### Warfare, Ethics, Ethology

Evolutionary fundamentals for conflict and cooperation in the lineage of Man

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#### ABSTRACT

The aim of this article is to set a macro-historical narrative concerning the emergence of warfare and social ethics as symplesiomorphic features in the lineage of *Homo sapiens*. This means that these two behavioral aspects, representative of a very selected branch in the phylogenetic tree of the Primate order, are shared by the two lineages of great African apes that diverged from a common ancestor around six million years in the past, leading to extant humans and chimpanzees. Therefore, this article proposes an ethological understanding of warfare and social ethics, as both are innate to the social high-specialized modular mind present in the species of genera *Pan* and *Homo*. However behavioral restraints to intersocietal coalitionary violence seems to be an exclusive aspect of the transdominial modular cognition that characterizes modern humans. Thus, if in the evolutionary *long durée*, warfare and restrictions to intrasocial violence both appear to be ethologically common to humans and chimpanzees to a certain extent, an ethics of warfare - and, of course, the cognitive capability for intersocietal peace - seems to be distinctly human.

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The aim of this article is to set a macro-historical narrative concerning the emergence of warfare and social ethics as symplesiomorphic features in the lineage of Homo sapiens. This means that these two behavioral aspects, representative of a very selected branch in the phylogenetic tree of the Primate order, are shared by the two lineages of great African apes that diverged from a common ancestor around six million years in the past, leading to extant humans and chimpanzee. This narrative is not intended to replace any well-established interpretations about war and peace sposed by social sciences and humanities in general; on the contrary, its objective is to add a new depth to these interpretations, from an evolutionary point of view. We hope that all contradictions brought forth by this "play of scales" can foster dialectical reflections about the relationship between social action and the historical durations, in the trail blazed by Braudel (2009) and Christian (2005).

There is a vast assortment of definitions - current

or obsolete - for these widespread phenomena we call warfare and ethics in human relations. But, in the perspective of this essay, most of them - if not them all - end up sharing a common limitation. The universality of these supposedly contradictory aspects of human behavior is a genuine stimulant for our imagination - that gives birth to a homo ethicus, or, in the Janus face, a homini lupus homini. Nonetheless, that same universality makes us lose grasp of the uniqueness of conditions that made possible intersocietal conflict in primate societies, and, even further, that had set in motion neurocognitive mechanisms devoted to mitigate or prevent the escalation of intragroup agonistic behavior. In the long dureé, and considering the evolutionary history of primates in general, the intersocietal coalitional violence (a broad definition that makes all human warfare nothing but a particular example of a general phenomenon) and the complex array of ethological <sup>1</sup> mechanisms in the unconscious

<sup>1</sup> Ethology, in general terms, is the study of animal behavior.

mind that gives foundation to ethical knowledge in Homo sapiens are absolutely exceptional. And we don't refer here to interpersonal violence, this common behavioral feature in the primate world, emerging as an evolutionary asset in the dispute over energy sources and reproductive opportunities. Some kind of primate sociability in the lineage of Man, emerging six million years before the present, has brewed up the context for the selection of intricate cognitive instruments, devoted to intragroup conflict resolution, based on complex status hierarchies, nonlethal violence, ritualizations and social stratagems. These phenomena, we believe, are mostly - but not exclusively - tributary to the rare development of masculine cooperative patrilineality, and, together, set intersocietal coalitionary lethal violence in motion. In this macro-perspective, humans and chimpanzees are the only species that make war. Furthermore, they are actors in a complex and daily social drama, in which the balance of power and prestige among "cooperative competitors" is highly volatile, and the potential for fratricidal lethal violence has to be kept under control by the operation of a well developed social modular mind. Humans and chimpanzees share warfare, ethological constraints to lethal violence among peers, and 98,8% of their genes. If this set of behavioral aspects hadn't emerged independently (homoplasically) in the two lineages that led, one to Pan troglodytes and other to Homo sapiens, it must have been manifest in species before the divergence, or, at least, in the last common ancestor (LCA) of humans and chimps. Would the behavioral potential for the projection of external power and for the deterrence of intrasocial conflict be phylogenetic <sup>2</sup>? In an evolutionary perspective, would warfare and ethics be the offspring of the same womb? And what's to say about an ethics of warfare?

# 1. Multissexual unstable sociability in the Early Eocene

The emergence of sociability among primates,

around fifty-two million years ago, didn't seem be a sufficient condition to generate a specific evolutionary context for the ethological foundations to warfare and ethics. Early Eocene <sup>3</sup> has brought, for some new putative species, the behavioral innovation of multissexual unstable groups, in detriment to the solitary life still led by other primate species, remnants of an even older paleocenic world. The main characteristic concerning these ancestral forms of sociability must have been an intense volatility regarding to the internal composition of social groups, with frequent processes of fusionfission, in response to demographic saturation and availability of resources. In these terms, both adult males and females tend to migrate from their natal groups to others, and in most cases, more than once in a lifetime. If we consider the eocenic climatic context of (natural) global warming, worldwide environmental homogeneity, the expansion of rainforest across the continents (including Antarctica), and the expansion of the overall energetic supply in most of the world ecosystems, we should infer that dispersion of individuals over the territory would be high, inasmuch as the risks of foraging dispersal (predation) would be offset by the richness (in qualitative and quantitative aspects) of nutrients supply.

Diurnality in primates could be associated with the development of this unstable sociability, with stereoscopic vision and with the expansion of depth perception. In arboreal species, the latter would enable organisms to pinpoint fruits and other nutritional high-value resources in conditions of visual pollution (closed canopy forests, with scarce luminosity), therefore opening to primates this rich ecological niche, put forth by the expansion of angiospermic vegetation. At the same time, and as a trade-off, diurnality placed them at a disadvantage to these species living in daylight, consubstantiated

<sup>2</sup> Are phylogenetic all characteristics inherited by a species from others in their direct ancestral line.

<sup>3</sup> Eccene is the geological period comprehended between 56 and 33,9 million years before the present, according to the International Commission on Stratigraphy (ICS). For more information about this subject see <u>http://www.stratigraphy.org/</u> <u>index.php/ics-chart-timescale</u>. The geochronology followed in this essay follows the international convention.

in an increased exposure to predation risk. Against that, gregariousness acted as an equilibrium strategy, enhancing the number of sensorial units willing to simultaneously scan around for potential threats, and sharing that information for mutual benefit. In that way, possibly, the unstable sociability among primates could have emerged: as an anti-predator strategy, merely pragmatic, unable to form neither lasting bonds among individuals, nor complex forms of cooperation and coalitions (Groves, Cameron, 2004: 36; Ladeia, Ferreira, 2015: 56-58; Shultz, Opie, Atkinson, 2011: 219; 222).

