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A REVISION OF THE GENUS ERIOSOMA AND ITS ALLIED GENERA IN JAPAN (HOMOPTERA: APHIDOIDEA)

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Abstract

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Nine species of *Eriosoma* and its allied genera, all leaf-roll aphids on Ulmaceae and occurring in Japan, are dealt with. Descriptions of gall-generations, exules, sexuparae and galls are given, with brief biological notes for some species. The species-complex hitherto called *Eriosoma japonicum* is classified into 6 species, including 5 ones new to science. A parasitic form of *Eriosoma yangi*, occurring on *Ulmus davidiana* var. *japonica*, is formally described as a new subspecies different from the nominate form on *Ulmus parvifolia* in not only behavior but also morphological characters of their fundatrices. The subdivision of *Eriosoma* is reconsidered in connection with the divergence and distribution of the host plants, and the *ulmi* group is newly proposed. A leaf-roll aphid associated with *Zelkova* is described as a new species belonging to *Hemipodaphis*, which has only been known from the morph occurring on the secondary host in India; on the basis of the new species *Hemipodaphis* is transferred to the Pemphigidae (Eriosomatinae) from the Hormaphididae. An aphid forming clustering galls on *Ulmus parvifolia* is identified with *Aphidounguis mali*, which has nothing to do with *Watabura nishiyae*. The phylogenetic position of leaf-roll groups within the Eriosomatinae is considered in terms of ancestral-descendant relationship. Based on the structure of the galls and the life-cyclic mode, leaf-roll groups are thought to maintain some fundamental characters of the supposed monoecious ancestral Eriosomatinae. As an appendix a new species, *Eriosoma lishanense*, is described from material collected on *Ulmus uyematsui* in Taiwan.

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INTRODUCTION

The taxonomic study of the subfamily Eriosomatinae (sensu Heie, 1980), the members of which are gall-makers on Ulmaceae in principle, still remains in a chaotic state. This is probably due to the fact that our knowledge of this group is largely limited to the species from Europe and North America. In this regard the eriosomatines of eastern Asia, where the genus *Ulmus* is thought to have had its center of diversification (Bate-Smith and Richens, 1973), will deserve much more attention in establishing a comprehensive classification of the subfamily.

This paper purposes to give information new to the current concept of the Eriosomatinae in revising the three poorly known genera *Eriosoma*, *Aphidounguis* and *Hemipodaphis*, which form simple, leaf-roll galls in common. Another purpose is to clarify the positions of these genera in the phylogeny of the Eriosomatinae with emphasis on some characteristics in their life-cyclic mode.

Eriosoma is a compact group morphologically, and has been represented by about 20 species (Heie, 1980). According to Eastop and Hille Ris Lambers (1976) the genus *Eriosoma* consists of three subgenera, *Eriosoma*, *Schizoneura* and *Colophina*. However, *Colophina* should be treated as a genus independent of *Eriosoma*. The subgenera *Eriosoma* and *Schizoneura* have generally been accepted on the basis of the characters of the exule first instar larvae. Hille Ris Lambers (1973) gave some basis for this division from a geographical aspect. According to him, all the Nearctic species belong to the subgenus *Eriosoma* and all the Palearctic ones to *Schizoneura*. Some new species from Japan are, however, obviously inharmonious with the concept of *Schizoneura*. In this paper, I pose a question as to the division between the subgenera *Eriosoma* and *Schizoneura* from a phylogenetic point of view, and propose to establish another phylogenetic group, the *ulmi* group, for some Palearctic species.

Special attention is paid to the fundatrix larvae. In the course of my ecological investigation of *Eriosoma* (Akimoto, 1981), it turned out that the fundatrix larvae play an important role in interspecific interactions at gall formation. Grounds for the identification of fundatrix larvae in my previous paper are given in this paper.

The genera *Aphidounguis* and *Hemipodaphis* have been monobasic. *Aphidounguis* was erected by Takahashi (1963) on the basis of material collected from the roots of the secondary host, apple trees. The type-species, *A. mali*, has been united by authors with *Watabura nishiyae* Matsumura, 1917, which is, however, indeterminable altogether. This problem is discussed and a reasonable taxonomic position is given for *A. mali* in this paper.

One species collected from leaf-roll galls on *Zelkova* in Sapporo is readily referable to the genus *Hemipodaphis*, of which the type-species was originally described as occurring on a lily-like plant, probably the secondary host, in West Bengal, India. Aoki (1978) has already remarked on the present species in his account of its aggressive behavior in the first instar against predators and tentatively regarded it as *Colopha* sp. near *C. caucasica*. In the present paper its taxonomic position is briefly discussed.

The type specimens of the new species described in this paper are deposited in the collection of the Entomological Institute, Hokkaidô University.

Key to East Asian species of Eriosoma and its allied genera

Emigrant

1 Fore wings with media not branched. Abdominal tergites with intersegmental pigmented bands. Cornicles present on abdominal tergite VI, hardly projecting, not surrounded by setae. Antennae short, dark pigmented, secondary rhinaria emerging as luminous lines. Tarsi thicker toward the apex. .... *Aphidounguis mali*

– Fore wings with media once branched. 2

2 Abdominal tergites without intersegmental pigmented bands. Cornicles not projecting, not sclerotized, not surrounded by setae. Antennae short. Genital plate with setae scattered over the posterior part, without anterior long setae. .. .. *Hemipodaphis persimilis*

– Abdominal tergites with intersegmental pigmented bands. Cornicles projecting, sclerotized, surrounded by setae. Antennae long. Genital plate with 2 long setae at the anterior part and shorter setae along the hind margin. 3

3 Antennal segments V and VI without secondary rhinaria, not intensively pigmented. Segments III and IV smooth, dark pigmented. Secondary rhinaria rather broad, arranged almost in parallel. 4

– Antennal segments V and VI with secondary rhinaria. Secondary rhinaria narrow. 7

4 Antennal segments V and VI quite shortened, each much shorter than IV, when combined together 0.11–0.13 times as long as the whole antennal length. Secondary rhinaria rather narrow. Interrhinarial parts conspicuously constricted..... ..... *Eriosoma moriokense*

– Antennal segments V and VI each almost as long as IV. 5

5 Antennae 1.43–1.73 mm long. Processus terminalis on the last segment very long, 0.066–0.076 mm long. ..... *Eriosoma longicornutum*

– Antennae shorter than 1.0 mm. Processus terminalis not so prominent. 6

6 Processus terminalis 0.020–0.025 mm long. The primary host plant: *Ulmus davidiana* var. *japonica*. ..... *Eriosoma auratum*

– Processus terminalis 0.035 mm long. The primary host plant: *U. uyematsui* in Taiwan. ..... *Eriosoma lishanense*

7 Antennae short, 0.53–0.57 mm long. Antennal segment III smooth, shorter than IV, V and VI taken together. ..... *Eriosoma yangi*

– Antennae longer than 0.70 mm long. Antennal segment III spinose. 8

8 Antennal segment V always shorter than IV. Antennal segment III longer than IV, V and VI taken together, with 24–30 secondary rhinaria arranged irregularly. ..... *Eriosoma harunire*

– Antennal segment V longer than (rarely as long as) IV. Antennal segment III shorter than IV, V and VI taken together, with 13–20 secondary rhinaria arranged almost regularly. ..... *Eriosoma japonicum*

Fundatrix adult and gall

1 Body with wax gland plates which lack a clear border and include indistinct, irregular-shaped cells. 2

– Body with wax gland plates which are sharply bordered by a rim and consist of granular cells. Antennae 3-segmented. Genital plate slightly pigmented, with setae at the posterior part, without long setae at the anterior part. Makes a gall of the clustering type, which includes several leaf-rolls on a shoot. Host plant: *Zelkova serrata*..... *Hemipodaphis persimilis*

2 Antennae long, 5- or 6-segmented. 3

– Antennae short, 4-segmented. Genital plate without anterior long setae. Antennal segment IV quite short relative to III. Makes a gall of the clustering type. Host plant: *Ulmus parvifolia*. ..... *Aphidounguis mali*

3 Antennae 6-segmented. Host plant: *Ulmus davidiana* var. *japonica*. 4

– Antennae 5-segmented. 6

4 Antennae 0.50–0.57 mm long. Antennal segment VI short, tapering. Segment III broad, about 0.04 mm wide. Early galls strongly twisted; with time, rolling becomes loose, and the gall turns reddish with waxy powder... *Eriosoma moriokense*

– Antennal segment VI not tapering, appearing rather truncated apically. 5

5 Body 2.44–3.00 mm long. Antennae 0.576–0.633 mm long. Antennal setae long, maximally 0.043–0.051 mm long on segment III. Rolling becoming strongly swollen, partially yellowish green. ..... *Eriosoma longicornutum*

– Body 1.81–2.38 mm long. Antennae 0.44–0.61 mm long. Setae on antennal segment III maximally 0.030–0.040 mm long. Rolling not swollen, yellowish green, losing flexibility in maturity. ..... *Eriosoma auratum*

6 Antennae 0.40–0.47 mm long. Segment III at the apical 1/3–1/2 with a circular membranous spot, which sometimes forms a complete division. Segments IV and V taken together longer than 0.7 times length of III. 7

– Segments IV and V taken together shorter than 0.7 times length of III, and darker than III. 8

7 Hind femur 0.343–0.414 mm (mean 0.387) long, and 0.211–0.262 (mean 0.230) times as long as body, which is 1.505–1.822 mm (mean 1.681) long. Host plant: *Ulmus davidiana* var. *japonica*.....*Eriosoma yangi parasiticum*

– Hind femur 0.313–0.384 mm (mean 0.355) long, and 0.186–0.218 (mean 0.199) times as long as body, which is 1.584–1.980 mm (mean 1.786) long. Host plant: *Ulmus parvifolia*. ..... *E. yangi yangi*

8 Host plant: *Ulmus uyematsui*, endemic to Taiwan. Antennae 0.501–0.541 mm long. Antennal segments IV and V more brownish than III. Segment V rather slender. Segment IV thicker toward the apex. Gall not swollen. .... *Eriosoma lishanense*

– Host plant: *Ulmus davidiana* var. *japonica*. Galls not swollen..... 9

9 Antennae 0.54–0.62 mm long. Antennal segment IV always longer than V. Segment V rather wide, 0.030 mm wide. Antennal setae long, maximally 0.043–0.046 mm long on segment III. Setae on legs long and thick, maximally 0.051–0.056 mm long on hind tibiae. Tarsi rather rectangular in profile, with slightly capitate dorso-apical setae. ..... *Eriosoma japonicum*

– Antennae 0.45–0.51 mm long. Antennal segment IV as long as or a little shorter than V. Segment V rather slender, 0.025 mm wide. Antennal setae short, maximally 0.032–0.035 mm long on segment III. Setae on legs short and thin, maximally 0.035–0.040 mm long on hind tibiae. Tarsi becoming narrower toward the apex, with acute dorso-apical setae. .....*Eriosoma harunire*

Fundatrix first instar larva

1 Ultimate rostral segment shorter than 0.095 mm..... 2

– Ultimate rostral segment longer than 0.100 mm..... 4

2 Antennae 4-segmented, short. Segment III conspicuously long. Segment IV shortened, tapering. Hind femorotrochanter 0.096–0.111 mm long. Host plant: *Ulmus parvifolia*. ..... *Aphidounguis mali*

– Antennae 5-segmented, 0.20 mm long. Segement III a little shorter than V. 3

3 Body 0.628 mm long on the average and hind femorotrochanter 0.121–0.136 mm (mean 0.128) long. Host plant: *Ulmus parvifolia* ..... *Eriosoma yangi yangi*

– Body 0.653 mm long on the average and hind femorotrochanter 0.136–0.156 mm (mean 0.146) long. Host plant: *Ulmus davidiana* var. *japonica*..... ..... *Eriosoma yangi parasiticum*

4 Antennal segment III a little longer than 0.83 times length of IV and V combined. 5

– Antennal segment III a little shorter than 0.71 times length of IV and V combined. Antennae about 0.20 mm long. Segment V much shorter than IV..... 6

5 Antennae 0.258 mm long. Antennal segment IV rather broad, maximally 0.028–0.030 mm wide. Ultimate rostral segment with almost straight blades. Hind

femorotrochanter 0.157–0.177 mm (mean 0.166) long. Abdominal tergites with oval sclerites, which include unpigmented cells..... *Eriosoma japonicum*

– Antennae 0.222 mm long. Antennal segment III slender, IV 0.023–0.025 mm wide. Ultimate rostral segment slender, slightly concave laterally. Hind femorotrochanter 0.137–0.157 mm (mean 0.147) long. Abdominal tergites with oval plates uniformly sclerotized. ..... *Eriosoma harunire*

6 In the second instar head with a broad, oval sclerite covering the dorsal surface and extending to the ventral side. ..... *Eriosoma auratum*

– In the second instar head always covered with some fragmentary irregular-shaped sclerites. ..... *Eriosoma moriokense*

Genus Eriosoma Leach, 1818

Type-species: *Eriosoma mali* Leach, 1818=*Aphis lanigera* Hausmann, 1802.

Fundatrix. Body oval, broad, wholly with wax gland plates each including indistinct small cells and not bordered by a distinct rim. Head and the basal part of legs strongly sclerotized. Legs, antennae and rostrum sclerotized, slender and comparatively long. Body wholly membranous except for genital plate, anal plate and cauda which are all weakly sclerotized and dark pigmented. Body setae short, acute apically, thinly scattered. Cornicles absent. Eyes represented by a triommatidion only. Antennae 6- or 5-segmented (when 5-segmented, often with a rudimentary trace of division), thinly with very short setae, slightly spinose. Antennal segment III longer than or almost as long as the succeeding segments taken together; last 2 segments darker in pigmentation and slightly imbricated. Processus terminalis on the last segment short. Rostrum reaching to middle coxae, or often beyond it, thinly with short setae. Ultimate rostral segment rather convex laterally. Genital plate disc-like, with transverse rows of denticles, and with a little more than 10 setae arranged neatly along the posterior margin and 1 pair of (rarely 3) longer setae at the anterior part. Spiracles without strongly sclerotized protomerites, with a distinct circular opening. Cauda small, semicircular, not sclerotized, with 1 pair of setae. Legs generally smooth, slightly with spinules on femora, thinly with short setae. Trochanter united with femur. Tarsi divided by a membranous intersegmental line. Some species with long and stout dorso-apical setae, which are capitate apically. Empodial setae almost as long as claws.

Emigrant. Antennae long, 6-segmented, rather narrow. Antennal segments III and VI (occasionally also V) with narrow secondary rhinaria. Antennal segment III the longest. Antennal segments V and VI with transverse rows of denticles, often imbricated, with primary rhinaria differing in shape among species. Abdomen with intersegmental, dark pigmented bands, which are divided into some fragments on the lateral side. Body setae rather long, thinly scattered, with an acute tip. Cornicles present on abdominal tergite V, projecting, weakly sclerotized, with a more sclerotized rim, surrounded by a little more than 10 setae. Genital plate disc-like, not uniformly pigmented, with transverse rows of denticles, with 1 row of setae at the hind margin and 1 pair of (rarely 3) longer setae at the anterior part. Second segment of tarsi slightly imbricated, with transverse rows of spinules, and with rather long setae. Apical part of tibiae slightly spinose. Fore wings with media once branched. Hind wings with 2 cubital veins.

Exule adult. Body oval, broad, wholly with long setae. Legs, antennae,

rostrum, clypeus and eyes sclerotized. Eyes represented by a triommatidion only. Legs long. Tarsi divided into two segments or incompletely divided by a membranous line. Femora and tibiae almost smooth. Except for the *ulmi* group and some North American species, setae on tibiae long, much longer than the width of tibiae, and tarsi intensively spinose, cone-shaped. Antennae 6-segmented. Segments III-VI spinose. Antennal setae long, longer than antennal width on segments III and IV. Rostrum reaching to between middle coxae and hind coxae, with short setae. Cornicles projecting, slightly pigmented, surrounded by long setae. Genital plate as in fundatrices and emigrants. Wax gland plates scattered all over the body, basically consisting of a large central cell and smaller circumferential cells, but showing great interspecific variation except for the *ulmi* group.

Eriosoma yangi Takahashi, 1939

Takahashi (1939) first described this species based on specimens collected at Fuchou, southern China, and, in the same paper, remarked that the specimens collected at Sapporo, northern Japan, were exactly identical to the Chinese specimens. Takahashi suggested that the host plant in China is probably *Ulmus*; if this is the case, the elm trees which occur around Fuchou doubtless correspond to *U. parvifolia*, according to Horikawa (1976).

Studies on interspecific interactions among *Eriosoma* species at Sapporo showed that the fundatrix larvae of *E. yangi* on *Ulmus davidiana* behave as an obligatory gall-parasite, always usurping embryo galls of other *Eriosoma* species (Akimoto, 1981). Without settling on a shoot stem for gall formation, they search for galls formed by other species, feeding on leaves and molting there at least to the third instar.

E. yangi also occurs in southwestern Japan on *U. parvifolia* (this knowledge comes from slide specimens collected by Drs. Takahashi and Aoki). Study was attempted to know the behavior of fundatrix larvae on *U. parvifolia* at Mihara, Ôsaka, on April 22nd-23rd, 1981. As a result, a decided behavioral difference was found between the fundatrices occurring on *U. davidiana* and those on *U. parvifolia*: the fundatrices on *U. parvifolia* have ability to form galls in the same manner as in other *Eriosoma* species, that is, they, while settling on a shoot stem, induce rolling on a distal leaf.

This behavioral difference required a careful comparison of their morphological characters. In the emigrants and exules no morphological characters to distinguish the two forms could be found. However, in the fundatrices there have been detected distinct morphological differences, which are supposed to reflect the genetic divergence between them by the reason mentioned below. The two forms may, therefore, be distinguished formally. They are treated here tentatively as different subspecies of the same species, because they appear also different in geographical distribution. Their exact relationship is to be investigated on the basis of further studies in central and southern Japan.

Eriosoma yangi yangi Takahashi

Eriosoma japonica: Sorin, 1977: 7.

Specimens examined. Fundatrix first instar larvae, 32 indvs., Mihara, Ôsaka, Honshû, 22 and 23 IV 1981, ex embryo galls or unfolding buds of *Ulmus parvifolia*.

Fundatrix adults, 4 indvs., Ôsaka, 20 V 1954 (Takahashi); 1 indv., Ôsaka, 23 V 1974 (Aoki), ex a gall; 6 indvs., Kyôto, 26 V 1982 (Yamaguchi), ex galls. First instar larvae borne by emigrants, 9 indvs., the emigrants collected at Mihara, Ôsaka 23 V 1974 (Aoki), ex galls.

Diagnostic characters for the adult and first instar larva of the fundatrix are shown in Table 2. Other characters are quite as in *E. y. parasiticum*.

First instar larva (progeny of emigrant). Description is mainly based on 9 specimens deposited by emigrants collected from galls on *Ulmus parvifolia*. Body length 0.495–0.523 (mean 0.511) mm. Antennae 5-segmented, 0.169–0.197 mm long or 0.32–0.38 times as long as body length. Length of segments (in mm): I 0.028–0.035 (0.031), II 0.025, III 0.043–0.051 (0.047), IV 0.033–0.040 (0.036), V 0.040–0.051 (0.046). Primary rhinaria present on segments IV and V, inflated and fringed with cilia, about 0.015 mm long in axial length on segment IV. Number of antennal setae on each segment as follows; I 2, II 2, III 4–5, IV 4–5, V 7. The longest setae on segment III 0.038–0.046 mm and apical setae on the last segment maximally 0.030–0.035 mm long. Antennal segments IV and V faintly spinose. Rostrum reaching to abdominal tergite IV. Ultimate rostal segment 0.086–0.088 mm long, with 8–9 accessory setae. Distal half of ultimate rostral segment faintly spinose and the remaining not. Wax gland plates present on head, thorax and abdomen. Abdominal tergites I-VII each with 1 pair of spinal and 1 pair of lateral wax plates, and tergites I-IV each with 1 pair of pleural plates. Lateral plates consisting of 1 large central cell and small circumferential cells arranged in a single or partially double row. Spinal plates on tergites I-V consisting of 2 or 3 same-sized cells, and those on tergites VI and VII composed of a mass of cells. Pleural plates consisting of 1 or 2 cells. Body setae long. Abdominal tergites I-V each with 3 pairs of setae arranged in spinal, pleural and lateral rows. The longest lateral setae on tergites III-V 0.040–0.046 mm long. Abdominal tergites VI and VII each with 2 pairs of setae located in spinal and lateral positions. Abdominal tergite VIII with 1 pair of long setae, of which the longer one is 0.051–0.066 mm long. Cornicle absent. Hind femorotrochanter 0.129–0.137 mm long. First and second tarsal segments united. Tarsi cone-shaped, strongly spinose. Tibiae slightly spinose. Setae on the first segment of hind tarsi 0.030–0.038 mm long. Length of hind tarsi 0.053–0.056 mm, and length of hind claws 0.023–0.025 mm. Empodial setae in hind tarsi fine and pointed at the apex, about 0.025 mm long, nearly as long as claws.

Embryo gall. Yellowish green. As usual in *Eriosoma* the leaf edge of one side is rolled toward the underside. A fundatrix generally forms one leaf-roll in a shoot.

Biological note. In my observations larvae of the first instar had emerged on the bursting buds of *U. parvifolia* by April 10th (in 1982) at Kagoshima, Kyûshû, and by April 22nd (in 1981) at Ôsaka, Honshû. All the larvae observed settled on the shoot stems of bursting buds, and none were found walking about or feeding on new leaves. The relationship between the position of a galled leaf and the settling site (Table 1) shows that most frequently the fundatrices settled on the shoot stem between the petiolar bases of the apical third and fourth leaves and induced rolling on the apical second, the same result as in the case of *E. harunire* reported in my previous paper (Akimoto, 1981).

Observation made at Kagoshima on April 10th 1982, however, showed that the *E. y. yangi* fundatrices have a habit of facultative gall intrusion like other

Table 1. Relationship between the settling site of the *E.y. yangi* fundatrix and the position of the produced gall on the elm shoot. Leaves are numbered from the top of a shoot.

Settling site	Gall position	Frequency (% in parentheses)
Petiole of leaf 2	On leaf 2	1(2.3)
Shoot stem between leaves 1 ane 2	〃 1	2(4.5)
Shoot stem between leaves 2 and 3	〃 1	5(11.4)
Shoot stem between leaves 3 and 4	〃 2	24(54.5)
Shoot stem between leaves 4 and 5	〃 3	8(18.2)
Shoot stem between leaves 5 and 6	〃 4	4(9.1)

Eriosoma species. Although this locality is outside the natural distribution of *U. parvifolia,* there are on the campus of Kagoshima University some planted trees of *U. parvifolia,* on which embryo galls of both *Aphidounguis mali* and *E. yangi* were abundant. An early gall was found to contain two fundatrix larvae (both of the second instar) of *A. mali* and *E. yangi.* Judging from the structure of the gall, the intruder was probably the *E. y. yangi* fundatrix. Yet, there was no indication of physical conflict between the two.

Distribution. Honshû (southwestern region) and Kyûshû; Korea, southern region; China, Fuchien-sheng (Fuchou).

Eriosoma yangi parasiticum, subsp. nov.

Eriosoma yangi: Akimoto, 1981.

This subspecies is distinguishable from the nominate one by slight, though distinct, quantitative differences between their fundatrices. In the first instar larvae of the fundatrices *E. y. parasiticum* is characterized by the femur always longer than (or rarely as long as) that of *E. y. yangi* and by the body length, on the average, significantly larger than that of *E. y. yangi* (Table 2). In the adult fundatrices *E. y. parasiticum* is still characterized by having a comparatively long femur, yet it is on the average smaller than *E. y. yangi* in body length. The difference in body size may be interpreted merely to be ecophenotypic. The *E. y. parasiticum* fundatrices spend some time of their life in searching for host galls, while the *E. y. yangi* fundatrices are wholly sluggish within their own galls, devoting themselves exclusively to feeding.

However, the larger hind femur length/body length value in *E. y. parasiticum* holds through the first instar to the adult, and this strongly suggests that the comparatively long femur is genetically dominated and adaptive in some way. In fact the *E. y. parasiticum* fundatrices are highly active in searching for host galls and in killing gall proprietors after having intruded into the galls. In addition, it is noteworthy that the *E. y. parasiticum* adult fundatrices have a smaller body width/body length value, that is, they are comparatively slender. This may also be associated with their high activity.

Table 2. Differences in size between *E. y. yangi* (Y) and *E. y. parasiticum* (P). Size in mm.

Fundatrix 1st instar larva

Character	Subspecies	Mean	*t*-test	Range	N	SD
Body length	Y	0.628	$t=3.69$	0.586-0.657	32	0.0210
	P	0.653	($P<0.01$)	0.596-0.707	34	0.0324
*Femur length	Y	0.128	($P<0.01$)**	0.121-0.136	32	0.0046
	P	0.146		0.136-0.157	34	0.0054
Femur length / Body length	Y	0.204	$t=8.51$	0.193-0.224	32	0.0070
	P	0.225	($P<0.01$)	0.200-0.242	34	0.0122

Fundatrix adult

Character	Subspecies	Mean	*t*-test	Range	N	SD
Body length	Y	1.786	$t=2.79$	1.584-1.980	11	0.1245
	P	1.681	($P<0.01$)	1.505-1.822	26	0.0952
Body width	Y	1.177	$t=4.12$	0.950-1.386	11	0.1302
	P	1.028	($P<0.01$)	0.871-1.188	26	0.0857
Femur length	Y	0.355	$t=5.00$	0.313-0.384	11	0.0201
	P	0.387	($P<0.01$)	0.343-0.414	26	0.0168
Femur length / Body length	Y	0.199	$t=7.38$	0.186-0.218	11	0.0100
	P	0.230	($P<0.01$)	0.211-0.262	26	0.0123
Body width / Body length	Y	0.658	$t=3.05$	0.600-0.729	11	0.0435
	P	0.612	($P<0.01$)	0.550-0.714	26	0.0413

* Femur length is measured in hind legs.
** In this case significance is self-evident.

There seems also to be no basis for the view that the larger body (in terms of the body length) in the first instar larvae of *E. y. parasiticum* is ecophenotypic. In the Pemphigidae the body size of fundatrix first instar larvae is completely determined by resource allocation in sexuparae (grandmothers), since sexuales (mothers) have only one egg and never feed. In *Tetraneura akinire* total amount of nutrition absorbed by a grandmother has a considerable influence on the clutch size but not on the size of the embryo itself (Yamaguchi, unpublished). It is very probable that the larger body size of the first instar larva has some significance in connection with the parasitic mode of life of *E. y. parasiticum*.

Another distinction between the two supposed subspecies lies in the state of dorso-apical setae on the tarsi of the second to fourth instar fundatrigenia larvae: in *E. y. yangi* these setae are always capitate apically, while in *E. y. parasiticum* quite acute. It seems that these setae generally function as sensory organs in walking. In the fundatrix first instar larvae of all *Eriosoma* species and the exule first instar larvae of the subgenus *Eriosoma* they are well developed and capitate and seem to perform an important function in dispersion and gall formation. However, it is unknown whether the capitate setae of *E. y. yangi* have any adaptive significance within the galls. At least, the fundatrigenia larvae of other *Eriosoma* species do not show a capitate tip in the dorso-apical setae of the tarsi.

Specimens examined. Emigrants, 10 indvs., Sapporo, Hokkaidô, 27 VI-8

VII 1978, ex galls; 1 indv. (holotype), Sapporo, 19 VI 1982, ex a gall. Fundatrix adults, 5 indvs., Sapporo, 24 VI 1978, ex galls. Fundatrix first instar larvae, 6 indvs., Sapporo, 25 V 1979, ex embryo galls. Sexuparae, 4 indvs., Sapporo, 23

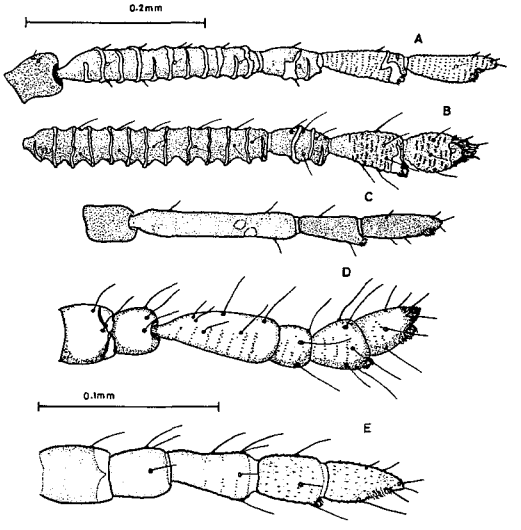

Fig. 1. *Eriosoma yangi parasiticum.* Antennae. A, emigrant; B, sexupara; C, fundatrix adult; D, exule adult; E, fundatrix first instar larva.

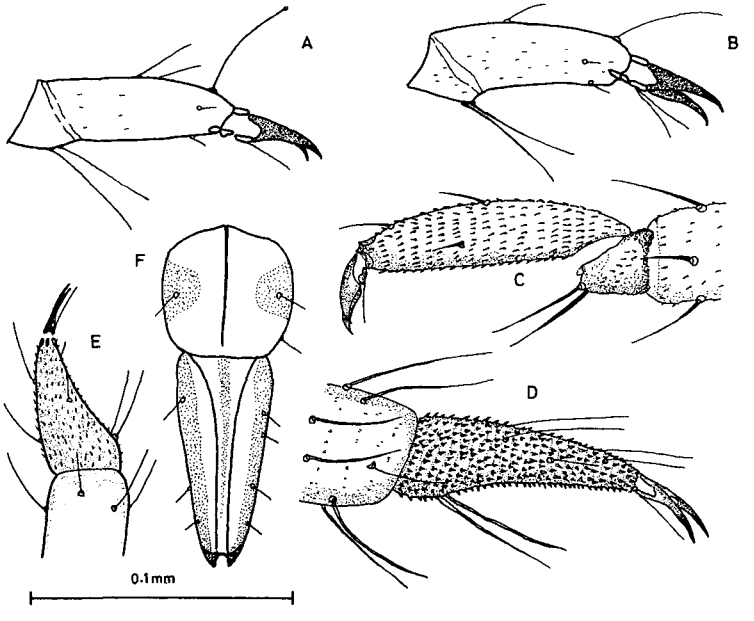

Fig. 2. *Eriosoma yangi yangi.* A, hind tarsus of the fundatrigenia 2nd instar larva. *E. y. parasiticum.* B-E, hind tarsus: B, fundatrigenia 2nd instar larva; C, sexupara; D, exule adult; E, first instar larva deposited by the emigrant. F, ultimate rostral segment of the fundatrix 1st instar larva.

