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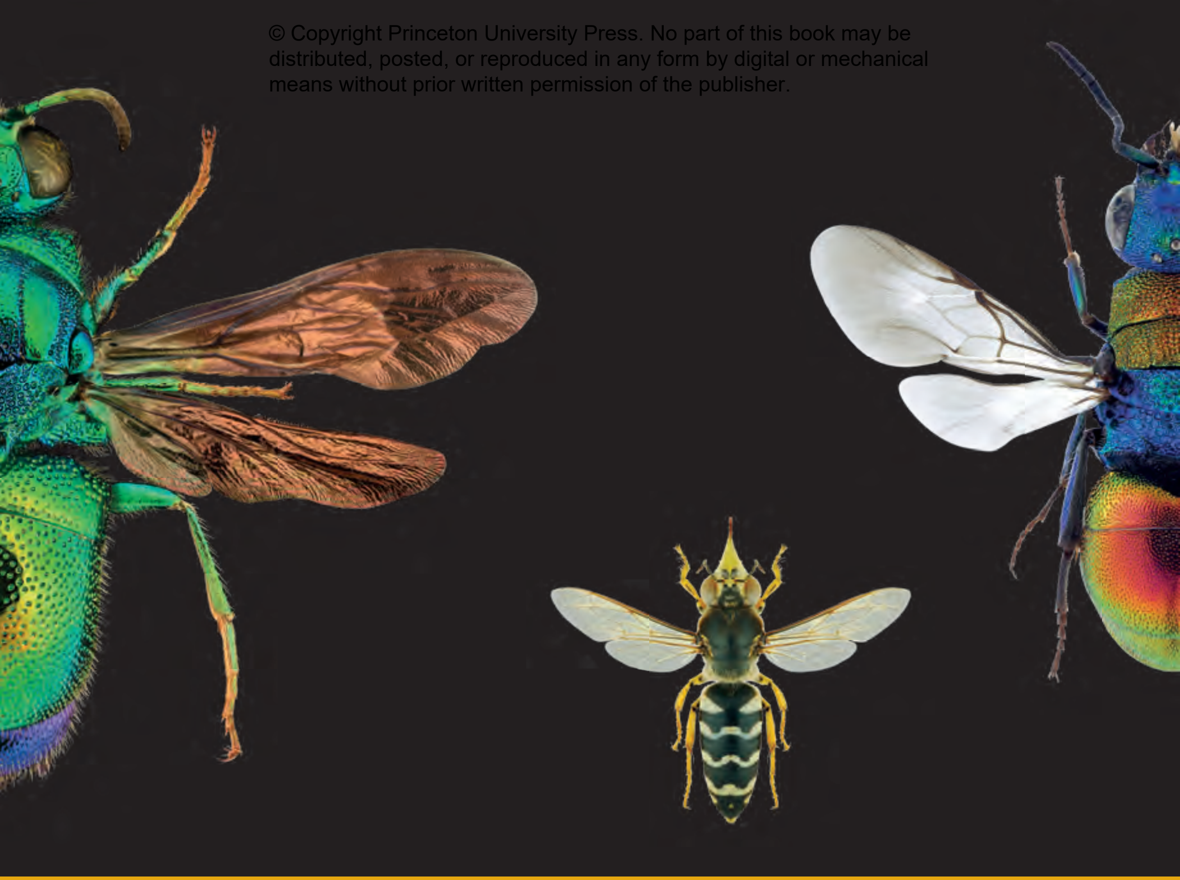
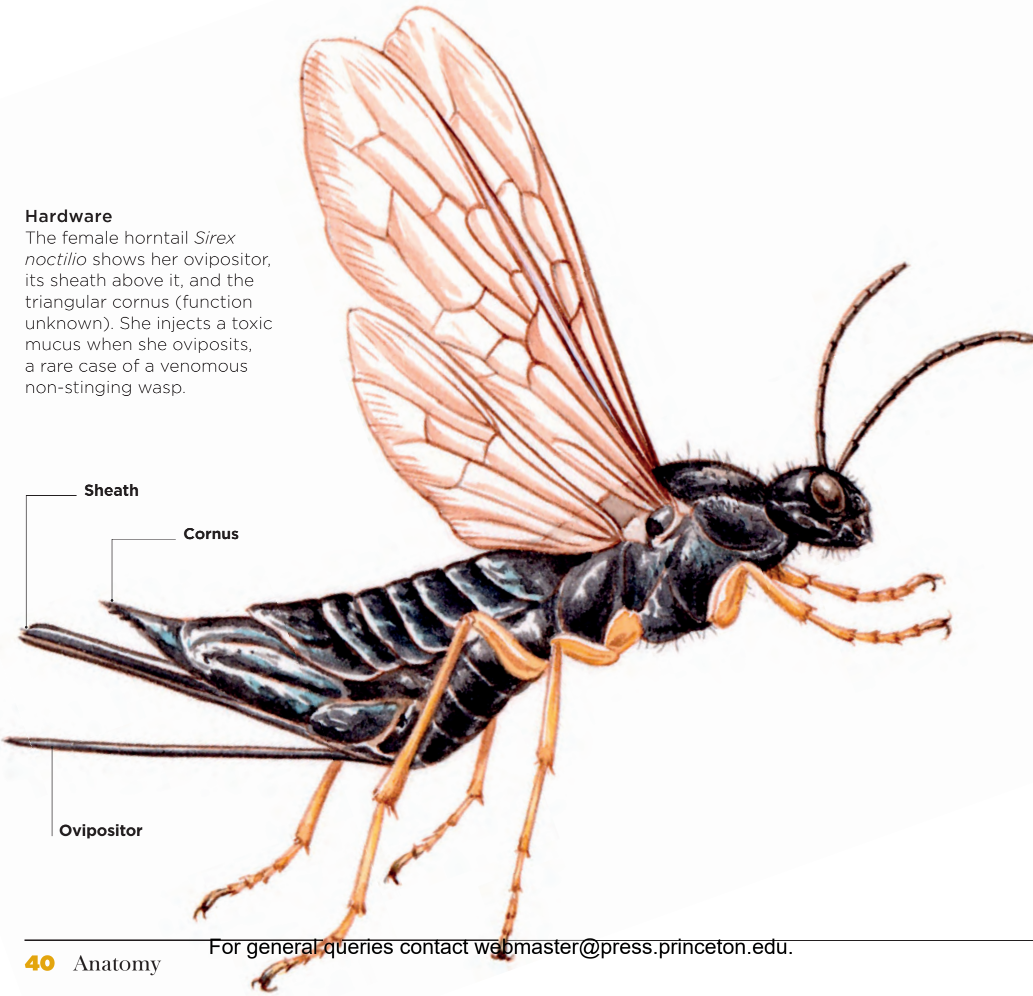


Sting and Venom

"Stinger" is a popular word for what is technically the "sting." It is unquestionably the greatest evolutionary achievement of wasps. What evolved initially as an egg-laying organ, the ovipositor, became weaponized. We are familiar with the sting as a tool of self-defense and colony defense in social wasps, but the primary purpose of the sting and its associated venom is to incapacitate struggling hosts or prey: inducing paralysis, temporary or permanent, is the goal. It is easier to transport, and/or lay an egg on, or in, a host if that animal is unable to flee, or offer resistance to the female wasp.

Hardware
The female horntail *Sirex noctilio* shows her ovipositor, its sheath above it, and the triangular cornus (function unknown). She injects a toxic mucus when she oviposits, a rare case of a venomous non-stinging wasp.



Venomous Needle
Normally retracted inside the abdomen, the sting of this female yellowjacket is here fully deployed. Above the sting is the exposed gonoplac, corresponding to the ovipositor sheath in non-stinging wasps.

