E.E. Sarmiento

Department of General Anatomy
University of the Witwatersrand
1 Jam Smuts Ave.
Johannesburg, South Africa
PO Wits 2050
and
Research Associate
Department of Mammalogy
American Museum of Natural
History
Central Pk. W. at 79th St.
New York NY 10024 USA

Cautious climbing and folivory: a model of hominoid differentation

Despite the large and growing number of Miocene fossil catarrhine taxa, suitable common ancestors of great apes and humans have yet to be agreed upon. Considering a) the conservative and primitive nature of the hominoid molar cusp pattern, and b) the variability of secondary dental features, it is difficult to discern whether a hominoid dentition is primitive, secondarily simplified to the primitive condition or too far derived to be ancestral to any of the living forms. Nonetheless, the inability to recognize a common ancestor is primarily due to the absence of a model of hominoid differentiation that provides a basis for its recognition. Vertical climbing as the limiting component of cautious climbing, explains all of the locomotor anatomy shared by living hominoids. Comparison of the shared derived characters of hominoids to those of forms which have converged on hominoids *i.e* colobines, atelines, lorisines, paleopropithecines and sloths suggest that early hominoids were probably folivores. In arboreal forms there is a strong link between a large body size, folivory and cautious climbing. Comparison of craniodental characters of committed folivores to committed frugivores from among each of the compared groups with the exception of lorisines, indicates that many of the distinguishing craniodental characters of humans and great apes are adaptations to folivory. Many of these characters, however, are also present in Jolly's seed eating complex. As such folivory may be the heritage factor which Jolly hypothesized to account for differential reduction of canines in fossil *Theropithecus* and hominids.

Key words: atelines, lorisines, sloths, colobines, diet, locomotion

Introduction

Present evidence, indicates that the hominoid divergence occurred some time in the Miocene (Hasewaga *et al.* 1984, 1985; Holme *et al.* 1989; Martin, 1990; Sarich and Wilson, 1967; Szalay and Delson 1979). Despite the large and growing number of Miocene catarrhine taxa, suitable ancestors of living hominoids have yet to be agreed upon. Although most of these fossil taxa possess the dentition parsimonious derivations predict for such ancestors, when more of their remains are uncovered, they fail to exhibit the shared cranial and postcranial hominoid morphology (Sarmiento, 1987). One possible reason for this phenomenon, lies in the conservative nature of the hominoid molar cusp pattern. The 4 cusp upper and 5 cusp lower molars of living hominoids dates back in time to the Oligocene (Gregory, 1922: Simons 1972). Although cranially and postcranially these Oligocene forms are barely catarrhines (Kay et al 1981), their molar cusp patterns are shared with modern hominoids. The hominoid cranial and postcranial morphology or incipient ones showing a trend in the hominoid direction do not appear in the fossil record until mid Miocene times (Sarmiento, 1987, 1988). Because it is conservative in nature, and shared by the ancestral catarrhines, the hominoid molar cusp pattern is not a good taxonomic indicator for distinguishing hominoids from each other or from their catarrhine ancestors. Alternately, secondary features of the molars i.e. development of cingula, cusp height, crown height, enamel thickness, enamel

wrinkling, cuspules and crests show too much variation within each of the genera of living hominoids to be diagnostic at higher taxonomic levels (Sarmiento, 1987). Although they are often the only alternative, use of such features is especially problematic when arguing ancestor descendant relationships of two forms over gaps of millions of years.

A nearly continuous fossil record which extends the hominid lineage back to the early Plio-pleistocene, provides a partial solution to this problem. The low cusps, and thick and wrinkled enamel of australopithecines (Robinson, 1956), and of Sivapithecines the earliest recognizable hominoids from the late Miocene (Gregory 1922), all suggest that these features were also exhibited by the ancestors of hominids and pongids. Unfortunately, many of the supposed hominoid fossils from the late Miocene also exhibit these features (Andrews and Tekkaya, 1980; Debonis and Melentis 1980; Leakey and Walker 1985; von Koenigswald, 1952; Wu 1984) detracting from their usefulness in distinguishing such ancestors. Given the large number of Miocene catarrhines with an ape-like molar pattern, and as much as a 15 million year gap between them and australopithecines, independent development of these few features in various lineages is not unexpected.

The failure to recognize hominid-great ape or hylobatid ancestors, however, is also in part due to the absence of a working model for hominoid origins which associates the shared hominoid specializations within an adaptive complex. Parsimonious reconstructions of the ancestral hominoid condition may apply to the whole of the evolving organism or to an interrelated adaptive complex, but not necessarily to localized unrelated features of the anatomy. Although on the basis of only the dentition, 4 cusp upper and 5 cusp lower molars with thick and wrinkled enamel are what a parsimonious derivation may predict, not all of these features may be compatible with the entire adaptive complex shared by hominoids. It is the purpose of this essay, therefore, to critically examine some of the models of hominoid differentiation and suggest a new one based on analogies to mammals which have converged on the specializations shared by living hominoids. It is hoped that through such an analysis the ancestral adaptations and associated dental features of early hominoids can be established.

Past Models of Hominoid Differentiation

Most models of hominoid differentiation are based on the following two concepts that find their origin in Lamarck's (1809) work i.e. a) the hominid pongid ancestor was at least partially if not fully arboreal and b) African apes are man's closest relatives. On the basis of these concepts, brachiation, knucklewalking and vertical climbing have been proposed as plausible models for the origin of our shared specializations. Although other models have been proposed, they fail to account for the shared derived morphology of hominoids (Lovejoy, 1981; Morgan 1972; Wood Jones, 1929) or to give full account to past theoretical models and their factual foundations (Schwartz, 1984). Usually these studies have focused on 'reputedly unique' traits or a unique correspondence between anatomy and behavior in single or disparate taxa. When studied systematically, these 'reputedly unique' traits are usually present in other closely related taxa, showing them to be related to other behaviors than those originally invoked by their model.

Brachiation

As first proposed by Keith (1923, 1934) the brachiationist model hypothesized a two stage ancestral origin. The first stage accounted for those features shared by living hominoids, and the second stage for those features shared by African apes and humans. Impressed by the

orthograde postures of hylobatids, and their evolutionary grade —one which he believed intermediate between pongids and monkeys—,Keith envisioned a similar form as the ancestral hominoid. Keith (1903, 1912, 1923, 1934) narrowly defined brachiation as the forelimb suspensory underarm pendular swing which is practiced almost solely by hylobatids. He postulated that increases in body size forced the hominid African ape ancestor to descend to the ground. This subsequent or "troglodytian" stage was modeled on chimpanzee behavior (Keith, 1923). He did not clarify, however, as to whether the "troglodytian" stage was largely opportunistic or consisted of acquiring a complex of terrestrial quadrupedal adaptations, and whether the increase in body size preceded or accompanied terrestrial behaviors. More importantly he does not interrelate those factors that must have accompanied increased terrestriality failing to present tangible adaptive mechanisms.

Although Gregory (1934) supported Keith's two stage model, his exposure to the African apes in their free-ranging habitat (Gregory and Raven 1937; Raven 1931) led him to a less rigid definition of brachiation. To Gregory brachiation included all forelimb dominated suspensory behavior. Moreover, he recognized (Gregory 1922) that the erect trunk postures of African apes more closely approximated human behaviors. In accordance with Morton (Morton 1924; Morton and Fuller 1952) he realized the ancestral hominoid was not exactly like any of the living apes. Nevertheless, both Keith and Gregory's models as well as those of their contemporaries (Hooton, 1946; Morton 1924) were based mainly on direct analogies to the living hominoids. Hylobatids loosely served as the prototype of the early hominoid ancestors, and chimpanzees the prototype of the early ancestors of humans and African apes. In this regard, these early theorists erroneously propounded a Lamarckian concept of the scala naturae. Because none of the living hominoids evolved the behaviors they are trying to explain, it is illogical to use them as the ancestral models for the origin of these behaviors.

Currently, Tuttle (1974, 1975a,b, 1981) ascribes to a single stage brachiation or hylobatian model in which hominid bipedality was gained largely in an arboreal setting prior to any terrestrial adaptations. He avoids the need for a second stage, because he believes comparative anatomy supports a prepongid divergence of hominids from the ancestral hominoid stock (Tuttle 1975b). According to Tuttle (1969a, 1974), if preadaptation to bipedalism occurred after an arboreal stage when both the ancestors of humans and chimpanzees were semi-terrestrial, a problem arises explaining the marked differences in the pelvic morphology of chimpanzees and humans, and the human pelvic tilt mechanism. Tuttle fails to recognize the elongated chimpanzee pelvis and associated reduction of lumbar vertebrae as the derived condition for pongids and hominids (Schultz 1961; Sarmiento 1985, 1987). In this regard, Tuttle must address why the hominid-African ape ancestor could not have initiated terrestrial behaviors with a higher number of lumbar vertebrae and a relatively shorter human-like pelvis. Although Tuttle (1974, 1975b) recognizes that this ancestor was not exactly a hylobatid, he also fails to integrate any of the features of his purported ancestor with an adaptive complex. More importantly, his failure to recognize a unique relationship between African apes and humans, and the associated shared terrestrial adaptations is both at odds with evidence from comparative anatomy (Sarmiento 1985, 1988, 1994) and biochemistry (Holme et al 1989).

Notably, Tuttle's single stage model for brachiation garners support from paleoanthropologists interpreting australopithecine postcrania (Zihlman, 1969; Zihlman and Bunker, 1979; McHenry and Temerin, 1979; Lovejoy, 1981; Rodman and McHenry, 1980; Robinson, 1972). Many see the compromise morphology of australopithecines as one between terrestrial bipedalism and arboreal climbing (Stern and Susman, 1981; Susman et al. 1984). Unfortunately, the often fragmentary and unassociated remains of these fossil taxa do

not provide anything better than interpretations. According to the author's studies the large similarities in the postcrania of australopithecine and African apes, more correctly associates these fossil with terrestrial quadrupedalism (Sarmiento, 1985, 1986, 1991, 1994).

Knucklewalking

Impressed by the similarities in the behavior, postures and anatomy of African apes and humans, Washburn (1950b) first proposed a knucklewalking model for the hominid-African ape ancestor. In effect this model is not much removed from that of Keith and Gregory's "troglodytean" stage in which the common ancestor is portrayed as a chimpanzee-like form. Washburn (1963, 1967, 1968) incorrectly uses knucklewalking as a label to define the entire locomotor anatomy and behavior, failing to mechanically associate a set of traits to the behavior itself. Knucklewalking is no more than a description of the use and posture of African ape manual phalanges, the remaining musculoskeletal system and associated behaviors remains undefined. Other behaviors could maintain different phalangeal postures, yet employ the same joint postures and segment movements throughout the body requiring a similar anatomy. Orang-utan knucklewalking postures (Tuttle and Beck 1972) further questions the validity of associating the entire musculoskeletal structure with phalangeal postures, since they lack the African ape knucklewalking phalangeal specializations. As suggested by orang-utan behavior, the musculoskeletal system of great apes shows a predisposition to knucklewalking hand postures. This predisposition and its associated anatomy must have arose as a response to the shared and/or ancestral behaviors of great apes.

Washburn's model has also been supported by paleontologists who interpreted the incipient hominoid morphology in the wrist of *Proconsul* (Conroy and Fleagle 1972), and the African ape-like features in the Olduvai hand (Robinson, 1972) as knucklewalking adaptations. Without a mechanical association of the fossil's wrist joint anatomy to knucklewalking, these interpretations suffer from the erroneous associations propagated by Washburn's model. Other behaviors carried out by hominoids placing similar requisites on the wrist could just as likely have been carried out with the given anatomy (Sarmiento 1985, 1987). When dealing with fossils, however, it is unclear whether Washburn ascribes to his knucklewalking model. In a concluding speech to the Berkeley symposium (Washburn, 1983), he emphasized the fully bipedal, but partially arboreal behaviors of australopithecines. This statement is more in line with a brachiationist philosophy.

Vertical climbing

This model arose in a large part from the realization by Kortlandt (1968) that relatively long arms and short legs, features shared by all the nonhuman homimoids were advantageous to climbing vertical supports (also see Klatsch, 1913). It has gained wide support from theorists which want to explain the shared locomotor anatomy of humans and great apes, and of those forms which have converged on great apes (Prost 1980). Static analyses of primate climbing have validated this model (Cartmill 1974, 1979; Jungers, 1977, 1978; Sarmiento 1985) providing explanations for the high intermembral index, reduction in the number of lumbar vertebrae and their capture by the ilia into the sacral region, the hip and thigh musculature, anterior displacement of the vertebral column relative to the trunk, shoulder mobility and musculature, forearm rotation, wrist joint anatomy, the intrinsic pedal musculature, foot mobility, a short trunk, relatively wide biacetabular

and biglenoid widths, and the torsions of the long bones of the upper and lower limbs, all features shared by humans and great apes and paralleled to some degree or another in atelines and lorisines (Cartmill 1974, 1979; Cartmill and Milton 1977; Jungers, 1977, 1978; Sarmiento 1985). Electromyographical and behavioral studies also suggest vertical climbing is central to the adaptations of great apes and humans (Stern and Susman, 1981) and is a link between bipedalism and brachiation (Fleagle et al, 1981). The unique and revolutionary behavioral studies of Prost (1965; 1980) likewise emphasize and confirm the influence vertical climbing has had in great ape and human adaptations.

Indirectly vertical climbing also explains the following great ape features; retroduodenal fixture, sinistral deviation of the heart, reduction in the number of tracheal rings, a pericardiophrenic ligament, a central tendon and flat topped configuration of the diaphragm, the formation of a pelvic diaphragm and the related loss of the tail. Associated with upright trunk postures, some of the non-locomotor features of the anatomy originally found their explanation in the brachiationist model (Keith, 1923). Vertical climbing as the limiting component of cautious climbing behaviors, however, associates all of the shared hominoid anatomy into a locomotor complex (Stern 1971; Cartmill and Milton 1977; MacArdle, 1981; Sarmiento, 1985, 1987) that solves the problem of moving within three dimensional framework of non- continuous supports. Because a) vertical supports present the extreme condition in which the animal assumes a vertical posture and all its mass must be supported by the frictional force it can create, and b) a cautious climber depends on the use of discontinuous supports of varying orientation and diameter for continuous movement—as opposed to leaping—, selective pressure would work on those features enhancing vertical climbing ability (Sarmiento 1985).

Despite its ability to explain a large number of shared features, vertical and cautious climbing has not been related by theorists to diet, social structure, life history or habitat of the individual. Comparison of the shared features of hominoids to those of groups which have been claimed to parallel or converge on the unique hominoid locomotor anatomy, i.e colobines (Napier, 1963) atelines (Erickson 1963; Stern 1971; Sarmiento 1983; 1985; 1988),lorisines (Cartmill and Milton 1977; MacArdle 1981) paleopropithecines (Walker 1967, 1974; Simons et al, 1992) and bradypodids (Schultz 1961; Mendel 1981a,b,1985; Sarmiento 1985, 1988) should present a more complete model of hominoid origins.

Hominoid Convergence and Divergence

In this model only those features exhibited by all members of the group which distinguish it from its sister group are considered. When features not shared by the group are included, but the evidence overwhelmingly suggest it is a distinguishing shared feature or trend, they are preceded by explanations in the form of a note. In none of the cases is the ancestral condition assumed for any of the groups. Table I summarizes the characters shared by each group which distinguish it from its sister group. These are listed without regard to their interrelationship and functional significance.

Due to the wide range of dietary specializations among hominiods and a generalized cranial (Vogel 1962) and dental anatomy (Sarmiento, 1987) the ancestral condition is not readily apparent. To avoid tautological arguments or ones based on scanty evidence, cranial and dental traits were compared for individual genera comprising each of the studied primate groups with the exception of lorisines (Table II), and will be discussed separately.

