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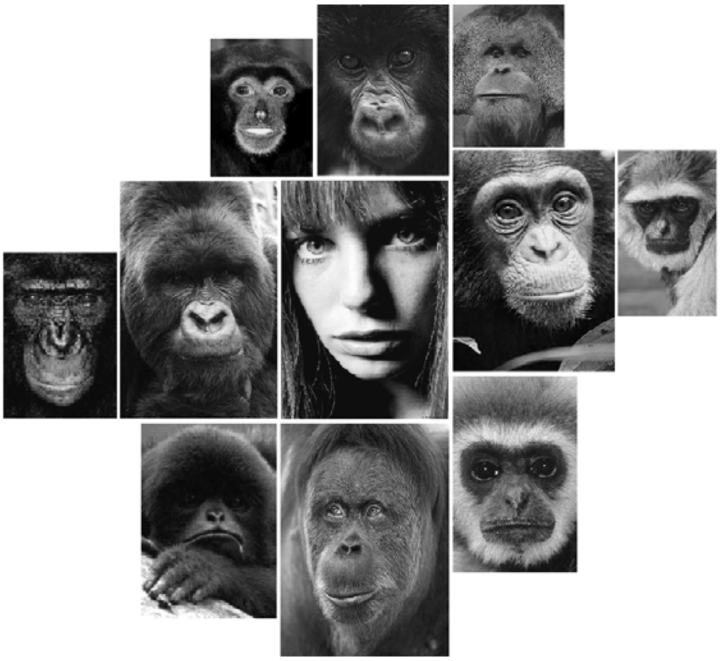
Cladistic analysis of reproductive, behavioral, sociobiological, and developmental traits in the Hominoidea

Bachelor thesis



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Summary:

The available information concerning reproduction, ontogeny, behavioral patterns and social relationships in all species of extant and some extinct were analysed cladistically. The character set was optimized on the phylogeny of the Hominoidea, and the particular common ancestors were reconstructed. The study reveals that all common ancestors (excluding the common ancestor of *Pan* spp.) showed more or less gorilla-like patterns of behavior and social system. The major outcome of this study is the finding that humans, despite universal assumptions, are (in terms of behavior and sociobiology) rather slightly derived gorillas than substantially derived chimpanzees.

Hereby I declare that I elaborated this bachelor thesis myself with use of the referred-to literature.

I declare that in conformity with the law § 47b Act nr. 111/1998 Collection of Law as amended, agree with publication of unshortened version of my bachelor thesis electronically by the Faculty of Sciences on a publicly accessible part of STAG database run by the University of South Bohemia in České Budějovice on its website.

In České Budějovice, April 22, 2008

Pavel Duda

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„We will only be able to appreciate real differences between humans and apes when we know their similarities.“

Jane Goodall

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INTRODUCTION

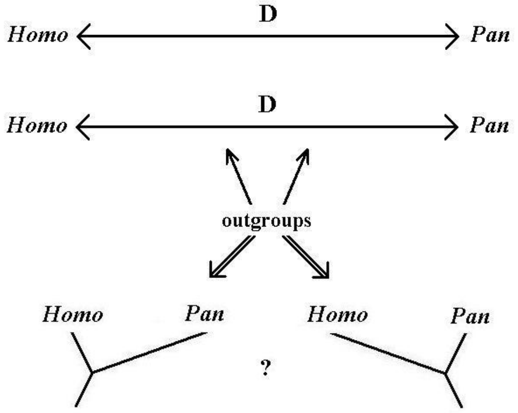
The bulk of sociobiological literature is dealing with the problem of fundamental reproductive, developmental, behavioral and especially sociobiological differences between humans and the rest of the Hominoidea, i.e. great apes (a chimpanzee and a bonobo, our closest relatives, and gorillas and orangutans) and lesser apes (gibbons and a siamang). Scientists usually point out to uniqueness of our life-cycle and strategies. Such attributes of human nature as parental care, monogamy, long-term male-female bonds, concealed ovulation, menopause and longevity are mentioned frequently. Humans are considered unique (or at least far more advanced than other apes) in many of these traits.

These ideas are concentrated in the Part Two of *The Third Chimpanzee* by Jared Diamond (1992). In the chapter „An Animal with a Strange Life Cycle“, the author wrote that „we rather than living apes are the ones whose life cycle diverged most from ancestral condition“ and that „we have to be content with merely inferring that conclusion from the fact that our life cycles are exceptional compared not just to living apes but also to other primates, suggesting that we were the ones who did more changing.“ Human is considered the most derived species of apes in all the features mentioned above.

Also Richard Dawkins (2004) in his *Ancestor's Tale* wrote that „Concestor one“ (the last common ancestor of human and both species of chimpanzees) was probably a chimpanzee-like arboreal ape. Assuming that humans evolved directly from "chimpanzee-like ancestors" (with the morphological and behavioral features of the recent species of *Pan*), we would really had to admit that humans diverged greatly in many aspects.

However, there is no *a priori* reason to assume that our social and mating system evolved from a chimpanzee-like basis. Both species of *Pan* can be significantly derived as well. This was supported recently by genetic evidence (Hopkin 2007, Bakewell *et al.* 2007), and morphological and behavioral features isolated chimpanzees from humans *and* the other great apes are well documented (Shoshani *et al.* 1996, Dixson 1998).

Comparison of two sister taxa (here: *Pan* and *Homo*) is a correct method to find the overall, "patristic" distance between them. Naturally, each individual difference between two sister taxa can be either an apomorphy of one taxon, or of the other, or possibly of both. The true "derivation load" (= number of apomorphies) of a taxon depends on the position of the root of this two-taxon tree: the common ancestor of the Hominini (= *Pan* + *Homo*) could be chimpanzee-like as well as human-like, and the information about outgroups (here: *Gorilla* and *Pongo*) is necessary to distinguish between the two possibilities.



Within the Hominoidea, many phenomenons considered to be uniquely human are in fact present in non-human species as well. Some form of substantial paternal care is known in gorillas (Maestripieri and Ross 2004) and in at least some species of gibbons (Palombit 1996). Females in geriatric population of western lowland gorillas in American zoos show obvious signs of the menopause (Atsalis *et al.* 2006). New data from long-term studies of the free-ranging orangutans (*Pongo abelii*) could suggest that, compared to the ancestral hominoid state, humans have undergone less of an increase in longevity than commonly assumed, and have experienced selection on earlier cessation of reproduction (Wilch, Utami *et al.* 2004). Also the gibbon monogamy with frequent intergroup (interfamily) interactions and the 12% level of extra-pair copulation (Reichard and Sommer 1997) is probably much more comparable to that of humans than we previously thought.

By all means, reconstruction of the common ancestors of the Hominoidea, Hominidae, Homininae, and Hominini is necessary for the human evolutionary psychology, which is strongly dependent on the concept of “environment of ancestral adaptation” (EAA). Although many suppositions were made about the sociobiological differences between human and non-human primates, no serious attempts have ever been made to analyze the conspicuous diversity of the human/ape behaviors phylogenetically. So far, human sociobiology is implicitly based on the linear, ladder-like reasoning (“from apes to human beings”) than on explicit evaluation of the phylogenetic trees.

The aim of this study is to analyze phylogenetically the available information concerning ecology, reproduction, ontogeny, behavioral patterns and social relationships in all species of extant and some extinct apes (sexual dimorphism), in order to reconstruct the particular common ancestors and the actual amounts of unique evolutionary novelties of individual species in question.

DIVERSITY OF THE RECENT SPECIES OF THE HOMINOIDEA

Diversity of the „biological“ characters of the individual Recent species of the Hominoidea is enormous, and the conventional dichotomy „*Homo* vs. rest of the (great) apes“ could only rarely be found. For more detailed comments and sources see Appendix.

1. Human (*Homo sapiens*)

Human is a bipedal, terrestrial ape inhabiting a wide range of habitats (originally probably savannah-like habitats).

Human has noticeable sexual dimorphism. Males are usually larger than females (although male stature is noticeably varying in the whole population), sexual dimorphism in canine size is insignificant, but sexual dimorphism in other physical features, especially in hormone-dependent sexual adornments is obvious. Males possess facial adornments like beard or loss of scalp hair that can results in baldness in some individuals, also more developed body and pubic hair. Females has large and prominent breast (these are developed before first pregnancy and breast enlargement is greater and begins earlier than in other hominoids). Fat allocation on the woman body is an important cue of female sexual attractiveness (although male preference for low waist-hips ratio is rather being culture specific, not universal like preferences for firm and symmetric breast).

Females do not posses any sexual skin swellings and ovulation is most probably concealed (females conceal ovulation not only to males, but even to themselves), although behavioral changes during the ovulation cycle have been detected (female proceptivity, mate-preferences, smell, fluctuating facial symmetry during cycle etc.). Females, however possess, plenty of features that are subjects to sexual selection (hair, facial symmetry, complexion, shape of the eyes, lips, etc.) Allocation of these features can be the outcome of human bipedality. Certain physical features (height, physique, facial and body symmetry etc.) play a role in male attractiveness as well. In most of the human societies, females are able to exert significant mate choice.

Males prefer to mate with younger, nulliparous females. Cross-cultural studies indicate that woman's sexual attractiveness generally peaks before motherhood and declines with age. Cues of female youth are thought to be attractive, because humans maintain long-term pair bonds, making reproductive value (e.g. future reproductive potential) particularly important to males.

Human is a moderately polygynous species. Polygyny is the prominent mating system (occurring in 84 % of 185 human societies considered), but harem polygyny is unusual. Another frequent mating system of human is monogamy (most individuals are monogamous). Polyandry occurs, but is extremely rare. Humans form unusually long-term pair bonds (maintained by frequent affiliative interactions, reassurance, non-conceptive sex, care for offspring, and intrasexual defense of mates and territory). Male rank and mating success are most likely to be positively correlated in many human societies. Extra-pair paternity is common, certainty of paternity of the dominant male (father) varies from about 80 to 100%. Degree of sperm competition is moderate in human (males have relatively small testicles).

Human males practice several mating strategies. Most usual is possessive strategy, when male monopolize female in the long term (marriage, partnership, or dating). Short-term male-female associations, comparable to consortships of other primate species, occur. Coercive matings (rape) are quite frequent in human, and some kinds of the coercive mating can be regarded as an alternative mating strategy.

Humans have sophisticated (although not necessarily more complex than some other ape species) precopulatory behavior. This includes communication and various activities (typically holding, touching, kissing, embracing, etc.). Just, like in other primates, engaging in eye contact plays crucial role. Humans have richly elaborated sexual behavior that often occurs in non-conceptive context.

Human pairs have sex quite often (mean copulatory frequency 0.025 / hour for North-American population). Mating is usually initiated by a female. Humans engage in various copulatory postures. Ventro-ventral (male superior) is the most frequent, but dorso-ventral and ventro-ventral with female on top and various other postures occur. Intromission duration varies. Human males are capable of achieving orgasm in less than two minutes, but intromission is usually longer, perhaps as a result of cultural evolution. Female is active during sexual intercourse. Majority of women (although the exact figure is most probably culture-specific and depends on number of factors) is capable of achieving orgasm. There is a positive relationship between female orgasm and amount of sperm retained, so it can enhance the probability of conception. Human males are unique among the apes (and primates) in two important features of genital morphology. Humans have the largest penis among great apes (twice as large as chimpanzees, whose penis is twice as large as in gorillas and orangutans) and they do not have baculum. The both characteristic can be interpreted as a result of sexual selection. Some types of sociosexual behavior occur in human that can be observed in other primate species as well (e.g. infantine sex-play).

Humans are non-seasonal breeders. Typical interbirth interval is 3-4 years (due to postpartum and lactational amenorrhoea in suckling mothers) but can markedly be reduced in absence of prolonged breastfeeding that leads to a loss of the regular intervals between successive births (“birth-spacing” according to Short 1994). Parental care in humans is greatly prolonged, including a long period of post-weaning nourishing and extended period of social learning. This is typical for most of the human cultures, including both hunter-gatherer societies and developed western society. Due to relatively short interbirth interval and need of prolonged parental care human female must care for two or more successive offspring. Human has substantial paternal care (including defending of the offspring, feeding, playing, learning etc.), but degree of paternal investment in the offspring varies greatly among human societies (and depends also on male’s physical attractiveness and other factors). Infanticide is prominent in humans, stepchildren are much likely to be killed than children living with natural parents. Parental infanticide (typically carried out by the mother) occurs as well, usually as a result of stress, severe environmental conditions, postpartum birth control or as an act of mercy. The onset of puberty in human is delayed compared to other great apes and noticeably varying in human populations, and it is affected by numerous factors. Major changes associated with puberty appear after 10 years of age. Menopause occurs in human females around 40 years of age. Considering the long lifespan it means that human female can spend considerable part of life as reproductively inactive.

