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ast month, I discussed the external anatomy of the honey bee. This month, I will turn my attention to the internal anatomy of the honey bee. I wanted to include high quality photographs of each organ discussed in this article so that the internal anatomy could be illustrated appropriately. However, such photographs are hard to acquire and nearly everything in a bee is creamy white or clear in appearance. Thus, the internal anatomy of a bee lacks visual stimulation, though the various parts are functional marvels. Rather than including color photographs that might be hard to understand, instead, I defaulted to using schematic drawings of some basic internal anatomy. I do not include images of everything I discuss. Instead, I would like to invite you to review the documents that I list in the Recommended Readings section of this article. All of the readings are fantastic references for helping you to understand and visualize bee internal anatomy in general. Some of the sources are even available for free online. As a final note, I list all of the anatomical features that I am discussing in **bold font** so that you can know exactly what I am trying to define.

ield Guide to

Circulatory System

Honey bees have an open circulatory system. This simply means that **hemolymph** (bee blood) does not pump through veins but rather freely circulates in the bee's body cavity. Hemolymph does not transport oxygen but rather transports nutrients and hormones to the various body tissues. Furthermore, hemolymph picks up waste products generated in the body and transports them to the excretory organs. Hemolymph also serves as a reservoir of food and can aid in heat transfer within the bee.

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How does the hemolymph get around to the various organs? Bees specifically and insects in general have a single vessel that runs from their abdomens, through their thoraxes and into their heads. This vessel is arranged dorsally, meaning that it runs down their back. The part of the vessel occurring in the abdomen is called the dorsal heart while the part in the thorax is called the dorsal aorta. The dorsal heart, the part in the abdomen, has small holes in its sides. These holes are called ostia. The dorsal heart pulses, pulling hemolymph through the ostia, into the vessel, and pumping it through the dorsal aorta in the thorax and into the head. From the head, the hemolymph percolates through the thorax and back into the abdomen. It bathes the various internal organs in route back to the abdomen. Once in the abdomen, the hemolymph absorbs nutrients acquired during food digestion and reenters the dorsal heart to start the cycle again.

Digestive System

The digestive system is composed of three main sections, the **foregut**, **midgut**, and **hindgut**. Interestingly enough, the three sections of the digestive tract form separately during bee development. The foregut (first third of the digestive tract) and hindgut (last third of the digestive tract) form as invaginations from either end of the developing bee. Imagine, for example, holding a balloon between the pointer fingers of both of your hands, with the fingers being on opposite sides of the balloon. Imagine, now, pushing your fingers toward one another, pressing both of the sides of the balloon in toward the center. This is a good model for how the digestive tract of the bee forms. The foregut and hindgut develop as invaginations from both ends of the bee. As a result, the foregut and hindgut are lined with the same material that lines the outside of the bee's body (cuticle), just like the two depressions on the balloon are lined by the external surface of the balloon. Practically speaking, this means that the foregut and hindgut are not sites for nutrient absorption in the bee since nutrients cannot traverse the cuticular lining of either section. In contrast, the midgut is not lined with cuticle, thus making nutrient absorption its primary function. Given that the foregut and hindgut are lined with cuticle, the lining of both are shed as a bee molts (sheds its exoskeleton) during larval development.

The foregut is composed of the mouth, esophagus, and crop (Figure 1) of the honey bee. Food enters the digestive tract through the mouth and travels down the esophagus and into the crop. The esophagus is simply a tube that runs from the mouth in the head, through the thorax, and into the crop in the abdomen. The crop, or honey stomach as it is called sometimes by beekeepers, is a spherically shaped organ in the abdomen that serves as a site for food storage, as a storage place for nectar bees collect from flowers and fly back to the hive, or as an initial site for the digestion of food in the bee. The crop can expand significantly when it is full of honey or nectar, so-muchso that the abdomen swells. The foregut and midgut are separated by a valve called the proventriculus which is located at the end of the crop. This valve can grind and pulverize food particles (such as pollen) and filter

