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THE EVOLUTIONARY ECOLOGY  
OF THE HOMINOIDEA

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## Introduction

Despite ever intensifying studies since the Second World War, the advance in the understanding of the Hominoidea has been patchy. In part this has because there have been too many assumptions; in part, because of accidents of history and accessibility. An example of both these factors is the concentration on Mountain Gorillas as representative of «the gorillas»: even a very recent sociobiological reconstruction (Ghiglieri, 1987) speaks of Mountain Gorillas as if they were the only gorillas, and it is true that for a long time the only really detailed available fieldwork was on this subspecies, although the observations since the late 1950s in West Africa of J. Sabater Pi (1966, 1977, etc.); Jones & Sabater Pi, (1971) indicate clearly that this is only very sketchily a valid proposition.

In what follows, I hope to show how an evolutionary perspective on hominoid interrelationships and their socio-ecology offers a possibility of shedding light on the phylogeny of the human/ape lineage in a holistic way, perhaps bringing together the results of morphology, physiology, psychology, and etho-ecology.

## Hominoid Cladistics

It is perfectly clear by now that, in Hominoid evolution, there was an initial split between the ancestors of the gibbons and those of the other taxa; the second of these lines then split into the orang-utan lineage and the human/gorilla/chimpanzee lineage; and the second of these underwent either a trifurcation or two closely spaced bifurcations. The gibbon/other split is conventionally viewed as being at family level, between the Hylobatidae (gibbons) and Hominae (others). The orang/other split within the Hominae is best given subfamily status: Ponginae (orang utan) and Hominae (chimpanzee, gorilla, human). The details of the proposal, and its supporting evidence, are set out in Groves (1986).

Within the Hominae, which view is correct? A three-way split, as the early Molecular Clock proponents had it? A split between human, on the one hand, and chimpanzee/gorilla, on the other, as Andrews (1987) argues? Or a split between gorilla, on the one hand, and human/chimpanzee, on the other, as Groves (1986) argues? The third split, though proposed only with some reluctance by Groves, is the one accepted by Ghiglieri (1987), and recently strongly supported by Goldman *et al.* (1987).

I will here construct my model around the third proposition, that the gorilla is the sister-group to human and chimpanzee. While some aspects of this decision will need to be discussed at the appropriate place, much of the model does not depend on it.

### The Ancestral Hominid

The Hylobatidae and Hominoidea are so fundamentally distinct that there would seem little possibility of reconstructing a morphotype or ecotype for the Hominoidea as a whole. None the less, they do all share a suite of derived features of their functional morphology, and Andrews (1982) has argued that, in the broad sense, ecological polarity can be worked out as well. Itani (1977) sees a social group based on the mated pair as primitive for the Hominoidea; in that this implies emigration of both sexes from their natal troop, something of the sort is necessary as a logical bridge between the gorilla or chimpanzee society, where female emigration is the pattern, and the more primitive troop of other primates where male emigration is the norm (even if, as we now know, female emigration does sometimes occur as well).

The ancestral hominid was, therefore, an arboreal frugivore living in loosely knit pairs, moving and feeding with forelimb-dominant modes. Size reduction, emphasis on brachiation, and intensification of the pairbond, lead to the Hylobatidae; size increase, more quadrumanous locomotion, and dissolution of the pair-bond, will lead to the Hominoidea. The importance of the combination of large body size and resource complexity for the evolution of intelligence has been stressed by such authors as Rodman (1979).

### The Hominine-Pongine Split

Ghiglieri (1977) compares the diets of the three Great Apes, but in the case of gorillas rests his case entirely on Mountain Gorillas (see his Fig. 1, p. 325). As shown long ago by Sabater Pi (1966, 1977), and amply confirmed by such authors as Tutin & Fernández (1985) and Calvert (1985), Western Lowland Gorillas, and to a lesser extent Eastern Lowland Gorillas (Goodall & Groves, 1977), are more frugivorous than are Mountain Gorillas. Similarly for habitats: Tutin & Fernández (1984) find that there is a good deal of habitat overlap between gorillas and chimpanzees in Gabon, even if the two species' preferred habitats are different (Jones & Sabater Pi, 1971).

