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Changing Paradigms in Insect Social Evolution: Insights from Halictine and Allodapine Bees

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Key Words

sex allocation, caste determination, phylogenetics, kin selection

Abstract

Until the 1980s theories of social insect evolution drew strongly on halictine and allodapine bees. However, that early work suffered from a lack of sound phylogenetic inference and detailed information on social behavior in many critical taxa. Recent studies have changed our understanding of these bee groups in profound ways. It has become apparent that forms of social organization, caste determination, and sex allocation are more labile and complex than previously thought, although the terminologies for describing them are still inadequate. Furthermore, the unexpected complexity means that many key parameters in kin selection and reproductive skew models remain unquantified, and addressing this lack of information will be formidable. At the same time, phylogenetic questions have become more tractable, and DNA sequence-based studies have resolved questions that earlier studies could not resolve, radically changing our understanding of the number of origins and losses of sociality in these bees.

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Eusociality: reproductive skew based on generational lines, mostly entailing reproductive mothers and worker-like daughters

Corbiculate apids: bees in the family Apidae with a corbicula, a "basket" of setae for transporting pollen

INTRODUCTION

Many social insect taxa display extreme forms of altruism, in which the reproductive trajectories of individuals are inflexible and determined before adulthood, leading to sharp reproductive skew between queens and workers. Understanding reproductive altruism was a major problem for Darwin and has been a focus for evolutionary biologists ever since. Trying to understand how eusociality has evolved has mostly been the precinct of comparative biology. Many taxa, such as termites, ants, stingless bees, and honey bees, are composed entirely of species in which sociality is complex, obligate, and there are no closely related solitary or weakly social taxa. For these groups it may be difficult or impossible to compare the consequences of individual strategies involving social and nonsocial options. For such groups it is also difficult to reconstruct feasible pathways that lead from solitary to social living, because remnants of transitory stages have been obliterated over evolutionary time, leaving only hypothetical solitary starting points and known advanced end-states. In addition, there are many other taxa in which forms of sociality vary greatly within and among species, forms of altruism vary from slight to extreme, and individuals are not consigned to specific roles for their entire lifetime. These latter groups provide the insights needed to understand how more advanced forms of sociality evolve (41, 46, 96).

Halictine and allodapine bees have been prominent for understanding how sociality has evolved from solitary ancestors for several reasons: Both groups include (*a*) many social species with facultative adoption of solitary or social roles by individuals, (*b*) relatively recent transitions between solitary and social living, and (*c*) substantial variability in the degree of sociality within and between extant species.

BACKGROUND AND NATURAL HISTORY

Eusociality is thought to have arisen at least five times in bees: once or maybe twice in the corbiculate apids, which comprise the orchid bees (Euglossini), bumble bees (Bombini), stingless bees (Meliponini), and honey bees (Apini); once in an ancestor of the extant allodapine bees (75); and three times within the Halictinae (4, 20). While the corbiculates have been the focus of much work on bee sociality, only the euglossines contain species that are not eusocial (9). This leaves only the halictines and allodapines as groups that span the full range from solitary to eusocial. Halictines and allodapines have evolved in different major clades of bees (**Figure 1**), and their biologies are also different. This review provides an overview of recent studies of social behavior and evolution in these two important lineages.

Halictines

The Halictinae is the largest and most diverse subfamily in the Halictidae, and among bees in general, it is the most interesting from the perspective of social evolution because of the sheer diversity of social systems it contains (46). The subfamily includes more than 2400 species of which we estimate around 830 are eusocial. Halictidae has a cosmopolitan distribution, with representatives on every continent except Antarctica. Seven genera and subgenera are thought to include obligately eusocialt species: *Halictus* (*Halictus*), *Halictus* (*Seladonia*), *Lasioglossum* (*Evylaeus*), *Lasioglossum* (*Dialictus*), *Augochlora*, *Augochlorella*, and *Augochloropsis*. In most cases, even closely related species show widely differing levels of social organization (94). Most eusocial halictine groups are from the Northern Hemisphere (e.g., *Halictus* and *Lasioglossum*), whereas the eusocial augochlorines (and Augochlorini in general) have their greatest diversity in the neotropical regions. Recent reports of eusociality in *Augochloropsis* (11) and facultative eusociality in *Megalopta* (2, 85, 93) suggest that eusociality may be more widespread in the Augochlorini than previously imagined.

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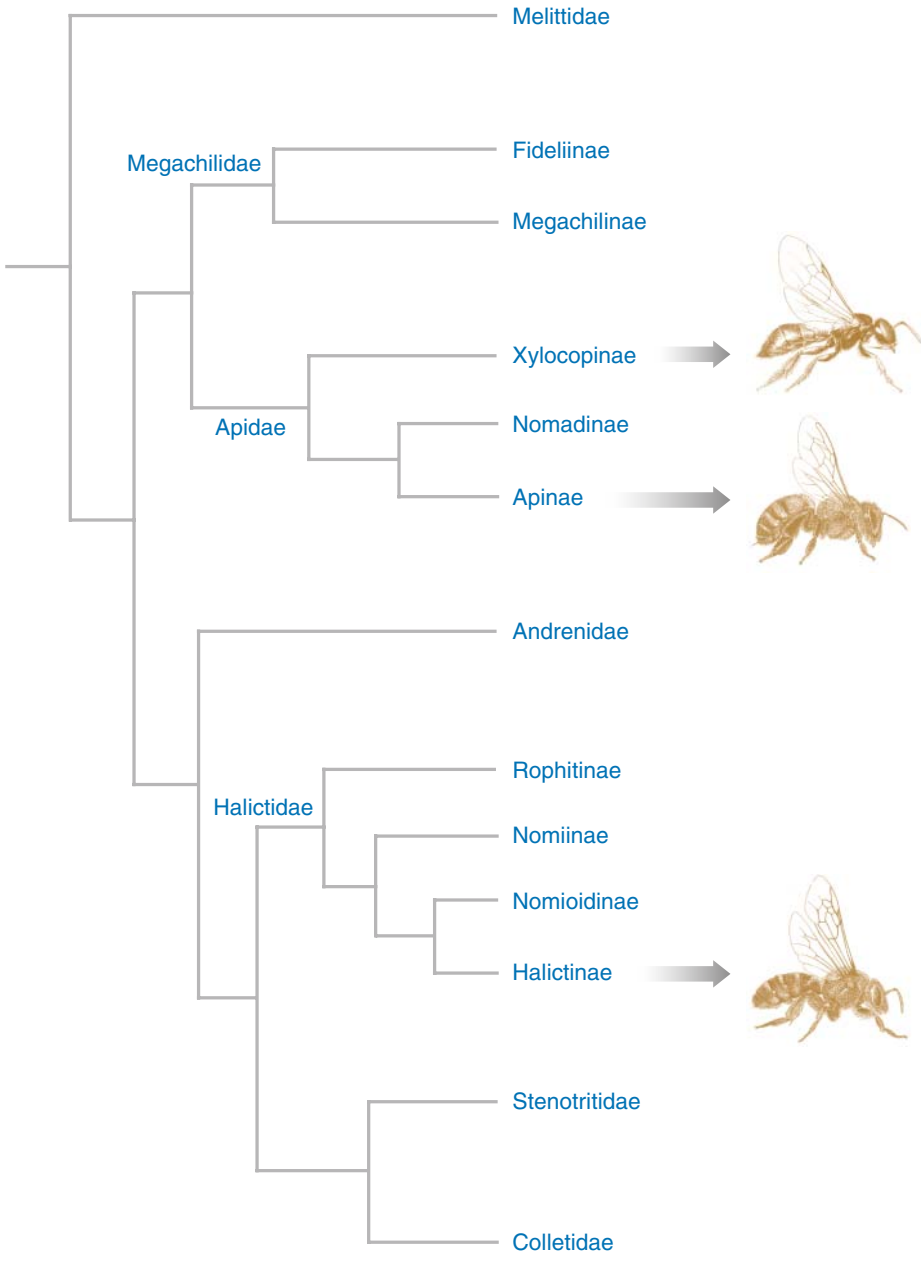

Figure 1

Phylogeny of the major bee groups with the position of halictines, allodapines (in Xylocopinae), and the corbiculate Apinae indicated. Modified from Danforth et al. (23a).