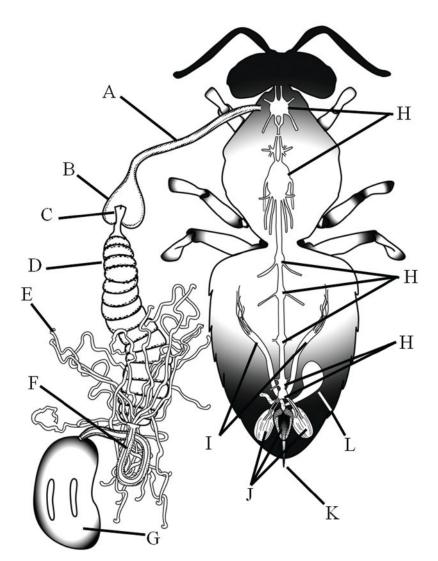


Figure 1. Internal anatomy of the honey bee. A – esophagus; B – crop; C – proventriculus; D – ventriculus (midgut); E – Malpighian tubules; F – ileum; G – rectum; H – ganglia; I – ovaries; J – sting apparatus; K – sting shaft; L – poison sac. Drawing by Kay Weigel, University of Florida. Published in Ellis, J.D., Atkinson, E.B., Graham, J.G. 2014. Honey bee biology. In: W. Ritter (ed) Bee Health and Veterinarians. OIE World Organization for Animal Health, Paris, France. pp. 15-28.

pollen out of the crop contents. Food passes through the proventricular valve and into the bee's midgut or **ventriculus** (Figure 1).

The midgut is the primary site of enzymatic digestion of food and absorption of nutrients. It is not lined by cuticle but rather is lined by the **peritrophic membrane**. This membrane likely protects the digestive cells (the cells that line the internal surface of the midgut) while allowing absorption of the nutrients straight into the hemolymph. Because the midgut is somewhat permeable, being so because of its function as the site of nutrient absorption, this is where many viruses and other bee pathogens enter the hemolymph. This is true especially for the *Nosema* pathogens (*N. apis* and *N. ceranae*) and some viruses.

Next along the digestive tract are the **Malpighian tubules** (Figure 1). These occur at the end of the midgut and are, essentially, spaghetti-like extensions of the tract that float freely in the bee's body cavity. The Malpighian tubules extract waste products from the hemolymph. They produce uric acid granules and help with osmoregulation (water management) within the bee.

The hindgut, or final section of the digestive system, is composed of the ileum (Figure 1) and rectum (Figure 1). The ileum, sometimes called the small intestines, is a short tube that connects the midgut to the rectum. The rectum is important for the absorption of water, salt, and other beneficial substances prior to waste excretion. There are small areas on the rectum called rectal pads. These sections reabsorb >90% of the water that was used by the Malpighian tubules to collect waste. The latter is an important function. Bees, like most insects, try to retain as much moisture as possible from the food they eat. Thus, they do not excrete nitrogenous wastes in a urine-equivalent as humans do. Instead, they reabsorb much of their water and tend to defecate moderately liquid to dry feces. Uric acid solids and other unused foodstuffs, such as the shells of pollen grains, are excreted as relatively solid feces.

Glandular System

The glandular system of a honey bee has four basic functions: (1) internal (within the body) and external (outside the body) communication, (2) food processing, (3) defense and (4) wax production. The glandular system includes a number of glands located throughout the bee's body. These glands are organs composed of clusters of cells that produce and secrete various products. Those glands that secrete products inside of the body to produce a change inside of the body are called endocrine glands while those that secrete chemicals through ducts to the outside of the body to produce a change in other organisms outside of the body are called exocrine glands. The chemicals released by endocrine glands into the body for internal signaling are called hormones while the chemicals released by exocrine glands outside of the body for external signaling are called pheromones.

The most notable hormone-producing glands are the **corpora allata** and the **prothoracic gland**. The corpora allata are paired glands behind the brain and these secrete juvenile hormone or JH into the bee's hemolymph. Juvenile hormone is a very important hormone in honey bees. It contributes to the regulation of bee development, reproduction, female caste determination, etc. The prothoracic gland secretes **ecdysone**, a hormone known to be an important regulator of the molting process in a bee.

