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Colophina clematis (Homoptera, Pemphigidae), an Aphid Species with "Soldiers"

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Synopsis *Colophina clematis* is a woolly aphid with a peculiar kind of dimorphism in the 1st instar larval stage: "primary-type" larva and the unusually characterized "secondary-type" larva. Some hypotheses explaining the biological role of secondary-type 1st instar larva were proposed and tested, and the following one is accepted as the conclusion of this paper: Secondary-type 1st instar larvae attack intruders, thus they serve for defending their colony from some predators; and they neither grow nor reproduce. Further problems are briefly pointed out.

I (1976) previously reported the occurrence of a peculiar kind of dimorphism in the 1st instar larva of *Colophina clematis*. What I call "primary-type" 1st instar larva is characterized by a long rostrum and practically uniform legs, while the "secondary-type" 1st instar larva by a short rostrum and enlarged fore and mid legs (Fig. 1). Primary-type 1st instar larvae are "normal" larvae, and grow to adults, which then produce larvae of both types. The function of the "abnormal" secondary-type 1st instar larvae has hitherto been unknown. The purpose of the present paper is to show it.

Matters in Question

Colophina clematis is a woolly aphid making a dense colony on the stem of *Clematis apiifolia* (Fig. 2). The colony is usually located near the ground and shaded by other plants. The life cycle of this aphid on *Clematis apiifolia* is rather simple. Apterous viviparae (exules) continue to reproduce parthenogenetically. Primary-type 1st instar larvae grow into apterous viviparae which produce larvae of both types. In autumn (in southern Kantô, in September and October), some of primary-type 1st instar larvae grow into alate sexuparae, which migrate to an unknown primary host plant. In late autumn (in southern Kantô, in November), primary-type 1st instar larvae are exclusively produced. They overwinter in the crevices of bark or in moss. It is unknown whether the apterous viviparae immediately originated from these overwintered larvae produce in spring larvae of both types. In autumn, secondary-type 1st instar larvae are very common in large colonies.

The matters in question are summarized as follows: 1) The dimorphism is confined to the 1st instar stage. Corresponding dimorphism is not found in the succeeding stages. 2) Moults of the primary-type 1st instar larvae can easily be found, while those of secondary-type 1st instar larvae have never been found.

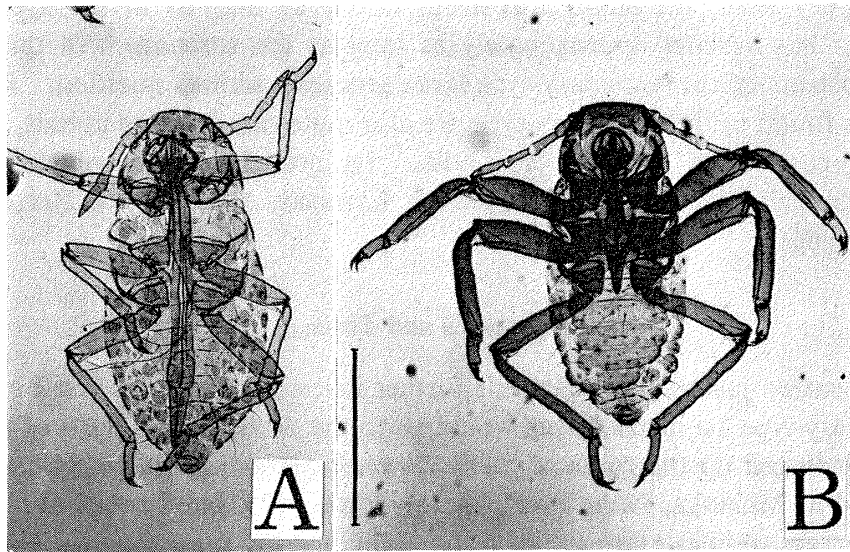


Fig. 1. Primary-type (A) and secondary-type (B) 1st instar larva. Scale: 0.5 mm.