#### 2. Climatic change, from the Oligocene to the Early Miocene: *Proconsul* and the matrilineal cooperative female sociability

With the relative environmental homogeneity of the Eocene giving place to gradual global cooling and aridification in the Eocene-Oligocene <sup>4</sup> transition, the African evolutionary board was distinctively disturbed, kickstarting a new context for speciations and extinctions. This worldwide climatic transformation was simultaneous to (and reinforced by) intense tectonic activity and orographic changes in the Early Miocene<sup>5</sup>, that resulted in the rising of the Himalayas, the Tibetan Plateau and the Ethiopian highlands. The geographic relief, thus, prevented the entry of moist air currents from the Indian Ocean, taking a heavy toll on East African ecosystems. As an environmental consequence, the territorial distribution of forest resources became even patchier, with the in-between spaces aridified in savannah-like form. The multiplicity of new niches ended up contributing to the selection of evolutionary innovations in the order of Primates.

Proconsulidae is a family of quadrupedal primates that encompasses a few miocenic species emerged around twenty-three million years ago, among which *Proconsul africanus* is the best known. Their dental anatomy is gracile; this suggests, in biomechanical terms, arboreal habits in tropical or subtropical closed forests, and a diet consisting of soft fruits and leaves, something very similar to their eocenic and oligocenic ancestors. In this species, the thin enamel layer all over the dentition is prone to wear due to abrasion (even in low levels), therefore increasing the shearing action of the cuspids. That is an adaptation commonly associated with primates occupying niches with plenty of soft and tender foods, that require little oral preparation and mastication (Pampush et al., 2013: 218).

Nonetheless, we should consider that environmental conditions on the Miocene of East Africa were creating a patchwork of forests ("isles") surrounded by savanna, and if proconsulids really depended on the exploitation of arboreal resources, these populations were certainly trapped inside these patches, with very likely effects on their social strategies. Inferring from the fossil register, if we also take in consideration the possibility of a reasonable level of sexual dimorphism in terms of body mass and shape/size of canine tooth (in Proconsul africanus, at least), we can suggest that males, corpulent and heavily-armed, were involved in intense levels of reproductive and territorial competition, based on agonistic behavior (intimidation, vocalizations, interpersonal violence).

According to this scenario of climatic change, arboreal life, spatial insulation of the natural resources and sexual dimorphism, we can suggest that proconsulids probably belonged to a group of pioneer primate species that first lived in stable societies. If we go further, and consider the reproductive and energetic costs imposed by intrauterine gestation and lactation, the access to high-quality and regularly supplied nutritional resources is the most important evolutionary demand in female energetic ethology. This is a central issue in the patterns of primate territoriality and social structure, which means to say that, in the Miocene of East Africa, where and when the most valuable forests were becoming even more isolated by vastitudes of arid plains, females belonging to

<sup>4</sup> The Oligocene was a geologic period comprehended between 33,9 and 23,03 million years in the past.

<sup>5</sup> The Miocene was a geologic period comprehended between 23,03 and 5,33 million years in the past.

arboreal species like proconsulids would seek to occupy and defend those secluded spaces. While climate and aridification were not harsh enough to deplete the nutritional value of resources concentrated in these forest patches - expanding the African savannah even more -, the ecological context would favor the exploitation by groups of kin-related females, cooperating to guarantee the access to preferred foods in the benefit of the genetic matrilinear community, and to exclude other groups of non-kin females. In the case of males, the energetic and reproductive demands are minimal (including gametic production), so the main challenge is to guarantee access to females. In this way, primate territoriality ends up being conformed mainly by female energetic strategies, since males just follow the patterns of spatial dispersion shown by female collectives. Therefore, males tend to migrate from their natal groups after reaching sexual maturity, in order to confront other males for sexual opportunities far away from their own genetic community.



In this simplified model, the darker the green, the richer the nutrients. A) High quality resources, deconcentrated in space. There is no circumstance for concentrating females in patches; and they forage alone and separate themselves from the others, avoiding competition with related females. Unstable groups emerge as anti-predation strategy. Males migrate from their natal groups when reaching maturity, as well as females. B) High and mediumquality resources are concentrated in homogeneous and large-scale patches. Kin-related females gather on these spots, which are rich enough for them to feed together, as long as unrelated females are kept at bay. The defense of the female genetic

pool prevails. Unrelated males gather around these females, fighting for sexual opportunities. C) High quality resources are extremely concentrated in uniform patches. Under these conditions, a lone male, if tough enough, is able to control the female foraging territory, excluding all competing males and establishing a harem. D) Quality of resources decreases, and the distribution pattern is maintained. Females scatter spatially in search of medium quality energy patches. Solidarity among females decays, as kin-related groups becomes counterproductive. There's opportunity for harems to continue, this time organized in patrilineal lines. It coincides with the sociability pattern present in *Gorilla* sp. E) Distribution of resources becomes heterogeneous. Kin-related female groups, already exhausted, become even less possible, as well as the harems. A lone male becomes unable to prevent the access of competitors as females spread to take advantage of scarce and scattered best quality resources. Harems are impossible, but patrilineality is preserved. Coalitions of kin-related males are formed, to dominate over dispersed females. It matches the sociability pattern in *P. troglodytes*. F) Resources becomes too poor and scattered, condemning permanent sociability. In Pongo sp., leads to female dispersion, to individual occupation of patches, and the formation of male super territories.

This scenario does not account for the emergence of intersocietal coalitional violence as a behavioral aspect, and seems reasonable to assume that it didn't exist in any primate species in the Early Miocene, even taking into consideration the possibility of stable sociability among kin-related females. Among proconsulids, is probable that uncooperative groups of non-kin males have been tolerated by the matrilineal collectives only if the territory and resources were compatible with the extenuating reproductive and energetic strategies of females. However, with the ongoing climate crisis in Early Miocene, and the possibility that supply and spatial concentration of natural resources have reached a critical threshold (Barnosky, Kratz, 2006: 528), these turbulent and competitive collectives of males could

have become an unbearable burden by pressing over the scarce food available and by the intense exercise of violence and harassment among themselves, generating increased levels of psychological stress, inducing to female reproductive suppression.