IX 1978; 1 indv., Sapporo, 18 IX 1980, ex the trunk of elm tree. Exule adult, 1 indv., Jôzankei, Hokkaidô, 3 X 1973 (Aoki), ex the root of *Salix* sp.

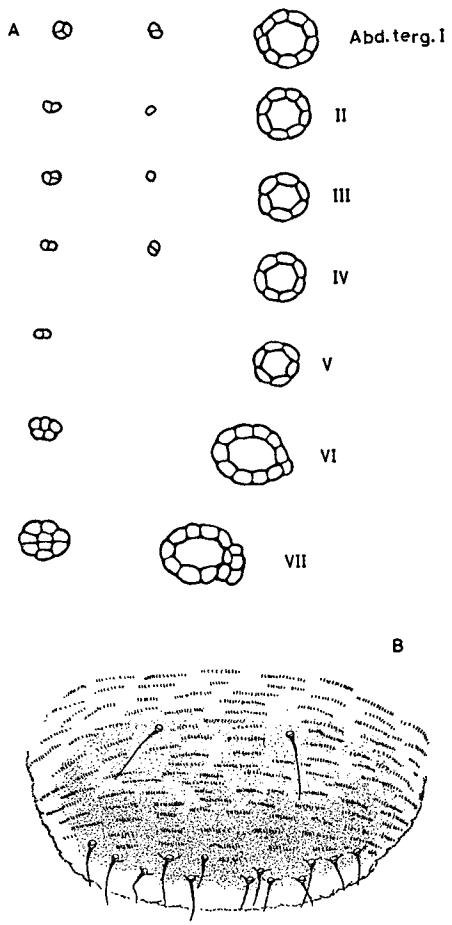

Fig. 3. *Eriosoma yangi parasiticum*. A, wax gland plates of the sexupara; B, genital plate of the emigrant.

Emigrant adult. Description is based on 10 specimens collected from galls on *Ulmus davidiana* var. *japonica*. Body 1.44–1.63 (mean 1.55) mm long. Head and thorax dark brown. Antennae and legs brown. No wax plate present. Antennae very short, 6-segmented, 0.53–0.57 mm long and 0.33–0.37 times as long as body. Antennal segment IV very short, always shorter than V; III shorter than IV, V and VI taken together. Processus terminalis on the last segment very short, about 0.020 mm long. Length of segments (in mm): I about 0.055, II 0.046–0.051 (0.047), III 0.190–0.230 (0.206), IV 0.058–0.071 (0.063), V 0.068–0.086 (0.080), VI 0.086–0.101 (0.094). Secondary rhinaria found on III and VI, rather slender, appearing as bright lines on the dark pigmented segments, irregular in shape and often connected with the adjoining rhinaria especially on IV, encircling about 1/2 the segment on ventral side. Antennal segment III with 10–13 and IV with 2 secondary rhinaria. Primary rhinaria present on V and VI, with a ciliate foramen, which is indistinct on V, and with a short irregular-shaped arm extending laterally; one on VI with a few accessory rhinaria fringed with cilia. Antennal segment VI with 5 thick and long setae at processus terminalis and 2 fine setae at the base; V with 3–4, IV with 2–4, and III with 8–10 fine setae. Antennal segments V and VI spinose, weakly imbricated. Ultimate rostral segment short, about 0.106–0.116 mm long, with many short setae. Abdominal tergites each with a very narrow and pigmented intersegmental band, which is often fragmented. Sclerotized cornicles present on tergite V, weakly projecting, surrounded by about 10 setae. Cauda short, 0.02–0.03 mm in axial length, with 2 setae. Genital plate entirely sclerotized, with 2 setae at the middle and 11–15 setae neatly arranged along the hind margin. A pair of sclerotized plates present laterally to genital plate, with a few spine-like setae. Hind femorotrochanter 0.38–0.41 mm long or 0.72–0.79 times as long as hind tibia. Setae on hind femora short, 0.025–0.030 mm long. Tarsi spinose;

first tarsal segment with 2 long setae, which are 0.028–0.033 mm long on the hind legs, and with 1 spine-like seta except on hind legs. Second segment of hind tarsi about 0.109–0.121 mm long. Fore wings with media once branched or rarely simple. Hind wings with Cu 1a and Cu 1b, but the latter often faint.

Fundatrix adult. Description is mainly based on 5 specimens collected from galls on *Ulmus davidiana* var. *japonica*. Body rounded, but slender in comparison with other species. Body 1.505–1.822 mm (1.681 [$\bar{x}$]±0.0373 [2SE], N=26) long and 1.58–1.65 times as long as broad. Body width 1.028 mm on the averege. Body width/body length 0.550–0.714 (mean 0.612). Body greenish grey in life. Antennae usually 5-segmented, 0.44–0.47 (0.45) mm long and about 0.27 times as long as body; segment III on the apical 1/3 with 1 or 2 circular membranous spots, which rarely form a complete division on the segment. Length of segments (in mm): I 0.056–0.061 (0.059), II 0.051–0.056 (0.052), III 0.172–0.222 (0.198), IV 0.073–0.081 (0.076), V 0.076–0.086 (0.080). Antennal setae comparatively short and fine; segment II with 2–3, III with 7–9, IV with 3–5, and V with 7–8 setae; the longest setae on segment III 0.025–0.035 mm long and 1.00–1.30 times as long as the diameter of the segment. Primary rhinaria present on IV and V. Antennal segments III-V weakly spinose, not imbricated. Ultimate rostral segment short, 0.101–0.111 mm long. Head weakly sclerotized with a pair of intensively sclerotized bars along the median line. Head with comparatively short setae, which are maximally 0.035 mm long. Thorax and abdomen membranous with ill-defined wax plates, which include many circular cells. Cornicles absent. Cauda and genital plate quite as in the emigrants. Legs more intensively sclerotized than in fundatrices of other *Eriosoma* species. Hind femorotrochanter 0.343–0.414 mm (0.387 [$\bar{x}$]±0.0066 [2SE], N=26) long and about 0.38 times as long as broad. Hind tibiae with thick setae, which are maximally 0.040–0.051 mm long and 1.29–1.43 times as long as the diameter of the hind tibiae. Second segment of hind tarsi about 0.081–0.091 mm long. Dorso-apical setae thick, capitate at the apex, maximally 0.040–0.051 mm long in hind legs. Empodial setae slightly longer than claws.

Fundatrix first instar larva. Description is mainly based on 6 specimens collected on unfolding buds of *Ulmus davidiana* var. *japonica*. Body length 0.596–0.707 mm (0.653 [$\bar{x}$]±0.0111 [2SE], N=34). Maximal width of body 0.263–0.318 mm, and 0.435 times as long as body length on the average. Body without visible wax gland plates. Head dorsally with a sclerite divided by a membranous median line and reaching to the ventral side. Antennae 5-segmented. Antennal segments IV and V with spinules and apical half of segment III with a few spinules. Length of segments as follows: I 0.030–0.035 (0.033), II 0.028–0.033 (0.030), III 0.051–0.056 (0.052), IV 0.035–0.040 (0.037), V 0.046–0.051 (0.048). Antennal segment I with 1–2, II with 2–3, III with 5, IV with 3–4, and V with 6–7 setae. The longest setae on segment III 0.023–0.025 mm long. Primary rhinaria present on segments IV and V, distinctly ciliate on V. Ultimate rostral segment short, convex laterally, 0.081–0.086 (0.082) mm long, with 9–11 accessory setae. Thoracic tergites each with circular or irregular-shaped setose sclerites. Pronotum with 1 pair of rather large marginal sclerites and 1 pair of small and irregular-shaped spinal sclerites. Meso- and metanotum with 1 pair of spinal sclerites, 1 pair of pleural ones and 1 pair of larger marginal ones. Spinal and pleural sclerites on meso- and metanotum with only 1 seta. Marginal sclerites on each notum with a few setae. Abdominal tergites I-V each with 1 pair of spinal, 1 pair of pleural and 1 pair of marginal oval sclerites. Tergites VI and VII each only with spinal and

marginal sclerites, which are often united to form a bar. Tergite VIII only with spinal sclerites. Each sclerite on abdominal tergites with 1 seta. The longest setae on sclerites of tergite VIII about 0.030 mm long. Hind femorotrochanter 0.136–0.157 mm (0.146 [$\bar{x}$]±0.00186 [2SE], N=34) long. Tibiae and tarsi not spinose. Setae on hind tibiae maximally 0.030 mm long. Tarsi indistinctly separated into 2 parts. Dorso-apical setae long and capitate at the apex, maximally 0.043–0.046 mm long on hind legs.

Second to fourth instar larvae. Sclerites on thoracic and abdominal tergites, though less sclerotized, are still found in the second instar larvae. Later, the body becomes membranous and inflates as the stage proceeds. In the *E. y. parasiticum* fundatrices, however, the abdomen is swollen to a less degree than in other *Eriosoma* fundatrices. Abdominal stigmata rather swollen, without a stigmal plate, with a rather large pore. Relative length of femora to body length is larger than in other *Eriosoma* species. Dorso-apical setae are long and capitate at the apex in all stages.

Sexupara. Description is based on 4 specimens collected on the trunk of *Ulmus davidiana* var. *japonica.* Body length 1.56–1.88 (mean 1.71) mm. Head, thorax, antennae and legs dark brown. Antennae short, 6-segmented, 0.579–0.645 mm long and 0.34–0.38 times as long as body. Antennal segment VI shortened and wide when compared with those of emigrants, appearing truncated apically. Processus terminalis on the last segment not prominent. Length of segments (in mm): I 0.056–0.066 (0.059), II 0.051–0.056 (0.052), III 0.243–0.303 (0.278), IV 0.71–0.076 (0.074), V 0.071–0.076 (0.074), VI 0.071–0.081 (0.078). Secondary rhinaria found on segments III and IV, narrower than those of emigrant, encircling a little more than 1/2 the segment. Antennal segment III with 13–16 secondary rhinaria, IV with 3. Primary rhinaria present on segments V and VI; on V shaped like a bar and partly inflated and fringed with cilia; on VI fringed with many cilia, with a few accessory rhinaria also fringed with cilia. Antennal setae on each segment as follows; I 3–5, II 3–5, III 12–13, IV 4–5, V 5, VI 5–6. The longest setae on segment III 0.025–0.040 mm long, and apical setae on the last segment maximally 0.015 mm long. Antennal segments V and VI spinose, weakly imbricated. Ultimate rostral segment 0.121–0.126 mm long, with about 11 accessory setae. Abdomen with narrow and sclerotized intersegmental bands. Abdominal setae short, maximally 0.035–0.046 mm long on tergite V. Cornicles present on tergite V, weakly sclerotized, surrounded by 10–12 setae. Wax plates present on head and abdominal tergites I–VII. Head with 1 pair of wax plates each consisting of 1 large central cell and, surrounding this, 5–8 smaller cells, which are absent in some specimens. Abdominal tergites I-IV each with 1 pair of spinal, 1 pair of pleural and 1 pair of lateral wax plates. Sometimes 1 wax plate of the pleural pair missing. Abdominal tergites V-VII each with 1 pair of spinal and 1 pair of lateral ones. Lateral wax plates each consisting of 1 large central cell and smaller surrounding cells. The row of circumferential cells always partially double on tergites VI and VII. Number of circumferential cells of lateral plates as follows: tergite I 8–11, II 5–11, III 5–6, IV 7–9, V 6–9, VI 10–14. Spinal wax plates consisting of a mass of same-sized cells; the number of cells in spinal plates as follows: tergite I 2–4, II-V 1–3, VI 4–8, VII 8–15. Number of cells of pleural wax plates 1 or 2 on tergites I-IV. Genital plate as in the emigrants. Hind femorotrochanter 0.420–0.516 mm long. Tarsi intensively spinose; first tarsal segment with 2 long setae, which are 0.038–0.051 mm long on hind legs; and with 1 spine-like

seta except on hind legs. Second segment of hind tarsi 0.096–0.111 mm long. Fore wings with media once branched.

Exule adult. Description is based on 1 specimen collected from the root of *Salix* sp. No characters have been found to differ from *E. y. yangi.* Body length 1.44 mm long. Body 0.60 times as wide as long, maximal width 0.87 mm. Head, antennae, legs and rostrum sclerotized and brownish. Antennae 6-segmented, 0.394 mm long and 0.27 times as long as body. Antennal segments all thick; segment III 0.35 times as wide as long at maximum. Segment IV shorter than V. Length of segments (in mm): I 0.053, II 0.046, III 0.129, IV 0.040, V 0.066, VI 0.061. Processus terminalis on the last segment not prominent. Antennal segments III-VI faintly spinose. Primary rhinaria present on segments V and VI, fringed with cilia. Antennal setae very long; number of setae on each segment as follows: I 3, II 4, III 11, IV 4, V 5, VI 8. The longest setae on segment V 0.066 mm; apical setae on the last segment maximally 0.025 mm long. Eyes represented only by a triommatidion. Rostrum reaching to middle coxae. Ultimate rostral segment 0.121 mm long, with several accessory setae, slightly spinose. Wax gland plates present on head, thorax and abdomen. Head with 4 pairs of wax plates: 1 pair at ventral side, 1 pair at frontal side, and 2 pairs at the central part and the hind margin of the dorsum. Wax plates at ventral side consisting of 1 large central cell and 6 smaller surrounding cells; those on dorsal side each consisting of 2 or 3 small cells. Pro-, meso- and metanotum and abdominal tergites I–VII each with 1 pair of spinal, 1 pair of lateral, and, except on V–VII, 1 pair of pleural plates (the spinal and pleural plates assumed to be present on the pronotum are invisible because of the fore legs superimposed on them in the specimen). Composition of thoracic and abdominal wax plates as in the sexupara. Body setae long; dorso-lateral setae on tergite V 0.071 mm long. Cornicles and genital plate as in the emigrants. Hind femorotrochanter 0.334 mm long. Legs with long setae; setae on tibiae maximally 0.061 mm long and 1.50 times as long as the diameter of hind tibiae. Tarsi intensively spinose, tapering; second tarsal segment of hind legs 0.081 mm long. Setae on the first tarsal segment of hind legs 0.056 mm long. Empodial setae a little longer than claws, 0.030 mm long on hind legs.

Distribution. Hokkaidô (Sapporo).

Eriosoma japonicum Matsumura, 1917

I could find no species which strictly agrees with Matsumura's (1917) original description, even after having sampled numerous galls. His description appears to consist of a mixture of characters of more than one species here recognized. Moreover, no type specimens are left. This situation, I guess, resulted from his belief that individuals collected from the galls on the same tree all belong to one and the same species. However, my ecological study showed that it is quite common for galls of more than one species to be formed on a single elm tree.

Matsumura described the antennae of the emigrant as follows: "The 3rd distinctly longer than the following joints taken together, rings of the 3rd joint about 17, the 4th 4, those of the 5th and 6th being not distinct, the 5th distinctly longer than the 4th". Only one species exactly agrees with the description in the relative lengths of segments IV and V and the number of secondary rhinaria, but disagrees in the antennal segment III slightly shorter than the succeeding segments

combined. Other described characters are found in more than one species. Therefore, I adopt the relative lengths of the antennal segments IV and V and the number of secondary rhinaria in newly defining *E. japonicum*, and apply the name to the species which agrees with original description in these characters.

E. japonicum thus redefined does not agree with Matsumura's description in the characters of the alatoid nymph. Obviously he confused different species in this stage, too.

Specimens examined. Emigrants, 3 indvs., Sapporo, Hokkaidô, ex galls on *Ulmus davidiana* var. *japonica*, 19 VI 1978; 7 indvs. (one the neotype), ditto, 22 VI 1979. Fundatrix adults, 1 indv., Sapporo, ex gall, 3 VI 1980; 2 indvs., ditto, 10 VI 1980. Fundatrix first instar larvae, 1 indv., Sapporo, ex bud of *U. davidiana* var. *japonica*, 10 V 1981; 4 indvs., ditto, 11 V 1981. Apterous exules, 4 indvs., Sapporo, ex roots of *Agrimonia pilosa*, 12 IX 1972 (Aoki); 1 indv., ditto, 14 IX 1972 (Aoki). Sexuparae, 2 indvs., Sapporo, ex the trunk of *U. davidiana* var. *japonica*, 19 IX 1980.

Emigrant adult. Description is based on 9 specimens collected from galls on *Ulmus davidiana* var. *japonica*. Body 1.38–1.75 (1.53) mm long. Head and thorax dark brown. Antennae and legs brown. No wax plate present. Antennae 6-segmented, 0.73–0.83 mm long and 0.50–0.55 times as long as body. Antennal segment III a little shorter than segments IV, V and VI taken together. Segment V usually longer than IV (rarely as long as IV). Processus terminalis on the last segment short, 0.025 mm long. Segment VI wide and a little warped at the apical 1/3. Length of segments (in mm): I 0.051–0.066 (0.058), II 0.046–0.058 (0.050), III 0.276–0.334 (0.312), IV 0.088–0.121 (0.104), V 0.101–0.131 (0.118), VI 0.106–0.126 (0.113). Secondary rhinaria present on III-V, rather slender, encircling a little less than 1/2 the segment, often connected with neighboring rhinaria, not much

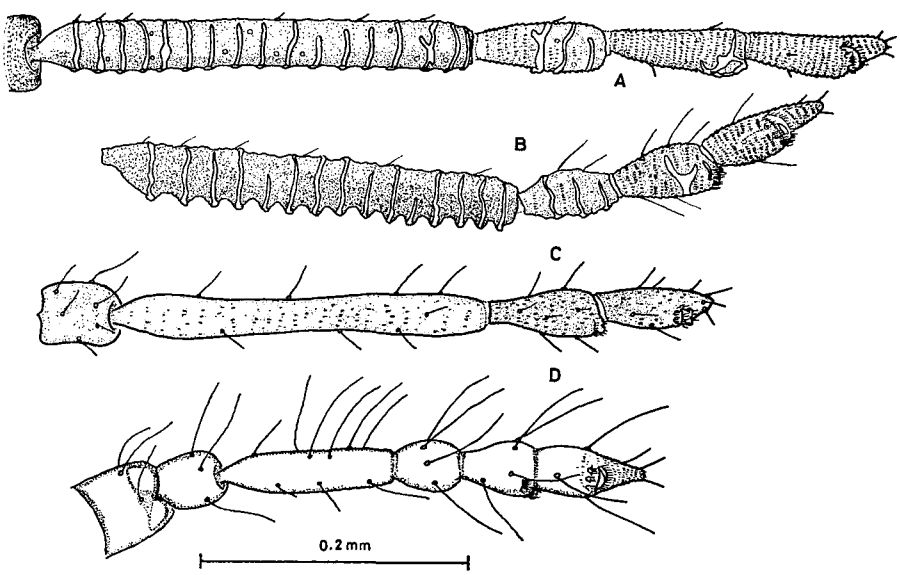

Fig. 4. *Eriosoma japonicum*. Antennae. A, emigrant; B, sexupara; C, fundatrix adult; D, exule adult.

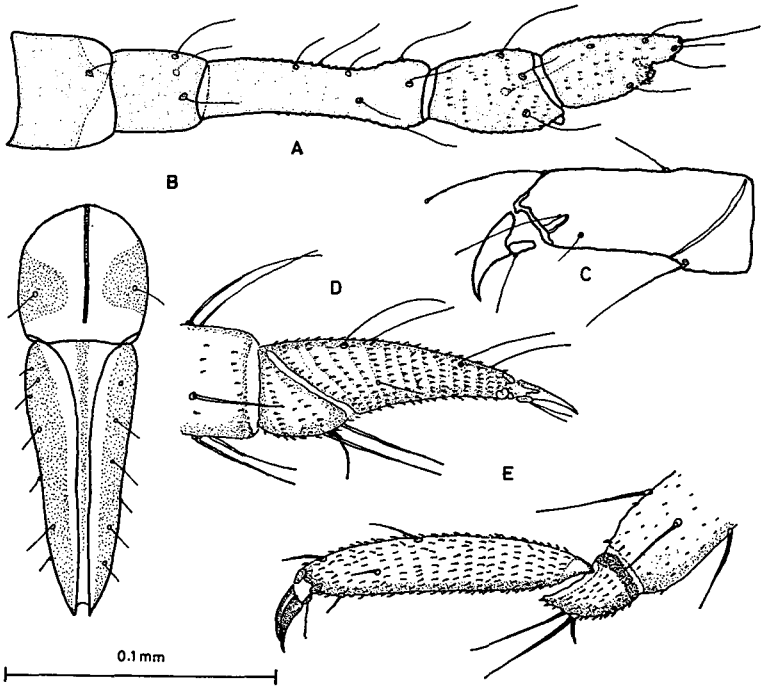

Fig. 5. *Eriosoma japonicum.* Antenna (A) and ultimate rostral segment (B) of the fundatrix 1st instar larva. C, hind tarsus of the fundatrix adult; D, hind tarsus of the exule adult; E, hind tarsus of the sexupara.

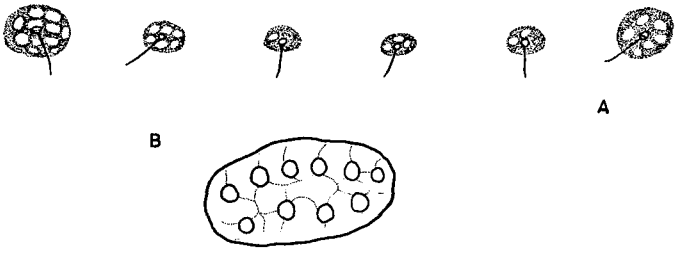

Fig. 6. *Eriosoma japonicum.* A, abdominal sclerites of the fundatrix 1st instar larva; B, wax gland plate of the exule.

upheaved, and covering only ventral side. Antennal segment III with 13–20 and IV with 1–5 secondary rhinaria, V often with a more slender secondary rhinarium. Primary rhinaria found on V and VI; one on V without a distinct foramen, with a secondary rhinarium-like structure extending around the segment; one on VI with a distinctly bordered foramen, from which an arm extends laterally, and with a few accessory rhinaria fringed with cilia. Antennal segment VI with 2–4 rather thick setae at processus terminalis, of which the longest one is 0.010–0.013 mm long, and with 3–4 fine setae at the base; V with 4–7, IV with 2–3, and III with 11–15 setae. Antennal segments III–VI weakly imbricated, intensively spinose, but segment III with some spinules only on the apical half. Ultimate rostral

segment about 0.116–0.131 mm long, with many short setae. Abdominal tergites each with a sclerotized intersegmental band, and with some fragmentary sclerites on the pleural part. Sclerotized cornicles present on tergite V, weakly elevated, surrounded by about 10 setae. Cauda semicircular, with 1 pair of setae at the middle. Genital plate with 2 long setae at the middle and 11–14 setae along the hind margin, almost entirely pigmented. A pair of sclerotized plates present laterally to genital plate, with a few spine-like setae. Hind femorotrochanter 0.46–0.53 (0.49) mm long. Setae on hind femora and tibiae short, 0.027–0.035 and 0.030–0.040 mm long, respectively. Tarsi intensively spinose; first tarsal segment with 2 long setae, which are 0.035–0.040 mm long, and with 1 spine-like seta. Second segment of hind tarsi 0.142–0.147 mm long. Fore wings with media once branched. Hind wings with Cu 1a and Cu 1b. Embryos extracted from the abdomen with spinose and cone-shaped tarsi, and with empodial setae a little longer than claws.

Fundatrix adult. Description is based on 5 specimens collected from galls on *Ulmus davidiana* var. *japonica*. Body broadly rounded. Body 1.81–1.94 (1.88) mm long and 1.46–1.61 times as long as broad. Body reddish brown in life. Antennae, rostrum and legs usually dark brown, strongly sclerotized. Wax gland plates ill defined. Antennae 5-segmented, 0.54–0.62 (0.58) mm long and 0.30–0.35 times as long as body. Antennal segment IV always longer than segment V. Antennal segment III with 1 or 2 unpigmented spots at distal 1/3. Antennal segment V rather wide, 0.030 mm wide. Length of segments (in mm): I 0.061–0.071 (0.067), II 0.056–0.061 (0.060), III 0.260–0.313 (0.288), IV 0.086–0.099 (0.093), V 0.071–0.091 (0.079). Primary rhinaria present on segments IV and V, fringed with cilia especially on segment V. Antennal segments III-V spinose, faintly imbricated. Antennal setae long; segment III with 13–18, IV with 6–8, and V with 6–9 setae. The longest setae on segment III 0.043–0.046 mm long, and 1.42–1.64 times as long as the diameter of the segment. Rostrum reaching to the middle coxae. Ultimate rostral segment 0.121–0.142 mm long, with relatively long setae. Head with a median sclerotized bar. Setae on head maximally 0.051–0.071 mm long. Thorax and abdomen membranous, with setae, which are maximally about 0.05 mm long. Wax gland plates each represented by an assemblage of indistinct cells. Cornicles absent. Genital plate and cauda almost as in the emigrants. Hind femorotrochanter 0.40–0.44 (0.42) mm long. Setae on femora and tibiae thick and long, maximally 0.051–0.056 mm long on hind tibiae, and 1.06–1.33 times as long as the diameter of hind tibiae. Tarsi not spinose and separated into 2 segments. Second segment of hind tarsi 0.083–0.091 mm long, rather rectangular and broad in profile. Dorso-apical setae slightly capitate at the apex and very long, 0.046–0.051 mm long. Empodial setae fine, about 0.030 mm long.

Fundatrix first instar larva. Description is based on 5 specimens collected on unfolding buds of *Ulmus davidiana* var. *japonica*. Body 0.616–0.778 (0.717) mm long, maximal body width 0.283–0.364 (0.326) mm and 0.454 times body length on the average. Head with a dorsal sclerite divided by a membranous median line and extending to the ventral side. Head with long setae which are 0.040 mm long maximally. Antennae 5-segmented. Antennal segments IV and V faintly spinose and apical half of segment III with a few faint spinules. Antennal segment IV rather broad, maximally 0.028–0.030 mm wide. Length of segments as follows: I 0.035–0.040 (0.039), II 0.030–0.040 (0.036), III 0.081–0.091 (0.084), IV 0.045–0.051 (0.048), V 0.051. Antennal segment I with 1–3, II with 3, III with 5–8, IV with

3–5, V with 6–7 rather long setae. The longest setae on segment III 0.030–0.035 mm long. Primary rhinaria present on segments IV and V, ciliate, and with accessory rhinaria on segment V. Ultimate rostral segment almost straight laterally, 0.101–0.106 (0.103) mm long, with 11–12 short accessory setae. Thoracic and abdominal tergites each with almost oval and setose sclerites including several unpigmented cells on the spinal, pleural and lateral position, but abdominal tergite VIII without pleural ones. Setae on the sclerites with an acute tip, about 0.025 mm long on the lateral position of abdominal tergite V. Hind femorotrochanter 0.157–0.177 (0.166) mm long. Tibiae and tarsi smooth. Setae on hind tibiae maximally 0.035–0.040 mm long. Tarsi separated by a membranous slit. Second segment of hind tarsi 0.056–0.066 (0.061) mm long. Dorso-apical setae long and capitate at the apex, 0.038–0.040 mm long on hind legs. Empodial setae a little longer than claws.

Apterous exule adult. Description is based on 5 specimens collected from the root of *Agrimonia pilosa*. Body oval, 1.56–1.69 (1.61) mm long. Head, antennae, legs and rostrum sclerotized and brown. Eyes represented by a triommatidion. Antennae 6-segmented, 0.460–0.549 mm long and 0.29–0.35 times as long as body. Antennal segment IV thick, 0.67–0.80 times as wide as long. Length of segments (in mm): I 0.056–0.066 (0.061), II 0.046–0.056 (0.049), III 0.159–0.197 (0.177), IV 0.051–0.066 (0.059), V 0.063–0.071 (0.067), VI 0.083–0.096 (0.091). Processus terminalis on the last segment rather prominent, 0.030–0.035 mm long. Antennae nearly smooth, slightly spinose on segments III-VI. Primary rhinaria present on segments V and VI, fringed with many cilia. Antennal setae very long; setae on each segment as follows: I 3–4, II 2–4, III 12–14, IV 4–5, V 5–6, VI 7–8. The longest setae on segment III 0.056–0.063 mm long; apical setae on the last segment maximally 0.025–0.028 mm long. Rostrum reaching to between middle coxae and hind coxae. Ultimate rostral segment 0.121–0.137 mm long, with 10–13 long setae, slightly spinose along labial groove. Wax gland plates present on thorax and abdomen. Head without wax plates. Pro-, meso- and metathorax and abdominal tergites I–VII each with only 1 pair of marginal wax plates. Wax plates often irregular in shape, laterally extended, more or less oval-shaped; including 7–15 small distinct cells and several larger, irregular-shaped cells bordered by indistinct lines which radiate from the smaller cells. Smaller cells 0.007–0.010 mm long in diameter. Body setae long; lateral setae on tergite V 0.076–0.086 mm long. Cornicles sclerotized and elevated, surrounded by 9–13 setae. Genital plate as in the emigrant. Hind femorotrochanter 0.339–0.377 mm long. Setae on legs thick and long; those on hind femora maximally 0.051 mm long and those on hind tibiae maximally 0.061–0.066 mm long. Tarsi cone-shaped, intensively spinose; second tarsal segments of hind legs 0.081–0.094 mm long. Setae on first tarsal segments of hind legs 0.043–0.056 mm long. Empodial setae fine, 0.035 mm long in hind tarsi.

