

the southern United States to southern South America with one genus in Australia; the Xeromelissinae are primarily South American; while the Neopasiphaeinae (surely the ugliest subfamily name among all bees) are found mostly in South America and Australia. Colletinae are found on all continents except Australasia and Antarctica, whereas the Hylaeinae are worldwide except for Antarctica.

See also Brood Cell; Classification; Mouthparts.

Communal

Most bees are solitary, with a single female occupying each nest. Some have queens and workers. But there are also bees that live in groups in an egalitarian fashion: they share a nest entrance but otherwise act as if they were solitary. In these communal nests, each female constructs her own brood cells, collects food for her own offspring and lays her own eggs. Communal behavior has arisen independently multiple times among the bees and communal societies may range in size from just two individuals to hundreds. Some of the largest communal groups have been found in a Brazilian species of *Exomalopsis* in which there were hundreds of females sharing a nest entrance and the nest had been occupied for multiple generations. Perhaps unsurprisingly for such an old and populous nest, it was also extremely deep. Other large communal societies have been found in some species of *Andrena* (suggesting that their oft-used common name “solitary mining bees” might not always be appropriate), some of their relatives in the Panurginae, and in some Australian *Lasiglossum* species.

An advantage of living in a communal society is that the nests are more difficult for intruders to access because there is more traffic at the nest entrance and more bees to detect an invader once it has entered. Perhaps a disadvantage is that it is more difficult for individuals to control cheaters—individuals that stay within the nest and lay eggs on pollen balls constructed by others.

A corollary of communal nesting is that males that emerge within one are surrounded by mating opportunities. This has resulted in some communal bee lineages evolving an aggressive male morphology.

See also Agapostemon; Dimorphic Males; Eusocial.

Corbicula

Corbiculae are a special kind of pollen transport structure defined as a bare area surrounded by hairs that hold the pollen in place. It is best developed in the appropriately named “corbiculate bees”: the orchid, bumble, honey and stingless bees. In most species in these groups, the hind tibia is largely concave and bare on the anterior surface while the dorsal and ventral margins possess curved hairs that help hold a pellet of pollen in place. These bees moisten the pollen with nectar and this helps ensure that pollen is not lost during transportation. But it is not only in the “corbiculate bees” that corbiculae can be found, and they are not only found on the metatibia. The mining bee genus *Andrena* have a propodeal corbicula—long curved hairs that surround the lateral surface of the last portion of the mesosoma, as well as a femoral one. Most colletids of the subfamily Xeromelissinae have a corbicula on their second metasomal sternum where dense, posteroventrally oriented hairs surround a

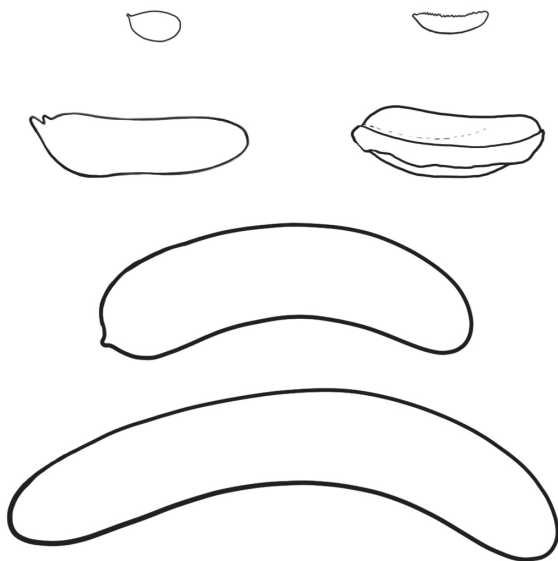
triangular bare area. Many bees that transport pollen on their hind legs have the ventral surface of the femur bald but surrounded by hair fringes that extend ventrally from both the anterior and posterior surfaces and, in *Andrena*, also basally from the trochanter. The Argentinean eucerine *Canephorula apiformis* is unusual in that the apical half of the hind tibia forms a corbicula whereas the basal half is entirely covered in hair.

See also Apidae; Pollen Acquisition.

Cuckoo Bees

Just like their avian namesakes, cuckoo bees do not make their own nests and do not collect food for their offspring. Instead, they lay eggs in the nests of other species and their offspring feed on the resources collected by the hosts. The switch from nest-building and food-collecting to cuckoo behavior (also called brood parasitism or clepto- or kleptoparasitism) has occurred multiple times among the bees—indeed, it has arisen multiple times in each of the three bee families in which it is found: Apidae, Halictidae, and Megachilidae.

Females of most cuckoo bees lay their egg in the brood cell while the host is out foraging. You can often see them flying around the surface of the ground (most, but not all, attack ground-nesting bees) searching for a host nest entrance. Sometimes, however, the host will come home to discover their enemy at work and so cuckoo bees are generally rather well defended, often with long stings, dagger-like mandibles, and a thick integument with lots of pits and ridges to deflect weapons away from the more vulnerable body parts. It is a safer bet to enter a nest when the host female has finished it.