Humans are gregarious with sophisticated social structure. Families (typically monogamous or polygynous) with several children of various age live within larger groups of more or less related or unrelated individuals. Intergroup interactions are frequent and also necessary for cohesion of larger social units. Various types of special relationships (both kin and non-kin) occur. All types of groups are usually dominated by male(s). Males dominate females, due to the strong tendency to form coalitions of both related and unrelated male individuals, but in some societies, male dominance is not pronounced or even apparent. Kin-associations, both male and female, play important role in all human societies. Female-female bonds can be also strong, oestrus synchrony occurs within some female social units.

Intergroup relationships vary across human societies from affiliative and friendly to rancorous or hostile. Strong competition for females and territory is common, intercommunity killings are frequent, and genocide occurs quite regularly. Veritable intergroup tolerance is rare.

Humans are omnivorous with diet based mostly on various reproductive parts of plants and supplemented by animal food. Varying degree of division of labour (foraging) by sex is characteristic. Human are capable of creating (exceedingly sophisticated) tools and weapons. They can cooperatively hunt various types of prey. Enormous variety of culture-specific behavior occurs among human societies.

2. Chimpanzee (*Pan troglodytes*)

Common chimpanzee is a quadrupedal ape that spends most of the time on the ground. Low degree of Bipedalism (almost all postural, not locomotor) occurs on arboreal substrates, and is mostly related to feeding and foraging behaviour. Chimpanzees inhabit forest and savannah habitats in tropical Africa.

Chimpanzees have moderate sexual dimorphism. Males are slightly larger than females and have moderately larger canines. Males do not possess any noticeable adornments, they only have wider faces than females.

Females posses large, prolonged sexual skin swellings with large oedema that lasts for about half of the menstrual cycle duration. Ovulation is detectable and advertised in chimpanzee female. Breast in female chimpanzee are markedly smaller than those of human females and develop in pregnancy.

Chimpanzee females in free-ranging populations are unable to exert significant mate choice. They can use indirect ways to affect paternity (such as termination of intromission before male’s ejaculation and post-copulatory calls). She may decline a male’s invitation to consortship. In contrast to humans, chimpanzee males prefer older females. Chimpanzees have promiscuous, multimale-multifemale mating system. There is no obvious correlation between male rank and mating frequency. Reproductive success of dominant males vary from 38–67% (average 50%) depending on the amount of competitors present. Degree of sperm competition is high, chimpanzee males have the largest testicles among primates.

Three distinct mating strategies occur in chimpanzee. In the opportunistic strategy (which is the most prominent), males from the group copulate repeatedly with a female, enabling each other to do so. Possesive strategy in chimpanzee means that dominant male temporarily monopolizes an oestrous female and does not let others to mate with her. Consortships occur too. In this case, a male (usually the dominant one) is followed by a female outside the group and mates with her. Such male-female associations vary greatly in duration (from few hours to several months). The occurrence and distribution of the mating strategies vary markedly among chimpanzee societies (e.g. no consortships occur in Mahale).

Copulatory frequency in chimpanzee is high (mean 0.52 / hour). Mating is usually initiated by male display and approach. Only one copulatory posture (dorso-ventral) occurs in chimpanzee with no exceptions. Copulation is very brief with intromission lasting from 5 to 10 seconds. Female is not active during intercourse, she sometimes rush off after mount is terminated.

Chimpanzee is the only ape in which copulatory plugs are known to occur, males possess long penis and reduced (shortened) baculum. In chimpanzee, three functions of sex exist: sex for reproduction, sex as a device of paternity confusion, and sex as a commodity (exchange for various favors, foodsharing, grooming etc.).

Chimpanzees are non-seasonal breeders. The typical interbirth interval is over five years, with one clear exception of the Bossou group. The age of first reproduction is 12–20 years for various chimpanzee populations. Parental care is prolonged (time to offspring independence is 6 years on average), but not comparable to that of human. Chimpanzee infant receives no direct and little indirect paternal protection and virtually none paternal care (except occasional play and some collective meatsharing), although chimpanzee males probably can recognize their own offspring. Raising an infant is very demanding for the chimpanzee mother. She must take care of it alone, and mother-offspring conflicts, such as refusal of suckling attempts and interference with mother's copulation, are common in chimpanzees. Infant mortality is high in chimpanzee (and chimpanzee has also the highest mortality through the whole lifespan), infanticide rate, on the other hand, is low. Puberty onset is delayed in chimpanzee and come up after sixth year of age. Chimpanzee longevity is comparable to that of humans (living in hunter-gatherer societies). No evidence has been found that menopause is a typical feature of chimpanzee life histories.

Chimpanzees are gregarious with social system often referred to as fusion-fission society. Function of the family is greatly reduced in chimpanzee, group size varies from about 20 to more than 100 individuals. Subgroup (party) usually consists of less than 7 chimpanzees (82 % in Gombe, 55 % in Mahale). Chimpanzee societies are characterized by male philopatry, strong male-male (both kin and non-kin) bonds, male alliances (various sociosexual behavior patterns occur in the males), male dominance over females, and surprisingly low degree of female-female affiliative interactions. Resident females often act aggressively towards immigrant females (this aggression, along with other factors can play a role in prolonged interbirth interval and low reproductive potential of chimpanzee female).

Chimpanzees are primarily frugivorous, supplementing the fruit with young leaf, stems, buds, bark, pith, seeds, and resins. They eat various animal foods, termites and other arthropods, small vertebrates, and they can cooperatively hunt mammalian prey (e.g. colobine monkeys). Cannibalism was observed in free-ranging chimpanzees. Chimpanzees are solitary foragers, members of the group do not maintain proximity during feeding, and disperse to feed in neighboring trees (even in periods of fruit abundance). Chimpanzees are unable to process terrestrial herbaceous vegetation and they can seasonally suffer from food stress. High degree of feeding competition may limit the group-size and affect various other ecological and sociobiological characteristics of the chimpanzee. There is often considerable overlap between the home ranges of adjacent communities and interactions are hostile. Intercommunity killings of both infants and adult group members occur and genocide was observed in chimpanzee

Chimpanzees are capable of using and even creating simple tools and weapons (used to hunt mammalian prey by savannah chimpanzees), they can handle the metatool. Various chimpanzee communities show wide range of culture-specific behavior.

3. Bonobo (*Pan paniscus*)

Bonobo is the closest relative of common chimpanzee, is slightly smaller, endemic to forest habitat of equatorial Africa. It can be regarded as terrestrial, but (like chimpanzee) spends considerable amount of time in the trees. Bonobo has the same level of sexual dimorphism as chimpanzee. Females posses large, prolonged, semipermanent sexual skin swellings with large oedema that are longer lasting than those of chimpanzee (nearly 80 % of the menstrual cycle) (Kalnova 2006). Female mate-choice is greatly limited in bonobo. Bonobo males do not show preference for certain females.

Bonobos have promiscuous, multimale-multifemale mating system. Male rank affects mating success, but inter-male tolerance is high and females mate with the most of non-kin males. Recent data suggests that bonobos are not less sexually competitive than chimpanzees. Top-rankig male(s) can be identified, based on small sample of "decisive aggressive interactions", but direct competition rate is low and relative ranking among other males unclear. Degree of the sperm competition is high, comparable to that of chimpanzees.

Majority of copulations is opportunistic in bonobos. Possesive mate guarding occurs in dominant male and regarding oestrous female.

Most copulations are initiated by a male. Copulatory frequency is high (mean 0.27 / hour). Two copulatory postures (dorso-ventral and male-superior ventro-vental) occurs in bonobo, but the dorso-ventral one is prominent (74 % of copulations observed). Intromission duration is from 10 to 15 seconds on average. Bonobos have richly elaborated sexual behavior that occurs without the constraint of a narrow window of fertility, and they use sex (in addition to functions mentioned in chimpanzee) for communicative purposes. Wide range of sociosexual behavior occurs, sex appears closely linked to the formation of the female-female alliances.

Bonobos are considered to be non-seasonal breeders although in Wamba bonobos a birth peak seems to occur during the light rainy season from March to May, just after the season with the least rainfall (Furuichi et al. 1998) The mean interval between live births of 4.8 years. Mother-offspring conflicts are rare in bonobos. No paternal care occurs. Bonobo infant mortality is much lower than that reported for chimpanzees, and some females simultaneously carried and nursed two successive offspring. Infanticide is virtually absent.

Bonobos live in fusion-fission groups. Both groups and parties are usually slightly larger than those reported in chimpanzees. Bonobo society is male philopatric, but with weak male-male bonds. Bonobo females, on the other hand, are highly affiliative to each other, despite they are unrelated genetically. Bonobo society is best characterized as female-centered and egalitarian with sex substituting for aggression. Female are able to cooperatively dominate males, they can defend themselves against occasional male aggression, or even retain food (fruit, meat) from adult males.

Bonobos are primarily frugivorous but unlike chimpanzees, they frequently exploit herbaceous vegetation. Bonobos are (at least partly) released from feeding competition.
Bonobo foraging behavior differs from that of chimpanzees. Bonobos eat together, especially during periods of abundant tree-fruit.

Bonobos do not made tools and they do not use tools in extent comparable to free ranging chimpanzees. Social hunting is not known in bonobos, they catch and eat small mammals (bushbabies etc.) occasionally, but meat proportion in the diet is probably marginal. Culture specific behaviour comparable to that of chimpanzee is was not observed in free ranging bonobos.

4. Gorillas (*Gorilla gorilla* and *Gorilla beringei*)

Gorillas are large terrestrial apes living in forests of equatorial Africa. Two species of gorilla are known: western lowland gorilla with wider distribution (some populations living sympatric with chimpanzee), and eastern gorilla (incl. mountain populations).

Gorillas are highly sexually dimorphic. Males are markedly larger than females, with large canines. Adult male (silverback) possesses a white saddle of short hair on back and a pat of fibrous/fatty tissue on the top of head. Gorilla females do not have sexual skin swellings, only slight tumescence of the labia occurs in mid-cycle.

Female mate-choice is limited in gorillas. Females usually strongly prefer to mate with the dominant male, who forcibly terminates copulations by others. Older silverback is generally more tolerant towards younger male (who is usually related to him), but female is generally unable to exert significant mate-choice.

Universal male preferences are difficult to assess, but silverback apparently invests differentially in relationships with individual females, but that does not regard only sexual relationships. Old males, for example, spend more time with mature daughters and granddaughters and give them agonistic support. Special relationships occur in gorillas and seem to be affected by length of the acquaintance.

Gorillas have polygynous mating system (harem-defense polygyny). Male rank and mating frequencies are positively correlated, male typically sires all offspring, although in the mountain gorilla groups up to three (exceptionally four) silverbacks are present. In western lowland gorilla groups there is usually only one silverback (sometimes the second is present, usually the maturing son of the dominant male who later emigrate).

Prevailing mating strategy is continuous mate guarding. Silverback monopolizes all females in the group, defending them and his offspring against other males. Subordinate males can stay (and "inherit" the group after silverback death) in natal group or emigrate and become solitary. Lone male can acquire female (usually the younger one) from an established group and thus form a new unit.

Gorillas do not engage in sexual activity as frequently as humans, chimpanzees or „hypersexual" bonobos. Mating is usually initiated by a female, who experience major increase in proceptivity during follicular phase (mid-cycle peak in sexual activity can be distinguished in all species of great apes including human). Dorso-ventral copulatory posture is prominent in both species of gorilla, but ventro-ventral male=superior occurs as well (more frequently in western lowland gorilla). Intromission duration is about 1.5 minutes. Female gorilla is active during sexual intercourse, complementing male's pelvic thrusts with visible pelvic thrusts of her own. Vocalization is given during intercourse, no post-copulatory calls occur. Gorilla males have small penis with baculum that is longer than that of chimpanzee, and have the smallest testicles of all great apes. Sperm competition is insignificant in gorillas. Sociosexual behaviour occurs in gorillas, but not in the same extent as in chimpanzees and bonobos.

