In the Beginning: The Bee Family Tree

Part II - Conclusion

by CONRAD BÉRUBÉ
Island Crop Management, Ltd.
Nanaimo, BC

Most beekeepers are aware that many people "outside the fold" often confuse bees with wasps and honey bees with other kinds of bees. Sometimes an inquisitive soul will offer for identification some exotic looking insect, fuzzy and bearing something like a hypodermic needle at the hind end. If the apiarist cannot immediately identify the creature, his visitor may mutter a disgruntled ". . .and I thought you were a beekeeper."

As a riposte in this situation and to offer some idea of the diversity and venerableness represented by the order Hymenoptera in general (of which over 100 thousand species have been described) and of the bees in particular: bees are today represented by over **20,000 modern species**[1]—as many different species of bees as there are individual honey bees in an average wild colony. The beekeeper, and most entomologists, may be excused for not being able to identify all such species off the top of their heads. However, a brief background in bee classification and natural history may fortify beekeepers called upon to proffer knowledge pertaining to their livestock's close relatives.

The 20,000 species of bees are grouped into about nine major families of 50 tribes[2] (the number may vary depending on the taxonomist). One can gain an understanding of the various adaptive stages that bees underwent in their evolution by looking at the group as a whole and at the different families of bees that exist today.

As mentioned (in part 1) bees possess hairs adapted for the collection of pollen. Such hairs comprise the *scopae,* bushy pollen-carrying areas, and the *corbiculae,* or pollen baskets, on the hindmost pair of legs that serve to carry pollen in some genera of bees. These differences reflect the change in behavior from providing the young with animal proteins as their growth medium, as wasps do, to the provision of nutrients of completely vegetal origin, pollen and nectar.

The majority of bee species are solitary and of a dimunitive size compared to the honey- and bumble-bees.[3] In solitary bee species, each female bee, after mating, builds its own nest and lays its eggs, then dies without ever seeing the new generation emerge. The nests are usually tiny, with minimal, if any, construction. Though most species of solitary bees merely dig tunnels in soft sand or soil, nests may be established within abandoned rodent burrows, plant stems or other small enclosures: leaf cutter bees (family Megachilidae) build miniature cups from leaf clippings inside the hollow stem of a plant, a neat circular cap sealing each of the thimble-shaped cups which are nested together in a column like drinking glasses stacked in a cupboard[4]; other species of solitary bees (Osmia) construct their cells only within the discarded shells of land snails[5]; yet others build several tubular galleries excavated within mud, sand or clay banks or cliffs and are thus collectively called **mining bees** (families Anthophoridae, Halictidae and Andronidae); **carpenter bees** (families Xylocopidae and Ceratinidae) chew their way into reeds, woody plants and even cured timbers.[6] To provision for their young each female gathers pollen and moistens it with nectar, forming a paste that is usually formed into a lump or pellet thereafter. A single egg is laid upon each pollen ball before the bee seals the cell and proceeds to build the next. In temperate climes the larvae which hatch from the eggs overwinter in their cells and emerge the following spring. In more tropical, warmer regions several generations of bees may be produced each year so that adult bees appear almost continuously.

Parasitic bees probably anticipated the stratagem of the cuckoo long before the bird had wafted into its peculiar mode of behavior. These bees will find their way into the nests of semi-social and social bees and lay their eggs in the cells intended for the brood of the host species. The **cuckoo bee** larvae will then destroy the host larvae and feed off the provisions brought to it by the oblivious hosts.[7]

Many mining bees and carpenter bees approach social behavior in their activities, nesting together in groups large enough to be considered colonies. The term semi-social is sometimes applied to this lifestyle, in which some group organization exists but in which there are no definite morphological caste distinctions (other than size). For instance some halictid bees, common in Europe and North America, produce an "early crop" of female offspring which do not mate, for the absence of males. These halictids, green and black and about half the size of honey bees, establish tributary galleries in the original tunnels which their mothers had drilled in the soil.[8] The term "**gyne**" is sometimes used to differentiate the single mated female, who established the parent nest, from her unmated daughters. As in other bee species, unmated reproductive females produce only male offspring (this type of reproduction without fertilization is called **parthenogenesis**). These males mate with a new generation of females produced by the gyne (who founded the colony) later in the summer. After the males, first-emerged females, and the old mated female die off in the fall, the newly mated females, the next generation of gynes, hibernate through the winter and then go on to repeat the cycle next spring. This pattern, in which no single colony exists for more than a season, is quite similar to that followed by the bumble bees, which are considered to be truly social (**eusocial**).

