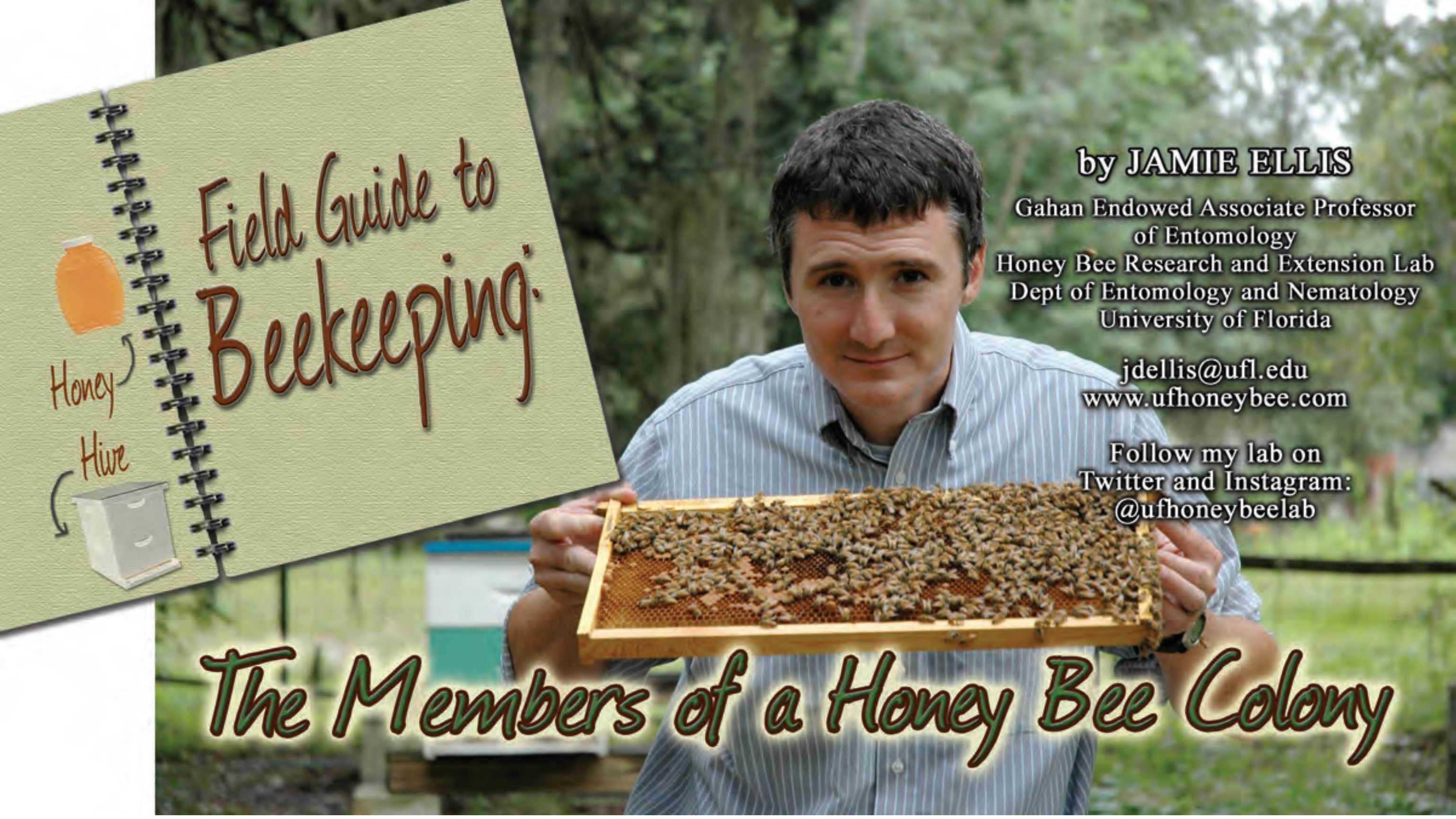

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The Members of a Honey Bee Colony

There is a lot of information one needs to know before keeping bees. Perhaps the most difficult part of getting started is learning all of the terminology associated with beekeeping. Beekeeping is, in fact, full of jargon. We put frames in supers. Bees pull comb and apply propolis to cracks and crevices around the hive. Worker bees like to waggle dance and drones leave the hive every day in search of a queen at drone congregation areas.

