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# THE EVOLUTIONARY ORIGINS OF KINSHIP STRUCTURES

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*Patrilineal kinship structures are among the most complex manifestations of the impact of kinship on human social life. Despite the fact that such structures take highly diverse forms across cultures, that they are absent in many human societies and, moreover, that they are not observed in other primate species, a comparative analysis of human and nonhuman primate societies reveals that human kinship structures have deep evolutionary roots and clear biological underpinnings. I argue here that the first patrilineal kinship structures came into being as the emergent products of the combination, in the course of human evolution, of ten biologically grounded components, seven of which are observed in our closest relative, the chimpanzee, the remaining three being consequences of the evolution of pair-bonding in humans. This indicates that contemporary patrilineal kinship structures are not cultural creations, but cultural constructs that built upon, and diversified from a rich biological substrate. The same reasoning applies to many other complex human kinship phenomena, such as marital arrangements. I conclude that models and theories from cultural anthropology must be compatible with the relevant biological evidence.*

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## **Introduction**

There seems to be a growing appraisal by cultural anthropologists that some of the most basic kinship features that humans share with other primates, such as kin groups, kin recognition, the tendency to favor one's kin, incest avoidance, and many others, reflect our common evolutionary history and biological heritage with those species (e.g., Godelier 2004; Jones 2004, 2010; Hill et al. 2011; Shenk and Mattison 2011; Trautman et al. 2011; Elsworth and Walker 2014; Schenk 2014; Hames, 2014; Stone 2014). Here I argue that primate studies not only help us understand the origins of kinship features that we actually *share* with other primates but, somewhat counter-intuitively, that they also shed light on the origins of complex kinship traits that other primates do *not* necessarily exhibit; traits that are uniquely human, such as patrilineal kinship structures. As will be shown, these traits may be explained as emergent products of the combination of more

elementary features present in other primates but not necessarily in the same species, that is to say, the combinations are uniquely human, but not the components. Fox (1975, 1980) made a similar argument when he reasoned that the two fundamental components of human kinship systems – kin groups and alliance (stable breeding bonds) – were present in other primates but not together in the same species. We now know that other primates, such as *Hamadryas* baboons, do combine the two features (Rodseth et al. 1991), but Fox’s principle is still very much relevant as I shall argue here in relation with other kinship traits.

The reasons I focus on patrilineal kinship structures are threefold: they are among the most complex manifestations of the impact of kinship on human social life, they illustrate the potency of kinship in generating group-level social structures, and they occupy a preponderant place in the anthropology of kinship (e.g., Stone 2014). Moreover, patrilineal kinship structures are not cross-culturally universal and like any other complex social phenomenon they exhibit a great deal of formal and semantic cultural variation. Thus, establishing that such structures have biological underpinnings should help dissipate the deeply erroneous idea that biologically-grounded social phenomena must necessarily be cross-culturally universal and uniform and, hopefully, it would constitute a strong case for integrating biology in the anthropology of kinship.

A kinship structure, whether patrilineal, matrilineal, or bilineal, is defined here as a consistent pattern of social relationships mapping a genealogical structure, regardless of whether the kinship structure itself is recognized as an entity or not. Social phenomena meeting that definition are observed in some primate species and their analysis offers a model of the conditions required for the evolution of matrilineal kinship structures, which in turn provides a phylogenetic model for the emergence of patrilineal kinship structures in humans. The present definition of kinship structure implies that human kinship systems were born as pedigree-based social networks whose members were, by definition, biological kin. This in turn means that the ethnographically well documented facts that kin terminologies commonly lump individuals differing in their degree of kinship in relation to ego or, on the contrary, separate kin who share similar degrees of relatedness (e.g., parallel and cross-cousins) are subsequent cultural outgrowths of genealogical substrates. As discussed below, the evolution of human cognitive abilities would have made it possible to conceptualize the criteria already used by nonhuman primates to differentiate their kin, which would have led to the advent of classificatory kinship, among other things. It follows that the genealogical grid cannot be dissociated from the analysis of human kinship (e.g., Schneider 1984; Read 2007, 2014).

