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etamorphosis is a word we use quite a lot in science. In the entomological sense, it is the process of transforming from an immature insect to an adult one. Insects undergo one of two types of metamorphosis. These are called incomplete (hemimetabolous) and complete (holometabolous) metamorphosis. Incomplete metamorphosis is where an insect passes through three life stages: the egg, the nymph and the adult. The nymphs look much like the adults; they simply lack wings (for those species that develop wings) and are smaller than the adults. Usually, the individual passes through multiple nymphal stages as it develops. They have to shed (molt) their exoskeleton (their outer shell or cuticle) to pass from a smaller sized nymph to a larger sized one, and from the last nymphal stage to the adult one. Crickets, grasshoppers, roaches and the true bugs (stink bugs, water bugs, etc.) develop this way. The principle drawback of this type of metamorphosis is that the immature individuals feed on the same foodstuffs as those on which the adults feed. Consequently, food competition between the adults and the immatures can be high when food availability is low.

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Complete metamorphosis is when the insect passes through four life stages: the egg, larva, pupa and adult. Generally speaking, the larva and the adult individuals are very different from one another in appearance, feeding habits, behavior, etc. Consequently, the adults and immatures usually do not compete for the same foodstuffs. The immature larvae feed and molt several times as they grow. The final larval molt ushers in the pupal stage. This stage is hallmarked by a period of fasting and often reduced mobility, but otherwise significant physiological activity in the individual. This is the point that the immature is progressing from a wormlike creature to that of an adult. The mature pupa molts a final time, yielding the adult form of the insect. Honey bees develop this way.

Honey Bee Development

What follows is a description of the development of a honey bee from egg to adult. Much of what I share I owe to the fantastic descriptions in Mark Winston's book *The Biology of the Honey Bee* and to the 2015 edition of *The Hive and the Honey Bee*. Please see the references section for more information on this topic.

The egg

A queen honey bee is capable of laying two types of eggs - fertilized ones and unfertilized ones. She is able to do this because she has a series of muscles she can use to control the release of sperm from her spermatheca (organ in her body in which she stores the sperm she collected from drones on her mating flight) while the eggs passes the spermathecal duct (duct leading from the spermatheca to the egg canal). An unfertilized egg results from the queen's decision to withhold sperm from the egg while the egg passes by the spermathecal duct. A fertilized egg results from her decision to release sperm while the egg passes the same. The egg is covered in a shell called the chorion. The anterior (top) end of the egg is permeable to sperm through a small area called the micropyle (a porous area on one end of the egg). The sperm enters the egg through the micropyle, thus resulting in a fertilized egg. Unfertilized eggs result in male (drone) honey bees while fertilized eggs result in female (queen or worker) ones. Interestingly, the queen has no ability to determine if the fertilized egg she lays will become a queen or a worker. That decision is left to the workers. She can skew the odds in her favor by laying fertilized eggs either in worker-sized cells or queen-sized ones. However, the adult workers elect to carry the immature to adulthood or abort the developing bee.

Egg deposition in a wax cell is a simple process. The queen honey bee pushes her abdomen into an empty cell and deposits the egg on the back of the cell. There, she affixes the egg to this location with a gluelike secretion. When freshly laid, the egg points from the back to the opening of the cell. Eggs begin to recline as they mature over the course of about three days (Tables 1, 2, and Figure 1). Thus, eggs from which larvae are ready to emerge lay on their sides, or nearly so, in the back of the cell.

There is nothing exciting about the physical appearance of a honey bee egg. They are pearly white and about 1.2 - 1.8 mm in length and 0.12 - 0.22 mg in weight. This length and weight can vary across the subspecies of honey bees, but also even among a queen's own progeny. They look similar to a small grain of white rice, being cylindrical, slightly curved and rounded on the ends. Eggs contain the egg cell (what will become the bee) and a large quantity of volk from which the immature draws its nourishment. You can see the body segments, including the head, of the developing embryo contained within if you view a late stage egg with a microscope.