Also, that should be the case for the development of one-male groups, or harems, in which a dominant male shows himself capable of establishing exclusivity of access to reproductive opportunities, represented by the existence of a stable collective of females. That privilege only becomes possible if the harem holder is able to sensorially watch over the estrous females, which is that made easier by spatially concentrated forests. Consequently, being able to protect the foraging territory where females live, a single dominant male could then use his improved physical and psychological weaponry to prevent access to other postulant males, in their search for reproductive wayouts. To the kindred females, the reduction of the amount of organisms alien to their genetic community - the migrant males - should represent less pressure over decisive energetic resources, therefore enhancing female reproductive fitness in group level. Harems were a very possible form of sociability among proconsulids, considering their morphological characteristics and the paleoecological conditions in which they probably lived. If this were the case, the harem strategy would have provoked high level of tension and interpersonal masculine violence. That conclusion is, as a matter of fact, supported by the dimorphic condition in proconsulids. Hence, intense agonistic behavior among unrelated and uncooperative males (especially in the presence of harem holders) is something that would prevent the emergence of that very special condition for primate warfare and for the ethological restraints to intragroup masculine conflict: patrilineal male coalitions (Cameron, Groves, 2004: 38-40; Foley, 2008: 220-227; Ladeia, Ferreira, 2015: 75; Nordhausen, Oliveira Filho, 2015: 36-37; Wrangham, Peterson, 1996: 131; 174-175).

# 3. *Afropithecus*: stable matriachies and the savannah

Afropithecids, a distinct family, diverged in Africa around eighteen million years in the past, having some proconsulid species as their most likely direct ancestor. Fossil record suggests that this new sort of primates have adapted some behavioral innovations, probably developed by their evolutionary forefathers, to a paleoecological context somewhat distinct. This behavioral heritage becomes even more relevant when we consider that an afropithecid was the presumed ancestor of all hominids, which includes, *lato sensu*, modern humans. In general, this extinct family had species morphologically quite distinct from the profile of their proconsulid ancestors, with whom they have coexisted. Their upper body morphology suggests they were brachiators <sup>6</sup>, which means that their main motor strategy consisted of suspensory locomotion in a forest environment, just like gibbons, and in a minor extent, chimpanzees and other extant great apes. The estimated average body mass of afropithecids is greater than what is expected from arboreal primates, which advocates in favor of semiterrestrial habits. Considering the body plan adapted to brachiation (more vertical posture, different from quadrupedal primates like proconsulids), the motor strategy employed by afropithecids on the ground could have been based on knuckle-walking (like extant gorillas and chimpanzees), an aspect that could have future consequences for the exercise of territoriality. Assuming the possibility of semiterrestrial behavior, coupled with the evidence for robust facial architecture, thick dental enamel and powerful chewing dentition, it is suggested that, unlike their ancestors, afropithecids occupied marginal habitats to the humid forests, with regular incursions into the savanna, from which they could have obtained fallback foods according to environmental fluctuations. Although the dry African

<sup>6</sup> Brachiation is a form of suspensory locomotion in which the animal moves hanging under tree branches, in vertical position.

plains offered mostly abrasive and hard provisions, afropithecids were adapted for the exploitation of niches opened by the aridification.

The expansion of nutritional opportunities for these species - inasmuch as they were capable not only of exploiting forest resources, but also those present in savannas and woodlands - altered the relationship between society and space for these primates. We must consider that the spatiality of resources is a dynamic phenomenon, and, thus, depends on energy processing and of thermoregulatory efficiency <sup>7</sup> of the motor strategies employed. Therefore, if for arboreal and thinenameled proconsulids these aridified habitats meant insurmountable barriers - which led their societies to concentrate in aisled forest patches -, for the more robust afropithecids, the savannah, to a greater or lesser extent, was also a space for foraging and exploration, which would have contributed to reduce the effects of demographic concentration on its social strategies.

Perhaps we should assume that, in this case, stable sociability - one of the primitive pillars for warfare and ethics - would have been contraindicated by the deconcentration of nutritional opportunities in the territory, which should have led - at least theoretically - to the spatial dispersion of females. That dispersion would be certainly counterproductive to the maintenance of permanent matrilineal female collectives, and hence, to the masculine sexual exclusivity strategies expressed, at the limit, by a successful harem behavior. All these facts would tend, if true to some extent, to conduct our afropithecid ancestors again to a profile of sociability very common to Eocene parameters - the unstable multisexual aggregation -, still practiced by many species of extant monkeys, especially New World

7 Knuckle-walking primates when moving terrestrially across open spaces (in savannah, with few trees), expose much of their body surface (head, shoulders, back) to the direct incidence of solar radiation, reasonably more than bipedal primates do. platyrrhines 8.

In spite of this possibility, the phylogenetic hypothesis of the transmission of stable sociability from proconsulids to hominids should not be discarded prematurely, since we have good examples of primates also capable of occupying vast territories - as we believe afropithecids could have been - but which preserve alternative forms of harem behavior and matrilineal feminine collectives, such as some species of papionins. Among geladas (Theropithecus gelada) for example, harems have been preserved, but given the expanded relative spatiality of natural resources (considering geladas are grazing primates), it became possible to form troops, that consist in a sort of "confederations of harems", composed of many reproductive units, each formed by related females and a dominant male, sometimes accompanied by a few subaltern males. This ethological pattern among geladas represents an aspect of morphological and behavioral flexibility present in variated degrees in all species. This means that there are "accommodation limits" through which an inherited aspect keeps being replicated - even in slightly modified forms -, in spite of the environmental change. Nonetheless, this limits can be broken by sudden or massive ecological transformation, giving rise to extinction / speciation processes. But, regarding afropithecids, we believe that is still defendable the hypothesis for the behavioral inheritance of matrilineal female collectives in one-male groups, especially if we consider that the same persists among some extant African primates, distantly descendant from that afropithecid radiation (Cameron, Groves, 2004: 39; Barnosky, Kraatz, 2007: 525; Foley, 2008: 150-151; 178-179; 183-184; Pampush et al., 2013: 222; Wrangham, Peterson, 1996: 56-59).

<sup>8</sup> Platyrrhines form a parvorder of primates that unites all New World monkeys. Unlike Old World catarrhines (such as humans, baboons, gorillas, chimpanzees, etc.), which have protruding noses facing downwards, platyrrhines have flat nostrils facing sideways. Some of its species have a prehensile tail, an evolutionary trace absent in all catarrhines.