The sting is usually retracted inside the abdomen of the female insect until deployment. Any visible filament, or spear- or needle-like extremity at the tip of the abdomen is either an ovipositor or, in the case of some male wasps, a pseudo-sting. The operative word is "usually." Nothing is ever simple in the wasp world.

Because the sting is derived from the ovipositor, it is valuable to compare the anatomy of the two. Neither is comparable to a hypodermic needle. What appears as a single structure is in reality composed of several parts that represent modifications of the terminal segments of the abdomen/metasoma. In a wasp ovipositor, two parallel, blade-like appendages form a channel down which eggs pass. Typically, the tips of each are serrated to facilitate entry into plant tissue or a host animal. They slide against each other alternately to advance the ovipositor into the tissues. The ovipositor is itself enveloped in a sheath composed of two halves of an additional appendage. The sheath filaments are stout, protecting the delicate ovipositor and serving as braces, like an oil-drilling derrick, if necessary, to penetrate a dense surface like wood.

A sting is built similarly to an ovipositor, but it lacks the sheath and is usually without teeth on the tips of the paired, piercing appendages. The result is a canal through which venom flows. Unlike the honey bee, which has barbs on the sting that anchor it in the wound, wasps can withdraw their sting for repeated use.

Venom is produced in one or more glands within the abdomen of the female. An increasing understanding of venom now defines it as basically any chemical or combination of chemical compounds that results in weakening or incapacitation of the host organism or victim. By that definition, the "non-venomous" horntail wasp, *Sirex noctilio*, envenomates conifer tree hosts with a cocktail that make the trees vulnerable to the fungus that is also introduced by the female wasp when she lays her eggs.

How is a Wasp Built to Sting?
The "wasp waist" allows multi-directional articulation of the abdomen to direct the sting wherever it is needed. The flexibility of the abdomen/metasoma/gaster itself allows the insect to contort its body to plunge its sting into struggling prey.

Top Ten Stingers

1. **Warrior wasp, Synoeca septentrionalis**
2. **Tarantula hawks, *Pepsis* spp.**
3. **Velvet ant, Dasymutilla klugii**
4. **Red-headed paper wasp, Polistes erythrocephalus**
5. **Red paper wasp, Polistes canadensis**
6. **Giant paper wasp, *Megapolistes* sp.**
7. **Yellow fire wasp, Agelaia myrmecophila**
8. **Glorious velvet ant, Dasymutilla gloriosa**
9. **Western yellowjacket, Vespula pensylvanica**
10. **Honey wasp, Brachygastra mellifica**

The most painful stings adapted from the "Schmidt Sting Pain Scale"

Sexual Dimorphism

Differences between male and female wasps are generally subtle, but the more practiced one becomes, the easier it is to identify each sex. Seasoned entomologists sometimes prank less-knowledgeable friends by freely handling male wasps that have no sting. Sometimes, the difference between males and females is so dramatic that one could be forgiven for assuming the two sexes are different *species*. Observable sex differences constitute sexual dimorphism.

Obviously, differences in genitalia exist between male and female wasps. Internally, males have testes, and females have ovaries. Male external genitalia are collectively the aedeagus, consisting of two penis valves framed by a pair of gonostyles, normally concealed in the abdomen. The corresponding female part is the vulva, the opening of the vagina. She is able to store sperm inside an internal pouch called the spermatheca. From it she releases sperm into her oviduct.

The Same But Different
Velvet ants, like *Nemka viduata* of Europe, demonstrate extreme sexual dimorphism. The male is winged, the female wingless. Their coloration differs as well.

False Sting
Males of some wasps like this thynnine wasp, *Myzinum* sp., have an intimidating but harmless "pseudo-sting." In other wasps it may be two- or three-pronged, rather than singular and hooked.

Males have more abdominal segments than females, and often a blunt, rounded, or toothed tip to the abdomen or metasoma. A trident or singular, menacing hook on the abdomen of a male wasp is called a pseudo-sting, and it protrudes from the last visible ventral segment. The abdomen or metasoma of a female wasp usually tapers to a point. There are species for which no males are known, either because females can reproduce without them, through parthenogenesis, or because we have yet to associate males with females. Males of the American Pelecinid, *Pelecinus polyturator*, are oddly scarce in most places where the species occurs.

One of the most striking examples of sexual dimorphism is in the velvet ants, family Mutillidae. Males are usually macropterous (fully winged) and females are brachypterous (wingless). There is often a size difference, too, males being larger in some instances. This is even more pronounced in some members of the family Tiphiidae where wingless females are a fraction of the size of males, and a male can carry his mate on the wing. In-flight sex of this nature is called phoretic copulation. There are wasps, like fig wasps in the family Agaonidae, in which the male is wingless, but the female is winged. Still other species demonstrate winged, wingless, or vestigial-winged (micropterous) individuals of either sex, as in the genus *Trimorus*, family Platygastridae.

Antennae of male wasps typically have more segments than those of females. The male's antennae may also be modified in various ways to better detect the sexual scents (pheromones) that females deploy to attract mates. Male paper wasps in the subfamily Polistinae have hooked antennae, and often pale faces, making them easy to identify.

Bizarre Variations

Wasps can look weird, and we sometimes do not understand why. They can have horns, or spikes, or spines, or other modifications that may leave you scratching your head. Their legs can be expanded like the biceps of a bodybuilder, or the antennae can be clubbed or comb-like. The puzzling strangeness of such insects is part of their appeal to entomologists and naturalists.

A frequent reason for modification of the wasp body is to better accomplish the tasks associated with the lifestyle of that species. Wasps that excavate burrows for nesting are termed "fossorial," and the females of most species have a series of stout spines on the front legs called the "tarsal rake." Watching a sand wasp fling large quantities of soil under and behind her as she digs gives one an appreciation of the utility of her built-in tools. Curling her "toes" enhances the effect, putting all the spines in the same plane as she tunnels quickly into a dune.

Modifications to legs help males of some species to grasp the female during courtship and mating, and/or help the male guard his mate from competing suitors. Male shield-handed wasps in the genus *Crabro* have the tibia segment of the front leg expanded into an opaque shield that filters light into a species-specific pattern when placed over the eyes of the female.

Strange Things
This small wasp, in the family Eucharitidae, has comb-like antennae, the better to detect scents of the opposite sex, or ant nests. It also has long spines on the rear of the thorax, of unknown function.

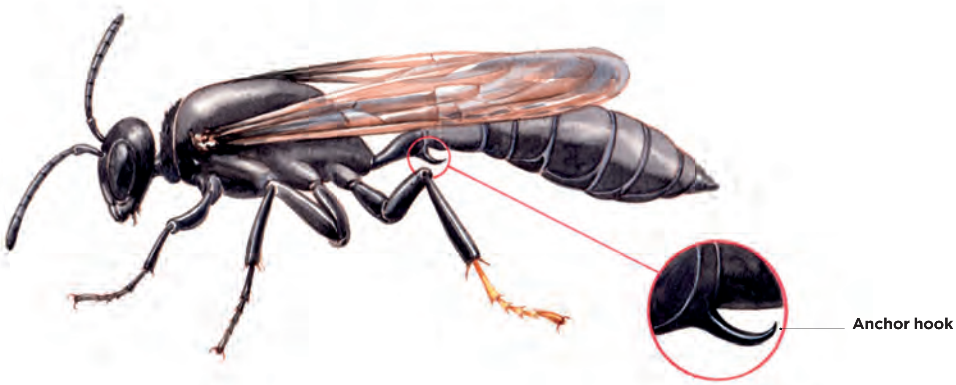
Tarsal Rake
This female European beewolf, *Philanthus triangulum* (left), possesses long spines on her front "feet" that help her dig a burrow quickly and efficiently. Many wasps in the Crabronidae, Sphecidae, and Pompilidae families have this adaptation.