Table 1 - Characters distingusihing hominoids as paralleled or converged upon by colobines, atelines, lorisines, paleopropithecines and sloths•

A=Shared characters distinguishing hominoids from cercopithecoids
B=Shared characters distinguishing colobines from cercopithecines
C=Shared characters distinguishing atelines from cebids
D=Shared characters distinguishing Lorisines from Galagines
E=Shared characters distinguishing Paleopropithecines from Indrids
F=Shared characters distinguishing Bradypodids from Myrmecophagids

X=presence of character
P=character is present, but does not distinguish between corresponding groups.
x=character may be indirectly inferred from fossil remains.
?= no information available as to it being a distinguishing character.

	A	B	C	D	E	F
LIFE HISTORY						
1) Long gestation period	X	X^a	X^b	X	?	X
2) Long infancy dependency	X	?	?	-	?	-
3) High interbirth interval	X	?	Xc	-	?	X
4) Long life	X	?	?	?	?	.?
5) Restricted to forests in tropical regions	X^d	X^e	P	P	P	P
6) Arboreal food sources wholely	f	X^g	P	P	?	X
BEHAVIOR						
7) Fully arboreal rarely descending to ground	h	X^i	P	X	?	X
8) Small daily range	j	-	X^k	X	?	X
9) Foraging in suspended postures below supports	X^l	X	X	X	x	X
10) Use of hand and/or foot in hook postures	X^m	X	X		x	X
11) Use of opposable pollical or hallucial grip in suspensory postures	-	-	-	X	-	-
12) Frequent use of vertical trunk postures	X	?	X	X		X
13) Enhanced adduction-abduction of upper and lower limbs	X	?	X	X	x	X
14) Enhanced adduction of wrist	X^n	X	X	X	x	X
15) Frequent bipedal behaviors when terrestrial	X		X		p	-
16) Forearm rotation marked	X		?		?	
17) Use of elbow and knee joint in extended postures	X		X	X	x	X
18) Slow deliberate movements	o		X^p	X	?	X
19) Cryptic habits				X		X
20) Leaps used to cross between supports	q	X	r			
21) Considerable mobility of foot including plantar flexion of midtarsal joint	X^s	?	X	X	x	X
LOCOMOTOR ANATOMY						
22) High percentage of slow twitch muscle fiber and associated vascular bundles.	?	?	?	X	?	X
23) Large body size	X		X		X	
24) High intermembral index	X^t		X	X	X	X
25) Relatively long hands, and feet consisting of elongated metatarsals metacarpals and phalanges	X^u	X	X	X	X	X

Table 1 (continued) - Characters distingusihing hominoids as paralleled or converged upon by colobines, atelines, lorisines, paleopropithecines and sloths

26) Pollex reduced or vestigial	X^v	X	X		?	X
27) Reduction of hallux	w	X			X	X
28) Reduction of index finger				X		
29) Loss or reduction of contrahentes in hands and feet	X	X	X		?	X
30) Loss or reduction of ulnocarpal articulation	X			X	?	Xx
31) Pisiform distally migrated	X		y	X	?	X
32) Tight mediolateral curvature of wrist joints	X^z	X	X	X	X	X
33) Ulnarly extended radial shelf omitting ulna from carpus	aa			X	?	
34) Wrist flexors large relative to extensors	X	?	X	?	X	X
35) Well developed shortheads of supinator and pronator	X					
36) Short olecranon process and deep olecranon fossa	X		X^{bb}	X	X	X
37) Medially projected medial epicondyle	X		X	P	X	X
38) High humeral torsion	X		X		X	X
39) Dorsal migration of scapula	X		X	X	?	X
40) Laterally directed glenoid of scapula	X		X	X	x	X
41) Long vertebral border	X	X	X	X	?	X
42) Long clavicle	X	X	X	X	?	
44) Variability in the # of cervical vertebrae	cc		dd	X	?	X
45) Relatively elongated dorsal spines on lower cervical upper thoracic vertebrae	X^{ee}	?	X	X	?	X
46) Anterior displacement of vertebral column relative to thorax	X	?	X	X	?	X
46a) Mediolaterally broad thorax	X	?	X	X	?	X
47) Wide biglenoid and biliac diameter	X	?	X	X	?	X
48) Reduced costal angle	X	X	X	X	?	X
49) Broad sternum especially manubrium	X	?	X	X	?	X
50) Reduction in the # of paired sternal ribs	X	X				
51) Thick and wide ribs				X		X
52) Less fasciculated extensor back musculature	X		X		?	?
53) Posterior placement of transverse process on lumbar vertebrae	X		X	X	X	X
54) Caudally directed lumbar spinous processes	X		X	X	x	X
55) Reduction in the # of thoracolumbar vertebrae	X		X		?	
56) Reduction in number of lumbar vertebrae	X		X		X	ff
57) Sacralization of lumbar vertebrae by iliac capture	X		X	X		
58) Increased number of sacral vertebrae	X			X	X	X
59) Coccygeal musculature refashioned into pelvic diaphragm	X		X		?	X
60) Absence or marked reduction of the tail	X			X	P	X
61) Prehensile tail			X			
62) Hip and thigh muscles enabling independent hip and knee joint movement	X		X	X	?	?
63) Underdevelopment or loss of the femoral fovea capitis	gg			X	X	X
64) Broad patella with shallow femoral groove	X		P	X	X	X
65) Plantaris tendon absent, feebly developed and/or inserting on heel	X		X	X	?	X

Table 1 (continued) - Characters distingusihing hominoids as paralleled or converged upon by colobines, atelines, lorisines, paleopropithecines and sloths

66) Well developed digital flexor originating from heel process	X		X	X	X	X
OTHER					
67) Reduction or absence of underfur and long coarse hair	X		X[hh]		?	X
68) Larynx showing marked specializations among the different taxa	X		X			
69) Reduction of subpericardial sinus	X		X			
70) Reduced number of tracheal rings	X		?			
71) Pericardiophrenic ligament	X		X		?	?
72) Sinistral deviation of cardial apex	X		?		?	
73) Dome shaped respiratory diaphragm with central tendon	X		X		?	
74) Retroduodenal fixture and various mesenteric adhesions preventing lapsus	X		X		?	?
75) Vermiform appendix	X			ii		
76) Complex stomachs or enlarged caecum for digesting cellulose		X	X[jj]		?	X
77) Low metabolism and/ or body temperature		X	?	X	?	X

References (table 1)

1) Chivers, 1977; Dixson, 1982; Doyle and Bearder, 1977; Eisenberg, 1977; Eisenberg and Maliniak, 1978; Ellefson, 1974; Goodall, 1986; Hill, 1967; Izard, 1987; Izard and Rasmussen, 1985; Lekagul and McNeely, 1977; MacKinnon, 1974; Nash and Harcourt, 1986; Nowack, 1991; Oates, 1977b; Rijsken, 1978; Roonwal and Mohnot, 1977; Rudran, 1973; Schaller, 1963; Schultz, 1942; Van Horn and Eaton, 1979.

2 and 3) Chivers, 1977; Dixson, 1982; Goodall, 1986; Eisenberg, 1977; Harcourt et al., 1980; Ellefson, 1974; MacKinnon, 1974; Nadler et al., 1981; Nowack, 1991; Rijsken, 1978; Symmington, 1988b; Tutin, 1980; Young et al., 1990.

4) Nowack, 1991

5) Bishop, 1979; Bleisch et al., 1993 - Hill, 1953,1962; Napier and Napier, 1967; Nowack, 1991.

6 and 7) Bishop, 1979; Bleisch et al., 1993 - Charles-Dominique, 1974,1977; Chapman, 1987; Chivers, 1974; Ellefson, 1974; Fooden, 1963, 1964; Fossey and Harcourt, 1977; Gautier et al., 1980; Hladik, 1977; Jones and Sabater Pi, 1971; Kano, 1983; Kavanagh and Dresdale, 1975; Klein and Klein, 1977; Leo Luna, 1981; Mac Kenzie, 1929; McKey et al., 1981; Milton, 1980,1984; Mittermeier and Combra-Filho, 1977; Nowack, 1991; Oates, 1977a,1977b,1978; Petter and Hladik, 1970; Rodman, 1979,1984; Soimi, 1986; Strier, 1991; Struhsaker, 1975,1978,1980; Subramoniam, 1957; Symmington, 1988a,b; Terborgh, 1983; Tutin and Fernandez, 1985; Wrangham, 1977.

8) Britton, 1941 Charles-Dominique, 1974,1977; Chivers, 1977; Defler, 1987; Ellefson, 1974; Estrada, 1984; Fossey, 1974; Gaulin and Gaulin, 1982; Izawa, 1987; Milton, 1980,1984; Nishimura, 1990; Nowack, 1991; Rijksen, 1978; Rodman, 1984; Struhsaker, 1975; Symmington, 1987,1988a,b; Wrangham, 1977.

9 and 10) Britton, 1941; Charles-Dominique, 1974; Chivers, 1974; Fleagle, 1976a,1976b,1977; Fossey and Harcourt, 1977; Galdikas Brindamour, 1979; Hunt, 1989; Jones and Sabater Pi, 1971; Klein and Klein, 1977; MacKinnon, 1974; Mendel, 1981a,1985; Milton, 1980, 1984; Mittermeier, 1978; Montgomery and Sunquist, 1978; Rose, 1979; Rijksen, 1978; Rodman, 1979; Sarmiento, 1985; Struhsaker, 1975,1980; Tuttle, 1970,1974.

11) Cartmill and Milton 1977; Charles Dominque, 1974; Dykyj, 1980.

12) Britton, 1941; Cartmill and Milton, 1977; Dykyj, 1980; Erikson, 1963; Fleagle, 1976a; Hill, 1962; Hunt, 1989; Mittermeier, 1978; Montgomery and Sunquist, 1978; Rijksen, 1978; Sarmiento, 1985; Stern, 1971.

13) Cartmill and Milton, 1977; Dykyj, 1980; Kortlandt, 1968; Hill, 1953,1962; Hunt, 1989; Mendel, 1981,1985; Sarmiento, 1985,1988.

14) Dykyj 1980; Hill, 1953 1962; Hunt, 1989; Mendel, 1981,1985; Sarmiento, 1985,1988. 1980; Tuttle, 1969c.

15) Carpenter and Durham, 1969; Hill, 1962; Nowack, 1991; Sarmiento, 1985; Stern, 1971.

16) Jenkins, 1981; Mendel, 1979; Sarmiento, 1985,1988.

17 and 18) Baldwin and Teleki, 1976; Britton, 1941;Cartmill and Milton, 1977; Charles-Dominique, 1974; Chivers, 1974; Dykyj, 1980; Fleagle, 1976a, b 1977; Fossey, 1974 Fossey and Harcourt, 1977; Galadikas Brindamour, 1978; Jones and Sabater Pi, 1971; Jungers et al., 1992; Kavanagh and Dresdale, 1975; Klein and Klein, 1977; MacKinnon, 1974; Milton, 1980,1984; Montgomery and Sunquist, 1978; Rijsken, 1978; Sarmiento, 1985; Schon Ybarra, 1984; Stern, 1971; Struhsaker, 1975,1980.

19) Aiello, 1978; Charles Dominique, 1974; Montgomery and Sunsquist, 1978; Nowack, 1991; Struhsaker, 1975.

20) Bleisch (personal communication); Fleagle, 1976ab,1977; Kortland, 1968; Mittermeir, 1978; Napier and Napier, 1967; Oates, 1977b; Rose, 1979; Struhsaker, 1975,1980.

21) Dykyj, 1980; Gebo, 1986; Mendel, 1981a,1985; Sarmiento, 1983,1985,1987, 1994; Strasser, 1989; Walker, 1967,1974.

22) Britton, 1941; Wislocki and Straus, 1932.

23) Ford and Davis, 1992; Godfrey, 1991; Nowack, 1991; Sarmiento, 1985; Schultz, 1953; Strasser, 1989,1992.

24) Erikson, 1963; Napier and Napier, 1967; Sarmiento, 1985 and authors unpublished measurements; Schultz, 1936, 1956; Straus and Wislocki, 1932; Walker, 1967,1974.

25) Britton, 1941; Etter, 1973,1974; Mendel, 1979,1981b; Midlo, 1934; Sarmiento, 1985, 1994; Schultz, 1963; Simons et al., 1992; Strasser, 1989,1992; Walker, 1967; 1974.

26) Britton, 1941; Hill, 1962; Lemos de Sa and Glander, 1983; Mendel, 1981b; Midlo, 1934; Miller, 1939; Sarmiento, 1985; Simons et al., 1992; Straus, 1942; Schultz, 1968; Wislocki, 1928; Yalden, 1972.

27) Britton, 1941; Sarmiento, 1993, 1994; Straus, 1942; Strasser, 1989,1992; Walker, 1967,1974; Wislocki, 1928.

28) Britton, 1941; Hill, 1953; Midlo, 1934; Miller, 1939; Straus, 1942.

29) Forster, 1917; Hill, 1953,1962,1970; Jouffroy and Lessertisseur, 1959,1960; Lertisseur, 1958; Makintosh, 1875; Marzke, 1971; Polak, 1908; Sarmiento, 1993, 1994; Straus, 1930.

30 and 31) Cartmill and Milton, 1977; Hill, 1962; Lewis, 1969; Mendel, 1979,1981b; Mivart and Murie, 1865; Sarmiento, 1988; Yalden, 1972;

32 and 33) Cartmill and Milton, 1977; Mendel, 1979,1981b; Sarmiento, 1988; Yalden, 1972; Ziemer, 1978.

34) Britton, 1941; Hill, 1953,1962; Makintosh, 1875; Meinke, 1911; Mendel, 1981b; Miller, 1921; Schon-Ybana, 1968; Tuttle, 1969b.

35) Sarmiento, 1985,1987.

36) Ford, 1980; Gebo, 1989; Miller, 1939; Sarmiento, 1985 (author's unpublished notes); Walker,   1967,1974; Ziemer, 1978.

37) Ford, 1980; Sarmiento, 1985 and author's unpublished notes); Simons et al., 1992.

38) Sarmiento, 1985; Walker, 1967,1974.

39) Britton, 1941; Cartmill and Milton, 1977; Erikson, 1963; Sarmiento, 1985; Schultz, 1960; 1961; Straus and Wislocki, 1932.

40) Britton, 1941; Cartmill and Milton, 1977; Erikson, 1963; Gregory, 1934; Keith, 1934; Sarmiento, 1985; Schultz, 1960,1961; Straus and Wislocki, 1932; Walker, 1967,1974.

41) Ashton and Oxnard, 1964; Erikson, 1963; Gebo, 1989; Miller, 1939; Roberts, 1974; Rosenberger and Strier, 1989; Sarmiento, 1985 (authors unpublished notes and measurements); Schultz, 1930,1942,1968.

42) Erikson, 1963; Miller, 1939; Roberts, 1974; Sarmiento, 1985,1987 (unpublished notes and measurements); Schultz, 1930,1937,1942,1968.

43) Britton, 1941; Sarmiento, 1985; Schultz, 1961; Straus, 1937; Straus and Wislocki, 1932.

44) Schultz, 1961; Straus and Wislocki, 1932

45) Sarmiento, 1985,1987; Schultz, 1960,1961; Straus and Wislocki, 1932.

46) Erikson, 1963; Sarmiento, 1985,1987; Schultz, 1960,1961; Straus and Wislocki, 1932.

47) Britton, 1941; Schultz, 1956; Straus and Wislocki, 1932; Walker, 1967,1974.

48) Erikson, 1963; Gebo, 1989; Sarmiento, 1985 (authors unpublished notes); Schultz, 1960,1961,1968.

49) Erikson, 1963; Sarmiento, 1985 (authors unpublished notes); Schultz, 1961.

50) Sarmiento (authors unpublished notes); Schultz, 1961.

51) Jenkins, 1970; Schultz, 1961

52) Keith, 1923; Hill, 1962.

53) Ankel, 1966; Sarmiento, 1985,1987,(authors unpublished notes); Schultz, 1961; Straus and Wislocki, 1932.

54) Mac Phee and Vuillaume-Randriamanantena, 1984; Sarmiento, 1985,1987; Schultz, 1961; Straus and Wislocki, 1932.

55) Erikson, 1963; Sarmiento, 1985; Schultz, 1961; Straus and Wislocki, 1932.