Allodapines

The allodapines (tribe Allodapini, subfamily Xylocopinae, family Apidae) form a relatively small group with at least 250 described species. They likely contain a much larger number of actual species, but because they are largely restricted to sub-Saharan Africa, Australia, and southern Asia, they have received relatively little taxonomic attention. Following Reyes (60) we regard previously recognized subgenera as genera, which means that the tribe currently contains 12 genera, of which 4 (*Inquilina*, *Effractapis*, *Eucondylops*, and *Nasutapis*) are obligate social parasites. The

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Subsociality: extended parent-offspring contact during offspring development

Semisociality: reproductive skew among same-generation adults that are jointly rearing brood, so that some adults adopt alloparental roles

Malagasy species currently placed in *Halterapis* form a distinct basal clade (80) and will eventually be accorded generic status.

The allodapines differ from nearly all other bees in that they do not rear their brood within cells—instead larvae are reared in a communal undivided tunnel excavated into the pithy centers of dead stems and branches or else in similar tunnels excavated by other burrowing insects and then reused by allodapines. Most species rear their larvae progressively throughout their development, a trait that is also different from nearly all other bees, although some species mass provision individual larvae (45) or groups of larvae (80) or they adopt a mix of mass and progressive provisioning strategies (45, 75).

Early studies suggested that some allodapines in apparently basal clades were solitary or only weakly social, leading to the notion that sociality had evolved de novo within extant clades (49, 96). Furthermore, some of these basal groups were complete or partial mass provisioners, suggesting that evolution of sociality was linked to a transition from mass to progressive provisioning.

FORMS OF SOCIAL ORGANIZATION

Although there was keen appreciation prior to the 1960s that insect sociality varied enormously in complexity, there was no systematic method for categorizing sociality into levels that might correspond to evolutionary steps from solitary behavior to complex societies. Building on a social classification scheme developed by Batra (3), Michener (44, 46) and Wilson (96) provided definitions for a range in forms of sociality based on cooperative nest use, reproductive division of labor, and generational overlap. The key grades of sociality, ranging from subsociality to eusociality, are outlined in the floating terms. Although used widely, this scheme has many problems, and Costa & Fitzgerald (12) ignited a debate on social terminology, resulting in proposals for a variety of alternative schemes over the next decade. The many subsequent proposals for alternative lexicons are summarized by Costa & Fitzgerald (13), though there is little consensus, with most studies now presenting brief explanations of the terms that they use and employing modifiers such as obligately, facultatively, weakly, and so on.

In both allodapines and halictines, and many other social taxa, the problem of ascribing terms of sociality to species is that relationships within colonies can vary both between colonies and over time. In the following sections we outline how these relationships can vary and how this creates difficulties for applying social terminologies to species.

Halictines

Because the kind of sociality exhibited in many species varies widely over the course of colony development, it is important to understand how colony composition can change over time. The diversity of halictine colony cycles is illustrated in **Figure 2**. The timing of brood production and whether females diapause before reproducing are the two crucial elements that distinguish different types of colony cycle demographically. When two additional behavioral elements, nest cohabitation by females and reproductive skew, are introduced, we obtain the critical dimensions necessary to define the various social grades observed in halictine bees.

Semisociality and eusociality are both caste-based social systems. The former has only been observed as an ontogenetic phase in eusocial colony development when colonies are sometimes jointly founded by multiple overwintered foundresses, most of which become worker-like subordinates and one of which becomes a dominant, queen-like individual. Eusociality is far more common. Two species, *Halictus ligatus* and *Lasioglossum malachurum*, are typical of temperate-zone eusocial species and are among the most widespread bees in North America and Europe, respectively, a testament to the ecological success of eusociality in these bees.

Two additional variations on the eusocial theme have been observed. In delayed eusociality, short breeding seasons lead queens and their daughter workers to hibernate before producing Brood 2 in the second year of the colony cycle (29). In perennial eusociality, currently known only in a single, unusual species, *Lasioglossum marginatum* (58), colonies last four to five years, producing a single brood of workers each year until the final year when both males and gynes are produced.

Although not as common as eusociality, egalitarian social behavior (i.e., communal nesting) is known in several genera and may be typical of Australian halictines (36, 37). Communal bees share nest architecture (for instance, a common nest entrance) but not brood care—each female provisions and raises her own offspring. Reproductive skew may arise among females, but as in solitary bees, skew should reflect the intrinsic reproductive abilities of individual females rather than social interactions among females. Is the sociality of communal bees more apparent than real? At incipient stages of social evolution, sociality might be an emergent property arising from associations among individuals with different propensities for performing different types of behaviors, rather than being the product of natural selection (35). Despite suggestions that communal behavior represents an intermediate step between solitary behavior and caste-based societies, in halictines the communal and eusocial behavior are more or less mutually exclusive phylogenetically (see below). Communal behavior may represent an intermediate step in reversions to solitary behavior, as recently suggested for *Halictus sexcinctus*, which variously exhibits eusocial, communal, and solitary colonies (63, 68).

Halictine social behavior is evidently highly flexible at a variety of levels. Ironically, a major step forward in understanding and defining social grade in halictine bees stemmed from the first observations of behavior that made it more difficult to justify the use of an inflexible social typology. First was the discovery of social polymorphism in the ordinarily eusocial species *Lasioglossum calceatum*, which is solitary and single brooded at high altitude, where the summer season is too short for a two-brood colony (69). Second was an intriguing phenomenon known as brood divalency (98–100). Yanega (98–100) showed that in an apparently typical eusocial population of *H. rubicundus*, females produced in the first brood were of two types: those that became workers and those that left the natal nest to mate and diapause, preparatory to becoming nest foundresses the following year. Brood divalency and facultatively solitary behavior (sometimes called facultative sociality, a convenient, but less phylogenetically correct, term) are probably related phenomena: *H. rubicundus*, like *L. calceatum*, is solitary at high altitudes (27a).

Quasisocial: cooperation between adults in the rearing of brood, but without reproductive skew

Allodapines

In allodapines, the difficulties of ascribing grades of sociality to particular species have long been recognized (46, 48). Colony composition and the relationships among colony members vary with colony development, and the problem is exacerbated by the long adult life spans of females (more than 18 months in some species; M. Schwarz, unpublished observations) and the lack of discrete generations in many groups. Three principal allodapine colony cycles are illustrated in **Figure 3**. **Figure 3*c*** shows a typical colony cycle for tropical species in which nests are founded solitarily, colony size and generational composition of adults vary over time, and nestmates can exhibit varying degrees of reproductive skew. Under the Batra-Michener-Wilson scheme, the solitary founded colony may be subsocial until the oldest daughters become adults. If these newly adult daughters then begin to help rear younger siblings without commencing their own reproduction, the colony becomes eusocial, and if the mother dies and all daughters become reproductive the colony can become quasisocial, but if the sisters exhibit marked reproductive skew, the colony

