

Monogamy, Strongly Bonded Groups, and the Evolution of Human Social Structure

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Human social evolution has most often been treated in a piecemeal fashion, with studies focusing on the evolution of specific components of human society such as pair-bonding, cooperative hunting, male provisioning, grandmothering, cooperative breeding, food sharing, male competition, male violence, sexual coercion, territoriality, and between-group conflicts. Evolutionary models about any one of those components are usually concerned with two categories of questions, one relating to the origins of the component and the other to its impact on the evolution of human cognition and social life. Remarkably few studies have been concerned with the evolution of the entity that integrates all components, the human social system itself. That social system has as its core feature human social structure, which I define here as the common denominator of all human societies in terms of group composition, mating system, residence patterns, and kinship structures. The paucity of information on the evolution of human social structure poses substantial problems because that information is useful, if not essential, to assess both the origins and impact of any particular aspect of human society.

It has been proposed, for example, that cooperative breeding (alloparenting) played a central role in the evolution of human cognition.^{1,2} Among the most basic evidence needed to assess the explanatory

power of this hypothesis, assuming that help was needed in rearing offspring, is information about the categories of individuals who were in a position to provide help at any point in human evolution. This was determined by the prevailing group composition, mating system, residence pattern, domain of kin recognition, and state of between-group relations. In short, it was determined by social structure. It is thus difficult to assess the potential impact of alloparenting on the evolution of human cognition without data on social structure. Discussions of the origins of specific components of human society are also dependent on information about social structure. For example, whether human monogamy evolved from a prior state of sexual promiscuity in multimale-multifemale groups or a prior state of generalized polygyny in groups composed of several one-male units generates different sets of models about its evolution.

The main reasons why the topic of social structure has been rather neglected by social evolutionary studies are clear. First, we lacked a comprehensive description of human social structure itself, without which it was hardly possible to address the issue of its evolution. Second, it is difficult to obtain comprehensive pictures of hominin social systems on the basis of paleo-anthropological data. The anatomical and artifactual markers of human behavioral and life-history patterns provide the most direct type of evidence on human social evolution, and both the variety and quality of those markers are growing at a fast rate. Using that information in association with behavioral data on extant primates makes it possible to infer several aspects of the social structure of particular hominin species.^{3,4} But however sophisticated such studies may be, they are intrinsically limited by the fact that social patterns leave few traces in the fossil record and the resulting reconstructions are fragmentary.

Another approach, adopted here, yields more comprehensive pictures of social structures, but has its own limitations. It consists in carrying out a comparative analysis of extant human and nonhuman primate societies as a means of characterizing modern human society in primatological, and hence, evolutionarily significant terms; defining a limited range of possibilities for the social structure of the *Pan-Homo* ancestor based on cladistic considerations; and inferring intermediate stages linking the two social structures on the basis of various constraints. The obtained sequence must be

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construed as the most parsimonious evolutionary pathway between the initial *Pan-Homo* social structure and modern human social structure; that is, there might have been a larger number of intermediate stages, but presumably not a smaller number. In other words, the intermediate stages would be necessary steps in the evolution of human society. As will be argued here, establishing such a sequence sets research questions that have not necessarily been given enough attention, generates new testable hypotheses about those questions, and contextualizes prior hypotheses on human social evolution. Moreover, given that this type of analysis is carried out independently of paleo-anthropological data, it is testable against those data. The main limitations of the present approach are that it is silent about the timing and duration of evolutionary events and that it does not necessarily include all stages of the actual sequence. My aim in this paper is to show that this mainly deductive and heuristic approach and the mainly inductive paleo-anthropological approach are fully complementary.

In earlier work, I provided a description of the unitary structure of human society and its evolutionary history by comparatively analyzing human and nonhuman primate societies.^{5,6} Here I push further the comparison of human society with multilevel societies, exemplified by hamadryas baboons and other species, the category of primate social organizations structurally closest to human society. Arguably, the relevance of this type of society for human evolution, in terms of possible homoplasies, is comparable to that of chimpanzee society, in terms of possible homologies. Using these two comparative bases, I propose a definition of human social structure and present an enhanced five-stage sequence describing its evolutionary history. I then show how the sequence crucially informs hypotheses and models about the origin of what appear to be two of the most consequential features of human society, monogamy and strong ties between groups.

HUMAN SOCIAL STRUCTURE

The human species is the only one whose unitary social structure is not readily recognizable and describable because it is concealed under a myriad of cultural expressions. Many other species have the dual capacity to create new behavioral patterns and adopt the innovations of others through various social learning processes, and hence to acquire cultural traditions. But the size of cultural repertoires in other species is extremely small, cultural change is barely cumulative, and most documented innovations are technologi-

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cal; only a few are social.⁷⁻¹⁰ Correlatively, behavioral categories vary little between groups of the same species, even though rates and intensities of interactions may vary a great deal. The relative paucity of cultural variation across conspecific groups is what makes it possible to discern some kind of unitary social structure or a limited set of social structures for any primate species – to speak, for instance, of chimpanzee social structure. In contrast, the cognitive underpinnings of innovation and social learning in humans are such that culture has thoroughly invaded the social realm. Humans ceaselessly invent new ways of communicating, courting, playing, fighting, or making alliances, and cultural change is fully cumulative. As a result, the unitary social structure of human societies has given

rise to multiple cultural versions and become barely visible underneath the resulting diversity. Hence, we have the concept of deep social structure to describe the common structural features of human societies.^{5,6} Only in humans is social structure a deep, hidden phenomenon.

In retrospect, the deep structure of human society could hardly be defined solely through the comparative analysis of human societies. The few sociocultural anthropologists who sought to identify so-called human universals (Brown's survey¹¹ is by far the most detailed) left out some important features of human society, including, for instance, the existence of lifetime bonds between cross-sex kin living in different groups and the bilateral recognition of in-laws. Such traits were missed because they are hardly recognizable as significant features in the absence of an outgroup (nonhuman) point of reference. To define what is specifically human and what is not, one must compare human societies with nonhuman societies. Such a comparative analysis leads me to define human societies as federations of multifamily groups. The modal composition of human groups is the community of conjugal families,¹² hereafter the multifamily group. Multifamily groups are large multi-male-multifemale groups in which adult males and females form stable breeding bonds, most of which are monogamous. Multifamily groups are always part of larger social entities, which themselves are part of still more inclusive entities such as a number of clans or villages forming a band and a number of bands forming a tribe. Thus, associations of multifamily groups have a multilevel and nested structure and exhibit high levels of between-group coordination; hence, my use of the word "federation."

Other primate species such as hamadryas baboons (*Papio hamadryas*), gelada baboons (*Theropithecus gelada*), and snub-nosed monkeys (*Rhinopithecus* spp.) have a nested structure. They are referred to as multilevel, or modular societies.^{13,14} Among hamadryas

baboons, for example, a number of one-male units (OMUs), most of which are polygynous, form a clan in which males are philopatric; other clans form a band that occupies a home range and appears to be the analogous counterpart of the multi-male-multifemale group in other baboon species.¹³ Bands may also merge into loose aggregations, or troops, around common resources or sleeping sites.¹⁴ Among *Rhinopithecus*, several OMUs may form a band, but higher levels of social organization are not reported.^{14,15}

From a structural viewpoint, human societies are multilevel societies but, as will be argued here, they have several distinctive features that can be grouped within three categories: (1) a highly composite mating system centered on enduring monogamous unions; (2) an unprecedentedly extensive domain of kin recognition and impact of kinship on social life; and (3) strongly bonded groups with high levels of between-group coordination.

A Composite Mating System

Compared to that of other primates, the human mating system is extremely flexible. It combines short-term and long-term mating bonds, and both types may be overt (known to all group members) or covert (unknown to a majority of group members and disapproved of). Overt enduring bonds (marital or marital-like unions) are either monogamous or polygynous; only rarely are they polyandrous. A mixed system of polygyny and monogamy prevails in more than 80% of human societies, whereas monogamy is strictly enforced in about 17% of societies.^{16–19} Monogamy is nonetheless the preponderant type of union worldwide because in societies practicing polygyny only a fraction of men have more than one wife.^{16–20} Covert enduring bonds show a different distribution. Monogamously mated men may have long-term bonds with other women (covert polygyny); monogamously mated women may also have more than one long-term partner (covert polyandry). Covert monogamous unions

also occur, for example when they are considered illicit for various reasons. As to short-term sexual bonds, they are frequent and characterize both sexes.^{20,21} They are often overt when they occur premaritally, but typically covert when they take place between marital partners.