## 4. The Middle Miocene and migrations across the Afroasiatic axis

The onset of the Middle Miocene, around fifteen million years ago, coincided with the expansion of polar ice caps and the lowering of sea levels, reaching a peak of intensity in the ongoing process of global cooling and aridification. Under these conditions, the northern portions of Eurasia became inhospitable to primates in general, while a milder and relatively homogenous biogeographic zone formed in the Sahara, East Central Africa, southern Europe, and the Levant. Many endemic African species are known to have migrated northward through the Mediterranean coast, and anthropoids also participated in these migrations. From these radiations out of Africa, many speciation processes have succeeded amongst the apes in Europe and Asia Minor without any significant impacts over the mainframe of social behavioral aspects, phylogenetically inherited by anthropoids from their afropithecid ancestors. Nonetheless, is important to note that from ten to seven million years ago, the moment of this primatological odyssey out of Africa, the reduction in diversity of the great apes species is impressive, something that probably have provoked the first major bottleneck in anthropoid evolutionary history. It is possible that this extinctionary context denoted that the behavioral and morphological portfolio based on robust dentition, semi-terrestrial locomotion and occasional exploitation of the savannah had met its limits of accommodation. In the final scene of that act, Graecopithecus freybergi or some close descendant species reached Mediterranean coast once again, escaping from the climatic aggravation in the north. The relevance of this species lies in the fact that perhaps it was the pivot of European anthropoid radiations across the Afro-Asian axis, where the harsh environment would put old social strategies once again to the test (Cameron, Groves, 2004: 41-42: 55-57; Ladeia, Ferreira, 2015: 76-77).

#### 5. Pongins in Asia: closed doors to warfare

Migrations from southern Asia to the Far East, as vectors of latitudinal expansion, were marked by the incidence of partially constant climatic conditions, although progressively aggravated by the advance of glaciers through the northern portions of Eurasia. This homogeneity gave birth to a set of similar evolutionary challenges from Anatolia to Southeast Asia, something suggested by the morphological similarity between the extinct Asian great apes and Pongo sp. (the two species of orangutans, restrict today to the islands of Sumatra and Borneo). They share an odontomorphological profile inherited from European ancestors that migrated through meridional zones - thick dental enamel, robust molars compared to the rest of the dentition - although, as already mentioned, these characteristics, by themselves, probably no longer guaranteed survival against the harsh seasonality and aridification. Thus, the Asian great apes should have been able to adapt to the extreme rarity of tropical forests, the impoverishment of nutrient supply, and the radical deconcentration of resources in southern Asia (lowland plains) through behavioral patterns present today in the last extant species of the subfamily Ponginae.

It is likely that stable matrilineal female collectives have become unviable; with scarce and extremely fragmented resources, either females would need to scatter around for food, or compete with one another in a very restricted territory, poor enough to supply the energy necessary for them all. In terms of kin selection, coinhabiting related females would inevitably lose reproductive fitness in the circumstance of fiercely struggling for food, whereas, if each of them migrate to different areas, the possibility of individual success would emerge without the otherwise necessary failure of one or more relatives in the survival race. This is what orangutans do: among them, matrilineal female cooperation does not exist, since each female with her immature offspring is fixed in a small arboreal patch, separated from others females, only with sufficient resources to maintain this stable family

unit. Group sociability is likewise dissolved, and consortia between males and females become temporary, creating a loose network of relationships over a vast territory.

For males, female territoriality prevents the traditional sexual exclusivity strategy (haremholding) given the practical inability to prevent access to competing males. Nonetheless, the ethology of sexual exclusivity remains relatively alive, as dominant males circulate terrestrially through various female-controlled patches (creating a super territory), attempting to secure their reproductive privileges and eliminate competitors, and, in this way, forming something like a "loose harem". The degree of uncertainty about paternity generated by that kind of female territoriality leads to a high level of competitive pressure among adult males, which is expressed by notorious sexual dimorphism, vocalization behavior (signaling the presence in the territory) and intense level of interpersonal violence. Thus, pongins represented an evolutionary dead end with regard to the ethology of warfare and ethics: the formation of matrilineal collectives, as well as of any patrilineal male group, cooperative or not, is prevented. The high degree of agonism 9 and of physical violence in particular does not advocate in favor of warlike behavior, nor does it generate a context demanding conflict resolution strategies (Cameron, Groves, 2004: 75-77; Foley, 2008: 218; Nordhausen, Oliveira Filho, 2015: 29; Wrangham, Peterson, 1996: 133-134).

#### 6. Gorillins in Africa: non-cooperative patrilineality inhibits coalitionary intersocietal violence

Pongins are primates not directly relevant to the phenomenon of intersocietal coalitionary violence and of ethics among modern humans, since they consisted of an evolutionary branch divergent from that which would result in the great African anthropoids. The last common ancestor of Asian pongins and African great apes lived about twelve million years ago, precisely in the period of radiations out of Europe. Rather, what interests us in particular are the hominids that have taken the way to Africa, coming from the north, since among them the ethology of warfare and ethics would take another decisive step.

The earliest species allocated under the Gorillinae subfamily emerged about ten million years ago, during the Late Miocene. These longitudinal migrations from Europe to the south represented the movement of species partially adapted to conditions of temperature and aridity more severe than those found in Central Eastern Africa. Thus, in a less rigorous environment than that existing all over the latitudinal range from Mediterranean Asia to the Malay Peninsula, some kind of permanent group sociability was still viable, and even more: if we take extant gorillas as reference, a harem sociability could be sustained. Although these migrant species found biomes less affected by climate change in African soil, the primitive strategy, based on robust dentition dependence, terrestrial knuckle-walking and opportunistic savannah exploitation, seems to have been abandoned. Odontomorphological profile of gorillins differs significantly from that of their European ancestors, indicating dietary specialization (again) in wet forest resources: once more among apes a graceful dentition emerges, with thin enamel, showing that reliance on this sort of retracting niche was still an option with evolutionary short-term returns. With natural resources less scattered than in southern Asian environments, although with inferior nutritional quality to that enjoyed by the ancient Eocene primates, the harem strategy could have been replicated by gorillins in Africa, but not the stable cooperative female matrilineality. With diminished quality and supply of resources, although distributed with some uniformity and concentration, female energetic ethology was somehow threatened. Female stable sociability continued to be advantageous - the advantages of gregariousness since Eocene times were well established at that time - but no longer among kin-related individuals. Among gorillins,

<sup>9</sup> It is characterized as agonistic any form of conflict behavior involving physical violence or intimidation.

the females are the ones that mainly migrate to other groups after reaching sexual maturity. This means that kin cooperation becomes unfeasible, and gregariousness occurs between unrelated individuals. The collapse of the female kin cooperation means that the empowerment for self-protection against males also cedes, giving space to the advancement of masculine reproductive agenda within these harem societies. The exercise of power and sexual exclusivity by a dominant male becomes compatible with maintaining one or more of his adult sons in the group (although these young males may also leave the group and fight for sexual privileges elsewhere). This kin-related males means more pressure over already scarce nutritional resources, reinforcing the female migration imperative (they leave their natal group in order to avoid disputing over resources with their relatives).