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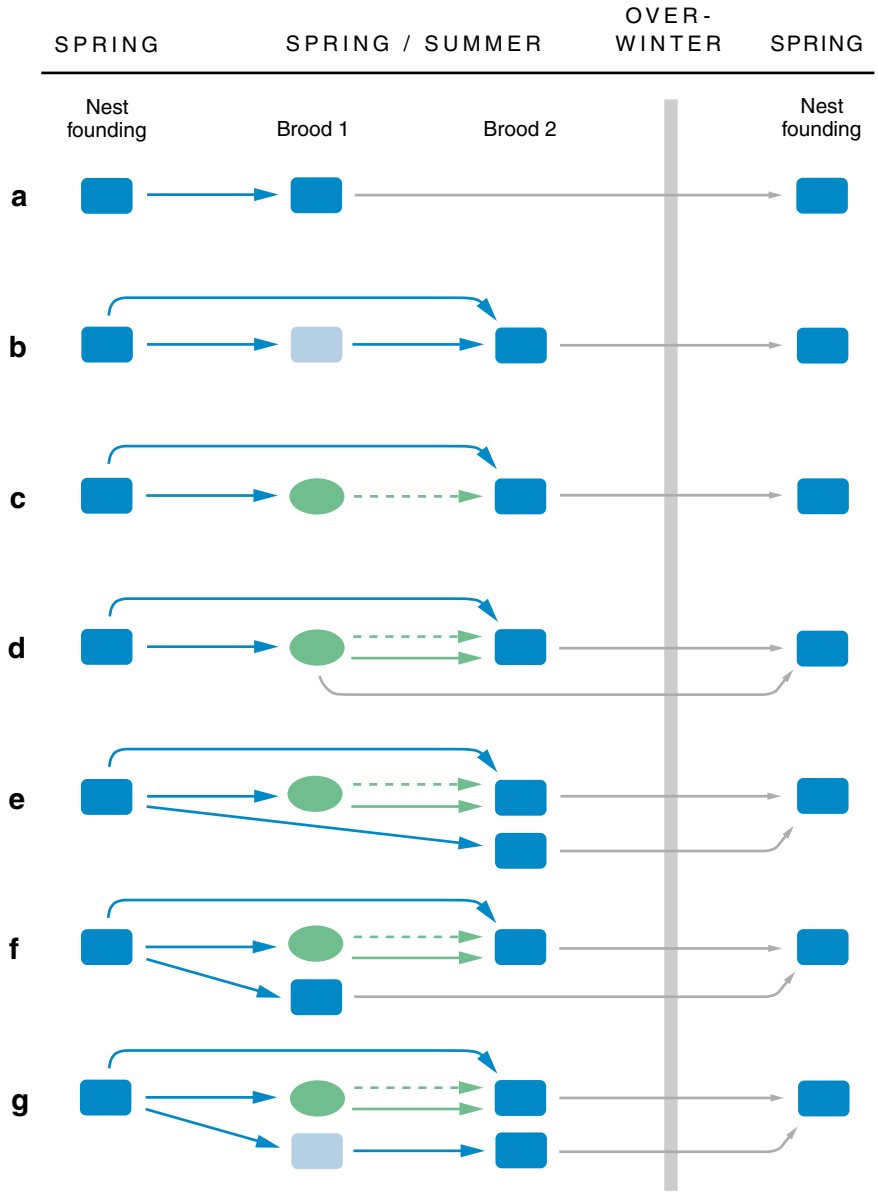
becomes semisocial. If, instead, social grade were based on levels of skew (82), this would also vary among colonies and over time. For example skew varies widely among colonies in species of the genus *Exoneura* (39, 40) and is responsive to the age and size of colonies, as well as to intracolony relatedness (39, 40, 70). Understanding social evolution in both allodapines and halictines depends on understanding the nature of queen-worker differentiation and how it arises in terms of both ultimate and proximate factors.

QUEEN-WORKER ROLES AND REPRODUCTIVE SKEW

While queen and worker castes may be readily distinguished in groups such as ants and



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honey bees, the more socially flexible systems in halictines and allodapines can make this problematic. In fact, such distinctions could be expected if species in these groups show incipient forms of sociality, but flexibility in social roles may represent an alternative end point to one in which queen-worker dimorphism is preimaginally determined.

Halictines

Traditional definitions of queens and workers apply reasonably well to eusocial halictines, if it is accepted that, as with definitions of social grade, caste is better defined as a somewhat fluid suite of characteristics. These characteristics include time of emergence, body size, whether females found nests, whether they overwinter, their reproductive status, and their social relationships with other adult females. Generally, queens are large-bodied individuals that overwinter (at least in temperate species), establish nests either singly or with other females, become highly worn, monopolize oviposition, and are assisted in raising their brood by other females that lay few or no eggs. Workers are small-bodied daughters that remain in the natal nest with their mothers, cooperate in the raising of younger brood that develop mostly from eggs laid by the queen, often mate and occasionally lay either gyne or male eggs, and, despite their name, often do less work than queens do (64, 65). Queens and workers can be discriminated independently of egg-laying status, which is necessary for non-teleological analysis of queen-worker reproductive skew.

The flexibility of halictine colony organization is due largely to the flexibility of female reproductive behavior (**Figure 2**). Adult females are totipotent: Any adult female is capable of expressing any of the reproductive strategies in a particular species's repertoire. This suggests that caste determination is mostly postimaginal, but preimaginal influences on caste cannot be ruled out. In *H. ligatus*, gynes eclose with abdomens full of fat stores that help them survive the winter, whereas workers do not. Because larvae develop in closed brood cells in underground nests, it is difficult to imagine that the cue leading to this developmental difference is anything other than nutritional (66). The main postimaginal influences include the

Figure 2

Variation in colony cycles and social behaviour in temperate zone halictids. For simplicity only female bees are represented. Major colony events are nest founding in spring, production of brood during spring and summer, and hibernation of overwintering females. Overwintering gynes that found nests following hibernation are represented by dark-blue rectangles, whereas females that found nests without first hibernating are represented as light-blue rectangles. Workers that remain in the maternal nest during production of Brood 2 are represented by green ovals. Solid blue and green arrows represent brood oviposition, and broken green arrows represent brood care by altruistic females. Gray arrows indicate females that overwinter. Most solitary halictids are univoltine (*a*), but some are bivoltine (*b*). In a classically eusocial halictid colony cycle (*c*), Brood 2 would develop from eggs laid by the queen, but most of their care and maintenance would be provided by nonreproductive workers. Although this colony cycle involves two separate broods, it is univoltine, as all brood are the queen's offspring. Partial bivoltinism (*d*) may occur in primarily eusocial halictids when workers lay male- or gyne-destined eggs or when, instead of working, they enter hibernation, becoming nest foundresses the following year. The most common form of social polymorphism (*e*) occurs in primarily eusocial species that become facultatively solitary by omitting production of Brood 1 (the worker brood); social polymorphism can occur within or among populations. Intrapopulation social polymorphism can also result from the phenomenon of brood divalency (*f*), in which Brood 1 is composed of two female castes, small workers that remain in the maternal nest and large gynes that immediately enter hibernation. Brood divalency may also be operating in cases in which Brood 1 females abandon the maternal nest to found their own nests in midsummer (*g*). Not shown is delayed eusociality in univoltine colonies, in which queens and workers both overwinter, raising males and gynes the following year.

