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BAG WORM

(*Thyridopteryx ephemeraeformis*)

Infestations of bagworms ravaged shade trees in nineteenth-century Philadelphia.

Figure 4.1 Bagworm bag in winter. It is on a recently planted street tree. It might contain bagworm eggs or parasites, or it might be empty. In September, male bagworm moths emerge from the bottom of their bags and fly to females, which mature, mate, and lay eggs inside their bags. In the spring the eggs hatch and larvae crawl out the bottom and make new bags, in which they develop.

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Joseph Leidy's report in 1862 to City Councils about insects injurious to shade trees describes five species, all Lepidoptera (moths) except one, a scale insect. The species that Philadelphians are most likely to see today, although infrequently and only in small numbers, is the bagworm, *Thyridopteryx ephemeraeformis,* which, according to Leidy:

> …is among the most curious of insects. It is common on our shade trees, but especially infests the maples, larches, and arborvitae. Just at this period, July, the writer observes a large number on the cypress trees in front of the United States Mint, on Chestnut Street. The worms, after escaping from the eggs, immediately compose for themselves cases composed of silk, interwoven with fragments of their food…As the worms grow, they enlarge their silken and leafy habitations, until they reach an inch or two in length. In the latter part of summer, these insects are often noticed dangling from the trees of our sidewalks, suspended from the boughs by a silken thread, and enclosed in a dark, rough, spindle-shaped sack. They never leave the latter, but when they have reached their full growth, they fasten their silken case securely to a branch of the tree, and within it undergo transformation into a pupa. From the latter is produced the moth, the male of which awaits the night to leave his habitation in search of a mate. The female never leaves her silken dwelling, nor does she even throw aside her pupa garment; it is her nuptial dress and her shroud. Within it she deposits her eggs, enveloped in the down stripped from her body. The eggs, thus protected and enclosed within the mother's habitation, remain suspended from the branches of the tree, secure from storms and the cold of winter, until the following season.
>
> They are easily destroyed. All that is required to get rid of them, is to remove their silken cases when the trees are trimmed in the spring. With the cases, the accumulations of eggs are destroyed, which otherwise would give origin to new colonies of worms.[1]

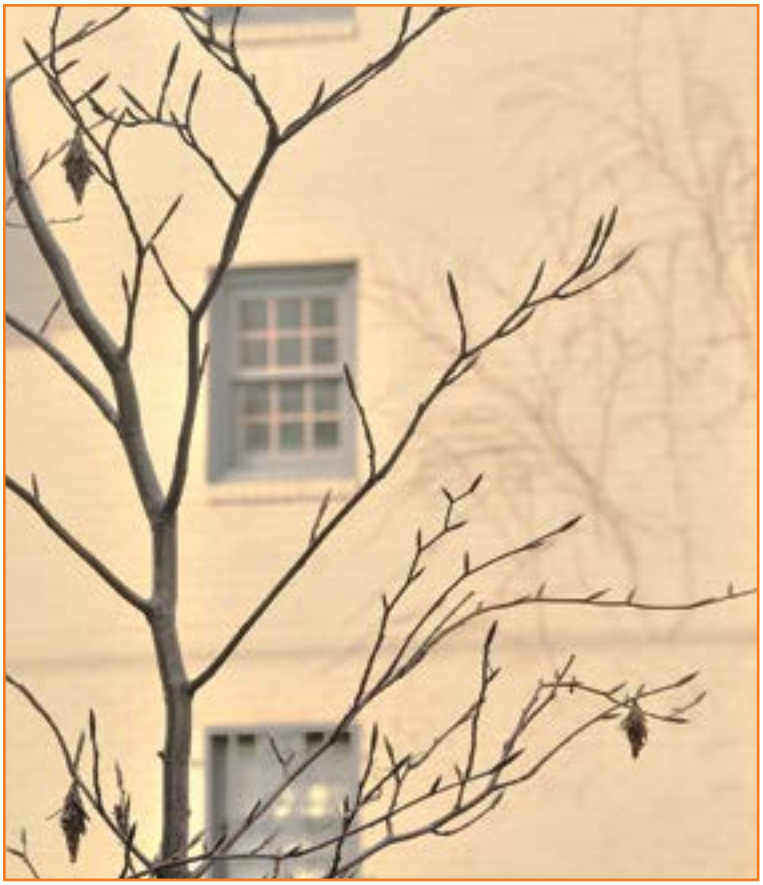

Figure 4.2 Group of three bagworm bags, including the one in figure 4.1.

Protection from the bag

The tough silken sacks that protect bagworms are covered with twigs and leaves that camouflage them and function like armor. They also shield them from solar radiation, wind, and rain. Although silken cocoons are commonplace during the immobile pupal stage of the life cycle of moths, the bagworm family, Psychidae, is unique for the portable sack its caterpillars carry.[2] The family includes 1,000 species worldwide,[3] but *Thyridopteryx ephemeraeformis* is the most conspicuous species in the northeastern United States,[4] where the term "bagworm" refers typically to just this species.

Leidy did not offer a clue to the mystery of how male bagworm moths manage to mate with flightless females enclosed within two defensive layers—pupal cases inside silk bags.

Mating through two defensive layers

In 1927, Frank Morton Jones, like Leidy a member of the Academy of Natural Sciences of Philadelphia, published a paper revealing how male bagworm moths penetrate the two enclosures that wall females off from the outside world. Mating takes place in September or October. Inside her pupal case, which in turn is inside her silk bag, the female is positioned head down, her genitalia facing the bag's top. At the bottom of the bag is a hidden opening through which the male will insert his genitalia at the tip of his abdomen. When ready to mate, the female—a maggot-like creature without wings, legs, antennae, or functional eyes—splits her pupal case open a crack near her head and emits a pheromone. Navigating using olfactory and visual cues, the male moth flies to the bag, grabs onto it, and probes its bottom with the tip of his abdomen, searching for the hidden opening. While the moth clings onto the outside of the bag, he inserts his genitalia, which occupy the tip of his abdomen, through the opening and then through the crack in the pupal case near the female's head. At this point, the male's genitalia are still far from the female's genitalia at the opposite end of the bag. The moth generates pressure that telescopes his abdomen and propels his genitalia past the female's head. The abdomen continues to elongate though the space between the female's body and the inside wall of the pupal case, finally apposing the genitalia of both sexes.[5]

After copulation, the moth's abdomen retracts to its normal length, and the moth flies away, capable of mating again. Almost immediately after mating, the female fills her pupal shell with eggs. Now in a shriveled, weak state, she exits her pupal case and seals the eggs inside. Contrary to Leidy's account, she then maneuvers herself through the hole in the bottom of the bag and drops to the ground to die. In the spring when the eggs hatch, the minute caterpillars emerge through the hole, crawling away onto nearby branches or floating away on strands of silk blown by the wind, to construct new bags.[6]

Figure 4.3 Moth (*Thyridopteryx ephemeraeformis*) reared from a bagworm feeding on eastern red cedar *(Juniperus virginiana)* planted along the Schuylkill River Trail. The moth is male and does not feed. To mate, he flies to a female confined inside her bag; her pheromone guides him. After landing on her bag, he inserts his genitalia (the orange structures at the tip of his abdomen) through an opening in the bottom of the bag and telescopes his abdomen inside the bag toward her genitalia at the top of the bag.

Thousands of eggs concentrated at one point

The capacity of this species to defoliate a tree is apparent from the size of a single brood: up to 1,200 eggs per bag.[7] Because the entire lot of eggs is stored in one bag, the release of bagworms is concentrated on a single point. One tree may harbor dozens of bagworm bags that collectively have the potential to release tens of thousands of bagworms. The larvae of this species can completely denude its host, although the host usually recovers.[8] Newly hatched caterpillars dangling on silken threads disperse by ballooning, blown by the wind to new host plants.[9] Bagworms have been recorded feeding on more than 128 species of plants in 45 families.[10]

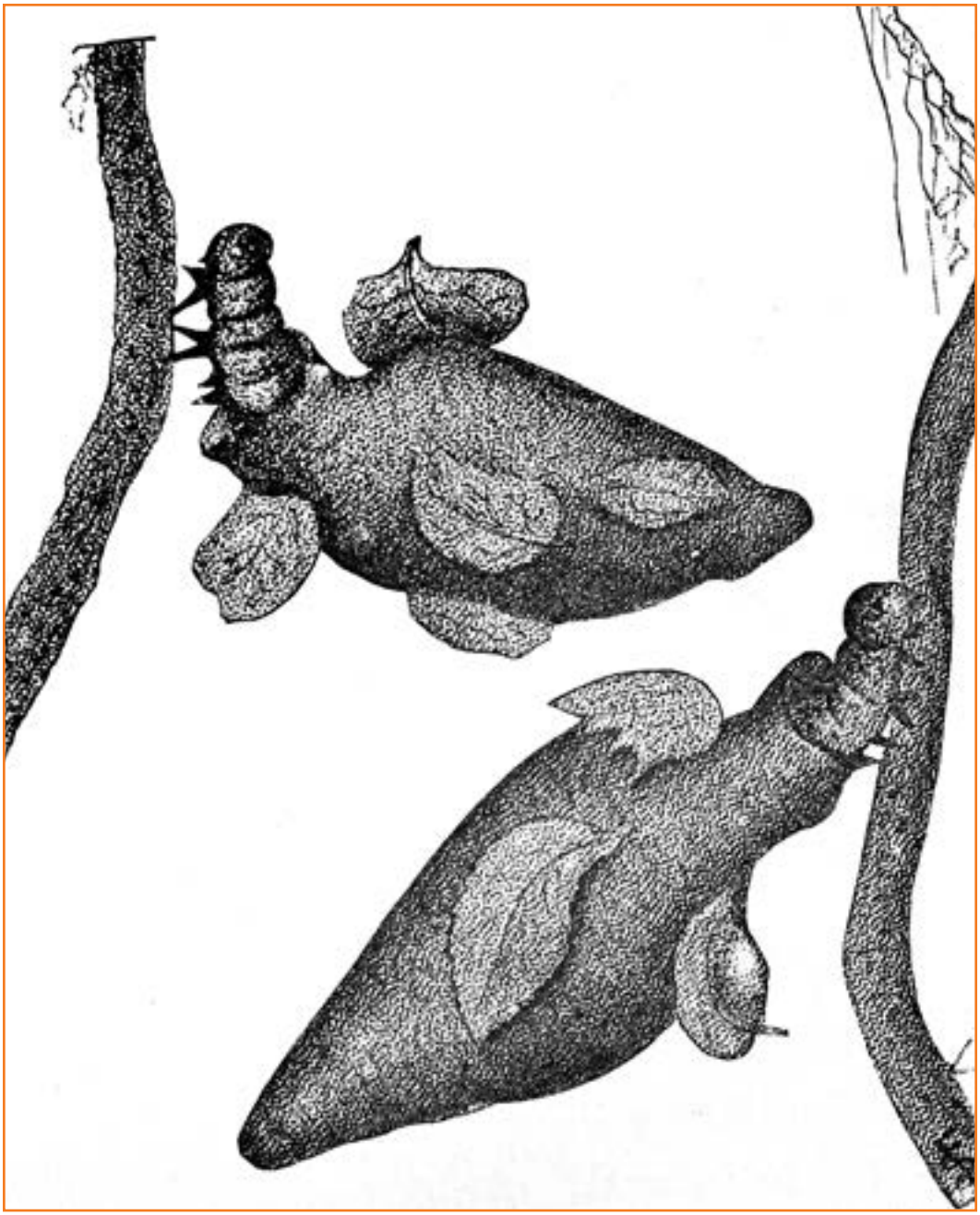

Figure 4.4 "How the bag-worms walk and climb." (Caption and cartoon from Henry McCook, *Tenants of an Old Farm. Leaves from the Note Book of a Naturalist. Illustrations from Nature.* [Fords, Howard and Hulbert, New York, 1889], 395.)

Infestations of bagworms in downtown Philadelphia are currently common only on recent plantings from nurseries. Why have bagworm infestations in Philadelphia declined since 1862, when Philadelphia City Councils enlisted Leidy's help in controlling them? In 1831 a horticultural report on Philadelphia's public squares indicated that horticultural development of Philadelphia's southwest square (now Rittenhouse Square) was a plan yet to be realized.[11] One hypothesis to explain the high prevalence of outbreaks of bagworms in nineteenth-century Philadelphia is that horticultural expansion required stock from nurseries, which then, like today, introduced bagworms that caused outbreaks.

More hypotheses to explain nineteenth-century outbreaks of bagworms

A second hypothesis is that enemies of bagworms in nineteenth-century Philadelphia had yet to establish populations sufficiently diverse and large to prevent outbreaks. Bagworms have been found to escape parasites by colonizing new areas and new host plants.[12] New plantings of municipal trees along streets and in other public places in the nineteenth century would have provided bagworms with host plants distant from established populations of specialized enemies, such as parasitic wasps. Joseph Leidy's report to City Councils in 1862 referred to a bagworm outbreak he had just witnessed on cypress trees in front of the United States Mint on Chestnut Street.[13] According to the escape-from-enemies hypothesis, this outbreak occurred because the bagworm's enemies had yet to colonize this area in numbers sufficient to keep the bagworm population under control.

Figure 4.5 Adult virgin female *Thyridopteryx ephemeraeformis* resembling a maggot, photographed in September. She developed in the bag of a bagworm I collected along Schuylkill River Trail in in August. Ordinarily, females mate and deposit their eggs inside their bags, and then, in a shrivelled state free of eggs, they emerge from their bags, drop to the ground, and die. Kept indoors and isolated from males, this female emerged as a virgin still laden with eggs. Whether she could have mated outside her bag is unknown. Her head and three pairs of diminutive legs are on the right; her genitalia are on the left.

Figure 4.6 Unidentified species of male ichneumon wasp attracted at night to black light in our backyard.

Figure 4.7 Unidentified species of female ichneumon wasp with long ovipositor, which she uses to lay eggs on (or in) her host. She was attracted at night to a pillowcase illuminated by black light in the rear of our home in Center City. Six species of ichneumon wasps are known to parasitize the bagworm (*Thyridopteryx ephemeraeformis*).

Figure 4.8 Plundered bagworm bag with interior silk exposed, September 16, 2013, along the Schuylkill River Trail, Center City. The predator had attacked most of the bagworm cases on this cultivated eastern red cedar, which hosted more than twenty. I did not witness this action. The ripping apart of bagworm bags (which are strong) attached to the tips of fine branches is consistent with depredation by white-footed mice (*Peromyscus leucopus*), nocturnal arboreal insectivores that prey on bagworms and inhabit Philadelphia.

A third hypothesis is that methods used to control bagworms in the nineteenth century were counterproductive. Leidy's recommendation to pick and destroy egg-laden bags in the winter had the potential for destroying parasitized bags by mistake, since the bags containing parasites or bagworm eggs look the same. Unintended destruction of parasites could be high if rates of parasitism were also high. Entomologists from the U. S. Department of Agriculture in the late nineteenth and early twenti-

eth century recommended spraying arsenic-based insecticides on trees infested with bagworm bags that could not be picked off by hand. This, too, may have killed parasites and interfered with biological control. Charles Valentine Riley, chief entomologist for the U.S. Department of Agriculture, recommended a simple modification of Leidy's approach: Instead of destroying bagworm bags, store them in a container that would allow parasites to fly out, but would deny newly hatched bagworms access to food and sites for ballooning.[14] I do not know whether Philadelphians tried this parasite-conserving method.

A fourth hypothesis is that shady promenades popular in nineteenth-century Philadelphia favored bagworm outbreaks. A recent horticultural restoration of the south garden of the Fairmount Water Works exemplifies such a promenade, planted with sweet gum cultivars and London plane trees emulating the design of Frederick Graff, Jr., one of the garden's nineteenth-century landscape architects.[15] The striking horticultural feature of this garden is the absence of flowerbeds. In 1874 Fanny Kemble, who lived on Rittenhouse Square, commented on the square's absence of flowerbeds and flowering shrubs.[16] Flowers provide food for ichneumon wasps, whose larvae are the primary parasites of bagworms. In a study designed to test the utility of flowers for control of bagworm infestations, it was found that bagworms feeding on shrubs surrounded by flowering forbs were parasitized at rates 71 percent higher than were bagworms feeding on shrubs not surrounded by flowers.[17]

A fifth hypothesis is that abundance of native host plants in nineteenth-century Philadelphia promoted infestations of bagworms. Populations of bagworms, which are native to North America, may be more likely to proliferate on native plant species compared to exotics, which took time to spread and naturalize in the Philadelphia area over the past two hundred years. Douglas Tallamy and his colleagues at the University of Delaware attempted to rear bagworms on sixteen species of exotic ornamentals currently naturalized in the mid-Atlantic area. Bagworms on thirteen of the species starved; those on the remaining three species grew at unsustainably low rates.[18] In another study, female bagworms feeding on Japanese maple *(Acer palmatum),* an exotic ornamental common in Center City, grew and matured normally, but did not produce eggs.[19]

A sixth hypothesis is that nocturnal darkness undisturbed by electric lighting promoted reproductive success of bagworms in nineteenth-century Philadelphia. Male bagworm moths fly to electric light, as demonstrated by their capture in electric light traps.[20] Bagworm moths in the laboratory live for only a day,[21] so moths diverted from mating to lamps might not have a second chance to mate. Electric lighting has been invoked to explain decreases in populations of moths in habitats already compromised by other disturbances.[22]

Despite the potential for artificial lighting to disrupt reproduction, its impact on populations of bagworms is doubtful. The moth's mating flights peak from 3 to 6 p.m. and are usually over by dusk.[23] *T. ephemeraeformis* may tolerate artificial lighting better than do most other moths; lamps cannot attract its wingless females, which mate and lay eggs in their bags. Flight to lamps may disturb bagworm moths less than their enemies, such as parasitic flies and wasps.[24]

Perpetual influx of new enemies

The decrease of outbreaks of bagworms in Philadelphia today compared to a century and a half ago is likely multifactorial in origin. Causes may have changed over time; in particular, bagworms in the city likely encountered a steady increase in enemies over the last century and a half. In 1986 *T. ephemeraeformis* was found for the first time to be parasitized by *Coccygomimus disparis,* an ichneumon wasp repeatedly introduced into North America from Asia from 1972 to 1984 to control the gypsy moth, *Lymantria dispar.*[25] In one survey published in 2005, *C. disparis* was the most common parasitoid found on *T. ephemeraeformis.*[26] (A parasitoid is a parasite that kills its host.) Enemies of *T. ephemeraeformis* include at least sixteen parasitoids, four predators, ten pathogenic fungi, a polyhedrosis virus, and bacilliform bacteria. These enemies include four orders and nine families of insects. Predators of bagworms include house sparrows and white-footed mice *(Peromyscus leucopus),* which inhabit Philadelphia.[27]

How long might it take for all potential enemies of *T. ephemeraeformis* to disperse into Philadelphia and establish populations here? In principle, evolution and importation of new enemies could continue indefinitely, a process exemplified by the annual influx of new viral strains that cause human influenza. The status of Center City as a nexus of commerce and transportation promotes this process.

Termination of recent outbreaks

During winter about a decade ago, I collected ten bagworm bags from saplings planted in Schuylkill River Park. I stored them in a breadbox to observe young bagworm larvae emerging from their mothers' bags. Bagworms had been partially defoliating trees in the park for several years. Four of the bags turned out to be empty; I had mistaken empty bags for egg-laden bags. Some of the empty bags may have been from males that had hatched in the fall, but others could have been leftovers from previous years. By leaving empty bags dangling conspicuously from branches, *T. ephemeraeformis* has established a system of decoys capable of fooling predators, including me.

The bags I collected yielded parasitic wasps and flies, but no bagworms. Leidy had observed wasps emerge from bags, but the attack rate in my small sample was 100 percent. I had hoped my removing bagworm bags from the trees in winter would reduce the infestation of bagworms, but I had succeeded only in removing the bagworm's natural enemies. I did not think to release the wasps back into the park. That summer I found no bagworms in Schuylkill River Park. The parasites had ended the outbreak of bagworms—despite my meddling.

Since then, I found new bagworm bags on newly planted river birches 100 meters away along the Schuylkill River Trail. A cluster of these trees had fifteen bagworm bags hanging from their branches, which showed moderate defoliation. This time I left the bags alone. After two years, I found no defoliation and no new bags.

Figure 4.9 Bag of the bagworm, *Thyridopteryx ephemeraeformis,* in winter on a river birch recently planted along the Schuylkill River Trail in Center City. New bags stopped appearing on these trees two years after appearance of the first bags.