

Kontyû, Tokyo, 49 (2): 355-336. June 25, 1981

## Observations on *Pseudoregma alexanderi* (Homoptera, Pemphigidae), an Aphid Species Producing Pseudoscorpion-like Soldiers on Bamboos

Shigeyuki AOKI, Shin-ichi AKIMOTO

Entomological Institute, Faculty of Agriculture, Hokkaido University,  
Sapporo, Hokkaido 060, Japan

and

Seiki YAMANE

Department of Biology, Faculty of Science, Kagoshima University,  
Kagoshima 890, Japan

**Synopsis** The following observations were made on a soldier-producing bamboo aphid, *Pseudoregma alexanderi*: 1) When tapped with the point of a pin, soldiers opened and closed their fore legs more frequently than normal 1st instar larvae. 2) Soldiers clasped, with their enlarged fore legs, insect predators artificially placed on the colony, and pierced the predators with their frontal horns. 3) Fourteen soldiers and 2 normal 1st instar larvae were found attacking an aphid competitor, *Astegopteryx bambucifoliae*, or wearing dead bodies of the latter on their heads. 4) Some soldiers as well as non-soldiers showed leg-shaking behaviour when disturbed. 5) Butting among colony members occurred frequently. 6) Soldiers sometimes attacked conspecifics. 7) *Synonycha grandis*, *Pseudoscymnus amplus*, and other unidentified predators were found feeding on *P. alexanderi*. 8) Alate sexuparae were found in May, but not in November and December. 9) Many normal 1st instar larvae were dispersed on the wind. Some problems regarding the life cycle and the soldiers are discussed.

*Pseudoregma alexanderi* is a hormaphidine aphid species known from Taiwan (TAKAHASHI, 1924, 1929; LIAO, 1976; AOKI & MIYAZAKI, 1978), Nepal (SHERMA, 1968) and north-eastern India (BASU, 1969; GHOSH *et al.*, 1974). This species makes large, dense colonies (Fig. 1B) on bamboos of the genus *Dendrocalamus*, *D. latiflorus* (TAKAHASHI, 1924, 1929; LIAO, 1976) and *D. strictus* (SHERMA, 1968).<sup>1)</sup> Besides normal 1st instar larvae apterous adults of *P. alexanderi* produce bizarre "pseudoscorpion-like" 1st instar larvae which are characterized by a large body size, enlarged fore legs, well-developed frontal horns with acute apices (Fig. 3A), and strongly sclerotized tergites. AOKI and MIYAZAKI (1978) supposed that the pseudoscorpion-like larvae are sterile soldiers, and cited some observations

1) TAKAHASHI (1929) recorded *P. alexanderi* also from "*Miscanthus* near a *Dendrocalamus* heavily infested by this aphid". Whether this *Miscanthus* species is a true host of *P. alexanderi* is uncertain.

supporting the hypothesis. However, the available information on *P. alexanderi* was admittedly scanty. In this paper we present further evidence to support the soldier hypothesis and report other observations on this aphid species.

## Methods

### 1. Colonies observed

Field observations were made by one of us (S. AOKI) at Sun Moon Lake, Nantou Hsien, Taiwan on December 11th–22nd, 1978, and by all of us at Chunyang near Wushe, Nantou Hsien on May 7th–12th, 1980. At Sun Moon Lake aphids in a large colony (Colony SML) of *P. alexanderi* on the ma bamboo *Dendrocalamus latiflorus* were mainly observed. Colony SML contained many pseudoscorpion-like 1st instar larvae or supposed soldiers.<sup>1)</sup> The aphids infested branchlets, slender culms and the underside of leaves. At Chunyang aphids in a huge colony (Colony CY) on *D. latiflorus* were mainly observed. Colony CY also contained many soldiers. The aphids infested branchlets, slender culms, the underside of leaves, and even thick culms (Fig. 1A). Unless otherwise stated, the following observations were made on these two colonies.

### 2. Identification of morphs

A) Specimens mounted on microscope slides. In aphid specimens which have been boiled in 10% KOH solution and mounted on microscope slides, it is easy to discriminate between the soldier, the normal 1st instar larva, the larvae of the 2nd to last instars, and the adult (see Fig. 1 in AOKI & MIYAZAKI, 1978).

B) Specimens in alcohol. In specimens preserved in alcohol it is possible under a dissecting microscope to discriminate the normal 1st instar larva from larvae of the 2nd to last instars by examining the dorsoapical setae on 2nd tarsal segments: the setae of the 1st instar are clearly longer than those of the later instars. The soldier can easily be discriminated from the other morphs by its enlarged fore legs. Intermediates between the soldier and the normal 1st instar larva occur, and they are difficult to classify unless mounted. However, since they are rare, the misidentification concerning them, if any, would not greatly affect the result of our observations.

C) Living aphids. Aphids were directly observed with the naked eye, or sometimes with the help of a hand-lens. As the aphids are comparatively large, it is easy to discriminate the soldiers from the other morphs in the field. In the field we considered the smallest individuals to be normal 1st instar larvae and the largest apterous ones to be apterous adults.