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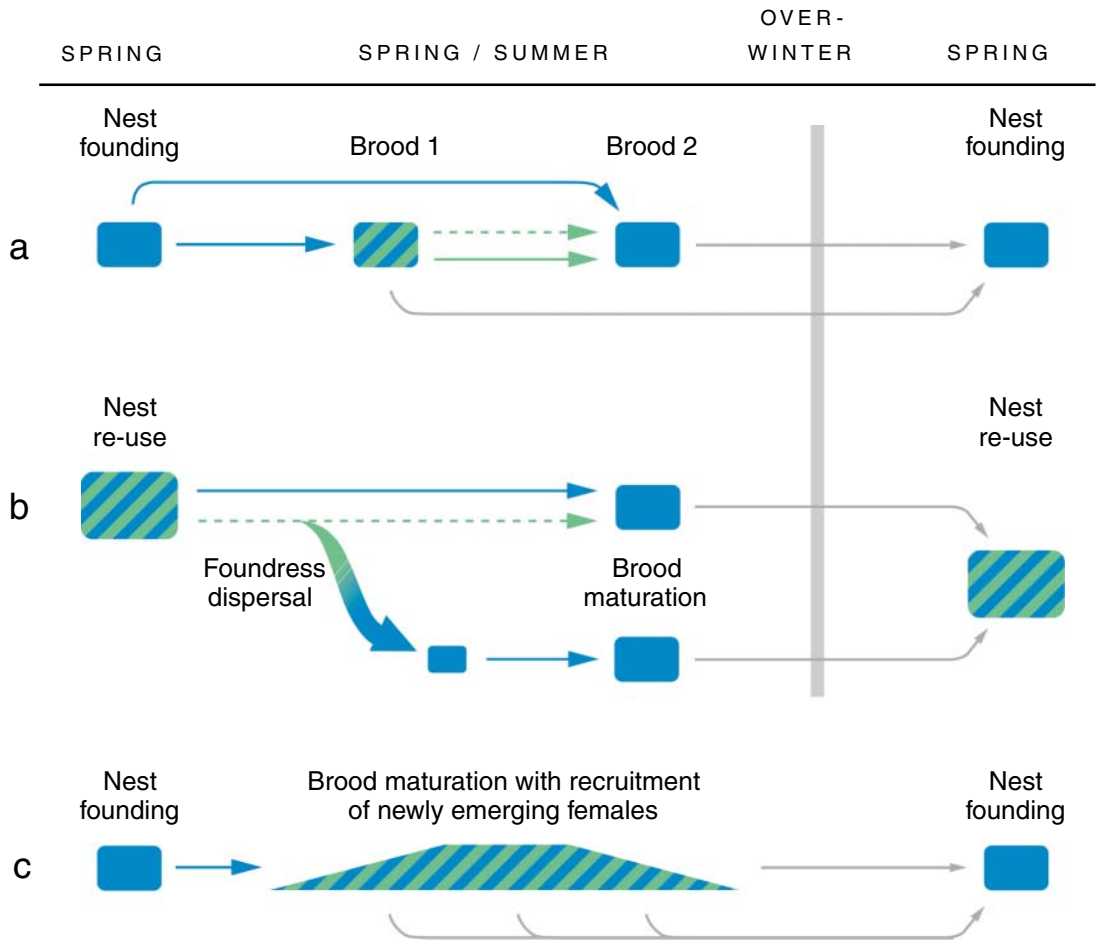

Figure 3

Three principal colony cycles for allodapines. Only female bees are represented. Blue rectangles represent reproductive females, and blue- and green-striped rectangles represent groups of females that may adopt either or both roles. Solid lines represent direct reproduction, and broken lines represent alloparental care. Because of communal brood rearing, some females may be parents and alloparents at the same time. (*a*) Represents a solitary founding species in a temperate habitat (e.g., *Exoneurella lawsoni*). Solitary females found new nests in spring and rear a first brood. Once this brood becomes adults, the foundress may continue oviposition and her adult daughters may then begin their own reproduction, become alloparents, or both. The resulting second brood disperses in the following spring as solitary founders. (*b*) Represents a temperate species in which spring colonies comprise a group of females that jointly share their natal nest (e.g., *Exoneura robusta*). Some females lay eggs in winter, whereas most do not. During spring some additional females become reproductive, but some others retain small ovaries. In late spring some of these females disperse into groups to cofound new nests, and all cofoundresses are reproductive, leaving behind a contingent of females in natal nests that remain as nonreproductive alloparents. Broods in both nest types reach maturity in late summer. (*c*) Represents a tropical or subtropical species in which colony cycles are aseasonal (e.g., *Macrogalea* spp.). New nests are founded by solitary foundresses that begin rearing a brood. Brood maturation is staggered, and as new females become adults they may become reproductive, engage in alloparental care, adopt both roles, or else disperse to found solitary nests. Pedigree relationships among females in such colonies can be both complex and fluid. Such colonies can persist for many generations, depending on how long the nesting substrate lasts.

social context of the nest into which a young female emerges, the time of year, and her nutritional status. Caste-switching is possible. For instance, replacement queens are workers that assume queen-like behavior on the death of the foundress queen, while overwintered gynes sometimes become worker-like subordinates in multifoundress nests. In the odd perennially eusocial species *L. marginatum*, caste appears to be completely determined by mating (58). Queens and workers are the same size and all overwinter, but queens live four to five years, whereas workers apparently live only about one year. In most nests only workers are produced and these nests open only for a few weeks in the spring so that pollen provisions can be brought into the nest. However, final-year nests produce both males and females. These nests open in late summer or early fall so that males can leave to find mates in other final-year nests. Plateaux-Quénu (58) showed that if males are introduced into closed nests that are still producing only workers, the workers will mate and become foundresses.

In eusocial halictines it may be useful to compare social grade among species in terms of criteria that correlate with the strength of queen-worker dimorphism. Using principal components analysis to uncover which social traits are most important, Michener's (46) comparative analysis revealed strong differences among taxa, suggesting that sociality, even eusociality, has evolved differently in each group. Subsequent studies focused on the *Lasioglossum* subgenera *Dialictus* (5) and *Evylaeus* (55, 97) and suggested that increasing strength of eusociality in halictine bees can be defined in terms of greater queen-worker size dimorphism, lower proportion of males produced in Brood 1 (which is usually produced solitarily by the queen), more workers produced in Brood 1, smaller proportions of workers that mate or have developed ovaries, and increasing colony size. Overall this suggests that the strength of eusociality is largely defined by two characteristics: the degree of queen-worker reproductive skew and colony size. Intriguingly, this has led to a new conundrum: Across species, greater skew is associated with larger colony sizes, but within species (in fact, within populations), the usual pattern is that greater skew is associated with smaller colony sizes (67, 87). Perhaps the evolution of stronger eusociality in halictine bees is dependent on the evolution of stronger queen control of worker behavior (97).

Allodapines

Early studies of allodapine bees suggested that for most species queen-worker roles were not easily recognizable. Michener (43, 45) outlined sociality in numerous allodapines from Africa and Australia. In one African species, *Halterapis nigrinervis*, colonies rarely contained more than one female and when they did, this apparently comprised an older, reproductive female and her recently eclosed daughters that were yet to disperse. In *Exoneurella lawsoni*, colonies comprised single female nests, with temporary matrifilial associations arising when the oldest brood reached adult eclosion while the foundress-mother was still rearing some younger brood (42). These two species seemed to represent the least social, indeed mostly solitary, end of the spectrum of sociality in allodapines. Studies on *Braunsapis* and *Exoneura* species (76, 79) indicate forms of sociality with varying levels of queen-worker differentiation, but in no case is any female constrained to the role of worker for her lifetime. Although ovarian differentiation among nestmates is often linked to body size, smaller females having smaller ovaries and often unfertilized, the mechanisms leading to reproductive differentiation were largely unknown.