56) Sarmiento, 1985; Schultz, 1961; Simons *et al.*, 1992; Straus and Wislocki, 1932.

57) Britton, 1941; Gebo, 1989; Sarmiento, 1985; Schultz, 1961; Straus and Wislocki, 1932; Walker, 1967,1974.

58) Erikson, 1963; Schultz, 1961; Sonntag, 1921; Straus and Wislocki, 1932.

59) Elftman, 1934; Elftman and Atkinson, 1950; Wilson, 1972.

60) Britton, 1941; Gebo, 1989; Sarmiento, 1985; Schultz, 1961; Straus and Wislocki, 1932; Walker, 1967,1974.

61) Hill, 1962; Schultz, 1961.

62) McArdle, 1981; Sarmiento, 1985; Schon, 1968; Stern, 1971; Uhlman, 1968.

63) author's observations; Mivart, 1866,1867; Owen, 1835a; Simons *et al.*, 1992; Walker, 1967,1974.

64) author's observations; Gebo, 1989; Mivart, 1867; Simons *et al.*, 1992; Walker, 1967,1974.

65) Hill, 1953,1962; Loth, 1908; Meinke, 1911; Sarmiento, 1983;

66) Gebo, 1986; Hill, 1953,1962; Jungers *et al.*, 1991; Sarmiento, 1983, author's unpublished notes; Sawalaschin, 1911.

67) author's unpublished notes; McKnab, 1978; Nowack, 1991.

68) Deniker and Boulart, 1886; Fick, 1895; Hill, 1962; Huxley, 1864; Primrose, 1899; Sonntag, 1923,1924.

69 and 70) Hill, 1962; Juraniec, and Szostakiewicz-Sawicka, 1968; Keith, 1923; Ruge, 1892,1910; Washburn, 1950a.

71) Deniker, 1885; Lineback, 1933; Narath, 1901; Washburn, 1950a.

72) Leidel, 1940; Ruge, 1892; Wasburn, 1950a;

73) Hill, 1962; Keith, 1923; Juraniec, and Szostakiewicz-Sawicka, 1968; Washburn, 1950a.

74) Deniker, 1885; Huntington, 1903; Keith, 1923; Kostanecki, 1926; Straus, 1934.

75) Chalmers Mitchel, 1905; Eggeling, 1920; Elftman and Atkinson, 1950; Forster, 1918; Huntington, 1903; Jacobs-Lagen, 1923; Kostanecki, 1926; Loghem, 1904, Lorin-Epstein, 1932; Straus, 1934; Treves, 1885.

76) Britton, 1941; Kostanecki, 1926; Langer, 1988; Owen, 1835b; Wislocki, 1928.

77) Britton, 1941; Hildwein and Goffart, 1975; McKnab, B.K. 1980,1986; Morrison and Sinois, 1962; Muller, 1979; Muller *et al.*, 1983; Nagy and Montgomery, 1980; Nicoll and Thompson, 1987; Thompson and Nicoll, 1986.

Notes

a) Based on the average length of the 5 main genera as compared to cercopithecoids of similar body size.

b) *Aloutta* the most primitive member of the group shows a much shorter gestation time than *Ateles*. *Brachytles* or *Lagothrix* gestation time has not been reported on.

c) Reported for *Ateles* only. *Aloutta* has a short interbirth interval coinciding with its short gestation.

d) Modern day humans have worldwide ditribution on all continents

e) *Presbytis* and *Rhinopithecus* have ranges that extend north of the tropics

f) Gorillas and humans have a mainly terrestrial food source. Chimpanzee's food source is partially terrestrial.

g) *Rhinopithecus* and *Presbytis* have a partial terrestrial food source.

h) Hylobatids and *Pongo* are mainly arboreal, chimpanzees are semi- terrestrial, and adult eastern gorillas and humans fully terrstrial.

i) *Rhinopithecus* and *Presbytis* are appreciably more terrestrial

j) Hylobatids and orang-utans have small ranges

k) Spider monkey have a large range and both large and small ranges have been reported for *Lagothrix*

l) Humans and gorillas are an exception

m) Humans and gorillas are an exception

n) Humans and gorillas are an exception

o) Orang-utans and gorillas are slow moving in trees.

p) The howler monkey, woolly monkey and wooly spider monkey.
all move slowly although the latter two may variably move quickly.

q) Chimpanzees and hylobatids leap

r) Spider monkeys and wooly spider monkeys leap

s) Humans are an exception

t) Humans are an exception

u) Humans and gorillas are an exception

v) Humans and hylobatids are an exception

w) Only in orang-utans.

x) Not in three toed sloth.

y) Seen in *Brachyteles* only.

z) Not present in gorillas or humans

aa) Present in orang-utans

bb) Not in the howler monkey, and less pronounced in *Lagothrix*

cc) Variability seems to be high in Orang-utans

dd) Variability seems to be high in *Lagothrix*.

ee) Not exhibited in humans

ff) In two-toed sloths only

gg) Absence of a fovea capitis is the usual condition in orang- utans and exhibited rarely in gorillas.

hh) Underfur present in *Lagothrix*, characters could not be verified for *Brachyteles*.

ii) *Nycticebus* has an appendix

jj) Stomach enlarged and U shaped in *Brachyteles* and *Ateles* and may participate in fermentation.

Table 2. The distinguishing craniodental characters among folivorous and frugivorous genera of the studied groups.

A) characters distinguishing *Gorilla* from *Pan*

B) characters distinguishing *Colobus* from *Cercocebus*

C) characters distinguishing *Brachyteles* from *Ateles*

D) characters seen in *Paleopropithecus*

X= distinguishing character present

P= character is present but does not distinguish between two genera

[a] characters present in orang-utans

[b] distinguishing characters present in Jolly's seed eating complex

[c] disinguishing characters present in Theropithecus and hominids not mentioned by Jolly (1970).

	A	B	C	D
1) Vertical ramus long, large surface area for masseter (enlarged gonial area)	X[a,b]	X	X	X
2) Coronoid process retroflexed	X		X	X
3) Post glenoid large	X[a]	X	P	X
4) Infratemporal fossa large	X[a]	X	X	X
5) Relatively *deep* mandibular articulation	X	X	X	X
6) Articular condyle mediolaterally wide, anteroposteriorly narrow	X[a]	X	X	X
7) Mental symphysis superoinferiorly wide, anteroposteriorly thick and rounded	X[a]	X	X	X
8) Reduction of premaxilla	X[b]	X	X	?
9) Curve of Spee pronounced	X[a]	X	X	X
10) Airorhynchy	[a]			X
11) Medial and lateral upper incisors tending to be equal in size, relatively small and allometrically reducing	X[b]	X	X	?
12) Lower incisors vertically set and nearly in the same frontal plane as the canines (latter statement not applicable for *Paleopropithecus*)	X[c]	X	X	X
13) Plane of incisor wear perpendicular to blade	X[c]	X	X	
14) Canine conical relatively smaller-less projection above tooth row, especially in females	X[a,b]	X	X	
15) Small diastema especially females	X[a]			
16) Oblique orientation of p3	P	X	P	?
17) Tendency to molarize P4 and p4, relatively larger talonid on p3 and p4 (applicable to p2 when present)	P	X	X	
18) Molars large, quadrate and crowded mesiodistally	X[ab]	X	X	X
19) m3>m2>m1	X	X	X	
20) Hypocone, hypoconulid large especially on M3 and m3 associated with larger talon and talonid	X	X	X	X
21) Molars with sharp crests and high crowns	X	X	X	X
22) Thin enamel	P	X	P	?
23) Wrinkled enamel	P	X		X

Notes

1) author's notes (1); Zingeser, 1973; Simons, 1972; Szalay and Delson, 1979.
2) author's notes; Zingeser, 1973.
3) author's notes; Lamberton, 1947.
4) author's notes; Lamberton, 1947.
5 and 6) author's notes.
7) author's notes Simons, 1972; Szalay and Delson, 1979.
8) author's notes.
9) author's notes; Simons, 1872; Szalay and Delson, 1979.
10) author's notes; Simons, 1972; Szalay and Delson, 1979.
11) author's notes; Eaglen, 1984; Godfrey *et al*, 1990; Rosenberg, 1992; Zingeser, 1973.
12) author's notes; Simons, 1972; Szalay and Delson, 1979; Zingeser, 1973.
13) author's notes; Zingeser, 1973; Rosenberger, 1992.
14) author's notes; Greenfield and Washburn, 1991; Simons, 1972; Szalay and Delson, 1979.
15) author's notes; Sarmiento, 1987; Zingeser, 1973.
16) author's notes; Sarmiento, 1987; Zingeser, 1973.
17) author's notes; Sarmiento, 1987; Szalay and Delson, 1979; Zingeser, 1973.
18) author's notes; Godfrey *et al.*, 1990; Gregory, 1922; Simons, 1972.
19) author's notes; Godfrey *et al.*, 1990; Zingeser, 1973.
20) author's notes; Godfrey *et al.*, 1990; Simons 1972; Szalay and Delson, 1979; Zingeser, 1973.
21) author's notes; Kay and Hylander, 1978; Lamberton, 1947; Szalay and Delson, 1979; Zingeser, 1993.
22) Martin, 1985; Kay, 1978; Zingeser, 1973.
23) author's notes; Kay and Hylander, 1978; Lamberton, 1947; Godfrey *et al.*, 1990; Simons, 1972; Zingeser, 1973.

(1) author's notes based on the comparison of; a) 25 male, 24 female lowland gorillas to 37 males, 30 females common chimpanzees (*Pan troglodytes*), b) 10 males, 8 females *C. polykomus* to 9 males, 8 females of *C. galeritus*, c) 8 males, 7 females *Ateles paniscus* to 2 males 3 females *Brachyteles arachnoides* d) 15 male orang-utans and 11 female orang-utans] and e) 4 males 4 females *Indri indri*]

Distinguishing Characteristics Common to the Groups

With the exception of humans and two genera of colobines all of the members of the groups comprising approximately 20 genera inhabited forests within tropical regions. The colobines, *Presbytis* and *Rhinopithecus* (Bishop, 1979; Jablonski, 1992; Bleisch *et al* 1993 inhabited forests in more northerly regions. The locomotor anatomy of *Paleopropithecus* (Walker, 1967; 1974; Simons *et. al*, 1992), suggests it was also a forest inhabitant regardless of what taphonomic evidence there may be to the contrary.

Except for African apes and humans most forms were fully arboreal rarely descending to the ground. Additionally, all forms depended on arboreal food sources, gorillas and humans again are an exception.

Solutions to Arboreality

The majority of the parallelisms and convergences in the locomotor anatomy among the groups have been interpreted as solutions to exploiting an arboreal habitat. These include relatively long hands and feet, reduction or loss of the pollex, reduction or loss of contrahentes in the hand, tight mediolateral curvature of the wrist joint, medially projected medial epicondyle, long vertebral border of scapula, large acromion and well developed coracoid,

and a reduced costal angle. The frequent use of vertical trunk postures, use of hands and/or feet in hook postures, enhanced adduction of wrist, adduction-abduction of upper and lower limbs, and use of elbow and/or knee joint in extended postures are corresponding arboreal characters. Although also seen in cautious climbers, those characters seen in colobines are more correctly related to the grasping ability necessary for stability on arboreal supports, and forelimb suspension in foraging postures. These characters are necessary for moving on all types of arboreal supports, but are especially benficial on relatively small ones. While a few of these characters are shared by their corresponding outgroup, and not distinguishing, they are nonetheless exhibited by all of the groups.

Cautious climbing

Those locomotor characters shared by all the groups not seen in colobines have been interpreted as correlates of cautious climbing behaviors, and its limiting component vertical climbing (Cartmill and Milton, 1977; Sarmiento 1983, 1985, 1987, 1988). These characters can be summarized as follows; high intermembral index, reduction or loss of the ulnocarpal articulation, distal migration of the pisiform, dorsal migration of the scapula, mediolaterally broad thorax, broad manubrium, long spinous process on the lower cervical and upper thoracic vertebrae, laterally directed glenoid, anterior displacement of the vertebral column relative to the thorax, posterior placement of the transverse processes of lumbar vertebrae, wide biglenoid and biliac diameters, increased number of sacral vertebrae, reduced number of thoracolumbar vertebrae, caudally directed lumbar spinous processes, less fasciculated back musculature, reduction or loss of tail, the hip and thigh muscular specializations, and the heel process and associated musculature. The corresponding behavioral characters are slow deliberate movements, a toe to heel foot grasp, hook postures of the foot, extension of hip and knee joint, and frequent bipedal behaviors when terrestrial. The high proportion of slow twitch or red muscle fibers and associated vasculature common to cautious climbers provides the prolonged contraction and endurance necessary for their slow deliberate movements (Sarmiento, 1985).

Folivory

With the exception of lorisines, *Ateles* and most hominoids, all of the forms are in large part folivores (Szalay and Delson 1979; Nowack 1991). Unlike ripe fruit, leaves are more or less uniformly distributed in tropical forests throughout the year, and are a resource that is compatible with the deliberate slow movement and small daily ranges seen in most members of the studied groups. Although readily available, leaves require a longer digestion time, are less nutritious and necessitate a greater intake per volume than fruit to provide comparable nutrients (Bauchop, 1978). Because leaves must be eaten in greater bulk, they require an *absolutely* larger gut, especially if housing the bacterial colonies necessary for cellulose digestion (Parra, 1978). Additionally, the fatty acids released by cellulose digestion (Bauchop and Martucci, 1968; Bauchop, 1978) do not provide an energy source as quickly convertible as the sugars in fruit, further emphasizing slow movements and also metabolism. Notably, fatty acids - as opposed to glucose or glycogen - are the necessary fuels for oxidative phosphorylation; the energy releasing reaction used by slow twitch muscle fibers. For these reasons, folivory is more common in slow moving forms with large body sizes, which have a smaller surface area to volume ratio, and hence lower metabolic needs. Larger body size relative to support size is also a correlate of arboreal cautious climbers (Cartmill and Milton,

1977; Cartmill 1979; Sarmiento, 1985). Thus the two are inextricably linked.

The reduction or absence of underfur in most of the large or medium-sized genera would seem to be at odds with a low metabolism Owing to a) the climate in tropical areas, b) the relative inactivity of these forms, and c) the rich vascularization of slow twitch muscle fibers, prolonged deliberate movement may be expected to raise body temperature. Additionally unlike glycolysis, oxidative phosphorylation the reaction associated with slow twitch muscles, releases substantial heat; both from uncoupling and movement down the energy gradient. The absence of underfur enables the dissipation of excessive body heat. This would be especially important in large forms with a low surface to volume ratio, and in those forms with a slow-climbing heritage which for one reason or another have increased their activity. The long coarse hairs, although not interfering with heat dissipation, serve to whisk away water and protect the skin from insects and scraping branches.

Lower metabolism is also partially a reason for the longer gestation time being a distinguishing character in most of the studied groups and interbirth interval a distinguishing character in hominoids, sloths and *Ateles*. Long gestation did not imply a size related phenomena, since comparisons were made to outgroup members of similar or larger size. Hylobatids, for instance, have a longer gestation period than all cercopithecoids and much longer than those in the same weight range (Table I; Nowack, 1991). Similarly two toed sloths are smaller in body size, but have a much longer gestation period than the giant anteater (Nowack, 1991). *Alouatta*, anatomically a non-committed cautious climber and the most primitive of the Atelinae (Rosenberger, 1979) has a larger body size and mass than spider monkeys (Ford and Davis, 1992), but a much shorter gestation period. (Despite its presently frugivorous nature, the anatomy of spider monkeys indicates a history of much stronger selection for the folivorous cautious climbing complex than has occurred in *Alouatta*). The development time of the embryo is limited by the animal's metabolism, as is its postnatal dependency period and the maternal recovery time between births. The less nutritious diet of folivores may require a longer recovery time. Although maternal increase in metabolism has been documented in primates (Richard and Nicoll, 1987), such an increase is limited both by the toxicity of the diet (Jansen, 1978) and by a low metabolic starting point.