Sexupara. Description is based on 2 specimens collected on the trunk of *Ulmus davidiana* var. *japonica*. Body length 1.53–1.69 mm. Head, thorax, antennae and legs dark brown. Antennae 6-segmented, 0.655–0.693 mm long and 0.41–0.43 times as long as body. Processus terminalis on the last antennal segment rather prominent. Segment V thickest at the apex, where it is 0.52–0.57 times as wide as its length. Length of segments (in mm): I 0.056–0.061, II 0.043–0.046, III 0.319–0.334, IV 0.071–0.078, V 0.071–0.078, VI 0.096. Secondary rhinaria present on segments III-VI, rather slender and irregular in shape, encircling about

2/3 segment III and less than half each segment IV, V and VI. Antennal segment III with 17 or 18, IV with 2 or 4, V with 2, and VI with 1 secondary rhinarium. Primary rhinaria present on segments V and VI, fringed with cilia, with a few accessory rhinaria on VI. Antennal setae longer than those of emigrants. Segment I with about 4, II with 4 or 5, III with 14 or 15, IV with 3 or 4, V with 5 or 8, VI with 6 or 7 setae. The longest setae on segment III 0.020–0.025 mm and apical setae on the last segment 0.013 mm long. Antennal segments IV, V and VI spinose, weakly imbricated. Ultimate rostral segment 0.121 or 0.126 mm long, with about 17 accessory setae. Abdomen with some weakly pigmented narrow intersegmental bands, which are fragmented on the pleural part. Abdominal setae on tergite V maximally 0.051–0.053 mm long. Cornicles as in the emigrants. Abdominal tergites I-VII each with only 1 pair of lateral wax plates, which are especially elongated on the tergites VI and VII. Wax plates consisting of 20–30 or more cells belonging to 2 types: some of them are smaller and well-shaped, others rather irregular in shape. Genital plate as in the emigrants. Hind femorotrochanter 0.425–0.460 mm long. Tarsi and apical parts of tibiae intensively spinose. First tarsal segment with 2 long setae, which are maximally 0.038–0.043 mm long on hind legs, and with 1 spine-like seta, which is always present even on hind legs. Second segment of hind tarsi 0.106–0.111 mm long. Fore wings with media once branched.

Gall. A fundatrix forms a single leaf-roll gall on a shoot. The gall is indistinguishable from that of *E. harunire*.

Distribution. Hokkaidô; Kyûshû (Kagoshima). Some specimens of the fundatrix were collected on *Ulmus davidiana* by Mr. Fujisawa in Seolag-san, Korea, May 25th 1982.

Eriosoma harunire, sp. nov.

Eriosoma harunire Akimoto, 1981 [nomen nudum].

Specimens examined. Emigrants, 1 indv. (holotype), Sapporo, Hokkaidô, ex a gall on *Ulmus davidiana* var. *japonica*, 7 VII, 1982; 2 indvs., ditto, 7 VII 1978; 3 indvs., ditto, 8 VII 1978; 4 indvs., ditto, 2 VII 1972 (Aoki). Fundatrix adults, 1 indv., Sapporo, ex a gall, 25 VI 1978; 1 indv., ditto, 27 VI 1978; 2 indvs., ditto, 10 VI 1979; 1 indv., ditto, 16 VI 1979; 1 indv., ditto, 17 VI 1979. Fundatrix first instar larvae, 1 indv., Sapporo, ex a gall, 24 V 1979; 4 indvs., ditto, 29 V 1979. Apterous fundatrigenia adults, 6 indvs., Sapporo, ex galls, 24 VI 1980. Sexuparae, 2 indvs., Sapporo, ex the trunk of *U. davidiana* var. *japonica*, 15 IX 1978; 2 indvs., ditto, 23 IX 1978.

Emigrant adult. Description is based on 9 specimens collected from galls on *Ulmus davidiana* var. *japonica*. Body 1.38–1.63 (1.49) mm long. Head and thorax dark brown. Antennae and legs brown. No wax plate present. Antennae 6-segmented, 0.79–0.89 mm long and 0.49–0.57 times as long as body. Antennal segment III longer than segments IV, V and VI taken together. Antennal segment IV always longer than segment V. Processus terminalis on antennal segment VI slender and rather long, 0.040–0.045 mm long. Length of segments (in mm): I 0.056–0.068 (0.062), II 0.046–0.056 (0.051), III 0.397–0.455 (0.416), IV 0.091–0.111 (0.097), V 0.086–0.106 (0.094), VI 0.111–0.121 (0.118). Secondary rhinaria very narrow, irregulary arranged and encircling about 1/3–2/3 the segments, not

much upheaved. Antennal segment III with 24–30, IV with 3–5, and, V with 0–3 secondary rhinaria. Primary rhinarium on segment V with no opening, similar to secondary rhinaria, but more irregular in shape, encircling about 2/3 the segment, partially fringed with cilia. Primary rhinarium on segment VI with a ciliate, indistinct and transverse foramen, from which an arm extends laterally around half the segment, and with a few ciliated accessory rhinaria. Antennal segment

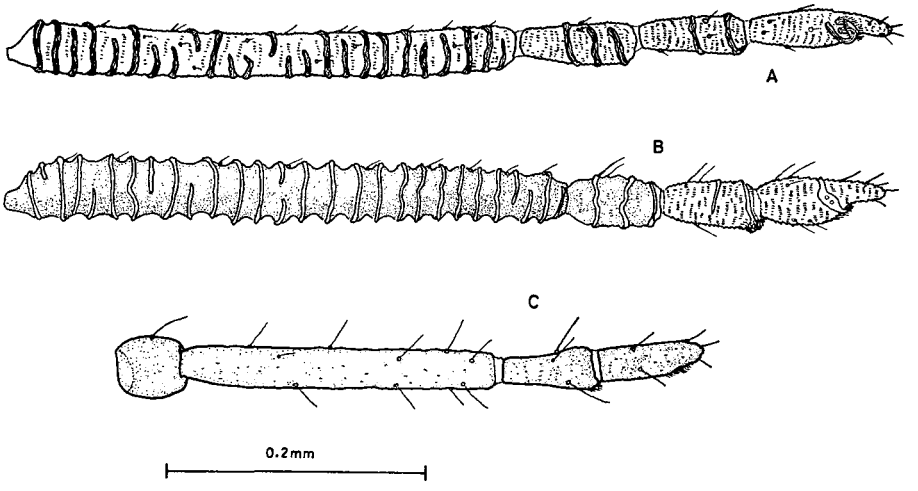

Fig. 7. *Eriosoma harunire.* Antennae. A, emigrant; B, sexupara; C, fundatrix adult.

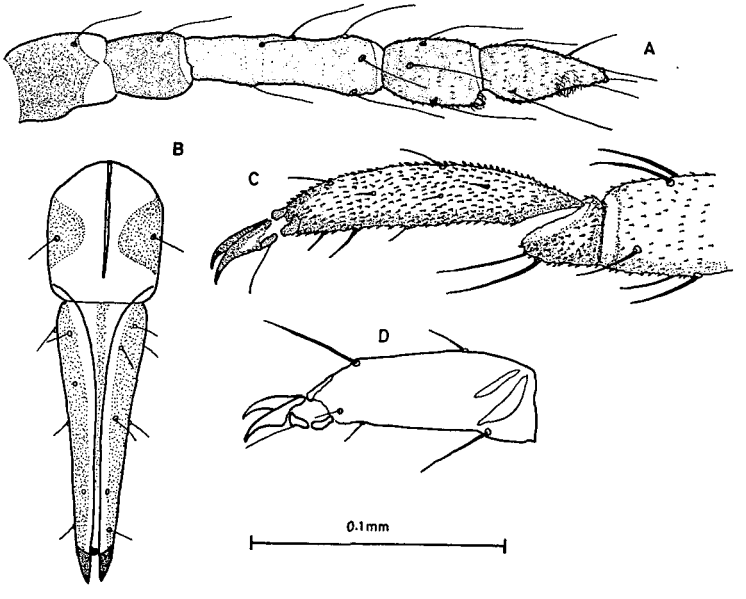

Fig. 8. *Eriosoma harunire.* Antenna (A) and ultimate rostral segment (B) of the fundatrix 1st instar larva. C, hind tarsus of the sexupara; D, hind tarsus of the fundatrix adult.

VI at processus terminalis with 5 relatively thick setae, of which the longest one is about 0.010 mm long, and at the base with 4–6 setae. Segment V with 3–5, IV with 3–4, and III with 11–12 shorter setae. Antennal segments III-VI rather imbricated, with transverse rows of spinules. Ultimate rostral segment about 0.137–0.142 mm long, with several short setae. Abdominal tergites each with a weakly pigmented intersegmental band. Sclerotized cornicles present on tergite V, weakly elevated, each surrounded by about 10 setae. Cauda semicircular, with 2 setae. Genital plate spinose and wholly pigmented, with 2 setae at the middle and about 10 setae along the hind margin. A pair of sclerotized plates present laterally to genital plate, with a few spine-like setae. Hind femorotrochanter 0.42–0.47 (0.45) mm long. Setae on hind femora and tibiae very short, maximally 0.020 and 0.035–0.038 mm long, respectively. Tarsi intensively spinose; first tarsal segment with 2 setae, which are 0.025–0.028 mm long on hind legs, and with 1 spine-like seta. Spine-like setae present even on hind legs. Second segments of hind tarsi 0.126–0.131 mm long. Fore wings with media once branched. Hind wings with Cu 1a and Cu 1b. Embryos within abdomen with spinose and cone-shaped tarsi, and with empodial setae a little longer than claws.

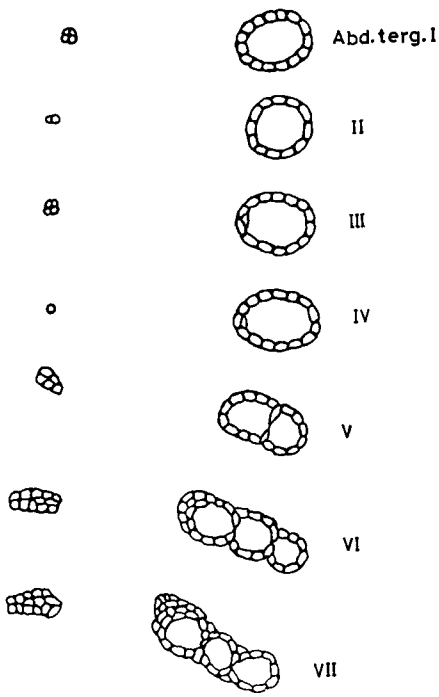

Fig. 9. *Eriosoma harunire.* Wax gland plates of the sexupara.

Fundatrix adult. Description is based on 6 specimens collected from galls on *Ulmus davidiana* var. *japonica*. Body broadly rounded. Body length 1.75–2.00 (1.88) mm long and 1.42–1.53 times as long as broad. Body brownish or greenish grey in life. Antennae, rostrum and legs pale brown on slide. Antennae weakly sclerotized, 5-segmented, 0.45–0.51 (0.48) mm long and 0.25–0.27 times as long as body. Segment IV not much constricted at the base; segment V not pointed at the apex, rather slender, 0.025 mm wide. Processus terminalis on the last segment stumpy. Length of segments (in mm): I 0.051–0.066 (0.061), II 0.051–0.056 (0.053), III 0.207–0.278 (0.241), IV 0.066–0.081 (0.075), V 0.071–0.086 (0.079). Antennal setae fine; segment II with 2–4, III with 9–11, IV with 3–4, and V with 6–7 setae. The longest setae on segment III about 0.032–0.035 mm long, and 1.08–1.17 times as long as the diameter of the segment. Antennal segments III-V faintly spinose. Antennal segments IV and V more pigmented than segment III. Rostrum reaching to middle coxae. Ultimate rostral segment comparatively long, 0.126–0.137 mm long with several accessory setae. Head with a weakly sclerotized bar along the median line. Setae on head maximally 0.051–0.061 mm long. Cornicles absent. Cauda and genital plate as in the emigrants. Legs short, weakly sclerotized. Hind

femorotrochanter 0.33–0.38 (0.36) mm long. Hind tibiae thinly with setae, which are maximally 0.035–0.040 mm long and 0.88–1.06 times as long as the diameter of the segment. Tarsi not spinose and separated into 2 parts. Second segment of hind tarsi 0.086–0.096 mm long, becoming narrower toward the apex. Dorso-apical setae rather long, but very fine, always acute at the apex, maximally 0.040–0.046 mm long.

Fundatrix first instar larva. Description is based n 5 specimens collected from embryo galls on *Ulmus davidiana* var. *japonica.* Body 0.616–0.677 (0.638) mm long, 0.489 times as wide as long on the average, maximal width 0.273–0.338 (0.312) mm. Body without visible wax gland plates. Head with a broad dorsal sclerite, which reaches to the ventral side. The sclerite with a median slit, but not definitely separated into 2 parts. Antennae 5-segmented. Antennal segment III rather slender and long. Segment IV 0.023–0.025 mm wide. Segments IV and V, and apical half of segment III thinly with spinules. Length of segments as follows: I 0.030–0.038 (0.034), II 0.025–0.030 (0.028), III 0.068–0.083 (0.075), IV 0.038–0.040 (0.039), V 0.043–0.051 (0.046). Antennal segment I with 2, II with 1–3, III with 5–8, IV with 4, and V with 7 setae. Setae on apical half of segment III, and also on IV and V long; segment IV with setae 0.035–0.040 mm long maximally. Apical setae on the last segment 0.023–0.025 mm long. Primary rhinaria present on segments IV and V, ciliate. Ultimate rostral segment slender, slightly concave laterally, 0.106–0.121 (0.113) mm long with 12–14 accessory setae. Rostral segment II with 2 a little pigmented transversal bars on apical 1/3 and 2/3 of the segment. Thoracic and abdominal tergites with small oval sclerites, which are about 0.02 mm in axial length and have 1 capitate seta. Pronotum with 1 pair of spinal sclerites and 2 pairs of lateral ones. Meso- and metanotum with 1 pair of spinal sclerites, 1 pair of pleural ones and 2 pairs of lateral ones often united. Abdominal tergites I-VI with 1 pair of spinal, 1 pair of pleural and 1 pair of lateral sclerites. Abdominal tergites VII and VIII without pleural sclerites, and tergite VIII also without lateral sclerites. The longest setae on lateral sclerites of tergite VI 0.028–0.030 mm long. Hind femorotrochanter 0.137–0.157 (0.147) mm long. Tibiae and tarsi not spinose. The longest setae on hind tibiae 0.030–0.040 mm long. Tarsi always separated into 2 segments, slender, 0.056–0.058 mm long. Dorso-apical setae long and capitate at the apex, maximally 0.040–0.043 mm long on hind legs. Empodial setae capitate at the apex and a little longer than claws, 0.025 mm long.

Apterous fundatrigenia adult. Description is based on 6 specimens collected from 2 galls on *Ulmus davidiana* var. *japonica.* Body more elongate than in fundatrix. Body 1.469–1.656 (1.562) mm long. Head with a sclerotized, lozenge-shaped median band dorsally, partially covered with many membranous cells surrounding the median band. Eyes consisting of 2 parts, multifacetted eye and triommatidion, the latter being also found in the fundatrix. Antennae 6-segmented, 0.642–0.710 (0.669) mm long and 0.40–0.46 times as long as body. Processus terminalis on the last segment rather long, 0.035–0.043 mm long. Length of segments (in mm): I 0.056–0.063 (0.059), II 0.051–0.058 (0.053), III 0.258–0.303 (0.277), IV 0.071–0.086 (0.079), V 0.078–0.086 (0.083), VI 0.114–0.124 (0.119). Primary rhinaria present on segments V and VI, inflated and fringed with cilia, with a few accessory rhinaria on segment VI. Setae on antennal segments: I 2–4, II 4–7, III 16–21, IV 3–4, V 3–6, and VI 4–5 at the base and 5 on processus terminalis. The longest setae on segment III 0.035–0.040 mm long; apical setae on the last segment 0.013–0.015

mm long. Antennal segments IV, V and VI rather spinose, and III faintly spinose. Rostrum reaching to between middle coxae and hind coxae. Ultimate rostral segment long, 0.137–0.144 mm long, with 12–17 accessory setae. Wax gland plates present on abdominal tergites, consisting of several cells, but indistinct and without a definite border. Setae on tergite V 0.048–0.056 mm long. Cornicles and genital plate as in the emigrants. Hind femorotrochanter 0.404–0.432 mm long. Setae on legs rather dense and long; those on hind tibiae maximally 0.040–0.048 mm long. Tarsi faintly spinose; second tarsal segment of hind legs 0.131–0.139 mm long. Setae on first tarsal segments of hind legs 0.046–0.051 mm long. Empodial setae shorter than claws, about 0.025 mm long on hind legs.

Sexupara. Description is based on 4 specimens collected on the trunk of *Ulmus davidiana* var. *japonica.* Body length 1.75–1.94 (1.82) mm. Head, thorax, antennae and legs dark brown. Antennae 6-segmented, 0.867–0.963 mm long and 0.46–0.55 times as long as body. Length of segments (in mm): I 0.061–0.071 (0.064), II 0.046–0.056 (0.051), III 0.470–0.551 (0.513), IV 0.091–0.101 (0.095), V 0.076–0.088 (0.082), VI 0.106–0.121 (0.111). Processus terminalis on the last segment comparatively long, 0.035–0.040 mm long. Secondary rhinaria found on segments III, IV and V, very narrow, irregularly arranged, hardly upheaved, encircling 1/2–3/4 the segment. Antennal segment III with 26–33, IV with 3–5, and V with 0–2 secondary rhinaria. Primary rhinaria present on segments V and VI, similar to secondary rhinaria and encircling about 1/2 the segment. A part of primary rhinaria fringed with cilia. Antennal setae on each segment as follows: I 2–4, II 5–6, III 18–26, IV 2–4, V 5–7, VI 10–13. The longest setae on segment III 0.028–0.035 mm long and apical setae on the last segment 0.015–0.020 mm long. Antennal segments V and VI spinose, weakly imbricated. Ultimate rostral segment 0.151–0.167 mm long, with about 8 accessory setae. Abdomen with narrow and sclerotized intersegmental bands. Abdominal setae on tergite V maximally 0.051 mm long. Cornicles as in the emigrants. Wax plates present on head and abdominal tergites I-VII. Head with 1 pair of wax plates each composed of 2–4 small cells. Abdominal tergites I-VII each with 1 pair of spinal and 1 pair of lateral wax plates. Lateral wax plates on tergites I-VI with 1 large central cell, which is surrounded by 13–18 smaller cells arranged in a single row, and those on tergites V-VII each with 2 or 3 large central cells and more than 30 smaller surrounding cells. Central cells appearing a little darker than circumferential smaller cells. Spinal wax plates consisting of same-sized cells; with 12–14 cells on tergite VII. Genital plate as in the emigrants. Hind femorotrochanter 0.526–0.602 mm long. Setae on hind tibiae 0.035–0.045 mm long. Tibiae on apical 1/3 and tarsi intensively spinose. First tarsal segment with 2 long setae, which are 0.033–0.040 mm long on the hind legs, and, except on hind legs, with 1 spine-like seta. Second segment of hind tarsi 0.116–0.125 mm long. Empodial setae slightly longer than claws, 0.025 mm long. Fore wings with media once branched.

Gall. A fundatrix forms a single leaf-roll gall on a shoot. The leaf edge of one side is firmly rolled toward the underside. The galls do not become inflated and distorted with growth, and keep green even after they have matured. Usually a lateral half of the leaf is rolled and the other remains unaffected.

Distribution. Hokkaidô; Kyûshû (Kagoshima). Some specimens of the fundatrix were collected on *Ulmus davidiana* by Mr. Fujisawa in Seolag-san, Korea, May 25th 1982.

Remarks. Dzhiblatze (1965) recorded "*E. japonica*" collected on *Ulmus pumila*

in the basin of the River Ussuri, and gave drawings for it. Her *E. japonicum* wholly differs from the species treated above and may be close to *E. harunire*. It is distinguishable from *E. harunire* in the following characters: the emigrants of *E. harunire* have 24–30 secondary rhinaria on antennal segment III, while those of Dzhiblatze's *E. japonicum* are shown to have 18–22; the ultimate rostral segment of the fundatrix is stumpier than in *E. harunire*. Moreover, the two differ in primary host plants: in Japan no galls of *E. harunire*, as well as of other *Eriosoma* species, have been found on *Ulmus pumila*, which was introduced from northeastern China and is now abundant in Sapporo. Therefore, *E. harunire* and Dzhiblatze's *E. japonicum* should be different species in spite of the supposed close relationship between them. None of the forms found in Japan exactly agrees with Dzhiblatze's species, which therefore should not be *E. japonicum* in any way.

Eriosoma nigrum, sp. nov.

Specimens examined. Apterous exule adults, 1 indv. (holotype), Jôzankei, Hokkaidô, ex the root of *Epilobium* sp., 3 X 1973 (Aoki); 2 indvs., ditto, 18 IX 1982 (Miyazaki & Aoki). Alate exules (reared to adults in laboratory), 5 indvs., Jôzankei, ex the root of *Epilobium* sp., 18 IX 1982 (Miyazaki & Aoki).

Apterous exule adult. Description is based on 3 specimens collected from the root of *Epilobium* sp. Body oval, dark pigmented all over except for dorsum, with long setae strewn over, 1.495–1.576 mm long. Head intensively sclerotized. Antennae 6-segmented, smooth, comparatively long, 0.581–0.609 mm long and 0.386–0.404 times as long as body. Antennal segment IV oval, segment V thicker toward the apical border. Segment VI comparatively slender; processus terminalis rather long, 0.040–0.045 mm long. Length of segments (in mm): I 0.061–0.066 (0.064), II 0.066–0.071 (0.067), III 0.217–0.242 (0.229), IV 0.053–0.061 (0.056), V 0.076–0.083 (0.078), VI 0.101–0.106 (0.103). Primary rhinaria present on segments V and VI, fringed with many cilia; one on segment VI with a transverse opening, from which a tonguelet projects, and with a few, ciliate accessory rhinaria; one on segment V without a distinct opening and accessory rhinaria. Secondary rhinaria absent. Antennal setae quite long, dense; the longest setae on segment III 0.066–0.076 mm long. Number of setae on each segment: I 3–6, II 5–7, III 22–25, IV 4–5, V 10–13, and VI 5 at the base and 5 at processus terminalis. Apical setae on the last segment 0.028 mm long. Rostrum reaching to a little beyond hind coxae. Ultimate rostral segment slightly spinose, 0.152–0.162 (0.158) mm long, with about 12 accessory setae. Wax gland plates present on head, thorax and abdomen, basically consisting of 1 large central cell and smaller cells surrounding the central one in a single row. Head with 2 pairs of wax plates: 1 pair on ventrum and the other on dorsum. Ventral wax plates with about 10 circumferential cells; dorsal wax plates with about 6. Pro-, meso- and metanotum and abdominal tergites I–VII each with 1 pair of spinal and 1 pair of lateral wax plates. Spinal wax plates with 2–5 circumferential cells, which sometimes do not completely surround the central cell, rarely without a central cell. The diameter of spinal plates on abdomen about 0.025 mm long. Lateral wax plates always larger than spinal ones, with 7–11 circumferential cells, which are sometimes partially arranged double. The diameter of lateral plates about 0.04 mm. Body setae very long, densely strewn all over. Lateral setae on abdominal tergite V maximally 0.131 mm long. Membranous and unpigmented bands or spots present along intersegmental lines,

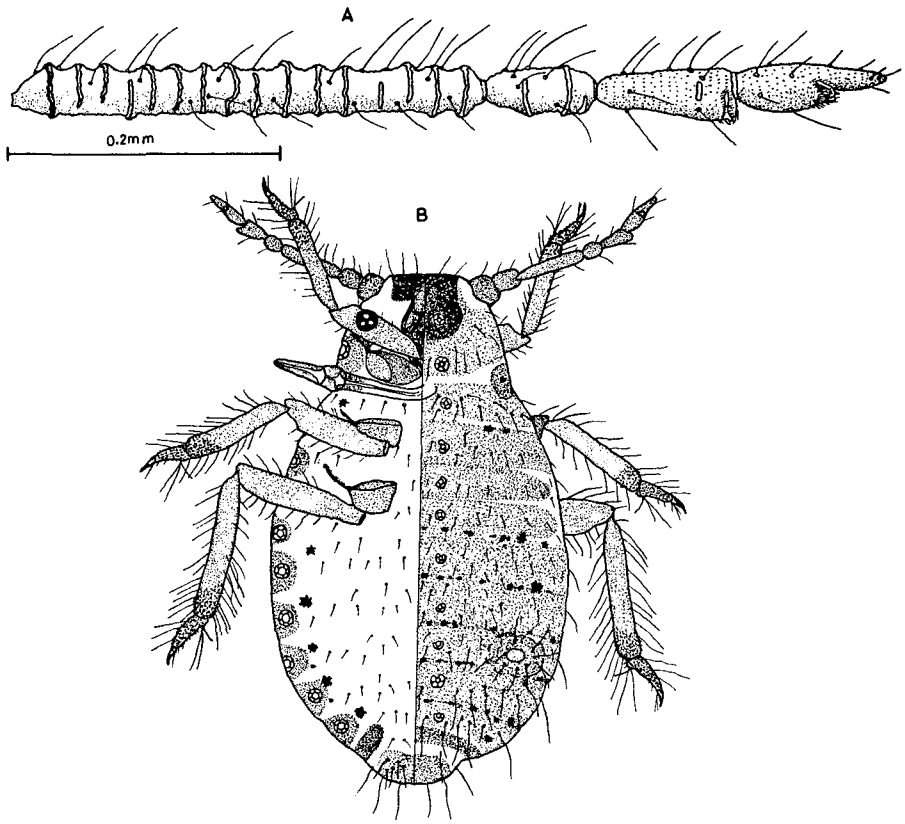

Fig. 10. *Eriosoma nigrum.* A, antenna of the alate exule; B, apterous exule adult.

and dark pigmented short bands and spots present also along intersegmental lines. Cornicles with an intensively sclerotized rim, projecting slightly, each surrounded by 11–13 long setae. Genital plate sclerotized, with 2 setae at the anterior part and 9–11 setae, shorter than the former, along the hind margin, and with many transverse rows of denticles. Hind femorotrochanters 0.374–0.414 (0.391) mm long. Legs densely covered with long setae; the longest setae on tibiae 0.10–0.11 mm long. Apical 1/3 of tibiae, and tarsi strongly spinose. First tarsal segment with 1 pair of setae, which are 0.096 mm long and with 1 shorter seta. Second tarsal segment of hind legs 0.106–0.109 mm long. Empodial setae longer than claws, 0.035 mm long.

Alate exule. Description is based on 5 specimens collected from the root of *Epilobium* sp. (reared to adults in laboratory). Body length 1.72–1.88 (1.80) mm long. Head, thorax, antennae and legs sclerotized, brown to dark brown. Body wholly covered with long setae. Antennae 6-segmented, 0.773–0.800 (0.784) mm long and 0.42–0.45 times as long as body. Processus terminalis on the last segment prominent and slender, 0.040–0.045 mm long. Antennal segment V much longer than segment IV, thicker toward the apical border. Segment III comparatively slender, about 0.035 mm wide. Length of segments (in mm): I 0.061–0.071 (0.066), II 0.071–0.076 (0.072), III 0.338–0.356 (0.346), IV 0.086–0.091 (0.088), V 0.096–0.106 (0.103), VI 0.111–0.116 (0.112). Secondary rhinaria present on segments III

and IV, slender, rather irregularly arranged, encircling a little more than half the segment. Segment III with 12–16 (15) secondary rhinaria and IV with 2 (rarely a rudimentary one present on segment V). Primary rhinaria present on segments V and VI, fringed with short cilia, with a transverse opening, from which a tonguelet projects; one on segment VI with a more irregular-shaped opening and with a few ciliate accessory rhinaria; one on segment V with a slit-like opening. Antennal setae comparatively long; the longest setae on segment III 0.051–0.061 mm long. Apical seta on the last segment about 0.020 mm long. Setae on antennal segments: I 5–6, II 5–7, III 22–23, IV 4–6, V 9–11, and VI 5–6 at the base and 5 at processus terminalis. Antennal segments V and VI intensively spinose and imbricated, other segments not. Ultimate rostral segment 0.167–0.172 mm long, with 15–17 long accessory setae, which are maximally 0.051–0.056 mm long. Abdominal tergites with dark pigmented intersegmental bands and spots. Abdominal setae long, maximally 0.061–0.076 (0.068) mm long on tergites V or VI. Cornicles present on tergite V, weakly sclerotized, slightly projecting, each surrounded by 11–15 setae. Wax gland plates present on head and abdominal tergites I-VII. Head spinally with 1 pair of incompletely circular, not sclerotized wax plates. Abdominal tergites I-VII each with 1 pair of spinal and 1 pair of lateral wax plates. Abdominal wax plates consisting of 1 slightly darker central cell and some surrounding cells. Spinal plates with 2–6 circumferential cells, which are almost as large as the central one and do not completely surround this. Lateral plates with 5–10 circumferential cells, whose number increases toward the hind margin of abdomen. Genital plate spinose, with 2 or 3 setae at the anterior part and 8 (in 1 instance 6) setae along the hind margin. Legs with long setae all over. Hind femorotrochanter 0.505–0.566 (0.530) mm long, with many long setae, of which the longest setae are 0.056–0.066 mm long. The longest setae on tibiae 0.066–0.068 mm long. Apical 1/5 of tibiae, and tarsi strongly spinose. First tarsal segment with 2 setae, which are 0.056–0.061 mm long on hind legs, and with 1 shorter seta. Second tarsal segment of hind legs 0.131–0.136 mm long. Empodial setae slightly longer than claws, about 0.030 mm long on hind legs. Fore wings with media once branched. Hind wings with 2 cubital veins.

Distribution. Hokkaidô (Sapporo).