The emergence of patrilineal links among African great apes in the Late Miocene does not signify the generation of cooperative relations among males. Sexual exclusivity, typical of harem regimes, is also a goal replicated in gorillin societies. To all kin-related males united in the same social group, except for the "silverback" <sup>10</sup>, submission to reproductive exclusion is the only option. One of these subaltern males will have access to regular sexual opportunities only after the death of the harem holder (often, his father), or after achieving dominance elsewhere. Domination also extends to females, whose ties of solidarity have been severed by the collapse of matrilineality: to control an increased level of conflict over nutritional resources, product of a non-kin stable female sociability, it is not uncommon for the silverback the exercise of non lethal violence over their female protégées. There is, so to speak, a high degree of inner peace and submission to instituted power, and in no respect an "ethology of rebellion" is manifested, as would become usual millions of years later, to the common ancestor between humans

and chimpanzees. There is no counter-hegemonic action, nor attempts to take power on the part of any members of the group; the threats to dominance usually happen in the circumstance of the arrival of young male migrants, who attempt to usurp the harem from an established silverback. Sexual exclusivity, as is customary, gives rise to a high degree of male interpersonal violence and sexual dimorphism. Again, despite the fact that two of the cornerstones of the ethology of warfare and ethics are present - stable sociability and patrilineality -, the harem regime and the lack of male intra-group kin cooperation makes this ethological phenomenon impossible (Foley, 2008: 224; Pampush et al., 2013: 217; Wrangham, Peterson, 1996: 147-149).

#### 7. Late Miocene and the last common ancestor to humans and chimpanzees: complex hierarchies and male cooperative patrilineality

With glaciation increasing its intensity in ends of the Late Miocene, climatic disruption reached a new critical threshold, causing niche-conservative primates such as gorillas to migrate, following the retraction of forest zones. At the same time, some opportunity to adaptation emerged for primate populations living in more marginal environments. The relative spatiality of resources for gracile and knuckle-walking anthropoids did not become so disperse as happened in southern Asia, yet the concentration suitable for the preservation of harem societies seemed to replicate only with difficulty. With increasingly rare food resources in the territory, these populations living in ecologically marginal regions, between savannas and forests, needed to spread more and more across the territory. As we know, this ultimately means that unrelated females, pursuing their energetic agenda, had to forage farther apart from each other. As it would also be the case among the pongins in their latitudinal migration across southern Asia, female spatiality formed a perimeter incompatible with the exercise of surveillance by a highly dimorphic male, willing to maintain his sexual exclusivity.

<sup>10 &</sup>quot;Silverback" refers to the dominant male in gorilla societies. The term derives from the silverish coloration displayed by the fur on the back of these primates after reaching sexual maturity.

Therefore, climatic extremes established for males a trade-off between the defense of their genetic community (patrilineality) and the exercise of individual reproductive agendas. In the case of Asian pongins, deprived of any inheritance of patrilineality behavior, this dilemma was null: the search for sexual exclusivity remained, despite the environmental circumstances, with a high degree of agonistic behavior among unrelated males. But, in the case of the last common ancestor to human and chimpanzees, the inheritance of patrilineality probably represented a factor that pointed the evolutionary arrow at unprecedented directions.

Instead of these ties between related males being dissolved, they become, on the contrary, even tighter, with the development of complex forms of male cooperation, a rare ethological condition. In the face of the impossible surveillance of the silverback over females, harems disappeared, and with them, the undisputed *locus* of male dominance. Avoiding fratricidal conflict for reproductive opportunities, in the circumstance of a "vacuum of power", these male patrilineal collectives organize themselves into complex status hierarchies. Without strict, gorillinstyle dominance, mating becomes a polygynandrous issue<sup>11</sup>, and male cooperation for the control of the foraging territory - and therefore, over nonkin females - arises. Kin-selection becomes clear, as individual reproductive agendas are relativized in face of the collective defense of male genetic community (against "alien" collectives of related males). With intragroup masculine agonistic behavior under control, interpersonal violence is reduced, as well as the level of sexual dimorphism. The emergence of complex ethological mechanisms for conflict management gives rise, then, to the rare phenomenon of intersocietal coalitionary violence (Aureli et al., 2008: 629-630; Foley, 2008: 230; Wrangham, Peterson, 1996: 52).

### 8. Post-harem sociability, cooperative patrilineality and intuitive ethics

Primates are imbued with an efficient general intelligence for problem-solving tasks. This implies that, in addition to simple inherited behavioral contents, their ethological portfolio includes learning mechanisms based on the interaction with the environment, with generic rules adjusted by trial and error. For most of the history of these species, accommodation to evolutionary challenges seems to have been possible by employing exclusively this sort of low-cost intelligence. The environmental context for the development of more specialized, energy-intensive types of cognition, seems to have emerged slowly, beginning ten million years ago, with the migrations back to Africa and Asia. These complex cognitive forms only become clearly visible with the modularization of social cognition, about six million years ago, with the emergence of the last common ancestor to humans and chimpanzees.

Highly specialized social cognition emerges as a mechanism of accommodation between competition and cooperation, between individual male reproductive agendas and stable post-harem patrilineality. In a context of dispute over sexual opportunities among related males, the fratricidal struggle is reduced to evolutionarily irrelevant levels through a complex capability to analyze the power locus of each member of the group in their relationships with the others, and to formulate hypotheses about the possibilities of rise and fall in the social pyramid for all the agents involved. From that natural proficiency in social strategy-making, an individual can trace his plans of preservation or conquest of status. The recognition of power and prestige levels of others, the temporary acceptance of one's own social condition, and the design of strategies for the contestation of hierarchy, in their own benefit and of their allies, appear as fundamental ethological guidelines among chimpanzees, and, presumably, also present in their last common ancestor with humans.