A longer gestation period may also in part be related to a small daily range, especially in an arboreal habitat where a considerable component of the animal's movements are against gravity. Considering the added weight of the embryo, long gestation times may prove too costly when moving about quickly and covering large areas.

Lorisines

The parallelisms between the non-folivorous lorisines and the cautious climbing folivores are instructive. Leaves and the cryptic and noxious insects consumed by lorisines are both high in toxins (Charles-Dominique, 1974; 1977; Petter and Hladik 1970; Subramoniam, 1957). The lower metabolism associated with slow deliberate movement may ease the deleterious effects of toxins slowing down their entry into the system, and increasing the time digestion can break them down. By moving slowly and deliberately, cautious climbers also protect themselves from the dangerous effects toxins can have on their coordination and reaction time. Such a toxic effect is more likely to prove fatal for arboreal leapers or acrobatic arealists which depend on quick reaction time and balance to secure stable supports. Furthermore, the cryptic noxious insects consumed by lorisines are not localized and do not require speed or special musculo-sensory coordination to catch. As a food resource, they share these harvesting properties in common with leaves (Charles-Dominique, 1974; 1977).

Differences Between Distinguishing Characteristics

The failure of hominioids to exhibit the distinguishing characteristics seen in the other groups are mainly due to the variation in behavior between the different genera of hominoids, and associated with the terrestrial behaviors of humans and the African apes (Sarmiento, 1985, 1988, 1993). Humans and gorillas exploit terrestrial food sources (Fossey and Harcourt, 1977) and chimpanzees a large daily range (Wrangham, 1977; Rodman, 1984). Correspondingly, humans and gorillas do not exhibit hook postures of the feet, marked mobility of the ankle joint, marked adduction of the wrist joint, relatively long hands and feet with long pedal and manual phalanges, and tight mediolateral curvature of the wrist joint (Sarmiento 1994). Additionally, humans do not exhibit a reduced pollex, a relatively long spinous process on the lower cervical and upper thoracic vertebrae, or a high intermembral index. Human and African ape terrestrial behaviors and the large number of underlying distinguishing characters these forms share with the other groups, indicate that their exceptional characters were relatively more recently derived from a cautious climbing arboreal ancestry (Stern, 1971; Sarmiento, 1983; 1985; 1987; 1988; 1994).

Colobines

A different solution for negotiating discontinuities in vertical supports accounted largely for the difference in distinguishing characters of colobines. Colobines depend on leaping to cross gaps in arboreal supports (Rose 1979). As a result, they do not show the high intermembral indices, hindlimb anatomy or lower back specializations seen in the other groups. It would seem all arboreal forms would benefit from those features in the lower limb and foot seen in cautious climbers, since they are in part adaptations to securing stable supportholds. However, the running and leaping behaviors necessitate lower back mobility, relatively long lower limbs, stable hip joint, a relatively rigid ankle joint and coordinated muscular action across two or more lower limb joints (Jolly and Gorton 1974; Sarmiento 1985). As such leaping is non-compatible with the lower limb and body anatomy of cautious climbers.

Brachiation: A Cautious Climber's Solution to Frugivory

Among the arboreal cautious climbers, the differences in distinguishing characters can be related to the types of arboreal food sources that are exploited. In tropical forests were almost all of the compared taxa are found, the main arboreal food sources for medium size non-carnivorous mammals are fruits and leaves (Clutton-Brock and Harvey, 1977; Gaulin and Konner, 1977; Gaulin, 1979). Unlike leaves which have a more or less continuous, all year round distribution throughout the forest, fruits last a limited time and are distributed seasonally at specific localities throughout the forest (Charles-Dominique 1977; Klein and Klein 1977; Rodman, 1979; Wrangham, 1977). To exploit their resources, fruit eaters must travel from locality to locality in search of fruit (Charles-Dominique 1977; Klein and Klein 1977; Rodman, 1973; 1979; Wrangham, 1977). To cover as many fruiting sites as necessary, minimize competition with other fruit eaters, and avoid predators that feeding fruit eaters may attract, fruit eaters must be able move relatively quickly in the trees and cover a considerable area throughout the forest.

Among the studied groups there seems to be a strong relationship between leaping or quick movements and fruit eating. As observed by Fleagle (1976b, 1977) in two sympatric

species of colobines, leaping is more common in the species consuming a higher percentage of fruit. Leaping and other quick movements are associated with white or fast twitch muscles fibers. Fruit contains sugars, the fuel for anaerobic glycolysis used by these fibers. All those arboreal forms sharing the slow climbing locomotor anatomy which do not engage in slow deliberate movements are fruit eaters which prefer ripe fruit i.e. *Ateles*, hylobatids and chimpanzees. Even among sloths, the two-toed sloth the quickest of the two forms, consumes a higher percentage of fruit (Britton, 1941; Montgomery and Sunquist, 1978; Nowack, 1991) .

Both *Ateles* and hylobatids have developed a brachiating habit which allows them to move rather quickly in the trees and cover a comparatively large range (Cant 1986; Gittins and Raemakers, 1980; Klein and Klein, 1997) . Chimpanzees are able to accomplish the same through terrestriality (Wrangham, 1977). In spite of lacking the leaping anatomy of colobines, spider monkeys, hylobatids and chimpanzees frequently leap to cross discontinuities in supports (Fleagle, 1976a; Kortlandt, 1968; Mittermeier, 1978; Susman 1984; Doran, 1989; 1992). Because a) *Ateles, Hylobates* and *Pan* share their locomotor anatomy with, and are also closely related to cautious climbers, and b) do not show apparent anatomical specializations for leaping or other quick movements, their locomotor behaviors are likely to be derived. A slow climbing heritage best explains why hylobatids and *Ateles* would have both evolved in parallel a method for collecting fruit divergent to that succesfully used by arboreal cercopithecines and non-ateline cebids, respectively.

Commitment and Heritage

Most of the other differences in distinguishing characters between groups reflect both heritage and commitment to other behaviors which sacrificed cautious climbing locomotor anatomy. Usually these characters are peculiar to the group itself or common to two of the groups. They are instructive, since they enable speculation as to the degree of commitment and development of distinguishing characters present in the hominoid ancestor.

Sloths appear to be the most committed cautious climbers given their inability when terrestrial to prop their bodies up above their limbs for support (Beebe 1927; Britton 1941; Mendel, 1981, 1985). This commitment is exhibited in the reduction and loss of two or more digits in the hands and feet, cryptic habits, a markedly reduced metabolism, and a high proportion of red twitch muscle fibers and associated vasculature. It is also reflected in variability in the number of cervical vertebrae a feature which is markedly constant among all mammals. In two-toed sloths a decrease in cervical vertebrae from seven to six probably provides the necessary stability to those back muscles originating from the vertebral spinous processes (rhomboids and trapezius) and inserting on the scapula. In doing so, however, it sacrifices neck mobility (Britton, 1941). The three-toed sloth, however, has increased the number of cervical vertebrae, so despite contraction of the back muscles necessary for scapular retraction and stability in hanging postures, the neck retains a wide range of mobility (Britton, 1941). The sloth's committed locomotor anatomy and behavior is complementary with a complex stomach specialized to digest leaves.

The cryptic habits of both sloths and lorisines relax those predator pressures maintaining the locomotor anatomy associated with escape, and enable a marked commitment to cautious climbing behaviors. Sloths and lorisines as suggested by their outgroups had nocturnal or crepuscular ancestors, a good starting point for enhancing cryptic behavior. Despite that reduction in size alleviates some of the selective pressures for the cautious climbing locomotor anatomy (Sarmiento, 1985), lorisines exhibit in common with sloths characters indicating a marked commitment, i.e. variability in the number of cervical vertebrae, a high percentage of

red twitch muscle fiber and reduction in the number of functioning digits in the hands and feet.

Although the differences in colobines may suggest less commitment to arboreal behaviors they are also in part a result of heritage. Cercopithecoids show strong cursorial adaptations that must have been common to the colobine ancestor. Running and leaping must have served as a viable solution for crossing gaps between supports, since colobines diverged from the ancestral cercopithecoid. Hence, leaping has been further selected for. Colobines in fact do show quite a few characters which are common to sloths, i.e. reduction or loss of the pollex and development of a complex stomach for leaf digestion. Moreover, they also exhibit incipient cryptic behaviors (Struhsaker, 1975; Nowack 1991).

Notably, spider monkeys and spider wooly monkeys both show a large U-shaped stomach which may have had, or has some ability for fermentation (Langer, 1988). [Although not a folivore, dietary studies show that *Ateles* a committed frugivore may consume a high percentage of leaves during particular times of the year (Chapman 1987; van Roosmalen 1980) suggesting some adaptation or possibly a recent heritage of folivory]. The vermiform appendix of hominoids is an organ of lymphoid tissue with the ability to produce antibodies and protect the caecum and colon from fluctuating levels of bacteria. As such, it may have developed to control bacterial colonies in a caecum that already participates in a restricted degree of hindgut fermentation. With better knowledge of its diet, the presence of an appendix in *Nycticebus* (Straus, 1934) could clarify the existence of this organ in hominoids.

Size

Many of the distinguishing characters common among the other groups, but absent in lorisines are size related features. Cartmill and Milton (1977) suggested that the high number of lumbar vertebrae are due to their smaller body size. Based on a vertical climbing model and the logarithmic properties of the friction coefficient, Sarmiento (1985) showed climbing would select for increasingly longer trunk with decreasing body size and vice versa.

Associated to trunk length, many of the visceral characters of hominoids that are absent or not as well developed in the other groups, are probably size related among cautious climbers. The reduction in the number of tracheal rings and in the size of the subpericardial sinus, the flat-topped diaphragm, the pericardiophrenic ligament, and sinistrial deviation of the cardial apex are features associated with packaging of the viscera in a relatively broad but short thorax (Washburn, 1950a). That these features seem to be most emphasized in the largest hominoids (Washburn, 1950a) suggests allometric decrease in thoracic length with increase in size (Sarmiento 1985).

The hand and foot grasps used by lorisines are also size related characters. For smaller forms, an opposable grip in which the organism actively applies a muscular force, is more stable and less costly relative to the supported weight than it is in large forms. This is due both to the logarithmic decrease in the friction coefficient and to relative strength with decrease in size (Cartmill, 1979; Sarmiento 1985). Additionally, unlike a hook grasp, that for effectivenes usually necessitates the ankle or wrist joint to be below the support, opposability allows supports to be grasped irrespective of their position relative to the animal's wrist, ankle or center of gravity (Sarmiento, 1985). Small animals are more apt to use supports as substrates, since their weight is less likely to bend the support, and their cheiridia is small enough to fully fit on the support.

For the same reason, pollical reduction is also more prevalent than hallucial reduction among all studied forms. Forelimbs are more likely to be used in suspension than hindlimbs —hindlimb

suspension inverts body posture (Sarmiento 1985). In this regard, the strong reduction of the hallux in orang-utans, a character expected in very committed cautious climbers is probably a closer reflection of their large size relative to the support. Because supports are more likely to bend under their weight, orang-utans are more prone to use hook postures of the feet.

There are some characters that seemed to be largely factors of heritage. Loss or reduction in the ulnocarpal contact in lorisines, hominoids and the two-toed sloth, but not in three-toed sloths and woolly spider monkeys is such a feature. As noted by the author (Sarmiento 1985, 1988) marked mediolateral curvature and mobility of the mid carpal joint, and radial loading postures are requisites of ulnocarpal reduction. When accompanied with distal migration of the pisiform the ulna losses it participation in the carpal joint. Despite the distal displacement of the pisiform in forms emphasizing ulnar loading or midcarpal mobility, the ulna remains as a participant in the joint. Both joints provide the emphasis on adduction flexion of a flexed wrist and adduction necessary in arboreal forms.

The loss or reduction of the tail in hominoids, lorisines and sloths can not be directly related to climbing behavior. As shown in atelines, tails when developed as prehensile organs serve to gain additional supportholds. In leaping colobines, the tail serves as balancing organ and in part helps the animal maintain its direction in mid-air (Rose, 1979). A non-prehensile tail or one without a tendency towards prehensility, presents additional surface area for heat loss, but provides no benefit. Without an apparent function in cautious climbing, the tail is a liability and hence selected against. Selection pressures for its reduction may be especially strong in forms with a low metabolism that undergo a seasonal energy debt as is common among folivorous primates.

The complete tail loss of hominoids and associated pelvic diaphragm, however, is also a feature seen in some macaques. These macaques which are neither arboreal folivores nor cautious climbers show complete tail loss and the formation of a hominoid like pelvic diaphragm (Eggeling 1896; Elftman 1932; Wilson 1972).In these forms, many of which live in colder climates, tail loss is probably also a result of heat conservation.

The forearm rotation of hominoids can also best be explained as a heritage feature. Although clearly advantageous to cautious climbing (Sarmiento 1985, 1987), forearm rotation and the development of the muscles associated to it is as marked or more marked in cercopithecoids than it is in any of the cautious climbing forms (Sarmiento, 1985). The unique and marked development of forearm rotation in hominoids depends on an ancestry that already exhibited some degree of enhanced rotation.

Similarities in the low number of paired sternal ribs in colobines and hominoids have no apparent correlation with behavior. The relatively shorter lumbar region of hominoids may necessitate a short sternum, so as not to compromise the size of the abdominal compartment and viscera. In colobines this may be the correlate of having a relatively large gut. Nevertheless, the absence of these distinguishing characters in the other forms suggest that it has a considerable heritage component between colobines and hominoids, both of which are catarrhines.

Marked laryngeal specializations are distinguishing characters of both atelines and hominoids. The parallel development of these structures have implications as to the home range, social system and population density of slow moving forms (Chivers 1974; MacKinnon 1974; Milton, 1980). The far-carrying vocalizations enabled by ateline and hominoid laryngeal specializations (Chivers, 1974; Ellefson, 1974; MacKinnon, 1974: Schon Ybarra, 1986) are a means of low energy intergroup interactions. As such they would be expected to develop in social, slow-moving, arboreal folivores with low energy expenditures.

Cranio-Dental Characters

Having established that folivory and cautious climbing constitutes an adaptive complex in large or medium size arboreal mammals, associated with the shared specializations of the pongid-hominid ancestor, cranial and dental characters can now be speculated upon.

Table II presents a comparison from among the studied groups of the distinguishing cranio-dental characters of folivores in comparison to frugivores. Hominoids and atelines both encompass genera with committed folivores and frugivores allowing for intragroup comparison. Colobines were compared to cercopithecines. Since it would be expected that the most committed forms would show more complete adaptations to either folivory or frugivory, comparisons are made between the most committed folivore vs. the most committed frugivore for each group as based on dietary studies, (Gautier-Hion 1978; Fossey and Harcourt, 1977; Klein and Klein, 1977; Milton 1984: Oates, 1977a, 1978; Struhsaker, 1978) i.e. *Ateles (A.paniscus)* and *Brachyteles*, *Pan (P.troglodytes)* and *Gorilla, Cercocebus (C galeritus)* and *Colobus (C. polykomus)*, respectively. The dental features present in *Paleopropithecus* a folivore (Simons, 1972) and the overlapping features exhibited in orang-utans and in Jolly's (1970) seed eating complex are also included for comparison.

Many of the distinguishing characters common to the leaf eaters focus on jaw use. In general, they reflect the need to generate and balance rotational forces in the frontal plane. The large and long vertical ramus with a large area of attachment for the masseter, and the large infratemporal fossa suggest large mandibular sling musculature, and considerable rotational forces in the frontal plane during unilateral chewing. The medio-laterally wide glenoid provides joint stability against these resulting rotational forces. The deep and thick mandibular symphysis, imparts rigidity to the mandible, so that muscular forces can be applied on the balancing side of the jaw.