A non-beekeeper would have had a hard time understanding anything I stated in the preceding paragraph. This illustrates the importance of learning to speak the beekeeping language before ever opening your first hive. Therefore, I am going to devote the next few articles in my column discussing common terminology associated with our craft, beginning with the members of the colony.

There are only three types of bees in the colony so one would think that learning the terminology associated with a colony's members would be easy. However, I feel it is useful to meet a colony's members and know how to discuss them correctly, especially given that they are the ones that advance the colony and with which a beekeeper must interact, nay, appease regularly. My strategy for emphasizing the terminology I am defining is by bolding the words that should be known and understood.

Adult honey bees

There are three types of bees in the honey bee colony. Some people say that there are three castes, and they are correct, in one sense. However, it may be more appropriate to say that there are two sexes of adult bees in the hive and only one sex (the female sex) has two castes. Regardless of how you define caste, there certainly are three types of bees in the colony and they are the queen, worker, and drone honey bees.

Queen honey bees (Figure 1) are the single most important honey bees in any colony. The typical honey bee colony usually only has one queen. I say *usually* because colonies often (maybe 5-10% of the time) have more than one queen, though this probably is only a temporary occurrence. I make this claim because I have conducted a lot of research using observation hives and I often see colonies with two queens. I am convinced that the reason we beekeepers do not notice this much is because we stop looking when we see the first queen.

Queen honey bees are not "queens" in the sense that they rule the colony and direct its intentions and behaviors. They do not govern the workers or otherwise tell any other bees what to do. They only make a handful of decisions, most notably: "I want to lay an egg," "this cell is clean and can receive an egg," "I am hungry," etc.

I do not want to over simplify the role the queen plays in the colony. The queen is the mother of all of a colony's members. During peak season, she can lay 2,000+ eggs per day, over 500,000 in her lifetime! She usually is the sole reproductive female in the nest. The workers take care of her, feed her, spread her pheromones (chemical signals) around the hive, etc. In fact, a queen's pheromonal bouquet helps to stabilize the nest and to keep the workers from rearing additional queens. Arguably, ensuring colony homeostasis (nest stability and continuity) is one of the most important functions of a queen.

Queen honey bees have many interesting attributes and behaviors. They result from fertilized (female) eggs. They are fed a considerable volume of food as an immature bee. This food, called royal jelly, pushes the female larva in the direction of becoming a queen. Queens only take 16 days to develop from egg to adult. They take one, at most two, true mating flights about one week after they emerge from their cell. They will mate with a wide range (5 - 30+ with the average being 10-17) of drones (male bees) on this mating flight and store all the semen they collect from the drones in a special organ inside their body. This organ, the spermatheca, can nourish the sperm it houses, keeping it ready for use at the queen's disposal.

Queens return to the hive after their mating flight and live in the colony, laying eggs, and otherwise surviving at the mercy of the worker bees within the nest. Queens can live 2+ years, though I suspect the majority of queens die within 6 months – 1.5 years of emerging as adult bees. I believe this to

(l) Figure 1. A queen honey bee. This is a newly emerged, virgin queen of Italian bee descent. (r) Figure 2. A worker honey bee. (Photographs by Mike Bentley.)

be true based on data on queen longevity in managed hives that have been published recently.

Worker honey bees (Figure 2), as the name implies, do all of the main tasks in a colony. Like queens, worker bees come from fertilized eggs and are female. This is very important and scientifically significant. Queen bees can elect to lay fertilized or unfertilized eggs (more on that later). All fertilized eggs result in female bees. Notice I said *female* bees. Every fertilized egg contains the potential to be either a queen or a worker honey bee. The deciding factor that directs the path of the immature female is the amount and type of diet it is fed as it develops. All female larvae receive the same food for the first few days of their lives. After this, worker bees change the volume and composition of food they offer to female larvae that they want to become queens. Queens get more food while developing than do worker bees. Perhaps this is an oversimplification, but queens are overfed workers and workers are starved queens.