Cuckoo Bee Eggs

This often requires more elaborate brood cell opening and resealing behaviors but has the advantage that the host is not likely to discover the invader.

Cuckoo bee females have to place their eggs carefully to make it less likely that the host will discover them. Cuckoo bee eggs are thus often diverse in structure compared to the simple banana-shape of other bee eggs. Egg-hiding is less important if the cuckoo attacks only completed nests.

See also Hospicidal; Ovaries, Ovarioles, and Oocytes; Social Parasitism.

Databases

It is becoming increasingly important to make the information from specimen holdings in museums widely available in the form of online databases. One reason is that it's not just biodiversity that is at risk of extinction; museum specimens themselves have been called "the endangered dead," because their maintenance is not cheap and there are so many other calls for financial assistance for research. But the information that has until recently been locked away in dusty cabinets is proving extremely important for understanding many issues, including the impact of climate change on the planet's most important pollinators.

Because museum collections go back for decades and even centuries, they can help document changing geographic distributions of species over time. Such studies have documented serious declines in some species and resulted in some bees being placed on national endangered species lists. One such study suggested why some bumble bee species are becoming threatened with extinction: while the southern distribution margins of northern hemisphere species were retracting northward, this was not compensated for by northward expansion at the northern edge of their ranges. The result is a decreased geographic range. That historical bee distribution records accurately track changing climate can be demonstrated by using old records of both bees and climate to predict where the species should be found now. Close agreement between predicted and observed current distributions suggests that the future distributions of the bees can be predicted under different scenarios of climate change with some accuracy.

Databases for wider ranges of bee species have demonstrated the unusual global pattern of bee species richness. There are more species in temperate zone deserts and semi-arid areas than in the tropics, a pattern that is unusual as most taxonomic groups show greatest diversity in the tropics.

See also Biogeography; Citizen Science.

Defecation

Both larval and adult bees have to defecate. The larvae are particularly interesting in how they achieve this because in most cases they store up all the waste from the food they consume during their growth and do not defecate until they have eaten it all. Thus, they avoid fouling their food. Indeed, in bees—as in the other Aculeata and Parasitica, the midgut doesn't even unite with the hindgut to permit defecation until late in larval growth. Before defecation, the fully grown larva is shiny because its skin is so stretched. As it starts to defecate it deflates somewhat, looking older and more wrinkly. Some bee larvae use their feces to line their brood cell, sometimes eating sand to make a tough, cement-like lining.

Adult bees have to defecate soon after emerging from the pupa as the waste resulting from all the metabolic activity of metamorphosis has to be expelled.

Honey bees can use mass worker defecation as a colony cooling mechanism. In 1981, the United States claimed that Russia had supplied the combatants in tropical Asia with mycotoxins that were detected in what was called “yellow rain.” It turned out to just be honey bees defecating en masse to cool down their

colony in the tropical heat. The “yellow rain” contained large amounts of digested pollen grains. Despite the scientific evidence, the United States has still not retracted the accusations.

See also Cocoon; Larva.

Digging

Studying bees that nest in the ground is not straightforward. Typically, to find out what the bee’s nest architecture is like, what its egg, larva, pupa, and cocoon (if it makes one) look like, or even to count the number of chromosomes it has—the researcher has to dig the nest up. This is easy if the nest is very shallow but can be very difficult indeed if there are numerous branches or diversions around tree roots or subsurface rocks. Some bee nests are so deep that the researcher must dig steps into walls of the hole they have dug to get out! Of course, the smaller the bee, the narrower the burrow and the more likely that the researcher will lose the plot.

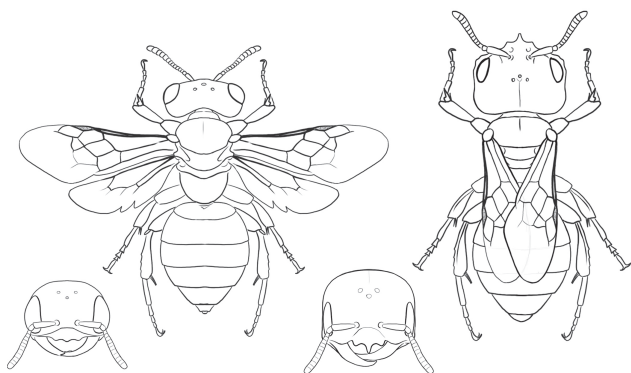
Different melittologists use different techniques to get data from burrowing bees. Some make a liquid slurry of plaster of paris that they squirt down the nest entrance. When hardened, this makes tracing the structure of the nest and finding all of its contents relatively easy. Others blow talcum powder down the nest entrance and then dig down perhaps using a grass blade to help follow the burrow. When bees nest in dense aggregations, it is impossible not to cut into multiple nests at a time. Both of these previous methods can be adapted by using multiple colors of powder whether in liquid or dry form. Still another approach is to plug the entrance, dig a “moat” around the nest and then

coat the outside of the block of soil with linen soaked in plaster of paris. When dry, the whole block can be transported back to the laboratory to be dissected from the comfort of a laboratory chair.