### **Matrilineal Kinship Structures in Primates**

Humans form large multimale-multifemale groups containing up to four generations of individuals, a composition that maximizes the diversity of kin types from ego’s perspective. Multimale-multifemale groups are also found in nonhuman primates. They may be divided into two categories according to their dispersal pattern, *female philopatry* or *male philopatry*. In female philopatric species, females stay and breed in their natal group, whereas males leave around puberty to breed in other groups. This dispersal pattern pro-

duces spatially localised and relatively extensive matrilineal lines containing three generations of individuals (rarely four), but small patrilineal lines because males leave their fathers' group. Reciprocally, in male philopatric species, the males stay put and the females leave, a pattern generating, this time, localized and relatively extensive patrilineal lines, but small matrilineal lines. Dispersal patterns thus determine which kin live together and have opportunities of recognizing each other. The word 'recognize' here neither means that nonhuman primates perceive genetic relatedness *per se*, nor that they necessarily conceptualize kin categories; it simply means that they interact preferentially with certain individuals, based on their kinship relation with them. For example, mothers are inferred to recognize their daughters based on the observation that they direct prosocial behaviors (approaches, vocalizations, lactation, ventral and dorsal transport, grooming, protection against aggressors, tolerance at food sites, and so on) at higher rates than they do so with less closely related, or unrelated individuals. Kin recognition thus refers to the differential treatment of individuals belonging to different kin categories.

A few definitions are useful at this stage. A *lineal* kinship relationship is a chain of parent-child links connecting two individuals either through the maternal line only (*maternal* kin) or the paternal line (*paternal* kin), in which one individual is ancestral to the other. A *collateral* relationship is a chain of parent-child links connecting two individuals, neither of whom is ancestral to the other. The *genealogical distance* between two kin is the number of parent-child links separating them, for example two links between grandmothers and grandchildren (lineal distance), and three links between aunts and nieces (collateral distance). Following Murdock (1949), I differentiate between ego's *primary kin* (ego's parents, children and siblings), *secondary kin* (the primary kin of ego's primary kin, such as ego's grandparents, uncles and nieces), *tertiary kin* (the primary kin of ego's secondary kin, such as great-grandparents and cousins), *quaternary kin* (the primary kin of ego's tertiary kin, such as second-degree cousins), and so on. Finally, the expression *domain of kin recognition* refers to the set of differentiated kin types from ego's perspective

Observational studies reveal that male philopatric species such as our closest relatives, chimpanzees and bonobos, exhibit small domains of kin recognition. Although males live with their paternal kin the available data indicate that the recognition of paternal kinship is absent or extremely fragmentary in those societies. In chimpanzees father-offspring recognition is inconsistent at best (Chapais 2008, in press; Langergraber 2012), which is not surprising given that chimpanzees are highly promiscuous sexually. If individuals cannot recognize their father on a consistent basis, it is unlikely that they recognize their father's kin, such as their paternal grandfather, uncles and cousins (Chapais 2008). Genotypic studies reveal that they do not recognize their paternal half-siblings either (Langergraber et al. 2007). In female philopatric species, by contrast, maternal kin recognition is rather extensive. Empirical studies (reviewed in Chapais 2008) show that females interact differently with their maternal kin depending on whether (1) ego's kin is a male or a female, (2) the actor, ego, is a male or a female, (3) ego is younger or older than its kin, (4) ego's kin belong to an ascending (senior) or descending (junior) generation, (5) the lineal distance between ego and its kin is different, and (6) the collateral dis-

tance between ego and its kin is different. The effect of each factor on how ego treats its kin is best appraised when all other criteria are held constant.

The effect of whether ego's kin is a male or a female is evidenced by the observation that ego interacts differently with its brothers and sisters for in this comparison all other factors are constant: ego's brother and sister are collateral kin belonging to the same generation, separated from ego by the same genealogical distance, and having similar ages (averaged over many dyads).

The effect of ego's sex on how ego treats its kin is illustrated by differences in how a male and a female interact with a sister, in which case, the two dyads (brother-sister and sister-sister) are collateral kin belonging to the same generation, sharing the same genealogical distance and having similar age differences on average.

Differences in how a female interacts with a younger sister and an older one illustrates the effect of ego's age relative to its kin. In this situation, the two types of sister dyads are collateral kin of the same sex belonging to the same generation and sharing the same genealogical distance.

Differences in how an adult female interacts with her mother and her daughter shows that she differentiates between individuals belonging to an ascending (senior) or a descending (junior) generation. To ego, both individuals are lineal kin of the same sex and same genealogical distance. They differ in age, however, which makes it possible that ego's differential treatment might reflect the effect of age rather than generation. This is highly unlikely, however, given that ego has a filial relationship with her mother and a parental one with her daughter, which points to the effect of generation *per se*.