Although the soldiers of *P. alexanderi* have a large variance in size, we did not find a clear bimodal pattern in the frequency of maximum cephalothorax lengths of 132 soldiers collected from Colony CY. In this paper, therefore, we do not discriminate between “major” and “minor” soldiers as did AOKI and MIYAZAKI (1978).

---

1) In the following they are simply called “soldiers”.

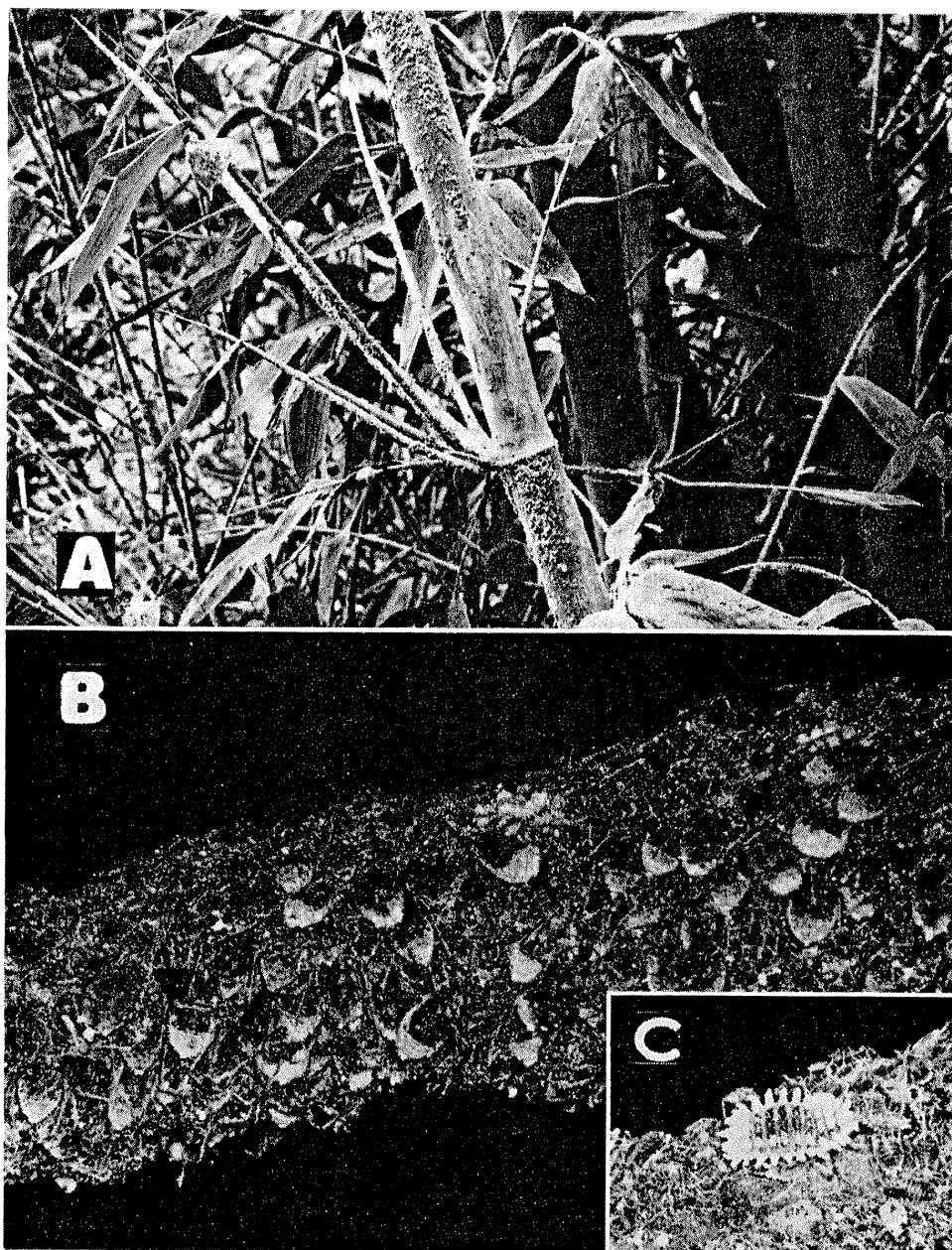


Fig. 1. A, a colony of *Pseudoregma alexanderi* on *Dendrocalamus latiflorus* (Colony CY); B, a bamboo branchlet heavily infested by *P. alexanderi* (Colony SML); C, a mature coccinellid larva in a colony of *Pseudoregma koshunensis*.

### Observations

#### 1. Reaction of soldiers to tapping with a pin

Like the soldier of *Colophina clematis* (AOKI, 1977) or *C. arma* (AOKI, 1980), the soldier of *P. alexanderi* opens and closes its fore legs quickly when lightly tapped on its frons with a pin or similar object. At Sun Moon Lake 140 soldiers and

Table 1. Reaction of soldier and normal 1st instar larva to tapping with a pin.