Tusks
Large male mason wasps in the African genus *Synagris* (below left) have bizarre horns on their jaws. They use these weapons against competing males while guarding nests from which a female is likely to emerge.

The faces of wasps can be adorned with a variety of structures. Males of some "tusked wasps" in the African genus *Synagris* have menacing horns sprouting from their jaws or face. They use these weapons primarily to battle for access to virgin females emerging from mud nests. They may also guard individual nests of females they have mated with, or patrol several such nests to defend against competing males. Males of the recently discovered "king wasp," *Megalara garuda*, family Crabronidae, from the Indonesian island of Sulawesi, also have exaggerated mandibles. We know nothing of their function. Female "warthog wasps" from Africa, *Genaemirum phacochoerus*, in the family Ichneumonidae, have odd projections on their "cheeks," perhaps helpful in bulldozing through the tunnels of their hosts: pupae of carpenterworm moths in the family Cossidae. The enormous compound eyes of male wasps in the subfamily Astatinae, family Crabronidae, meet at the top of the head—all the better to watch for females passing by.

Even the abdomen of a wasp can be bizarre. Take the "handle" on the front of the abdomen of tiny female wasps in the genus *Inostemma*, family Platygastridae. The projection serves to house the long, retractable ovipositor she uses to lay eggs in galls made by gall midges.

Ventral Spine
Males of the organ pipe mud dauber, *Trypoxylon politum* (below), have a menacing hook that they use to anchor themselves in nests that they guard from predators, parasitoids, and competing males.



PROFILE

Dryinid Wasps

Family Dryinidae

The family Dryinidae does not have a standard common name, but calling them “scissor-handed wasps” would be appropriate. These are small, ant-like wasps with prominent eyes, the females of most species possessing mind-boggling adaptations of their front feet.

Family Dryinidae

SPECIES	~1,100
DISTRIBUTION	Worldwide except for Antarctica
SIZE	0.08–0.43 inches (2–11mm)
AMAZING FACT	Females of many species have pincers

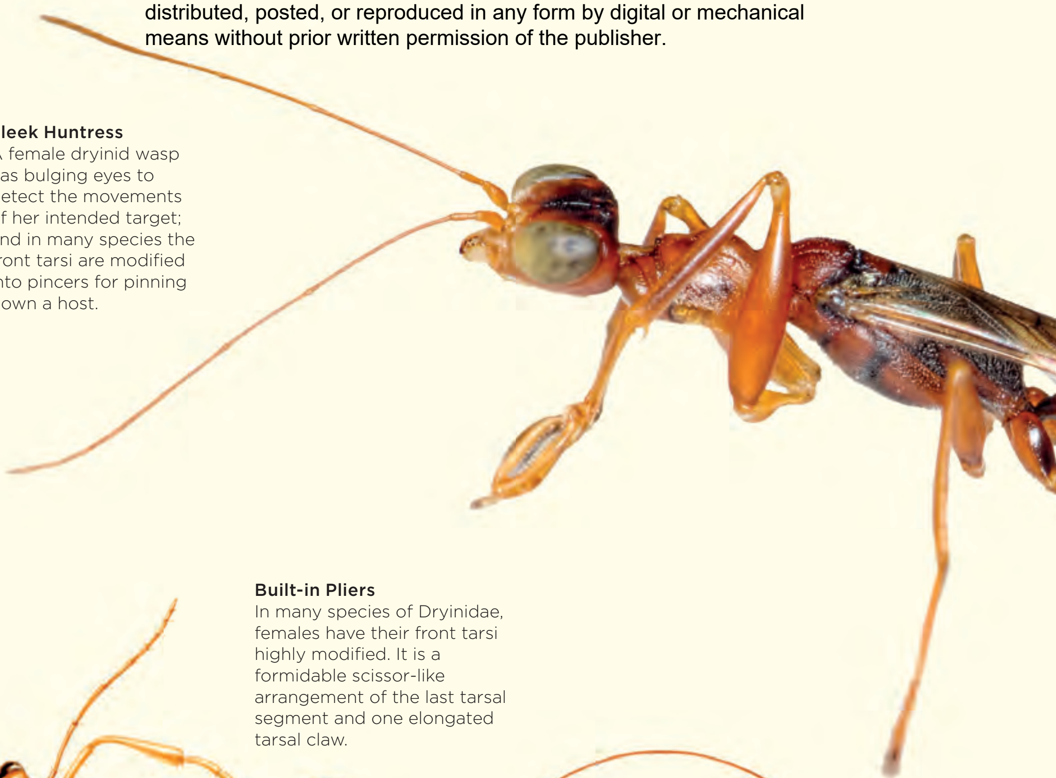
Actual size

Small but Mighty
Adult dryinid wasps average around 0.2 inches (5mm), and rarely exceed 0.43 inches (11mm). What females lack in size they make up for in ferocity.

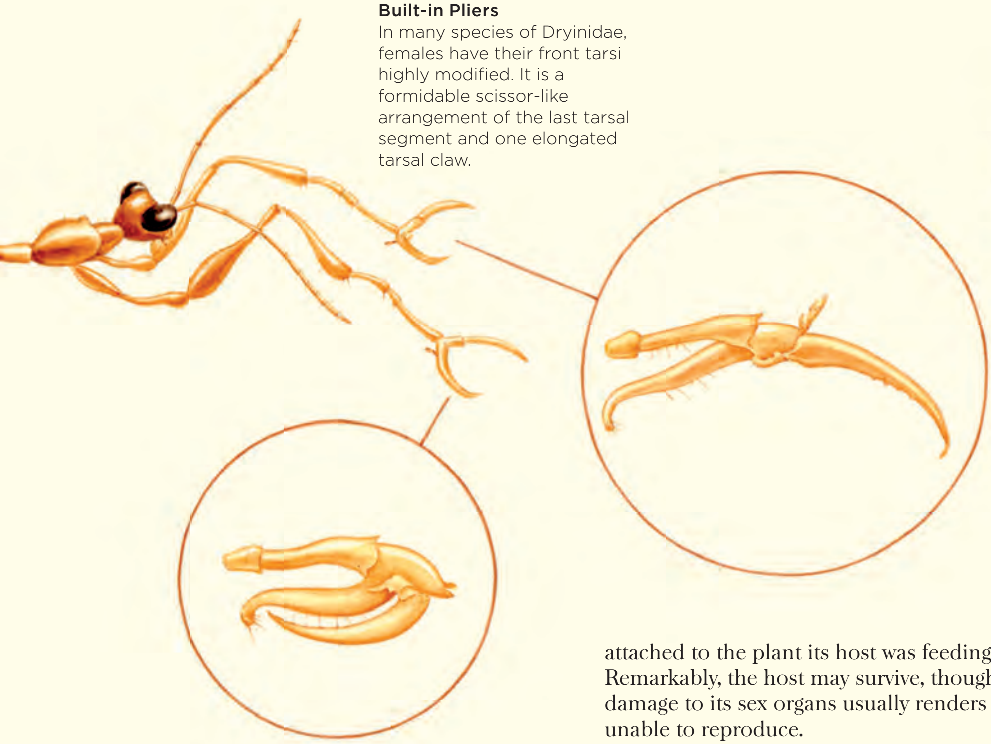
Stuck on You
The larva of a dryinid wasp has formed a hardened sack for protection as it sucks the blood of its host, the nymph of a planthopper, *Siphanta acuta*, in Tasmania.