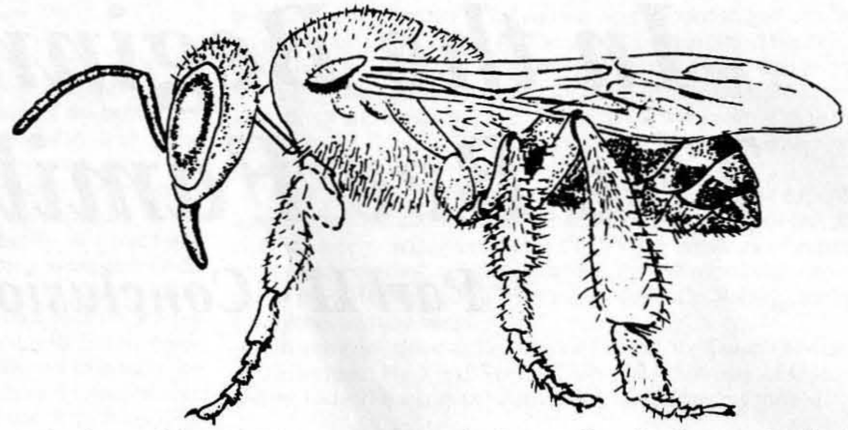
To review (from part 1), eusocial behavior is defined by:

1) Communal brood care, in which individuals care for larvae that are not their own.

2) A reproductive division of labor in which many colony members are sterile, creating morphologically distinct castes.

3) An overlap existing such that the parent generation is assisted by offspring in the rearing of additional generations.[9]

The bumblebees (family Bombidae – sometimes grouped with the Apidae), honey bees (family Apidae) and stingless bees (family Meliponinae) have distinct castes, a clear indicator of the division of labor that is a requisite for social behavior. Although it is the manifestation of instinctual and physiologically dictated activity, the cooperation and concerted effort displayed by the social bees, and social insects in general, convey the same benefits toward survival of the species as do the social arrangements amongst humans. Members of the population specialize in certain functions, and communicate with one another in their allotted activities, allowing the exploitation of resources and completion of necessary tasks to progress at a much more efficient level than that possible for a single individual working alone. In other words, many hands or, in this case, tarsal claws, make light work. Queens, freed from the necessity of food gathering, can produce enormous quantities of eggs—over 1,500 per day, in the case of honey bees, during the peak of rearing season. Workers, relaying information about the location of attractive food sources, can lay-in enormous surpluses of food, allowing the colony to survive through the winter (and making possible the honey industry). Organized defense of the colony, while expending a few workers, is obviously much more effective and less hazardous, to the next generation, than would be a single brood-rearer warding off an attack on her solitary nest. It is little wonder, then, that social bees are distributed throughout the earth's diverse ecosystems. From frigid climes within the arctic circle to sultry tropical habitats, social bees play an important ecological role as pollinators.



Author's rendition of *Trigona prisca*, a stingless meliponine bee—a fossil of which was preserved in Cretaceous amber 74-96 million years ago (sketch by author, after Grimaldi)

Bumblebees may well be considered the next step in sociability from the halictid bees.[10] The behavior of the halictid females is determined more by temporal factors, when they emerge in the season, than by any inherent physiological differences between the gyne and her daughters. Bumblebee castes, on the other hand, seem based on more discernable physiological differences. Bumblebee queens are larger than their worker daughters, called "**callows**", and seem to have greater reserves of fat, perhaps ensuring them the longer life-span required of the queen.[11] However, there are none of the dramatic visible differences of body structure (other than size) as among the honey bees, as the queen, in order to establish a colony, must possess the instruments of food gathering herself before she can relinquish this task to her offspring.

Emerging from her winter dormancy, a mated bumblebee queen will begin to search for a nesting site, such as an abandoned rodent burrow, soft humus which she can cement into a dome with nectar and salivary secretions, or simply a sheltered spot on the forest floor.[12] She begins preparing for her first clutch of brood by constructing a honeypot from wax which is secreted from glands on her abdomen. This honeypot is used, of course, to store the nectar which the queen collects, along with pollen, as food for both herself and her offspring. This reserve of food is used during the night or in inclement weather when the queen cannot leave the nest to forage, and must be close to her brood to incubate them against the cold—to which they are very susceptible. The pellets of pollen that she brings back to the nest are dropped on the floor until there is enough, made pasty with some of the nectar, to gather into a ball, upon which the bee lays a single egg. She seals this into a small wax cell she has constructed for the purpose and continues to gather nectar and pollen, and to knead together these balls of bee-bread or honey loaves until she has a neat little cluster of cells. This cluster will be enlarged with subsequent clutches, since each cell is used only once for brood rearing and is then used for storage, until it forms an extensive horizontal comb. She warms these cells with her own body and tries to protect them from parasites and predators. She will leave the nest periodically to collect more pollen and nectar which she mixes together and squirts into the cells.[13] (This behavior is called **progressive feeding** and is another distinction from the non-social and semi-social bees which use **massive provisioning.** In the massive provisioning strategy enough stores are laid-in to last the larva throughout its period of development in the cell.)