The flexibility of the human mating system contrasts markedly with the situation in other multilevel primate societies. In those species, a majority of reproductive units are polygynous (for example, among hamadryas baboons n females per OMU = 2–3, range = 1–9; among gelada baboons: n = 3.5–4, range = 1–12).^{4,13} This implies that a substantial fraction of males have no

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females at any one time. There are no enduring polyandrous unions and only a minority are monogamous. Human societies are the only multilevel societies in which reproductive units are entirely or primarily monogamous. Structurally speaking, the human multifamily group is a particular form of multi-OMU group in which most stable sexual bonds are monogamous.

A further distinctive feature of the human mating system is the collective nature of mate selection. Among other primates, mate selection is a dyadic activity involving the partners themselves, whereas in humans the widespread practice of marital

arrangements^{22,23} shows that mate selection and the formation of marital unions are integral parts of cooperative agreements between the partners' kin groups, in which kinswomen and kinsmen are used as currencies of exchange. Marrying one's daughter or sister creates obligations of reciprocity in the receiving family or group in terms of physical resources, future marriage partners, or political alliances.²⁴ Although nonhuman primates do engage in reciprocity through the exchange of services such as grooming, support in conflict, and access to food, they are not known to exchange social partners. Moreover, it is unlikely that they regularly engage in human-like contingent reciprocity (giving conditionally upon receiving).^{25,26} In humans, the conjunction of various factors, including the capacity for robust contingent reciprocity, the possibility of controlling the behavior of others through language, and the recognition of in-laws (or affines) presumably set the stage for using mating bonds as a means of alliance formation.

Extensive Kinship Networks

Another key aspect of the human multifamily group is the sheer extent of kin recognition. Humans recognize their relatives on both the female line (matrilineal) and the male line (patrilineal). Kinship is fully bilateral (mother's and father's sides) and independent of whether kin are coresident or not. In small-scale societies, this translates into group-wide and supragroup kinship networks in which individuals may trace kinship links with a majority of group members and interact differentially on that basis. The situation is very different among other primates. In species forming large bisexual groups and breeding promiscuously (no stable breeding bonds), kin recognition through females (matrilineal kinship) is well developed, especially when females are the philopatric sex.^{27,28} This reflects the existence of long-term bonds between mothers and offspring. However, kin recognition through males (patrilineal kinship) is either absent or

fragmentary and, when detected,²⁹ is manifest in extremely low rates of interaction compared to matrilineal kinship.^{5,30} A similar situation prevails in male philopatric societies in which males live with several patrilineal kin types. Among chimpanzees, for example, paternal siblings do not appear to recognize each other.^{31,32} Paternity translates into remarkably weak effects on social interactions between fathers and offspring,³¹ and it is unlikely that individuals recognize their father's kin. What is lacking to generate patrilineal kinship in such species is a systematic means of paternity recognition based on long-term bonds between fathers and offspring, and stemming from the existence of stable breeding bonds between mothers and fathers.⁵

Interestingly, from that perspective, multilevel primate societies feature stable breeding bonds and hence, father-offspring recognition. However, a majority of those species, notably gelada baboons and Asian colobines, exhibit female philopatry and male dispersal,^{14,33} which precludes the formation of patrilineal kinship networks. An interesting exception is hamadryas baboons, among which males of the same clan, and hence of the same band, are philopatric,^{4,14} recognize their father (the OMU's leader), and grow up with full-siblings and paternal siblings.³⁴ Leaders of the same clan and band may thus be related to each other as half-brothers, full-brothers, fathers and sons, and so on. If males were to form long-term cooperative partnerships with their fathers, they might, in theory, be in a position to recognize some of their father's kin on the basis of associative processes similar to those involved in the recognition of matrilineal kin in female philopatric species.³⁵ But although males of the same clan interact with each other,⁴ they do so only infrequently, owing to the intensity of male sexual competition. It is doubtful that patrilineal kinship translates into differentiated relationships in that species. In sum, the domain of kin recognition in other multilevel societies is quite limited compared to the situation among humans.

Federations of Strongly Bonded Groups

One of the most salient features of human society is the existence of strong social ties between groups. The two most basic categories of strong bonds at work are those between biological kin and between in-laws.^{5,6} Both types of bonds stem from exogamy. By definition, exogamy implies that a child has a father born in one group and a mother born in a different group, and thus has relatives living in at least two groups. This creates the potential for kinship bonds between the two groups, provided kin living in different groups visit each other, which is the rule among humans.¹² Bonds between two in-laws, or affines, stem

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from the connection of a kinship bond to a pair-bond through the intermediary of an individual present in both dyads – for example, a woman linking her brother to her husband or her father to her husband's father. Affinal kinship, or the structural linkage of pair-bonds and kinship bonds, is a major human originality.^{5,36,37}

Strongly bonded groups appear to be uniquely human. Relations between groups among other primates are generally hostile. Also, there are no social entities larger than the local group and no multigroup structures, including in chimpanzees and bonobos. Exceptions are found in some multilevel societies.

For example, among hamadryas and gelada baboons, multi-OMU groups may occasionally assemble in larger aggregations at common resources. However, such aggregations are relatively inconsistent and loose.^{4,14} Among hamadryas baboons, moreover, males and females are philopatric at the level of the band except when females are abducted by males from other bands.^{4,38} This precludes the formation of bonds between kin and between "affines" living in different bands. For these reasons, I use the expression "weakly bonded" to describe relations between multi-OMU groups in multilevel primate societies.

A correlate of the existence of strong bonds between multifamily groups in humans is the flexible character of residence patterns. Both men and women may move between allied groups; dispersal is bisexual and so is residence.⁵ Correlatively, human residence patterns are remarkably flexible and variable across societies, with adult individuals of both sexes living with their male and female kin.^{39–41} Significantly, lifetime relationships between cross-sex kin among humans, particularly between brothers and sisters, are a distinctive feature of human society's deep structure.^{5,6} In contrast, residence patterns among other primates forming multimale-multifemale groups are usually much less flexible. Dispersal and philopatry are most often strongly sex-biased, so that adult cross-sex kin, such as brothers and sisters, rarely live together.

Three additional characteristics justify using the word "federation" to describe human societies: multifamily groups commonly interact with each other as collective entities (that is, members coordinate their actions toward shared objectives); several groups can coordinate their actions in relation to several other groups (multigroup coordination); and there is, in theory, no upper limit on the number of nested levels of social organization. In comparison, within-group coordination is extremely limited in other multilevel societies, multigroup coordination probably is

TABLE 1. The Main Distinctive Features of Human Social Structure, the Federation of Multifamily Groups, From a Comparative (Interspecific) Perspective

Multifamily group as modal group type
Monogamy/polygyny mix as modal mating system
Variable levels of premarital and postmarital sexual promiscuity
Cooperative mate selection (marital arrangements)
Father-offspring recognition based on stable mating bonds
Lifetime bonds between dispersed kin, in particular between cross-sex kin
Bilateral kin recognition (mother's and father's sides), independent of coresidence
Bilateral recognition of affines (husband's and wife's sides), independent of coresidence
Exogamy and dual-phase residence
Bisexual residence and dispersal; hence, flexible residence patterns
Strong bonds between interbreeding groups based on biological and affinal kinship
Nested organization of social groups
Group-wide coordination based on shared objectives
Multigroup coordination
Number of nested levels of social organization theoretically unlimited

almost absent, and there is a fixed limit to the number of nested levels of social organization.^{13,14} Table 1 summarizes the distinctive features of human society.

A FIVE-STEP EVOLUTIONARY SEQUENCE

How did the uniquely human federation of multifamily groups evolve? The proposed sequence, depicted in Figure 1, includes five stages, from the *Pan-Homo* ancestor (phase 1) to the federation of multifamily groups (phase 5). It should be noted that the sequence applies specifically to a single evolutionary line, that leading to *H. sapiens*; it certainly does not exhaust the diversity of hominin social structures.

The reasoning starts with the observation that most human groups have a multifamily composition and that such a composition reflects the conjunction of two structural features that usually do not co-occur in the same primate species: the multimale-multifemale group and stable breeding bonds, or OMUs. This raises the question of why the two features came together in the first place. From a strictly logical and structural viewpoint, four possibilities are determined by the social structure of the *Pan-Homo* ancestor (Table 2). First, that initial social structure might have been the independent OMU. This implies that the grouping of independent OMUs into multi-OMU groups would have

taken place after the *Pan-Homo* split, at some point in the human lineage. Second, the *Pan-Homo* ancestor might have exhibited the multi-OMU group itself, in which case both the multimale-multifemale composition and OMUs would have characterized the earliest hominins. Third, the *Pan-Homo* ancestor might have formed multimale-multifemale groups and bred promiscuously, in which case stable breeding bonds would have evolved after the *Pan-Homo* split and substituted for sexual promiscuity, with this generating multi-OMU groups. Finally, the *Pan-Homo* ancestor might have exhibited neither a multimale-multifemale composition nor OMUs; it might have been characterized by a different social structure, in which case both features would have evolved in the human lineage.