I hope you grasp the significance of this concept. A queen *could* have been a worker while a worker *could* have been a queen. Their environment (i.e. the amount and type of food they received) dictated their future. I would like to state this another way. Workers possess all the same genes that queens possess and *vice versa*. Thus, the real difference between queens and workers is the turning on and off of certain genes and gene combinations, or the level of expression (how long a gene is turned on) of a given gene in both types of bees. Queens and workers share *all* the same genes but are otherwise two different bees.

I recognize that my discussion of queen and worker genetics may appear to be a digression, but I believe it is of critical importance. Consider this practical example: queens can live 2+ years while workers live 6 weeks to 6 months. Two bees with the same DNA have two completely different lifespans. This has considerable implications for the biology of aging. Furthermore, workers and queens look nothing alike, share no tasks, and are behaviorally, morphologically, and physiologically different, yet the same blueprint was used to build both – fascinating.

Ok, so that tantrum highlighted the nerd in me. I will refocus my discussion on worker bees specifically. Worker honey bees take 21 days, more or less, to develop from egg to adult. They possess a few, key morphological adaptations that queen bees do not have. For example, worker bees have stingers that possess significantly sized barbs, making workers more apt to leave the stinger behind in their stung victim. The barbs on a queen's stinger are reduced, making it possible for a queen to sting her victim repeatedly. Furthermore, worker bees have a pollen basket which is a special feature on their hind leg that they use to transport pollen. Queens do not possess a pollen basket since they do not forage for pollen.

Unlike the worker caste of many other social insects, worker honey bees are not born into a task in which they remain their whole life. Instead, they progress through a fairly predictable series of tasks that ultimately end in the workers' employment as forager bees, a task that claims the lives of all of its practitioners. We call this task progression **temporal polyethism** (literally: time-related "many" behaviors) or **age related division of labor**, the latter being the term most used by beekeepers. Not all workers do all tasks, but all workers progress through many of the tasks in a predictable order. Worker bees are the nursery workers, the queen attendants, the colony's architects, the cleaning staff, the undertakers, the guards, and the food processors and gatherers. They do all of these tasks selflessly, even being willing to forfeit their life for the good of the colony.

Figure 3. A drone (male) honey bee. The large compound eyes are the most notable feature of a drone. (Photograph by Mike Bentley.)

Drone honey bees (Figure 3) result from the queen's conscious decision to lay an egg that she does not allow sperm to contact. Therefore, drone honey bees are produced from unfertilized eggs and are haploid; they contain half of a complete set of chromosomes (see my article in the *American Bee Journal* September 2014 issue for an explanation of this process). Drones are the male honey bees. Arguably, they have the easiest life of all bees in the colony.

Drones take about 24 days to develop from egg to adult. Being haploid, they receive all of their DNA from their mothers. They have no fathers, though they do have grandfathers, but only maternal ones.

Drones get a bad rap in colonies and they are plagued with unfavorable PR. This, largely, is because drones sit around the colony much of their lives, doing little-to-nothing to contribute to the colony's function, while consuming their fair share of the food resources. They are the largest, by volume, bees in the nest (Figure 4), so they can put a significant dent in the colony's resources, so-much-so that the worker bees will evict the drones from the hive during times of the year that drones are not needed. This occurs usually as colonies are preparing for the coming winter.

When are drones needed? They are needed during mating season, when colonies are making new queens and preparing to swarm. Drones spend the first few days/weeks of their lives lounging around the colony, maturing sexually, and learning the hive's location in the environment. When ready (i.e. when sexually mature), the drones will leave the nest and coalesce at drone congregation areas (DCAs), areas where drones from many of the area's colonies congregate. Here, the drones wait for virgin queens to buzz through the area on their mating flights. Drones race to any new queen present in the area and try to mount and mate the queen. Drones outnumber queens by the thousands. Thus, most drones never fulfill their lifelong dream of fertilizing a queen. So it goes.

Drones possess a few anatomical features that are unique to them, though the absence of one anatomical feature in particular, the sting, makes them defenseless when harassed. They do have large eyes which they likely use when searching for queens flying in DCAs. Drones otherwise are large, have rounded abdomens, and fuzzy.