There is no question but that gorillas and chimpanzees are terrestrially adapted compared to the orang-utan: plantar dermatoglyphics are as strongly developed as palmar; the talus is broad; the calcaneus has a broad talon; the power arm of the foot is lengthened as a proportion of the lever arm; and the carpus is more close-packed, with fusion of os centrale to the

scaphoid and a conjunct rotation mechanism in the midcarpus; finally the brachial index is low, always below 100 (Groves, 1986). In these features they resemble the human condition, suggesting very strongly that the ancestral Hominine was at least partially terrestrial. In that both gorillas and chimpanzees move quadrupedally by knuckle-walking, it is at least worth asking whether this ability too characterized the ancestral Hominine; that humans do not knuckle-walk, whereas gorillas and chimpanzees have a complex of functional specialisations for this activity, is the main reason why Andrews (1987) supports the model of chimpanzee/gorilla association to the exclusion of human, but as humans are not quadrupedal such anatomical specialisations are not in question, and I suppose could have been lost subsequent to the adoption of habitual bipedalism.

The terrestrial anatomical features of gorillas and chimpanzees are supported by some features suggesting that a move out of dense primary forest, into at least potentially more open habitats, was part of the same picture. From the list in Groves (1986) we have the following: (1) apocrine glands are, in the Homininae, largely replaced over most of the body surface by eccrine glands, with their superior thermoregulatory capacity; (2) the scalp is more densely haired than the rest of the head and body, in effect acting as an enhanced shield against solar radiation. In psychological testing the gorilla and, to a lesser extent the chimpanzee, are less distracted by irrelevant foreground visual features than is the orang-utan (Rumbaugh, 1974). To these we should perhaps add the greater sociability.

Greater social complexity in the Homininae is shown in many ways, quite aside from the simple fact that they live in social groups while the orang-utan is solitary. The orang-utan has a sternal gland (Geissmann, 1987); in this it resembles at least some taxa of Hylobatidae, and a very wide range of other primate species, so is evidently a primitive feature. The Homininae, however, have no sternal glands but instead a complex axillary organ, whose development is at best rudimentary in the orang-utan. It is not known whether orang-utans scent-mark, but that both humans and gorillas make use of their axillary organs for (subconscious?) communication is very evident, and it may be that chimpanzees do also (but, if they do, the scent is not detectable to the human nose). On the analogy of New World Monkeys, a means as pectoral sniffing, rubbing, or marking; it would not be suitable for convective dispersal like axillary odour, while axillary odour would have little value except in a social group, in a relatively open environment.

The behaviour of gorillas and chimpanzees, as of humans, is fundamentally social. Dixson (1981) notes a variety of facial gestures of communicative value: frown, smile, nervous lip-tuck, tongue extrusion during concentration, yawning under stress rather than as a display. Gorillas and chimpanzees have white pygal tufts when young (infants and early juveniles), with the potential to act as social signals; as humans lack much pigmented body hair, this feature is of course not in question in our species.

Vocalisations are highly developed in gorillas and chimpanzees, with a

very wide repertoire. The middle ear is larger than in the orang, or in any other primate, perhaps permitting a perception of unusually soft auditory signals. Other sounds—drumming on trees in chimpanzees, and on the chest in gorillas—are added to vocalisations to extend auditory communication over greater distances. Vocal communication among group members continues to be maintained during the night (Groves & Sabater Pi, 1985).

Chiglieri (1987) points out that in the Hominae female exogamy is the usual system; male exogamy is much less common—the reverse of the normal primate troop migration strategy. Thus, association between females, being between unrelated individuals, is loose at best, and initially at least is due entirely to their mutual attraction to the males. In the orang-utan, on the other hand, the females disperse only short distances, so that within a restricted area all females are effectively kin; while males may, at any rate, disperse very widely.