See also Aggregation; Brood Cell; Nesting Sites; Snapping.

Dimorphic Males

In some bee species, the males come in two different size classes: small, normal-looking individuals and unusually large ones. The smaller males behave like males of most bees—they fly around looking for females on flowers or other rendezvous areas such as shrubs with particularly glossy leaves or around the nest site where virgin females may be emerging. The larger males generally have such disproportionately large heads that in some cases they have been called “walking heads” and



Dimorphic Males: *Macropoda portalis*

may be sufficiently ungainly that they are incapable of flight. These individuals are “built like tanks,” but why? Extreme male dimorphism seemingly occurs only in species that nest communally. Any male emerging within a communal nest has plenty of mating opportunities with the daughters of the other females that provisioned the nest in the previous generation. Thus, their fighting morphology increases their chances of obtaining multiple mates. These big-headed males may never leave their natal nest and battles between them have been observed to go on for hours, often ending fatally for the loser.

Other bees have more continuous variation in size of their males with similar, but not so extreme, strategies. The larger males will fight for mating opportunities, sometimes digging down to where virgin females are emerging while smaller ones try to avoid potentially damaging combat by searching for mating opportunities using more traditional means.

See also Communal; Mating.

Division of Labor

In insect societies, different individuals take on different tasks. The most common and best known is a reproductive division of labor where queens do all, or at least a disproportionate amount, of the egg-laying and little to none of the other tasks, while the workers (who are all female) have little or no direct reproduction but perform all or most of the remaining tasks. In honey bee colonies, this reproductive division of labor is usually complete, with workers laying no eggs unless the queen is lost. Stingless bee workers often lay eggs but these serve a

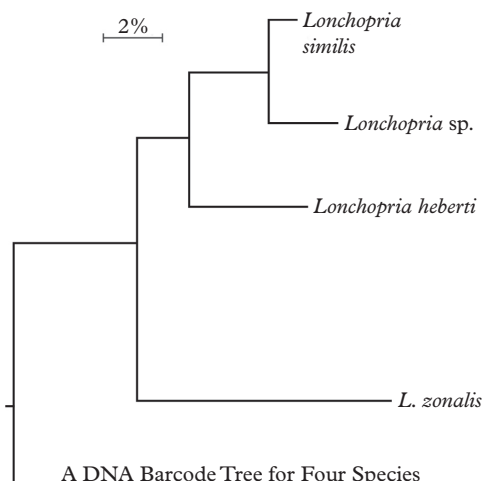
nutritive function and are eaten by the queens. But in most social bees including bumble bees, most social halictines, and some carpenter and reed bees, there is competition over oviposition, especially when it comes to male production. In bumble bees, the competition between workers and queen and among workers can result in the queen's death and some workers causing the death of the offspring of the queen and / or other workers.

Behavioral differentiation often occurs at finer scales. Most social halictines will have one worker that concentrates on guard duties while some neotropical stingless bees evolved a large soldier caste in response to the evolution of robber bees. Honey bees have specialized undertakers that can detect a dead bee within half an hour and many social bees have "police" that eat eggs laid by rebellious workers.

See also Apis; Eusocial; Meliponini; Robber Bees.

DNA Barcoding

With almost 21,000 described species and some genera containing over 1,000 species, bee identification can be extremely difficult and time-consuming. Even for genera with a few species, it is often difficult to separate the morphological signal that indicates species level differences from the morphological noise that is intraspecific variation. Fortunately, there is an entirely different approach that can help: DNA barcoding. This method, an invention of the Canadian biologist Paul Hebert, uses small pieces of mitochondrial DNA (typically a 658 base pair region of the cytochrome oxidase gene COI) to identify specimens. Mitochondrial DNA



is good for this task in animals because it is inherited only from the mother and does not recombine. As a result, any mutation will be passed down to the offspring and subsequent generations and any further mutations in that lineage will crop up only in combination with the previous one. Thus, differences accrue over time and we usually end up with larger DNA sequence divergence between species than there are within species. There is no absolute rule as to how many differences there must be for two individuals to belong to different species. With 658 base pairs, thirteen differences give an approximately 2 percent divergence, but in some cases sequence divergence between morphologically distinct species can be zero. As always in science, it is best to get as much data as possible, and so integrating

morphological with DNA data is often particularly beneficial. Discovery of DNA barcode differences within “one species” often leads to the discovery of morphological differences and the description of new species. Another great advantage of the method is that it helps associate the sexes, which is not always as straightforward as one might imagine, given that most bees are highly sexually dimorphic. DNA barcoding approaches can also be used to discover what species are found in mass samples.

See also Classification; New Species.

Endemic A taxonomic group that is only found in one geographic area is said to be endemic to that area. While there are numerous species or genera that are endemic to a particular country, geographic region, habitat, or biome, some whole subfamilies are endemic: the Callomelittinae and Euryglossinae are endemic to Australia, the Scapterinae to Africa, and the Xeromelissinae to South America—with a few species getting into Central America and one into the Antilles.