Chimpanzees and humans share a common

<sup>11</sup> In polygynandrous regimes, males and females select occasional sexual partners without establishing stable bonds. Of course, polygynandry does not imply an equal distribution of reproductive opportunities. High-ranking individuals are favored, even though reproductive exclusivity (harem-like) is absent.

ancestor that most likely lived in stable societies with patrilineality and male patrilocality, marked by the high degree of uncertainty about the privileges and limits concerning each of the members of the social group. The relative simplicity of gorillinian harem hierarchies - in which male reproductive dominance was clear, monocratic, and subalternity was a common condition to all other members of the group - was replaced by a kind of intragroup "systemic chaos", in which multiple echelons in the hierarchical pyramid emerge, and the constant struggle for social ascension (masculine, especially) becomes widespread. This could have represented a favorable context for the dissolution of permanent sociability (given the potential for intragroup aggression), but in the lineages descending from the LCA<sup>12</sup>, the survival of patrilineality ended up guaranteed by the emergence of this modular, high-cost social cognition, that coincides with the expansion of brain allometry in the Panini (the chimpanzee lineage of species, extinct and extant) and Hominini (all bipedal anthropoids emerged after the divergence with the first chimpanzees), when compared to the older anthropoids in the evolutionary tree.

The emergence of mental modules dedicated to the management of social relationships means that the stereotyped and generalized cognitive mechanisms produced at low cost by general intelligence have become insufficient to generate effective responses in a context of excessive "moving parts" (information) in social mechanics. The focus of modularity is not on its innate content, but on the ability to formulate testable hypotheses about the behavior of third parties, involving or not the presence of the observer. It is an extension of the cognitive complexes linked to the so-called "theory of mind" (ToM) present in different degrees of complexity throughout the Primate family. The ability to assess mental states is based on the modelization of reactions the subject would expect of himself if hypothetically immersed in a certain situation being observed but experienced by others, something that involves a reasonable degree of empathic skills. The extrapolation of these

hypotheses must be calibrated according to the object's individual temperament (which is previously known, by definition) and to the circumstances of the action; the use of generic, standardized learning rules for strategic social decision-making, in the conditions of complexity present in these post-harem anthropoid societies, would result in a high probability of error.

It is difficult to support the idea that in the lineages of humans and chimpanzees, sociability is the product of social learning. Chimpanzees can be taught by humans to perform tasks in captivity that in their natural habitats would not be developed, since they do not fulfill any relevant evolutionary role (sign language and the production of lithic tools are two good examples). For such activities, chimpanzees employ their general intelligence, which functions as a kind of multi-purpose learning tool, producing simple results after some trial and error, but at low energy cost. As far as modularized social behavior is concerned, there is very little that can be taught to a chimpanzee, or that they should teach one another: even individuals born in captivity intuitively develop, at the right age, the social skills necessary for the intense "machiavellian" status games, which demonstrates their innateness. Thus, dedicated mental modules, that enable an individual to understand the functioning of social hierarchies and to devise status strategies, emerge with age, just like definitive teeth.

The modularity of social cognition seems to allow chimpanzees to develop some form of self-awareness, something suggested by mirror recognition tests. However, circumscribed to the scope of ethology, this awareness is far from equivalent to the *self*, the transdominial and transmodular holistic consciousness that only recently emerged in the evolutionary history of *Homo sapiens*. The modular social intelligence in chimpanzees seems isolated from the general intelligence, unable to interact fluidly with other non-modularized cognitive domains, so that these great apes become aware of themselves and of others only as social actors, and in the universe of social relationships. There is no substantive evidence of

<sup>12</sup> Last common ancestor to humans and chimpanzees.

the use of material culture - related to the technical aspects of the general intelligence - for leverage in status disputes. There is not yet any symbolic dimension of material culture that is instrumentalized in order to transmit social information, to signal the hierarchical locus occupied by an individual, or to disguise the occupation of a lower echelon in the stratification pyramid. With the modular social mind incapable of accessing other cognitive domains, and placing them at its service, chimpanzees do not seem capable of complex mental simulations regarding foraging or tool-use issues, involving conspecifics. The general intelligence operates unconscious domains, incapable of producing mental perceptions and self-representations. This condition, though highly derived when comparing chimpanzees to other primates, is primitive in view of the cognitive transdominiality of modern humans.

Despite its insularity, the social modular mind has allowed the establishment of innate patterns and ritualistic norms in the struggle for intragroup power. From the behavior of chimpanzees in natural habitat, we know that these dominance clashes between two adult males can last for many months, and can be marked by intense demonstrations of agonism. It is common for the contestant male refusing to perform rituals of submission to the dominant male, rituals that are regularly attended by the other members of the group, as a form of reassertion of loyalty bonds, recognition of their place in the hierarchy, and stability of the social body. These loyalty rituals involve body postures and gestures, such as bowing down before the dominant male, or demonstrating what some primatologists call a "scared smile." As part of their power-signaling repertoire, dominant males tend to touch the shoulder of lower-status chimpanzees, and being touched this way is something that a contestant male tends to avoid at all costs in his struggle for ascension. These displays of intimidation, aggressiveness, and power are closely watched by all members of the group, who, over time, tend to give their support to one side or the other.

As the estrangement between factions builds

up, daily coalitions for specific tasks - foraging, grooming <sup>13</sup>, etc. - tend to become more volatile. Both the dominant male and his challenger seek to intimidate the females of the group, forming alliances with different subaltern males. What the disputants seek is the political support of the females themselves. The struggle for support is also reinforced by the increase in social time spent with each female and her offspring, through the practice of grooming. Allied subaltern males tend to help in keeping oppositionist females at bay, denying them the opportunity for hindering the adversary's efforts of socialization and support-gaining. What these lower-ranking males seek, therefore, is to climb steps in the hierarchy in virtue of the eventual victory of their "candidate", something that should provide increased reproductive advantages to them. In the end, after intense struggle for dominance, all the members of the group tend to converge to support one of the competitors, isolating the other. From there, the demonstrations of agonistic behavior on the part of the victorious male tend to slow down; the leader takes a conciliatory and pacifying stance, mediating conflicts between females and assisting weaker or less prestigious males against stronger opponents. At some point the process of contesting the hierarchy resumes, which often involves radical recomposition of alliances.

