CHAPTER 1 Introducing the Arachnids

Tested by 400 million years of a changing planet, arachnids have evolved many strategies for survival. Combining the ancient with the new has produced a diversity of species of every color and shape. Despite this, one key characteristic is shared by all arachnids: two chelicerae, used for piercing, grasping, or chewing up food. In this case, each scorpion chelicera has a fixed and movable finger, giving this scorpion a somewhat toothy "smile."

If "alien" means strange, arachnids are arguably among the most alien of Earth's inhabitants. The archetypal arachnid possesses eight legs, eight beady, unblinking eyes, fangs or pincers, and venom. In addition, the hardened exoskeleton and the multi-jointed legs convey an almost mechanical quality to this living creature; arachnids seem to have stepped right out of the movie *War of the Worlds* and scuttled into our living rooms. Finally, most are small, fast, and nocturnal, and are therefore difficult to observe. Consequently, the human imagination fills in the gaps in our knowledge, creating fearsome creatures. Ironically, the arachnids that exist in the real world rival anything that our imaginations could conjure. As a group they are many things: tough, resourceful, beautiful, and incredibly diverse—but hardly terrifying. Getting to know these small neighbors who share our planet is immensely rewarding and never dull.

First of all, arachnids are arthropods. Arthropods are characterized by segmented bodies, jointed appendages, and an exoskeleton. This exoskeleton, or cuticle, is composed of layers of waxes, proteins, and chitin. Chitin, which is composed of a derivative of glucose (*N*-acetylglucosamine), is combined with other substances that enhance its function as protective armor. In many terrestrial arthropods such as insects and arachnids, the chitin is embedded in a proteinaceous matrix of sclerotin. Sclerotin imparts the brown color to many arthropods; as proteins become cross-linked in the sclerotin, it becomes tougher, harder, and darker in a process called tanning. Immediately after molting, arthropods are pale and their cuticle is soft. Over a period of hours or days, as the sclerotin proteins become cross-linked, the cuticle darkens and hardens. In other arthropods such as crustaceans, calcium carbonate is combined with the chitin in a process of biomineralization. This gives the crustacean the perfect armor, combining hardness and resiliency. The major drawback of an exoskeleton is that the arthropod must molt in order to grow in size. Molting is a risky business; the arthropod is susceptible to predation during this time, and sometimes the process of molting itself can lead to injury or death. Despite this, arthropods have been extraordinarily successful from an evolutionary perspective.

Arthropods make up more than 80 percent of all known species of animals, with more than a million described species and millions more yet to be described. Included in this group are hexapods (six-legged arthropods such as insects and springtails), crustaceans (such as crabs, lobsters, shrimp, and pillbugs), myriapods (centipedes and millipedes), and the chelicerata (including horseshoe crabs, arachnids, and sea spiders).

Arachnids have two main body sections (also known as tagmata) and six pairs of basic appendages. The front of the body is called the prosoma or the cephalothorax; it includes both the head and the thorax fused together. The back of the body is the opisthosoma or the abdomen; it contains most of the reproductive and food storage capacity. In some arachnids (such as spiders) these body divisions are clearly evident, but in others (such as mites and harvestmen) the two body divisions merge together without a clear line of demarcation.

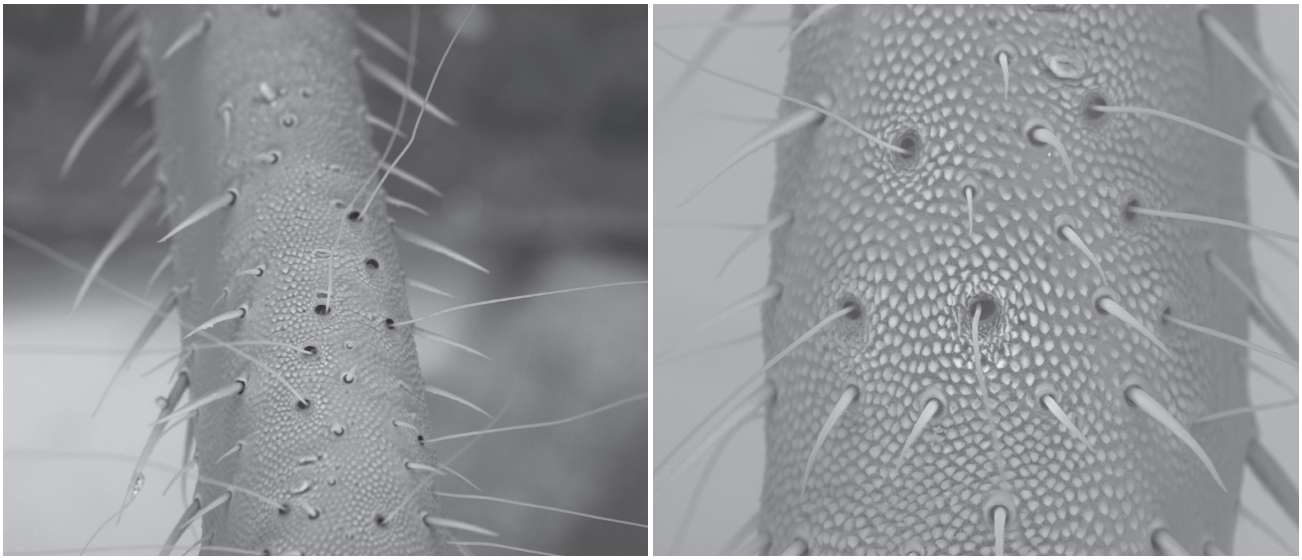
Most arachnids have six pairs of appendages at maturity. First and foremost are the appendages that give the subphylum Chelicerata its name: the chelicerae. The most common form of chelicera is a pair of claws consisting of a fixed upper finger and a movable lower finger. Because the arachnid has a pair of chelicerae, it therefore has two of these "hands," each with its own complement of fingers. This undoubtedly is extremely valuable during the manipulation and mastication of prey. Having two hands is certainly far more effective than having only one hand, especially when attempting to cut up food. Many arachnids have some version of these clawlike chelicerae. Exceptions include some mites that have evolved specialized chelicerae for piercing and sucking and spiders that have a single fang as part of each chelicera instead of the two clawlike fingers. In addition, spider chelicerae are even more specialized, being used like hypodermic needles to inject venom into prey. Some species of pseudoscorpions have a special structure on each pincerlike chelicera called a galea. The galea is a spinneret, delivering silk used for building nests. Male mites of some species may also possess specialized structures on the movable finger of their chelicera used for transferring sperm. This may be a fingerlike projection (the spermadactyl), or an opening that receives the spermatophore (the spermatotreme).