Does all this, then, involve a dietary shift? From a superficial inspection of Chiglieri's (1987) Fig. 1, it would appear not; but the gorilla's greater herbivory (even in the relatively more frugivorous Western Lowland Gorilla) and the diversity of non-fruit items, notably vertebrate prey, consumed by many populations of chimpanzees, seem to put a different complexion on this. From the list in Groves (1986), we can select the following derived features of the Hominae which would seem to be related to diet: (1) shortened premolar row compared to molars, with implied heavier chewing mechanics; (2) dental eruption delayed, compared to epiphyseal closure, suggesting complexification of masticatory apparatus; (3) well defined frenulum, implying a tongue that is muscular and active in chewing; (4) a lengthened gut, especially the small intestine; (5) the presence of brow ridges and (associated?) frontal sinuses, providing a buttressing mechanism for masticatory action. In addition, Glaser (1986) records that in any Homine the ability of the Taster genotype to detect Phenylthiocarbamate (though it is polymorphic in all) is considerably greater than in the orang-utan. This substance, PTC, has a most unpleasant bitter taste and is related to compounds occurring in members of the plant family Cruciferae; as thiocarbamates have a thyroid-depressant activity, lowered taste thresholds would be advantageous in species which eat, even if episodically, large amounts of non-fruit vegetable matter.

There is a final observation which may be more difficult to explain in these general terms: the presence of noticeable cranial asymmetry in many gorillas (Groves & Humphrey, 1973), chimpanzees and humans, but not in the orang-utan. The suggestion that this relates to lateralised brain function, via lateral predominance of jaw function in at least the Mountain Gorilla (Groves & Humphrey, 1973), raises questions of what function this would serve in the reconstructed hominine morpho/ecotype, and how the apparently equally intelligent orang-utan can do without it.

### The Human/Chimpanzee Ancestor

Numerous features are listed by Groves (1986) as being synapomorphic for human and chimpanzee. As noted above, this question can still not be considered closed, but for the moment the simplest explanation for the existence of the shared derived characters—that they derive from a common ancestor, rather than that they are parallelisms—will be adopted.

Humans and chimpanzees share the characteristic of homomorphic upper incisors, rather than I<sup>2</sup> being much smaller and differently shaped; the incisor row is thereby given a longer cutting edge. The foliate papillae are lateral in position on the tongue rather than dorsal; as this is where sour tastes are predominantly received, it implies that gustation is further modified from the primitive state. In both humans and chimpanzees the most striking non-fruit dietary component is vertebrate prey, though stems and other herbaceous material are also consumed. Sabater Pi (1977) found that combined sweet and sour tastes predominate in the diet of chimpanzees as of gorillas, but that bitter tastes are absent; while according to Glaser (1986), the chimpanzee tastes PTC at still lower concentrations than the gorilla, though not to sourness in apes, so the link to tongue morphology remains unclear; but the avoidance of bitter tastes seems eminently explicable on physiological grounds.

Humans and chimpanzees share a reduction in hair density over the gorilla; not easy to interpret, but the simple fact should be carefully noted before we sail off into speculation about hair reduction during specifically human evolution.

In chimpanzees puberty is delayed past 7 years of age, thus approaching the human condition. The whole of development seems delayed: Piagetian stages during the early (Sensorimotor) period are passed through more slowly than in the gorilla, if rather more quickly than in the human child (Doré & Dumas, 1987).

Chimpanzees, like humans, live in communities, within which there is a fusion-fission type of sociality. Conceptions occur within consortships in chimpanzees; human marital and quasi-marital relationships are conventionally seen as indefinite prolongations of these consortships (Groves & Sabater Pi, 1985), but in human societies the other form of sexual activity seen in chimpanzees, promiscuity, is muted. Correlated with the high rates of sexual activity, and implied sperm competition, are the elongated penis and enlarged testes and pendulous scrotum; but the baculum, for reasons not understood, is reduced (chimpanzee) or lost altogether (human). The multi-male social organisation results in reduction of sexual dimorphism, at least in size (males weight 120-135% of females on average), though in such aspects as hair distribution, and presence of female sexual signals (perineal swelling in chimpanzee, permanent breasts in human), other aspects of sexual dimorphism are exaggerated.