Notable exocrine glands include the mandibular glands in queens, the Nasonov glands near the tip of the upper side of a worker bee's abdomen, the glands associated with bee defense, and the glands associated with bee "footprint pheromones." All of these glands produce products that maintain the social homeostasis of the colony.

Queen mandibular glands are glands located around the queen's mouthparts that secrete a number of compounds that the queens pass to workers while being fed. These compounds inhibit the rearing of new queens, inhibit the development of worker ovaries, attract drones outside the hive, help stabilize swarms, and stimulate foraging and brood rearing, all among other suspected tasks.

There are a number of pheromones produced by a bee that serve as location signals for other bees. **Nasonov glands** are activated at water sites, colony entrances, swarm clusters, etc. Essentially, the Nasonov pheromone is a homing pheromone. It is used to call other bees to a single location. **Trailing** or **footprint pheromones** are believed to be produced by the bee and deposited as it walks. It is not known whether these pheromones are deposited by glands in the **tarsi**, or bee foot, or the abdomen as it drags while the bee walks. Honey bees also produce two different alarm pheromones, one from **the mandibular gland** (located near the mouthparts) and the second from the **sting gland** (located near the rear of the bee). The mandibular gland produces 2-heptanone while the sting gland produces isopentyl acetate. The latter is deposited on a victim that has been stung, thus telling other attacking bees where to sting.

Brood produces an array of pheromones from multiple glands. These pheromones communicate the brood's food needs to worker bees. Brood pheromones also aid in the inhibition of worker ovary development. It is possible that pheromones produced by older larvae tell the worker bees that their cells need to be capped.

Glands located inside the bee are important for food production and handling as well. Nurse worker bees secrete the food that larval honey bees eat. This food is secreted mainly by **hypopharyngeal glands** and **mandibular glands** located in the bee's head. The hypopharyngeal glands are the largest glands in the worker honey bee. They are well developed in nurse bees. The mandibular glands produce some components of bee saliva and royal jelly. Adult worker, drone and queen bees have large **salivary glands** that occur in a bee's head and thorax. These glands secrete compounds that aid in the digestion of food.

Finally, worker bees have **wax glands** that secrete **beeswax** onto various **wax plates** located underneath their abdomens. These glands produce the beeswax that the bees use as a major part of the hive construction materials. Bees usually need a major supply of incoming nectar before they will be stimulated to secrete wax.

Nervous System

The nervous system of a bee is similar to that of other insects. It consists of a brain located in the bee's head and a nerve cord that is located on the ventral (under) side of a bee's body (Figure 1). The bee's brain is mostly the center of bee sensory perception and processing. It is composed of various lobes or swollen sections of nerve cells that unite to process and respond to certain types of information. Almost everything that a bee uses to sense the outside world is connected to the brain. For example, the main sections of the brain are the antennal lobes (these receive information from the antennae), the optic lobes (centers of the brain receiving information from the bee's eyes), and the mushroom bodies (these have a role in a bee's ability to learn, remember, and act on information).

Information perceived by the brain produces a response by the bees that sends signals down the ventral nerve cord through one or more of the seven **ganglia** (nerve centers – Figure 1) located throughout the bee from the head through the abdomen. These ganglia coordinate the bee response to any stimuli perceived by the bee. Generally speaking, these ganglia control the nervous function for the section of the bee's seg-

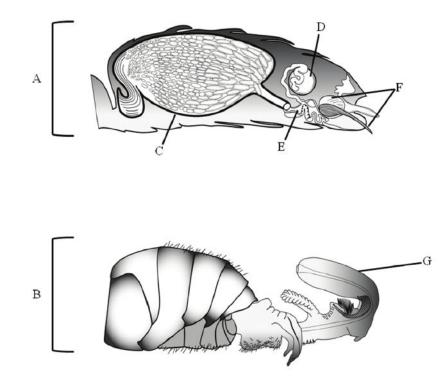


Figure 2. Queen and drone reproductive anatomy. A – queen abdomen (lateral internal view); B – drone abdomen (external view with reproductive organs everted); C – Ovary; D – spermatheca; E – oviduct; F – sting apparatus; G – endophallus. Drawing by Kay Weigel, University of Florida. Published in Ellis, J.D., Atkinson, E.B., Graham, J.G. 2014. Honey bee biology. In: W. Ritter (ed) Bee Health and Veterinarians. OIE World Organization for Animal Health, Paris, France. pp. 15-28.

mented body in which the ganglia is found. For example, the **subesophageal ganglion** is a ganglion in the bee's head that is connected to various components of the bee's mouthparts, thus controlling mouth movement and function. There are other ganglia located throughout the bee's body and these mostly control bee locomotion or general movement in their respective sections.

Muscular System

Honey bees move and movement requires **muscles**. Honey bees have muscles located throughout their bodies, with greater concentrations of muscle located mainly in the areas that move the bee. These areas of muscle concentration include in the legs, in the head (to move the mouth parts), and in the thorax (to move the wings). There are, of course, muscles in much of the rest of the body, but more in these noted areas.

The muscular system has multiple functions. These include body support, maintenance of a bee's posture, movement of the limbs, movement of the wings, locomotion, opening and closure of the **spiracles** (the openings on the side of the bee that let air in/out of the body), operation of pumps such as poison glands, and the generation of heat by shivering.

The thorax is filled with muscle, principally to move the wings that power bee flight. The muscles in the thorax do not attach directly to the wings, but rather to the inner surfaces of the thorax. Thus, these muscles are referred to as **indirect flight muscles** since they do not power the wings directly. Essentially, there are muscles in the thorax that are arranged vertically and muscles that are arrange horizontally. The **vertical muscles** pull the upper plate of the thorax down, causing the wings to go up. The **horizontal muscles** compress the thorax from front to back, causing the top of the thorax to squeeze up and the wings to go down. Thus, the bee's thorax changes shape rapidly as the bee flies.

Reproductive System

There are three types of bees in a honey bee colony and two are considered the **reproductives**, or the bees in the hive that contribute to reproduction. These are the queen and drone bees. Worker bees, the third type of bee in the nest, are female and do possess the ability to contribute to reproduction, but they are believed to do so under strict conditions under which the colony has failed to make a new queen.

Queen honey bees are the reproductive female in the nest and they possess special or enhanced anatomical structures that support reproduction. First, they have two large **ovaries** (Figure 2) in their abdomens and the ovaries are composed of about 150 or so **ovarioles** (Figure 2). The ovarioles are long tubules that contain various developmental stages of eggs and the **nurse cells** that support them. The less mature eggs, or **egg cells**, occur at the end of the ovariole oriented toward the bee's head, while the more developed eggs travel down the ovariole positioned toward the end of the ovary facing the rear tip of the bee's abdomen.

Eggs that are about to be laid by the queen pass from the ovariole into the lateral oviduct connected to the given ovary. The lateral oviducts are tubes that extend from both ovaries and unite into a single oviduct called the median oviduct. The mature egg passes from the ovariole, through its respective lateral oviduct and into the median oviduct. Once the egg is here, the queen can control whether or not the egg is fertilized with sperm provided by the drone. The queen possesses a special organ in her abdomen called the spermatheca (Figure 2). The spermatheca holds and nourishes all of the sperm that the queen collected from her multiple drone partners. The queen has a special valve that she can open to release sperm from the spermatheca to fertilize eggs as they pass through the median oviduct.

Worker honey bees possess significantly reduced ovaries that contain around five or so ovarioles. They rarely have a spermatheca, though some workers of some subspecies of honey bees (such as Cape honey bees) can have a spermatheca, even one that is quite large.

Drone, or male, honey bees have a somewhat complex reproductive system. Immature drones have large **testes** that are composed of tubules in which sperm are produced and mature. Drones reach sexual maturity around 12-13 days after emerging. By this time, the testes have reduced in size significantly since the sperm have migrated to the **seminal vesicles**. These vesicles are sausage-shaped organs that grow in size as sperm migrate from the testes to fill them. They serve as the home of the sperm until they are expelled from the body while copulating with the queen.

