CONTENTS

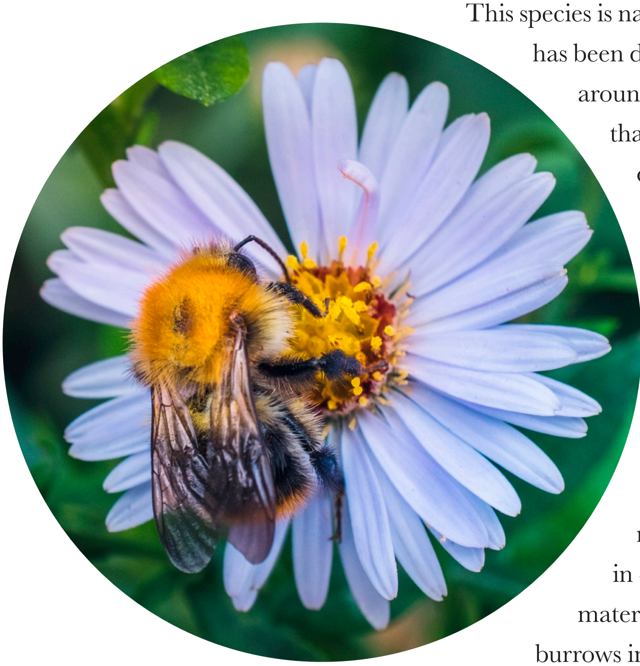
INTRODUCTION

When most people think of bees they imagine an insect about 3/8 inch (1 centimeter) in length, mostly brown or orange-brown, that lives in enormous, socially complex societies with a single queen and thousands of workers inside a hive. These bees can communicate the location of good food resources through a dance that takes place in the dark but that tells nearby bees which direction to go (in relation to the sun) and how far to travel to find the nectar and pollen they need.

However, most bees are nothing like the one I describe above—the domesticated Western Honey Bee (*Apis mellifera*). This species is native to Africa and southern Europe, but has been domesticated for centuries and transported around the world. It is just one among more than 20,000 species of bee that have been described, almost none of which are anything like it.

In contrast to the Western Honey Bee, the average bee lives a solitary existence in a hole in the ground and will interact with others of its species only for mating, egg-laying (hardly an interaction really!), and perhaps fighting over nest ownership. The second most common lifestyle for bees is nesting in cavities, again primarily solitarily, in plant material such as pithy stems, and in old beetle burrows in wood.

BELOW | A bumble bee *Bombus pascuorum* collects resources from a flower.



The third most common mode of "beeing" is perhaps even less expected: going against the old adage "as busy as a bee," perhaps a fifth of all bee species do no work whatsoever, with the females laying their eggs in the nests of other bees that do the work of nest construction and food collection for them. These are the cuckoo bees. Still other bees make their own nests in abandoned snail shells; on the surface of rocks, stones, or vegetation; inside animal dung; and even in hollow man-made objects such as patio furniture, keyholes, or the fuel lines of crashed aircraft.

ABOVE | The worker honey bee in the center right is performing the waggle dance, while those in the ring around it pay attention. In this way the onlookers find out where good resources may be found.

ABOVE | One of the world's smallest bees (*Perdita minima*, 1/16 in/1.6 mm long), sits on the antenna of a very large bee (*Xylocopa* sp., 1½ in/38 mm long) in a composite image.

SOCIAL BEES

Like the Western Honey Bee, some other bees live in complex societies. For example, there are at least seven other species of honey bee, one of which is also domesticated in eastern Asia (it is called the Eastern Honey Bee, *Apis cerana*, to differentiate it from the Western species most people know about). Some of these social bees do not nest inside hives, but instead construct their nest on the surface of a tree branch or trunk, on the outside of a building, or on a rock face.

There is also a group of several hundred bee species, restricted to the tropics, called stingless honey bees, which have complex social lives but in ways that differ fundamentally from those of the domesticated honey bees. The bumble bees, comprising several hundred species, are also social. Their societies start off in spring with a single individual that raises a small brood of workers, which in turn help raise more workers—until later in the year, when males and the following year's queens are produced (only a single batch of workers is produced in those species living in colder climates).

Even social bees have other bees that are their natural enemies. Stingless bees suffer from robber bees, which steal both their food and their home (dismantled bit by bit, like taking a neighbor's house down brick by brick to enlarge your own while also raiding their fridge), and the bumble bees include among their ranks socially parasitic bumble bees, in which a single female invades the nest, suppresses the queen (sometimes killing her), and gets the workers to raise her own offspring.

BEE DIVERSITY

Bees are remarkably diverse, not just in nest site choice or social organization, but also in appearance. The smallest bees are less than 1/16 inches (2 millimeters) in length, and occur in two taxonomic groups: the fairy bees (page 176), which are mostly solitary; and some species among the stingless honey bees, which have complex societies with perhaps 600 individuals living inside a nest the size of a walnut. At the opposite extreme are several bees that can be called giants. If it's the longest bee you're after, then that's *Megachile pluto*, a resin bee that nests inside termite nests and is known from a few islands in the Pacific Ocean.

In contrast, the heaviest bees are probably the queens of some species of bumble bee. Bees also come in a wide variety of shapes, from long and narrow to almost spherical. And they come in all colors of the rainbow, as well as black and white. Many of them do not look like what most people would think of as a bee because they are almost bald and/or have the yellow and black stripes usually associated with wasps. In fact, there are so many bees that don't look like bees and so many other insects that do look like bees that there have been books published on bees that depict other insects on their cover.

So, given all this diversity and confusion, what are bees?

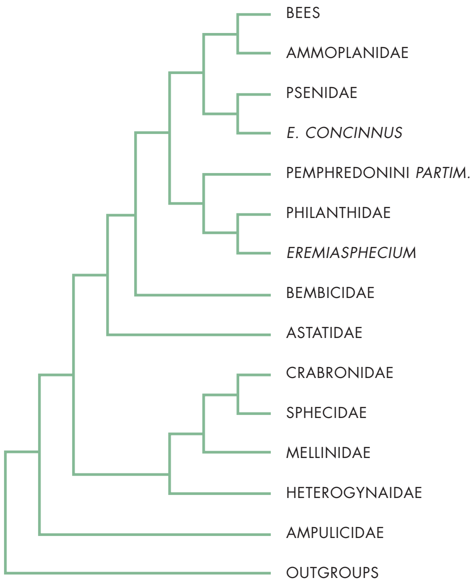
BELOW | A short fat bee *Pachyanthidium* sp. and a long thin bee *Geodiscelis longiceps* demonstrating differences in overall shape among bees.

WHAT ARE BEES?

EVOLUTIONARY ORIGIN OF BEES

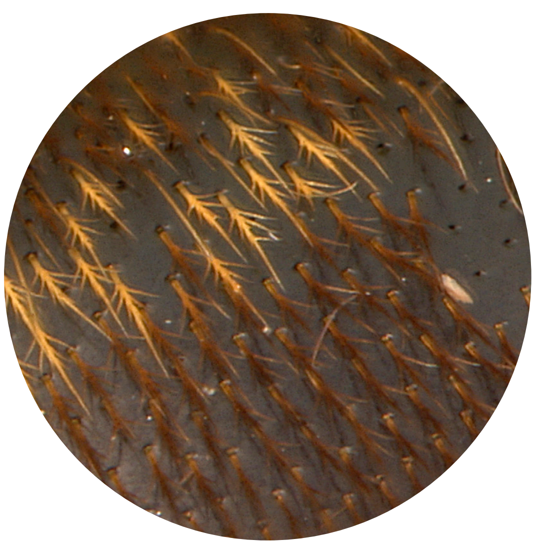
To an evolutionary biologist, the simplest answer to this question is that bees are wasps that went down the food chain to collect pollen instead of other animals (or parts of them) as a protein source for their offspring. Bees also collect nectar, not only as an energy source for their own individual activities,

BELOW | A female *Trachusa integra*. The white metasomal scopal hairs can be seen.