The chimpanzee community is based on a male kin-group; females

transfer between communities. Ghiglieri (1987) stresses that this relationship is more rigid and absolute than among gorillas, and resembles the majority of human societies. It is within these communities that the fusion-fission sociality takes place. Males cooperatively patrol boundaries in the chimpanzee, and in both chimpanzees and humans they also cooperate in community and territory (or quasi-territory) defence, which actively may degenerate into lethal conflict.

Tool-use and even tool-making is confined, among the Hominoidea (and, in its intellectual associations, apparently among animals), to humans and chimpanzees, although orang-utans and gorillas can acquire this ability in captivity.

The picture of a human/chimpanzee common ancestor, then, is one of an open forest or woodland living species, partly terrestrial, periodically at least not frugivorous, occasionally eating meat, using tools, living in communities marked by cooperation between males, perhaps territoriality and labile social associations within the community, including sexual consorts. The intellectual demands of such a social life might in turn necessitate a longer period of pre-adult life, a longer learning phase.

### The Evolution of the Gorilla

By trying to work out what is in common between sister-groups (or supposed sister-groups), and examining these features to see whether they can be fitted into a pattern, I have tried to reconstruct morpho/ecotypes of (1) the ancestral Hominine, and (2) the common ancestor of the chimpanzee and human. Now is the time to look at each of the three living species individually, to see how each differs from this reconstruction, and if thereby any light can be shed upon the evolutionary routes involved.

The gorilla prefers forest regrowth habitats, though it does occur in primary dense forest as well (Jones & Sabater Pi, 1971). Specifically, in Gabon the gorilla exists at high density in thick, undisturbed secondary forest, and coastal scrub (Tutin & Fernández, 1984); these are all biomes which are uniquely high in representation of the sapling layer (2 to 5 metres) and, usually, the herb layer. The distribution is decidedly patchy, compared to that of chimpanzees; it presumably reflects the overwhelming terrestriality of the gorilla, although the young do climb trees to obtain and throw down food for the heavy adults (Sabater Pi, 1977). Although avoiding direct human contact, and recently disturbed areas, they are rarely too far from human habitation (Jones & Sabater Pi, 1971; Groves & Sabater Pi, 1985), which provides an abundance of the ground herbage which is, even given greater frugivory in some areas than others, their chief diet. There is a sense, then, in which the gorilla can be called a mild commensal species. Everywhere, the gorilla has preferred food species, which form a third to a half of the diet: *Gallium* in the Virunga Volcanoes, *Aframomum* in Equatorial Guinea. The diet is rather unvaried in the Virunga Volcanoes, but much more diverse in West Africa and

Kahuzi-Biega. Much of the diet is sweet, or sweet/sour tasting (Sabater Pi, 1977); it avoids food that is high in tannin, and prefers foods of high digestibility, not unexpected in a herbivore without gastric specialisations (Calvert, 1985).

The gorilla has a large kidney compared to humans and chimpanzees, according to the tabulation of Groves (1986), perhaps connected to the high protein levels in the diet as analysed by Calvert (1985).

In its social organisation, the gorilla diverges strongly from the chimpanzee/human type in its rigidity: formal troops with harem relationships within each, i.e. if more than one silverback lives in a given troop, then each has his exclusive mates among the females. Female exogamy is, however, usual as in other Hominiinae, but male exogamy is also usual, though not invariable, quite opposite to humans and chimpanzees. The females in a troop are bonded to each other only insofar as they are mates of the same male: the silverbacks in a troop—and in both the Virunga Volcanoes and in West Africa, 35–36% of troops do have more than one silverback, though only 23% of *G.g. graueri* (Harcourt *et al.*, 1981)—are, on the other hand, close kin such as father and son.

The female gorilla has among the most restricted periods of receptivity among the higher primates, 3 to 4 days. At this time, they develop very small sexual swellings. They appear to be proceptive, however, over the whole of the sexual cycle. The male thus has a very circumscribed sex life, and very small testes and scrotum, with also very small penis which is not a display organ. The male's huge size and silvery dorsal saddle are quite unmistakable attributes of somatic display, as is his chest-beat, his powerful—and frequent—vocalisations, and perhaps his pungent, choking axillary odour which may have a sexual role (Dixson, 1981), though in my experience it also effectively silently communicates alarm among the troop: when the odour fills the air, the troop becomes quiet and unobtrusively slips away.