The larva

Queen, worker, and drone larvae hatch from eggs that are about three days old,

Table 1. The development of honey bee instars. How to understand this table: the life stage in (A) undergoes the development activity in (B) to become the life stage in (C)							
(A) Life Stage	(B) Developmental Activity	(C) Life Stage 1st instar larva					
egg	larval emergence from egg						
1st instar larva	1st molt	2nd instar larva					
2nd instar larva	2nd molt	3rd instar larva					
3rd instar larva	3rd molt	4th instar larva					
4th instar larva	4th molt	5th instar larva (prepupa)					
5th instar larva (prepupa)	5th molt	6th instar pupa					
6th instar pupa	6th molt (eclosion)	teneral adult bee					
teneral adult bee	emergence from cell						

though this range can vary significantly (Table 2, Figure 1), especially across the different races of honey bees. For example, the eggs of African-derived bees tend to hatch hours earlier than those of Europeanderived ones. Larvae do not hatch in the sense that they break out of the egg chorion like birds do their egg shells. Instead, the chorion dissolves gradually as the larva inside becomes active.

Honey bee larvae, much like the eggs from which they emerged, are somewhat non-descript. They are plump, worm-like creatures, pointed at the head end and rounded at the tip of what will become their abdomen. They are white, pliable, and somewhat mobile, despite their lack of appendages. They also lack significant external features (i.e. no eyes, wings, legs, antennae, etc.). Larvae lie on one side of their bodies, in the back of a cell, with one side facing the back wall and the other facing the cell opening. The position in which they lie aligns the tip of their head close to the tip of what will become their abdomen. Thus, they effectively lie in the shape of a letter "C", hence the common beekeeper reference to them as "C-shaped larvae".

The non-descript larvae have some important morphological characteristics. First, they possess basic mouthparts on the head. These they use to **imbibe** (eat) the food placed before them by their adult sisters. Second, larvae are segmented, having a head and 13 additional segments (three will become the thorax and the remaining ten the abdomen), with each section delineated by a ringed restriction of the body. The best way to visualize this is to imagine stacking a few marshmallows end upon end. After a placing a few large marshmallows, you start to use progressively smaller ones until you get to a small end, 14 marshmallows in total (one for the head and the remaining 13 for the rest of the body). The larval body looks sectioned in this way when viewing it closely. Each of these separate sections (what would be a single marshmallow in my analogy) becomes something different on the adult bee. Third, both sides of a larva's body are lined with small holes called spiracles (ten pairs, two pairs on two of three thoracic segments and eight pairs on eight of ten abdominal segments). These spiracles are the openings through which air passes into/out of the larva. You can actually see these move when looking at a larva under a dissecting microscope. Fourth, their bodies are filled with a massive digestive system, including a large midgut (where nutrient adsorption happens) and hindgut (where wastes are processed and expelled from the body). They possess accessory features such as salivary glands and excretory tubules, the latter facilitating waste handling. This internal anatomy says a lot about what larvae are built to do - and that is eat. Nearly everything inside a larva is primed to receive and digest food. Consequently, they gain massive amounts of weight during this life stage. Finally, the larvae possess silk glands internally, on the ventral (belly) side of its body. It uses these glands to produce silk with which they spin silken cocoons when they are ready to pupate. The silk is secreted and manipulated from the mouth of the larvae. The silk glands become the thoracic salivary glands in the adult bee.

The larva that emerges from the egg is referred to as the 1st instar larva. An **instar** is a period of insect development between molts. Insects cannot grow the same way mammals grow. They are covered in a

Table 2. The length of time the honey bee castes spend in the various developmental stages. All numbers are reported as days. Due to the nature of ranges and averages, the adult emergence ranges and averages for the three castes (bottom row) are not a sum of the ranges and averages for each developmental stage.

