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Bees (Hymenoptera: Apoidea: Apiformes)

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Bees essentially are wasps that turned to pollen for dietary protein. A combination of distinctive features, taken together, make bees unique among insects. (i) Sociality, characterized by overlapping generations, cooperative brood care and a reproductive division of labor between fertile queens and sterile female workers, has evolved multiple times within the bee lineage. Presumptive intermediate stages of sociality are represented by at least several living species, and thus are available for observation, evolutionary study, and experimental manipulation. (ii) Bees, unlike most other herbivorous insects, dine solely on pollen and nectar or floral oils. This dietary transition from their carnivorous ancestors was accompanied by the evolution of branched body hairs which aid bees in picking up pollen, plus modification of the hind legs or ventral abdominal surface for carrying large loads of pollen. These features typically distinguish bees from wasps. (iii) Unlike most insects, each adult female of every non- parasitic bee species, whether social or not, rears her young in a nest. Thus, all food and shelter needs of bee larvae are provided by their mother, or one or more sisters if the species is social, or the host female if the species is parasitic. (iv) From the central nest, females daily venture forth repeatedly on spatially extensive foraging trips to acquire floral resources for their brood. These trips require remarkable navigational skills equaled by few other insect taxa. (v) As a consequence of their extensive foraging at flowers, bees have become the primary biotic agents of pollination for continental floras worldwide. No other animal group so dominates this, or the other great plant-animal mutualism, seed dispersal.

Evolutionary History

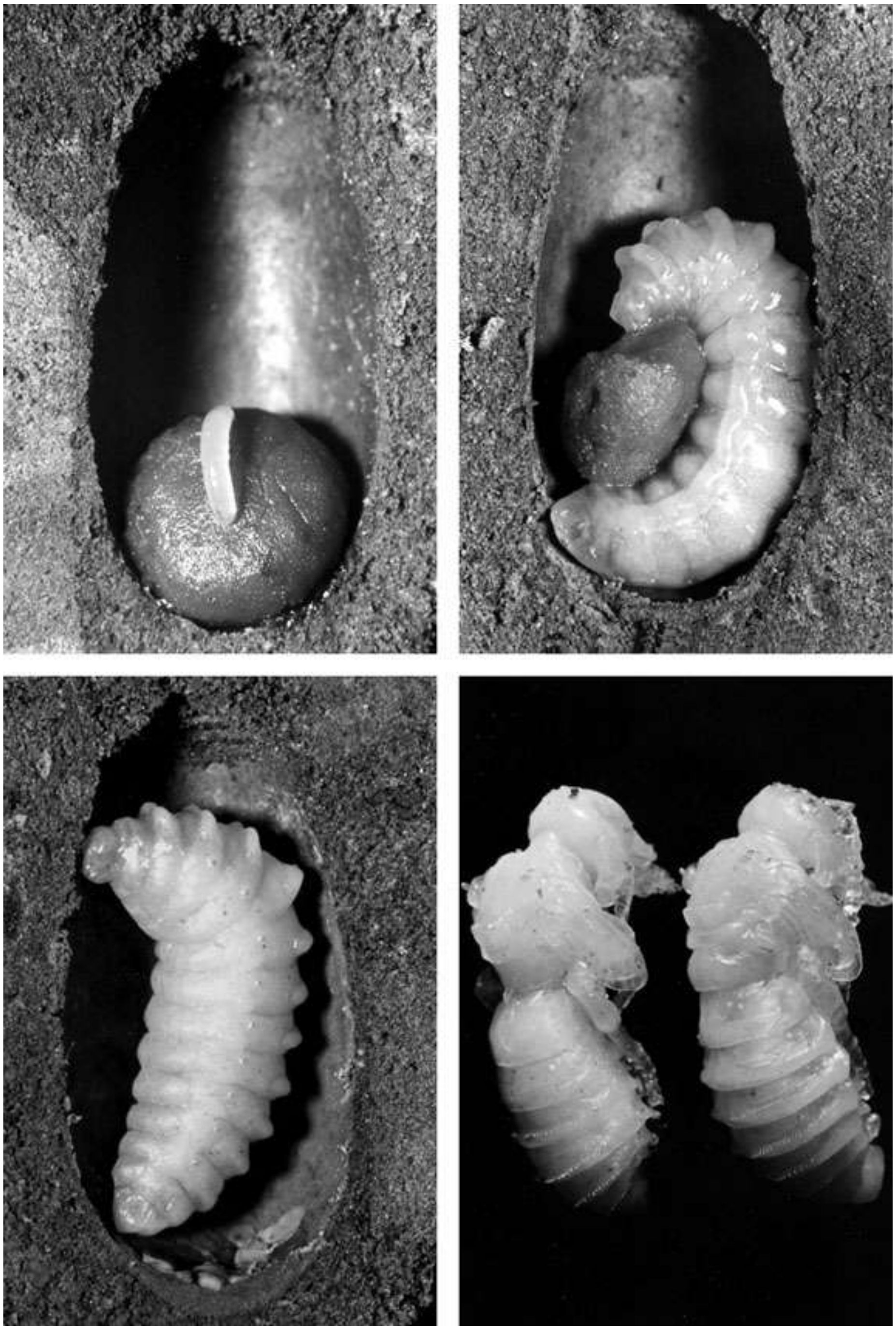
Bees (Hymenoptera: Apoidea: Apiformes) likely arose in the Cretaceous, perhaps 120 million years ago, when they diverged from the carnivorous habits of their closest relatives, the sand wasps (Hymenoptera: Apoidea: Spheciformes). Flowering plants (angiosperms) had made their debut by this time. Most paleontological material consists of bees entombed in amber (polymerized tree resins) millennia later. Specimens from the Eocene (40 million years ago) are common. They are typically workers of the stingless bees (Meliponini) that probably became mired while gathering resin to seal their nest cavities. These represent highly evolved social genera that remain extant today, suggesting a much earlier origin for bees. Tantalizing casts of much earlier fossil nest cells are also reported, but their identity remains controversial.