Interestingly, cladistic inferences about the social structure of the *Pan-Homo* ancestor are compatible with the first three possibilities, so the fourth will not be invoked here, though this does not imply that it may be discarded. Gorillas form independent OMUs. If one assumes that gorilla-like and human-like OMUs are homologous, which means that stable breeding bonds in humans and gorillas have a common origin, it follows that the trait characterized the *Gorilla-Pan-Homo* ancestor. If the grouping of independent OMUs into multi-OMU groups occurred after the *Pan-Homo* split, one obtains the first logical

possibility (pathway A in Fig. 1). Alternatively, if the grouping took place before the *Pan-Homo* split, this produces the second logical possibility (pathway B in Fig. 1).

The third logical possibility listed earlier finds cladistic support in the assumption that the multimale-multifemale composition is homologous between humans and chimpanzees and characterized the *Pan-Homo* ancestor,⁴² so that stable breeding bonds evolved after the *Pan-Homo* split (pathway C in Fig. 1). Several arguments support the view that those bonds would have been initially polygynous, resulting in multi-OMU groups, rather than primarily monogamous, resulting in multifamily groups. First, polygyny is the rule in all multilevel primate species, presumably because the spatial cohesiveness of females in multi-OMU groups allows males to herd more than one female.⁴³ Second, the transition from the sexually promiscuous multimale-multifemale group to the multi-OMU structure receives support from phylogenetic analysis of the evolution of the multi-OMU composition from a multimale-multifemale ancestor in baboons.⁴⁴ Third, all theoretical models on the fractionation of multimale-multifemale groups into multi-OMU groups, including the ecological, time constraint, social, and social brain models,¹⁴ predict the formation of polygynous, not monogamous, units. Fourth, the alternative transition, from chimpanzee-like sexual promiscuity to human-like monogamy, which is often assumed, is unlikely, as I will discuss.

Phase 1, the social structure of the *Pan-Homo* ancestor, is thus represented by three possible social structures in Figure 1: the single OMU, the multi-OMU group, and the sexually promiscuous multimale-multifemale group. The important point, as far as the present argument is concerned, is that regardless of the relative merit of these three possibilities, they converge on the existence of the multi-OMU group, either before the *Pan-Homo* split (pathway B) or immediately after (pathways A and C). Given that multi-OMU groups in multilevel primate societies,

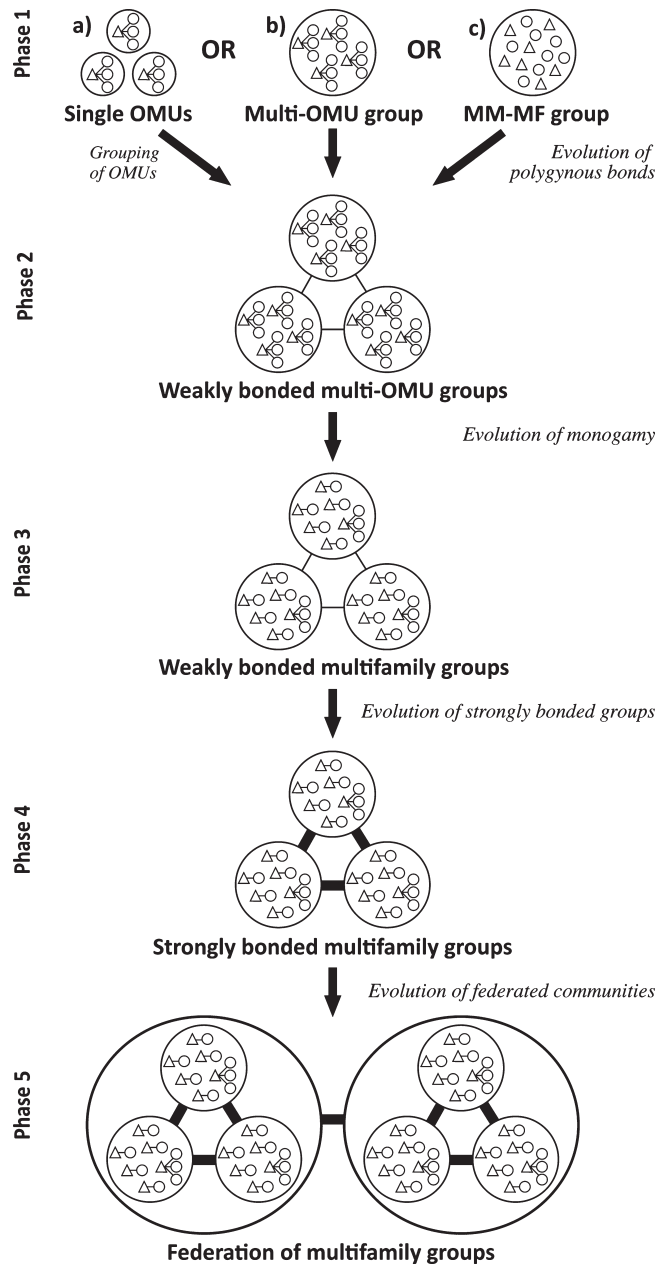


Figure 1. A schematic representation of the evolutionary history of human social structure, the federation of multifamily groups. Phase 1 characterizes the *Pan-Homo* ancestor and is represented by three possible social structures (see Table 1). Thin lines represent weak bonds between groups. Thick lines represent strong bonds based, minimally, on biological kinship and affinal kinship. Triangles, males; circles, females. MM-MF: multimale-multifemale group.

particularly hamadryas and gelada baboons, may form larger aggregations around common resources, phase 2 is depicted in Figure 1 as being characterized by weakly bonded multi-OMU groups.

The main difference between multi-OMU groups and human-like multifamily groups is that the former

are composed mostly of polygynous units, whereas the latter are composed mostly of monogamous units. This points to a parsimonious pathway between the two states, one involving the evolution of constraints on the capacity of males to monopolize several females. The evolution of constraints on polygyny, resulting in

monogamy, thus produces phase 3, which features weakly bonded multifamily groups.

Phase 4 coincides with the evolution of strong bonds between multifamily groups, or the primitive tribe. "Tribe" is used here in its generic sense to refer to the first stable multigroup social structures. As will be argued later, at this early stage in the evolution of multigroup structures, relations between groups would have been limited to a state of mutual tolerance favoring, for example, the bilateral transfer of individuals between groups and reciprocal access to territories.

More sophisticated aspects of between-group relations, notably group-wide coordination, multigroup coordination, and supratribal levels of social organization, had to await phase 5 in the evolution of human society, the federated community. The high levels of within- and between-group coordination characterizing human societies rest on specific cognitive abilities: the capacity to recognize one's membership in a group and the membership of others in the same group (shared membership), to agree explicitly with fellow group members on common objectives, and to modify one's behavior in relation to ongoing changes in the behavior of others (shared intentionality).^{45,46} Accordingly, the transition from the primitive tribe to the federated community would have coincided with the evolution of cognitive abilities such as minimal levels of symbolic communication and a human-like theory of mind.

The proposed five-step sequence with its corresponding four transitions was meant to include the minimal number of steps required to go from the social structure of the *Pan-Homo* ancestor to human social structure. The sequence shows how the complexity of human society may have evolved from simpler states and thus provides a historical type of explanatory value. The sequence does not say why the transitions took place; it does not specify the events and selective pressures that might have driven them. However, it points to the existence of such events and selective pressures;

TABLE 2. Four Structural Possibilities for the Evolution of Multi-OMU Groups From the *Pan-Homo* Ancestor and Their Corresponding Cladistic Assumptions

Social structure of <i>Pan-Homo</i> ancestor	Changes occurring in human lineage	Assumptions
Independent OMUs	Grouping of OMUs	OMUs homologous in humans and gorillas. Grouping of OMUs after <i>Pan-Homo</i> split
Multi-OMU group	None	OMUs homologous in humans and gorillas. Grouping of OMUs before <i>Pan-Homo</i> split
MM-MF composition, sexual promiscuity	Stable breeding bonds	MM-MF ^a composition homologous in <i>Pan</i> and <i>Homo</i>
Other social structure	MM-MF composition, stable breeding bonds	Neither MM-MF composition nor OMUs are homologous in humans and African apes

^aMM-MF : multimale-multifemale

it also specifies both the prior social state on which the corresponding selective pressures would have operated and the resulting social state. Those constraints substantially limit the set of possible hypotheses for each transition. In what follows, I illustrate the principle by concentrating on two transitions, that from phase 2 to phase 3, the origins of monogamy, and from phase 3 to phase 4, the origins of strongly bonded groups.