The next pair of appendages are the pedipalps. Pedipalps are basically modified legs, and arachnids have evolved an array of variations depending on how

Equipped with a fixed and a movable finger, each scorpion chelicera operates like a hand but is the functional equivalent of jaws. Since the scorpion has a pair of these chelicerae, food can be cut up and masticated during preoral digestion. During this process, digestive fluids are mixed with the masticated katydid, turning it into a liquefied mush. The scorpion ingests only the liquid food: hence the term "preoral digestion." Many arachnids have some version of this form of chelicerae.

1. Instead of having a fixed and movable finger, each spider chelicera has a single fang. These fangs are specialized for injecting venom. A small hole near the tip of each fang provides an opening for the venom to pass into the prey. The subterminal position of the hole reduces the chance of it becoming plugged. The fangs of mygalomorphs such as this tarantula are mostly downward pointing, somewhat like the teeth of a saber-toothed cat.

2. In araneomorph spiders like this jumping spider, the fangs work like pincers.



Long, delicate setae called trichobothria move if there is the slightest disturbance in the air. Each trichobothrium is set in a cuplike socket in which there are dendritic nerve endings. These hairs are sensitive to sound as well as air currents, allowing the arachnid to detect moving prey at a distance. In fact, the trichobothria are so sensitive that some arachnids are capable of detecting and capturing a buzzing fly in midair. These trichobothria are from the walking leg of an amblypygid.

the pedipalps are used. In wind spiders (Solifugae), the pedipalps are elongated and resemble long legs; however, they are used primarily in a sensory capacity. In addition, the solifuge palp has a special suctorial organ at the tip of each palp, which assists it in grasping prey as well as in climbing. Other pedipalps resemble claws or pincers. Scorpions, pseudoscorpions, amblypygids, and vinegaroons have robust pedipalps that are utilized in a variety of ways. Scorpions not only use their palps to grasp prey, but the male scorpion also uses his palps to hold the claws of the female while performing his courtship dance. Some species of pseudoscorpions have venom glands in their palps; therefore, they can simultaneously grasp and envenomate their prey. Vinegaroons use their lobsterlike claws for prey capture as well as for digging. The vinegaroon must have an efficient way to carry out the soil that it has loosened as it digs its burrow; the palps function like the bucket of a bulldozer. Harvestmen (Opiliones) have a wide range of different palps. *Protolophus* shows extreme sexual dimorphism in the size and structure of its palps. The males have large palps that can be used to wrestle a female prior to mating, whereas the females have small palps, each with two delicate fingers. Harvestmen such as *Sclerobunus* and tiny *Sitalcina* have raptorial palps with which to grasp prey. Each palp is armed with a row of spines; hence their family name Phalangodidae reflects the palp's resemblance to the line of soldiers holding long spears (the phalanx) used during Alexander the Great's campaigns. Mites have a variety of palps that may be modified for prey capture in predaceous mites, hold-fast structures in parasitic mites, or food filters in microbivorous species. The hollow specialized setae (eupathidium) on the tips of the palps of spider mites (Tetranychidae) have evolved to deliver silk instead of functioning primarily as sensory structures. The majority of arachnid palps are also armed with an array of specialized sensory hairs for the detection of water, food, disturbances in air currents, and temperature measurements. Finally, spiders present one of the most extreme examples of sexual dimorphism and specialized structure in their palps. The female has simple, leglike palps, while the male has complicated palps used for transferring sperm to the female.

The next four pairs of appendages are the legs. In wind spiders, vinegaroons, amblypygids, schizomids, palpigrades, and many mites, the first pair of legs is functionally sensory rather than being used for locomotion. In harvestmen, the second pair of legs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Given the diversity of arachnid lifestyles, it is not surprising that arachnids have evolved many kinds of pedipalps.

FACING PAGE:

1. Armed with impressive spines, the raptorial palps of the amblypygid *Paraphrynus carolynae* are its sole tool for capturing prey. These palps open on a horizontal plane.

2. The pedipalps of male spiders are highly specialized structures used for transferring sperm to the female. They must be loaded with sperm prior to courtship, a process called sperm induction.

3. Vinegaroons use their palps for digging and carrying soil. Living underground, they must dig their own burrows.

4. Pseudoscorpions have venom in the fingertips of their clawlike pedipalps. This cricket died within seconds of being stabbed with the tip of the pedipalp.

5. Some harvestmen like this *Sclerobunus* have raptorial, spiny palps used for prey capture. These palps open on a vertical plane.

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serves in this capacity. These sensory legs may be referred to as antenniform legs, especially the extremely elongated and delicate first pair of legs found in the amblypygids and the vinegaroons. Specialized setae on sensory legs detect chemical traces or air movement. The sensory legs of arachnids are held out in front as they walk, tapping the ground at frequent intervals in order to "taste" or feel the substrate in search of food, water, or mates. Hard ticks (Ixodida) have a specialized sensory structure on the tarsus ("foot") of the first pair of legs referred to as Haller's organ. This organ detects chemicals, heat, and humidity, assisting the tick in finding a host. As the tick waits on vegetation, it stretches out its front legs, "questing" for a host from which it will take a blood meal. Many arachnid tarsi are endowed with specialized hairs or structures that enable them to cling to vertical surfaces. In many spiders, brushlike scopula hairs serve this function, whereas pseudoscorpions have a little pad called the arolium between the two claws on each tarsus that allows them to walk on vertical surfaces or the underside of an object. This is an extremely useful adaptation, since pseudoscorpions frequently live and hunt on the underside of rocks.

