

# Eusociality: Origin and consequences

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**In this new assessment of the empirical evidence, an alternative to the standard model is proposed: group selection is the strong binding force in eusocial evolution; individual selection, the strong dissolutive force; and kin selection (narrowly defined), either a weak binding or weak dissolutive force, according to circumstance. Close kinship may be more a consequence of eusociality than a factor promoting its origin. A point of no return to the solitary state exists, as a rule when workers become anatomically differentiated. Eusociality has been rare in evolution, evidently due to the scarcity of environmental pressures adequate to tip the balance among countervailing forces in favor of group selection. Eusociality in ants and termites in the irreversible stage is the key to their ecological dominance and has (at least in ants) shaped some features of internal phylogeny. Their colonies are consistently superior to solitary and preeusocial competitors, due to the altruistic behavior among nestmates and their ability to organize coordinated action by pheromonal communication.**

In eusociality, an evolutionarily advanced level of colonial existence, adult colonial members belong to two or more overlapping generations, care cooperatively for the young, and are divided into reproductive and nonreproductive (or at least less-reproductive) castes. The phenomenon is well marked and nearly confined to insects, especially ants, bees, wasps, and termites, where it has been subject to a large body of mostly specialized research scattered across disciplines from genetics to paleontology. It has long been the conviction of researchers on social insects that common principles exist at the organismic and superorganismic levels, thus between individual insects and the tightly integrated colonies they compose (1, 2). Parallels have been persuasively drawn between the self-construction of organisms from molecules and tissues and that of superorganisms from interacting entire organisms (3). The principles can be further parsed into two segments of the time scale: the developmental decision rules that assemble organisms and colonies in each generation and the origin of these rules through evolutionary time.

Focusing here on the second principle, evolutionary process, we suggest how three seemingly disparate evolutionary phenomena can be causally linked: the selection forces that generate and shape eusociality, the rareness of the origin of eusociality, and the ecological hegemony of eusocial insects.

## The Forces of Natural Selection

Research during the past half century has incrementally clarified the nature of the collective forces that create and shape eusociality. At the most basic level, an allele or ensemble of alleles prescribing phenotypic plasticity that includes self sacrifice of some members

of groups will spread if the positive intergroup component of the altruists' fitnesses exceeds the negative within-group component of the altruists' fitnesses (4–6). Altruism is defined as behavior that benefits others at the cost of the lifetime production of offspring by the altruist. The forces that determine this outcome are group selection, the differential survival and reproduction of entire cooperative groups as a result of the frequency of the eusociality alleles in each; individual direct selection, accruing from the differential personal survival and reproduction of each of the colony members; and kin (indirect) selection, which we define here in the original narrow sense as the favoring or disfavoring by individuals of collateral relatives, i.e., relatives other than personal offspring. The inclusive fitness of the prescribing genotype, of individual colony members and hence statistically the colonies they compose, is the nonadditive product of the three forces. The definition of kin selection in the commonly used broad sense, which folds in individual direct selection as well, produces results that are consistent with those from the narrow sense but intuitively less clear and less practicable in application. It also leads to such confounding statements as “solitary species evolve by kin selection.” When the broad definition of kin selection is used (offspring included), colony selection and kin selection are reduced to just alternative ways of viewing change in the frequency of eusociality alleles in a population structured by relatedness (4, 5). This formulation raises basic theory to a high level of mathematical inclusiveness and abstraction, but it departs from the earlier and very heuristic narrow definition of kin selection; further, the dynamical terms of the population genetic models composing the

theory are difficult to relate to the complexities of tangible social phenomena.

We suggest that each force can be heuristically classified as binding or dissolutive in its effect on colony cohesion and either strong or weak in its relative power. The degree of relatedness, the similarity across the whole genome of individuals as a result of recent common ancestry, is a factor that biases the direction and strength of the forces. When elevated, say by lower individual dispersal rates, relatedness can bring alleles for presociality and eusociality together more quickly. If it brings such genes together more frequently due to shared microhabitat preference, mate choice, or other biological traits, it can have the same effect. Relatedness can also increase variance in presocial and eusocial alleles among groups, thus quickening the pace of colony selection. But relatedness is relevant only insofar as it affects the frequency of alleles that prescribe social behavior. Eusociality arises by the superiority of organized groups over solitaires and cooperative preeusocial groups. It can, in theory at least, be initiated by group selection in either the presence or absence of close relatedness and, when close relatedness exists, also in the presence or absence of kin selection. Conversely, eusociality cannot arise without the driving force of group selection, regardless of the degree of relatedness within local populations or cooperative aggregations.