In the 1980s a series of studies on an Australian allodapine, *Exoneura robusta*, began to uncover mechanisms of reproductive differentiation. During winter, colonies show high levels of ovarian differentiation; each colony contains one or two reproductive queens and the remaining nestmates have small ovaries. Queens inhibit ovarian enlargement in their

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Preimaginal caste determination: in which the caste that an individual adopts is determined prior to becoming an adult

nestmates (78), and this interference is mediated pheromonally (52). It was not known what initially established this dichotomy until a series of experiments (81) showed that winter queens were the first females among their brood cohort to reach adult eclosion. Even eclosing one day before a nestmate was enough to allow a female to become dominant (81). Interestingly, during this period of reproductive differentiation in autumn and winter, queens are the guards within nests, spending nearly all their time at the nest entrance (32). Bull et al. (6) hypothesized that because the order of adult eclosion determined reproductive dominance, dominant females may guard their nest entrance to police mating by their subordinates, thereby ensuring that subordinates did not mate in autumn and therefore were unable to produce daughters that might become rivals for the queen's offspring. They found that guarding queens did indeed distinguish among subordinates that had been, or had not been, in physical contact with males. In *E. robusta*, solitary nesting females have low fitness owing to brood predation (72, 73, 76), and this means that a guarding female that controls entry to the nest may wield substantial power by refusing entry to subordinates that would otherwise have to nest solitarily. These studies indicate that in *E. robusta*, queen-worker differentiation is behaviorally mediated, but that the mechanisms underlying this are surprisingly complex.

One key discovery was made by Houston (33), who reported marked morphological differentiation between queens and workers in the Australian bee *Exoneurella tridentata*. Colonies of this semiarid species are the largest known for allodapines (in excess of 50 females) and queens are two to three times larger than workers. Workers have typical adult allodapine female morphology, but queens have the distal part of their metasoma greatly expanded into a shovel-like tip and strongly rugose metasomal terga (33, 34). Queens often had greatly worn wings and in some cases were unable to fly. Queen-worker differentiation in this species occurs prior to cessation of larval feeding, indicating preimaginal caste determination (34). The mechanism behind this is unknown, as all larvae are reared in a contiguous clump in a common burrow and allodapine larvae are capable of movement within these burrows so that adult females are unable to restrict feeding to only some larvae (79). Indeed, queen-destined larvae occur in the midst of their worker-destined sibling larvae (34). The possibility of a genetic basis to queen-worker differentiation cannot be ruled out in this species.

Strong queen-worker differentiation has also been found in the Malagasy bee *Halterapis minuta*, in which queens are markedly larger than their workers and workers are apparently sterile (80). However, in other allodapines, queen-worker differentiation is less clear-cut. In *Brevineura xanthoclypeata*, females below a certain size never reproduce, but above this size reproductive skew is variable, though still size based (89). In still another species, an undescribed *Macrogalea* from Malawi, the role of relative body size as a determinant of reproductive hierarchies is mediated by age. Thompson & Schwarz (88) found that all newly eclosed females reproduce without any evidence of hierarchical structure, but that among older females that have already laid their first egg clutches, there is a strong size-based hierarchy. In this species brood development is staggered, and egg laying is continuous as new females eclose and older females move into nonreproductive roles. Allowing all young females to lay eggs may provide staying incentives, so that they remain in the nest as alloparents to help rear the communal brood. However, the value of older females as alloparents is likely much lower and therefore their reproductive status is more likely to be contested.

SEX ALLOCATION AND INTRACOLONY RELATEDNESS

Sex allocation and intracolony relatedness are tightly linked in social evolution and are key to understanding conflicts and cooperation in

haplodiploid societies (17). However, studies on halictines and allodapines have focused on different mechanisms that lead to sex allocation patterns, with halictine studies examining conflict over male and female investment and allodapine studies exploring the consequences of cooperation among nestmates. This could reflect some key differences in the ecology of these two groups, but sex allocation paradigms may have been applied to the two groups with some bias.

Halictines

Until the 1990s it generally seemed that eusocial halictines conformed to the classical expectation (31, 91) that worker altruism could be explained by kin selection. Specifically, it was assumed that if relatedness is high enough and sex allocation is skewed at the correct mathematical level, then worker altruism must be explained by kin selection. Hamilton's Rule describes exactly how many kin workers must be raised if kin selection is a sufficient explanation for helping behavior by workers. Yet there has been almost no effort to determine whether workers' cooperative efforts actually result in the production of numerically sufficient brood to tip Hamilton's Rule in their favor. In *L. malachurum*, it appears that worker fitness would be higher if workers used the pollen supplies that they bring to the colony to provision their own eggs instead of the queen's (65). In other words, workers appear not to raise sufficient kin to compensate them for the sacrifice of their own offspring.

Analyses based on allozyme, microsatellite, and DNA fingerprinting techniques suggest that in four eusocial species, *Lasioglossum zephyrum* (18), *L. laevissimum* (56), *L. malachurum* (57, 68), and *Augochlorella striata* (=*aurata*) (50, 51), colony genetic structure is consistent with the hypothesis that a singly mated queen monopolizes oviposition and is assisted by daughter workers in raising reproductive daughters and sons. In each of these species, various exceptions occur that lower relatedness among nestmates, including multiple mating by queens, brood parasitism and nest usurpation by foundresses, more than one queen per nest, and worker reproduction of both diploid and haploid eggs. Overall, these exceptions appear to have little impact on population-wide relatedness patterns. However, in a fifth species, *Halictus ligatus* (67), queens on average mate twice, so relatedness among sisters is considerably lower (around 0.5), and this has important consequences for sex allocation (see below). Thus mating frequency of queens is an important determinant of eusocial colony organization. Relatedness is probably considerably lower in communal than in eusocial halictines: In *Lasioglossum hemichalceum* low average intracolony relatedness (about 0.13) results from female natal dispersal, a mechanism to avoid inbreeding (38).

Sex allocation data have been difficult to collect in halictines because the often extended period of gyne and male emergence means that older brood may emerge before younger brood have even been laid as eggs, making it difficult to accurately determine colony sex ratios, especially in species with large colony sizes. Moreover there is a lack of consensus about how sex allocation is to be measured. Should males of the worker brood be included if their destiny is to mate with workers? Should reproductive workers be counted as workers or as reproductives? Even if these issues are resolved, the classic models by Trivers & Hare (91) are based on the implicit assumption that male and female production is simultaneous. The significance of this assumption is underappreciated, although preferred queen and worker allocation ratios in species with extended brood emergence periods may be different from 3:1 and 1:1 (67).

Despite these concerns, sex allocation patterns in eusocial halictines correlate with colony relatedness structure. In *L. laevissimum* (56), a female/male investment sex ratio of about 2.2:1 is ideal for neither queens nor workers but is closer to the classic 3:1 ratio preferred by workers. Moreover, the sex

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ratio of individual colonies correlates with the relatedness asymmetry between workers and their sisters versus their brothers, suggesting that workers recognize the relatedness structure in their own colonies relative to the population mean and adjust the investment ratio accordingly. In *A. striata* (= *aurata*) (50, 51), experimentally orphaned (parasocial) nests produced significantly more males than did queen-right (eusocial) nests, suggesting that workers could both detect the relatedness of the primary egg-layer (or her brood) and then manipulate the sex ratio in their own best interest. In *H. ligatus*, it seems more likely that queens control the sex ratio: Queens produce males before workers become reproductive, thus biasing the population sex ratio toward males and forcing workers to allocate reproductive effort toward the production of gynes, whether they are the queen's daughters or grand-daughters (67).

Allodapines

Given that the generational composition of allodapine colonies can follow complex patterns over time, intracolony relatedness is likely to vary similarly. Using allozyme data, Schwarz (71) showed that in *E. robusta* intracolony relatedness was moderately high for females reusing their natal nests ($r \approx 0.4$) or cofounding new nests ($r \approx 0.6$). Schwarz & Blows (74) showed that this ability to recognize kin when cofounding did not depend on familiar landmarks and that even large groups of colonies assorted along kin lines when dispersing. Tierney et al. (89) also found moderately high intracolony relatedness in the genus *Brevineura*, and Hurst (34) found that for *Exoneurella tridentata*, intracolony relatedness was consistent with a situation in which colonies have a single once-mated queen that produces the worker brood. However, in *E. robusta* and *E. nigrescens*, dispersing females sometimes nest with nonrelatives (40, 84). Langer et al. (39) showed that for *E. robusta*, intracolony relatedness influences reproductive skew, group productivity, and colony-rearing efficiency, findings that support a Tug-of-War model (59a) for reproductive skew in social groups.