Inside the cells, the eggs hatch into larvae, then become pupae and finally break out of their cells and emerge as adult bumblebees which will soon take over entirely the duties of food gathering, and cell building—allowing the queen to devote all her energies to egg laying. The queen continues to lay worker eggs until the fall, when the colony may consist of several hundred bees (and in rare instances a thousand or more). Then, gynes and drones are produced. It is most likely the activities of the callows that accounts for the change in caste production. Once a certain"critical mass" is reached in the number of callows, the colony is able to increase the amount of food provided to each larva. Concurrent production of reproductive females with males, which

Stingless bees. A, Nest in a constructed hive; B, closeup of nest showing bees, brood, and honey storage area. (From S.E. McGregor's book, *The Pollination of Cultivated Crops*, USDA-ARS, Washington, D.C., 1976)

require less food than even callow larvae, allows the investment of still greater food resources per female larva, reared under massive provisioning. This massive provisioning, in which the larva has merely to open its mouth to obtain food rather than waiting to be fed, allows for the development of the fatty deposits and larger body size characteristic of bumblebee queens. These queens will mate with drones from their own or neighboring colonies. With the encroaching cold, all except the new batch of mated queens, who seek sheltered places to hibernate, have died. In the spring the process begins all over again. Of course, this is all how it should work ideally and only a small percentage of colonies are successful enough to produce new queens.

Stingless bees and honey bees exhibit the greatest degree of caste differentiation. The queens, workers and drones can quickly be identified from one another on the basis of differences in body structure.[14] In fact, so adapted are these bees to living a social existence that none could survive long apart from the hive. The drones and queens lack the body structures and behavior for food gathering. A lone worker would quickly die of exposure without the warmth and protection of her sisters. And, of course, a colony left queenless will quickly die out without a steady stream of fresh workers to renew its numbers, unless it can rear a new queen from one of the orphaned brood. For these bees sociality is survival.

"Stingless" bees (which do, in fact, possess vestigial internal stings though not the musculature to extrude them as weapons), or meliponids, are native to all of the tropics, different genera being found in South and Central America, Africa, Asia and Australia. (It is this type of bee that a fossil specimen preserved in amber for 80 million years, the oldest known fossilized bee, most closely resembles—christened *Trigona prisca* the bee is very similar in structure to *Trigona cilipes,* a present-day native of the South American tropics[15]. The presence of *Trigona prisca* would befit the tropical clime in which basked Mesozoic New Jersey, where it was found.)

In Africa and South and Central America certain species of these bees have, for centuries, been provided with hive-boxes in which to nest to facilitate harvest of the honey they produce.[16] The meliponids produce honey of a variety of qualities, depending on the species of bee and floral resources the bees use—such honey is more commonly employed for purposes of folk medicine rather than as a food and many of these honeys are particularly prized as eye ointments. In some instances, as among the Maya of Central America[17], a rich beekeeping lore has developed around the culture of these bees. In classical Mayan days the honey of meliponid bees was used to brew a potent mead-like drink called *pulque* which was an important feature at religious and civic functions—there were even bee gods, Noyumcab and Ah-Mucencab, to whom elaborate ceremonies were dedicated to ensure a copious honey crop[18].

The nests of the stingless bees are surrounded by an envelope or sheath of material similar to the papery covering constructed by paper wasps. This consists of an outer *batumen* and an inner *involucrum.* The batumen is frequently quite hard and durable and is made of laminate plates which may contain any and all of mud, dung, chewed wood fibers, and plant resins, all of which the bees collect and cement together with saliva and wax. The involcrum may consist of several layers of a more papery consistency. Most meliponid species build their nests within cavities, such as hollow trees or abandoned sections of termite mounds—I have even seen colonies of one species in the rotting timbers of Mayan ruins—thus the nest architecture is not readily apparent. More easily observed are the entrance tubes that are under the constant vigilance of guard bees. These tubes and the involucrum to which they connect are made of mud, plant resin, fecal matter, wax or a combination of these. The architecture is often distinctive to the species constructing it. (The black, oozing appearance of the entrance tube constructed by one type of bee is referred to by locals in Central America as "*el culo-de-chucho*" which translates, roughly <and more genteelly>, as "the doggie's bottom".) Trumpet-shaped or cylindrical entrance tubes, may be closed at night to protect against the parasitizing flies and raiding ants which constantly harangue the colonies. The tubes lead into labyrinthine chambers in which honey is stored in thimble-sized spherical honey-pots and brood cells are constructed in single-sided horizontal clusters which may spiral around themselves to form staircase-like helixes. The complex structures are connected to the enclosing envelope by wax supporting sprues, giving the whole nest the appearance of some abstract sculpture awaiting casting.

