Well-Developed Gall Tissues Protecting the Gall Wasp, *Andricus mukaigawae* (MUKAIGAWA) (Hymenoptera: Cynipidae) against the Gall-Inhabiting Moth, *Oedematopoda* sp. (Lepidoptera: Stathmopodidae)

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Gall parasitism by moth larvae in the unisexual galls produced by *Andricus mukaigawae* (MUKAIGAWA) on *Quercus serrata* THUNB. in Nose, Osaka, Japan, was surveyed by dissection of the galls. Almost all moth larvae found in the galls were *Oedematopoda* sp. This is the first record of this genus from insect galls. Overall, 53.4% of *A. mukaigawae* galls examined were attacked by the moths, but *A. mukaigawae* larvae were fed on by moth larvae in 12.7% or less of the galls examined. Larval feeding habits of *Oedematopoda* sp. were examined under laboratory conditions. The moth larvae were able to feed on *Q. serrata* leaves, but preferred unisexual galls of *A. mukaigawae*. Furthermore, almost all larvae tested fed on artificially exposed larvae or pupae of *A. mukaigawae* or larvae of *Synergus japonicus* WALKER, although the results of gall dissection indicate that the moth larvae were usually cecidophages and seldom became predators of the gall-formers or inquiline gall wasps under natural conditions. Thus, the well-developed parenchymatous tissues surrounding the sclerenchymas protect the gall-formers or inquiline gall wasps in *A. mukaigawae* galls from attack by moths.

Key words: gall, cecidophage, predator, Stathmopodidae, Cynipidae

INTRODUCTION

Gall-formation has evolved principally in seven orders among Insecta, and many insects are associated with galls, as parasitoids, predators, inquilines, successori, etc. (MANI, 1964). Gall-parasitic moths have been recorded in ten families of Lepidoptera: Stathmopodidae (MORIUTI, 1982), Cosmopterigidae (TAKAHASHI, 1935; CALTAGIRONE, 1964; PRICE and CRAIG, 1984), Momphidae (CLANCY et al., 1986), Sesiidae (ENGELHARDT, 1946), Tortricidae (CARLETON, 1939; PATOČKA, 1960; KOPELKE, 1982; YOSHIYASU, 1986; ABE, 1990; SCHÖNROGGE et al., 1995), Cochylidae (KUROSU and AOKI, 1988), Pyralidae (TAKAHASHI, 1935; YOSHIYASU, 1986; ABE, 1990; KUROSU and AOKI, 1991), Geometridae (KOPELKE, 1987), Nolidae (ITÔ and HATTORI, 1982) and Noctuidae (ABE and SANARI, 1991; SULAIMAN BIN and YUKAWA, 1992; ABE, 1995). Larvae of these moths utilize galls as a food resource and a shelter against natural enemies and bad weather conditions. Some of them specialize in gall-feeding and others do not.

The effect of gall-parasitic moths on the survival of gall-formers has been studied in only a few cases, with variable results. *Characoma ruficirra* (HAMPSON) (family: Noctuidae) and *Andrioplecta pulverula* (MEYRICK) (family: Tortricidae) attack 34.0% of unisexual galls of *Trichagalma serratae* (ASHMEAD), but neither species usually has a significant effect on the survival of the gall-former (ABE, 1995). Only 1% of the stem-galling sawfly, *Euura lasiolepis* SMITH, were killed by larvae of the cosmopterigid, *Batrachedra striolata* ZELLER (PRICE and

CRAIG, 1984). Each gall produced by the aphid *Ceratovacuna nekoashi* (SASAKI) contains about 10 subgalls, and larvae of the cochylid *Eupoecilia ambiguella* (HUBNER) were found to invade 38.3% of the subgalls and fed on the aphids as well as the gall tissues (KUROSU and AOKI, 1988). Larvae of *Nola innocua* BUTLER (family: Nolidae) feed on gall tissues of aphids on *Distylium racemosum* SIEB. et ZUCC., and gall deterioration occurs. As a result, the gall-forming aphids die, so that this moth is a most important mortality agent in the galls (ITÔ and HATTORI, 1983).

Preliminary observations suggested that some larvae of *Oedematopoda* sp. (family: Stathmopodidae) feed on larvae of the gall wasp *Andricus mukaigawae* (MUKAIGAWA) in addition to the gall tissues, so I examined the effect of the moth on the survival of the gall wasp under natural conditions. In addition, the larval feeding habits of the moth were examined under laboratory conditions.

MATERIALS AND METHODS

Gall wasp studied. The biology of the unisexual generation of *Andricus mukaigawae* in Nose, Osaka Prefecture, Japan, can be summarized as follows. Unisexual galls of *A. mukaigawae* develop from buds of *Quercus serrata* THUNB. in June. Each gall has a sclerenchyma embedded in acorn-shaped parenchymatous tissue, which is surrounded by numerous lanceolate spines (ABE, 1986); the sclerenchyma contains a nutritive layer and larval chamber in which one gall wasp exists. The diameter of the mature gall is generally more than 20 mm, and the parenchyma is well developed with a hard consistency. Pupation and adult eclosion begin in mid September and early October, respectively. Unisexual adults emerge from their galls from mid-December to January.

Gall-inhabiting moths studied. I collected unisexual galls of the gall wasp *A. mukaigawae* in Japan and obtained stathmopodid moths emerging from the galls. The data were as follows. One ex, Chojabaru, Oita Prefecture, coll. x-1985, em. xi-1985; 1 ex, same locality, coll. x-1985, em. iv-1986; 1 ex, Katsunuma, Yamanashi Prefecture, coll. 19-x-1983, em. 5-v-1984; 10 exs, Nose, Osaka Prefecture, coll. 29-i-1992, em. 4-8-iii-1992 (under room temperature). These moths were identified as *Oedematopoda* sp. by Drs. S. MORIUTI and Y. YOSHIYASU. This moth is close to, but distinct from, *O. ignipicta* (BUTLER), whose larvae are known to be predators of aphids. This is the first record of this genus from insect galls (MORIUTI, pers. comm.). *Oedematopoda* sp. has occasionally been obtained from *Quercus* galls produced by two insect species other than *A. mukaigawae*. By the courtesy of Mr. Y. GYOUTOKU, I have examined two *Oedematopoda* sp. moths emerging from unisexual galls of *Trichagalma serratae* on *Quercus acutissima* CARRUTH. (1 ex, Hisaishi, Kugino-mura, Kumamoto Prefecture, coll. 15-ii-1996, em. 5-v-1996 (Y. GYOUTOKU); 1 ex, Kikuyo-machi, Kumamoto Prefecture, same coll. and em. date and same collector). Further, I obtained one *Oedematopoda* sp. moth emerging from a gall produced by the gall midge, *Ametrodiplosis acutissima* (MONZEN), on *Q. acutissima* (1 ex, Nose, Osaka Prefecture, coll. 12-iii-1996, em. 26-iv-1996).

Examination of galls. There were numerous 1–2 m high *Q. serrata* trees in a forest at Shimoda, Nose, and unisexual galls of *A. mukaigawae* were abundant on these. Fifteen *Q. serrata* trees bearing unisexual galls of *A. mukaigawae* were randomly chosen for the examination of galls. On 15 September 1992, all unisexual galls of *A. mukaigawae* were collected from the 15 trees. They were examined in the laboratory for openings on their surface produced by moth larvae, and then dissected to check for *A. mukaigawae*, inquiline gall wasps, moths and parasitoids.

Laboratory experiments. Two experiments, enforced feeding and food choice experiments, were conducted to examine the feeding habits of *Oedematopoda* sp. larvae, using larvae randomly chosen from those collected as described in "Examination of galls." All experiments were carried out at 25°C, under 15L : 9D. To prevent desiccation, 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 the experiments. Moth larvae were never tested more than once. After the experiments, they were reared with gall tissues as a food source until pupation, to clarify their stage during the experiments.

Twenty-seven *Oedematopoda* sp. larvae were used in the enforced feeding experiment to determine whether or not the moth larvae fed on each of the following four kinds of foods. Soon after removal from the galls, each larva was placed in (1) a 20-ml plastic Petri dish (37 mm dia.) containing a unisexual larva of *A. mukaigawae*, a unisexual pupa of *A. mukaigawae*, or a larva of an inquiline gall wasp *Synergus japonicus* WALKER, or (2) a 115-ml plastic Petri dish (90 mm dia.) with a fresh young leaf of *Q. serrata*. 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 *Oedematopoda* sp. larvae. Each larva was placed at the mid-point between a leaf and a gall in a 115-ml Petri dish and allowed to feed for 48 h. At 12, 24, 36 and 48 h after the beginning of the experiment, I observed the larva, the leaf and the gall in each Petri dish. The galls into which moth larvae had bored by 48-h were left for 5 days under the same conditions. After 5 days, the galls were dissected to determine whether the moth larvae had fed on the inhabitants within the larval chambers.

The larvae and pupae of *A. mukaigawae* and the larvae of *S. japonicus* used in these experiments were removed from unisexual galls just before the start of the experiment; the leaves were young (opened in August), with a midrib length of 5 cm and with no trace of having been fed on, taken from a tree at the experimental farm immediately before the start of the experiment (the petiole was immersed in a 1-ml glass vial containing water); the galls had a maximum diameter of 20–26 mm and no sign of previous moth attack.

RESULTS

Gall invasion by moths and gall types

The results of dissection of the unisexual *Andricus mukaigawae* galls are shown in Table 1. Attack by the moth larvae on the galls was easily recognized by the apertures produced. Moth larvae and/or faeces were present in the galls with openings but were not found in the galls without openings. No moth pupa or pupal exuvia was found in the galls examined. Overall, 53.4% of the 118 galls examined were attacked by moth larvae, but *A. mukaigawae* larvae were fed on by moth larvae in only 12.7% or less of the galls examined. All larval chambers with holes made by moth larvae were empty. Only parenchymatous tissues and lanceolate spines were fed on by moth larvae in the attacked galls which had larval chambers without holes. Eighty-three *Oedematopoda* sp. and one *Andrioplecta pulverula* larvae were found boring into the galls. Thus, almost all the attacks on the galls were made by *Oedematopoda* sp. Live *A. mukaigawae* were found as fully fed larvae or pupae in their larval chambers.

Independent of the moth attack, the galls examined were classified into (1) immature galls without larval chamber which were small (maximum diameter < 15 mm), possibly due to physiological deterioration of gall tissues; (2) normal galls which had *A. mukaigawae* but did

Table 1. Number of galls containing and not-containing live inhabitants in galls with and without signs of moth feeding. One hundred and eighteen unisexual galls of *Andricus mukaigawae* were collected from a forest in Nose, Osaka, and dissected.

A. Galls with signs of moth feeding

Gall types	No. of galls		
	Inhabitants within larval chambers were fed on	Gall-formers or inquilines were not fed on	Total
Normal galls	15	17	32 ^a
Inquiline galls	4	27	31 ^a
Total	19	44	63

^a No. of galls containing moth larvae was 30 for normal galls and 26 for inquiline galls.

B. Galls without signs of moth feeding

Gall types	No. of galls		
	Without live inhabitants	Containing live gall-formers or inquilines	Total
Immature galls	4	0	4
Normal galls	3 ^b	5	8
Inquiline galls	5 ^c	38	43
Total	12	43	55

^b Larvae of gall-formers died from fungal deterioration.

^c Inquiline wasps had already emerged.

not contain inquiline gall wasps; and (3) inquiline galls containing inquiline gall wasps. No parasitoid was found in any of the 118 galls examined. Fourteen of the 118 galls were completely destroyed by feeding moth larvae. It was uncertain whether these galls were immature, normal or inquiline galls. In Table 1, the completely-destroyed galls were assumed to be normal galls for evaluating the effect of the moth larvae on the survival rate of *A. mukaigawae*, so this effect may have been overestimated. No significant difference in survival rate of *A. mukaigawae* was found between the normal galls with ($17/32 = 0.53$) and without ($5/8 = 0.63$) signs of moth feeding, even assuming that some of the completely-destroyed galls were not normal galls (FISHER's exact probability-test, $p > 0.072$).

The inquiline galls constituted 62.7% of the galls examined. This percentage might be an underestimate, because all the completely-destroyed galls were assumed to be normal galls. All the inquiline gall wasps were identified as *Synergus japonicus* by the author. No larval chambers of *A. mukaigawae* were found in the galls containing *S. japonicus*. *S. japonicus* consists of two biological species, tentatively named *Synergus* sp. A and sp. B (ABE, 1992). The structure of the gall showed that all the inquiline gall wasps examined were *Synergus* sp. A. As pointed out by MASUDA (1959), *A. mukaigawae* adults do not emerge from galls containing *Synergus* sp. A or B, because larvae of the inquiline gall wasps grow faster than the gall-former and eventually the larvae of the latter cease to develop. *Synergus* sp. A is trivoltine,

Table 2. Enforced feeding experiment of *Oedematopoda* sp. larvae

Food provided	No. of larvae tested	No. of larvae which fed on the food provided
<i>Andricus</i> larva	5	4
<i>Andricus</i> pupa	3	2
<i>Synergus</i> larva	9	9
<i>Quercus</i> leaf	10	9

Table 3. Food choice experiment of *Oedematopoda* sp. larvae between the *Andricus* gall and the *Quercus* leaf

No. of larvae tested	No. of larvae which fed on gall only	No. of larvae which fed on leaf only	No. of larvae which fed on both foods
10	9	0	1

and its second and overwintering generations utilize unisexual galls of *A. mukaigawae* (ABE, 1992). The second generation of *S. japonicus* emerged from 5 inquiline galls and larvae of the overwintering generation were found in 69 inquiline galls. Moth larvae attacked 44.9% of inquiline galls which fostered the overwintering generation of *S. japonicus*, and some of the inquiline larvae were fed on by moth larvae in 5.8% of the inquiline galls.

Laboratory experiments

The results of the enforced feeding experiment with *Oedematopoda* sp. larvae are shown in Table 2. Almost all larvae tested fed on larvae or pupae of *A. mukaigawae* or larvae of *S. japonicus*. Also, nine of ten larvae tested fed on the *Q. serrata* leaves. The result of the food choice experiment is shown in Table 3. All larvae tested preferred the galls. One of ten larvae tested also fed on a *Q. serrata* leaf before boring into the gall. This larva stayed on the leaf for 12 h after the beginning of the experiment, but was seen boring into the gall at 24, 36 and 48 h after the beginning of the experiment. The other nine larvae were observed boring into the galls at 12, 24, 36 and 48 h after the beginning of the experiment. None of the 10 larvae made holes into the larval chambers, but all of them fed on parenchymatous tissues and the bases of lanceolate spines of the galls.

One *Oedematopoda* sp. larva feeding on the *A. mukaigawae* pupa, one feeding on the *S. japonicus* larva, and one feeding on the *Q. serrata* leaf in the enforced feeding experiment were in the penultimate stadium, because they molted only once before cocoon formation after the experiment. The other *Oedematopoda* sp. larvae used in the two experiments were in the last stadium, since they made cocoons and pupated soon after the experiments ended.

DISCUSSION

The collection data of *Oedematopoda* sp. indicate that this moth specializes in gall-feeding on *Quercus* spp. Adults of the overwintering generation of this moth emerged in spring, but unisexual galls of *Andricus mukaigawae* and *Trichagalma serratae* appear in summer on the host plants (ABE, 1986, 1995). Thus, *Oedematopoda* sp. is considered to have more than one

generation a year.

The inquiline gall wasp, *Synergus japonicus* was the most important mortality factor for *A. mukaigawae* in galls on *Quercus serrata* in Nose, because 62.7% or more of the galls examined were inquiline galls (Table 1). Overall, 53.4% of the galls examined were attacked by moth larvae (mainly *Oedematopoda* sp.), but *A. mukaigawae* larvae were killed by the moth larvae in only 12.7% or less of the galls examined. Almost all *Oedematopoda* sp. larvae fed on *A. mukaigawae* and *S. japonicus* which had been artificially exposed to them (Table 2), but were usually cecidophagous and seldom became predators of the two wasp species within their larval chambers under natural conditions (Table 1). When the parenchymatous tissues were fed on by moth larvae, *A. mukaigawae* in their larval chambers were not harmed (Table 1). Probably, the well-developed and hard parenchymatous tissues surrounding the sclerenchyma protect the wasps from damage by the moths. There exists the possibility that such parenchyma in *A. mukaigawae* galls has evolved to counter the gall-parasitic moths.

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