Group selection which with the addition of cooperative behavior becomes colony selection, is the result of the interaction of entire groups with their environments (6, 7–11), conditioned by the efficiency of their internal opera-

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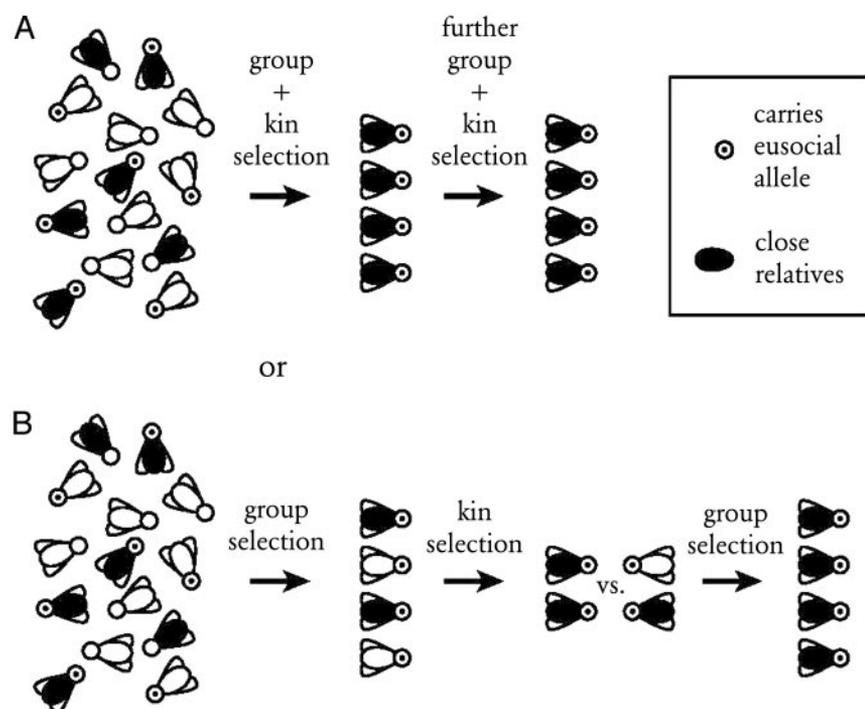
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tions (12). It promotes harmony among group members and genetic fitness of the group as a whole, once colony level is attained, and its effect is thereby inherently binding. Individual direct selection and kin selection play out in the social interactions of the colony members. By pitting individual members and nepotisms against one another, individual direct selection tends to reduce colony harmony and genetic fitness. Depending on circumstance, kin selection can be either binding or dissolutive, the latter by competition among nepotistic subgroups. In all of this multilevel theater of evolution, the gene remains the unit of selection, whereas the target of selection can be the individual, the group, or nepotistic alliances or otherwise biased actions within the group.

### The Point of No Return

An abundance of evidence suggests that the strength of the biasing role of relatedness within a species depends on the stage of its social evolution. The key transition occurs at a point in colony evolution that can be conveniently called the point of no return (13). Beyond this level, it is impossible, or at least difficult and uncommon, for a species to regress from the eusocial to a more primitively eusocial, presocial, or solitary condition.

When in evolution does eusociality become irreversible? We infer that this comes very early in the evolution of that condition, in particular when an anatomically distinct worker caste first appears, hence when a colony can most meaningfully be called a superorganism. Three lines of solitary halictine bees and one of allodapine apid bees are known to have originated from primitively eusocial lines, in which the worker caste was not yet anatomically distinct (14, 15). In contrast, not a single such reversal is known among the >11,000 described species of ants (family Formicidae) or 2,000 described termites (order Isoptera). Both of these taxonomic groups contain many species with relatively primitive social organizations, but whose worker caste is anatomically distinct or else are social parasites derived from lines in which this trait previously existed and that now depend on host workers. The same evidence concerning the lack of evolutionary reversal is offered by the scores of lines of polistine and vespine wasp species that possess an anatomical worker caste. The only known exceptions to this rule are several lines of thrips (16) and aphids (17) that have lost the nonreproductive soldier caste and hence reverted from eusociality to cooperative breeding.



