# ARACHNIDS

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## GLOSSARY

**booklungs** One to four pairs of abdominal respiratory organs consisting of a thin, multifolded membrane (the book's "pages") over which blood circulates and that is open to an air-filled cavity on the outside, itself open to the exterior via a spiracle. Gases passively diffuse back and forth across the membrane.

**chelicerae (chelate)** The first pair of preoral appendages. They are at most three segmented, usually two, and usually the distal segment acts against the penultimate to grab or hold prey or objects. If the basal segment has a finger-shaped outgrowth against which the distal segment operates, the chelicerae are chelate (as in scorpions or harvestmen). If not, the chelicerae are subchelate, as in spiders and tailless whip scorpions. In parasitic mites the chelicerae are modified into piercing stylets.

**monophyly** A true, historical, evolutionary lineage consisting of an ancestor and all of its descendants; defined by shared, derived characters.

**ovoviviparous** Young are born alive, but the mother simply retains eggs within her body until they hatch.

**paraphyly** A group consisting of an ancestor and only some of its descendants. Defined by primitive characters.

**pedipalps** The second pair of preoral appendages. They are multisegmented and primitively leg-like. They may be raptorial or sensory (like antennae) or used as walking legs.

**phoresy** A method of long-range dispersal in which the dispersing animal attaches itself to another animal (e.g., beetle, wasp, or bird) that carries the disperser along with it until the disperser drops off or disembarks.

**polyphyly** A group in which the most recent common ancestor of the included taxa is excluded from the group. Defined by convergent, nonhomologous characters.

**spermatophore** A chitinous container produced by the male to hold sperm. It may be attached to the substrate for the female to find or passed to the female from the male during mating.

**spinnerets** Usually three, rarely four pairs of modified terminal abdominal appendages in spiders bearing one to hundreds of hollow spigots from which silk is drawn.

**tracheae** A system of hollow, branched or unbranched air-conducting tubes used for respiration, opening via abdominal spiracles. They may or may not extend into the cephalothorax or legs.

**trichobothria** Long, delicate, slender setae set in broad, shallow innervated sockets in the cuticle. Trichobothria are sensitive to vibration or near-field air movement and are a major sense organ of arachnids.

TABLE I

| Latin name | Common name | No. of Families | No. of Genera | No. of Described species |
|---|---|---|---|---|
| Arachnida | Arachnids | 648 | 9241 | ±92,680 |
| Araneae | Spiders | 108 | 3200 | ±37,000 |
| Palpigradi | Micro-whip scorpions | 2 | 6(5) | 80 |
| Uropygi | Whip scorpions | 1 | 16 | 101 |
| Amblypygi | Whip spiders, tailless whip scorpions | 5 | 20 | 126 |
| Schizomida | Schizomids | 2 | 31 | 195 |
| Solifugae | Wind spiders | 12 | 153 | 1,065 |
| Pseudoscorpiones | Pseudoscorpions | 24 | 430 | 3,100 |
| Ricinulei | Ricinuleids | 1 | 3 | 53 |
| Opiliones | Harvestman | 44 | 1554 | ±4,500 |
| Scorpiones | Scorpions | 18 | 156 | 1,260 |
| Acari | Mites, ticks | 431 | 3672 | 45,200 |

ᵃ Modified from Adis and Harvey (2000), with data for the Acari from Walter and Proctor (1999).

Arachnida is a class of the huge phylum Arthropoda. Familiar arachnids are spiders, scorpions, ticks, mites, and harvestmen, but arachnids include many lesser-known terrestrial arthropod groups as well.

## I. OVERVIEW OF ARACHNIDA

The known diversity of arachnids is approximately 640 families, 9000 genera, and 93,000 species (Table I), but there are many thousands of new mite and spider species still undescribed and hundreds to thousands of undescribed species in the remaining orders. Together with the marine horseshoe crabs (Xiphosura) and sea spiders (Pycnogonida), arachnids comprise the arthropod subphylum Chelicerata, named for the characteristic first pair of preoral appendages, the chelate, or pinching, mouthparts. In some arachnid groups the chelicerae are further modified into venomous fangs or piercing stylets to suck body or plant fluids. Arachnids are the only terrestrial chelicerates. Along with the insects, arachnids are by far the most species-rich, abundant, and widely distributed terrestrial arthropods. Acarologists (scientists who study mites and ticks) estimate that there may be as many mite species as beetles, implying that total extant arachnid diversity may exceed 1 million species. Arachnids are an important component of every terrestrial ecosystem, but, apart from several specialized mite lineages, none are aquatic or marine. Although most arachnids share many ancestral similarities in body plan and lifestyle, many extremely specialized groups exist, especially among the mites (Acari).

Although arachnids are commonly mistaken for some sort of peculiar insect, the groups are quite distinct and only distantly related. Arachnids have four pairs of walking legs rather than three (except the young stages of mites and the related Ricinulei), only two (not three) major body parts, and simpler chelate mouthparts rather than the more complex feeding apparatus of insects. The anterior body part is specialized for locomotion and the posterior for digestion and reproduction. Arachnids lack the wings, antennae, and compound eyes usual in insects. In many groups the first pair of walking legs (e.g., amblypygids, uropygids, schizomids, solifuges, palpigrades, and many mites) are elongate and function in much the same way as insect antennae. Figure 1 depicts a consensus view of the position of arachnids in the arthropod evolutionary tree.

Arachnids and hexapods (which insects dominate) differ in fundamental ways, possibly because their marine ancestors were already distinct lineages in the Silu-
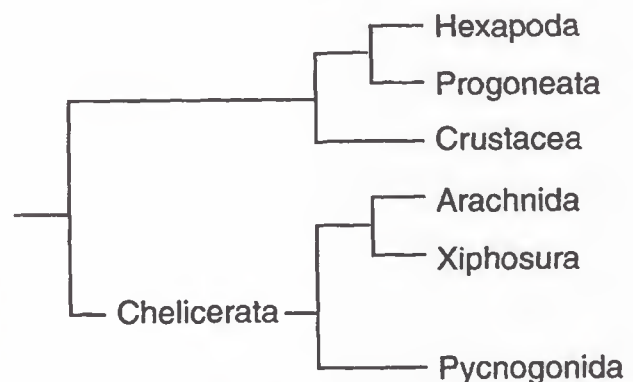


FIGURE 1  Phylogenetic position of Arachnida among arthropods.

rian and both colonized land independently. They therefore solved the fundamental challenges of terrestrial existence (support, breathing, water balance, reproduction in dry environments, and nitrogenous waste management) in different ways. The arachnid skeleton is hydraulic; arachnids, except scorpions and pseudoscorpions, lack extensor muscles at key joints. Instead, the animal pumps blood into the limb to extend it. The basic arachnid uses two (or four) pairs of book lungs (gas-permeable, gill-like membranes with blood on one side and open to the air on the other) to exchange carbon dioxide for oxygen rather than tracheae. Many arachnids possess rudimentary tracheal systems that supplement or replace book lungs, but ventilation is passive, not active. Unlike insect tracheae, arachnid tracheae generally do not ramify throughout the entire body or penetrate inside body cells. For all these reasons, insect tracheae more efficiently deliver oxygen directly to tissue, and insects in general can lead more energy-intensive lifestyles than arachnids. Arachnids have significantly lower metabolic rates than other terrestrial arthropods, especially insects. Whereas male insects transfer sperm directly to the female using an intromittent organ, in most arachnids males either ejaculate onto a special structure and carry the sperm mass with a specialized appendage until the female is encountered or they deposit the sperm mass in a specially built receptacle (spermatophore) fixed to the substrate, which the female picks up. Major exceptions include the harvestmen, astigmatic mites, and spider mites, which transfer sperm to the female by means of an intromittent organ, and the water mites (Prostigmata: Hydracarina), which transfer sperm directly by opposing the male gonopore to the female gonopore.

Arachnids are peculiar among animals in using guanine (three nitrogen atoms per molecule) as well as the much more common uric acid (two nitrogen atoms per molecule) to eliminate nitrogenous wastes. Insects have compound eyes, which provide relatively excellent vision. Arachnids lost compound eyes early in their evolutionary history but retain usually one to five (commonly four) pairs of simple eyes, much inferior in acuity to compound eyes. Schizomids, palpigrades, ricinuleids, mites, and other mainly litter-dwelling arachnid groups are nearly always blind. Vision is much less important to arachnids than vibration. Many structures (slit sense organs, trichobothria, and lyriform organs) are specialized to detect minute vibrations and slight air currents.

Arachnids are also peculiar in that species of most arachnid groups digest food externally. They have a strong pumping stomach that rhythmically vomits and sucks digestive juice through a preoral cavity formed by the basal articles of the pedipalps back and forth over their prey. The process continues until only the hard, indigestible parts of the prey remain. Only liquids or very small particles are actually ingested. Some major groups of arachnids have internal digestion, however. Opilionids and several groups of mites are particulate feeders, and parasitism of plants, vertebrates, and invertebrates has arisen repeatedly in the mites. External digestion is a major obstacle to life in fresh water or the sea. Arachnids are also notable for their ability to withstand starvation. Fasts of weeks or even months are routine for larger arachnids. Some scorpions and mygalomorph spiders live for more than 1 year without food, and adult soft ticks (Argasidae) can survive for years without feeding.