Brood

Brood is the term used to describe, collectively, all of the immature stages of honey bees. Honey bees undergo complete metamorphosis. This simply means that they pass through egg, larval, pupal and adult stages while developing, similar to what butterflies do. The egg, larval, and pupal stages are considered the immature stages of the honey bee; thus, they also are considered the brood stage of honey bee development. There are two subgroups of brood: uncapped and capped brood. Any cell that contains brood is called a **brood cell**. Bees build the cells out of wax, with new wax cells starting off a creamy white color and darkening progressively to almost black the more often they are used to house developing brood.

Uncapped brood

Eggs and larvae develop in open, or uncapped, cells. **Uncapped brood** refers to egg and larval honey bees. Both egg and larval stages are visible in brood cells since they are not hidden behind a wax capping.

Honey bee **eggs** (Figure 5) are cylindrical with rounded tips, white, and about 1.5 mm in length. They are curved slightly. Queen honey bees lay (or **oviposit**, meaning "to lay an egg") a single egg at the base of a brood cell. Queens control the sex of the egg by releasing or withholding sperm from the spermatheca while the egg is being oviposited into the cell. Eggs receiving sperm become females while eggs from which sperm are withheld become males. New queens may deposit multiple eggs per cell, but this quickly corrects itself, usually within 7-14 days. Worker bees may start to lay in the absence of a queen and given the colony failed to rear a new queen. **Laying workers** (workers who begin to lay eggs in the absence of a queen) usually oviposit multiple eggs per cell. Workers cannot mate and only produce unfertilized eggs. A colony headed by laying workers is doomed given its ability to produce only drones.

All eggs, fertilized and unfertilized alike, take about three days to hatch. **Larvae** are

Figure 4. A worker and drone honey bee. This photograph shows the size relationship between the two bees, with the worker in the upper center of the photograph and the drone in the lower center of the photograph. (Photograph by Mike Bentley.)

the bee life stage that emerges from eggs. Larvae are grub-like in appearance and creamy in color, the latter because they are full of fat bodies that occupy much of the space in a larva's body. Honey bee larvae are veracious feeders, this being what they spend most of their time doing.

Shortly after emerging from an egg, a young larva lies on one of its sides on the bottom of the cell in which it is developing. At this stage, it curls into a position resembling the letter "C" (hence sometimes being called **C-shaped larva** – Figure 6) and is flooded with food provided to it by its older sister workers who are acting as nurse bees. Very young larvae, in fact, float in a pool of the milky-white brood food secreted for them from glands in the nurse bees' heads. Beekeepers call this stage of larval development **milk brood** (Figure 6) since it looks as if the young larvae are floating in a pool of milk.

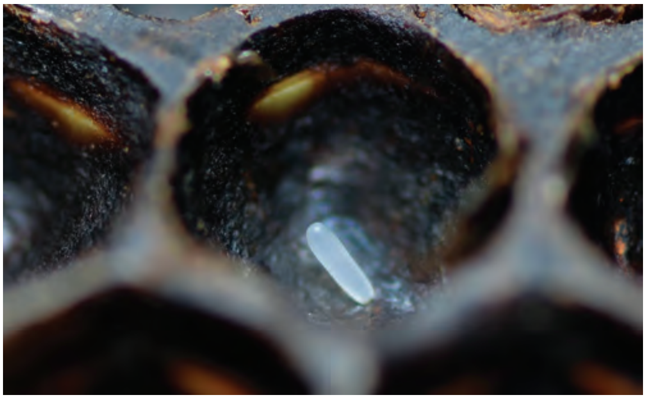
Nurse bees provisionally feed young larvae and continue to feed worker and drone larvae this way. They may visit cells of developing worker and drone larvae in excess of 2,500 times during the larva's development. On the other hand, they begin to mass provision queen larvae about three-to-four days after they emerge from eggs and continue to do so throughout the young queens' development. Female larvae directed toward queens by their older worker sisters are given so much food that they do not consume all of it before progressing into the pupal life stage.

Older drone and worker larvae begin to grow, swelling to a size that allows them to occupy their cells fully (Figure 7). At this point, the food given to these larvae is not visible as it is consumed rapidly by the developing larvae. Larvae that finish eating (and, therefore, growing), defecate and begin the transition to pupae. Adult worker bees recognize that the larvae have reached this level of readiness and they cap the cell in which the larvae are developing. This ends the uncapped stage of brood development.

