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Cleptoparasitic Life of the Tachinid Fly, *Symmorphomyia katayamai* MESNIL et SHIMA, in the Nest of Host Wasps Hunting the Chrysomelid-larva Prey

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Abstract Previous knowledge about the tachinid cleptoparasite, *Symmorphomyia katayamai* MESNIL et SHIMA (Diptera, Tachinidae), a specific attacker on the chrysomelid-larva hunter, *Symmorphus* spp. (Hymenoptera, Eumenidae), was corrected by observing (1) the activities of host wasps and other insects at nesting sites and colonies of the chrysomelid prey, (2) the developmental process of the tachinid larva, and by inspecting (3) the cell contents of the host nests. No visits by *S. katayamai* to the host wasp's nesting sites were observed, in spite of the remarkably high percentage of cleptoparasitism on the wasp's nests. It was confirmed that the larva of *S. katayamai* first has the endoparasitoidal stage on any one of chrysomelid larvae stored in the nest cell. Two puparia of presumably *S. katayamai* were obtained through rearing chrysomelid larvae collected on the host plant that a female fly had visited. The female reproductive organs of *S. katayamai* had the structure typical to the ovoviviparous tachinine flies which produce numerous first-instar larvae. A cleptoparasitic life style of *S. katayamai* is probably derived from the fundamental one of the endoparasitoid on chrysomelid larvae by the phoresy-like access into the nests of *Symmorphus* wasps.

Key words: *Symmorphomyia katayamai*; Tachinidae; cleptoparasite; parasitoid; *Symmorphus*; chrysomelid larva.

Introduction

Plenty of prey stored in a nest cell of solitary wasps are attractive food resources for not only the wasp's progeny but also some specialized cleptoparasites, which normally can not collect individuals of prey. Many taxonomically different groups of insects are known as cleptoparasites attacking on solitary wasps. Some major groups are hymenopteran cleptoparasites. They can be divided into the following two groups: (1) those derived from nesting ancestors, for example, sphecid cleptoparasites belonging to the genus *Stizoides* (hosts: grasshopper hunter, *Prionyx* spp.) and (2) those from groups including many parasitoid species, for example, some chrysidid "cuckoo wasps" such as *Chrysis coerulans* (hosts: twig-nesting Eumenidae spp.). Other major groups belong to Diptera, especially a specialized cleptoparasitic subfamily Miltogramminae of Sarcophagidae. The subfamily contains several genera. Each of the genera has its unique method of attack. So-called "satellite flies" of the genera such as *Amobia* and *Senotainia* follow wasps laden with a prey or material for nest closure and locate their nests. They then perch near the nest entrance and wait for opportunities to larviposit into the cells or on the prey (EVANS & EBERHARD, 1970).

This paper reports the habit of the unique tachinid cleptoparasite, *Symmorphomyia katayamai* MESNIL et SHIMA (Diptera, Tachinidae), which is a specific attacker on the chrysomelid-larva hunters, *Symmorphus* spp. (Hymenoptera, Eumenidae). This fly was described taxonomically as a new genus and species (MESNIL & SHIMA, 1977). A general habit of this fly was considered to be almost the same as one of the sarcophagid satellite flies (IWATA, 1978a, 1978b). Other informations, making mention of its habit (SHIMA, 1989b; ITINO, pers. comm.), were based on the observations by Dr. K. IWATA and by Mr. H. KATAYAMA, because of scarce chances to encounter large colonies of host wasps. I observed nesting activity of two species of host wasps, *Symmorphus decens* (KOSTYLEV) and *S. foveolatus* GUSSAKOWSKIJ, inspecting cell contents of their nests in detail, where many individuals of this tachinid cleptoparasite were obtained. My some observations showed that the habit of the tachinid fly was considerably different from what had been recognized. Some lines of evidence reveal a unique triangular-relationship among the hunting wasps, their specific prey and the specific tachinid cleptoparasite, which provides an important insight on the formation of cleptoparasitism.

Materials and Methods

Study site

Field observations were carried out in the Branch of Field-Study and Education, *Gakushu-no-Mori*, of the Kobe Municipal Arboretum on the west slope of Mt. Futatabi, Kobe, Hyogo Pref. (11.3 ha, long. 135°10′27″E, lat. 34°44′2″N, alt. 367 m) during the spring—early summer of 1991–1994. The study site and its peripheral area are covered with temperate deciduous woods and afforestations of the Japanese cedar, *Cryptomeria japonica* D. DON, and the Japanese cypress, *Chamaecyparis obtusa* ENDL. *Wisteria floribunda* DC., a host plant of *Phytodecta rubripennis* BALY that is the only prey of *S. decens*, forms large vines in the edge of woods along open valleys and stretches many shoots to the shaded areas. Most colonies of *P. rubripennis* were found on such shoots. *Alnus pendula* MATSUMURA, a main host plant of *Linaeidea aenea* LINNÉ that is a main prey-species of *S. foveolatus*, forms shrubberies on steep banks along the surrounding passes. These shrubberies were planted within these decades. Several species of *Salix*, both native and planted, grow beside streams. Colonies of *Plagiodera versicolora* LAICHARTING, a second prey-species of *S. foveolatus*, occur mainly on the shrub of *Salix integra* THUNB. growing along the small stream and on one big tree of *Salix chaenomeloides* KIMURA in a valley in the arboretum. A small number of *Juglans mandshurica* MAXIM. grow at a model orchard, and a big tree of *Pterocarya rhoifolia* SIEB. et ZUCC. beside the stream. Almost all colonies of *Gastrolina depressa* BALY, another prey-species of *S. foveolatus*, occur on *J. mandshurica*.

Activities of host wasps and related insects

The nesting activity of host wasps (see Appendix for their biology) was observed at some trap-nest shelves during the nesting periods. Those nesting shelves were divided into two types: old ones where the wasp's colonies had established previously and the others newly set up every year. At these new shelves, the observation colonies of host wasps originated in setting some overwintered nests or releasing newly emerged wasps, where over 120 reed tubes were provided as nesting substrates before the nesting season. Furthermore additional reed tubes were sometimes supplied. Female wasps were individually marked with acrylic lacquer paint. The nesting activity of wasps was observed for 4–8 hours almost every day in suitable weather conditions. The following items on behavioral aspects were recorded: (1) time of returning, (2) time of departure, (3) type of load (prey or materials of cell-partition, *etc*.), (4) interactions between wasps and (5) interactions between wasps and natural enemies such as satellite flies. Some of these data were used for the analysis of the relationship between the cleptoparasite's activity at a wasps' nesting site and the intensity of parasitism. All newly occupied nest tubes were numbered, and the final mud plugs of completed nests were marked every evening. In 1991 and 1992, intensive observations were made on locating colonies of chrysomelid prey and interactions among related insects at a hunting site of wasps. Intra-nest behavior of female wasps was observed in 1991 and 1992 by using several see-through nest tubes whose side wall had a clear plastic window.

