

A COMPARATIVE APPROACH
TO THE TAXONOMY AND PHYLOGENY OF *PAN*

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INTRODUCTION

In the dim light of dawn a nest high in the canopy rustles with the movements of its inhabitants. The sun appears on the horizon as a slender male chimpanzee emerges, followed by a female. An infant clinging to the female's belly yawns, grasping its mother's hair in tiny, tight fists as it stretches against her. After a moment of quietly gazing at each other the adults silently swing to an adjacent *Antiaris* tree which is laden with ripe, red fruits, and begin a leisurely breakfast.

One familiar with *Pan* behavior might discern from this limited description that the "chimpanzees" in question are *P. paniscus* a species (or subspecies) of the genus *Pan* which displays marked contrast to the behavior of *P. troglodytes*. What is not so easily discernable is *P. paniscus*' place in the phylogeny and taxonomy of *Pan* and of anthropoids in general.

Schwarz (in Horn 1980) was first to formally describe *P. paniscus* in 1929, relegating it to subspecies level based on the skull and skin of a female collected near Befale and a male skull from Djombo (in Susman 1984). Schoutenden corroborated this opinion with behavioral data from a captive *paniscus* compared to the behavior of a captive *troglodytes* (Susman 1984). Coolidge (1933) initially proposed that Schwarz' designation of *Pan saryus paniscus* be changed to a species status, *P. paniscus*. He supported his contention with previous reports and the gracile skeleton of a small female. Additionally, he suggested that the behavior and morphology of *paniscus* made it a probable candidate for a living model of early hominids.

Since then many have supported or contradicted the taxonomy and phylogeny of *paniscus*. Zihlman et al. (1978, 1983) suggest that *paniscus* may be a living example of a Ramamorph or some other precursor of *Australopithecus*, *Pan* and *Gorilla*. J. E. Cronin (1977) supports this view utilizing immunological testing of albumin and transferrins from *Pan*, *Homo* and *Gorilla*. Although these samples demonstrate more similarities between *paniscus* and

troglydites than between any other species (thus supporting close phylogenetic ties), gel electrophoresis suggests a greater diversity within *paniscus*. Cronin suggests this diversity indicates *paniscus* may be a primitive rather than derived form; a relict of a species that gave rise to all three African anthropoid lineages. Stanyon et al. (1986) offer chromosomal evidence of *paniscus* as a separate species and as the best model for the common ancestor of humans and African apes. Horn (1979) concedes the possibility of *paniscus* as an extant form of a protohominid but reserves his opinion until the taxonomic issue is satisfactorily settled. Horn (1979) notes that *paniscus* and *troglydites* exhibit morphological and size differences similar in kind to lowland and highland *gorillas* as evidence of *paniscus* subspecies status. From allometric comparisons of *paniscus* and *troglydites* morphology McHenry and Corruccini (1981) conclude that observed differences between the two are due to allometry and neither resemble *Homo* more than the other in cranial, postcranial or dental features.

The 1984 publication *The Pygmy Chimpanzee* offers numerous opinions on this debate including a comparative study by Socha who discovered many differences in red cell antigens between *paniscus* and *troglydites*. Unlike *troglydites*, *paniscus* demonstrates only one blood group in the ABO system in a sample of 14 wild and captive bonobos. Other systems also demonstrate this lack of polymorphism. Sarich (1984) provides another molecular perspective using electrophoresis and mtDNA cloning techniques. Electrophoretic data concur with Socha's as 13 of 20 bands between *paniscus* and *troglydites* demonstrate the same mobility when *Pan*, *Gorilla* and *Homo* are compared. mtDNA results show an accumulation of 6% change since the separation of these three lineages with 4% change in both *Pan* species. Laitman (1984) demonstrates a lack of exocranial flexion in *paniscus* similar to other non-human primates and unlike the obvious flexion in humans. Kinzey (1984) adds to the argument in favor of species designation and against a phylogeny **ancestral to *Homo*** with dental evidence. He establishes clear differences between *paniscus* and *troglydites* but maintains that both share more characteristics with each other than either does with *Homo*. Shea (1986) support's Coolidge's claim of species level with an allometric study of scapular form. The observed differences in

scapular morphology are discussed with reference to locomotor patterns and phylogeny.