Remarks. In the Eriosomatinae the anholocyclic life mode tends to concentrate in forms living on grass roots as secondary hosts, e.g. *Tetraneura* and *Colopha*. In the genus *Tetraneura* almost all the species have a holocyclic mode accompanied by an anholocyclic one, in which the population can expand its distribution by the production of alates (Moldvilko, 1935; Hille Ris Lambers, 1970; Zwölfer, 1958); the resultant distribution is extremely extensive nearly all over the world. By contrast there have been few records of a complete anholocyclic life mode in *Eriosoma*. Especially, the production of alate exules occurs only in the well-known case of *E. lanigerum*. It has been ascertained that *Eriosoma nigrum* is maintained by anholocyclic generations producing alates on the roots of *Epilobium* sp. Material of this species including alates was collected on the host plant on 18 September, when the sexuparae of other *Eriosoma* species were remigrating to *Ulmus*. All the alates contained embryos which were equipped with a rostrum. This means that they were alate exules. Through all my sampling investigations around Sapporo I have found no form of gall-making generations corresponding to the exule of *E. nigrum*.

Eriosoma ulmi group

The *ulmi* group is here recognized on the basis of characters given below. In Japan *E. auratum*, sp. nov., *E. longicornutum*, sp. nov., and *E. moriokense*, sp. nov., belong to this group, which includes 6 other species (see under *Eriosoma ulmi* group and other Palearctic species).

Fundatrix adult: Body generally large, broad. Antennae 6-segmented (5-segmented in *E. lishanense*). Genital plate often with more than 2 long setae at the anterior part, and with about 10 setae arranged, often irregularly, along the hind margin. *Emigrant*: Antennae 6-segmented, without secondary rhinaria on segments V and VI. Secondary rhinaria rather broad, arranged in paralell. Segments III and IV (except for the basal parts) not imbricated, without spinules. Primary rhinaria present on segments V and VI, with a distinct and circular opening. Segments V and VI intensively spinose, but not deeply pigmented. Segments III and IV dark pigmented, and the secondary rhinaria on them looking as darker lines. Genital plate as in fundatrices. Setae occurring along the hind margin of genital plate readily distinguishable from those at the anterior part. Second tarsal segment slightly imbricated, thinly with transverse rows of spinules, with rather long setae. Dorso-apical setae slightly shorter than empodial ones. First tarsal segment with 3–3–2 setae. Apical part of tibiae with a few spinules. *Exule adult*: Legs completely smooth. Tarsi not tapering, distinctly divided into 2 segments. Setae on legs stout, acute at the apex. Tarsi with a few very short setae, which are much shorter than claws. Empodial setae absent, if present rudimentary and quite feeble. Wax gland plates consisting of 1 large central cell and circumferential cells arranged in a single row, arranged in spinal and lateral rows. *Exule first instar larva*: Body covered with long setae. Tarsi united and cone-shaped, spinose, without empodial setae. Apical 1/2 of tibiae spinose. *Sexupara*: Antennal segments V and VI without secondary rhinaria. Antennal setae longer than in emigrants. Wax gland plates degenerated, merely forming dark pigmented rings or cells. Tarsi not wholly spinose, with transverse rows of spinules, with short setae not extending beyond claws.

Eriosoma auratum, sp. nov.

Eriosoma auratum Akimoto, 1981 [nomen nudum].

Specimens examined. Emigrants, 1 indv. (holotype), Sapporo, Hokkaidô, ex a gall on *Ulmus davidiana* var. *japonica*, 26 VI 1982; 2 indvs., Shiretoko-Goko, Hokkaidô, ex a gall, 12 VII 1972 (Aoki); 2 indvs., Miyakonojô, Kyûshû, ex galls, 29 IV 1972 (Aoki) (embryos examined); 4 indvs., Sapporo, ex a gall, 26 VI 1978. Fundatrix, 1 indv., Sapporo, ex a gall, 10 VI 1978; 2 indvs., ditto, 4 VI 1979; 1 indv., ditto, 5 VI 1979; 1 indv., ditto, 25 VI 1979; 1 indv., ditto, 14 VI 1980. Fundatrix second instar larvae, 1 indv., Sapporo, ex an embryo gall, 24 V 1979; 3 indvs., ditto, 25 V 1979; 1 indv., ditto, 24 V 1980. Apterous fundatrigeniae, 1 indv., Sapporo, ex a gall, 14 VI 1980; 2 indvs., ditto, 19 VI 1980. Sexuparae, 1 indv., Sapporo, ex the trunk of *U. davidiana* var. *japonica*, 15 IX 1980; 2 indvs., ditto, 18 IX 1980; 1 indv., ditto, 19 IX 1980.

Emigrant adult. Description is based on 8 specimens collected from galls on *Ulmus davidiana* var. *japonica*. Body length 1.56–1.88 (1.71) mm. Head and thorax dark brown. Antennae and legs brown. Abdomen pale brown. No wax

plate present. Antennae 6-segmented, 0.74–0.92 mm long and 0.44–0.59 times as long as body. Processus terminalis on segment VI very short, 0.020–0.025 mm long. Length of segments (in mm): I 0.056–0.061 (0.058), II 0.046–0.053 (0.050), III 0.394–0.495 (0.424), IV 0.096–0.124 (0.106), V 0.081–0.101 (0.090), VI 0.073–0.091

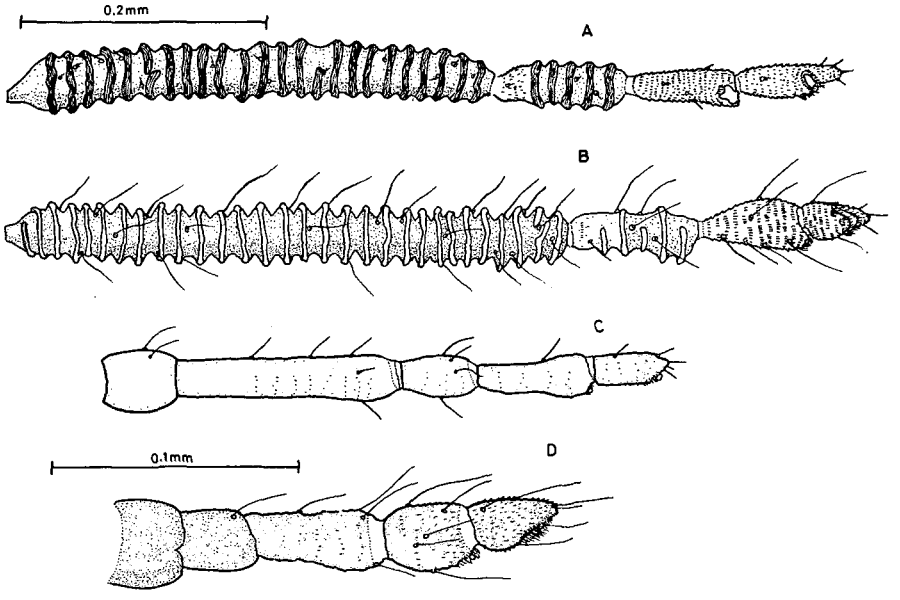

Fig. 11. *Eriosoma auratum*. Antennae. A, emigrant; B, sexupara; C, fundatrix adult; D, fundatrix 1st instar larva.

(0.085). Secondary rhinaria present on segments III and IV, regularly arranged, encircling a little more than 1/2 to 2/3 the segment, covering only ventral side. Antennal segment III with 23–30 and segment IV with 3–6 secondary rhinaria. Primary rhinaria found on segments V and VI, with a ciliate, distinctly bordered foramen, from which a tonguelet projects; one on VI with a few accessory rhinaria, which are semicircular and fringed with cilia. Antennal segment VI with 5 apical setae, 0.013 mm long, at processus terminalis and 1–2 setae at the base, V with 5–6 setae, II–IV each with a few shorter setae. Antennal segments V and VI spinose and imbricated. Ultimate rostral segment about 0.106–0.116 mm long with several short accessory setae. Abdominal tergites each with a sclerotized intersegmental band and with some fragmentary sclerites on pleural part. Sclerotized cornicles present

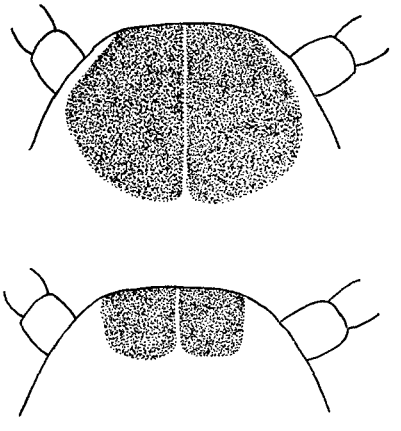

Fig. 12. *Eriosoma auratum*. Head of the fundatrix 2nd instar larva. Above, dorsal view. Below, ventral view.

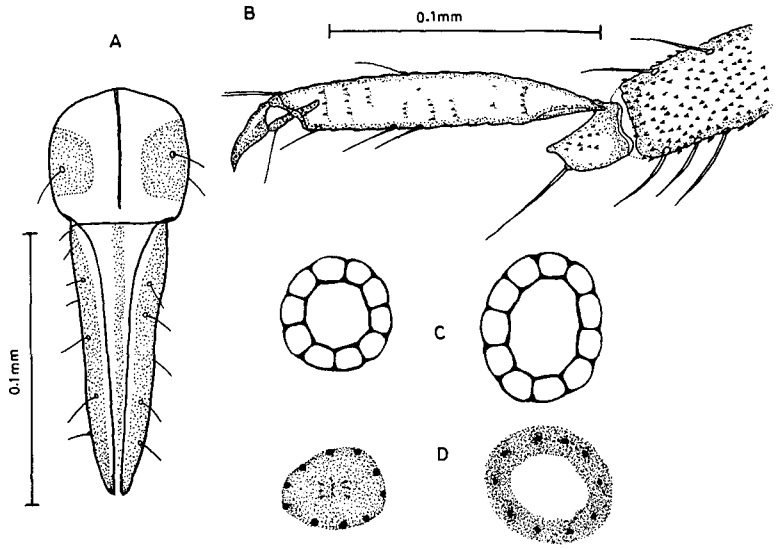

Fig. 13. *Eriosoma auratum.* A, ultimate rostral segment of the fundatrix 1st instar larva; B, hind tarsus of the sexupara; C, wax gland plates of the 1st instar larva deposited by the emigrant (left, spinal plate; right, lateral plate); D, wax gland plates of the sexupara.

on tergite V, weakly elevated, each surrounded by about 6–8 setae. Cauda semicircular, with 2 setae. Genital plate spinose, with 2 or more setae at the anterior part and 9–14 along the hind margin, pigmented except for the central part. A pair of sclerotized plates present laterally to genital plate, with a few spine-like setae. Hind femorotrochanter 0.47–0.53 (0.50) mm long. Setae on hind femora and tibiae respectively 0.035–0.040 and 0.038–0.045 mm long. Tarsi with a few spinules; first tarsal segment with 2 long setae, which are 0.046–0.051 mm long on hind legs, and, except on hind legs, with 1 spine-like seta. Second segment of hind tarsi 0.131–0.134 mm long. Fore wings with media once branched. Hind wings with Cu 1a and Cu 1b.

Embryos of emigrants. Description is based on 9 specimens extracted from abdomen of emigrants. Body 0.435–0.513 mm long. Wax gland plates present on head, thorax and abdomen. Pro-, meso- and metathorax and abdominal tergites I-VII with 1 pair of spinal and 1 pair of lateral wax plates. Abdominal tergits VIII with only 1 pair of spinal plates. Spinal and lateral plates consisting of 1 large central cell and a single row of smaller surrounding cells, on tergites II-V including 10–11 smaller cells. Body setae long. Abdominal tergites I-VI with 1 pair of spinal, 1 pair of lateral and 1 pair of pleural setae; VII with 1 pair of spinal setae and 1 pair of lateral setae; VIII only with 1 pair of spinal setae. The longest setae on tergite V 0.051–0.056 mm long. Tarsi spinose, cone-shaped, without empodial setae.

Fundatrix adult. Description is based on 6 specimens collected from galls on *Ulmus davidiana* var. *japonica.* Body broadly rounded, 1.81–2.38 (2.07) mm long and 1.28–1.68 times as long as broad. Body greyish green in life. Legs, antennae and rostrum pale brown, very weakly sclerotized. Wax plates indistinct. Antennae 6-segmented, 0.44–0.61 (0.54) mm long and 0.22–0.30 times as long as

body. Antennal segment IV sometimes not completely divided from segment III, segment V thickened at distal half. Length of segments (in mm): I 0.056–0.081 (0.064), II 0.051–0.061 (0.057), III 0.152–0.268 (0.197), IV 0.046–0.068 (0.058), V 0.071–0.091 (0.078), VI 0.061–0.081 (0.067). Primary rhinaria found on segments V and VI, with a circular foramen fringed with very short and fine cilia. Antennal setae comparatively long; setae on segments: II 1–3, III 4–6, IV 4–5, V 1–4, and VI 5 at processus terminalis and 1–2 at the base; the longest setae on segment III 0.030–0.040 mm long and 1.00–1.40 times as long as the diameter of the segment. Antennal segments III-VI faintly spinose, not imbricated. Antennal segments V and VI more pigmented than the other segments. Rostrum reaching to middle coxae or often a little beyond them. Ultimate rostral segment 0.121–0.152 mm long with 10–13 very short setae. Head sclerotized along the median line and rarely at the basal part of antennae. Head with long setae, maximally 0.051–0.071 mm long. Genital plate as in the emigrant. Hind femorotrochanter 0.36–0.51 (0.42) mm long. Hind tibiae thinly with short setae which are maximally 0.025–0.035 mm long and 0.67–0.87 times as long as the diameter of hind tibiae. Tarsi not spinose and separated into 2 parts. Second segment of hind tarsi about 0.081–0.101 mm long. Dorso-apical setae rather thick, slightly capitate at the apex, about 0.035–0.040 mm long.

Fundatrix first instar larva. Not distinguishable from the corresponding stage of *E. moriokense.* Only antennal and rostral characters should be given on the basis of 3 specimens collected from embryo galls on *U. davidiana var. japonica.* Antennae 5-segmented, spinose on segments IV and V. Segment III thicker toward the apex, V short. Length of segments (in mm): I 0.033–0.038, II 0.030–0.033, III 0.051–0.056, IV 0.040–0.045, V 0.035–0.043. Antennal segment I with 2, II with 2, III with 6 or 7, IV with 4 or 5, and V with 7 or 8 setae. Ultimate rostral segment 0.101–0.106 mm long, convex laterally.

Fundatrix second instar larva. Description is based on 5 specimens collected from galls on *U. davidiana* var. *japonica.* Body 0.346–0.435 (0.392) mm long, 0.48–0.53 times as wide as long, maximal width 0.356–0.460 mm. Body without visible wax gland plates. A broad, oval dorsal sclerite on head reaching to ventral side. The sclerite separated into 2 parts by a median slit. Antennae 5-segmented. Antennal segment III rather short. Segment V thick, 0.55–0.61 times as wide as the axial length. Segments III, IV and V with a few spinules. Length of segments as follows: I 0.030–0.040 (0.036), II 0.030–0.035 (0.032), III 0.061–0.068 (0.065), IV 0.043–0.051 (0.046), V 0.040–0.046 (0.044). Antennal setae fine and short. Number of setae on each segment as follows: I 2, II 2, III 6–10, IV 4–5, V 7. The longest setae on segment IV 0.030–0.040 mm, and apical setae on the last segment 0.015–0.018 mm long. Primary rhinaria present on segments V and VI, fringed with fine cilia. Ultimate rostral segment 0.099–0.116 (0.110) mm long, with 12–16 accessory setae. Rostral segment II with 2 rather sclerotized transversal bars at apical 1/3 and 2/3 of the segment. Thoracic tergites almost membranous except for 3 pairs of sclerites, below which the legs occur. Spiracles on meso- and metanotum rather sclerotized and prominent. Abdominal tergites membranous. Abdominal setae maximally 0.035–0.038 mm long. An oval sclerotized stigmal plate present above the pore. Hind femorotrochanter 0.147–0.167 (0.160) mm long. Tibiae and tarsi not spinose, thinly with some setae. The longest setae on hind tibiae about 0.025 mm long. Tarsi separated into 2 segments, thick especially on fore and mid legs. Dorso-apical setae 0.030–0.033 mm long, capitate at

the apex. Empodial setae faintly capitate at the apex, about 0.025 mm long.

Apterous fundatrigenia adult. Description is based on 3 specimens collected from 3 galls on *Ulmus davidiana* var. *japonica*. Body more elongate than that of fundatrix. Body length 1.530–1.906 mm. Head, legs and rostrum weakly pigmented. Head almost sclerotized, sometimes with a few, not sclerotized cells. Eyes consisting of 2 parts: multifacetted eye and triommatidion. The latter occurring at the posterior margin of the former. Antennae 6-segmented, 0.612–0.688 mm long and 0.36–0.39 times as long as body. Antennal segment V longer than IV and almost as long as VI. Segment III with a few, unpigmented spots. Length of segments (in mm): I 0.061–0.068, II 0.051–0.061, III 0.260–0.298, IV 0.066–0.076, V 0.081–0.094, VI 0.086–0.099. Primary rhinaria oval, distinct, with very short cilia, present on segments V and VI, with a few accessory rhinaria on VI. Antennal setae short and fine; setae on segments: I 2–3, II 2–3, III 16–22, IV 4–5, V 5–7, and VI 1–3 at the base and 5 at processus terminalis. The longest setae on segment III 0.030–0.033 mm, and apical setae on the last segment 0.010–0.013 mm long. Segments III-VI faintly spinose. Rostrum reaching to middle coxae. Ultimate rostral segment 0.109–0.119 mm long, with 9–10 setae. Wax gland plates present on abdominal tergites, consisting of several cells, but indistinct and without a definite border. Setae on tergite V 0.046–0.051 mm long. Cornicles slightly projecting, surrounded by about 9 setae. Genital plate as in fundatrices. Hind femorotrochanter 0.402–0.465 mm long. Tibiae thinly with short setae, which are maximally 0.025–0.040 mm long on the hind legs. Tarsi not spinose. First tarsal segment with 2 long setae, which are 0.040–0.046 mm long on hind legs, and, except on hind legs, with 1 spine-like seta. Second tarsal segment of hind legs 0.114–0.121 mm long. Empodial setae shorter than claws, 0.028–0.030 mm long on hind legs.

Sexupara. Description is based on 4 specimens collected on the trunk of *Ulmus davidiana* var. *japonica*. Body length 1.69–2.00 (1.84) mm. Head, thorax, antennae and legs dark brown to black. Antennae 6-segmented, 0.763–0.834 mm long or 0.39–0.48 times as long as body. Antennal segments V and VI distinctly shortened. Processus terminalis on the last segment shortened. Length of segments (in mm): I 0.061–0.063 (0.061), II 0.046–0.056 (0.051), III 0.399–0.480 (0.436), IV 0.101–0.121 (0.110), V 0.071–0.081 (0.075), VI 0.056–0.066 (0.060). Secondary rhinaria present on segments III and IV rather broad, regularly arranged, encircling about 3/4 the segment. Antennal segments III with 16–28, and IV with 4–5 secondary rhinaria. Primary rhinaria present on segments V and VI, fringed with cilia especially on segment VI. Antennal setae more numerous and longer than in the emigrant. Antennal segment I with 3–5, II with 3–4, III with 20–27, IV with 6–7, V with 6–8, and VI with 5–6 setae. The longest setae on segment III 0.056–0.066 mm and apical setae on the last segment 0.015 mm long. Antennal segments V and VI intensively spinose, weakly imbricated. Ultimate rostral segment 0.119–0.131 mm long, with 12–14 accessory setae. Abdomen with weakly sclerotized intersegmental bands. Abdominal setae on tergite V maximally 0.051–0.066 mm long. Cornicles present on tergite V, weakly sclerotized, each surrounded by 9–11 setae. Wax gland plates present on head and abdominal tergites I-VIII. Head with 1 pair of circular wax plates. Abdominal tergites I-VII each with 1 pair of spinal and 1 pair of lateral wax plates, and tergite VIII with only 1 pair of spinal ones. Lateral plates with an irregular-shaped central cell surrounded by blackish frame, where several reduced cells are found as spots;

spinal plates circular, wholly blackish. Lateral plates larger than spinal plates on each tergite. Genital plate spinose, with 2 or 3 setae at the anterior part and 10–16 setae along the hind margin. Hind femorotrochanter 0.528–0.571 (0.544) mm long. Tarsi not very spinose; first tarsal segment with 2 long setae, which are 0.046–0.051 mm long on hind legs. Second segment of hind tarsi 0.121–0.131 mm long. Fore wings with media once branched.

Gall. A fundatrix forms one leaf-roll gall on a shoot. Leaves are rather tightly rolled downward along the edge. Usually a lateral half of the leaf is rolled and the other side is hardly affected. The rolled part is not very inflated. The galls tend to turn yellowish green and lose flexibility as they mature. It is easy to distinguish them from the galls of *E. harunire* and *E. japonicum*.

Distribution. This species occurs all over Japan, from Shiretoko, Hokkaidô to Kagoshima, Kyûshû. Moreover, I have had the opportunity to examine one gall, supposedly of this species, collected by Mr. Fujisawa in Seolag-san, Korea; although one fundatrix included in the gall is prominently smaller than the Japanese form in body size and femur length, it well agrees with the latter in other characters.

Eriosoma moriokense, sp. nov.

Eriosoma moriokense Akimoto, 1981 [nomen nudum].

Specimens examined. Emigrants, 4 indvs., Morioka, Honshû, ex *Ulmus davidiana* var. *japonica*, 26 VI 1972 (Oku); 4 indvs., Sapporo, Hokkaidô, ex galls on *U. davidiana* var. *japonica*, 26 VI 1978; 4 indvs., Jôzankei, Hokkaidô, ex galls, 9 VII 1978; 1 indv. (holotype), Sapporo, ex a gall, 1 VII 1982. Fundatrix adults, 1 indv., Sapporo, ex a gall, 15 VI 1972 (Aoki); 1 indv., Bibai, ex a gall, 16 VI 1972 (Aoki); 4 indvs., Sapporo, ex galls, 10 VI 1978. Fundatrix 2nd instar larvae, 1 indv., Sapporo, ex a gall, 27 V 1978; 4 indvs., ditto, 30 V 1979. Apterous fundatrigenia adults, 3 indvs., Bibai, ex a gall, 16 VI 1972; 2 indvs., Sapporo, ex galls 29 VI 1980. First instar larvae deposited by emigrants, 15 indvs., Sapporo, 3 VI 1973 (Aoki). Sexuparae, 2 indvs., Sapporo, ex the trunk of *Ulmus davidiana* var. *japonica*, 18 IX 1980; 2 indvs., ditto, 19 IX 1980. Exule adult, 1 indv., Sapporo, ex the root of *Sedum* sp., 24 IX 1982 (Miyazaki & Aoki).

Emigrant. Description is based on 8 specimens collected from galls on *Ulmus davidiana* var. *japonica*. Body length 1.63–2.18 (1.93) mm. Head and thorax dark brown. Antennae and legs brown. No wax plate present. Antennae long, 6-segmented, 1.06–1.46 mm long or 0.659–0.739 (0.690) times as long as body. Antennal segment III long; segments V and VI shortened, when combined together 0.11–0.13 times as long as the whole antennal length. Processus terminalis on the last segment, 0.030–0.035 mm long and 0.40–0.50 times as long as thesegment. Length of segments (in mm): I 0.061–0.081 (0.066), II 0.051–0.071 (0.060), III 0.672–0.914 (0.792), IV 0.157–0.245 (0.190), V 0.061–0.083 (0.069), VI 0.056–0.083 (0.075). Secondary rhinaria narrow, found on III and IV, encircling 1/2–2/3 the segment. Interrhinarial parts constricted conspicuously. Segment III with 33–41 and IV with 7–9 secondary rhinaria. Primary rhinaria present on V and VI, with a ciliate transverse foramen, from which a tonguelet projects; one on VI with a few accessory rhinaria, which are semicircular and fringed with cilia. Antennal setae fine; segment VI with 4–5 apical setae, 0.013 mm long, at processus terminalis and with 1–2

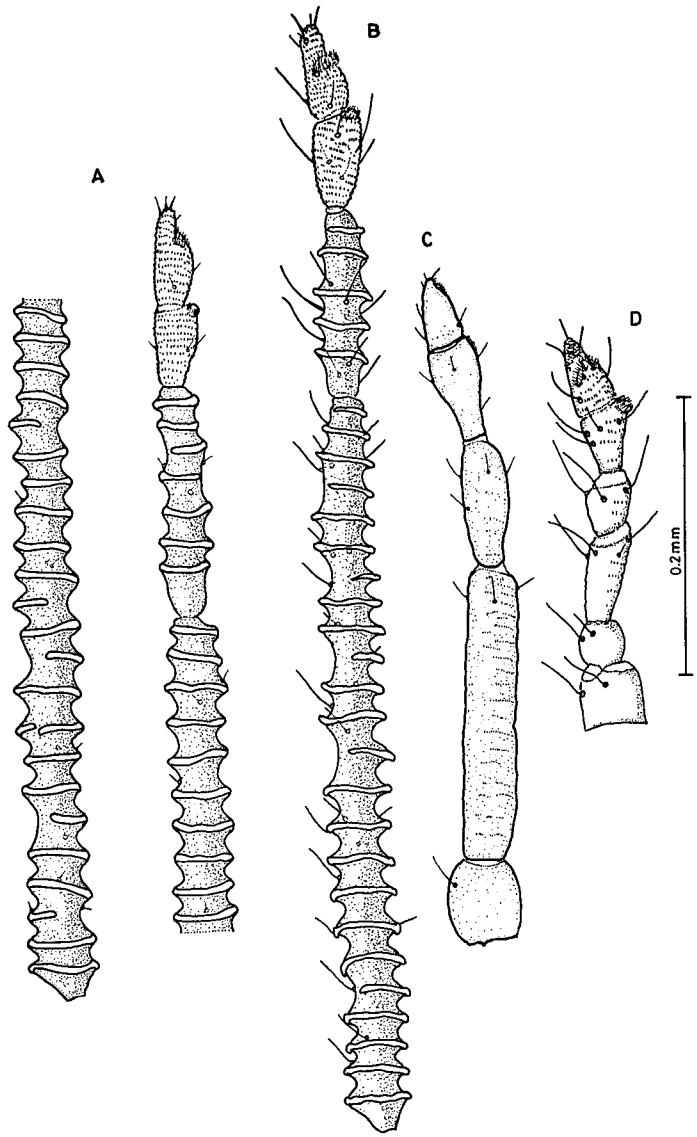

Fig. 14. *Eriosoma moriokense*. Antennae. A, emigrant; B, sexupara; C, fundatrix adult; D, exule adult.

setae at the base, V with 5–6 and II–IV each with a few shorter setae. Antennal segments V and VI imbricated and spinose. Segment IV spinose at the base. Ultimate rostral segment 0.116–0.131 mm long, with several fine accessory setae. Abdominal tergites each with a sclerotized intersegmental band and with some fragmentary sclerites on the pleural part. Sclerotized cornicles present on tergite V, slightly projecting, each surrounded by 8–10 setae. Genital plate spinose, with 1 pair of setae at the middle and 9–15 setae along the hind margin, pigmented except for the central part. A pair of sclerotized plates present laterally to

genital plate, with many spine-like setae. Cauda semicircular with 2 setae. Hind femorotrochanter 0.48–0.61 (0.57) mm long. Setae on hind femora and tibiae short, respectively 0.030–0.035 and 0.028 –0.035 mm long. Tarsi faintly spinose; first tarsal segment with 2 long setae, which are 0.040–0.046 mm long on hind legs, and, except on hind legs, with 1 spine-like seta. Second segment of hind tarsi 0.121–0.162 mm long. Fore wings with media once branched. Hind wings with Cu 1a and Cu 1b.

Fundatrix adult. Description is based on 6 specimens collected from galls on *Ulmus davidiana* var. *japonica*. Body broadly rounded, 2.22–2.38 (2.30) mm long and 1.42–1.61 times as long as broad, red brown in life. Legs, rostrum and

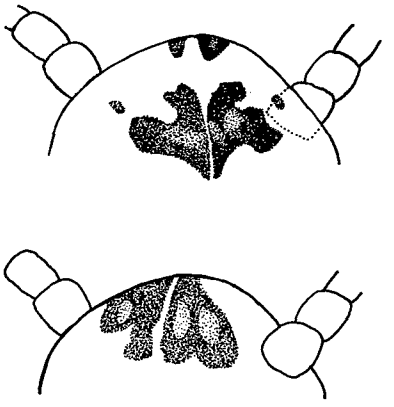

Fig. 15. *Eriosoma moriokense.* Head of the fundatrix 2nd instar larva. Above, dorsal view. Below, ventral view.

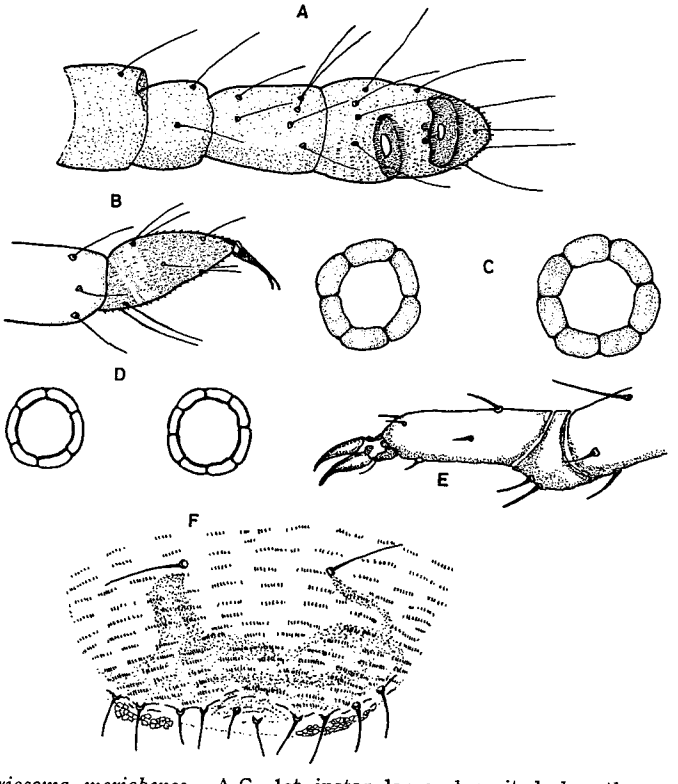

Fig. 16. *Eriosoma moriokense.* A-C, 1st instar larva deposited by the emigrant; A, antenna; B, hind tarsus; C, wax gland plates (left, spinal plate; right, lateral plate). D, wax gland plates of the exule adult; E, hind tarsus of the exule adult; F, genital plate of the emigrant.