The effect of genealogical distance between lineal kin is exemplified by differences in how females interact with their mother (1 parent-child link) and with their grandmother (two links), and by differences in how they interact with their daughter (one link) and granddaughters (two links). To ego, all those individuals are lineal kin of the same sex. But note that those behavioral differences may also reflect the effect of belonging to an adjacent or a nonadjacent generation in relation to ego (whether ascending or descending).

Finally, the effect of genealogical distance between collateral kin is exemplified by the observation that females have much higher rates of prosocial behavior with their sisters than with their female cousins. From ego's perspective, sisters and cousins are collateral kin belonging to the same sex, generation and age group, but while sisters are separated from ego by two parent-child links, cousins are by four.

The fact that those factors affect how nonhuman primates interact with their kin does not imply that animals conceptualize sex differences, relative age, ascending versus descending generation, lineal distance, and collateral distance. It means, minimally, that they use proxies, behavioral or phenotypic, that correlate with those factors. The upshot is that in female philopatric species a female recognizes a substantial fraction of her coresident maternal kin, including, her sisters, brothers, mother, daughters, sons, grandchildren, great-grandchildren, grandmother, greatgrandmother and, less systematically, her aunts and nieces, whereas her cousins and other collateral relatives are treated as nonkin (Chapais 2008). In other words females recognize their primary kin, some of their secondary

kin, but usually not their tertiary kin. The recognition of maternal kin stems from the existence of lifetime bonds between mothers and daughters and appears to involve primarily familiarity and association-based processes (Rendall 2004). In those species young females come in contact with their sisters, grandmothers, aunts and other kin types on a regular basis thanks to the enduring bonds their mothers maintain with those kin. The mother's mediation sets in motion at least two distinct and complementary processes likely involved in kin recognition (Chapais 2008). First, because the mother spends different amounts of time in proximity with her own mother, sisters, nieces, and so on, her daughter accumulates different levels of developmental familiarity with each of those kin, which roughly match her degrees of genetic relatedness with them (Chapais 2001; Chapais and Bélisle 2004). At the same time the daughter is in a position to learn the specific characteristics of the relationships her mother maintains with her various relatives in terms of degree of proximity, grooming rates, willingness to protect them against certain individuals, and so on. The capacity of nonhuman primates to recognize the relationships of others – i.e., for ego to recognize the relationship between two other individuals – is well documented (Cheney and Seyfarth 2004; Seyfarth and Cheney 2012). Importantly, both processes of maternal kin recognition require mothers and daughters to maintain lifetime bonds with each other.

The spatial localization of females and the differentiation of kin types in female philopatric species translate into the existence of patterns of social relationships that map the genealogical (matrilineal) structure; in other words, they produce kinship structures. Social relationships in nonhuman primates are manifested in recurrent patterns of interactions between females involving the maintenance of proximity, bilateral grooming, co-feeding (tolerance at food sites), protection against aggressors, coalitions, conflicts over resources and access to social partners, reconciliation, and dominance relationships (Mitani 2009; Silk 2010). For reviews of the influence of maternal kinship on behavior in primates, see Paul and Kuester (2004); Silk (2009), Berman (2011), Langergraber (2012), and contributions in Chapais and Berman (2004).

A particularly salient manifestation of matrilineal kinship structures in many philopatric primate species is that maternal kinship determines the structure of the dominance hierarchy. The influence of kinship is so preponderant that knowledge of the genealogical structure makes it possible to predict the dominance rank of all females. In those species a female comes to rank immediately below her mother. As a result, matrilineal lines are ranked in relation to each other (Chapais 1992, 2004). Sons may also inherit their mother's rank initially, but they cannot transmit it to their offspring if only because they leave their natal group at puberty. The transmission of status is thus a unisexual/unilineal process, with the sons being excluded from the line of descent. It is also a social, not a genetic, process, which involves a consistent pattern of maternal favoritism, with mothers supporting their daughters in their conflicts against lower ranking females. In some species, mothers also support their younger daughters against older ones so that the former outrank the latter around puberty. This determines rank relations between aunts and nieces and between cousins.

A further aspect of matrilineal kinship structures in female philopatric groups is that the latter typically split when they become too large, which suggests that group fissions help reduce feeding competition. When groups split they do so along maternal kinship lines (Chepko-Sade and Sade 1979; Okamoto 2004; Di Fiore 2012). A simple explanation is that members of a matriline or sub-matriline are strongly bonded to each other so they tend to leave together. This results in the formation of two maternal kin groups, as first remarked by Fox (1980).