**Fig. 1.** The two competing hypotheses of the origin of eusociality in insects and thence before the point of no return. The first (A) holds that in the earliest stage, kin selection is binding, making close relatedness a key feature; if combined with group selection, kin selection favors primitively eusocial colonies in a population of solitary or preeusocial insects (far left). The second hypothesis (B), newly presented here, holds in contrast that group selection is paramount as the binding force, and kin selection is minor or absent as a binding force for the group as a whole and weakly dissolutive if it forms competing groups. Relatedness, in hypothesis B, is increased as group selection cleanses the dissolutive nepotisms effect of kin selection. The empirical evidence appears to favor, but does not conclusively prove, B.

### The Origin of Eusociality

A key question remaining is whether, in fact, relatedness is an important biasing factor and hence kin selection an important force in the origin and maintenance of eusociality. For the origin and evolution of eusociality before the point of no return, a new and alternative model should be considered. The two competing hypotheses can be compared as follows (see also Fig. 1).

**Model A.** In the standard model, altruism originates by selection of its prescribing alleles through a kin network. Kin selection is thus strongly binding, whereas individual direct selection is dissolutive. Group selection from environmental pressure and kin selection drive the system. Close genetic relatedness precedes the origin of eusociality.

**Model B.** In the alternative model, which we propose here, altruism originates by group selection of prescribing alleles whose phenotypic expression is flexible, directing individuals to become reproductives or workers according to physiological or behavioral cues. Kin selection can be absent, weakly binding, or weakly dissolutive, according to evolutionary

stage and circumstance, but it does not join group selection from environmental pressure in driving the system. Close genetic relatedness arises from eusociality but is not a necessary precondition.

In the second model, alleles exist that induce cooperation and possess phenotypic plasticity, which includes a nongenetic worker caste. If these alleles are favored by sufficiently powerful colony selection, eusociality can originate when founding members of the primitive colonies have low relatedness or, in theory (and albeit unlikely), none at all (18, 19). What counts is the common possession of eusociality alleles, not relatedness. However, the probability that others share such alleles is obviously higher in closely related than in unrelated individuals (after all, when such an allele arises, it most likely spreads in a population of relatives).

Thus, if the second, opposing hypothesis is correct, the high relatedness generally observed in even the evolutionarily primitive colonies could be more a consequence than a cause of eusociality and not a necessity for its origin. Preeusocial groups formed of parents and offspring would automatically have close kinship. In the hypothe-

sis we offer here, groupwide relatedness is raised in the following two steps: group selection leads to eusociality with little or no binding kin selection, then further group selection raises the degree of relatedness by reducing the dissolutive effects of selfish individual behavior and (in the event binding kin selection occurs) nepotistic competition arising from the kin selection that variously favors different genetic subgroups. Another way of expressing the process is that as the degree of relatedness drops, the dissolutive effect of individual selection and kin selection increases, and as the degree of relatedness rises through group selection, the dissolutive effects of individual selection and kin selection decline. Close relatedness at the outset accelerates the concentration of eusociality genes but does not work as a selective force. Although quickly favored by group selection, close relatedness is not a form of kin selection, which is the preferential favoring of collateral relatives (i.e., not including offspring) within groups according to their degree of relationship.

Evidence from living presocial and primitively eusocial species that might distinguish between the two hypotheses and shed light on the importance of genetic relatedness is still tenuous. But it is at least consistent with the second hypothesis, namely that relatedness is less powerful a factor and kin selection often more dissolutive in the early stages of colonial evolution than previously suspected. Xylocopine carpenter bees, which are facultatively semisocial and possibly examples of an early stage in the origin of eusociality, often form pairs, which then divide into queen and worker roles by means of a dominance order. Subordinates prefer to stay if unrelated but to leave if related. The result is consistent with kin selection, but the effect is dissolutive rather than binding (20). Thus, group selection appears not to be yet strong enough to counteract dissolutive kin selection. Groups of bees in the allodapine genus *Exoneura* have higher per capita productivity when the members are closely related but individual reproduction approaches uniformity, as expected from group selection, and, if sustained in the absence of sufficiently strong colony selection, would seem to preclude the origin of an altruistic worker caste (21). In the very primitively eusocial wasp *Eustenogaster fraterna*, founding females have lower relatedness than sisters and, due to high adult turnover, the relatedness of unmated females to female brood is far lower ( $r = 0.210 \pm 0.171$ , 95% confidence intervals) (22). Among somewhat primitively eusocial paper wasps

(*Polistes*), females act less aggressively toward genetic relatives than toward nonrelatives but do not favor close over distant relatives when founding colonies (23). Similar results obtained from the primitively eusocial wasps of the genus *Ropalidia* demonstrate that relatedness plays no significant role in eusocial organization (24).