	Reaction		Total number of tests
	+	-	
Soldier	102	38	140
Normal 1st instar larva	8	62	70

70 normal 1st instar larvae were tapped with the point of a pin, and their reactions were recorded. When the aphid opened and closed its fore legs quickly against the pin within five taps, it scored a positive reaction; otherwise a negative one. The same individual may occasionally have been tested more than once. As shown in Table 1, the soldier reacted to the tapping with a pin significantly more frequently than the normal 1st instar larva ( $\chi^2=70.61$ ,  $P<0.001$ ).

## 2. Attacks on potential predators by soldiers

AOKI and MIYAZAKI (1978) reported an observation that a soldier of *P. alexanderi* clutched at a coccinellid larva (*Synonymcha grandis*) which was artificially placed on the colony. In order to confirm that soldiers of *P. alexanderi* attack potential predators, and to see whether the soldiers pierce animals with their frontal horns, the following experiment was carried out at Sun Moon Lake.

Four syrphid larvae and 3 hemerobiid larvae, which were preying on other aphid

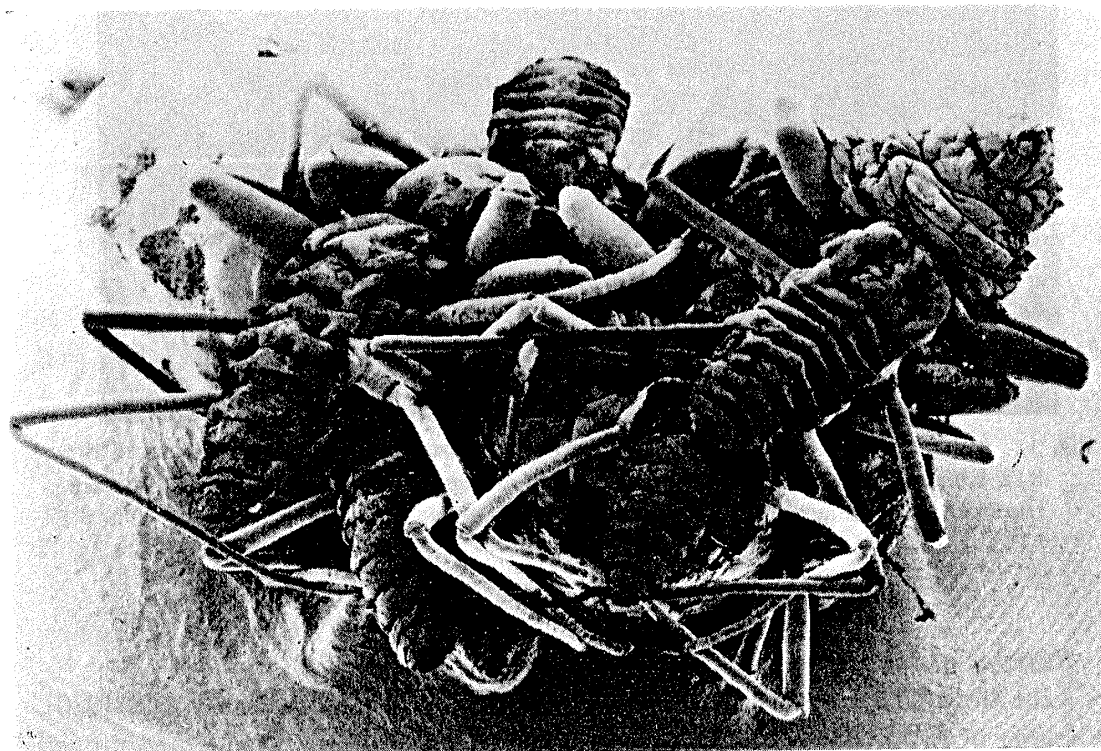


Fig. 2. Soldiers attacking a syrphid larva.

species without soldiers, were collected from leaves of a bamboo species. These predaceous larvae were placed on Colony SML one by one. The result was that every predaceous larva was attacked by a number of soldiers (Fig. 2), and either fell from the colony or was immobilized. The predaceous larvae together with the soldiers attached to them were deposited in alcohol, and later they were examined under a dissecting microscope in the laboratory. Some of the soldiers entirely inserted their frontal horns in the body of the predator being clasped (Fig. 3B). One more replication of the experiment, using a syrphid larva which had been preying on *Astegopteryx bambucifoliae* on *D. latiflorus*, was carried out at Chunyang with the same result.

At Chunyang attack on other insects by soldiers in natural conditions was observed twice: 1) A soldier opened and closed its fore legs quickly against a calliphorid fly which was licking honeydew in the aphid colony. 2) When a cantharid beetle (*Themus* sp.) alighted in the aphid colony, a number of soldiers immediately clutched at the legs and mouthparts of the beetle. Then the beetle fell from the colony together with the soldiers attached to it.