Females may be fully winged, but in a number of species are wingless (apterous), or have the wings reduced to non-functional pads (brachypterous). Males of most species have wings, a few being brachypterous, but all lack the intimidating hardware of the female’s forelegs. Why the sexual dimorphism? Males do not wrestle host insects in hand-to-hand combat.

The scissor-like front tarsus of the female is a marvel of evolutionary engineering. One of the two claws is elongated into a blade-like appendage. The last (fifth) tarsal segment to which the claws are attached is expanded laterally to make the opposing “grip” against which the articulated claw compresses. Lacking a paralyzing sting, she uses these handy weapons to securely grasp a host and drive an egg between its abdominal segments. Nymphs and adults of leafhoppers in the family Cicadellidae, or planthoppers in the Delphacidae, Flatidae, and related families, serve as hosts for various dryinids. The adult female wasp will also kill hosts on occasion to feed herself, one of the few adult solitary parasitoid wasps known to engage in such predatory behavior.



Sleek Huntress
A female dryinid wasp has bulging eyes to detect the movements of her intended target; and in many species the front tarsi are modified into pincers for pinning down a host.



Built-in Pliers
In many species of Dryinidae, females have their front tarsi highly modified. It is a formidable scissor-like arrangement of the last tarsal segment and one elongated tarsal claw.

The dryinid larva that hatches from the egg develops initially as an internal parasite, but as it grows it eventually bursts the seams of its host, its hindquarters oozing between the host's body segments. The soft body of the larva is protected by a hardened sac called a thylacium, formed from its molted exoskeletons. When finished dining, the dryinid larva releases itself to enter the pupa stage in the soil, or attached to the plant its host was feeding on. Remarkably, the host may survive, though damage to its sex organs usually renders it unable to reproduce.

In rare instances, a single egg laid by the mother wasp will split into multiple, viable embryos (polyembryony, page 52). Under this scenario, the larvae remain internal parasites for the duration of their youthful lives.

Dryinidae are collectively found all over the world, with roughly 1,100 species in 58 genera and 11 subfamilies.

3

Metamorphosis

Purpose in Transformation

The Wasp Life Cycle

All wasps are holometabolous insects. That sounds frightening, but all it means is that they undergo complete metamorphosis. This is a complicated, advanced life cycle shared by ants, bees, beetles, flies, butterflies, moths, scorpionflies, caddisflies, lacewings and their kin, and fleas. Grasshoppers, cockroaches, mantids, true bugs, and other insects experience gradual or simple metamorphosis, with their juvenile stages growing incrementally and attaining a reproductive system—and maybe wings—with the last molt into adulthood.

The miraculous passage of wasps through egg, larva, pupa, and adult stages confers a number of advantages over simple metamorphosis. Each stage in the life cycle can be dedicated entirely to one or two functions. The larva stage can feed on one resource while the adult feeds on another, reducing or eliminating generational competition. One stage may excel over other stages in withstanding environmental extremes such as cold winters or hot summers. Complete metamorphosis usually results in faster growth than simple metamorphosis. Yet, there is more fluidity in the process than the four distinct stages would suggest. The final imago is almost literally imagined in the immature phases. Hormones play a pivotal role in all of this.

There are seemingly infinite variations on the theme of metamorphosis. Some wasp species that form plant galls alternate generations between a sexually-reproducing one and a generation without males. Female parasitoid wasps of some species are able to lay eggs that habitually split into dozens, hundreds, or even thousands, of additional embryos. A few wasps that are parasites of parasites undergo radical transformations within the larval stage in a phenomenon known as hypermetamorphosis, a strategy for seeking elusive hosts. You are unlikely to see a wasp egg, larva, or pupa because they are usually concealed underground, in plant tissue, inside another insect, in a paper or mud nest, or in a cocoon. It may come as a surprise to learn that a wasp may live the bulk of its life in one of those immature stages instead of as an adult.

Species that have only one generation per year are termed "univoltine." Other species may be bivoltine or multivoltine, with two or more generations each year. The duration of a life cycle for a given individual may vary even more. Wasps that feed as larvae inside plant seeds may be dormant for two or three years if conditions are not favorable for their emergence as adults.

An utterly unique feature of the order Hymenoptera is the manner in which sex is determined at birth. Fertilized eggs become females, and unfertilized eggs yield males. Consequently, females have two sets of chromosomes, males only one. This is haplodiploidy, a puzzling attribute that continues to confound entomologists.

Egg
An adult female social wasp, *Ropalidia* sp. in Thailand (above), has laid an egg in one of the cells of her paper nest. Within the egg, a yolk furnishes nutrition for the developing larval embryo.

Pupa
The pupa of a bethylid wasp (family Bethylidae) (right) is revealed inside a kernel of grain damaged by its host, the lesser grain borer beetle, *Rhyzopertha dominica*. The wasp helps keep this pest in check.

The Egg: Embryogenesis

The ovum is the incubation stage of a future wasp, its sex already determined by its mother. Female wasps are able to store sperm in an organ called the spermatheca, and release the male sex cells at will. Eggs pass down the oviduct and, if fertilized, are destined to become female wasps. Unfertilized eggs will be male wasps.

Comb Home
A colony founding female paper wasp, *Polistes metricus*, is guarding the eggs inside the cells of her young nest.

Survival of this most vulnerable stage in the life cycle usually hinges on the mother wasp placing her eggs in the optimal location or circumstance for the next stage: the larva that will hatch from the egg. Sawflies and gall wasps must oviposit in the correct host plant. Parasitoid wasps must divine the identity of a host, as well as its location, sometimes concealed deep inside a tree trunk. Solitary stinging wasps lay a single egg upon paralyzed or deceased hosts they conceal in a cavity, burrow, or mud nest, or in some instances lay an egg in an empty cell before hosts are harvested. Social wasps lay one egg in each cell in the paper or mud comb. Where necessary, the eggs are cemented in place with secretions from Dufour's gland, an organ inside the adult female's abdomen.

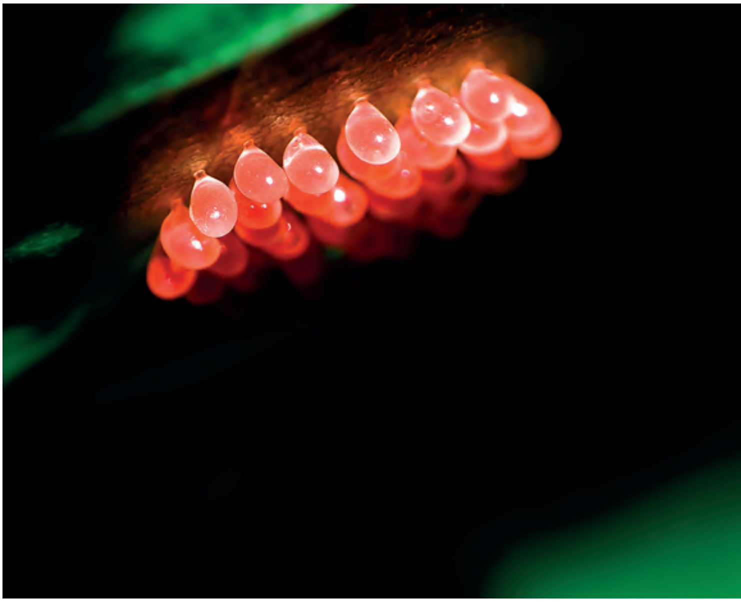
There are plenty of exceptions to straightforward scenarios. Some wasps "broadcast" scores of eggs, scattering them in places where the host organism is likely to come to them, instead of the female wasp searching for victims. In such cases the host usually ingests the leathery or hard-shelled eggs, which then hatch inside the host. Few offspring will reach the proper destination this way. The opposite approach is to lay fewer eggs, but protect them. Some sawfly species invest in parental care, the mother wasp fiercely guarding her clutch of eggs, and the young larvae that hatch, against predators and tiny parasitic wasps.