Also arguing against a strong biasing role of relatedness and binding force of kin selection in the origin of eusociality is the collapse of the “haplodiploid hypothesis,” an early and once persuasive stanchion of the standard model, due to the discovery in recent years of enough phylogenetically separate lines (9) to render the association of haplodiploidy and eusociality originations statistically independent.

Finally, the rarity of the evolutionary origin of eusociality also appears to argue against the standard model and favor its alternative, a point to be elaborated shortly.

### Beyond the Point of No Return

In the later stages of eusocial evolution, past the point of no return, the favoring of close collateral kin has been depicted as dissolutive in some respects but also, and much more importantly (with some writers demurring to variable degree), as a strong binding force crucial to the maintenance of altruism and eusociality. A growing body of evidence of several kinds now suggests otherwise. It includes the rarity of male production by workers in colonies of social hymenopterans (ants, bees, and wasps), with one single-mated queen, contrary to the prediction from models of narrow kin selection (25); the lack of favoring bias by workers of their respective mothers in colonies with multiple queens, also at variance with traditional expectation (26, 27); and the existence of unexpected low degrees of relationship, in some cases approaching background values, in many species of ants (27). Moreover, nestmate recognition in the social Hymenoptera is by colony scent, which turns out to be a complex gestalt of hydrocarbons absorbed into the outer cuticle of the exoskeleton, shared by food exchange and grooming, learned by imprinting, and largely independent of kinship in composition (25, 28). In an ant checked for such correlations (*Pogonomyrmex occidentalis*), colonies with low relatedness among the workers have overwhelmingly higher growth and reproduction rates than those with high worker relatedness (29). This effect, favoring group selection as opposed to kin selection as the binding force, may be due to improved genetic resistance to disease or to the enhancement of divi-

sion of labor by genetic proneness to specialization by the workers.

At the same time, a great many studies have implicated kin selection as a weak dissolutive force arising from nepotism and conflict among colony members. Its principal documented effect is the perturbation of sex investment ratios in the social Hymenoptera away from the expected 1:1 Fisherian balance. The perturbation stems from the haplodiploid mode of sex determination in the Hymenoptera, which causes ratios in singly mated mother queens (1:1) to differ from those of her daughter workers (more investment in new virgin queens than in males) (4, 5).

A second phenomenon possibly biased by relatedness and established in the later, irreversible stage of eusocial evolution is policing, the use of harassment or selective egg removal to restrict reproduction to the reproductive individual. Kin selection has been strongly indicated as a binding force in one species of social wasps, where policing decreases with the relatedness of the workers (30). On the other hand, the role of kin selection has been eliminated altogether in favor of group selection in the Cape race of the honey bee (31) and several species of ponerine and formicine ants (32–36).

### The Rariness of Eusociality

The colonial insects thus seemingly command us to turn back to the external environment and group selection and away from a preoccupation with abstract models of kin selection if we are to best understand the origin and maintenance of eusociality. That frame shift is consistent with a remarkable phenomenon that has been in plain sight but largely overlooked by investigators: the phylogenetic rarity of eusociality. Of the  $\approx 2,600$  living taxonomic families of insects and other arthropods currently recognized, only 15 are known to contain eusocial species (13, 24, 37). Because six of the eusocial families are termites, the living species of which apparently derived from a single phylad, whereas eusociality of halictid bees originated in three independent events (15), the total number of known origins of eusociality in arthropods is 12.