Patterns of colony productivity have the potential to influence sex allocation if female-biased investment leads to larger, more productive colonies in subsequent generations. In fact, female-biased sex allocation was recognized as widespread in African allodapines even in early studies (45) and was also reported for the mostly subsocial Australian species *Exoneurella lawsoni* (42). For the African species it was thought that the bias was due to the existence of worker-like females (45), which should not be counted when reckoning female investment. For *E. lawsoni*, the bias may have been due to a recent loss of sociality whereby selection had not yet restored unbiased investment patterns (42).

In 1988 Schwarz (72) reported strongly female-biased patterns in *E. robusta* and attributed these to local resource enhancement (LRE). LRE arises because colony-level efficiency, measured as the per capita number of brood, increased dramatically with colony size, and larger colony sizes could be achieved by female-biased allocation. Female bias in *Exoneura angophorae* (15) and *E. nigrescens* (73) was also attributed to LRE, with both species exhibiting the predicted pattern of maximum bias in the smallest colonies, and decreasing bias in larger colonies. Building on an earlier experimental study that showed that recently eclosed adult daughters would complete rearing of their younger, immature siblings in the event of orphaning (7), Bull & Schwarz (8) argued that in *E. nigrescens* there were strong benefits in producing daughters first (protogyny) so that alloparents would be available in the case of brood orphaning. They found that the first brood produced in this univoltine species was indeed mostly daughters, and argued that if such daughters acted as alloparents, then investment in them should not be entirely counted as sexual investment. They found that if such insurance daughters were not counted when reckoning sexual investment, then predicted sex

ratios closely matched observed investment. It is interesting that for temperate allodapines, where brood develop as a cohort, protogyny is the rule, whereas protoandry is most common for nearly all other Hymenoptera. This unusual prevalence of protogyny fits with the hypothesis that alloparents are important for brood survival—if alloparents are critical, then it is likely important to have them in place as soon as possible.

Other allodapine studies have also found that allocation bias is greatest for smaller colony sizes. These patterns have been found for species in which mean and maximum colony sizes can be very small (1) or very large (88), but importantly they all appear to be attributable to positive fitness interactions among close relatives arising from the benefits of larger adult groups sizes. One important result from these studies is that females closely adjust the sex of their offspring according to colony size, indicating that they assess colony size accurately. Indeed, in one *Macrogalea* species, sex allocation patterns change dramatically as colony size moves from six to seven females per nest (88). The ability to accurately assess colony size and adjust fertilization of eggs accordingly is another indication that social behavior in allodapines is much more sophisticated than earlier studies had assumed.

The different approaches to sex allocation studies in halictines and allodapines reflect emphases on queen-worker control of allocation in the former group and nonlinear fitness interactions among female kin in the latter. This could be due to key differences in the social biology of the two groups. In allodapines, brood are highly vulnerable to enemies at the nest, so that colony size and the existence of alloparents become critical elements to reproductive success. For small colonies, attaining optimal group size as quickly as possible is important and this can be realized by overproduction of daughters. However, in halictines, brood have the physical protection of cells and their survival is likely less impacted by colony size (but see Reference 85). At the same time, no allodapine studies have examined the possibility of worker control over sex allocation, and no halictine studies have examined LRE as a possible factor.

ENVIRONMENTAL FACTORS IN THE EXPRESSION OF SOCIALITY

The social variability characteristic of halictine bees has often been thought to be associated with climatic variability, specifically the length of the summer breeding season and temperature, both of which can vary latitudinally, altitudinally, or even locally. In bees that live for approximately one year, the requirement for sequential production of two or more broods within a single season has important consequences for colony social organizations. Eusociality can be expressed only in environments with summers long enough for sequential production of first a worker and then a reproductive brood, so obligately eusocial species are limited mostly to environments with sufficiently long breeding seasons. Socially polymorphic and delayed eusocial species are more flexible, and communal bees may also be more suited to environments with short seasons.

Within obligately eusocial species, two contrasting latitudinal gradients in colony social organization have been identified. Because longer breeding seasons lead to extended colony cycles and larger colony sizes, in warmer climates queens must interact with more (and sometimes larger) workers. In *H. ligatus*, this results in weaker queen control of worker behavior and decreased reproductive skew (67). In *L. malachurum*, the tendency for queens to lose control of worker behavior when nests are large is seen in northerly populations (87), but not in southerly populations (65). This suggests that one of the important factors driving social evolution and increasing strength of eusocial colony organization is the increasing ability of the queen to dominate the behavior of workers, especially in terms of preventing worker oviposition.

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An important question concerns the extent to which geographic and environmentally organized (92) variation in social behavior represents phenotypic plasticity or underlying genetic variation. Several lines of circumstantial evidence suggest that in socially polymorphic species expressed social phenotype results from an interaction between genotype and local environmental conditions. The best approach to investigating such questions would be to conduct transplantation experiments for populations that differ in their sociality (e.g., between low- and high-altitude populations in which one is social and the other is solitary). Although this has not yet been carried out under field conditions, a laboratory experiment with *L. albipes* (59) suggested that bees raised under the alternative environmental conditions tended to retain their original social phenotype. A second line of evidence using phylogeographic analysis of *H. rubicundus* suggested that solitary and eusocial populations in North America represent more or less separate lineages established at different times (86).

Cronin & Schwarz (16) showed that for two Australian allodapines, broad social and sex allocation patterns did not vary over a latitudinal range spanning subtropical to cool, temperate environments, but that in one species, the more tropical populations produced two broods instead of only one brood per year, increasing the opportunities for alloparental care of younger siblings. In a further study, Cronin (14) transplanted colonies from the northern and southern populations of these species and found that although latitude influenced some life-history traits, this was not large compared with variation within natural populations. It seems that for allodapines, climate does not have the large impact on intraspecific sociality that it has for halictines.

PHYLOGENETICS

The phylogenies of social taxa are critical for inferring the origins and losses of social behavior. Before the advent of molecular data, phylogenies were often based on problematic data involving difficulties in character-coding polarity, and sometimes relied on the same behavioral traits whose evolution was being inferred. Recent molecular studies of halictines and allodapines have led to some radical changes in our understanding of their evolution.

Halictines

Poor understanding of the phylogenetic relationships within and among social lineages hindered studies of social evolution in halictine bees for many decades. In the absence of a clear phylogenetic framework, even the number of independent derivations of eusociality could not be accurately estimated: Estimates ranged from five origins of eusociality to "many" (27, 46, 54).

Phylogenetic studies of relevant eusocial lineages began in the 1960s with Eickwort's studies of the Augochlorini (26). While Eickwort (26) did not explicitly map sociality onto his phylogenies, his trees were of immediate use in interpreting patterns of social evolution. For example, his uniting of the genera *Augochlora* and *Augochlorella* suggested a single origin of eusociality in the tribe Augochlorini.

Subsequent reanalyses of the Eickwort (26) data matrix (23, 28) yielded largely congruent results. However, the tree topologies also implied that eusociality could revert to solitary nesting because some members of the genus *Augochlora* (e.g., *A. pura*) are solitary species (23). Although these early studies based on morphology provided important insights into social evolution, it was really the larger and more diverse tribe Halictini (49) for which phylogenies were needed. Halictini encompasses more than 2000 species, including the largest and most socially variable genera, *Halictus* and *Lasioglossum*. This group is notoriously difficult taxonomically and has been called "morphologically monotonous" (49) and

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"monotonous and uninteresting bees. . .that differ by such insignificant and elusive characters that they are the despair of taxonomists" (95).

