also be associated with terrestrial quadrupedality (Sarmiento, 1994; this study).

The cranial and gnathic characters—(i.e.,

reduction of the anterior dentition, parabolic dental arcade, flat molar wear, a deep and anteroposteriorly narrow glenoid with an articular eminence, a markedly shortened basisphenoccipital, a tympanic plate acting as the posterior buttress for the jaw joint, a tympanic crest and vagina suggesting a robust and elongated styloid process, a variably notched, laterally placed and inferiorly projected mastoid, a strongly developed jugular process, and a mandible with a vertically set ascending ramus; Hylander, 1988; Kimbell, et al., 1988; Sarmiento, in prep. b)—confirm the postcranial characters in assigning Swartkrans to a second stage of hominid divergence. A brain that is larger relative to body size than those of Sterkfontein or Hadar australopithecines (McHenry, 1992) along with evidence of tool and fire use (Brain and Shipman 1993; Brain and Sillen, 1988), indicate that these hominids were on the threshold of developing a complex culture. Nevertheless, the presence of at least two genera at Swartkrans (Robinson, 1953; Clarke et al., 1970), the absence of associated postcranial remains, and marked differences in the size of some skeletal remains (cf SKX 5020 and Sk 84) create some uncertainty as to which genera the cultural remains and postcrania belong to, as well as to the relative brain size of these taxa. With fossil frequencies as high or higher than baboons and/or geladas (*Simnopithecus*) (Brain and Watson, 1992; Watson, 1993), the robust australopithecines must have existed at relatively high densities in proximity to the site of deposition, providing further evidence of stage II adaptations.

#### MAKAPANGSAT

Some dental and cranial remains from Makapansgat are similar to those from Sterkfontein (MLD 37/38), representing a similar stage in hominid evolution. Other remains are more similar to those from West Turkana and Hadar (i.e., MLD 2; but see Aguirre, 1970). The known postcrania are too fragmentary to resolve the overall locomotor behaviors of these fossils. A uncataloged proximal manual phalanx is similar in dimensions to those from Sterkfontein (author's notes). Seemingly humanlike, the infant hip bones (MLD 7 and MLD 25) come from a different

section of the cave at much higher levels than those that yielded the australopithecine remains (Hughes and Kitching, personal commun.). As such, there is no basis for assigning these pelvises to *Australopithecus*. Paleoecology of the deposits suggests closed woodland to riverine forest environments (Rayner et al., 1993, 1996). The cave is large and has a complicated depositional history with both wet and dry phases (Brain, 1981; Vrba, 1979), and an unknown temporal span unlikely to reflect a single environment or depositional event (Rayner et al., 1993). Considering morphological similarities to Sterkfontein member 4 and East African Pliocene fossils, the Makapansgat australopithecines represent both a hominid on the threshold of stage II and a stage I hominid, respectively. The infant hip bones underscore the cave's long depositional history and are best referred to *Homo*.

#### KROMDRAAI

The partial crania of the type specimen of *Paranthropus robustus* TM 1517 found at Kromdraai probably indicates a stage II hominid. The associated postcranial remains are too fragmentary to reveal behaviors. A fragmentary ilia and the original humeral, ulnar, and talar fragments found by Broom (Broom and Scheppers, 1946; Straus, 1948) are similar in size to those of the smaller of the two taxa from Swartkrans. Recently recovered tools from the hominid bearing Kb member further emphasize the similarities to Olduvai and Swartkrans (Young et al., 1997).

#### OLDUVAI

Closely approximating the human condition, the os coxa (OH28) shows all the characters which distinguish Swartkrans from Hadar and Sterkfontein australopithecines. Compared to Hadar or Sterkfontein, the Olduvai foot bones (OH 8), also show marked progress toward the human condition (i.e., a talus with a large and distinct articular area for the spring ligament set at discrete angles to the navicular and sustentacular surfaces, elongation of the cuboid and cuneiforms, a more humanlike navicular with a shallow talar surface set nearly parallel to the entocuneiform articular plane, a straight medial subcutaneous surface of the entocuneiform, a

nearly planar first tarso-metatarsal joint, and the dimensions of the distal hallucial phalanx [OH 10]; Day and Napier, 1964; Sarmiento, 1991; author's notes).