ABOVE | A phylogenetic tree of the apoid wasps, showing that the origin of bees is deeply nested among these wasps.

BELOW | Bees have branched hairs, although the form of the branching is diverse—even differing on different parts of the body of a single individual.



but also as a carbohydrate source for their offspring (some bees collect oils for the same purpose). When a yellowjacket (these are not bees, although in some parts of the world they are called meat bees) disturbs your outdoor barbecue or picnic and tries to snatch pieces of hamburger, it is finding a protein source for its juvenile nestmates back home. It might also try to take some jam or other sweet substance from you, which it will use for its own energy needs rather than as food for its relatives.

Bees arose from within a particular group of wasps, tiny little thrips-hunting species, well over 100 million years ago. Clearly it was advantageous to change food sources—there are more than 20,000 extant bee species, yet fewer than 200 wasp species in the group that comprises the closest bee relatives, even though both groups have had the same length of time to diversify.

BEE OR WASP?

However, how do you know whether a particular insect is a bee or not? This is a more difficult question than you might have imagined, knowing now how variable bees are in size and appearance. The answer is not very satisfying: bees have branched hairs somewhere on their bodies, whereas wasps generally do not (but irritatingly, there are a few exceptions). Searching for branched hairs on a bee can take some time, and in some species this defining characteristic is found on a minority of body parts.

LEFT | This *Andrena* female has a very full scopal load—the hind tibiae, hind femora, and propodeal corbicula on each side are packed with white pollen. Having such a diverse range of body parts to transport pollen is somewhat unusual.

RIGHT | Bees of the genus *Hylaeus*, such as this *H. variegatus*, are relatively bald and do not carry pollen back to their nest on an external scopa, instead transporting it inside their gut.

Another characteristic that helps indicate whether a particular insect is a bee is that a particular part of the hind leg is relatively flat and wide, whereas in wasps the same part is usually cylindrical (there are exceptions, however, as in some bees the same part is entirely cylindrical). There are also differences in the structure of the sting apparatus.

None of these characteristics is useful in helping you tell whether an insect flying around in your backyard is, or is not, a bee, and nobody in their right mind would want to cut open the sting apparatus of an insect to find out whether it is a bee or not. There is an easier answer for those patient enough to watch what the insects in their gardens are doing: female bees will actively collect pollen to store on their bodies, usually their hind legs or the underside of their metasoma. However, this strategy fails in the case of bees that take pollen back to the nest inside their digestive system, such as masked bees, and cuckoo bees, which don't collect pollen at all.

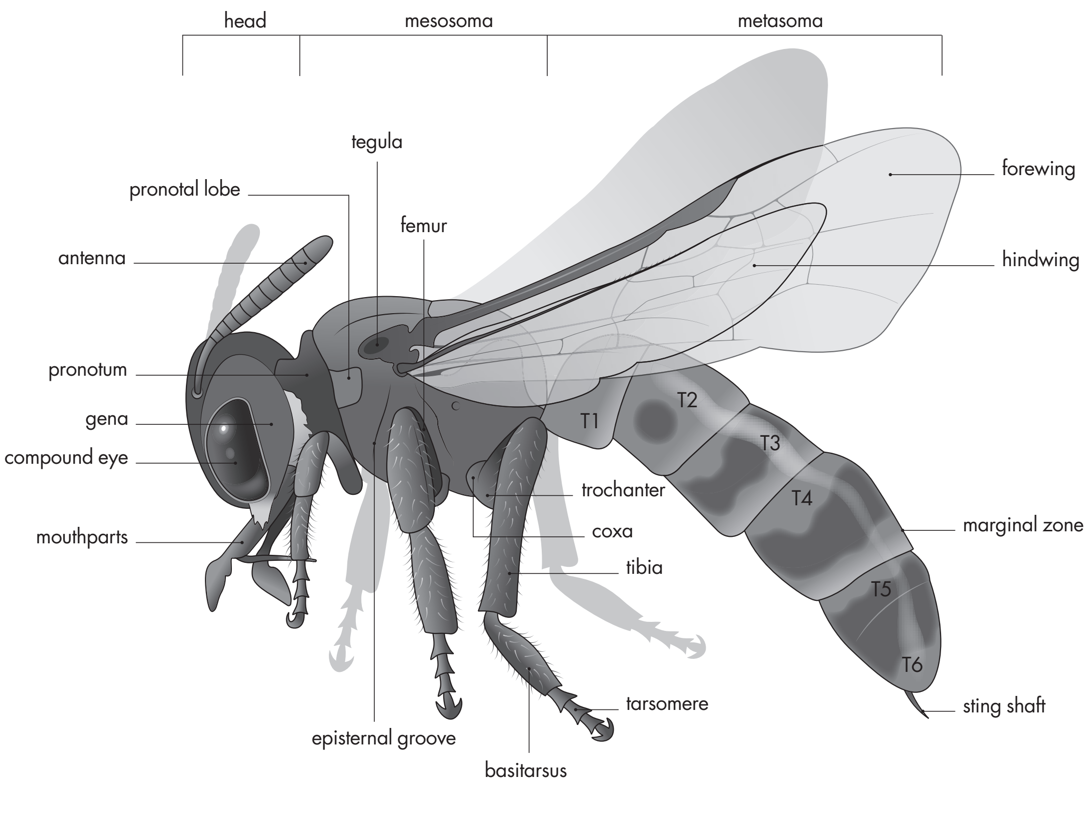
Of course, male bees don't collect pollen and are little more than volant sperm donors. Although these can perhaps be identified as bees, because they usually look like slimmer versions of the bees that are collecting pollen and seem to spend most of their time flying around searching for these similar females.

BEE ANATOMY

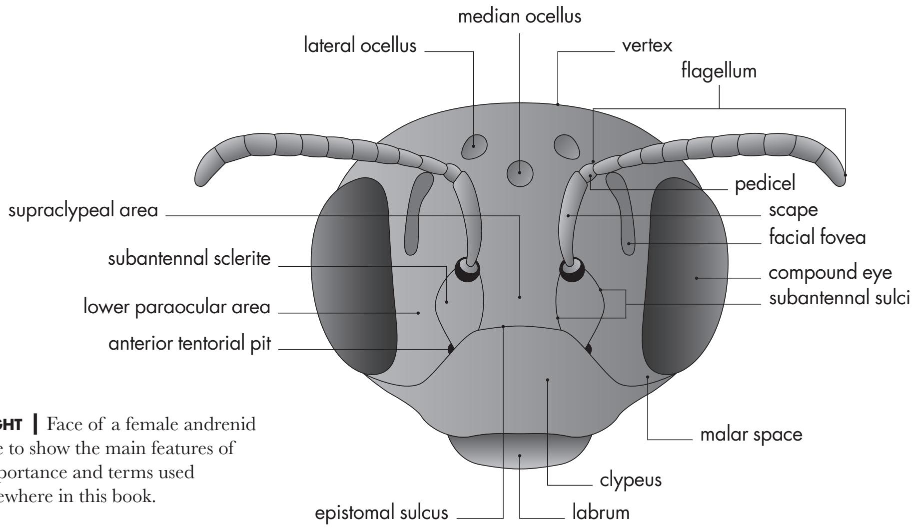
In common with all other insects, the bee body can be divided into head, thorax, and abdomen. But unlike in other insects (other than their waspy relatives), the bee abdomen is not what it seems, because the narrow waist is actually at the junction between the first and second segments of the abdomen. In other words, the ancestor of bees and wasps evolved to have a modified structure so that the first segment of the abdomen is broadly fused to the thorax, and the junction between the first and second segments is very narrow.