Matrilineal kinship structures thus exhibit the following components: (1) a multi-male-multifemale group composition maximizing the domain of maternal kin recognition; (2) a pattern of female philopatry and male dispersion producing spatially localized matriline, with this resulting in (3) the female kin group being the outbreeding unit; (4) lifetime bonds between mothers and daughters, which is a necessary condition for (5) the operation of familiarity and association-based mechanisms of kin recognition centered on the mother as a point of reference; (6) the occurrence of various types of cooperative activities among females, such as grooming and alliance formation; (7) kinship biases in the patterning of those cooperative activities; (8) status differentials between females in the form of stable dominance relationships; (9) the transmission of status from mothers to daughters; and (10) a pattern of group fission along maternal kinship lines, or matriline segmentation. Table 1 summarizes the ten components.

This analysis provides a *primate model* of kinship structures, according to which some sort of matrilineal kinship structure is bound to emerge in any primate species meeting those conditions, including hominins. The general character of that model lies in the nature of its components. Three of these (components 1, 6 and 8) are phylogenetically primitive and rather common features of primate societies that are neither specific to kin-

**Table 1: Components of Matrilineal Kinship Structures  
in Female Philopatric Primate Species**

- |    |  |
|----|--|
| 1  | Multimale-multifemale group                  |
| 2  | Spatially localized matriline                |
| 3  | Female kin group as outbreeding unit         |
| 4  | Lifetime mother-daughter bonds               |
| 5  | Familiarity-based kin recognition mechanisms |
| 6  | Cooperative activities among females         |
| 7  | Kinship biases in cooperation                |
| 8  | Female dominance relationships               |
| 9  | Maternal transmission of status              |
| 10 | Group fission along maternal kinship lines   |

ship, nor restricted to primates.

Four other components are specific to kinship and reflect directly what may be called the *intrinsic properties* of kinship (properties that apply to animals in general). Three of these properties are that kinship determines social motives, engenders genealogical structures, and is a permanent characteristic of dyadic relations. The first property is now overwhelmingly documented throughout the animal kingdom: kinship promotes prosocial behavior between relatives. Kin selection theory is the primary mechanisms involved. Briefly, when a female unilaterally protects a kin against an aggressor or a predator, she does not gain any direct (personal) benefits, whether immediate or delayed. On the contrary, she incurs costs, but by reducing the likelihood that her kin will be wounded or killed, she obtains indirect fitness benefits amounting to a fraction of the direct benefits accruing to her kin, that fraction being determined by their degree of genetic relatedness. In addition to explaining unilateral and bilateral altruism between relatives, kin selection may also explain why cooperation (including reciprocity) is frequent among relatives. When a female cooperates with a kin she benefits in two different ways: she obtains the direct (personal) benefits of the cooperative act – as she does when interacting with a nonkin – and she also derives the indirect fitness benefits previously mentioned (Wrangham 1982). Thus, others things being equal, such as the relative competence levels of potential partners (Chapais 2006), cooperation between kin pays more than cooperation between nonkin. This first property of kinship accounts for component 7 and 9 of matrilineal kinship structures (Table 1). It is worth recalling that the prosocial property of kinship does not imply that kinship should engender cooperation between kin irrespective of circumstances – that it is deterministic. It means that kinship is a prosocial factor interacting with several other variables, such as residence patterns and types of descent, which markedly affect the availability of kin as social partners and hence whether or not certain kin will engage in cooperative activities.

The second intrinsic property of kinship is that sexual reproduction produces chains of parent-child links, or genealogical structures, in which individuals are connected to each other either lineally or collaterally. When this property combines with sex-biased philopatry, in this case female philopatry, it generates spatially localized matrilineal structures (component 2).

The third intrinsic property of kinship is that it is, by definition, a permanent (lifetime) characteristic of the relation between two individuals. This property, in combination with the first one (kinship promotes prosocial behavior) entails that kinship has the potential to create enduring biases in altruism and cooperation between individuals, provided the latter recognize each other as kin and have opportunities of interacting with each other on a regular basis. In other words kinship promotes the formation of long-term dyadic social relationships. This property explains component 4.

The last three components of matrilineal kinship structures are correlates or consequences of other components. Component 3 (female kin group as outbreeding unit) is a direct consequence of female philopatry and male dispersal. Component 5 (familiarity-based, mother-centered kin recognition) results from the interplay of lifetime mother-daughter bonds with the cognitive abilities allowing primates to utilize their mother as a mediator of social interactions. Finally, component 10 (matriline segmentation) results



from interactions between a multimale-multifemale composition, increases in group size, and kinship biases in prosocial behavior (property 1).