DESCRIPTIVE GENUS MORPHOLOGY

It is apparent that the taxonomic position of *paniscus* and its relevance for hominid evolution remain ambiguous. Although molecular biology has made the argument for species level more vigorous a survey of the characteristics of the different forms of *Pan* might better elucidate not only the most appropriate taxonomic level for *paniscus* but its relationship to *troglydytes* and the homonid lineage. Molecular biology provides the most rigorous test of taxonomic and phylogenetic associations, including that of *paniscus* to the hominids. However, the preponderance of non- molecular data requires a review of that which is often cited as a supportive, sometimes definitive argument for the use of *paniscus* as a human prototype.

Such a survey requires a description of the accepted members of the genus *Pan*. Yet even the genus designation proves problematic. Tuttle (1987) contends knuckle-walking is the determining feature of *Pan*. Thus *troglydytes*, *paniscus* and *gorilla* should be subsumed under *Pan*: *Pan (Pan) paniscus*, *Pan (Pan) troglydytes* and *Pan (Pan) gorilla*. Szalay (1979) explains that the **assumption** of these three species under the genus *Pan* reflects a close relationship to *Homo*, thereby distinguishing these species from Asian apes (*Pongo*). However, this phylogeny is based only on a few phenotypic characters and does not address the issue of *gorilla* subspecies (species) **or** morphological differences between the three African lineages. Most continue to place *gorilla* in a separate genus (Richards 1986, Groves 1989). Until recently Groves (1970) also supported *gorilla* as a species of the genus *Pan*. Subsequent investigations have convinced him that two subfamilies (*Ponginae* and *Homininae*) dividing the Asian and African Hominoidea into the genera *Pongo*, *Gorillini*, *Panini* and *Hominini* is more parsimonious. Concerning the subspecies of *Pan*, Hill (1969) recognized four: *Pan troglydytes* verus, *P. t. troglydytes*, *P. t. schweinfunhi* and *P. t. koolakamba*. These 4 species range from western to eastern equatorial Africa.

P. t. verus have light-colored faces at birth which darken with age, retaining mask-like splotches. They have large, pale ears, pale palms and soles and white beards. *P. t. troglodytes* is known as the black-faced chimp. Though pale-faced at birth, the face, ears, palms and soles are dark at maturity. They have few or no white chin hairs and are thought to be recently extinct from the south bank of the Zaire in Angola.

P. t. schweinjuni is the eastern or long-haired chimp. Neonate faces are pale but mature to a brown hue which matches their ears, palms and soles. As the common name implies, they have long cheek whiskers and body hair, though few white chin hairs.

P. t. iwolakamba is the least known and not recognized by all taxonomers. Shea (1984) has suggested they are hybrids of *gorilla* and *P. troglodytes* but this has not been substantiated. Unlike other chimps, infants have blotchy, brown faces which become prognathic and black with maturity. They share such features with *gorilla* as small ears and padded nasal alae and, in general, do give the appearance of a *troglodytes/gorilla* hybrid.

P. paniscus is considered by Hill (1969) to be a separate species of *Pan* which is confined to the west bank of the Zaire river (in early accounts referred to as the Congo) and west of the Lualaba river. Hill (1969) reported that the body weight of *paniscus* was less than half that of *troglodytes*. However, more recent studies indicate that although overall *troglodytes* are larger, *P. t. schweinjuni* weights overlap with those of *paniscus*. *Paniscus* are reported to have black faces (except around the mouth), ears, palms and soles from infancy. However, like *troglodytes*, captive *paniscus* are sometimes lighter. Adults often retain the white perianal tuft from infancy and the hair on the cheeks and body is long. Species specific alopecia seen in *troglodytes* is absent and the ears are small, similar in size to *Homo* and *gorilla*. Besides an overall slender build and a more 'gibbon-like' scapula (long and narrow perpendicular to the scapular spine) *paniscus* demonstrates a more rounded cranium with less facial prognathism than *troglodytes* and have been likened to juvenile *P. t. schweinjuni* (Coolidge 1933, Hill 1969, Shea 1984).

MOLECULAR COMPARISONS

As previously noted, *paniscus* demonstrates little polymorphism in its blood groups (Socha, 1984). Conversely, serological polymorphisms in *troglydytes* and *Honw* are numerous. *Troglydytes* are either type A or 0 whereas all *paniscus* tested were Type A. While *paniscus* A antigens are indistinguishable from human A antigens, the A antigens on red cells of *troglydytes* differ from humans. *Troglydytes* are either M or MN and *paniscus* samples are all M (Socha 1984). The *troglydytes* V-A-B-D system (an extension of the MN system) demonstrates 16 types yet only one type is found in all 14 *paniscus* samples (Socha 1984). The R-C-E-F system (an extension of the human Rh-Hr group) demonstrates at least 24 types in *troglydytes* but only a single irregular type is found in *paniscus* (Socha 1984).