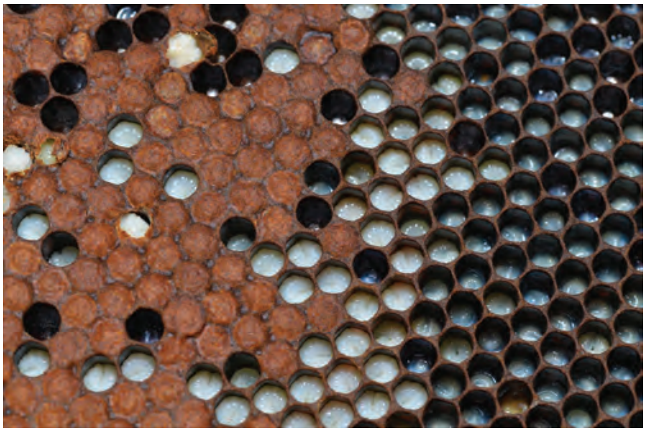
Capped brood

The term **capped brood** refers to the honey bee developmental stages that occur in a capped brood cell. They have completed the egg and larval stages by the time they are capped so they only have the prepupal and pupal stages left. The **prepupal** stage is not really a formal stage like that of an egg or larva, but rather the period of transition from the larval to the pupal stages. In essence, a larva repositions itself in the cell immediately after the cell is capped. It moves from the c-shaped position in which it was laying on its side to an elongated position where its head it just under the cell capping and it is laying on its back.

The prepupal stage is brief as the developing immature quickly transitions into the **pupal** stage (Figure 8). Pupal honey bees do not eat, defecate, or move. This is less a growth stage (the bee is not getting larger)



(l) Figure 5. A honey bee egg. Much of the cell's walls were removed so that the photographer could capture the image. The queen glues the egg in an upright position to the back of the cell. (r) Figure 6. Milk brood and c-shaped larvae. Larvae lie in the back of a cell in the shape of a letter "C," thus earning the name C-shaped larvae. Young larvae float in a pool of milky white brood food. Beekeepers refer to this stage of brood development as milk brood. There are four cells containing eggs in the photograph. Can you find them? (Photographs by Mike Bentley.)




(l) Figure 7. Brood cells containing larvae and pupae. In general, the immatures in this image progress in age from right to left. Milk brood is present in the open cells on the right and older larvae in open cells in the middle. The prepupae and pupae are developing in capped cells on the left. (r) Figure 8. Purple-eyed pupae. The cappings of these pupal cells have been removed to expose the developing worker pupae underneath. Pupae begin development fully white (pupa furthest to the left in the center row). The eyes (both compound eyes and the three ocelli arranged in a triangular pattern between the compound eyes) darken first. Pupae with dark eyes are called purple-eyed pupae. Worker and drone bee pupae develop on their backs, with their bellies facing up (as seen in this photograph). (Photographs by Mike Bentley.)

but rather a developmental stage where the body and its contents are redesigned/repackaged from that of a grub to that of a functioning adult.

The body of the grub-like prepupae begins to differentiate, with the head, wing and leg buds, and abdomen beginning to form. Young pupae are fully white but resemble the adult bee they are striving to become. At this point, the pupa's body must harden, or sclerotize, and gain color. The first part of a pupa to do this is its eyes. Bees have five eyes, two large compound eyes and three small ocelli located between the compound eyes. The eyes darken to black quickly, but appear purple during a pupa's early development. Many beekeepers call these individuals **purple-eyed pupae**. This term simply refers to young pupae because only young pupae have purple eyes.

Prepupae and pupae develop exclusively in capped brood cells, under wax cappings. This is significant because some of the pests and/or pathogens that impact honey bees can cause the brood cell capping to become sunken, perforated, or removed altogether. In the latter case, you can see the developing prepupae or pupae. You should never be able to see these life stages since they should be developing under wax cappings. Furthermore, and generally speaking, brood cappings are domed, with the dome extending away from the developing bee within the cell. Sunken, perforated cappings can be a sign of brood stress or disease.