It follows that some property of nature has set a very high bar for the attainment of eusociality. The inhibiting property is most likely to be the dissolutive force of individual direct selection. Even the large number of phyletic lines where individuals nest in aggregates and disperse to a limited degree, including those that reproduce by cloning ( $r = 1$ ), have not in the vast majority of cases vaulted the bar. It seems to follow that

only some additional extraordinary circumstance or set of circumstances in their prior history and in the environmental challenge they faced lifted them over the bar. When those rare conditions exist, it is not difficult to imagine how the plasticity of a single genome can be molded by group selection first to create cooperative breeding and then caste systems (the defining property of eusociality). The adaptive programming of phenotypic plasticity to fit environmental contingency is a well established principle of genetics (38). So even if colony selection renders some individuals sterile drudges or suicidal defenders, it does not matter, because neither deviants who leave to try their luck as solitaires nor colonies weakened by their deviancy can compete against well integrated colonies of the same species. Even if workers retain the ability to reproduce and dissolutive individual selection remains potentially strong, their prudent cooperation could be enhanced by programming into the hereditary social repertory through the acceptance of “bribes” of small amounts of reproduction bestowed by the dominant queens or by the dominant collectivity of nestmates, or else the prospect of assuming the role of primary reproductive in the event of the death of the queen (39).

### Colony Selection as the Driver

The defining nature of the programs of developmental plasticity in insect superorganisms can be more clearly visualized by the metaphor of the colony as a factory inside a fortress. The factory is the egg-laying queen together with the nurse workers who rear the young to maturity, whereas the fortress is the nest and the workers who build, repair, and guard it (12, 40).

Several evolutionary rules have emerged from decades-long studies of the insect fortress and factory. All point to ecological colony selection as the strong binding force of eusocial evolution. First is the necessity of preadaptation. The known eusocial phyletic lines with primitive species still living stand out among closely related solitary phyletic lines in adaptations that evidently predisposed them to forming colonies. In the Hymenoptera, for example, at least seven independent lines among the 60,000 or so known species of wasps and bees (with ants added, composing the division Aculeata of the hymenopteran suborder Apocrita) have evolved eusociality, evidently from ancestral species that built nests and fed their larvae with prey or pollen. In contrast, not one of the >70,000 known sawflies (suborder Symphyta) and parasitic hymenopterans (division Parasitica of the Apocrita) are

eusocial, and in none extant do adults build nests or provision their young. Other eusocial species, those outside the Hymenoptera, have descended from species adapted to unusually well protected microhabitats that can be most effectively used and defended by groups. They include green-wood borings (the ambrosia beetle *Austroplatypus*) (41), plant galls (aphids and thrips) (42, 43), and, in the one known example among crustaceans, cavities in sponges (*Synalpheus* snapping shrimps) (44).

A second rule is consistent with the first: the key adaptation that led to eusociality is defense against enemies, specifically predators, parasites, and competitors (9, 45). Numerous studies, especially those on ants, have shown that groups are more effective in defense than solitary individuals and large groups more effective than small groups. In more advanced species, with larger mature colonies and recruitment communication, colonies gain further advantage from their superior foraging methods (25, 46).

Along with the establishment of the fortress has been the evolutionary development of the factory. The division of labor has grown stronger along phyletic lines, first between reproductives and workers and then within the worker caste. Communication has grown in complexity. Judging by comparison among living species, signals of fertility status and colony recognition were first; then alarm signals; next, recruitment to food sources and new nest sites by successful foragers; then mass foraging and, depending on the timing and spatial distribution of resources, long-lasting trunk trails; and finally, territorial defense by territorial pheromone marking, ritualized tournaments, and other sophisticated exchanges (25).

Correlative studies across large numbers of eusocial insect species provide strong evidence that the colony life cycle of each species, along with the details of its caste and communication system, has been shaped by the particular environments in which the species occurred through evolutionary time. The most important predictor of evolved social complexity is mature colony size (25, 46). Among species of eusocial bees and wasps, for example, an evolutionary increase in the populations was generally accompanied by elaboration of the division of labor, together with increased complexity in the modes of caste determination and changes in the modes of fertility signaling. Caste shifted from a flexibly behavioral relationship among anatomically similar females to complete dimorphism in which the status of colony members is deter-

mined in larval life or even in part genetically (13, 37).

Among the >11,000 known species of ants, mature colony size, varying by six orders of magnitude, is correlated with sociobiological trends parallel to those of bees and wasps. It is also manifestly adapted to nest sites and food habits particular to each species in turn. At one extreme are the tens of workers of some predatory ponerine colonies that occupy preformed cavities in decaying vegetation and specialize variously on polyxenid millipedes, centipedes, beetles, and other restricted prey. At the other extreme are the gigantic colonies of African driver ants, with >20 million workers, that live in large excavated soil cavities and hunt in armies for a wide range of arthropod and small vertebrate prey (25).

