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Host specificity and host recognition in a chemically-defended herbivore, the tenthredinid sawfly *Rhadinoceraea nodicornis*

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Abstract

The sawfly *Rhadinoceraea nodicornis* Konow (Hymenoptera: Tenthredinidae) is a member of a closely related group of species, the tribe Phymatocerini, which feed on the Liliales and Ranunculales. It is known to sequester steroid alkaloids from its host plants, species in the genus *Veratrum* (Liliales: Melanthiaceae), and to use them as a defence against predators. There are known chemical relationships between the hosts of *R. nodicornis* and hosts of related sawfly species. We tested whether the *R. nodicornis* larvae would accept hosts of closely- and more distantly-related sawflies, but found that they accepted only plant species in the genus V*eratrum*. This specificity was apparently innate, as it was independent of early larval experience. A feeding bioassay showed that the steroid alkaloids from *Veratrum nigrum* were phagostimulatory for *R. nodicornis* larvae, suggesting that they may be involved in host recognition. We discuss the possibility that the evolution of recognition of specific compounds may represent the mechanism of host radiation within the Phymatocerini.

Introduction

Most phytophagous insects specialise on a limited number of host plant species. Since the work of Fraenkel (1959) and Ehrlich & Raven (1964), host-plant chemistry has been widely invoked in the explanation of both host-use patterns of individual species and of patterns of insect species-radiation between different hosts. Constraints operating on host recognition abilities can act as a restriction on the ability to recognise some plants as hosts as a corollary to improved recognition of others (Bernays, 1996). There may also be a trade-off between the ability to cope with one particular group of toxic plant secondary chemicals and the ability to utilise food sources with different chemistries. This may be particularly the case where insects have evolved such an intimate relationship with their host-plant that they are able to adopt the chemistry in the plant to their own ends through sequestration. Strong selection from predators is likely to act against individuals which feed on plants from which they cannot obtain defensive compounds, driving the evolution of species which recognise and specialise in feeding on those plant species on which they are chemically defended (Bernays & Graham, 1988). There are some exceptions, but most insects that sequester chemicals for their defence are monophagous or specialists on one closely-related group of host plants (Duffey, 1980; Rowell-Rahier & Pasteels, 1992). There are also examples from phylogenetic studies of insect groups that appear to have used secondary chemicals sequestered by many species in the group as 'guide posts' in shifts to new host species, although the process is far from universal, with shifts also to groups with an entirely different host chemistry (Dobler, 2001; Wahlberg, 2001).

Sawflies in the tribe Phymatocerini feed on plants from two orders, the Liliales and Ranunculales. Literature sources (Liston, 1995) suggest that each sawfly species is restricted to one plant genus, although

this remains to be tested rigorously. The two plant orders are not closely related but share some common elements of secondary chemistry, notably the steroid saponins and steroid alkaloids, two groups of structurally similar compounds made through the same biosynthetic pathway which occurs in many Liliales and some Ranunculales (Frohne & Jensen, 1992; Colombo et al., 1990). These compounds are highly toxic to non-adapted insects (Velbinger, 1947; Harmatha, 2000). At least three of the phymatocerine sawfly species are known to sequester the steroid saponins or steroid alkaloids from their host plant and use them for their own defense (Schaffner et al., 1994; Schaffner & Boevé, 1996; J.-L. Boevé & R. Rozenberg, unpubl.; F.V. Vencl & U. Schaffner, unpubl.). The pattern of host-use within the Phymatocerini suggests a potential role for the common chemistry of the two plant orders in their use as hosts by related sawfly species. Host recognition in the sawflies might be mediated by the sequestered steroids, or by secondary chemicals that indicate their presence.

Rhadinoceraea nodicornis Konow is the most well-studied species in the Phymatocerini. This species occurs in Europe and feeds on two species of false helleborine, the montane grassland species *Veratrum album* L. and the woodland species *V. nigrum* L. (Liliales, Melanthiaceae). Testing larval acceptance of a range of other plants from these habitats found no other plants that the species would accept (Schaffner, 1994). Both *Veratrum* species contain a mixture of steroid alkaloids known as ceveratrum alkaloids. Schaffner et al. (1994) showed that the larvae sequester some elements of this mixture without modification, modify and sequester others, and degrade or excrete the remainder. They found that sequestered alkaloids are present in the haemolymph, and that this is repellent to ants, which are a key group of predators in the sawfly's natural habitat. When ants consumed haemolymph in sugar solution, it was highly toxic to them. In addition, in field observations and laboratory trials Schaffner et al. (1994) found that larvae themselves were ignored or rejected by ants and spiders, which suggested that sequestration provides this species with an effective defence against predation.