BELOW | Side view, of a *Protandrena* female to show the three main body parts with hairs removed. The mouthparts are partially extruded and thus are not accurately in position. The head is rotated somewhat ventrally to the far side.

MAIN PARTS OF A BEE

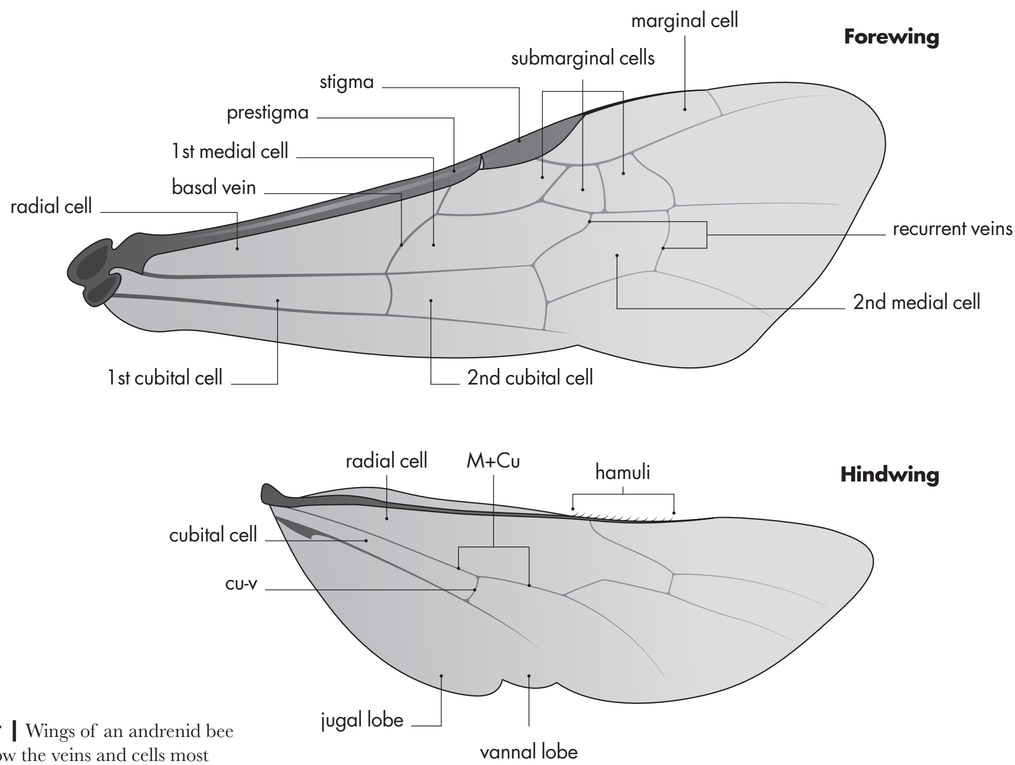


PARTS OF A BEE'S HEAD



RIGHT | Face of a female andrenid bee to show the main features of importance and terms used elsewhere in this book.

TYPICAL CELLS AND VENATION OF A BEE



RIGHT | Wings of an andrenid bee to show the veins and cells most commonly mentioned in the text.

As a result, we need different words for "the thorax plus the first segment of the abdomen" (i.e., the part between the neck and the other narrow part of the body) and "the abdomen minus its first segment." These words are "mesosoma" and "metasoma"—meaning *mid-body* and *hind body*.

ABOVE LEFT | A female *Andrena labialis*. Although of two families, the adjacent images show two things: the difference in number of antennal "segments" between males and females and the fact males generally have hairier faces than females.

ABOVE | A male *Megachile* showing the longer antennae typically found in males and the modified front legs that are used for the sexually selected, melittological version of "guess who" in some species of the genus.

RIGHT | This *Nomada panzeri* is cleaning its antenna by drawing it through the space formed by the foretibial spur and forebasitarsus.

HEAD

As in other insects, the bee head has compound eyes, ocelli (three tiny facets that generally measure light intensity), antennae, and the complex suite of features that make up the mouthparts. As discussed below, the details of the structure of the mouthparts are extremely important in bee classification and evolution. The antennae are important in helping us find which sex a bee is: in all but a few cases, there are 13 subdivisions of the antenna in males and 12 in females.

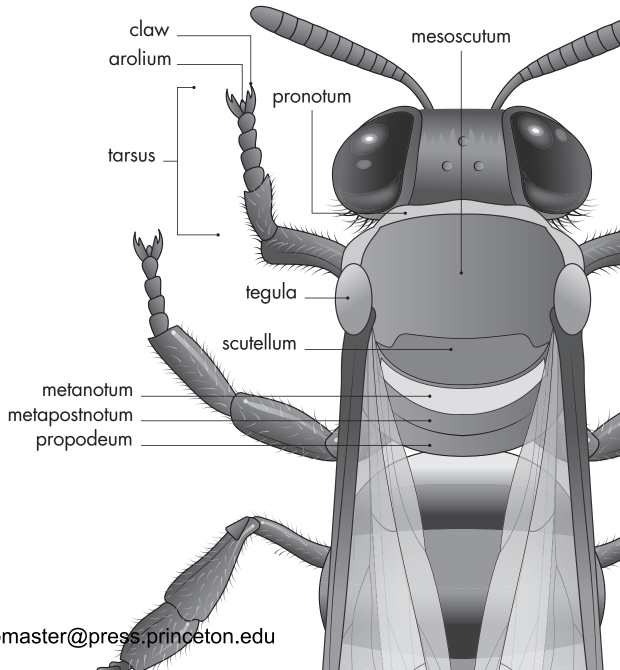
MESOSOMA

The mesosoma bears three pairs of legs and two pairs of wings. Although it often looks as if bees have only one pair of wings, this is because the two wings on each side are held together in flight by a row of hooks, called hamuli. Located on the front edge of the hindwing, these grip into an elongate gutter on the posterior margin of the forewing.

Each leg is subdivided into five sections: a basal coxa, a small trochanter, an elongate femur, a similarly elongate tibia, and a subsegmented tarsus, the basal segment of which is usually quite long. The tibiae bear one or two apical spurs, that on the foreleg forming part of the antenna-cleaning apparatus. Many bees (often only the females) have a triangular or U-shaped protrusion at the base of the hind tibia—this is the real "bee's knees," in that it helps the insect obtain purchase on the walls of its burrow. Called the basitibial plate, it is generally found in ground-nesting bees and not in those that nest in stems and the like, although here again there are exceptions.

The mesosoma is technically divided into four segments. The first three make up the true thorax and each bears a pair of legs, and the second and third segments bear the wings. As mentioned above, the fourth segment of the mesosoma is the first segment of the true abdomen, called the propodeum. What appears to be the dorsal surface of the propodeum is actually an extension of the third segment of the thorax and is called the metapostnotum in most modern literature on bees. The second segment of the mesosoma is much larger than the others and houses most of the flight muscles. Dorsally, it is subdivided in a way that makes it look as if multiple segments are involved. Fortunately, there are some bees in which these parts are color coded.

BELOW | Dorsal view of the head and mesosoma of an andrenid bee to show terms used frequently in this book.



LEFT | The six metasomal segments can be counted in this female *Andrena*. The fifth one has a hairy pre-pygidial fimbria and the sixth is small, but just visible, beneath it.

BELOW LEFT | A *Colletes hederae* male obtaining nectar. It is easy to see that this is a male because there is a white band at the apex of each metasomal tergum except the last, which is all black, and there are seven terga (females have six).

ABOVE | Only female bees have a sting, although this remains housed inside the metasoma unless the bee is going to use it. This is the sting of a bumble bee.