Perception of the environment is dependent on and limited by the kinds of sensory structures present. An arachnid's cuticle is analogous in function to our ears, nose, taste buds, and temperature receptors. For many arachnids, the cuticle is as important as eyes are to humans. Long, delicate trichobothrial hairs are "touch-at-a-distance" receptors, sensitive to any air disturbance as well as low-frequency vibrations (sound), alerting an arachnid to the presence of predator or prey. A spider can capture a buzzing fly even if its eyes are completely covered. Slit sensilla on the legs may also be used for detecting and locating potential prey. These narrow slits in the cuticle are covered by a thin, easily deformed membrane. Substrate vibrations deform the slit and trigger a nerve impulse, allowing the arachnid to locate moving prey. A single spider may have more than 3,000 slit sensilla, most of which are located on its legs. Although different slit sensilla serve in different capacities, it is thought that some slit sensilla may also function as the "ears" of some arachnids. It is only logical that there is some receptor for spiders to "hear" the stridulation produced by a potential mate during courtship. Specialized hairs of many kinds cover the typical arachnid, including tactile hairs that detect touch and contact chemoreceptive ("taste") hairs that have an open pore at the tip for detecting molecules. Other structures in the cuticle may also be used in olfaction, such as tarsal (foot) organs consisting of small pits that may function primarily as hygroreceptors, detecting changes in humidity. Some structures may be specific to a certain group of arachnids. Only scorpions have the comb-shaped pectines, used for mechanoreception as well as for detecting chemical traces, and only the solifuges have malleoli (racquet organs) used for chemoreception.

For many arachnids, the eyes are of secondary importance compared to cuticular sensory structures. Despite this fact, many arachnids do have eyes, and these eyes can play a significant role in their ability to function. Arachnids have two types of eyes: the main (or median) ocelli and the secondary ocelli. The first type of eyes, the median ocelli, are seen as a pair of eyes on top of the cephalothorax in many orders of arachnids, including the scorpions, vinegaroons, amblypygids, harvestmen, and solifuges. Spiders also have main ocelli, the anterior median eyes, which in jumping spiders form detailed images and may be able to detect colors as well as ultraviolet light. The secondary ocelli correspond to the lateral ocelli in many arachnids. These were compound eyes in ancestral scorpions, as is still seen in their cousin the horseshoe crab. These compound eyes evolved into the simple ocelli that are found in modern scorpions. In some groups such as scorpions, there may be up to five lateral ocelli on each side of the cephalothorax. In many arachnids such as wolf spiders, the secondary ocellus has a tapetum which enhances sight in dim light and is responsible for the "eye-shine" of reflected light from these eyes.

Arachnid eyes are covered by a thin, transparent layer of cuticle that protects their eyes against damage and desiccation. Consequently, arachnids do not have eyelids and therefore cannot blink. Instead, jumping spiders clean their eyes with a quick brush using their fuzzy pedipalps to wipe off any dust. Because the front of the eye is covered with this layer of rigid cuticular exoskeleton, the front of the eye must remain stationary. However, in jumping spiders, the back of the anterior median eye can move. These eyes are roughly conical in shape, and the narrow base of the cone rests in a harness of muscles that can move it. Consequently, the area of the retina (at the base of the eye) can be shifted, aiming the vision of the jumping spider. Of course, the

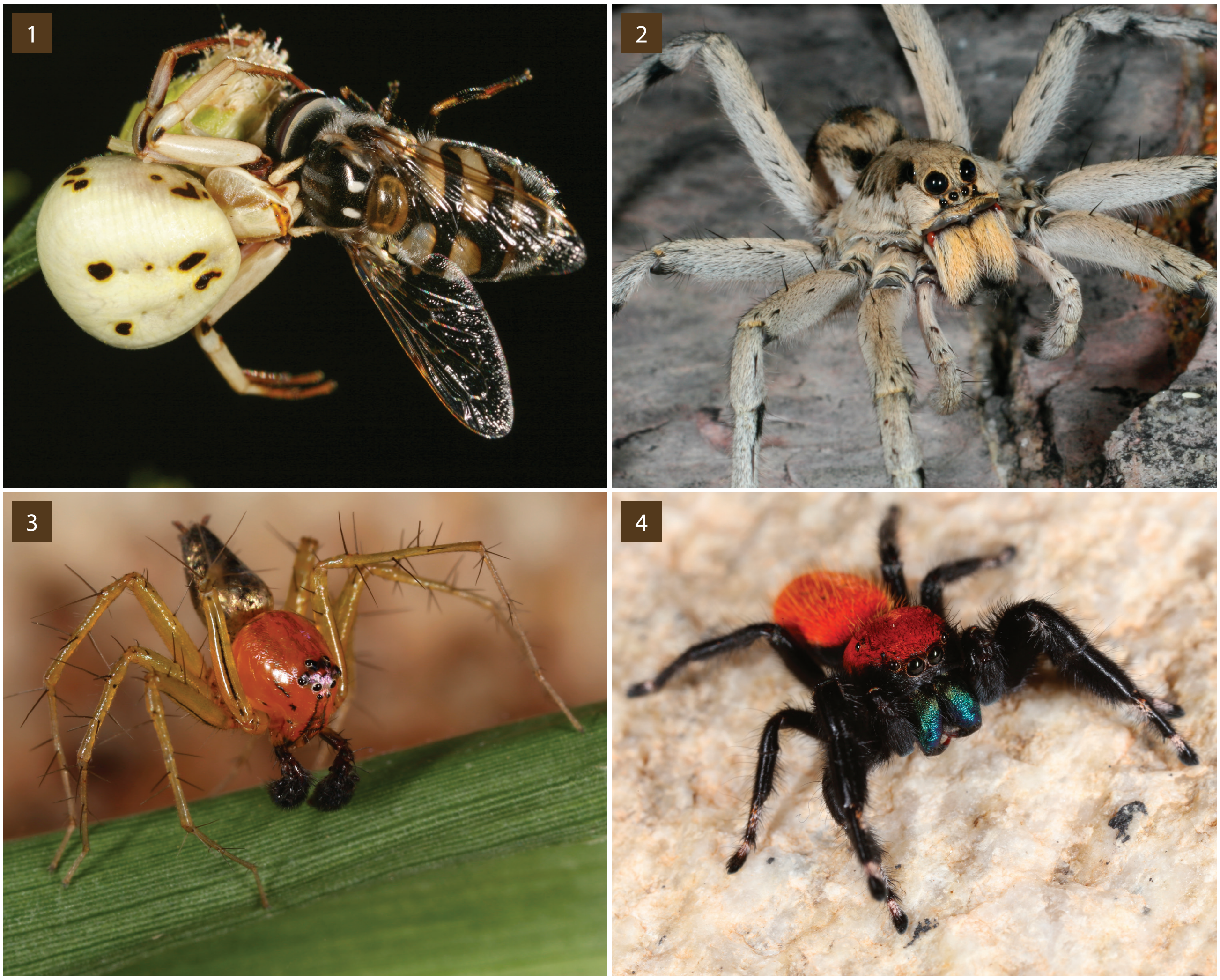
Extremely sensitive to light, scorpion eyes have their own built-in sunglasses. A larger pair of median eyes is in the center, flanked by several pairs of lateral eyes (in this case, 6 lateral eyes). Many other orders of arachnids share this general eye arrangement.