A PHYLOGENETIC FRAMEWORK FOR THE EVOLUTION OF MONOGAMY

Although the evolutionary significance of male provisioning in contemporary foraging societies is still debated,^{47,48} empirical evidence may be brought forward to support the view that human monogamy evolved as a sexual and mate guarding strategy, and/or as a survival strategy featuring mutual provisioning and the division of labor, and/or as a parenting strategy involving protection, information transfer, and provisioning by both parents.^{49–54} It has also been proposed that monogamy in primates, including humans, evolved to prevent infanticide by males.^{55–57} Clearly, then, the multifunctional nature of human pair-bonds makes it difficult to infer the origin of monogamy based on functional analyses alone. This is precisely why a consideration of the evolutionary history of human social structure may prove useful: It suggests a stepwise

evolution of the human family's components and functions.⁴³

An Unlikely Transition

In earlier studies, the state that preceded monogamy was not specified⁵⁴ or monogamy was seen as evolving from a prior state of sexual promiscuity.^{49,52,58,59} A direct transition from chimpanzee-like sexual promiscuity to monogamy appears unlikely, though not impossible. That transition typically is associated with the view that human pair-bonding originated in male parental effort. In a recent attempt to verify that possibility, Gavrilets⁶⁰ showed mathematically that the transition was possible if one assumes that the costs of maternity had increased and females needed provisioning; males were in a position to provision them; food-for-sex exchanges were preexisting; and females were faithful to males who provisioned them. This is an interesting finding in itself, even though food-for-sex exchange among chimpanzees is a debated issue.^{61,62} But the main reason for doubting the proposed sequence is that it sees the three major components of modern pair-bonds, sexual, parental, and economic, as evolving simultaneously. The tendency to assume that all aspects of a complex evolutionary phenomenon necessarily arose simultaneously as part of the same functional system is referred to here as the adaptive suite pitfall. Evolutionary change is rather typically stepwise, cumulative, and opportunistic, often building on exaptations.

For example, a phylogenetic analysis of the distribution of pair-bonding and paternal care in mammals points to a sequential evolution of the two components,⁶³ with pair-bonding evolving as a mating strategy and paternal care evolving subsequently, if need be. Difficulties with phylogenetically compressed models of the evolution of the human family are compounded when such models further assume that the whole adaptive suite characterized the earliest hominins,⁵⁹ who were otherwise typical primates in terms of life-history, growth patterns, and brain size, with no special needs calling for male provisioning.

The promiscuity-to-monogamy transition is also less parsimonious than a transition in two stages, from promiscuity to polygyny and from there to monogamy. The switch from sexual promiscuity to polygyny involves a single change, from short-term to long-term mating bonds; the only variable involved is the duration of bonds. As noted, that change, the fragmentation of multimale-multifemale groups into multi-OMU groups, receives phylogenetic and theoretical support. The next transition, from polygyny to monogamy, also implies a single change, a reduction in the number of females per male. In contrast, a direct transition from promiscuity to monogamy implies mechanisms simultaneously driving both changes. That such a transition is mathematically possible does not imply that it is phylogenetically realistic.

In a recent phylogenetic analysis of primate social systems, Shultz,

Opie, and Atkinson⁶⁴ showed that monogamous pairs and polygynous units evolved from large multimale-multifemale aggregations, a finding that apparently lends support to the sexual promiscuity-to-monogamy transition. But these authors were concerned with the evolution of independent pairs and polygynous units, not with the evolution of multifamily groups or multi-OMU groups. They did not differentiate these as a separate type of social structure, but instead lumped them with multimale-multifemale groups. Those findings therefore do not apply to the origin of human monogamy.

The Evolution of Monogamy From Polygyny

According to the present view (Fig. 1), monogamy evolved out of polygyny, a possibility that appears to have been rather neglected in earlier studies. This transition raises the question of how males might have benefited from a reduction in the size of their reproductive unit. The proposition here is that monogamy resulted from an increase in the costs of polygyny. I consider four different types of costs, which constitute as many hypotheses about the origin of monogamy: the costs of paternal provisioning (paternal load hypothesis), the costs of physical conflicts between males (leveling hypothesis), the costs of sexual competition in terms of its negative effects on male cooperation (trade-off hypothesis), and the energetic costs of guarding several spatially dispersed females (ecological hypothesis). My objective is to illustrate the range of possibilities raised by the polygyny-to-monogamy transition; it is not to argue in favor of a particular hypothesis.

The paternal load hypothesis posits a rise in the costs of raising children as a result, for example, of increased body size and/or brain size, slower maturation rates, and increased altriciality – whatever the nature of the ecological or nutritional factors that might have started the process. In that context, the leaders of polygynous units would have

been selected to provision their females. But the provisioning of several females would have been costly, if possible in the first place, and rather inefficient from the females' viewpoint. Soon the males would have been selected to reduce the size of their reproductive unit up to the point that maximized offspring survival, possibly the monogamous unit. Males would have gone from a strategy that maximized mating effort and minimized parental effort to a strategy that minimized mating effort and maximized parental effort. For males to forego mating opportunities for paternal investment, one must assume the selection of males with lower motivations for polygyny or higher motivations for paternal investment, as well as the outcome, a preponderance of intrinsically monogamous males. The paternal load hypothesis is therefore not easily compatible with the widespread distribution of polygyny in human societies.^{16–19}

According to the next three hypotheses, monogamy evolved from polygyny as a sexual and mate-guarding strategy independently of any change in the costs of raising children (Fig. 2). The leveling hypothesis^{5,43} invokes a rise in the costs of physical aggression between males. Among mammals in general, clear discrepancies in physical power between males translate into significant differences in their capacity to defend females. It follows that any factor that reduces discrepancies in physical strength should reduce variation in the size of polygynous units. Arguably, the invention of weapons, from uncarved stones to bows and arrows, and their use against conspecifics, substantially reduced discrepancies in actual power between larger and smaller individuals. Physically stronger individuals could still overpower weaker opponents, but the latter could easily wound or kill stronger opponents when they were vulnerable (inattentive or sleeping). Moreover, the efficiency of projectile weapons⁶⁵ depends less on sheer physical power than on skills. When male competition came to rely on cunning and skills in the use of weapons, in addition to sheer physical strength, the capacity of stronger males to monopolize

several males decreased. Generalized (hamadryas-like) polygyny could no longer be the rule. According to this hypothesis, polygyny was thwarted, but the motivation for polygyny was not necessarily selected against. The outcome would have been a preponderance of monogamous unions with a minority of polygynous unions when conditions allowed.

The trade-off hypothesis also invokes a rise in the costs of male competition, but this time in terms of lost opportunities for cooperation between male competitors. The underlying principle is that the higher the degree of mutual dependence between two individuals, the higher the social costs of conflicts between them. One expects such costs to have increased substantially following, for example, the evolution of big-game hunting, with its associated high levels of cooperation between hunters, or the intensification of between-group conflicts and its requirement in terms of within-group male coalitions. In relation to this principle, Flinn, Geary, and Ward⁶⁶ stressed the relatively low levels of sexual competition characterizing coresidential males among humans as compared to other primate species and suggested that such high levels of tolerance among males might reflect, among other factors, the importance of male coalitions in conflicts. Whatever the exact nature of male cooperative activities, the associated increase in mutual dependence would have favored the evolution of some trade-offs between sexual competition and cooperation. The likely outcome would have been reduced variation in the size of polygynous units, or a drift toward monogamy.