Nest structure and cell contents of host wasps

Almost all nests inspected in 1991 and 1994, and several ones in 1992 and 1993 were collected and dissected 1–7 days after completion of each nest. While the others in 1992 and 1993 were done after the nesting seasons. In 1991, the nests were sampled mainly from the old nest-shelves and subsidiarily from the new one. In 1992, the nests of *S. foveolatus* were sampled only from the old nest-shelf. While, in 1993 and 1994, all nests were collected only from the new nest-shelf. The cell contents were spread on a white paper by the cell individually and inspected in detail. Pellets clotted with taint gravy from consumed prey were softened in 10% potassium hydroxide solution. Debris in each cell was spread in 50% ethanol. Then they were examined. Inner walls of open nest tubes were also examined carefully. The examined contents of each cell were stored in a vinyl sample-tube (7 mm dia. × 4 cm long) with cotton plugs. The samples which contained an egg or larva of host wasp, unconsumed prey, or maggots of flies were checked every day or two during their developmental periods.

Female internal reproductive organs of Symmorphomyia katayamai

In 1992, three females of *S. katayamai* were dissected, and their internal reproductive organs were observed under a binocular microscope. Two of them were collected on May 11 in 1992 when they emerged from host's nests, and were dissected two days later. The other emerged from a storage of examined cell contents on May 17 in 1992, was reared with male flies, and then she was dissected 17 days later.

Results and Discussion

Seasonality of S. katayamai

S. katayamai emerged from the nests made in 1991 during the emergence periods of both host species which had overwintered outdoors (Fig. 1). Although the dates of emergence of these insects were not checked daily in 1993 and 1994, no individual of these species emerged before spring. On the other hand, all individuals of sarcophagid cleptoparasite, *Amobia* sp., emerged from the nests within the season in 1991. For example, five individuals from a nest of *S. decens* made on May 24–25 emerged on June 15–18, and four individuals from two nests of *S. foveolatus* made on July 2–3 emerged on July 22–25. The results suggest that *S. katayamai* has univoltine life-cycle almost coincident with its host wasps.

For the time lag of the nesting periods a little less than one month between *S. decens* and *S. foveolatus* (Fig. 2), it was suspected that *S. katayamai* would emerge in the order corresponding to nesting period of each host if the tachinid adapted to the life cycle of each host. Then the relation between the date of completion of each nests containing *S. katayamai* and the date of fly emergence in the following year was examined in Fig. 3. There is a significant difference between *S. decens* and *S. foveolatus* on the periods in which the cleptoparasitized nests were constructed (MANN–WHITNEY U-test, $p < 0.001$), but no significance between two hosts on the periods of emergence of *S. katayamai* from the nests (MANN–WHITNEY U-test, $p = 0.59$). There is also a weak but significant correlation between the date of nest completion and the date of fly emergence (KENDALL's correlation test, $p = 0.0445$). However, this seems to be a superficial correlation owing to small sample size for *S. decens*, which nests in relatively early season. On the other hand, when identical data points were classified by sex of the emerged flies, it shows that males of *S. katayamai* tend to emerge

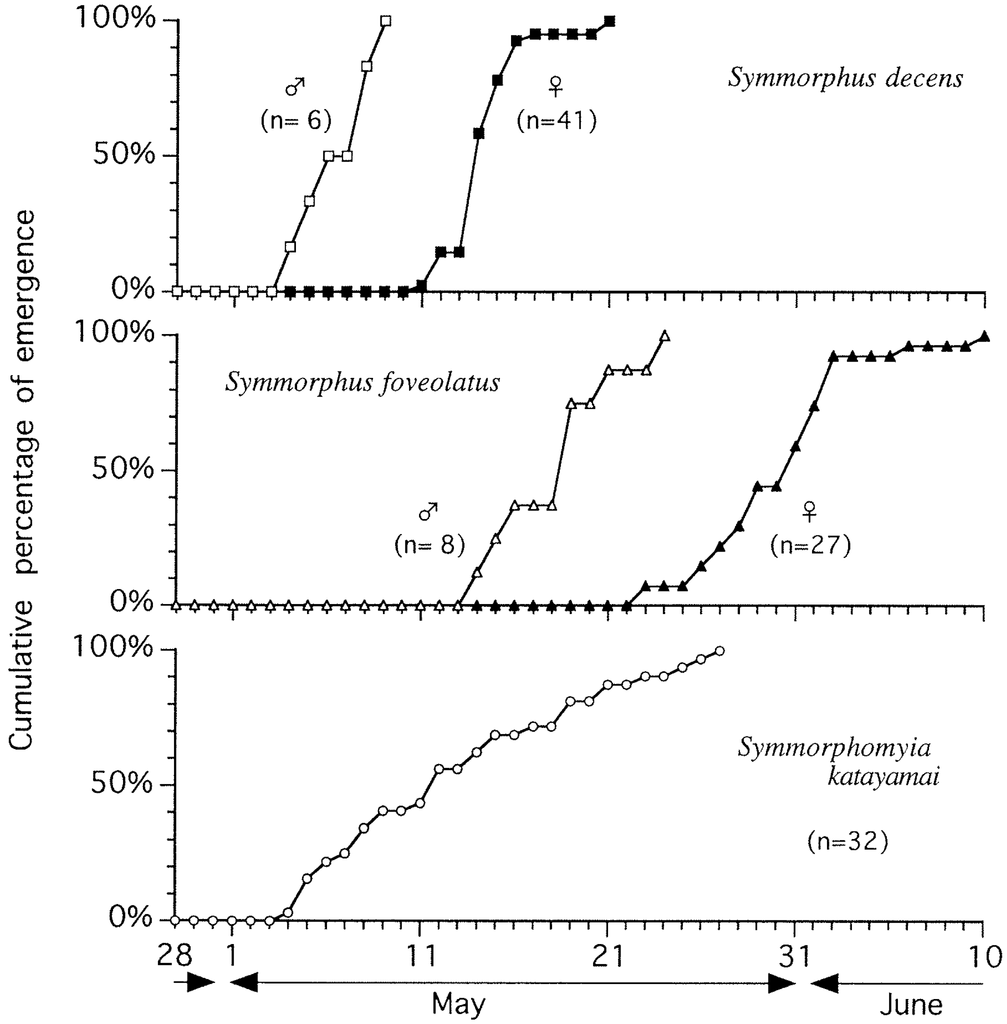

Fig. 1. The cumulative emergence curves of two host wasps, *Symmorphus decens* and *S. foveolatus*, and of the cleptoparasitic tachinid fly, *Symmorphomyia katayamai*, at the study site in 1992. All of these insects were collected from the nests made in 1991, and overwintered in vinyl sample-tubes under the outdoor condition on the campus of Kobe Univ., and then were sent back to the study site at the beginning of March in 1992.

significantly earlier than females (KRUSKAL–WALLIS test, $p<0.001$). In other words, *S. katayamai* is protandrous.