As a first step towards understanding the host-use patterns of the Phymatocerini, we set out to define the host range of *R. nodicornis* in a phylogenetic context by testing larval acceptance of hosts used by other sawfly species in the tribe. It is possible that larvae might feed to some extent on these plant species which they do not normally encounter but which have a similar secondary chemistry. In addition, we wondered whether the observed patterns of specific host recognition were innate or were learnt by the experience of neonate larvae. As with almost all tenthredinids, the eggs of this sawfly are laid into the plant tissue and larvae eat a hole in the leaf in order to emerge. Conditioning to a particular host plant after some initial experience has been recorded for oligophagous sawfly larvae (Martens, in Heitland & Pschorn-Walcher, 1993). We therefore also tested how larval host acceptance might be affected by feeding experience during hatching. Finally, we hypothesised that larval discrimination should be at least partly based on recognition of characteristic plant chemistry, potentially either the sequestered steroid alkaloids or an indicator of their presence, and so we investigated the possibility that these alkaloids have a role in larval host recognition using a simple bioassay.

Materials and methods

Host-specificity testing: host acceptance. For the host specificity testing, we adopted a strategy based on a phylogenetic approach: we tested the normal hosts, as controls, and then the hosts of other species of *Rhadinoceraea*, including another *Veratrum* species, *V. californicum*, which is native to North America and does not grow in the range of *R. nodicornis*. We then tested hosts of other Phymatocerini that feed on the Liliales and of phymatocerines that feed on Ranunculales. Finally we used the host of an outgroup species, *Tomostethus nigritus* (Fab.), which is in the same subfamily (Blennocampinae) but not the same tribe of sawflies (Tomostethini rather than Phymatocerini) and feeds on a plant from the Oleales, *Fraxinus excelsior* L.. We also used one species from the Liliaceae, *Convallaria majalis* L., that as far as is known is not eaten by any sawfly species, as a 'botanical outgroup', expecting that even if everything else was accepted this would be rejected. Our selected plants and the sawfly species that normally feed on these are shown in Table 1. Plants for testing were obtained from the field or from organic nurseries and grown in a soil-based compost with a slow release fertiliser.

In each feeding trial, ten Petri-dishes were set up for each plant species. Each contained one small leaf (or a cut piece about 3 cm square for plants with large leaves) placed onto filter paper dampened with tap water. A single larva was placed carefully onto each leaf. After 24 h the leaves were examined for signs of

Table 1. Selected test-plants and the sawflies that normally feed on them. Sawfly names are based on Liston (1995). Plants marked * were tested in the year 2000 and those marked ** in 2001. All plant and sawfly species are native European species except *R. aldrichi* and its host *V. californicum*, which are native to North America

Plant species and family	Plant order	Normal host of:
Veratrum album L. (Melanthiaceae) *&**	Liliales	*Rhadinoceraea nodicornis* (Konow)
Veratrum nigrum L. (Melanthiaceae) *	Liliales	*Rhadinoceraea nodicornis* (Konow)
Veratrum californicum Durand (Liliaceae) *	Liliales	*Rhadinoceraea aldrichi* MacGillivray
Lilium martagon L. (Liliaceae) *	Liliales	*Rhadinoceraea bensoni* Beneš
Iris pseudacorus L. (Iridaceae) *	Liliales	*Rhadinoceraea micans* (Klug)
Polygonatum multiflorum All. (Liliaceae) *	Liliales	*Phymatocera aterrima* (Klug)
Convallaria majalis (Liliaceae) *	Liliales	None
Helleborus viridis L. (Ranunculaceae) **	Ranunculales	*Monophadnus monticola* (Hartig)
Helleborus foetidus L. (Ranunculaceae) **	Ranunculales	*Monophadnus latus* (A. Costa)
Ranunculus lanuginosus L. (Ranunculaceae) **	Ranunculales	*Monophadnus pallescens* (Gmelin)
Clematis recta L. (Ranunculaceae) **	Ranunculales	*Eurhadinoceraea ventralis* (Panzer)
Fraxinus excelsior L. (Oleaceae) **	Oleales	*Tomostethus nigritus* (Fabricius)

feeding damage and the larvae examined to check if they had material in the gut. The number of larvae that had fed was recorded. We used neonate or early instar larvae in these trials as they are more susceptible to starvation over short time periods. Many of those that did not feed over the 24 h period of the trial died during or soon after the experiment. We therefore considered that very young larvae would be more likely to feed on marginally acceptable hosts over this time.