The vertical set of the ramus, also suggests the reactionary force of occlusion is greater for small angular displacements at the jaw joint. With increasing radial excursion the masseter's moment arm is sacrificed. A slightly raised articular planum increases the gap between the occluding molars without sacrificing the masseter's moment arm (Sarmiento in prep). Despite a long molar row, the curve of spee insures that the force of occlusion is more or less constant along the molars. The curve achieves this by setting the reactionary force normal to the occlusal plane of each molar, at approximately the same perpendicular distance from the jaw joint (Sarmiento in prep). The curved molar set also helps to maintain an even distance between molars (regardless of their position on the molar row) so that the entire row can come down at once on the bolus increasing the effectiveness of each stroke. The retroflexed coronoid process indicates a posterior pull of the temporalis muscles probably necessary to balance the anterior component of the powerful masseter. All of these jaw characters are necessary to shear and triturate a large bolus of leaves, separating the liquid and solutes from the fiber, and also increasing the number of leaf particles, their total surface area and hence the speed of digestion.

The common molar characters are all suggestive of maximizing the volume of leaves processed per mandibular stroke. The large molar surface area, tendency for molarization of the premolars, and large hypocone and hypoconulid all increase the available tooth area for processing leaves. In large forms maximising occlusal area is especially important, given its proportional decrease with increase in the animal's volume. The high crown, crests, and thin enamel of molars insures that with wear enamel and dentine will alternate, maintaining sharp cutting edges for the lifetime of the animal.

A relatively less projecting canine in males and the near absence of canine projection in females is also related to maximizing occluding surface. The potential shearing and triturating

surface of the premolars is not sacrificed for canine honing. Although some social systems may select for the large projecting canines and the associated honing premolars in males (Kay et. al 1988), the apparent correlative response between canine size in the two sexes (Greenfield 1992) would be selected against in folivores. As seen in *Brachyteles* relaxation of the social pressures on male canine size (Milton 1985) results in a short almost non-projecting canine and added surface area on premolars (Kay *et al*, 1988; Remane, 1960; Zingeser, 1973) for processing leaves.

A number of the dental characters are associated with the vertical set of the incisors and maximizing the force applied when their occlusal surfaces are brought together. These characters are also important for leaf processing. Reduction of the premaxilla, reduction of the diastema, oblique set of the p3, and incisors set in almost the same frontal plane as the canines, all reflect the incisor row's proximity to the jaw joint. The vertical set of the incisors and the similarity in their size creates a straight cutting edge perpendicular to the incisor blade. These characters in combination provide powerful edge on edge occlusion of incisors to crop leaves and stems into small pieces before being processed by the molars (Rosenberger 1992). Considering, a) the poor nutritional content of leaves per volume, b) the amount of leaves that must be processed and c) the benefit of breaking up the leaves in as many pieces as possible to extract their nutrients and/or speed up fermentation (Parra, 1978), those characters optimizing the energy of mastication in a folivore would be selected for.

Enamel wrinkling a character common to most of the folivores probably also improves the leaf shearing and triturating function of molars. On new or slightly worn molars it presents a file like occluding surface. With a weaker jaw and an undeveloped gastrointestinal tract this helps infants and juveniles break up leaves into finer pieces (Gordon, 1980; Walker and Murray, 1975). With increased wear, wrinkling disappears completely. The flatly worn occlusal surfaces of adult hominoids are probably compensated by a longer mature gastrointestinal tract and a greater force of mastication. In this regard, crushing the leaf to extract its liquid is probably all a less committed, large-sized folivore without a complex stomach needs to do.

Shared Characters of the Hominoid Dentition

Considering the above analysis, a number of dental traits which were noted by the author in a past study (Sarmiento, 1987) to be shared characters of hominoids can be related to leaf eating. These include, a p3 with an obliquely directed axis, a crushing surface on p3, a mesiodistally short canine and premolar, development of 6th cusp on m3, enamel wrinkling on molars, pronunced cingula, reduction or absence of diastema in females, and a tendency to diminish or lose the p3 sectorial function (and hence develop a buccolingual crest and/or a lingual cusp on the p3). All these traits may have first appeared in hominoids as a response to increasing the efficiency of leaf eating. They have probably been maintained by a significant percentage of leaf eating in all the large bodied non-human hominoids (Fossey and Harcourt 1977; Hladik, 1977; Rodman, 1979).

Similarities Between Folivores and Small Object Feeders

Comparison of the folivorous craniodental characters to the distinguishing characters proposed by Jolly (1970) to be common to hominids and *Theropithecus* shows a wide overlap. The a) mediolaterally broad anteroposteriorly narrow mandibular condyle and corresponding glenoid fossa, b) large and vertical ascending ramus, c) a large mandibular body in the region of the molars, d) incisors relatively small and allometrically reducing, e) mesiodistally crowded molars, f) a reduced premaxilla, and g) a reduced canine are all distinguishing characters of folivores also exhibited in Jolly's seed eating complex. Although

not in opposition to Jolly's (1970) hypothesis, it indicates a folivorous hominoid ancestor may be the heritage factor which Jolly hypothesized to account for the differential reduction of canines in hominids and fossil *Theropithecus*.

This morphological link between folivory and granivory is biologically real. *Colobus satanas* a structural and taxonomic folivore is the most committed granivore as indicated by its diet (McKey, 1978).

The characters common to folivores also appear to be common to hard object feeders. Orang-utans can be distinguished from chimpanzees by many of the same characters that distinguished gorillas. It can be argued, however, that orang-utans are semifolivorous forms. As observed by Rodman (1979) for half of the year orang-utans spend as much or more time feeding on leaves than fruits. During this time orang-utans spent approximately 30% of their feeding time on fruit (Rodman 1979) the rest of their time was spent feeding mainly on bark,flowers and leaves. Hard object feeding may explain why orang-utans did not develop the fragile convoluted crests and high crowned molars of committed folivores. Nevertheless, leaf eating could be placing considerable limiting pressures on their dental traits. These could have had as a much influence in shaping orang-utan craniodental features as hard object feeding.

Reconstruction of the Hominoid Ancestor

In part a reconstruction of a hominoid ancestor's cranio- dental features depends on how committed it was to cautious climbing and folivory. Among primates, the dichotomy between fruit eaters and folivores is not so clear cut as the labels indicate. Most folivorous primates do eat a considerable percentage of fruit (Hladik and Hladik, 1972; Chivers, 1977; Gaulin and Gaulin, 1982;. Conversely, frugivores eat leaves (Hladik, 1977; 1978; MacKinnon and MacKinnon, 1978; Rodman 1979;). Frugivores emphasizing folivory and those forms without specializations for leaf digestion, tend to eat younger leaves containing less cellulose, alkaloids and tannins, and more nutrients (Glander, 1978, 1982). Those committed folivores exploiting fruits tend to eat unripe ones (Wasser 1977). Lower in sugars, but higher in toxins, unripe fruit is probably closer in its composition of nutrients and secondary compounds to young leaves (Milton, 1980). In contrast to ripe fruit, the lower concentration of sugars in unripe fruit would not promote dangerous levels of bacterial proliferation in the complex stomach of folivores. Additionally, unripe fruit does not attract as many competitors or predators and, hence is more accessible to a slower moving folivore.

Considering that no living hominoid even those that are mainly folivorous i.e. gorillas (Fossey and Harcourt, 1977), have developed a complex stomach for cellulose digestion (Kostanecki, 1926; Elftman and Atkinson 1950; Langer 1988), it is unlikely that the hominoid ancestor possessed one. This would be consistent with the degree of commitment exhibited by the distinguishing characters in the hominoid locomotor anatomy. The a) retention of 5 digits in the hands and feet, b) retention of 7 cervical vertebrae, c) retention in most of a fovea capitis, d) ability to prop their body up on their limbs, e) the development of terrestrial behaviors and a terrestrial food supply in some taxa and f) non-cryptic habits, all indicate hominoids aren't as committed to a cautious climbing complex as are sloths or lorisines. All the other distinguishing characters of the locomotor anatomy and lifestyle of hominoids in common with these other groups, indicate an ancestry with a level of commitment slightly more than, or comparable to that of atelines. The spatulate central incisors shared by all great apes is a frugivorous dental character that also argues for a less committed folivorous ancestry. Whether ancestral hominoids ever possessed the shearing crests, thin enamel and high

crowns seen in the folivorous forms is up to fossil record to answer. Nevertheless, all hominoids do exhibit a number of shared ancestral traits associated with folivory.

The Fossil Record

Oreopithecus the only Miocene fossil catarrhine which has postcranial adaptations that would be expected in a hominoid ancestor (Sarmiento 1987), has an ornate dental morphology of a browser (Simons, 1972). This is considered by some to be too specialized to have given rise to the dentition of humans and great apes (Szalay and Delson 1979). This is despite the fact that it too has relatively low cusps, and thick enamel, and that its premolar canine complex is very similar in detail to that of the earliest australopithecines (Sarmiento, 1987). As outlined in this study its supposedly 'specialized dentition' indicating folivorous dietary adaptations, is just what would be expected in a hominoid ancestor of great apes and humans. Both its postcranial adaptations and its dental anatomy (Sarmiento, 1987) suggests that selection for a cautious climbing folivorous complex had already been operating for some time. Earlier hominoids or those that had just begun to differentiate from cercopithecoids can not be expected to show as committed a hominoid morphology.

The subsequent origin of African apes and humans from the hominoid ancestor is a point which has not been addressed in this study. Differences in the shared derived characters of living hominoids versus those of hominids and African apes does not indicate there would be *marked* differences between the last common ancestor of each of the two groups. Considering morphological links between folivory, hard object feeding and Jolly's seed eating complex, the impetus for increased terrestriality in human and African ape ancestors may just as likely have been the exploitation of seeds and consequently grains and other small food objects. The subsequent divergence of chimpanzees and gorillas may have been based on moving away from what would become the hominid resource. In this regard, it may be difficult to recognize the most recent African ape human ancestor or the early chimpanzee and gorilla ancestors as separate from hominids. At least dentally they probably would show smaller canines and the large molars of a folivore turned granivore.

Testing the Model

As noted by Jolly (1970) the nature of an evolutionary model is such that it cannot be readily tested experimentally. Its major test lies in its plausibility. It must organize the data from comparative anatomy, behavior and the fossil record comprehensively with a minimum of justifications. The model presented here achieves this goal accounting for shared hominoid features in locomotor anatomy, visceral anatomy, diet, lifestyle, behavior, reproduction, dental traits and fossil evidence. Additional tests for this model can come from additional examination of parallel adaptations in other living forms.

According to this study a closer analogy than that made by Jolly (1970) between *Theropithecus* and hominids should exist between humans and a folivore that has become a seed eater and a small object feeder. Although its divergence from *Papio* may be analogous to the divergence of *Homo* from *Pan*, *Theropithecus* lacks the folivorous ancestry for developing the hominid features. In this regard, one of the more northerly distributed genera of colobines *Rhinopithecus* has been observed consuming as much as fifty percent of its diet terrestrially as seeds, herbs and other small food objects (Bleisch personal communication). As such, it can be used to further test the proposed model. Its similarity to hominids has been remarked on as early as Gregory (1922) and recently by Peng *et al* (1985). Cranially it

exhibits, an inferiorly oriented foramen magnum, a short basisphenoccipital, markedly large, quadrate and mesiodistally crowded molars, tympanic vagina, an ossified styloid, a relatively deep glenoid fossa, lateral position of the postglenoid process so as to align with the tympanic plate, orthognathic face, the development of a supraorbital bar, eyes set far apart associated with superoanteriorly shifted ethmoid, and slight postorbital constriction, Females also show a parabolic dental arcade, a small canine and the total absence of a diastema. All of these features are characteristic of the hominid family (Jolly 1970; Sarmiento in prep.). Notably, as meured from twelve skulls, it has a very large cranial capacity relative to body size. Further work on the anatomy and behavior of this poorly know form as well as that other primates and convergent non-primate mammals may further serve to test the proposed model.

References

Aiello A., 1978. *Sloth hair unanswered questions*. In (G.G. Montgomery ed.). *The ecology of arboreal folivores*. pp. 213-218 Washington DC: Smitsonian Institution Press.

Ankle F., 1966. *Morphologie von Wiberlsaule und Brustkorb*. Biblio. Primatol. no. 4, Basel: Karger

Andrews P.J. and Tekkaya, 1980. *A revision of the turkish Miocene Hominoid* Sivapithecus metai. Palaeontology 23:85-95.

Ashton E.H. and Oxnard C.E., 1964. *Functional adaptations in the primate shoulder girdle*. Proc. Zool. Soc. London. 142:49-66.

Baldwin L.H. and Teleki G., 1976. *Patterns of gibbon behavior on Hall's Island Bermuda*. In (D.M. Rumbaugh ed.). Gibbon and Siamang vol 4 pp. 21-105 Basel: S. Karger.

Bauchop T., 1978. *Digestion of leaves in vertebrate arboreal folivores*. In (G.G. Montgomery ed.). The ecology of arboreal folivores, pp.193-204. Washington DC: Smithsonian Institution Press.

Bauchop T. and Martucci R.W., 1968. *Ruminant-like digestion of the langur monkey*. Science 161:698-700.

Beebe W., 1927. *The three toed sloth* Bradypus cuculliger cuculliger Zoologica vol. 7 #1

Bishop N.H., 1979. *Himalayan langurs: Temperate colobines*. J. Hum. Evol 8:251-281.

Bleisch W., Cheng A., Ren X., and Xie J., 1993. *Preliminary results from a field study of wild Guizhou snub-nosed monkeys*, Rhinopithecus brelichi. Folia primatol. 60: 72-82.

Britton S.W., 1941. *Form and function in the sloth*. Quart. Rev. Biol. 16:13-34, 190-207

Cant J.H., 1986. *Locomotor and feeding postures of spider and howling monkeys: Field study and evolutionary interpretation* Folia Primatol. 49:90-105.

Carpenter C.R. and Durham M.N., 1969. *A preliminary description of suspensory behavior in nonhuman primates*. Proc. 2nd Int. Congr. Primatol. Atlanta, vol.2 pp. 147-154. Basel: Karger.

Cartmill M., 1974. *Pads and claws in arboreal primate locomotion*. In (F.A. Jenkins Jr. ed.). Primate Locomotion, pp. 45-83. New York: Academic Press.

Cartmill M., 1979. *The volar skin of primates: Its frictional characteristics and their functional significance*. Amer. J. Phys. Anthrop. 50: 497-510.

Cartmill M. and Milton K., 1977. *The lorisiform wrist joint and the evolution of brachiating adaptions in the Hominoidae*. Amer. J. Phys. Anthrop. 47: 249-272.

Chalmers Mitchel P., 1905. *On the intestinal tract of mammals* Trans. Zool. Soc. London 17:437-536.

Charles-Dominique P., 1974. *Ecology and feeding behavior of five sympatric species of lorisids in Gabon*. In (R.D. Martin, G.A. Doyle, and A.C. Walker ed.) Prosimian Biology, pp.131-150. Pittsburgh: University of Pittsburgh press.

Charles-Dominique P., 1977. *Ecology and Behavior of Nocturnal Primates*, New York: Columbia University

press.

Chapman C., 1987. *Flexibility in the diets of three species of Costa Rican primates.* Folia Primatol. 40:90-105.

Chivers D.J., 1974. *The Siamang in Malaysia. A Field Study of a Primate in a Tropical Rain Forest.* Contr. Primatol. vol. 4 Basel: Karger.

Chivers D.J., 1977. *The lesser apes.* In (H.S. Rainier and G.H. Bourne, eds.) Primate Conservation, pp. 539-598. New York: Academic press

Clutton-Brock T.H. and Harvey P.H., 1977. *Primate ecology and social organization.* Journal of Zoology (London). 183:1-39.

Conroy G.C. and Fleagle J.G., 1972. *Locomotor behaviors in living and fossil pongids.* Nature 237:103-104.

DeBonis L. and Melentis J., 1980. *Nouvelles remarques sur l'anatomie d'un primate hominoide du Miocene Ouranopithecus macedoniensis Implications sur la Phylogenie des hominoides.* Cr. Acad. Sci. Paris, 290:755-758.

Defler T.R., 1987. *Ranging and the use of space in a group of woolly monkeys (Lagothrix lagothricha)* in the NW Amazon of Columbia. Int. J. Primatol. 8:420.