METASOMA

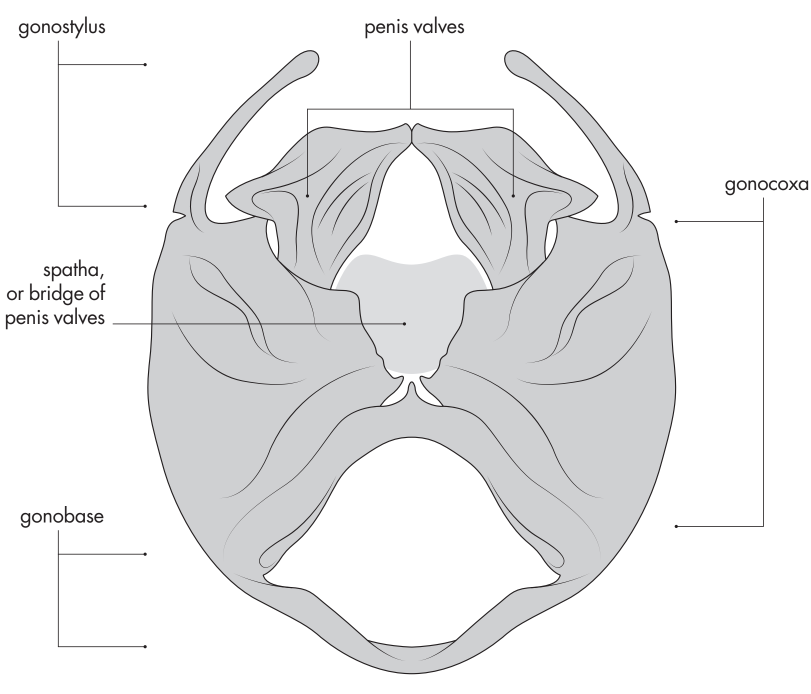
The metasoma is divided into segments that, as in the antennae, also differ in number between males and females: females have six and males seven externally visible segments. I say "externally visible" here because both sexes have segments that are telescoped inside the apex of the metasoma, forming the sting apparatus in females and the genitalia in males. These sex-delimited sets of structures are both highly complex and highly variable.

From the sting apparatus, let us consider just the sting shaft—perhaps the best part to choose, because it is the one you can easily see when it pierces your flesh if you have annoyed a bee. In some bees the shaft is curved downward, in some it is curved upward, and in others it is perfectly straight. It also varies considerably in length. Some bees, especially some cuckoo bees, have a sting that is very long and narrow, and that sometimes can even be completely extruded from the body at the end of a structure called the furcula, which might function somewhat like an atlatl (spear-thrower). In other bees, including the stingless honey bees and some different lineages of cuckoo bees, the sting shaft is reduced to practically nothing. Such bees are incapable of inflicting pain with their sting (though the stingless honey bees have other ways of tormenting animals that threaten their nest).

The male genitalia are also remarkably diverse, often even among closely related species. Indeed, it is often necessary to study the male genitalia to be able to identify an individual to species level, because the rest of the body may be indistinguishable among closely related species but the genitalia obviously diagnostic. This is a common feature in insects—indeed, even in animals in general.

BELOW | Ventral view of the genital capsule of a male apid bee.

BEE GENITALIA

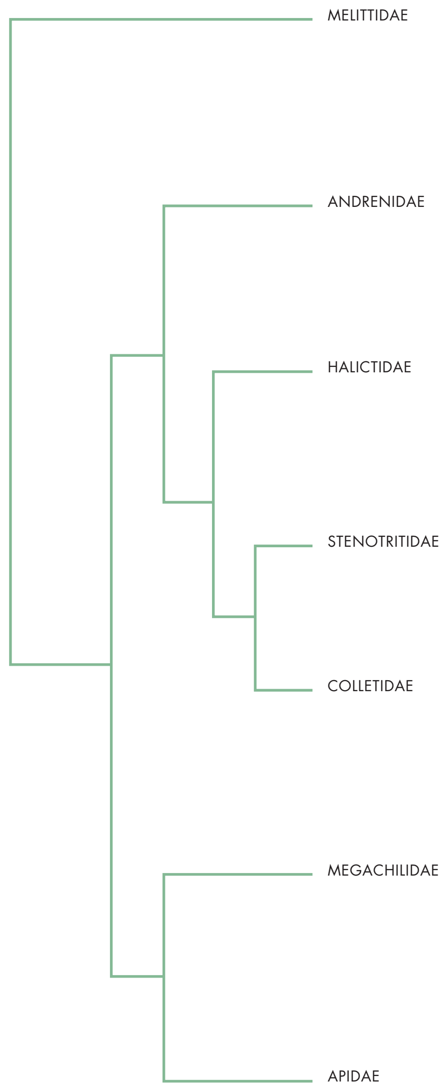


BEE CLASSIFICATION

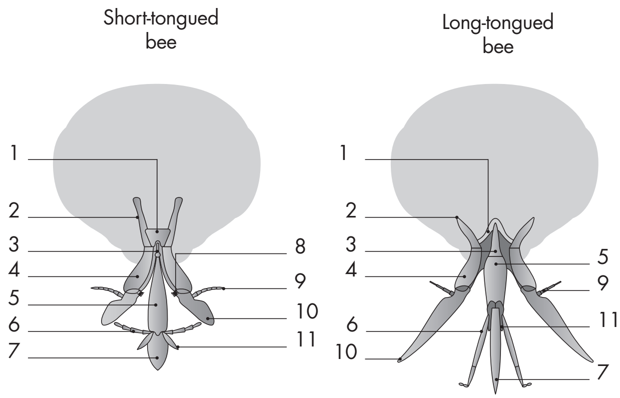
As usual when experts are involved, bee classification can be a controversial topic. We know that bees arose from among a particular group of wasps, although precisely where in the wasp tree the branch that led to bees diverged is something that not all bee experts yet agree on. There is also disagreement as to how many groups there are at the coarsest level of classification found among bees, which taxonomists call the family level.

In the UK and Brazil, some researchers consider bees to belong to a single family. While other numbers have been considered at one time or another, the most widespread view is that bees make up seven different families. Here, I follow the latter approach, the one advocated by the renowned American melittologist Charles Michener (1918–2015), who spent more than 80 years publishing research articles on bees and had in his prodigious memory a larger proportion of humanity's entire knowledge of bees than anyone else will ever possess.

Some of the controversy over bee classification has arisen from comparing results from traditional morphological analyses with those obtained from DNA sequences. Neither approach is perfect. As most people are not overly interested in the niceties of DNA sequences, it is more illuminating (not to mention aesthetically pleasing) to consider the morphological features that support particular taxonomic groups among the bees. The most fundamental of these groups are the seven families, and to understand how bee experts divide them up we need to pay attention to bee mouthparts and pollen-collecting structures.



ABOVE | The most widely accepted phylogenetic tree for the families of bees.



LEFT | The major difference between short- and long-tongued bee mouthpart morphology is in the structure of the labial palps. Generally, long-tongued bees have two long and two short palpomeres, with the latter at right angles to the former, and short-tongued bees have four equal-sized and equal-oriented palpomeres.

1: lorum, 2: cardo, 3: mentum, 4: stipe, 5: prementum, 6: labial palpus, 7: glossa, 8: lacinia, 9: maxillary palpus, 10: galea, 11: paraglossa.

CLASSIFYING BEES BY TONGUE LENGTH

Living descendants of the group of wasps that bees diverged from more than 100 million years ago fuel their predatory activities through imbibing sugary solutions—most commonly nectar from flowers, but also other sources such as extrafloral nectaries on plants, honeydew from aphids, and so on. But they do not collect nectar as a food for their offspring. Most bees do collect nectar, adding it to the pollen they provide to their offspring: it helps bind the friable pollen into a pollen ball, in addition to providing energy.

Having to collect so much nectar for each offspring places a great burden on the efficiency of the structures that bees use to obtain the sweet solution. So, as soon as the proto-bee arose from the pre-bee wasp, it had to evolve efficient mouthparts for nectar uptake. As a result, bee mouthparts went wild and adaptive radiation provided divergences in structure that were passed on to descendants in each lineage; today, we can study these in order to classify our bees.