Gorillas are non-seasonal breeders with shortest interbirth interval among apes (with the exception of reduced interbirth interval in modern human societies), about 3-4 years that is more affected by ecological and social factors than by gorillas biology. The age of first reproduction is lower than in the other great apes (8.7-12.8 years in *Gorilla beringei*) Gorilla infant receives direct paternal protection, and substantial paternal care occurs in gorillas. This includes guarding, social play and learning. Male infants play more than female infants did, and both male and female infants prefer to play with males rather than with females.

Infant mortality is moderate (higher in mountain gorillas) and infanticide (following dead or ousting of the dominant male) is common. Other males attempt to kill the offspring of a rival, therefore, the paternal protection is crucial for infant survival. Puberty onset is delayed, comparable to that of chimpanzee; gorilla females experience menopause.

Gorillas are gregarious with harem social structure. Harem can be compared to human family. Gorillas are considered to be male philopatric (although not all females leave natal group and not all males stay). Males dominate females.

Mountain gorillas are folivorous supplementing terrestrial herbaceous vegetation by forest fruit, western lowland gorilla is more frugivorous / omnivorous, but broadly exploiting terrestrial herbaceous vegetation. Gorilla groups do not suffer from food stress and the group members maintain proximity during feeding. Gorillas do not eat meat.

Intergroup encounters of mountain gorillas are related to acquisition of females and are extremely hostile. Close-range displays and fights of silverback are common. Intergroup encounters of western lowland gorillas are rather associated with access to and defense of food resources and they are relatively peaceful. Cases of extreme intergroup tolerance are known.

Gorillas do not use tools in the same manner as chimpanzees, primitive tool-use during fording and male displays was observed in western lowland gorilla. There is no evidence for culture-specific behavior in gorillas (at least nothing that would be comparable to human or chimpanzee).

5. Orangutans (*Pongo pygmaeus* and *Pongo abelii*)

Orangutans are large arboreal apes. Two species (Bornean orangutan and Sumatran orangutan) inhabit forested areas of Indonesia.

Orangutans express high degree of sexual dimorphism in body weight and canine size. Adult male possesses noticeable (and species-specific) androgen-dependent adornments (fibrous/fatty cheek „flanges“, a hump on top of head, beard, and long hair on shoulders, back and arms).

Orangutan females do not posses any sexual skin swellings. Female mate-choice is possible in orangutan. Females strongly prefer to mate with the adult, dominant males. It has been suggested that females may seek out flanged males for protection from harassment by unflanged (non-dominant) males. Little is known about the orangutan male mate preferences, but considering the absence of menopause in orangutan females, it is probably not correlated with age.

Mating system of orangutan is a dispersed harem polygyny. The orangutan males are of two, distinct adult morphs. The flanged males possess sexual adornments, are twice the size of the unflanged males, and produce loud “long calls” to advertise their presence. The unflanged males, on the contrary, are of about the same size as females, and lack the secondary sexual characteristics possessed by flanged males. These adult morphs pursue two distinct mating strategies.

The mating strategy of a flanged, dominant male is referred to as “call and wait” strategy and is comparable to consortship and/or possessive tactics in other ape species. Female seeks out the dominant male when she is most fertile and mates with him. Such association lasts for several days. The unflanged-male mating strategy is referred to as „sneak and rape“.

Unflanged males suffer little energetically from the association with females, compared to the flanged males, allowing them to spend more time close to females. Copulations are forced. Females strongly resist mating with the unflanged males, although copulation usually ensues. This resistance is unique among non-human primates. Unflanged males, until recently, were thought to have limited reproductive success but recent genetic analyses have shown that, in a population of Sumatran orangutans (*Pongo abelii*), the unflanged males fathered 6 out of 10 offspring born over a 15-year period for which paternity could be determined. Similar findings were gained through studies of the Bornean orangutans. Both adult morphs have considerable reproductive success, and the sneak and rape is a frequency-dependent strategy. Penis and testes size of orangutan are comparable to that of gorilla, although slightly larger.

Normal (self-imposed) mating is initiated by females. Orangutan males are surprisingly passive during copulation. Prominent mating posture is ventro-ventral (female superior). Median copulation duration is about 14 minutes (maximum 46 minutes).

Orangutans are non-seasonal breeders (although most matings occur in the heaviest fruiting months) with longest inter-birth interval among apes (6-8 years in Bornean orangutan, 8-10 years in Sumatran one). The age of first reproduction is 13–18 years (with mean 15.4 for Sumatran and 15.7 for Bornean orangutans, they have later age at first reproduction than chimpanzees). Parental care is prolonged, no paternal care occurs. Adult males sometimes leave the area after the females they had mated with become pregnant, or gave birth. Puberty onset is delayed, comparable to that of other great apes excluding human (female orangutans become sexually active at the average age of 12.3 years), but male can arrest their development towards the flanged morph for a variable period between one and twenty-five years of age. Infant mortality is very low, infanticide has never been observed. Orangutans have the slowest life history pace among non-human primates. Longevity estimates from the wild indicate life spans of over 50 years, with no evidence for menopause.

Orangutans are female-philopatric.

Orangutans are non-gregarious. Solitary lifestyle is most likely enforced by continuous food-stress and arboreality (orangutans are almost completely arboreal except for occasional forays on the ground) of a considerably large ape. Orangutans are frugivorous (with higher degree of folivory in Bornean species), and ripe fruit is scarce in forests of Borneo and Sumatra. Orangutans are supplementing fruit by young leaves, flowers and bark, insects (mainly ants, termites, and crickets), and an occasionally eggs. In the nutritionally more abundant forests of Sumatra, so called mass fruiting years (typical for dipterocarp rainforests) occur, when the normally non-gregarious orangutans gather to feed.

Encounters between flanged males are always aggressive, with the loser fleeing. Unflanged males, on the other hand, are generally quite tolerant towards one another.

Both species of orangutan exhibit tool use (but not tool-creating) abilities comparable to those of chimpanzee, and geographic variations in their cultural diversity were found.

6. Gibbons (*Hylobates, Hoolock, Nomascus,* and *Symphalangus*)

Gibbons are small arboreal apes living in forested areas of South-East Asia. Their body weight and canine size sexual dimorphism is inconsiderable. Males possess some androgen-dependent adornments (e.g. black pelage, preputial tufts). Some species do exhibit patterns of sexual dichromatism and ontogenetic color change.

Females of some species (especially *Hylobates lar*) are known to possess small sexual swellings.

Monogamy, moderate polygyny, and (possibly) polyandry occur in gibbons. Possesive strategy can be considered the only mating tactics in all gibbon species.

Dominant male’s (father’s) paternity success is possibly 100 %, sperm competition is minimal; extra-pair copulations, however, occur (frequency depends on population density and the frequency of intergroup encounters). Copulation frequency is lower than in the great ape species, but probably higher than previously assumed.

Gibbons are thought to live in nuclear families consisting typically of 2-6 individuals, including a pair of breeding adults who maintain lifelong, sexually monogamous relationships. Monogamy is generally thought to be maintained by intrasexual defense of territory.

Gibbons are non-seasonal breeders. New data suggests that interbirth intervals may often exceed the 2- to 3-year interval, commonly attributed to these species. Puberty is reached earlier (less than 5 years of age) in gibbons than in other ape species.

Paternal care in varying extent occurs, substantial paternal investment is known in the siamangs (*Symphalangus syndactylus*). Infant mortality varies, but is generally lower than that of chimpanzee or gorilla. Infanticide has never been observed in the gibbons.

There is no apparent dominance of one sex over other in gibbons. Behavioral observations suggest that gibbons are male-philopatric (shorter dispersal distances are probably more common in males). Dispersing young usually obtain mates by replacing adults in the existing territories, which creates non-nuclear families. Social relations within such a heterogeneous group remain harmonious.

Intergroup encounters are relatively peaceful, displays and chasing occurs along with the intergroup infantine play and affiliative behavior.

Gibbons are primarily folivorous /frugivorous, proportion of leaves, flowers, ripe fruit etc. varies among species.

No tool use or cultural diversity has been observed in gibbons.

MATERIAL AND METHODS

1. Taxon sampling and character data

All the Recent ape species (*Homo sapiens, Pan troglodytes, P. paniscus, Gorilla beringei, G. gorilla, Pongo pygmaeus, P. abelii, Hylobates lar, H. klossii, H. agilis, H. moloch, H. muelleri, H. pileatus, Nomascus concolor, N. nasutus, N. gabriellae, N. leukogenys, Hoolock hoolock,* and *Symphalangus syndactylus*) were analysed, and eleven cercopithecoid species (*Papio anubis, M. mulatta, M. fuscata, M. nigra, M. radiata, M. arctoides, Cercopithecus aethiops, Miopithecus talapoin, Theropithecus gelada, Erythrocebus patas*, and *Presbytis potenziani*) were used as outgroups (*P.s potenziani* as a rooting outgroup). Altogether 23 species (or genera) of extinct apes (*Aegyptopithecus zeuxis, Proconsul, Laccopithecus robustus, Dianopithecus progressus, Chororapithecus abyssinicus, Dryopithecus, Ouranopithecus, Oreopithecus, Sivapithecus, Gigantopithecus, Lufengopithecus lufengensis, L. chiangmuanensis, Khoratpithecus, Ardipitecus ramidus, Australopithecus anamensis, A. afarensis, A. africanus, Paranthropus robustus, P. boisei, Homo hablis, H. erectus, H. neanderthalensis,* and archaic *H. sapiens*) were also included, if some data on sexual dimorphism in the body size and canine size (as approximation of the species sociobiology and mating system) are available.

The main sources for collecting the data used as a character matrix were the extensive monography *Primate Sexuality* (Dixson 1998), article assemblage *Great Ape Societies* (McGrew *et al.* 1996), and numerous journal sources (see Appendix). I made an effort to use data from free-ranging populations of apes as much as possible. However, in some species, like western lowland gorilla and bonobo, strong bias toward captive data is a general rule (Lockwood *et al.* 2007).

Because direct human-ape comparison can be very tricky and attempts to find ape homologues of all human behavioral traits (like art or religion) could be misleading, I choosed the opposite approach. During the character scoring, the comparative data for as many species of great and lesser apes as possible were collected first. Afterwards I looked for their possible human homologues.

Regarding the human data, comparison with other apes is not the only problem. It is quite obvious that some data on human sexual behavior would be inaccurate and biased, while others would be unavailable at all. It is mostly because such information is acquired by questionnaires or enquiry, and humans strongly tend to lie, conceal or overstate, and to exaggerate the oddities concerning sex (Frynta, pers. comm.). For basic developmental and sociobiological characteristics (lifespan, interbirth interval, etc.) the data from hunter-gatherer societies were preferred. In other features, data from more tribes were included (Norwegians or Knickerbockers are considered „tribes“ as well as Yolngu Aborigines), assuming that many features of human sexuality and other behavioral patterns do not change much due to cultural revolution, sexual revolution, social welfare etc. Nevertheless, I must note that some of these traits, for example the intromission duration, are considered to be culture-influenced (Dixson 1998).

2. Datasets and phylogenetic analyses

The suitable characters (with more than one state, where character states for at least three species were known, and such that were certainly not synonymous with others) were translated into character matrix using Winclada software (Nixon 1999).

Because of polymorphic nature of many characters, four datasets were created. In one, called „polymorphic“, all character states observed in the species were scored using the polymorphic coding, regardless their quantitative distribution. In the second, „monomorphic“ matrix, only the most prominent state was coded. For example, in human, the character „Mating system“ has all possible states known among apes (with the exception of promiscuous mating system) coded in the polymorphic matrix, but in the monomorphic matrix, the human is coded as „moderately polygynous“ species, because polygyny occurs in 84 % of 185 human societies for which sufficient information could have been obtained (Ford and Beach 1952) and some of our morphological and anatomical characteristics are indicative of a polygynous ancestry (Short 1980). Finally, the human and ape polymorphisms were resolved to formed two more datasets, “Pan” (human, chimpanzee, and bonobo were recoded to be as similar as possible) and “Gorilla” (human and gorillas were recoded to be most similar).

Characters from behavioural dataset were optimized parsimoniously on the cladogram based on recent syntheses of morphological and molecular data (Shoshani et al. 1996, Pilbeam 1996, Takacs et al. 2005, Whittaker et al. 2007). The NONA (Goloboff 1999) software was used (option “unam”).

RESULTS AND DISCUSSION

1. The data matrix

In the final form, the dataset includes 32 Recent species and 65 characters, i.e. 2,080 character states. In the "polymorphic" matrix, there were 51 polymorphic character states; in the "monomorphic" one, the number of polymorphisms was reduced to 19. The overall amount of ambiguous (i.e. unknown, inapplicable, and polymorphic) character states is 27-29 % in all data matrices.

