Relationships between the Gall Wasp, *Trichagalma serratae* (ASHMEAD)
(Hymenoptera: Cynipidae), and Two Moth Species,
Andrioplecta pulverula (MEYRICK) (Lepidoptera: Tortricidae) and
Characoma ruficirra (HAMPSON) (Lepidoptera: Noctuidae)

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Gall parasitism by moth larvae of unisexual galls produced by *Trichagalma serratae* (ASHMEAD) in Nose, Osaka, Japan was surveyed by dissection of galls. Larvae or pupae of *Andrioplecta pulverula* (MEYRICK) and *Characoma ruficirra* (HAMPSON) were found in the galls. The two moth species did not significantly affect the survival of *T. serratae* on seven of the eight trees examined. Overall, attack by *Megastigmus habui* KAMIJŌ was the most important mortality factor for the gall wasp after gall initiation. Larval feeding habits of the two moth species were examined under laboratory conditions. *A. pulverula* larvae were able to feed on *Q. acutissima* leaves, but preferred unisexual galls of *T. serratae*. Some of the *A. pulverula* larvae boring into the galls fed on the larval cells and their inhabitants. The moth is therefore usually a cecidophage, but often becomes a predator of the gall wasp. Like *A. pulverula*, *C. ruficirra* larvae were able to feed on *Q. acutissima* leaves, but preferred *T. serratae* galls. However, the *C. ruficirra* larvae boring into the galls did not attack the larval cells, though they could feed on *T. serratae* larvae that had been artificially exposed. Thus, the larval cell wall of *T. serratae* functions as a barrier against *C. ruficirra* larvae. This moth is regarded as a commensal of *T. serratae*.

Key words: gall, cecidophage, commensalism, predator, *Trichagalma serratae*

INTRODUCTION

As pointed out by MCNEILL and SOUTHWOOD (1977), gall tissues generally contain more nitrogen and amino acids than normal plant tissues. Consequently, as well as providing shelter, galls may provide a high-quality food supply not only for the gall inducers but also for other gall inhabitants.

Gall parasitism has evolved in some taxonomic groups of Insecta. Among Lepidoptera, gall-parasitic moths have been recorded in the Momphidae, Cosmopterigidae, Tortricidae, Pyralidae, Geometridae, Nolidae and Noctuidae (CLANCY et al., 1986; YOSHIYASU, 1986; KOPELKE, 1987; ABE and SANARI, 1991). However, feeding habits and damage to gall-inducing insects have been investigated for only a few species (CALTAGIRONE, 1964; ITŌ and HATTORI, 1982; PRICE and CRAIG, 1984; KOPELKE, 1987; SULAIMAN BIN and YUKAWA, 1992).

In 1991, I discovered that larvae of two moth species attack unisexual galls of the gall wasp *Trichagalma serratae* (ASHMEAD) in Kyoto and Osaka Prefectures, Japan. Some larvae were fixed in 80% ethanol, and others were reared until adult eclosion in our

laboratory. The two species were identified as *Andrioplecta pulverula* (MEYRICK) and *Characoma ruficirra* (HAMPSON) by Drs. F. KOMAI and Y. YOSHIYASU, respectively. *A. pulverula* adults are known to emerge from unisexual galls of the gall wasp *Andricus mukaigawai* (MUKAIGAWA) (ABE, 1990), and *C. ruficirra* is known to be an important pest of chestnuts (SEKIGUCHI, 1978). The importance of cecidophagous moths as mortality factors for gall inducers has not been investigated in detail, except for *Nola innocua* BUTLER (ITÔ and HATTORI, 1982). *N. innocua* was one of the most important mortality factors for aphids within galls on *Distylium racemosum* SIEB. et ZUCC. The moth larvae usually feed on gall tissues alone, though they can feed on gall-inducing aphids. As a result of attacks by the moth, gall deterioration occurs and consequently the gall-inducing aphids die, because they feed on sap from the gall tissues. This is not the case for the association between *T. serratae* and the two moth species, because preliminary observation showed that the gall wasps eclosed in the larval cells, even if the gall walls had been fed on by moth larvae. In the present study, I examined the influence of the two parasitic moths on the survival of this wasp under natural conditions. Furthermore, the larval feeding habits of the two species were examined under laboratory conditions.