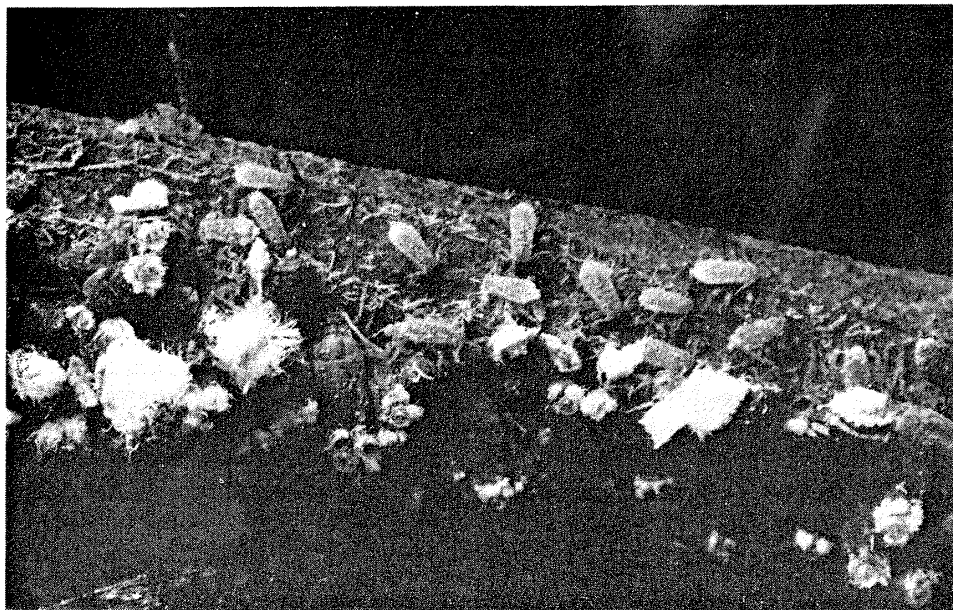


Fig. 2. An autumnal colony of *Colophina clematis*. Secondary-type 1st instar larvae are scattered on the upper surface of the stem. Larvae with wing pads appear.

Furthermore, though I examined more than 200 mounted specimens of the secondary type, none of them was found to have formed the 2nd instar skin inside. 3) It seems that secondary-type 1st instar larva does not excrete honeydew. And 4) the short rostrum and enlarged fore and mid legs of secondary-type 1st instar larva are of course unusual. The reason for the long rostrum in comparison with the body length in the primary-type 1st instar larva could easily be explained. These larvae, together with grown larvae and adults, suck the sap on the stem, probably from the

phloem. They need, therefore, a rostrum nearly as long as in the aged stages (this species has a stylet approximately as long as the rostrum). In this regard the short rostrum of the secondary-type larva arouses a serious question. Enlarged legs such as found in the secondary type are also quite rare in other aphids, with the only known case of the "pseudoscorpion-like" 1st instar larva of *Oregma*, in which, too, their function is unknown (HILLE RIS LAMBERS, 1966; HILLE RIS LAMBERS and BASU, 1966).

Hypotheses and Tests

The situation just mentioned needs further investigations. At first I supposed that secondary-type 1st instar larvae would go to the subterranean parts of *Clematis apiifolia*. I dugged up the roots of a few *Clematis*-plants with large aerial colonies of the aphid at Morioka, Iwate Pref., on July 29th, 1975, but I could not find any heavy subterranean infestation sufficient to strengthen my supposition.

Thereafter, a peculiar behavior of secondary-type larvae was found. When lightly tapped on the frons by the apex of a pin, they raise the fore legs and open and close them quickly. They often clutch at the pin. Such a reaction was not observed in the primary-type 1st instar larva at all (Table 1).

Table 1. Reaction of primary-type and secondary-type 1st instar larva to the tapping by a pin.