Provoked by the breakdown of harem dominance and by the preservation of male patrilineality, is the high degree of social uncertainty caused by the expansion of group size, the main reason for the development of an intuitive ethics in the lineages departing from the LCA to humans and chimpanzees? Functioning as a genuine prosocial ethological restrain, it rules the procedures of internal dispute for power, reduces the degree of male interpersonal violence (although it does not eliminate it), and establishes when and how a struggle cycle ends. Unlike chimpanzee cultures,

<sup>13</sup> Grooming is an important social ritual among primates. Its primary purpose lies on removing parasites and dirt, for hygiene purposes. However, the role of grooming as a social act transcends that dimension, functioning as an important instrument for tightening affective bonds.

with socially transmitted practices and behaviors (by observational learning) exclusive to certain groups, a common core of sociability parameters and internal conflict resolution emerges innately in all groups of chimpanzees, in nature or in captivity (Aureli et al., 2008: 632; 636-637; Bauernfeind et al., 2013: 263-264; 271-273; Foley, 2008: 207-210; Mithen, 2002: 67-71; 102-111; 126-131; 139-142; Nordhausen, Oliveira Filho, 2015: 36-38; Wrangham, Peterson, 1996: 128; 143-144; 186)

### 9. Intersocietal conflict and exhaustion of social cognition

If the development of social cognition results in innate ethical standards in intragroup relations, intersocietal relations are precisely characterized by the absence of ethological restraints and rules concerning the management of social hierarchies. Among the common chimpanzees (*Pan troglodytes*) and, probably, the LCA, contact between social groups is restricted to coalitional violence aimed at eliminating foreign males, abducting fertile females, and disarticulating enemy communities. There are no cognitive mechanisms of pacification or containment of the lethal conflict between these societies.

Social groups occasionally split after struggles for dominance in the internal sphere. Socioenvironmental limits are exerted over the cohesion of chimpanzees groups, something that involves a delicate balance between spatial distribution of natural resources and demographic factors. When these limits are exceeded, and a new cycle on the struggle for power begins, the breakup of the social macro-unit may be the result. One indication that political struggle may cause secession comes from the group segmentation into factions of relationship: the tendency to alternate partners in foraging and grooming gives way to more limited and repeated choices, with individuals reinforcing their social ties more often with certain partners than with others. As defections normally conclude a dominance struggle, with one of the competitors being abandoned by its supporters and progressively isolated by a growing

majority, another important sign of secession in progress lies in the sustained allegiance of factions to their leaders. Then, the social fracture becomes visible in the very configuration of group spatiality: each faction, although inhabiting the same localities, will tend to rest apart from each other. Division goes on with the separation of distinct foraging grounds to each of the cliques, a situation considered of paramount importance in the secession process.

Being separated the two social units with their respective dominant males and hierarchical pyramids, small temporary subgroups will be formed in short time to fulfill daily tasks. One of these (not so daily) tasks consists in the exercise of intersocietal coalitionary violence. Incited by the dominant male (in most cases) through gestures and vocalizations, companies of adult males can be formed and march to the territory of the "enemy" group, sometimes accompanied by one or two nulliparous females. These initiatives are neither defensive measures or reactive patrols, nor byproducts of foraging expeditions. Leaving rich opportunities for obtaining food behind, these companies march with the sole purpose of bringing lethal violence to the "other." Before raids begin, signals of the opponent's presence (sounds in particular) provoke anxiety, only controlled by gestures that ensure trust and loyalty among fellow chimpanzees (touches, hugs). As we know, the ecological conditions in which chimpanzees live (and the LCA have lived, we presume), with scattered nutritional resources, leads to the temporary fission of permanent groups for the practice of foraging, and this fact creates the opportunity awaited by an aggressive band: to catch a lonely and unwary enemy male, distracted while feeding. Unlike warfare among human nations, chimpanzee clashes are necessarily asymmetric. With an erroneous assessment of circumstances that eventually results in contact between a company and a numerically equivalent group of enemies, the raids are always aborted, and the attackers flee in hurry, back to their homeland.

But if the situation is propitious, the companies of males are able to cooperate efficiently to isolate

and lead the opponent to death. If more than one opponent is found, and the numerical advantage remains unequivocal for the attackers, the raid may continue with the tactic of isolating the enemy, denying them the opportunity to cooperate. Nulliparous females and young males accompanying the raiding party usually just observe all the action without engaging in it. Incursions ends after the opponent's death, and may involve peculiar ethological demonstrations, such as the emasculation of dying enemies or the consumption of their blood. Retreat to home territory does not occur before some coercion (non-lethal violence and intimidation) has been made on enemy young females (if available), in order to convince them to join the victorious party. The abduction of females happens either by their (forced) migration or the incorporation of their foraging territory, as soon as there are few enemy males capable of defending it. In a postharem society with male patrilineal cooperation, the incorporation of new females into the social macrounit ensures that all males engaged in intersocietal coalitional violence may find opportunities to enhance their reproductive fitness in some degree, if they cooperate. The reproductive dimension of coalitional violence also gains visibility through the practice of infanticide after abduction: the first offspring born to newly incorporated females tends to be killed by males, while subsequent generations are preserved. In a polygynandrous regime, there is no guarantee of paternity, and this fact tends to restrain male attacks against infants; but in the case of the absorption of foreign females, the possibility of alien paternity for the first generation is reasonable, and infanticide aims to ensure the "purity" of the patrilineal genetic community.

Lethal aggression is not exactly a rare ethological phenomenon among mammals, but the lion's share in such cases involves infanticide or the dispute over scarce natural resources, both practiced on individual level. In reproductive competition, interpersonal duels are equally common, and can result in lethality. In ethological terms, lethal aggression among adults is a very costly behavior: in circumstances of

symmetry of power, it can result in the death of the victim or/and of the aggressor. Thus, lethality can be ethologically fixed as agonistic behavior when: 1) it increases the reproductive fitness of the aggressor; 2) it occurs under risk-controlled conditions. This is the rationale for infanticide, arguably the most common category of lethal violence: the risks involved will be null if infants are not protected by highly dimorphic females (which is not the case among anthropoids), by dominant males in harems or by the cooperation of multiple males in social regimes such as those of chimpanzees. Thus, what makes intersocietal coalitional violence follow the way of lethal aggression is precisely the imbalance of power, the asymmetry involved in the cooperative tactic. Ethologically, the balance of power is an effective mechanism of deterrence, and what male coalitions do is exactly breaking this equilibrium. Considering that chimpanzee raiders rarely suffer any harm, the physical elimination of competing males can bring advantageous fruits in terms of the reproductive agenda for the cooperative victors.