A fundamental divergence that must have occurred relatively soon after the origin of bees was the development of the long-tongued bee morphology, a feature that is shared by two of the seven families (the Apidae and Megachilidae). While this usually does involve a long glossa (the section of the mouthparts that might truly be called a tongue), the real distinguishing feature is the size and orientation of some subdivided, rather leg-like structures (called labial palps) that flank the glossa. In the long-tongued bees there are (with, as always, some exceptions) two very long basal palpomeres, followed by two very short ones that are more or less at right angles to the basal pair. The long ones are flat or concave along their inner margin. In contrast, in the short-tongued bees (the remaining five families) all four palpomeres are usually (there are exceptions here also) similar in length and cylindrical in shape.

LONG-TONGUED BEES

The two long-tongued bee families can be most readily differentiated (in females of nest-building forms at least) by the location of a group of pollen-carrying hairs called the scopa. In the Megachilidae the scopa is primarily on the underside of the metasoma, whereas in Apidae it is primarily on the hind leg. Males and cuckoo forms

of the two families can be told apart perhaps most easily by the shape of the labrum—a flap in front of the mouthparts like an upper lip. In the Megachilidae this is broadest at its very base, whereas in the Apidae it is a little narrower there than it is below. Unfortunately, to observe this it is necessary to open up the mandibles, and these are so strongly closed, especially in Megachilidae, that a beginner (and sometimes even those with considerable experience) may decapitate the specimen in the attempt to identify which family it belongs to.

SHORT-TONGUED BEES

Among the short-tongued bee families, observers must examine a wider range of structures to be reasonably confident of a correct assignment. If the bee's glossa is at least weakly concave at the apex (some have a deeply forked glossa), then the individual belongs to the family Colletidae. An apically concave glossa is a feature these bees share with the wasps, and for a long time many entomologists thought that this suggested the colletids were the first bee family to diverge, with a more pointed tongue being a morphological

ABOVE LEFT | A female mining bee, *Anthophora bimaculata*, on Common Fleabane (*Pulicaria dysenterica*) in the UK, with pollen on the scopa on her hind leg.

ABOVE | The leafcutter bee *Megachile centuncularis* feeding from Common Marigold (*Calendula officinalis*) with pollen on the ventral surface of the metasoma.

RIGHT | Close-up view of the malar areas, labrum, and mandibles of the Himalayan honey bee *Apis laboriosa* to show the narrowing of the labrum towards the base.

feature that originated in the common ancestor of the rest. We are now confident that this was not the case; the concave apex of the colletid glossa is related to a novel use of the tongue.

Colletids are often called cellophane bees because they line their brood cells with a cellophane-like layer (sometimes two or three layers) that acts as a means of waterproofing the brood cell. This material comes from a gland in the bee's metasoma and is applied to the walls of the brood cell with the tongue, which is used like a paintbrush—it clearly wouldn't work as well if it was sharply pointed. This helps prevent the pollen mass from becoming moldy if it is too damp or from desiccating if it is too dry. As it is only the females that work at nest construction and thus need a paintbrush-like tongue, it is perhaps not surprising to find a few species of colletid in which the males have a pointed tongue (and have to be identified to the right family either by using other structures or, more easily, by otherwise looking like the females of their species).

The closest relatives of the Colletidae are members of the Stenotritidae, the smallest family of bees, with only 21 described species, all of which are restricted to Australia. They are large, very fast-flying bees, with a tongue that is bluntly rounded rather than concave or pointed.

The Andrenidae is a large, diverse family that is found worldwide except for Australia, where they are entirely absent. A defining characteristic of all female and almost all male Andrenidae is the two sulci descending from each antenna, where most bees have just one. The stenotritids also have two subantennal sulci, albeit in a somewhat different form, but as they are only found in Australia and andrenids are found everywhere except Australia, there is no risk of confusing them.

The Halictidae have a truly global distribution (except Antarctica), but a larval melittologist may

have to work hard to be certain of an identification. In most but by no means all halctids, a particular vein—the basal vein—is strongly bent near its base. In most other bees this is fairly straight or evenly curved, or if curved it is not most strongly so at the base. To be absolutely certain of the exceptions, you either have to get to know the bees more personally at lower taxonomic levels, or look for a tiny, usually hairy lobe, called the lacinia. This is usually at the base of a structure called the galea. In halictids it is in the "wrong" position, further toward the base of the mouthparts. So, if the lacinia (which is always hard to find) isn't where it should be, either it's there and you haven't noticed it or you have a halictid (or any of a small group of andrenids, which can be identified by the subantennal sulci, as discussed above).

This leaves us with the second-smallest bee family, the Melittidae, with just over 200 species. To be certain you have a melittid, look at the tongue yet again. If your specimen has the short-tongued bee structure (labial palpomeres all similar in size and shape) *and* a V- or Y-shaped structure known as the lorum with the narrow part toward the tongue base, then it is a melittid. These bees are absent from South America and Australia, so if you are looking at species from either of those continents, you don't need to worry about this family.

TAXONOMY FOR THE BEGINNER

By now you may have given up on becoming a bee taxonomist. Please don't; it is a great deal of fun and, in general, it is easier to learn the overall appearance of a group of bees than it is to identify

ABOVE | A sleeping aggregation of *Colletes* males.

ABOVE RIGHT | A *Dasypoda hirtipes* female with a full scopal load returns to her nest in the ground.

LEFT | A female *Thyreus waroonensis* searches for the nest entrance of its host.

them by dissecting their mouthparts. Finding out which family a bee belongs to is often the most difficult step in identification in the earlier stages of someone's bee obsession. This is why many geographically restricted identification guides often skip the family level entirely, enabling the user to get straight to the genus level. Indeed, as you look through the generic-level treatments in this book you will find plenty of examples of completely unrelated bees that look, superficially at least, more similar to one another than to their closer relatives. Some of the most striking examples can be found on pages 113, 119, and 220 for very hairy bees, and 109, 126, 154, and 191 for relatively bald ones; some unusually wasp-like bees can be seen on pages 53, 71, 144, and 194.

BEE-NESTING BIOLOGY

Consider the life of an average insect such as a butterfly or grasshopper. After mating, the females wander around looking for suitable places to lay their eggs. For the butterfly this is usually a plant species, one that the caterpillar eats. You can watch cabbage white females flitting to and fro among garden vegetables. After laying a few eggs, they will fly away to lay elsewhere. Most insects take their eggs to where the food is. In contrast, bees bring the food back to where their offspring are (or will soon be): they take pollen and nectar back to the nest. But first, the female has to construct a nest.

NEST SITES

Most bees nest in the ground, with different species preferring different soil types and different kinds of ground cover. Most prefer drier, grainier soils as these are easier to dig into. And most seem to prefer sparsely vegetated ground, perhaps because there's less chance that growing root systems will disrupt their nest. That said, it's easier to find bee nests where there is less vegetation to obscure the entrances, so the proportion that nest in more densely vegetated ground is likely underestimated simply because they are more

RIGHT | Some bees, such as this *Gronoceras felina*, build their nests on the outside of a surface. In this instance a nest made of mud and resin is anchored to the branch of a shrub.

LEFT | A tumulus of sandy soil around the entrance to a *Dasypoda hirtipes* nest.

BELOW | Nests of *Xylocopa californica* revealed in sotol (*Dasylirion* sp.) stalks that have been split down the middle. The brood cells are separated by disks of chewed sawdust.

difficult to find. Despite these overall preferences, some bees preferentially nest in densely grassed lawns and may be pests of golf courses. Some bees prefer to nest on slopes, others on flat ground, and still others in vertical banks. The insects often favor south-facing slopes (in the northern hemisphere, or north-facing ones in the southern hemisphere) because of the increased warming effects of the sun. That said, some cool-adapted bees can persist in warmer climates by nesting on the shadier side of a hill. To a bee, the sandy mortar between bricks in a wall, or dried-mud adobe, is like a cliff and can provide suitable opportunities for nesting, with some species preferring such substrates.