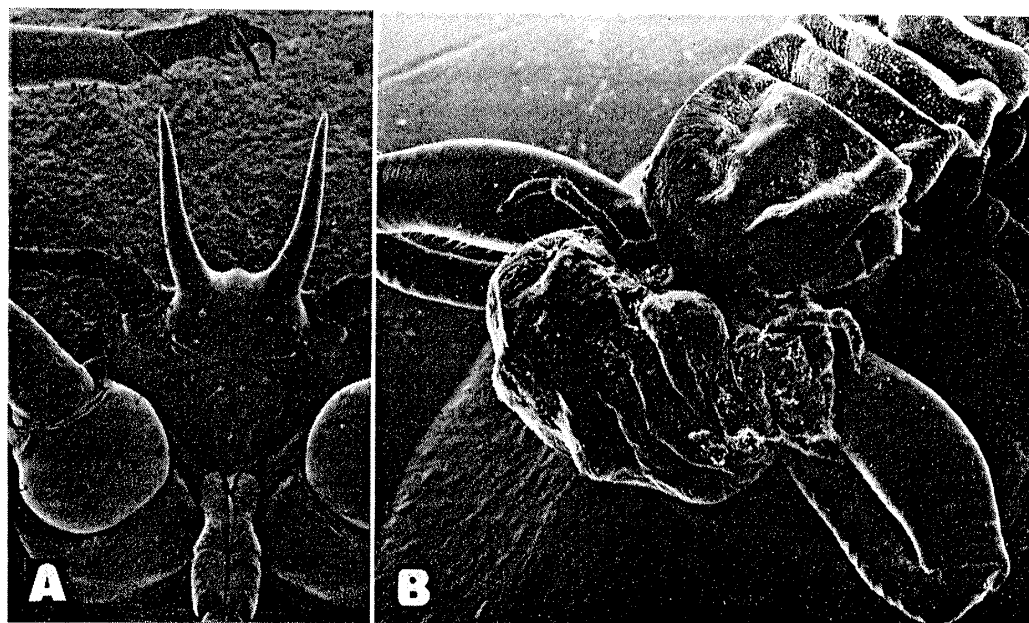


Fig. 3. A, head of soldier (ventral view); B, a soldier clasping a syrphid larva with its enlarged fore legs, and piercing the larva with its frontal horns.

### 3. Attacks by soldiers on a competitor, *Astegopteryx bambucifoliae*

*Astegopteryx bambucifoliae* is a hormaphidine aphid attacking leaves of several bamboo species. This species produces no soldiers on bamboos. According to LIAO (1976) its host plants are *Dendrocalamus latiflorus*, *Bambusa dolichoclada*, *B. edulis*, *B. oldhami*, *B. stenostachya* and *Phyllostachys lithophia*. At Chunyang a few *Dendrocalamus latiflorus* plants with colonies of both *Pseudoregma alexanderi* and *Astegopteryx bambucifoliae* were found. From these colonies a number of

*P. alexanderi* soldiers which were in the act of attacking *A. bambucifoliae*, or which wore dead bodies of *A. bambucifoliae* on their frontal horns, were collected. They were deposited in alcohol, and later examined under a dissecting microscope in the laboratory. Although some of the victims had detached themselves from the *P. alexanderi* soldiers in alcohol, 14 of the soldiers were still clasping and/or piercing *A. bambucifoliae* aphids when examined (Table 2). Two normal 1st instar larvae of *P. alexanderi*, which were identified by mounting on microscope slides, were also found to have attacked *A. bambucifoliae*.

Soldiers of *P. alexanderi* do not always attack *A. bambucifoliae* immediately. A number of *A. bambucifoliae* aphids were observed walking in the colonies of *P. alexanderi*, apparently without causing the attack by the soldiers.

Table 2. *Pseudoregma alexanderi* attacking *Astegopteryx bambucifoliae*, collected from *Dendrocalamus latiflorus* at Chunyang.

<i>Soldier:</i>	
6*	clasping and piercing <i>A. bambucifoliae</i> .
2:	clasping but not piercing <i>A. bambucifoliae</i> .
6:	with the dead body of <i>A. bambucifoliae</i> on its head.
<i>Normal 1st instar larva:</i>	
1:	clasping and piercing <i>A. bambucifoliae</i> .
1:	with the dead body of <i>A. bambucifoliae</i> on its head.

\* Including 2 soldiers attacking a single individual of *A. bambucifoliae*.

#### 4. *Leg-shaking behaviour*

TAKAHASHI (1921, 1923) reported that the apterous adults and larvae of *Pseudoregma bambucicola* lift and shake their hind legs when disturbed. Such a habit was also observed in *Pseudoregma alexanderi* at Sun Moon Lake. When a branchlet of *Dendrocalamus latiflorus*, on which *P. alexanderi* formed a dense colony, was lightly shaken, many of the aphids simultaneously lifted their abdomens and hind legs, and then moved their hind legs up and down, their fore and mid legs remaining *in situ*. Synchronized with the occurrence of this behaviour, many droplets of honeydew fell from the colony. Repeated observations confirmed that the apterous adults, larvae and soldiers of *P. alexanderi* show this leg-shaking behaviour. However, some of the soldiers excitedly walked about on the bamboo branchlet instead of showing this behaviour.

According to TAKAHASHI (1921) similar leg-shaking behaviour commonly occurs in the genera "*Macrosiphum*" (Aphidinae) and "*Pterochlorus*" (Lachninae), and BLACKMAN (1974) mentions the occurrence of such a behaviour in *Aphis fabae* (Aphidinae) and in *Tuberolachnus salignus* (Lachninae), but as far as we know nobody has yet explained the function of this behaviour.