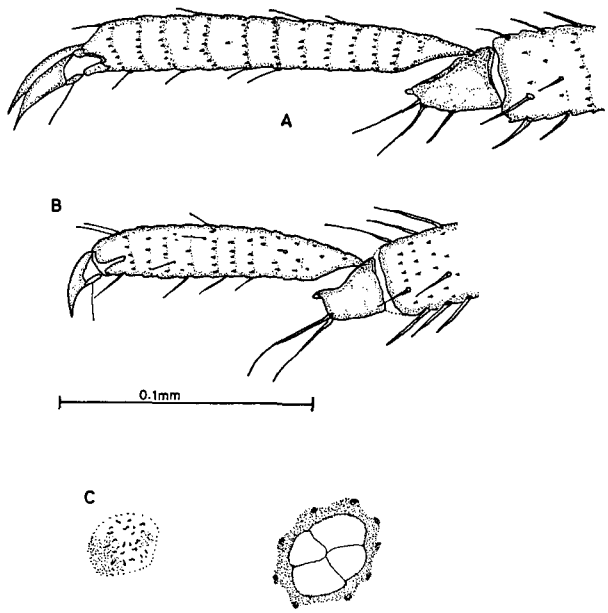

Fig. 17. *Eriosoma moriokense.* A, hind tarsus of the emigrant; B, hind tarsus of the sexupara; C, wax gland plates of the sexupara (left, spinal plate; right, lateral plate).

antennae brown to pale brown. Wax gland plates indistinct. Antennae 6-segmented, 0.50–0.57 (0.53) mm long or 0.22–0.24 times as long as body. Antennal segment III broad, about 0.04 mm wide. Segment V constricted at the base and thickened at the apex. Segment VI relatively short, cone-shaped. Length of segments (in mm): I 0.061–0.081 (0.071), II 0.056–0.063 (0.059), III 0.187–0.258 (0.210), IV 0.066–0.096 (0.079), V 0.068–0.086 (0.075), VI 0.056–0.066 (0.061). Primary rhinaria present on V and VI, inflated and fringed with cilia. Antennal setae fine and relatively short. Number of setae on each segment as follows: II 2–3, III 3–5, IV 3–4, V 2–3, and VI 3 at processus terminalis and 1–2 at the base; the longest antennal setae on III 0.020–0.025 mm long and 0.50–0.71 times as long as the diameter of the segment. Antennal segments III-VI spinose, not distinctly imbricated. Rostrum reaching to middle coxae. Ultimate rostral segment 0.126–0.137 mm long, with 7–9 very short setae. Head with a sclerotized, irregular-shaped median bar, which is more or less heart-shaped on the dorsum, and with a narrow sclerotized bar surrounding the most part of the base of each antenna. Setae on head maximally 0.040–0.046 mm long. Thorax and abdomen membranous, with setae maximally 0.045 mm long. Cornicles absent. Genital plate spinose, wholly pigmented, with 1 pair of setae at the anterior part and 9–11 setae along the hind margin. Cauda semicircular, with 2 setae. Hind femorotrochanter 0.39–0.43 (0.42) mm long. Hind tibiae thinly with very short setae, which are maximally 0.020–0.025 mm long and 0.55–0.82 times as long as the diameter of hind tibiae. Tarsi not spinose, separated into 2 segments. Second segment of hind tarsi 0.083–0.096 mm long. Dorso-apical setae very short and fine, 0.028–0.033 mm long, pointed at the apex.

Fundatrix second instar larva. Body 0.768–0.879 (0.824) mm long, 0.51–0.56

times as wide as long at maximum, without visible wax gland plates. Appendages weakly sclerotized. Head always covered with some fragmentary irregular-shaped sclerites; 1 pair of small sclerotized fragments on the dorsum and another pair on the frontal part; the frontal ones are bridged to the former by narrow sclerotized bars. Antennae 5-segmented. Antennal segment III rather short, often with a trace of division. Segments III, IV and V with a few spinules. Length of segments as follows: I 0.030–0.040 (0.036), II 0.030–0.035 (0.033), III 0.061–0.071 (0.066), IV 0.038–0.043 (0.040), V 0.035–0.043 (0.040). Antennal setae extremely fine and short. The number of setae on each segment as follows: I 2–3, II 2, III 7–8, IV 4, V 7. The longest setae on segment IV 0.018–0.025 mm long, and apical setae on the last segment 0.008–0.010 mm long. Primary rhinaria present on segments IV and V, fringed with fine setae. Rostrum reaching to hind coxae. Ultimate rostral segment 0.101–0.116 (0.106) mm long, with about 14 very fine accessory setae. Rostral segment II with 2 rather sclerotized, transversal bars at apical 1/3 and 2/3. Thoracic tergites membranous except for 3 pairs of pleural sclerites, below which the legs occur. Spiracles on meso- and metathorax rather sclerotized and prominent. Abdominal tergites membranous, and the setae short, maximally 0.030–0.032 mm long. Spiracles found on abdominal tergites I-VII. An oval, sclerotized stigmal plate present above the pore. Hind femorotrochanter 0.157–0.172 (0.164) mm long. Hind tibiae thinly with very fine and short setae, which are maximally 0.020–0.028 mm long. Tibiae and tarsi not spinose. Tarsi thick, separated into 2 segments. Dorso-apical setae 0.028–0.030 mm long, capitate at the apex. Empodial setae very fine, a little longer than claws, 0.018–0.020 mm long.

Apterous fundatrigenia adult. Description is based on 5 specimens collected from 2 galls on *U. davidiana* var. *japonica*. Body more elongate than in the fundatrix. Body length 1.88–2.13 (1.98) mm. Legs, rostrum and antennae weakly sclerotized and brownish. Head with a sclerotized median bar, from which 2 broad transverse bars, dorsal and ventral, stretch to the base of each antenna. Eyes consisting of 2 parts: multifacetted eye and triommatidion, the latter occurring at the posterior margin of the former. Antennae long, 6-segmented, 0.713–0.801 mm long and 0.36–0.43 times as long as body. Antennal segments V and VI relatively very short. Segments III and IV with unpigmented spots which are often elongate. Length of segments (in mm): I 0.068–0.076 (0.073), II 0.053–0.056 (0.055), III 0.334–0.410 (0.373), IV 0.096–0.106 (0.099), V 0.071–0.076 (0.074), VI 0.073–0.091 (0.080). Primary rhinaria found on segments V and VI, oval, with a few accessory rhinaria on segment VI. Antennal setae short and fine; setae on segments: I 2–4, II 3–4, III 8–18, IV 3–4, V 3–4, and VI 1–2 at the base and 4–5 at processus terminalis. The longest setae on segment III 0.020–0.025 mm, and apical setae on the last segment 0.008–0.010 mm long. Antennal segments III–VI spinose. Rostrum reaching to middle coxae. Ultimate rostral segment 0.121–0.131 mm long. Wax gland plates present, but indistinct and without a definite border. Setae on tergite V 0.051–0.061 mm long. Cornicles as in emigrants. Genital plate and cauda as in fundatrices. Hind femorotrochanter 0.495–0.536 (0.516) mm long. Setae on tibiae short, maximally 0.020–0.030 mm long on hind legs. Tarsi not spinose; first tarsal segment with 2 long setae, which are 0.035–0.040 mm long, and, except on hind legs, with 1 spine-like seta. Second tarsal segment 0.144–0.162 mm long on hind legs. Empodial setae shorter than claws, 0.025–0.028 mm long on hind legs.

Sexupara. Description is based on 4 specimens collected on the trunk of *U.*

davidiana var. *japonica*. Body length 1.38–1.69 mm. Head, thorax, antennae and legs brown to dark brown. Antennae rather slender, 6-segmented, 0.812–0.903 (0.845) mm long. Antennal segments V and VI strongly shortened. Processus terminalis on the last segment short and stumpy. Length of segments (in mm); I 0.051–0.061 (0.058), II 0.046–0.056 (0.050), III 0.445–0.531 (0.504), IV 0.116–0.137 (0.131), V 0.051–0.063 (0.060), VI 0.056–0.071 (0.062). Secondary rhinaria present on segments III and IV, very slender, rather irregularly arranged, encircling a little more than 1/2–3/4 each segment. Antennal segment III with 20–23 and IV with 4–5 secondary rhinaria. Interrhinarial parts rather constricted. Primary rhinaria present on segments V and VI, indistinct in shape, fringed with dense cilia, with a few accessory rhinaria on segment VI. Antennal setae more numerous and longer than in emigrants. Antennal segment I with 3–5, II with 2–6, III with 19–24, IV with 6–8, V with 5–6, and VI with 5–7 setae. The longest setae on segment III 0.038–0.046 mm and apical setae on the last segment 0.013–0.015 mm long. Antennal segments V and VI intensively spinose, weakly imbricated. Ultimate rostral segment 0.111–0.119 mm long, with about 12 accessory setae. Abdominal tergites with weakly sclerotized intersegmental bands or fragmentary sclerites. Abdominal setae on tergite V maximally 0.040–0.046 mm long. Cornicles present on tergite V, weakly sclerotized, each surrounded by 14–16 setae. Wax gland plates present on head and abdominal tergites I-VIII. Head with 1 pair of wax plates, which consist of irregular-shaped circles and are not sclerotized. Abdominal tergites I-VII each with 1 pair of spinal and 1 pair of lateral plates, and tergite VIII only with 1 pair of spinal ones. Spinal plates without distinct border, reduced to spots. Lateral plates with a blackish circular frame, from which a few partitions stretch to the center but often do not form complete cells. Genital plate as in emigrants. Hind femorotrochanter 0.435–0.485 (0.459) mm long. Setae on femora and tibiae long, 0.046–0.051 mm long respectively on hind legs. Tarsi spinose; first tarsal segment with 2 long setae, which are 0.030–0.040 mm long on the hind legs, and, except on hind legs, with 1 spine-like seta. Second segment of hind tarsi 0.101–0.111 mm long. Fore wings with media once branched.

Exule adult. Description is based on a single specimen collected from the root of *Sedum* sp. Body oval, 1.31 mm long. Antennae, legs and rostrum sclerotized and brown. Other parts generally membranous. Eyes represented by a triommatidion only. Antennae 6-segmented, smooth, short, 0.268 mm long and 0.20 times as long as body. Antennal segment V thicker toward the apex. Segment VI cone-shaped. Length of segments (in mm): I 0.045, II 0.030, III 0.061, IV 0.035, V 0.045, VI 0.051. Processus terminalis on the last segment stumpy. Primary rhinaria present on segments V and VI, fringed with many cilia; one on segment VI with a transverse opening, from which a tonguelet projects, and with a few, ciliate accessory rhinaria. Secondary rhinaria absent. Antennal setae thin and comparatively short; the longest setae on segment III 0.040 mm long. Number of setae on each segment: I 2, II 2, III 4, IV 4, V 4, and VI 2 at the base and 4 at processus terminalis. Apical setae on the last segment short, 0.013 mm long. Rostrum reaching to the hind margin of middle coxae. Ultimate rostral segment 0.096 mm long, with 6 pairs of setae; the longest one 0.040 mm long. Wax gland plates present on head, thorax and abdomen, consisting of 1 large central cell and smaller surrounding cells arranged in a single row. Head with 4 pairs of wax plates; 1 pair at ventrofrontal position, 1 pair at frons, 1 pair at dorsofrontal position and 1 pair at dorsal spinoposterior position. Ventrofrontal pair with 8

circumferential cells, dorsofrontal one with 5, and spinoposterior one with 6. Pro-, meso-, and metanotum, and abdominal tergites I-VII each with 1 pair of spinal and 1 pair of lateral wax plates. Segment VIII with 1 spinal pair only. Spinal plates with 5–8 and lateral ones with 6–8 circumferential cells. The diameter of spinal plates on abdominal tergite V about 0.048 mm. Lateral wax plates always a little larger than spinal ones in all thoracic and abdominal segments. Body setae feeble, short and thin; the longest one on abdominal tergite IV 0.040 mm long. Cornicles with a sclerotized rim, slightly projecting, each surrounded by 10 setae. Genital plate pigmented, with 2 long setae at the anterior part and 9 setae along the hind margin. Hind femorotrochanter 0.247 mm long. Legs wholly smooth, thinly covered with short and stout setae. Hind tibiae with 24 setae, of which the longest one is 0.035 mm long and 1.17 times as long as the diameter of the segment. Tarsi not completely separated into 2 segments. First tarsal segment of hind legs with 1 pair of stumpy setae 0.01 mm long. Second tarsal segment of hind legs 0.066 mm long. Empodial setae feeble and rudimentary.

Gall. Fundatrices often transform whole leaves. Early galls are strongly twisted. As the galls mature, they become loosened, so aphids inside often become visible. Mature galls are reddish or brownish and covered thinly with waxy powder. One or 2 small galls are usually formed on more distal leaves in addition to the main gall on the same shoot. Like the clustering gall of *Aphiodunguis mali*, the additional ones are inhabited by migratory larvae from the main gall.

Distribution. Hokkaidô; Honshû. Probably this species is distributed also in Korea: the species described by Paik (1972) as *Eriosoma* sp. B seems to agree with *E. moriokense*.

Biological note. As an example of the defensive behavior of aphids Aoki (1978) reported that the first instar larvae of "*Colopha* sp. near *caucasica*" (=*Hemipodaphis persimilis*, sp. nov.), which does not produce the sterile "solider" caste, attack predators which invade the galls. A similar but much less violent aggressive behavior was observed in the 2nd and 3rd instar larvae of *E. moriokense*. In laboratory I put syrphid or lepidopterous larvae into galls, which were collected on June 24th–28th, 1978. Although soon retrieved from the galls, the intruders were clutched by 5–7 larvae every time. The aphid larvae pricked the skin of the intruders with the stylet. I could not ascertain, however, that their stylets really penetrated the skin. In the case of *Hemipodaphis persimilis*, the first instar larvae soon appear on the surface of the galls and walk about actively in response to an impact to the galls. But the larvae of *E. moriokense* were sluggish in the galls and hardly responded to physical stimuli. Alternatively, yellow brownish fluid secreted from cornicles of larvae released an aggressive behavior. When I put near larvae forceps which were smeared with the secretion at the tip, several larvae clung to the forceps and tried to sting them with the stylet. First and fourth instar larvae showed no aggressive behavior. Such a moderate aggressive behavior does not seem to have a full defensive effect against the predation of syrphid larvae or anthocorid bugs. In fact, the galls of *E. moriokense* are frequently invaded by them like those of other *Eriosoma* species, whose larvae show no aggressive behavior at all.

Eriosoma longicornutum, sp. nov.

Eriosoma grossulariae: Akimoto 1981.

Specimens examined. Emigrants, 4 indvs., Jôzankei, Hokkaidô, ex a gall on *U. davidiana* var. *japonica*, 9 VII 1973 (Aoki); 2 indvs., Abashiri, Hokkaidô, ex a gall on *U. laciniata*, 7 VII 1974 (Aoki); 3 indvs. (one the holotype), Sapporo, ex a gall on *U. davidiana*, 24 VI 1978. Fundatrices, 4 indvs., Sapporo, ex galls, 6 VI 1978. Apterous fundatrigenia adults, 4 indvs., ditto, 21 VI 1978. First instar larvae

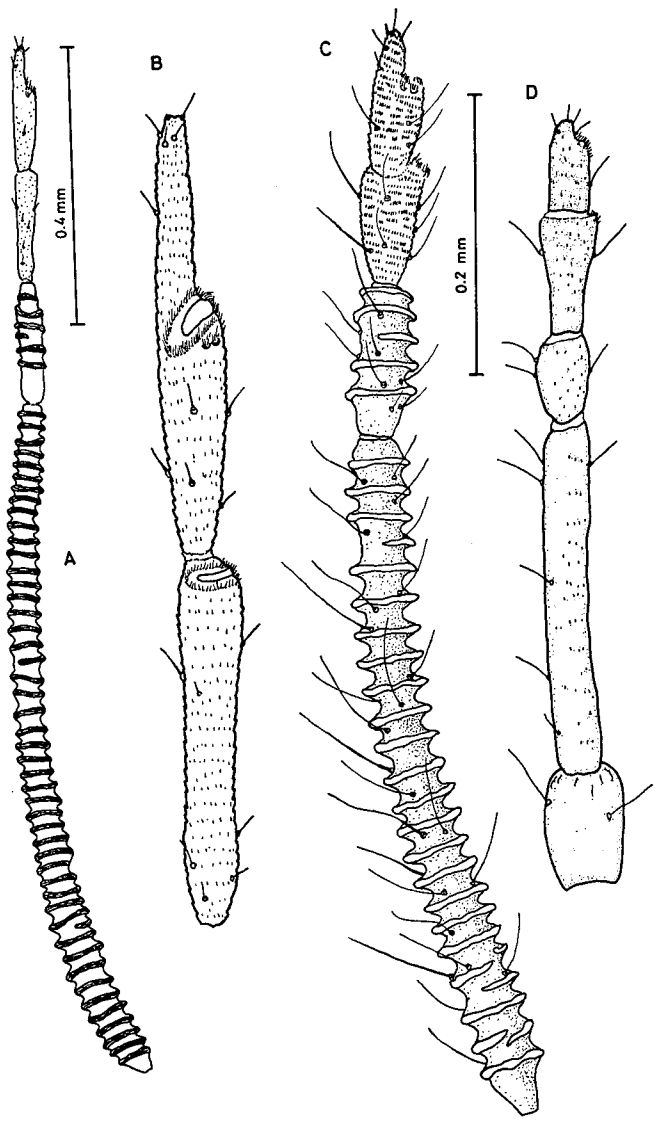

Fig. 18. *Eriosoma longicornutum*. Antennae. A, emigrant; B, antennal segments V and VI of the emigrant; C, sexupara; D, fundatrix adult.

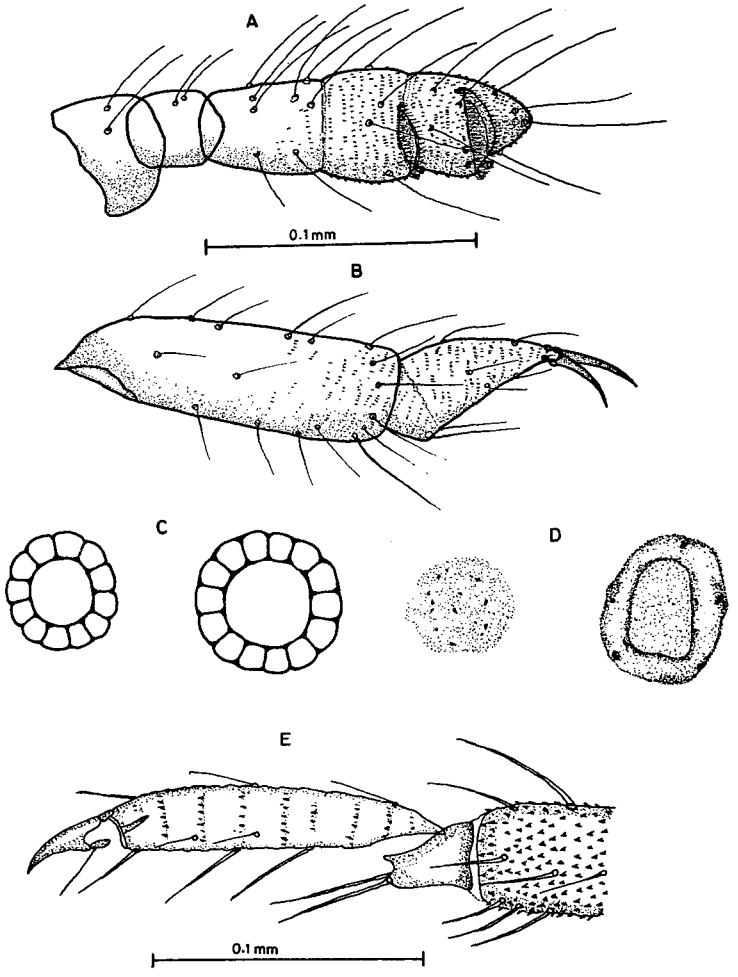

Fig. 19. *Eriosoma longicornutum*. A-C, 1st instar larva deposited by the emigrant; A, antenna; B, hind tarsus; C, wax gland plates (left, spinal plate; right, lateral plate). D, wax gland plates of the sexupara; E, hind tarsus of the sexupara.

(progeny of emigrants), 24 indvs., Jôzankei, ditto, 9 VII 1973 (Aoki). Sexupara, 1 indv., Sapporo, ex the trunk of *U. davidiana*, 19 X 1980.

Emigrant. Description is based on 8 specimens collected from galls on *Ulmus davidiana* var. *japonica* and *U. laciniata*. Body long, 2.00–2.94 (2.50) mm long. Head and thorax dark brown. Legs and antennae brown. No wax gland plate present. Antennae very long, 6-segmented, 1.43–1.73 mm long and 0.49–0.73 times as long as body. Processus terminalis of segment VI very long, about 0.066–0.076 mm long. Length of segments (in mm): I 0.076–0.091 (0.082), II 0.066–0.096 (0.076), III 0.778–1.010 (0.893), IV 0.162–0.182 (0.171), V 0.152–0.172 (0.163), VI 0.177–0.212 (0.193). Secondary rhinaria present on segments III and IV, broad, about 0.008 mm wide, regularly arranged, encircling about 3/4 the segment, strongly upheaved, not covering the dorsal side. Antennal segment III with 36–

46 and IV with 6–8 secondary rhinaria. Primary rhinaria found on segments V and VI, each with a ciliate, suboval foramen, from which a tonguelet projects; one on segment VI with a few accessory rhinaria fringed with cilia. Antennal segment VI with 4 thick setae, maximally 0.015–0.020 mm long, at the apex of processus terminalis and 1 seta at the middle of processus termialis. Antennal segments V and VI intensively spinose and imbricated. Ultimate rostral segment long, about 0.16–0.17 mm long, with many short setae. Abdominal tergites each with a sclerotized intersegmental band and with some fragmentary sclerites on the pleural part. Sclerotized cornicles present on tergite V, weakly elevated, each surrounded by about 9–16 setae. Cauda rather pointed at the apex, with 2 setae near the apex. Genital plate spinose and wholly pigmented, with 1 pair of setae at the middle and 12–22 shorter setae along the lateral and hind margin. A pair of sclerotized plates present laterally to genital plate, with many spine-like setae. Hind femorotrochanter 0.71–1.00 (0.82) mm long and 0.62–0.69 times as long as hind tibiae. Setae on hind femora and tibiae long, 0.061–0.071 and 0.053–0.076 mm long, respectively. Tarsi faintly spinose; first tarsal segment with 2 long setae, which are 0.040 mm long on the hind legs, and, except on hind legs, with 1 spine-like seta. Second segment of hind tarsi 0.187–0.228 mm long. Fore wings with media once branched. Hind wings with Cu 1a and Cu 1b.

Fundatrix adult. Description is based on 4 specimens collected from galls on *U. davidiana* var. *japonica.* Body broadly rounded. Body 2.44–3.00 (2.70) mm long and 1.45–1.58 times as long as broad, yellowish green in life. Legs, antennae and rostrum dark brown. Antennae 6-segmented, 0.576–0.636 mm long and 0.22–0.26 times as long as body. Segment V constricted at the base. Length of segments (in mm): I 0.068–0.081 (0.078), II 0.061–0.073 (0.069), III 0.217–0.263 (0.241), IV 0.061–0.073 (0.067), V 0.081–0.099 (0.087), VI 0.071–0.076 (0.073). Antennal setae relatively long; setae on segments: II 3–4, III 5–8, IV 4, V 4–5, and VI 4 at processus terminalis and 2–3 at the base; the longest setae on III 0.043–0.051 mm long and 1.29–1.58 times as long as the diameter of the segment. Antennal segments V and VI spinose, III and IV faintly spinose. Rostrum reaching to middle coxae. Ultimate rostral segment 0.137–0.144 mm long, with several short setae. Head with a sclerotized bar between the bases of antennae and with a heart-like sclerite on dorsal position; setae on head long, maximally 0.046–0.066 mm long. Cornicle absent. Wax gland plates present on abdominal tergites, consisting of many cells, but indistinct and without a definite border. Genital plate as in emigrants. Hind femorotrochanter 0.485–0.566 (0.520) mm long. Hind tibiae thinly with relatively long setae, which are maximally 0.040–0.048 mm long and 0.75–1.00 times as long as the diameter of hind tibiae. Tarsi not spinose and separated into 2 parts. Second segment of hind tarsi about 0.091–0.101 mm long. Dorso-apical setae long and thick, slightly capitate at the apex, 0.043–0.046 mm long. Empodial setae nearly as long as claws, about 0.033 mm long.

Apterous fundatrigenia adult. Description is based on 4 specimens collected from 1 gall on *Ulmus davidiana* var. *japonica.* Body more elongate than in fundatrices, large, 2.63–2.84 (2.67) mm long. Head with 2 rather cross-shaped sclerites, one dorsal and the other ventral; their extensions united at the frons. Legs and rostrum weakly pigmented and pale brown in slide specimens. Eyes consisting of 2 parts: composed eye and triommatidion, the latter occurring at the posterior margin of the former. Antennae very long; 6-segmented, 1.203–1.297

(1.253) mm long and 0.46–0.49 times as long as body. Processus terminalis very long, 0.053–0.056 mm long. Length of segments (in mm): I 0.086–0.096 (0.092), II 0.076–0.081 (0.080), III 0.581–0.652 (0.608), IV 0.126–0.137 (0.129), V 0.157–0.182 (0.163), VI 0.172–0.195 (0.182). Secondary rhinaria absent. Primary rhinaria oval, fringed with short cilia, present on segments V and VI, with a few accessory rhinaria in segment VI. Antennal setae long; setae on segments: I 6–10, II 5–7, III 25–30, IV 4–6, V 8–11, and VI 3–5 at the base and 4–5 at processus terminalis. The longest setae on segment III 0.043–0.056 mm long, and apical setae on the last segment 0.013–0.015 mm long. Antennal segments III-VI faintly spinose. Rostrum reaching to middle coxae. Ultimate rostral segment 0.177–0.182 (0.179) mm long. Wax gland plates indistinct. Setae on tergite V maximally 0.066–0.076 mm long. Cornicles, genital plate and cauda as in emigrants. Hind femorotrochanter 0.632–0.678 mm long. Setae on tibiae maximally 0.046–0.051 mm long on hind legs. Tarsi not spinose; first tarsal segment with 2 long setae, which are 0.051–0.053 mm long, and, except on hind legs, with 1 spine-like seta. Second tarsal segment 0.172–0.179 (0.175) mm long on hind legs. Empodial setae shorter than claws, about 0.030 mm long on hind legs.

First instar larva (progeny of alate emigrant). Description is mainly based on 24 specimens deposited by emigrants collected from galls on *Ulmus davidiana* var. *japonica*. Body length 0.525–0.621 (0.569) mm. Antennae 5-segmented, 0.179–0.205 mm long or 0.32–0.34 times as long as body, the separation between segments III and IV and also between segments IV and V indistinct. Length of segments (in mm): I 0.030–0.048 (0.037), II 0.023–0.028 (0.025), III 0.040–0.051 (0.046), IV 0.035–0.043 (0.038), V 0.043. Primary rhinaria present on segments IV and V, inflated and fringed with cilia. Antennal setae long; number of setae on each segment as follows; I 2, II 2, III 7–8, IV 4, V 6–7. The longest setae on segment III 0.061–0.066 mm long; apical setae on the last segment maximally 0.051–0.058 mm long. Antennal segments III, IV and V faintly spinose, but the posterior half of segment III without spinules. Rostrum reaching to abdominal tergite V. Ultimate rostral segment faintly spinose, 0.094–0.096 mm long, with 10–15 accessory setae. Wax plates present on head, thorax and abdomen, consisting of 1 large central cell and circumferential cells arranged in a single layer. Head with 4 pairs of wax plates: 2 pairs on the ventral side, 1 pair along the dorsal posterior margin of head and 1 pair on the frons. Pro-, meso- and metathorax and abdominal tergites I-VII each with 1 pair of spinal and 1 pair of lateral plates. Abdominal tergite VIII with only 1 spinal pair. Wax plates on abdominal tergites III-V each consisting of 9–15 (mean 12) cells and 0.030–0.038 mm long in diameter. Body setae long. Abdominal tergites I-VI with 3 pairs of setae located in spinal, pleural and lateral positions. The longest ones on tergites III-V 0.056–0.071 mm long. Cornicles absent. Hind femorotrochanter 0.134–0.139 (0.136) mm long. Tarsi cone-shaped, spinose, and tibiae also with a few spinules on the distal half. Setae on first segment of hind tarsi 0.035–0.046 mm long. Second tarsal segment 0.056–0.058 mm long on hind legs. Length of hind claws 0.028–0.030 mm. Dorso-apical setae of hind tarsi fine and pointed at the apex, about 0.030 mm long. Empodial setae absent on all legs.