Another extraordinary strategy is polyembryony. Members of four families of Hymenoptera are able to inject a single egg into a host and then have the embryo split into many more: upward of 2,000 additional embryos in some cases. If this sounds somewhat familiar it is because this is the same phenomenon that produces twins or multiple human babies per single conception.

Subduing another organism, even another insect or a spider, is fraught with danger, so many wasps evolved venomous stings as a way to make the host more…compliant. This usually translates to complete paralysis—temporary or permanent—so that attaching or injecting an egg is an easier task.

Ovipositing
A female Krug's sawfly, *Sericocera krugii*, lays her eggs on the leaf of a sea grape, *Coccoloba uvifera*, in Puerto Rico.

Ova
The eggs of a Krug's sawfly are opalescent red, indicative of a foul taste or poisonous nature. The mother wasp must lay her eggs on the proper host plant or her larvae will starve.



SPOTLIGHT ON

Rose Sawflies

Arge ochropus is one of several sawfly species that go by the name "rose sawfly," exposing one of the problems with common, English names. As one might expect, rose sawflies are considered pests due to their larval appetites for these ornamental garden shrubs. Still, they are an example of the life cycle of sawflies in general.

The female of *Arge ochropus* lays 15–18 eggs in the host plant by using her toothed, blade-like ovipositor to saw a groove in a stem or shoot and inserting her ova inside. She can lay around 35–50 eggs total during her lifespan, according to one laboratory study. The oviposition scar may become blackened and distorted. Early instar larvae feed together on the underside of leaves, scraping the lower epidermis of the leaf and/or flower buds. Later instars disperse to feed singly, chewing through leaves at the edge. Larval development through five instars takes about 24 days. Mature larvae measure 25mm, and drop to the ground to pupate in brown, double-walled cocoons they form in the soil. Pupation lasts about 14 days under laboratory conditions.

Third and fourth instar larvae are well-defended, and advertise the fact with a bright yellow head and broad dorsal stripe that contrasts with numerous black spots. Each abdominal segment is covered with 226 individual bristles that function as mechanoreceptors to detect the slightest touch. Should an ant or other small predator contact the spines, the larva suddenly raises its abdomen to expose seven ventral glands, one per segment, that emit repellent, volatile chemicals. These alone may send the ant running, but if the antagonist persists, it may imbibe worse toxins that leave it nearly paralyzed, staggering away in retreat.

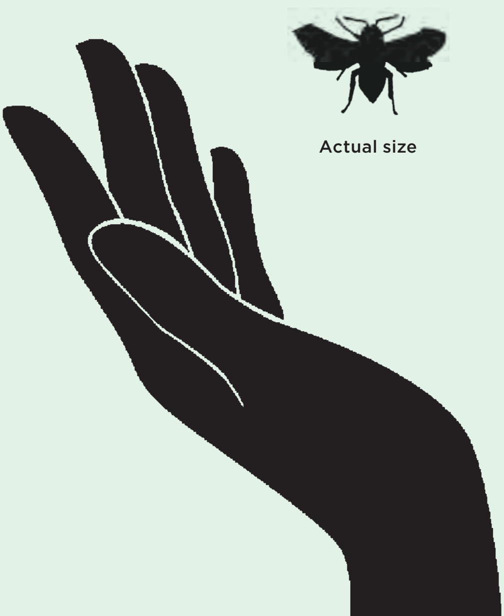
Native to Europe and Asia, including the Middle East and western Siberia, *Arge ochropus* usually has one generation each year. First-generation adults are seen in late April and early May, with second-generation adults appearing in July and August. The adult female is 7–10mm in length, and both sexes feed on pollen, especially that of umbelliferous flowers.

Damage to roses can harm growth and flowering; skeletonizing of leaves is common. This species has recently become established in Canada (Ontario, Quebec) and the northeast U.S.A. (Vermont, Massachusetts, New York, and Michigan).

Colorful
The adult rose sawfly, *Arge ochropus*, is a lovely insect. Its antennae have only three segments each, the last one a long, undivided segment. This is a trait of all argid sawflies.

Chowing Down
The larva of the rose sawfly munches greedily on a rose leaflet. It adopts a defensive posture here, to warn that it can secrete a foul substance if further antagonized.

Stingless Vegetarian
Rose sawflies may mimic in color and shape wasps that can sting.



Actual size

Mating
Male and female large rose sawflies *Arge pagana*, copulate back-to-back. Different wasps have different orientations during mating, depending in part on the configuration of their genitalia.

The Larva: An Eating Machine

Teenagers are the eating and growing phase of the human lifetime, and the larva stage is the equivalent for wasps. The larva usually represents the greatest percentage of time in the total life cycle, and often includes a prepupa stage that undergoes diapause to endure winter. Diapause is characterized by dramatically reduced metabolism, and temporarily arrested development. Dedicated as they are to feeding and growing, wasp larvae generally sacrifice the mobility and armor of the adult.

Larva and Food
Contents of a nest of the grass-carrier wasp *Isodontia mexicana*, dumped on a table, show the larva amid a cache of paralyzed katydids that it is consuming. Black specks are the larva's frass (faeces). Nests of *Isodontia* are in linear cavities partitioned with grass.

Vulnerable
The larval members of a colony of social wasps, *Ropalidia fasciata*, are protected by an adult female. Each larva is ensconced inside a paper cell where its only responsibility is to eat and grow.

Despite their soft, flexible bodies, there is a limit to the elasticity of the larval exoskeleton. The larva must molt periodically, shedding the old exoskeleton and expanding before the new one hardens. Intervals between molts are called instars. There are an average of 3–5 instars, but the number and duration of each varies according to sex, amount of food available, environmental conditions, and species identity. Molting (ecdysis) and growth are regulated by hormones, the most important being juvenile hormone or "JH." JH maintains the expression of juvenile characteristics but, inside, the blueprint for an adult wasp is already in place. "Imaginal discs" destined to become wings, legs, compound eyes, and antennae are triggered by other hormones.

Foods high in protein fuel growth, but sawflies and their kin, and gall wasps, consume cellulose as larvae. Securing enough nutrition from plants necessitates eating large quantities, and digesting it with the help of symbiotic microbes in the gut of the insect. Most wasp larvae feed on other invertebrates. The food source (host) is living, paralyzed, or deceased, depending on the wasp species.

Most parasitoid wasp larvae live on or within insect larvae, insect eggs, or spiders. A few are hyperparasites: parasites of other parasites that must find a host within a host, say a braconid wasp larva inside a caterpillar. Hyperparasites undergo hypermetamorphosis whereby the larvae change drastically. The family Perilampidae includes such examples. The first instar perilampid larva is a planidia, an active, host-seeking missile. Once a host is located, it attaches, and the succeeding instars are plump couch potatoes by comparison.

Stinging parasitoid wasps are provided for by their mother. She collects at least one host, usually an insect or spider, paralyzes it, and caches it in an underground burrow, pre-existing cavity in wood or other material, or inside a mud cell. She lays a single egg, seals the nest, and departs. The larva that hatches from the egg consumes the food, which won't rot because it is still living. Social wasps kill prey outright, chew it up, and bring it back to the nest where the prey is distributed to the larvae living in the cells of the comb.