Diversity and Distribution

There are more species of bees today than the sum total of mammals, reptiles, amphibians and birds; 19,000 species of bees have been described, perhaps another 10,000 await discovery. They are distributed among only seven families. The largest genus (*Andrena*) has 1,400 described species; many have more than 100. Bees are native to all continents but Antarctica. Few species are found on isolated oceanic islands, but ranges of some hardy species extend well north of the Arctic Circle. Only social bees achieve maximum diversity in lowland tropical rainforests. Non-social (or solitary) species are most diverse in drier, more seasonal biomes of the world' s temperate zones. These include the Mediterranean Basin and areas of similar climate around the world (e.g., western South Africa, southern California, central Chile and Argentina, much of Australia) and the more vegetated, warm deserts (e.g., Sonoran, Chihuahuan and Colorado deserts of the southwestern U.S. and adjacent Mexico). Warmer grasslands also can be productive, such as the Great Plains of the U.S. In these regions, several hundred bee species can be easily expected in any given locality.

Development and Life Cycle

Like other insects with complete metamorphosis, bees pass through four discrete life stages (Fig. 25). Bee eggs are sausage-shaped. Those of the solitary, non-parasitic species can be proportionally huge for an insect; eggs of some large carpenter bees (*Xylocopa*) are 16 mm long. Non-social bee species are much less fecund than most insects, laying only 10–25 eggs in their lifetimes, averaging one to two per day. As with other Hymenoptera, progeny sex is determined by egg fertilization: male eggs remain unfertilized and are thus, haploid. Bee larvae are gently curved, soft, white, blind, largely immobile and defenseless grubs. Only specialized instars of some cleptoparasitic species are mobile and armed with powerful mandibles, adaptations that they use to assassinate host larvae before consuming the host' s provision masses.



Bees (Hymenoptera: Apoidea: Apiformes), Figure 25 Bee life cycle, illustrated using the alkali bee, *Nomia melanderi* (Halictidae): (top left) egg atop a completed provision mass. Note the polished waterproof cell lining applied to the soil matrix; (top right) third instar larva feeding on remaining provision; (lower left) prepupa, the post-feeding larval resting stage; (lower right) two pupae (removed from their nest cells) (photos by William Nye).

Larvae of nearly all solitary species and most eusocial species receive an individual cache, or mass provision, of pollen moistened with nectar, or occasionally, floral oils.

Provision shape and consistency varies from firm, spherical pellets to a soupy gruel on which the larva actually floats. Larvae pass through four molts (so five instars) to accommodate their rapid growth, consuming their provision mass in a few weeks. Larvae do not defecate until they are mature. Once the provision mass is consumed, larvae of many (but not all) species then spin a cocoon. The final larval stage is the prepupa, which is more robust and resistant to desiccation than the earlier instars, but still grub-like. This is the typical resting, or diapause, stage for those temperate-zone species whose single adult generation flies later in spring or summer. Unlike most other insects, bees do not weather inhospitable seasons as pupae. Rather, bee pupae are quite delicate, resembling waxen versions of the adult. If a bee species is one that flies in the early spring (allowing little warmth for further development), then the pupal stage lasts only a few weeks, yielding an adult that will remain in the cocoon (or nest cell) to overwinter. Some halictids (sweat bees), as well as bumble bees, emerge as adults, mate, and then disperse before overwintering.

Nesting

All larval bees live in a nest selected, constructed, maintained, defended and provisioned by their mother, sisters (social species) or host (parasitic bee). A genus of bee often can be recognized by its nesting substrate and nest architecture. Most bee species nest underground, typically exca vating a central, cylindrical tunnel that is either partitioned into nest cells, or from which lateral tunnels branch that terminate in nest cells. Soil cliffs as well as more horizontal surfaces are used. Excavated soil on horizontal surfaces is often heaped in a small cone or delta of irregularly sized pellets, the “tumulus.” Nest depths differ among species, ranging from a few centimeters to several meters if in sandier soils. Cells are often egg- or barrel-shaped, just large enough for a mother bee to fit with her assembled provision mass. Cell walls are commonly smoothed, even polished, usually with the addition of a secreted waxy or membranous waterproof lining, or alternatively, plant resin. Other bee species nest above ground, excavating pithy stems of plants or adopting abandoned tunnels chewed by wood-boring larvae of beetles and some other insects. Some carpenter bees (*Xylocopa*) can chew tunnels directly into sound wood. The highly social honey bees and stingless bees often build their nests in hollow tree cavities. Free-standing nests are made by a few paleotropical honey bees (pendant wax combs) and a few other bees (mostly orchid bees and some megachilids that use clay or resin).