MATERIALS AND METHODS

Gall wasp studied. According to my observation, the biology of the unisexual generation of *T. serratae* in Nose can be summarized as follows. Unisexual galls of *T. serratae* appear on twigs of *Quercus acutissima* CARRUTHERS in August. Each gall is covered with spines and has a larval cell which contains a larva of the gall wasp. The mature gall is hollow and the larval cell is attached to the bottom of the gall. The size of the cavity increases with gall development. The maximum diameter of the mature gall is 10–15 mm. Pupation and adult eclosion begin in late September and mid-October, respectively. Unisexual adults emerge from their galls from mid-December to January. Some of the galls remain on the twigs until the following summer.

Examination of galls. Eight *Q. acutissima* trees which bore unisexual galls of *T. serratae* at Nose were chosen for the examination of galls. These trees stood on the south edge of a paddy field in a line running from east to west for 50 m. Tree no. 1 was ca. 7 m high and the other trees were 2.5–3.5 m in height. Tree no. 1 bore at least 1,000 fresh unisexual galls of *T. serratae*. On 27 September 1992, all fresh galls of *T. serratae* on seven of the eight trees (trees no. 2–8) were collected and 205 fresh galls were collected randomly from tree no. 1. On 6 December 1992, an additional 364 galls were collected from tree no. 1. All the galls collected were brought back to the laboratory and examined for openings on their surface produced by moth larvae. They were then dissected to check for larvae, pupae or faeces of the moths, irrespective of whether openings were present. Furthermore, larval cells of all the *T. serratae* galls were dissected to examine their inhabitants. Parasitoid larvae attacking *T. serratae* were reared at room temperature to obtain adult wasps.

Laboratory experiments. Enforced feeding and food choice experiments were conducted to examine the feeding habits of *A. pulverula* and *C. ruficirra* larvae collected from unisexual galls of *T. serratae* on *Q. acutissima* trees in Nose in September, 1992. All experiments were carried out at 25°C, under a 15L:9D photoperiod. To prevent dryness, a moistened cotton pad (20 mm × 20 mm × 2–3 mm) was placed on the bottom of each of the plastic Petri dishes used in these experiments. The moth larvae were never tested more than once. Many of the *A. pulverula* larvae used in both experiments were probably last stadium,

on the basis of the width of their frontoclypeus (0.35–0.54 mm).

Twenty-seven *A. pulverula* and 14 *C. ruficirra* larvae were used in an enforced feeding experiment to determine whether or not moth larvae fed on each of three foods. Soon after removal from the galls, each larva was placed in (1) a 115-ml plastic Petri dish (90 mm dia.) with a unisexual gall of *T. serratae*, (2) a 20-ml plastic Petri dish (37 mm dia.) containing a unisexual larva of *T. serratae*, or (3) a 115-ml plastic Petri dish containing a fresh young leaf of *Q. acutissima*. The moth larvae were then allowed to feed for 48 h.

To determine the food preference of the moth larvae, a food choice experiment was conducted using 10 *A. pulverula* and 10 *C. ruficirra* larvae. Each larva was placed at the midpoint between a leaf and a gall in a 115-ml Petri dish and allowed to feed for 48 h.

The foods used in the two experiments had the following characteristics. First, the maximum diameter of the galls was 10–15 mm, and they bore no signs of moth attack. Second, each unisexual larva of *T. serratae* was removed from a unisexual gall immediately before the start of the experiment. Third, a young leaf (opened in August) with a midrib length of 5 cm, without any trace of having been fed on, was taken from a tree at the experimental farm immediately before the start of the experiment. The petiole of the leaf was immersed in a 1-ml glass vial containing water.

In both experiments, the galls into which moth larvae had bored were left for 5 days under the same conditions after the 48-h period. After 5 days, the galls were dissected to find out whether the moth larvae had fed on larval cells and their inhabitants within the galls.

RESULTS

Examination of galls

The results of dissection of unisexual *T. serratae* galls are shown in Table 1. Attack by the moth larvae on the galls was easily recognized by the apertures produced. Moth larvae, pupae or faeces remained in the galls with openings but were not found in galls without openings. No pupal exuviae were found in the galls examined. The moths found in these galls were identified as *A. pulverula* and *C. ruficirra* by Drs. F. KOMAI, Y. YOSHIYASU and the author. No other species was found boring into the galls. Thus, the openings on the gall surfaces were most likely made by the two species identified. I could not find any difference in the shape of the openings produced by the two moth species. On 27 September, 1992, 28 larvae of *A. pulverula* and 19 of *C. ruficirra* were found in 25.5% of the *T. serratae* galls with openings; no moth larva was found in galls without openings. No gall contained more than one moth larva. Almost all (27 out of 28) *A. pulverula* larvae were probably last stadium, on the basis of the width of their frontoclypeus (0.38–0.54 mm). The remaining larva was most likely younger (width of frontoclypeus: 0.22 mm). All of the 19 *C. ruficirra* larvae were last stadium, because pupation soon occurred in the laboratory. On 6 December, 20 *A. pulverula* larvae and 5 *C. ruficirra* pupae were found in 13.0% of the *T. serratae* galls with openings, and no moth larva or pupa was found in galls without openings. All of the *A. pulverula* larvae were probably last stadium on the basis of the width of their frontoclypeus (0.41–0.53 mm). Most *C. ruficirra* larvae escape from chestnuts shortly before pupation in the autumn (SEKIGUCHI, 1978). Hence, some *C. ruficirra* larvae might have escaped from the *T. serratae* galls before their examination.

On 27 September, 34.0% of galls had openings produced by moth larvae. Larval cells and their inhabitants had been fed on by moth larvae in 40.2% of these galls. No

Table 1. Gall parasitism by moth on unisexual galls produced by *Trichagalma serratae* (ASHMEAD) at Nose, Japan

	27 September									6 December
	Tree 1	Tree 2	Tree 3	Tree 4	Tree 5	Tree 6	Tree 7	Tree 8	Total	Tree 1
1. No. of galls examined	205	7	15	16	17	48	86	147	541	364
2. No. of galls with openings produced by moth larvae	92	0	0	5	4	1	24	58	184	192
(% of 2 to 1)	(44.9)	(0)	(0)	(31.3)	(23.5)	(2.1)	(27.9)	(39.5)	(34.0)	(52.7)
3. No. of galls in which larval cells and their inhabitants were fed on by moth larvae	19	0	0	3	4	1	13	34	74	43
(% of 3 to 1)	(9.3)	(0)	(0)	(18.8)	(23.5)	(2.1)	(15.1)	(23.1)	(13.7)	(11.8)
(% of 3 to 2)	(20.7)	(0)	(0)	(60.0)	(100)	(100)	(54.2)	(58.6)	(40.2)	(22.4)
4. No. of galls in which larval cells contained parasitoid larvae	89	0	0	8	9	4	21	38	169	156
(% of 4 to 1)	(43.4)	(0)	(0)	(50.0)	(52.9)	(8.3)	(24.4)	(25.9)	(31.2)	(43.1)
5. No. of <i>Andrioplecta pulverula</i>	3	0	0	1	0	0	2	22	28	20
6. No. of <i>Characoma ruficirra</i>	14	0	0	0	0	0	2	3	19	5
7. No. of galls containing moths	17	0	0	1	0	0	4	25	47	25
(% of 7 to 1)	(8.3)	(0)	(0)	(6.3)	(0)	(0)	(4.7)	(17.0)	(8.7)	(6.9)
(% of 7 to 2)	(18.5)	(0)	(0)	(20.0)	(0)	(0)	(16.7)	(43.1)	(25.5)	(13.0)
8. No. of immature galls possibly due to physiological deterioration of gall tissues	13	3	1	0	0	17	3	32	69	15
(% of 8 to 1)	(6.3)	(42.9)	(6.7)	(0)	(0)	(35.4)	(3.5)	(21.8)	(12.8)	(4.1)
9. No. of galls in which gall wasp larvae died from fungal deterioration	0	0	0	1	1	4	0	3	9	39
(% of 9 to 1)	(0)	(0)	(0)	(6.3)	(5.9)	(8.3)	(0)	(2.0)	(1.7)	(10.7)
10. No. of galls containing live <i>T. serratae</i> without openings	45	4	14	3	3	22	41	26	158	57
(% of 10 to (1-2))	(39.8)	(57.1)	(93.3)	(27.3)	(23.1)	(46.8)	(66.1)	(29.2)	(44.3)	(33.1)
11. No. of galls containing live <i>T. serratae</i> with openings	39	0	0	1	0	0	8	14	62	53
(% of 11 to 2)	(42.4)	—	—	(20.0)	(0)	(0)	(33.3)	(24.1)	(33.7)	(27.6)

Table 2. Enforced feeding and food choice experiments on *Andrioplecta pulverula* (MEYRICK) and *Characoma ruficirra* (HAMPSON)

Food	<i>Andrioplecta pulverula</i> (MEYRICK)		<i>Characoma ruficirra</i> (HAMPSON)	
	No. of larvae used	No. of larvae feeding	No. of larvae used	No. of larvae feeding
<i>Trichagalma</i> larva	10	2	8	7
<i>Trichagalma</i> gall	6	5	—	—
<i>Quercus</i> leaf	11	2	6	6
<i>Trichagalma</i> gall	10	G: 8	10	G: 8
+ <i>Quercus</i> leaf		B: 1		B: 1

G indicates that the larva fed only on the gall. B indicates that the larva fed on both foods.

significant difference in survival rate of *T. serratae* was found between the galls with openings and those without openings on trees no. 1, 4, 5, 6 and 8 (trees 1 and 8: χ^2 -test, $p > 0.70$; trees 4, 5 and 6: FISHER'S exact probability-test, $p > 0.40$). On tree no. 7, however, survival rate was significantly higher in the galls without openings than in those with openings (χ^2 -test, $p < 0.01$).

All unisexual *T. serratae* were found as fully fed and mature larvae and as adults in their larval cells on 27 September and 6 December, 1992, respectively. The most important mortality factor for the gall wasp after initiation of galls was parasitoid attack in trees no. 1, 4, 5, 7 and 8. After rearing the parasitoid larvae, only *Megastigmus habui* KAMIJO emerged. From the larvae collected on 27 September and 6 December, 1992, 43 female and 38 male adults and 88 female and 63 male adults of this wasp were obtained, respectively. Moth larvae possibly fed on parasitoid larvae within larval cells of the gall wasp, so that the mortality caused by the parasitoids may have been underestimated. Gall development was poor on trees no. 2 and 6.

Laboratory experiments

The results of the enforced feeding and food choice experiments with *A. pulverula* larvae are shown in Table 2. In the enforced feeding experiment, 2 of the 10 larvae fed on the gall wasp larvae. Also, five of the six larvae bored into the galls and fed on the gall walls; three of the five fed on the larval cells and their inhabitants. Furthermore, 2 of the 11 larvae fed on the *Quercus* leaves. In the food choice experiment, nine larvae bored into the galls and fed on the gall walls; four of the nine fed on the larval cells and their inhabitants. One of the nine also fed on a *Quercus* leaf before boring into the gall.

Table 2 also shows the results of the enforced feeding and food choice experiments for *C. ruficirra*. In the enforced feeding experiment, seven of the eight larvae fed on the gall wasp larvae. Also, all six larvae fed on the *Quercus* leaves. In the food choice experiment, 9 of the 10 larvae bored into the galls and fed on the gall walls, but there was no sign of attack on the larval cell within each gall. The other larva died without feeding, and one of the nine larvae also fed on the leaf before boring into the gall. Cocoon formation occurred during and after the experiments, showing that 23 of the 24 larvae were last stadium. The single larva that died during the food choice experiment was also most likely last stadium, judging from the width of its frontoclypeus.

DISCUSSION

As a whole, the percentage of unisexual *T. serratae* galls with openings produced by moth larvae was higher than that of galls containing parasitoid larvae (Table 1). However, gall parasitism by moth larvae was not the most important mortality factor for the gall wasp. Except for tree no. 7, the survival rate of *T. serratae* did not decrease significantly when moth larvae bored into the galls. This is explained by the fact that adult eclosion of the gall wasp occurs within the larval cell, even if a moth larva has fed on the gall wall. The results of the laboratory experiments indicate that *A. pulverula* larvae boring into the galls also often feed on the larval cells and their inhabitants, and that *C. ruficirra* larvae never feed on them. Unlike *N. innocua* attacking aphid galls, therefore, the cecidophagous moths usually do not significantly affect the survival of *T. serratae*.

Moth larvae were found in 25.5% of the *T. serratae* galls with openings on 27 September, 1992 and in 13.0% of the galls on 6 December. Thus, one moth probably uses more than one gall during its larval stage.

A. pulverula has been recorded from unisexual galls of *Andricus mukaigawai* (MUKAIGAWA) (ABE, 1990). Probably, this moth is specialized for cynipid galls. Larvae of *A. pulverula* pass the winter in *Trichagalma* galls; adults of the overwintering generation emerge in spring and summer (ABE, unpublished data). In spring, the bisexual generation of *T. serratae* produces galls on male catkins of *Q. acutissima*, and that of *A. mukaigawai* does so on leaves of *Q. serratae*, *Q. mongolica* and *Q. dentata* (MASUDA, 1972; ABE, 1986). Nonetheless, the maximum length of these galls is ca. 3 mm, so that they are not large enough to provide shelter for the moth larvae. Since unisexual galls of *T. serratae* and *A. mukaigawai* are produced in summer and remain fresh until autumn, larvae of the first generation of *A. pulverula* may invade galls of other members of Cynipidae in spring. The present results indicate that *A. pulverula* larvae boring into *T. serratae* galls often feed on the larval cells and their inhabitants, in contrast to *C. ruficirra* larvae. Thus, *A. pulverula* is usually a cecidophage but often becomes a predator of *T. serratae*.

C. ruficirra is known to be an insect pest of chestnuts and to produce four or five generations per year on chestnut trees in Japan (SEKIGUCHI, 1978). Adults of the overwintering generation of this moth emerge in April and those of the first generation do so in June (SEKIGUCHI, 1978). Thus, this moth cannot complete its annual life cycle if it depends on *T. serratae* galls.

SEKIGUCHI (1978) reported that pupae of *C. ruficirra* overwinter in unisexual galls of *T. serratae*. The present study demonstrated that *C. ruficirra* larvae feed on *T. serratae* galls, a new host record for this moth. Moreover, although these larvae can feed on *Q. acutissima* leaves, they prefer the galls. Cecidophagy of *Hydrillodes lentalis* GUENEE and *Lophomilia takao* SUGI has been recorded among Noctuidae (SULAIMAN BIN and YUKAWA, 1992; ABE and SANARI, 1991). Larvae of the former species usually feed on dead leaves (OWADA, 1982), and *Quercus glauca* THUNB. is recorded as a host plant of the latter (SUGI, 1982). Similarly to *C. ruficirra*, neither species appears to be specialized for gall feeding.

The present results indicate that *C. ruficirra* larvae feed on gall walls, and not on larval cells of *T. serratae*, though they could feed on the gall wasp larvae that had been directly exposed to the moth in small Petri dishes. Hence, the larval cell wall of *T. serratae* functions as a barrier to *C. ruficirra* larvae. Even if *T. serratae* galls are attacked by *C. ruficirra* larvae, adult eclosion of *T. serratae* always occurs in the larval cells. Thus, *T. serratae* avoids the harmful effects of the *C. ruficirra* larva, and the moth larva benefits from the gall wasp by

using the gall as a food resource and refuge. Therefore, this gall wasp-moth relationship is regarded as commensalism.

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