2. Character evolution

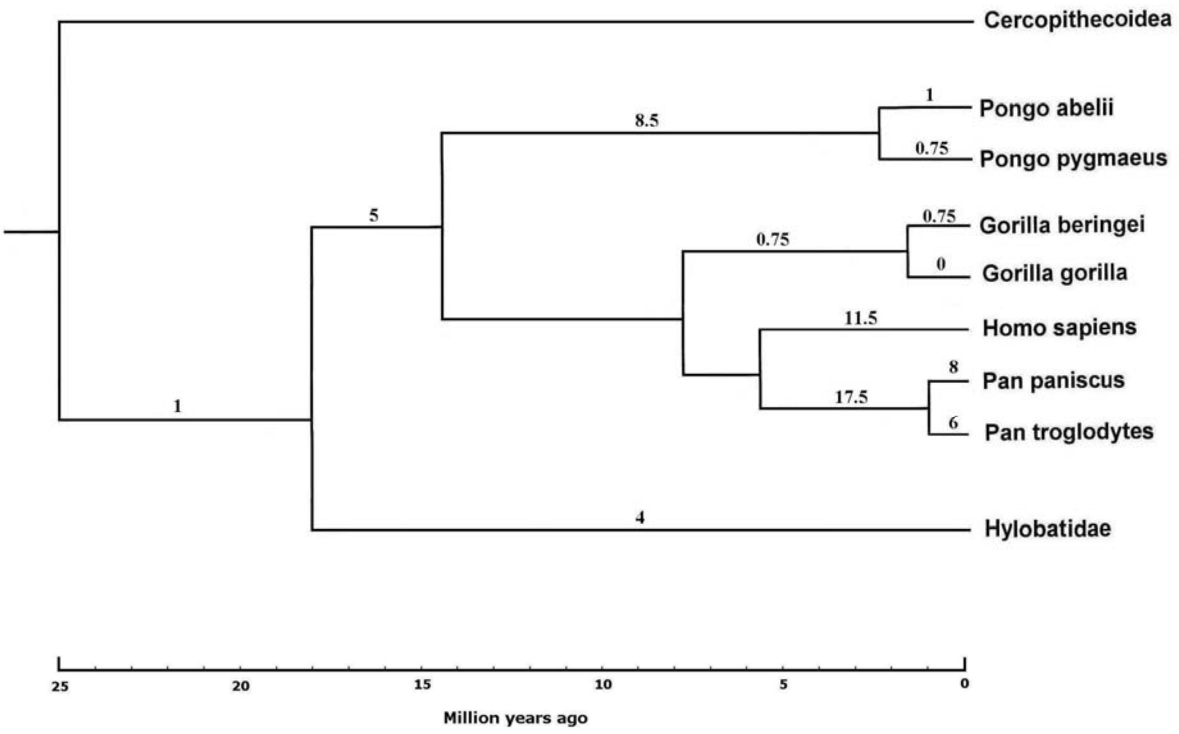
Optimization of the "biological" characters on the hominoid phylogeny allowed to reconstruct the hypothetical common ancestors and to infer the "derivation load" of the individual species and clades. Analysis of four datasets revealed that effect of various polymorphism-coding on the lengths of important branches was negligible (Table 1).

The tree branch leading to *Homo sapiens* is actually one of the longest (11-13 autapomorphies). However, some other branches are of comparable lengths (*Pongo* 7-9, *Pan paniscus* 8) or even considerably longer (*Pan* 17-18).

Table 1: Lengths of significant branches (= number of autapomorphies of the taxon given) according to „polymorphic", „monomorphic", „Pan", and „Gorilla" datasets

	Polymorphic	Monomorphic	Pan	Gorilla	mean
Hominoidea	1	1	1	1	1
Hylobatidae	4	4	4	4	4
Hominidae	5	5	5	5	5
Pongo	7	9	9	9	8.5
P. pygmaeus	0	1	1	1	0.75
P. abelii	1	1	1	1	1
Homininae	1	1	1	1	1
Gorilla	0	1	1	1	0.75
G. gorilla	0	0	0	0	0
G. beringei	1	1	0	1	0.75
Hominini	6	6	6	6	6
H. sapiens	11	13	11	11	11.5
Pan	18	17	17	18	17.5
P. troglodytes	6	6	5	7	6
P. paniscus	8	8	8	8	8

Fig. 1. Phylogeny of the Hominoidea, based on recent consensus of morphological and molecular data, with times of divergence indicated (Haaf *et al.* 1995, Zhang *et al.* 2001, Glazko and Nei 2003, Thalmann *et al.* 2005, Won and Hey 2005, Ebersberger *et al.* 2007). Mean lengths of significant branches based on optimization of behavioral data on the phylogeny are shown above the branches.



3. Reconstruction of development, behavior and socioecology of the hypothetical common ancestors

3.1. Common ancestor of *Pan* and *Homo*

The animal referred to as “Concestor one” by Dawkins (2004) that lived some 5-6 million years ago (Ebersberger *et al.* 2007), was most likely gregarious, mostly terrestrial ape that spent substantial time in the trees and showed a low degree of postural (probably arboreal) bipedalism.

This ape had marked sexual dimorphism in both body weight and canine size, with males possibly having some androgen-dependent sexual adornments. Females did not possess noticeable sexual skin swellings. Other physical cues of female sexual attractiveness like large prominent breast were not present, at least not in the extent comparable to females of recent

Homo. Ovulation was not concealed. The penis was moderately lengthened, comparable to recent chimpanzee, and baculum was present, possibly reduced to some degree.

Female personal mate choice might have been possible, patterns of male mate choice are unknown, and it is impossible to assess whether females experienced menopause or not. “Concestor one” lived in gorilla-like polygynous groups with males exerting consortship/mate guarding mating strategy. Male rank and mating frequency were positively correlated. Nocturnal copulations and mate guarding might have been present. Female was the initiator of most copulations, intromission duration was most likely more than one minute. Prominent copulatory posture was dorso-ventral. It is impossible to resolve whether sex in the non-conceptive context occurred and how elaborated the sexual behavior was, but some additional functions of the sexual activity (like paternity confusion) might have been present.

Onset of puberty was slightly delayed comparable to recent hominoid species, but not as delayed as in *Homo*. Parental care, paternal protection and some degree of the paternal care were present, infant mortality was moderate, with unclear significance of the intra- and intergroup infanticide. Slow life history pattern, similar to the extant great apes (delayed puberty, long interbirth period, long lifespan), was present in the “Concestor one”.

Society was male-centered, patterns of philopatry unknown. Family as a functional social unit was present, possibly within larger social units consisting of unrelated individuals. Special relationships (e.g. friedships between male and female, long-term social bonds) probably existed in this society, but degree of the male-male and female-female plotting and the potential existence of coalitions are impossible to resolve. Intergroup encounters were moderately aggressive, comparable to extant western lowland gorillas.

This species was primarily frugivorous, with meat proportion in the diet unknown, and with social foraging behavior. The degree of tool-usage is impossible to assess, some cultural diversity might have been present.

3.2. Common ancestor of *Pan* spp.

The bonobo and the common chimpanzee are estimated to have diverged approximately 0.86-0.89 million years ago (Won and Hey 2005). According to the parsimony optimization, the common ancestor of both species of *Pan* already showed reproductive, behavioral, developmental, and sociobiological patterns similar to that present in his recent descendants. However, some characteristics of the *Pan* ancestor are impossible to determine, especially those regarding social and feeding ecology (although it was certainly mostly frugivorous), as interactions between the sexes are obviously different in the common chimpanzees and bonobos and in their closest “outgroups” (humans and gorillas). Extent of tool usage and culture-specific behavior is unclear as well. Mating system was polygynandrous, dominant male paternity success was reduced, and mate guarding only occasional. Most matings were initiated by males, copulations were brief, and other behavioral traits resembling Recent *P. troglodytes* were present.

3.3. Common ancestors of Hominidae and Hominoidea

The common ancestor of the Hominidae lived approximatelly 12-15 million years ago (Glazko and Nei 2003) and common ancestor of the Hominoidea some 15-25 million years ago (Haaf *et al.* 1995). Results of the optimization suggest that reproductive, behavioral and developmental traits and sociobiology were generally identical in both.

Both were gregarious, arboreal apes showing moderate degree of (at least) canine size sexual dimorphism, with males possibly having some sexual adornments and female lacking sexual skin swellings (although small swellings might have been present in common ancestor of Hominoidea). Ovulation was detectable. The penis was short, baculum present.

Female mate-choice was possible, degree of sperm competition moderate, and male rank and copulatory frequency were positively correlated. Common ancestor of the great apes was polygynous; common ancestor of both great apes and gibbons might have been monogamous, but probably exhibited some degree of polygyny. The prevailing mating strategy was possessive mate-guarding. Matings were female-initiated, and intromission duration probably more than one minute long. The primary copulatory posture was dorso-ventral.

Infants received some degree of paternal protection, but no substantial paternal care was present. Onset of puberty was only slightly delayed compared to the cercopithecines, and the lifespan was lower compared to recent great apes. Females most likely were not experiencing menopause.

These species lived in multimale-multifemale groups that were male-centered. Oestrous or breeding synchrony might have occurred among females within the group. Intergroup encounters were moderately aggressive.

Both ancestors were primarily frugivorous with collective foraging.

3.4. Extinct apes

Patterns of sexual dimorphism in extinct hominoids are also indicative of polygynous ancestry. Parsimonious optimization of data regarding fossil remains shows that basal hominoid lineage expressed high degree of sexual dimorphism in body weight and in canine size. The loss of dimorphism in body weight in gibbons and its reduction in the Hominini occurred independently, as well as the loss of canine-size dimorphism in gibbons and modern humans (in the human lineage, the onset of reduction of the sexual dimorphism took place in *Homo erectus*).

4. Evolutionary origin of the human uniqueness

Table 2: Representation of features of human behavior, sociobiology, and development, found in common ancestors of Hominoidea and Hominidae, common ancestor of Hominini and features regarded as human autapomorphies, based on the behavioral dataset

Hominoidea and Hominidae	Hominini	*Homo*
52,8%	9,4%	37,8%

4.1. The old hominoid components of the human biology

The phylogenetic analysis suggests that most of the fundamental characteristics of human behavior, sociobiology, and development are in fact evolutionary older and were already present in common ancestors of Hominoidea and Hominidae. Altogether they cover more than half of the characters analysed.

They include basic patterns of sexual dimorphism in body weight and canine size (that are still present in humans, although reduced to some degree), presence of androgen-dependent adornments in adult males, possible suppression (arrest) of male development, no (or only small) sexual skin swellings in female, possible oestrous synchrony within some female social units, polygynous (or ocasionally monogamous) mating system with positive correlation of male rank and mating frequency and significant paternity success of dominant male), possessive/consortship mating strategy, medium testes size and no copulatory plugs (moderate degree of sperm competition), copulatory patterns (initiation of copulation by female, intromission duration about 2 minutes, some female activity during copulation and possibly female orgasm), slow life-history pattern (delayed puberty, interbirth period about 4 years, and long lifespan), parental care, weaning longer than two years, direct paternal protection and some (possibly substantial) paternal care, and the social structure (families or harems, male dominance, social foraging and moderately aggressive intergroup encounters).

4.2. Synapomorphies of the Hominini (Homo + Pan)

The following behavioral, ecological, and sociobiological characteristics (less than 10 % of human features) can be regarded as apomorphies of the common ancestor of *Pan* and *Homo*: higher degree of terrestriality, lower degree of vocalization (used for long-distance communication), culture-specific behavior, additional functions of sexual activity (like exchange for favors and paternity confusion), and possibly also the patterns of philopatry and intergroup relationships. Some penis enlargement and reduction of baculum might have been present.

4.3. The unique human apomorphies

The following human characters concerning behavior, ecology, sociobiology and development (more than one third of the human features) are the true, unique autapomorphies: They include:

- reduced sexual dimorphism in body weight, loss of sexual dimorphism in canine size;
- male's preference for young, nulliparous females (Muller *et al.* 2006);
- further penis enlargement and loss of baculum;
- presence of non-behavioral cues of female sexual attractiveness (prominent breast development, fat allocation, facial symmetry etc., that are considered true signals of female reproductive potential and overall health (Moller *et al.* 1995, Marlowe 1998) and their allocation might be an outcome of the human bipedality;
- blurring the ovulation signaling (concealed or non-advertized ovulation) in females;
- high proportion of non-conceptive sex, sex in private, and lower copulatory frequency
- further delayed puberty onset;
- post-weaning nourishing of children till early adulthood;
- substantial paternal care, noticeable infanticide rate and parental infanticide;
- degree of omnivory, and significant meat proportion in the diet

.