	Queen			Worker			Drone		
	Stage	Range	Average	Stage	Range	Average	Stage	Range	Average
Egg	Egg	2-6	3	Egg	2-6	3	Egg	2-6	3
Larva	Uncapped Larva	3-5	4.6	Uncapped Larva	4 - 11	5.5	Uncapped Larva	4 - 7	6.3
	Capped Larva	*	0.5	Capped Larva	*	0.5	Capped Larva	*	2
	Prepupa	2.5 – 3.5	2	Prepupa	2.5 – 4.5	2.5	Prepupa	2-4	3
Pupa	Pupa	4 - 5	4.5	Pupa	8 - 9	8	Pupa	8-9	9
Adult	Teneral Adult	0.5 – 1	0.5	Teneral Adult	0.5 - 1	0.5	Teneral Adult	0.5 - 1	0.5
	Emergence	14 - 17	16	Emergence	16 - 24	21	Emergence	20 - 28	24



cuticle that only permits minor expansion before it has to be shed and replaced. Thus, the 1st instar feeds, grows, and molts to become a 2nd instar larva. A larva molts five times, meaning that there are 5 instar stages in a larva (Table 1). The first four instars last about one day each. The 5th instar larva often is called the prepupae, as it is the stage that occurs immediately before the pupal stage (Table 1 and Figure 1). This stage takes place in a capped cell and is when the larva elongates in the cell (i.e. its body is oriented with the cell) to a new position where its head is located just beneath the cell capping rather than lying in a shape of a "C" in the back of the cell.

Insect molting is governed, in part, by two hormones: ecdysone and juvenile hormone (JH). Ecdysone is secreted by the prothoracic gland (a gland located in the thorax, on the side where the head connects). JH is secreted by a paired set of glands, the corpora allata glands, located at the base of the head. When JH levels are high, ecdysone stimulates larva-to-larva molts. When JH levels decrease, ecdysone stimulates the larva-to-pupa molt. Ecdysone stimulates the pupa-to-adult molt when JH levels are low or nearly absent.

All larval development, growth, molting, etc. is made possible by the food that they consume while they are young. The drone and worker larvae are fed **brood food** while the developing queens are fed **royal jelly**. The adult nurse worker bees secrete these foodstuffs from glands in their heads. Generally speaking, brood food (the worker and drone diet) is produced by combining the secretions from **hypopharyngeal glands** (clear liquid with high protein content) and **mandibular glands** (white liquid containing mostly lipids). The diet of worker larvae contains 20 - 40% white and 60 - 80% clear component the first two days. Following this (day 3 onward), the white component is no longer added to the diet. Drones are fed similarly to workers, but their diet tends to have higher protein and carbohydrate levels than that of workers and they consume significantly more food than do workers. Honey and pollen likely are added to the mixture the final two days of larval worker development in the open cells (days 4 and 5). Brood food fed to drones has increased quantities of honey and pollen in the diet as the drone larvae age. Interestingly, pollen appears to supply little of the nitrogen required by the developing larvae. Brood food contains only about 12% sugar for first 3 days of larval development and around 47% sugar on the 4th and 5th days. Glucose is the dominant sugar in the food of young worker/drone larvae while fructose is the dominant sugar in the food of the older ones.

Worker and drone bees are fed provisionally, meaning that the adult nurse worker bees will put their head into the cell and place a small amount of food in front of or on the developing larva. In fact, a cell can be visited 5,000+ times by nurse bees while it is open, with the larva contained within being fed by the nurses 1,000 - 2,000 of those visits. The larvae spin in a circle, constantly consuming the food that is placed in front of them by their adult sisters.

The youngest drone and worker larvae are provided more food than they can eat initially. They, then, can be seen in the back of their cells floating in a small pool of the milky-looking brood food. Beekeepers often call this the **milk brood** stage. Older larvae tend to eat their food nearly as quickly as it is placed in their cells by their adult nurse sisters. The developing worker and drone larvae grow to fill their cells completely. Though they are fed up to a few thousand times, they still are not provided all of the food they could consume. This is evidenced by the fact that female larvae fed even more food become queens. Thus, workers and drones are put on a carefully controlled, restricted diet to get them to their ultimate adult bee destiny. It is not known fully how adult nurse workers know that a larva wishes to be fed. It is possible that there is a hunger signal that hungry larvae use to convince their adult nurse sisters to feed them.