## A. Reproduction and Growth

Like all arthropods, arachnids grow by molting their exoskeletons and expanding the larger skin beneath with blood pressure before it hardens into the usual tough covering. The number of molts to maturity varies widely between 3 and 10–12; five is perhaps the most common. Life spans also vary greatly. The majority of mites and spiders live less than 1 year, but several years is common among the larger forms, and mygalomorph spiders can live 20–30 years in captivity. Some arachnids cease molting at adulthood but others continue to molt periodically until death.

The ancestral reproductive pattern of sperm transfer is via spermatophore, modified in spiders, harvestmen, mites, and ricinuleids. Except among permanently social species and many mites, the sex ratio is equal, and parthenogenesis is rare. In the vast majority of species, males and females meet only to mate; cohabitation and parental care are uncommon. Nevertheless, various spiders, scorpions, schizomids, uropygids, and amblypygids may carry and feed their young, and in some harvestmen the male cares for the eggs in a specially built nest. Pseudoscorpion females nourish eggs with secretions from their bodies, and scorpions bear only live young. Females commonly guard their eggs until they hatch, but the young are usually abandoned soon thereafter. Mites are more diverse in reproductive strategies than nonacarine arachnids.

## B. Ecology

Despite huge numbers of species (Table 1), arachnid biology is coherent in many ways (even though exceptions to nearly every generalization exist). Most arachnid orders consist of fluid-feeding predators, and predation still dominates these groups today. However, opilionids and two of the three orders of mites are

particulate-feeders on detritus, fungi, and small invertebrates. Additionally, parasitism of vertebrates, invertebrates, and plants has arisen numerous times within the Acari and radiations within these lineages account for most of the 45,000 described species of mites.

Non-acarine arachnids tend to be at the top of the terrestrial invertebrate food chain wherever they occur. At one site in Israel, mites comprised 35% of the total soil arthropod population; in the Amazon ranges from 35 to 55% have been reported. Some harvestmen eat dead or decaying animal or plant material. Arachnids are generally nocturnal, despite numbers of diurnal harvestmen, spiders, and mites. Nocturnal forms hide in dark crevices and burrows during the day; several orders are morphologically specialized to inhabit small spaces. With the exception of the wind spiders (Solifugae), arachnids tend to be torpid and sedentary—none fly, for example, nor do any move constantly like ants or other active insects. The basic arachnid forages with a "sit and wait," solitary strategy. They move rarely and wait for prey to encounter them. Prey is then seized with a quick strike and immobilized. Highly organized social systems are known only in a few spiders, but loose aggregations (spiders, harvestmen, and pseudoscorpions) are not uncommon, usually in response to high prey density or limited refugia. Most arachnids are well adapted to last for long periods (weeks or months) without food; in the laboratory some have survived for more than 1 year. Only jumping spiders among arachnids have notably good vision; otherwise, they orient primarily via vibrations and touch.

Arachnids occupy all terrestrial habitats—deserts, forests, tundra, grasslands, mountaintops, soils, litter, caves, etc. Hydrachtinid mites (approximately 5000 species) are important components of most freshwater ecosystems; other mites are parasites of marine organisms, whereas others inhabit marine sediments, including the deepest oceanic trenches. Otherwise, arachnids are exclusively terrestrial. A few groups, such as scorpions and wind spiders, conserve body water as well as any arthropod and thus tend to dominate in deserts. The majority needs moist conditions to survive. Schizomids, palpigrades, and ricinuleids are apparently restricted to the interstices of moist tropical and subtropical leaf litter or equally constant and moist habitats.

## C. Phylogeny and Taxonomy

The most commonly encountered arachnids are spiders, scorpions, harvestmen, and mites, but the class contains seven smaller groups of terrestrial arthropods less familiar to the general public (Fig. 1). The largest and heaviest arachnid is the African scorpion *Pandinus imperator*,

which may reach a length of 18–20 cm. The smallest are perhaps the gall mites at 80 $\mu$m. No group of arachnids is well-known by vertebrate, butterfly, or vascular plant standards. Popular manuals are available for only a smattering of the most common species of spiders in Europe, North America, and Japan; all others require technical literature and specialist knowledge to identify. Myriad species are undescribed and undiscovered; at best, the approximately 93,000 known arachnid species are but one-third of the probable total, and probably much less. Most undescribed arachnid species are mites.

The study of arachnids is called arachnology. The principal international scientific society for nonacarines has approximately 600 members but many more belong only to regional societies. The taxonomy of arachnids is still a monumental task and an obstacle to better ecological and biotechnological understanding of arachnids, but the number of arachnid taxonomists is small and decreasing, and new students are not being trained. There are no comprehensive arachnology texts appropriate for university teaching (three exist for Acari), although modern "biologies" are available for spiders, scorpions, solifuges, pseudoscorpions, and various aspects of mite biology.

## D. Paleontology

Arachnida were among the earliest terrestrial animals. The marked similarity between fossil and recent forms in overall body plan and morphology suggests few changes over hundreds of millions of years. The earliest sites for terrestrial arachnids are Early Devonian (400 Ma) and Late Silurian (414 Ma); the extinct arachnid order Trigonotarbida figures prominently, but mites are also present. The fossil record of all arachnids is comparatively poorly known. The 13 living and extinct orders are still known from less than 50 major time horizons since the Silurian; gaps remain more common than fossils. Arachnids seem to have invaded land in the Silurian and reached a pinnacle of ordinal diversity by the Carboniferous. The latest dates for the extinct orders Trigonotarbida and Phalangiotarbi are Permian and Carboniferous, respectively. No order seems to have succumbed to the end Cretaceous event that eliminated the dinosaurs. The earliest arachnid fossils are aquatic scorpions from the Late Silurian. Spiders, pseudoscorpions, terrestrial scorpions, and mites are known from the Devonian. The scorpion-like Eurypterida, which are sister to true Arachnida, also may have become extinct at the Permo–Triassic boundary; the youngest fossils are also Carboniferous. The phylogeny in Fig. 2 implies that many arachnid clades must predate all scorpion fossils; an alternate opinion, based on less
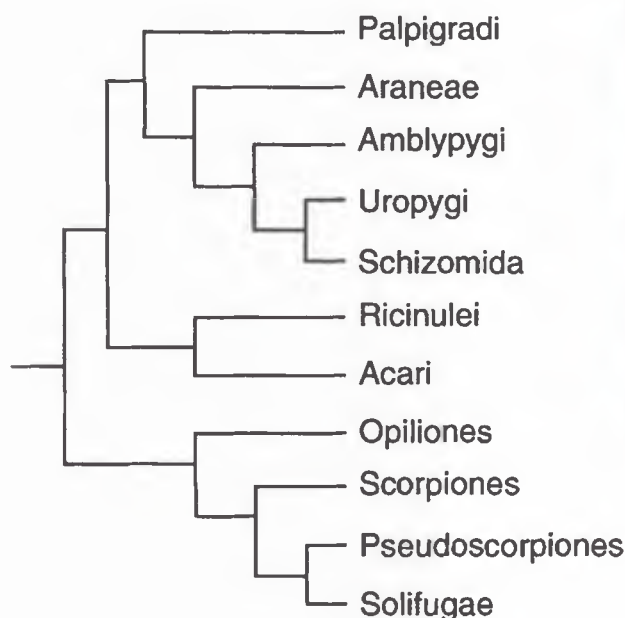
FIGURE 2 Phylogeny of arachnid orders.



FIGURE 3 Spider (Araneae: Ctenidae, *Cupiennius* sp.) (photograph by Jonathan A. Coddington).

evidence, is that scorpions instead are sister to eurypterids, and that the phylogeny of Fig. 2 will be shown to be incorrect. Small size may explain the rarity of schizomid and palpigrade fossils, but mites in the Devonian show that small arachnid fossils can persist. Given the sparse record, it may well be that all arachnid orders were distinct and essentially modern in appearance by end Silurian–Early Devonian times. The most detailed arachnid fossils are "inclusions" in amber, which is fossilized gum or tree sap. The organisms became caught in the wet sap and were fossilized along with the sap. Cenozoic amber arachnid fossils 40–80 million years old can mostly be placed in modern genera; in some cases, the fossils are difficult or impossible to distinguish from modern species. Ecological relations are also preserved: Parasitic mites occur on their insect hosts, for example, thus documenting the antiquity and diversity of mite parasitism.

## II. ARANEAE

Araneae is the second largest arachnid order with 108 families, 3200 genera, and approximately 37,000 species described (second to mites). Spiders are distinguished from other arachnids by their silk-producing spinnerets at the end of the abdomen and the prosomal poison glands exiting through their chelicerae modified as fangs (Fig. 3). Spiders are among the very few animals that use silk throughout their entire lives. A narrow stalk joins the abdomen to the prosoma, allowing great flexibility and precise orientation of the abdominal spinnerets. Pedipalps are leg-like and short. Colors are predominantly dull tans, browns, and blacks, but spiders are occasionally very colorful, even iridescent. The abdomen of most spiders shows no trace of ancestral segmentation, unlike that of other arachnids. The Neotropical tarantula *Theraphosa leblondi* (Theraphosidae) is the largest spider at about 10 cm in body length. The smallest spiders are the tiny orb-weaving Symphytognathidae; adults are less than 1 mm long.

## A. Ecology

Spiders are very abundant. One calculation estimated 5 million animals per hectare in an English meadow. Another found 29,000 per cubic meter in an English sewage treatment plant. These are extreme values, but "average" nondesert habitat probably supports at least 1 and as many as 800 spiders per square meter. Many spider species disperse by ballooning. Ballooning spiders spin a silk line until it is caught by the wind and lifted aloft—potentially for hundreds or thousands of kilometers. One study estimated that 216,000 spiders per hectare may balloon into tilled fields during the growing season. Point diversities per hectare may vary from 100 species in moderate temperate zones to 600 or more in the wet tropics. Boreal diversities are less, perhaps 20–50 species per hectare.