Figure 4 shows the daily number of newly founded nests of the host wasps and the ratio of nests cleptoparasitized by *S. katayamai* in 1993 and 1994. Abandoned nests before provisioning or the destroyed and usurped nests by other individuals were, however, not included here. The sub-periods (I), (II), *etc.* in Fig. 4 were determined according to the limitation on the small expected values in Chi-square test for the temporal distribution of the cleptoparasitized nests, where "expected value"="no. of founded nests in a sub-period"×"total no. of

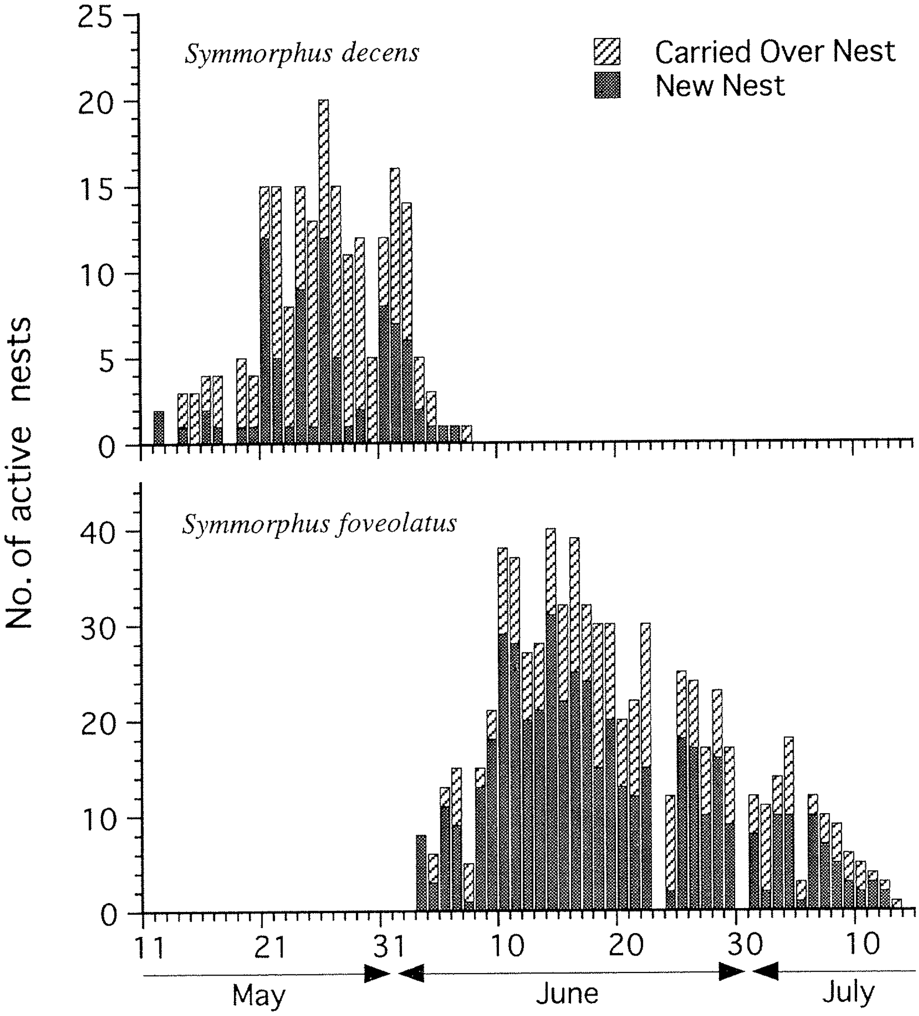

Fig. 2. The nesting periods of two species of *Symmorphus* in the observed nesting sites in 1992.

cleptoparasitized nests"/"total no. of founded nests". There was no significant difference between the observed values and the expected ones (One group Chi-square test, $p=0.52$ for *S. decens* in 1993, $p=0.24$ for *S. foveolatus* in 1993, $p=0.44$ for *S. decens* in 1994, $p=0.88$ for *S. foveolatus* in 1994). The results show that the cleptoparasitism occurred throughout the nesting seasons of host wasps when the number of nest tubes was taken as a unit of counting. In *S. decens*, however, nests made at the beginning of its nesting season were not damaged so much from the viewpoint that the number of cells was taken as a unit of counting, since the unparasitized ones of those nests that were made earlier had relatively many cells (see Appendix and Fig. 7A).

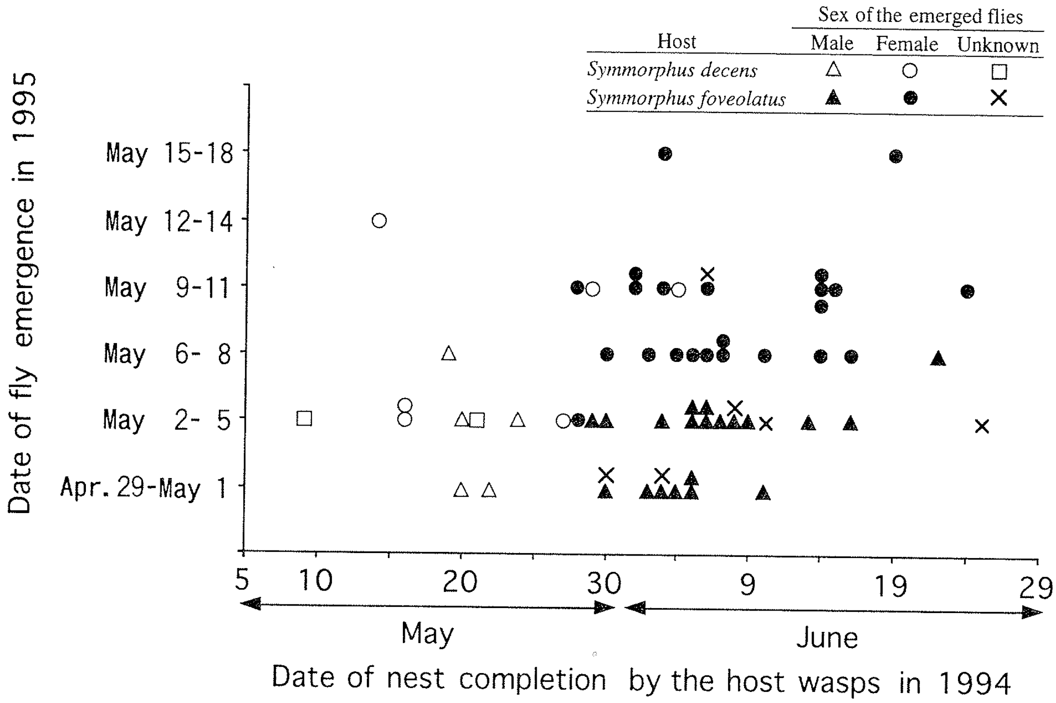

Fig. 3. The relation between the date of nest completion by the host wasps and the date of emergence for the individuals of *Symmorphomyia katayamai.*