Sexupara. Description is based on only 1 specimen collected on the trunk of *Ulmus davidiana* var. *japonica*. Body 2.44 mm long. Head, thorax, antennae and legs dark brown. Antennae much shorter than those of emigrants, 6-segmented,

0.935 mm long and 0.38 times as long as body. Antennal segments V and VI especially shortened and thicker than in emigrants. Processus terminalis on the last segment not so prominent, about 0.040 mm long. Length of segments (in mm): I 0.083, II 0.056, III 0.506, IV 0.109, V 0.084, VI 0.094. Secondary rhinaria present on segments III and IV, rather broad, regularly arranged, encircling about 2/3 the segment, but not covering the dorsal surface. Antennal segment III with 25 (24 on the opposite antenna) and IV with 5(4) secondary rhinaria. Primary rhinaria present on segments V and VI, fringed with cilia, inflated, with a few accessory rhinaria on segment VI. Antennal setae more numerous and longer than in emigrants. Setae of antennal segments: I 4, II 5, III 28, IV 8, V 12, and VI 4 at the base and 5 at processus terminalis. The longest setae on segment III 0.076 mm and apical setae on the last segment 0.018 mm long. Antennal segments V and VI intensively spinose and weakly imbricated; the other segments without any spinules, not imbricated. (Ultimate rostral segment not measurable.) Abdominal tergites each with a sclerotized intersegmental band and with some fragmentary sclerites on pleural part. Abdominal setae long, maximally 0.068 mm long on tergite V. Cornicles present on tergite V, weakly sclerotized, slightly projecting, surrounded by 13 (14) setae. Wax gland plates present on head and abdominal tergites I-VII (wax plates of tergite VIII invisible in the specimen examined). Head with 1 pair of wax plates which are irregular circles. Abdominal tergites I-VII each with 1 pair of spinal and 1 pair of lateral wax plates. Lateral gland plates with a pigmented, irregular-shaped central cell surrounded by a more pigmented frame. Spinal gland plates reduced and indistinct, weakly pigmented and without any cells. Genital plate spinose and pigmented, with 2 long setae at the anterior part, 1 seta at the central part, and 13 setae along the hind margin. Hind femorotrochanter 0.688 mm long. Tarsi not very spinose; first tarsal segment with 2 long setae, which are 0.048 mm long, and, except on hind legs, with 1 spine-like seta. Second segment of hind tarsi 0.126 mm long. Empodial setae as long as claws, 0.025 mm long on hind legs. Fore wings with media once branched and hind wings with 2 cubital veins.

Gall. A fundatrix generally forms one leaf-roll gall on a shoot. A leaf edge of one side is rolled toward the underside. The rolled part becomes strongly swollen, having a large opening, and turns yellowish green as they mature. The other side of leaf remains unaffected. The galls are easily distinguishable from those of other species.

Remarks. In my previous paper (1981) this species was identified with *E. grossulariae*, which was originally described from Europe. Subsequent detailed inspections showed a clear discontinuity between the Japanese and European forms. The Japanese form apparently shows larger values for measurements of many parts in all the morphs, but there may remain for such quantitative differences the possibility that the difference is merely ecophenotypic. However, Dr. Danielsson (pers. comm.) pointed out that the exule first instar larvae (progeny of emigrants) of these forms differ in the character of wax gland plates: the cells of the ring are smaller and more circular in the European form. This fact may support the view that the two forms represent distinct species.

The galls of *E. longicornutum* have been collected not only on *Ulmus davidiana* var. *japonica* but also on *U. laciniata*, though much less frequently, while no galls of other *Eriosoma* species have been collected on the latter plant.

Distribution. Hokkaidô.

Genus Hemipodaphis David, Narayanan & Rajasingh, 1971

Tyep-species: *Hemipodaphis monstrosa* David, Narayanan & Rajasingh, 1971.

Fundatrix adult. Body oval, very broad. Wax gland plates scattered wholly on the dorsum, distinct, rather irregularly circular, sharply bordered by a dark rim, consisting of many granular cells. Pronotum with 4, meso- and metanotum and abdominal tergites I-VI each with 8, and VII with 4 wax plates. A V-shaped wax plate present on VIII. Head, legs, antennae, tip of rostrum, eyes and clypeus strongly sclerotized. Genital plate, anal plate and stigmal plates slightly sclerotized and weakly pigmented. Body setae stout and short, thinly scattered, longer toward the posterior margin of body. Eyes represented only by a triommatidion. Antennae very short, 3-segmented, not imbricated, smooth. Two primary rhinaria present, one at the apex and the other a little more basally, on segment III. Antennal setae stumpy. Processus terminalis on the last segment hardly prominent. Rostrum reaching to between middle coxae and hind coxae. Ultimate rostral segment tapering, with edges rather straight, with a few short setae. Genital plate disc-like, with transverse rows of denticles, uniformly weakly pigmented, with a little more than 10 setae along the hind margin and without any setae at the anterior or central part. Cornicles absent. Cauda reduced to a quite small, semicircular projection, with 1 pair of stout setae. Legs wholly smooth, short, with short and stout setae scattered over. Trochanter and femur united. Tarsi completely separated into 2 segments. Dorso-apical setae much shortened and rudimentary. Empodial setae shorter than claws.

Emigrant, Antennae 6-segmented, very short, narrow, dark pigmented wholly. Secondary rhinaria present on segments III-V, quite narrow, regularly arranged in paralell. Segment V longer than IV. Primary rhinaria present on segments V and VI. Segments I-IV and basal half of V smooth, not imbricated, VI spinose and imbricated. Abdomen without pigmented intersegmental bands, not sclerotized except for anal and genital plates. Cornicles present on abdominal tergite V, not projecting, nor sclerotized, only showing a very small rimmed opening. Abdominal setae scanty and short. Genital plate disc-like, dark pigmented only on the posterior part, with many very short setae along the hind margin; the marginal setae not arranged in a single row, and some setae spreading to the central part of genital plate, thus "anterior setae" indistinguishable. Second tarsal segment imbricated, intensively spinose, rarely with a few setae. Apical part of tibiae slightly imbricated. Empodial setae slightly longer than claws. One pair of setae on first tarsal segment quite short. Fore wings with media once branched and hind wings with 2 cubital veins.

Hemipodaphis persimilis, sp. nov.

This genus, which has been known only by the exule of the type-species, is characterized by having many nodules all over the dorsum of the body and a quite long stylet nearly three times as long as the rostrum. There is another species referable to the genus. It lives in leaf-roll galls on *Zelkova serrata* at Sapporo, northern Japan, where this plant was introduced from Honshû. Aoki (1978) in his report on the aggressive behavior of its first instar larvae treated it as "*Colopha* sp. near *caucasica*". Later he collected its galls on *Zelkova* at Ôtawara, Tochigi Pref., Honshû. He suggested to me that this species belongs to *Hemipodaphis* by

having a very long stylet in the larvae borne by the emigrants.

The long stylet and the nodular dorsum certainly point to the possibility that the leaf-roller on *Zelkova* belongs to the genus *Hemipodaphis*. I have, however, no exule specimens of this species to compare with the description of the type-species from India, owing to the total absence of knowledge as to the exule generation in Japan. Moreover, there is no records on the primary hosts in India. Comparisons in corresponding stages are, therefore, impossible, and there is no way of deciding whether the aphids from Japan and India are conspecific or not. Yet, the characters of the embryos of the emigrants are basically the same as those of the exule larvae, and the wax gland plates seem preferable for a useful comparison, for my taxonomic study on the Eriosomatinae has shown that the shape and arrangement of the wax plates are quite stable through all the developmental stages.

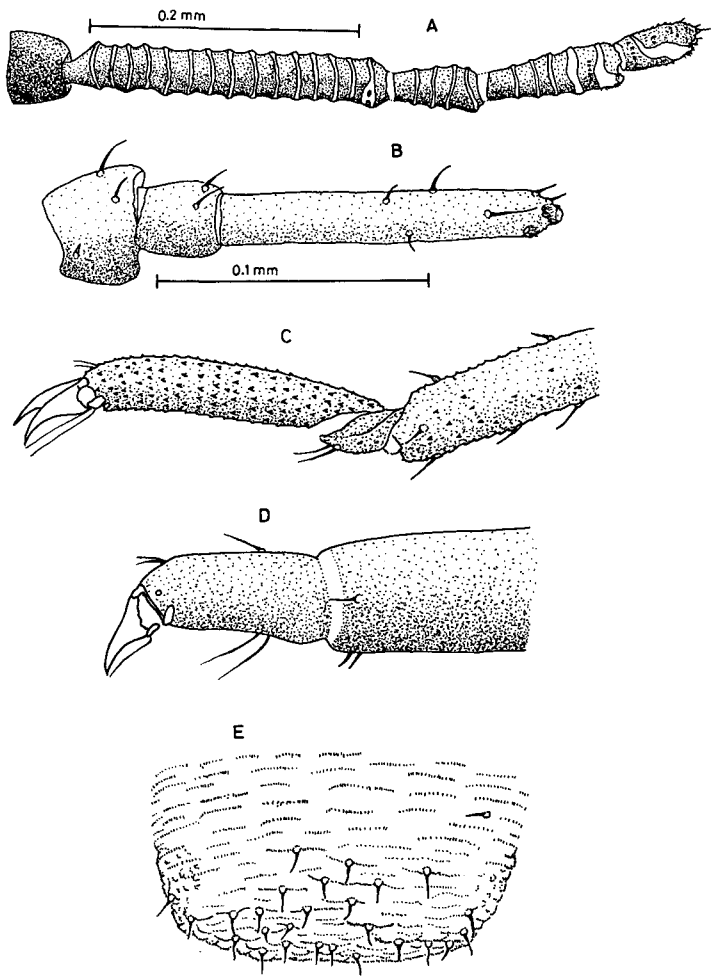

Fig. 20. *Hemipodaphis persimilis*. A, antenna of the emigrant; B, antenna of the fundatrix adult; C, hind tarsus of the emigrant; D, hind tarsus of the fundatrix adult; E, genital plate of the emgirant.

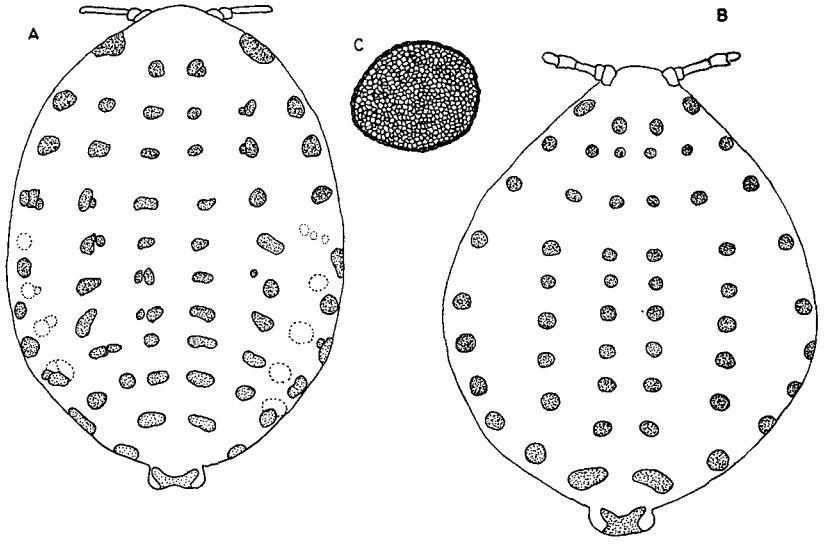

Fig. 21. *Hemipodaphis persimilis.* Arrangement of wax gland plates in the fundatrix adult (A) and the fundatrigenia adult (B). C, wax gland plate of the fundatrix.

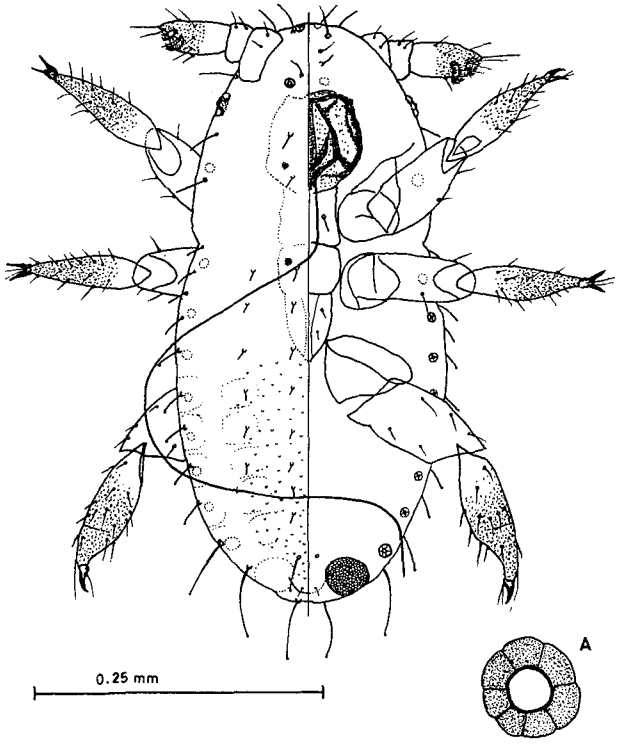

Fig. 22. *Hemipodaphis persimilis.* First instar larva deposited by the emigrant. A, wax gland plate in abdominal tergite VI.

As a result of my comparison some differences have been found between the first instar larvae (embryos of the emigrants) of the Japanese form and the description of the Indian form as follows: (1) The Japanese form show one pair of lateral wax plates on each of the abdominal tergites I-VI and one pair of pleural ones on the tergite VII, while the Indian form has one pair of pleural and one pair of lateral wax plates on the tergite I, one pair of lateral ones on each of the tergites II-V, and one pair of pleural ones on the tergite VIII. (2) In the Indian form the wax gland plates are with a thick and dark rim, while in the Japanese form they show merely a simple border. (3) The Indian form is, through whole developmental stages, equipped with a median cauda-like protuberance with some setae at the posterior margin of the body, and with subprotuberances at both the lateral sides of the median one, while the Japanese form lacks any protuberances.

Considering a great distance between India and Japan, plus these morphological differences, the view may be accepted that these forms represent different species. There is no species of *Zelkova* over the West Bengal region in India. This means that the populations there are maintained only by parthenogenetic generations.

David et al. (1971) suggested that this genus belongs to the *Thoracaphis*-group in the Hormaphididae owing to the long stylet. However, although there is a remarkable morphological specialization in the exule generations, the primary host plant and the characteristics of the generations on the primary host, especially the structure of the gall and the morphology of the fundatrix and the emigrant, indicate that this genus is a member of the Eriosomatinae.

Specimens examined. Emigrants, 1 indv. (holotype), Sapporo, Hokkaidô, ex a gall on *Zelkova serrata*, 3 VIII 1981; 4 indvs., ditto, 28 VIII 1972 (Aoki); 4 indvs., ditto, 29 VIII 1973 (Aoki). Fundatrix adults, 3 indvs., Sapporo, ex galls, 13 VI 1978; 2 indvs., ditto, 17 VI 1978. Apterous fundatrigenia adults, 6 indvs., ditto, 15 VII 1978. Progeny of emigrants, ditto, 29 VIII 1973 (Aoki).

Emigrant. Description is based on 8 specimens collected from galls on *Zelkova serrata.* Body 0.57–0.72 (0.62) mm long. Head, thorax and antennae dark brown, and legs brown. No wax plate present. Antennae 6-segmented, 0.503–0.573 (0.530) mm long or 0.77–0.90 times as long as body. Antennal segment III nearly as long as or a little longer than IV, V and VI taken together. Segment V always longer than IV or VI. Segments I-IV and basal half of V not imbricated and not spinulose, but apical half of V and VI with a few minute spinules scattered. Processus terminalis on segment VI not projecting, about 0.01 mm long. Length of segments (in mm): I 0.045–0.056 (0.050), II 0.043–0.051 (0.046), III 0.212–0.242 (0.226), IV 0.051–0.076 (0.059), V 0.076–0.096 (0.086), VI 0.051–0.066 (0.060). Secondary rhinaria very slender, encircling about 1/2–2/3 the segment. Segment III with 15–22 secondary rhinaria, IV 2–4, V 2–4, VI 0–1. Primary rhinaria present on segments V and VI, with a ciliate, transverse foramen, from which an irregular-shaped arm extends laterally around half the circumference of each segment. Primary rhinarium on segment VI with a few, ciliated accessory rhinaria. Processus terminalis on antennal segment VI with 2–3 thick setae, of which the longest one is about 0.01 mm long. Setae on antennal segments : I 1–3, II 1–2, III 0–2, IV 0–2, V 1–3, basal half of VI 0–1 shorter setae. Ultimate rostral segment 0.157–0.172 (0.164) mm long with a few inconspicuous, accessory setae. Abdominal tergites membranous, without any pigmentation except for cornicles or spiracles. Cornicles present rather laterally, weakly projecting, weakly pigmented,

without any cilia. Longest diameter of cornicles about 0.02 mm long. Cauda semicircular, dorsally with 1 pair of setae. Genital plate with transverse rows of spinules, weakly pigmented at the posterior part, with 24–27 setae arranged irregularly along the hind margin. A pair of pigmented plates present laterally to genital plate, with a few spine-like setae. Hind femorotrochanter 0.328–0.359 (0.340) mm long. Setae on hind femora and tibiae very short and feeble, maximally 0.010 and 0.015 mm long respectively. Femora and tibiae smooth, while tarsi spinose. First tarsal segment with 2 setae, which are about 0.018 mm long on hind legs, and without spine-like setae. Second segments of hind tarsi 0.116–0.126 mm long. Empodial setae a little longer than claws, about 0.03 mm long on hind legs.

Fundatrix adult. Description is based on 5 specimens collected from galls on *Zelkova serrata*. Body broadly rounded. Body 1.52–2.03 (1.74) mm long and 1.25–1.47 times as long as broad. Head, legs, antennae and rostrum brown. Body wholly covered with circular wax gland plates. Antennae short, smooth, and not imbricated; 3-segmented, 0.495–0.545 mm long, 0.13–0.16 times as long as body and 0.83–0.96 (0.89) times as long as femorotrochanter. Antennal segments I and II normal, but succeeding segments fused to form segment III, which is slender, a little narrower toward the base and apex, about 0.051 mm wide. Processus terminalis on segment III not projecting. Length of segments (in mm): I 0.056–0.061 (0.057), II 0.045–0.051 (0.048), III 0.141–0.167 (0.150). Two, apical and subapical, primary rhinaria present on segment III, each with a tonguelet projecting from a foramen. Apical rhinarium surrounded by a few, ciliate accessory rhinaria. Secondary rhinaria absent. Antennal setae fine; number of setae on each segment as follows: I 1–2, II, 2, III 8–10. The longest antennal setae on III 0.023–0.025 mm long. Rostrum reaching to between middle coxae and hind coxae. Ultimate rostral segments 0.126–0.146 (0.138) mm long with a few very short accessory setae. Head wholly sclerotized, with relatively long setae, of which the longest ones are 0.045–0.051 mm long. Wax gland plates present on thorax and abdomen. Prothorax with 1 pair of spinal and 1 pair of lateral gland plates; lateral gland plates located anterior to spinal gland plates at the level of clypeus. Meso- and metathorax and abdominal tergites I-VI with 1 pair of spinal, 1 pair of pleural and 1 pair of lateral gland plates; abdominal tergites II–VI each with 1 pair of additional gland plates on the ventral side. Abdominal tergite VII only with 1 pair of spinal and 1 pair of lateral gland plates. An irregular-shaped wax gland plate present just above anal plate, and its furcate tails extending to cauda. Thoracic and abdominal wax gland plates circular to elongate, often with a division or completely separated into 2 smaller gland plates, rimmed by a row of dark cells. Inner circles comprising an assemblage of numerous brighter cells. Genital plate disc-shaped, weakly sclerotized, with 8–11 setae. Anal plate projecting, with long setae; the longest one about 0.051 mm long. Hind femorotrochanter 0.268–0.313 (0.288) mm long. Tibiae and tarsi smooth. Tibiae thinly with setae; the longest one about 0.030 mm long on hind legs. Tarsi not separated into 2 segments, 0.066–0.076 (0.070) mm long on hind legs. Empodial setae present, but fine and not longer than claws.

Apterous fundatrigenia. Description is based on 6 specimens collected from a gall on *Zelkova serrata*. Body broadly rounded. Body 1.34–1.63 (1.46) mm long and 1.26–1.41 times as long as broad. Head, legs, antennae and rostrum pale brown. Body wholly covered with circular wax gland plates. Antennae smooth

and not imbricated; 6-segmented, but rarely 5-segmented, 0.571–0.722 (0.628) mm long, 0.20–0.22 times as long as body and 0.94–1.10 times as long as femorotrochanter. Antennal segments III and IV rarely fused, with a trace of division between. Length of antennal segment III variable. Antennal segment V thickened toward the apex. The width of antennal segment III 0.025–0.030 mm. Processus terminalis on segment VI not projecting. Length of segments (in mm): I 0.035–0.056 (0.044), II 0.045–0.051 (0.048), III 0.053–0.091 (0.069), IV 0.035–0.043 (0.038), V 0.053–0.073 (0.063), VI 0.045–0.056 (0.052). Primary rhinaria present on segments V and VI, with a tonguelet projecting from a foramen; one on segment VI with a few ciliate accessory rhinaria. Secondary rhinaria absent. Antennal setae fine and thin; number of setae on each segment as follows: I 2–3, II 1–3, III 0–1, IV 0–1, V 2–4, VI 3–6. The longest setae on segment V about 0.015 mm long. Rostrum reaching to between middle coxae and hind coxae. Ultimate rostral segment 0.131–0.162 (0.146) mm long, with a few very short accessory setae, the blade almost straight, not very tapering. Head wholly sclerotized, with relatively long setae, of which the longest ones are 0.030–0.040 mm long. Abdominal tergites membranous. Cornicles absent. Setae on abdominal tergite III about 0.045–0.051 mm long. Wax gland plates present on thorax and abdomen. Prothorax with 1 pair of spinal and 1 pair of lateral gland plates; lateral gland plates located anterior to spinal ones at the level of the cavities of fore coxae, and spinal ones posterior to the cavities of fore coxae. Meso- and metathorax and abdominal tergites I-IV with 1 pair of spinal, 1 pair of pleural and 1 pair of lateral wax gland plates. Abdominal tergites V and VI with 1 pair of spinal and 1 pair of lateral wax gland plates, and tergite VII only with larger spinal ones. One irregular-shaped wax gland plate present just above anal plate, its furcate tails extending to cauda. Thoracic and abdominal wax gland plates circular to elongate, without any divisions at all, rimmed by a row of dark cells. Inner circles comprising numerous brighter cells. Genital plate disc-shaped, wealky sclerotized, with 13–21 setae. Hind femorotrochanter 0.288–0.333 (0.312) mm long. Tibiae and tarsi smooth. Tibiae thinly with setae; the longest ones about 0.030–0.035 mm long on hind legs. Tarsi not separated into 2 segments, 0.071–0.106 (0.091) mm long on hind legs. Empodial setae present, but quite fine and much shorter than claws. Anal plate projecting, with long setae, the longest setae about 0.091 mm long.

Progeny of emigrants. Description is based on 6 specimens deposited by emigarnts collected from 1 gall on *Zelkova serrata.* Body 0.485–0.515 (0.504) mm long, or 2.15–2.27 times as long as broad. Eyes represented only by a triommatidion. Antennae broad, 3-segmented, 0.106–0.116 (0.112) mm long or 0.21–0.23 times as long as body. Antennal segments following segment II fused to form segment III. Length of segments (in mm): I 0.025–0.030 (0.027), II 0.020, III 0.061–0.066 (0.065). Two primary rhinaria present on subapical position and apical 2/5 of segment III, fringed with cilia, with an elongate foramen, from which a tonguelet projects; subapical one with a few ciliate accessory rhinaria. Antennal setae long; apical setae on segment III 0.040–0.043 mm long. Number of setae on each segment as follows: I 2, II 2, III 11–12. Apical 2/3 of segment III with transverse rows of denticles. Segments I and II smooth. Rostrum reaching to the cavities of hind coxae. Ultimate rostral segment smooth, with 2 pairs of setae at apical 1/3 and 2/3 of the segment, 0.058–0.065 (0.061) mm long. Stylet much longer than rostrum, reaching beyond the posterior margin of body, nearly as long as body, about 0.45–0.51 mm long. Wax gland plates present on head, thorax

and abdomen. Head with 2 pairs of wax gland plates located on the frons and the dorsal posterior margin respectively. Wax gland plates on head consisting of 1 central bright cell and 2–4 surrounding cells. Pro-, meso- and metathorax with 1 pair of spinal and 1 pair of lateral wax gland plates (metathoracic ones often indistinct), and abdominal tergites I-VI only with 1 pair of lateral ones located on rather ventral surface. Thoracic and abdominal wax gland plates similar to cephalic ones, circular, comprising a single central cell surrounded by darker cells, about 0.01 mm long in diameter on abdominal tergite V. Abdominal tergite VII with 1 pair of larger circular wax plates located ventrally and comprising same-sized cells, some of which are brighter than others. Body setae long, capitate at the apex. Pronotum with 2 pairs of spinal and 2 pairs of lateral setae. Meso- and metanotum with 1 pair of spinal, 1 pair of pleural and 2 pairs of lateral setae. Abdominal tergites I-IV with 1 pair of spinal, 1 pair of pleural and 1 pair of lateral setae. Abdominal tergites V-VII only with 1 pair of spinal and 1 pair of lateral setae. Lateral setae on tergite V 0.048–0.051 mm long. Tergite VIII rather spinally with 1 pair of long and stout setae about 0.056 mm long. Hemispherical nodules scattered over the spinal to pleural surface of abdominal tergites. Cornicles absent. Hind femorotrochanters 0.121–0.126 (0.123) mm long, smooth. Tibiae and tarsi fused to show a mere indistinct division. Apical half of tibiae spinose with about 13 stout setae maximally 0.023 mm long. Tarsi cone-shaped, spinose, 0.040–0.043 mm long on hind legs. Length of hind claws 0.023–0.025 mm long. Empodial setae fine and long, reaching to beyond the tip of claws, 0.025–0.030 (0.028) mm long. Dorso-apical setae finer but longer than empodial ones, 0.045–0.051 mm long.

Gall. Fundatrices form clustering galls composed of several rolled leaves of one shoot. In early galls, fundatrices are found within one leaf-roll. Other leaf-rolls are inhabited with time. Mature leaf-rolls are thinly covered with waxy powder.

Distribution. Hokkaidô (Sapporo); Honshû (Ôtawara, Tochigi Pref.).

Remarks. Leaf-roll aphids of *Zelkova* have been known in the genus *Byrsocryptoides* (two species) and *Colopha* (*C. caucasica*) so far, all recorded on *Z. carpinifolia* in Gruziya, USSR (Dzhibladze, 1960, '65). As to *Colopha caucasica*, the gall structure and host plant suggest a remote relationship to the genuine *Colopha* species, which form pouch galls on *Ulmus*. It may belong to *Hemipodaphis*, but all depends on whether the exule larvae have a stylet much longer than the rostrum or not.

Although a close relationship between *Byrsocryptoides* and *Hemipodaphis* is also suggested from the gall structure and wax gland plates of fundatrigeniae, there seem to be some important differences. In *Byrsocryptoides* the embryos of emigrants have a rostrum reaching to about three-quarters of the body length and 70–80 μ long in the apical segment (Stroyan, 1963), while in *Hemipodaphis* the exule larvae have a rostrum a little shorter than half the body length and about 60 μ long in the apical segment. (Stroyan does not remark on the stylet of *Byrsocryptoides*.) Moreover, *Byrsocriptoides* and *Hemipodaphis* may be separated by the following differences: (1) apterous fundatrigeniae of *Byrsocryptoides* have wax gland plates composed of small-facetted cells, but the individual cells are much larger than in *Hemipodaphis*; (2) alates of *Byrsocriptoides* have an unbranched media in the fore wings and one cubital vein in the hind wings, while the alates of *Hemipodaphis* have a once-branched media in the fore wings and two cubital veins in the hind wings.

The genera which form galls on *Zelkova*, i.e., *Hemipodaphis* (including "*Colopha*" *caucasica*), *Colophina* and *Byrsocryptoides*, are thought to constitute a phylogenetic group. They are commonly characterized by the wax gland plates which are sharply rimmed and consist of clear same-sized cells in the generations of both primary and secondary hosts.

Another genus, *Gharesia*, which has been recorded only on the secondary host, is doubtless a member of this group so far as based on the wax gland plates. In spite of the absence of the knowledge on the primary host, I would like to point out the possibility that the host is (or once was) a species of *Zelkova*. Further aspects in biogeography and phylogeny will be treated elsewhere.

Genus Aphidounguis Takahashi, 1963

Type-species: *Aphidounguis mali* Takahashi, 1963.

Fundatrix adult. Body oval and quite broad; wax gland plates without a clear rim, consisting of irregular-shaped, small cells. Legs, antennae, rostrum, stigmal plates, clypeus and eyes sclerotized, brownish, but head, genital plate and anal plate very weakly sclerotized and thinly pigmented. Legs and antennae shortened and feeble. Body setae very thin. Eyes represented only by a triommatidion. Antennae 4-segmented. Antennal segment IV very short, tapering, showing a slight imbrication. Segments III and IV weakly spinose. Processus terminalis on the last segment very short. Antennal setae very short, thinly scattered. Primary rhinaria present on segments III and IV. Rostrum short, reaching to between fore coxae and middle coxae. Ultimate rostral segment with very short setae, convex laterally. Genital plate disc-like, with transverse rows of denticles, not uniformly pigmented, with setae arranged not neatly along the hind margin and often scattered over the central part, and with 1 pair of longer setae at the anterior part. Cornicles absent. Cauda semicircular, slightly sclerotized on the dorsum, with 1 pair of setae. Legs wholly smooth, thinly with fine and short setae. Trochanter and femur united. Tarsi separated into 2 segments by a membranous line, but the division often incomplete. Dorso-apical setae on tarsi rather short, with a slightly capitate tip. Empodial setae almost as long as or a little longer than claws.

Emigrant: Antennae very short, 6-segmented, rather broad. Secondary rhinaria present on segments III-VI, quite narrow, arranged almost in parallel. Primary rhinaria present on segments V and VI. Segments I-IV smooth, segment V slightly spinose and segment VI more intensively spinose. Segment VI slightly imbricated. Antennae wholly dark pigmented and secondary rhinaria emerging as luminous lines. Abdomen with dark pigmented intersegmental bands, which are rather broad in the spinal area and reduced to fragmentary spots in the pleural area. Body setae very short and thin. Cornicles present on abdominal segment VI, small, with a clear opening, hardly projecting, slightly sclerotized, not surrounded by setae. Genital plate almost as in fundatrices, with setae occurring along the posterior margin and extending toward the central and anterior parts, thus the anterior setae indistinguishable from the marginal ones. Second tarsal segment slightly imbricated, thicker toward the apex, wholly with spinules, with a few very short setae. Empodial setae very fine, as long as claws. First tarsal segment with 1 pair of fine setae and 1 spine-like seta. Tibiae slightly spinose at the apical part. Fore wings with media not branched. Hind wings with 2 cubital veins.