Larvae for the trials in the year 2000 were collected as first and second instars from *V. album* plants from montane field sites at different altitudes from May to July. *Rhadinoceraea nodicornis* is univoltine but adult emergence and egg-laying times vary according to climate and altitude. In order to use larvae while they were as small as possible, we distributed all field-collected individuals within a day of their collection randomly between selected treatments and did not standardise age or moulting condition. The duration of each trial was much longer than the non-feeding phase of moulting larvae. In 2001, larvae were reared from eggs laid by females emerging in culture in April. After allowing these females to mate they were given pieces of cut *V. album* leaves (approximately 2 cm × 2 cm) on dampened filter paper in 9 cm Petri-dishes in a incubator at 17 °C and L16: D8. Eggs laid hatched after about ten days in these conditions and neonate larvae were used in trials.

In addition, in 2000, we were able to collect a small number of early instar larvae from woodland sites with *V. nigrum* in southern Switzerland. Adults fly in April at this warm-climate site. At this time, the number of test plant species available was limited, in part because it was early in the growing season for northern Switzerland; the larvae were tested on *V. nigrum*, the alternative host *V. album*, two other hosts of *Rhadinoceraea* species (*Lilium martagon* L, *Iris pseudacorus* L.) and the non-host plant *C. majalis*.

Host specificity testing: the role of experience. To obtain larvae that had hatched without experience of feeding on the host-plant, we caged four *R. nodicornis* females with *V. album* leaves in 9 cm Petri-dishes in an incubator at 17 °C, L16: D8 for several days to lay eggs. When the 90 eggs laid were about five days old (when the eyes of embryos had become visible), we dissected out the eggs from two-thirds of each leaf under a microscope, and placed them onto wet filter paper in a 9-cm Petri-dish. We then cut the leaves into two pieces, one containing all the remaining eggs. One half of the dissected eggs were then replaced into the depressions in the other part of the leaf from which eggs had been removed, carefully smoothing the loose flap of leaf tissue over them; these served as controls for any effects of the dissection process on subsequent larval behaviour or survival. A little water was dripped onto each replaced egg to compensate for the reduced humidity caused by wounding the leaf. The dissected, replaced, and unmanipulated (normal) eggs from each female were placed in separate dishes back into the incubator until the eggs hatched. Eggs were not washed, as they are very fragile and we wished to minimise manipulation; in any case, many of the compounds that might affect larval host choice, such as steroid

alkaloids, are not water soluble. It should be noted that hatching larvae do not eat the chorion of the eggs.

Hatching larvae were tested singly in a no-choice test as described above on each of three host plants from the Liliales, *V. album*, *P. multiflorum*, and *L. martagon*, with ten larvae on each plant from normal, replaced, and dissected eggs. To check that the manipulation treatments did not adversely affect larval establishment on the host, all larvae on *V. album* were reared individually in their Petri dishes. Every two days they were fed fresh sections of *V. album* leaf and the dishes re-lined with fresh moistened filter paper. The larvae were weighed after five days and their survival was monitored until the larvae reached the prepupal phase (the species overwinters in the soil in this phase). Mean weights were compared between egg manipulation treatments using a one-way ANOVA to see if the manipulation had affected establishment on the host.

Host acceptance and host chemistry: a feeding bioassay. To test whether host acceptance was at least partly determined by the alkaloids which the larvae sequester, we used a feeding bioassay. We applied 20 μl of 1 M sucrose solution in water to 1.5 $\times$ 1.5 cm filter paper squares and allowed the squares to dry completely. We then applied either 20 μl of test solution or 20 μl of solvent (as controls) to the squares and again allowed them to dry. This volume was sufficient to just wet the entire filter paper square. Test solutions used were a whole leaf extract of *Veratrum nigrum* in methanol (MeOH), with MeOH-treated controls, and a complete alkaloid extract of *Veratrum nigrum* in dichloromethane (CH_2Cl_2) prepared from a methanol whole leaf extract, with CH_2Cl_2 – treated controls. *Veratrum nigrum* was used because preliminary bioassays had suggested that larvae respond more strongly to *V. nigrum* than *V. album* methanol extracts. Methods for extract preparation were as follows:

(1) Whole leaf extract: 40 g of *V. nigrum* leaves were collected in Ticino, Switzerland, on 20/6/01 and kept initially in a cool box at about 5 °C and then stored overnight at 2 °C. The following day when they were chopped finely and left to extract in 100% MeOH at room temperature for 24 h. The leaf/MeOH mixture was then stored at 5 °C.