	Total number of tests	Reaction	
		+	-
Secondary-type	50	39	11
Primary-type	50	0	50

When the larva raised fore legs and opened and closed them quickly, it scored a positive reaction; otherwise negative one. It seemed that larvae walking on the stem react readily. Therefore, walking larvae were selectively tested for both types. The same individuals may have been tested more than once. This experiment was carried out at Fujisawa, Kanagawa Pref., on September 8th and 14th, 1976. Aphids reared on a potted *Clematis apiifolia* were used.

On this observation another hypothesis seemed to me possible: the secondary-type 1st instar larvae disperse by clutching at other active insects visiting the colony of this aphid, as in Javanese pseudococcids, *Hippeococcus* spp., which are closely associated with the ant *Hypoclinea gibbifer* (REYNE, 1954; WILSON, 1971: 421-422). To test this hypothesis I carried the following experiment. I pinned a living ant (*Formica fusca japonica*) on a colony of *Colophina clematis* reared on a potted *Clematis apiifolia*. The result was that when the ant struggled, secondary-type larvae approached to the ant and climbed on it (Fig. 3). This seemed to support the hypothesis. However, the hypothesis predicts the existence of closely associated insects, too. Therefore, I examined field colonies of this aphid for them, but the

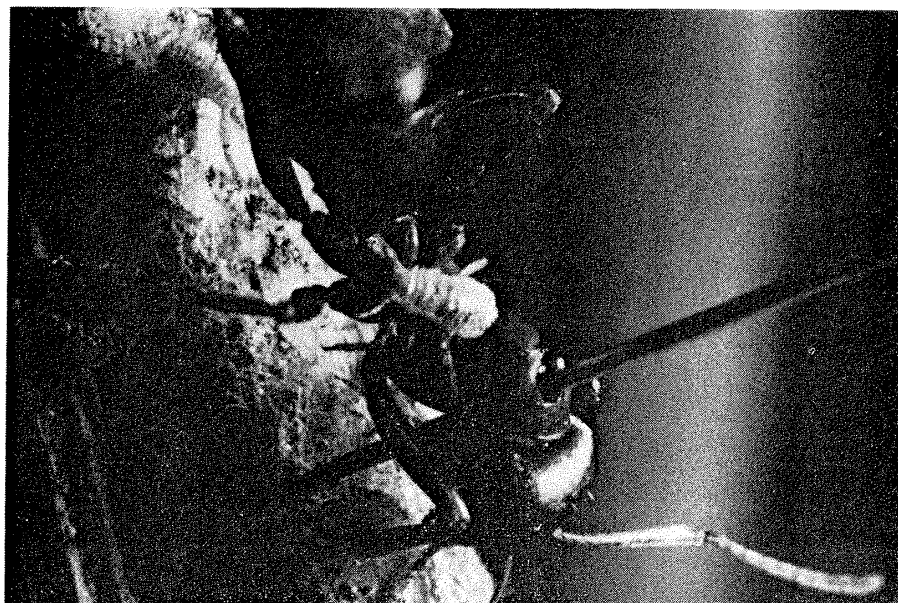


Fig. 3. A secondary-type larva climbing on a pinned ant.

results were negative. I examined 4 large colonies of *Colophina clematis* at Takao-san, Tokyo Distr., on October 1st, 1975, seven colonies at Haruyama, Iwate Pref., on September 16th, 1976, and more than 10 colonies at Takao-san, Tokyo Distr., on September 30th, 1976. Perhaps, some ants may collect fallen droplets of honeydew on the ground. But, there seems to be no ant closely associated with the aphid and collecting the honeydew directly from the latter.