A karyological comparison of *paniscus*, *troglydytes* and *Honw* indicates that although there is a high degree of similarity among the three, *paniscus* is more specialized than either *troglydytes* or *Honw* (Stanyon et al. 1986).

MORPHOLOGY

Much of the morphological comparisons between *troglydytes* and *paniscus* have been discussed in previous sections. However, some characteristics not specifically mentioned are noteworthy. Although McHenry (in Susman 1984) postulates that *paniscus* and *troglydytes* show similar morphology of 47 separate postcranial features, he also makes note of over 2 dozen features that differ. Most of these relate to morphological differences affecting locomotion, such as scapular shape and bones associated with intermembral indices. Of these he includes narrower chests and longer hind limbs (thus a lower intermembral index) in *paniscus* relative to *troglydytes*. Nishida and Hiraiwa-Hasegawa (in Smuts 1986) describe *paniscus* as having a shorter clavicle, smaller molars (Kinzey 1984), and less sexual dimorphism than *troglydytes*. In general, the morphology of *paniscus* is described as paedomorphic in comparison with

trogodytes (McHenry 1984, Horn 1979, Shea 1984, Coolidge 1933).

ECOLOGY AND DEMOGRAPHY

Both *trogodytes* and *paniscus* are found in primary and secondary forests in equatorial Africa. *Trogodytes* is also found in woodland and savanna areas, and *paniscus* in swamp forests (Nishida et al. 1986, Horn 1975, Kano 1980, Kuroda 1980, Tuttle 1987). Range sizes for *trogodytes* and *paniscus* are 6 to >278 km and 22-58km, respectively (Tuttle 1987). Variation of range size seems strongly influenced by region. In densely wooded regions *trogodytes* has smaller home ranges (5-38 km) and larger ranges in sparsely wooded areas (25-560 km). Regional differences are also associated with *paniscus* group size (ca. 22 km at Lomako and 40-50 km at Wamba, Nishida et al. 1987).

Trogodytes and *paniscus* are both considered omnivores with a preference for ripe fruits (Tuttle 1987, Nishida et al. 1987, Badrian and Malenky 1984). Both eat invertebrates although *paniscus* consumes a wider variety. Unlike *paniscus*, *trogodytes* utilizes tools in foraging for termites and driver ants (Cousins 1978, Goodall 1968). Both are assumed to hunt although this behavior has been observed only in *trogodytes*. *Paniscus* have been observed eating small animals and remains of snakes have been found in their fecal matter (Badrian and Badrian 1977). *Paniscus* is believed to rely heavily on tubers and fibrous foods and has been observed digging *shimoukiro*, a mushroom native to the Zaire basin (Kano 1979). There have also been unsubstantiated reports of *paniscus* catching mud fish in this area.

Locomotion between feeding sites is generally arboreal for *paniscus* while *trogodytes* usually descend and travel terrestrially between sites. However, *paniscus* and *trogodytes* are generally considered to be terrestrial knuckle-walkers. Like *trogodytes*, *paniscus* often flee terrestrially when disturbed. Yet, due to their light frame and slender scapula, they are able to locomote arboreally much faster than *trogodytes* (Susman et al. 1980, McHenry 1984).

Group sizes are similar in both species although *paniscus* tends towards a larger basic

unit group (Nishida et al. 1987, Kano 1979). Most party groups (temporary associations) number < 6 in *trogodytes* and > 6 in *paniscus*. However, sex ratios are quite different between the two. Although both species exhibit all male groups, bisexual groups of approximately equal ratios are the norm for *paniscus* and multimale associations are more common to *trogodytes*. When bisexual associations do occur in *trogodytes* groups they are usually characterized by a higher number of females than males (Nishida et al. 1987, Kano 1982).

BEHAVIOR

Although many molecular, morphological and ecological differences exist between *paniscus* and *trogodytes* perhaps the most obvious differences are behavioral. Marked differences in nesting, affiliative behaviors, agonistic interactions and tool use are noted.