range of movement of the retina is somewhat limited, so the jumping spider orients its cephalothorax in order to better see any disturbance that the smaller eyes had detected.

Instead of forming high-resolution images as jumping spider eyes do, scorpion eyes are specialized for detecting very low levels of light. They even have pigment granules within their eyes that help shield their highly sensitive retinas during the day, comparable in function to sunglasses.

Many arachnids have other light-sensitive structures, although some of these are not fully understood at this time. Some of these are found in unexpected areas of the body, such as the metasoma (tail) of the scorpion, or the tarsi (feet) of snake mites.

The central nervous system (analogous to our brain and spinal cord) processes all the incoming sensory input and controls the response of the animal. In general, arachnids have two major components to their central nervous system: a supraesophageal ganglion or nerve mass (the brain) and a subesophageal ganglion or mass. The brain controls and receives input from the eyes, while the subesophageal ganglion or nerve mass controls the legs and pedipalps while receiving signals from cuticular sensory structures. In the case of scorpions, additional ganglia control other



Spiders have diversified into a bewildering array of more than 45,000 species. The arrangement of their eyes is a useful tool in identifying them to family.

1. Crab spiders (Thomisidae) have 2 rows of fairly small eyes, often on tubercles, 4 eyes to a row.

2. Wolf spiders (Lycosidae) see well even at night with their large posterior eyes. The 4 anterior eyes are located in a straight row just above the chelicerae.

3. Lynx spiders (Oxyopidae) have 6 conspicuous eyes arranged in a roughly hexagonal arrangement. Two tiny eyes are facing forward, just below the conspicuous eyes.

4. Jumping spiders (Salticidae) are characterized by their large, forward-facing anterior median eyes.

body regions. The cheliceral ganglion wraps around the digestive tube between the supraesophageal nerve mass and the subesophageal nerve mass. It controls the chelicerae. Seven other ganglia are located down the length of the scorpion's body: three in the mesosoma and four in the metasoma (tail). These are all connected by nerve cords and control the opisthosoma, including the action of the aculeus (stinger). Adult spiders have only two major ganglia: the supraesophageal and subesophageal ganglia. The supraesophageal ganglion consists of the "brain" in addition to the cheliceral ganglia. Together, these control the eyes as well as the chelicerae, pharynx, and venom glands. The subesophageal ganglion receives cuticular sensory input and controls motor neurons to the legs and extremities. However, the embryonic development of the spider reveals that this compact arrangement exists only after individual ganglia migrate into the prosoma from the abdomen during development and fuse together to form the impressive subesophageal ganglion. Most other arachnids have some variation of this arrangement. Harvestmen have a large neural mass that consists of two major sections. The protocerebrum together with the deutocerebrum controls the eyes and the chelicerae, while the subesophageal ganglion controls the palps, legs, and opisthosoma. In solifuges, the dorsal cerebral ganglion controls the eyes and chelicera, while the subesophageal ganglion controls the palps, walking legs, and the structures associated with the opisthosoma. Vinegaroons, tailless whipscorpions, schizomids, palpigrades, and mites share this arrangement with slight variations. Pseudoscorpions have a single cerebral ganglion surrounding the esophagus. It is remarkable that these relatively simple arachnid central nervous systems can handle complex tasks involving learning and memory.

Together, the respiratory system and the circulatory system deliver oxygen to the various organs and also remove carbon dioxide, a waste product of respiration. There are three possible respiratory systems found in arachnids: book lungs, tracheae, and cuticular respiration.

The most conspicuous of these are the book lungs, appearing as paired whitish areas just under the cuticle on the ventral surface of the abdomen. The number of book lungs varies with the type of arachnid. Scorpions have four pairs of book lungs while vinegaroons, amblypygids, and mygalomorphs have two pairs. Schizomids and many modern spiders have only one pair of book lungs. Each book lung consists of alternating layers of lamellae and air. The thin parallel layers are stacked such that they resemble the pages of a bound book, giving book lungs their name. Contained within the lamellae is the hemolymph (blood), which picks up oxygen and releases carbon dioxide while passing through the book lung. Because the cuticle of the lamellae is extremely thin, gas exchange can readily occur by diffusion as the hemolymph flows through these hollow, flattened structures. The many stacked layers maximize the available surface area needed for gas exchange. The book lung works somewhat like a bellows, powered by the pumping of the heart. As blood pressure increases during systole, the lamellae fill with hemolymph and the air spaces become compressed. These open up again during diastole, when blood pressure decreases. A small slit opening to the outside allows fresh air to enter the spaces between the lamellae. Although this slit can be opened or closed by muscular control, respiration in arachnids is considered passive compared with ours.

Book lungs are not very efficient; consequently, the arachnids who depend entirely on book lungs for oxygen cannot sustain a high activity level for long. Tarantulas, vinegaroons, and amblypygids are capable of extremely rapid sprints of short duration, but then they must stop while they "catch their breath," figuratively speaking. During these recovery periods, lactic acid is oxidized. A more efficient delivery system consists of tracheae. These hollow tubes open to the outside air and pass into the body, delivering oxygen directly to the interior. Arachnids and insects have independently evolved this system of respiration. Solifuges, ricinuleids (hooded tickspiders), harvestmen, pseudoscorpions, and some mites have tracheae. Many "modern" spiders have both tracheae as well as one pair of book lungs, and some species of spiders have only tracheae. Arachnids with tracheae can maintain a higher activity level for a longer time than arachnids that have only book lungs. However, even the tracheae of arachnids is still inefficient compared with our respiratory system, which employs a diaphragm and lungs.

The third method of respiration is through the cuticle. This is found primarily in tiny arachnids such as palpigrades and some mites. Cuticular respiration requires a large surface area compared with the mass of the animal, thereby limiting it to tiny animals. A thin cuticle is advantageous for this type of respiration. Palpigrades have an extremely thin, weakly sclerotized cuticle that is probably well adapted for cuticular respiration in moist environments.

The hemolymph of arachnids, like the blood of vertebrates, transports oxygen and carbon dioxide; however, instead of being red in color like our blood, arachnid blood is somewhat blue in color. This color is due to hemocyanin (containing copper) in their blood instead of hemoglobin (containing iron). Hemocyanin has been around for a very long time and is found in both mollusks and arthropods. The oxygen-carrying capacity of hemocyanin is significantly lower than that of hemoglobin. It remains a mystery why such a relatively poor transport molecule should be conserved for so many millions of years. The answer may lie in the fact that arachnids do not use specialized cells to package the hemocyanin; these enormous molecules are freely circulating in the hemolymph. In contrast, hemoglobin is contained within specialized red blood cells whose sole purpose is to transport hemoglobin. If large numbers of the red blood cells are lysed (broken open), the free hemoglobin is actually toxic to many organs of the body. In fact, free hemoglobin can kill the organism. Ultimately, there may be a greater net efficiency in having to manufacture only the transport molecule without complex cellular packaging; however, there must be a concurrent low metabolic rate for this strategy to succeed. Low oxygen use, a large food storage capacity, and long periods of inactivity may collectively contribute to a survival strategy of low energy use. This strategy may make the difference between life and death during lean times.

The circulatory system works with the respiratory system to supply oxygen and energy to all parts of the body. Humans have a closed circulatory system whereby blood is enclosed within arteries and veins. Arachnids have a circulatory system which is partly open and partly closed. The heart is tubular in shape and lies lengthwise inside the opisthosoma. It pumps hemolymph to the arteries, which in turn branch into smaller vessels. From there, the oxygenated blood is distributed throughout the body, right to the tips of the extremities. The branched arterial blood vessels are open at the end, allowing oxygenated hemolymph access to the tissues. The arachnid arterial system is primarily a closed system, open only at the tips of the smallest arterial vessels; however, the arachnid's return blood flow system is very different from ours. Arachnids do not have a venous system of blood vessels. Instead, the hemolymph flows freely within the body, traveling along a gradient of progressively decreasing pressure. Eventually the hemolymph collects in spaces called lung lacunae and from there is routed through the book lungs (if there are book lungs) before returning to the heart.

All the energy for fueling this system must come from food. Most but not all arachnids are predators. Noteworthy exceptions are the harvestmen (Opiliones) and some mites. Many species of harvestmen are omnivorous, feeding on an incredibly wide variety of plants, animals, and fungi. Mites include a vast array of different species with different lifestyles. Among mites are predators, parasites, fungivores, herbivores, and detritivores. Harvestmen and some species of mites ingest particulate food, but most arachnids ingest only liquefied predigested food.

Wastes are concentrated and excreted by several systems. Intestinal cells within the digestive diverticula synthesize guanine, a nitrogenous waste product, and route it into the intestine to be excreted with the feces. Guanine is relatively insoluble in water and so precipitates out as a white paste, thereby conserving water. Another important system for nitrogenous waste removal consists of the Malpighian tubules. These tubules are found between the gut diverticula and empty out into the intestine. Their role is to extract nitrogenous wastes from the hemolymph and convert these wastes into the largely insoluble guanine, adenine, hypoxanthine, and uric acid, to be excreted later. Malpighian tubules are found in many orders of arachnids, including spiders, scorpions, vinegaroons, and others. A final set of excretory organs consists of the coxal glands. These glands open at the base (or coxa) of the legs and are probably important in ion and water balance. Fluid from these glands is released only during feeding and may assist in processing food for digestion.

Arachnids have a stunning variety of reproductive strategies. The transfer of sperm may involve the pedipalps (spiders), an intromittant organ (harvestmen and some mites), or spermatophores (scorpions, amblypygids, vinegaroons, pseudoscorpions, some solifuges, and some mites). Some transfer sperm directly from the male's genital opening to the female (some solifuges). In some arachnids, no mating is necessary; these species are parthenogenetic and consist only of females. Finally, in some species, males can be produced from unfertilized eggs and females are produced from fertilized eggs. The many different methods of reproduction reflect the fact that arachnids have been diversifying and adapting to changes on this planet for a very long time. The ability to colonize ephemeral habitat with only one individual (as is possible in parthenogenetic species) may be more important than the ability to recombine genes (as is seen in sexual reproduction).

Arachnids have been on Earth for at least 400 million years. In an attempt to tease out the story of their evolution, several different types of data are considered. Morphology, embryology, and DNA

1. The spermatophore of the vinegaroon was deposited by the male and picked up by the female.

2. Harvestmen transfer sperm directly via an intromittent organ. The male in this pair is on the right.

3 and 4. The pedipalp of the male spider is specialized for transferring sperm to the female. The male spider must load his pedipalps with sperm prior to courting the female. The male is the smaller of this mating pair.

Eurypterus remipes. Eurypterids, also known as sea scorpions, were distant relatives to our modern arachnids. The chelicerates split into two major groups: one clade contained eurypterids and horseshoe crabs, while the other clade included all the arachnid orders.

sequencing all contribute evidence that can be used to construct cladograms depicting the phylogeny, or evolutionary history, of a group of related organisms. The addition of fossils from extinct taxa presents additional challenges. Fossils cannot provide DNA or developing embryos; they are limited to the partial morphology of an organism. What they do provide is a glimpse of creatures that may have been extinct for hundreds of millions of years, creatures whose lives from the distant past are intertwined with the lives of their living relatives today, linked forever by their phylogenetic relationships. The inclusion of fossils may therefore provide additional pieces of the puzzle, filling gaps in the evolutionary picture.

The process of constructing cladograms may at times resemble the story of the blind men and the elephant; each cladogram may be significantly different from the others depending on what data are included and how that data are analyzed. Consequently, there is no consensus on the exact phylogeny of the arachnids. Despite this, some interpretations of arachnid evolution do have support across a broad base.

The first challenge consists of determining where chelicerates belong in relation to other arthropods. One classification scheme placed arachnids, horseshoe crabs, and sea spiders on one branch (the Chelicerata) and all the other arthropods, including crustaceans, insects, and myriapods, on the other branch (the Mandibulata). Another analysis incorporating molecular evidence (RNA and DNA) as well as data on embryonic development has generated a different model. The Arthropoda once again split into two groups, but in this case one clade consists of the Parahexapoda (including chelicerates and myriapods) while the other clade includes the Pancrustacea (including crustaceans and Hexapoda, such as insects).

The earliest record of a possible chelicerate dates from the Cambrian Period, 542 to 488 million years ago. Better techniques for processing fossils, including improved imaging technology, have revealed detailed structures locked away in rock for millions of years. Orsten limestone nodules from Sweden contain the remains of many fossilized invertebrates. The chitinous cuticles of these tiny invertebrates were phosphatized and silicified, preserving them in a matrix of limestone. The limestone can be removed with acid, leaving the microscopic fossils intact. Electron microscopy is then used for generating images of these minute and ancient fossils. A tiny protonymph larva of a sea spider (Pycnogonida) dating from the Upper Cambrian Period was discovered in this way. This larva possessed chelicerae, also known as cheliphores in sea spiders. Only 270 micrometers in length (just over a quarter of a millimeter) and approximately half a billion years old, this larva provides us with evidence that chelicerates appeared very early in the Paleozoic Era.

The exact position of sea spiders within the arthropod cladogram remains controversial. However, many agree that the remaining chelicerates break down into two major clades. Most horseshoe crabs (Xiphosura) along with the extinct sea scorpions (Eurypterida) and Chasmataspidida (which shared characteristics with both sea scorpions as well as horseshoe crabs) form one clade. The sister group to this aquatic clade of chelicerates contains all twelve living arachnid orders as well as four extinct orders of arachnids. It is noteworthy that with the exception of some derived species of aquatic mites and one species of aquatic spider, virtually all the extant species of arachnids are terrestrial. This is in contrast to those most ancient chelicerates (horseshoe crabs, sea scorpions, etc.), which lived exclusively in a marine environment. The aquatic lifestyle of the earliest creatures reflects the story of life on Earth; the marine environment was the cradle of these early life forms in part because the land was still barren and inhospitable. The colonization of land by plants started in the Ordovician Period 488 million years ago with nonvascular plants such as mosses and liverworts. As plants continued to evolve during the remainder of the Paleozoic Era, the face of the land changed. Plants were the catalyst for the diversification of terrestrial arthropods, directly providing food for herbivores, as well as indirectly supporting detritivores and predators, including arachnids. Sometime before the Silurian Period the ancestral arachnids probably started living on land. Their descendants diversified, filling a variety of newly available niches. Many of today's arachnid orders made their first appearance during the Silurian, Devonian, and Carboniferous periods. The following is a list of the arachnid orders along with the time period during which they are known to have appeared, as seen in the fossil record; however, this fossil record may demonstrate "sampling bias." The extremely fragile creatures such as palpigrades may only rarely become preserved as fossils, compared with more durable arachnids such as the scorpions.

A clade referred to as the Tetrapulmonata is well accepted among many arachnologists. As its name would imply, the Tetrapulmonata group includes several orders that possess four book lungs. These include Amblypygi (tailless whipscorpions), Thelyphonida (vinegaroons), Araneae (spiders), and the extinct orders Haptopoda and Uraraneida. The group also includes Schizomida (short-tailed whipscorpions), although they have only one pair of book lungs. The spiders considered closer to the ancestral form, such as Liphistius and the mygalomorphs, have two pairs of book lungs. Other spiders that have only one pair of book lungs (or none) are thought to be derived and

EXTANT ARACHNID ORDERS

Scorpiones (scorpions)—Silurian
Pseudoscorpiones (pseudoscorpions)—Devonian
Opiliones (harvestmen)—Devonian
Acariformes (mites)—Devonian
Amblypygi (tailless whipscorpions)—Carboniferous, or possibly Devonian
Araneae (spiders)—Carboniferous
Thelyphonida (Uropygi,vinegaroons)—Carboniferous
Schizomida (short-tailed whipscorpions)—Carboniferous
Solifugae (wind spiders or camel spiders)—Carboniferous
Ricinulei (hooded tickspiders)—Carboniferous
Parasitiformes (ticks and mites)—Cretaceous
Palpigradi (microwhipscorpions)—Tertiary

EXTINCT ARACHNID ORDERS

Trigonotarbida—Silurian-Permian
Urananeida—Devonian-Permian
Phalangiotarbida—Devonian-Permian
Haptopoda—Carboniferous

Eleven arachnid orders at a glance:

1. Scorpiones
2. Pseudoscorpiones
3. Schizomida: short-tailed whipscorpions
4. Thelyphonida (Uropygi): vinegaroons, whipscorpions
5. Solifugae: wind spiders
6. Palpigradi: microwhipscorpions
7. Amblypygi: tailless whipscorpions
8. Araneae: spiders
9. Opiliones: harvestmen
10. Acariformes: mites
11. Parasitiformes: ticks
12. Parasitiformes: opilioacarids and other mites

The Acariformes and the Parasitiformes both contain mites. However, it appears that these two major groups of mites may have evolved independently and might not be closely related.

The order Ricinulei has not been included since it does not occur in the southwestern United States. Although hooded tickspiders historically occurred in Texas, they have not been found in the United States in recent times.