Pithy stems can be relatively easy to dig into, and many bees use dry raspberry canes or other stems to nest in. Other bees will be able to use a stem only if something else has hollowed it out first. The harder the wood, the more effort it takes to chew a burrow to make a nest, so lots of bees that nest in harder wood rely on other insects (often beetles) to do the hard chewing for them. Some large carpenter bees can chew their way through quite hard wood, and they and other species with similar nest site preferences can be pests in wooden buildings.

Other hollow structures can also be used as nests, ranging from snail shells to cavities in brick walls. There have been cases of bees plugging up stethoscopes in a field hospital or rendering keyholes unusable. However, claims that bees were the cause of a plane crash through plugging up fuel lines have been shown to be false, with nesting beginning after the crash occurred: bees not guilty.

NEST FORMS AND CONSTRUCTION

Relatively few bees construct a nest on a surface by molding resin, mud, or a ball of plant hairs into a structure for brood cells. Some will decorate such nests with gravel and make a mosaic. Even rarer substrates that bees make nests in include dry dung, plant galls, termite nests, and rodent burrows (particularly popular among some bumble bees).

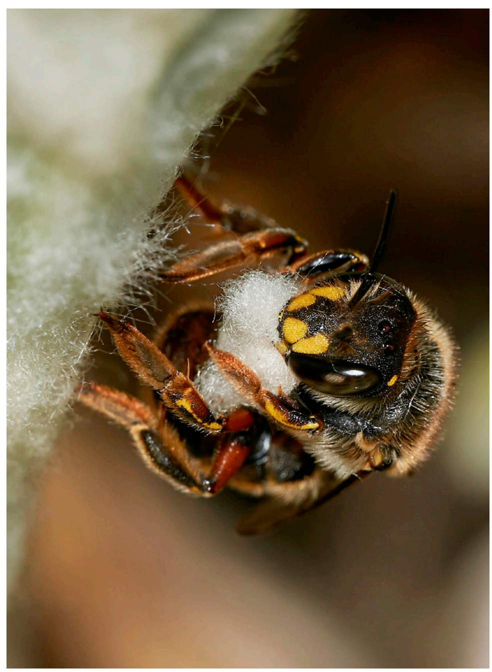
Bee nests in the ground are usually not simple tunnels. Inside each nest a female will construct brood cells, one for each offspring. Some species build these adjacent to the main tunnel, while others dig side branches with one cell at the end of each. Others build the cells in clusters, sometimes constructing a cavity around them, while others make a row of brood cells connected end to end. Some bees make shallow nests, sometimes just beneath the soil surface. The deepest nests ever found were more than 16 feet (5 meters) deep.

The brood cells are where the bee offspring develop, and they have to be constructed with care. They are usually lined with waterproofing materials, most commonly waxy glandular secretions that make the inside of the brood cell look shiny. These serve both to keep excess water out of the brood cell and to maintain appropriate levels of humidity inside, so that the food supply does not go moldy or dry out. In a few species the brood cell lining is unusually thick and serves as an additional food source for the larvae. Cellophane bees make a polyester brood cell lining, and so the offspring literally develop inside a plastic bag. The provisions their mother gathers are often relatively liquid made possible by the lining's greater leak-proofing properties. Other bees line their brood cells (and often the entire burrow) with extraneous materials: pieces of leaves or petals, resin, and even pieces of plastic bag or kitchen tile caulking have been used in some cases. Attentive wool carder bee mothers shave hairs from plant leaves and construct a large fluffy ball, which they hollow out before collecting food for their offspring. You have to admire a mother that makes a pillow for her offspring to grow up inside as well as collecting all the food it needs.

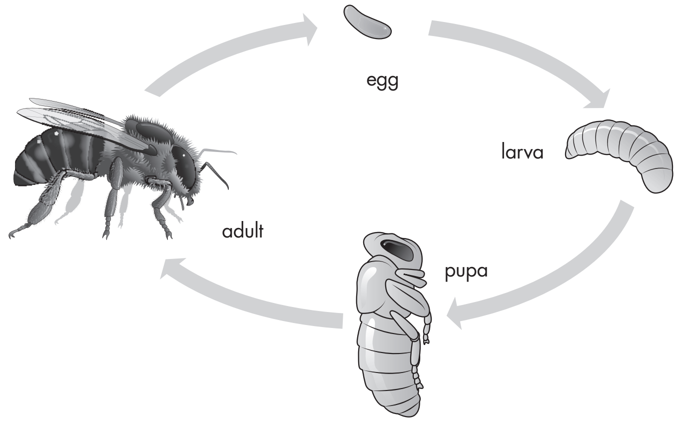
LEFT | An opened brood cell of a *Megachile*. To the left is the pollen and nectar mixture that has yet to be consumed by the larva, which is to the right. Note the leaf sections that surround the contents of the brood cell.

BELOW LEFT | A brood cell cluster of a *Bombus pascuorum*. The large queen is to the left and a recently emerged worker is at the bottom.

BELOW | A female *Anthidium manicatum* forming a ball from the hairs she has shaved from the surface of a leaf.



THE BEE LIFE CYCLE



RIGHT | The life cycle of an individual bee. The adult female lays an egg, which hatches into the first-instar larva. The larva sheds it exoskeleton several times before pupating. The pupa starts out white, then gradually darkens as the adult develops within.

Bees start life as an egg, usually banana-shaped, laid on top of a pollen ball. Cuckoo bees are more diverse in egg structure, as they have to place the egg in a way that reduces the chance of detection by the host bee. As a result, cuckoo bee eggs are often flattened on one side or at one end and flush with the brood cell surface, with the rest of the egg buried in the brood cell wall.

The bee mother determines which sex her offspring will be: if she passes stored sperm over the egg as it passes through her reproductive tract, then it will be a female (with rare exceptions); if she does not, it will become a male. In other words, male bees result from unfertilized eggs and females from fertilized ones. This unusual form of sex determination is also found in wasps, ants, sawflies, thrips, and some other arthropods.

As a result of their rather easy lifestyle inside a brood cell, with all the food they will ever need, bee larvae are morphologically rather simple "couch potatoes," especially in comparison to the elaborate forms found among caterpillars, which have to fend for themselves "outdoors." Like all juvenile insects, bee larvae have to shed their exoskeleton (which includes the lining of the gas-exchange tubes that run through their bodies and much of the lining of their digestive system) in order to grow, because their exoskeleton is rather inflexible and cannot stretch much. This is akin to needing only five sets of clothes from birth to adulthood, as bee larvae must "change their skins" a number of times between hatching from the egg and becoming fully grown. Then the larva molts to the pupal stage.

Bee pupae have the same overall structure as the adult, except that the wings are reduced to little flaps and the legs and antennae are held close to the body. Pupae start out the same white color as the larvae, but gradually darken as the integument of the adult forms beneath the translucent pupal skin. Upon emerging from the pupa, the wings expand as blood is pumped into them. Once the exoskeleton has hardened and the wings have dried, the adult is ready to leave its natal nest and fly.

The timing of the life cycle with the seasons varies greatly among bees, with different species being active as adults at different times of year. Many of the earliest spring bees have overwintered as adults and will have completed their brood production by the time the season's willow catkins have faded. Others will pass the cold season as fully grown larvae, and then pupate and develop into adults once the weather warms. Desert bees survive—sometimes for years—as fully fed larvae, ready to pupate as soon as soil humidity levels suggest that it has rained enough for flowers to start developing.