Another point worth considering with brood concerns a queen's **brood pattern**, as determined by presence, shape and density of capped brood on a given comb. Loosely speaking, a brood pattern is the shape of the area on a comb containing brood. Queen honey bees typically begin laying eggs in the center of an empty frame and in a spiral pattern radiating from the center of the frame. A busy queen in peak season can fill one side of a single frame in one day, but it may take a little longer depending on her propensity to move to other frames before finishing the one she started. If you could remove all parts of a hive except the developing brood, you would have something roughly the shape of a squashed basketball. Generally speaking, the combs located in the middle of the nest have more brood while the combs on the outer part of the nest contain less, with a decrease in the amount of brood per comb from the inner to the outer combs. Any given frame has an oval-shaped brood pattern, as seen in Figure 9. This produces a total brood nest that is rugby ball-shaped on any one comb, but squashed basketball-shaped when considered as a whole.

In an ideal situation, most of the brood present on one side of one frame should be about the same age, give or take a few days. Given that brood develop under cappings for 10 or more days, most of the brood on one side of one frame should be capped roughly about the same time, again, within a few days of one another. This ultimately tends to produce frames that contain exclu-


(l) Figure 9. Solid brood pattern. Only a few cells in this comb do not contain brood (<5%). (r) Figure 10. Moderately spotty brood pattern. About 10% of the cells are empty while the rest contain capped brood. (Photographs by Jamie Ellis.)

sively capped brood and these frames can be used to judge a queen's brood pattern.

Among other reasons, queens are considered good if they have a **solid brood pattern** (Figure 9). This simply means that there are very few cells containing no brood scattered among a majority of cells containing brood. For example, look at Figure 9 and notice how the vast majority of this frame contains capped brood. There are only a few cells in which no immature bees are developing, perhaps <5% in fact. In this case, the queen laid eggs in most of the cells, missing only a few cells as she marched across the frame producing offspring.

In Figure 10, the brood pattern becomes less solid and spottier, hence beekeepers calling this a **spotty brood pattern**. Interestingly, the brood pattern seen in Figure 10 retains the same overall shape as that seen in Figure 9; it simply has more cells that contain no developing brood than does the frame in Figure 9. The brood pattern seen on the frame in Figure 11 is considerably spottier, and significantly less desirable. First, the brood pattern has irregular edges (i.e. it no longer is shaped like a rugby ball). Furthermore, there are a number of empty cells scattered among cells containing brood. In fact, as many as 50% of the cells within the pattern are empty. Beekeepers find this very undesirable.

What causes a spotty brood pattern? I have heard many answers to this question. First, a queen can be a poor queen meaning that she may not have mated well, may not produce a lot of eggs, or otherwise may be compromised in another way. The combs may contain pesticide residues. The immature bees may be affected by pests/parasites and be removed from the combs by bees responsible for aborting sick brood. Another leading cause of spotty brood patterns lies with inbred queens. There are times when queen honey bees are forced to mate with their brothers if the density of colonies is low in the wild. For example, imagine having one honey bee colony and with no feral colonies anywhere nearby. Any new virgin queen produced by the colony will have access only to drones from her hive when visiting the drone congregation areas. Thus, she is doomed to mate exclusively with her brothers, resulting in inbred progeny. Worker bees can detect inbred eggs and abort them after the queen oviposits them. The result is a spotty brood pattern. You can have the best laying queen on the planet, but suffer from a spotty brood pattern if the queen is unfortunate enough to have mated with her brothers. Beekeepers usually replace queens producing a spotty pattern quickly.

Figure 11. Spotty brood pattern. Looking only at the area containing capped brood, >30% of the available cells do not contain capped brood. (Photograph by Jamie Ellis.)

As noted, queen, worker, and drone honey bees take 16, 21, and 24 days to develop from egg to adult, respectively. Once the pupa has developed into an adult, he/she chews through the capping of his/her cell, emerges from the cell, and proceeds to become a significant contributor to the life of the colony. These **newly emerged bees** (Figure 12) have a wet, hairy appearance. Their bodies are soft, they are somewhat clumsy, and they cannot sting. Now their bodies finish hardening as they feed and begin contributing to a colony's workforce. Most bees go on to be productive members of the insect societies in which they live.

Figure 12. An adult worker bee beginning to emerge (A) and immediately after successful emergence (B). Note in photograph A how the worker is using her two front legs to try to pull herself out of the cell. The newly emerged worker bee has a "wet" appearance and cannot sting. (Photographs by Mike Bentley.)