Behavior of Symmorphomyia *larvae in the host nests*

Figure 5 shows how larvae of *S. katayamai* behaved in the wasp's nest. Two larvae of *S. katayamai* occurred in two of the three cells (cell #1 and cell #3) respectively in this nest. The larva of *S. katayamai* that had broken out of cell #1 penetrated both one empty cell and the next cell (cell #2), and began to devour prey stored there. Such sweepingly destructive activity by cleptoparasite larvae was observed in every cleptoparasitized nests. Although both the larvae in Fig. 5 were still alive at inspection, only one individual grew into a puparium in almost every cleptoparasitized nest no matter how excess amount of prey was there, since the larvae attack each other before long in every nest tube containing more than one fly larvae. For the nest tubes cleptoparasitized by *S. katayamai*, the number of nests containing one survivor and one or more dead larvae and the total number of nests containing more than one individuals dead or alive were as follows respectively: 7/8 for *S. foveolatus* in 1992; 1/3 for *S. decens* in 1993; 10/11 for *S. foveolatus* in 1993; 4/6 for *S. decens* in 1994; 8/9 for *S. foveolatus* in 1994.

When eggs (or young larvae) of the wasps and their prey only were transferred into individual vinyl tubes from cells of the nests dissected one or a few days after completion, it was observed in several cases that a larva of *S. katayamai* appeared from one individual of prey: [1] a fly larva appeared on June 23 and began to devour egg of *S. foveolatus* and its prey, larvae of *L. aenea*, which

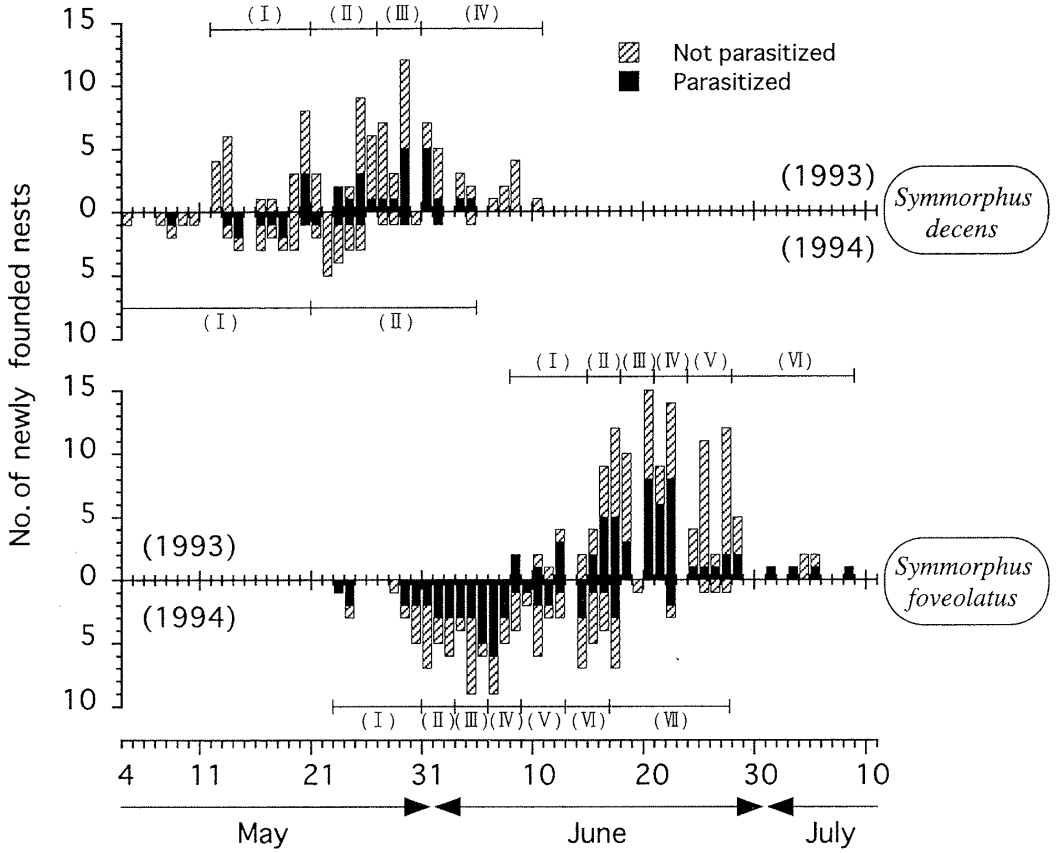

Fig. 4. The temporal change of the ratio of nests cleptoparasitized by *Symmorphomyia katayamai* for two species of host wasps in 1993 and 1994. See the text for the sub-periods (I),(II), *etc.*

were collected from the nest completed on June 20 in 1991; [2] a fly larva appeared on July 19 from one individual of prey, larva of *L. aenea*, in the nest completed on July 18 in 1992; [3] a fly larva appeared on July 24 and devoured larva of *S. foveolatus* and its prey, larvae of *L. aenea*, which were collected from the nest completed on July 14 in 1992; [4] two fly larvae appeared on May 27 from each individual of prey, larva of *Phytodecta rubripennis*, in two cells respectively of the nest of *S. decens* made during May 20–21 in 1992. In the last case, one of the fly larvae was about to break the integument of prey whose interior of the body was consumed at all and to come out of it (Fig. 6A). No egg shells like oviparous tachinid flies' were found on every individual of prey containing a fly larva, on the other individuals of prey stored with them and on the internal walls of the nests. These suggest that *S. katayamai* has the phase of endoparasitoid on a chrysomelid larva before the phase of cleptoparasite on a nest of the *Symmorphus* wasps.