The brood food fed to developing queens is called royal jelly. Royal jelly contains mostly the white component (mandibular gland secretion) the first three days of the larva's development and then equal parts white and clear secretions (the latter, from the hypopharangeal glands) throughout the rest of the queen's development. Royal jelly contains more sugar than does brood food. In fact, it is about 34% sugar or more, mainly in the form of glucose. Glucose is the dominant sugar in royal jelly throughout the developing queen's life. Sugar is a feeding stimulate, thus causing developing queens to eat more food, further encouraging their growth as queens. The female larvae remain totipotent during the first three days of their lives, meaning that they can become queens or workers up to three days after hatching, despite the differences in diet quality fed to developing queens and workers. The caste (queen or worker) is determined by the time the 3rd instar is reached.

In contrast to how worker and drone larvae are fed, queen honey bee larvae are mass provisioned. They are fed so much, in fact, that they are not able to eat all of the food their sisters provide to them. There is leftover food in the queen's cell when she emerges as an adult. The queen's diet is about 11.9% protein, 67.1% moisture and 4.3% lipids. The diet also contains royalactin, a protein once believed to be the

main factor leading to the development of queens rather than workers, though this was shown recently not to be the case. Instead, the high sugar content of royal jelly causes the developing queen to eat more food. This, in turn, triggers the larva's production of JH. Worker larvae also produce JH, but in much lower quantities than that produced by queens. In general, queen larvae have high JH titers (levels) on day 3 of larval develop, right at the time they become destined for royalty. In contrast, the worker larvae have lower titers of JH at day three. In fact, the JH levels in queen larvae at 72 hours after emerging from their eggs is 10× more than that in workers of the same age. During the first three days of development, when the larvae can be either a queen or a worker, a wide array of genes become active. These genes remain active in the developing worker. However, royal jelly down-regulates (lowers the expression of) some of these genes and a distinct set of caste-related genes are upregulated (increased expression).

I want to make a final note about caste determination in the female larva. Oueens could have become workers and workers become queens. They both possess the same genes the other possesses. Thus, the differences in queens and workers are not a function of unique or differing genomes. Instead, it is the turning on/off of certain genes that ultimately produces queens or workers. Imagine two long walls, facing one another, with hundreds of light switches arranged side-by-side down both walls (one wall the mirror image of the other). Imagine again that the first light switch on the first wall is 1A (wall 1, light switch A) and its counterpart on the second wall is 2A. 1A and 2A turn on their respective lights that otherwise produce the same brightness and intensity of light (i.e. they are genes that code for the same thing). The difference between queens and workers is not that one has a certain set of light switches while the other has a completely different assortment of switches. Rather, it is that one may have light switch A on while the other has light switch A off. Sometimes, it is not that one switch on one wall (let us say 1T) is always on while its corresponding switch on the other wall (2T) is always off. It could be that 1T is on half of the day while 2T is on only a quarter of the day. In this case, 1T would be upregulated (on or expressed more) than 2T, which is downregulated (on or expressed less). Similarly, the on/ off nature of corresponding genes (like the light switches in my analogy), and how long they are on/off make the difference between queens and workers. Something, then, controls whether a switch is on or off and how long it remains in that position. This is the science of epigenetics (epimeaning above the gene). In this instance, something higher than the gene controls the "on/off" nature and "duration of expression" of the gene.

In the case of queens and workers, DNA methylation helps control the caste fate

of the female larvae. **DNA methylation** is when a **methyl group** is added to the DNA base pairs **cytosine or adenine**. This renders the gene unable to be expressed (the light switch is always off). The methylation pattern is different in queens and workers, meaning that the corresponding expression patterns of the genes of queens and workers is different. All of this starts with the varied diets that a single female receives. Fascinating, is it not?

The final stage of larval development, the 5th instar, is the prepupal stage. This is the life stage of the immature bee that spins the cocoon and defecates for the only time it will while young. The silk spinning organ (the spinneret) is between some of the immature bee's mouthparts. A duct leads from the silk glands to the spinneret, opening in the mouthparts. The prepupa uses its spinneret to manipulate the silk while spinning a cocoon for itself, which is what the prepupa spends the last amount of time as a larva doing. The prepupa defecates early in cocoon construction. Until this time, the excretory tubules and midgut were closed off from the proctodeum (larval hindgut) until the larva finished feeding. Thus, the larva was unable to defecate. After this, the tubules and midgut open into the hindgut, thus allowing their contents to be discharged from the anus into the back of the cell.