In sum, matrilineal kinship structures, as they are defined here, appear to be emergent and contingent products of the co-occurrence in the same species of a limited number of components stemming from the intrinsic properties of kinship, or reflecting basic primate behavioral adaptations. Matrilineal kinship structures, therefore, existed well before they were conceptualized and recognized as such.

### **The Origins of Patrilineal Kinship Structures**

Structurally speaking, patrilineal kinship structures are the mirror image of matrilineal structures. One may thus expect patrilineal kinship networks to emerge whenever the ten components of matrilineal structures, adjusted for sex, co-occur in the same species, namely: (1) a multimale-multifemale group composition maximizing the domain of paternal kin recognition; (2) a pattern of male philopatry and female dispersion producing spatially localized patrilineal kin groups, with this resulting in (3) the male kin group being the outbreeding unit; (4) lifetime bonds between fathers and sons, which is a necessary condition for (5) the operation of familiarity and association-based mechanisms of kin recognition centered on the father as a point of reference; (6) the occurrence of various types of cooperative activities among males, such as grooming and alliance formation; (7) kinship biases in the patterning of those cooperative activities; (8) status differentials between males in the form of stable dominance relationships; (9) the transmission of status from fathers to sons; and (10) a pattern of group fission along paternal kinship lines, or patrilineal segmentation (Table 2).

As pointed out earlier, patrilineal kinship structures are not observed in other primates, they are uniquely human. Remarkably, however, our closest relatives, chim-

**Table 2: Components of Hypothetical Patrilineal Kinship Structures in Male Philopatric Species**

- 1 Multimale-multifemale group
- 2 Male philopatry and female dispersion
- 3 Male kin group as outbreeding unit
- 4 Lifetime father-son bonds
- 5 Familiarity-based kin recognition mechanisms
- 6 Cooperative activities among males
- 7 Kinship biases in cooperation
- 8 Male dominance relationships
- 9 Paternal transmission of status
- 10 Group fission along paternal kinship lines

panzees and bonobos, exhibit seven of the ten components. The three ones missing (com-

ponents 4, 9 and 10) all stem from the same source: a mating system based on sexual promiscuity. In the absence of stable breeding bonds fathers and children cannot recognize each other on the basis of their common association to the same female and hence cannot form lifetime bonds (component 4). Such bonds in turn are a necessary condition for the paternal transmission of status (component 9). Were chimpanzees forming stable breeding bonds, and considering that males establish stable dominance relationships, fathers would be in a position to help their sons in their conflicts against lower-ranking males – as females help their daughters in female philopatric species –, a situation conducive to the formation of patrilineal status hierarchies, the analogue of matrilineal dominance systems.

Similarly, lifetime father-child bonds are a necessary condition for the recognition of paternal kinship, without which group fissions cannot proceed along paternal kinship lines (component 10). Like other primates, chimpanzees differentiate their coresident maternal kin using the same (if not cognitively more sophisticated) familiarity and association-based mechanisms of recognition centered on the mother. Males recognize their mother and maternal siblings but, owing to female dispersal, they are usually not in a position to recognize their mother's kin, nor their sisters' children (Chapais 2008, in press; Langergraber et al. 2009). Interestingly, however, anecdotal evidence indicates that when a female fails to emigrate and hence reproduce in her natal group, her sons may develop preferential bonds with their maternal grandmother and maternal uncles (Goodall 1990). Taken together this evidence suggests that if chimpanzees could recognize their father they would be able to recognize some of their father's kin through the same types of association-based processes females use to recognize their mother's kin in female philopatric species (Chapais 2008). Given that group fissions have been observed in chimpanzees (Goodall 1986; Wilson and Wrangham 2003), one may speculate that the recognition of paternal kinship would translate in those fissions proceeding along paternal kinship lines (patriline segmentation), for the same reasons they take place along maternal kinship lines in female philopatric species. Group fissions along paternal kinship lines are well documented in humans (Evans-Pritchard 1940; Chagnon 1979; Hunley et al. 2008; Walker and Hill, 2015).