Gorilla troops are not territorial. There is however a possibility, raised by Goodall & Groves (1977), that two or three troops may together form a sort of community, sharing parts of their home ranges with each other but excluding other such «communities». This model could readily be tested in the field, and its corroboration or refutation might have implications for social evolution reconstructions, such as the present model.

The gorilla would, then, have diverged from its common ancestor with the chimpanzee/human stock to become a more herbivorous, secondary-growth species, living in close-knit social groups with male exogamy as well as female; everything about its social organisation is male-dominated—the male is conspicuous in every way, in his enormous size and silvery saddle, in his tremendous display; he makes most of the vocalisations; the females seem to interact only as a byproduct of interacting with him. This may be a rather crude overstatement, but the contrast with human and chimpanzee societies is difficult to overemphasise. Yet there is a common basis, and as suggested above the gorilla is clearly a modification from a Hominine stock.

Finally: is the gorilla, really, a montane-adapted species? I argued this long ago (Groves, 1971): I am somewhat less certain now. The population

density differences, relied upon to show how well-adapted the gorilla is to the *Hagania* forests of the Virunga Volcanoes, have been reduced if they have not vanished (Harcourt *et al.*, 1981); instead, we have a picture of a species very patchily distributed, wherever there is suitable habitat in the form of abundant ground vegetation, and such habitat may be montane, but can also be lowland secondary forest or ticket (Tutin & Fernández, 1984), or even anthropogenic (Jones & Sabater Pi, 1977; Sabater Pi, 1977). The restricted environment of the Virunga Volcanoes leads to what appears to be a rather impoverished diet; more plant species are recorded as being eaten in West Africa (Sabater Pi, 1977) and even in Kahuzi-Biega, than in the highest altitude habitats. The broad chest could be, in part at least, simply allometric; the broad nostrils in fact characterise lowland *G.g.gorilla* more than the other two subspecies! Seeing the western lowland gorilla as closer to the species morphotype might, given its still quite frugivorous diet, make sense of Shea's (1983) puzzlement the absence of significant functional reorganisation of the facial skeleton in gorilla evolution.

#### The Chimpanzee as a Primitive Survivor

Groves (1986) found that the chimpanzee possesses remarkably few autapomorphic (uniquely derived) features, given its sister-group relationship to humans. The same appears true of its eho/ecological characteristics: reconstructing the human/chimpanzee common ancestor takes us a very short distance away from the chimpanzee itself. Possibly it is more arboreal, a secondary reversion: some of its uniquely derived characters include a long foot, and a shortened caecum (greater frugivory than in the common ancestor?). The social organisation does suggest, too, an increased tendency towards promiscuity in sexual behaviour during its evolution: long thin glans penis, functioning as a display organ; very high sperm density; huge female sexual swelling.

The chimpanzee's population density is higher in forest and woodland (Gombe, Kibale, Budongo) than in either dense forest or savannah (Ghiglieri, 1987; Tutin & Fernández, 1984). To this extent, therefore, Kortlandt's (1963 *etc.*) model of 'dehumanization' might have merit; but the tool-use and community social organization, to name but two aspects of behaviour which unite chimpanzee and human, need not have evolved independently parsimony suggests, as argued here, that they characterized the last common ancestor.

If the series of dichotomous splits used here as a basis for argument are correct, what of the misgivings of Andrews (1987) about such characters as knuckle-walking and enamel thinning which lead him to favour a gorilla-chimpanzee clade rather than a chimpanzee-human one? As suggested above, knuckle-walking specialisations would not be expected to occur in modern humans, which are not quadrupedal at all: australopithecine forelimbs might be expected to preserve traces of such features, if they were present in a common Hominine ancestor, which already seems possible (see evi-

dence cited in Groves, 1986). Martin (1985) showed that the mode of formation of the dental enamel of chimpanzees and gorillas is similar to humans and quite unlike orang-utans, for all that the proportions of fast-forming and slow-forming enamel are different, producing the two end-products 'thick' in the human case and 'thin' in the two African apes by quite a simple change. The mode of enamel formation could, then, have gone through either the human 'thick' stage, so that the thin chimpanzee and gorilla enamel would be evolved in parallel, or a 'thin' stage, so that human thick enamel would be a reversal, without much substantial evolutionary change being called upon.