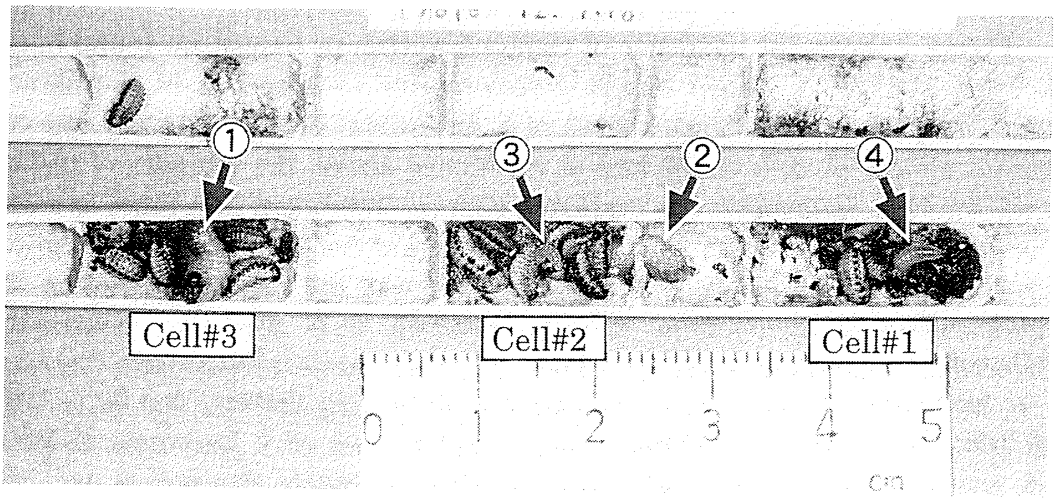

Fig. 5. The interior view of the host's nest cleptoparasitized by two larvae of the tachinid fly, *Symmorphomyia katayamai* (A pair of halves of the split nest tube is shown). This three-cellular nest of *Symmorphus foveolatus* was dissected four days after completion, in which all cells had been provisioned with larvae of *Linaeidea aenea*. Cell #1, empty cell, Cell #2, empty cell and Cell #3 were arranged in the direction from blind end to open end of the nest tube. Arrow 1 shows one of the tachinid larvae, which was devouring the chrysomelid prey in the cell. Arrow 2 shows the other larva, which was penetrating into the next cell (Cell #2) and beginning to devour the prey there. Arrows 3 and 4 show the young larvae of the host wasp, which were destined to be killed by the tachinid larvae.

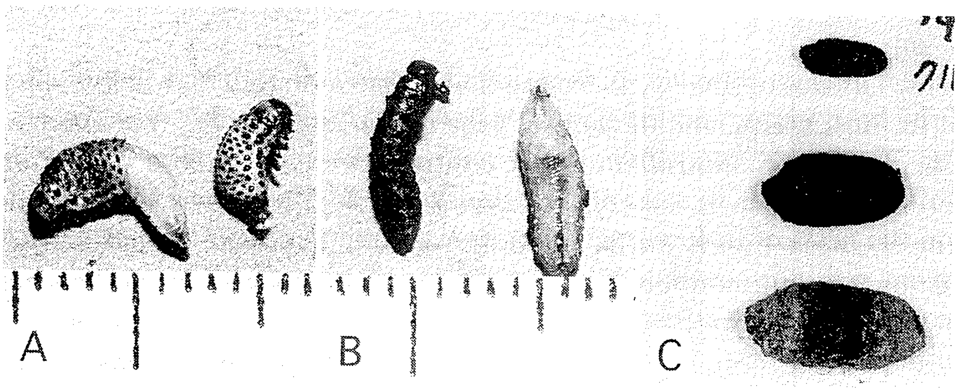

Fig. 6. The tachinid larvae and puparia. A: The larva of *Symmorphomyia katayamai* coming out of a consumed chrysomelid-larva (left) and a normal chrysomelid-larva (right), *Phytodecta rubripennis*, which were stored in a nest of *Symmorphus decens*. B: The larva of probably *Symmorphomyia katayamai* (right) which had come out of the consumed chrysomelid-larva (left), *Gastrolina depressa*, having lived on the host plant. C: The small puparium of probably *Symmorphomyia katayamai* which consumed one chrysomelid larva having lived on the host plant (top), the puparium of *S. katayamai* from a single-cellular nest of *S. foveolatus* (middle), and the puparium from a three-cellular nest of *S. foveolatus* (bottom).

Intensity of cleptoparasitism by S. katayamai *on the host nests*

Figure 7 shows the incidence of cleptoparasitism or parasitism found in the inspected nests of *S. decens* and *S. foveolatus* for each species of the natural enemies to those wasps. Since a larva of *S. katayamai* occurring in any one cell destroys almost all cells in the nest as mentioned above, the intensity of cleptoparasitism by *S. katayamai* was evaluated with the number of nest tubes as a unit of counting but the number of cells, even if the number of cells per nest varied. It is clear from this figure that *S. katayamai* was the major one among the cleptoparasites to *Symmorphus* species, especially to *S. foveolatus* constantly. Furthermore, one thing should be added. All of the nests infested with Phoridae sp. or *Melittobia* sp. were found only on the old nesting shelves, that is, in 1991 and 1992 (see Materials and Methods) except for one of *S. foveolatus* in 1993. This seems to result from that those parasites propagate themselves over the host's nesting site from the already infested nests there (IWATA, 1975). By contrast, the nests cleptoparasitized by *S. katayamai* were found on the new nesting shelves, that is, in 1993 and 1994 no less frequently than on the old ones for *S. foveolatus* (Chi-square test, $p=0.65$); and, for *S. decens*, those were found more frequently on the new ones (Chi-square test, $p<0.05$ in comparison between the data in 1991 and two others, $p>0.45$ in comparison between 1993 and 1994). Therefore, it is unlikely that females of *S. katayamai* deposit their eggs or larvae in the host's nesting site where they have emerged.

Confirmation for the ovi-(larvi-)position of S. katayamai *outside the host wasp's nesting site*

Some females of *Amobia* sp. occasionally visited on both new and old nesting sites of the host wasps, and the typical behavior as "satellite fly" was observed on each site. Visits by *S. katayamai*, to the contrary, were never observed during the period of observations in spite of the remarkably high percentage of cleptoparasitism on the nests of host wasps. Did the tachinid fly attack the nests when the observation was not continued? In order to examine the relation between the occurrence of cleptoparasitism by *S. katayamai* in the nest and the probability of their visits to the nest, the contingency table analysis was applied. Data of

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Fig. 7. The incidence of cleptoparasitism or parasitism by each species of the natural enemies found in the inspected nests of two species of *Symmorphus* wasps. A: For *S. decens* in 1991, 1993 and 1994. All inspected cells were provisioned with larvae of *Phytodecta rubripennis*. B: For *S. foveolatus* in 1991–1994. In 1991, the inspected cells were provisioned mainly with larvae of *Linaeidea aenea* and subsidiarily with larvae of *Plagiodera versicolora* and *Gastrolina depressa*. In the other years, all the inspected cells were provisioned with larvae of *Linaeidea aenea*. C: Percentage of the nest tubes cleptoparasitized by *S. katayamai* and by *Amobia* sp. during 1991–1994, without distinction of the number of cells in each nest.