According to this reasoning the key event that brought about the evolution of the first patrilineal kinship structures in hominins was the combination of a chimpanzee-like social organization – essentially, a multimale-multifemale group composition and a pattern of male philopatry – with a mating system featuring stable breeding bonds. Human groups combine the two traits. They are stable associations of predominantly monogamous units, or communities of conjugal families (Rodseth et al. 1991). Even though polygyny is practiced in about 80% of human societies (Murdock and White 1969; Low 2003), only a minority of men have more than one wife in any society (Marlowe 2003; Apostolou 2007; Layton, O'Hara, and Bilsborough 2012). In other primate species forming stable associations of reproductive units, the latter are polygynous as a rule so a fraction of adult males have no females at any point in time (Grueter et al. 20102; Swedell 2011). Although polygyny allows father-child recognition (Colmenares 2004), it is doubtful that males recognize their paternal kin in those species. A majority of them, notably

gelada baboons and Asian colobines, are female philopatric (Le Roux et al. 2011; Grueter et al 2012), which precludes the formation of patrilineal kinship networks. An interesting exception is the Hamadryas baboon, a male philopatric species (Grueter et al. 2012; Swedell and Plummer 2012). However, as argued elsewhere (Chapais 2013), the high intensity of male sexual competition in that species translates into low levels of prosocial (cooperative) interactions between harem leaders and adult males in general. If only for that reason, young males can hardly recognize their father's kin based on his association patterns with other males. Thus, from the perspective of the present model, Hamadryas baboons would lack condition 6 (cooperative activities among males) to form patrilineal kinship structures, an hypothesis that remains to be empirically verified. This reasoning implies that monogamy, with its substantially lower levels of sexual competition, would have been a prerequisite for the evolution of patrilineal kinship structures among hominins.

The proposition that the first patrilineal kinship structures emerged in the human lineage subsequently to the evolution of monogamy in male philopatric, multimale-multifemale groups (Chapais 2008, 2014) provides what may be called a phylogenetic model of patrilineal structures. The rationale underlying that type of model holds in two principles. First, the human phenomenon under study must break down into a number of building blocks that have their own evolutionary history and biological underpinnings; in other words it must be shown to be the emergent product of those components merging together. Second, there must be solid evidence that the phenomenon's building blocks were assembled together in the course of human evolution. In the present case, the ten components stem from four possible evolutionary sources. Some components are basic features of primates in general (e.g., cooperative activities, male hierarchies), others are likely homologous similarities between chimpanzees, bonobos and humans (e.g., multimale-multifemale composition, male philopatry), while still others are specific human adaptations (e.g., monogamy), or consequences of the conjunction of the previous three categories (e.g., paternal transmission of status, patrilineal segmentation).

Phylogenetic models of human social phenomena provide virtual images of the simplest and most primitive versions of complex social patterns, before the latter underwent processes of cognitive enhancement and cumulative cultural elaboration that led to their present forms. In what follows I consider some of those processes.

### **The Cognitive Enhancement of Primitive Patrilineal Structures**

The main argument developed here is that the evolution of the capacity to conceptualize the criteria already used by nonhuman primates to differentiate their kin played a central role in the transition from primate-like kinship structures to human kinship structures, in which the correspondance between biological kin types and culturally defined kin types is considerably blurred.

We saw that primates differentiate their maternal kin based on criteria such as sex, age, generation, lineal distance, and collateral distance. An important question concerns the extent to which they conceptualize those criteria. Nonhuman primates form mental representations of objects and individuals. As argued by Cheney and Seyfarth (2007: 261)

the observation that monkeys recognize a female by voice alone, “regardless of whether she is giving a grunt, a contact bark, or a threat-grunt, and regardless of whether she is grunting loudly or softly, or vocalizing in a calm or agitated manner (...)” and despite the “fact that the calls of an individual may grade acoustically into the calls of another” strongly suggests that monkeys have a mental representation of the individual they listen to. Not only may nonhuman primates realise that several distinct cues or behavioral manifestations refer to the same entity, in this case an individual, they may also recognize that different entities share a number of commonalities and belong to the same category. Experimental findings show that apes classify objects in different categories according to their properties, which testifies to their having some kind of concepts about those categories (Spinozzi 1996; Tanaka 2001). With respect to kinship, there is limited evidence that monkeys perceive properties common to the same type of kin dyads, such as siblings (Dasser 1988). There is even evidence that wild baboons are able to recognize that two individuals belong to the same matriline or to different ones, which suggests that they might recognize matrilineal entities (Bergman et al. 2003). But even assuming that nonhuman primates have mental representations – some sort of primitive concepts – about children, mother, siblings, or larger groups of kin, whether they have more abstract ones like same-generation kin, senior generation kin, lineal kin, collateral kin, paternal kin, and so on appears unlikely.