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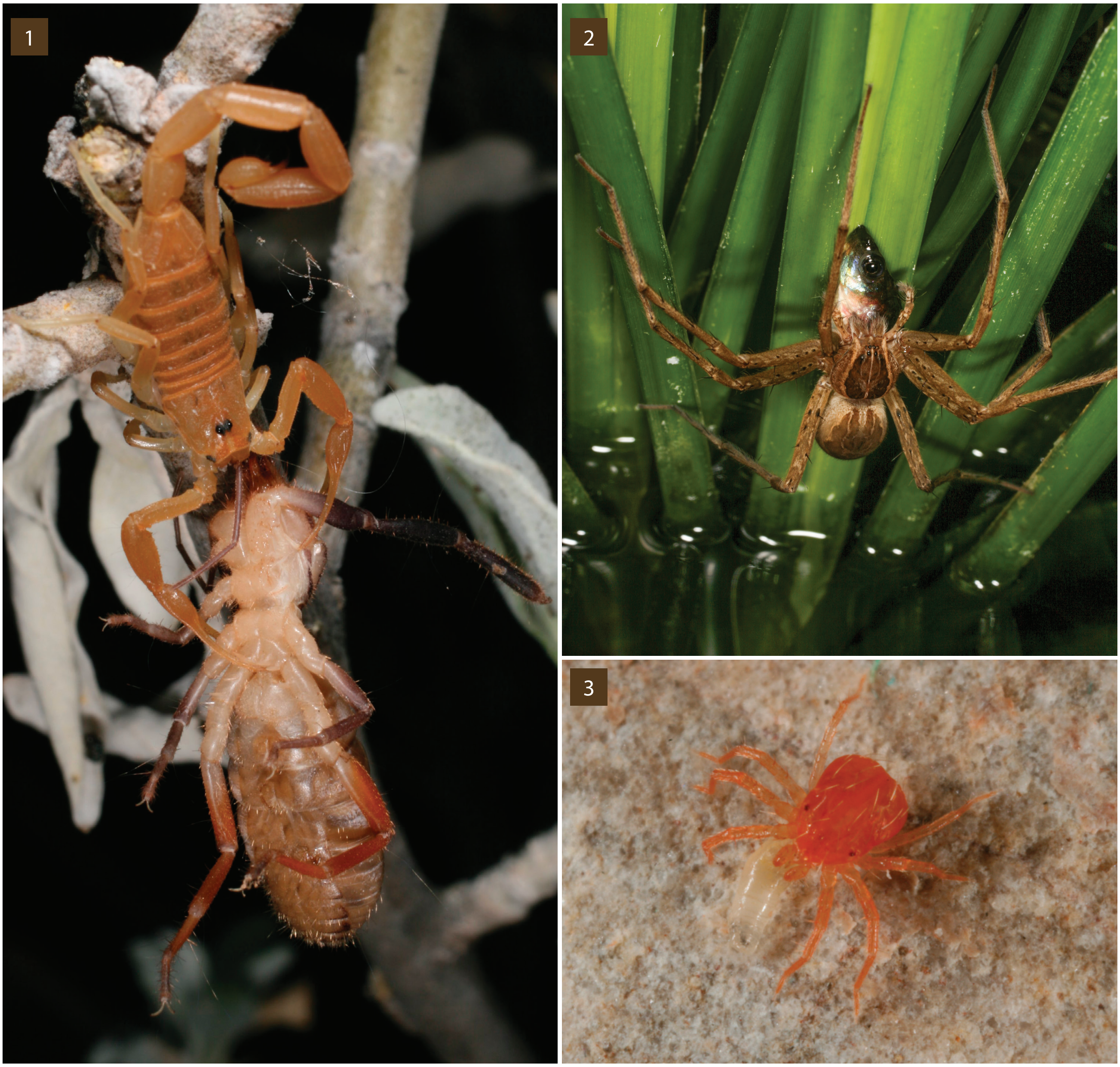
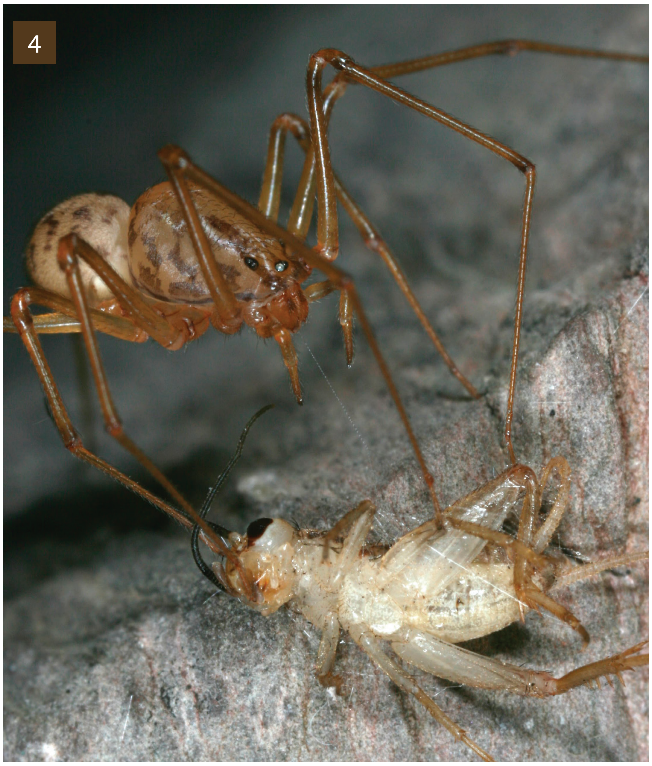


Millions of years of diversification and adaptation have produced a stunning repertoire of hunting strategies among the arachnids.

1. The business end of the scorpion is at the tip of its "tail," armed with a needle-sharp aculeus and a supply of venom. This scorpion has been able to overpower a solifuge as large as itself.

2. Fishing spiders like this *Tinus peregrinus* capture fish just at the surface of the water. After immobilizing its prey with venom, the spider must carry it up out of the water in order to feed; otherwise the enzymes needed for predigestion would be diluted out.

3. *Anystis* mites also use venom for prey capture. Known as whirligig mites, these little predators run rapidly in circles hunting other small invertebrates like this fly larva.