But can the intersocietal relations among our closest evolutionary relatives be subject to the ethology of conflict resolution, to that intuitive ethics we are talking about? Was the LCA able to behave, in the intersocietal universe, guided by cognitive instruments of violence management? In the context of a modular social intelligence - an exemplary mechanism for ordering relationships in an intragroup systemic chaos - there are clear limits related to brain capacity. Encephalization quotient <sup>14</sup>, neocortical volume, the demography of the groups, and grooming time are associated variables. When the volume of social information produced by the increasing number of simultaneous relationships exceeds the processing limits of the modularized mind, coordination and cooperation become less and less viable. So, the larger the groups, the more social time is needed to strengthen the bonds. In these terms, greater will be the demand on the

<sup>14</sup> The encephalization quotient expresses the ratio between mean brain volume and the expected volume for the brain in isometric (proportional) conditions with the rest of the body.

cognitive apparatus to collect information on the status of others, in order to build hypotheses about the social ascension strategies. The overload of social information makes most of the efforts to status assessment vague, creating an anomalous situation in which the instruments of conflict management lose effectiveness. Factionalism gradually emerges in the groups in response to the inability to identify correctly the status of once close individuals. As the demand for mental processing intensifies beyond the cognitive capacity of these primates, cognitive tools will continue to be pressed, something that results in pathological behavior and psycho-emotional suffering. The definitive fission of the macro-unit then acts as a homeostatic phenomenon, bringing the pressure over social mental modules to equilibrium. Once split, the two newly formed groups will have brought their demographic contingent to cognitively manageable limits back. (Aielo, Dunbar, 1993: 184-185; Aureli et al., 2008: 627; 637; Bauernfeind et al., 2013: 275-276; Ferguson, Beaver, 2009: 291; Mithen, 2002: 140-141; Wrangham, Peterson, 1996: 5-18; 158-159; 162-170; 179).

# Final considerations: the ethics of warfare is an apomorphic condition in *H. sapiens*

Since the LCA, chimpanzees and most of the hominins would be unable to incorporate their intersocietal relations into the field of intuitive political ethics, something that makes the most recent developments in recent evolutionary history of H. sapiens quite unusual: the emergence of behavioral modernity, of transdominial consciousness and of abstract thought, about forty thousand years ago. In this long evolutionary trajectory since six millions years ago, classifying an conspecific as "foreigner" is a product of the disposal of excessive social information. The "other", once disconnected from a social macro-unit, does not occupy any place in the internal hierarchy, and ceases to be the object of innate cognitive processes dedicated to conflict management. Somatic signals displayed by chimpanzees facing the "enemy" suggest that,

unlike their ingroup fellows, aliens are treated as game animals. In an act of intersocietal coalitionary violence, aggressors make vocal and gestural signals that coincide with the act of pursuing an escaping prey. "Dechimpization", that is, the cognitive process of re-signifying the nature of a chimpanzee conspecific, is something that seems to be universal and ethological in the lineages departing from the LCA, and not a socially learned procedure to control an supposedly innate aversion to murder. If so, it should be restricted to certain groups of chimpanzees, as are the various facets of material culture in this species. Reframing the alien's condition functions as an ethological artifice aimed at triggering responses from the sympathetic nervous system associated with the exercise of lethal violence, such as in hunting, and this is in no way related to any defensive reaction. Chimpanzees are able to ignore the presence of other potentially dangerous primates, such as baboons, with which they occasionally compete for food. The presence of these primates does not trigger ethological reactions associated with intersocietal coalitionary violence, despite the fact that they pose a real potential threat. The baboon is not the enemy, but a chimp belonging to another social macro-unit is.

It is symptomatic that the foreigner represents the uncertainty in its highest degree, since it belongs to the universe of the "non-social", absent either from the base and from the top of the pyramid, ignoring both dominance and submission. Being impossible to identify its hierarchical locus, there are no possible strategies to be planned concerning him, making social modular cognition useless. Averse to order and representing the outer chaos of a world devoid of instruments of conflict management, to aliens only annihilation is due, and to their females, the opportunity to be integrated in the universe of ethologically controlled social relations. Since primates rely on sensory mechanisms for identifying consanguinity - something that belongs to the personal unconscious in human mind, as potentially suggested by the Oedipus myth - we are invited to ponder about how strong environmental

and cognitive pressures must be in leading to the breakup of patrilineal communities and to the "dechimpization" (or dehumanization) of the "other", with whom, once, kinship relations were recognized. When lethal violence comes to the intersocietal stage, it represents, somehow, ethological-sanctioned fratricide, in complex and unstable equilibrium with the very exercise of cooperative patrilineal sociability (Mithen, 2002: 308-309; Ferguson, Beaver, 2009: 287; Roscoe, 2007: 485-486; 491).

These cognitive mechanisms of intragroup conflict management (which, in the interaction between the transdominial consciousness, the personal unconscious and the vast ethological universe of the collective unconscious, would be called "ethical thought" in *H. sapiens*) are symplesiomorphic <sup>15</sup> in humans and chimpanzees, and subject to disruptions of pathological nature. Likewise, the capacity for intersocietal coalitionary violence (with claws, teeth, swords or nuclear weapons) seems to manifest itself as a symplesiomorphic condition in these two lineages departing from the LCA. What seems to be clearly apomorphic <sup>16</sup> is the ability of *H. sapiens* to have an ethics of warfare, the power to formulate abstract norms that determine the limits and parameters of the exercise of intersocietal violence, and, eventually, denying this own violence. Nonetheless, pacifism and the norms of warfare, in this case, seem far from being an ethological condition, deposited in the human collective unconscious: they depend exclusively on the exercise of transdominial consciousness. On the other hand, intergroup violence and dehumanization, although strongly opposed by domains of the conscious mind, find firm rest in the recesses of the collective

unconscious, inherited from a turbulent evolutionary past.

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<sup>15</sup> Symplesiomorphy is a primitive characteristic shared by two or more species that is not crucial to define any of these species in particular. *H. sapiens*, for example, has no tail, such as gorillas; therefore this is not a condition that defines modern humans or gorillas.

<sup>16</sup> Apomorphy is an innovative characteristic present in a particular species, that makes it differs from all its ancestors. Bipedal locomotion is probably an apomorphy in the lineage of the hominins, that makes them distinct from their last common ancestor with chimpanzees (and from chimpanzees themselves).

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