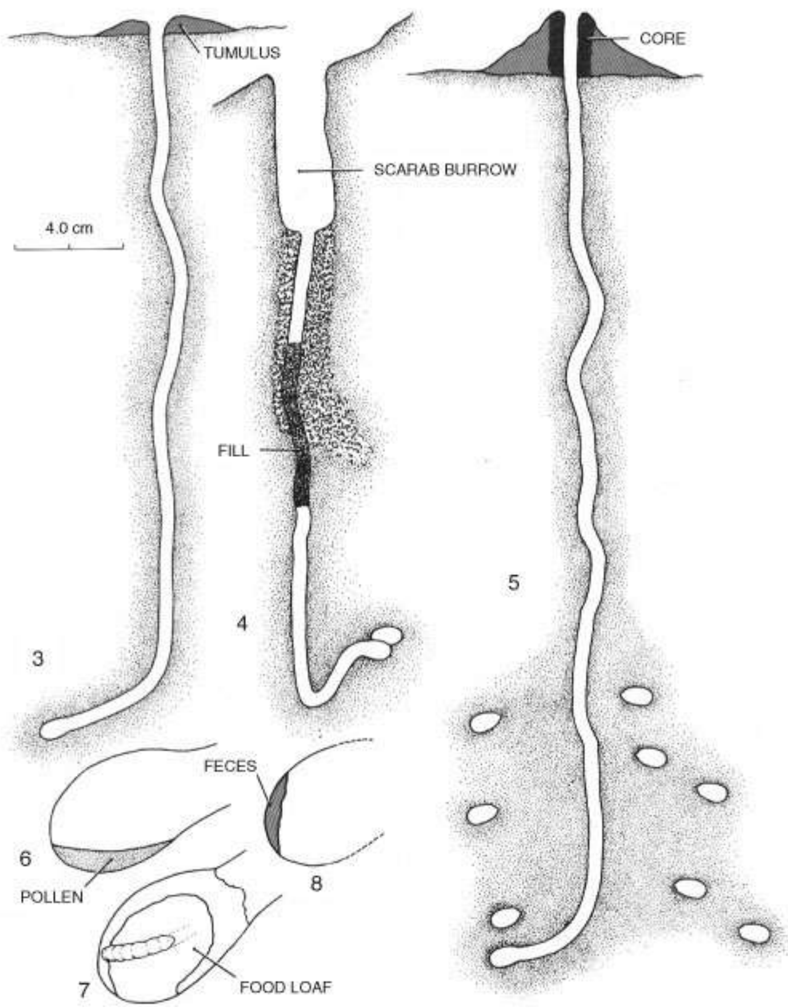
Mating Biology

Male bees do not contribute to nesting (excavation, foraging, defense) (Fig. 26). With few exceptions, males are not welcome in the nest. They spend their days patrolling for receptive conspecific females, and their nights sleeping on flowers or vegetation, or in shallow burrows underground. Males of various species enhance their encounter rates with females using one or more search and/or advertisement strategies employing scent and vision. Among non-social species, males are often protandrous, emerging some days before females of the year. Males of floral specialists may patrol preferred floral hosts, especially if females of their species mate repeatedly during their lifetimes. Males also may patrol nesting sites; among species whose females mate but once and whose nests are aggregated, males may compete intensively to find freshly emerged virgin females, guided by the virgin female’s scent. Conversely, males may apply scent-marks to attract females to a sort of trapline that males patrol. These can sometimes extend for hundreds of meters. Honey bees, some bumble bees and large carpenter bees maintain aerial territories. Some orchid bees reportedly form “leks” perfumed with scents synthesized from floral oils of orchids. A few recent cases report flightless males that linger in their natal nests to mate with their sisters. In general, courting and mating are brief affairs for bees. Most species are monandrous, each female mating but once in her lifetime. All female bees are able to store live sperm to varying degrees; at the extreme, queens of social species store live male sperm for months or even years. Hence, sperm often outlive the male bees that produce them.

Bees (Hymenoptera: Apoidea: Apiformes), Figure 26 Mating adults (above), male atop female (photo by William Nye); aggregation of males (center) sleeping together atop plant stem (photo by William Nye); female at nest entrance (below). (photo by James Cane).

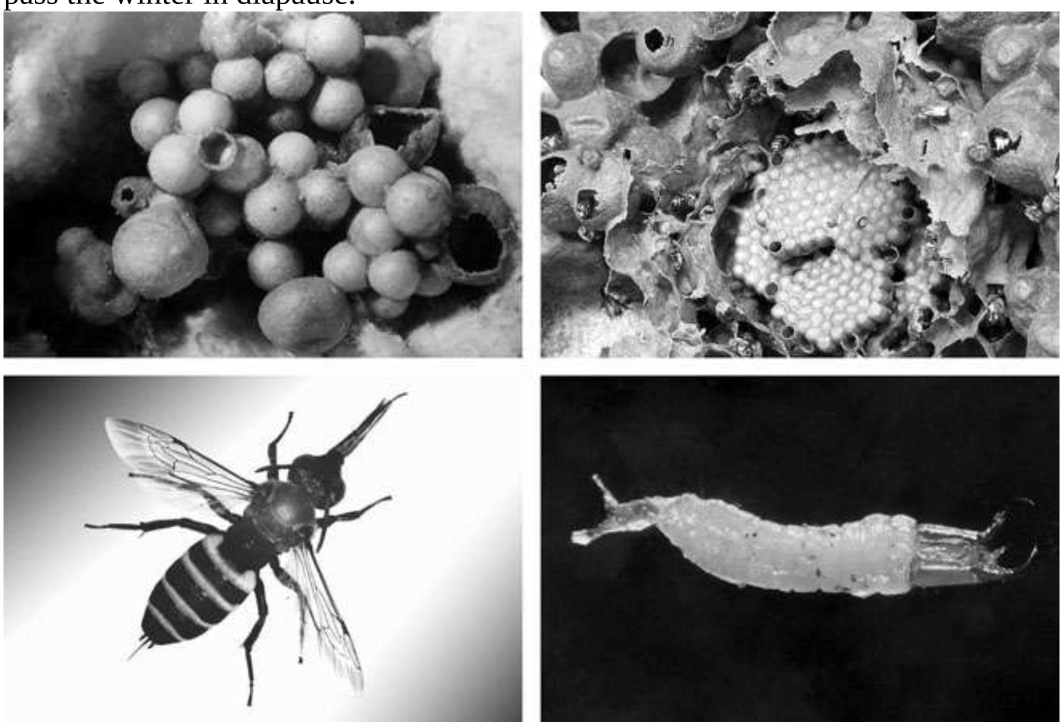
Sociality

Bees have lineages representing all degrees and hypothesized evolutionary steps of sociality, including reversion to solitary habits. Populations of a few species range from solitary to social depending on ecological circumstance. Less social arrangements include: communal species, wherein reproductive females sometimes share in a single nest’s construction and defense but otherwise act solitarily; semisocial colonies founded by a group of (likely) sisters; subsocial species in which mothers actively care for growing daughters, that in turn may linger as adults to aid their mother; and several other much rarer arrangements. Many non-social species, especially ground-nesters, will nest gregariously (Fig. 27) in populous aggregations of hundreds to many thousands of individuals. During adult activity, these bee “cities” can be dramatic, with a dense traffic of foragers and patrolling males producing a loud, daylong hum.