(2) Complete alkaloid extract: Following the method in Schaffner et al. (1994), 40 g of leaves of *V. nigrum* plants from the same origin but grown in pots in the institute garden since April 2000 were cut and left to air-dry on 15/6/01. They were chopped and extracted initially in 300 ml MeOH, then evaporated to about 90% dryness. 200 ml H_2SO_4 (pH3) was added and the mixture washed three times with 3 $\times$ 150 ml CH_2Cl_2. The pH was adjusted to 8.5 with 1 M NaOH and the alkaloids extracted from the solution by shaking it with three aliquots of 150 ml CH_2Cl_2. Each CH_2Cl_2 aliquot was decanted from the MeOH, with which it is immiscible, before the next was added; the three were then pooled. The extract was stored at room temperature as the alkaloids are stable under these conditions (Schaffner, pers. obs.).

The experiment was carried out on 23/7/01, one month after the extracts were prepared.

Plastic boxes 18 $\times$ 13 cm and 6 cm deep were lined at each end with wet filter paper, leaving a dry area of 12 $\times$ 13 cm in the centre. A pair of filter paper squares treated with a test substance were weighed and placed in this dry area on one diagonal of a square in each box; a pair of the control squares were weighed and placed on the opposite diagonal. Squares weighed about 40 mg each. Papers were spaced at a distance of 4 cm apart, edge-to-edge. We set up 12 boxes with whole-leaf extract squares plus controls, and 12 with the alkaloid extract and controls, giving 12 replicates for each experiment. The aim of this design was principally to test whether the alkaloid extract stimulated feeding, with the whole leaf extract experiment as a standard for comparison. Eight *R. nodicornis* larvae were added to each box and the lids were put on. Larvae had been collected from *V. album* plants at an Alpine field site in late July, a few days before the experiment, and maintained on *V. album* leaves in an incubator at 17 °C constant temperature with a L16: D8 photoperiod. They were sorted by size and a matched mixture of sizes added to each box; the majority were 4th and 5th instars with one late 3rd instar per box. Larvae were left in the boxes at ambient conditions (maximum temperature 25 °C, minimum 20 °C, approximately 16 h daylight) for 24 h. The boxes formed a sealed environment in which the filter paper squares quickly became moist, even though they were not directly wetted. After 24 h the box lids and the larvae were removed and the squares allowed to air dry for 24 h, and then reweighed. The weight of filter paper consumed was calculated for each pair of treatments in each box.

For each dataset – whole-leaf and alkaloid extract trials – data were analysed as a comparison between the amount of feeding (measured as weight of paper consumed) on the treated and control filter papers. A potential problem in analysing multiple-choice feed-

ing experiments comes from the lack of independence between the amount consumed from simultaneously-offered treatments, which violates the assumption of independence of treatments made in using univariate parametric analyses. Following the suggestion of Roa (1992), the comparisons were therefore conducted using the Hotelling's T^2, which is the multivariate equivalent of the t-test and does not require such an assumption.

Results

Host specificity testing. As shown in Table 2, larvae of *R. nodicornis* were extremely host-specific. They fed on the two European members of the genus *Veratrum*, accepting either species readily irrespective of their original host, and also on *V. californicum*, the North American species of the same genus. But they would not feed on any other members of the same plant order, even those which were hosts for congeneric sawfly species, nor would they feed on the Ranunculaceae used by other closely related sawflies (Table 1). They also rejected *F. excelsior*. Where tested, larvae originating from *V. nigrum* showed the same pattern of host specificity as those from *V. album*. When plant species were rejected, there were no signs of damage to the test leaf – on these hosts, larvae generally walked over the leaf surface for a few minutes, at most, before leaving the leaf and searching the dish.

Host specificity and larval experience. There was no evidence that host specificity was affected by early larval experience. All larvae tested fed on *V. album*, regardless of whether they had fed on this plant during the hatching process, and none on either of the other hosts. Larvae from all origins survived for the first five days on *V. album*; all but one survived to the pre-pupal phase. The larva that died was from a dissected egg; it did not grow well and died after a week. Mean weights (and standard error) after five days for each group of ten were: larvae of normal origin 3.48 mg (0.23), larvae from dissected eggs 4.02 mg (0.25), larvae from eggs replaced into leaves 3.61 mg (0.25). These were not significantly different (one-way ANOVA $F_{1,29} = 2.34$. $P = 0.279$). There was therefore no evidence that egg manipulation led to differential establishment of larvae.

