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Gall Formation by *Eriosoma* Fundatrices and Gall Parasitism in *Eriosoma yangi* (Homoptera, Pemphigidae)

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Synopsis *Eriosoma yangi* fundatrices usurp galls of other *Eriosoma* species. Such a habit has not been reported for any aphid so far. The fundatrix of a gall-forming species settles on a young elm shoot and induces a gall on a leaf a little away from its feeding site. On the other hand, the *E. yangi* fundatrix walks about actively on young leaves, and molts there usually until the 3rd instar. It does not form its own gall, but intrudes into a gall of other *Eriosoma* species. After the intrusion, *E. yangi* somehow kills the original gall proprietor. *E. yangi* is an obligatory parasite on the galls of other *Eriosoma* species.

The aphids of the genus *Eriosoma* make leaf-roll galls on elm trees. This genus is distributed throughout the Holarctic region, and includes 20 known species (HEIE, 1980). Except for some species, they perform host alternation between *Ulmus* spp. as primary hosts and various shrubs as secondary hosts. The leaf-roll galls are simple in structure (Fig. 1) and not completely closed.

Although the single name *E. japonicum* has generally been applied to the aphids of this genus in Japan, at least six different species occur in Hokkaido. Of the five species other than the true *E. japonicum*, three are new to science, and one is conspecific with *E. grossulariae* which has long been confused with *E. ulmi* (DANIELSSON, unpublished). The remaining species, *E. yangi*, has already been described by TAKAHASHI (1939) based on Chinese specimens. He mentioned that this species is distributed also in Japan, but his record has long been neglected.

Galls of these species are morphologically very similar to one another, and galls of more than one species are frequently found in proximity on the same elm twig at Sapporo, northern Japan. In 1978 I noticed that fundatrices of *E. yangi* were often walking about on leaves, and that they often coexisted with other species' fundatrices in one and the same gall.

The purpose of this paper is to describe 1) gall formation by *Eriosoma* fundatrices, 2) the intrusion of *E. yangi* fundatrices into other species' galls, and 3) the interaction between *E. yangi* and the host species.

The three new species, *E. harunire* AKIMOTO (MS), *E. auratum* AKIMOTO (MS) and *E. moriokense* AKIMOTO(MS), will be described in my revision of the Japanese species of *Eriosoma*.

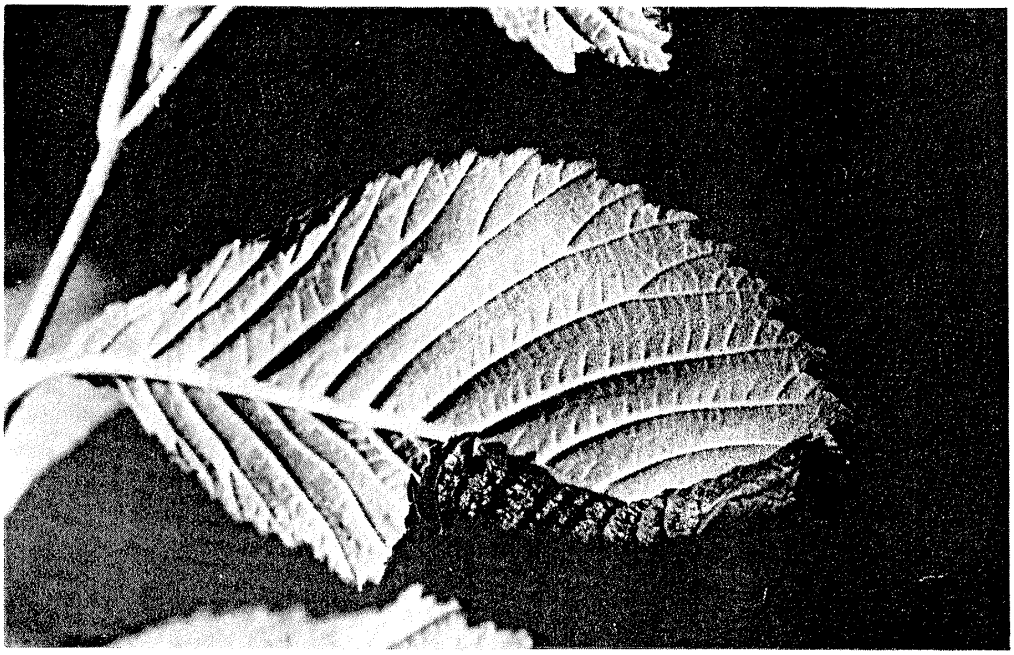

Fig. 1. A gall of *E. harunire* on an elm leaf.