Trogodytes generally build nests each evening in the lower part of the canopy. Adult females share nests with their infant but older juveniles often construct nests of their own adjacent to the mother. Adults rarely share nests and nests are loosely clumped (Goodall 1968, Tuttle 1987). *Paniscus* also build fresh nests each evening, though higher in the canopy. These are **reported** as high as 82 meters from the ground (MacKinnon 1976). However, Hom (1980) reports that nests were no higher than 25 meters. The discrepancy may be due to regional differences between the Lamako community and Lac Tumba. Although there are similarities in distribution of nests *paniscus* demonstrate more tolerance of nest sharing.

Affiliative behaviors are also unique in *paniscus*. These roughly consist of grooming, rump-touching, genital- genital rubbing and appeasement gestures such as brief grooming and presenting. The highest frequency of grooming is between mother and dependent infant (Badrian and Badrian 1984). Among adults the highest frequency is between males and females, followed by female/female and male/male grooming. Among *trogodytes* male/male grooming accounts for **most adult grooming**, followed by female/female and then male/female grooming (Nishida et al. 1987). Rump touching and genital-genital rubbing (GG rubbing) are

common and unique gestures of *paniscus*. Rump touching by males (lightly touching the rump of another with rump or hands) is seen in many contexts, although it is thought to be a form of greeting. Like GG rubbing it is exhibited as appeasement behavior or in the context of social or feeding excitement (Kano 1982, Kuroda 1980, Badrian and Badrian 1984). GG rubbing between females is observed in similar contexts and often associated with estrus females. It appears to be a mechanism for decreasing tension and strengthening bonds between females. Females rub the clitoride regions of their perianal areas against one another, in either a standing or reclining ventro-ventral position. Anatomical differences may contribute to the expression of this behavior as the labia majora and clitoris of *paniscus* are located more ventrally than that of *trogodytes* (Kuroda 1980). Other forms of appeasement include brief grooming bouts and submissive presenting. Females are sometimes observed grooming a male for several seconds before passing him on a branch or narrow path (Kuroda 1980). In contrast, anogenital contact between adult male *trogodytes* is restricted to periods of intense social excitement, such as during fights, feeding bouts or inter-community interactions. GG rubbing is uncommon in female *trogodytes* although genital inspection is common (Tuttle 1987). Appeasement gestures demonstrated by *trogodytes* usually reflect current male status. Anogenital contact is usually performed by a lower ranking animal to a higher one. This can involve manual contact with the thigh, scrotum or perianal area. Other appeasement gestures of *trogodytes* include crouching, 'fear grins', kissing, patting, presenting, mounting and pant-grunts (Tuttle 1987).

Play also distinguishes the two species. Although adult *trogodytes* do engage in play behavior with one another, this occurs mostly in captivity where other forms of social stimulation are often sparse. Wild *paniscus* adults have been reported to play with one another regularly. The main contexts of this play appear to be courtship and feeding. Kuroda (1980) reports "sexual play" between males and females before and after copulation. This includes kissing, patting, play biting and one of the few vocalizations described: a soft [hagg...J uttered during play and occasionally during copulation. Feeding often involves a snatch/resnatch game where two or more individuals take turns repeatedly 'stealing' food from each other with no

apparent agonistic behavior. Adults also play with infants though females play with them more actively and males generally let the juveniles climb them. The [hagg...] pant and penile erection are not exhibited by juveniles during play as is common in adult play (Kuroda, 1980). The [hagg...] vocalization may be similar to the 'laugh' vocalized by *troglydytes* (Goodall 1968). However, juveniles and adult *troglydytes* often vocalize in this manner during play.

Food sharing is common to both *paniscus* and *troglydytes* but is expressed in different forms. Sharing of vegetable matter is rare among *troglydytes* and is generally exhibited by mothers towards infants. Meat sharing is more common to *troglydytes*. Meat is generally shared between adult males although females are given pieces or allowed to take or beg portions. Goodall (1986) reports that a good deal of social excitement accompanies the disbursement of meat including squabbles, kissing and general reassurance and appeasement behaviors. By comparison *paniscus* regularly share vegetable matter. Adult females often share with unrelated juveniles but there is little sharing between males (Kuroda 1980, 1984). Although there is little aggression during these feeding bouts GG rubbing and snatchlresnatch games are often components of large, intense feeding groups.