Deniker J., 1885. *Recherches anatomiques et embryologiques sur les singes anthropoides: Foetus de Gorille et de gibbon.* Arch Zool. Exp. Gen. ser. 2,3. Suppl. 1-265

Deniker J. and Boluart H. 1886. *Les sacs laryngiens des singes anthropoides* Journal de l'Anatomie et de la Physiologie. Paris 22: 51-62.

Dixson A.F., 1982. *The Natural History of the Gorilla.* New York: Columbia Univ. press.

Doran D.M., 1989. *Chimpanzee and pygmy chimpanzee positional behavior: The influence of body size, morphology and ontogeny on locomotion and posture.* Ph.D. Thesis, Stony Brook: SUNY.

Doran D.M., 1992. *Comparison of instantaneous and locomotor bout sampling methods: A case study of adult male chimpanzee locomotor behavior and substrate use.* Am. J. Phys. Anthrop. 89:85-99

Doyle G.A. and Bearder K.S., 1977. In (H.S. Rainier and G.H. Bourne, eds.) *Primate Conservation,* pp. 2-37. New York: Academic press

Dykyj D., 1980. *Locomotion of the slow loris in a designed substrate context.* Amer. J. Phys. Anthrop. 52:577-586.

Eaglen R.H., 1984. *Incisor size and diet revisited: The view from a platyrrhine perspective.* Am. J. Phys Anthrop. 64:263-275

Eggeling von H., 1896. *Zur Morphologie des Dammmuskulatur.* Morph. Jahrb. Bd. 24:311-631.

Eggeling von H., 1920. *In wie weit is der Wurm fortsatz am menschlichen blindarm ein rudimentares Gebilde.* Anat. Anz. Bd. 53:401-428.

Eisenberg J.F., 1977. *Comparative ecology and reproduction of New World monkeys.* In (D.G. Kleiman, ed.) The Biology and Conservation of the Callithricidae, pp. 13-22. Washington D.C.: Smithsonian Inst. Press.

Eisenberg J.F. and Maliniak, E. 1978. *Reproduction by two-toed sloth Choloepus hoffmani in captivity.* Amer. Assoc. of Mammalogist Abstr. Tech. Pap. 58th Annual meeting pp. 41-42.

Elftman H., 1932. *Evolution of the pelvic floor of primates.* Am. J. Anat. 51:307-346.

Elftman J.F. and Atkinson W.B., 1950. *The abdominal viscera of the gorilla.* In (W.K. Gregory ed.) Anatomy of the Gorilla, pp. 197-204. New York: Columbia University press.

Ellefson J.O., 1974. *A natural history of white-handed gibbons in the Malayan penninsula.* In (D.M. Rumbaugh ed.) Gibbon and Siamang, vol. 3, pp.1-136. Basel: Karger.

Erikson G.E., 1963. *Brachiation in New World monkeys and in anthropoid apes.* Symp. Zool. Soc. London 10: 135-164.

Estrada A., 1984. *Resource use by Howler monkeys in the rain forest of los Tuxtlas, Vera Cruz, Mexico.* Int. J. Primatol. 5: 105-131.

Etter H.F., 1973. *Terrestrial adaptations in the hands of the cercopithecinae.* Folia primato. 20: 331-350.

Etter, H.F., 1974. *Morphologisches und metrisches vergleichende Untersuchung am Handskelett rezenten Primaten.* Gegenb. Morpholo. Jb., 120: 153-171.

Fick R., 1895. *Vergleichend anatomische studien an einem erwachsenen orang-utang.* Arch. Anat. Physiol., Anat Abth., 1-96.

Fleagle J.G., 1976a. *Locomotion and posture of the Malayan siamang and implications for hominoid evolution.* Folia Primatol. 26: 245- 269.

Fleagle J.G., 1976b. *Locomotion, posture and habitat utilization in two sympatric Malaysian leaf monkeys (Presbytis obscura and Presbytis melalophus)* Yrb. Phys. Anthrop. 20:243-251

Fleagle J.G., 1977. *Locomotor behavior and muscular anatomy of sympatric Malaysian leaf monkeys.* Amer. J.

Phys. Anthrop. 46:297- 307.

Fleagle J.G., Stern J.T., Jungers W.L., Susman R.I., Vangor A.K. and Wells J., 1981. *Climbing a biomechanical link with brachiation and bipedalism* Symp. Zool. Soc. London 48:359-373.

Fooden J., 1963. *A revision of the woolly monkeys* (genus Lagothrix) J. Mammal. 44:213-247

Fooden J., 1964. *Stomach contents and gastrointestinal proportions in wild shot Guianan monkeys.* Amer. J. Phys. Anthrop. 22:227-232

Ford S.M., 1980. *A systematic revision of the platyrrhinni based on features of the postcranium.* Ph.D. Thesis, Univ. of Pittsburgh.

Ford S.M. and Davis L.C., 1992. *Systematics and body size: Implications for feeding adaptations in New World monkeys.* Amer. J. Phys. Anthrop. 88(4): 415-468.

Forster A., 1917. *Die muscle contrahentes und interosei manus in der saugetierreihe und beim menschen.* Arch. Anat. Physiol., Anat. Abt. 101-378.

Forster A., 1918. *Zur anatomie des primaren peritoneumfalten des Calcalapparates und der recessus ileo-calcalis.* Arb. Anat. Inst. Weisbaden 56:1-170

Fossey D., 1974. *Observations on the home range of one group of mountain gorillas (Gorilla gorilla beringei).* Anim. Behav. 22:568- 581.

Fossey D. and Harcourt A.H. 1977. *Feeding ecology of free-ranging mountain gorillas (Gorilla gorilla beringei).* In (T.H. Clutton- Brock ed.) *Primate Ecology*, pp. 415-499. London: Academic press.

Galidikas-Brindamour B.M.F., 1979. *Orang-utan adaptation at Tanjung Puting Reserve: Mating and Ecology.* In (D.R. Hamburg and E.R. McCown eds.). *The Great Apes*, pp. 194-233. Menlo Park: Benjamin Cummings.

Gaulin S.J.C., 1979. *A Jarman/bell model of primate feeding niches.* Human Ecol. 7:1-19.

Gaulin S.J.C. and Konner, M., 1977. *On natural diet of primates, including humans.* In (R.J. Wurtman and J.J. Wurtman eds.). Nutrition and the Brain, pp. 1-86. New York: Raven press.

Gaulin S.J.C. and Gaulin C.K., 1982. *Behavioral ecology of Alouatta seniculus in Andean cloud forrest.* Int. J. Primat. 3:1-32.

Gautier-Hion A., 1978. *Food niches and coexistence in sympatric primates in Gabon.* In (D.J. Chivers and J. Herbert eds.). Recents Advances in Primatology vol.1 Behavior, pp. 269-286. New York: Academic press.

Gautier Hion A. and Emmons, L.H. and Pobost, G., 1980. *A comparison of the diet of 3 major groups of primary consumers of Gabon (Primates squirrels and ruminants)* Oecologia (Berlin) 45:182-189

Gebo D.L., 1986. *The anatomy of the prosimmian foot and its application to the primate fossil record.* Ph.D. thesis. Duke University.

Gebo D.L., 1989. *Postcranial adaptations and evolution in the lorisidae.* Primates 30(3):347-367.

Gittleman J.L. and Thompson S.D., 1988. *Energy allocation in mammalian reproduction.* Am. Zool. 28:863-868.

Gittins J.P. and Raemakers J.J., 1980. *Siamang, lar and agile gibbons.* In (D.J. Chivers ed.). Malayan Forrest Primates, pp. 63- 105 New York:Plenum press.

Glander K.E., 1978. *Howling monkey feeding behavior and plant secondary compounds: a study of strategies.* In (G.G. Montgomery ed.) The ecology of arboreal folivores. pp. 561-574. Washington DC: Smithsonian Institution Press,

Glander K.E., 1982. *The impact of plant secondary compounds on primate feeding behavior.* Yrbk. of Phys. Anthrop. 25:1-18.

Goodall J., 1986. *The chimpanzees of Gombe Patterns of Behavior.* Cambridge: Harvard Univ. Bellknap press.

Godfrey L.R., 1991. *How big were the giant lemurs of Madagascar?* Am. J. Phys. Anthrop. Suppl. (Abstract) 12:80.

Godfrey L.R. Simons, E.L., Chatrath, P.S., and Rakotosamimanana B., 1990. *A new fossil lemur (Babakoia, Primates) from Northern Madagascar.* C.R.S. Acad. Sci. Paris 310:81-87.

Gordon K.D., 1980. *Dental attrition in the chimpanzee (Pan troglodytes verus): a scanning electron microscope study.* Ph.D. Thesis, Yale.

Greenfield L.O. and Washburn, A. 1991. *Polymorphic aspects of male anthropoid canines.* Amer. J. Phys. Anthrop. 84(1):17-34.

Greenfield L.O., 1992. *A non-adaptive dental trait.* Int. J. Primatol. 13: 631-657.

Gregory W.K., 1922. *Origin and Evolution of the Human Dentition.* Baltimore: Williams and Wilkins.

Gregory W.K., 1934. *Man's place among the anthropoids.* Oxford: Clarendon Press.

Gregory, W.K. and Raven, H.C., 1937. *In Quest of Gorillas.* New Bedford, Mass: Darwin Press,

Harcourt A.H., Fossey D., Stewart K.T., and Watts D.D., 1980. *Reproduction in wild gorillas and some comparisons with chimpanzees.* J. Reprod. Fert., Suppl. 28: 59-70.

Hasewaga M., Kishino H. and Yano T., 1984. *Estimation of branching dates among primates by molecular clocks*

of nuclear DNA which slow down in Hominoidea. J Hum. Evol. 18:461-476.

Hasewaga M., Kishino H. and Yano T. 1985. *Dating of the human ape split by a molecular clock of mitochondrial DNA.* J. Hum. Evol. 22:16-174.

Hildwein G. and Goffart M., 1975. *Standard metabolism and thermoregulation in a prosimian Perodicticus potto.* Comp. Biochem. Physio. A: Comp. Physio. 50:201-213.

Hill C.A., 1967. *A note on the gestation period of the siamang Hylobates syndactylus. Int. Zoo Yrbk.* 7:93-94.

Hill W.C.O., 1953. *Primates: Comparative Anatomy and Taxonomy. I. Strepsirrhini.* Edingburgh: Edingburgh Univ. Press.

Hill W.C.O., 1962. *Primates: Comparative Anatomy and Taxonomy. V. Cebidae* Part B. Edingburgh: Edingburgh Univ. Press.

Hill W.C.O., 1970. *Primates: Comparative Anatomy and Taxonomy, VII.Cynopithecidae,* New York: Wiley.

Hladik C.M., 1977. *Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on the diet* In (T.H. Clutton-Brock ed.). Primate Ecology, pp.481-501. New York: Academic press.

Hladik C.M., 1978. *Adaptive strategies in primates in relation to leaf eating.* In (G.G. Montgomery ed.). The ecology of arboreal folivores, pp.215-254. Washington DC: Smitsonian Instituition Press.

Hladik C.M. and Hladik A., 1972. *Disponibilities alimentaires et domaines vitaux des primates a Ceylon.* Terre Vie. 26:149-215

Holme E.C., Pesole G., and Saccone C., 1989. *Stochastic models of molecular evolution and estimated phylogeny of nucleotide substitutions in the hominoid primates.* J. Hum. Evol. 18:775-799.

Hooton E.A., 1946. *Up From The Ape.* New York: MacMillan.

Hunt K.D., 1989. *Positional behavior in Pan troglodytes at the Mahale mountains and the Gombe stream national parks, Tanzania.* Ph.D. Thesis. Univ. of Michigan.

Huntington G.S., 1903. *The anatomy of the Human Peritoneum and Abdominal Cavity Considered from the Standpoint of Development and Comparative Anatomy.* New York: Philadelphia press.

Huxley T.H., 1964. *The structure and classification of the Mammalia.* The Medical Times and Gazette. Vol. 1 and Vol. 2

Izard M.K., 1987. *Lactation length and three species of galago.* Am. J. Phys. Anthrop.

Izard M.K. and Rasmussen T.D., 1985. *Reproduction in the slender loris (Loris tardigradus malabaricus)* Amer J. Primat. 8:153-165.

Izawa K., 1987, *Group sizes and composition of primates in the upper Amazon basin.* Primates 17:367-399.

Jablonski N.G., 1992. *Upper limb morphology and locomotion in the Yunnan snub-nosed langur. Rhinopithecus bieti.* Am. J. Phys. Anthrop. Suppl. (Abstract) 14:94.

Jacobs-Lagen E., 1923. *Das Schgleimhaut relief des Prosimien- Rumpfdarma mit beitrager zur kenntnis der Kerkringschen Faltensysteme der Anthropoiden und des Menschen.* Jan. Zschr. Naturwies. 64:1-90

Jansen D.H., 1978. *Complications in interpreting the chemical defenses of trees against tropical arboreal plant-eating vertebrates.* (In G.G. Montgomery ed.). The ecology of arboreal folivores, pp.73-84. Washington DC: Smitsonian Institution Press.

Jenkins F.A. Jr., 1970. *Anatomy and function of expanded ribs in certain edentates and primates.* J. Mammal. 51:288-301.

Jenkins F.A. Jr., 1981. *Wrist rotation in primates: a critical adaptation for brachiators.* Symp. Zoo. Soc. London vol. 48, pp. 429-451.

Jolly C.J., 1970. *The seed-eaters: A new model of hominid differentiation based on a baboon analogy.* Man 5:5-26.

Jolly C.J., 1972. *The classification and natural history of Theropithecus (Simopithecus)(Andrews 1916) baboons of the African Plio-pleistocene.* Bull. Brit. (Nat. Hist.) Mus. Geol. 22:1-122.

Jolly C.J. and Gorton J.T., 1974. *Proportions of the extrinsic foot muscles in some lorisoid prosimians.* In (R.D. Martin, G.A. Doyle, and A.C. Walker, eds.). Prosimian Biology, pp. 801-811 Pittsburgh: University of Pittsburgh press.

Jones C. and Sabater Pi J., 1971. *Comparative ecology of Gorilla gorilla (Savage and Wyman) and Pan troglodytes (Blumenbach)in Rio Muni, West Africa.* Biblio. Primat. No. 13 Karger, Basel

Jouffroy F.K. and Lessertisseur J., 1959. *Reflexions sur les muscles contracteurs des doigts et des ortiels (Contrahentes digitorum) chez les primates.* Ann. des Sc. Nat. Zool., Ser. 12, 1: 211-235.

Jouffroy F.K. and Lessertisseur J., 1960. *Les specialisations anatomiques de la main chez les singes a progression suspendue.* Mammalia 24: 93-151.

Jungers W.L., 1977. *Hindlimb and pelvic adaptations to vertical climbing and clinging in Megaladapis, a giant sub-fossil prosimian from Madagascar.* Yrbk. Phys. Antrhop. 53:471-478.

Jungers W.L., 1978. *The functional significance of skeletal allometry in Megaladapis in comparison to living*

prosimians. Amer. J. Phys Anthrop. 49:303-314.

Jungers W.L., Godfrey L.R., Simons E.L., Chatrath P.S. and Rakotosamimanana B., 1991. *Phylogenetic and functional affinities of Babakotia (Primates) a fossil lemur from northern Madagascar.* Proc. Nat. Acad. Sci. USA 88:9082-9086.

Juraniec J.and Szostakiewicz-Sawicka H., 1968. *The central tendon of the diaphragm in primates.* Folia Morphol. 27:183-194.

Kano T., 1983. *An ecological study of the pygmy chimpanzees (Pan paniscus) of Yalosidi, Republic of Zaire.* Int. J. Primatol. 4(1):1- 31.

Kavanagh M. and Dresdale L., 1975. *Observations on the wooly monkey (Lagothrix lagothricha) in Northern Colombia* Primates 16:285-294.

Kay R.F., 1978. *Molar structure and diet in extant Cercopithecidae.* In (P.M. Butler and K.A.Joysey eds.). Development, Function and Evolution of Teeth, pp. 309-339. London: Academic Press.