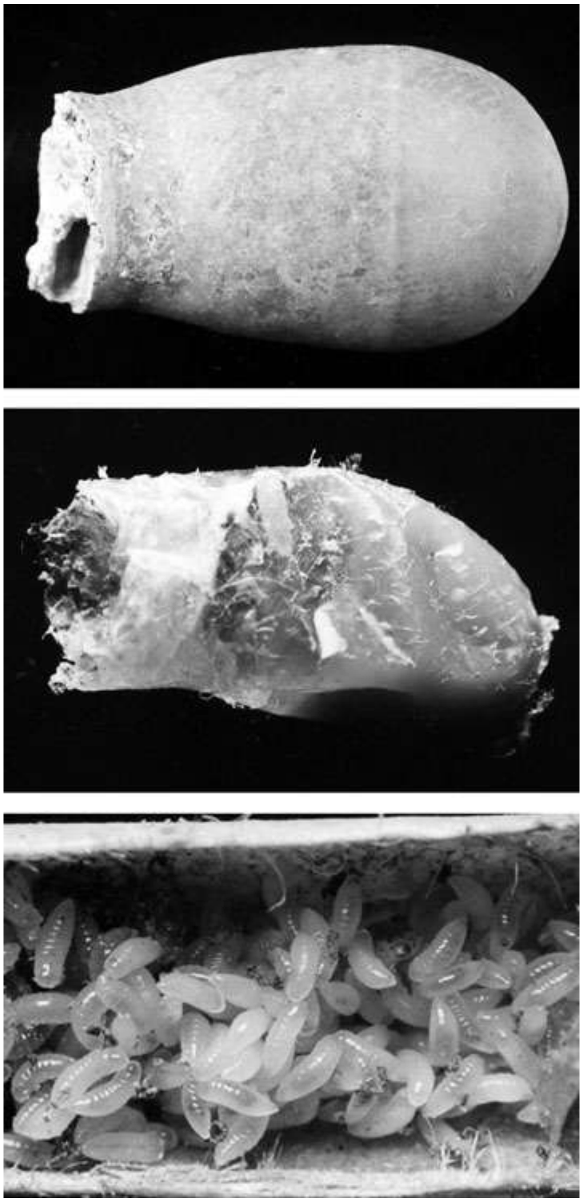


Bees (Hymenoptera: Apoidea: Apiformes), Figure 27 Gregarious nesting (above left) showing dark soil tumuli atop a square meter of soil surface (photo by James Cane); core (1 cu. ft.) of nesting soil (above right) from alkali bee nesting aggregation, showing numerous white prepupae in their individual nest cells (photo by William Nye); schematic (below) of an excavated subterranean nest of the neotropical bee *Tapinotaspis tucumana* (Apidae). Nests and enlarged views of three nest cells (Reproduced with permission from the American Museum of Natural History. Artwork by Jerome Rozen, Jr.).

The hallmarks of higher sociality ("eusociality") are an overlap of generations (mothers and daughters), cooperative brood care by workers, and reproductive division of labor (queens and workers). Workers are rarely, if ever, mated, and so, if they lay eggs, these are male. For primitively eusocial species (some sweat bees and carpenter bees, nearly all bumble bees), nests are founded in the spring by a single, mated female (gyne), as with solitary species. In rare cases, there are several foundresses. This mother bee builds a nest and prepares cells. Each cell receives a ball (Figs. 28 and 29) of pollen moistened with nectar and a single egg. The cell is then sealed. Emerging daughters remain with the nest rather than dispersing, helping their mother construct, provision and defend her nest. The original foundress, mother to the nest, then becomes the colony's primary egg-layer (queen). The more eusocial species have morphologically distinct queens and workers. Primitively eusocial colonies grow to, at most, a few hundred workers. Late in the summer or early autumn, reproductives are produced, and mate; only the future queens pass the winter in diapause.



Bees (Hymenoptera: Apoidea: Apiformes), Figure 28 Laboratory nest of the bumble bee *Bombus morrisoni* (Apidae) (above left) showing nest cells and honey pots clustered amid insulative cotton batting; Nest of a Brazilian *Melipona* sp. (Apidae)(above right). The thin pliable sheets of the involucrum (i) have been peeled back to reveal the topmost tier of horizontal combs (c). Between the involucrum and the wall of the cavity are the large pollen pots and honey pots (h). Honey is visible in those pots that remain open (Photo by James Cane); adult female of the cleptoparasitic bee, *Triepeolus dacotensis* (Nomadinae) (lower left). Note paucity of hairs, lack of pollen-transporting structures, and the exserted sting; first instar "assassin" larva of *Triepeolus dacotensis* (Nomadinae) (lower right). Note its long recurved mandibles, which are used to grip and kill the host egg or young larva. Subsequent instars resemble normal bee larvae (photos by William Nye).



Bees (Hymenoptera: Apoidea: Apiformes), Figure 29 Cast of nest cell of *Anthophora* (Apidae) (above); provisioned nest cell of ground-nesting *Colletes* (Colletidae), showing the thin, translucent membrane made of secreted polyesters (center) (photos by James Cane); larvae of parasitic *Melittobia* wasps (Hymenoptera: Eulophidae) in nest cell of an *Osmia* bee (below) (photo by William Nye).

Only the stingless bees (Meliponini) and honey bees (*Apis*) are highly eusocial. Most reside in the humid tropics. Their colonies are tightly integrated and perennial, populated by thousands of workers headed by long-lived queens that are dependent on worker care.

Their colonies reproduce by "fissioning," when swarms of workers accompany a queen to found a new colony.

Foraging

Except for queens and drones of highly eusocial species, all bees visit flowers. For males and individuals of cleptoparasitic species, it is only for self-maintenance and sometimes mates. All other females seek, gather and transport nutritious substances (typically pollen and nectar) and sometimes, nesting materials for their progeny. Species of honey bee size will regularly fly a kilometer or more to desirable bloom. Using the sun and local landmarks for navigation, they can then fly directly home at 15–25 kilometers per hour to find a nest entrance that is often no bigger than the bee, and, in the case of gregarious species, that is imbedded in an aggregation of hundreds or thousands of like-looking entrances of their conspecifics.

Bees always take nectar at flowers. Nectar powers bees' flight and contributes carbohydrates and water to larval diets. Typical nectar sugars are glucose, fructose and sucrose. Few nectars are toxic. A retractable, complex proboscis allows bees to sip or lap nectar. A bee's access to nectar is constrained by body size, tongue length, and the flower's dimensions. Some carpenter bees, stingless bees and bumble bees regularly rob deep, tubular flowers of their nectar by perforating the corolla near its basal nectaries. Perhaps because bees can readily assess nectar volume, sugar constitution and its concentration, individuals and species can and will compare nectar yields of various flowering species, optimally choosing the most rewarding species at any given time. Some flowers, mostly tropical, secrete calorically rich oils rather than nectar. These are mopped or wiped up by bee species that have pads and "squeegees" of hairs specialized for the task, to be incorporated into larval provisions and sometimes, nest cell linings. Some ground-nesting species and many eusocial species synthesize and secrete their own calorically rich substances that they blend into progeny provisions.

Bees also seek pollen at flowers, which is their key dietary source of proteins, fats, minerals and sometimes starches, for themselves and their offspring. Pollen, of course, also contains the male gametes of flowering plants, so it really serves two reproductive purposes, plant ovule fertilization and bee reproduction. No effective dietary substitute for pollen has yet been devised for bees. Few animals match the nitrogen assimilation efficiency of bees, despite the indigestibility of the external shell, "exine," of pollen grains.