The hand bones also approximate those of humans more closely than those of Hadar. As in humans, the hamate's (OH7) 4th and 5th metacarpal facets are poorly divided and do not extend onto the hamulus. The first carpometacarpal articulation is broad, but with an even milder curvature than seen in humans (Trinkaus, 1989). The length, robusticity, and general dimensions of the manual phalanges correspond with those from Swartkrans, especially the distal pollical phalanx (Sarmiento, in prep. a; Sussman, 1994).

Cranially and dentally, some Olduvai remains have similarities to the progressive forms at Sterkfontein (Sts 19, Stw 53, Sts 53; Robinson, 1965; Sarmiento, 1993, in prep. b; Tobias, 1988, 1991a) and others to the robust Swartkrans hominids (Tobias, 1967). As for Swartkrans, both the cranial and postcranial remains of the two taxa and the presence of tools (Leakey, 1971) point to a second stage of hominid adaptation. As predicted by the model, tooth root development of OH 16 indicates that the most progressive form (i.e., *Homo habilis*) lacked the prolonged maturation period characteristic of humans (Dean 1995). The paleoecology of Olduvai confirms open-habitat conditions (Peters and Blumenschine 1996).

#### OMO

Hominid remains from the Omo river valley are relatively few, nonassociated, and fragmentary (Feibel et al., 1989; Howell et al., 1987). Although not closely similar in anatomical detail to those of Sterkfontein or Swartkrans, most postcranial remains suggest a commitment to terrestriality near or at the second adaptive stage of hominid divergence. A proximal pedal phalanx (28-1973-4570) is the exception, showing the more generalized proportions of a stage I hominid (author's notes). Clearly belonging to a stage II hominid, a first metacarpal (323-1976-897) approximates in dimension SKX 5020 (author's notes), the largest of the two first metacarpals from Swartkrans. As in Olduvai and Swartkrans, both a robust (75-1969-14a, 323-1976-896) and gracile hominid (L.894-

1) can be recognized (Boaz, 1988; Deloison, 1986; Howell et al., 1987).

#### LAKE TURKANA AND KANAPOI (EASTERN RIFT VALLEY KENYA)

Representing a wide range of ages and also habitats (Coffing et al., 1994; Feibel et al., 1989; Leakey et al., 1995), the few associated skeletal remains known from Lake Turkana are badly fragmented (Grausz et al. 1988; Walker et al., 1982). Considering the variety of taxa represented by the cranial and gnathic remains (Wood, 1991) and the limited association of postcrania, reconstructing behaviors is tenuous at best. With some exceptions, all East Turkana cranial remains seem to indicate at least a second stage of hominid divergence, which is confirmed by the humanlike postcrania (e.g., KNM-ER 1481, a complete femur; KNM-ER 3228, an os coxa; KNM-ER 803, an associated skeleton). Above 2.4 Ma (Feibel et al., 1989), the skull from West Turkana (KNM-WT 17000; Leakey and Walker, 1988; Walker and Leakey, 1988), exhibits a generalized condition diagnostic of the first stage of hominid divergence.

Based mainly on their resemblance to KNM-WT 17000, Hadar, Makapansgat, and/or Kanapoi hominids, a first stage probably also applies to the older gnathic remains from both west (KNM-WT 8556, 16006, 16005) and east Lake Turkana (KNM-ER 2602-2606; KNM-ER 20419-20432, 30200) (Coffing et al., 1994; Leakey et al., 1995; Walker and Leakey, 1988).