It is impossible to assess whether female menopause is a human autapomorphy or not. Mating system and strategies related are rather conservative evolutionarily in human, but strict monogamy and polyandry (although negligible) are autapomorphies of individual human populations. Also the coercive strategy (rape) as a part of male „arsenal" of mating strategies can be regarded as a human autapomorphy (similar strategy evolved in orangutan independently).

CONCLUSION

The common ancestor of the Hominini (*Pan* + *Homo*) as well as common ancestors of Hominidae and Hominoidea showed more or less gorilla-like behavior, mating system and sociobiology. Ergo, despite universal assumptions, humans should rather be regarded as slightly derived gorillas than substantially derived chimpanzees. Consequently, the phylogenetic analysis of the observed ape diversity seems to falsify most conventional (“chimpanzee-centric”) sociobiological theories about biological roots of the origin of the humans.

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APPENDIX - Character list

Char. 1 - Dominant male paternity success (%)

State 0 - 100% - 80%
State 1 - 80% - 60%
State 2 - 60% - 40%
State 3 - 40% - 20%
State 4 - 20% - 0%

Sources: Dixson (1998), Reichard and Sommer (1997), Utami et al. (2002), Simmons et al. (2004), Setchell et al. (2005), Alberts et al. (2006), Goossens et al. (2006), Harrison and Chivers (2007), Inoue and Takenaka (2008)

Data for gibbons were not obtained directly from paternity analysis, but extrapolated from EPC (extra-pair copulations) frequency, which is 12 % in a free-ranging population of white-handed gibbons (*Hylobates lar*) in Thailand's Khao Yai rainforest (Reichard and Sommer 1997) and is probably much lower in other populations and in other gibbon species (Harrison and Chivers 2007).

Char. 2 - Male rank and mating frequencies positively correlate

State 0 - yes
State 1 - no (no correlation found)

Sources: Kano (1992), McGrew et al. (1996), Dixson (1998), Matsubara, M. 2003, Setchell et al. (2005), Alberts et al. (2006), Inoue and Takenaka (2008)

In the vast majority of primate multimale-multifemale groups male rank and mating frequencies are positively correlated. Alpha male copulate with females more often than beta male and so on. The same correlation occurs in monogamous families or in one-male groups, where dominant male (the father) performs the majority of copulations (although he might no be the only one who copulate with female and some EPC (performed by peripheral solitary males or fathers from adjanced families/groups) might occur). Significant correlation of male rank and copulation frequencies has never been found in chimpanzee (*Pan troglodytes*) (Dixson 1998). In bonobo (*Pan paniscus*), contradictory data exist. In Wamba population, positive correlation was previously found (Kano 1992), but more recent data suggests that „there is no consistent relationship between male rank order and mating success and it is unclear if male bonobos are less sexually competitive than male chimpanzees" (McGrew *et al.* 1996). Outside Hominoidea, male rank and mating frequencies usually show positive correlation with exception in Japanese macaque (Macaca fuscata) where female prefers to mate with low-ranking (peripheral) adult males, and the long-term tenure of the alpha-male within the group affects his mating success negatively (Inoue and Takenaka 2008).

Char. 3 - Adult male morphs (occasional suppression of male development)

State 0 - one adult morph
State 1 - two adult morphs

Sources: Dixson (1998)

In some species of monkeys and apes (typically in the polygynous ones) two distinct forms of postpubertal, (at least potentially) reproductively active adult male are present as a possible effect of inter-male competition (e.g. silverback and blackback in gorillas, flanged and unflanged male in orangutan). These morphs differs especially in weight and presence of androgen-dependent adornments. It is not clear if this phenomenon occurs in human males as well. Growth of external genitalia, pubic hair, larynx and muscularity show great individual variation, and social factors might be involved (Dixson 1998). However, although human males show enormous variability in appearance, there is no clear distinction between two types („masculine" and „feminine", for instance). This variability is distributed gradually on a large scale, and it is therefore impossible to resolve whether human possess these character or not.

The purpose of this character is to express that in certain species of apes (and in one species of monkey – mandrill) postponing or suppressing of development of sexual dimorphism (see characters 33 –35) occurs, probably due to a presence of another adult, dominant male and this dimorphism of males (although sexually dimorphic traits are not homologous) leads to dimorphic strategy of female acquisition in this species.

Char. 4 - Possesive mate-guarding of an alpha-male

State 0 - permanent
State 1 - occasional (regarding only oestrous or peri-ovulatory females)
State 2 - none

Sources: McGrew et al. (1996), Dixson (1998), Marlowe (2000), Matsubara (2003)

Char. 5 - Onset of puberty

State 0 - reached at 2-5 years
State 1 - slightly delayed, reached usually around 5 years of age
State 2 - delayed, reached at 6-10 years
State 3 - further delayed, noticeably varying, reached typically at >10 years

Sources: Marshall and Tanner (1986), Shoshani et al. (1996)

Char. 6 - Copulatory postures

State 0 - dorso-ventral (foot clasp on non-foot clasp mount)
State 1 - ventro-ventral (male superior)
State 2 - ventro-ventral (female superior)

Sources: Kinsey et. al. (1948), Koyama (1971), Dixson (1998)

The most prominent copulatory posture among primates is dorso-ventral (with foot-clasp in many species of monkeys). Ventro-ventral copulatory posture was observed among various hominoid species, e.g. *Symphalangus syndactylus, Pongo pygmaeus* (in *Pongo* it is female superior). In chimpanzee (*Pan troglodytes*) the mating posture is invariably a modified dorso-ventral one. The bonobo (*Pan paniscus*) is more versatile in its copulatory behaviour (about 25 % of copulations is ventro-ventral, the rest is dorso-ventral). Gorillas practise both positions, but prefers the dorso-ventral one. Ventro-ventral (male superior) position is usual among human. It is prefered by great majority of American couples (as well as Alorese, Balinese, Lepcha, Trobrianders, Trukese, and many others). Numerous copulatory postures (more or less derived from the three basic postures considered here) were reported from humans. Humans are (as well as bonobos, gorillas and orangutans) polymorphic in this character, but with one prominent posture.

Char. 7 – Interbirth interval (in free-ranging populations)

State 0 - typically between 1-3 years
State 1 - typically <5 years
State 2 - slightly prolonged, typically 5-6 years (excluding the Bossou group)
State 3 - prolonged (6-8 years)
State 4 - prolonged (8-10 years)

Sources: Howell (1979), Hayssen et al. (1993), Wich et al. (2004), Short (1994), Wrangham et al. (1994), McGrew et al. (1996), Furuichi et al. (1998), Palombit (1995)

In this character, intervals between two successive live births in free-ranging populations, with nursing and surviving offspring (otherwise it is usually shorter), were considered. In cases where lifespan in wild is not known, I used data from captivity (some outgroups and gibbons).

Human interbirth interval is actually quite short compared to other great apes, but extreme shortened interbirth interval in modern western society is a result of abandonment of the prolonged breastfeeding that began some 4,000 b.c. (Short 1994). Normal interbirth interval (with postpartum and lactational amenorrhea) among !Kung hunters-gatherers in Africa is 3-5 years (average 4.1) (Howell 1979)).

Chimpanzees (*Pan troglodytes*) have prolonged interbirth interval, propably due to their social and mating system rather than due to reproductive physiology. This can be supported by long-term observations of community of *Pan troglodytes* in Bossou (southeastern Guinea). The Bossou group is isolated from other chimpanzee groups (their territory is surrounded by human settlements) and therefore Bossou chimpanzee societies are of „non-fusion-fission“ type. Interbirth intervals are shorter (usually <5 years) due to different social relationships (parties include larger percentage of community members, parties are permanent, and the dominant males actively maintain the group cohesion) (Wrangham *et al.* 1994). In the rest of chimpanzee populations, interbirth interval is longer (5.1–6.2 years; see Wich *et al.* 2004) due to “harsher” social conditions. Mother must carry the infant alone and she receives no support from its father. Mother-offspring conflicts, such as refusal of suckling attempts and interference with mothers’ copulation, are common (Furuichi *et al.* 1998). The fact that resident females often act aggressively towards immigrant females (Wrangham *et al.* 1994) may also add to a prolonged interbirth interval; all this affects not only interbirth interval, but the age at first birth as well (it is higher in chimpanzee than in gorilla and bonobo) (Wich *et al.* 2004). Seasonal food scarcity and low level of fruit sharing (except mother-offspring sharing) between chimpanzees can also play significant role in this phenomenon.

Mean interbirth interval of 4.8 years in bonobo is shorter than those reported on chimpanzees, and some females simultaneously carry and nurse two successive offspring. The mother-offspring conflicts are rare in bonobos (Furuichi *et al.* 1998).

Interbirth interval of both species of gorilla is shorter, comparable to that of human, most likely due to group cohesion, protective function of an adult male (silverback), substantial paternal care, less seasonal food availability, and low degree of female-female aggressive interactions (males usually intervene to end conflicts between females) (McGrew *et al.* 1996). Gorilla females also have lower age at the first birth (Wich *et al.* 2004) and higher reproductive potential as a result (births by 40 years of age: average 4.4 for chimpanzee, average 7.1 for gorilla) (Wrangham *et al.* 1994).

The longest interbirth interval among apes has been found in orangutan species (with average interbirth interval 6.1, 7.0, and 7.7 years in various populations of *P. pygmaeus* and 9.3 years in *P. abelii*). This is probably caused not only by the orangutan ecology and social organization, but also by their reproductive physiology (*P. abelii* has longer interbirth interval than *P. pygmaeus*, despite both species have virtually identical social system, and Sumatra is richer in fruit than Borneo; Wilch *et al.* 2004).

Char. 8-10 – Social system

Char. 8 - Family as a certain social unit

State 0 - no (function of family reduced)
State 1 - yes (family is a main functional social unit)

Char. 9 - Social unit that goes beyond family's scope

State 0 - no cohesive social units (except family)
State 1 - yes (cohesive social units consisting of less-related individuals)

Char. 10 - Male absence

State 0 - no (continuous presence of (alpha) male within the group (family))
State 1 - yes ((dominant) male is unable to maintain proximity to the group)

Sources: Tenaza (1975), Temerin (1980), Wrangham et al. (1994), McGrew et al. (1996), Palombit (1996), Reichard and Sommer (1997), Dixson (1998), Marlowe (1999), Marlowe (2000), Harrison and Chivers (2007), Frynta (pers. comm.)

	Homo	*Pan*	*Gorilla*	*Pongo*	*Hylobates*
family	√		√	√	√
other social units	√	√			
male absence				√	

In order to avoid often puzzling and not easily comparable terms from primatological literature that are used to name several types of primate societies, I worked with these three character-based system. This system draws a distinction between two basic types of the social units. The first type can be regarded as s family (human, gibbon, gorilla…), without reference to number of group members, male-female ratio, or mating system. In such units long-term social bonds are typical, dominance rank is evident and group cohesion is maintained by dominant male or by dominant members of the both sexes (in gibbons and humans).

Other social units go beyond the family scope and consist of less related individuals (like for example human village or fusion-fission society of chimpanzee). In context of such social units, family does not play a vital role, dominance rank is sometimes unclear (especially in bonobo), and cohesion of such a group is not maintained by the dominant male (father) or female. Such units are generally less stable. In chimpanzees and bonobos, existence of such social units imply that families (in the usual sense of the word) do not exist.

This leads to conclusion that human is the only species among apes who posses levels of social organization (we have a gorilla-like social system embedded within the chimpanzee-like one). We have cohesive families, but they are in continual contact with other members of a wider society, and the member transfer among social units is permanent (not as frequent as in chimpanzees, however).

The gibbon families are also cohesive and they are working on the similar principles as human ones. for example some aspect of territoriality and monogamy in Kloss' gibbon (*Hylobates klossii*) display striking similarity to the humans (Tenaza 1975). Despite the fact that among-group interactions in some gibbon populations can be quite frequent (Reichard and Sommer 1997), gibbons do not have any stable social units above the family level.

What is, in this context, the social system of orangutan that is usually referred to as non-gregarious? The gorilla-like sexual dimorphism suggests that the orangutans, in fact, live in secondarily dispersed families. The similar conclusions were received from paleontological and paleoclimatological evidence (Harrison and Chivers 2007) and long-term ethological studies. The orangutan groups seem to be dispersed due to continuous food scarcity and probably also due to secondary arboreality of the species (Temerin 1980). Orangutans can be regarded as „miserable“ gorillas (see comment on char. 11 – Mating system). There is a growing consensus that the orangutan social system has evolved recently from a gorilla-like base (Harrison and Chivers 2007). Function of the third character - „male absence“ - is to express the „misfortune“ of the orangutans („enforced non-gregariousness“). In their habitat, adult orangutan alpha male (father) is unable to maintain proximity to his females.

Char. 11 - Mating system

State 0 - monogamy (1-1) (maintained by intrasexual defense of teritory)
State 1 - moderate polygyny (about 1-3 females to one male)
State 2 - female-defense (harem) polygyny (>5 females to one alpha-male)
State 3 - promiscuous (multimale-multifemale, polygynandric)
State 4 - polyandry (1 female and 2 or more males)

Sources: Haimoff et al. (1987), McGrew et al. (1996), Jiang et al. (1999), Marlowe (2000), Dixson (1998), Leutenegger and Lubach (2005), Harrison and Chivers (2007)

Human possess all types of the mating systems that are known among monkeys and apes (except the chimpanzee-like promiscuous mating system, which can possibly occur but would be highly aberrant). Polyandry is marginal mating system (2 %), monogamy is usual, and the most prominent mating system is the (moderate) polygyny (84 % of 185 human societes considered) (Dixson 1998), where one male is able to maintain more than one female.

It is not clear how the mating system of orangutan should be interpreted. Although it is sometimes compared to the dispersed mating system of some nocturnal prosimian species (pottos, galagos etc.), or to the promiscuous mating system (with each female mating with more than one male, and each male mating with more than one female), it is apparent that orangutan mating system most closely resembles that of gorilla than any other living ape. Orangutan groups are dispersed due to continuous food scarcity. Ancestral state was probably the harem polygyny, but the later change of the food availability caused that full-time gregariousness was no longer energetically tolerable and, as a result, females dispersed more widely in search of food and adult/flanged males were no longer able to effectively guard a harem of females. A niche for a quiet, quick, opportunistic “sexual predator” (unflanged male) then became available (Harrison and Chivers 2007), but flanged males are still trying to exert exclusive sexual relationships with females, despite they fail to do so. Mating system of orangutan is therefore interpreted here as (dispersed) harem polygyny (Harrison and Chivers 2007), or „roving-male polygyny“ (McGrew *et al.* 1996).

Char. 12-15 – Mating strategy/tactics

Char. 12 - Opportunistic mating

State 0 - absent
State 1 - present (more than five adult males opportunistically mate with a female repeatedly)

Sources: Goodall (1986), Kano (1992), McGrew et.al. (1996), Dixson (1998), Frynta (pers. comm.)

Char. 13 - Consortship

State 0 - absent
State 1 - present (male / female follows partner usually outside the group)

Sources: McGrew et al. (1996), Dixson (1998), Kálnová (2006)

Char. 14 - Possessive mating (mate guarding)

State 0 - absent (male do not shows tendency to exert long-term monopolization of female(s))
State 1 - present (male monopolize and actively defends female(s))

Sources: Dixson (1998), Marlowe (2000)

Char. 15 - Coercive mating (rape)

State 0 - absent (coercive strategy was not recorded / impossible to resolve)
State 1 - present (coercive strategy or rape occur within this species)

Sources: Dixson (1998), Thornhill and Palmer (2000), Thornhill and Palmer (2001), Utami *et al*. (2002), Tainaka, Yoshimura and Rosenzweig (2007), Harrison and Chivers (2007), Frynta (pers. comm.)

I distinguish four basic types of mating strategies. Opportunistic tactics is the most common strategy in the promiscuous mating system where each male mates with more than one female and each female mates with more than one male. This is the mating system that occurs especially bonobo, where number of males mate repeatedly with more females. The sperm competition is the most important in such species (see character 42).

In the common chimpanzee (*Pan troglodytes*), opportunistic matings occur along with other mating strategy: the consortship, temporary association of male (typically the dominant one) and female who follows him, usually outside the group. (in chimpanzees and also gorillas but not in all species in which consortships occurs). The length of such male-female association vary greatly, from a few hours to few months (Dixson 1998, Kálnová 2006). Dominant chimpanzee (and bonobo) males occasionally monopolize oestrous females, not allowing others to mate with them (see character 4). The occurrence and distribution of the mating strategies vary markedly among separate chimpanzee societies (McGrew *et al.* 1996).

The next strategy is the possessive mate guarding. Dominant male (but not necessarily the alpha male as the human dad (husband) is also a dominant male in this context) monopolizes one or more females, mates with her/them and defend her/them actively against other males' mating attempts. This includes long-term mate guarding like human marriage, plural marriage or partnership, gibbon pair-bonds, long-term mate guarding in harems of the mountain and western lowland gorillas, and also limited mate guarding in the Bornean and Sumatran orangutan.

The last mating tactics is the coercive one, that can be also referred to as rape. This strategy occurs in unflanged males of both species of orangutan (sneak and rape strategy) (e.g. Dixson 1998, Harrison and Chivers 2007, Utami *et al*. 2002), and also as a mating strategy under certain circumstances in human males (Thornhill and Palmer 2000), although there certainly does exist more than one type of rape among humans. Forced copulation occurs in some non-human primate species. It was observed in a captive group of bonnet macaque (*Macaca radiata*), or in mating aggregation of the wooly spider monkeys (*Brachyteles arachnoides*) (Dixson 1998).

Each character implies presence/absence of this type of mating strategy/ tactics in question in the given species. More than one strategy occurs in the most of the species of monkeys and apes, and there is plenty of combinations possible. Sometimes one male is able to switch between strategies (human, gorillas etc.), in some species, each strategy is bound to a certain class of the males (Orangutan flanged male: Consortship/possesive; unflanged male: Coercive. Patas monkey dominant male: Possessive; peripheral male: opportunistic etc.)

Char. 16 - Ovulation

State 0 - detectable
State 1 - concealed

Sources: Andleman (1987), Diamond (1992), Dixson (1998), McGrew et al. (1998), Marlowe (2004), Roberts et al. (2004), Sievert and Dubois (2005), Kalnova (2006), Havlicek et al. (2006), Gangestad and Thornhill (2008), Frynta (pers. comm.)

In contrast to many primate species, human ovulation can be regarded as concealed for both men ad women. Women who think they know when they ovulate, actually do not (some of them are able to succesfully recognize they ovulate in about half of the cases) (Sievert and Dubois 2005). Previous suggestions that ovulation may not be concealed in human living under natural conditions with minimal hygiene has been disproved. For example, the Hadza conception beliefs do not suggest that ovulation is more detectable in humans under more natural conditions (although Hadza know that pregnancy is caused by sex, most of them say conception occurs right after the menstruation ends; Marlowe 2004). Some authors suppose that human ovulation is actually detectable, for some physical and behavioural cues of human oestrus does exist (smell, fluctuating female facial attractiveness during cycle, female mate preferences etc.) (Roberts et al. 2004, Gangestad and Thornhill 2008) and it should be regarded as non-advertized rather than concealed (Havlicek et al. 2006). Despite these facts, compared to our closest animal relatives, human ovulation is virtually undetectable and it should be regarded as concealed (at least in this context).

Although gorilla females do not have exaggerated sexual skin swellings, small tumescence of circumvulval area ensures that at least a female can be sure, when she may ovulate, and this is accompanied by apparent behavioral change. Female "success ratio" - proportions of her sexual presentations that were accepted by the male - peaks sharply during the labial tumescence period (Dixson 1998). In the chimpanzees, this phenomenon is even more apparent.

It is difficult to assess whether ovulation is detectable in orangutans, because the female does not possess any swellings (the orangutan female has apparent swellings only during pregnancy – like the gorilla) (Kálnová 2006) and she actively blurs the ovulation signalling, perhaps in order to avoid infanticide (McGrew et al. 1998).

Among non-hominoid primates, it was found that female vervet monkeys (*Cercopithecus aethiops*) successfully conceal their time of ovulation from males. It is apparent that concealed ovulation reduces the vulnerability of a female and her offspring to potentially infanticidal males (Andleman 1987).

Char. 17 – (Exagerrated) sexual skin swellings

State 0 – absent (or only slight tumescence of circumvulval area)
State 1 - present (small swellings)
State 2 - present (large, prolonged or semipermanent swellings)

Sources: Dixson (1998), Nunn (1999), Kálnová (2006), Bareli et al. (2007)

Char. 18 - Oestrus synchrony

State 0 - yes (oestrous or breeding synchrony within some female social units occurs)
State 1 - no (although some older contradictory data could exist)

Sources: Kálnová (2004)

Char. 19 - Baculum (os penis)

State 0 - present
State 1 - reduced/shortened
State 2 - absent

Sources: Shoshani et al. (1996), Dixson (1998)

Char. 20 - Penis length (when erect)

State 0 - short (up to 50 mm)
State 1 - lenghtened (80 mm on average)
State 2 - further lenghtened (median 130 mm)

Sources: Dahl (1994)**,** Shoshani et al. (1996), Dixson (1998)

Char. 21 - Mating usually initiated by

State 0 - female
State 1 - male

Sources: McGrew et al. (1996), Dixson (1998), Nadler and Collins (1991), Frynta (pers. comm.)

Char. 22 - Intromission duration

State 0 - > 1,5 min
State 1 - < 1 min
State 2 - < 20 s

Sources: Kinsey et al. (1948), Adams and Schoel (1982), Dixson (1998), Frynta (pers. comm.)

There are considerable differences in the duration of copulation among great apes. In both species of *Pan*, intromission is brief. In common chimpanzee (*Pan troglodytes*) copulation involves in average of just 8.8 pelvic thrusts and last on approximately seven seconds. A comparable pattern occurs in bonobo (*Pan paniscus*) (mean duration 12.2 seconds). Similar type of intromission (single, brief) occurs in many non-human primate species (e.g. *Papio anubis, Macaca mullata, Theropithecus gelada, Erythrocebus patas* etc.). In stumptail macaques (*Macaca arctoides*) non-dominant males copulate longer (more than 3 minutes), while dominant male engages in only brief intromissions (less than 1 minute). Gorillas have slightly prolonged intromission (mean duration 96 seconds and 27.5 thrusts). Orangutans have markedly prolonged intromission (median 14 minutes, maximum 46 minutes). What is the typical intromission duration in human? Human copulation is propably comparable to that of the gorillas, for orangutan copulation is too long and differs from that of human in other ways (e.g. orangutan male is startlingly passive during copulation). The majority of men questioned by Kinsey et al. (1948) told they were able to achieve ejaculation in less than 2 minutes during intercourse. This raises the possibility that brief copulation is normal for human beings and that the more prolonged copulation is a result of cultural evolution rather than of sexual selection. The question is, however, whether the Kinsey‘s data can be regarded as reliable.

Char. 23 - Female is active during sexual intercourse

State 0 - yes (female "complements" males pelvic thrusts etc.)
State 1 - no particular female activity

Sources: Dixson (1998)

The behaviour considered in this character includes female physical activity (complementing males pelvic thrusts, holding, touching, embracing etc.). Female copulatory (or postcopulatory) calls are considered a diferrent type of behaviour (see character 28).

Char. 24 - Intermale (adult) relationship: tolerance level among males (within the group)

State 0 - alpha-male does not tolerate proximity/presence of other adult males
State 1 - alpha-male tolerates presence of other male(s), but not matings
State 2 - males are tolerant, enables each others to mate with female(s)

Sources: McGrew et al. (1996), Dixson (1998), Lappan (2007), Harrison and Chivers (2007), Tainaka et al. (2007)

Char. 25 - Female personal mate-choice possible

State 0 - no (female has a little opportunity to choose their mates)
State 1 - yes (female can exert significant mate-choice among resident males)

Sources: McGrew et al. (1996), Dixson (1998), Harrison and Chivers (2007), Frynta (pers. comm)

Presence of this character implies that female has the opportunity to choose her mates, regardless the type of mating system and presence of the dominant male. In gorillas the females strongly prefer the dominant males and spend more time close to them, interacting affinitively with them more than with their subordinates (McGrew *et al.* 1996). However, if female prefer (from whatever reasons) non-dominant male, she is unable to put her choice into effect, because the silverback will forcibly terminate the mount. Female gorilla cannot exert personal mate choice for other than dominant male within the group. The way she can exert her choice is to leave the group with younger male (and thus establish a new group) or to move to another established group (Dixson 1998). Gorilla is then polymorphic in this character.

Orangutan female, on the other hand, has the opportunity to choose always, because dominant male is not permanently present. Orangutan females actively seek dominant (flanged) males and respond to their calls, and refuse mating attempts of the unflanged males (Dixson 1998).

In chimpanzee, female has a little opportunity to choose her mate. She copulates with number of males. She can only use some indirect, probably not very efficient ways to affect paternity (see characters 27 and 28).

Significant female mate choice certainly works in many human societies, where dominance is not the only cue of male attractiveness.

Gibbon female has the opportunity to choose her mate in the same manner as human female (she is able to accept or refuse the suitor and she has opportunity to cheat on him subsequently).

In the gregarious species, possibility of the female mate-choice is most certainly influenced by sexual dimorphism.

Char. 26 - Female orgasm

State 0 - present
State 1 - no / female shows no apparent signs of orgasm

Sources: Kinsey et al. (1953), Dixson (1998)

In human, female orgasm is the well-known phenomenon and there is no doubt about its existence. More than 90 % of North American women can reach orgasm (although it is usually reached by additional manual stimulation after or before intercourse (Kinsey *et al.* 1953). Several attempts has been made to find out if females of non-human primates an apes can experience orgasm. Its occurrence has been sufficiently proved in *Macaca arctoides* (Dixson 1998). Lesser apes do not shows apparent signs of orgasm. In great ape species, question of orgasm occurrence remains open, although some behavioral and physiological responses, that could be associated with orgasm were observed (e.g. laughing vocalization during masturbation in chimpanzee females, activity during copulation and complementing of male pelvic thrusts in gorilla and orangutan females). However, it is unlikely, that chimpanzee and bonobo female could experience orgasm during intercourse, due to brief intromission duration, indifferent female response and hasty termination of copulation (see characters 22, 23 and 27). Post-copulatory calls of chimpanzee occurs right after termination of the mount and can be interpreted rather as a female signal to other males, increasing male-male competition than as a sign of a sexual climax (see character 28).

Char. 27 - Female sometimes terminate coppulation once ejaculation has occured or even before that

State 0 - no (not reported)
State 1 - yes (this behavioural pattern is present)

Sources: Dixson (1998), Frynta (pers. comm.)

This, from our point of view eccentric behavioral pattern, has been observed in common chimpanzee and bonobo and in several species of monkeys (Dixson 1998). In chimpanzee female dart forward once ejaculation has occurred or terminate the mount even before male ejaculate. This phenomenon can be referred to as a device of female mate-choice in highly promiscuous chimpanzee society, where bonds between male and female are weak, and female has a little opportunity to choose their mates copulating with all mature (unrelated) male members of the group in order to ensure paternity confusion and, therefore, the future safety of her offspring.

Char. 28 - (Post)copulatory calls (as a device of postcopulatory female choice)

State 0 - no postcopulatory calls or seldom (in 10 % of copulations or less)
State 1 - postcopulatory calls occur and fit this pattern

Sources: Dixson (1998), Maestripieri and Roney (2005)

Char. 29 – Nocturnal coppulations / mate guarding

State 0 - no / never recorded
State 1 - recorded but infrequent, probably insignificant for reproduction
State 2 - yes; consortships continues at night, partners maintain proximity
State 3 - yes; prevailing and fundamental in this species

Sources: Goodall (1986), Dixson (1998)

Char. 30 - "Friendship" between male (non-dominant) and female

State 0 - no / impossible to resolve
State 1 - possible / characteristic

Sources: Dixson (1998), Frynta (pers.comm.)

„Friendships“ in this character means that some male and some female conspecifics form long-term associations, spending time together more frequently than with others (as seen in *Papio anubis*). Such associations involve grooming, huddling, reassurance and sleeping together. Male forms attachment to the infants of female friends and can behave protectively towards them and their mother. „Friendships“ can be regarded as special form of consortship, but they are not sexual relationships, although there is a possibility of having sex with female friend and there is some probability that the male friend is father of her infants. Spending time with them, playing with them and protective behavior can be regarded as a form of paternal or quasi-paternal care. Long-term associations equivalent to friendships described in olive baboons have also been found among rhesus (*Macaca mulatta*) and Japanese macaque (*Macacaca fuscata*).

Long-term associations between the sexes, quite comparable to those seen in some species of monkeys, certainly play significant role in human societies, but it is difficult to assess if similar phenomenon occurs among great ape species and which type of relationship in e.g. gorilla society is homologous to human and baboon male-female friendship.

Char. 31 - Sexual interference / harassment or interruption of copulation by adult female

State 0 - no / not observed
State 1 - high-ranking adult female sometimes harass copulations by others

Sources: Dixson (1998)

Char. 32 - Sexual interference / occasional harassment and interruption of copulation by infants and juveniles (as manifestation of the mother-child conflict)

State 0 - no / not observed
State 1 - infants and juveniles sometimes harass copulations by adults

Sources: Goodall (1986), Dixson (1998), Furuichi et al. (1998)

Char. 33 - Sexual dimorphism in body weight (male:female)

State 0 - strong, marked (from 1.6 to 2.6:1)
State 1 - moderate (from 1.2 to 1.6:1)
State 2 - insignificant, small (from 0.9 to 1.2:1)

Sources: Dixson (1998), Clutton-Brock et al. (1977), Frayer and Wolpoff (1985), Breuer, Robbins et al. (2007)

Char. 34 - Sexual dimorphism in canine size

State 0 - males canine markedly larger than females
State 1 - males canine moderately larger than females
State 2 - insignificant canine size dimorphism

Sources: Plavcan and van Schaik (1992), Shoshani et al. (1996), Weston et al. (1997), Dixson (1998), Kelley (2005)

Char. 35 – Sexual dimorphism in androgen-dependent secondary sexual adornments of adult males (beard, mane, pelage, "flanges", color skin etc.)

State 0 - present
State 1 - absent

Sources: Dixson (1998)

Various secondary sexual adornments are quite common in males of apes and monkeys. These structures show marked variability. Almost every species has specific type of adornments (only human males posses beard, only gorilla silverback has a „silver“ saddle of short hair on back and a pat of fibrous tissue on top of head, only adult-type orangutan males have fatty cheek-flanges, only males in some gibbon species posses a preputial tuft, only geladas males have long capes of hair on shoulders and red sexual skin on chest, and so on). These structures are not homologous in terms of morphology and anatomy; however, their life-strategy purpose is apparently identical. The purpose of this character is to express that (some) males of some species invest in secondary sexual adornments, while others do not.

Char. 36 – Paternal care: Protective function of an adult male

State 0 - alpha male actively defends his offspring
State 1 - infants receives no direct paternal protection

Sources: McGrew et al. (1996), Dixson (1998), Buchan et al. (2003)

Char. 37 – Infant (preweaning) mortality

State 0 - low (up to 20 %)
State 1 - moderate (around 30 %)
State 2 - high (>40 %; and also highest mortality through the whole lifespan)

Sources: McGrew et al. (1996), Furuichi et al. (1998), Dixson (1998), Wilch et al. (2004), Broom et al. (2004), Takahata et al. (1998), Bezerra et al. (2007)

Char. 38 - Infanticide

State 0 - yes (prominent; quite commonly follows takeover)
State 1 - yes (observed but limited, up to 10 % of total infant mortality)
State 2 - no (never seen)

Sources: Goodall (1986), Dixson (1998), Furuichi et al. (1998), Mori, Iwamoto and Bekele (1997), Broom, Borries, and Koenig (2004), Yamada and Nakamichi (2006)

Char. 39 - Parental infanticide

State 0 - absent
State 1 - present

Sources: Nordlund and Temrin (2007), Trautmann-Villalba and Hornstein (2007), Frynta (pers. comm.)

Char. 40 - Female attractiveness correlates with her age

State 0 - no correlation
State 1 - positively (male prefer older or higher-ranking and parous females)
State 2 - negatively

Sources: Dixson (1998), Muller et al. (2006), Setchell and Wickings (2006)

In human, features of feminine facial beauty are considered to be neotenous and human males prefer young females with no offspring over others. Chimpanzee males despite their promiscuous mating system also prefer some females over others. However, in contrast to humans, chimpanzee males prefer older females (Muller *et al.* 2006). In mandrill, alpha male prefer high ranking, parous (therefore older) females over low-raking nulliparous ones.

Char. 41 - Additional functions of sexual activity

State 0 - none (practice sex with some EPC, possibly paternity confusion)
State 1 - present (paternity confusion + exchange for favours)
State 2 - one more present (+ communication sex, female plotting)

Sources: Wrangham (1993), Dixson (1998)

The purpose of this character is to formulate bonobo’s apomorphy – the „hypersexuality”. Only bonobos use sex purely for communication about social relationships, while in common chimpanzees there are only three distinctive functions of sexual activity (Wrangham 1993).

This „communication sex" seems to play important role in the female-female relationships and maintaining alliances, and is unique among apes.

Char. 42 – Testes size (expressing degree of sperm competition)

State 0 - Small (mean combined testes weight <10 g)
State 1 - Medium (mean combined testes weight <50 g)
State 2 - Large (mean combined testes weight >50 g)
State 3 - Large (mean combined testes weight >100 g)

Sources: Shoshani et al. (1996), Dixson (1998), Dixson and Anderson (2004), Simmons et al. (2004)

Char. 43 - Copulatory plugs are known to occur

State 0 - no
State 1 - yes

Sources: Dixson (1998)

Char. 44 - Philopatry (dispersal patterns)

State 0 - female (female remains in natal group or migrate near, male leaves)
State 1 - male (female transfer between groups, male stays or migrate near)

Sources: McGrew et al. (1996), Lappan (2007), Charpentier et al. (2007)

Char. 45 – Menopause

State 0 - Present
State 1 - Absent

Sources: Wich et al. (2004), Muller et al. (2006), Atsalis and Margulis (2006), Thompson et al. (2007)

Menopause of human female has long been considered unique among primates (Diamond 1992). It was found recently that western lowland gorillas (*Gorilla gorilla gorilla*) experience behavioral and physiological patterns associated with reproductive aging and menopause that are similar to human patterns.(The survey was done on the aging population of western lowland gorillas in American zoos.).The patterns found included increased variability in cycle length and peak progestogen values, and frequent insufficient increases in progestogen levels during the luteal phase in geriatric females. About 23 % of geriatric females are acyclic (menopausal), and another 32 % show variable hormonal patterns suggesting the perimenopause.

Considering that maximum longevity in captive female gorillas is 52 years, with poor reproductive prognosis beginning from the age of 37, it is apparent that both perimenopause and menopause characterize aged female gorillas, which may experience a postreproductive lifespan of > 25 % of their lives (Atsalis and Margulis 2006).

Chimpanzee and orangutan females, on the other hand, show no sign of menopause and they are able to reproduce into their forties (and more orangutan females may do so, as a result of our age estimation; Wich *et al.* 2004).

Mean age of menopause among hunter-gatherer females is 39 years. Chimpanzee and human birth rates show similar patterns of decline beginning in the fourth decade, suggesting that the physiology of reproductive senescence was relatively conserved in human evolution. However, in contrast to humans, chimpanzee fertility declines are consistent with declines in survivorship, and healthy females maintain high birth rates late into life. Thus, it is likely that menopause is not a typical characteristic of chimpanzee life histories (Thompson *et al.* 2007), considering also the fact that chimpanzee males prefer to mate with old females while human males do not (Muller *et al.* 2006).

Char. 46 - Diet

State 0 - primarily herbivorous (arboreal leaves or terrestrial herbaceous vegetation)
State 1 - primarily frugivorous (arboreal fruit)
State 2 - omnivorous (mostly reproductive parts of plants + animal foods)

Sources: McGrew et al. (1996), Urban and Francl (2008), Fuentes (1996)

Char. 47 - Food scarcity

State 0 - the main elements of the diet are abundant (or substitute is available)
State 1 - the main elements of the diet are scarce (=> impact on social system)

Sources: Wrangham et al. (1994), McGrew et al. (1996)

Presence of this character implies that individuals of this species suffer (seasonally or continuously) from food stress. This can affect their feeding competition, degree of food sharing, foraging patterns, party size and other social factors and behavioral patterns.

This regards especially the fruit-eating species (orangutans, chimpanzees, gibbons etc.), but not bonobos that apparently suffer much less from feeding competition (bonobos do not live sympatrically with frugivorous western lowland gorillas and they, in contrast to chimpanzees, can feed also on terestrial herbaceous vegetation, a continuously available food resource; Wrangham *et al.* 1994).

Char. 48 - Feeding / foraging patterns

State 0 - members of the group maintain proximity during feeding
State 1 - the group disperse during feeding / solitary foraging

Sources: Wrangham et al. (1994), McGrew et al. (1996)

Char. 49 – Meat proportion in diet / hunting

State 0 – significant (active social hunting of mammalian prey with tool usage)
State 1 - occasional (small prey; no cooperative hunting)
State 2 - virtually no meat in diet

Source: Wrangham et al. (1994), McGrew et al. (1996)

Char. 50 - Higher-ranking females tends to have shorter interbirth interval

State 0 - yes
State 1 - no

Sources: Watts (1991), Wich et al. (2004)

Char. 51 - Length of parental investment is affected by sex of the infant

State 0 - no (the same for both male and female infants)
State 1 - maternal investment is longer-lasting when infant is a male

Sources: Watts (1991), Furuichi (1998), Wich et al. (2004)

Char. 52 – Habitat

State 0 - arboreal
State 1 - terrestrial

Sources: McGrew et al. (1996)

Char. 53 – Cultural diversity

State 0 - absent
State 1 - present (local diferences in tool use, plant use, vocal behaviour etc.)

Sources: Wrangham et al. (1994), Leca et al. (2007), van Schaik and Knott (2001), van Schaik et al. (2003), Cipolletta et al. (2007)

Cultural diversity in tool use, plant use, and various behavioral patterns is known among populations of common chimpanzee (*Pan troglodytes*). Cultural traditions comparable to those observed in chimpanzee have not been found in bonobo (*Pan paniscus*). The question of cultural diversity of behavior among western lowland gorilla populations remains open (e.g. Cipolletta *et al.* 2007).

Geographic variations in some aspect of behavior (eg. tool use, nest building behavior) were found in both species of orangutan (van Schaik and Knott 2001). Moreover, as expected under cultural interpretation, a correlation between geographic distance and cultural difference, a correlation between the abundance of opportunities for social learning and the size of the local cultural repertoire, and no effect of habitat on the content of culture were found (van Schaik et al. 2003).

Japanese macaque (*Macaca fuscata*) shows signs of cultural behavior. So called “stone handling” behavior is socially transmitted across generations forming a behavioral tradition. Various stone handling patterns show geographically patchy distributions and are referred to as local variants or stone handling traditions (Leca *et al.* 2007).

Char. 54 - Lifespan (in free-ranging populations)

State 0 - assumed lifespan typically <20 in the wild
State 1 - assumed lifespan typically <40 in the wild
State 2 - slow life-history pattern (typical lifespan <50 in the wild)

Sources: Wich *et al.* (2004)

Char. 55 – Parental care: father-offspring interactions

State 0 - virtually none
State 1 - occasional (play, some foodsharing etc.)
State 2 - substantial, characteristic paternal care (protection, play, learning etc.)

Source: Maestripieri and Ross (2004), McGrew *et al.* (1996), Palombit (1996), Marlowe (1999), Marlowe (2000), Tanhehco (2000), Buchan et al. (2003), Lehmann et al. (2006), Charpentier et al. (2007), Sear and Maceb (2008)

Char. 56 - Weaning

State 0 - <2 years
State 1 - >2 years

Sources : Short (1994), Hayssen et al. (1993), Nowell and Fletcher (2007), Dupras and Tocheri (2007)

Char. 57 – Postweaning nourishing

State 0 - none or insignificant
State 1 - substantial, long-lasting

Sources: Short (1994), Diamond (1992)

Char. 58 - Male-male interactions, degree of cooperation, coalitions

State 0 - weak male-male bonds, no coalitions occur
State 1 - coalitions of two or more related or unrelated males rarely occur
State 2 - strong male-male bonds, characteristic tendency to form coalitions

Sources: Wrangham et. al. (1994), McGrew et. al. (1996)

Char. 59 - Female-female interactions, degree of cooperation among females

State 0 - relatively weak female-female bonds, no female coalitions
State 1 - strong female affiliation, significant cooperation among females

Sources: Wrangham et. al. (1994), McGrew et. al. (1996), Tanhehco (2000)

Char. 60 - Female-male relationship

State 0 - unequal (male dominant, female gains status through male)
State 1 - equal (there is no apparent dominance of one sex over another)
State 2 - females dominate males (male gains status through mother)

Sources: Wrangham et. al. (1994), McGrew et. al. (1996), Palombit (1996), Sicotte (2002)

Char. 61 - Intergroup encounters / relationships

State 0 - affiliative (intergroup tolerance, feeding, infantine play etc. occur)
State 1 - encounters relatively peaceful (males display chasing... fights rare)
State 2 - hostile (strong competition, intercommunity killing /genocide occurs)

Sources: Goodall (1986), Diamond (1992), Wrangham et. al. (1994), McGrew et. al. (1996), Reichard and Sommer (1997), Boesch (2007), Robbins and Sawyer (2007)

The most vicious intergroup encounters (state 2) are usually related to acquisition of females (not to defense of food resources or home range). Close-range displays are common (74 %) and fighting between silverbacks not unusual (17 %) in the case of mountain gorilla (*Gorilla beringei beringei*) (McGrew *et al.* 1996). The same is true for encounters of flanged males of orangutans. Intergroup encounters of southern lowland gorillas, on the other hand, are related mostly to access to and defense of food resources and they are relatively peaceful (state 1) with distance between group ranging from 50 to 300 m. Only 7 % (3 of 43) observed encounters escalated to fighting (McGrew *et al.* 1996). Intergroup encounters in gibbons show many similarities with those of western lowland gorillas. There is also extensive overlap of home ranges (64 % in *Hylobates lar*) and, therefore, the encounters are quite frequent. There is a plenty of behavioral patterns that have „defensive“ function, male display and chasing are frequent and fights are rare (8-9 %) (Reichard and Sommer 1997). Affiliative behavior is also quite frequent (phenomenons as grooming and intergroup play between infants). Case of the extreme tolerance is known in western-lowland gorilla from Nouabalé-Ndoki, where 4 groups and one lone male were seen on one site together peacefully (displays observed but no fightings). The encounters in chimpanzees can be quite hostile. Lethal aggression occurs within and between social units in some populations. Intercommunity killings are a rare but widespread phenomenon among chimpanzees (Boesch 2007). Cases when one chimpanzee group successively eliminates another are known and well-documented (Goodall 1986). It is not clear if the intergroup aggressivity in chimpanzees is driven by acquisition of resources and territory, or by acquisition of females, but it is apparently quite „human-like“, only slower and less efficient (Diamond 1992)

It is not clear how should the orangutans be scored in the data matrix. Group encounters in orangutans can be categorized as hostile (quite similar to those in mountain gorillas) but the „group“ means only one adult male (or occasionally, a male with a female) in this case. The subadult, unflanged males, on the other hand, are tolerant. This character is, by my opinion, meaningless for orangutans, because they do not have the groups comparable to those of other monkeys and apes. For the male-male tolerance see character 24.

Char. 62 - Vocalization rate (primarily by males)

State 0 - high (loudcalls)
State 1 - low (and less suitable for long-distance communication)

Sources: McGrew et al. (2007)

Char. 63 - Tool use (in free-ranging groups)

State 0 - no tool use reported
State 1 - simple (stone-handling, throwing etc.)
State 2 - variety of tools is used, metatool use (three-stone test)

Sources: Galdikas (1982), Goodall (1986), Wrangham et al. (1994), Dixson (1998) van Schaik and Knott (2001), McGrew et al. (2007), Leca et al. (2007), Wittiger and Sunderland-Groves (2007), Cipolletta et al. (2007), Pruetz and Bertolani (2007), Mercader et al. (2007)

Chimpanzees not only use, but also produce various types of tools. They can even made weapons (spears, javelins) to hunt mammalian prey (Pruetz and Bertolani 2007), they can use metatools (Wrangham et al. 1994). Material culture of chimpanzees is probably very old. It was proved by the paleontological evidence that chimpanzees did not learn how to use tools through interactions with human (Mercader et al. 2007).

Bonobos do not use tools in the same manner as chimpanzees, although "there is no obvious ecological reason why (bonobos) should not use elementary technology in extractive foraging, e.g., termite-fish, ant-fish, ant-dip, honey-dip, to obtain social insects" (McGrew et al. 2007).

The Cross River gorillas (*Gorilla gorilla diehli*) occasionally use objects (tree branches, fistfuls of grass) for throwing during displays. This behavior can be possibly learned through interactions with humans (Wittiger and Sunderland-Groves 2007). Gorillas do not use tools to obtain social insects in the same manner as chimpanzees (Cipolletta *et al.* 2007).

Both species of orangutan exhibit tool use abilities comparable to those of a chimpanzee. Orangutans were observed to build nests, use overhead covers, break, wave, drop and throw branches and vegetation, and also to manipulate twigs and branches in play. In addition, Tanjung Puting orangutans manipulated and crashed snags and wiped their faces with crumpled leaves. One adult female constructed a nest-like structure to bridge a narrow river and a wild adult male once was observed scratching himself with a stick broken from a dead branch (Galdikas 1982). Ex-captive (rehabilitant) orangutans released into the forest use tools in a variety of contexts. Rehabilitant female orangutans were seen using twigs or leaves to stimulate their genitalia (Dixson 1998).

Primitive tool use (stone handling behavior) is known among free ranging populations of the Japanese macaque (*Macaca fuscata*) (Leca *et al.* 2007).

Char. 64 – Mean (hourly) copulatory frequency

State 0 – <0.01
State 1 - <0.1
State 2 - >0.1
State 3 - >1
Sources: Dixson (1998)

Char. 65 - Prominent breast development in females

State 0 - absent
State 1 - present

Sources: Low et al. (1987), Low et al. (1988), Moller et al. (1995), Dixson (1998), Marlowe (1998)

Characters not included into analysis

Some characters were not included to the final dataset for various reasons. Some of them were not representative enough for the Hominoidea as a whole. Some characters have identical character states in the all species considered (e.g. mating season – all apes are non-seasonal breeders). Others could not have been processed and included in the matrix due to the lack of sufficient information for more than one species (e.g. effect of facial fluctuating asymmetry on sexual attractiveness of male or female). Finally, some characters were excluded because of significant overlap with the other, included characters.
They include:

- Social organization: Number of dominant males, Adult non-dominant males, subadult males, females, infants and juveniles in the group;
- Group stability: frequency of intra-troop transfers;
- Sexual dimorphism: Sexual dimorphism in vocal anatomy ; sexual dimorphism in vocal display;
- Sexual attractiveness: Female attractiveness correlates with waist-hips ratio ; Fluctuating asymmetry affects sexual attractiveness;
- Sperm competition: Presence of structurally abnormal ("kamikaze sperm") spermatozoa in ejaculate;
- Psychological changes in female during menstrual cycle: female sexual attractiveness peaks during follicular phase ; Female is more sexually active during follicular phase (mid-cycle peak in sexual activity) ; Female sexual preferences vary across the menstrual cycle;
- Time of menarche;
- Menstrual cycle length;
- Incest avoidance: Close associations in childhood inhibit sexual attraction later in life;

- Mating season;
- Skewed birth sex ratio;
- Skewed mortality-sex ratio;
- Proceptive behavior in female (Precopulatory behavior, Flirting) ; Patterns of precopulatory behavior in male;
- Occurrence of masturbation in females ; males;
- Self-awareness level: ability of self-recognition in the mirror ; gender identity level;
- Sociosexual behavior (sexual patterns occurrence during social activities): male's erection as a visual display; male's erection during play or grooming ; sociosexual behavior in females; infantine sex play (sexual intercourse simulation etc.);
- Homosexuality: Occurrence of homosexual behavior in males ; females;
- Age at first born;
- Neonatal mass (weight of living newborn);
- Presence and duration of postpartum amenorrhoea;
- Nursing frequency;
- Female reproductive potential;
- Sex differences in play;
- Division of labor by sex;
- Rate of food sharing: In males ; In females; Between the sexes;
- Occurrence of food begging;
- Multiple partner mating (in female) ; EPC occurrence