Kay R.F., Fleagle J.G. and Simons E.L., 1981. *A revision of the Oligocene apes of the Fayum Province Egypt.* Am. J. Phys. Anthrop. 55:293-322

Kay R. F. and Hylander W.L., 1978. *The dental structure of mammalian follivores with special reference to primates and phalangeroids (Marsupalia).* In (G.G. Montgomery ed.): The ecology of arboreal folivores. pp.173-192. Washington DC: Smithsonian Institution Press.

Kay R. F., Plavacan J.M., Glander K.E, and Wright P.C., 1988. *Sexual selection and canine dimorphism in New World primates.* Amer. J. Phys Anthrop. 77:385-397.

Keith A., 1903. *The extent to which the posterior segments of the body have been transmuted and suppressed in the evolution of man and allied primates.* J. Anat. Physiol., London. 37: 18-40.

Keith A., 1912. *Certain phases in the evolution of man.* Brit. Med. J. 1: 734-737, 788-790.

Keith A., 1923. *Man's posture: Its evolution and disorders.* Brit. Med. J. 1:451-54, 499-502, 545-48, 587-90, 624-26, 669-72.

Keith A., 1934. *The Construction of Man's Family Tree.* Watts, London.

Klatsch H., 1913. *Die erwerbung der auftrehen haltung un ihre folgen.* Anat. Anz. suppl. 44:161-186.

Klein L.L. and Klein D.J., 1977. *Feeding Behavior of the Columbian spider monkey.* In (T.H. Clutton-Brock ed.) Primate Ecology, pp. 154-181. London: Academic press.

Kortlandt A., 1968. *Handgebrauch bei Freilebenden Shimpansen.* In (B. Rensch ed.). Handgebrauch und Verstandigung bei Affen und Fruhmenschen, pp.59-102. Bern: Hans Huber.

Kostanecki K., 1926. *Le caecum des vertebres.* Bull. Int. Acad. Cracovie Cl. Sci. Nat. Suppl.

Lamarck J.B.. 1809. *Philosophie Zoologique ou Exposition des considerations relative al'Histoire Naturelle des Animaux etc.* Paris: J.B. Ballier.

Lamberton C.L., 1947. *Contribution a la connaissance de la faune subfossile de Madagascar. Note XVI: Bradytherium ou Paleopropithique?* Bull. Acad. Malagache (Nuov. Ser.) 26:89-140.

Langer P., 1988. *The Mammalian Herbivore Stomach. Comparative anatomy, Function and Evolution.* Stuttgart: Gustav Fischer.

Leakey R.E.F. and Walker A., 1985. *New higher primates from the early Miocene Buluk, Kenya* Nature 318: 173-175.

Leakgul B. and McNeely J.A. 1977. *Mammals of Thailand.* Bangkok li: Sahakarnbhat.

Leidel G., 1940. *Zur Anatomie des Anthropmorphes herzen.* Morph. Jb 84:457-490.

Lemos de Sa R.M. and Glander K.E., 1993. *Capture techniques and morphometrics for the wooly spider monkey or muriqui (Brachyteles arachnoides).* Am. J. Primatol. 29:145-153.

Leo Luna M., 1981. *First field study of the yellow tailed wooly monkey Oryx* 15:386-389

Lewis O.J., 1969. *The hominoid wrist joint.* Amer. J. Phys. Anthrop. 30: 251-267.

Lessertisseur J., 1958. *Doit-on distinguer deux plans de muscles interosseux a la main et au pied des primates?* Ann. Sci. Nat. Zool. Biol. Anim. Ser. 11, 20: 77-103.

Lineback P., 1933. *The respiratory digestive and urinary system* In (C. Hartman and W.L. Straus eds.) Anatomy of the Rhesus monkey pp 210-230. Baltimore: Williams and Wilkins.

Loghem van J.J., 1904. *Das Colon und Mesocolon der Primaten.* Petrus Camper Nederlandische Bijdragen tot de Anatomie 2:350-347.

Lorin-Epstein M.J., 1932. *Evolution und Bedeutung des wurmfortsatzes und der valvula ileocecalis im Zusammanhang mit der Aufrichtung des Rumpfes.* Zschr. Anat. und Entwick. 97:68-144.

Loth E., 1908. *Die aponeurosis plantaris in der Primatereihe. Mit spezieller Berucksichtingung des Menschen.* Morph. Jahrb. 38:194- 322.

Lovejoy C. O., 1981. *The origin of man.* Science 211:341-351

MacArdle, J.E., 1981. *Functional Morphology of the hip and thigh of the Lorisiformes.* Contr. Primatol. vol. 17 Basel: Karger.

MacKenzie J.M.D., 1929. *Food of the slow loris Nycticebus coucang.* J. Bombay nat. Hist. Soc. (1929):971-1000

MacKinnon, J.R., 1974. *The behavior and ecology of wild orang-utans (Pongo pygmaeus).* Anim. Behav. 22: 3-74.

MacKinnon J.R. and MacKinnon K.S., 1978. *Comparative feeding ecology of 6 sympatric primates in West Malaysia.* In (D.J. Chiver and J. Herbert eds.). Recent Advances in Primatology, pp. 305-321. New York: Academic press.

Mac Phee R.D. and Vuillaume-Randriamanantana M., 1984. *Hand and foot of Paleopropithecus, anatomy and function.* Amer. J. Phys. Anthrop. Abstract 63:189.

Makintosh H. W., 1875. *On the muscular anatomy of Choloepus didactylus.* Proc. Roy. Irish Acad. 2nd ser. 2:66-78.

Martin R.D., 1990. *Primate origins and evolution.* New Brunswick: Princeton University Press.

Marzke M.W., 1971. *The origin of the human hand.* Amer. J. Phys. Anthrop. 34: 61- 84.

McHenry H.M. and Temerin L.A., 1979. *The evolution of human bipedalism: Evidence from the fossil record.* Yrbk. Phys. Anthrop. 22:105-131.

McKey D.B., 1978. *Soils vegetation and seed eating by black colobus monkeys.* In (G.G. Montgomery ed.). The ecology of Arboreal Folivores, pp. 423-427. Washington DC: Smitsonian Instituition Press.

McKey D.B., Gartlan J.S., Watterman P.G. and Choo G.M., 1981. *Food selection by black colobus monkey (Colobus satanas) in relation to plant chemistry.* Biol. J. Linn. Soc. 16:115-146.

McKnab B.K., 1978. *Energetics of arboreal folivores.* In (G.G. Montgomery ed.) The ecology of arboreal folivores, pp. 153-162. Washington DC: Smithsonian Institution Press,

McKnab B.K., 1980. *Food habits and energetics and the population biology of mammals* Am. Nat. 116:106-124.

McKnab B.K., 1986. *The influence of food habits on the energetics of eutherian mammmals* Ecol. Mono. 56(1):1-19.

Meinke F., 1911. *Morphologisches untersuchungen uber die myologie an den extremitaten bei Bradypus trydactylus.* Morph. Jb. 42: 309-360.

Mendel F.C., 1979 *The wrist joint of two-toed sloths and its resemblance to brachiating adaptations of the Hominoidea.* J. Morph. 162: 413-424.

Mendel F.C., 1981a. *Use of Hands and feet in two toed Sloths, Choloepus hoffmani during climbing and terrestrial locomotion.* J. Mammalogy 62:413 421

Mendel F.C., 1981b. *Hand of two-toed sloth: Its anatomy and potential use relative to the size of the support.* J. Morphology 169:1-19.

Mendel F.C., 1985. *Use of hands and feet in three toed Sloths, Bradypus tridactylus during climbing and terrestrial locomotion.* J. Mammalogy 66:359-366

Midlo C., 1934. *Form of hand and foot in primates.* Am. J. Phys Anthrop. (o.s.) 19: 337-389.

Miller R.A., 1939. *Functional adaptation in the forelimb of the sloth* J.Mammal. 16:38-51

Milton K., 1980. *Foraging strategy of howler monkeys.* New York: Columbia Univeristy press.

Milton K., 1984. *Habitat, diet and activity patterns of free- ranging wooly spider monkeys (Brachyteles arachnoides E. Geoffroy 1906)* Int. J. Primatol. 5:491-514.

Milton K., 1985. *Multimale mating and absence of canine tooth dimorphism in wooly spider monkeys (Brachyteles arachnoides)* Amer. J. Phys. Anthrop. 68:519-523.

Mittermeier R.A., 1978. *Locomotor posture* in Ateles geoffroy and Ateles paniscus. Folia primatol. 30:161-193.

Mittermeier R.A. and Coimbra-Filho A.F., 1977. *Primate conservation in Brazilian Amazonia.* In (H.S. Rainier and G.H. Bourne eds.). Primate Conservation, pp. 117-166. New York: Academic Press.

Mivart St. G., 1866. *Contributions towards a more complete knowledge of the skeleton of primates. Part I The appendicular Skeleton of Simia.* Trans. Zool. Soc. London (1886):175-225.

Mivart St. G., 1867. *On the appendicular skeleton of primates.* Phil. Trans. Roy. Soc. London. 157:299-429.

Mivart St. G. and Murie J. 1865. *Observation on the anatomy of Nycticebus tardigradus.* Proc. Zool. Soc. London. (1865):240-256

Montgomery G.G., and Sunquist M.E., 1978, *Habitat selection and use by two-toed and 3 toed sloths.* In (G.G. Montgomery ed.). The ecology of arboreal folivores, pp.329-359. Washington DC: Smithsonian Instituition Press.

Morrison P.R., and Sinois J. Jr., 1962. *Body temperature in two Brazilian primates.* Boletin de Faculdad de Filosofia, Ciencias y Letras Universidad de Sao Paulo 24:167-178

Morgan E., 1972. *The Descent of Woman.* New York: Stein and Day

Morton D.J., 1924, *Evolution of the human foot.II.* Amer. J. Phys.Anthrop. 7: 1-52.

Morton D.J. and Fuller D.D.,1952. *Human Locomotion and Body Form. A study of Gravity and Man.* Baltimore:

Williams and Wilkins Co.

Muller E.F., 1979. *Energy metabolism thermoregulation and water budget in the slow loris Nycticebus coucang* Comp. Biochem physio. A: Comp. Physio. 64:109-119.

Muller E.F., Kazan J.M.Z. and Maloiy G.M.O., 1983. *Comparative study of the basal metabolism and thermoregulation of a folivorous (Colobus guereza) and an omnivorous (Cercopithecus mitis) primate species.* Comp. Biochem Physio. a: Comp. Physio 74:319-322.

Nadler R.D., Graham C.E. and Kling O.R., 1981. *Postpartum amenorrhea and behavior of apes.* In (C.E. Graham ed.). Reproductive Biology of the Great Apes, pp 69-81. New York: Academic press.

Nagy K.A. and Montgomery G.G., 1980. *Field metabolic rate water flux and food consumption in three toed sloth B. variegatus.* J. Mammal. 61:465-472.

Napier J.R., 1963. *Brachiation and brachiators* Symp. Zool. Soc. London 10:183-194

Napier J.R. and Napier P.H., 1967. *A Handbook of Living Primates.* New York: Academic press.

Narath A., 1901. *Der bronchialbaum der Saugetheire in des Menschen.* Bibl. Med. Stuttgart Abt A. Heft 3:1-380

Nash and Harcourt A.H., 1986. *Social organization of galagos in Kenyan Wasta forrest.* Amer. J. Primatol. 10:357-69

Nicoll M.E. and Thompson S.D., 1987. *Basal metabolic rates energetics and reproduction in Therian mammals marsupials and placentals compared.*In (A.S. Loudon and P. A. Racey eds.) Reproduction Energetics in Mammals, pp. 7-24. Oxford: Clarendon press.

Nishimura A., 1990. *A sociological and behavioral study of wooly monkeys Lagothrix lagothricha in the Upper Amazon.* Sci. Eng. Rev. Doshisha University 31:87-121.

Nowack R.M., 1991. *Walker's Mammals of the World.* 5th ed. Baltimore: John Hopkins Univ. press.

Oates J.F., 1977a. *The guereza and its food.* In (T.H. Clutton-Brock ed.) Primate Ecology. pp. 276-321. London: Academic press.

Oates J.F., 1977b. *The guereza and man.* In (H.S. Rainier and G.H. Bourne, eds.) Primate Conservation, pp. 419-467. New York: Academic press.

Oates J.F., 1978. *Water-plant and soil consumption by guereza monkeys (Colobus guereza): a relationship with mineral and toxins in the diet?* Biotropica 10:241-253.

Owen R., 1835a. *On the osteology of the chimpanzee and the orang- utan.* Trans. Zool. Soc. London I:343-380.

Owen R., 1835b. *On the saculate form of the stomach as it exits in the genus Semnopithecus.* Trans. Zool. Soc. London I:65-70.

Parra R., 1978. *Comparison of hindgut and foregut fermentation in herbivores.* In (G.G. Montgomery ed.). The ecology of arboreal folivores, pp.205-230.. Washington DC: Smithsonian Instituition Press.

Peng Y., Ye Z., Zhang Y., Liu R., 1985. *Observations on the position of the genus Rhinopithecus in phylogeny.* Acta Theriol. Sinica 5:173-181.

Petter J.J. and Hladik C.M., 1970. *Observation sur le domaine vital et la densite de population de Loris tardigradus dans le forest de Ceylon,.* Mammalia 34:394-309.

Polak C., 1908. *Die anatomie des genus Colobus.* Verh. Konniklijke Akad. Wetenshappen te Amsterdam II (14) 2:139-154.

Primrose A., 1899. *The anatomy of the orang-utang (Simia satyrus).* Trans. Roy. Soc. Canad. Inst. 6: 507-598.

Prost J.H., 1965. *A definitional system for the classification of primate locomotion.* Amer. Anthrop. 67:1198-1214.

Prost J.H., 1980. *Origin of bipedalism.* Amer. J. Phys Anthrop. 52: 175-190.

Raven H.C., 1931. *The gorilla the greatest of all apes.* Nat. Hist. 31(3): 231-242.

Remane A., 1960. *Zahne und Gebiss.* Primatologia III(2):637-846 Basel: Karger.

Richard A. F. and Nicoll M.E., 1987. *Female social dominance and basal metabolism in Malagasy primates Propithecus verrauxi.* Amer. J. Primat. 12: 309-314.

Rijksen H.D., 1978. *A Field Study on Sumatran Orangutans,* Ecology Behavior and Conservation, Wagenigen.

Roberts D., 1974. *Structure and function of the primate scapula.* In (F.A. Jenkins ed.). Primate Locomotion, pp. 171-200. New York: Academic Press.

Robinson J.T., 1956. *The dentition of the Australopithecinea,* Transvaal Mus. Mem. 9.

Robinson J.T., 1972 *Early Hominid Posture and Locomotion.* Chicago: Univ. of Chicago.

Rodman P.S., 1973. *Population composition and adaptive organization among orangutans of the Kutai Reserve.* In (R.P. Michael and J.H. Crook eds.). Comparative Behavior and Ecology of Primates, pp. 171-209. New York: Academic Press.

Rodman P.S., 1979. *Feeding behavior of orang-utans of the Kutai Nature Reserve East Kalima.* In (D. Hamburg ed.). Perspectives of Human Evolution. Vol 4, pp 383-413. New York: Addison Wesley.

Rodman P.S., 1984. *Foraging and social systems of orang-utans and chimpanzees.* In (P.S. Rodman and J.H. Cant,

eds.). Adaptations for Foraging in Non-Human Primates, pp. 134-160. New York: Columbia Univ. press.

Rodman P.S. and McHenry H.M., 1980. *Bioenergetics and the origin of human bipedalism.* Amer. J. Phys. Anthrop. 52:103-106.

Roonwal M.L and Mohnot S.M., 1977. *Primates of South Asia: Ecology, Sociobiology and Behavior.* Cambridge: Harvard Univ. press.

Rose M.D., 1979. *Positional behavior of natural populations: some quantitative results of a field study of Colobus guereza and Cercopithecus aethiops* In (M.E. Morbeck, H. Preuschoft, N. Gomberg, eds.). Environment Behavior and Morphology. Dynamic Interactions in Primates, pp 75-94. New York: Fischer.