In any case, when the evolution of human cognitive abilities made it possible for hominins to develop that kind of abstract concepts, this entailed they were able to group together individuals who shared specific characteristics, irrespective of other, differentiating characteristics. For instance, a concept referring to siblingship implies the capacity to lump a number of individuals regardless of differences in sex and age, based on the perception that they share attributes that might relate, for instance, to the nature of their relationships with the same mother. Similarly, a concept about ‘senior generation,’ from ego’s perspective, implies grouping in the same class the members of a senior generation irrespective of variation in sex, age and genealogical distance. Thus, the conceptualization of the criteria used to differentiate kin types lies at the very foundation of the classificatory character of human kinship – *classificatory kinship*. Accordingly, conceptualization would have played a central role in the transition from strictly genealogical kinship, in which different kin types often have different degrees of genetic relatedness to ego, to classificatory kinship, in which individuals differing in their degree of relatedness with ego may nonetheless be grouped together. Kin terminologies vary markedly in this respect. For example, some terminologies group all members of an ascending generation in relation to all members of a descending generation, whereas other terminologies distinguish between kin belonging to odd generations in relation to ego (parents and children) and kin belonging to even generations (grandparents and grandchildren) (Goodenough 1970). The point here is not that the conceptualization of kinship criteria produced universal categories of kin types, but that it was a necessary condition for the advent of classificatory kinship.

At the same time, conceptualization allowed the differentiation of a much larger array of kin types compared to the situation in other primates. For example, by combining

the concept of generation with that of collateral kin, it became possible to differentiate between collaterals belonging to different generations, such as first, second and third-degree cousins. Thus, on the one hand, conceptualization substantially enlarged the set of kin types potentially differentiated by humans compared to other primates while, on the other hand, making it possible to lump several different biological kin types in the same category.

An interesting question is whether categories like first and second-degree cousins could be differentiated based on conceptualization but prior to the evolution of language. It has been argued by many linguists, psychologists and philosophers that the capacity to have mental representations of individuals, objects, actions, events and relations between things preceded the evolution of language and that in fact such knowledge provided the very mental categories needed for language to evolve. Put differently, humans would have had a language of mental representations, or *language of thought* (Fodor 1975), well before they were able to communicate linguistically. This principle also applies to the ontogeny of language acquisition and would help explain why young children learn languages so easily (for a discussion of the subject from a comparative, phylogenetic perspective, see Cheney and Seyfarth 2007: 248-272). Applied to kinship, the language of thought hypothesis implies that some sort of kin classifications based on prelinguistic conceptual categories antedated language-based kin terminologies. Whatever the exact nature of those categories, there is little doubt that the possibility of linguistically labeling kin types must have contributed importantly to the expansion of the domain of kin recognition in humans (e.g., Jones 2004, 2010; Barnard 2008).

Another major consequence of the evolution of human cognitive abilities on kinship was the recognition of deceased kin, lineal or collateral. Humans are told by group members about the existence of dead ancestors and can refer to them by their names. In combination with the concept of lineal kin, the recognition of deceased ancestors made it possible to recognize chains of mother-daughter links composed of dead female ancestors (matrilineal descent), and chains of father-son links including dead male ancestors (patrilineal descent). Implied here, descent would have emerged in the human lineage when the primate capacity to recognize lineal kin combined with the cognitive abilities underlying higher-order conceptualization and the identification of deceased ancestors. The recognition of descent in turn was a necessary condition for the perception of matrilineal and patrilineal social entities, that is, as entities whose members, by virtue of descent from a common, recollected ancestor, share a number of prerogatives, rights and duties. Prior to the advent of conceptualization, matrilineal and patrilineal were mere primate-like patterns of social relationships matching genealogical structures. With conceptualization, matrilineal and patrilineal evolved into *matrilineages* and *patrilineages* in the anthropological sense of the term: kinship structures recognized as such and constituting political and economic units.

In an attempt to demonstrate that similarities between human lineages and primate matrilineal were superficial and no more than metaphorical, Fortes (1983) noted that “human lineages are groups of people conceptually rather than physically distinguished (...). They are not primarily breeding groups but political, economic and religious sub-divi-

sions of a larger society (...) [that] “exist not by virtue of the transitory dyadic relationships of successive generations of females but by reason of elaborately conceptualized and institutionalized models, rules and norms of social and personal relationships.” “Above all”, he added, “they represent a dimension of human social existence that is surely lacking in other primate species” namely, “the incorporation into the life of a human society of the sense of its continuity in time, more exactly, of its having a past and a future” (Fortes 1983: 19). Far from discrediting the evolutionary connection between primate matrilineal and human lineages, Fortes’s argument provides an accurate description of the consequences of human cognitive abilities on our primate heritage with respect to descent and lineages.

