6

AILANTHUS WEBWORM MOTH

(*Atteva aurea*)

While cynthia moths in Philadelphia went extinct, another ailanthus moth thrived—the ailanthus webworm moth.

Figure 6.1 Ailanthus webworm moth taking nectar at white snakeroot (*Ageratina altissima*), a common wildflower in Center City.

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In 1911 Carl Ilg, an entomological laboratory assistant, submitted a one-paragraph note to *Entomological News, and Proceedings of the Entomological Section of the Academy of Natural Sciences of Philadelphia:*

> It was at the later part of August when I was out collecting, that my attention was called to a web which looked to me like a spider's nest, on a small ailanthus bush. By investigating more closely, I saw a chrysalis suspended in the web. Not knowing what it was, I took it home, and several days after, a small moth emerged and proved to be *Atteva aurea.* As I knew the food plant now, I looked in the same neighborhood and found several similar webs containing newly hatched, as well as full grown, larvae and also chrysalids in them. The full grown larva is about 1¼ inches long, blackish, with a distinct brown stripe all along its back, while the sides are dotted with fine white spots…As far as I could find out, there is no record as to food plant or life history of this little moth, but should any other collectors have made any observations in this respect, I would like to hear from them.—Carl Ilg, 2728 Somerset St., Philadelphia.[1]

Figure 6.2 Pupa of ailanthus webworm moth in its web. The web is in an ailanthus sapling growing along the Schuylkill River Trail in Center City. Until Carl Ilg of Philadelphia discovered such a pupa and identified the moth that emerged from it, nobody knew that the species made webs or that it ate ailanthus.

A mystery solved and a mystery created

Ilg's discovery solved a mystery. In 1857 Asa Fitch, entomologist for New York state, described *Atteva aurea*—but only the moth. Fitch had never seen the moth's larva and did not know the identity of its food plant.[2] The fact that its life history had gone unrecognized for so long is remarkable given the moth's beauty: it has four metallic gold bands offset by brilliant white spots embedded in iridescent blue and black. It is 12 millimeters (half an inch) long. Its species name, *aurea,* is from *aureus,* meaning "golden" in Latin. Ilg's discovery led to the moth's common name, "ailanthus webworm moth."

Ilg solved one mystery but created another: where did *Atteva aurea* come from? It could not be native to Philadelphia, since ailanthus, its only host plant here, is not native. It is not known from Europe or Asia. The specimen Fitch described came from Savannah, but the same puzzle existed in both cities.

Daniel Janzen, ecologist at the University of Pennsylvania, has been conducting a long-term inventory of moths in a Costa Rican nature preserve, *Área de Conservación Guanacaste.* His inventory includes two confusing species of *Atteva* with wing patterns that look almost identical. Using DNA fingerprinting and other data, he and his colleagues compared these two species with *Atteva aurea* collected in North America, including the mid-Atlantic region and Canada. They concluded that one of the two species in Guanacaste is *Atteva aurea*. They also determined that a species of *Atteva* in southern Florida is also *Atteva aurea*. Thus Philadelphia's ailanthus webworm moth ranges from Costa Rica to Canada.[3] In Guanacaste[4] and southern Florida[5] it feeds on the paradise tree, *Simarouba glauca,* which, unlike ailanthus, is native to tropical and subtropical areas in North and Central America. *Simarouba glauca* and *Ailanthus altissima* belong to the same family, Simaroubaceae.[6]

These findings lead to a hypothetical scenario explaining the mystery of the origin of the ailanthus webworm moth in Philadelphia. The chain of events begins around 1784 when William Hamilton introduces *Ailanthus altissima* into North America by planting it in Woodlands, his estate in west Philadelphia. When the distribution of ailanthus trees extends around the country, it approaches populations of *Atteva aurea* feeding on the paradise tree in Florida. *A. aurea* then encounters ailanthus trees for the first time and begins to feed on this close relative of its native host plant. Thriving on ailanthus trees, it expands its range north, moving into ailanthus's new territory, including Savannah by 1857, Philadelphia by 1911, and later, urban and suburban areas throughout the eastern half of this country and southern Canada.[7] One variant of this scenario is possible: *A. aurea* may have switched to ailanthus in southern Texas, which like Florida has native plants in the family Simaroubaceae.[8]

Differences between the cynthia moth and ailanthus webworm moth

In Philadelphia the ailanthus webworm moth is the most common moth at flowers such as goldenrod during the day in late summer and fall. What might account for this species' survival, in contrast to the extinction of *S. cynthia,* in Philadelphia? One might suppose the two species would share the same fate, since they have so much in common: both are moths that arrived in Philadelphia over a century ago and are specialized feeders on the same plentiful host plant. *A. aurea,* however, is smaller— about one fifth as large by wingspan—requiring less food for development and offering potential predators fewer calories and a smaller target. During the day its caterpillars are protected inside a web, in contrast to *S. cynthia,* whose caterpillars are fully exposed.

The most obvious difference, however, is in behavior and coloration. *A. aurea* is brilliantly colored and visits flowers during the day, whereas *S. cynthia* flies at night, and in the adult stage does not feed.[9] While visiting flowers, *A. aurea* is indifferent to its surroundings, in the sense that it does not fly away when a person approaches it. This fearlessness makes it easy to photograph. The overall syndrome—daytime flight, bright colors, and insensitivity to danger—is common in bees and wasps, but rare in moths. The three traits suggest that *A. aurea* possesses some kind of protection. Since it cannot sting or bite and has no sharp spines or urticating hairs, one might suspect that *A. aurea*'s protection is chemical, and its bright colors *aposematic,* warning potential predators.

Aposematic coloration

In Philadelphia, the most familiar example of a chemically defended species is the monarch butterfly, whose conspicuous black and orange pattern distinguishes it from other species at a distance of a dozen yards or more, barring confusion with its mimic, the viceroy butterfly, which is rare here. In Philadelphia, monarch caterpillars feed mostly on common milkweed, *Asclepias syriaca,* which is widely scattered in old fields in Fairmount Park. Like the monarch butterfly, the monarch's caterpillars are distinctively marked. They have bold yellow, black, and white stripes along their entire length. Feeding on milkweed blossoms, the caterpillars contrast sharply against the pink flowers. Any milkweed patch of a dozen or more stalks is likely to host other conspicuously colored insects, including bright red and black beetles (*Tetraopes tetrophthalmus*) and bugs (*Lygaeus kalmii and Oncopeltus fasciatus*).

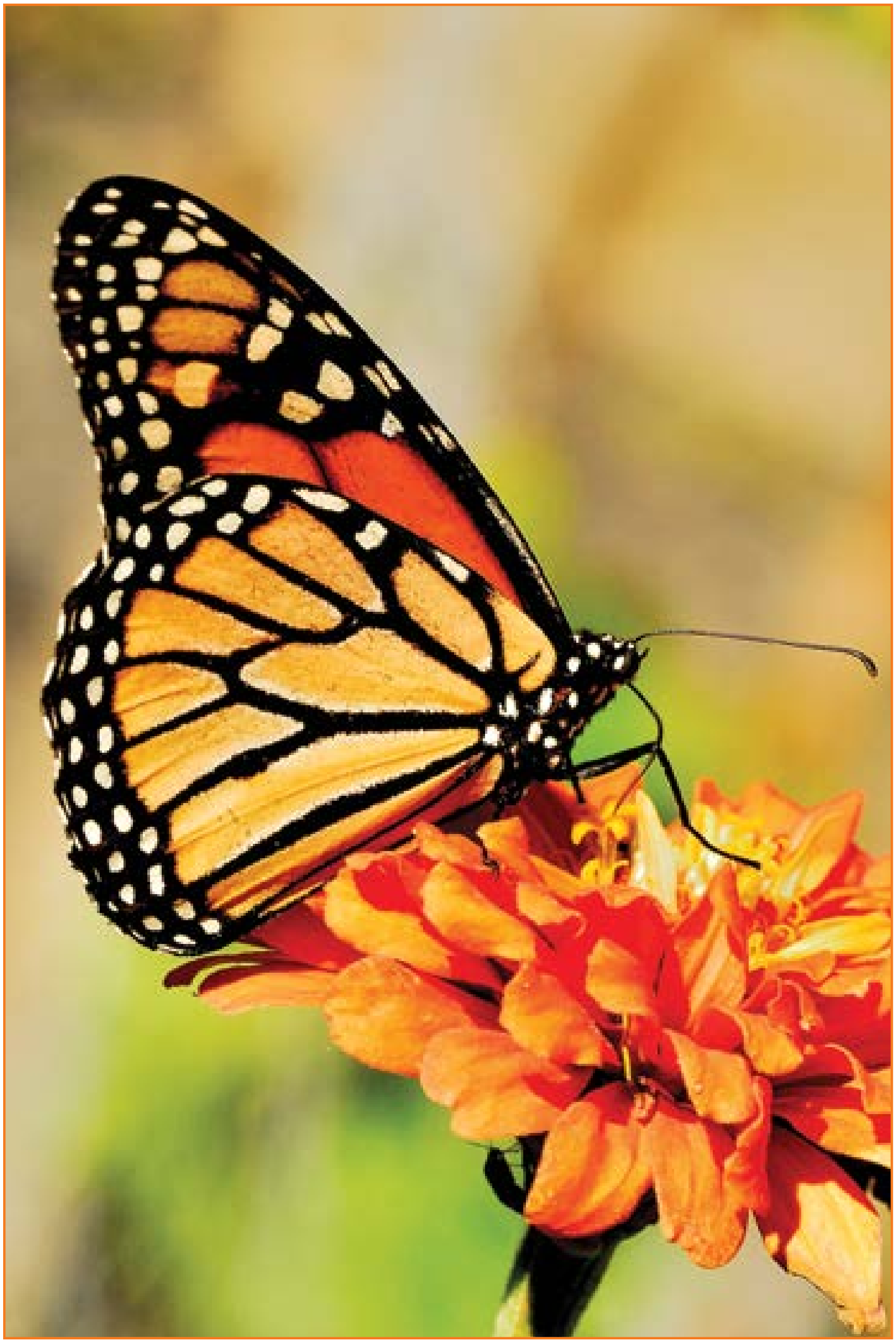

Figure 6.3 Monarch butterfly (*Danaus plexippus*) taking nectar in the community garden at 25th and Spruce Streets in Center City. It is poisonous and aposematic (warningly colored).

Figure 6.4 Monarch caterpillars on tropical milkweed (*Asclepias curassavica*) in a garden in Center City. Like monarch butterflies, they are aposematic. They obtain their protective poisons from milkweed and retain them after they undergo metamorphosis into butterflies.

Figure 6.5 Large milkweed bug (*Lygaeus kalmii*) on common milkweed (*Asclepias syriaca*) off Martin Luther King Drive in Fairmount Park. Like the monarch butterfly, it is aposematic.

Figure 6.6 Red milkweed beetle (*Tetraopes tetrophthalmus*), another aposematic species, on common milkweed in Fairmount Park.

The showy species noted above all contain cardenolide poisons that match those present in their milkweed (*Asclepias*) food plants.[10] One might hypothesize that these insects gain protection by sequestering noxious chemicals synthesized by milkweed. Lincoln Brower, who took me on as an assistant in college, tested this hypothesis. He succeeded in breeding a strain of monarch caterpillars that ate cabbage. I recall his frustration when he tried to select such a strain and the elation when caterpillars finally started eating cabbage—and then pupated and hatched into monarch butterflies. Caged blue jays initially rejected all monarch butterflies offered on sight, but they were eventually conditioned to eat cabbage-reared monarchs, which they consumed without ill effects. When Brower substituted monarchs reared on milkweed *(Asclepias curassavica)* for those reared on cabbage, the jays vomited within fifteen minutes of eating even one. As described by Brower and colleagues:

> In great contrast to the cabbage-fed monarchs, those reared on *Asclepias curassavica* caused all eight birds to become sick. Ingestion of these was followed uniformly by violent retching and vomiting of the partially digested insects and fluid…Other less objective indications of unpalatability included excessive billwiping, crouching, alternate fluffing and flattening of the feathers, erratic movements about the cage, jerky movements of head, wings, and thoracic regions, partial closure of the eyes, eating of sand, twitching, and a generally sick appearance.[11]

One might suspect that *Atteva aurea,* like the monarch, is unpalatable due to poisons it sequesters from its host plant. Its host plant belongs to a family that makes bitter compounds known as quassinoids. Leaves from *Ailanthus altissima* have yielded forty-nine volatile compounds with diverse biological activity: cytotoxic, phytotoxic, antiproliferative, antifeedant, insecticidal, and insect growth regulating.[12] Two investigators reported that birds find *A. aurea* unpalatable, but the number of observations was small.[13] No studies have investigated the chemical composition of *A. aurea*.

Richard Peigler, an expert on the ailanthus silkmoth, *Samia cynthia,* wrote:

> I agree that *Atteva* is aposematic, but I do not have any evidence that *Samia* moths are also toxic. Blue jays did swoop down and catch and eat flying *cynthias* that I released into my back yard in South Carolina.[14]

Other protective traits

The dramatic coloration of *Atteva aurea* might have functions unrelated to poisons. Its uniqueness could discourage predation by birds that avoid novelty.[15] Birds avoid attacking prey they perceive as unfamiliar. Ray Coppinger, working with Lincoln Brower, found that hand-raised blue jays and red-winged blackbirds in cages tended to reject novel-appearing insects offered as food. He demonstrated that rejection of novel insects was due to novelty per se and not experience or innate preference.[16] Sexual selection may also favor evolution of bright colors.

Poisons may protect *A. aurea* from birds, but not from other predators, such as insects. Ants, tachinid flies, and *Polistes* wasps attack monarch eggs and larvae, which in one study had survival rates of less than 12 percent.[17]

A. aurea's web provides barriers against invertebrate attack. The caterpillars stay motionless inside their web during the day; they leave it to feed only at night. Diurnal parasitic wasps would have to penetrate a hatchwork of threads to reach larvae in the web. A unique feature of *A. aurea's* web is that all life stages except adults occupy it simultaneously. Moths lay eggs in the web, and caterpillars develop and pupate in the web.[18] A bird that attacked a noxious caterpillar in the web would presumably learn to avoid other caterpillars in the web. Since the web hosts more than one generation of *A. aurea,* this protective benefit could span generations.

Fungal threat to ailanthus trees

A. aurea is the most common moth attracted to outdoor lighting in our backyard in Center City. Despite its abundance, the moth's host plant in Pennsylvania is susceptible to an emerging lethal contagion. In 2003 a verticillium wilt was discovered to be killing ailanthus trees in the Tuscarora State Forest about 210 kilometers (130 miles) west of Philadelphia. Mark Schall and his colleagues at Pennsylvania State University have been investigating this outbreak. By 2008, Schall estimated that the fungal pathogen, probably a strain of *Verticillium albo-atrum,* had killed 10,000 ailanthus trees.[19]