Then, the alternate hypothesis was as follows: Secondary-type 1st instar larvae attack intruders, thus they have a function in defending their own colony from some predators. To see whether the secondary-type larvae react against other animals, I put a young lepidopterous larva (*Phalera flavescens*) on a colony of *Colophina clematis* reared on a potted *Clematis apiifolia*. This experiment was carried out at Fujisawa on September 10th–14th, 1976. When the lepidopterous larva moved, secondary-type larvae approached to the larva and climbed on it, as in the former experiment using an ant. I repeated this experiment five times. In every case except one in which the lepidopterous larva attached to the stem with silken thread, the lepidopterous larva wriggled and soon fell from the stem. The fallen lepidopterous larva was further attacked by secondary-type larvae walking on the ground. In every case, the lepidopterous larva died within a few hours. One lepidopterous larva was attacked by 66 aphid larvae. Some secondary-type larvae attached so tightly to the lepidopterous larva (Fig. 4) that they did not drop from the latter when together deposited in alcohol. It seems that the enlarged fore and mid legs of secondary-type larva serve very well for clinging to larviform animals with soft skin. I observed under a dissecting microscope that some of these secondary-type larvae inserted their stylets in the body of the lepidopterous larva, although

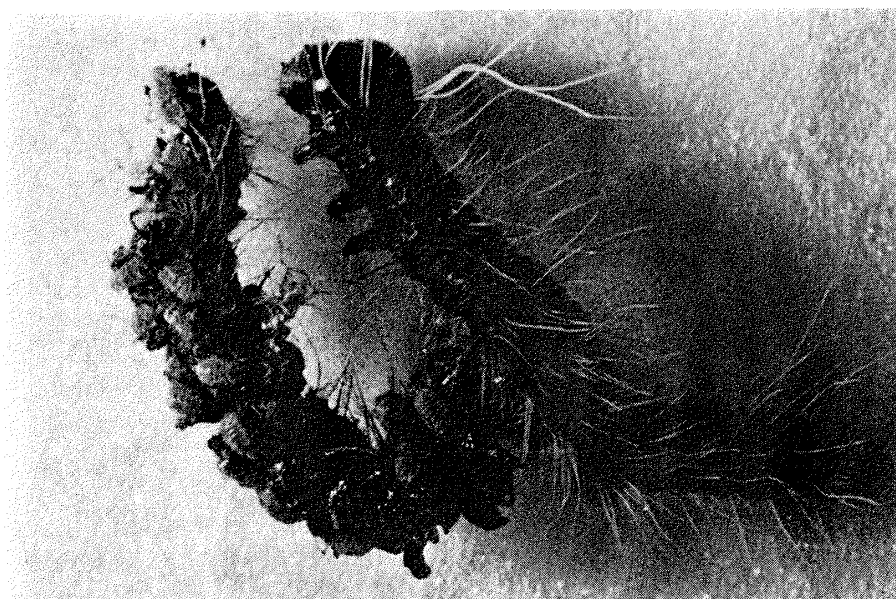


Fig. 4. Secondary-type larvae attaching to a lepidopterous larva (left).

the protracted part of the stylet was at best ca. 0.05 mm. long. The result corroborates the third hypothesis and refutes the second one, because there is no "need" for the rider to insert its stylet into the body of its carrier.

The next problem is whether the observed aggressive behavior is really effective against the possible predator. Syrphid larvae were collected from the leaves of *Cornus controversa* at Sapporo, Hokkaido, on September 25th and 26th, 1976; they were feeding on the sexuparae and perhaps also the sexuales of *Anoecia* sp. They were not identified. Using them, I carried an experiment, in the same way as for the *Phalera flavescens* larva, at Sapporo on September 26th and at Fujisawa on September 27th–29th. The result was about the same as for the *Phalera flavescens* experiment. I repeated this experiment seven times. In some cases, the syrphid larva sucked on 1 or 2 aphids before the attack of secondary-type larvae. When attacked by aphid larvae, the syrphid larvae wriggled and fell from the stem together with the aphid larvae attaching to them. At least in one case, it was clearly observed that the syrphid larva discharged a slimy exudation. The fallen syrphid larvae were further attacked by secondary-type larvae walking on the ground. In every case, the syrphid larva was killed by the aphid larvae. Some of secondary-type larvae inserted their stylets in the syrphid larvae as in the former experiment using the lepidopterous larvae. The conclusion seems to be unavoidable that secondary-type larvae can function very well in defending their colony from such predators as syrphid larvae. And if some polyphagous syrphids actually lay eggs near the colony of this aphid, this aggressive behavior undoubtedly secures an advantage. On one occasion, I found a syrphid egg adhering near a colony of this aphid on a potted *Clematis apiifolia* (at Fujisawa, on October 6th, 1976). Its fate could not be pursued.