4. Spitting spiders capture prey by squirting two streams of sticky glue and silk from their tiny fangs, fastening the prey to the substrate.

5. Armed with massively powerful chelicerae, the solifuge energetically attacks and tears apart its prey. These solifuges have no venom; therefore, they must use speed and strength to overpower prey.

6. Using aggressive chemical mimicry, bolas spiders release fake female moth pheromones in order to lure male moths within striking distance. Once the male moth flies close enough, the bolas spider swings the sticky blob, hits the flying moth and captures her dinner. Photo by Matt Coors

more modern from an evolutionary perspective. The order Uraraneida is of special interest. These extinct arachnids date from the Devonian Period through the Permian Period, 416 to 251 million years ago. They share several characteristics with the Araneae (spiders), including silk glands and a naked cheliceral fang. However, this order differed from spiders in that it had a flagellum (similar to a vinegaroon's) and lacked spinnerets. Uraraneida is considered a sister group to Araneae and therefore by inference provides clues regarding the ancestors of spiders.

A controversial area of arachnid phylogeny involves the Acari (ticks and other mites). Traditionally, mites were considered to belong to a single group based in part on having a hexapodal (six-legged) larva. Within this group were two superorders: the Acariformes (also known as Actinotrichida) and the Parasitiformes (also known as the Anactinotrichida). The Acariformes is a highly diverse group containing a vast number of species found in almost every conceivable niche throughout the globe. Included within the Acariformes are the "typical" mites, such as red spider mites and velvet mites. The earliest unquestioned records of acariform mites date to the Devonian Period, 416 to 359 million years ago, preserved in the Rhynie chert of Scotland and the Gilboa Formation in New York State. Molecular data suggest that they occurred even earlier, during the Silurian Period, 444 to 416 million years ago. In contrast to the acariform mites, the earliest parasitiform mites do not appear until much later, during the Mesozoic Era, 251 to 65 million years ago (contemporary with the dinosaurs). The Parasitiformes contain the Ixodida (ticks), Mesostigmata (including many phoretic and parasitic mites), Holothryrida, and Opilioacarida (the "harvestmen" mites). Altogether the parasitiform mites make up only about one-third of the total number of described Acari.

Independently generated cladograms based on molecular data compared with cladograms that include fossil data both strongly support the concept that Acari is not monophyletic; in fact, it most likely evolved from two separate lineages of arachnids. The Acariformes are an ancient group probably most closely related to the Solifugae (camel spiders). The Parasitiformes are a more recently evolved group. They may be more closely related to Ricinulei (hooded tickspiders) or possibly to pseudoscorpions than they are to the acariform mites; however, as mentioned earlier, agreement has not yet been reached on the exact structure of the arachnid family tree, so further developments may yet modify the model.

All the extant orders of arachnids are included in this volume except for the hooded tickspiders (Ricinulei), which do not currently occur in the southwestern United States. Phalangiotarbida, Trigonotarbida, Uraraneida, and Haptopoda have become extinct, and are therefore also excluded.

From the Equator to the Polar regions, arachnids can be found on every continent of our planet in every imaginable environment. They can be found in deserts and in lakes, in jungle canopies and in underground caves. They ride the winds thousands of feet above the earth and survive buried deep in the soil. They have survived profound changes on the face of the planet during the past 400 million years. Land masses have converged forming supercontinents, only to break up and drift apart again but in a different configuration. Mountains rise up and climates change. Jungles, savannas, and deserts appear and disappear; nothing is spared from change over time. In addition to abiotic challenges, millions of other species of organisms have evolved during this period. Some were prey, some were predators, and some were competitors.

The arachnids described in the following chapters are the living legacy of these millions of years of diversification and adaptation. Their defense mechanisms, reproductive strategies, and hunting methods have been refined and perfected by natural selection over the eons, at times producing extreme solutions to challenging problems.

Ironically, natural selection has sometimes produced diametrically opposite solutions to a particular problem. For example, many arachnids use mimicry as protection against predation. This mimicry may take the form of camouflage, making the animal virtually invisible in its environment. An opposite kind of mimicry may actually attract attention with bright warning colors, imitating the appearance of stinging insects such as wasps. In another example of evolution producing opposite extremes, some spiders may be solitary and fiercely territorial, while other species even within the same family may be completely social, cooperatively catching prey and collectively raising their young. The metabolism and reproductive rates of arachnids may demonstrate opposite extremes as well. Ticks have such a slow metabolism that some have been known to survive for 10 years without food, while some mites can fit an entire life cycle into a brief 34 hours.

Arachnids present a puzzling paradox. By necessity, their brains are quite tiny, and therefore their cognitive capabilities are presumed to be correspondingly small. However, some arachnids have unequivocally demonstrated a degree of plasticity in their behavior and a remarkable capacity for storing information and problem solving that seems impossible given these minute brains.

It is in the categories of hunting and defense that arachnids have evolved almost every imaginable strategy, and even a few strategies that may be beyond the imagination. In the realm of hunting, trapdoor spiders pop up out of the ground, raft spiders capture fish at the surface of the water, pirate spiders lure their quarry by imitating prey, bdellid mites "tag" their prey with silk, oecobiid spiders race around giant ants in order to hobble them, bolas spiders lure their prey with fake pheromones, pseudoscorpions have venom in their claws, scorpions have venom in their "tails," and spitting spiders spit out two narrow streams of glue mixed with silk. Of course, web spiders construct an ingenious variety of traps and snares using the phenomenal material we call silk. In the line of defense, vinegaroons and schizomids spray acetic acid, green lynx spiders spray venom, harvestmen release a veritable cocktail of repugnant chemicals, and crab spiders produce pigment to match the color of the flowers they sit in.

Arachnids present the perfect combination of form and function, illustrating the integration of anatomy, physiology, chemical capabilities, and behaviors. These creatures are simultaneously ancient and modern, living fossils in some respects and nimble opportunists in other ways. In the following chapters, their stories will rival the best science fiction fantasies. Welcome to the world of the arachnids.

This tiny *Bellota* from Arizona is only about a tenth of an inch (3 mm) long, the same size as the shiny black ants it mimics. Despite their small size, jumping spiders demonstrate a surprising degree of intelligence.