#### 5. *Butting behaviour*

The apterous adult and normal larvae of *Pseudoregma alexanderi* have a pair of frontal horns which are shorter than those of the soldier (see Fig. 28 in LIAO,

1976; Fig. 1 in AOKI & MIYAZAKI, 1978). At Sun Moon Lake apterous adults and larvae were frequently seen to butt their conspecific fellows with their short frontal horns. The attacker usually put its fore legs not on the body of the other aphid but on the plant, and butted the latter quickly and repeatedly. Some soldiers were also observed to show this behaviour. This behaviour differs from "true" attacks by the soldier, in that the attacker does not clasp the other aphid and apparently does not injure it. In 19 such butting interactions recorded, 18 attackers soon stopped their butting and went away. But one apterous adult attacker butted a later instar larva upward in the rear, and forced the latter to raise its abdomen, and further butted it repeatedly until it went away, when the attacker occupied the position which it had occupied. Why the aphids butt conspecifics remains unclear.

Similar intracolony butting was also observed in *Ceratovacuna nekoashi* on *Eulalia viminea* and in *C. lanigera* on *Miscanthus* sp. (AOKI, unpublished observations). Both species have larvae and apterous adults with similar frontal horns (TAKAHASHI, 1958; RUEDA & CALILUNG, 1975), but neither of them produces pseudoscorpion-like soldiers.

#### 6. Attacks on conspecifics by soldiers

At Sun Moon Lake attack on conspecific fellows by soldiers was observed three times under natural conditions: 1) A soldier clasped a young stationary larva suddenly, but almost immediately detached itself. 2) A soldier clasped the abdomen of an apterous adult which was butting another individual. The soldier soon detached itself from the adult. 3) A soldier clasped a young larva which was walking toward the soldier. Then the clasped larva became stationary, and the soldier detached itself from the larva.

In all of the cases the soldier did not pierce the sufferer with the frontal horns. But at Chunyang one soldier was found clasping another soldier and piercing it with the frontal horns.

#### 7. Occurrence of predators on *Pseudoregma alexanderi*

A) *Synonycha grandis* (Coccinellidae). SHERMA (1968) recorded *Synonycha grandis* as a predator of *P. alexanderi* in Nepal. A larva of *S. grandis*, about 13 mm long, was found feeding on *P. alexanderi* near Colony CY.

B) *Pseudoscymnus amplus* (Coccinellidae). A number of adults of *Pseudoscymnus amplus* were found in colonies of *P. alexanderi* at Chunyang. Many adults of *P. amplus* were also collected from colonies of *Pseudoregma bambucicola* (at Sun Moon Lake from November 21st to December 4th, 1977) and *Pseudoregma koshunensis* (at Sun Moon Lake on December 11th–22nd, 1978), both of which produce many pseudoscorpion-like soldiers on bamboos. Some adults of *P. amplus* were observed preying on *P. bambucicola* in the aphid colony. An adult of *P. amplus* was seen laying her eggs in a colony of *P. koshunensis*.

C) A coccinellid larva. A number of larvae of a coccinellid species (Fig. 1C) were found in colonies of *P. alexanderi* at Chunyang and Sun Moon Lake. These coccinellid larvae were feeding on *P. alexanderi* without causing any attack by its

soldiers. In Colony SML, a later instar larva of *P. alexanderi* was seen to butt a larva of this coccinellid as well as a conspecific fellow. Curiously, the coccinellid larvae, when immature and coated with little wax, so much resembled its prey that we had difficulty in detecting them in the aphid colony. Larvae of this coccinellid were also collected from colonies of *Pseudoregma bambucicola* (at Sun Moon Lake from November 21st to December 4th, 1977) and *Pseudoregma koshunensis* (at Sun Moon Lake on December 11th–22nd, 1978). It is possible that these larvae are of *Pseudoscymnus amplus*, but we have not yet confirmed the relation between the larvae and the adults.

D) A moth larva making a silk nest. A number of larvae of a moth species living in silk nests were found in colonies of *P. alexanderi* at Sun Moon Lake. Some of them were seen feeding on the aphid. When one of the moth larvae was ejected from its nest by pecking the nest with a pincette, a soldier attacked the moth larva.

E) A syrphid larva. A syrphid larva was seen feeding on aphids in a colony of *P. alexanderi* at Wushe on May 12th, 1980. No soldiers were attacking the syrphid larva. However, when the syrphid larva was picked up and placed on some soldiers, the soldiers clutched at the syrphid larva and the larva fell from the aphid colony. It is uncertain whether this syrphid species usually feeds on *P. alexanderi* without causing attack by its soldiers.