Schall reported that the fungus spreads rapidly from tree to tree. It can overwinter in infected ailanthus trees or on fallen leaves. The primary infection begins in the spring and spreads circumferentially around the tree and up and down the trunk until the tree dies. Trees experimentally inoculated with the fungus died within one season. In severely affected parts of the forest, the fungus wiped out the entire ailanthus canopy and half of ailanthus seedlings and sprouts. Seedlings of red maple, striped maple, and sweet birch began to fill in forest gaps caused by deaths of ailanthus.[20] Schall and his colleagues are investigating the application of *Verticillium albo-atrum* as a biocontrol agent against ailanthus, which is classified as an invasive species in Pennsylvania.[21]

To what extent verticillium wilt will reduce the distribution of ailanthus over time is hard to predict. Its hyphal resting structures do not tolerate acidic soils.[22] It may have difficulty propagating in urban leaf litter, which tends to get discarded. *Verticillium* is a fungal genus with ten recognized species.[23] *V. albo-atrum* is highly adaptable, with strains differing in virulence and host specificity.[24] In the Tuscarora State Forest, the strain's lethality appears specific to ailanthus, but worldwide *V. albo-atrum* and other members of the genus *Verticillium* have infected over 200 species of plants[25] and have been blamed for billions of dollars in annual crop damage.[26]

Figure 6.7 Woodlands cemetery, formerly William Hamilton's estate, site of the introduction of *Ailanthus altissima* into North America around 1784. It is located in west Philadelphia, a short walk from Center City. A fungal contagion has been discovered to be killing stands of ailanthus trees 210 kilometers to the west of here. The lethal infection is a kind of verticillium wilt.

Although the recent establishment of ailanthus in North America began when William Hamilton imported it to his estate in Philadelphia,[27] ailanthus fossils in North America span approximately 40 million years, from the early Eocene to the middle Miocene. These fossils accompany fossils from temperate plant genera that, unlike ailanthus, never died out.[28] Why ailanthus disappeared in North America while so many other members of its fossil temperate plant community survived is unknown, but one possibility is an ailanthus-specific pathogen like the fungus currently attacking it in Pennsylvania.

The rapid colonization of *A. aurea* in Philadelphia and farther north is remarkable for an insect originating in subtropical and tropical habitats. Conceivably, the recent spread of *A. aurea* into North America represents repopulation of ancestral territory. Whether a progenitor of *A. aurea* was present in temperate North America in the Eocene when ailanthus grew here is unknown. The genus *Ailanthus* and its family Simaroubaceae are believed to have originated in North America,[29] so the moth and its host plant could have evolved here together. On the other hand, *A. aurea* belongs to a pantropical genus (*Atteva*) of fifty-three species,[30] pointing to a tropical, not temperate, origin. An unanswered question is whether *A. aurea* overwinters in Philadelphia or whether it annually recolonizes the region by migration from the south.

Survival of populations of ailanthus webworm in Philadelphia

The survival of the ailanthus webworm moth but not the ailanthus silkmoth in Philadelphia is a mystery. Adaptive traits that favor the ailanthus webworm moth include webs, small size, aposematic coloration, and probably poisons. These advantages alone do not resolve the paradox; the ailanthus silkmoth flourished in Philadelphia in the nineteenth and early twentieth century despite its lack of such traits.

When populations of the ailanthus webworm moth expanded north from their home ranges in subtropical and tropical America, they likely left behind native enemies such as parasites that were intolerant of cold or otherwise maladapted to temperate North America. Perhaps Philadelphia endowed the ailanthus webworm moth with a refuge from its tropical enemies.

The theory that the ailanthus webworm moth in Philadelphia escaped tropical enemies does not explain the ailanthus webworm moth's survival in Philadelphia. While the moth in late summer and early fall is abundant, the damage its larvae inflict on ailanthus trees is minor. Some forces are reining in populations of the ailanthus webworm moth while simultaneously allowing them to propagate.

The difference in the fate of the two exotic ailanthus moths defies easy explanation. Perhaps parasites of the ailanthus webworm moth, in contrast to those of the cynthia moth, do not have alternate hosts; or perhaps lowering the population density of *A. aurea* lowers its vulnerability to enemies, be they pathogens, parasites, or predators.