Host acceptance and host chemistry. Larvae of *R. nodicornis* were stimulated to feed on whole leaf-extract applied to sugared filter-paper; feeding from whole leaf extract-treated squares was significantly higher on average than from controls (Hotelling's $T^2 = 42.90$, $F_{2,10} = 214.52$, $P < 0.001$) and in all 12 replicates there was more consumption of extract-treated papers than controls. The applied alkaloid extract similarly stimulated feeding, although apparently to a lesser extent (Figure 1); again, there was significantly more feeding on treated papers than the equivalent sugared and solvent-treated control (Hotelling's $T^2 = 2.25$, $F_{2,10} = 11.23$, $P = 0.006$), and in ten out of the 12 replicates there was more feeding on the treatment, with one tie.

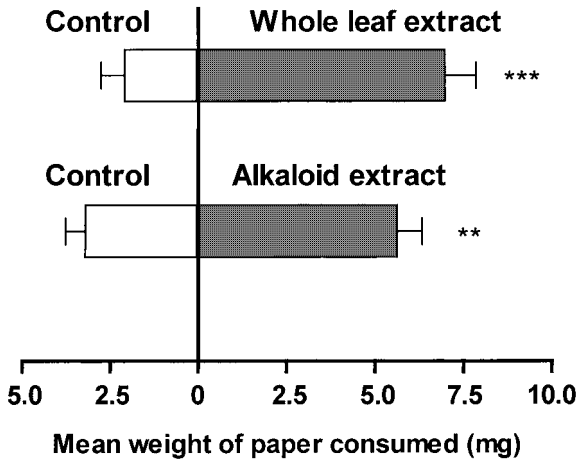

Figure 1. Mean weight of treated filter papers consumed by *R. nodicornis* larvae feeding in bioassay. On average, the total weight of each treatment available per box was 80 mg (2 × 40 mg). Larvae were therefore eating just under 10% of the available extract-treated papers and less of the controls. Significance of differences between pairs of extract and control treatments are shown after the bars (*** = $P < 0.001$, ** = $P < 0.01$); see text for details of analysis.

Discussion

It is clear from our results that *R. nodicornis* is a highly host-specific insect, and they suggest that this specificity is based on host secondary chemistry. Larvae accepted three species of the steroid-alkaloid-containing host genus *Veratrum*, even though one was not a native host. However, they would not accept any other plants tested, not even Liliales such as *L. martagon* or *P. multiflorum* which include the chemically-similar steroid saponins and are hosts of closely-related sawflies. Results of egg dissection experiments suggested that this specificity was not a function of early larval feeding experience. In a bioassay, an extract of the steroid al-

Table 2. Host plant acceptance by *R. nodicornis* larvae. +++ indicates that 100% of the larvae tested accepted and fed normally on the plant, − − − indicates that none did. [a&n] shows those plants where larvae originating from both *V. album* and *V. nigrum* were tested; results were the same for both. $n = 10$ for all trials

Plant order								
Liliales	Species	*V. album*	*V. nigrum*	*V. californicum*	*L. martagon*	*I. pseudacorus*	*P. multiflorum*	*C. majalis*
	Feeding	+++[a&n]	+++[a&n]	+++	−−−[a&n]	−−−[a&n]	− − −	−−−[a&n]
Ranunculales	Species	*H. viridis*	*H. foetidus*	*R. lanuginosus*	*C. recta*			
	Feeding	−−−	−−−	−−−	−−−			
Oleales	Species	*F. excelsior*						
	Feeding	−−−						

kaloids from *V. nigrum* had a phagostimulatory effect on the larvae.