#### 8. Occurrence of alate aphids

TAKAHASHI (1929) recorded a few alate aphids of *P. alexanderi* in April at

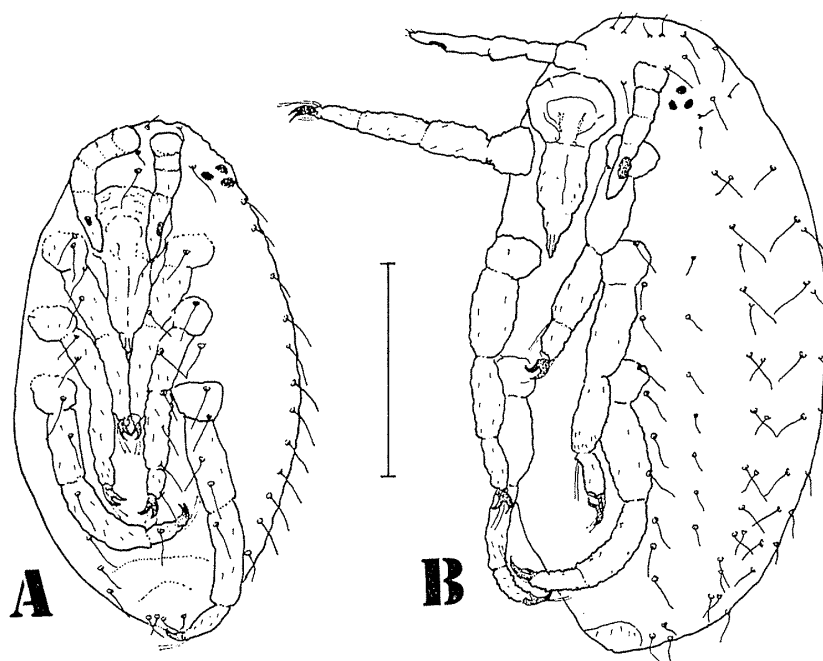


Fig. 4. Embryos taken out from alates (ventral view): presumed male (A) and presumed oviparous female (B). Tergal setae on the opposite side are also shown. Scale: 0.2 mm.



Fenchihu, Alishan, Taiwan. No alate aphids were detected in the colonies of *P. alexanderi* observed at Sun Moon Lake in December 1978. At Chunyang in May 1980 a number of alate aphids and alatoid larvae were collected from colonies of *P. alexanderi*. Thirty of these alates were macerated and mounted on microscope slides, and their embryos were examined. All of the alates were thought to be sex-uparea which emigrate to the primary host and not to be secondary migrants between bamboos, because the embryos (Fig. 4) in their abdomens are dimorphic in size (*i.e.* presumed males and females) and lacked such frontal horns as occurring in the 1st instar larva on *Dendrocalamus latiflorus*. The primary host of *P. alexanderi* is unknown.

#### 9. *Dispersal of 1st instar larvae on the wind*

A great number of normal 1st instar larvae in Colony CY were observed dispersing on the wind. Even a gentle breeze dispersed many aphids. In order to confirm whether the dispersing individuals on the wind were really normal 1st instar larvae, we blew aphids off leaves and twigs of the bamboo into a paper bag. They were preserved in alcohol and later identified under a dissecting microscope in the laboratory. Of 2076 aphids collected, 2044 (98%) were normal 1st instar larvae.

How far the normal 1st instar larvae disperse on the wind is not clear. On May 10th we found 16 normal 1st instar larvae on the tip of a stick at a distance of about 20 m from Colony CY, the nearest colony to the stick.

Dispersal of small apterous individuals on the wind is known in the woolly apple aphid *Eriosoma lanigerum* (HOYT & MADSON, 1960), and well known among coccids and mites (*e.g.* HOELSCHER, 1967).

Many adults, larvae of various instars, and soldiers were walking about on the ground below Colony CY. These individuals may play a role in short-distance dispersal.

#### 10. *Percentage of soldiers*

We cut off a branchlet from the bamboo on which Colony CY was made, and collected all of the aphids on the branchlet except for a number of normal 1st instar larvae which fell when disturbed. The aphids were preserved in alcohol, and later identified under a dissecting microscope. Of 3956 aphids contained in the sample, five were alates and 140 (3.5%) were soldiers.

### Discussion

#### 1. *Life cycle*

Although the available information is scanty, the life cycle of *Pseudoregma alexanderi* in Taiwan is supposed as follows: Apterous viviparous females propagate parthenogenetically through the year on *Dendrocalamus latiflorus*, and produce many pseudoscorpion-like soldiers at least from October to December, and in April and May. The soldiers neither moult nor reproduce. In April and May

alate sexuparae are produced, and they are thought to migrate to the primary host if it is present. These sexuparae are probably the only alate individuals produced on *D. latiflorus*.

We know no record of this species on *D. latiflorus* from June to September in Taiwan. But it is unlikely that all normal larvae become alate sexuparae in May and no aphids remain on *D. latiflorus* through summer, because, if so, it would be hard to explain why the dispersal of normal 1st instar larvae occurred in May.

According to LIU (1970) *Dendrocalamus latiflorus* is a bamboo introduced into Taiwan from southern China to which it is native.<sup>1)</sup> It is, therefore, possible that *P. alexanderi* is also an introduced species and lacks its primary host in Taiwan.