#### A Word on Human Evolution

Compared to the human/chimpanzee morphotype, humans have evolved fast and far. Bipedalism and habitually upright posture; enlarged brain; canine reduction and orthognathly; long thumb and manual dexterity; reduced body hair, and sexual differentiation in its distribution; prolonged gestation and growth; long pendulous penis, very low sperm density, loss of sexual swelling but permanent mammary enlargement, prolonged (quasi-permanent) consortships; diversified diet including much carnivory; large parotid glands; increased number of vallate papillae, enhanced ability to detect bitter substances; these are among the characteristics evolved in the human stem since its individualisation. If it has done nothing else, this essay will have been a success if it has emphasised the extent to which the specifically human attributes not only depend fundamentally on their hominoid, hominid and hominine background, but are actually an intensification of characters already foreshadowed in hominoid evolution as a whole.

#### Acknowledgements

It should be obvious by reading this essay that I owe a great intellectual debt, as well as a debt in many practical ways, to Jorge Sabater Pi. I have enjoyed discussing some of the questions raised, and not perhaps answered all that satisfactorily, in this paper with Peter Andrews, Lawrence Martin, Sandy Harcourt, and the late Dian Fossey.

TABLE 1. TAXONOMY OF THE HOMINIDAE  
(AFTER GROVES, 1986)

SUBFAMILY PONGINAE		
Genus <i>Pongo</i>		orang-utan
<i>Pongo pygmaeus pygmaeus</i>		Bornean orang-utan
<i>Pongo pygmaeus abelii</i>		Sulatran orang-utan
SUBFAMILY HOMININAE		
Tribe Hominini		
Genus <i>Pan</i>		Common Chimpanzee
Genus <i>Pan troglodytes</i>		Central African Chimpanzee
<i>Pan troglodytes verus</i>		West African Chimpanzee
<i>Pan troglodytes schweinfurthii</i>		Eastern Chimpanzee
<i>Pan paniscus</i>		Pygmy Chimpanzee
Tribe Gorillini		
Genus <i>Gorilla</i>		Gorilla
<i>Gorilla gorilla</i>		Western Lowland Gorilla
<i>Gorilla gorilla gorilla</i>		Eastern Lowland Gorilla
<i>Gorilla gorilla beringei</i>		Mountain Gorilla

## RESUMEN

No obstante la enorme proliferación de estudios que referentes a la ecología evolutiva de los *Hominoides* han sido publicados a partir de la segunda guerra mundial, nuestro conocimiento sobre esta cuestión continúa siendo muy fragmentario, parcial y hasta contradictorio, como intentamos demostrar en este trabajo.

Opinamos que solamente los estudios evolutivos referentes a la sociología de estos primates superiores (*Ponginae*, *Homininae*, *Panini* y *Gorillini*) contemplados desde una amplia perspectiva filogenética y valorando, ponderadamente, los resultados de los estudios: psicológicos, eto-ecológicos, fisiológicos y morfológicos, pueden aportar información, científicamente válida, para una comprensión realmente holística, de esta apasionante problemática.

## SUMMARY

A large number of studies concerning the evolutionary ecology of the *Hominoides* have been published since the second world war. Despite this proliferation our understanding of the subject is still fragmentary, partial and contradictory, as we intend to show in this paper.

In our opinion evolutionary studies of the socioecology of the higher primates (*Ponginae*, *Homininae*, *Panini*, *Gorillini*) must be carried out after weighing the results of psychological, ethoecological, physiological and morphological research and viewing the whole field in a wide phylogenetic perspective. Only this way of research may supply information scientifically valuable to understand this dramatic subject in a true and holistic manner.

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## CONDUCTA Y EVOLUCIÓN: HISTORIA Y MARCO DE UN PROBLEMA

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