PROFILE

Paper Wasps

Polistes spp.

Provided you are brave, paper wasps in the genus *Polistes* offer a unique opportunity to witness a wasp's life cycle. The uncovered combs of these social insects are a window into metamorphosis, though a curtain of silk conceals the pupa. You may want to use binoculars, the zoom feature on your camera or phone, or a telescope, depending on your fear threshold. There are more than 200 species of *Polistes* on Earth, and their personalities vary.

Genus *Polistes*

SPECIES	>200
DISTRIBUTION	Worldwide except for Antarctica
SIZE	~0.3–1.5 inches (8–38mm)
AMAZING FACT	Inspired modern paper manufacturing

Actual size

Social Architect
Female paper wasps are all capable of reproducing, but only the dominant female (gyne) in a given colony does so. She bullies her cohorts into raising her offspring and expanding the nest.

Besides individual transitions, paper wasps have a colony life cycle. *Polistes* is Greek for "city founder," and one or more female foundresses establish a single nest. These are gynes, females that reproduce but do not differ in size or form from other females. One female eventually asserts dominance, and suppresses the development of functional ovaries in her daughters, who will be *de facto* workers. Nests are constructed of wood or plant fibers chewed into pulp and formed into paper. A thick pedicel suspends the comb from a branch, palm frond, or other surface. A small number of hexagonal cells is built, and a single egg laid in each.

Hard Worker
A female European paper wasp, *Polistes dominula*, performs many duties for her colony: she forages for prey, feeds other nestmates, feeds her larval siblings, helps build additions to the nest, and guards against predators and parasitoids.

Reaching Capacity
As it grows, the paper wasp larva fills the entirety of its confining hexagonal cell. Soon it will spin a silken dome over the opening in preparation for entering the pupa stage.

Transformation
Appearing inert on the outside, paper wasp pupae undergo radical changes internally. The closer they get to the time of emergence to adulthood, the darker the pupae become.

Newly Minted
The newest product from the paper wasp factory is an adult that chews her way through the silken cap that protected her in the pupa stage.

In temperate *Polistes* species, the foundress produces new gynes in late summer or autumn, along with males. In tropical species, this happens at other times, as dictated by wet and dry season variability in food abundance, and other factors. In *Polistes biglumis*, a high-elevation European species with a brief nesting window, females that lose their own nest may usurp the foundress of another nest. In fact, most nests of this species represent offspring from multiple females. *Polistes metricus* of the eastern U.S.A frequently re-uses old nests, maintains multiple active nests, and may share nests with other paper wasp species.

A study of *Polistes cinerascens* in Brazil found the duration of one colony cycle, from founding to producing reproductives, averaged 200 days with 94 adults produced. There were up to four generations per year with an egg stage that lasted 13 days. All larval paper wasps go through five instars before pupating; the larva stage lasts about 24 days in *P. cinerascens*. An adult emerges from the pupa in 22 days. The pupa stage of the temperate *Polistes dominula* lasts 10–14 days. Adult *Polistes* live about 38 days.

The Pupa: Epic Reorganization

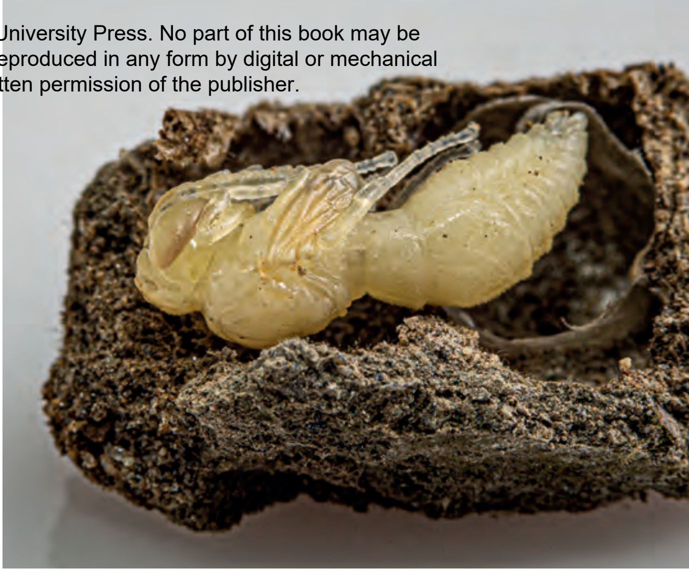
The pupa appears inert externally, so is often referred to as the "resting stage" between larva and adult. Nothing could be farther from the truth. The pupa might better be termed the reorganizational stage, since that is what is transpiring internally. Like the larval stage, the pupa is usually hidden from view inside a nest or gall or plant stem, or within a cocoon, or in a cocoon *and* a nest. Resembling a ghostly adult, the pupa is pale initially, darkening as the adult insect takes shape. Nearly all wasp pupae are exarate, meaning the appendages are free from the main body. Many pupae in the Chalcidoidea are obtect, with appendages adhered to the body wall.

Bird Poop?
The pupa of the ichneumon wasp *Charops annulipes* is concealed within a silken black and white cocoon that resembles a bird dropping. The disguise protects the vulnerable pupa from parasitoid enemies.

Transitioning from lumpy larva to sleek, alert, active adult is no mean feat. Much can go wrong if the correct genes are not turned on, or off. Timing of hormone releases, and proper cellular responses to them, are critical. Juvenile hormone is no longer manufactured, signaling the cessation of juvenile programming and the end of larval anatomy, and the onset of construction of the adult central nervous system, and triggering of the imaginal discs into differentiating appropriate adult body parts.

Let us return to the larva for a moment, as it sets the stage for the pupa. Larvae of many wasps pass unfavorable environmental conditions as prepupae, and often protect themselves by spinning cocoons. Labial glands in the mouth of the larva excrete silk that the insect weaves around itself, helping to insulate it from excessive cold and offering a barrier to parasites. Once ensconced inside the cozy capsule, the larva may go into diapause, a state of torpor in which metabolism decreases drastically, and all growth and development ceases. By this point the larva has accumulated enough fat reserves to resume development on the far side of diapause. In the case of most social wasps, each larva simply spins a silken dome over the opening of its paper cell, and overwintering is accomplished by

Ghostly
The pale creature encased in a mud capsule is the pupa of a mason wasp, genus *Ancistrocerus*. This is an example of an exarate pupa: the appendages are free from the body of the insect.



Fluffy
The cottony "cloud" on a pine needle represents communal cocooning by braconid wasp larvae of the subfamily Microgastrinae. The remains of their caterpillar host may lie underneath the woolly ball.