EASTOP and HILLE RIS LAMBERS (1976) listed 11 *Pseudoregma* species from the world, but among them there is no species whose primary host is known. Since some species of closely related genera, e.g., *Ceratovacuna nekoashi* (SHIBATA, 1955) and *Astegopteryx styracophila* (HILLE RIS LAMBERS, 1953), have primary hosts belonging to the genus *Styrax*, *Pseudoregma* species may also be (or have been) associated with *Styrax*, as TAKAHASHI (1958) suggests for *P. bambucicola* and *P. panicola*.

## 2. *Are the pseudoscorpion-like larvae really soldiers?*

From the above observations it is unquestionable that the pseudoscorpion-like soldiers of *P. alexanderi* play a defensive role against insect predators. In addition, at least when the soldiers clasp such a relatively large predator as a syrphid larva and fall from the colony together with the predator, they obviously behave like a self-sacrificing "kamikaze" attacker. There is good evidence to assert that the soldiers never moult and eventually die without producing progeny. No exuviae of the soldiers have hitherto been found. AOKI and MIYAZAKI (1978) examined 123 mounted specimens of the soldier, and found that none of them had the skin of the next instar inside. Among its relatives, *Pseudoregma bambucicola*, *P. panicola* and *Ceratovacuna japonica* also produce pseudoscorpion-like soldiers. Although we examined the mounted specimens of 233 *P. bambucicola*, 13 *P. panicola* and more than 100 *C. japonica* soldiers, none of them had the skin of the next instar inside.

It may be a good test of our assertion to see whether the ovary of the old soldier is developed. As is well known (e.g. KENNEDY & STROYAN, 1959; BLACKMAN, 1974; HEIE, 1980), viviparous aphids usually already have embryos before they are born. Therefore, if the soldiers of *P. alexanderi* are really sterile, their ovaries should be less developed than those of the normal 1st instar larvae.

## 3. *Preadaptation of the frontal horns*

Unlike *Colophina* spp. (AOKI, 1977, 1980), *Astegopteryx styracicola* (AOKI, 1979 a), *Pemphigus dorocola* and *Colopha* sp. (AOKI, 1978), the soldier of *P. alexanderi* has frontal horns with which it pierces predators or competitors, instead of using its stylets. What was the function of the frontal horns when they were not so

1) SUZUKI (1978) is of opinion that *D. latiflorus* is native to Burma.

well developed and were useless for piercing? The non-soldier individuals of *P. alexanderi* have shorter horns, and they use the horns for butting conspecifics. Therefore, although it is not clear why the aphids butt conspecific fellows, we suggest that the frontal horns originally evolved "in order to" butt conspecific fellows effectively, and then the function of the horns changed, in the normal 1st instar larva from which the soldier caste derived, so as to pierce predators or competitors. The occurrence of intracolony butting in *Ceratovacuna nekoashi* and *C. lanigera*, which do not produce pseudoscorpion-like soldiers, may support our hypothesis.

Another possibility is that the horns originally evolved in order to butt allo-specific aphids. However, such a behaviour, if it occurred, has not yet been observed in extant species without soldiers.

#### 4. *Aphid soldiers and kin selection theory*

As DAWKINS (1979) pointed out, kin selection theory predicts that altruistic behaviour can readily evolve in the clonal colony of the aphid species adopting cyclic parthenogenesis (see also HAMILTON, 1964, 1972). Therefore, it may not be surprising that soldiers or the like have been found to occur in several aphid species (e.g., AOKI, 1977, 1978, 1979 a, b). However, in the case of *Pseudoregma alexanderi* there is some circumstantial evidence which suggests that its colony is not always a pure clone. First, although alate aphids which disperse between bamboos are not produced, it was observed that many normal 1st instar larvae disperse on the wind. If these larvae reach other colonies of *P. alexanderi*, or if more than one larva from different clones makes a new colony, then the resultant colonies will not be pure clones. Second, if a colony of *P. alexanderi* were almost always a pure clone, the observed intracolony butting could not be interpreted as a "selfish" behaviour which is detrimental to the whole colony, because such a behaviour could not evolve by interclonal selection.

If the aphid colonies producing soldiers are not pure clones, such "cheaters" as producing fewer or no soldiers can evolve, and the situation would not be so simple as DAWKINS (1979) envisioned for *Colophina clematis* (cf. AOKI, 1980).

**Acknowledgement** We thank Dr. R. BLACKMAN (British Museum) for his useful comment on the manuscript, Dr. M. MIYAZAKI (National Institute of Agricultural Sciences) for his taking photographs (Figs. 2 & 3), Prof. H. SASAJI (Fukui University), Prof. T. NAKANE (Kagoshima University) and Mr. S. TSUKAGUCHI (Osaka Prefectural University) for their kindness in identifying predators, and Mr. and Mrs. S. CHUNG (Puli) and Mr. and Mrs. C. WU (Puli) for their hospitality in Taiwan. This paper comprises part of S. AOKI's thesis submitted to Hokkaido University in partial requirements for the degree of Doctor of Agriculture. One of us (S. AOKI) is grateful to Prof. T. NAKASHIMA (Hokkaido University) for his kind advice.