The advent of classificatory kinship certainly blurred the correspondance between biological kin types and culturally defined kin types, but the fact that it initially proceeded along the criteria used by nonhuman primates to differentiate their kin implies that human kinship structures cannot be dissociated from the genealogical grid. What is more, classificatory kinship includes additional criteria belonging to that grid, but which are not used by other primates, namely, bifurcation and affinity. Humans classify their kin according to whether they are related to an individual through the mother or the father (e.g., matrilineal and patrilineal aunts). Bifurcation is not possible in other primates forming multimale-multifemale groups if only because, as we saw, sexual promiscuity prevents systematic father-offspring recognition so that individuals are not in a position to recognize their paternal relatives. However, distinguishing between the close associates of one’s mother and those of one’s father appears to lie well within the cognitive capacities of apes. This suggests that the bifurcation criterion, in its simplest form, became operative among hominins following the evolution of pair-bonding and the advent of fully bilateral kinship.

Humans also take into account whether they are related to a kin through a marital tie or not. Affinal kinship is a uniquely human phenomenon, as first noted by Fox (1980), and the relevant distinctions made by people vary across cultures. In-laws may be labeled differently depending on the number of marital ties separating them from ego, whether that number is odd or even, whether the marital ties belong to a junior or senior generation, and so on (Goodenough 1970). Regardless of such distinctions, exogamy being the rule in humans many of ego’s affines reside in groups other than ego’s group. Thus for a man to recognize the husband of his sister married and living in another group, the husband and his sister must maintain contact on a regular basis. The recognition of in-laws thus depends on intergroup visiting and the existence of lifetime bonds between noncoresident, cross-sex kin, two uniquely human phenomena. This explains why affinal kinship is limited to our species. Affinal kinship, nonetheless, has deep evolutionary roots (Chapais 2014). Bonds between affines reflect enduring linkages between a kinship bond and a pair-bond through the intermediary of an individual connecting the two dyads – e.g., a woman linking her brother to her husband. Kinship bonds and pair-bonds are common in nonhuman primates, but they usually do not co-occur in the same species. Moreover, even if they did, the absence of intergroup visiting would preclude the formation of relationships between affines. Following the evolution of the first between-group

alliances in the human lineage – what I referred to elsewhere as the *primitive tribe* (Chapais 2008) – individuals were in a position to recognize the spouses of their kin married in other groups. Cognitively speaking, recognizing affines involves perceiving associations between individuals and the characteristic of their relationships; it involves the same basic processes underlying the recognition of consanguineal kin (Chapais 2008). In short, affinal kinship, like matrilineal and patrilineal kinship, is an evolutionarily composite phenomena.

## **Conclusion**

Patrilineal kinship structures are complex, group-level social phenomena exhibiting a great deal of cultural variation. As such they appear to be cultural *creations*, the result of collective decisions taken in the context of some sort of tribal gatherings that took place in our distant past, and hence in the absence of any significant biological constraint affecting their general form and content (e.g., Allen 2008). The alternative proposed here is that contemporary kinship structures are cultural *constructs*, the outcome of cumulative cultural elaborations that initially built upon a rich biological substrate comprising genealogical structures, the primate criteria of kin differentiation, the intrinsic properties of kinship, and a number of primate cognitive and social adaptations.

Although I concentrated here on kinship structures the same reasoning applies to other complex human kinship phenomena, including marital arrangements (Chapais 2014). Like patrilineal kinship structures, marital arrangements are uniquely human, they are absent in many societies, and the forms they take vary substantially across groups. Nonetheless marital arrangements share a number of basic properties, in particular the parental control of marital unions, the centrality of the principle of conditional reciprocity, and the high value of children as currencies of exchange. A phylogenetic comparative analysis suggests that matrimonial exchange emerged from the conjunction of several biological components in the course of human evolution. Several of those components relate to consanguineal and affinal kinship and are an integral part of our primate heritage, whereas others are uniquely human cognitive abilities.

If we accept that the present phylogenetic approach provides solid evidence that a number of complex human kinship patterns have biological underpinnings, anthropological models and theories ignoring that information will necessarily have to account for the actual effects of biological factors in terms of cultural factors. This is bound to introduce a number of flaws in the corresponding models. I conclude that theories purporting to explain the same phenomena but issued from different disciplines, such as cultural anthropology and evolutionary anthropology, must necessarily resolve their contradictions and be compatible with each other. It is certainly possible to build theories in disciplinary silos – whether anthropological, psychological, or biological – but their validation depends ultimately on the extent to which they are congruent with theories issued from distinct levels of analysis.

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