Aphidounguis mali Takahashi, 1963

Watabura nishiyae: Hille Ris Lambers, 1967.

Specimens examined. Emigrants, 3 indvs., Kyôto, Honshû, ex a gall on *Ulmus parvifolia*, early June (without exact date), 1980 (Yamaguchi). Fundatrix adults, 4 indvs., ditto, mid June, 1982 (Yamaguchi). Fundatrix first instar larvae, 6 indvs., Tôkyô, ex unfolding buds, 14–19 IV 1981. Apterous fundatrigeniae, 3 indvs., Kyôto, ex a gall, early June, 1980 (Yamaguchi).

Emigrant. Description is based on 3 specimens collected from galls on *Ulmus parvifolia*. Body length 1.56–1.66 mm. Head and thorax dark brown. Antennae and legs brown. No wax plate present. Antennae short and rather thick, 6-segmented, 0.508–0.587 mm long and 0.34–0.38 times as long as body. Antennal segment III 0.15–0.18 times as wide as long, a little shorter than IV, V and VI taken together. Segments IV, V and VI almost equal in length. Processus terminalis on the last segment stumpy, 0.020–0.023 mm long. Length of segments (in mm): I 0.051–0.061, II 0.043–0.051, III 0.205–0.233, IV 0.071–0.094, V 0.066–0.081, VI 0.073–0.076. Secondary rhinaria very narrow, found on III-VI, regularly arranged, encircling 2/3 the segment, but covering only ventral side. Segment III with 15–18, IV 5, V 3–4, and VI 2–3 secondary rhinaria. Primary rhinaria present on V and VI, joined to a secondary rhinarium and irregular in shape, fringed with cilia on segment VI. Antennal setae very short and fine; apical setae on the last segment longest, 0.010–0.015 mm long. Antennal segment VI spinose and V faintly spinose. Ultimate rostral segment short, 0.099–0.106 mm long. Abdominal tergites each with 1 sclerotized intersegmental band, which is reduced to fragmentary sclerites on the pleural side. Cornicles present, but located near to genital plate, not surrounded by any setae, not projecting, without a rim within the opening. Diameter of cornicles 0.020–0.025 mm long. Genital plate spinose and wholly pigmented, with 20–25 setae. Several setae present in the central part. Cauda semicircular, with 2 setae. Hind femorotrochanter 0.379–0.415 mm long. Setae on hind tibiae short, maximally 0.020–0.025 mm long. Tarsi slightly spinose, becoming thicker toward the apex. First tarsal segment with 2 setae, which are 0.020–0.030 mm long on the hind legs, and with 1 spine-like seta (also present on hind legs). Empodial setae almost as long as claws, about 0.025 mm long on hind legs. Second segment of hind tarsi 0.094–0.111 mm long. Fore wings with a simple media. Hind wings with Cu 1a and Cu 1b.

Embryos of emigrants. Tarsi cone-shaped, spinose, without empodial setae, with only a single claw, which is straight and 0.02 mm long on hind legs. Wax gland plate present on each of thoracic and abdominal tergites, arranged in spinal and lateral rows, elongate in shape, consisting of 2 types of cells: 1 to 3 central circular cells and circumferential more elongate cells arranged radially.

Fundatrix adult. Description is based on 4 specimens collected from galls on *Ulmus parvifolia*. Body oval, convex dorsally, very weakly sclerotized, with short setae thinly scattered, without distinct wax gland plates. Legs, rostrum and antennae brown. Body 1.97–2.25 (2.09) mm long and 1.57–1.80 times as long as broad. Head dorsally with a median sclerotized band divided by a median line, and with a pair of smaller, band-shaped sclerites near antennal bases. Antennae 4-segmented, 0.323–0.356 (0.338) mm long, 0.15–0.17 times as long as body, 0.99–1.08 times as long as femorotrochanters. Antennal segment III slender, narrower

to the base, 0.025 mm wide at the middle, occasionally with a membranous spot at the apical 1/3. Processus terminalis on the last segment not projecting. Length of segments (in mm): I 0.045–0.061 (0.056), II 0.051–0.061 (0.055), III 0.172–0.192 (0.182), IV 0.040–0.051 (0.045). Antennal setae thinly scattered, short and fine. Number of setae on antennal segments: I 2, II 2, III 7–8, IV 5–6. The longest setae on segment III 0.025–0.030 mm long. Primary rhinaria present on antennal segments III and IV, with a tonguelet projecting from a foramen. A few accessory rhinaria surrounding primary one on segment IV. Antennal segments I and II smooth. Segment III with spinules scattered thinly all over, and segment IV with

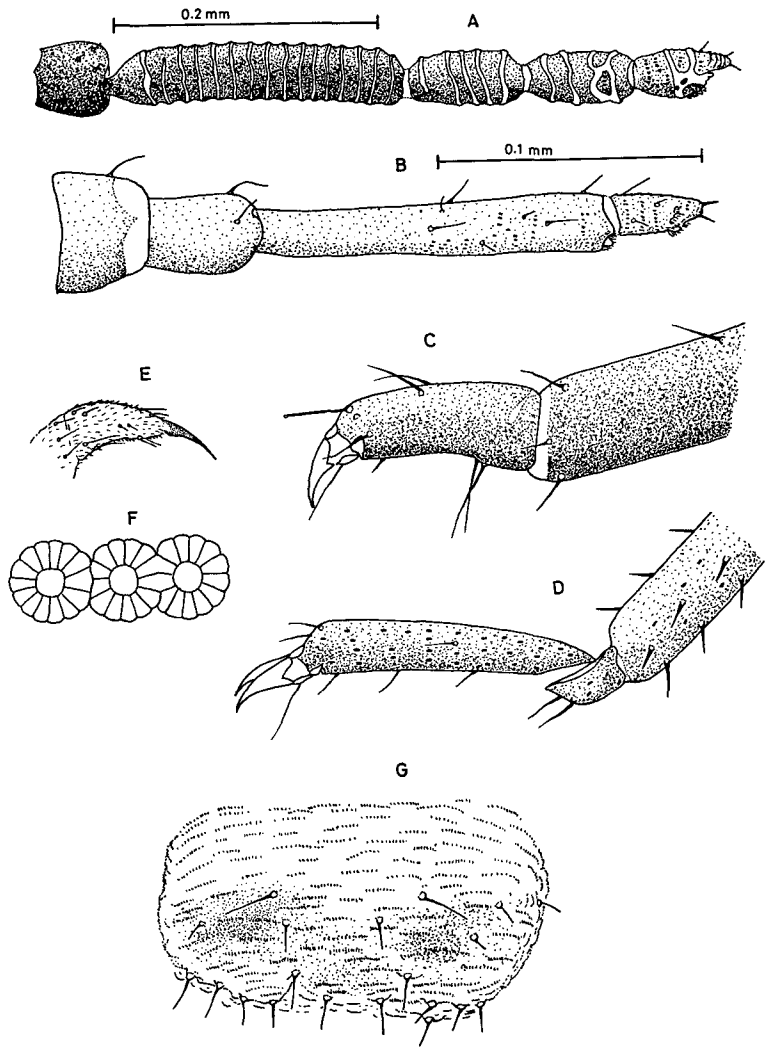

Fig. 23. *Aphidounguis mali.* A, antenna of the emigrant; B, antenna of the fundatrix; C, hind tarsus of the fundatrix; D, hind tarsus of the emigrant. Hind tarsus (E) and wax gland plates (F) of the 1st instar larva deposited by the emgirant. G, genital plate of the emigrant.

a few transverse rows of spinules. All segments not imbricated. Rostrum reaching to between fore coxae and middle coxae. Ultimate rostral segment short, 0.096–0.101 mm long, with 6–9 short accessory setae. Thorax and abdomen with indistinct circular wax gland plates, which lack a clear border. Abdominal setae short, maximally about 0.040 mm long on abdominal tergite VI. Cornicles absent. Genital plate weakly pigmented, with transverse rows of spinules, with 2 long setae at the anterior part and 16–21 shorter setae scattered over the posterior part. Cauda semicircular, dorsally pigmented, with 1 pair of setae on the dorsal surface. Hind femorotrochanter 0.308–0.343 (0.328) mm long. Tibiae and tarsi smooth. Tibiae thinly with setae, of which the longest one is 0.035 mm long on the hind legs. Tarsi showing an abortive division, 0.076–0.081 (0.078) mm long. Long setae on the base of tarsi (first segment) 0.045 mm long. Empodial setae fine and short, 0.020–0.025 (0.022) mm long on hind legs, nearly as long as claws. Dorso-apical setae stout but short, about 0.030 mm long, not acute at the apex.

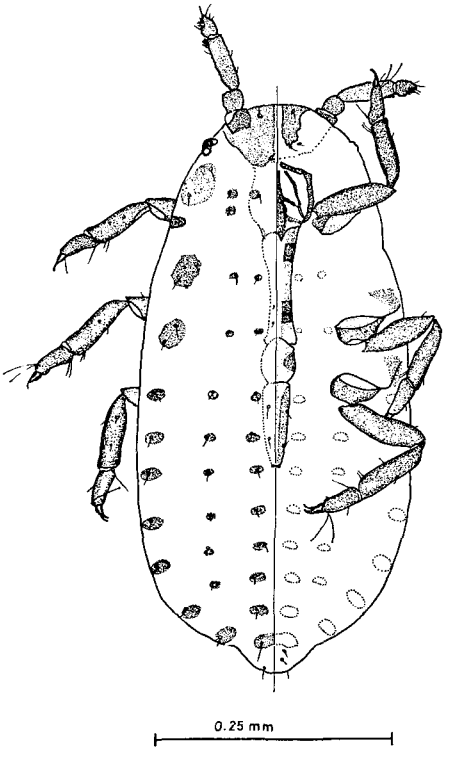

Fig. 24. *Aphidounguis mali*. Fundatrix first instar larva.

Fundatrix first instar larva. Description is based on 6 specimens collected on unfolding buds of *Ulmus parvifolia*. Body 0.566–0.677 (0.615) mm long, 0.488 times as wide as long on the average, maximal width 0.283–0.333 (0.300) mm. Body wholly weakly sclerotized, without visible wax gland plates. Head with a sclerite broadly covering the dorsal surface, reaching to the ventrum, and divided into 2 parts by a median slit. Antennae 4-segmented, very short and rather broad. Segment III conspicuously long, becoming thicker toward the apex. Segment IV shortened, tapering. Processus terminalis on segment IV not prominent. Segment III, except for basal 1/3, and IV spinose, not imbricated. Length of segments as follows (in mm): I 0.025, II 0.020–0.023 (0.021), III 0.058–0.061 (0.060), IV 0.023–0.030 (0.026). Antennal segment I with 2–3, II with 2–3, III with 6–9, and IV with 8 short setae. The longest setae present on the apex of antennae, about 0.020 mm long, and longest setae on segment III 0.018 mm long on the average. Primary rhinaria present on segments III and IV, ciliate on IV. Ultimate rostral segment rather short, convex laterally, 0.083–0.091 (0.088) mm long, with about 10 very short setae. Thoracic and abdominal tergites each with small oval sclerites arranged in spinal, pleural and lateral rows, but abdominal tergites VII and VIII without pleural sclerites and VIII further without lateral ones. Thoracic lateral plates larger, with 2 setae, and other plates with only 1 seta. Setae on the sclerites very short, acute, 0.013 mm long on lateral ones of

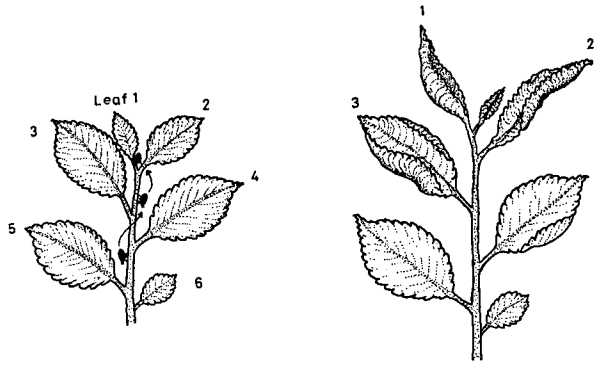

Fig. 25. Gall formation in the *Aphidounguis mali* fundatrix. Left, developing shoot. Right, completed clustering gall.

abdominal tergite VI. Legs wholly smooth, very weakly sclerotized. Hind femorotrochanter 0.096–0.111 (0.104) mm long. Tarsi broad, not separated into 2 segments but often with a trace of division, 0.043–0.048 (0.045) mm long. Dorso-apical setae capitate at the apex, 0.035–0.040 (0.037) mm long on hind legs. Empodial setae a little longer than claws, 0.020 mm long.

Apterous fundatrigenia. Description is based on 3 specimens collected from galls on *Ulmus parvifolia.* Body rather elongate, about 1.59 mm. Legs, rostrum and antennae sclerotized and brownish. Head with a median sclerotized bar which widely covers the head on the dorsal side, and with a pair of sclerotized bars surrounding each base of antennae. Eyes consisting of two parts: multifacetted eye and triommatidion. Antennae short, 6-segmented, 0.440–0.483 mm long and 0.28–0.30 times as long as body. Antennae very thick; segment III about 0.28 times as wide as long. Segment III with a few circular, unpigmented spots. Processus terminalis on the last segment 0.025–0.030 mm long. Length of segments (in mm): I 0.056–0.061, II 0.061–0.066, III 0.147–0.162, IV 0.051–0.061, V 0.056–0.061, VI 0.066–0.076. Primary rhinaria present on segments V and VI, fringed with cilia. Antennal setae short and fine; segment I with 2–4 setae, II with 3–4, III with 7–11, IV with 3–4, V with 4–5, and VI at the base with 2 and on processus terminalis with 5. The longest setae on segment III 0.025 mm, and apical setae on the last segment 0.013 mm long. Antennal segment VI spinose and III-V slightly so. Rostrum short, reaching between fore coxae and middle coxae. Ultimate rostral segment 0.096–0.106 mm long, with 7–8 accessory setae. Wax gland plates present on abdominal tergites, consisting of cells, but indistinct and without a definite border. Setae on tergite V maximally 0.040 mm long. Cornicles present near genital plate or often at the level of genital plate, without surrounding setae, and without a rim. Diameter of cornicles 0.025 mm long in axial length. Genital plate pigmented and spinose, with 1 pair of long setae at the anterior part and with 16–19 setae at the central part or along hind margin. Hind femorotrochanter 0.354–0.374 mm long. Tarsi not spinose. First tarsal segment with 2 long setae, which are 0.035–0.038 mm long, and with 1 spine-like seta (present also on hind legs). Second tarsal segment 0.101 mm long on hind legs. Empodial setae a little shorter than claws, 0.025 mm long on hind legs.

Distribution. Honshû (southwestern region); Kyûshû.

Remarks. Although Hille Ris Lambers (1967) regarded *Aphidounguis mali* Takahashi, 1963, as a synonym of *Watabura nishiyae* Matsumura, 1917, his treatment includes some serious problems. First of all, it must be pointed out that *W. nishiyae* is undeterminable from the description, while no type specimens remain. Mysteriously, Matsumura (1931) remarked that *W. nishiyae* has *Zelkova* as a primary host and *Sasa* sp. as a secondary host; this is obviously incompatible with the original description, where it was stated that the alates were collected on *Malus pumila* and *Cydonia vulgaris*. It is certain that the species Matsumura (1931) referred to is identical with *Colopha moriokaensis* (sensu Eastop & Hille Ris Lambers, 1976), which forms galls on *Zelkova*, and obviously differs from *W. nishiyae* described by Matsumura (1917). Some Japanese workers followed Matsumura (1931) and accepted *W. nishiyae* as a gall-maker on *Zelkova* (Takahashi, 1931; Shinji, 1941; Tanaka, 1961), although Shinji and Tanaka, following Barker's (1920) remark, referred it to *Dryopea*.

Aphidounguis mali was described by Takahashi (1963) on the basis of material collected from apple roots, but at that time the gall-generations on the primary host were unknown at all. Later, Hille Ris Lambers (1967) correctly identified Japanese specimens collected from galls on *Ulmus** as *A. mali* based on the characters of embryos extracted from emigrants. However, simultaneously he suggested that the emigrants well agree with Matsumura's and Shinji's descriptions of *W. nishiyae*, and treated *Aphidounguis mali* as a synonym of *Watabura nishiyae*. As mentioned above, however, what Shinji described as *W. nishiyae* is undoubtedly identical with *Colopha moriokaensis* on *Zelkova*. Moreover, there is some disagreements between *A. mali* and Matsumura's original description of *W. nishiyae*. Matsumura stated that *W. nishiyae* (sexuparae ?) is characterized by having one oblique vein on the hind wings and by the antennal segment IV shorter than the segment VI; while in the emigrants of *A. mali* there are two cubital veins on the hind wings and the antennal segment IV is longer than the segment VI. This suggests that Hille Ris Lambers' treatment is uncorrect. The opinion is held that *Watabura nishiyae* Matsumura (1917) and *Aphidounguis mali* are quite different species.

Biological notes. The fundatrix of *Eriosoma* indirectly induces a distal leaf of a new shoot to roll downwards on one side while settling on the shoot stem at some distance from the leaf (Akimoto, 1981). A similar, but partially altered way is employed by *Aphidounguis mali* in gall formation. In this species a completed gall comprises several rolled leaves on one shoot – a clustering gall.

The behavior of the fundatrix in forming the clustering gall on *U. parvifolia* was observed at Kitanomaru Park, Tôkyô, on April 13th-19th, 1981, when new buds of *U. parvifolia* were rapidly developing. One fundatrix individual employed for observation was first found to have settled on a shoot stem immediately under the petiole of leaf 2 (see Fig. 25) on April 14th, when the shoot was 7 mm long and

* Hille Ris Lambers (1967) recorded *Aphidounguis mali* from *Ulmus davidiana* var. *japonica*. This is probably an error. Although I have extensively studied galls on *Ulmus*, the galls of *A. mali* have been discovered not from *U. davidiana* but from *U. parvifolia* only. *Ulmus parvifolia* occurs in temperate to subtropical climates, and is distributed over southern China (including Taiwan) and southwestern Japan. The exules of *A. mali* also have been discovered only in southwestern Japan, from apples.

no leaves showed distortion. During my observation this individual left the settling site a few times, walking about on the stem and petioles, but each time returned to the original site. On April 15th it was found remaining there, but on the 17th it was settling on the petiolar base of leaf 1. On the 19th leaves 1 and 2 showed signs of rolling, and the fundatrix was found within the roll of leaf 2. The shoot reached 17 mm long at that time. The wandering habit was also observed for other individuals of *A. mali*. All this suggests that the shift of settling sites causes several leaves of one shoot to roll. Chemical stimuli from one settling site may influence only the leaf immediately above the settling site.

The fundatrix of *A. mali* forms two to six leaf-rolls on one shoot and occupies one of them, leaving the others empty. The leaves unoccupied, as well as the one occupied, continue to roll with the developement of the shoot. This may show that the chemical stimuli given by the fundatrix when it was feeding on the shoot stem are sufficient to complete leaf-rolls. Interestingly, all the leaf-rolls of one shoot become fully occupied by mid July. Part of the fundatrix offspring borne in the maternal leaf-roll doubtless migrate into existing empty leaf-rolls.

It seems that *Hemipodaphis persimilis*, which forms a similar clustering gall, migrates in the first instar. I often found several leaf-rolls only inhabited by a few young larvae in mid June. Since at that time the maternal gall still includes only a few tens of aphids, the migration cannot be simply ascribed to overcrowding within the gall. This suggests that the larvae borne in the early stage of the breeding period of fundatrices serve migration in *H. persimilis*. The same would be expected for *A. mali*.

Positions of Eriosoma, Aphidounguis and Hemipodaphis in the phylogeny of Eriosomatinae

The concept of punctuated equilibria claims that a species once established persists in a stasis without substantial changes (Eldredge & Gould, 1972; Stanley, 1979). Accepting it, we may suppose that sometimes the ancestral (stem) species of a taxon still exists so far as the environment to which it was adapted has remained substantially unchanged. Even if the ancestral species has been extinct, we may expect that some species of the taxon remain in almost the same environment that the ancestral species once lived in, and that such species maintain a mode of life quite approximating to that of the ancestor. The maintenance of a practically ancestral mode of life should inevitably be connected with a morphological stasis concerning characters associated with that mode. Thus, it may be reasonable to specify the primitive species within a taxon in terms of aspects in life history, even if they have derived characters in some features. While evaluation of characters in terms of relative primitive-derived (plesiomorph-apomorph) relationship is essential to cladistic analysis, the relationship among the extant forms is interpreted there always as divergent but not as ancestral-descendant in any case. Yet, so far as the punctuation concept is valid, the ancestral-descendant relationship is undoubtedly one of the most fascinating and promising themes in systematics.

In the following lines I will try to see if it is possible to recognize the ancestral, or nearly the ancestral, mode of life in the extant Eriosomatinae. I would like to limit my discussions to some aspects in the gall-formation for the sake of simplicity. In fact, not only the gall structure itself but also the manner in the gall-formation

is in close association with other aspects in the life cycle of a species, and is essential in considering the evolutionary adaptation in the Eriosomatinae.

Monoecious life cycle of the ancestry

According to Heie (1967), the Pemphigidae trace their origin back to the Permian of the Paleozoic era and had their early evolution on gymnosperms. Based on his opinion, it may follow that some pemphigids were associated with early members of some groups of angiosperms in the Cretaceous, the ancestral Pemphidinae with, say, the ancestral *Populus*, the ancestral Fordinae with the ancestral Anacardiaceae (*Pistacia* and *Rhus*), and the ancestral Eriosomatinae with the common ancestor of *Ulmus* and *Zelkova*, which are, according to Bate-Smith & Richens (1973), most closely related in the Ulmaceae. This last is suggested from the fact that the Eriosomatinae have advanced their divergence along two pathways on *Ulmus* and *Zelkova*, on each of them there being found an evolutionary series of primitive-derived species (Akimoto, unpublished). Thus, the acquisition of the common ancestor as host must have occurred before the late Cretaceous, when *Ulmus* appeared at first (Bate-Smith & Richens, 1973) and probably *Zelkova* did, too. I postulate that early eriosomatines had a monoecious mode of life on the common ancestor of *Ulmus* and *Zelkova* and later acquired a heteroecious mode, which, according to Moldvilko (1928), has been maintained as a consequence of the consistent adherence of the fundatrices to the primary hosts. The evolutionary course of specialization in gall formation may have demanded a considerably long time, committing the fundatrices only to a particular host plant. Otherwise, the whole life cycle would have easily been switched over to the secondary host, if this was superior in resource value. In fact, this switchover often occurred in other aphid groups (Hille Ris Lambers, 1950; Eastop, 1973).

Relationship between ancestral Eriosomatinae and Ulmaceae

It should be kept in mind that the ancestral Ulmaceae must have been greatly different from the current forms in some phenological habits. In the present, *Ulmus* and *Zelkova* develop new buds only once a year in spring, so that the environment surrounding the aphids comes to deteriorate toward summer (Dixon, 1971, '73). Historically this must have evolved a heteroecious life mode in Eriosomatinae associated with *Ulmus* and *Zelkova*. Yet, it is unlikely that the ancestral Ulmaceae had the same habit in the environment of their time. A critical problem here is the period in a year during which the ancestral Ulmaceae supplied new leaves available to the aphids.

As members of the Arcto-Tertiary flora *Ulmus* and *Zelkova* diverged brilliantly and evolved to current forms in the high latitudes from the late Cretaceous to the early Tertiary (Chaney, 1947; Tanai, 1972; Takahtajan, 1969; Stebbins, 1950). According to Axelrod (1959, '66), however, their ancestral forms, as well as the ancestors of other deciduous trees, had accomplished the optimal development in the tropical uplands by the early Cretaceous before their migration to the high latitudes. Still now *Ulmus lanceaefolia* is distributed in the tropical uplands of North Sumatra and South Celebes (Touw and Van Steenis, 1968). In a subtropical environment with a periodically semiarid climate, where deciduous habit is supposed to have evolved in the early Cretaceous (Axelrod, 1966), ancestral plants possibly used to develop new buds over a considerably long period, even if they had no evergreen

habit. This is suggested from the case of *Celtis sinensis* (belonging to the Ulmaceae), which is distributed from the temperate to the subtropical region. The plant is completely deciduous in the temperate climate of Japan, while developing new shoots all the year round, especially at early ages, in the subtropical climate of Taiwan (Takahashi, 1928). Moreover, *Celtis* includes completely evergreen members (Axelrod, 1966). The yearlong growth of new shoots is probably due to the secondary extension of shoots. In *Ulmus davidiana* and *U. parvifolia* I observed that part of the shoots extend secondarily in early summer. Postvernal shoot-growth may be quite scanty in amount, but, even so, it may give significant influence on the life cycle of some insects parasitic on the plant. Takahashi (1928) observed in Taiwan that on *C. sinensis* a leaf-cutting weevil (*Paroplapoderus vitticeps* Jekel), which utilizes new leaves only, formed cladles through a year. Similarly, the supposed pseudo-evergreen habit of the common ancestor of *Ulmus* and *Zelkova* would have allowed the ancestral Eriosomatinae to have a monoecious life mode.

Without secondary hosts, the ancestral Eriosomatinae might have utilized the host plants so as to maximize on them the number of their offspring prior to sexual reproduction. Therefore, it is quite possible that in the past apterous fundatrigeniae took over some generations within the galls until the time when the rate of population growth began to decline. Even if the ancestral Ulmaceae continued to supply new shoots available to the aphids, individual galls or shoots inhabited by aphid colonies eventually lost with time their value as resource. As Aoki (1976) mentioned, this may inevitably have led to the production of alates for migration to young shoots available. Moreover, it can also be assumed that apterous individuals migrated from their old gall to secondarily extended part of the shoot, having formed new ones by themselves.

Gall structure and secondary hosts

In the extant species of Eriosomatinae two main types of galls, open and closed galls, can be distinguished. The open galls are mainly leaf-rolls (with the exception of *Colophina* galls (Aoki, 1980)), while the closed ones are all pouch-like (Table 3). Pouch galls obviously need a peculiar transformation of the leaf tissue. It is more important that the life mode of pouch-gall aphids seems to be undetachably connected with herbaceous plants as secondary hosts (Table 3). Within the pouch gall there is usually only one generation following the fundatrix generation owing to the nature of the gall (among the pouch-gall aphids *Colopha* is the only group producing apterous fundatrigeniae (Moldvilko, 1935)). It may be said in general that the pouch-gall aphids take full advantage of the most nutritious new leaves only, without the risk of being attacked by predators. On the other hand, on the herbaceous secondary hosts they are guaranteed of a high growth rate during summer. Thus, the main stage of population increase has been transferred to the generations on the secondary host. *Kaltenbachiella japonica* exceptionally has no secondary hosts, and all larvae borne by the fundatrix grow to sexuparae in the pouch gall. Even in this case, there is only one generation in the gall after the fundatrix generation. This suggests that the life history of *K. japonica* is merely secondarily deviated from the typical life mode of the pouch-gall aphids. The life mode of the pouch-gall aphids is obviously much advanced and largely different from the one assumed for the ancestral Eriosomatinae.

Table 3. Host plants and types of galls in the genera of the Eriosomatinae.

Genus	Species number	Primary host	Secondary host	Attacking part	Type of gall
Eriosoma	26	various species of *Ulmus*	various species of Pomaceae and various herbaceous plants	stem, root and shoot	leaf-roll (often clustering type)
Aphidounguis	1	*U. parvifolia*	*Malus*	root	leaf-roll (clustering gall)
Shizoneurella	1	*U. villosa*	*Malus*	root	?
Shizoneurata	1	?	*Crataegus*	?	?
Tetraneura	20	Group F and G of *Ulmus*	various species of Gramineae or Cyperaceae	root	pouch gall
Colopha	4*	Group C of *Ulmus*	*Carex*	root	pouch gall
Kaltenbachiella	4	Group F and G of *Ulmus*	Labiatae	subterranean parts	pouch gall
Hemipodaphis	2	*Zelkova*	? (lily-like plant)	root	leaf-roll (clustering gall)
Byrsocriptodies	2	*Zelkova*	?	?	leaf-roll (clustering gall)
Colophina	2**	*Zelkova*	*Clematis*	stem and root	intergrading type between leaf-roll and pouch gall
Paracolopha	2***	*Zelkeva*	*Phyllostachys*, *Arundinaria* and *Sasa*	root	pouch gall
Gharesia	1	*Zelkova* (?)	Cryperaceae	stem	?

* *C. compressa*, *C. graminis*, *C. kansugei*, and *C. ulmicola*; ** *C. clematis* and *C. arma*; *** *P. morrisoni* and *P. moriokaensis* (=*Colopha moriokaensis*, sensu Eastop & Hille Ris Lambers, 1976).

On the other hand, the leaf-roll aphids pass more than one generation within the galls on the primary hosts. In *Aphidounguis* and *Hemipodaphis* most of the fundatrix offspring grow to apterous fundatrigeniae, thus increasing gall generations. Especially in *Hemipodaphis* the succession of generations in the gall generally lasts until autumn. *Eriosoma* comprising many species shows a wide variation in the continuation of gall generations.

It seems that the mode of life with such a clustering gall as found in *Aphidounguis*, *Hemipodaphis* and some species of *Eriosoma* approaches to the supposed monoecious mode in the ancestral Eriosomatinae. In the foregoing section it is supposed that in the ancestral forms the colony was lasting by utilizing galls produced by turns, for example, on secondarily extending shoots. In some species of the Pemphiginae, which are a group close to the Eriosomatinae and also gall-makers, this tendency in fact emerges as the secondary galls that the migratory larvae from the maternal gall form (Börner and Heinze, 1957; Aoki, 1975). On the other hand, in extant eriosomatines forming the clustering gall, the fundatrix prepares spare leaf-rolls for the following generations and the larvae borne in the maternal leaf-roll migrate into the spare ones. In both the cases, the larval

migration from the maternal galls is deemed to be a primitive habit, which has escaped from the ancestral stock.