The larval stage of bee development varies somewhat between the various races of honey bees. African-derived bees, for example, generally have shorter development periods than do European-derived bees. By the time the larvae are ready to pupate, they have gained 900 (worker), 1700 (queen), and 2300 (drone) times their weight as an egg, weighing 140, 250, and 346 mg, respectively. Their length changes significantly as well, with workers growing from 2.7 mm to 17 mm and queens from 4.2 mm to 26.5 mm.

The pupae

The developing prepupae molts (5th molt) into a pupae (6th instar), though it does not shed its prepupal cuticle initially. Therefore, the external body wall of the pupa is developing within the final larval cuticle. Following this, the pupa pushes through the prepupal cuticle head and thorax first. Once it sheds its cuticle, it looks like a white adult bee with wings that appear as small pads attached to thorax. The antennae, legs, and wings of the pupa are everted, i.e. now visible outside the body. The compound eves and adult mouthparts are also present. Otherwise, the young pupa looks much like a slightly more-developed larva. The three segments that compose the thorax are of equal size in the young pupa. There is no wasp waist (no restriction between the thorax and abdomen) present in the young pupal bee. The early precursors to the sting are developing and visible on the underside (ventral surface) of the posterior (end or tip) of the abdomen.

As the pupa ages, its head, thorax, abdomen, eyes, antennae, mouthparts, and

legs become discernable. Only the wings remain undeveloped at this stage. The middle segment of the thorax expands significantly, much-more-so than the first and third segments. The wasp waist remains absent. The cuticle darkens as the pupae ages. This darkening (scleritization) occurs in such a predictable fashion that it can be used to age the pupae. At this stage, the pupae do not grow in size or change much externally. Instead, the pupal stage is when the tissues in the body begin to reorganize and develop into the organs recognized in the adult bee. The muscles and various organ systems undergo massive changes. The larval tissues break down through a process of programmed cell death while adult structures form through the birth of new cells.

The pupae resembles an adult bee when it is developed fully. Its thorax is separated from the abdomen by a restriction between the first and second abdominal segments, the wasp waist. The first abdominal segment is fused to the thorax and, functionally, becomes part of it. This small part of the abdomen is called the **propodeum** (the part of the abdomen fused to the thorax). The rest of the abdomen, segments two through ten (all after the restricted waist), are collectively called the **gaster**.

Adult

Once the adult inside the pupal cuticle finishes developing, it will split the pupal cuticle headfirst, emerge from the cuticle (eclose, or the shedding of the pupal cuticle), spend some time in its cell maturing as a teneral (soft-bodied) adult (also called the imago), and emerge from the cell at a fairly predictable time (Table 2, Figure 1). The teneral adult remains inside the cell for several hours as its new cuticle hardens. This newly eclosed adult uses its mandibles to perforate its cell's capping and rotates within cell to open the cell from the inside. Once emerged and on the comb, the teneral adult unfolds its wings and antennae and allows body hairs to dry. It can take eightto-ten days for the teneral adult to complete maturation after emerging from the cell. Its cuticle hardens for the first 12 - 24 hours. It usually looks "soft and fuzzy" during this period. The teneral adult cannot sting as the sting is too soft to penetrate the skin of an antagonist.

The teneral adult also undergoes additional internal maturation. The glands and fat bodies develop further, this aided by the consumption of pollen. Young adult workers start eating pollen the first few hours after emerging from their cells. Their pollen consumption peaks about 5 days post emerging. Young adult workers that fail to consume enough pollen experience poor glandular development and have shorter lifespans. Interestingly, the young adult queens and drones get most of their protein from brood food fed to them by workers. A lot of their early pollen and nectar consumption contribute to their reproductive development.

Workers have a wide-ranging longevity from a few days to almost a year. Seasonal factors, food availability, nutrition, work life, race, etc. all influence worker longevity. Workers can live 15 - 38 days in summer (short lives because they work themselves to death), 30-60 days in spring and fall, and 140 - 320 days in winter. Drones can live 14 – 43 days in spring, but up to 90 days in autumn. That said, they usually do not survive that long in autumn given that their sister workers eject them from the nest in an effort to conserve honey stores heading into winter. Queens are the longest-lived honey bees, surviving one-tothree years. Remarkably, a queen living up to eight years has been documented.