Although *paniscus* are not the only apes to copulate ventrally they are the only *Pan* species observed-to do so (Horr 1972). Copulation is often initiated by one of the individuals gazing intently at the other, usually when the male's penis is erect. Badrian and Badrian (1980) recorded ventro-dorsal matings 74% of the time and ventro-ventral 26% of the time (N=70). These data are similar to Kano's (1980) observations of 62% ventro-dorsal and 35% ventro-ventral (N=106). Three percent of these began ventro-dorsal but were completed ventro-ventral. Kuroda (1984) observed an increase in gazing and soft vocalizations during copulation and Kano (1980) states that all females uttered screams at completion. Badrian and Badrian (1980) reported that most copulations were silent and ventro-ventral copulation was more frequent between adults and juveniles (1984). Although *troglydytes* also exhibit visual contact (such as ventro-dorsal copulation accommodates) and copulatory pants (Tuttle 1987), ventro-ventral copulation between adults is clearly a *paniscus* feature.

Little is known of the menstrual cycle of *paniscus* from wild or captive studies. However, data from preliminary investigations indicate *paniscus* experience a relatively longer estrus cycle and more anovulatory cycles than *trogodytes* (Badrian and Badrian 1984, Kano 1980, Nishida et al. 1987). They also exhibit shorter postpartum anestrus cycles. *Trogodytes* remain anestrus for 3-6 years and *paniscus* for about 1 year post-partum (Nishida, et al. 1987).

Agonistic interactions among *paniscus* have been of particular interest to investigators. Kuroda (1984) determined that, when provisioned, *paniscus* were no less agonistic than *trogodytes*. These behaviors were, however, less intense and/or prolonged than *trogodytes*'. Although many reports of *paniscus* describe them as generally non-aggressive there are numerous examples of mild aggression and aggressive displays reported. These include branch-dragging, kicking, and drumming on tree trunks (Badrian and Badrian 1980, Kuroda 1980, 1984, Kano 1980). Such behaviors are qualitatively different from the impressive bipedal and quadrupedal charge displays of *trogodytes*. An addendum to these features is the vocalizations associated with particular behaviors. Many sources maintain a lack of vocal expression in *paniscus* that characterizes *trogodytes* behavior. *Paniscus* exhibit few or no vocalizations in association with feeding, grooming, appeasement behaviors, copulation, playing or **agonistic** behaviors within the group (Kuroda 1980, Kano 1980). Vocalizations have been reported during agonistic interactions with other communities (Badrian and Badrian 1984, Kuroda 1980) or when startled by humans or elephants (Badrian and Badrian 1980).

Dominance ranking is an important feature in the lives of *trogodytes* and male-male bonding and alliances are characteristic of dominance relationships. Males rise to high rank through aggressive displays and physical confrontations. Coalitions between males which may afford passage to higher status are formed and strengthened through grooming and supportive actions. This creates an unsteady status for males and the male ranking is generally temporary. *Paniscus* males also exhibit a dominance ranking although status is maintained mostly through **avoidance** behaviors. However, Kuroda (1980) reports that most agonistic encounters were between males. Male *paniscus* are generally dispersed throughout the group. Unlike

trogodytes, *paniscus* males tend not to associate with males but with females. Thus status is generally stable due to lack of male interaction. Like male *paniscus*, female *trogodytes* do not frequently associate with other females, except relatives. They too demonstrate fairly stable dominance rankings. Unambiguous dominance ranking has not been demonstrated for female *paniscus*. Like male *trogodytes*, they exhibit unique behaviors that would seem to serve as coalescing behaviors in same-sex relationships. GG rubbing and non-kin food sharing are such female bonding behaviors.

Trogodytes are well known for their different forms of tool use (Goodall 1968). In contrast, *paniscus* evidence a general lack of tool use with the exception of using leafy branches for rain cover (Kano 1982b). However, this may be a notable distinction, as *trogodytes* tend to simply sit in the rain.

SUMMARY

Early taxonomic and phylogenetic designations were hindered by a severe lack of data. Taxons and evolutionary associations were often assigned on the basis of only one or two samples of morphology and/or behavior. Currently, molecular evidence proves the most rigorous test of phylogeny and, although sample sizes remain small, sufficient data have been amassed to begin to speculate on the taxonomy and phylogeny of *Pan*.