Endemic groups often arose in the area where they remain restricted. Geographic barriers often preclude their dispersal elsewhere. Australia clearly has oceanic barriers, making it unlikely that bees can easily get to other parts of the world from there. Chile, while having a very long border with adjacent countries, has the hyperarid Atacama Desert to the north, oceans to the south and west, and the Andean peaks to the east, and as a result a large proportion of its bee species are found in no other countries.

When isolated islands are colonized by a bee, they may undergo multiple speciation events there. Examples include *Hasinamelissa*—a genus of reed bee with twenty-five species all restricted to Madagascar—and the neopasiphaeine *Nesocolletes*, which is restricted to New Zealand where there are seven species.

See also Biogeography; Databases.

Eusocial

By definition, a eusocial organism has cooperative brood care, overlapping generations, and a reproductive division of labor between parents and offspring. In bees, there are no kings (unlike in termites, but as in ants and yellowjackets): eusocial bee societies generally consist of a queen and her worker daughters. While most bees are solitary, with a single female constructing a nest and brood cells, foraging for resources to construct pollen balls and laying eggs, in eusocial societies the queen does most of the egg-laying and the workers do most of the foraging and other colony tasks.

We can divide eusocial societies into two broad types: those in which there is a solitary phase at the beginning of the colony cycle and those in which there is never a solitary phase. In the latter, new bee colonies are started by a queen and a group of workers, usually by swarming. This type is commonly referred to as “advanced eusocial” and the colonies are usually perennial. Honey bees and stingless bees have this type of eusocial organization. Bumble bees and some halictines have their colony initiated by a single female foundress that starts a nest and produces a brood of workers all by herself. Once the female offspring reach adulthood, they become workers

and do the foraging and nest maintenance and guarding tasks, leaving their mother, the queen, to concentrate on egg-laying. With few exceptions, such primitively eusocial colonies last less than a year. While there may be a single brood of workers as in some bumble bees in very cold climates, or cool temperate climate halictines, most bumble bees and some halictines produce workers continually until males and next year's queens are produced later in the summer.

See also Haplodiploidy; Queen; Worker.

Flies as Natural Enemies of Bees

Many predatory flies will attack adult bees and suck their juices. Prime among these are the robber flies (Asilidae), some populations of which will persist through attacking bees that nest in dense aggregations. Some other flies oviposit in adult bees and their offspring develop within the doomed host. Within the scuttle fly family, Phoridae, there are some that are termed “bee-killing flies,” tiny insects, 2–3 millimeters in length, known only from warmer parts of the western hemisphere. They have two modes of attack—flying at a stationary or flying bee and ovipositing on them or landing near where a bee is resting, curling their ovipositor forward beneath their bodies and running at their victim wielding the ovipositor like a sword. These are specialized behaviors and, as may be expected, work well where large numbers of bee hosts may be found; consequently, these flies mostly attack social species such as stingless bees, honey bees, and bumble bees. The other main group of adult bee-attacking flies are the thick-headed flies, Conopidae. These follow the first

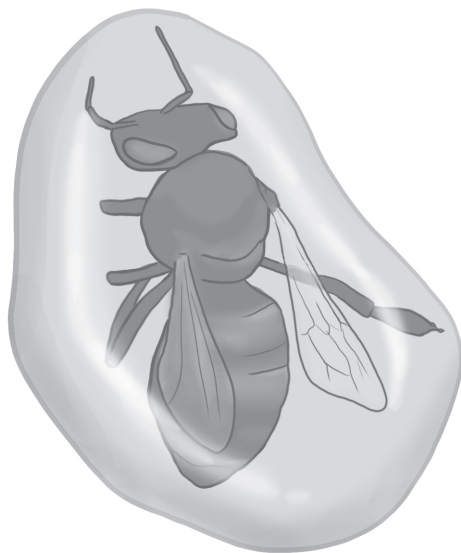
of the two tactics of the bee-killing flies and insert a barbed egg into the membrane between the segments of the bee host. Both these types of dipterous enemy develop as larvae inside the body of the adult bee.

Other flies develop on bee larvae or just the food provided for them. Best known among the former are the bee flies, family Bombyliidae, which flick eggs into the nest entrances of their hosts where the larva waits until the host larva is fully grown before attacking. Species of *Leucophora*, satellite flies of the family Anthomyiidae, will follow female bees returning to the nest and can be seen flying close behind them even as the potential host zigzags in escape maneuvers. The offspring of these flies eat the food that was meant to be eaten by a bee larva.

See also Beetles as Natural Enemies of Bees; Stylopids; Wasps as Natural Enemies of Bees.