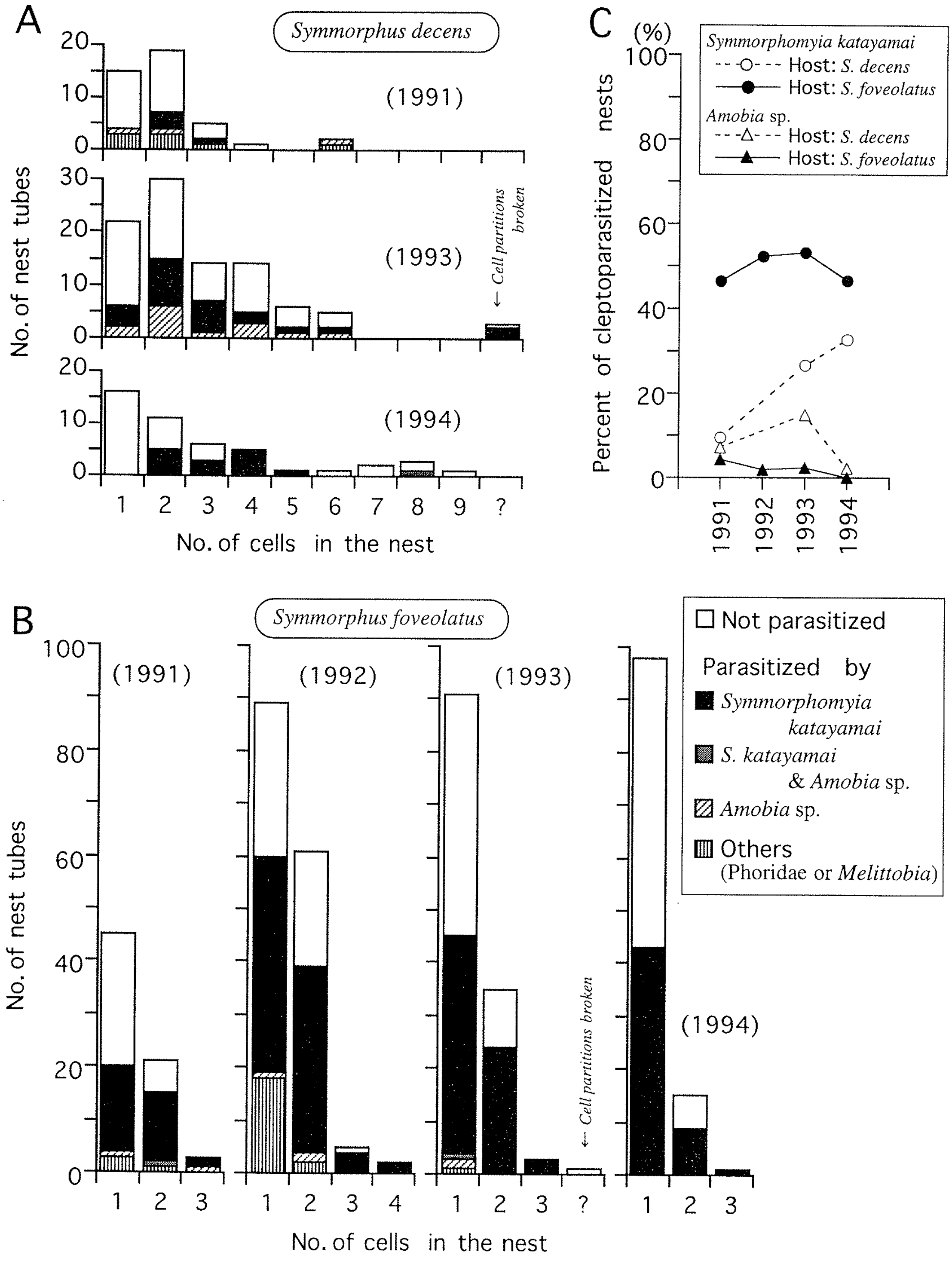
A
Symmorphus decens
(1991)
(1993)
(1994)
No. of nest tubes
0
10
20
30
← Cell partitions broken
1
2
3
4
5
6
7
8
9
?
No. of cells in the nest
C
(%)
100
80
60
40
20
0
Percent of cleptoparasitized nests
Symmorphomyia katayamai
Host: S. decens
Host: S. foveolatus
Amobia sp.
Host: S. decens
Host: S. foveolatus
1991
1992
1993
1994
B
Symmorphus foveolatus
(1991)
(1992)
(1993)
(1994)
No. of nest tubes
100
80
60
40
20
0
← Cell partitions broken
1
2
3
4
?
No. of cells in the nest
□ Not parasitized
Parasitized by
■ Symmorphomyia katayamai
▩ S. katayamai & Amobia sp.
▨ Amobia sp.
▥ Others (Phoridae or Melittobia)

Fig. 7.

Table 1. The contingency table of the relation between the occurrence of cleptoparasitism by *Symmorphomyia katayamai* in the nest and the probability of visiting to the nest by it, for the single-cellular nests of *Symmorphus foveolatus*.

Cleptoparasitism by *S. katayamai*		Count (Expected)	Observation during the wasp's nesting		Total	Chi-square test	Fisher's exact prob. test
			No	Yes			
1992	+		27	14	41		
			(27.8)	(13.2)		ns	ns
	–		32	14	46	(p=0.7115)	(p=0.8191)
			(31.2)	(14.8)			
		Total	59	28	87		
			Observation during the whole process of provisioning and closing the cell				
			No or Imperfect	Perfect			
1993	+		34	7	41		
			(34.6)	(6.4)		ns	ns
	–		42	7	49	(p=0.7163)	(p=0.7757)
			(41.4)	(7.6)			
		total	76	14	90		
1994	+		35	7	42		
			(36.25)	(5.75)		ns	ns
	–		47	6	53	(p=0.4515)	(p=0.5522)
			(45.75)	(7.25)			
		Total	82	13	95		

single-cellular nests were classified according to whether it was observed during provisioning and cell-closure constructing by the host wasp (Table 1). Although the data for *S. decens* could not be used because of the small number of cleptoparasitized single-cellular nests (see Fig. 7A), the results of this analysis never contradict with the notion that the nests to which the tachinid fly did never have access can be cleptoparasitized no less than ones which it could do. On the other hand, the nests visited by *Amobia* sp. were most likely cleptoparasitized at the significantly higher ratio than the other nests in 1993 when the relatively large number of nests were cleptoparasitized (Table 2, see also Fig. 7A). If *S. katayamai* has the same tactics for cleptoparasitism as *Amobia* sp., the visit by *S. katayamai* to the host wasp's nest must be observed. Therefore it follows that the direct visit by *S. katayamai* to the host's nesting site is improbable, and the tachinid fly is likely to have access to wasp's nests in some way outside the nesting site.

Table 2. The contingency table of the relation between the occurrence of cleptoparasitism by *Amobia* sp. in the nest and the probability of visiging to the nest by it, for *Symmorphus decens* and *S. foveolatus* in 1993.

Cleptoparasitism by *Amobia*		Count (Expected)	Visiting by the fly to the wasp's nest on constructing			Fisher's exact prob. test
			Unknown	Observed	Total	
S. decens nest	+		6	8	14	
			(10.02)	(3.98)		sg.
	−		67	21	88	(p=0.0214)
			(62.98)	(25.02)		
		Total	73	29	102	
S. faveolatus nest	+		1	2	3	
			(2.78)	(0.22)		sg.
	−		102	6	108	(p=0.0133)
			(100.22)	(7.78)		
		Total	103	8	111	

Female activity of S. katayamai *in the study site*

A few adults of *S. katayamai* were observed just twice in the field of study site except when the tachinids rested at the entrances of host nests during post-emergence sclerotization. On May 21 in 1992, a fine and warm day, a female adult of *S. katayamai* visited a tree of *Juglans mandshurica* in the model orchard of the arboretum and rested on the fresh leaves of the tree, occasionally flying around. At that time, larval colonies of *Gastrolina depressa* grew on that tree. For several days thereafter, a few dozens of male wasps of *S. foveolatus* were swarming. Furthermore a visit of a female wasp of *S. foveolatus*, investigating some colonies of chrysomelid larvae by tapping the substrate with her antennae, was observed on June 1, when hunting behavior did not occur, however. On May 22 in 1994, two adult flies of *S. katayamai* were observed to visit the same *Juglans* tree, when larval colonies of *G. depressa* and swarming of several males of *S. foveolatus* were there. One of the two flies was netted and identified distinctly. These observations suggest that *S. katayamai* may have contact with its host wasps on the wasp's hunting site, that is, the host plant for the chrysomelid prey.

The tachinid larva hides in the chrysomelid larva on the host plant

It was 22 individuals of the second or third instar larvae of *Gastrolina depressa* that were collected from the colonies on the *Juglans* tree mentioned above on June 1 in 1992. They were reared in the laboratory. On June 4, a tachinid larva came out of the mature chrysomelid larva (Fig. 6B). On June 8, another tachinid larva came out of the chrysomelid prepupa that had remained at the same developmental stage since June 4. This larva died, but the first one became a small puparium on June 7 (the top in Fig. 6C). It had consumed just one chrysomelid larva. It was compared with two puparia of *S. katayamai* from a single-cellular nest and a three-cellular nest of *S. foveolatus*, respectively. Although the adult fly unfortunately did not emerge from the small puparium in the next spring, its shape was identical with the puparia of *S. katayamai* except its size (Fig. 6C).

The structure of the female internal reproductive organs of S. katayamai

Figure 8 shows the female internal reproductive organs of an individual of *S. katayamai* two days after emergence (A) and of another 17 days after emergence (B). It should be noted that the long expanded *oviductus communis*, which looks like a loop and thick string (at the center of Fig. 8B), contained numerous embryos without chorion. In addition, the *oviductus communis* was surrounded with well-developed tracheoles. These characteristics suggest strongly that *S. katayamai* is an ovoviviparous species which produces numerous larvae.

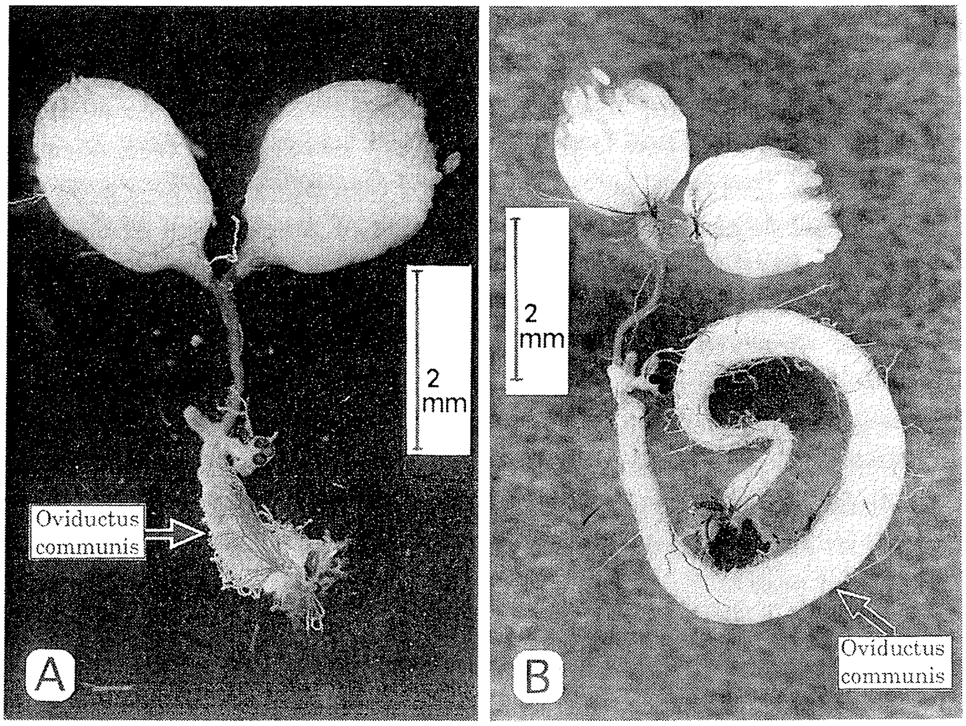

Fig. 8. The female internal reproductive organs of *Symmorphomyia katayamai* two days (A) and 17 days (B) after emergence. The elongated *oviductus communis* of B contained numerous embryos.

General Discussion

IWATA (1978a, 1978b) reported the habit of *Symmorphomyia katayamai* according to his observation and Mr. H. KATAYAMA as follows: "The fly locates the host wasp's nest by following the wasp, and then perches near the nest entrance to wait for the chance to larvi- or oviposit. When the wasp departs from the nest, the fly deposits one to three larvae or eggs into the nest." Such a behavior of the tachinid fly is almost identical with the typical one of miltogrammine satellite flies. The present study, however, was not consistent with this report. No visits by *S. katayamai* to the host wasp's nesting sites were observed in spite of the remarkably high percentage of its cleptoparasitism on the nests. If *S. katayamai* has the same mode of cleptoparasitism as the miltogrammine satellite fly, such as *Amobia*, we can not explain why visits by *S. katayamai* to the host nests were never observed. Then, how do larvae of *S. katayamai* sneak into the host nests?

Some lines of evidence can be obtained from inspections of cell contents in host nests. Undoubtedly, the larva of *S. katayamai* has the endoparasitoidal stage in the interior of the chrysomelid larva's body before it behaves as the cleptoparasite in the host wasp's nest. It is almost certain that larvae of *S. katayamai* parasitize chrysomelid larvae—they can be potentially hunted by the *Symmorphus* wasps—on plants, because the puparia peculiar to *S. katayamai* were obtained from mature larvae of *G. depressa* on the *Juglans* tree where a female of *S. katayamai* visited.

MESNIL & SHIMA (1977) have considered that *S. katayamai* belongs to *Cleonice-Gastroptilops* group of the subfamily Tachininae, judging from the morphological characters. They have pointed out that the genus *Cleonice*, closely related to *Symmorphomyia*, is a parasitoid on certain chrysomelid larvae. Furthermore, the structure of female reproductive organs of *S. katayamai* is typical of the tachinine flies which produce numerous first-instar larvae of planidium type or short-range-host-searcher type (SHIMA, 1989a). These agree with the presumption that larvae of *S. katayamai* first, as the endoparasitoid, enter into the bodies of chrysomelid larvae on plants. Here, it is worth mentioning that keen competition among the tachinid larvae encountering each other in a host's nest is probably reflection of the attribute of solitary endoparasitoids. In addition, from a comparison of the life cycle between *S. katayamai* and *Amobia* sp., it seems reasonable to assume that the univoltine life cycle of *S. katayamai* may help synchronize with the population dynamics of certain chrysomelid larvae rather than that of *Symmorphus* wasps.

After all, the cleptoparasitic life style of *S. katayamai* seems to be derived from the linkage of a few additional key factors with the fundamental life style of the endoparasitoid on chrysomelid larvae. One of the key factors is the phoresy-like habit that a larva of this tachinid fly sneaks into the host wasp's nest through the chrysomelid larva—as prey of the wasp—parasitized by the fly, and another is that the tachinid larva devours *Symmorphomyia*-free individuals of chrysomelid prey also (and the wasp's young larva or egg) in the nest cell after consuming the first one which it endoparasitized.

Relationship among the sphecid wasps, *Solierella* spp., their prey, lygaeid nymphae, and the chrysidid cleptoparasite, *Pseudolopyga taylori* (BODENSTEIN), is probably analogous with that among *Symmorphus* wasps, the chrysomelid larvae and *S. katayamai.* Females of *P. taylori* oviposit in first or early-second-instar nymphae of a lygaeid bug. Chrysidid eggs hatch but do not develop. If some of the parasitized lygaeid nymphae, when they became fourth or fifth instar, were hunted by a *Solierella* wasp and stored with other *Pseudolopyga*-free lygaeids in a nest, the chrysidid larvae could then develop. They emerge out of the lygaeids which they have endoparasitized as second instar, consume the sphecid progeny and the other stored lygaeids in the nest cell (CARRILLO & CALTAGIRONE, 1970). Chrysididae is considered to be the group in which most of the members are parasitoids on the hosts such as nesting wasps and bees rather than cleptoparasites despite the common name "cuckoo wasp" (IWATA, 1971, 1978a). *P. taylori* and *S. katayamai* may represent respectively the origins of cleptoparasitic branches in two parasitoid phyla. From this point of view, IWATA's report that *S. katayamai* behaved like the miltogrammine satellite fly can not be denied entirely. Or otherwise we may have to consider the possibility that *S. katayamai* has the alternative tactics for access to the host wasp's nests, since the local populations of *S. katayamai* may encounter a new niche in the Kinki-Hokuriku district, which is the range of *S. decens.* The distribution of this wasp leans to more southern area in Japan than that of the other *Symmorphus* wasps (YAMANE, 1990), perhaps in connection with the distributions of its prey, *P. rubripennis*, and the host plant of the prey, *W. floribunda.*

The following matters remain to be investigated: (1) to observe directly the ovi- or larvi-positing behavior of adult females of *S. katayamai* to colonies of chrysomelid prey, (2) to find out the way in which the young larvae of *S. katayamai* enter the chrysomelid larvae on the host plants and (3) to evaluate the proportion in which the chrysomelid larvae on the host plants are parasitized by the tachinid larvae for different species of the chrysomelids, different colonies or different periods. These investigations will bring some important bits of information to consideration about the influence of the cleptoparasitic pressure by *Symmorphomyia katayamai* on the intra- or inter-specific prey-preference by *Symmorphus* wasps.

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Appendix: *Biological sketch of host wasps*

Symmorphus decens (KOSTYLEV) is a slender eumenid wasp. The full body lengths of newly emerged females range from approximately 11.5 mm to 13.5 mm (HAMANISHI, unpublished). It occurs in Honshu, Shikoku, Kyushu, and East Siberia (YAMANE, 1990). This species is univoltine, overwintering at the prepupal stage, and its nesting activity is observed in May and June in the Kinki district, Honshu. It was reported that their nests contained one or two brood cells and one to three empty cells in narrow tubes such as wheat straws used for thatched roofs (IWATA, 1938, 1978b). But I observed that their nests often contained a little more cells, 1 to 9, more continuously in reed tubes 5 mm in diameter and 200 mm in length. Cell partitions (0.5–1 mm thick) and final entrance plug (2 mm thick) are made of fine soil or clay. The brood cell is provisioned with 4 to 11 mature larvae of a chrysomelid beetle, *Phytodecta rubripennis* BALY (YAMANE, 1990 after IWATA, 1938, 1978b).

Symmorphus foveolatus GUSSAKOWSKIJ has almost the same size as above-mentioned species, but is slightly more slender. It occurs in Hokkaido, Honshu, Shikoku, Kyushu, East Siberia, and Korea (YAMANE, 1990). This species is also univoltine, overwintering at the prepupal stage, and its nesting activity is observed from mid-May to July in the Kinki district, Honshu. It was observed that their nests contained one to six brood cells and one to three empty cells in narrow tubes such as wheat straws, slender bamboo stems, reed tubes, and rarely deserted beetle burrows in wood (IWATA, 1938). But again I observed less, usually 1 to rarely 3, brood cells. Cell partitions and final entrance plug are made of mud. IWATA (1938, 1978b) reported that female wasps of *S. foveolatus* exploited the mature larvae of chrysomelids, *Gastroidea atrocyanea* MOTSCHULSKY on *Rumex* spp. and *Plagiodera versicolora* LAICHARTING on *Salix* spp., as prey in Ikeda, Osaka, and that the number of prey larvae per cell ranged 4 to 31, depending on their body size. I observed, however, that *S. foveolatus* utilized the mature larvae of three chrysomelids, mainly *Linaeidea aenea* LINNÉ on *Alnus pendula* MATSUMURA and *A. japonica* STEUD. (4 to 11 per cell), and subsidiarily *Plagiodera versicolora* on *Salix* spp. (23 to 45 per cell) and *Gastrolina depressa* BALY on *Juglans mandshurica* MAXIM. (7 or 8 per cell) in Mt. Futatabi, Kobe (HAMANISHI, 1996).

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