Spiders are the only animals to use silk throughout their lives. Silk is one of the strongest and toughest natural fibers known and compares favorably with the best man-made filaments. Eight different kinds of spider silk have been discovered, but the maximum made by

any single species is seven. Orb web spinners, for example, make two varieties of stiff, tough silk for weight-bearing structural fibers and safety lines, cement to fix silk to itself and substrate, sticky silk or glue to capture prey, rubbery silk to carry the sticky silk in the web, specialized silk for eggsacs, and thin, weak silk spun as multiple fibers to wrap prey, cradle eggs, and for other general purposes. All spiders are capable of spinning silk as soon as they leave the eggsac, and all make at least safety lines ("draglines") and the cement to attach them to substrate. Approximately half of spider species spin webs to capture prey. Web architectures are taxonomically specific and provide many clues for reconstructing spider evolution. The remaining spiders are ambush predators such as the crab spiders, which lurk inside flowers to attack pollinators, tube or retreat dwellers that forage in the very limited area at the burrow mouth, or vagabond predators such as wolf, ground, or jumping spiders.

## B. Reproduction and Growth

Reproduction in spiders requires the male to ejaculate sperm onto a specially constructed sperm web. He then sucks up the sperm into specialized sperm transfer organs at the pedipalpal tips. Only adult males have such structures; their form is usually species-specific. With his palps filled, the male then searches for females. Females are usually more sedentary than males. Life is short for adult males, both because of predation and because they eat little as adults. The duration of courtship and copulation varies from seconds to days, but it ends with the insertion of the male pedipalp and transfer of sperm into the female gonopore. Females store the sperm and sometime later construct a silken eggsac into which 1–2500 eggs are placed. Eggs are fertilized only as they exit the female's body. Parental care is rare and highly variable, ranging from simple guarding of eggsac to actively feeding the babies. In at least one crab spider the female dies as the juveniles emerge from the eggsac, which then eat their mother's body. About 20 species of spiders are extremely social. Males are rare (1:40–100), generations overlap, food is shared, and prey capture and brood care are cooperative. Colony sizes range from a dozen to several thousand individuals.

## C. Phylogeny and Taxonomy

Spiders are the seventh largest zoological order on Earth (after Coleoptera, Hymenoptera, Lepidoptera, Diptera, Hemiptera, and Acari), and of these they are the only one for which all taxonomic literature is fully cataloged. Catalogs greatly facilitate all kinds of research because scientists can easily determine the current taxonomic status and history of any described species and thus decide whether a given specimen belongs to a described species or not. At higher taxonomic levels (approximately, family) a basic, first-draft phylogeny is nearly complete. At the species level the easiest species-specific characters are found in the male and female genitalia. Species boundaries in spiders are generally clear-cut. However, the species taxonomy of spiders is based overwhelmingly on morphology. If more costly and sophisticated molecular methods were routinely applied, the number of distinguishable spider "taxa" would certainly increase.

The fundamental phylogenetic division in spiders is between the primitive mesotheles (spinnerets towards the middle of the abdomen) and the opisthotheles (spinnerets terminal). Within opisthotheles there are again two basic groups, the mygalomorphs (tarantulas and their allies) and araneomorphs (so-called "true" spiders). Mesotheles and mygalomorphs are not particularly diverse at the species level; araneomorphs currently include 94% of all known spider species and this disparity will certainly increase. Within araneomorphs the basal taxa are a few relictually distributed families in north and south temperate regions. Araneomorph haplogynes are diverse, but again comprise relatively few species. The araneomorph Entelegynae includes the bulk of modern spiders. Seven spider families currently contain more than 1000 species—all are entelegyne.

During a recent 39-year period, an average of 314 new species were described per year (12,200 total), but an annual average of 104 old names were synonymized, for a net gain of approximately 200 species per year (8800 total). Estimates of total spider diversity range from 76 to 170,000. Lower estimates mostly extrapolate from the proportions of new versus known species in taxonomic publications or are based on comparisons to well-known groups. The higher estimates take into account that many regions, particularly those richest in spider species, are disproportionately undercollected. In any case, the real diversity of spiders will never be known because a potentially great fraction will certainly go extinct before being discovered, much less described.

### 1. Major Lineages

### a. Mesothelae

Liphistiidae is the only extant family and is limited to areas of Southeast Asia and Japan. Only a few dozen

species are known, but some are common where they occur. Liphistiids retain many primitive morphological features, such as eight (rather than six or fewer) segmented spinnerets that insert anteriorly rather than terminally on the semi-segmented abdomen. Their biology may likewise represent the ecological "ground plan" for spiders. Liphistiids live in silk-lined tubes equipped with rudimentary trap doors in banks and cave entrances. Sometimes, silk "trip lines" lead away from the burrow entrance to extend the sensory radius of the animal. They are nocturnal, ambush predators. They live for 5–8 years, are remarkably sedentary, and consume a catholic diet of mainly walking prey.

## b. Mygalomorphae

Mygalomorphs include the tarantulas or baboon spiders (Theraphosidae), trap-door spiders (Ctenizidae, Actinopodidae, Migidae, etc.), purse web spiders (Atypidae), funnel web spiders (Hexathelidae), and several other families with no common name. Mygalomorphs number 15 families and approximately 2200 species, but several of the families are para- or polyphyletic. A more realistic estimate is 20–30 "family-level" groups. Like mesotheles, mygalomorphs tend to live in burrows and forage at the burrow entrance or for a very limited distance around it. Some theraphosids are arboreal and spin elaborate silken retreats. Diplurids make extensive webs but are virtually unique among mygalomorphs. The venomous Australian funnel web spiders (*Atrax and Hadronyche*: Hexathelidae) were responsible for many deaths until an antivenin was developed in the 1980s. The large theraphosid baboon spiders are not seriously venomous to humans, despite their popular reputation.

## c. Araneomorphae

Araneomorphs include approximately 94% of known spider species. Even the most primitive araneomorphs are very different from mygalomorphs and mesotheles. Basal araneomorphs tend to be much smaller, and most are obligate web spinners with elaborate spinnerets capable of making adhesive "cribellate" silk. Cribellate silk is adhesive due to the extremely fine threads drawn from the cribellum, the very modified and fused anterior pair of spinnerets. Adhesive silk makes feasible a greater variety of web architectures, and these basal araneomorphs spin elaborate catching webs. The sister group of all remaining araneomorphs is the family Hypochilidae; its dozen or so species are limited to the Appalachian Mountains, a few places in western North America, and equally restricted sites in China.

i. *Haplogynae*  Haplogynae comprises 17 families of spiders of diverse habits and worldwide distribution. Filistatidae are cribellate web-spinning spiders. Their web architecture is not much different from that of the mygalomorph diplurids—a sheet that narrows to a silk-lined retreat in a tube or crevice. Diguetids make dry silk webs. The majority of haplogynes are leaf-litter specialists and are vagabond, webless predators. The venomous brown recluse spiders (Loxosceles spp.) are haplogyne sicariids. The sister group of *Loxosceles* in southern Africa (Sicarius) has also been implicated in medically serious bites.

ii. *Entelegynae*  The remaining 70 families of spiders are the Entelegynae. Entelegynes share many evolutionary novelties. Females have a convoluted abdominal plate protecting their gonopore, which male genitalia must navigate successfully to achieve insemination. Sperm are stored in a unique "flow-through" system so that the female reproductive tract has two apertures to the outside. Female entelegynes also make special silk used exclusively in eggsacs, although its exact role is unknown. The lateral eyes possess a canoe-shaped tapetum that in some spiders enables orientation via polarized light. Although the higher phylogeny has been worked out for many entelegyne lineages, some very large ones remain unstudied, and the relationships between entelegyne lineages are also controversial.

Lycosoidea includes 11 families of mainly hunting spiders, some with common names: lynx, wolf, fishing, or tropical wolf spiders. Lycosidae (wolf spiders) and Pisauridae (fishing spiders) are common, cosmopolitan lycosoid spiders. Lycosoids occur in all terrestrial habitats, and some are semiaquatic in their ability to run across the surface of the water or dive beneath the surface. Web spinning is rare among lycosoids; some may have regained it after evolutionary loss. Most species are vagabond predators or, occasionally, tube dwellers. Active at night, they move sporadically or wait until prey approaches and then attack with powerful front legs and chelicerae. They are built strongly and run and jump with agility. The South American ctenid *Phoneutria* is venomous to humans.

Dionycha includes 17 families of spiders with two tarsal claws and a tuft of hair rather than the more common three claws and no claw tufts. The monophyly of Dionycha is by no means certain. Dionycha are also hunting spiders and have habits similar to those of lycosoids. Crab spiders (Thomisidae) wait for insect prey in flowers. Jumping spiders (Salticidae), the largest spider family, can be very brightly colored and often prefer to jump rather than walk. Their vision is superior

to any other arachnid; salticids are the only sizable spider lineage that is strictly diurnal.

Orbiculariae includes 14 families of spiders and approximately 12,000 species. Most orbicularians spin prey-catching webs, but a few groups have secondarily lost the web-spinning habit. The primitive web architecture seems to be the orb—the classic spider web of radially symmetric, stiff, dry spokes supporting a spiral of sticky silk—but more orbicularian species have lost or modified the orb architecture than retained it. Web spiders rely exclusively on webs for prey capture. Araneidae (common orb weavers), Linyphiidae (sheet weavers), and Theridiidae (cobweb weavers) are the largest families. The venomous widow spiders (*Latrodectus*) are theridiids and are distributed worldwide; several species are spread by humans and are now cosmopolitan.