Observations

1. *Gall formation by Eriosoma fundatrices*

Observations on gall formation were made in 1980 on the campus of Hokkaido University where elm trees (*Ulmus davidiana* var. *japonica*) of various sizes grew in the semiurban environment. Many galls of *Eriosoma* were found on comparatively small, young elm trees available for observations and experiments. Microscopic inspection of mounted specimens was the only way to determine the species of fundatrices. The field identification of the fundatrices was not practical. In most cases, the gall-forming species were *Eriosoma harunire* and *E. auratum*, and they occupied 71.1% and 24.3%, respectively, of a sample of 239 fundatrices.

1.1. General observations on gall formation

Having hatched from the overwintered egg laid on the bark of elm, the fundatrix larva travels to a bud. I found fundatrix larvae on buds for the first time on May 14th in 1979 and May 21st in 1980. When the bud was still tight, the fundatrix larva temporarily fed on the surface of the bud. As the bud began to burst, it settled down just inside an axil to feed usually on the young shoot and rarely on the petiole of a new leaf. The fundatrix concealed itself within the bud which had just been unfolded, but then revealed itself with the rapid expansion of the shoot and the leaf. Once had settled, the fundatrix stayed to feed on the young shoot or the petiole (Fig. 2A). I have not observed it feeding or walking on leaves.

One of the distal leaves on the shoot attacked by a fundatrix was rolled downward from the edge, while the fundatrix was still feeding on the shoot (Fig. 2B). Thus, an *Eriosoma* fundatrix induces a gall a little away from its feeding site. After

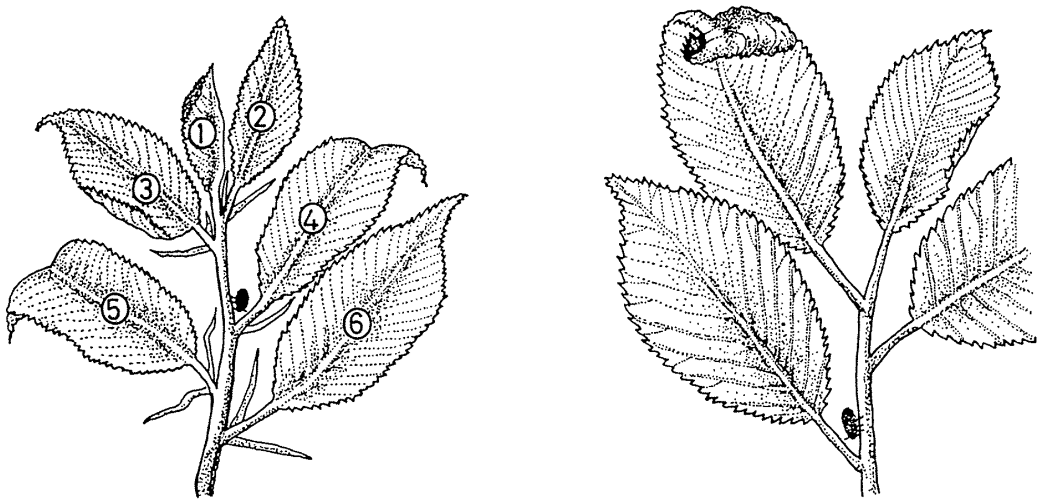

Fig. 2. A, an unfolding bud (shoot) with a fundatrix of the gall-maker; the fundatrix is feeding between leaves 3–4 on the shoot. B, An early gall on leaf 2.

Table 1. Relationship between the feeding site of *Eriosoma* fundatrices and the gall position on each shoot.

Feeding site	Gall position	Frequency (%)
Petiole of leaf 2*	On leaf 2	2 (5.0)
Between leaves 2–3	〃 1	6 (15.0)
Petiole of leaf 3	〃 3	1 (2.5)
Between leaves 3–4	〃 2	23 (57.5)
〃 3–4	〃 3	1 (2.5)
〃 4–5	〃 3	4 (10.0)
〃 5–6	〃 4	3 (7.5)

* Elm leaves are alternate on the opposite sides of a shoot. Leaves are numbered from the apex to base of each shoot (Fig. 2A). A fundatrix feeds on the petiole of a leaf or on a shoot between leaves.

a young leaf had been rolled downward, the fundatrix larva stopped feeding and got into the leaf roll. On the evening of June 2nd, 1979, I observed a fundatrix larva moving to the leaf roll formed on the morning of the same day.

1.2. Feeding site and gall position

The relationship of the gall position to the initial feeding site was examined for 40 buds from May 22nd to June 1st, 1980 (Table 1). The results show that fundatrix larvae did not necessarily induce curlings on the leaves nearest to their feeding sites. In 92.5% of the buds examined, the distal leaves on the same side as the feeding sites were rolled. In 7.5% fundatrices fed on petioles and the leaves on the petioles were rolled. The leaves starting to roll ranged from 2.0 to 3.7 cm

in length (measured from the petiolar base to the top). The age of leaves susceptible to gall formation may be limited.

1.3. The period for gall formation

On May 24th and 25th of 1980, 17 fundatrix larvae were removed from the buds they had settled on to other buds with the aid of a small brush. Of them 11 formed galls on the new buds. They took 5–8 days (average 6.3) to settle in the rolled leaves. The leaf was rolled not gradually but rapidly within a day or so. Fundatrices of *E. harunire* always molted to the second instar after settling in the galls. However, second instar larvae of *E. auratum* were often found feeding on young shoots. After the occupation by aphids the leaf rolled further with its expansion.

1.4. Failure in gall formation

During May 22nd–June 1st, 1980, the percentage of fundatrices which failed to form galls was determined based on 86 fundatrices in 61 buds. Their feeding sites were recorded on May 22nd, and then the fundatrices were checked every day. By June 1st, 17 (19.8%) of them disappeared from their sites. Probably, the failure for the most part resulted from the strong wind which injured buds bitterly on May 26th. Another reason for the failure might be the selection of leaves unsuitable for gall formation. For example, when the 17 fundatrices mentioned above (1.3) were transferred to more or less unfolded buds, 3 fundatrices abandoned the new feeding sites in 2 or 3 days, moved to the leaves which were not eventually rolled, and disappeared in a few days.

1.5. Multiple occurrence of fundatrices

It was often observed that more than one fundatrix larva settled on a single shoot. Of the 61 buds examined, 17 (27.9%) harbored more than one fundatrix. As a result, more than one gall was formed on a shoot. Moreover, some fundatrix larvae happened to be feeding simultaneously in close proximity. One fundatrix moved into a rolled leaf on June 2nd, and another which had been feeding in close proximity intruded into the same rolled leaf on the next day. Galls with more than one conspecific fundatrix were often found in every gall-forming *Eriosoma* species collected in the present study.

2. *The behavior of fundatrix larvae of E. yangi on leaves*

The behavior of *E. yangi* fundatrices on growing leaves was observed on the campus of Hokkaido University in 1979 and 1980.

2.1. General observations on *E. yangi* fundatrices

In the third week of May of 1979 and 1980, first instar larvae of *Eriosoma* began to appear on buds, which were still folded. Fundatrix larvae of *E. yangi* were almost as abundant as those of *E. harunire*. More than one *E. yangi* fundatrix larva (sometimes about 10 individuals) was often feeding together. I also observed that an *E. yangi* fundatrix and an *E. harunire* fundatrix were feeding together on the same bud.

By the end of the fourth week of May, buds began to unfold and grew to about 3 cm in length. Juvenile elm leaves in a tight bud are folded along veins and there are also shallow folds between veins on the underside of developing leaves. As soon as buds unfolded, most fundatrix larvae of *E. yangi* moved into underside folds of leaves and began to feed. None settled on a young shoot. They frequently changed their feeding sites, moving about on young leaves and shoots, and molted on buds or leaves, where their exuviae were frequently left. From the fourth week of May to the first week of June, fundatrix larvae were observed walking actively on the surface of leaves and petioles especially when it was hot and sunny. They wore waxy secretion only on the apical part of the abdomen.

Fifty-nine fundatrices walking on leaves were collected from May 24th to June 4th in 1978 and 1979 and mounted. All of them were *E. yangi* of the first to fourth larval instars, and no adult fundatrices were found. Of the 29 fundatrices collected since June 1st, 24 (82.8%) were third instar larvae and only 3 were fourth (final) instar larvae. The number of fundatrix larvae on leaves decreased gradually and almost vanished by the end of the first week of June.

2.2. Intrusion into the galls of other *Eriosoma* species

Experiments were carried out to know why *E. yangi* fundatrices were walking about on leaves and shoots. On May 31st, 1979, a twig with *E. yangi* fundatrices was selected for observation in each of three trees, and tanglefoot was smeared at the base to prevent the fundatrices from escaping. As some exuviae were left, probably some of them were in the second or third instar.

Twig A had 12 rather developed leaves, where 24 fundatrices of *E. yangi* were found on May 31st. Twig B had 7 buds just unfolding and about 3 cm long. The condition of the buds seemed to be suitable enough for fundatrices to induce galls, so far as judged from the observations on other *Eriosoma* species. There were 13 fundatrices of *E. yangi* on May 31st. Twig C had 7 rather developed leaves and 2 neighboring leaves each with an early-stage gall of another *Eriosoma* species. There were about 20 fundatrices of *E. yangi*. On 31 May I removed all inhabitants of the galls.

On Twigs A and B, the number of fundatrices reduced gradually and by June 10th they completely disappeared without forming any galls. Although some individuals were trapped in the tanglefoot band, none seemed to have escaped through the barrier. This suggests that the *E. yangi* fundatrix cannot complete development on the leaves. The two galls on Twig C were opened on June 3rd. They were both invaded by *E. yangi*, containing 5 and 8 fundatrices, respectively. From these experiments it can be concluded that *E. yangi* does not form its own galls, but intrudes into the galls of other *Eriosoma* species. It is not certain why the *E. yangi* fundatrix adult cannot survive outside the gall. Prehaps its largely inflated abdomen makes the support of body quite difficult at an exposed site.

2.3. Failure of gall intrusion

KOACH and WOOL (1977) reported that the galls of rare species of the subfamily

Table 2. Successful intrusion of galls by *E. yangi* fundatrices.

Twig	No. of buds (shoots)	No. of galls formed	No. of *E. yangi* fundatrices found at first	No. of *E. yangi* fundatrices from galls	% intrusion
D	31	1	12	4	25.0
E	25	4	37	23	62.2
F	27	0	45	—	—
G	24	1	38	11	28.9
H	12	0	90	—	—

Fordinae occurred generally on the same host tree over a few years. Likewise, galls of different species of *Eriosoma* more or less concentrated on certain elm trees in the studied site, where the gall density was not so high. Many fundatrices of *E. yangi*, however, were often found on some elm trees with a very few *Eriosoma* galls. Although *E. yangi* fundatrices were frequently found in such galls, some of them might fail to intrude into the galls.

To assess the success of gall intrusion on trees of low gall density, five twigs (D–H) with many fundatrices of *E. yangi* were selected in two elm trees. These twings were about 0.5–1 m long and their bases were smeared with tanglefoot. Twigs D, E and F were observed from May 21st, 1979, Twigs G and H from May 25th, and all fundatrices on each twig were counted. At that time many of them seemed to be 2nd instar larvae. On Twigs D and E, galls of other *Eriosoma* species were formed 4 days later and on Twig G on the next day. On Twigs F and H, no galls were formed, and there were 45 and 90 fundatrices of *E. yangi*, respectively. They decreased gradually and vanished by June 10th. Since there were no dead bodies on the 5 twigs, the fundatrices were probably thrown off by physical effects such as wind and rain. On June 5th, when all the exposed fundatrices disappeared from the twigs with galls, all galls were collected and *E. yangi* fundatrices were counted. The results are shown in Table 2. On Twigs D and G, more than 70% of the fundatrices failed to intrude into galls, and probably died. *E. yangi* fundatrices may have been too numerous for the available galls on these twigs. However, there was enough space in the galls for many more fundatrices. In fact I have found a gall embracing as many as 19 fundatrices. It seems unlikely that fundatrices occupying a gall exclude new-comers. Aggressive interaction among *E. yangi* fundatrices was not observed at least outside galls.

The low intrusion rates on Twigs D and G seem to have resulted from the high death rate of the fundatrices during gall searching. Fundatrices which hatched on trees of low gall density may suffer a high death rate due to prolonged searching time. Therefore, the success of *E. yangi* fundatrices is profoundly affected by the host selection of the sexuparae (autumn migrants). If the latter can select a host tree which attracts sexuparae of gall-forming species, their progeny will enjoy ample opportunity for intrusion. Although *E. yangi* sexuparae may have evolved the same host preference as that of gall-forming species, they may settle, by chance, on a host

tree selected by few sexuparae of gall-makers. Alatae are generally weak fliers and are likely to be carried on the wind rather than to control their flight direction. In trees with few galls, the usurping startegy of *E. yangi* fundatrices is obviously risky. It is questionable what sort of selection pressure has made *E. yangi* an obligatory gall parasite.

2.4. Intrusion into galls under formation

On May 21st, 1980, while a fundatrix of a gall-forming *Eriosoma* (probably *E. harunire*) was feeding on a young shoot, an *E. yangi* fundatrix, probably of the 1st instar, was found to be "waiting" for the completion of curling on the leaf. In addition, I frequently observed that, while the gall-producer still remained at the initial feeding site, *E. yangi* fundatrices had already intruded into the gall at its early stage of formation. Probably, the earlier *E. yangi* fundatrices get into galls, the more profit they would derive. When galls at an early stage of formation were not available in close proximity, they may walk about in search of them.

I cannot specify the factors eliciting the searching activity of *E. yangi* fundatrices. However, they seem to be quite sensitive to the distortion of leaves. When *E. yangi* fundatrices appear on leaves, knit-leaf nests of lepidopterous larvae (probably *Acleris bascana*) are common on elm trees. Several *E. yangi* fundatrices were found in many of those nests, especially on twigs with few *Eriosoma* galls.

3. *Usurpation of Galls*

To examine the interaction between the invader and the original proprietor, 125 and 159 galls were collected from May 24th to June 17th in 1979 and 1980, respectively, from elm trees planted at regular intervals on both sides of a road. In this spot the gall density was rather low. In both years, the first galls were formed around May 24th, and by June 17th fundatrices were all mature and often began to give birth to larvae.

The sampling period was divided into every five days (SP I, SP II, . . . SP V). The number of galls collected is given in Table 3. For each gall all fundatrices and dead bodies, if present, were mounted to determine their species and instars (Canada balsam was mainly used for mounting fundatrix larvae, and gum-chloral mountant for fundatrix adults). Galls collected in the later sampling periods were frequently attacked by predators. Severely attacked ones were discarded.

Galls of *E. harunire* were the most common, and those of *E. auratum* came next. *E. moriokense* and *E. japonicum* were rare and galls of *E. grossulariae* were not found. The galls of different species could not be distinguished by their appearance.

The sampled galls were divided into 3 types: galls inhabited only by the

Table 3. The number of galls sampled.

	SP I (24.V–28.V)	SP II (29.V–2.VI)	SP III (3.VI–7.VI)	SP IV (8.VI–12.VI)	SP V (13.VI–17.VI)
1979	18	36	33	22	16
1980	15	54	47	20	23

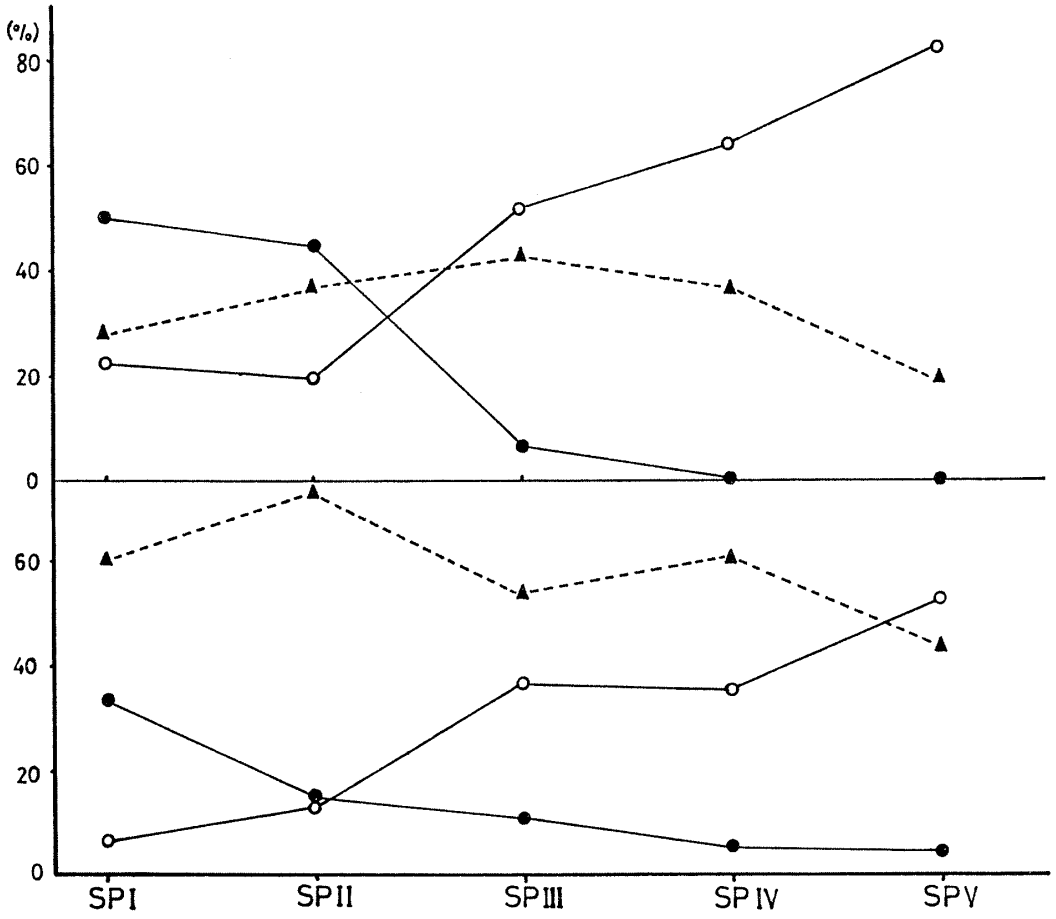

Fig. 3. Changes in percentage frequency of three types of galls with time in 1979 (above) and in 1980 (below).
▲---▲: Type A (gall-maker); ●—●: Type B (gall-maker+*E. yangi*); ○—○: Type C (*E. yangi*).

gall-maker (Type A), those by both *E. yangi* and the gall-maker (Type B), and those only by *E. yangi* (Type C).

3.1. Changes of gall inhabitants

Figure 3 shows changes in percentage of the three types of galls with the sampling time. Similar tendencies were found in 1979 and 1980. In 1980, however, the density of *E. yangi* relative to that of the gall-makers was lower than in 1979.

Fundatrices of *E. yangi* and the gall-making species frequently coexisted in early galls. Of the galls collected in SP I (first 5 days), Type B was 50.0% in 1979 and 33.3% in 1980. The frequency of this type decreased gradually with time. In SP IV and SP V, no galls of Type B were collected in 1979, and only 2 in 1980 (see below). On the contrary, the frequency of Type C (including only *E. yangi*) increased gradually. Of the galls collected in SP V, Type C was 81.3% in 1979 and 52.2% in 1980. The frequency of galls inhabited only by the gall-maker (Type A) held almost constant in both years.

Table 4. The species and instars of dead fundatrices found in galls invaded by *E. yangi* fundatrices.

Species	L1	L2	L3	L4	A	Total
E. harunire	3	8	4	3	2	20
E. auratum	1*	3	2	2	2	10
E. moriokense	0	1	0	0	0	1
E. japonicum	0	0	1	3	1	5
Total	4	12	7	8	5	36

L1~L4, first to fourth larval instars; A, adult.

* I could not distinguish 1st instar larvae of *E. auratum* from those of *E. moriokense* in this study, but circumstancial evidence suggested that this larva was probably *E. auratum*.

Dead fundatrices of the gall-making species were often found in galls invaded by *E. yangi*. Forty-six and 42 galls, all of which harbored at least 1 *E. yangi* fundatrix, were collected during SP III–SP V, in 1979 and 1980, respectively. Dead fundatrices of the gall-maker were found in 23.9% and 28.6% of them.

These results can be explained by assuming that the *E. yangi* fundatrices somehow kill the original proprietors of the galls they invaded and thus usurp the galls. All the galls of Type C examined, however, did not contain dead fundatrices of the gall-maker. As the galls of *Eriosoma* are not completely closed, corpses may easily be lost by wind or rain.

A question may still arise whether the dead fundatrices found in the galls of Types B and C were really attacked by *E. yangi* or not. Galls of *Eriosoma* are attacked intensively by many predators, such as anthocorid bugs, syrphid larvae, etc., and fundatrices killed by them are often left. In such cases, however, dead fundatrices are found flattened, since the predators absorb their body fluid. The dead fundatrices in the galls invaded by *E. yangi* did not bear such a symptom of predation. I could not observe how *E. yangi* killed the original gall proprietor. However, it was doubtless that the death of the latter was due to the presence of the former.

3.2. Dead fundatrices of the original gall proprietor

All dead fundatrices were mounted, and their species were determined. Even deformed bodies of dead fundatrices were easily identified. The dead fundatrices were of various instars (Table 4). This suggests that the time of killing activity of *E. yangi* is not strictly restricted.

3.3. How does *E. yangi* kill the gall proprietor?

Two possibilities may be suggested. Firstly, *E. yangi* may attack the gall proprietor with the stylet. BANKS *et al.* (1968) reported that starved larvae of *Myzus persicae* and *Megoura viciae* attacked with their stylets other individuals of the same colony and absorbed the body fluid. *E. yangi* fundatrices, even after having invaded galls, were still active, while the proprietor became sluggish soon after the settlement in the gall. However, if *E. yangi* attacks the proprietor intensively, dead fundatrices should be more uniform in age than observed (Table 4). Moreover, this hypothesis

fails to explain why the original proprietor sometimes coexists with the invader for a long time.

The second possibility is that the movement or presence of *E. yangi* in the gall may exert some fatal stress on the proprietor. PARNELL (1964) reported the inquilinism of a gall midge, *Trotteria sarothamni*, within the pod gall induced by another gall midge, *Asphondylia sarothamni*. He concluded that the larvae of the latter die from mechanical pressure exerted by the inquiline.

3.4. Failure in gall usurpation

Three instances of failure in the gall usurpation by *E. yangi* were observed.

a) A gall collected in SP III, 1979, included 1 dead 3rd instar fundatrix of *E. yangi* and 1 living adult fundatrix of *E. harunire*. It could not be determined whether the death was by the counterattack of the *E. harunire* fundatrix or by any other cause.

b) A gall collected in SP V, 1980, included 1 adult fundatrix of *E. yangi* and 1 adult fundatrix of *E. harunire*. Both fundatrices gave birth to larvae. They, however, occupied the sites apart from each other within the gall. Their offspring surrounded their own mothers, and did not mix.

c) Another gall also collected in SP V, 1980, contained 1 adult fundatrix of *E. yangi* and 1 adult fundatrix of *E. harunire*.

3.5. *E. yangi* as an obligatory gall parasite

The relationship between *E. yangi* and the gall-forming *Eriosoma* species can be regarded as a sort of parasite-host relationship. This can compare with social parasitism or "cuckoo parasitism" in social Hymenoptera. In social wasps, queens perform a variety of parasitic activities between or within species about the nest foundation. Concerning the evolution of obligatory parasitism in social wasps, TAYLOR (1939, cited from WILSON, 1971) stated: "at the first step to parasite, queens may have tended to usurp the reproductive position in alien colonies of their own species. Then, with further evolution, they may extend this behavior to colonies of other closely related species. Eventually they may come to depend on interspecific parasitism altogether."

Likewise, the evolution of obligatory gall parasitism in *E. yangi* may have gone through some precursory steps. Probably, one of such steps is that a fundatrix of gall-forming species intrudes into a conspecific gall. Galls inhabited by more than one conspecific fundatrix were also reported in *Eriosoma ulmi* and *E. anncharlotteae* (JANISZEWSKA-CICHOCKA, 1969; DANIELSSON, 1979). JANISZEWSKA-CICHOCKA recorded a gall including 33 fundatrices of *E. ulmi*. It is unlikely that so many fundatrices induce a single gall simultaneously. Her observation suggests that some fundatrices may invade the gall formed by other conspecific individuals. At present, however, it is unclear whether the intrusion of conspecific fundatrices reduces the profit of the original gall proprietor. In fact, I could not observe that any particular fundatrix dominates over others in the same gall in producing offspring. Therefore, it is quite questionable that the intrusion into conspecific galls can be regarded as

parasitism. Nevertheless, the peculiar type of parasitism of *E. yangi* has no doubt been derived from such more general relationships between conspecific fundatrices of the gall-maker.

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