Fossil Bees

The fossil record for bees is reasonably good. Indeed, some amber fossils are of such high quality that the specimen can be studied in as much detail as a recently collected one and in much better detail than a recently collected specimen that hasn't been looked after properly. Amber is the fossilized resin from trees and so it is not surprising that amber fossils often represent bees that collect resins, such as some stingless bees. Compression fossils form in sedimentary deposits and the structures of the original animal are often distorted through flattening. Wings are nice and flat and compression fossils often show their structure remarkably well. As it is often useful, or even necessary, to include



Bee in Amber

characteristics from wing veins to identify a bee specimen, bee wings in compression fossils often allow remarkably accurate placement within bee phylogenies. Such placements allow researchers to anchor parts of a phylogenetic tree to a particular period in geological time allowing inferences on how, when, and where certain groups of bees diversified. However, reassessment of decisions on the precise classification of some fossils often results in changes to their previously accepted placement. Nonetheless, a paper published in 2023 used data from 185 fossils to generate the most comprehensive calibrated phylogeny for bees so far.

Not only the bees themselves may be found in the fossil record, but also their nests, pollen, and natural enemies. However, suggestions of surprisingly ancient bee brood cells from such ichnofossils are generally considered imprecisely identified.

See also Biogeography; Classification.

Guards

Bee nests contain a large number of resources and other organisms, including other individuals of the same bee species, may seek to steal the resources or consume the bee's developing offspring. Even the nest itself is a valuable resource because of the effort required to construct it. Thus, bees need to defend these resources and one way they do this is by guarding the nest entrance, which is often done by blocking it with their heads. Solitary bees cannot guard their nests while foraging and may close the entrance when they leave. Social bees often post a single guard at the nest entrance and this individual will try to prevent the entry of natural enemies and unrelated individuals of the same species.

A guard of a social bee should only let her nestmates into the nest. But how do they tell nestmates from other individuals? A series of elegant experiments conducted in the 1970s raised bees with different parentage within the same nest and then investigated whether the guards let in their own relatives that had been raised in other nests or individuals that were close relatives of their nestmates that had also been raised in different nests. The results showed that the bees learned the odors of their nestmates and let similarly smelling bees into the nest but refused entry to their own relatives that had been raised

elsewhere. Thus, it seems that the guards do not smell themselves to compare their own odors to those of bees trying to get into their nests, but they memorize the odors of their nestmates and let those that smell like them in while refusing access to their own genetic relatives.

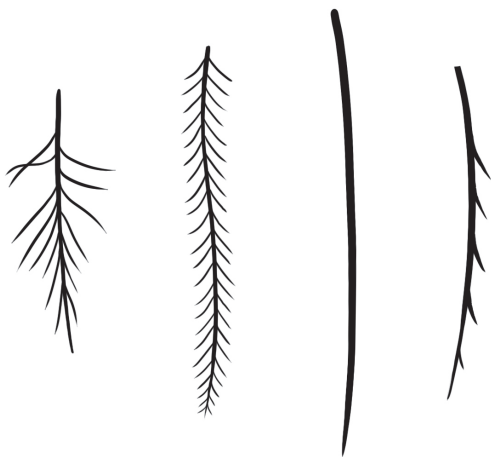
The stingless bee *Tetragonisca angustula* stations hovering guards outside the nest entrance as well as additional guards that remain around the entrance. If a robber bee is detected prospecting for a nest to invade, the guards attack it. They also attack larger groups of marauding robber bees recruited to the fray.

See also Cuckoo Bees; Eusocial.

Hairs

It is the nature of the hairs on a bee that helps define them as bees: they have branched hairs somewhere on their bodies, whereas wasp hairs lack branches. Unfortunately, there are exceptions. Some velvet ants (a group of wasps with wingless females) also have branched hairs. Conversely, and somewhat irritatingly, it may take a long time to find branched hairs among the simple hairs on a bee's body.

The pattern of branches on a bee hair is endlessly variable. Some might have a single branch, others multiple branches but only on one side of the shaft, while some have branches on opposite sides of the shaft like a bird feather, and still others have branches coming out in all directions like a Christmas tree. Some hairs are very long, others very short, and hairs of any length can be fine or thick. Short, thick hairs can look like scales and are particularly common lying flat on the body surface of some groups of cuckoo bees. Longer, thick hairs may



Hairs

look like spines or be modified into special structures to scrape open the oil-containing cells of some plants. Most bees have a wide range of different hair types on their bodies, even on the same body part. Some oil collecting bees have a scopa comprised of fine, feathery hairs with long branches as well as long, thick, simple ones mixed among them. The latter give structural integrity to what is really a mop aiding in the retention of oily liquid.

Two ideas have been put forward to explain the origin of branched hairs in bees: either they aid in trapping pollen for transport, or they serve to prevent tiny particles of nesting substrate from lodging between the different parts of the exoskeleton.

See also Corbicula; Oil Bees; Pollen Acquisition; Scopal Hairs.