Rosenberger A.L., 1979. *Phylogeny, evolution and classification of New World monkeys.* Ph.D. Dissertation City Univ. New York.

Rosenberger A.L., 1992. *Evolution of feeding niches in New World monkeys.* Am. J. of Phys. Anthrop. 88(4):525-562.

Rosenberger A.L. and Strier K.B., 1989. *Adaptive radiations of the Ateline primates.* J. Hum. Evol. 18:717-750.

Rudran R., 1973. *The reproductive cycle of two species of langur with relation to environmental factors.* Folia Primatol. 19:41-60.

Ruge G., 1892. *Die Grenzlinien der Pleura-sacke un der Lagerung des Herzens bei Primaten inbesondere bei den Anthropoiden: Zuegnisse fur die metamere Verkurzung des Rumpfes.* Morph. Jb. 19:149-249.

Ruge G., 1910. *Grenzen der Pleurasacke der Affen und des Menschen.* Morph. Jb. 41:1-109

Sarich V.M. and Wilson A.C., 1967. *Immunological time scale for hominoid evolution.* Science 158:1200-1204.

Sarmiento E.E., 1983. *The significance of the heel process in anthropoids.* Int. J. Primatol. 4(2):127-152.

Sarmiento E.E., 1985. *Functional differences in the skeleton of wild and captive orang-utans and their adaptive significance.* Ph.D. Thesis New York University.

Sarmiento E.E., 1986. *The evidence for terrestrial quadrupedalism in the Hominid lineage.* Am. J. Phys. Anthrop. (Abstract) 66(1):226.

Sarmiento E.E., 1987. *The phylogenetic position of Oreopithecus and its significance in the origin of the Hominoidea.* Amer. Mus. Novitates # 2881

Sarmiento E.E., 1988. *Anatomy of the hominoid wrist joints, its evolutionary and functional implications.* Int. J. Primatol. 9:281- 345

Sarmiento E.E., 1991. *Functional and phylogenetic implications of the differences in the pedal skeleton of australopithecines.* Amer. J. Phys. Anthrop. (Abstract) 12:157-158.

Sarmiento E.E., 1994. *Terrestrial traits in the hands and feet of gorillas.* Amer. Mus. Nat. Hist. Novitates # 3091.

Sawalaschin M., 1911. *Der musculus flexor communis brevis digitorum pedis in der primatenreihe mit spezielier Berucksichtigung des Menschlichen varietaten.* Morphol. Jahrb. 42: 557-663.

Schaller G.B., 1963. *The Mountain Gorilla: Ecology and Behavior.* Chicago: Univer. Chicago press.

Schon Ybarra M.A., 1968. *The muscular system of the red howling monkey* U.S. Nat. Mus. Bull. 273:1-185.

Schon Ybarra M. A., 1984. *Locomotor postures of red howlers in deciduous forrest savanna.* Amer. J. Phys. Anthrop. 63:65-76.

Schon-Ybarra M. A., 1986. *Loud calls of adult male red howler monkeys (Alouatta seniculus).* Folia primatol. 48:284-316.

Schultz A.H., 1930. *The skeleton of the trunks and limbs of higher primates.* Hum. Biol., 2: 303-438.

Schultz A.H., 1936. Characters common to higher primates and characters specific to man. *Quart. Rev. Biol.* 11: 259-283; 425- 455.

Schultz A.H., 1937. *Proportions, variability and assymetries of the long bones of the limbs and clavicles of man and apes.* Hum.Biol., 9: 281-328.

Schultz A.H., 1942. *Growth and development of the proboscis monkey.* Bull. Mus. Comp. Zool. 89:277-314.

Schultz A.H.,1953. *The relative thickness of the long bones and the vertebrae in primates.* Amer.J.Phys.Anthrop., 11: 277-311.

Schultz A.H., 1956. *Postembryonic age changes.* Primatologia: 1: 887-964.

Schultz A.H., 1960. *Einege Beobachtungen und masse am skelet von Oreopithecus.* Z. Morph. Anthropol. 50:136-149.

Schultz A.H., 1961. *Vertebral column and thorax.* Primatologia 4(Lf. 5): 1-66.

Schultz A.H., 1963. *Relations between the lengths of the main part of the foot skeleton in primates.* Folia.Primat. 1:150-171.

Schultz A.H., 1968. *The recent hominoid primates* In (S.L. Washburn and P.C. Jay, eds.). Perspectives on Human Evolution *1*, pp. 122-195. New York: Holt, Rinehart and Winston, Inc.

Schwartz J.H., 1984. *The evolutionary relationships of man and orang-utans.* Nature 308:501-505.

Simons E.L., 1972. *Primate Evolution*. New York: MacMillan

Simons E.L., Godfrey L.R., Jungers W.L., Chatrath P.S., Rakotosamimanana B., 1992. *A new subfossil lemur, Babakotia, and the evolution of the sloth lemurs*. Folia Primatol. 58:197-203

Soini P., 1986. *A synecological study of a primate community in the Pacaya-Saimiria National reserve Peru* Primate Conserv. 7:63-71.

Sonntag C.F., 1921. *A contribution to the anatomy of the three-toed sloth (Bradypus tridactylus)*. Proc. Zool. Soc. London. 21: 157- 177.

Sonntag C.F., 1923. *On the anatomy, physiology and pathology of the chimpanzee*. Proc. Zool. Soc. London. 23: 323-429.

Sonntag C.F., 1924 *On the anatomy, physiology and pathology of the orang-outan*. Proc. Zool. Soc. London. 24: 349-449.

Stern J.T., 1971. *Functional myology of the hip and thigh of cebid monkeys and its implications for the evolution of erect posture*. Biblioth. Primatol., 14: 1-318.

Stern J.T. and Susman R.L., 1981. *Electromyography of the gluteal muscles in Hylobates, Pongo and Pan, implications for the evolution of hominoid bipedality*. Amer.J.Phys. Anthro. 55: 153-166.

Strasser E., 1989. *Form, function and allometry of the cercopithecoid foot*. Ph.D. Thesis. New York: CUNY.

Strasser E., 1992. *Hindlimb proportions, allometry and biomechanics in Old World monkeys*. Amer. J. Phys. Anthrop. 87:187- 213.

Straus W.L. Jr., 1930. *The foot musculature of the highland gorilla*. Quart. Rev. Biol. 5:261-317.

Straus W.L., 1934. *The thoracic and abdominal viscera of primates with special reference to the orang-utan* Proc. Am. Philo. Soc. 76:1-85.

Straus W.L., 1937. *Cervical ribs in the Wooly monkey* J.Mammal. 18:241-242.

Straus W.L., 1942. *Rudimentary digits in primates*. Quart. Rev. Biol. 17:228-243.

Straus W.L. and Wislocki G.B., 1932. *On certain similarities between sloths and slow lemurs*. Bull. Mus. Comp. Zool. Harvard. 74:45-56.

Strier K.B., 1991. *Diet in one group of spider monkey or Muriquis* (Brachyteles arachnoides) Amer. J. Primatol. 21:113-126.

Struhsaker T.T., 1975. *The red Colobus monkey*. Chicago: University of Chicago press

Struhsaker T.T., 1978. *Food habits of five monkey species in the Kibale forrests Uganda*. In (D.J. Chivers and J. Herbert eds.). Recents Advances in Primatology vol.1 Behavior, pp. 269-286. New York: Academic press.

Struhsaker T.T., 1980. *Comparison of the behavior and ecology of the red colobus and redtail monkey in the Kibale forrest Uganda*. Afr. J. Ecol. 18:35-51.

Subramoniam S., 1957. *Some observations on the habits of the slender loris Loris tardigradus (Linneaus)*. J. Bombay Nat. Hist. Soc. 54:387-398

Susman R.L., 1984. *The locomotor behavior of Pan paniscus in the Lomako forrest*. In (R.L. Sussman ed.) The pygmy Chimpanzee: Evolutionary Biology and Behavior, pp. 369-393. New York: Plenum press.

Susman R.L., Stern J.T. Jr. and Jungers W.L., 1984. *Arboreality and Bipedality in the Hadar Hominids*. Folia primatol. 43:113-156.

Symington M.M., 1987. *Ecological and social correlates of party size in the black spider monkey* Ateles paniscus chamek. Ph.D. Thesis Princeton University.

Symington M.M., 1988a. *Food composition and foraging party size in the black spider monkey Ateles paniscus chamek Behavior*. 105:117- 134.

Symington M.M., 1988b. *Demography ranging patterns and activity budgets of black spider monkeys Ateles paniscus chamek in the Manu National Park Peru*. Am. J. Primatol. 15:45-67.

Szalay F.S. and Delson, E., 1979. *Evolutionary History of the Primates*. New York: Academic press.

Terborgh J., 1983. *Five New World Primates. A study in Comparative Ecology*. Princeton: Princeton University Press.

Thompson S.D. and Nicoll M.E., 1986. *Basal metabolic weight and the energy of reproduction in therian mammals*. Nature 321:690-696.

Treves F., 1885. *Lectures on the anatomy of the intestinal canal and peritoneum in man*. Brit. Med. J. I

Tutin C.E.G., 1980. *Reproductive behavior of wild chimpanzees in the Gombe National park, Tanzania*. J. Repro. Biol. 28: 23-59.

Tutin C.E.G. and Fernandez M., 1985. *Foods consumed by sympatric populations of Gorilla gorilla gorilla and Pan troglodytes troglodytes in Gabon, some preliminary data*. Int. J. Primatol. 6:27-43.

Tuttle R.H., 1969a. *Knuckle-walking and the problem of human origins*. Science 166:953-961.

Tuttle R.H. 1969b. *Quantitative and functional studies on the hands of the Anthropoidea. I. The Hominoidea. J.*

Morph. 128: 309-363.

Tuttle R.H., 1969c. *Terrestrial trends in the hands of the anthropoidea: A preliminary report.* Proc. of the 2nd Int. Congr. Primatol. vol 2. pp. 192-200. Basel: Karger.

Tuttle R.H., 1970. *Postural, propulsive and prehensile capabilities in the cheiridia of chimpanzees and other great apes.* In (G.H. Bourne, ed.). The Chimpanzee. Vol. II.pp. 167-253. Baltimore: Univer. Park Press.

Tuttle R.H. 1974. *Darwin's Apes, dental apes and the descent of man: normal science in evolutionary anthropology.* Curr. Anthrop. 15:389-426.

Tuttle R.H. 1975a. *Knuckle-walking and knuckle-walkers: a commentary on some recent perspectives of hominoid evolution.* In (R.H. Tuttle ed.). Primate Functional Morphology and Evolution. pp. 203-212. The Hague: Mouton.

Tuttle R.H. 1975b. *Parallelism, Brachiation and Hominoid Phylogeny.* In (W.P. Luckett and F.S. Szalay eds.). Phylogeny of the Primates. pp. 447-480.New York: Plenum Press.

Tuttle R.H. 1981. *Evolution of hominid bipedalism and prehensile capabilities.* Phil. Trans. Roy. Soc. 292: 89-94.

Tuttle R.H. and Beck B.B., 1972. *Knucklewalking hand postures in an orang-utan Pongo pygmaeus.* Nature 236:33-44.

Uhlman K., 1968. *Huft und Oberschenkel-muskulatur systematische und vergleichenden Anatomie.* Primatologia 4(10):1-442

Van Horn R.N. and Eaton G.C., 1979. *Reproductive physiology and behavior in Prosimians.* In (G.A. Doyle and R.D. Martin eds.) The Study of Prosimian Behavior pp.79-122. New York: Academic press.

Van Roosmalen M.G.M., 1980. *Habitat preferences diet feeding behavior and social organization of the black spider monkey Ateles paniscus chamek in Surinam.* Ph.D. Dissertation, University of Wageningen, The Netherlands.

Vogel C., 1962. *Morphologische studien am gesichtsschadel Catarrhiner Primaten.* Biblo. Primatol. 4:1-226.

von Koenigswald G.H.R., 1952. *Gigantopithecus blacki a giant fossil hominoid from the pleistocene of south China.* Anthrop. Pap. Amer. Mus. Nat. Hist. 43:291-326.

Walker A.C., 1967. *Locomotor Adaptations in Recent and Fossil Madagascan Lemurs.* Ph.D. Thesis University of London.

Walker A. C., 1974. *Locomotorn adaptations in past and present prosimian primates.* In (F.A. Jenkins ed.). Primate Locomotion, pp. 349-381. New York: Academic press.

Walker P. and Murray, P., 1975. *An assessment of masticatory efficiency in a series of anthropoid primates with special reference to the colobinae and the cercopithecinae.* In (R. Tuttle ed.). Primate Functional Morphology and Evolution, pp 135-150. The Hague: Mouton.

Washburn S.L., 1950a. *Thoracic viscera of the gorilla.* In (W.K. Gregory ed.) Anatomy of the Gorilla, pp. 189-195. New York: Columbia University press.

Washburn S. L., 1950b. *The specializations of man and his place among the catarrhine primates,* Cold Harbor Symp. Quant. Biol. Vol. XV: Origin and Evolution of Man, pp. 37-52. Cold Spring Harbor, Long Island

Washburn S. L., 1963. *Behavior and Human Evolution* In (S.L. Washburn ed.). Classification and Human Evolution. pp. 190-201. Chicago: Aldine.

Washburn S.L., 1967. *Behavior and the orgin of man: The Huxley memorial lecture.* Proc. of the Roy. Anthrop. Inst. of Gr. Brtn and Irlnd. pp. 21-27.

Washburn S.L., 1968. *Speculations on the problem of man's coming to the ground.* In (B. Rothblatt ed.) Changing Perspectives on Human Evolution, pp. 193-206. Chicago: University of Chicago Press.

Washburn S.L., 1983. *Audiotape recording of the concluding speech to the symposium on Hadar hominids,* held April 1983 in Berkeley CA. Institute of Human Origins..

Wasser P.M., 1977. *Feeding, ranging and group size in the Mangabey Cercocebus albigena.* In (T.H. Cluttonbrock ed.). Primate Ecology. pp. 183-222. London: Academic press.

Wilson D.R., 1972. *Tail reduction in Macaca.* In (R.H. Tuttle ed.). Functional and Evolutionary biology of Primates, pp. 241-261 Chicago: Aldine-Atherton.

Wislocki G.B., 1928. *Observations on the Gross and microscopic anatomy of the sloth (Bradypus grisseus grisseus* and *Choloepus hoffmani)* J. Morphophysio. 46:317-377.

Wislocki G.B. and Straus W.L., 1932. *On the blood-vascular bundles in the limbs of certain edentates and lemurs.* Bull. Mus. Comp. Zool., 74: 1-16.

Wood Jones F., 1929. *Man's Place Among the Mammals.* New York: Longmans, Green and Co.

Wrangham R.W., 1977. *Feeding behavior of chimpanzees in Gombe National park Tanzania.* In (T.H. Cluttonbrock ed.). Primate Ecology.pp. 504-538. London: Academic press.

Wu R., 1984. *A revision of the classification of the Lufeng great apes.* Acta Anthrop.Sinic. 6:265-271

Yalden D.W., 1972. *The form and function of the carpal bones in some arboreally adapted primates.* Acta Anat. 82: 383-406.

Young A.L., Richard A.F., and Aiello L.C., 1990. *Female dominance and maternal investment in strepsirrhine primates.* Am. Nat. 135:473-488.

Ziemer L.K., 1978. *Functional morphology of the forelimb joints in the woolly monkey Lagothrix lagotricha.* Contr. Primatol. 14:1-130.

Zihlman A.L., 1969. *Human locomotion a reappraisal of the functional and anatomical evidence.* Ph.D. Thesis, University of California at Berkeley

Zihlman A.L. and Bunker L., 1979. *Hominid bipedalism: Then and now.* Yrb. Phys. Antrhop. 22:132-162.

Zingeser M.R., 1973. *Dentition of Brachyteles arachnoides with reference to Alouattine and Atelinine affinites.* Folia primatol. 20:351-390.