## III. SCORPIONES

About 1256 species of scorpions are currently known in 156 genera and 18 families (Fig. 4). Scorpions are one of the better collected arachnid groups so that huge



FIGURE 4  Scorpion (Scorpiones: Vaejovidae, *Uroctonus* sp.) (photograph by James C. Cokendolpher). See also color insert, this volume.

increases in diversity are not as likely as in mites or spiders. Estimates of total diversity run as high as 7000 species. All scorpions have large, obvious pedipalps modified as pincers, both body regions are broadly joined, the distal abdomen is narrowed into a flexible tail bearing a venomous stinger at the end, and ventrally. The abdomen bears a pair of comb-like sensory appendages known as pectines. Colors vary from translucent to brown or black. Curiously, they fluoresce under ultraviolet light, a discovery that has galvanized recent field research on these animals. The longest is *Hadogenes troglodytes* at 21 cm, but *Pandinus imperator* is nearly as long and much heavier. The external morphology of recent scorpions is impressively similar to Silurian fossils. Formerly scorpions were thought to be the sister group of all other arachnids because they closely resemble the extinct marine eurypterids that are the sister group of all arachnids. Better analysis of morphological data (Fig. 2), weakly corroborated by molecular evidence, suggests that scorpions are more deeply imbedded in the arachnid clade and merely retain many primitive features. The issue is controversial.

Scorpions are the only arachnids with a narrow post-abdomen ("tail") terminating in a venomous sting. The sting is most often used for defense, although scorpions will sting large or strong prey. The sting of most scorpions is painful—like wasp or hornet stings—but not dangerous. Characteristically, scorpions with slender pedipalps are more prone to sting their prey, whereas those with robust pedipalps tend to crush prey. The Central American genus *Centruroides*, Brazilian *Tityus*, and Old World *Androctonus*, *Leiurus*, *Mesobuthus*, and *Parabuthus* are very venomous and medically important. In Mexico, *Centruroides* spp. sting 300,000 and kill 1000 people annually; *Androctonus*, *Leiurus*, and *Mesobuthus* kill thousands annually in Egypt and Pakistan alone. Excepting ticks that spread disease, scorpions are by far the most dangerous arachnids to humans. Scorpions are correspondingly prominent in mythology and folklore (e.g., the zodiacal constellation "Scorpio"). Scorpion venoms typically contain multiple low-molecular-weight proteinaceous neurotoxins. Scorpion blood inactivates scorpion venom, but if the venom is injected directly in a nerve, the animal rapidly dies. *Parabuthus transvaalicus* and *P. villosus* squirt venom to damage corneas, like spitting cobras.

## A. Ecology

Scorpions are most diverse in deserts or similar dry areas, although they are reliably present in moist ecosystems if the temperature is not too cold. They now occur

on all major landmasses except Antarctica. Favored habitats are burrows, under bark, stones, or logs, or inside small crevices. Burrows may be as deep as 40–80 cm, serving to escape the hot daytime temperatures in deserts. Because they like hard substrates and dry conditions, scorpions adapt well to human structures. Most scorpions are ground dwelling, but many species are arboreal, especially in the neotropics. In canopy fogging at four Amazonian sites in Peru, all of approximately 100 specimens were Buthidae (J. Ochoa, personal communication). A few are limited to lightless caves.

Scorpions are almost invariably nocturnal, although the African P. villosus is predominantly diurnal. The eyes seem to detect luminosity at best. Prey movements are detected by tarsal sense organs at distances up to 15 cm, and prey are attacked in a single motion. At distances up to 30 cm prey are located through orientation responses. The large, pincher-like pedipalps immobilize prey; thereafter, pieces are torn off by the chelicerae and digested in the pre-oral cavity before being sucked into the gut. Scorpions can be important consumers in some communities. In Israel, Scorpio maurus annually ate an average of 11% of the isopod population, which was not the only item in their diet. At moderate densities of 1.5 kg/ha, Urodacus yaschenkoi ate an annual average of 7.9 kg/ha of prey. Cannibalism and predation by other scorpion species are thought to be the most important sources of mortality, but other top invertebrate predators (e.g., spiders) and vertebrates are also important scorpion predators. Generally, mortality is highest immediately after birth, lower for intermediate-aged animals, and high for adults (e.g., 65, 30, and 60%, respectively, per year for the Australian Urodacus manicatus). Scorpion mortality is particularly high among males because of their high activity levels and mobility during the breeding season. Cannibalism by females is a significant cause of male death. Biased adult sex ratios of 1.2–1.4 : 1 are typical. Communal behavior, however, does occur. For example, family groups up to 15 individuals of the Brazilian Opisthacanthus cayaporum cooperate to construct and occupy communal chambers in the center of termite mounds. The African Heterometrus spp. also construct and share a communal burrow, inhabited by individuals of various ages. "Piles" of 20–30 individuals of Centruroides exilicauda are found in the winter months. Groups of 5 individuals of Mesobuthus martensi, all of the same age and all with their heads oriented toward a central spot, have been found under wet rocks in the intertidal zone.

The vast majority of scorpion species are subtropical or tropical. Point diversity (the number of species sym-patric at one site) peaks in subtropical deserts and is particularly high (6 or 7, with a maximum of 12) in Baja California. Two to three species per site is more usual. Vaejovis littoralis reaches unusually high densities (8–12/m²) in the drift line along the Gulf of California. The North American Paruroctonus boreus occurs as far north as British Columbia and Alberta, and the European Euscorpius germanus reaches the southern Alps. Even tropical scorpions sometimes inhabit extreme conditions; Orobothriurus crassimanus was collected at 5560 m in the Peruvian Andes.

## B. Reproduction

Reproduction in scorpions is via a spermatophore attached to the substrate. The male completes production of the spermatophore inside his body, deposits the sperm inside, and attaches the spermatophore to the substrate, all the while holding on to the female during preliminary courtship. The spermatophore is "spring-loaded" and catapults the sperm mass into the female gonopore when a lever is touched. Scorpions are exclusively ovoviviparous or viviparous. The 1–105 young are born live and cling to the mother for the first few molts. A few species are parthenogenetic. Scorpions live 4 or 5 years (rarely 8); they do not molt as adults.

## C. Phylogeny and Taxonomy

The higher classification of scorpions has changed dramatically as classical data have been reinterpreted phylogenetically. The old system proposed a few, huge, polyphyletic families about which nothing much in general could be said; now 16 or 18 families with increasingly coherent biologies are recognized. Species limits in scorpions are often difficult because scorpion genitalia are usually not species-specific. By tradition, scorpion taxonomists use the subspecies category more than most arachnologists. About 150 subspecies are recognized in addition to the 1260 species, but because these are easily distinguished they are probably distinct species. A classic example is the 25 non-overlapping, fully distinct subspecies of Scorpio maurus. Species-level taxonomic characters include the surface sculpturing of the exoskeleton, morphometric data, the number and position of pedipalpal trichobothria, and the hemispermatophores—internal male structures that produce the spermatophore.

### 1. Major Lineages

The basal division in Scorpiones is between the buthoids and remaining scorpions. New and Old World

buthids are also distinct lineages. Scorpionoids and the vaejovoid–chactoid lineage are the remaining major scorpion lineages. Chaerilidae and Pseudochactidae (*Chaerilus*, 21 species; *Pseudochactus ovchinnikovi*, from Kazakhstan) are monogeneric and enigmatic; they are like none of the other scorpion families and their relation to other major lineages is obscure. They may be basal buthoid groups.

Buthidae is the largest and most widely distributed scorpion family with approximately 74 genera and 531 species. Buthidae is most diverse in the African tropics and Palearctic regions. Buthids tend to have slender, elongate pincers, a robust tail, and usually a tubercle under the sting. All scorpions considered dangerous to humans are buthids. Buthids are also the most diverse ecologically and occupy humid, mesic, and dry habitats. The small family Microcharmidae is an Afrotropical buthid segregate with two genera and six species.

The Scorpionoidea (36 genera and 355 species) is a large, monophyletic lineage that includes Bothriuridae, Diplocentridae, Heteroscorpionidae, Hemiscorpiidae, Ischnuridae, Scorpionidae, and Urodacidae. Scorpionidae lack a tubercle under the sting and the sides of the sternum are parallel. The family contains the genus *Scorpio* from the Mediterranean and Near East, much mentioned in classical Greek, Egyptian, and Christian myths, and *Pandinus*, the giant African black scorpion. The longest and heaviest scorpions are scorpionids, which are exclusively Old World.

The relationships and monophyly of the vaejovoid–chactoid lineages (43 genera and 495 species: Chactidae, Euscorpiidae, Iuridae, Scorpiopidae, Superstitionidae, Troglotayoscidae, and Vaejovidae) are the most problematic areas of scorpion higher taxonomy and phylogeny. The large families Iuridae and Chactidae, in particular, are doubtfully monophyletic, although each includes many clearly valid groups. Together, the vaejovoid–chactoid lineages comprise about one-fourth of known scorpion species, including the most common species in North America.

## IV. OPILIONES

The described world fauna of Opiliones (harvestmen or daddy long legs) comprises approximately 44 families, 1554 genera, and about 5000 species (Fig. 5). The largest harvestman is *Trogulus torosus* at 2.2 cm long. The anterior and posterior body regions are broadly joined and the abdomen is rather short, giving the body a wider and rounder appearance than those of other
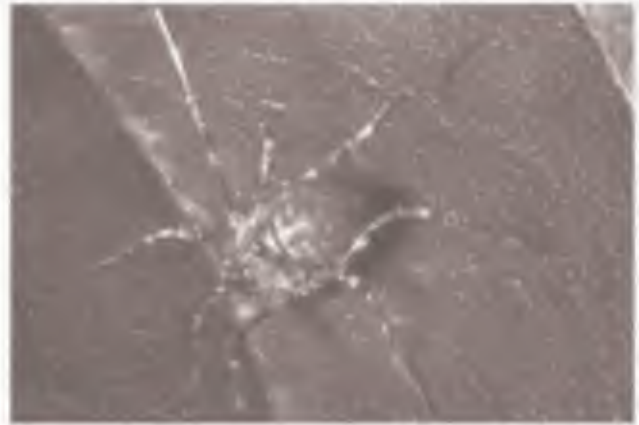


FIGURE 5   Harvestman (Opiliones: Phalangiidae, *Hadrobunus* sp.) (photograph by Jonathan A. Coddington).

arachnids. The second pair of walking legs is usually the longest. Opilions have just two eyes (cave or litter groups are sometimes blind). All harvestmen have a pair of glands that open via large pores on the anterolateral margins of the body; the function of their secretions is apparently diverse. Harvestmen are the only arachnids in which males have a penis. Females have a long, flexible, and extensible ovipositor (as do many mites). The most common group in north temperate regions, the Phalangioidea (daddy long legs), have soft and flexible bodies, weak mouthparts, and extremely long legs (commonly 15 times the body length), but just as many harvestmen are fantastically armored with bizarre, huge chelicerae, raptorial pedipalps, and short, stiff legs. Others are mite-like, and still others are dorsoventrally flattened. Colors are usually subtle patterns of brown, gray, or black, but tropical forms can rival anything seen in spiders or mites. In the long-legged forms, the distal leg tip is divided into numerous false segments that form a prehensile tip. It can be wrapped around objects to achieve a very firm and adaptable grip. The long second legs may double as feelers.

The respiratory system is exclusively tracheate. The very long-legged Phalangioidea have accessory spiracles on distal leg articles. Touch and vibration perception, as in most other arachnids, seems to be the dominant sense. The eyes at best distinguish light and dark and direction of light. Opilions consume a broader diet than any other arachnids other than mites. The basic pattern is predation, but some, for example, specialize on snails, which are otherwise rarely consumed by nonacarine arachnids. Opilions also are known to eat dead insects, fruit, and decaying vegetable matter. Unlike other arachnids, harvestmen can ingest solid particles, as shown by sclerotized bits in their excrement.

Many harvestmen defend themselves against attack by shedding legs. One study of two species in Louisiana found that about half the animals had lost one leg, but less than 10% lacked three. Seven-legged harvestmen seem to survive and function as well as intact animals. A shed leg continues to jerk and twitch attractively for minutes, permitting the harvestman to escape. All harvestmen have paired "repugnatorial" glands on the front margin of the body. When legs are pinched a droplet of fluid appears at the orifice which may be dabbed on an attacker with a leg or allowed to evaporate. The secretions can also help aggregating species to find each other, and some show broad antibiotic and antifungal activity, presumably useful to litter and soil-dwelling forms. Quinones are a major ingredient. Soil-dwelling harvestmen and the short-legged Laniatores are slow compared to long-legged harvestmen.

## A. Ecology

In general, harvestmen prefer moist, or at least not xeric, environments. The mite-like Cyphophthalmi live in dark leaf litter, caves, or under stones. The largely tropical and usually short-legged Laniatores move slowly over vegetation or the forest floor. The usually long-legged Eupnoi can be anywhere, but their very long legs with prehensile tips are specialized for crossing the large gaps between the leaves of trees, shrubs, and herbs. The northern European opilionid fauna comprises approximately 24 species and that of North America approximately 235 species. In temperate regions, diversities of more than a dozen species per hectare are uncommon.

## B. Reproduction

Uniquely among non-acarine arachnids, sperm transfer occurs via the male penis. Mating occurs quickly and seemingly without courtship. The male faces the female and pushes the penis underneath her body or between her chelicerae and into the gonopore. After insemination, the sexes separate and continue their solitary wanderings. Females use their long, flexible ovipositors to deposit eggs in suitably protected areas. Trogulids deposit their eggs only in empty snail shells, and other groups oviposit beneath stones, deep into soil, underneath bark, or in bore holes in plant stems left by insects, usually abandoning the eggs once laid. Newly hatched animals are active and resemble adults. Five to eight molts to maturity are common. An unusual reversal of sex role occurs in the Panamanian harvestman *Zygopachylus albomarginis*. Males fight to occupy existing mud nests or construct their own. Females wander between nests, courting the males, mating, and ovipositing in a series of nests. They have nothing more to do with the offspring. Males accumulate eggs of different ages and from different females and defend the eggs against conspecifics and ants.

## C. Phylogeny and Taxonomy

The phylogeny of Opiliones has recently been clarified at the superfamily level, but many additional changes are expected in familial arrangements. Some families seem to be based only on primitive features (e.g., Travuniidae, Phalangodidae, and Triaenonychidae). Eupnoi and Dyspnoi classically formed the suborder Palpatores, but increasing evidence indicates that this taxon is paraphyletic. The number of recognized families has approximately doubled in the past 20 years. At the species level the morphology of male genitalia is especially diagnostic.

### 1. Major Lineages

#### a. Cyphophthalmi

This suborder contains five (or six) families and about 100 species. It is sister to all remaining Opiliones (the "Phalangida"). Cyphophthalmi are eyeless, live in deep moist leaf litter or caves, and range in size from 1 to 7 mm. The animals have a hardened plate covering the entire dorsal surface, and they resemble mites. *Siro* is North American and European, but the family also occurs in Southeast Asia, Turkey, Japan, Mexico, and South Africa. Life spans of up to 7 years have been reported.

#### b. Eupnoi

This group contains two superfamilies, including the classic daddy long legs (Phalangioidea: Phalangiidae, Sclerosomatidae, Megalopsalididae, and Neopilionidae) of soft-bodied, long-legged harvestmen. *Phalangium opilio* is common around buildings and introduced throughout the world. The sclerosomatid *Leiobunum* spp. are common in North American and European forests, in which they move easily across the upper vegetation. They are predators and scavengers. Caddoidea includes only one or two families of harvestmen with enlarged eyes and short legs, sometimes common on tree trunks.

#### c. Dyspnoi

This group also includes two superfamilies, but has many fewer species than Eupnoi. Ischyropsalidoidea

contains three families and just seven genera. *Ischyropsalis* is European and feeds on snails. Troguloidea contains four families, two monogeneric and several genera in the remaining families. *Nemostoma* is common in caves. Trogulidae are peculiar harvestmen that look like giant, flattened mites. Legs are very short. Trogulids live under stones and in leaf litter; snails are an important part of their diet.

### d. Laniatores

This group is morphologically more diverse than the previous groups and tends to be more diverse in the tropics, including many colorful species. Three superfamilies are recognized: Traviunoidea (4 families), Oncopodoidea (1 family), and Gonyleptoidea (18–20 families). Colloquially, laniatorids are known as "short-legged" harvestmen because the most common laniatorids do have short legs, but some agoristenids, cosmetids, gonyleptids, caelopygines, progonyleptoidellines, and mitobatines have legs comparable in length to those of Palpatores. The Gonyleptoidea contains 18–20 families with raptorial pedipalps for prey capture and enlarged fourth coxae with spreading appendages—perhaps a defense against being swallowed whole by predators or dragged down the burrow of a parasitoid. Gonyleptidae are typical heavily armored and spiny, often colorful, and usually larger than 4 mm. They are exclusively Neotropical and, with more than 100 genera, are one of the largest families. The closely related Cosmetidae superficially resemble gonyleptids—large, heavily armored, often colorful, and slow-moving New World harvestmen. Phalangodidae is a large cosmopolitan family of more than 150 genera defined mainly by the features they lack. For years it has been used to file taxa with no obvious relatives, and therefore its biology makes little sense. Although most diverse in the northern neotropics, their distribution includes southern North America. Their pedipalps are flattened with spiny margins.

## V. SMALLER ARACHNID ORDERS

Amblypygi (whip spiders or tailless whip scorpions), Uropygi (whip scorpions or vinegaroons), Schizomida (no common name), and Palpigradi (micro-whip scorpions) are all small, unfamiliar arachnid groups that are closely related to each other and to spiders (Fig. 2). Like primitive spiders, all have two pairs of abdominal book lungs, although the second pair is missing in the tiny Schizomida and palpigrades lack both. The first pair of walking legs is elongate and feeler-like, with false articulations in the terminal articles to promote flexibility. Pseudoscorpiones (pseudoscorpions), Solifugae (wind spiders), and Ricinulei (no common name) are a miscellany of remaining arachnid orders related to various orders already discussed, as illustrated in Fig. 2.

## A. Amblypygi

Approximately 125 species of amblypygids in 20 genera and 5 families are known (Fig. 6). The American *Acanthophrynus coronatus* is the biggest, at about 4.5 cm in body length. The usual adult body size is about 4–6 cm. The first walking legs of amblypygids are enormously long, and fully stretched a large animal can span 50 cm. Whip spiders have no tail, and their pedipalps are modified into fierce-looking, spiny raptorial appendages. Amblypygids are easily recognized by their extremely long front legs and raptorial pedipalps. Colors are dull brown or black. The body is flat and leg insertion twisted so that limbs fold in the same plane as the body (like a crab), permitting the animals to edge through thin openings such as cracks in hollow trees. They move sideways more easily than forward or back. Amblypygids hunt by drifting their long front legs gently over the surface around them to locate prey and using their raptorial pedipalps to pounce. Like spiders, all the abdominal ganglia have migrated into the prosoma in which, fused, they form a brain. Reproduction is via a spermatophore. Like uropygids, amblypygid females carry their egg clutches inside a membrane of dried mucus glued to their ventral abdomens. The 15–50 young hatch and remain inside this membrane until they have undergone their first molt. The young cling to the mother for a short time.



FIGURE 6  Whip spider or tailless whip scorpion (Amblypygi: Phrynidae, *Phrynus* sp.) (photograph by Jonathan A. Coddington). See also color insert, this volume.

Whip spiders live in subtropical and tropical areas, in forests and often in caves. They are exclusively nocturnal and fairly common. During the day they hide in hollow trees or logs, under loose bark, or under large logs. Only one species lives in leaf litter and is not known to burrow. Their diet seems to be a broad range of smaller arthropods in their environment.

## B. Uropygi

About 100 species of whip scorpions are known in 16 genera and one family, Thelyphonidae (Fig. 7). At 7.5 cm, the largest is *Mastigoproctus giganteus* of North America, but 3–5 cm is usual. Whip scorpions are easy to recognize by the long posterior whip or flagellum (highly modified terminal abdominal segments). Colors are brown to black. Uropygids have defensive anal glands that accurately spray an acid-smelling fluid at attackers. The smell explains the common name "vinegaroon." The fluid of *M. giganteus* is 85% acetic acid but it also contains substances to reduce the surface tension of the epicuticle so that the acetic acid can spread widely and penetrate. Vinegaroons are supposedly not sensitive to their own spray. Reproductive habits are known only for a few species, but presumably sperm transfer occurs via a spermatophore glued to the substrate in all species. Some species have a lengthy courtship—10 hr to several days. Females keep their 12–40 eggs attached to their ventral abdomen. Female *Thelyphonus* build a deep burrow and do not feed while guarding the eggs for 4 or 5 weeks. Uropygids may live 6–8 years or even longer.

Uropygids are tropical to subtropical animals. They hide in leaf litter, burrows, under logs and rocks, and inside dark crevices or holes during the day, emerging



FIGURE 7 Whip scorpion (Uropygi: Thelyphonidae, *Mastigoproctus* sp.) (photograph by Jonathan A. Coddington). See also color insert, this volume.



FIGURE 8 Schizomid (Schizomida: Hubbardiidae) (photograph by Jeremy A. Miller).

at night to hunt. Not much is known about their prey, but presumably it consists of other small ground-dwelling insects, arachnids, and crustaceans, which they crush between their pedipalpal segments prior to ingestion.

## C. Schizomida

About 200 species in 30 genera and two families (Protoschizomidae and Hubbardiidae) are known (Fig. 8). Schizomids (there is no common name) are most like tiny uropygids, but the abdominal flagellum is short (three segments but rarely five). Colors are usually light yellow to tan to dull green. Assiduous searching in moist tropical litter usually turns up a schizomid. The largest schizomid known is *Agastoschizomus lucifer* at about 12.7 mm long, but 3 mm is typical. Most schizomids lack eyes entirely and live in moist tropical or subtropical leaf litter, under stones, in logs, moist crevices, caves, and so on. Reproduction is via a spermatophore attached to the substrate, after which females lay 6–30 eggs that are glued to the ventral female abdomen until the young emerge. At two Amazon sites schizomid abundances ranged from 5 to 110 animals per square meter per month.

Like the uropygids they have been reported to produce a defensive chemical smell. They can move backwards rapidly and have enlarged femora apparently used to hop backwards.

## D. Palpigradi

There is only one family (Eukoeneniidae) with five or six genera and about 80 species. Palpigrades (micro-

whip scorpions) are tiny, light yellow to white, delicate soil and leaf litter specialists with a cosmopolitan distribution. The largest is *Eukoenenia draco* at 2.8 mm long, but 1 or 2 mm is typical. They resemhle the young of Uropygi. Like whip scorpions, they have a wide preabdomen and a multi-segmented whip-like postabdomen. Like many soil organisms, palpigrades lack most of the organ systems required by large animals that live in drier and less constant environments. They lack eyes, respiratory organs, and a circulatory system but have innervated setae that detect vibrations. Most species are known from the tropics; several palpigrades apparently live in intertidal or shallow marine habitats. *Eukoenenia janetscheki* was the only species found at two Amazon sites, but it was fairly abundant (30–120 animals per square meter per month).

## E. Ricinulei

One family (Ricinoididae), three genera, and 53 species of ricinuleids are known (Fig. 9). Ricinuleids, like schizomids and palpigrades, are soil-dwelling specialists. The largest is *Ricinoides afzelli* at 10 mm. long, but most are 3–5 mm. Unlike the preceding forms, ricinuleids are heavily armored with a thick exoskeleton and a kind of visor or flap (the cucullus) that folds over the mouthparts. Colors are reddish to brown or black. Males have third legs modified for sperm transfer. Some have "eye-spots" that are able to sense light. Females lay one or two eggs at a time, which they may carry about with them. Adults may live 10 years. Formerly

thought to be extremely rare, ricinuleids are not uncommon in Neotropical leaf litter. They are also known from Africa, but not from the Asian tropics.

## F. Pseudoscorpiones

About 3100 species of Pseudoscorpions (or "false scorpions") have been described, classified in approximately 430 genera, 24 families, and two suborders (Epiocheirata and Iocheirata) (Fig. 10). The North American fauna comprises about 350 species. One local fauna in the Amazon comprised nine species and Mediterranean ecosystems around Perth, Australia, and other Old World tropical moist ecosystems are comparable (M. Harvey, personal communication). Pseudoscorpions look like tiny scorpions without the tail and pectines. Colors are tan to dark brown or black. Their chelate pedipalps can have venom glands and the chelicerae have silk glands. The largest is *Garypus titaneus* at 12 mm long, but most are 2 or 3 mm. They are flattened for life in crevices, usually under bark or in leaf litter, but a few forms live on ocean shores where they are truly intertidal. Numerous species live among the hairs of mammals where they feed upon other arthropod parasites. At least one species has the body, legs, and palps modified for living on a Celebese rat. *Chelifer cancroides* is cosmopolitan and lives in houses where it hunts book lice and other small insects. Pseudoscorpions are sometimes found in aggregations of dozens of individuals. Reproduction, as in most other arachnids, is via a spermatophore. The female builds a silken nest



FIGURE 9 Ricinuleid (Ricinoididae) (photograph by Jonathan A. Coddington). See also color insert, this volume.



FIGURE 10 Pseudoscorpion (Pseudoscorpiones: Neobisiidae, *Tartarocreagis infernalis* (Muchmore) (photograph by James C. Cokendolpher).

and secretes a "brood sac" attached to her body and in which she nourishes the 3–40 embryos with maternal secretions. Juveniles leave the mother soon after hatching. Pseudoscorpions are famous for their tendency to disperse by phoresy. Mature females (rarely males or juveniles) use their pedipalps to hold onto larger insects, which carry them from place to place as they fly about. Phoretic specimens in fossil amber show that this behavior is at least 10 million years old.

## G. Solifugae

About 1065 species of solifuges are known, grouped in about 153 genera and 12 families (Fig. 11). The greatest known diversity occurs in Namibia. Wind spiders (sun spiders or camel spiders) look somewhat like hairy, stout, fast-running spiders, but their chelicerae are fearsomely enlarged and both the leg-like pedipalps and the long and slender first legs are used as feelers. The fourth femurs bear ventral sensory structures shaped like inverted mushrooms. Colors are tan to sandy yellow. The largest is *Galeodes caspius* at 7 cm, but 2 or 3 cm is usual. Wind spiders can run extremely fast (53 cm/sec) for short bursts, but like most arachnids they cannot sustain rapid locomotion for long periods. The solifuge respiratory system is only tracheate and is comparable in complexity to that of insects. They are generally nocturnal and exclusively carnivores and, like any of the larger arachnids, will take small mice, lizards, amphibians, and so on if the opportunity arises. A few species feed only on termites. Unlike most other arachnids, solifuges are active, cursorial predators. Wind spi-

ders are most common in tropical and subtropical dry or desert regions, but they are absent from Australia. Many inhabit burrows, where they may stay up to 9 months of the year, depending on rainfall. Reproduction is via spermatophore, which the male produces during courtship and transfers into the female gonopore with his chelicerae. The female digs a deep burrow to deposit egg masses that may contain 5–164 eggs. Females may lay 1–5 egg masses. Some females remain with the eggs until hatching. Newly hatched wind spiders are gregarious and remain in the burrow for the first two molts.

## VI. ACARI

Mites and ticks are classified as Acari, from a Greek word meaning a thing too tiny to be divided (Fig. 12). At more than 45,000 species, Acari is already the most diverse arachnid order, but acarologists estimate that between half a million and more than 1 million species actually exist. Despite being far more abundant and diverse than any other order of arachnids, mites and ticks are nonetheless much less familiar to most people than spiders, harvestmen, or scorpions. Likewise, scientific knowledge of mites lags far behind our understanding of most other arachnid groups. The primary reason for both public and scientific ignorance of mites is their small size.

Since we sometimes find them on ourselves and our pets, because they are relatively large, and because of their role as serious vectors of human disease, the ticks are probably the most familiar group of mites. In fact, ticks (which have their own name only because of their



FIGURE 11   Wind spider or solifuge (Solifuga: Eremobatidae) (photograph by Jonathan A. Coddington). See also color insert, this volume.



FIGURE 12   Free-living yellow moss mite (Acari: Penthalodidae, *Stereotydeus* sp.) (photomicrograph by David Evans Walter; scale bar = 100 μm).

importance to humans) represent a small offshoot on the evolutionary tree of mites. Other kinds of mites are vastly more common and diverse than the ticks and include not only other parasites but also followers of many other ways of life. In this article, unless otherwise distinguished, the term *mites* is intended to include ticks and will be used interchangeably with Acari.

The Acari are distinguished from other arachnids principally by the lack of conspicuous body segmentation, the broad union of the leg-bearing part of the body (the podosoma) with the posterior part (the opisthosoma) to form a single unit (idiosoma), the aggregation of the mouthparts into a distinct anterior body region (the gnathosoma), and the first active immature stage, the larva, having only three pairs of legs. The gnathosoma is not a true head, like that of an insect, in that it possesses neither eyes nor antennae and does not contain the brain. (Most mites have no eyes at all, but those that do bear them on the idiosoma. The brain is situated anterior to the stomach in the idiosoma.) Although usually compact in form, like that of a spider mite or tick, the overall shape of the mite body varies greatly. Species that live in polypore fungi or hair follicles are elongated to fit their habitat, and mites found deep in soil tend to be worm-like. Ticks and some other mites can tolerate enormous distention of the body wall to accommodate food.

Like other chelicerate arthropods, mites have no antennae, but in many groups the first pair of legs carry chemosensory and tactile organs and are not used, or little used, for locomotion. The pedipalps, integrated laterally into the gnathosoma, are also primarily sensory in function. The chelicerae, the primary food-getting organs, vary greatly in form, in accord with the varied feeding habits of mites. In many species, the chelicerae of males are so modified for sperm transfer that adult males scarcely feed.

## A. Ecology

Mites are found in virtually every habitat on Earth. On land, legions of free-living mites populate soils in all habitats, often numbering in the hundreds of thousands per square meter in the soil (50,000–250,000 per square meter, down to 5 cm depth, in forests; 20,000–100,000 in grasslands; and 500–1000 in deserts). In many soils, including deserts, mites can be found at depths up to 10 m, where they follow plant root systems. Although the habits and behavior of many soil mites remain a mystery, it is known that soil mites fill many ecological roles. Many eat decaying organic matter (and the microorganisms it contains); others consume fungi, algae,

and bacteria; and still others are predators, feeding on nematodes, other mites, or various stages of insects. Oribatid mites in the soil facilitate plant growth by dispersing the spores of mycorrhizal fungi, which form mutually beneficial and often essential associations with higher plants.

Mites are common and often abundant on plants, on which many species feed on leaf, stem, or root tissue by piercing cell walls. Others specialize on plant reproductive parts, including nectar, pollen, and fruit. Still other plant-dwelling mites are fungivores (eating fungi on leaves or stems) or predators, mostly of plant-feeding mites. Unlike life in the soil, life on plant surfaces constantly threatens mites with desiccation. Hiding from direct sun on the underside of leaves offers some protection because the "boundary" layer of still air is kept relatively moist by plant transpiration.

In addition, many plants produce domatia—hollow, mite-sized cavities or pockets in the leaf. The adaptive function of domatia is controversial, but experiments have shown that removal of domatia from some plants that normally have them reduces the density of beneficial predatory mites and increases the density of herbivorous mites.

Some fungus-feeding mites have specialized cavities or pouches in the body wall (sporothecae) in which they carry spores or propagules of fungi that they depend on for nourishment.

Parasitic and phoretic mites exploit most terrestrial vertebrate species, most other arthropod groups, mollusks, and even marine invertebrates (Fig. 13). Most species of birds, for example, generally support many "feather" mite species found nowhere else. Four or five different, host-specific species inhabit different feather



FIGURE 13 Parasitic sejine mite (Acari: Sejiidae, *Epicroseius* sp.) (photomicrograph by David Evans Walter).

types (flight feathers, tail feathers, or body feathers), whereas different species live on the surfaces of feathers, others in the interior lumen of the quills, others on or in the skin, and yet others in the nasal passages. One particular species of parrot hosts more than 20 species of feather mites. Bird nests support additional, phoretic species that feed on debris or on other nest associates. Both parasitic and phoretic species generally colonize young birds while in the natal nest and travel with the host until it builds its own nest. Similar sets of species inhabit the bodies of mammals and reptiles and, to a lesser degree, amphibians.

Mites are also common associates of insects and other invertebrates. Some are parasitic and deleterious to their hosts, such as the tracheal mite and *Varroa* mite parasites of honeybees or moth ear mites. Some are commensal (e.g., feeding on insect waste products). Others are believed to benefit the host, perhaps by consuming other harmful mites, parasitic nematodes, or decaying matter that would otherwise nourish fungi or bacteria that might threaten the host or its young. Some insects have acarinaria, special pockets in the outer body wall, that are routinely occupied by phoretic mites. The very existence of acarinaria, which have no other known function other than to house and transport mites, is evidence for a net beneficial relationship between these mites and their insect hosts. Parasitic mites have been shown to be capable of mediating horizontal gene transfer between insect host species.

All ticks require blood from a vertebrate host for development and reproduction but live off the host when not feeding or mating. Chiggers and many other mite species must live a portion of their lives, and others all their lives, as parasites of animals. Other mites exploit animal hosts not for food but strictly for transport—a phenomenon called phoresy (see the following section). Parasitism is thought to have evolved, in some lineages, from phoretic associations.

Mites are common and diverse inhabitants of freshwater and marine habitats. In fresh water, adults and nymphs prey on other mites, crustaceans, and aquatic insects. The larvae of aquatic mites are commonly parasitic on insects and crustaceans, and nymphs and adults of unionicolid mites parasitize bivalve mollusks. Other aquatic mites graze algae and fungi growing on aquatic plants. Mites are common on seashores, including the intertidal zone. The sea is home to predatory and algae-feeding mites. Some mites have been found at depths up to 7000 m at hydrothermal vents, and one group lives in the gut of sea cucumbers. Mites are the only arachnids found in the ocean depths.

Closer to home, even the cleanest office, classroom, or home normally supports dust mites (e.g., *Dermatophagoides* spp.), which live on organic matter in house dust. Some mites are stored-product pests, feeding on grains, cheese, and other dry foods. Even more intimately, as you read this encyclopedia there is a very good chance that the follicles and sebaceous glands of your forehead or eyelids house normally benign, microscopic mites (*Demodex* spp).

## B. Reproduction and Dispersal

Reproductive patterns in mites are remarkably diverse. Many mites are ordinary diploids (having an equal number of chromosomes from each parent) with two sexes, requiring fertilization by the male for females to reproduce. In other groups, males are absent, and females bear female young from unfertilized eggs. In still other mites (e.g., spider mites), females require sperm from a male to produce (diploid) daughters, but sons are haploid (they have only the maternal chromosomes) since they are produced from unfertilized eggs. In other species (e.g., some phytoseiid mites), both sexes are diploid and all eggs require fertilization to develop, but only the mother's chromosomes are active in males (called paternal genome loss).

Modes of sperm transfer are diverse. Some mites transfer sperm directly through copulation, using legs, palps, or other specialized body parts to accomplish the transfer. Other mites rely on spermatophores placed on the substrate, with or without active enticement of the female to take up the sperm.

Development of the egg takes place in most mites after oviposition. In some species (e.g., moth ear mites and hummingbird flower mites) the eggs are laid *communally*. In other mites, the young leave the mother's body as active larvae. In some mites (e.g., *Siteroptes graminum*) sisters and brothers both hatch and mate within the mother's body, and both mother and sons die when the fertilized daughters emerge—truly material for a Greek tragedy.

The development of most mites includes one or more active stages between egg and adult. (Some Heterostigmata have no active immature stages.) In nearly all groups, the first active immature stage, called the larva, has three pairs of legs, and later stages, including the adult, have four pairs. (The plant-parasitic Eriophyoidea are exceptional in having two pairs of legs in all active stages, and females of many species of insect-parasitic Podapolipidae have three, two, or even only one—the anterior—pair of legs.) The number of nymphal stages between larva and adult varies from none to three, depending on the group. Several groups

of mites have metabolically inactive stages that can endure stressful periods. Life expectancy among mites also varies widely. Some mites live only about 1 week or so (e.g., hummingbird flower mites), whereas others require several years to complete the life cycle (e.g., certain ticks, oribatid mites, and water mites).

Because mites are so small and (unlike most insects) are wingless, selection for effective dispersal from one food patch to another has produced many special adaptations. Parasitic mites, for example, must have a way to find a new host—or ensure that their offspring do—before the current host dies or becomes unsuitable. In the case of plant-feeding mites, some species disperse aerially, either by simple passive transport in the wind or, in the case of some spider mites (Family Tetranychidae), by "ballooning" on strands of silk. (The silk-producing glands in these mites are not homologous to those of spiders.) Other plant-feeding mites disperse phoretically on plant-visiting animals. For example, nectar- and/or pollen-feeding insects and birds on all continents carry nectar- and/or pollen-feeding mites as hitchhikers—a way of life that has many independent evolutionary origins.