## References

- AOKI, S., 1977. *Colophina clematis* (Homoptera, Pemphigidae), an aphid species with "soldiers". *Kontyû, Tokyo*, **45**: 276-282.
- 1978. Two pemphigids with first instar larvae attacking predatory intruders (Homoptera, Aphidoidea). *New Entomologist, Ueda*, **27**: 67-72.
- 1979 a. Further observations on *Astegopteryx styracicola* (Homoptera: Pemphigidae), an aphid species with soldiers biting man. *Kontyû, Tokyo*, **47**: 99-104.
- 1979 b. Dimorphic first instar larvae produced by the fundatrix of *Pachypappa marsupialis* (Homoptera: Aphidoidea). *Ibid.*, **47**: 390-398.
- 1980. Life cycles of two *Colophina* aphids (Homoptera, Pemphigidae) producing soldiers. *Ibid.*, **48**: 464-476.
- & M. MIYAZAKI, 1978. Notes on the pseudoscorpion-like larvae of *Pseudoregma alexanderi* (Homoptera, Aphidoidea). *Ibid.*, **46**: 433-438.
- BASU, A. N., 1969. Further records of new and little known aphids (Homoptera) from West Bengal, India. *Orient. Ins.*, **3**: 355-371.
- BLACKMAN, R., 1974. Aphids. 175 pp. Ginn and Co. Ltd., London and Aylesbury.
- DAWKINS, R., 1979. Twelve misunderstandings of kin selection. *Z. Tierpsychol.*, **51**: 184-200.
- EASTOP, V. F., & D. HILLE RIS LAMBERS, 1976. Survey of the World's Aphids. 573 pp. W. Junk, The Hague.
- GHOSH, M. R., P. K. PAL, & D. N. RAYCHAUDHURI, 1974. Studies on the aphids (Homoptera: Aphidoidea) from eastern India, 21. The genus *Astegopteryx* KARSCH and other related genera (Homaphidinae), with descriptions of three new genera and two new species. *Proc. zool. Soc., Calcutta*, **27**: 81-116.
- HAMILTON, W. D., 1964. The genetical evolution of social behavior, I & II. *J. theoret. Biol.*, **7**: 1-52.
- 1972. Altruism and related phenomena, mainly in social insects. *Ann. Rev. Ecol. Syst.*, **3**: 193-232.
- HEIE, O. E., 1980. The Aphidoidea (Hemiptera) of Fennoscandia and Denmark, I. Fauna Entomologica Scandinavica, vol. 9. 239 pp. Scandinavian Science Press Ltd., Klampenborg.
- HILLE RIS LAMBERS, D., 1953. Notes on aphids from *Cocos nucifera*. *Agric. J. Fiji*, **24** (3 & 4): 1-3.
- HOELSCHER, C. E., 1967. Wind dispersal of brown soft scale crawlers, *Coccus hesperidum* (Homoptera: Coccidae), and Texas citrus mites, *Eutetranychus banksi* (Acarina: Tetranychidae) from Texas citrus. *Ann. ent. Soc. Amer.*, **60**: 673-678.
- HOYT, S. C., & H. F. MADSON, 1960. Dispersal behaviour of the first instar nymphs of the woolly apple aphid. *Hilgardia*, **30**: 267-299.
- KENNEDY, J. S., & H. L. G. STROYAN, 1959. Biology of aphids. *Ann. Rev. Ent.*, **4**: 139-160.
- LIAO, H.-T., 1976. Bamboo aphids of Taiwan. *Quart. J. Taiwan Mus.*, **24**: 499-586.
- LIU, Y.-C., 1970. Colored Illustrations of Important Trees in Taiwan. 538 pp.
- RUEDA, L. M., & V. J. CALILUNG, 1975. Biological study of the sugar cane wooly aphid, *Ceratovacuna lanigera* ZEHNTNER (Hemiptera: Aphidoidea: Pemphigidae) of five varieties of sugar cane. *Philipp. Ent.*, **3**: 129-147.
- SHERMA, K. C., 1968. Biological notes on the aphids of Nepal. *Nepal. J. Agric.*, **3**: 105-132.
- SHIBATA, B., 1955. Ecological studies of plant lice (IX), with special reference to the ecological cycle. *Bull. Coll. Agr. Utsunomiya Univ.*, **3**: 1-8. (In Japanese.)
- SUZUKI, S., 1978. Index to Japanese Bambusaceae. 384 pp. Gakken Co. Ltd., Tokyo.
- TAKAHASHI, R., 1921. Aphididae of Formosa, I. *Rept. no. 20, Dept. Agr. Govt. Res. Inst. Formosa*, pp. 1-97.
- 1923. Ditto, II. *Rept. no. 4, Ibid.*, pp. 1-173.
- 1924. Ditto, III. *Rept. no. 10, Ibid.*, pp. 1-121.
- 1929. Notes on some Formosan Aphididae, I. *Trans. nat. Hist. Soc. Formosa*, **19**: 92-103.
- 1958. On the aphids of *Ceratovacuna* in Japan. *Kontyû, Tokyo*, **26**: 187-190.