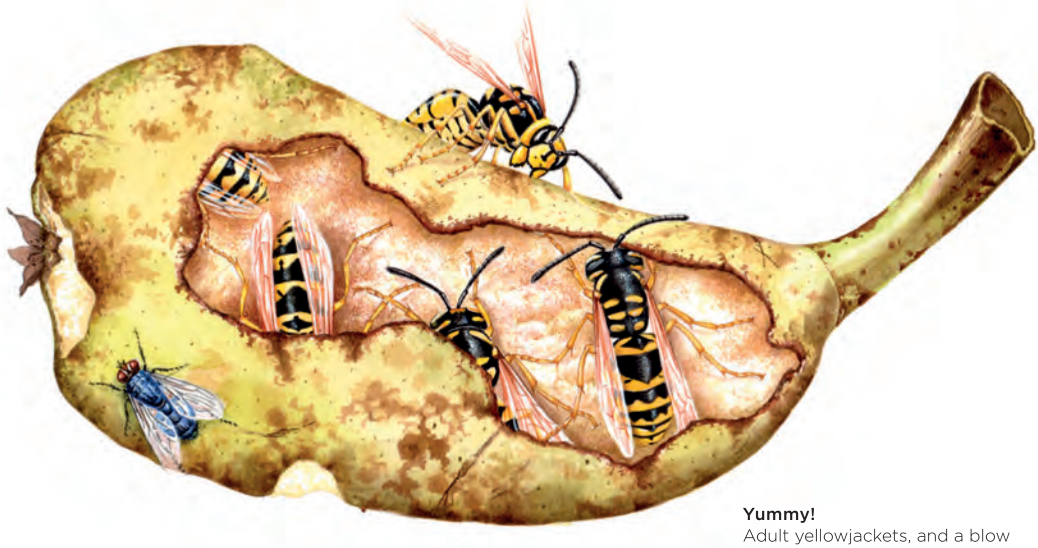
Not Eggs
The "balloons" on this Carolina Sphinx moth caterpillar (*Manduca sexta*), are cocoons of a braconid wasp in the genus *Cotesia*. Dozens of wasp larvae have been feeding internally, and have finally erupted synchronously to pupate.

adult females. Some gregarious internal parasitoids (endoparasitoids) erupt from their host in unison, spinning small cocoons that may be mistaken for eggs. This is a common phenomenon observed on caterpillars.

Revving up the metabolism machine again, some larval tissue is destroyed in the course of creating the adult. Other cells are re-purposed, at the behest of hormones targeting specific gene locations. Once the process is complete, an adult wasp emerges from the pupa. It may need to chew its way out of a cocoon and/or a mud plug, or through a layer of plant matter, or some other barrier to its freedom. Not every wasp succeeds in breaking out.

The Adult: Mating and Host-finding

The life of an adult wasp is all about finding a mate (males), procreating (both sexes), and providing for the next generation (females). It is also left to females to disperse to new or better habitats. There is much work to be done, but first to fuel up.



Yummy!
Adult yellowjackets, and a blow fly, feed on a rotting pear. Ripe fruit provides carbohydrates that the adult insects need for their bustling lifestyle. Fermenting? All the better.

Whereas the larva stage needed protein to grow, adult wasps require carbohydrates to stoke their metabolic furnace. Flower nectar is the wasp equivalent of our energy drinks, so you will often find wasps on blooming plants. When nectar is scarce, wasps avail themselves of alternatives. This includes sweets from extrafloral nectaries, specialized structures that produce nectar apart from flowers. Sunflowers (*Helianthus* spp.) possess them, for example. Plant galls may also exude nectar. Sap oozing from wounds on trees, all the better if fermenting, also suffices. Overripe fruit is another resource some wasps exploit. A favorite indulgence is "honeydew," the liquid wastes excreted by aphids, scale insects, planthoppers, treehoppers, and related true bugs that live in groups. Aphid colonies may attract scores of wasps of diverse families, as well as bees, flies, ants, and other insects.

In temperate climates, adult females of some species overwinter, and these we see early in spring. They include ichneumon wasps, paper wasps, yellowjacket queens, hornet queens, solitary cutworm hunters, and cricket-seekers. Having mated the previous autumn, they are now free to hunt and nest without being bothered by overzealous males.

Among solitary wasps, males are usually the first to emerge from nests, and they immediately seek virgin females. Strategies vary, but a primary method is to simply force themselves onto the opposite sex. A tumbling ball of male wasps wrestling over a female concealed somewhere inside their frenzied mass may injure one or more parties. Less chaotic approaches to mating include staking out a landmark where a male can see females approaching, and from where he can chase away competing males. Male wasps of some species establish territories, sometimes scent-marking like a cat. In a few species, males assist females *after* mating, guarding the nest while the female is gathering building material or hunting for prey.

It is a naturally human desire to see other animals as inferior to us, but wasps give us ample reason to call our superiority into doubt. Female wasps are capable of astounding feats of fearlessness, strength, navigation, and parental care. Their instincts maintain enough plasticity to allow them to overcome novel problems. They lack a mammalian level of intellect, yet they not only survive, they thrive, in a diversity of ecosystems.

Calling All Males
A wingless female flower wasp in Australia, family Thynnidae, emits a pheromone and waits for a much larger, winged male to sweep her off her perch. This is her only way to reproduce, get to a nectar source, and find her way to a more distant, favorable habitat.

Honeydew Addict
Many wasps, like this diminutive cuckoo wasp, *Pseudomalus auratus*, crave the sugary liquid waste (honeydew) produced in copious amounts by aphids, scale insects, treehoppers, other sap-sucking bugs, and even some kinds of galls.

PROFILE

Emerald Cockroach Wasp

Ampulex compressa

One of the shining heroes of the wasp world is *Ampulex compressa*, the emerald cockroach wasp. True to its name, it dispatches cockroaches of the genus *Periplaneta* in an especially macabre manner. The female wasp stings the roach in the thorax to stun it, then uses her jaws and upper lip (clypeus) as a clamp to seize the roach by its hood-like pronotum. She then stings it in a nerve center under its head. The venom acts to suppress her victim's ability to move voluntarily. She amputates the roach's antennae, drinking what fluid leaks out. Using the shortened antennae like a horseman uses reins, the wasp then guides the roach to an appropriate natural cavity that will serve as its tomb. Once inside, the wasp lays her egg at the base of the roach's middle leg. She then carefully plugs the entrance to the cavity with debris and leaves.

Family Ampulicidae

SPECIES	~170
DISTRIBUTION	Worldwide, mostly tropical
SIZE	0.2–1.3 inches (5–33mm)
AMAZING FACT	All species use cockroaches as hosts

Actual size

Roach-master
Ampulex compressa is the largest species in its family, but still smaller than its cockroach host, measuring 0.7–0.98 inches (18–25mm) compared to the roach's average 1.6 inches (40mm) length.

A Lip With Grip
The clypeus (face plate below the eyes) and jaws of *Ampulex* work like a clamp to grip the edge of a cockroach's carapace, so the wasp can sting it underneath.

Life Cycle
A female wasp has stung her cockroach victim into a cooperative state and drags it where she wants by its antennae. Another sting at the nest paralyzes it permanently. Her egg has hatched and the larva feeds externally, then internally. A new wasp emerges from the body cavity of its now deceased host.

Inside the nest, a larva hatches from the egg in three days, puncturing the cuticle of its still-living host, and begins to suck its blood. The larva does a remarkable thing in spitting out copious amounts of an antimicrobial cocktail that "disinfects" the roach prior to feeding. The larva spends two instars as an external parasitoid, using its piercing mandibles to feed.