The role of steroid alkaloids in providing anti-predator defence in *R. nodicornis* (Schaffner et al., 1994; Schaffner & Boevé, 1996) reinforces the adaptive value to the insect of specialising on plants that produce these compounds. Steroid alkaloids have been reported from all *Veratrum* species investigated, as well as the closely related genera *Stenanthium*, *Schoenocaulon*, and *Zigadenus* (Kupchan et al., 1961). Furthermore there are several North American species of *Rhadinoceraea* that feed on species of *Veratrum* (including *V. californicum*) or *Zigadenus* (Smith & Dearman, 1990), which supports the suggestion of a link between the distinctive alkaloid phytochemistry and the host use of these sawflies. Analysis of steroid alkaloids of the two European *Veratrum* species from Swiss populations has been concentrated on one main sub-group, the ceveratrum alkaloids. Profiles of these alkaloids are subtly different in the two plant species; the main alkaloid in *V. album* is the ester 3-angeloyl-zygadenine (Schaffner et al., 1994; Gfeller et al., 1995) whereas in *V. nigrum*, the main component is the non-esterified alkamine, zygadenine (H. Gfeller, U. Schaffner & J.-L. Boevé, unpubl.). However, the ceveratrum alkaloids found in the haemolymph of *R. nodicornis* larvae are the same for animals reared on both plant species, principally 3-acetyl-zygadenine (another ester of zygadenine) and also zygadenine itself (Schaffner et al., 1994; Gfeller et al., 1995; H. Gfeller, U. Schaffner & J.-L. Boevé, unpubl.). For larvae reared on *V. album* there is evidence that the metabolism of the plant alkaloids into those sequestered by the larvae takes place in the gut, where the angeloyl group is split from the ester to make zygadenine which is then acetylated (Schaffner et al., 1994). Both plants also have traces of other alkaloids, such as protoveratrine B, which are not sequestered by the larvae. Unfortunately, although some steroid alkaloids have been reported from the third *Veratrum* species we tested *V. californicum* (Browne et al., 1984), the ceveratrum alkaloids of this species do not seem to have been studied, so at present we do not know the extent of its chemical similarity to the two European species.

Our results represent the first indication that steroid alkaloids have a phagostimulatory effect on the herbivores that sequester them. Although we cannot fully exclude the presence of additional compounds in the alkaloid extract, the characteristic amphoteric behaviour that makes alkaloids soluble in polar solvents at low pH and then soluble in non-polar solvents at high pH is unusual, and this technique should be efficient for the preferential extraction of this class of compounds (Majak et al., 1992). Given that it is one of the compounds sequestered, and that it was the principal ceveratrum alkaloid found in chemical analyses of *V. nigrum*, it is interesting to consider whether the phagostimulatory activity found in our complete alkaloid extract of *V. nigrum* is principally due to zygadenine (H. Gfeller, U. Schaffner & J.-L. Boevé, unpubl.). Comparison with the activity of a similar extract of *V. album* and with purified compounds may help to clarify this question. It would seem to be parsimonious for species that sequester allelochemicals from specific host plants to recognise their hosts, at least in part, by detecting those chemicals. There are a handful of cases where phagostimulation by sequestered allelochemicals has been demonstrated (Rowell-Rahier & Pasteels, 1992). For example, curcubitacins act as feeding stimulants to *Diabrotica* beetles, which sequester these bitter-tasting chemicals and probably use

them in anti-predator defence (Metcalf, 1986), and the lepidopteran *Uresiphita reversalis* sequesters and is stimulated to feed by quinolizidine alkaloids (Montllor et al., 1990). As far as we are aware this is the first report of this phenomenon in sawflies.

As free-living sawflies have to feed on host tissue on hatching in order to emerge from the plant, the early experience of the hatching larvae may lead to a form of host learning that contributes to the high specificity of these insects. Our dissection experiments cannot rule out some chemical transfer across the egg membrane while the egg is in contact with plant tissue, as has been proposed to occur with the externally-laid eggs of the Australian moth *Othreis fullonia* and its host-plant *Erythrina variegata* (Sands & Chan, 1996). This is very difficult to exclude with insects that lay obligately into leaf tissue. Nevertheless, we have been able to demonstrate that for *R. nodicornis* host specificity persists in larvae from eggs dissected from the plant, and so is not derived from plant cues encountered by hatching larvae. This strongly suggests an innate pattern of host acceptance.

It should be noted that monophagy is a common condition in sawflies; about 45% of tenthredinid sawflies are monophagous (Heitland & Pschorn-Walcher, 1993). A wider phylogenetic approach to the host range of the Phymatocerini and the chemistry of their hosts is needed in order to address the question of the evolution of host-specificity in *R. nodicornis*; we are currently involved in such a study. Sequestration of chemically related host-plant compounds is known from three of the phymatocerine sawflies (Schaffner et al., 1994; Schaffner & Boevé, 1996; J.-L. Boevé & R. Rozenberg, unpubl.; F. V. Vencl & U. Schaffner, unpubl.) and may be a more general feature of the group. If similar host-specificity exists among other phymatocerines, and if these species have specific host recognition mechanisms using cues derived from sequestered chemicals, this may provide an evolutionary explanation of the radiation of this group of species onto plant taxa which share similar chemistries but are not all closely related.

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