In contrast with the rigid species-specificity to the primary host, the eriosomatines generally show a relatively wide range of the secondary hosts. For example, the exule of *E. yangi* is collected on the roots of *Salix* sp. (willow) and *Fragaria ananassa* (strawberry). Evidently the exule is able to accept an extensive repertoire of food plants and reproduce on them. It is reasonable to suppose that the migrating alates choose as secondary hosts such plants as realize the most numerous remigrating ones through clonal series on them. The adoption of the secondary host therefore seems to depend on how easily the plant is procurable on one hand and on how much it is suitable for the growth of the aphid on the other hand. It is noteworthy that woody plants belonging to the Rosaceae (e.g. *Malus* and *Crataegus*) are included in the secondary hosts of some leaf-roll aphids. Notice that woody plants are decidedly inferior to herbaceous plants in Nitrogen content (wood: 0.03–0.25% of dry weight, grasses: 0.9–4.0% of d.w.) (Mattson, 1980). Although herbaceous plants had certainly appeared by the Eocene (Stebbins, 1950), their rapid diversification and prosperity occurred in semiarid climate after the Miocene and especially in the Middle Pliocene (Axelrod, 1948). The presence of woody secondary hosts in some leaf-roll aphids may show that the mode of life in these aphids can trace back to their ancestor which had already acquired a heteroecious mode before the appearance of herbaceous plants in prosperity, and that the choice by the ancestor has been preserved in them probably because of some constraint posed on the exules. In the species of *Eriosoma* having herbs as secondary hosts, two cases must be distinguished. Some species may have transferred secondarily to herbaceous plants from woody Rosaceae. This case seems to be applicable to species having herbaceous Rosaceae as secondary hosts (e.g. *E. japonicum*). In a few other species the adoption of the secondary host was probably made after the pervasion of herbs, whether the choice concerned speciation events or not. *Eriosoma patchiae* may accord with this case, because it is profoundly connected with the primary host, showing long lasting gall-generations and facultative host-alternation. The combination of simple leaf-roll galls and woody secondary hosts is also found in Pemphiginae: the aphids of Prociphilini (sensu Heie, 1980), which all form simple galls on several primary hosts, have coniferous trees as secondary hosts.

On the other hand, there are no pouch-gall aphids having woody plants as secondary hosts. This may mean a relatively recent origin of them. In any case there is a greater weight of the secondary hosts in the population growth of the pouch-gall aphids. In this regard the pouch-gall aphids may be unavoidably linked to the primary hosts.

In conclusion, the concurrence of some characteristics in life mode, i.e. leaf-roll galls, extended reproduction within the gall, and woody secondary hosts, in the same group probably shows that the group closely approximates the ancestral stock of the Eriosomatinae.

The manner of gall formation

The primitiveness of the leaf-roll aphids is also suggested by the manner of gall formation. The fundatrix induces the transformation of a leaf by sending a plant hormon-like substance contained in the saliva (Miles, 1968). This is remotely

controlled by the aphid which has settled on the shoot stem bearing the leaf to be affected (Akimoto, 1981). On the other hand, in the pouch-gall aphids the fundatrix settles on the surface of a leaf and inflates the specific settling site downward.

It is worth pointing out that there is among the leaf-roll aphids a species showing a primary step toward the habit of forming a pouch-gall. *Eriosoma lanuginosum* transforms an elm leaf into a largely inflated pouch. The developmental process of this gall is illustrated by Shaposhnikov (1968). The illustration shows that the fundatrix of *E. lanuginosum* first induces a simple rolling on the leaf edge of one side as in other *Eriosoma* species, and that subsequently a part of the leaf-roll begins to inflate upward, involving other parts of the leaf in the inflation. Obviously, the gall formation of this species proceeds through two different stages. The primary rolling is doubtless caused by the aphid settling on a shoot stem as in other species of *Eriosoma*. On the other hand, the leaf inflation probably follows the intrusion of the fundatrix into the roll. This aphid may represent a transitional stage between the leaf-roll aphids and the pouch-gall aphids, the primary stage having been lost in the course of evolution of the pouch-gall aphids.

During the gall formation, the fundatrix of a leaf-roll aphid can stay under the protection within developing buds, while the fundatrix of a pouch-gall aphid must stay exposed on the surface of a leaf without any protection against fluctuating humidity or other external physical conditions. This is probably the reason for the fact that in *Tetraneura* spp. and *Colopha moriokaensis*, which form pouch-galls, the skin of the fundatrix first instar larva is more or less sclerotized throughout. This character appears to be an apomorphic character through all the species of the Pemphigidae. By contrast, *Eriosoma*, *Aphidounguis* and *Hemipodaphis* are membranous except for weakly sclerotized patches.

Conclusion

Based on the discussions above, the leaf-roll aphids can be considered to have preserved some features of the supposed ancestral life cyclic mode of the Eriosomatinae. Apart from apparent secondary deviations, e.g. *E. gillettei*, none is known to have a monoecious mode of life on the primary host. However, the ancestral mode may be partially traced in *E. patchiae*, in which host-alternation is facultative and part of alates grown in the gall bear sexuales on *Ulmus* (Marchal, 1933). I think that the heteroecious mode started with woody Rosaceae as secondary hosts and later expanded on other diverse plant groups in association with speciation events and spreading distributions.

Although *Eriosoma*, *Aphidounguis* and *Hemipodaphis* are tentatively lumped together as primitive genera, some differences can still be recognized among them. Therefore, there is a possibility that more primitive forms can be detected among them. To proceed along this line, we need to make a detailed morphological comparison and to take up some biogeographical aspects. This will be done elsewhere.

Subgroups within the genus Eriosoma

Subdivision of the genus Eriosoma into two subgenera

In dividing *Eriosoma* into two subgenera only some characters of the tarsi in the exule first instar larvae have been adopted. The ecological meaning of the

tarsal characters, however, has not been known. It seems to me that the characters of this feature reflect biotopes. In such a feature, parallel evolution of characters may occur among different lineages.

According to Börner & Heinze (1957) and Hille Ris Lambers (1973), the subgenus *Eriosoma* (with *Colophina* included in Hille Ris Lambers' classification) is distinguishable from *Schizoneura* by having the following characters in the exule larvae: (1) smooth tarsi, (2) developed dorso-apical setae with a capitate tip, (3) segmented and not cone-shaped tarsi, (4) curved claws. It seems that these characters except (1) more or less reflect a high walking activity in the exule larvae and have been favored on such secondary hosts as enable the larvae to disperse freely.

It has been observed in *E.* (*E.*) *lanigerum*, which forms the colonies on stems or twigs, that the first instar larvae walk about actively on twigs in dispersion. Likewise, *E.* (*E.*) *crataegi* and *E.* (*E.*) *herioti* colonize on the aerial parts of the secondary hosts (Börner & Heinze, 1957), so that they are expected to be active in the first instar larvae. It is notable that *Colophina* also forms its colonies on the aerial parts of the host plant. In this regard, parallelism may be invoked to explain the agreement between *Colophina* and the subgenus *Eriosoma* in the characteristics of the tarsi, because the disagreement between them in the structure of the galls and the plants they are associated with (Aoki, 1980) seems to be significant. If that is the case, the inclusion of *Colophina* within the subgenus *Eriosoma* or even the genus *Eriosoma* is not correct phylogenetically. I strongly incline to the view that *Colophina* is a distinct genus.

On the other hand, all the known Eurasian species of the genus *Eriosoma* are recorded from the roots when they occur on the secondary hosts. Such a closed environment as roots may not demand a high activity of the first instar larvae. Undeveloped dorso-apical setae, unsegmented and cone-shaped tarsi, and straight claws in the first instar larvae of the subgenus *Schizoneura* may suggest a rather sessile life mode on the roots of the secondary hosts. Yet, it is obscure whether the spinose tarsi of the Eurasian *Eriosoma* have any adaptive significance in the hypogeous environment or not. Rather, this character seems to be unstable through the whole Eriosomatinae. For example, in the genus *Tetraneura*, of which all species live on the roots of grasses, the spinose tarsi appear in a rather sporadic fashion among species (Hille Ris Lambers, 1970).

There is quite little possibility that the hypogeous forms compose a phylogenetic group distinct from the aerial group. Although Hille Ris Lambers (1973) seems to imply that different phylogenetic groups of *Eriosoma* have been formed between Eurasia and North America, another interpretation seems to be possible. *Ulmus* had already diversified into the extant subgroups in Eurasia before it migrated to North America through the Bering Strait during the early Tertiary (Pielou, 1979; Bate-Smith & Richens, 1973). Therefore, it is very probable that *Eriosoma* had also been divided into some subgroups by the early Tertiary. In the present, some subgroups of *Ulmus* are distributed disjunctly in Eurasia and North America. Similar patterns of distribution are expected for *Eriosoma*.

Eriosoma ulmi group and other Palearctic species

The *ulmi* group, called as such in the description of species, is worth taking up prior to the division of *Eriosoma* into subgenera. It is a compact subgroup within

the genus *Eriosoma* and differs from the other Palearctic species in the following characters: (1) antennal segments V and VI of the alates without secondary rhinaria, (2) tarsi of the exule first instar larvae spinose and cone-shaped, but those of the exule adult completely smooth and not tapering, (3) tarsi of the exule larvae without empodial setae at all, (4) wax gland plates arranged in spinal and lateral rows, each consisting of a large central cell and circumferential cells arranged regularly in a single row, (5) first tarsal segments of alate with 3–3–2 setae, (6) antennae of the fundatrix adult 6-segmented, (7) wax gland plates of the sexupara degenerated in comparison with those of the exule.

This group includes the following species: *E. ulmi*, *E. grossulariae*, *E. ann-charlotteae* and *E. sorbiradicis*, occurring in Europe; *E. auratum*, *E. longicornutum*, *E. moriokense* and *E. lishanense*, occurring in eastern Asia; and *E. kashimiricum*, occurring in India.

E. sorbiradicis is considered to be wholly anholocyclic (Danielsson, 1979) and has a small body size. With the reduction of body size some appendages show simplification. Yet, having characters (2), (3) and (4), it seems to belong to the *ulmi* group. The primary hosts of the *ulmi* group belong to the groups F and G of *Ulmus* (in the classification proposed by Bate-Smith & Richens, 1973), which are regared as advanced types within the genus and distributed broadly over Eurasia and North America. The exules of the *ulmi* group are found abundant on *Ribes* (or *Vitis*, after Moldvilko, 1935) in Europe, but the exules of *E. moriokense* are known to occur on the roots of *Sedum* sp. in Japan. A remote relationship between *Ribes* and *Sedum* suggests that the secondary hosts are not always restricted to a particular plant group. The taxonomy and biology of the European species of the *ulmi* group are given in detail by Danielsson (1976, '82).

The *lanuginosum* complex (Danielsson, 1982) probably forms another phylogenetic group within the Palearctic members of *Eriosoma*. There are other Palearctic species occurring mainly in eastern Asia and agreeing with one another at least in the following characters: (1) antennal segment V with secondary rhinaria, otherwise with a primary rhinarium whose arm stretches and encircles the segment like a secondary rhinarium, (2) through all the stages of the exule the tarsi are spinose and cone-shaped, (3) the first instar larvae of the exule with empodial setae nearly as long as the claws, (4) wax gland plates of the sexupara is as in the exule. These characters are found in the following species: *E. yangi*, *E. harunire*, *E. japonicum* and *E. nigrum*, occurring in eastern Asia; *E. patchiae*, occurring in Europe; and probably *E. gomboriense*, occurring in Gurziya, USSR. Nevertheless, in the exules of these species, the arrangement and shape of the wax gland plates do not give a support for the view that all these species form a phylogenetic stock. The genus *Eriosoma* has been defined by the wax gland plates arranged in spinal and lateral rows. But this definition is violated by *E. yangi* and *E. japonicum*. The exule of *E. yangi* has pleural rows of plates in addition to those two rows, although lacking pleural plates on the tergites V-VII, while that of *E. japonicum* has only the lateral rows of plates which are greatly different in appearence from those of the other species.

Some species in North America have smooth tarsi through all the stages of the exule; by contrast, the East Asian species show spinose and cone-shaped tarsi in all the stages. Intervening between them, the *ulmi* group has spinose and cone-shaped tarsi in the first instar larvae and smooth and untapering tarsi in the adults. This

again suggests that it is unnatural to divive the genus *Eriosoma* on the basis of spinosity in the tarsi of the first instar larvae only.

Chromosome numbers in Eriosoma

The karyotypes of Japnanese species were studied by Dr. R. Blackman. *E. harunire*, *E. moriokense*, *E. yangi*, *E. longicornutum* and *E. japonicum* all agree in having 2n=10, while only *E. auratum* has 2n=12 (pers. comm.). Either of the North American *E. lanigerum* and *E. crataegi* has 2n=12 (Kuznetsova and Shaposhnikov, 1973). Interestingly, the *ulmi* group includes both karyotypes.

Appendix: Eriosoma lishanense, sp. nov., from Taiwan

In the course of my survey in Taiwan in 1980, I collected at Lishan (2000 m alt.), Taitung-Shen, many leaf-roll galls on *Ulmus uyematsui*, which is endemic to mountainous parts of Taiwan. The galls were all of the same species and included many apterous fundatrigeniae, some fundatrices and only two emigrants, which are similar to the corresponding morphs of *E. auratum*. Characteristics of the emigrants and embryos within their abdomens show that this species belongs to the *ulmi* group. But, unlike the other members of the group, the antennae of the fundatrix are 5-segmented. Although *Ulmus uyematsui* is tentatively thought of as forming an isolated group, group D (Bate-Smith & Richens, 1973), the association of a member of the *ulmi* group and a simultaneous finding, on the same host, of *Tetraneura yezoensis*, which is common on *U. davidiana* and *U. laciniata* in Japan, suggest a close relationship among these elm species.

Specimens examined. Emigrants, 1 indv. (holotype), Lishan, Taitung-Shen, Taiwan, ex a gall on *Ulmus uyematsui*, 3 V 1980; 1 indv, ditto, 29 IV 1980. Fundatrices, 4 indvs., Lishan, Taitung-Shen, ex galls, 29 IV 1980. Apterous fundatrigenia adults, 5 indvs., ditto.

Emigrant. Description is based on 2 specimens collected from galls on *Ulmus uyematsui*. Body 1.44–1.50 mm long. Antennae and legs brown. No wax plates present. Antennae 6-segmented, 0.819–0.852 mm long and 0.57 times as long as body. Processus terminalis on the last segment rather long, about 0.035 mm long. Length of segments (in mm): I 0.058–0.061, II 0.051–0.053, III 0.404–0.440, IV 0.111, V 0.096, VI 0.094–0.096. Secondary rhinaria present on segments III and IV, regularly arranged, encircling 1/2–2/3 the segment, covering only ventral side.

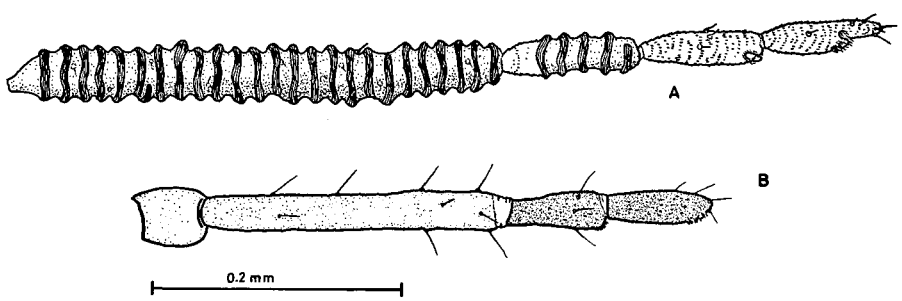

Fig. 26. *Eriosoma lishanense*. Antennae of the emigrant (A) and the fundatrix adult (B).

Antennal segment III with 23–26 and IV with 5 secondary rhinaria. Primary rhinaria found on segments V and VI, with a ciliate, transverse foramen, from which a tonguelet projects; one on VI with a few accessory rhinaria, which are semicircular and also fringed with cilia. Processus terminalis on the last segment with 4 stout setae, 0.010 mm long, at the apex and with 1 seta at the middle. Segments I-V with a few, much shorter setae. Antennal segments V and VI spinose and imbricated. Ultimate rostral segment 0.111–0.116 mm long, with several short accessory setae. Abdomen with weakly sclerotized intersegmental bands, which are indistinct on segments VI, VII and VIII. Sclerotized cornicles present on tergite V, weakly elevated, each surrounded by 8–9 setae. Cauda semicircular, with 2 setae. Genital plate spinose, marginally pigmented, with 2 setae at the anterior part and 9–13 setae along the hind margin. A pair of sclerotized plates present laterally to genital plate, with a few spine-like setae. Hind femorotrochanter 0.495–0.526 mm long. Setae on hind femora and tibiae 0.033 and 0.046–0.051 mm long respectively. Tarsi faintly spinose; first tarsal segment with 2 long setae, which are 0.038–0.040 mm long on the hind legs, and except on hind legs, with 1 spine-like seta. Second segment of hind tarsi 0.137–0.147 mm long. Fore wings in 1 specimen with media once branched, but in the other twice branched. Hind wings with Cu 1a and Cu 1b.

Embryos within the abdomen of emigrants. Features other than legs are indistinct, and wax gland plates are invisible. Tarsi cone-shaped, intensively spinose, completely without empodial setae.

Fundatrix. Description is based on 4 specimens collected from galls on *Ulmus uyematsui*. Body broadly rounded. Body length 1.88–1.94 (1.89) mm. Body 0.60–0.67 times as wide as long. Legs, rostrum and antennae sclerotized, pale brown to brown. Wax plates indistinct. Antennae 5-segmented, 0.501–0.541 (0.526) mm long or 0.26–0.29 times as long as body. Antennal segment III often with a spot, not sclerotized, at distal 1/3 of the segment. Antennal segments IV and V more brownish than III. Length of segments (in mm): I 0.053–0.066 (0.061), II 0.051, III 0.228–0.260 (0.248), IV 0.076–0.086 (0.081), V 0.076–0.094 (0.085). Primary rhinaria present on IV and V, fringed with cilia. Antennal setae fine and short. Antennal segments II with 3, III with 10 or 11, IV with 3 or 4, and V with 6 or 7 setae. The longest setae on III 0.030–0.033 mm long and 1.08–1.33 times as long as the diameter of the segment, and spinal setae on the last segment 0.015 mm long. Antennal segments IV and V spinose and III with a few spinules; these segments not showing distinct imbrication. Rostrum reaching to a little beyond middle coxae. Ultimate rostral segment relatively long, 0.142–0.152 mm long, with 14–16 very short setae. Head wholly sclerotized, with setae maximally 0.053–0.056 mm long. Thorax and abdomen membranous, with setae maximally 0.035 mm long. Cornicles absent. Genital plates spinose and wholly pigmented with 1 pair of setae at the anterior part and 13–14 setae along the hind margin. Cauda semicircular, with 2 setae. Hind femorotrochanter 0.364–0.404 (0.379) mm long. Hind tibiae with long setae which are maximally 0.040–0.051 mm long and 1.19–1.29 times as long as the diameter of the segment. Second segment of tarsi indistinctly separated from first segment, smooth, 0.081–0.096 mm long on hind legs. Dorso-apical setae rather long, 0.040–0.051 mm long and pointed at the apex.

Apterous fundatrigenia adult. Description is based on 5 specimens collected from 3 galls on *Ulmus uyematsui*. Body more elongate than in fundatrices. Body length 1.56–1.63 (1.63) mm. Legs, rostum and antennae weakly sclerotized and

brownish. Head almost wholly sclerotized, the sclerotization divided into many cells especially on the dorsal side. Eyes consisting of 2 parts: multifacetted eye and triommatidion, but the former often hardly developed. Antennae 6-segmented, 0.619–0.746 (0.681) mm long and 0.40–0.46 times as long as body. Antennal segments IV-VI more pigmented than III. Processus terminalis long, about 0.040 mm long. Length of segments (in mm): I 0.058–0.071 (0.065), II 0.051–0.058 (0.054), III 0.238–0.308 (0.276), IV 0.066–0.083 (0.075), V 0.083–0.101 (0.091), VI 0.116–0.126 (0.121). Primary rhinaria found on segments V and VI, fringed with cilia, with a few accessory rhinaria on VI. Antennal setae rather long; setae on segments: I 2–3, II 3–5, III 12–14, IV 3–4, V 4–5 and VI 4–5 at the base and 5 at processus terminalis. The longest setae on segment III 0.040–0.051 mm long, and apical setae on the last segment 0.015–0.020 mm long. Antennal segments III-VI faintly spinose. Rostrum reaching to between middle coxae and hind coxae. Ultimate rostral segment long, 0.147–0.152 mm long. Wax gland plates indistinct. Setae on tergite V 0.040–0.066 mm long. Cornicles slightly projecting, each surrounded by 10–12 setae. Genital plate as in fundatrices. Hind femorotrochanter 0.402–0.447 (0.424) mm long. Setae on tibiae rather long, maximally 0.046–0.051 mm on hind legs. Tarsi slightly spinose, first tarsal segment with 2 long setae, which are 0.046–0.051 mm long, and 1 spine-like seta. Spine-like setae always present also on hind legs. Second tarsal segment 0.126–0.139 mm long on hind legs. Empodial setae shorter than claws, 0.025 mm long on hind legs.

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References

Akimoto, S. 1981. Gall formation by *Eriosoma* fundatrices and gall parasitism in *Eriosoma yangi* (Homoptera, Pemphigidae). Kontyû, Tokyo, 49: 426–436.

Aoki, S. 1975. Descriptions of the Japanese species of *Pemphigus* and its allied genera (Homoptera: Aphidoidea). Ins. matsum. n.s. 5: 1–63.

——— 1967. Mordvilko's theory on the origin of heteroecy in aphids. Rostria 26: 189–197. (in Japanese).

——— 1978. Two pemphigids with first instar larvae attacking predatory intruders (Homoptera, Aphidoidea). New Entomol. 27: 7–21.

——— 1980. Life cycles of two *Colophina* aphids (Homoptera, Pemphigidae) producing soldiers. Kontyû, Tokyo, 48: 464–476.

Axelrod, D.I. 1948. Climate and evolution in Western North America during Middle Pliocene time. Evolution 2: 127–144.

——— 1959. Poleward migration of the early angiosperm flora. Science 130: 203–207.

——— 1966. Origin of deciduous and evergreen habits in temperate forests. Evolution 20: 1–15.

Baker, A.C. 1919. An undescribed species of *Dryopea* injurious to *Phyllostachys* (Aphididae-Hom.). Proc. ent. Soc. Wash., 21: 104–106.

Bate-Smith, E.C. and R.H. Richens, 1973. Flavonoid chemistry and taxonomy in *Ulmus*. Biochemical Systematics 1: 141–146.

Börner, C. and K. Heinze, 1957. Aphidina-Aphidoidea. In P. Soraure: Handbuch der Pflanzenkrankheiten, 2. Teil, 4. Lief. Homoptera II: 1–402.

Chaney, R.W. 1947. Origin and development of natural floristic areas with special reference to North America. Tertiary centers and migration routes. Ecol. Monographs. 17: 139–148.

Danielsson, R. 1979. The genus *Eriosoma* Leach in Sweden, with descriptions of two new species. Studies on Eriosomatidae I (Homoptera, Aphidoidea). Ent. scand. 193–208.

——— 1982. The species of the genus *Eriosoma* Leach having *Ribes* L. as secondary hostplant (Homoptera, Aphidoidea). Ent. scand. 13: 341–358.

David, S.K., K. Narayanan and S.G. Rajasingh, 1971, A new genus and four new species of aphids (Homoptera) from India. Oriental Insects, 5: 557–570.

Dixon, A.F.G. 1971. The life-cycle and host preferences of the bird cherryoat aphid, *Rapalosiphum padi* L., and their bearing on the host alternation in aphids. Ann. appl. Biol. 68: 135–147.

——— 1973. Biology of Aphids. London: Edward Arnold. 58 pp.

Dzhibladze, A.A. 1960. New species of aphids of the subfamily Eriosomatinae on *Zelkova carpinifolia* from Georgia. Trans. Inst. Zool. Acad. Sci. Georgian S.S.R. 17: 229–238. (in Russian).

——— 1965a. A new aphid species *Byrsocryptoides zelkovaecola* Dzhibl., sp. n. (Homoptera: Aphidoidea, Eriosomatidae) from Georgia. Soobsnch. Akad. Nauk gruz. SSR, Tbilisi. 37: 427–433. (in Russian)

——— 1965b. A new aphid species *Eriosoma gomboriense* Dzhibl., sp. n. (Homoptera: Aphidoidea, Eriosomatidae) from Georgia. Soobsch. Akad. Nauk gruz. SSR, Tbilisi. 37: 163–169. (in Russian).

Eastop, V.F. 1973. Deduction from the present day host plants of aphids and related insects. In Van Emden, H.F. (ed.), Insect/plant Relationships. 157–178. Blackwells, Oxford.

Eastop, V.F. and D. Hille Ris Lambers, 1976. Survey of the World's Aphids. Junk, the Hague. 573 pp.

Eldredge, N., and S.J. Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism, p. 82–115. In T.H.N. Schopf (ed.), Models in Paleobiology. Freeman, Cooper and Co., San Francisco.

Heie, O.E. 1967. Studies on fossil aphids (Homoptera: Aphidoidea), especially in the Copenhagen collection of fossils in Baltic amber. Spolia zool. Mus. Haun., 26.

——— 1980. The Aphidoidea (Hemiptera) of Fennoscandia and Denmark. I. Fauna Entomologica Scandinavica, Vol. 9. 236 pp. Scandinavian Science Press Ltd. Klampemborg, Denmark.

Hille Ris Lambers, D., 1950. Hostplants and aphid classification. 8th internat. Congr. Ent. Stockholm 1948: 141–144.

——— 1967. Notes on some Japanese Eriosomatinae (Homopt., Aphididae) and their life cycle. Entomologishe Berichten, Deel 27: 86–89.
——— 1970. A study of *Tetraneura* Hartig, 1841 (Homoptera, Aphididae), with descriptions of a new subgenus and new species. Boll. Zool. agr. Bachic., ser. II, 9, 1968–69: 21–101.
——— 1973. A new genus and species of Aphididae (Homoptera) from Florida. The Florida Entomologist. 56: 295–299.
Horikawa, Y. 1976. Atlas of the Japanese Flora. An introduction to Plant Sociology of East Asia. Gakken Co., Ltd. Tokyo. Japan. 862 pp.
Kuznetsova, V.G., and G. Kh. Shaposhnikov, 1973. The chromosome numbers of the aphids (Homoptera: Aphidinea) of the world fauna. Entomological Review, Washington, 52: 78–96
Marchal, P. 1933. Les aphides de l'orme et leurs migrations. Ann. Epiphyt. 19: 207–329.
Matsumura, S. 1917. Synopsis of the Pemphigidae of Japan. In: A Collection of Essays for Mr. Yasushi Nawa. 39–94. Gifu. Japan.
——— 1931. Illustrated Insects of Japan-Empire. 1497 pp.
Mattson, W.J. Jr. 1980. Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. Syst. 11: 119–161.
Miles, P.W. 1968. Insect secretion in plants. Ann. Rev. Phyiopath. 6: 137–166
Moldvilko, A.K. 1928. The evolution of cycles and the origin of heteroecy in plant-lice. Ann. Mag. nat. Hist. 10: 570–582.
——— 1935. Die Blattläuse mit unvollständigem Generationszyklus und ihre Entstehung. Ergebn. Fortshr. Zool. 8: 36–328.
Paik, W.H. 1972. Illustrated Encyclopedia of Fauna & Flora of Korea, 13, Insecta 5, 751 pp. (in Korean).
Pielou, E.C. 1979. Biogeography. A Wiley-Interscience Publication. 335 pp.
Shaposhnikov, G. Kh. 1956. Phylogenetic basis of the classification of Anuraphidina, and their connection with plants. Trud. zool. Inst. Akad. Nauk SSSR, Moscow 23: 215–320. (in Russian).
Shinji, O. 1941. Monograph of Japanese Aphids (in Japanese). Tokyo, 1215 pp.
Sorin, M. 1977. Aphids parasitising trees (6). Forest Pest, Tokyo, 26: 4–13. (in Japanese)
Stanley, S.M. 1979. Macroevolution: Pattern and Process. W.H. Freeman, San Francisco.
Stebbins, G.L. 1950. Variation and Evolution in Plants. Columbia University Press.
Stroyan, H.L.G. 1963. A new genus and species of Eriosomatinae (Homoptera: Aphidoidea) from the North-West Himalayas. Proc. roy. ent. Soc. Lond. (B) 32: 81–85.
Takahashi, R. 1928. Field observations on leaf-cutting weevils and consideration on the relationship between the life histories of herbivorous insects and their host plants. Zoological Journal, Tokyo, 40: 199–206. (in Japanese).
——— 1931. Aphididae of Formosa, part 6. Dept. Agric. Formosa Rept. 53: 1–127.
——— 1939. Some Aphididae from South China and Hainan (Homoptera), IV. Trans. nat. Hist. Soc. Formosa. 29: 141–146.
——— 1963. Two new genera and five new or little known species of Aphididae from Japan (Homoptera). Kontyû, Tokyo, 31: 159–168.
Takahtajan, A. 1969. Flowering Plants: Origin and Dispersal. Smithsonian institution Press, Washington, D.C.
Tanai, T. 1972. Tertiary history of vegetation in Japan. In Floristics and Paleofloristics of Asia and Eastern North America. (A. Graham ed.). Elsevier Publishing Company, Amsterdam.
Tanaka, T. 1961. The rice root aphids, their ecology and control. No. 10, Special Bull. Coll. Agrical. Utsunomiya Univ., Utsunomiya, Japan. (in Japanese).
Touw, A., and C.G.G.J. Van Steenis, 1968. Note on *Ulmus* in Malesia. Blumea 16: 84.
Zwölfer, H. 1958. Zur Systematik, Biologie und Ökologie unterirdisch lebender Aphiden (Homoptera, Aphidoidea). I-IV. Z. angew. Ent. 40: 182–221, 528–575; 42: 129–172; 43: 1–52.