A small diameter of the external acoustic meatus, a planar glenoid joint, a horizontally disposed tympanic plate, and relatively large incisors (Leakey et al., 1995) confirm a first hominid stage for the Kanapoi craniodental remains. Unfortunately, the postcrania of these earlier forms are too few and fragmentary to corroborate the cranial characters or to diagnose any specific locomotor behaviors. The alleged bipedal characters in the Kanapoi tibia (Leakey et al., 1995) are also common to quadrupeds.

An undoubted representative of the genus *Homo* (Walker, 1993), the Nariokotome boy (KNM-WT 15000) exhibits a nearly modern postcrania (Walker and Leakey, 1993). The absence of hands and feet and unfused and



undeveloped epiphyses result in ambiguity when interpreting the detailed anatomy. Some peculiarities in the scapula (Walker and Leakey, 1993) and in the orientation and size of the spinous process of the lumbar and cervical vertebrae (Latimer and Ward, 1993) point to postural differences and may represent differences in the duration or developmental stages of bipedal behaviors relative to modern humans. Full development of the secondary sexual characteristics of the skull in adult males may have given this taxon a less progressive or humanlike appearance than exhibited in the immature KNM-WT 15000 individual.

#### FOSSIL PHYLOGENY

As presented, the fossil evidence closely fits the postulated two-stage model of hominid divergence. With decreasing age of deposits (i.e., Kanapoi, Alia bay [Leakey et al., 1995]; Hadar [Walter, 1994]; Sterkfontein, Makapansgat, and Kromdraai [McKee et al., 1995; Vrba, 1982; Kuman 1994, 1996; Young et al. 1997]; Omo [Feibel et al., 1989]; Olduvai [Hay, 1971]; Swartkrans and east Lake Turkana [Brain, 1981; Feibel et al., 1989]; and Nariokotome [Brown and McDougall, 1993]), hominid fossils become increasingly committed to open habitats, sacrificing a generalized structure. Because shifts to open habitats among hominoids may have occurred on more than one occasion, these adaptive stages need not reflect ancestor-descendant relationships. Both geladas and hamadryas baboons have arisen on separate occasions from a generalized baboon or baboon-like cercopithecine (Jolly, 1965, 1972), suggesting that multiple invasions of open habitats by generalized "hominids" may also have occurred—a suggestion that is supported by the sympatry of *Homo* and robust australopithecine at many Pleistocene hominid sites.

Seemingly, the fossils fail to provide evidence as to the human–African ape divergence. Considering that (1) many Western Rift primates are also found along the Eastern rift (Fleagle, 1988; Nowack, 1991), and (2) humans and two species of African apes coexist sympatrically along the Western Rift 600 km from the nearest australopithecines

sites, it is odd that the ancestors of the semi-terrestrial African apes have not been found in the wetter habitats of the East African Plio-pleistocene (Kimbel, 1995; Kimbel et al., 1996; White et al., 1993; WoldeGabriel et al., 1994; but see Edelstein, 1987, and Verhaegen, 1990, 1994, 1996). Because stage I hominids exhibit very few characters that are derived in the human direction, it may prove difficult based on fragmentary fossil remains to distinguish them from early African apes. When recognizing a relatively reduced anterior dentition and canine, a well-formed femoral bicondylar angle, an ischial spine, and a short ilia with five or more lumbar vertebrae as the primitive human–African ape condition (de Bonis et al., 1990; Sarmiento, 1985a, 1987a, 1995; this study), a hominid designation for all of the Hadar australopithecines is not so clear cut. The absence of a C7-1st rib articulation (Ohman, 1986), a more inferiorly disposed nuchal crest, a humanlike talar trochlea (Latimer et al., 1987), and short pedal and manual digits, argue for a hominid designation. A supraorbital foramen as opposed to a fissure (Rak et al., 1996), a conical thorax (Schmid, 1983), and gorillalike morphologies of the navicular, supraorbital bar, and zygomatic arch (author's notes) align it more closely to African apes. In either case, deriving humans or African apes from the Hadar australopithecines must invoke reversals.