Phylogenetic studies using allozymes were the first attempts to reconstruct patterns of social evolution in halictine bees (53, 61), but they were based on limited taxa because of the difficulty of preserving specimens for allozyme analysis. DNA sequence-based studies addressed relationships on a global scale in Halictinae, and generic relationships among the Halictini appeared later (19, 25). These studies demonstrated that eusociality had arisen once within the two closely related eusocial genera *Halictus* and *Lasioglossum* and that within these genera there had been multiple reversions to solitary nesting (22, 24, 25). In fact, these studies were the first to suggest that the diversity of social systems in halictine bees could be best explained by few origins and multiple losses rather than by multiple origins (22).

Most of the intergeneric relationships within Halictini have since been analyzed (20, 21). We can now say with confidence that eusociality arose just three to four times in the halictine bees: once (or twice) in Augochlorini, once in the common ancestor of *Halictus*, and once within the genus *Lasioglossum*. Most recently, Brady et al. (4) combined fossil and molecular data to estimate the antiquity of eusociality in halictine bees (**Figure 4**). Their results indicate that eusociality in halictine bees is recent (roughly 20 to 22 Ma) relative to other eusocial lineages of Hymenoptera, and that the origins of eusociality were virtually simultaneous during a period of global warming (the mid-Miocene climatic optimum). That eusocial origins could be favored by periods of global warming is especially plausible because today many social halictine species show altitudinal and latitudinal gradients in social behavior (62, 86). The relatively recent origin of eusociality in halictine bees also helps explain why there is so much intra- and interspecific variation in social behavior within halictine bees.

Allodapines

The first phylogenetic study of allodapines was conducted by Michener (47), who argued on cladistic and phenetic grounds that *Halterapis* + *Compsomelissa* formed the sister group to all other remaining allodapines. Using additional taxa and characters, Reyes (60) came to the same conclusion and placed the rare Middle Eastern genus *Exoneuridia*, not included in Michener's study, as the sister clade to the Australian exoneurines (*Exoneura*, *Exoneurella*, *Inquilina*, and *Brevineura*). Both studies assumed that mass provisioning in *Halterapis* represented retention of an ancestral trait found in all other Xylocopinae, and concluded that among allodapines progressive provisioning had evolved twice, with larval appendages being lost once. Because *Halterapis* appeared to be solitary, and sociality in *Compsomelissa* was weak at most, these phylogenies also implied that the transitions from mass to progressive provisioning, and from solitary to social behavior, occurred among the extant lineages. However, arguments that *Halterapis* represents a plesiomorphic retention of mass provisioning are problematic because it involves oviposition before provisioning, whereas in other Xylocopinae the cell is provisioned first (75).

DNA sequence-based phylogenetic studies present a picture different from that presented by morphological studies. Schwarz et al. (75) found an arrangement of basal nodes completely different from that of Michener (47) and Reyes (60), such that *Macrogalea* became the sister clade to all other allodapines, while *Halterapis* grouped with *Allodapula* and *Compsomelissa* in a much more distal group of bifurcations. This rearrangement of relationships indicates that sociality is plesiomorphic for allodapines and has two major consequences.

The first consequence concerns provisioning strategies: Mass provisioning in *Halterapis* must be a derived trait, and in fact it is quite different in nature from the provisioning

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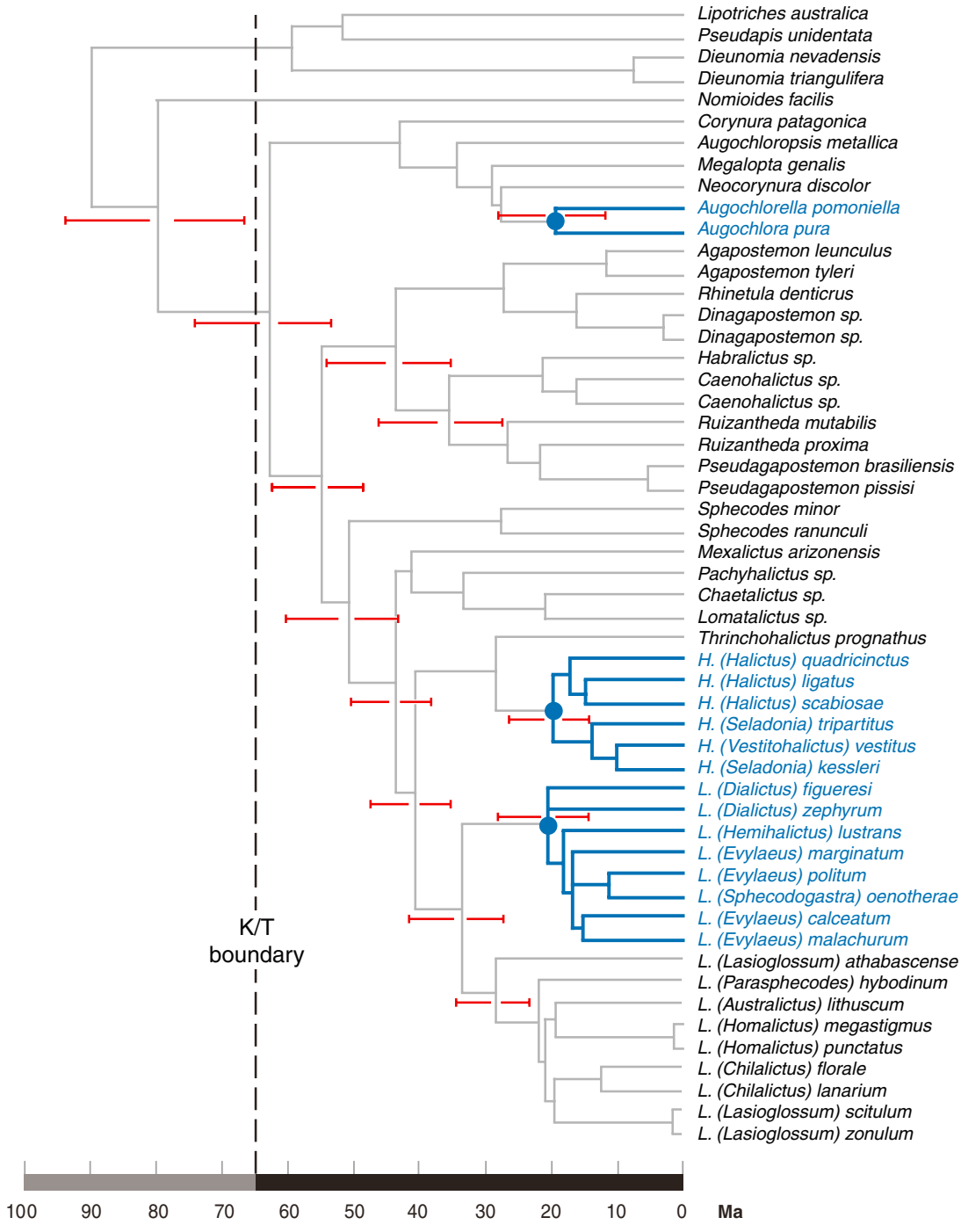

Figure 4

Chronogram of the halictines modified from Reference 4 and derived from Bayesian phylogenetic and dating analyses. Social origins are indicated by blue circles, and confidence limits for key nodes are indicated by red error bars. The Cretaceous/Tertiary boundary is indicated by a vertical dashed line.

of cells in other Xylocopinae, but not different from partial mass provisioning in genera that belong to the same clade as *Halterapis* (75). The second consequence is linked to recent studies of social behavior. Tierney et al. (90) and Thompson & Schwarz (88) found that the genus *Macrogalea* also exhibits complex sociality and sex allocation patterns, and Silberbauer & Crewe (83) and Chenoweth & Schwarz (10) found that *Halterapis nigrinervis* is social rather than solitary and has well-developed size-based reproductive hierarchies. These findings indicate that sociality is plesiomorphic for the allodapines and that there have been no losses of sociality in the tribe. The absence of reversions to solitary behavior in allodapines contrasts strongly with halictine studies and is somewhat surprising given that in nearly all allodapines all females are totipotent and are capable of nesting solitarily.