Molecular, morphological, ecological and behavioral data support *P. paniscus* as a "group of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr 1970). They are reproductively isolated not only geographically, as are the subspecies of *Pan*, but ecologically and, to some extent, behaviorally. *Paniscus'* specialized morphology and behaviors demonstrate speciation due to the geographic isolation of their range on the left bank of the Zaire river (MacKinnon 1976). Molecular data are evidence that this isolation is indeed speciation (Stanyon et al. 1986). Such geographic isolation has even been proposed as the impetus for the splitting of the three African hominoids (Kortlandt 1972).

The phylogeny of *Pan* is a more delicate issue and one is tempted to follow Marks' (1989) sage advice and "leave the chimp-gorilla-human clade as a sniglet". Yet naivete and the purpose of this article demand a proposal of phylogeny. Given the present data, neither species of *Pan* can be considered more closely related to *Homo*. Molecular analysis has repeatedly been demonstrated to be the most accurate tool for deciphering the relatedness of these species. Most of these analyses have demonstrated decreased diversity for *paniscus* as compared to *troglydytes* or *Homo*. These data suggest that *paniscus* is more specialized than either *troglydytes* or *Homo* and therefore, is most likely derived from *troglydytes*. Only Cronin (1977) reports increased genetic diversity in *paniscus*. However, this result may be indicative of autoapomorphic characters and could still be evidence of specialization in *paniscus*.

"Morphological, ecological and behavioral data are generally supportive of close phylogenetic ties to *troglydytes*. These characters, especially behavioral data, have often been advanced as

evidence of *paniscus* as the prototype of early humans. Although behavioral differences can often result in reproductive isolation, behavioral similarities do not necessarily reflect the closeness of phylogenetic ties. All extant genera of *Pan* and *Homo* exhibit adult play, non-kin food sharing and adult bonding behaviors in various forms. All display aggressive behaviors to varying degrees. And even GG rubbing has been reported not only in female *paniscus* but also in female *trogodytes* (personal communication).

Data demonstrate many similarities and dissimilarities in the expression of behaviors among the species of *Pan* and the genus *Homo*. Care must be taken not to anthropomorphize any particular species' repertoire in comparison with human behavior, as humans (and many other species) display a wide range of behavioral expressions. Molecular data indicate only that species designation is appropriate for *paniscus*, that all three are closely related, and that the two species of *Pan* are more closely related to each other than either is to *Homo*. When behavior is used in support of discussions of these relationships the effect of captivity, cultural and individual variation and geographic isolation on the expression of behavior must be seriously considered. What is already evident is the remarkable behavioral plasticity demonstrated by *Pan* and *Homo* and the many evolutionary solutions with which *Hominoidea* has met environmental challenges.

REFERENCES CITED

- Badrian A. and N. Badrian
 1980 "The Other Chimpanzee." Animal Kingdom, 83(4):9-14.
- 1984 "Social Organization of *Pan paniscus*." The Pygmy Chimpanzee, R. Susman, ed., Plenum Press: New York, pp. 325-346.
- Badrian, N. and R. Malenky
 1984 "Feeding Ecology of *Pan paniscus* in the Lomako Forest, Zaire." The Pygmy Chimpanzee, R. Susman, ed., Plenum Press: New York, pp. 325- 346.
- Coolidge, H. S.
 1933 "*Pan paniscus*, Pygmy Chimpanzee South of the Congo River." American Journal of Physical Anthropology 18:1-59.
- Cousins, D.
 1978 "The Diminutive *Pan*." International Zoo News 25(2):5-11.
- Cronin, J.
 1977 "Pygmy Chimpanzee (*Pan paniscus*) Systematics." American Journal of Physical Anthropology 47: 125.
- Goodall, J.
 1968 "The Behavior of Free-Living Chimpanzees in the Gombe Stream Reserve." Animal Behaviour Monographs 1: 161-311.
- 1986 The Chimpanzees of Gombe. Belknap Press: Massachusetts. Groves, C. P. 1970 Gorillas. Arthur Barker, London.
- 1989 A Theory of Human and Primate Evolution. Oxford University Press: New York
- Hill, W. C. O.
 1969 "The Nomenclature, Taxonomy and Distribution of Chimpanzees. The Chimpanzee, Vol. 1, G.H. Bourne, ed., University Park Press: Baltimore.
- Horn, A.
 1975 "Adaptation of the Pygmy Chimp to the Forests of the Zaire Basin. American Journal of Physical Anthropology 42:307.
- 1979 "The Taxonomic Status of the Bonobo Chimpanzee." American Journal of Physical Anthropology 51:273-282.
- 1980 "Some Observations on the Ecology of the Bonobo Chimpanzee Near Lake Tumba, Zaire." Folia Primatol. 34:145-169.
- Horr, D.
 1975 "The Borneo Orang-utan." Primate Behavior, L.A. Rosenblum, ed., Academic Press: New York, vol. 4, pp.307-324.
- Kano, T.
 1980 "Social Behavior of the Wild Pygmy Chimpanzees of Wamba: A Preliminary Report." Journal of Human Evolution 9:243-260.