Halictidae

The Halictidae is a diverse group of mostly small to moderate sized bees. Possession of a basal vein that is strongly curved toward its base diagnoses most members of the family, but as always there are exceptions. There are four subfamilies. Rophitinae is a small group of mostly oligolectic and largely northern hemisphere bees. The Nomiinae are generally larger often with remarkably elaborate secondary sexual characteristics in males with an almost worldwide distribution. The Nomioidinae is a small group of small bees from the warmer parts of the eastern hemisphere. Most Halictidae belong to the Halictinae, and one of its genera—*Lasioglossum*—has almost 1,900 species, more than any other bee genus, and is found in all areas of the globe that are not covered in ice. This genus has been called “the bane of taxonomists” and “morphologically monotonous” and it is impossible to identify most of its species in many parts of the world, though considerable progress has been made recently by a few dedicated melittologists who like a challenge.

Halictids have the broadest range of social behavior of any group of bees; just the genus *Lasioglossum* contains almost all named categories of social organization (and cleptoparasitism and social parasitism as well). While many species are solitary, some have queens and workers that are so different, they look as if they belong to different species. Others have relatively large colonies with minimal externally visible differences between castes (dissect them and you’ll find the queen has better developed ovaries than do the workers), which might differ only slightly in average size. One species has

colonies that last five years and its queens live longer than do honey bee queens.

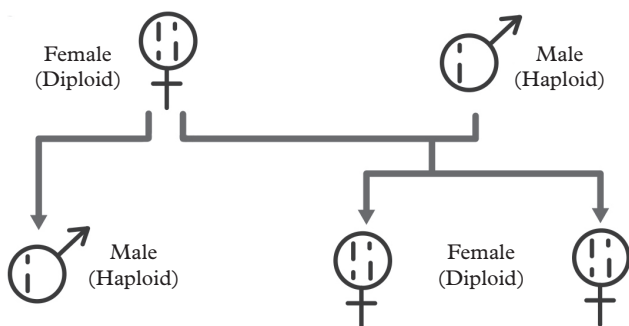
A common name often applied to some halictids is “sweat bee,” because they often land on exposed human skin to obtain nutrients.

See also Alkali Bee; Classification; Oligolectic; Social Parasitism.

Haplodiploidy

Bees and other Hymenoptera have a different mechanism for determining the sex of an individual than do most other organisms: males are haploid—resulting from unfertilized eggs—and females are diploid. That is a slight oversimplification, however. The details are that in bees there is a single gene locus that determines sex: if an individual is heterozygous at that locus, then it is a female. But if there is only one type of sex allele at the locus then that individual is a male. If an egg is not fertilized, then there can be only one sex allele and the egg becomes a haploid male. But if a female bee mates with a male that shares one of her two sex alleles, half of her diploid offspring will be homozygous at the sex locus and will become diploid males. Such males seem to be a drain on the population as they may be sterile, produce triploid offspring, or simply not survive long enough to reproduce.

There are additional ramifications of this unusual sex-determining mechanism. First, females can produce male offspring without having mated. Second, a mated female can decide whether to produce a haploid or a diploid offspring and only pass sperm over the egg as it passes through her reproductive tract if the objective is



Haplodiploidy

to produce a female. In eusocial bees, this permits the production of broods containing only worker daughters, rather than males. Additionally, as males are commonly smaller than females (exceptions include species in which males are aggressively territorial), a mass provisioning mother can modify her decision as to which sex to produce based on the amount of food available at the time she lays the egg.

See also Eusocial; Kin Selection; Provisioning.

Hive

The term hive is applied to eusocial species with large colonies that nest inside a structure, as honey bees and stingless bees do. Stingless bee hives are by far the most diverse and their entrances are often elaborated into beautiful flower-like openings while others are simple tubes that are sometimes translucent, looking like a plastic straw. Brood cells of stingless bees are either formed in seemingly disorganized clusters or in a more

regularly arranged comb. Unlike honey bees, stingless bee combs are usually horizontal and often arranged in a spiral and they are usually separated from the food storage pots by layers of wax and / or resin and the whole nest is surrounded by tougher outer layers.

A great advance in beekeeping arose with the development of the Langstroth hive, invented by Reverend Lorenzo Lorraine Langstroth (1810–1895) and patented in 1852. His design made use of his discovery that bees would not build comb or fill a space with propolis or wax if it was between approximately 6 and 9 millimeters in width. Consequently, by hanging movable combs vertically, separated by such a space, and with a lid allowing access to the hive from above, the new design was a great improvement on earlier ones. The same technology is used for the eastern domesticated honey bee, *Apis cerana*, as well as the more common western one.

See also *Apis*; *Clan Apis*; Eusocial; Meliponini.

Holotype

When someone calls an organism by its scientific name—its genus and species—how do they know they have identified it correctly? Ultimately, all identifications har-ken back to a single specimen, the one upon which the original species description was based. This specimen is called the holotype. While the regulations as to how to describe a species in a valid manner have changed over time (for example, purely electronic publication of names has only been permitted since 2012), currently, the actual individual described is the holotype and all others mentioned along with the original description are termed paratypes.