Pollen, in most cases, dusts the foraging bee as a powder that lodges in the vesture of branched hairs that envelop its body. Harvest may be enhanced by buzzing, biting, scraping and scrabbling. Many specialized structures, hairs and behaviors of foraging females then work in concert to efficiently groom and accumulate pollen from the body for transport. Pollen is transported in a brush of hairs called a "scopa," often on the hind legs (or under the abdomen of megachilids). A few taxa carry pollen internally in their crop (e.g., Hylaeus). Bumble bees, honey bees, orchid bees and stingless bees carry pollen in a pollen basket, or “corbicula,” on the hind leg, a smooth, slightly concave surface surrounded by guard hairs that holds a damp pollen pellet.

Anthers of some flowers (e.g., tomato and blueberry) shed their pollen through apical pores or slits like a salt shaker. These require vibration to dispense their content of pollen. Some bees shake this pollen free by battering or stroking the anthers with their legs, while others bite the anthers to squeeze out pollen. Species of many genera can shiver their flight muscles while on the flower, sonicating these anthers to eject their content of pollen. This buzzing is audible. The effect can be duplicated with a vibrating tuning fork. Bumble bees frequently use this method of pollen extraction, even for flowers with anthers of normal morphology.

Many bee species are floral generalists (“polylectic”), taking pollen from many taxa of flowers, a necessity for the long-lived colonies of social bees. Foraging individuals often will display floral constancy, selectively visiting sequences of conspecific flowers on a given foraging trip, despite the availability of alternatives. Such preferences are labile, perhaps reflecting learning or memory constraints. In contrast, a third or more of the non-social species in a community may be “oligolectic.” This is a fixed species-specific predilection to collect pollen from the same small subset of available flowering species, commonly one or several related genera within a plant family. Such unwavering fidelity is particularly common among desert bee faunas and vernal bees of the temperate zone. The reason(s) for oligolecty are not fully understood. In some cases, oligoleges seem to accumulate at reliable pollen hosts that produce generous quantities of pollen (e.g., willow, sunflowers, creosote bush, and blueberries). For other species, the association seems to reflect phenological specializations (e.g., crepuscular flowers, early spring blooms) or more or less private floral resources eschewed by other species (e.g., oil flowers of *Lysimachia* and their associated *Macropis* bees). Unlike insect herbivory, host chemical defenses rarely, if ever, dictate floral specialization by bees.

Pollination

Bees are the most important and cosmopolitan biotic pollination agents in most continental habitats, and for most prevalent plant families, such as the Asteraceae, Fabaceae, Lamiaceae, Orchidaceae, Rosaceae and Solanaceae. Few nocturnal flowers are pollinated by bees. Reciprocal co-evolution between bees and their flowers seems, at best, diffuse in nearly all cases, although adaptations that enhance attraction, resource extraction and pollination are evident everywhere. Most collected pollen ends up in a larval provision, not on a flower’s stigma, but bees are still vastly more efficient than wind in moving pollen to receptive flowers. Bees are essential pollinators of some vegetable crops (or their seeds), many prominent fruit and seed-oil crops, forage legumes and a few nut or fiber crops. Crops that contribute the starches and refined sugars to the human diet are typically wind-pollinated or vegetatively propagated. Home and market gardeners benefit from pollination services of wild bees. In large mechanized agriculture, however, only hived honey bees can generally supply the millions of inexpensive foragers needed for pollination. In the past half-century, though, a growing minority of tree fruit, forage seed and greenhouse crops are benefiting from pollination services of managed solitary bees and bumble bees (rather than honey bees), a trend that seems likely to continue, given their often superior pollination efficiencies and the devastating effects of new pest problems suffered by honey bees.

Diseases, Parasites and Predators

Among insects, the superior life expectancies of bees result largely from superior maternal care of offspring. Females actively deter predators and parasites by biting, stinging and by use of chemical repellents. Nest cells are waterproofed and possibly fumigated with applied glandular secretions or plant resins. Despite such extensive maternal care and defenses, bees are nonetheless plagued by diseases, parasites and predators. Feeding larvae, in particular, succumb to various viral, bacterial and fungal diseases. Microorganisms commonly spoil provision masses, too. Nematodes and mites (mostly external) are ubiquitous bee parasites. Many larval insects devour the contents of bee nests, including clerid and meloid beetles. Others are internal or external parasitoids, including chalcidoid wasps, bombyliid flies and strepsipterans. The elaborate structural defenses of stingless bee nests attest to the intense predation pressures of ants and social parasites of the tropics. Adult bees are subject to the myriad predators of other mobile insects.

Cleptoparasitic, or cuckoo bees, are analogous to cowbirds and European cuckoos, surreptitiously inserting their eggs into the provisioned nest cells of their bee hosts. There are thousands of cleptoparasitic species, most associated with specific genera of host bees. They directly or indirectly exterminate the host larva, ultimately consuming its provision. Adult females spend much of the day searching for and evaluating host nests. They display numerous subtle adaptations to conceal their eggs from the host female and repair damage incurred to nest cells during oviposition. Odor concealment and mimicry may be practiced as well. Social bee species (other than *Apis*) host their own parasitic bees, often evolving from within their host’s genus. Psithyrus queens usurp bumble bee nests, enslaving unwitting host workers to produce parasite progeny. Robber genera among the stingless bees (e.g., *Lestrimelitta*) raid host nests for honey and pollen.

Conservation

Human activities also can harm bees. Bees tend to be sensitive to broad-spectrum insecticides, which if used indiscriminately or carelessly by farmers or homeowners during bloom, can poison adults, or later, their progeny. No genetic resistance has been shown. Herbicides, when used to kill wildflowers, remove available forage for bees. Habitats and constructs that are extensive, monotonous and inhospitable (e.g., lawns, parking lots, wheat fields) fail to fulfill bees nesting and/or foraging needs, although bees can readily fly through a finer patchwork mosaic of these features if interspersed with favorable nesting and foraging habitats. Unlike accidental or misguided introductions of plants, vertebrates and shellfish, exotic bees have generally been of little ecological consequence, although ill-guided international trade (or smuggling) of honey bees and bumble bees has been disastrous in some recent cases. The greatest risk attending intercontinental transport of live bees is likely to be the inadvertent transport of diseases and pests, such as those that are currently devastating apiculture, especially *Varroa* and tracheal mites.

The Families of Bees

Seven families of bees are currently recognized. The Colletidae, Halictidae, Andrenidae, Melittidae and Stenotritidae are grouped as short-tongued bees, while the Megachilidae and Apidae are long-tongued bees. The five more common families are considered here.

Family Colletidae: Yellow-Faced, Masked and Plasterer Bees

Distribution: Worldwide, but Greatest Diversity is in the Southern Hemisphere, Including Australia. This is probably the oldest extant bee family. No studied species nests socially. Pollen is transported dry in hair brushes of the hind leg (e.g., *Colletes*) or mixed with nectar and carried internally in the crop (e.g., *Hylaeus*). Their tongue tips are distinctively bilobed. They nest underground, or rarely, in mortar and even sandstone (e.g., *Colletes*), in pithy stems (e.g., *Hylaeus*), or adopt holes in wood. The plasterer bees are so named for the peculiar, secreted, transparent, polyester membranes used to waterproof their nest cells; those of *Hylaeus* contain silk strands. *Hylaeus* (=*Prosopis*) (570 species) and *Colletes* (330 species) are the commonly encountered genera in the U.S. and Europe; *Leioproctus* has 300+ species in Australia and temperate South America; *Nesoprosopis* has radiated in the Hawaiian Islands, where many of its species appear to be endangered. This subgenus contains the only cleptoparasites in the family. *Hylaeus* may be the most cosmopolitan of all bee genera, found on all continents but Antarctica as well as many oceanic islands, their dispersal facilitated by their stem-nesting habits.

Family: Andrenidae

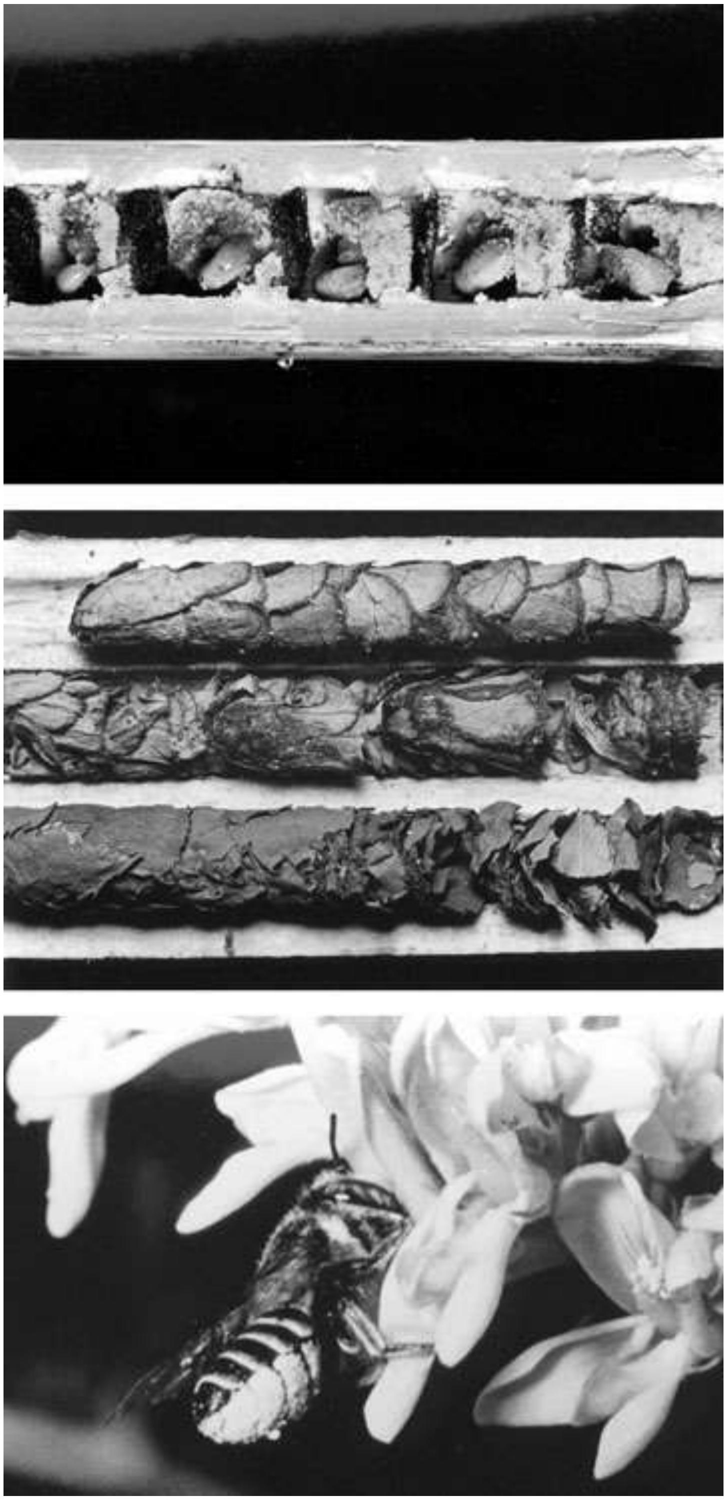
Distribution: Worldwide, Except Australia, Rare in the Moist Tropics. Species of this family nest underground. The family includes two enormous genera: *Andrena* (1,400 species, ubiquitous in north temperate regions) and *Perdita* (600 or more species, mostly of the American Southwest and northern Mexico). *Perdita* are small-bodied, including the tiniest bee, *Perdita minima* (slender, 2 mm long, 1/3 mg). A few species of *Perdita*, *Andrena* and *Panurgus* nest communally; no studied andrenid is social. There are no cleptoparasitic species in this family. Pollen is carried on the hind legs, and in some species, is moistened with nectar. Probably all *Perdita* are oligolectic, as are the majority of *Andrena* and species of other genera.

Family Halictidae: Sweat Bees, Alkali Bee, etc

Distribution: Worldwide. Most halictids are small or medium sized. Some taxa are commonly known as sweat bees because they alight on people's skin to lap up sweat for the salts that it contains. Many halictids are darkly colored, others are a brassy or brilliant emerald green. Some *Nomia* have striking pearly green or orange abdominal bands. Pollen is carried on the hind legs, typically dry. Their nests are burrows in soil, or occasionally, rotting wood, sometimes in dense aggregations. The common, cosmopolitan cleptoparasite genus in the family is *Sphecodes* (250 species). Halictids illustrate an unprecedented diversity of social organization, particularly among the 1,000+ species of *Lasioglossum.*

The alkali bee, *Nomia melanderi*, is the world's only intensively managed ground-nesting bee. In regions of the western U.S., alfalfa (=lucerne) seed growers construct large subirrigated nest sites with salt-crusted surfaces. Densities of 400 nests/m^2 over a hectare or more can be obtained with this gregarious bee. Nest sites can remain populous for more than 50 years. Another effective alfalfa pollinator, *Rhophitoides canus*, is less intensively managed in regions of eastern Europe for alfalfa seed production.

Family Megachilidae: Leaf-Cutting Bees, Mason Bees, Carder Bees and Others
Distribution: Worldwide. The common names for groups in this large family refer to the remarkable diversity of exogenous materials that they typically use to line or construct their nest cells. Many nest above ground in twigs, stems and wood, and will readily adopt drilled holes in these substrates (termed "trap nests"). A few even nest in abandoned snail shells. *Megachile* and others line their nest cells, and partition and cap their nest tunnels, with strips and disks neatly cut from leaves or petals; other species build with leaf pulp, resin, nectar, mud, plant hairs, or pebbles. Foraging females of non-parasitic species can be easily recognized, as they are unique in (Fig. 30) carrying pollen in a scopa solely beneath the abdomen. Nearly all species are solitary. There are several cleptoparasitic genera (notably *Coelioxys*, 300 species). *Megachile* is a cosmopolitan genus (900+ species); *Osmia* (300 species) are common in the Northern Hemisphere. The world's longest bee is *Megachile pluto* at 39 mm. Many megachilids are important pollinators, especially for plants in the pea and clover family (Fabaceae). The cavity- nesting species are the most successful stowaways in transoceanic travel.



Bees (Hymenoptera: Apoidea: Apiformes), Figure 30 Nest of *Osmia* (Megachilidae) in reed, split open to reveal partitioned nest cells each occupied by a single larva with its mass provision of pollen moistened with nectar (above); three nests of a leaf-cutting bee (*Megachile*: Megachilidae), consisting of a linear series of cells each wrapped with cut leaf pieces (center); female of the alfalfa leaf cutting bee, *Megachile rotundata*, visiting alfalfa flowers (below). Note the pollen load carried dry in a scopa of hairs beneath her abdomen. To the right is a "tripped" flower, the staminal column pressed against the banner petal. Good alfalfa pollinators trip the flowers frequently (photos by William Nye).

The alfalfa leaf-cutting bee, *Megachile rotundata*, came to the U.S. from the Near East as a stowaway before 1937. Burgeoning feral populations of this bee prospered in the semi-arid western U.S. The species' value as an alfalfa pollinator soon became apparent. A multimillion-dollar industry developed in North America for cheaply mass rearing of this species for sale to alfalfa seed growers. Wooden or foam boards, each with several thousand nesting holes, are placed in shelters in alfalfa fields. Each shelter receives 50,000 or more females. This bee is versatile, pollinating other crops too, such as hybrid canola and various vegetable seeds.

Several species of mason bees in the genus *Osmia* are more recently being managed in Japan, the U.S. and Europe to pollinate tree crops in the rose family, such as apples, plums, sweet cherries and almonds. One of these species has been dubbed "the blue orchard mason bee." Only 250–300 blue orchard bees are needed to pollinate as many apple or cherry flowers as two to three hives of honey bees.

Family Apidae: Carpenter Bees, Orchid Bees, Bumble Bees, Stingless Bees, Honey Bees

Distribution: Worldwide. This family is large, ecologically diverse and continues to be taxonomically perplexing. One or more tribes of this family is most closely related to the lineage that evolved into today's highly eusocial Apinae. Many cleptoparasitic species are included (1,600 species). This unwieldy group is best recognized by its constituent tribes, of which there are many. Select ones are treated here.

Subfamily Nomadinae: Cuckoo Bees

Distribution: Worldwide. This is the largest group of cleptoparasitic bees (Nomada alone has 800 species). Most species are glossy, quite hairless and wasp-like with a rugged exoskeleton. They can commonly be seen patrolling low over the ground for host nests.

Subfamily Xylocopinae: Carpenter Bees

Distribution: Worldwide. Carpenter bees typically excavate nests above ground in pithy stems or even bore into sound wood. Cells are unlined. Most species are solitary, but some are subsocial or even primitively eusocial. Females overwinter as mated adults; they can be very long-lived. The large carpenter bees (*Xylocopa*) are primarily tropical. They can resemble bumble bees, but have a smooth, glossy dorsal abdomen and transport their pollen dry. *Xylocopa* pollinate commercial passion fruit; they are also adept nectar robbers. Males of some *Xylocopa* hover for hours in aerial territories, pursuing any and all small airborne objects. The small carpenter bees (*Ceratina*) nest in dead stems of roses, sumac, elderberry and some grasses.

The Corbiculate Apinae: Orchid Bees, Bumble Bees, Stingless Bees, Honey Bees

Distribution: Worldwide. This quartet of tribes contains all of the highly eusocial bees, as well as the primitively eusocial bumble bees and the mostly solitary orchid bees. All secrete wax, which they incorporate into their nest structures. They carry pollen on a specially adapted, smooth region of the hind leg referred to as the pollen basket or "corbicula." Taxonomists formerly grouped these four tribes as a separate family.

Tribe Euglossini: Orchid Bees

Distribution: New World Tropics, from Central Mexico into Argentina. The orchid bees are so named because the males collect scents from orchid flowers and, in the process, pollinate the orchids. The orchids provide no food, but rather produce scents which male euglossines collect and place in a glandular pocket of their enlarged hind legs. These perfumes attract mates. Several species have intricate male displays. These large bees are flying jewels, sporting metallic emerald, cobalt, violet and bronze colors as well as red, orange and yellow. They are important pollinators of many endangered tropical orchids and probably the Brazil nut, too.

Tribe Bombini: Bumble Bees

Distribution: The Americas, Europe, Asia, North Africa. Bumble bees (*Bombus*) are large, furry, often black and yellow, orange or red bees. They are common in the world's cooler climates, following mountain ranges into the tropics. Few species live in deserts or rainforests. They nest shallowly underground, often in abandoned rodent nests, or sometimes above ground, either in tree cavities or, less commonly, beneath a leaf heap on the forest floor. They actively brood larvae to warm them, and fan their wings at the colony entrance to cool its contents. Few other bees can fly in cooler weather. *Bombus* consists of primitively eusocial species and a lesser number of social parasites. They are important pollinators in alpine, boreal and subarctic habitats. Queens of species such as *B. nevadensis* and *B. dahlbomi* are the world's most massive bees, weighing a gram or more (the weight of a raw almond).

