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Oak apple gall (*Andricus quercuscalifornicus*) on valley oak (*Quercus lobata*). Photograph by G. Frankie.

CYNIPID-INDUCED GALLS AND CALIFORNIA OAKS

by Kathy Schick

Watching a tiny female *Andricus fullawayi* wasp through a magnifying glass, I am amazed at the amount of time she spends carefully grooming her wings and antennae with the special combs on her front legs. As I wait anxiously to see where she will fly to lay her eggs, she crawls awkwardly, brushing her antennae against the twig to test its odors. She takes her time. More than 20 minutes elapse after I release her from the rearing container before she finally becomes airborne.

Suddenly, a gust of wind sweeps the tiny wasp into the branches of a nearby valley oak (*Quercus lobata*) and she is lost to sight. I wonder where this tiny creature is going, and whether her offspring will develop within a gall on the stem, leaf, flower, or root of an oak tree.

Like many other cynipid wasps, this tiny, ungainly female is smaller than this typeset number "1," yet she and other gall wasps have managed to colonize every native oak tree species in California. They trick their host trees into forming striking plant growths called galls, filled with nutritive tissues. The galls provide food and shelter for the developing larvae of the wasps.

Oak gall wasps are members of the insect order Hymenoptera, family Cynipidae, and tribe Cynipini. Unlike bees, ants, and stinging wasps, in which the ovipositor has evolved into a stinger, cynipid wasps have retained ovipositors with which they can carefully position their eggs inside plant tissues without harming any plant cells.

The most primitive living

relatives of modern cynipid wasps use their long ovipositors to lay eggs into the larvae of wood-boring wasps and beetles, much as their earliest ancestors probably did. From such primitive ancestors two modern families of wasps evolved:

Wasp of *Andricus quercuscalifornicus* (top) on gall. Photograph by K. Schick. • Spindle gall (bottom), unisexual generation of *Heteroecus pacificus*, on *Quercus vaccinifolia* (huckleberry oak). Photographs by K. Schick.

Figitidae, which parasitize the larvae of flies; lacewings and other wasps; and Cynipidae.

Apparently early in their evolutionary history, ancestors of cynipid wasps began to skip the insect host and consume plant tissue directly through gall induction. The oldest known fossil cynipid galls, approximately 115 million years old, are found in Cretaceous deposits.

Regular readers of *Fremontia* will be familiar with some of the exotic and bizarre shapes of modern cynipid galls on blue oak (*Quercus douglasii*) from the excellent photographs in an article over a decade ago by Russo (1990). Each species of cynipid wasp induces its oak host to form a unique shape of gall. While many other gall-inducing insects, such as tenthridinid wasps, inject chemicals into plant tissue along with their eggs so that gall formation begins before larvae emerge, gall induction in Cynipidae begins in response to chemicals secreted by growing wasp larvae.

Cynipid galls are more complex than galls of many other insects. They contain several tissue layers and a separate central chamber for the developing larva. Cynipid larvae complete their development by becoming pupae and then adults, before they emerge from their galls to lay eggs for the next generation.

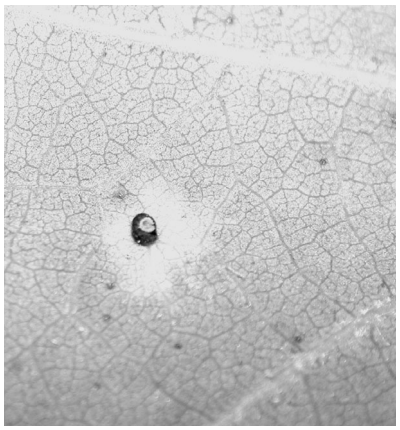
Galls may contain a single larva, as do those of the jumping gall *Neuroteras saltatorius*, a tiny spherical structure about the size of this "o" which forms on the underside of oak leaves. These tan-colored galls hop up and down under *Quercus lobata* oaks from June through August in the Central Valley of California. The dropping galls jump around for a while after they fall from the leaves, eventually maneuvering themselves into crevices in the ground where they will endure the winter, and from which the adult females will emerge in early spring.

Other cynipid galls may contain more than one larva such as the large "oak apple" gall induced on *Quercus lobata* by the wasp *Andricus quercuscalifornicus* (see photographs, page 15). This stem gall gets as big as a baseball and may contain as many as 16 developing larvae. The galls generally start forming in early spring and grow into round green spheres that resemble juicy green apples, even to the point of developing a reddish blush when they mature. The color quickly fades and the drying galls turn beige during the summer. The wasps within finish pupation and emerge as adults in autumn, leaving the gall behind on the tree. After the first year, old galls turn black, covered in sooty mold.

ALTERNATION OF GENERATIONS

Distinctly different galls—often on different parts of the host tree—are produced not only by different wasp species, but also by different generations of the same cynipid species. Most cynipid species in the oak-galling tribe Cynipini have two alternate generations each year: a bisexual generation with both males and females developing in spring galls, and a unisexual generation of only females in autumn galls. This phenomenon of alternating generations is called *heterogony* and results in females so different from those of their alternate generations that many were originally described as separate species, sometimes even in separate genera.

The unisexual generation of the wasp *Antron douglasii* produces striking pink star-like spiny turbans in summer on the leaves of *Quercus lobata*, *Q. dumosa* (Nutall's scrub oak), and *Q. douglasii*. The bisexual generation of this wasp produces twig galls that look like large white semi-translucent mistletoe berries in early spring, later fading and hardening to woody knobs. Wasps



Jumping gall, the unisexual generation of *Neuroterus saltatorius*, under *Quercus lobata* leaf. Photograph by G. Frankie.

emerging from these spring galls were first placed in the genus *Dryophanta* because they looked so strikingly different from their alternate generation.

Surprisingly, even though their homes are so distinctive and thus the insects should be easy to locate, scientific knowledge of the gall wasp fauna in California is far from complete. Many oak galling species have yet to be described, and alternate generations are currently known for fewer than a fourth of the 122 described California species.

In the British cynipid fauna, which is well known, some cynipids species are known to have alternate generations on separate oak tree species, as well as strikingly different morphologies and colors with size ranges differing more than fivefold.

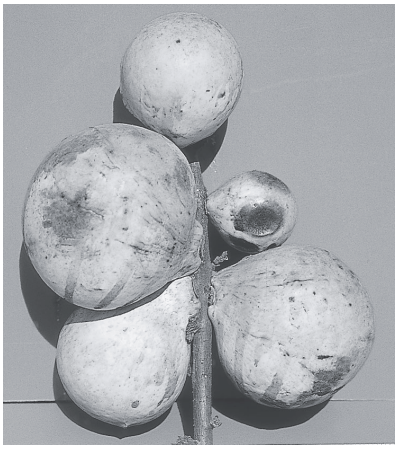
After many years of caging *Andricus quercuscalifornicus* wasps on young oak trees, which then produced new oak apple galls within these cages during the second year, I suspect this species has lost its alternate generation. If an alternate generation does exist, the adults must be significantly smaller than the unisexual generation and must induce inconspicuous galls on stems or leaves. Only after several more years of study will we truly understand heterogony for this single species. Finding alternate generations for the remaining cynipid species in California will require a lifetime of study.

A COMMUNITY OF WASPS IN AN OAK GALL

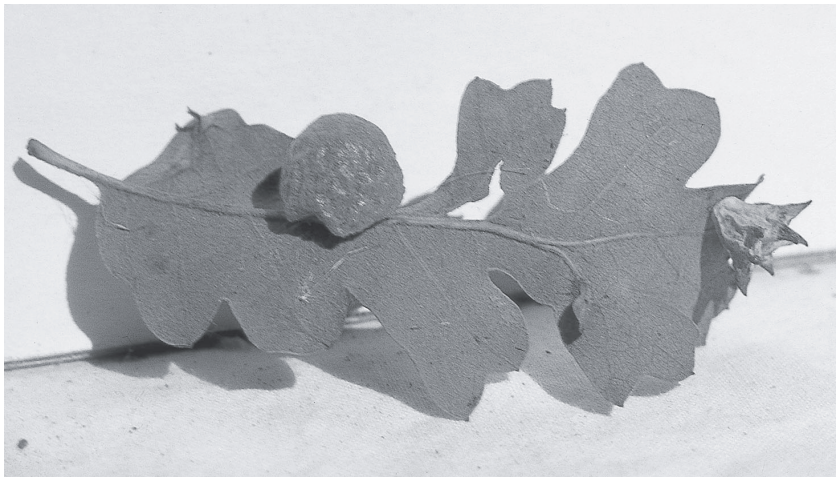
At first glance, an oak gall might seem an ideal refuge from predators and other dangers to young larval insects. Oak galls are especially rich in tannins, much more so than normal plant organs, so the gall tissue should not be especially attractive to plant-eaters. However, these galls cannot move so they are predictable food resources, attracting herbivores as well as insect-eaters. Also abundant in oak galls are two other groups of wasps: herbivorous inquiline ("guest") cynipid wasps and very specialized parasitoids in the superfamily Chalcidoidea.

The inquiline wasps all belong to the tribe Synergini within the family Cynipidae and appear to have lost the ability to secrete gall-inducing chemicals. Instead, they locate developing galls into which they lay their eggs. When inquiline larvae emerge they may consume all the nutritive cells, starving the gall-inducer. Some species may even deliberately kill the gall-inducing larva in order to consume its food resource.

A very few cynipid inquilines actually induce changes in the shape of the gall, indicating that they have not entirely lost the ability to secrete appropriate chemicals. One such inquiline species in the genus *Synergus* causes unisexual galls of *Heteroecus pacificus* forming on either *Quercus chrysolepis* (canyon oak) or *Q. vaccinifolia* (huckleberry oak) to change from a narrow spindle shape to a rounded globular shape. I have dissected these galls and found as many as five larval chambers for the smaller inquiline wasps around a single central chamber for the larger gall-inducer, all of which



Oak apple gall (*Andricus quercuscalifornicus*) (right), on valley oak (*Quercus lobata*). • Three galls on leaf of *Quercus lobata* (below): clockwise from tip, *Antron douglasii*, *Besbicus conspicuous*, and *Xanthoteres clavuloides*. Photographs by G. Frankie.



apparently matured and emerged as adults.

Parasitoids are similar to predators in that they kill their host animal, and they are also similar to parasites in having a single host animal for their entire lifetime. The majority of chalcid parasitoids found in oak galls lay their eggs in cynipid larvae. The growing larvae of the parasitoids slowly consume developing cynipid larvae or pupae. These wasps come in an amazing array of forms and colors, and I am constantly amazed at the number of different parasitoid species found on each cynipid species.

One of my favorite oak gall parasitoids, *Torymus californicus*, belongs to the calcid wasp family Torymidae and can be reared from *Andricus quercuscalifornicus* oak apple galls. The female of this species is a metallic coppery red with a long, pin-like ovipositor extending twice the length of her body. The long ovipositor allows the female parasitoid to lay her egg directly into the cynipid larva deep in the gall. The male of this species is metallic green and much smaller than the female. These parasitoids emerge from old oak galls in late spring after the season's galls are nearly half their mature size.

EFFECTS ON THE OAKS

A quick glance at any California woodland will reveal some oak trees with numerous galls while neighboring oak trees remain virtually gall-free. Scientists are only beginning to understand the mechanisms gall wasps use to turn on certain plant genes with auxin-like chemicals, and the corresponding immune response of the trees. While there is an energy cost to the oak tree that grows galls, most healthy oak trees have more than enough energy left over from photosynthesis to spare tissue and sugar to shelter a community of wasps. However, problems can arise when individual trees are diseased or stressed.

Callirhytis quecussuttoni, a common gall wasp on *Quercus agrifolia* (coast live oak) and *Q. wislizeni* (interior live oak) forms a large spherical stem gall slightly smaller than a tennis ball in the center of a twig. This gall appears to block vascular tissues, and frequently all of the branch extending past the gall dies. At any given time many *Quercus agrifolia* trees along the coast in Monterey County will be growing several of these galls and appear rather ragged. But the majority of cynipid galls are not nearly so stressful to the host tree as is this species.

A very unusual situation has recently developed in Canada. Since 1986, people on Vancouver Island have observed a tragic interaction between their Garry oaks (*Quercus garryana*) and the jumping gall wasp, *Neuroterus saltatorius*. The jumping gall wasp had moved north into this area only a few years earlier and for reasons still not clearly understood, it induces many galls to form close together on Garry oak leaves.

The brown spots of necrosis around each growing gall are not a problem in California, where these same wasps induce only a few galls on each leaf, but they cause entire leaves to die when galls grow too densely in Canada. Some of the Vancouver Island Garry oaks actually lose all their leaves mid-summer as a result of this abundance of galls, and even a formerly healthy tree will die after two or three years of mid-summer leaf loss. Many heritage trees have died as a result.

There seems little danger that the Canadian problem with *Neuroterus saltatorius* will ever occur in California. One major difference between Californian and Canadian populations of this wasp is the percentage of galls that are parasitized. When I have collected and reared these galls in California, 80 to 90 percent of the galls yield parasitoids instead of gall-inducers. When my Canadian colleagues have made similar collections on Vancouver Island, they find far lower rates of parasitism in galls, which they believe is a result of their cooler, wetter weather. Death of these Canadian trees may also be related to the recent introduction of two species of oak phylloxera to western Canada.

The Vancouver Island oak-cynipid interaction is an extreme exception to the norm of gall wasp and host tree interactions. California cynipid galls provide colorful and spectacular decoration to our oak woodlands, costing trees only a tiny fraction of the energy they gain through photosynthesis and providing homes for a diverse and interesting wasp community.

REFERENCES

Csóka, G. et al. 1998. *The biology of gall-inducing arthropods.* Forest Service, US Department of Agriculture, St. Paul, MN.

Duncan, R.W. 1997. *Forest pest leaflet #80: Jumping gall wasp.* Pacific Forestry Centre, Victoria, BC.

Meyer, J. 1987. *Plant galls and gall inducers.* Gebrüder, Borntraeger, Stuttgart, Germany.

Redfern, M, and R.R. Askew. 1992. *Naturalists' handbooks 17: Plant galls.* Richmond Publishing Company, Slough, England.

Russo, R. 1990. Blue oak: A gall wasp nursery. *Fremontia* 18:68–71.

——. 1979. *Plant galls of the California region.* Boxwood Press, Pacific Grove, CA.

Shorthouse, J.D., and O. Rohfritsch. 1992. *Biology of insect-induced galls.* Oxford University Press, New York, NY.

Weld, L.H. 1957. *Cynipid galls of the Pacific Slope.* Privately printed, Ann Arbor, MI.

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