BEE FOOD AND POLLINATION

ABOVE | This *Scaptotrigona depilis* larva is preferentially feeding on *Zygosaccharomyces* fungi growing on its brood-cell lining rather than on the pollen and nectar in the brood cell.

BELOW | This *Agapostemon* female is using sonication or "buzz pollination" on a pale meadow beauty blossom. The pollen grains can be seen like shooting stars.

Most bees are mass provisioners, meaning that all the food required for the development of the larva is collected before the egg is laid. This is like collecting 18 years' worth of groceries, piling them inside a room, giving birth, and then leaving your child to develop alone. In most cases, the food is pollen and nectar, although some bees replace nectar with floral oils. However, it has recently been suggested that much of the nutrition most developing bees get does not come directly from the floral sources collected by the mother, but from microbes that grow on the pollen and nectar mixture. In other words, much of the nutrition the bee larva gets is probiotic. Certainly some bees that make a very liquidy provision mass have brood cells that smell "yeasty," indicating that fermentation has taken place. Some bee larvae have even been shown to preferentially consume the fungi growing around the edges of their brood cells.

ABOVE | As the genus name suggests, *Nolanomelissa toroi* females collect pollen only from flowers of plants in the genus *Nolana*.

With the enormous diversity of flowers available to any mother, how does she choose which ones to visit? Some species are oligolectic, which means they will collect pollen from only one, or a few closely related, plant species. An example of such a species is the sundrop sweat bee (*Lasioglossum oenotherae*), which like its closest relatives collects pollen only from evening primroses, including the horticultural sundrops that many people in eastern North American cities have in their gardens. These are flowers that open at night or under the low light intensities associated with dawn or dusk. Thus, the sundrop sweat bee is active in the early hours of the morning and goes to bed "for the night" at 9 a.m.! At the opposite end of the spectrum are bees that will visit almost any flowering plant for resources, our domesticated Western Honey Bee coming close to that. Most bees fall between these extremes, and it is normal for the insects to visit a wider range of flower species for nectar than for pollen.

While most nest-building, food-collecting bees have developed special hairs to carry pollen—the scopa, usually on the hind leg or the underside of the metasoma—others have evolved mechanisms to obtain pollen in less usual ways. A particularly interesting example is the genus *Samba* (page 48), where the bee uses the mandibles, midlegs, and hind legs simultaneously to obtain pollen. Likely the most common additional adaptation for collecting pollen is buzz pollination.

Many flowers have pollen on the inside of their anthers rather than easily accessible on the outside, so it has to be shaken out of the anthers if the bee is to get it. Buzzing bees seem preadapted to do this: they land on the flower, hold it tightly with their mandibles and/or legs, and vibrate their flight muscles. The result is usually a fairly high-pitched buzz, and the pollen pours out of the anther and collects on the hairs on the bee's body. Blueberries and other ericaceous plants require buzz pollination, as do Tomato plants (*Solanum lycopersicum*) and a wide range of wildflowers.

As some bees visit only one or a few species of flowers for pollen, do the plants rely on the insects for pollination? It is generally true that bees rely on particular flowering plant species more than particular flowers need the bees, thus, with exceptions (such as some cacti where most pollination results from visits of a single bee species), it is a somewhat one-sided relationship.

SOCIAL BEES

LEFT | Most stingless bees have beautiful nest entrances. In this instance *Pariotriogona klossi*—a tear-drinking bee—has built a nest on a limestone cliff, and the nest has numerous tubular entrances that lead to a conduit and thence a fissure in the cliff wall.

RIGHT | Bumble bee colonies are initiated by a foundress in spring. She produces a brood of workers that labor to increase the colony size before there is a switch to the production of males and the next generation of reproductive females. This drawing shows a species with a long colony cycle; some species produce males and next year's queens in mid-summer.

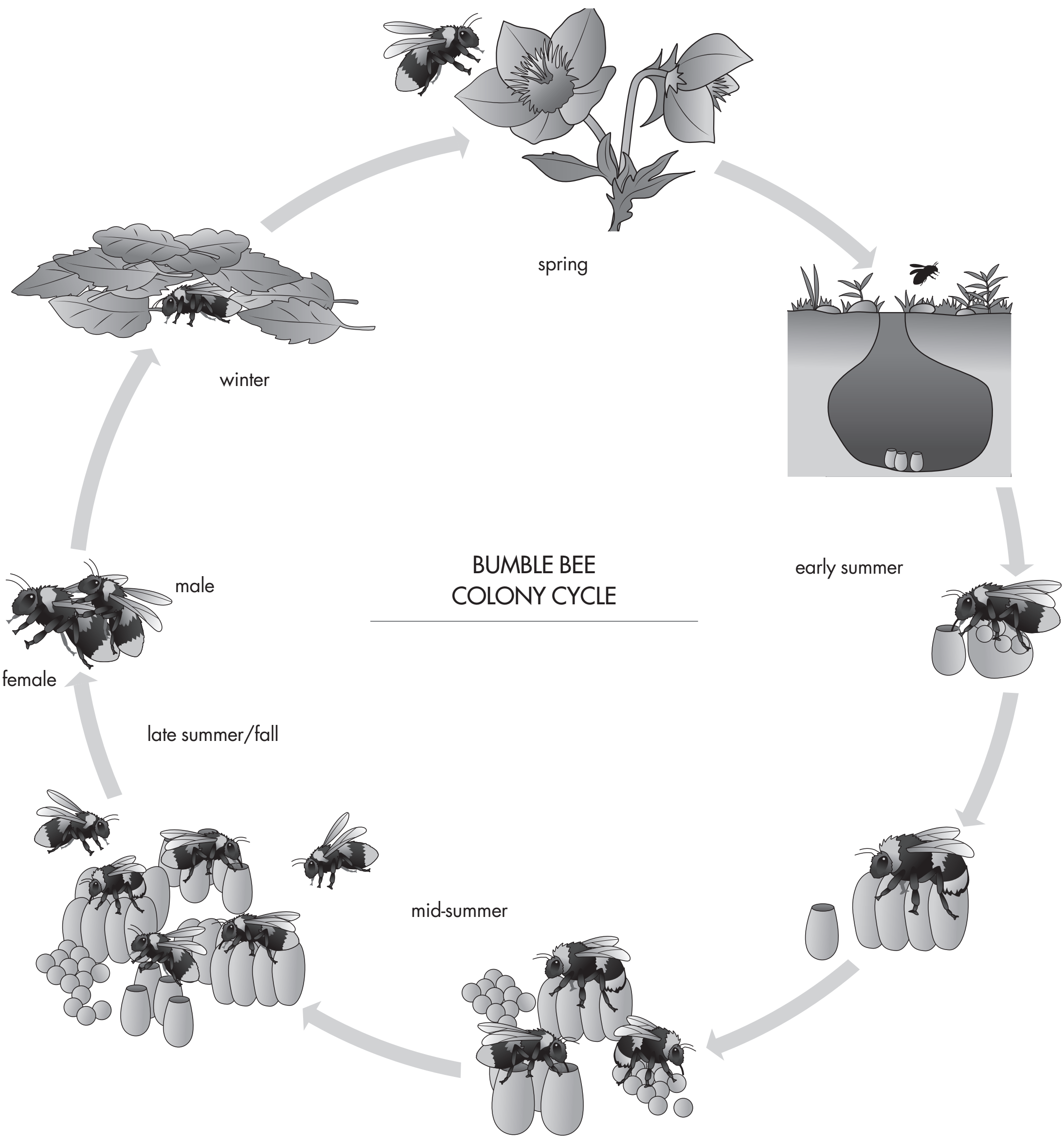
As discussed at the start of the chapter, most bees are solitary. However, several hundred species are incapable of living outside of a large perennial colony headed by a queen that survives for several years. Honey bees and stingless honey bees fit that description, as does *Lasioglossum marginatum*, a very unusual sweat bee with queens that live five or six years—longer even than honey bee queens (pages 106–7).