The ecological hypothesis rests on the energetic costs of guarding several spatially dispersed females. Those costs would become prohibitive to polygynous males if, as a result of a change in ecological niche, individuals regularly had to disperse widely over large home ranges to obtain their food. Such a ranging pattern would force males into monogamy. Among non-human primates, ecologically induced monogamy is associated

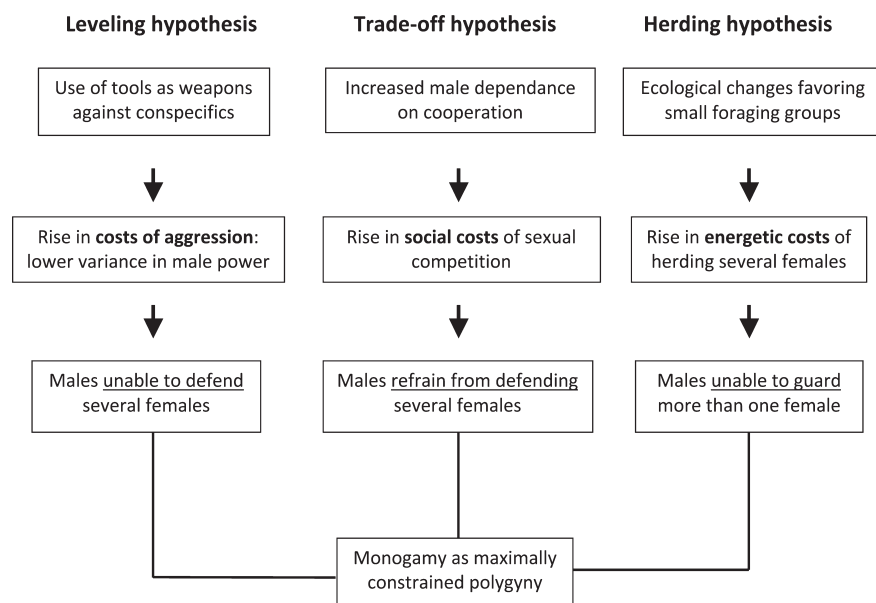


Figure 2. Three hypotheses according to which monogamy evolved from polygyny as a mating strategy and as a result of different types of constraints on polygyny.

with territorial monogamy,⁶⁷ not with group living, as in the present case. But the observation that nuclear families in hunter-gatherer societies may forage independently and coalesce on a regular basis¹⁶ points to the adaptiveness of this pattern.

The leveling, trade-off, and ecological hypotheses are not mutually exclusive. The use of weapons in conflicts, a greater reliance on economic or coalitional cooperation among males, and an ecology-based increase in the costs of female guarding may have had a cumulative impact on both the feasibility and profitability of polygyny. From that perspective, it is difficult to ignore the potency of constraints on polygyny in explanations of the origin of monogamy.

The polygyny-to-monogamy transition imposes constraints on other hypotheses about the origin of monogamy. I consider two examples. Some data support the view that monogamy evolved to prevent infanticide, for example in gibbons.⁶⁸ But for the infanticide hypothesis to explain the evolution of human monogamy from a prior state of polygyny, one must posit that monogamously mated females incurred lower risks of infanticide than did polygynously mated females. This is not immediately obvious, given that in both situations females benefit from the

protection of a male. In any case, this prediction, in theory, is testable. The other example concerns the role of concealed ovulation in the evolution of monogamy. A common view, derived from the assumption that monogamy evolved from sexual promiscuity in chimpanzee-like groups, is that the loss of sexual swellings in females forced males into continuous mate guarding and stable breeding bonds to ensure paternity.^{59,69} But it is likely that sexual swellings in chimpanzees and bonobos are a derived trait, which implies that the *Pan-Homo* ancestor lacked sexual swellings and that hominins did not experience a “loss of estrus.”^{70,71} Moreover, even assuming that polygynously mated hominins (phase 2 in Fig. 1) had sexual swellings, as might be inferred from the fact that multilevel primate species such as hamadryas baboons have them,⁷⁰ the loss of those swellings could not be explained as a strategy to induce males into forming stable breeding bonds because this was already the case.

The Initial Monogamous Family

The last three hypotheses locate the origin of monogamy in its mating and mate guarding function, the implication being that the economic

and parental dimensions of the human family – the sexual division of labor – evolved subsequently. It must be noted, however, that some building blocks of the modern sexual division of labor probably were already in place at phase 3, an early phase in evolution of the family.⁴³ As bipeds, early hominins had the capacity to transport food and other objects and to practice occasional gathering in order, for example, to eat in safer locations. They probably exhibited sex biases in their subsistence activities, comparable to the male hunting bias and female tool-using bias of chimpanzees.⁷² In all likelihood, they were also disproportionately tolerant of each other when feeding on concentrated and defensible resources, as indicated by the occurrence of food transfers between pair-bonded mates and between consort partners among other primates.^{73,74} On this basis, one may infer that upon the evolution of monogamy, sexual mates already co-fed on resources that either one had transported. Hence, they practiced an embryonic and *de facto* form of “mutual provisioning.”⁴³

Another correlate of the initial family concerns the relative power of sexual mates. Among mammals in general, monogamy is associated with low levels of sexual dimorphism and hence with relatively low discrepancies in physical power between males and females. In humans, moreover, the evolution of monogamy allowed females to recognize and form long-term preferential bonds with their patrilineal kin, including their father. After the primitive tribe (phase 4) had evolved, any adult female was an integral part of an unprecedentedly solid network of kinship-based alliances. This was a drastic departure from the situation in other large mixed-sex primate groups, in which there are no bonds between adult females and their patrilineal kin.^{5,6} Monogamy thus substantially increased the coalitional power of females in relation to unrelated males and, at the same time, reduced the extent of sexual dimorphism. The upshot is that females would have been better able to resist male coercion, refuse

potential suitors, and choose their mating partners on the basis of their own criteria and those of their kin allies, a novelty with potentially far-reaching consequences.

The Sexual Division of Labor

I consider two possibilities for the evolution of the sexual division of labor, which I refer to as the economic pathway hypothesis and the parental pathway hypothesis. Again, my aim here is mainly to illustrate the range of possibilities. According to the economic pathway hypothesis, sexual mates became partners in subsistence well before they were partners in raising children. Among the possible driving forces of economic collaboration is the invention of cooking. As Wrangham⁷⁵ has convincingly argued, cooking increased the digestibility of several food types and substantially enlarged the diet of hominins. In hunter-gatherer societies, cooking is done by women and lies at the very heart of economic interdependence between spouses. Wrangham reasoned that cooked food was a highly prized resource and that, upon adopting it, females became so vulnerable to marauding males that they needed a male protector, with whom they shared cooked food. Here would lie the origin of pair-bonds. But monogamy might well have predated the invention of cooking, in which case cooking would have operated as a major incentive for the development of economic collaboration. Indeed, cooking dramatically increased the proportion of the daily diet that was gathered rather than eaten on the spot. Given the food-sharing biases characterizing sexual partners in primates, it is likely that pair-bonded hominins pooled the food they gathered and cooked it on a single fire. Thus, the conjunction of pair-bonding, regular food gathering, central-spot food processing, tolerated co-feeding, and sex biases in subsistence activities would have set the stage for further levels of coordination and sexual specialization in subsistence activities.