The abdomens of drones also contain an endophallus (Figure 2). This is the equivalent of the penis in mammals. The endophallus is stored inside of the drone's body. During storage, the endophallus is inverted, or turned inside out. The endophallus is forced out of the abdomen when the drone copulates with the queen. At this point, what was the inside of the endophallus while in the body becomes the outside of the endophallus when pushed from the body. It takes much of the drone's hemolymph to force the endophallus out of the body. Thus, the everted drone becomes paralyzed and ultimately dies as a result of forcing out his endophallus and copulating with the queen.

Respiratory System

Honey bees, like other insects, respire. Respiration is simply gas exchange. Bees breathe, but not in the same way that humans and other mammals do. Honey bees do not have lungs, neither are they able to take breathes actively. Instead, their respiration is a bit more passive.

Oxygen rich air enters the bee's body through small openings called **spiracles** that are located down both sides of a bee's body. There are three pairs of spiracles on the bee's thorax and seven pairs on the abdomen. These spiracles lead to small **trachea** that widen to form **air sacs**. The air sacs are located throughout the bee's thorax and abdomen. These large air bags serve as bellows to move air into and out of the body. Small branches or tubes emerge from the air sacs and are called **trachea** (the bigger of the tubes) and **tracheoles** (the smaller of the tubes), the latter in which oxygen exchange occurs. The trachea are ringed by spiral thickenings of cuticle (**taenidia**) in their walls while the tracheoles have no such thickening.

Conclusion

There are a number of internal anatomical features that I did not discuss, mainly because I felt that a discussion of these minor parts was not appropriate for a general overview of honey bee internal anatomy. However, the readings that I recommend contain amazing photographs and drawings and a thorough explanation of all of the major internal and external features of the honey bee. I believe a knowledge of honey bee anatomy is useful to beekeepers because it helps one understand the basic systems that support bee, and ultimately colony, life. I hope that you will explore this topic further, especially if you want to be amazed by the stunning creature with which we interact.

Recommended Readings

 Carreck, N.L., Andree, M., Brent, C.S., Cox-Foster, D., Dade, H.A., Ellis, J.D., Hatijina, F., vanEngelsdorp, D. 2013. Standard methods for *Apis mellifera* anatomy and dissection. In. V. Dietemann; J.D. Ellis, P. Neumann (Eds) The COLOSS BEEBOOK, Volume I: standard methods for *Apis mellifera* research. Journal of Apicultural Research, 52(4): 40 pp. http://dx.doi.org/10.3896/ IBRA.1.52.4.03.

*This publication is available freely online here: http://www.ibra.org.uk/ articles/Standard-methods-for-Apismellifera-anatomy-and-dissection. It contains a table of bee internal and external anatomy that I believe you will find most useful.

2. Dade, H.A. 2009. Anatomy and Dissection of the Honey Bee. International Bee Research Association, Cardiff, UK. 178 pp.

*This is a reprint of a classic book on honey bee anatomy. It is very affordable and a must have for any beekeeping library.

- Goodman, L. 2003. Form and Function in the Honey Bee. International Bee Research Association, Cardiff, UK. 220 pp. *This book includes a large number of excellent photographs and drawings of honey bee anatomy. It is a masterpiece on this topic.
- 4. Koeniger, G., Koeniger, N., Ellis, J., Connor, L. 2014. Mating biology of honey bees (*Apis mellifera*). Wicwas Press, Kalamazoo, MI, USA. 155 pp.

*The authors of this book go into considerable detail discussing the reproductive anatomy and physiology of honey bees.

- Snodgrass, R.E. 1910. The Anatomy of the Honey Bee. U.S. Government Printing Office. Washington, D.C., U.S.A. 166 pp.
 - *This is one of the original books on honey bee anatomy. In fact, I find many of the drawings in this book in other published works on honey bees.
- 6. Stell, M.I. 2012. Understanding Bee Anatomy: A Full Color Guide. The Catford Press, Middlesex, UK. 208 pp.
 *To my knowledge, this is the most recent major work published on honey bee anatomy. The photographs are stunning and the book is very affordable.





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