The origin of colonies with mature colony populations of  $10^5$  and higher, bolstered by major innovations in colony organization, is a rare event, like the origin of eusociality itself. The weaving of arboreal nests from larval silk has originated in ants only three times worldwide. Army-ant behavior, marked by mass foraging, has appeared perhaps six times. Within this ensemble, swarm-raiding, in which the foraging army advances over a broad front, has appeared three times, in *Dorylus*, *Eciton*, and *Pheidologeton*, respectively. Fungus gardening has evolved only once in ants, in the New World Attini, and within this tribe, it has advanced to the use of fresh foliage only once also, in the monophyletic leafcutter complex of *Acromyrmex* and *Atta* (25).

### Eusociality and Preemptive Ecological Success

The breakthrough by two of the lines to eusociality has conferred on them spectacular ecological success. Although ants and termites together compose only 2% of the  $\approx 900,000$  insect species known globally, they make up more than half the insect biomass. Their dominance is ecological in origin. Colonies control nest sites and foraging grounds in competition with solitary insects. They use chemical communication to assemble nestmates and organized maneuvers to defeat adversaries. The disposition of workers to risk or surrender their lives enhances the genetic fitness of the mother colony. In general, ants in particular dominate the central, more stable areas of habitats, whereas solitary insects are best able to flourish in the peripheral, more ephemeral areas (25, 45).

How did this hegemony arise? The modern ant family (Formicidae) is dominated by four subfamilies, including the Ponerinae, a member of the anatomi-

cally and behaviorally relatively primitive poneromorph group of subfamilies, and the more advanced Myrmicinae, Dolichoderinae, and Formicinae. Each of these “big four” far exceeds in number of genera, global range, and local abundance any of the 17 other currently recognized living subfamilies, including five other poneromorph subfamilies. The origin of the contemporary ecological success of the ants is essentially the history of these four groups. Although still largely speculative, the following ecological history of the dominant groups can be drawn from fossil evidence and phylogenetic reconstructions of the modern fauna (47), combined with the natural history of the dominant groups (25, 48). Ants arose in the ground layer of the tropical Cretaceous angiosperm and angiosperm–gymnosperm mixed forests, or else they penetrated this habitat early in their evolution and began to diversify within it. The poneromorphs, including the stem clade of the present-day Ponerinae, gained an early advantage as predators of arthropods and flourished thereafter in the broad array of niches opened by this specialization. The myrmicines also proliferated in the ground layer, mostly as predators but also (in

many lines) as granivores and collectors of homopteran sugary excreta. During the Eocene, the dietary versatility of the myrmicines promoted their advance into other habitats. The same expansion occurred even more disproportionately in the formicines and dolichoderines, with a large number of species spreading both upward into the tropical forest canopies, which they now dominate in good part as cryptic herbivores on enriched sap transmitted as excrement by homopterans (49), and outward into temperate forests and xeric habitats around the world. By the mid-Eocene, ants had become numerically dominant insects. The history of the ants thus appears to have started with ecological preemption based on eusociality in the late Cretaceous or early Paleogene and to have continued with subsequent dynastic expansions into environments beyond the tropical forest ground layer (47).

### Broader Implications

In the ants and other social insects, we are thus privileged to see not only how complex societies have evolved independently of those of humans and in a different sensory modality (mostly chemosensory versus audiovisual) but also,

with increasing clarity, the relations between levels of biological organization and the forces of natural selection that formed and shaped them. We have also begun to glimpse, albeit still dimly and in fragments, connections between major features of the sociobiology, ecology, and biogeography of these insects.

If the conclusions drawn here about eusociality in insects and other arthropods are correct, they could have implications for advanced social behavior outside the arthropods. Rarity and the preeminence of group selection in unusual environments that favor cooperation are shared by the bathyergid rodents, the only highly eusocial phylad known in the vertebrates. Rarity of occurrence and unusual preadaptations characterized the early species of *Homo* and were followed in a similar manner during the advancement of the ants and termites by the spectacular ecological success and preemptive exclusion of competing forms by *Homo sapiens*.

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