Cooking is only one category of activities among others that might

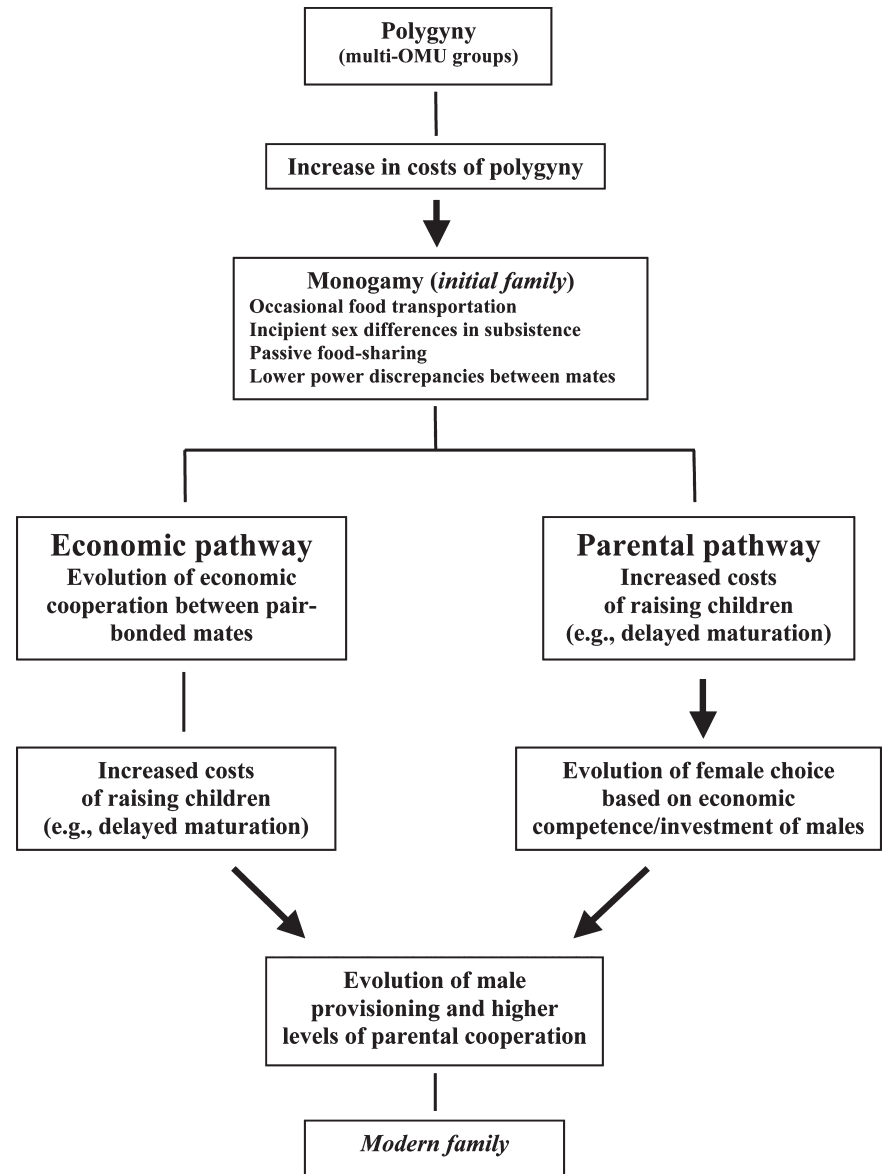


Figure 3. Two possible pathways for the evolution of the economic and parental dimensions of the modern family, assuming that monogamy evolved as a result of constraints on polygyny. Arrows indicate selective pressures, lines the passage of time.

have driven economic cooperation between pair-bonded mates; big-game hunting is another because it also involved food transportation and central place processing.⁴⁹ Whatever the exact force at work, the economic pathway hypothesis states that economic cooperation *per se* had long preadapted hominins for paternal provisioning when the costs of raising children eventually began to increase (Fig. 3).

The parental pathway hypothesis, in contrast, posits that it was the increase in the costs of raising

children that selected for paternal provisioning and the sexual division of labor. The characteristics of the initial monogamous family, including occasional food gathering, sex biases in subsistence activities, food sharing, and father-offspring recognition, had already set the stage for the evolution of paternal provisioning. But an additional factor, increased female choice, which appears to have been neglected in previous discussions, may have played a key role in launching systematic male provisioning. As

monogamy and patrilineal kin recognition increased the coalitional power of females in relation to unrelated males, a female and her allies were better able to choose a male partner on the basis of his capacity to provision and protect the female and her children. This profound change in the dynamics of mate selection would have moved male competition from the arena of physical dominance to the arena of economic competence and paternal provisioning (Fig. 3). From that perspective, therefore, the economic dimension of the human family originated in its parental function and primarily benefited mothers, whereas in the previous hypothesis it originated in its survival function and benefited both sexes equally.

THE EVOLUTION OF STRONGLY BONDED GROUPS

The present framework for the evolution of human social structure also sets constraints on models about the origin of the first multigroup structures. It sees the origin of the primitive tribe in multifamily groups associating together. In earlier work, I discussed the possibility that the first groups to establish strong bonds with each other were daughter-groups issued from the fission of a larger group.⁵ Group fissions are documented in nonhuman primates, including chimpanzees, with large bisexual groups dividing into two daughter-groups that eventually cease interacting with each other.^{76,77} Assuming that group fissions characterized hominins, all groups were initially independent or weakly bonded entities (Fig. 4). But after hominins had evolved the means to form strong bonds between groups, daughter-groups were strongly bonded and part of the same small-scale tribe, and daughter-tribes were part of larger social entities. The nested structure of between-group relations mapped their history.

This model provides an evolutionary explanation for the observation that among hunter-gatherers it is not the tribe, but the band that is the exogamous unit (people marrying

between bands).¹⁹ Chimpanzee communities are outbreeding units. In the present model, bands of hunter-gatherers are the homologous counterparts of chimpanzee communities. This means that bands were exogamous before the evolution of the primitive tribe and remained so thereafter. The model also explains why between-group hostility among hunter-gatherers mostly takes place between tribes,⁷⁸ not between bands of the same tribe: the latter were pacified in relation to each other. In a recent discussion of the evolution of multigroup structures, Layton, O'Hara, and Bilsborough¹⁹ argued for the reverse process: Tribes would have emerged not from bands associating with each other, but from large communities subdividing into bands that remained together thereafter. To argue that, they assumed that the chimpanzee community and the human tribe were homologous entities and that the chimpanzee community was, in fact, a multilevel society comprising three levels of social organization, with mother-offspring units constituting the minimal level. This assertion contradicts the very definition and classification of primate multilevel societies.^{13,14}

In contemporary human societies, alliances between groups involve various types of activities, such as trade, reciprocal access to territories, marital arrangements, cooperative activities between kin and affines, war alliances, athletic games, feasts, and others. In trying to understand the emergence of multigroup structures, a pitfall would consist in using recently evolved aspects of between-group relations to explain their very origin. For example, trade and economic agreements are central components of between-group relations among hunter-gatherers, but they involve cognitively sophisticated processes and are more likely to be a consequence rather than the ultimate source of between-group ties. The present model of the origin of strongly bonded groups relies on the most basic bonding factors in primates: sex and kinship. Significantly, those processes closely match Lévi-Strauss's marriage-based alliance theory, an anthropological model of

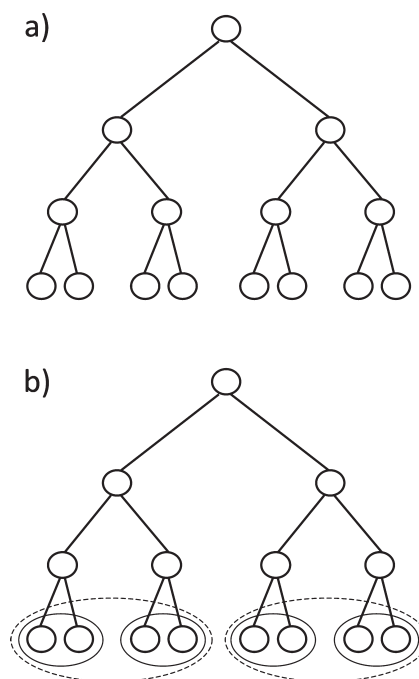


Figure 4. A schematic representation of the evolution of the first multigroup structures through a combined process of group fission and association. Circles, multifamily groups. Lines represent the fission of a group into two daughter-groups. A. Before between-group pacification, all groups are independent entities. B. After between-group pacification, multigroup structures map the history of group fissions.

between-group alliances.²⁴ Although the two models were derived from entirely different theoretical perspectives, they converge on the view that pair-bonding, kinship, and exogamy are the most basic components of between-group alliances.^{5,6}

Based on cladistic considerations, the model posits male philopatry and female dispersal as characterizing the earliest hominins.^{6,42} The mixed nature of residence patterns in hunter-gatherers³⁹⁻⁴¹ does not contradict that view. Bisexual dispersal and flexible residence patterns are seen as requiring between-group pacification, and hence as evolving only after the evolution of the primitive tribe (phase 4). The key aspect of the model is the evolution of patrilineal kinship networks, a uniquely human trait.^{5,6} Stage 2 in the evolution of human social structure is characterized by multi-OMU groups (Fig. 1). In such groups, individuals recognize both their mother and father.

Box 1. Glossary

Affines - in-laws; the relatives of one's spouse or stable sexual mate; the spouses of one's relatives.

Federation of multifamily groups - the denomination proposed here to characterize human societies in relation to other primate societies. "Federation" refers to the following criteria: strongly bonded groups, group-wide coordination, and multigroup coordination.

Monogamy - the term is used here as shorthand for social monogamy, a stable breeding bond between one male and one female, which, unlike sexual monogamy, does not exclude extra-pair sexual activity.

Multifamily group - type of multi-OMU group in which most reproductive units are monogamous. Humans form multifamily groups.

Multilevel society - among non-human primates, a society composed of two to four nested levels of social organization. Human societies are a particular type of multilevel society.

Multimale-multifemale group - group composed of several males and females breeding promiscuously, so that there are no stable breeding bonds between particular males and females.

Multi-OMU group - cohesive group composed of several one-

male units (OMUs), the majority of which are polygynous.

Strongly bonded groups - groups linked by actual social relationships between particular kin and between particular in-laws and possibly other individuals, and manifest in the context of group meetings or intergroup visiting. Strongly bonded groups probably are uniquely human.

Weakly bonded groups - groups forming temporary aggregations around common resources. Those aggregations appear to involve no actual relationships between particular kin or "in-laws." In multilevel primate societies, multi-OMU groups may form such aggregations.

However, as discussed, the intensity of male sexual competition is apparently not conducive to the development of kin-differentiated networks of cooperative relationships among males, through which individuals would be in a position to recognize their father's relatives. The evolution of monogamy (stage 3) would have removed that obstacle, for it coincided with a substantial reduction in levels of male sexual competition. By enabling the recognition of patrilineal kin, monogamy would have brought about a dramatic expansion of the domain of kin recognition.