Conclusion and Further Problems

From the above experiments and considerations, I now accept the following hypothesis which is the conclusion of the present paper: Secondary-type 1st instar larvae attack intruders, thus they serve for defending their colony from some predators; and they neither grow nor reproduce. So, I reject my previous suggestion (AOKI, 1976: 136) that the secondary-type 1st instar larva grows to the adult.

I admit that at least two important problems remain unsolved. First, the food of the secondary-type larva is still unknown. As discussed above, it is improbable that it absorbs the phloem sap of *Clematis apiifolia* because of its very short rostrum. It may feed on none. However, it should be noted that some individuals lived for 10 days or more. On October 8th, 1976, I put a mark with a pink paint on 120 individuals of the secondary-type larva reared on a potted *Clematis apiifolia* at Fujisawa. At least one individual was alive and still active on October 18th. Second, there exist actual predators. Although this aphid seems comparatively predator-free, I found two predaceous species on its colony. One is the coccinellid *Pseudoscymnus pilicrepus* collected at Takao-san on November 8th, 1975, as a larval stage. The other is an unidentified mature syrphid larva collected at Haruyama on September 16th, 1976. It is unknown whether these predators can stand the aphid attack or they can feed without causing the aggression of secondary-type larva.

There may be other aphid species with such larvae as found in *Colophina clematis*. The "pseudoscorpion-like" larva of *Oregma* may be of this kind. I found larvae of this type also in *Ceratovacuna japonica*.¹⁾ When lightly tapped on the frons by the head of an insect pin, these larvae raise the fore legs and open and close them quickly, quite in the same way as in the secondary-type larvae of *Colophina clematis* (Aoki, unpublished data).

Lastly, if my conclusion is true, the secondary-type larvae are "soldiers". Such altruistic individuals are well known in social Hymenoptera and Isoptera. They have evolved by "kin selection" in broad sense, where the mother producing larvae of both kinds has a selective advantage. HAMILTON (1964) made up a special model of "kin selection". It may be predicted from his theory that true sociality should occur more frequently in groups with haplodiploidy than in those without it (WILSON, 1971: 329; but for critique, see GHISELIN, 1974: 137, 228-233). I do not know how many occurrences of true sociality among animals without haplodiploidy would be sufficient to refute his theory. The existence of soldiers in aphids should take part in one of the gravest problems against his theory, however.

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1) *Oregma* and *Ceratovacuna* are related very closely with each other, and some taxonomists treat them as a single genus.

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References

- AOKI, S., 1976. Occurrence of dimorphism in the first instar larva of *Colophina clematis* (Homoptera, Aphidoidea). *Kontyû, Tokyo*, **44**: 130-137.
- GHISELIN, M. T., 1974. *The Economy of Nature and the Evolution of Sex*. 346 pp. University of California Press, Berkeley.
- HAMILTON, W. D., 1964. The genetical evolution of social behavior, I & II. *J. theoret. Biol.*, **7**: 1-52.
- HILLE RIS LAMBERS, D., 1966. Polymorphism in Aphididae. *Annu. Rev. Ent.*, **11**: 47-78.
- , and A. N. BASU, 1966. Some new or little known genera, subgenera, species and subspecies of Aphididae from India (Homoptera, Aphididae). *Ent. Bericht.*, **26**: 12-20, 27-36.
- REYNE, A., 1954. *Hippeococcus* a new genus of Pseudococcidae from Java with peculiar habits. *Zool. Mededel., Leiden*, **32**: 233-257.
- WILSON, E. O., 1971. *The Insect Societies*. 548 pp. Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts.