How do inquilines and parasitoid wasps locate the galls they use?

Orientation, chemical signals, gall characteristics, vibrations, and examples from the world of gall wasps

Key idea
A tiny wasp does not simply search for “a particular gall” using a single sense. The search is probably a multi-stage process: long-range orientation using the host plant and odours, short-range searching using visible and chemical characteristics of the gall, and finally assessment of the concealed host through contact, mechanical, or chemical signals.

1. Long range	2. Short range	3. Contact	4. Assessment	5. Decision
Oak / plant	Gall	Antennae	Ovipositor	suitable host?
Odour plume	Shape • colour • position	Touch • smell	Vibrations	Oviposition

Important limitation: For many oak gall communities, the precise mechanism by which galls are located has not yet been established experimentally. This is particularly true for inquilines such as Synergus, where direct evidence for individual locating cues is considerably more limited than it is for well-studied parasitoids.

1. What does a tiny wasp actually have to find?

A gall wasp produces a gall that conceals its larval stage within plant tissue. For a parasitoid arriving later, the situation is therefore unusual: the actual host is hidden from view and is often only a few millimetres in size. The gall is simultaneously a refuge, a food source, and a point of orientation.

Two ways of life – two search problems

- **Parasitoids / parasitoid wasps: The larva must use an animal host. The gall therefore first has to be found as a “host-bearing structure”; the hidden host must then be located and accepted.**
- **Inquilines: They live inside a gall produced by another gall wasp and mainly use its tissues or the resources provided by the gall. Their search is therefore directed more towards a suitable gall than towards a single host larva.**

Searching in oak gall wasps is shaped by a particularly complex mosaic
Oak galls differ in gall type, plant part, shape, size, surface, developmental stage, tree species, and season. The associated parasitoid and inquiline community is therefore not assembled at random. For West Palaearctic oak galls, it has been documented that the associated fauna is strongly influenced by gall morphology, position on the tree, developmental timing, and host tree.

This does not automatically mean that the wasp consciously “identifies” each of these individual features. Some may simply act as innate preferences: particular odours, shapes, or plant structures may trigger searching behaviour.

2. The first level: odour and host plant

Many parasitoids use volatile organic compounds (VOCs). These may come directly from the plant, from the gall, or from plant parts altered by the infestation. In gall wasp systems, gall formation can alter the plant’s odour profile, creating a kind of chemical “fingerprint”.

What might the wasp detect by smell?

- **Odour compounds produced by the host plant itself.**
- **Altered plant odours caused by gall formation or feeding/manipulation.**
- **Volatile compounds released from the gall tissue.**
- **In some systems, indirect cues indicating the presence of a living host inside the gall.**

Well-documented example: Quadrastichus mendeli and the eucalyptus gall wasp Leptocybe invasa
In an experimental study, the parasitoid Quadrastichus mendeli preferred odours from eucalyptus plants damaged by the gall wasp over odours from mechanically damaged or undamaged plants. Several individual odour compounds also triggered measurable responses in the antennae. This clearly shows that a parasitoid can detect an infestation through plant-derived odour signals without having to see the gall-wasp larva.

But caution is needed with oak galls

For oak cynipids, it has long been suspected that the odour, shape, size, and position of the gall play a role in its discovery. However, the literature explicitly emphasises that relatively little is still known about the specific locating cues used by oak gall wasps. Recent studies confirm that at least some parasitoids can perceive volatile compounds associated with cynipids.

3. The second level: sight, shape, colour, and position

Once a wasp reaches the vicinity of a suitable plant, the search becomes much more precise spatially. At this stage, visual and structural characteristics of the gall may become important.

Why is gall shape so useful?

- **Many gall species have a highly characteristic shape.**
- **The gall occurs on a plant part characteristic of the species: bud, leaf, catkin, twig, fruit, etc.**
- **Colour and surface structure change as the gall develops.**
- **Size and degree of maturity may indicate whether a suitable host is actually present.**
- **The position on the plant drastically reduces the number of possible "candidates".**

This is particularly interesting in oaks
The two generations of many oak gall wasps can produce completely different galls. A parasitoid species that specialises in or prefers a particular generation therefore does not simply find "the gall-wasp species", but potentially a very specific gall type at a particular time of year and on a particular part of the plant.

Studies of oak gall communities show that sexual and asexual generations often support different parasitoid communities. This is strong evidence that timing and gall type are important ecological filters.

A possible search sequence

Long range	Tree / plant chemistry	"Worth searching here."
Intermediate	Gall type / position / shape	"This gall fits."
Short range	Antennae / touch / odour	"There is something interesting here."
Contact	Ovipositor / mechanical signals	"The host is here."

4. The third level: touch, vibrations, and "tapping"

Some parasitoid wasps can locate concealed hosts using mechanical information. This does not necessarily mean that they "hear" a vibration produced by the host itself. In certain species, the wasp generates a signal by tapping or vibrating the substrate and evaluates the mechanical response. This behaviour is described as vibrational sounding.

How does the basic idea work?
The wasp touches or taps a substrate such as a stem, wood, or plant tissue. Mechanical waves spread through it and are influenced by structures inside. Specialised sensory organs on the legs and modified antennae may be involved in this form of host location. The method is particularly interesting for concealed, immobile hosts.

Important: This is not automatically the mechanism used by every gall wasp

Vibrational sounding is well studied in parasitoid wasps in general, but this does not justify concluding that, for example, every Torymus or every eulophid finds a gall in this way. For oak cynipids, the precise contributions of individual sensory channels are even less completely understood.

A good comparative example

Pimpla turionellae can locate concealed, immobile hosts in plant structures using mechanical signals. Experiments show that this form of host location is influenced by temperature and by the physical properties of the substrate. This demonstrates how finely tuned a mechanical locating system can be.

At a gall, a wasp could therefore theoretically combine several types of information: Where is the gall? – What is its structure? – Is there a suitable host inside? These levels should be distinguished biologically.

5. What happens directly at the gall?

Once the wasp has found a potentially suitable gall, a second kind of decision begins: Is this gall actually suitable? Parasitoids may examine the gall with their antennae, insert the ovipositor, or investigate the surface in detail.

The ovipositor is more than a "drill"

- **It can penetrate the gall wall.**
- **It allows the egg to be laid at a very precisely selected location.**
- **In some parasitoid wasps, chemosensory structures on the ovipositor can provide information about the substrate and/or the host.**
- **In species with a long ovipositor, the wasp can reach hosts located deeper inside; other strategies involve laying eggs very early in gall development.**

Example from oak galls

In oak cynipids, parasitoids differ, among other things, in how deeply they can reach a host. A long ovipositor can facilitate access to larvae located deep inside the gall. Another strategy is to oviposit very early in gall development and wait for the host to develop. This means that the wasp does not later have to overcome the thicker gall wall.

Why this matters for identifying your specimens
For the oak galls you are studying, the combination of gall type + generation + oak species + developmental timing is therefore valuable not only for the later identification of the emerged wasp. It can also help explain why particular inquilines and parasitoids occur in exactly this gall at exactly this time.

6. And how do inquilines such as Synergus find their galls?

Here, a little more scientific caution is needed. For many inquilines, the specific sensory physiology underlying gall location is less well studied than it is in classical parasitoids. Nevertheless, there is strong ecological evidence that inquilines do not colonise galls indiscriminately.

What the data clearly show

- **Synergus species can be associated with particular groups of oak galls.**
- **In oak inquilines, host tree, gall type, and gall morphology play an important role in the observed host ranges.**
- **The composition of inquiline and parasitoid communities depends strongly on gall species, position on the tree, and season.**
- **The direct question "Which molecule does a female Synergus detect by smell and therefore fly specifically towards this gall?" remains unanswered for many species.**

This is therefore the most scientifically cautious wording
We know that the appropriate gall is located and deliberately used; however, for every inquiline species we do not know which sensory cues control the entire search process. A combination of several signals is probably involved here as well.

Connection with Andricus grossulariae

For your specific system, the information "Andricus grossulariae, bisexual generation" is particularly valuable. In oak cynipids, the associated communities of the two generations often differ markedly. An inquiline specialised in a particular gall type must therefore coincide precisely, both in time and space, with the occurrence of that gall.

This does not necessarily mean that the wasp can "recognise" the gall from a great distance. Instead, it may be a stepwise process: suitable oak → suitable season → suitable plant part → suitable gall → chemical/physical assessment.

7. Four examples for comparison

Example 1 – Quadrastichus mendeli: chemical orientation

This eulophid parasitises the invasive eucalyptus gall wasp Leptocybe invasa. Experiments showed a preference for odours from plants damaged by the gall wasp. This is a particularly clear example of the use of plant-mediated chemical signals.

Example 2 – oak cynipids and their Chalcidoidea: gall type as an ecological filter

In parasitoids of oak gall wasps, the community as a whole is strongly influenced by gall morphology, position on the tree, season, and host tree. This shows that a wasp does not simply search for “oak”, but selects from a complex range of galls.

Example 3 – vibrational sounding: mechanical host location

In certain parasitoid wasps, the substrate is actively investigated mechanically. This allows the wasp to obtain information about concealed hosts. The strategy is particularly impressive because the host does not have to be visible from the outside.

Example 4 – fig gall wasps and their parasitoids: odour + direct chemical assessment

In fig systems, the role of volatile compounds and chemical assessment has been particularly well studied. Parasitoids can respond to odours from syconia containing their gall wasp hosts; during the subsequent decision, chemical information detected by the ovipositor may play a role. This system provides an excellent example of how long- and short-range signals can work together.

> **Key point**
> **The farther the wasp is from the gall, the coarser the information available to it. As it gets closer, the signals become more specific: plant → gall type → surface → concealed host. This is not a rigid recipe, but a multimodal search system.**

8. What we know – and what remains unresolved

Question	State of knowledge
Do parasitoids use odours?	Yes, this is well documented for many parasitoids; plant VOCs associated with galls may also be relevant.
Are oak gall types important?	Yes. Gall morphology, position, season, and host tree clearly influence the associated fauna.
Do wasps use vibrations?	Well documented in certain parasitoid wasps; it cannot be generalised to every gall wasp.
Is host location in Synergus fully understood?	No. Host ranges and ecological associations are better known than the specific sensory mechanisms involved in gall location.
Does a wasp recognise “the right species” from a single signal?	Probably not in most cases. A multimodal, hierarchical search is the more plausible model.

For practical collecting and rearing

- **Always document the gall together with the exact host plant, locality, date, and plant part.**
- **For gall wasps, record the generation whenever possible (sexual/bisexual or asexual).**
- **Photograph the gall shape and stage of maturity before storing the galls.**
- **Document emerged inquilines and parasitoids separately from the original gall type.**
- **For unusual finds, the combination of host + gall + generation + date is often more valuable than simple photographic similarity.**

Especially with Synergus, a carefully documented rearing can therefore be of enormous taxonomic value: the gall provides the ecological context, while the adult wasp provides the morphological characters – only together do they provide a robust identification.

Sources and further reading

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Note on the scientific interpretation
The literature on gall location must distinguish between parasitoids in general, parasitoids of gall wasps, and inquilines. A mechanism demonstrated experimentally in one parasitoid wasp species must not automatically be extrapolated to all parasitoid wasps or to Synergus.