Bumble bees are important pollinators of several crops, especially red and crimson clover. The honey bee proboscis is too short to probe such deeply tubular flowers. Bumble bees, having longer tongues, work these flowers efficiently. Bumble bees have been imported into New Zealand and Chile for clover pollination. They aid in the pollination of several other crops like alfalfa, and several fruits, especially blueberries, cranberries and kiwi. A multimillion-dollar global business has emerged from Europe for year-round propagation of disposable bumble bee colonies to pollinate greenhouse vegetables like tomatoes, peppers, eggplants and squashes. Introduction of these few managed species outside of their native ranges can lead to feral populations that pose problems for native *Bombus* and perhaps other bees.

Tribe Meliponini: Stingless Bees

Distribution: Old and New World Tropics. The stingless bees are highly eusocial, and as a group, exhibit a sweeping diversity of adaptations and natural history traits. Their permanent colonies can be populous, containing between 300 and 80,000 workers. Although stingless, many can defend their nests with irritating bites sometimes accompanied by caustic secretions. Queens are morphologically distinct from workers, their status sometimes determined genetically, in other cases as an individual larva's reproductive gamble. Of the 260 known species, 70% are found in Central and South America. They are the most common insects in Dominican and Baltic amber.

Stingless bees usually build nests in tree hollows, although some species nest on exposed surfaces, in underground cavities, or in termite or ant nests. Workers fashion a hard shell of "batumen" for the nest, consisting of wax blended with resin, mud or vegetation. Intricate nest entrance platforms and tubes are fashioned from wax, resin, or even plant latex. Within this shell, honey and pollen are stored in large irregular waxen pots. These rim the brood chamber, whose exterior is delineated by layers of pliable, delicate sheets of the "involucrum," made of insulative wax imbued with resin. Within this chamber are the waxen combs dedicated to brood rearing, grouped in horizontal tiers supported by thin pillars, reminiscent of nests of hornets or yellow-jacket wasps. Cells are typically mass provisioned with pollen, honey, and in some genera, glandular secretions (in a few cases, consisting of digested carrion). Some genera (e.g., *Lestrimellita*) rob nests of other stingless bees for their honey and pollen stores.

Colony fission is unlike *Apis*, because for meliponines, the new home is selected and furnished before the swarm issues from the parent colony. Workers assemble a complete new nest using materials transported from the parent colony. Only then does a group of workers and new queen fly to the new nest. The old queen is too large to fly and remains with the parent colony and its workers.

Workers of some stingless bees recruit nestmates to food sources, but in ways different from *Apis*. Scouts of some species scentmark trails from productive flowers to the nest, depositing mandibular gland secretions on surfaces every few meters. Returning to the nest, this scout buzzes loudly; the longer the buzz, the greater the distance of the food from the colony. The scout's behavior excites others which follow the odor trail to the resource. This method of recruitment communicates not only the direction and distance of food from the nest, but can lead other foragers directly to the food at any height by means of the odor trail. This three-dimensional road map is especially adaptive in towering tropical forests where flowers are frequently found high in the leafy canopy.

Stingless bees benefit people in several ways. In the Neotropics, *Melipona* colonies are cultured for honey in special wooden hives, although yields are meager (2–5 pounds per year). Stingless bees pollinate numerous tropical crops, but their economic impact has not been widely estimated. Stingless bees are promising pollinators for greenhouse crops.

Tribe Apini: True Honey Bees

Distribution: Europe, Asia, Africa, Now Introduced to all Continents Except Antarctica. There are 11 currently accepted species of true honey bees, all of the genus *Apis*. These are very different from all other bees, such that their evolutionary origins and ancestry remain unresolved. The genus is largely restricted to tropical Asia. Taxonomic diversity is centered in Indonesia, Malaysia and the Philippines, where new species continue to be discovered. Only the familiar western honey bee or "hive" bee, *A. mellifera*, is also native to Europe, northern Asia, and most of Africa. Its colonization of cooler regions was facilitated by its honey storage habits that fuels the workers' warming of their brood. Because we value this species for honey, wax and pollination, and can manage it in transportable hives, it has been further introduced throughout most of the world.

The western honey bee is among the most studied animals on the planet. Certainly their hallmark behavior is the remarkable abstract dance language performed by foragers and scouts for precisely communicating distance, direction and quality for resources, translating the direction of gravity into celestial bearings. Once thought unique to *Apis mellifera*, this and other behaviors now have been observed and studied for some of the lesser-known species of *Apis*, too.

Colony activities of *Apis* require sophisticated coordination. Much of the information is communicated olfactorily using pheromones. Like the Meliponini, all *Apis* are highly eusocial, maintaining populous perennial colonies. Queens, drones and workers are morphologically distinct. Among bees, only worker *Apis* have a barbed sting that lodges in the skin and continues to pump venom even after the worker bee has been killed and swept away. Colonies reproduce by fissioning, again like stingless bees, but in *Apis*, it is the old queen that departs with the swarm, whose workers then scout out a suitable nesting site at which they must construct their combs unassisted by the parent colony. This seems a riskier strategy, but it does allow swarms to disperse more widely. Honey bees thermoregulate their colonies using evaporative as well as convective cooling. Some tropical species undertake mass defecation flights to further nest cooling. Only *Apis* produce the familiar waxen vertical combs of uniform hexagonal cells that are reused over and over to house pollen, nectar (as honey) or progeny, although the wax itself cannot be recycled. Very unusual for bees, larval honey bees are fed progressively rather than with a cache of food, which together with the uniform comb dimensions, yields adults of very consistent size.

Species of *Apis* can be assigned to one of three groups, based on body size and nesting habits. Two dwarf honey bees, exemplified by *A. florea*, have small colonies of a few thousand small workers that construct beneath a branch a single exposed comb the size of a waffle. The top of this comb is broadened horizontally; recruitment dances performed on this surface are oriented simply in the direction of the food source. Several giant honey bees (e.g., *A. dorsata*) also build a single exposed vertical comb, often in conspicuous groups, but beneath a stout branch or cliff. Living curtains of the huge workers envelop the massive comb; when disturbed, they pour off *en masse* to assail any intruder. They are nonetheless robbed for honey. The remaining species of *Apis* build nests that consist of multiple wax combs housed in a hollow tree or rock cavity. Cavities enhance defense and insulation, but present problems with ventilation for temperature, humidity and atmospheric control. The most familiar representatives of this group are *A. cerana* and *A. mellifera*, which share many similarities, including their management in hives.

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