This causes some practical problems, which include issues associated with the often substantial variation within a species. No single taxonomist will have access to all the necessary holotypes for a particular group of bees. So many will use identification keys written by people who hopefully did study the relevant holotypes. Sometimes researchers will have a synoptic collection of specimens identified by an expert who may or may not have seen the relevant holotypes. This protocol suggests that holotypes receive a lot of study and as they are usually old and often fragile, they frequently become damaged: some have the head glued to the body backward, some are completely missing the head, some are missing all the body parts that could conceivably fall off. Thus, the most important specimen that represents the species, the holotype, is often a wreck. There are regulations that enable designation of replacements for such damaged specimens, or those that have been lost—for example, if the museum holding them is destroyed by fire or warfare.

See also New Species.

Honey

Honey is concentrated nectar that bees store as food. Very few of the more than 20,900 described bee species make honey. The dozen or so species of honey bees (genus *Apis*) and the other perennially social group of corbiculate bees—the stingless honey bees with over five hundred species—make quite a lot of honey, while bumble bees might, at best, have a few tablespoons of it at a time. Most honey that people add to their tea, breakfast cereal, or desserts comes from just one species—the domesticated western honey bee. Its

honey is stored in combs that beekeepers provide and from which the honey is easily extracted, although wild honey bee honey can be harvested through honey-hunting, which destroys the nest. Stingless and bumble bees store honey in little pots that often resemble a bunch of grapes. Extracting honey from their nests is more destructive in that the pots themselves have to be cut open. Stingless bee honey is generally more runny, acidic, and has a more complex flavor than *Apis* honey.

Honey color, consistency, and flavor all depend on the resources that are available for the bees to forage from—which are usually flowers, but also include extrafloral nectaries and honeydew produced by insects such as aphids. By collecting honey at a time when the hive is surrounded only by flowers of a particular type, beekeepers can get honey with the specific flavors of the nectar of that plant. Manuka honey from bees that have collected nectar only from the manuka tree in New Zealand is particularly prized, although more honey is sold under the name “manuka honey” than the bees visiting all the world’s manuka trees could possibly produce. Buckwheat honey has a particularly strong flavor.

In addition to its nutritional and gastronomic features, honey has medicinal uses, perhaps most commonly as a cough suppressant. However, honey should never be given to babies as it can cause infant botulism.

See also Apis; Bumble Bees; Hive; Mead; Nectar; Stingless Bee.

Honey Bee Declines

Previously referred to as Colony Collapse Disorder, the phenomenon is now known to be more complex with

different symptoms in different parts of the world. While small proportions of colonies are usually lost during the winter, unusually heavy colony mortality rates were first observed toward the end of the twentieth century. Current understanding suggests there is no single cause, although application of a new group of pesticides—neonicotinoids—seems to have coincided with its spread. Unlike earlier pesticides that are used when a pest outbreak has happened or is predicted to happen soon, neonicotinoids are used as a prophylactic, often applied to the seeds before planting, whether a pest outbreak is expected or not. It is not surprising that there have been numerous legal battles over neonicotinoids between beekeepers and the pesticide industries. Early field studies were criticized by industry for not being performed under controlled laboratory conditions and laboratory experiments were criticized for not reflecting realistic conditions in the field. But the relationship between these pesticides and colony losses is not simple. Research has shown that there is an interaction between fungicides and neonicotinoids in increasing colony losses. Additionally, the pesticides weaken the immune response of bees and their usage also coincided with the spread of both new diseases and mites that can transmit them.

See also Agriculture; Mites; You Can Help the Bees.

Hospicidal

Cuckoo bee larvae hatch from the egg in a brood cell that may contain a living host egg or larva, and sometimes there may be additional cuckoo bee eggs or larvae also. With the potential for so much competition for the finite resources of just one pollen ball, it is not



A Hospicidal Cuckoo Bee Larva Attacks the Host Larva

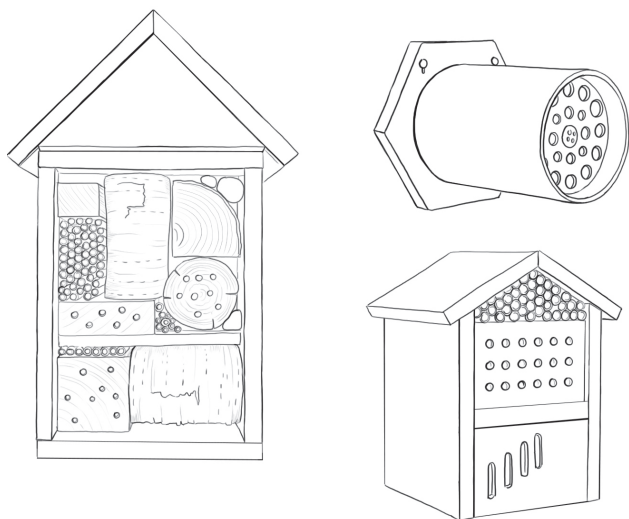
surprising that newly emerged cuckoo bee larvae are usually armed with enormous sickle-shaped mandibles and sometimes with sharp points on the labrum. The megachilid genus *Stelis* is an exception in that most of the host killing seems to take place when the cuckoo larva is in its last instar. These sharp armatures are used to slice away at, or puncture, host eggs and larvae or those of other cuckoo individuals. These hospicidal—host killing—larvae move about the brood cell to remove all competition and so they often have fleshy appendages that help them traverse the entire pollen ball. These larvae must often be very busy, as up to six other cuckoo eggs have been found within the same brood cell such that the winner would have to murder seven times—the host's offspring, as well as other cuckoo bee larvae. The morphological weapons are usually reduced in subsequent molts as they are no longer needed once all the competition has been eliminated.