Two recent studies (30, 77) have estimated the ages of key allodapine nodes, which is important for understanding how long sociality has been in place and what kinds of geographical events may have shaped the distribution of allodapines. These studies indicate a surprisingly ancient origin for allodapines, >40 Ma (**Figure 5**), which fits with the surprising complexity found in numerous species but negates the previous paradigm of allodapines representing recent evolutionary steps into sociality (48, 96). Phylogeographic analyses indicate an origin in tropical Africa, followed by four dispersals into Madagascar, a single ancient transoceanic dispersal into Australia, a single dispersal (of *Braunsapis*) into Asia, and then a subsequent dispersal into northern Australia. The timings of dispersal into Asia and then into northern Australia by the derived genus *Braunsapis* are typical of Indian Ocean Rim taxa. However, much earlier transoceanic dispersal from Africa to Australia is puzzling, and Schwarz et al. (77) suggested this may have been enabled by island-hopping across remnants of the now-submerged Kerguelen Plateau in the southern Indian Ocean.

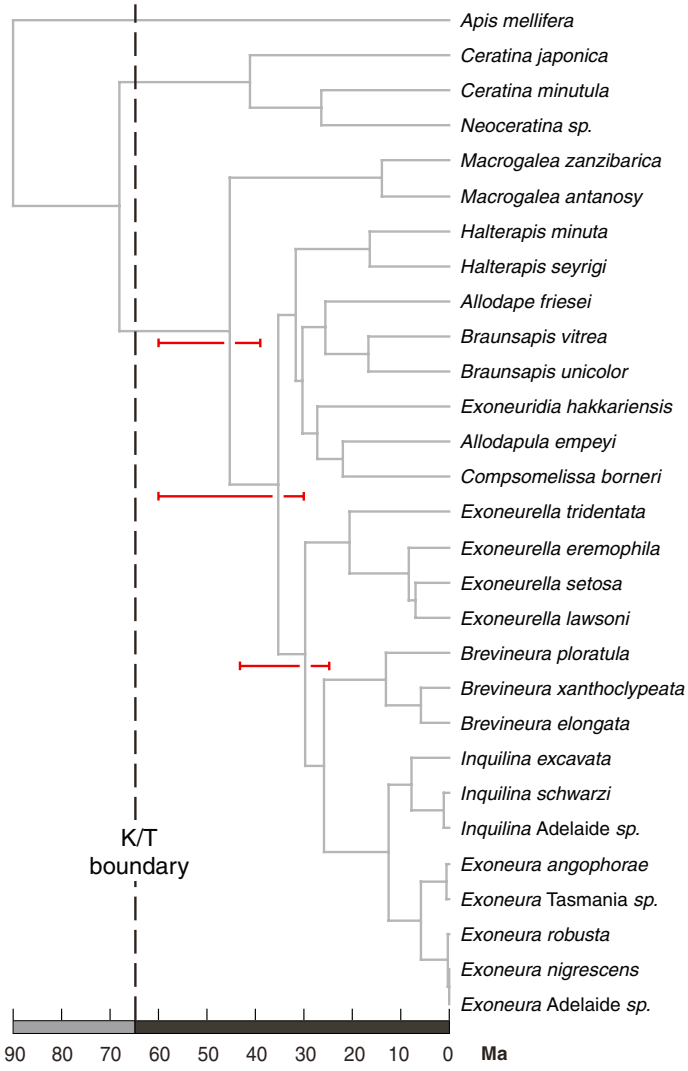

Figure 5

Chronogram of the allodapines modified from Reference 77 and derived from penalized likelihood transformation of a Bayesian phylogram based on three gene regions. The Cretaceous/Tertiary boundary is indicated by a vertical dashed line. Red bars indicate 95% central distribution limits for the ages of key nodes.

CONCLUSIONS

Considerable advances in our understanding of halictine and allodapine bees have been made since the 1980s. For both groups, the levels of complexity and lability in social organization have turned out to be greater than had been thought. One consequence of this

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is that terminologies for social organization are more difficult to apply, but a more important implication is that testing kin selection and reproductive skew models has become formidable for many species with interesting forms of sociality. At the same, inferring phylogenetic history has become more straightforward, and this has dramatically changed earlier paradigms. We are much more confident about the number of origins and losses of sociality in the two groups, which are very different from earlier expectations. Whereas sociality has been lost repeatedly in the halictines, there have been no losses in allodapines. Future work is required to comprehend this important difference, because it is key to understanding how sociality is maintained and how it may have first evolved.

SUMMARY POINTS

1. The halictine and allodapine bees have long been model systems for understanding social evolution in insects because of their diversity in forms of sociality, ranging from solitary to highly eusocial. Recent studies have extended this diversity, although it is now known that there are no strictly solitary allodapines.
2. Lexicons for describing sociality in these bees are fraught with problems because the grades of sociality can vary widely within species, both among colonies and over stages in colony development. Even colonies at similar stages of development can differ strongly in the degree of reproductive skew and future reproductive trajectories of totipotent females.
3. Flexibility in individual roles and in the social structure of colonies is often much greater than had been anticipated and points to levels of complexity and responsiveness to proximate conditions that were not anticipated in earlier studies. This means that key parameters required for assessments of kin selection and reproductive skew models become difficult to measure.
4. Patterns of sex allocation in both groups can be complex but overall suggest that different selective factors operate on allodapines and halictines. However, researchers themselves have approached sex allocation in the two bee groups from different angles, and further empirical work is needed to compare factors underlying sex allocation in the two groups.
5. DNA sequence-based analyses of both bee groups have led to phylogenetic patterns different from those of earlier morphology-based studies. For halictines these patterns suggest fewer origins of sociality, but many more losses. For allodapines, they indicate only a single origin and no losses.
6. The prospects for phylogenetic comparative approaches to social evolution in these bees are enormous. Future progress will require measurements of social and life-history parameters that are comparable across a wide variety of species, a difficult task given the problems described above.

FUTURE ISSUES

1. Assessing kin selection and associated reproductive skew models requires knowledge of many parameters, such as constraints to independent living, yet for most species

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the only parameter that has been well quantified is relatedness. Effort is required to measure the other variables, but this calls for detailed work that allows direct comparisons between species that might differ in key life-history traits.

2. The recent development of robust phylogenies creates the prospect for inferring evolutionary pathways from solitary to eusocial, and for assessing putative causal factors underlying key transitions. However, for many key taxa, critical social, life-history, and ecological traits still need to be determined. Choice of focal taxa needs to be guided by phylogenetic knowledge.
3. Studies to date have estimated the ages of some key phylogenetic nodes, but for many clades, especially allodapines, there is a lack of internal calibration points. Where fossils are not present, there may be prospects for using geological events, such as island formation, to provide calibration data.
4. Agreement on terminologies for social organization is needed for researchers to effectively compare different taxa. Experience over the past 15 years has shown this is not easily achieved, but development of a consensus lexicon will greatly help synthetic approaches to social evolution.

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