The developmental timeline of queens, workers, and drones has built in variation, mainly owing to temperature and nutrition. When nest temperatures fall below 35°C, individual bee development can be delayed up to 5 days. Brood located on the periphery of the comb, for example, takes longer to develop, likely because their temperature is not regulated as tightly as that for the brood developing in the center of the nest.

It appears that brood mortality is somewhat low, but extremely variable, under normal conditions, with about 94% of eggs surviving to larvae, 86% to sealed brood, and 85% to adult bees. Drones and queens seem to have a lower survival rate of around 56% and 53%, respectively, from egg to adult. Lots of factors contribute to varying brood survival rates. This includes, but is not limited to, a colony's queen status, nutrition, where on the comb the brood is, time of year, disease, pesticides, inbreeding, etc. Most brood failing to develop is eaten by workers.

Conclusion

I want to conclude by noting that there is a really good video available online in which you can see bees develop. You can find the video here: https://www.youtube. com/watch?v=f6mJ7e5YmnE. I think the video is a great supplement to what I discussed herein. As a result, I would like to point out a few things that you should look for throughout the video. I apologize to those of you without internet access. If this describes you, you likely can go to your local library and view it on a public computer there.

What to notice:

- The video opens with an egg standing in the back of a cell. The egg has started to lean somewhat as the developing embryo contained within prepares to emerge from the egg. A close inspection will reveal that the developing embryo inside begins to look like a larva immediately before it hatches from the egg chorion. You can see the body become segmented as the embryo develops. The chorion is lost altogether during hatching.
- In the next scene (around second 6), small worker larvae are seen floating in

a pool of brood food. The video moves quickly. This allows you to notice how mobile the larvae actually are. They spin in their cells as they eat the food in which they are sitting. Pay close attention to the head of any larva. You can see the larvae moving their heads as they eat the brood food.

- Around second 16, you will see a pupa inside its molted prepupal cuticle. The astute bee biologist will notice that this image is not oriented correctly. Honey bees develop on their backs in their cells, not their bellies. Essentially, the video is upside-down at this point. Nevertheless, it remains an amazing video.
- The individual in this scene has molted (thus, is a pupa) but has not shed its cuticle. I want you to notice a couple of things in this scene. First, you can clearly see the pupa developing underneath the cuticle. Second, you can see the prepupal skin stretch, especially around the head/thorax and abdomen/ thorax junctions. This skin stretches as the pupa within begins the process of shedding this prepupal skin. By the end of this scene, the pupa is emerging from its prepupal skin much like a cicada does during summertime, head and thorax first.
- The following scene (second 25) shows some prepupae (which look like larvae standing in their cells, pointy head facing the cell opening; upper left and second cell from the bottom right), some new, young pupae (just shed their prepupal cuticle so they look like a cross between a prepupa and a pupa; upper center), and some older pupae (look like white adult bees; upper right and lower left). The cell cappings have been removed to facilitate viewing. This scene also shows a Varroa moving between the open cells. One of the most interesting things about this image is that the young pupae quickly grow up before your eyes and look like more established pupae (like white adult bees) late in the scene.
- The next scene (second 31) shows the face of a developing pupa (cell capping removed). It is oriented incorrectly, upside-down again. Despite this, it probably is my favorite scene in the entire video. If you look closely, you will see the head tissues between the eyes reorganize to form parts of the bee's brain, optic lobes, etc. It is simply fascinating. The pupa's body begins to darken (sclerotize) as well. The eyes gain their pigmentation.
- The final scene (second 44) shows, again, the bees developing upside-down. You see a number of late stage pupae (6th instar cell cappings removed) getting ready to shed their pupal cuticle and become teneral adults. Notice the two darker bees on the bottom row (the two rightmost bees). Their pupal cuticles begin to shrivel on their heads right before they eclose. They,

then, shed that cuticle and become teneral adults that will remain in the cell a few hours before chewing their way out of the cell as emerged adults.

The honey bee is a marvelous creature. I hope that you agree.

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