A Tripartite Relationship Between a Woodrot Fungus, a Wood-boring Sawfly, and the Giant Ichneumonid Wasp

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One of the joys of mycology is that there is always more than meets the eye at first glance. Every mushroom has a story if you dig deep enough. Take the ubiquitous turkey tail; probably the most common mushroom on the planet. No matter how small the patch of woods, no matter how dry the season—it can even be found in the dead of winter, the previous season's growth on a downed log, dried-out and faded.

But wait… what's this? Upon closer inspection it's not a turkey tail at all, but a somewhat similar looking little polypore. The little bit of green on the top belies its disguise (Fig. 1). This is no turkey tail but none other than the mossy maze polypore, *Cerrena unicolor* (Fig. 2). But dig a little deeper still, as this is only the beginning our story…

The lifecycle of *Cerrena* is much more complicated and fascinating than you can imagine and involves a huge symbiotic wood wasp plus an even larger parasitic wasp. I first came across this story many years ago while reading a 2003 edition of *Sam's Corner.* The "Sam" was venerated northeastern naturalist Sam Ristich. He was loved by all who ever met him, knew everything about every organism in the forest, and was only too eager to share his knowledge with anyone curious. "The Remarkable Story of the Wood Fungus *Cerrena* (*Daedalea*) *unicolor*, the Horntail Wasp *Tremex columba*, and the Ichneumonid wasp *Megarhyssa"* stuck with me over the years and through personal observations of the players involved, I am able to add a bit more information to the story.

The horntail wasp (*Tremex columba*) is a very large (about 2 inches long) wood-boring wasp (family Siricidae). Also called sawflies, horntails get their name because of the upturned

Figure 1. *Cerrena unicolor*; photo by B. Bunyard.

horn-like spike (cornus) on the last segment of the abdomen (Fig. 3). (Many sources erroneously say that this is the ovipositor, or egg-laying apparatus; the ovipositor is actually the much longer structure that looks like a stinger.) Worldwide there are about 100 species of siricids in 11 genera; in North America there are six genera (Smith and Schiff, 2002). No native siricids are known to be of tremendous economic importance as a forest pest, and thus they are poorly studied.

There are countless species of wood-boring insects on the planet and in all cases, including siricid wasps, none of them make enzymes to digest wood cellulose. In order to utilize cellulose, all wood-boring insects must live in symbiotic relationship with microbes that produce cellulase enzymes (Buchner, 1965). Siricids rely on basidiomycete white rot fungi, even transporting these fungi to the wood source (Cartwright, 1929; 1938). These symbioses are mutualistic, as both partners benefit; the wasps are enabled to utilize a large energy resource in the forest and the fungus benefits in not only being transported to a specific host tree, but by the insect carrying the fungus past the tree's first line of defense (the corky bark) and into the interior wood. Tabata and Abe (1995) showed that in the case of the horntail wasp, oidia (conidia, or asexual spores) and mycelium are carried within special abdominal glands in the female wasp called mycangia. (Oidia are very simple conidia, arthrospores really, resulting from repeated fragmentation of mycelial tips.) When the horntail lays eggs inside the tree, oidia pass from mycangium through ducts to the ovipositor. No doubt *Cerrena* fruitbodies produce heavy loads of sexual basidiospores that result in successful infestation of wood, but compared with the insect as vector, the former seems much more haphazard. And without the involvement of *Tremex* spp., infestation into a living tree is probably even less likely.

Adult horntails are known to lay eggs in dead as well as living trees, but (in the case of living) usually select host trees

***Cerrena unicolor* (=*Trametes unicolor*, *Daedalea cinerea*) occurs in overlapping clusters on broad-leaved trees, stumps, and logs (occasionally on conifer wood) and thought to be initially parasitic on living trees, becoming saprobic on the dead wood. The brackets can remain on the log year-round. Appearance of brackets is similar to that of the turkey tail but with several notable differences. The flabellae (fan-shaped brackets) are wavy and densely hairy on top, whitish gray/brown, concentrically zoned, and often *covered with algae* giving them a green appearance. The underside is whitish to ash gray, *maze-like* and becoming almost tooth-like at maturity. The spore print is white.**

that are already weakened or dying as a result of some other disease (Smith and Schiff, 2002). The most common host tree is beech (*Fagus grandifolia*) and to some extent sugar maple (*Acer saccharum*) (Stillwell, 1964). As mentioned, the host tree is inoculated with the fungus at the time of oviposition. The female horntail drills under the bark of the tree (Fig. 4) where the eggs are then deposited 2-15 mm deep into the sapwood (Stillwell, 1964). A single female may lay several hundred eggs among many oviposition tunnels in a single tree. As with other hymenopterans, fertilized eggs will become females and unfertilized eggs will become males. Eggs typically take a few weeks to hatch (but may not hatch until the following year) and it's thought that the lag period allows for the fungus to begin growing and digesting the wood. Upon hatching, the horntail larvae bore tunnels through the wood (up to 1 m in length) but it's unclear if they are consuming wood *and* fungal material; some scientists have suggested that the larvae may be getting all their nutrition from the fungal material alone (Gilbertson, 1984). Larvae will mature and pupate within the wood; emergence as adults occurs via exit holes bored to the surface and adults emerge from July through October. Stillwell (1964) found that larvae do not live past the first instar (first molting) when grown in the absence of the fungus.

Many more horntail larvae do not make it to adulthood because they are killed by an amazing parasitoid wasp,

The ichneumonid wasps of the genus *Megarhyssa* (four North American species) and of closely related genera parasitize larvae of wood wasps and wood-boring beetles. The Ichneumonidae *is the largest family of insects* and comprises well over 3,000 species in North America alone! Ichneumonids are parasitoid wasps; some, like *Megarhyssa* spp. are the largest of parasitoids. Adults often feed on body juices of hosts and larvae feed on immature stages, such as larvae and pupae of butterflies and moths (Lepidoptera), beetles (Coleoptera), flies (Diptera), and sawflies and wasps (Hymenoptera). Ichneumonids are valuable control agents of many noxious insect pests. Some species attack spiders or are hyperparasites (parasites that feed on other parasites) and, thus, might not be considered to be beneficial insects in all cases. Most species overwinter in the cocoon as a mature larva, although some spend the winter as adult females. There may be one to 10 generations produced annually depending on the species. Ichneumonids are generally considered to be harmless but although species of *Megarhyssa* cannot sting, some species are capable of stinging when improperly handled.

Figure 2. Detail of underside (hymenium) of *Cerrena unicolor*; photo courtesy J. Justice.

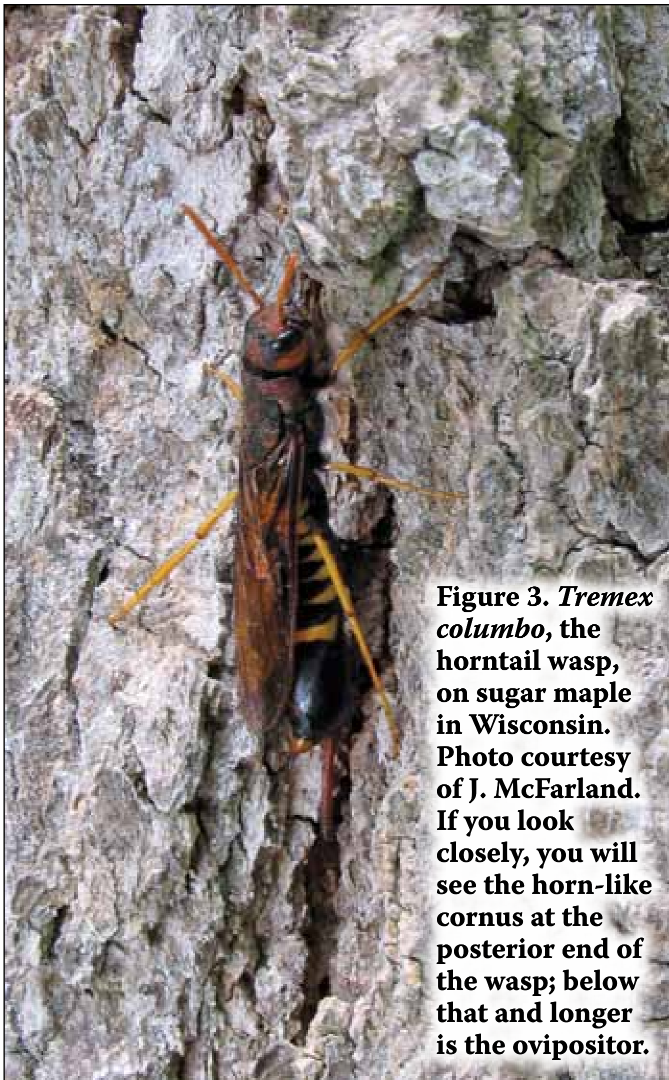

Figure 3. ***Tremex columbo*****, the horntail wasp, on sugar maple in Wisconsin. Photo courtesy of J. McFarland. If you look closely, you will see the horn-like cornus at the posterior end of the wasp; below that and longer is the ovipositor.**

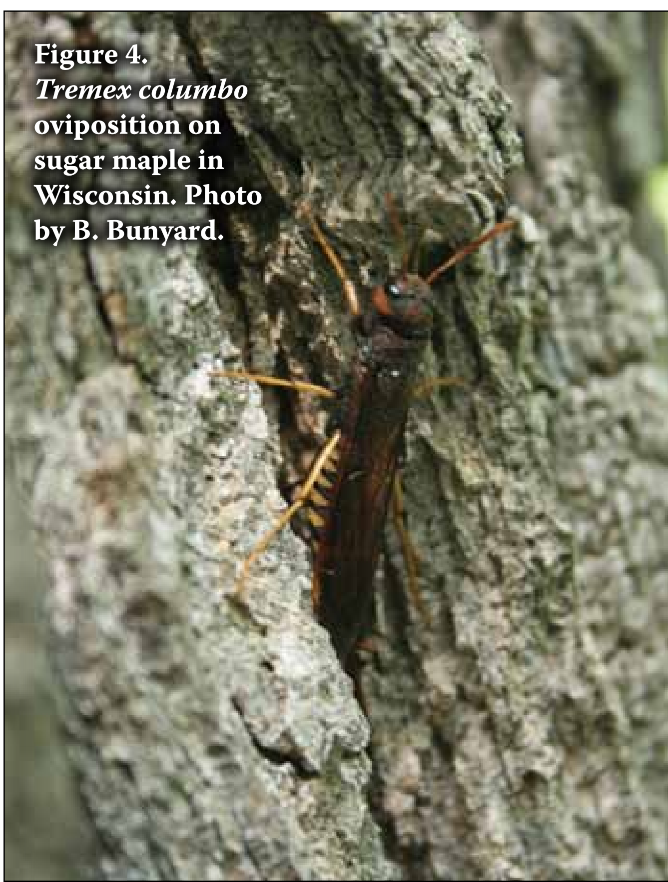

Figure 4. ***Tremex columbo*** **oviposition on sugar maple in Wisconsin. Photo by B. Bunyard.**

Figure 5. *Megarhyssa atrata* oviposition on beech in Maine. Photo courtesy of B. Woo. If you look closely, you will see the female's ovipositor has been inserted into an exit hole, presumably of a horntail.

Figure 6. *Megarhyssa atrata* oviposition on beech in Wisconsin; photo by B. Bunyard.

the giant ichneumonid wasp (*Megarhyssa atrata*, and *M. macrurus*; Figs. 5-8). The giant ichneumonid (family Ichneumonidae) is a parasitoid with a single host: horntail wasp larvae. Besides its alarming size, the coloration of *Megarhyssa* spp. also make them quite striking to see. But its most notable feature is the long "tail" that extends *four to six inches beyond the tip of the abdomen* (Fig. 9). This tail may look like an incredibly wicked stinger, but is the ovipositor and supporting structures, used to insert eggs into wood where its host (the developing horntail larvae) exist. The ovipositor "tail" of the female actually consists of three filaments. The central part is the ovipositor, capable of drilling through wood. Although appearing as a single filament, it is actually made of two parts that interlock, slide against each other, and are tipped with the cutting edge. Although very thin, it is a tube and the egg moves down the minute channel in its center during egg-laying. The ovipositor is normally sheathed within two other thin filament structures that are protective in function, do not assist with drilling and bow outward prominently (Figs. 5-7) around the insect during egg laying. Males are smaller (Fig. 8), lack the ovipositor, and have a blunt tip of the abdomen.

Both horntails (*Tremex* spp.) and ichneumonids (*Megarhyssa* spp.) are in the insect order Hymenoptera (commonly called sawflies, bees, wasps and ants), so they are both wasps, but very different types of wasps. Siricids are sawflies, which are primitive/basal, non-stinging wasps with large saw-like ovipositors (rather than "stingless wasps;" "Stingless" usually refers to stinging hymenopterans that have secondarily lost the ability to sting, such as stingless bees, which have evolved from stinging bees).

The female *Megarhyssa* can be seen searching the same logs and stumps used by the female horntail, although they tend to be present a bit later in the summer. So, how does the giant ichneumonid find the horntail larvae tunneling deep in the dead wood? Sam Ristich claimed that the fungus, *Cerrena unicolor*, played a role. Indeed, an insidious symbiotic alliance with the parasitoid—sort of a double-cross. He wrote that "the fungus produces a pheromone that lures the female ichneumonid wasp" to the area. I've seen no other reference to the production of secondary metabolites or any other odorous attractants but Tabata and Abe (1995) reported that *Cerrena unicolor* mycelia grown in culture produce a horrible odor. Other sources claim that the parasitoid detects the vibrations of host larvae within the wood with their antennae (and I have witnessed "antennae sensing" on logs but it might be more complicated than simply detecting vibrations). No matter how *Megarhyssa* does it, developing horntail larvae are detected under the bark by the female and she subsequently drills into the wood to the tunnel of the horntail larva. *Tremex* larva are paralyzed with a sting (from the ichneumonid) after which the parasitoid egg is laid. The ichneumonid larva feeds on the horntail larva, consuming it completely within a couple of weeks. It then pupates in the host insect tunnels and the adult *Megarhyssa* emerges the following spring.

I have personally observed oviposition of both wasp species on several occasions. Usually the females are quite focused on their business and will allow you to approach closely and to

Figure 7. (Above left) *Megarhyssa macrurus* female during oviposition; photo by R. Heidt.

Figure 8. (Above right) *Megarhyssa macrurus* male on beech in Wisconsin; photo by B. Bunyard.

take photos. Oviposition can take place over a long period of time, even an hour or more, so you may have time to set up a tripod and reflectors should you happen upon these amazing creatures in your woods.

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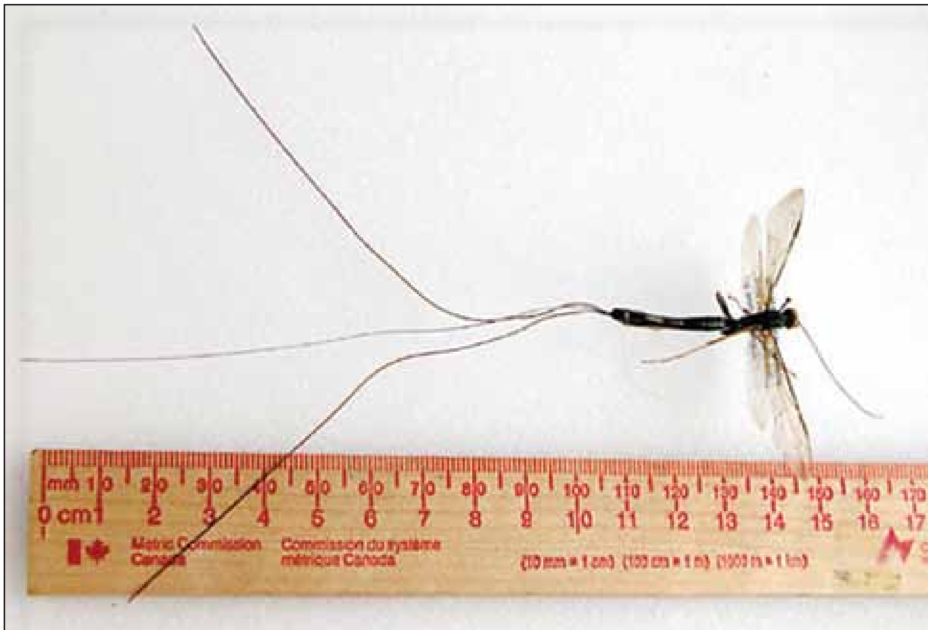

Figure 11. Naturalist Sam Ristich, photo courtesy R. Ristich.

Figure 9. (Above) *Megarhyssa atrata* being sized up—that's one large wasp! Photo courtesy of M. Turgeon.

Figure 10. (Right) Joseph McFarland prepares to photograph *Tremex columbo*. Photo by B. Bunyard.