- 1982 "The Social Group of Pygmy Chimpanzees of Wamba" *Primates* 23(2): 171-188.
- 1982b "The Use of Leafy Twigs for Rain Cover by the Pygmy Chimpanzees of Wamba" *Primates* 23(3):453-457.
- Kano, T. and M. Mulavwa
1984 "Feeding Ecology of the Pygmy Chimpanzees of Wamba." *The Pygmy Chimpanzee*, R.Susman, ed., Plenum Press: New York, pp.233-274.
- Kinzey W.
1984 "Dentition of the Pygmy Chimpanzee." *The Pygmy Chimpanzee*, R.Susman, ed., Plenum Press: New York, pp.65-87.
- Kuroda, S.
1980 "Social Behavior of the Pygmy Chimpanzee." *Primates* 21(2):181-197.
- 1984 "Interaction Over Food Among Pygmy Chimpanzees." *The Pygmy Chimpanzee*, R.Susman, ed., Plenum Press: New York, pp. 301-324.
- Laitman, J. and R. Heimbuch
1984 "A Measure of Basicranial Flexion in the Pygmy Chimpanzee." *The Pygmy Chimpanzee*, R.Susman, ed., Plenum Press: New York, pp. 49-63.
- MacKinnon, J.
1984 "Mountain *Gorillas* and Bonobos." *Oryx* 13(4):372-382.
- Marks, J.
1989 "The Hominin Clade." *Science* 22Dec:p 1645.
- Mayr, E.
1970 *Populations, Species, and Evolution*. Harvard University Press: Cambridge.
- McHenry, H.
1984 "The Common Ancestor: A Study of the post- cranium of *P. paniscus*, Australopithecus and other hominoids." *The Pygmy Chimpanzee*, R.Susman, ed., Plenum Press: New York, pp. 201-230.
- McHenry, H. and R. Corruccini
1980 "*Pan paniscus* and Human Evolution." *American Journal of Physical Anthropology*. 54:355-367.
- Meyers-King, L.
1989 Personal Communication.
- Nishida, T. and M. Hiraiwa-Hasegawa
1987 "Chimpanzees and Bonobos: Cooperative Relationships Among Males." *Primate Societies*, B. Smuts, ed., University of Chicago Press: Chicago, pp.165-178.
- Richard, A.
1985 *Primates in Nature*. W.H. Freeman and Co.: New York.

- Sarich, V.
1984 "Pygmy Chimpanzee Systematics." The Pygmy Chimpanzee, R.Susman, ed., Plenum Press: New York, pp. 201-230.
- Shea, B.
1986 "Scapula Form and Locomotion in Chimpanzee Evolution." American Journal of Physical Anthropology 70:475-488.
- Socha, W.
1984 "Blood Groups of Pygmy and Common Chimpanzees: A Comparative Study." The Pygmy Chimpanzee, R.Susman, ed., Plenum Press: New York, pp. 201-230.
- Stanyon, R., B. Chiarelli, K. Gottlieb and W. Patton
1986 "The Phylogenetic and Taxonomic Status of *Pan paniscus*." American Journal of Physical Anthropology 69:489-498.
- Susman, R., ed.
1984 The Pygmy Chimpanzee. Plenum Press: New York.
- Szalay, F. and E. Delson
1979 Evolutionary History of the Primates. Academic Press: New York.
- Tuttle, R.
1987 Apes of the World. Noyes Publications: New Jersey.
- Zihlman, A., J. Cronin, D. Cramer and V. Sarich
1978 "Pygmy Chimpanzee as a Possible Prototype for the Common Ancestor of Humans, Chimps and *Gorillas*." Nature 275:744-746.
- Zihlman, A and J. Lowenstein
1983 "Ramapithecus and *Pan paniscus*: Significance for Human Origins." New Interpretations of Ape and Human Ancestry, Ciochon, R. and R. Corruccini, eds., Plenum Press: New York, pp. 677-694.