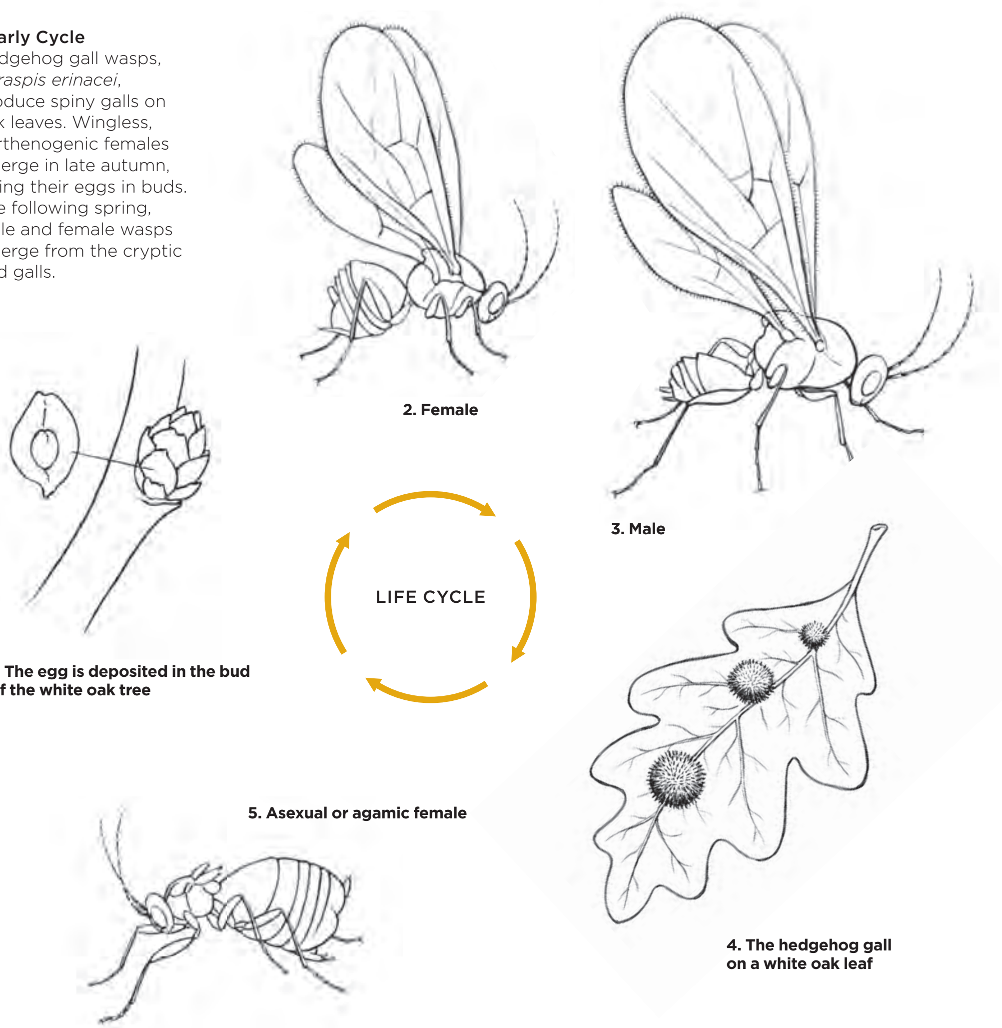
Molting to the third instar, about seven days since it hatched from the egg, the larva now has more blunt jaws that it uses to tunnel inside the roach. This finally causes its death, as it consumes all muscle and internal organs, save for the digestive tract and Malpighian tubules. Once it has finished dining, the mature wasp larva spins a cocoon around itself, still within the empty husk of the roach. The entire egg-to-adult cycle takes around six weeks, and the adult female wasps may live for several months.

Averaging 0.86 inches (22mm) in length, the female emerald cockroach wasp is one of the larger members of the family Ampulicidae, formerly treated as a subfamily of the thread-waisted wasps (Sphecidae). There are roughly two hundred species in six genera. This species is found in Africa, Asia, Australia, and many tropical Pacific islands. Much smaller, duller species occur in North America, but Ampulicidae in general are overwhelmingly tropical, and all known species have cockroach hosts

Alternation of Generations

Interestingly, some gall wasps in the family Cynipidae practice heterogony. That is, they have a life cycle of alternating generations between a traditional sexual generation involving males and females, and an asexual generation of females that reproduce without males via parthenogenesis. This bizarre pattern is limited to gall wasps of the subfamily Cynipinae living on oak or sycamore trees, as far as we know. The genera *Andricus*, *Cynips*, and *Neuroterus* demonstrate the typical form of heterogony.

Yearly Cycle
Hedgehog gall wasps, *Acraspis erinacei*, produce spiny galls on oak leaves. Wingless, parthenogenic females emerge in late autumn, laying their eggs in buds. The following spring, male and female wasps emerge from the cryptic bud galls.



How is this possible? We know that haplodiploidy applies to all wasps: males come from unfertilized eggs, females from fertilized eggs. How can you get both males *and* fertile females without mating? You cannot have it both ways! Apparently, you can if you have two types of asexual females. Androphores are females that produce haploid eggs through meiosis. These eggs will result in males. Gynephores are females that produce diploid eggs that become sexually reproducing females. Asexual in this context means a female that reproduces without mating with a male (parthenogenesis).

One female, however, can only produce males or females, depending on whether she is an androphore or gynephore. Confused? It turns out that in polar opposite to all other wasps, these particular cynipids, in the *sexual* generation (females and males), cannot produce males from unfertilized eggs. Mating with males will produce only androphore females or gynephore females, depending on the individual (sexually reproducing) female. In conclusion, there are two types of females in each of the generations. Males are produced only by certain females of the asexual generation.

The galls most obvious to us are growths on the leaves or twigs or limbs of oaks. The insects inside represent the generation of asexual females only. These females are frequently wingless, and typically emerge in late autumn. They lay their eggs in the developing buds of the host. A tiny gall forms on the scales of the bud. In late spring or early summer of the following year, the sexual generation of males and females emerges from these bud galls. They are winged and disperse to start the cycle again. The asexual generation alone may require one year, or a year for each generation. This can vary by species and/or depend on environmental conditions.

Cramped Quarters
This cross-section of an oak marble gall (right) shows the mature larva of the wasp *Andricus kollari*, in the central compartment, folded in half and about to pupate.

There are other deviations from the above, namely in the sycamore gall wasp, *Pediaspis aceris*, and some oak gall wasps, including *Biorhiza pallida* and some *Andricus* species. Some individual, asexual (parthenogenic) generation females of *Biorhiza pallida* can produce both females *and* males, for example. Lest your mind be bent no farther, take comfort in the fact that the genetic origins of heterogony are completely unknown, even to scientists.

Oak Apple
Unlike the dense, woody marble galls on stems, oak apple galls are on leaves, and spongy on the inside (below). A central chamber, suspended by a web of filaments, is where the wasp larva feeds.

4

Beauty
Purpose Expressed in Structural Design

Iridescence and Aposematism

Few people consider wasps to be beautiful creatures until confronted by their diversity. The endless variety of shapes, sizes, colors, and patterns serves the extraordinary array of lifestyles these insects lead. What passes for mere beauty to us is vital to the survival of the organism that wears the exoskeleton.

Hard to Miss
The bold colours of an eastern velvet ant, *Dasymutilla occidentalis* of North America, warn of her sting. Males are winged and do not sting, but they are seen less often than the conspicuous females.

The armor itself, regardless of color, serves several functions. Perhaps the most important is waterproofing. This has less to do with a terrestrial insect drowning than it does with that insect losing water through evaporation and transpiration. Spiracles—the breathing holes of insects—can be closed if necessary, but usually remain open. The exoskeleton also affords increased durability in the face of environmental wear and tear. Chitin, the major building material of insect armor, resists abrasion, splitting, and other forms of damage while discouraging predator attack. The cuticle of a cuckoo wasp or velvet ant may be exceptionally dense, even compared to other wasps, but it is still covered in sensilla, usually in the form of hairs. These setae detect changes in air movement, sense vibrations, or perceive chemical cues.

Many of the bright colors of wasps serve notice of their ability to defend themselves with a venomous sting, should circumstances call for such desperate measures. These visual advertisements are called aposematic colors or “warning colors.” They may include iridescent colors like blue, especially if paired with a contrasting color. Metallic colors can be aposematic, oddly camouflaging (metallic green in some instances), or aid in thermoregulation. Wasps covered with patches of short, dense, silver or gold hairs reflect a great deal of incoming solar radiation, preventing the insect from overheating in extremely hot, dry habitats.

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