Other species have annual colonies, started in spring by a single overwintered female—the foundress—that mated late the previous year and has stored sperm so she can fertilize eggs after emerging from diapause (dormancy). Bumble bees (page 206) are the best-known examples of species that form annual colonies, which can get quite large, with hundreds of workers. There are also lots of sweat bees with annual colony cycles, although most of them are much smaller with perhaps half a dozen workers at most. There are even examples where the average number of workers is less than one—meaning that some females in the population are entirely solitary, whereas others have just one or two workers.

The types of social insects we are most familiar with—in addition to the bees mentioned above, yellowjackets, hornets, and ants—are all eusocial, meaning that normally the workers are the daughters of the queen and help her raise the next generation. But there are other forms of social life among the bees. A few bee species have workers that are sisters to the reproductively dominant queen in what is termed a semisocial society. This is rare when it is the only form of social organization, but more common as a phase during the cycle of a colony that is eusocial at some point.

It can arise in two ways: either as a grouping of sisters in spring, in which the dominant one remains as a queen when the brood develops and the society becomes eusocial; or if the queen in a eusocial society dies and is replaced by one of her daughters. In the latter case, usually the oldest or the largest daughter becomes the replacement queen and her sisters collect the food on which she then lays her eggs.

Some bees share a nest but once underground act as if they are solitary. In these communal societies the bees share a nest entrance but have their own branches below ground, construct their own brood cells, collect their own pollen and nectar, and lay their own eggs. This is more like an apartment building style of living, as opposed to an extended single-family dwelling.



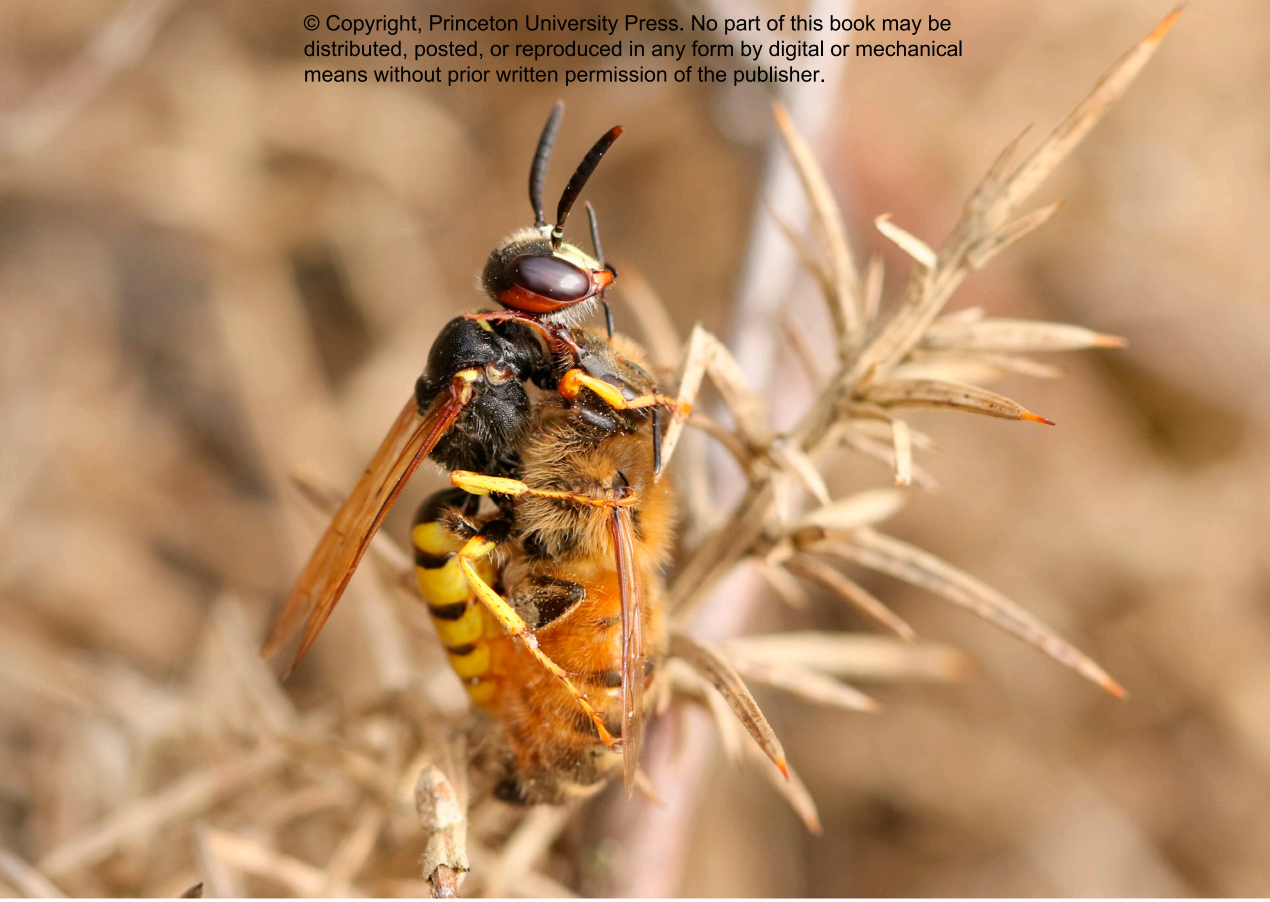
ENEMIES

CUCKOO BEES

Bees make large amounts of nutritious food available for their offspring, but those resources can be stolen by other animals. Prime among these thieves are other bees known as cuckoo and socially parasitic bees. Bees seem to have evolved cuckoo bee behavior on many occasions, and while the precise number remains unknown (as new cuckoo bee lineages are discovered every now and then), such larceny has arisen at least 19 times during bee evolution. Some origins involve few species that are very closely related to their hosts, while others involve hundreds. One group of the family Apidae, the Nomadinae, contains more than 1,600 species of mostly wasp-like bees that lay eggs on provisions provided by hosts from five of the seven bee families, including other apids.

ABOVE | This *Sphecodes* female is leaving its host nest, perhaps after having laid an egg on a pollen ball constructed by the host.

RIGHT | This female *Philanthus triangulum* wasp has paralyzed a honey bee worker, which it will place in a brood cell along with others before laying an egg. The wasp larva will then eat the paralyzed bees.



Cuckoo bees have a variety of ways of entering a host nest. Most enter and lay an egg while the host female is out foraging, while others break in after the nest is completed. The latter must have structures that permit a break-in—for example, if the host is a cellophane bee, then the cuckoo has to cut through the plastic and often has saw- or forceps-like structures at the tail end that facilitate this.

While some cuckoo bee females eat the egg they find in a completed brood cell, most leave it to their offspring to make sure the host offspring is dispatched: early-instar cuckoo bee larvae often have long sickle-shaped mandibles with which they slice and dice the host egg or early-stage larva (and other cuckoo bee early stages if the brood cell has been attacked more than once). Some particularly enterprising cuckoo bee mothers lay their egg directly on the egg of the host, and the newly hatched cuckoo larva (which develops more quickly than the host egg) then consumes the contents of the host egg before consuming the provisions.

Bees that lay eggs in the nests of social bees have more fearsome obstacles to overcome. Some do so by brute force, with heavily armored bodies that can withstand the attacks of the workers as they attempt to defend their colony and strong mandibles and/or stings that can maim or kill the defenders. Others use stealth. Some cuckoos of communal bees have relatively flat bodies that make them less noticeable among the thrum of activity as they go up and down the brood tunnels. Others have evolved to become social parasites that take over the society they invade.

(continued...)

INDEX

All index entries relate to bees, unless otherwise specified (e.g., wasps).

Families, subfamilies, and tribes are in Roman type; genera and species are in *italics*.