As argued at length elsewhere,^{5,6} in this novel context females were in a position to develop strong, intimate relationships with their patrilineal kin over several years before moving to another group (for example, female chimpanzees emigrate at around 11 years of age). After entering a new group, a female formed a mating bond with a male, himself bonded to several male kin. Thus, from then on, transferred females were simultaneously bonded to particular males in both their natal group (consanguineal ties) and their group of adoption (affinal ties). When two multifamily groups came

into contact as part of the same loose aggregation (stage 3), adult males from one group would recognize their female kin living in the other group and refrain from attacking them and their newborn offspring, a situation that set the stage for actual between-group kinship bonds. At the same time, transferred females would create familiarity biases between their kin and their long-term sexual partners (for example, between brothers-in-law or fathers-in-law and sons-in-law), with this instigating between-group affinal bonds. The outcome of the two categories of processes operating concurrently would have been a state of mutual tolerance between interbreeding groups.

The resulting primitive tribe presumably exhibited several new features that characterize modern human societies. These include multigroup social networks; peaceful relations between groups belonging to the same tribe; bisexual dispersal and the ensuing diversification of residence patterns; lifetime bonds between cross-sex kin, which set the stage for phenomena like avuncular relationships; incipient mating biases between affines (for example, levirate,

sororate, sister exchange, and cross-cousin unions); and the potential for bilateral grandmothing.^{5,6}

CONCLUSION

The interest of the present, mainly deductive approach to the study of human social structure lies in three points. First, the proposed sequence points to issues that have not been given enough attention. For example, whether the multifamily composition of human groups evolved through the subdivision of multimale-multifemale groups into multi-OMU groups or through the grouping of autonomous polygynous units needs further research. Notably, small-scale⁷⁹ and large-scale comparative phylogenetic analyses of primate social structures are needed,⁶⁴ but ones in which multilevel societies are treated as a separate category in relation to other categories of social structures.

Second, the sequence sets phylogenetic and structural constraints on existing hypotheses; for example, a direct transition from sexual promiscuity to a community of monogamous families appears unlikely. As another example, the potential impact of cooperative breeding on

human evolution^{1,2} would have been greatest after the evolution of the primitive tribe because by then an individual's social network included kin on both the mother's and father's sides, in addition to affines. This leads to the idea that the expansion of cooperative breeding in phase 4 might have selected for the cognitive changes, such as theory of mind and shared intentionality, that would eventually enable hominins to move to the federated community (phase 5) and its high levels of between-group coordination.

Third, the sequence generates new hypotheses. This was exemplified with the evolution of monogamy and the sexual division of labor. All six hypotheses are testable because they predict different temporal relations between the markers of pair-bonding (low sexual dimorphism), increased maternity costs (delayed maturation, brain size), and subsistence activities such as cooking or cooperative hunting. For example, the paternal load hypothesis for the polygyny-to-monogamy transition predicts that low levels of sexual dimorphism and delayed maturation evolved concurrently, whereas the leveling hypothesis predicts that low levels of sexual dimorphism predated delayed maturation and coincided with the anatomical markers of weapon-induced wounds. Similarly, the competing hypotheses that cooking or big-game hunting either brought about pair-bonding or followed the evolution of pair-bonding predict distinct temporal relations between the markers of pair-bonding and those of cooking or big-game hunting.

The present sequence of social structures was developed independently of paleo-anthropological data and thus can be tested against those data. One expects specific temporal relations between the anatomical and artifactual markers corresponding to the behavioral and life-history correlates of each phase. For example, the sequence predicts that male philopatry predated bisexual dispersal, polygyny predated the human-like monogamy/polygyny mix, monogamy predated the primitive tribe, and important cognitive

changes predated the federated tribe. Such predictions are testable⁸⁰ and debatable.⁸¹

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REFERENCES

- Hrdy SB. 2009. Mothers and others: the evolutionary origins of mutual understanding. Cambridge, MA: Harvard University Press.
- Burkart JM, Hrdy SB, van Schaik C. 2009. Cooperative breeding and human cognitive evolution. *Evol Anthropol* 18:175–186.
- Foley R, Gamble C. 2009. The ecology of social transitions in human evolution. *Philos Trans R Soc B* 274:2195–2202.
- Swedell L, Plummer T. 2012. A papionin multilevel society as a model for hominin social evolution. *Int J Primatol* 33:1165–1193.
- Chapais B. 2008. Primeval kinship: how pair-bonding gave birth to human society. Cambridge, MA: Harvard University Press.
- Chapais B. 2010. The deep structure of human society: primate origins and evolution. In: Kappeler PM, Silk JB, editors. *Mind the gap: tracing the origins of human universals*. Berlin: Springer, p 19–51.
- Tomasello M. 1999. The cultural origins of human cognition. Cambridge, MA: Harvard University Press.
- Mc Grew W. 2004. The cultured chimpanzee. Cambridge: Cambridge University Press.
- van Schaik C. 2004. Among orangutans: red apes and the rise of human culture. Cambridge, MA: Harvard University Press.
- Whiten A. 2010. Ape behavior and the origins of human culture. In: Kappeler PM, Silk JB, editors. *Mind the gap: tracing the origins of human universals*. Berlin: Springer, p 429–450.
- Brown DE. 1991. Human universals. Boston: McGraw Hill.
- Rodseth L, Wrangham RW, Harrigan AM, et al. 1991. The human community as a primate society. *Curr Anthropol* 32:221–254.
- Swedell L. 2011. African papionins: diversity of social organization and ecological flexibility. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, editors. *Primates in perspectives*. New York: Oxford University Press, p 241–277.
- Grueter CC, Chapais B, Zinner D. 2012. Evolution of multilevel social systems in non-human primates and humans. *Int J Primatol* 33:1002–1037.
- Kirkpatrick RC. 2011. Asian colobines: diversity among leaf-eating monkeys. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, editors. *Primates in perspective*. New York: Oxford University Press, p 189–202.
- Low BS. 2003. Ecological and social complexities in human monogamy. In: Reichard UH, Boesch C, editors. *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. Cambridge: Cambridge University Press, p 161–176.
- Marlowe FW. 2003. Paternal investment and the human mating system. *Behav Processes* 51:45–61.
- Henrich J, Boyd R, Richerson PJ. 2012. The puzzle of monogamous marriage. *Philos Trans R Soc B* 367:657–669.
- Layton R, O'Hara S, Bilsborough A. 2012. Antiquity and social functions of multilevel social organization among human hunter-gatherers. *Int J Primatol* 33:1215–1245.
- Fortunato L, Archetti M. 2010. Evolution of monogamous marriage by maximization of inclusive fitness. *J Evol Biol* 23:149–156.
- Schmitt DP. 2005. Fundamentals of human mating strategies. In: Buss DM, editor. *The handbook of evolutionary psychology*. Hoboken, NJ: John Wiley & Sons, p 258–291.
- Apostolou M. 2007. Sexual selection under parental choice: the role of parents in the evolution of human mating. *Evol Hum Behav* 28:403–409.
- Walker RS, Hill KR, Flinn MV, et al. 2011. Evolutionary history of hunter-gatherer marriage practices. *PLoS ONE* 6: e19066.
- Lévi-Strauss C. 1969. The elementary structures of kinship. Boston: Beacon Press.
- Silk JB. 2007. The strategic dynamics of cooperation in primate groups. *Adv Stud Behav* 37:1–40.
- Brosnan SF, Silk JB, Henrich J, et al. 2009. Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task. *Anim Cogn* 12:587–597.
- Kapsalis E, Berman CM. 1996. Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*). I. Criteria for kinship. *Behaviour* 133:1209–1234.
- Chapais B, Savard L, Gauthier C. 2001. Kin selection and the distribution of altruism in relation to degree of kinship in Japanese macaques (*Macaca fuscata*). *Behav Ecol Sociobiol* 49:493–502.
- Widdig A. 2007. Paternal kin discrimination: the evidence and likely mechanisms. *Biol Rev* 82:319–334.
- Rendall D. 2004. Recognizing kin: mechanisms, media, minds, modules, and muddles. In: Chapais B, Berman CM, editors. *Kinship and behavior in primates*. New York: Oxford University Press, p 295–316.
- Lehmann J, Fickenscher G, Boesch C. 2006. Kin biased investment in wild chimpanzees. *Behaviour* 143:931–955.
- Langergraber KE, Mitani JC, Vigilant L. 2007. The limited impact of kinship on cooperation in wild chimpanzees. *Proc Natl Acad Sci USA* 104:7786–7790.
- Le Roux SR, Beehner JC, Bergman TJ. 2011. Female philopatry and dominance patterns in wild geladas. *Am J Primatol* 73:422–430.
- Colmenares F. 2004. Kinship structure and its impact on behavior in multilevel societies. In: Chapais B, Berman CM, editors. *Kinship and behavior in primates*. New York: Oxford University Press, p 242–270.
- Berman CM. 2004. Developmental aspects of kin bias in behavior. In: Chapais B, Berman CM, editors. *Kinship and behavior in primates*. New York: Oxford University Press, p 317–346.
- Chapais B. 2011. The deep social structure of humankind. *Science* 331:1276–1277.
- Fox R. 1980. The red lamp of incest. New York: Dutton.

- 38 Swedell L, Saunders J, Schreier A, et al. 2011. Female "dispersal" in hamadryas baboons: transfer among social units in a multi-level society. *Am J Phys Anthropol* 145:360–370.
- 39 Marlowe FW. 2004. Marital residence among foragers. *Curr Anthropol* 45:77–284.
- 40 Hill KR, Walker RS, Bozicevic M, et al. 2011. Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science* 331:1286–1289.
- 41 Walker RS, Beckerman S, Flinn MV, et al. 2012. Living with kin in lowland horticultural societies. *Curr Anthropol* 54:96–103.
- 42 Wrangham R. 1987. The significance of African apes for reconstructing human social evolution. In: Kinzey WG, editor. *The evolution of human behavior: primate models*. Albany: State University of New York Press, p 51–71.
- 43 Chapais B. 2011. The evolutionary history of pair-bonding and parental collaboration. In: Salmon C, Shackelford T, editors. *The Oxford handbook of evolutionary family psychology*. New York: Oxford University Press, p 33–50.
- 44 Barton RA. 1999. Socioecology of baboons: the interaction of male and female strategies. In: Kappeler PM, editor. *Primate males: causes and consequences of variation and group composition*. Cambridge: Cambridge University Press, p 97–107.
- 45 Tomasello M. 2008. *Origins of human communication*. Cambridge, MA: MIT Press.
- 46 Tomasello M, Moll H. 2010. The gap is social: human shared intentionality and culture. In: Kappeler PM, Silk JB, editors. *Mind the gap: tracing the origins of human universals*. Berlin: Springer, p 331–349.
- 47 Gurven M, Hill K. 2009. Why do men hunt? A reevaluation of "man the hunter" and the sexual division of labor. *Curr Anthropol* 50:51–74.
- 48 Hawkes K, O'Connell JF, Coxworth JE. 2010. Family provisioning is not the only reason men hunt: a comment on Gurven and Hill. *Curr Anthropol* 51:259–264.
- 49 Kaplan HS, Hill KR, Lancaster JB, et al. 2000. A theory of human life history evolution: diet, intelligence and longevity. *Evol Anthropol* 9:156–185.
- 50 Hawkes K. 2004. Mating, parenting, and the evolution of human pair bonds. In: Chapais B, Berman CB, editors. *Kinship and behavior in primates*. New York: Oxford University Press, p 443–473.
- 51 Quinlan RJ. 2008. Human pair-bonds: evolutionary functions, ecological variation, and adaptive development. *Evol Anthropol* 17:227–238.
- 52 Kaplan HS, Hooper PL, Gurven M. 2009. The evolutionary and ecological roots of human social organization. *Philos Trans R Soc B* 364:3289–3299.
- 53 Hill K, Barton K, Hurtado M. 2009. The emergence of human uniqueness: characters underlying behavioral modernity. *Evol Anthropol* 18:187–200.
- 54 Flinn MV, Quinlan RJ, Coe K, et al. 2007. Evolution of the human family: cooperative males, long social childhoods, smart mothers, and extended kin networks. In: Salmon CA, Shackelford TK, editors. *Family relationships: an evolutionary perspective*. Oxford: Oxford University Press, p 16–38.
- 55 van Schaik CP, Dunbar RIM. 1990. The evolution of monogamy in large primates: a new hypothesis and some crucial tests. *Behaviour* 115:30–62.
- 56 Smuts BB. 1992. Male aggression against women: an evolutionary perspective. *Hum Nat* 3:1–44.
- 57 Palombit RA. 2010. Conflict and bonding between the sexes. In: Kappeler PM, Silk JB, editors. *Mind the gap: tracing the origins of human universals*. Berlin: Springer, p 53–83.
- 58 Fisher H. 2006. *Why we love: the nature and chemistry of romantic love*. New York: Henry Holt.
- 59 Lovejoy CO. 2009. Reexamining human origins in light of *Ardipithecus ramidus*. *Science* 326:108–115.
- 60 Gavrilets S. 2012. Human origins and the transition from promiscuity to pair-bonding. *Proc Natl Acad Sci USA* 109:9923–9928.
- 61 Gomes CM, Boesch C. 2009. Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS ONE* 4:1–6.
- 62 Gilby I, Emery Thompson M, Ruane JD, et al. 2010. No evidence of short-term exchange of meat for sex among chimpanzees. *J Hum Evol* 59:44–53.
- 63 Brotherton PMN, Komers PE. 2003. Mate guarding and the evolution of social monogamy in mammals. In: Reichard UH, Boesch C, editors. *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. Cambridge: Cambridge University Press, p 42–58.
- 64 Shultz S, Opie C, Atkinson QD. 2011. Stepwise evolution of stable sociality in primates. *Nature* 479:219–222.
- 65 Churchill SE, Rhodes JA. 2009. The evolution of the human capacity for "killing at a distance": the human fossil evidence for the evolution of projectile weaponry. In: Hublin JJ, Richards MP, editors. *The evolution of hominin diets: integrating approaches to the study of Paleolithic subsistence*. Berlin: Springer, p 201–210.
- 66 Flinn MV, Geary DC, Ward CV. 2005. Ecological dominance, social competition, and coalitional arms races: why humans evolved extraordinary intelligence. *Evol Hum Behav* 26:10–46.
- 67 van Schaik C, Kappeler PM. 2003. The evolution of social monogamy in primates. In: Reichard UH, Boesch C, editors. *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. Cambridge: Cambridge University Press, p 59–80.
- 68 Borries C, Savini T, Koenig A. 2011. Social monogamy and the threat of infanticide in larger mammals. *Behav Ecol Sociobiol* 65:685–693.
- 69 Alexander RD, Noonan KM. 1979. Concealment of ovulation, parental care and human evolution. In: Chagnon NA, Irons W, editors. *Evolutionary biology and human behavior: an anthropological perspective*. North Scituate, MA: Duxbury Press, p 436–453.
- 70 Dixson AF. 1998. *Primate sexuality: comparative studies of the prosimians, monkeys, apes, and human beings*. Oxford: Oxford University Press.
- 71 Dixson AF. 2009. *Sexual selection and the origins of human mating systems*. Oxford: Oxford University Press.
- 72 McGrew WC. 1992. *Chimpanzee material culture: implications for human evolution*. Cambridge: Cambridge University Press.
- 73 Wolovich CK, Perea-Rodriguez JP, Fernandez-Duque E. 2007. Food transfers to young and mates in wild owl monkeys (*Aotus azarai*). *Am J Primatol* 69:1–16.
- 74 Van Noordjwick MA, van Schaik CP. 2009. Intersexual food transfer among orangutans: do females test males for coercive tendency? *Behav Ecol Sociobiol* 63:883–890.
- 75 Wrangham RW. 2010. *Catching fire: how cooking made us human*. New York: Basic Books.
- 76 Wilson ML, Wrangham RW. 2003. Inter-group relations in chimpanzees. *Ann Rev Anthropol* 32:363–392.
- 77 Okamoto K. 2004. Patterns of group fission. In: Thierry B, Singh M, Kaumanns W, editors. *Macaque societies: a model for the study of social organization*. New York: Cambridge University Press, p 112–116.
- 78 Rodseth L, Wrangham R. 2004. Human kinship: a continuation of politics by other means? In: Chapais B, Berman CB, editors. *Kinship and behavior in primates*. New York: Oxford University Press, p 389–419.
- 79 Grueter CC, van Schaik CP. 2010. Evolutionary determinants of modular societies in colobines. *Behav Ecol* 21:63–71.
- 80 Copeland SR, Sponheimer M, de Ruiter DJ, et al. 2011. Strontium isotope evidence for landscape use by early hominins. *Nature* 474:76–78.
- 81 Koenig A, Borries C. 2012. Hominoid dispersal patterns and human evolution. *Evol Anthropol* 21:108–111.