Inside the nest, activities follow very much the same routines as among honey bees, though the bees are generally smaller and the nests less populous (bees of the genus Melipona are typically about 8mm <1/4 in.> long, while the related genus Trigona, has species that approach the 16mm. length of the honey bee; a colony with 5,000 members would be considered at the large end of the scale for the meliponids).[19] The queen concerns herself only with laying eggs. The workers attend to her care and to that of the developing brood, as well as to the food gathering and construction needs of the colony. It is the workers, as well, who guard the entrances and, though bereft of the use of their stings, the fierce biting and caustic salivary acids that many species can secrete are formidable enough to afford adequate protection from most invaders. As in all bees, the males contribute nothing more to the colony than their body warmth which helps to incubate the nest—and the service of passing on the colony's genes to a future generation, which is, after all, the name of-the-game in biological systems.

There are six to eight species of true honey bees, or apine bees, depending on who you ask. Although most readers will be intimately familiar with much of the biology of honey bees, the general habits of the genus as a whole deserve a brief examination. The nests of all honey bees are vertical and double sided: *Apis florea, Apis andreniformix, Apis dorsata*, and the closely related *Apis laboriosa* (which some taxonomists believe should be considered a race of *Apis dorsata*) each produce a single, exposed comb. The first two species each produce a single comb that is about the size of a person's open hand, the latter two species each produce a comb that can exceed the size of an average door. The other prominent species of honey bee, *Apis mellifera, Apis cerana and Apis vechti* (alternately call *Apis koschevnikovi*)[20], build multiple-comb nests, usually in enclosed places and so from an early period were enticed to inhabit the myriad types of structures used as hives world-wide.[21]

Interestingly, no true honey bees, that is, no species of the genera Apis, is native to the western hemisphere.[22] *Apis laboriosa* seems to be confined to the Himalayas whereas *Apis dorsata* is found throughout Southeast Asia and the Philippines. *Apis florea* and *Apis andreniformis* are found in a slightly smaller area of the same region[23]—although *Apis florea* has recently been found as far west as north Africa (though the population was most likely introduced there from Pakistan)[24]. *Apis cerana* is distributed from Japan and Southeast Asia and across the Indian subcontinent. *Apis vechti* is essentially a larger, reddish version of *Apis cerana* and both are found on the island of Borneo[25]. *Apis mellifera*, the common honey bee, is native to the extremely diverse conditions encountered from the temperate forests and farmlands in northern Europe through the gamut of African desert, savannah and jungle back into the temperate regions of the southern cape.[26]

It is believed that *Apis mellifera* evolved from a common ancestor with the slightly smaller *Apis cerana*, attaining its present attributes within the last 25 million years.[27] The colonial life of all of the apid bees is quite similar and is roughly the same as that of the stingless bees. The notable difference is in the size of the populations (around 20,000[28] individuals for an average colony) and in the nest structure in which large quantities of honey are stored in distinct areas apart from the brood. The large quantities of honey and its storage around the brood nest, where it acts as an insulator against extremes of temperature, is an adaptation necessary for the bees to survive as a colony through seasonal changes in which there may be absolutely no food source available, other than the golden treasures of pollen and nectar they have stocked away. This arrangement also results in quantities of stored honey within relatively easy access to raiding human honey hunters who, for as long as anything warranting the adjective 'human' has existed, have followed the lure of honey bees' delectable caches. Because *Apis dorsata, Apis laboriosa* and *Apis florea* will not remain confined in box hives, the harvesting of their wild combs has rarely progressed beyond more than simple looting, although even this has stimulated a rich legacy of bee-lore in the regions where they are found. In contrast, the various degrees of apiculture developed with the common honey bee has lead to introduction of *Apis mellifera* to virtually all parts of the globe.

Given these contemporary counterparts to ancient ancestors, it is still sometimes difficult to retrace the evolutionary stages through which the honey bee has passed. The natural origins of the honey bee are very bit as fascinating as any myth pertaining to the creation of this marvelous creature.

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