Some groups of mites have special, non-feeding stages adapted for phoretic dispersal. In others, adults and sometimes later nymphal stages mount phoretic hosts to reach new hosts or habitats when local mite population density becomes high, when the host is ready to disperse (e.g., emerging adult insects), or when a food plant becomes unsuitable.

## C. Phylogeny, Taxonomy, and Current Knowledge

Only 90 species of Acari were known to Linnaeus, all of which he placed in the genus *Acarus*. Currently, perhaps 45,000 species in 431 families and 3672 genera have been described compared to 30,000 species estimated 30 years ago. The rate of description of new species is still very high—several hundred species per year—and every systematic acarologist has dozens or hundreds of undescribed species sitting on shelves in vials of alcohol, awaiting description and classification. In fact, the taxonomic impediment to full knowledge of the Acari is monumental:— The number of practicing, modern mite systematists is no more than 50, and the rate of training of new systematists is alarmingly low. Moreover, exploration and species discovery in tropical forests (especially the forest canopy), lakes, and streams is still in its earliest stages. Most estimates of the total world fauna of Acari range from 500,000 to more than 1 million species, but some acarologists even suggest

that mites rival insects in worldwide number of species. In any case, mites represent by far the most species-rich and ecologically diverse arachnid group. Table 1 gives summary data on mite diversity.

### 1. Major Lineages

Given the highly incomplete knowledge of the Acari, it is not surprising that their phylogeny, classification, and nomenclature are far from settled. It is generally recognized, however, that the Acari comprise three lineages that diverged from one another in very ancient times: the Opilioacariformes and Parasitiformes (which together constitute the Anactinotrichida) and the Acariformes (which constitute the Actinotrichida). Their relationships to one another and to non-acarine arachnid groups have been debated for decades, but the current opinion appears to be that the Acari, so defined, is a monophyletic group.

The taxonomic rank of acarine lineages is also controversial. The tradition among zoologists in general and arachnologists is to treat Acari as an order, but acarologists now treat it as a subclass or even a class, with subsidiary mite taxa then being orders or superorders. Clearly, this is not the place to attempt a resolution of this controversy. The taxonomy in the following sections reflects the prevailing acarological point of view that major groups should rank as orders, despite the incongruity with the rest of this article.

### a. Order Opilioacariformes

The small order Opilioacariformes (with 17 species described of an estimated 85–170 total) with a single family (Opilioacaridae) are large mites (1.5–2.3 mm in length) that somewhat resemble small harvestmen. Some genera occur in dry climates, often under litter or stones, and others in tropical forest litter, where they feed as omnivores or predators.

### b. Order Parasitiformes

The Order Parasitiformes includes three Suborders: Holothyrida, Mesostigmata, and Ixodida.

i. *Suborder Holothyrida.* The Holothyrida is a small group (with 32 species described, of an estimated 160–320 total) of large (2–7 mm) saprophagous and predaceous mites of temperate and tropical forest litter, known only from Pacific-Indian Ocean islands and the Australasian and Neotropical regions.

ii. *Suborder Mesostigmata.* The cosmopolitan suborder Mesostigmata, in contrast, is extremely rich in species (with 11,632 species described of an estimated

100,000–200,000 total) and diverse in habits, ranging in size from 0.2 to 4.0 mm. Mesostigmatic mites range from saprovores (eating dead or decaying organic matter), fungus feeders, predators living in soil, litter, beach wrack, dung, or rotting wood, to pollen and nectar feeders. Repeatedly, mesostigmatic lineages have evolved close relations with other arachnids (spiders, amblypygids, and scorpions), myriapods, insects, and vertebrates and their nests. Some are endoparasitic (living inside vertebrate respiratory tracts), and others are ectoparasitic. Many others are phoretic, with a variety of feeding habits. Some prey on mite and insect pests of orchards and stored food products. Some of these beneficial predators have been genetically engineered to be more acaricide resistant, enhancing integration of biological and chemical control of pest mite species.

iii. *Suborder Ixodida.* With 880 species described, of an estimated 1000–1200 total, the ticks (suborder Ixodida) are taxonomically the best-known major group of Acari primarily because of their medical and economic importance. Ticks are considerably larger than most other Acari; adults range in size from 1.7 to 12.7 mm in the unfed state. All ticks feed on the blood of terrestrial vertebrates as ectoparasites. (Sea snakes also have ticks.) Ticks are capable of carrying and transmitting to humans and their domesticated animals more kinds of disease-causing organisms than any other group of blood-feeding arthropods. These agents include viruses, spirochaetes, rickettsiae, anasplasmas, bacteria, piroplasma, and filariae. Important tick-borne human diseases include Russian spring–summer encephalitis, Colorado tick fever, African relapsing fever, Lyme disease, Rocky Mountain spotted fever, Siberian tick typhus, Q-fever, monocytic and granulocytic ehrlichiosis, Kyasanur forest disease, and tularemia.

c. Order Acariformes

The order Acariformes comprises three suborders— Prostigmata, Astigmata, and Oribatida—with a fourth group, the Endeostigmata (120 described species, perhaps 1200–2400 total) of uncertain rank and affinities but often treated as Prostigmata.

i. *Suborder Prostigmata.* Prostigmatic mites (with 17,000 described species of an estimated 320,000– 640,000 total) range in size from 0.1 to 2 mm, with a few of the giant red velvet mites as large as 16 mm, and vary widely in body form, color, habitat, and feeding adaptations. They include predatory and omnivorous species living in organic strata of soils and on algae, lichens, mosses, trees, and shrubs. The Prostigmata also include obligately plant-feeding groups, including the spider mites (Tetranychoidea), false spider mites (Tenuipalpidae), and eriophyoid mites, many of which are serious economic pests of field crops, orchards, and greenhouse plants, in some cases acting at vectors of damaging plant viruses. Some groups inhabit the soil; species of the family Nematalycidae have been found at depths of up to 3 m in sand dunes. Species of at least five families of prostigmatic mites are known from Antarctica, and others live in caves. Some prostigmatic groups live in the sea, where they are predaceous or algivorous. Many families of this order are specialized for life in springs, streams, rivers, waterfalls, lakes, bogs, or aquatic interstitial habitats of all descriptions. Some groups live in thermal waters; mites of the genus *Thermacarus* inhabit hot springs, thriving in water up to 50°C, in which the larvae parasitize amphibians. As in the Mesostigmata, parasitism has arisen repeatedly in independent lineages within the Prostigmata. Some are ectoparasites of slugs, scorpions, insects, or vertebrates; some are parasitoids of eggs or larvae of insects; and some are endoparasites of insect respiratory and reproductive organs, vertebrate respiratory tracts, the quills of birds, the skin of turtles, the mantle cavity of mollusks, the guts of echinoderms, or the gills of decapod crustaceans. A few species in the order are vectors of human disease (scrub typhus), and some cause mange and other skin diseases in domesticated animals. *Demodex* spp, which live (generally benignly) in hair follicles and sebaceous glands of the human face, are prostigmatic mites, as is the straw itch mite *Pyemotes tritici*, which can cause severe skin lesions in humans.

ii. *Suborder Oribatida.* The Oribatida is remarkable in being the only major group of mites in which a great diversity of species (11,000 described species of an estimated 33,000–110,000 total) has evolved without the evolution of parasitism. Although a few species are phoretic as adults on insects, the rest of this vast radiation are free-living inhabitants of the soil, forest litter, tree holes, bark, twigs, leaves, mosses, lichens, algae, freshwater vegetation, bogs, and the intertidal zone. Most oribatid mites feed on fungi, but some consume dead woody material or algae, and a few are predators on nematodes, rotifers, and other small invertebrates. Oribatida (and many species classified as Astigmatata, which are actually derived oribatids) feed on particulate matter. Through their feeding, they help to maintain soil structure. Unknown for other mites, many oribatid species sequester calcium and other minerals in their thickened cuticle. As with Prostigmata, oribatid species are also found on continental Antarctic.

Some oribatids are intermediate hosts of cestode tapeworms whose final hosts are herbivorous mammals. Oribatid mites range in size from 0.2 to 1.5 mm.

iii. *Suborder Astigmata.* The Astigmata, closely allied to the Oribatida, are primarily associates of arthropods, vertebrates, and other animal groups, although a few species are free-living in all life stages (with 4500 described species of an estimated 90,000–180,000 total). This lineage is thought to be derived from within the Oribatida, but a revised classification, with names of major groupings to reflect this relationship, has yet to be promulgated. A key evolutionary innovation of the Astigmata is a nonfeeding, immature stage especially adapted for phoretic dispersal or tolerance of adverse conditions. Astigmatic mites include fungus feeders, a few plant feeders, a few predators, and mites with mouthparts specialized for filter feeding in water. Some feed on algae in the intertidal zone, in water-filled tree holes, or in sap exudates. Several groups inhabit the nests of insects, mammals, and birds as ectoparasites or commensals. The specialized deutonymphs in several families are parasitic in the hair follicles of mammals. The insect hosts of some species produce acarinaria. One group lives as commensals on the gills of hermit crabs. A large radiation of astigmatic mites lives on feathers and within quills of birds as well as in the avian respiratory tract and air sacs. Another group has radiated among mammals as parasites of the skin, hair, follicles, respiratory passages, ears, and even (rarely) the digestive tract. Some astigmatic mites feed in dung or carrion, and others are important pests of stored food products, including not only grains but also stored meat and dried fish. This order also includes house dust mites (*Dermatophagoides* spp.), the itch or scabies mite (*Sarcoptes scabiei*), and mange mites.

## Acknowledgments

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