If the cuckoo is one that oviposits in cells that the host has already completed and sealed, it is important for the eggs to develop rapidly such that dispatching the host egg or larvae—and those of any other cuckoo bee individuals, can be completed as soon as possible. Developing quickly gives the hospicidal larva an advantage.

See also Cuckoo Bees; Larva.

Hotels

Bee hotels are human-made aggregations of tubular cavities made for bees to nest inside. They come in all shapes and sizes and are usually made of wood, cardboard, canes, or pithy stems (or combinations thereof) that mimic naturally occurring cavities that many bees use for their nests. Some of them are beautiful works of art. The tunnels are usually of a range of sizes to attract species of different sizes. Making bee hotels has become something of a cottage industry and even some chain stores carry them with the exhortation to “help the bees.” Unfortunately, this claim is not based on much hard evidence. A detailed study showed that half of the occupied hotel tubes were inhabited by wasps and that approximately half of the bee or wasp inhabitants were introduced, exotic species. While there’s nothing wrong with solitary cavity-nesting wasps (indeed, they help control pests in the garden) most people would prefer to help native bees rather than potentially invasive exotic species. Also lacking are long-term studies that show a beneficial effect of bee hotels. Because they provide artificially dense nesting opportunities, as the bees would not usually nest in such close proximity, there



A Variety of Bee Hotel Designs

is potential for natural enemy populations or diseases to build up and have a negative impact on the bees (and wasps). Long-term studies are needed to assess the advisability of encouraging people to purchase a bee hotel.

See also Aggregation; You Can Help the Bees.

Integumental Coloration

Both the underlying integument and the overlying hairs of bees can have various colors. The underlying integument is dark brown to black in most bees, though dull metallic colors throughout or orange or

red—particularly on the metasoma—are common. Yellow markings are also common, especially on the face of males and / or as bands on the metasoma, and less commonly as markings on the mesosoma. Some bees have very complicated arrangements of yellow markings against a dark background, as in the appropriately named small carpenter bee *Ceratina hieroglyphica*. A few bees are entirely pale colored, pale yellow, tan, or orange—or, very rarely, pale green. Pale colors are disproportionately found in either very small bees, such as fairy bees, or in nocturnal ones. These colors are caused by pigments in the integument, although in bees with a transparent, or semi-transparent integument, the colors may come from the internal organs.

Metallic coloration is an entirely different matter and arises in two ways. Most metallic bees get their colors from structural effects caused by nanostructures of the body surface. Most metallic bees are green or bluish, but some are orange, red, or purple, and a few have the entire rainbow. Orchid bees and many Halictinae such as *Agapostemon* are the best-known, brilliantly metallic, colored bees. The other way of obtaining metallic coloration arises from an effect like a sheen of oil on water. These metallic colors are relatively faint.

See also Agapostemon; Mimicry; Nocturnal and Crepuscular Bees; Orchid Bees.

Introduced Species

An introduced species is one that has been taken to outside its native range, accidentally or on purpose, by humans. Relatively few bees have been introduced on purpose, perhaps only 25 percent of the approximately

eighty species known to have been translocated outside where they naturally occur. Most were transported to aid in pollination; these include the alfalfa leafcutting bee, moved from Europe to North America for alfalfa pollination, and various orchard bees (*Osmia*: Megachilidae) that have been taken from the eastern hemisphere to North America for pollination of fruit tree crops.

Bees accidentally transported to new parts of the globe most often arrived inside wooden structures and so, although the majority of bees nest in the ground, only approximately a dozen species out of the eighty introduced bees do so. It has been suggested that one such soil-nester was transported from Europe to the East Coast of North America in ballast used to weigh down ships with dirt while their holds for the return journey would have brought fish to Europe for Friday dinner.

An introduced species becomes an invasive species when it has a negative ecological impact within the new range. *Megachile sculpturalis*, the Asian giant resin bee (Megachilidae), brought to North America from Asia, takes over the nesting tunnels of native large carpenter bees, sometimes gumming up the homeowner bee with resin. One way in which invasive bees can have a negative impact on species in the introduced region is through the vectoring of pathogens to which the local native bees have no experience and little immunity. The decline of the South American *Bombus dahlbomii* is thought to have been caused through disease transmission from introduced European bumble bees.

See also Biogeography; Endemic.

(continued...)