Considering that two or more hominid taxa invaded open habitats and the associated parallelisms or reversions that would have developed, deciphering fossil relationships, especially when relying on nonassociated and fragmentary remains, is problematic. Principally, too much can be made of trends in quantitative characters in localized anatomy, without evidence as to the overall morphological or ecological trends shown by the organism, or even knowledge as to the morphology corresponding to species differences (Tobias, 1991a). For instance, the relegation of South African australopithecines to a side branch of hominid evolution (White et al., 1981), despite a complex of cranial and postcranial characters shared by Swartkrans robusts and modern humans exclusive of Hadar hominids (this study, Sarmiento, in prep. b; Skelton et al., 1984; Susman, 1989, 1994;

Susman and Stern, 1991; Tobias, 1988) is based largely on a reduced anterior dentition and an erroneous application of Dollo's principle of irreversibility. A reversal in the trend to reduce the anterior dentition in the transition from stage II hominids to *Homo* is actually expected with the postulated shift from a seed-eating to a meat-eating diet (Jolly, 1970). In this regard, the more conservative and generalized stage I hominids may appear dentally to be more similar to *Homo* and difficult to distinguish as separate (Robinson, 1965). The nondental characters that, along with anterior dental reduction, are used to place the robust grade on a side branch of hominid evolution (Robinson, 1967, 1972; White et al. 1981) are sexually dimorphic, size dependent, and/or notoriously variable in catarrhines (i.e., development of tori, and sagittal and nuchal crests, development of muscular attachment areas, and facial morphology; Schultz, 1963b) and likely to be paralleled without leaving evidence of it in the anatomy.

Regardless of whether a more generalized open-habitat taxon (Tobias, 1991b) or one of the known lineages of the more committed robust australopithecines is nearer to the ancestry of *Homo*, it is uncertain if the perceived morphological differences could have prevented gene flow between robusts and human ancestors. Returning to the cercopithecine analogy, it is significant that anubis baboons naturally interbreed with both geladas and hamadryas baboons. Although all three may be considered different species (Jolly, 1993), the hamadryas and anubis baboons share a similar morphology, exhibiting dental, cranial, and postcranial specializations contrastingly different to those of geladas (Jolly 1965, 1972). There is no known clue in the skeletal morphology of these three taxa, which show they can, or cannot, interbreed. Although it is unknown if the human ancestor arose from a robust grade, the strong likelihood of gene flow between this ancestor and some robust lineages would have produced hybrids that blur morphological distinctions and refute the evolutionary dead-end status of robusts. More accurate taxonomies and phylogenies will depend on associated and more complete fossils, a more continuous fossil record, and a clearer un-

derstanding of the variation and sexual dimorphism of the living great apes.

## CONCLUSIONS

The model presented is based on a systematic approach for understanding human evolution and the premise that closely related taxa with a largely common anatomy will encounter similar adaptive problems in similar environments and arrive at similar solutions. The model interprets interactions between each taxon's structure and the environment as a natural experiment that reveals the nature of selection pressure and adaptations. Whenever possible, a complex of characters associated with a specific function (or adaptation) was analyzed to separate shared-inherited structure from parallelisms. Without contrary evidence, the model postulates parsimonious evolutionary pathways with the minimum of reversals. In those cases where it argues for reversals or parallelisms without direct anatomical proof, it does so (1) to avert hypotheses of reversals or parallelisms in characters that are too complex not to leave anatomical proof, and (2) on the premise that the characters are quantitative in nature and labile at the taxonomic or phylogenetic level concerned. The model accounts for distinguishing external, sexual, craniofacial, dental, locomotor, visceral, developmental, and behavioral characters of humans. It reconciles most of the evidence from anatomy, behavior, ecology, molecular biology, and the fossil record, presenting a novel synthesis to test against new data.

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