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DESCRIPTIONS OF THE JAPANESE SPECIES OF PEMPHIGUS AND ITS ALLIED GENERA (HOMOPTERA : APHIDOIDEA)

By SHIGEYUKI AOKI

Abstract

AOKI, S. 1975. Descriptions of the Japanese species of *Pemphigus* and its allied genera (Homoptera: Aphidoidea). *Ins. matsum. n. s.* 5: 1–63, 20 tabs., 23 figs. (20 text-figs., 3 pls.).

Seven species of *Pemphigus* and its allied genera occurring in Japan are dealt with. Descriptions of the adult and 1st instar larva of the fundatrix, emigrant and exule are given. *Pemphigus microsetosus* is new to science, and *Pemphigus saliciradicis* is new to Japan. *Pemphigus niisimae* is transferred to *Epipemphigus*. An attempt is made at the taxonomic evaluation of the 1st instar larval characters. *Thecabius* and *Parathecabius* are criticized, and are tentatively included in *Pemphigus*.

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Contents

Introduction

The insects of the genus *Pemphigus* and its allied genera are gall-makers prominently associated with *Populus* species. Certain authors (e.g. Börner 1952, Börner and Heinze 1957) have attempted the so-called generic classification of them without overwhelming success. The difficulty of constructing a sound classification of these insects is mainly due to the morphological uniformity of the exules strikingly contrasted with the diversity of the gall inhabitants. Though there are a number of works describing these pemphigids, not much attention has been paid to the 1st instar larvae of various generations. In these pemphigids, the 1st instar often plays a special biological role; e.g. the fundatrix 1st instar larvae hatch from the eggs overwintering in bark crevices and migrate to leaves or shoots, and the emigrant 1st instar larvae of certain species emigrate from the leaf bearing the primary gall to another leaf to make the secondary gall. Therefore, a comparative study on this stage is important in biology and hence in taxonomy. The main purpose of the present paper is to give descriptions of the pemphigids occurring in Japan, with the hope of finding clues to some problems of their phylogeny.

The species treated here are referable to the Pemphigini (sensu Börner 1952, see also Hille Ris Lambers 1966a), which involve *Thecabius*, *Parathecabius*, *Pemphigus*, *Pemphiginus* and *Epipemphigus*. However, I am much inclined to the opinion that the genera mentioned are rather tentative ones, and only two genera are recognized in this work. In the course of the present study, many exules of this group were collected from the roots of *Erigeron annuus*, *Cryptotaenia japonica*, *Rumex* sp., etc., and many sexuparae were collected from the trunk of *Populus maximowiczii*, but they are omitted from the present paper because of the difficulty to join them with respective spring gall-making forms.

Main morphological characters adopted here are tabulated in Tables 1–5. Terms peculiar to the life cycle of this group are mainly based on Hille Ris Lambers (1966b). The type specimens of the new species described in this paper are deposited in the collection of the Entomological Institute, Hokkaidô University.

Description and discussion

Pemphigus orientalis (Mordvilko) n. comb.

Thecabius affinis orientalis Mordvilko 1935: 67.
Thecabius populiconduplifolius ?: Essig and Kuwana 1918: 106.
Pemphigus ranunculi Shinji 1922: 533 (nec Kaltenbach 1843[1)], nec Davidson 1910[2)]).
Prociphilus ranunculi: Shinji 1941: 1088; Paik 1972: 613.
Thecabius orientalis: Paik 1972: 626.
Thecabius affinis: Holman and Szelegiewicz 1972: 5.

Fundatrix. First instar larva differs from adult in many respects, whereas 2nd to last instar larvae are similar to adult in general.

1) Monographie der Familien der Pflanzenläuse (Phytophthires), 1. Teil. Die Blatt- und Erdläuse. Aachen. 223 pp. (after Zwölfer 1957 & 1958).
2) Further notes on the Aphididae collected in the vicinity of Stanford University. J. Econ. Ent. 3: 372–381 (after Palmer 1952).

Fundatrix 1st instar larva (Fig. 1, A–C).

Description is based on 10 moults left in primary galls on *Populus maximowiczii* (Sapporo, Hokkaidô; 20 v–8 vi, 1973).

Body without visible wax gland plate. Thoracic and abdominal tergites not extensively sclerotized, but only the small regions within which 1 or 2 setae (1 on abdominal tergites I–VII) occur are weakly sclerotized. Antenna (Fig. 1, B) usually 5-segmented (one specimen with 4-segmented right antenna), but segments III and IV with a non-functional articulation; number of setae on each segment as follows: I: 3–5 (usually 4), II: 2, III: 0, IV: 3, V: 2+5; the longest seta on V (except terminal setae) *ca.* 0.017–0.025 mm.; primary rhinaria distinctly ciliate, on IV *ca.* 0.007–0.010 mm. and on V *ca.* 0.010–0.015 mm. in axial length; III–V spinose. Ultimate rostral segment (Fig. 1, C)[1] without accessory seta. Fore femur not enlarged. Tarsi (Fig. 1, A) 2-segmented, spinose; 1st segment with a pair of long pointed setae, which are *ca.* 0.035–0.043 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium; the empodial setae bent and capitate, extending a little beyond the apices of claws; the lateral setae long, usually capitate but less remarkably than the empodial setae. Abdominal tergites I–VI each with 3 pairs of setae, the longest one on tergite III *ca.* 0.010–0.013 mm.; abdominal tergite VII with 2 pairs of setae; abdominal tergite VIII with a pair of setae, the longer one *ca.* 0.015–0.020 mm.; cauda sclerotized, with a pair of setae; anal plate with 4 (rarely 5 ?) setae. Cornicle absent.

Measurements of 10 specimens in mm. Antennal segments (I–V): 0.042 (0.037–0.048), 0.042 (0.037–0.048), 0.034 (0.027–0.040), 0.029 (0.027–0.035), 0.090 (0.080–0.098); ultimate rostral segment (in 9 specimens) 0.078 (0.075–0.080); 2nd segment of hind tarsus (in 7 specimens) 0.082 (0.077–0.088).

Fundatrix adult (Fig. 1, D–H).

Description is based on 9 specimens collected from primary galls on *Populus maximowiczii*. Measurements of certain parts and collection data in Table 6.

Antenna (Fig. 1, E) 5-segmented, the articulations all functional; number of setae on each segment as follows: I: 4–6, II: 3–8, III: 1–5, IV: 3, V: 2+5; the longest seta on V (except terminal setae) *ca.* 0.017–0.023 mm.; III the longest, about as wide as IV, IV somewhat wider than V; primary rhinaria ciliate, on IV *ca.* 0.012–0.018 mm. and on V *ca.* 0.017–0.025 mm. in axial length. Ultimate rostral segment (Fig. 1, F) very short, faintly spinose, with 1 or 2 accessory setae at middle. Thorax usually not sclerotized except on sides of prothorax, rarely prothoracic tergite sclerotized somewhat strongly. Tarsi (Fig. 1, D) 2-segmented, spinose; 1st segment with a pair of long setae and sometimes with 1 or 2 secondary setae, which are *ca.* 0.037–0.045 mm. in maximum length on hind tarsus; 2nd segment with some accessory setae, the empodial setae *ca.* 0.010–0.015 mm. in maximum length on hind tarsus. Thoracic and abdominal wax gland plates usually with separated facets (Fig. 1, H), but on posterior abdominal segments often with facets appressed together (Fig. 1, G), their distribution is as follows: spinal ones on thoracic tergites I–III and abdominal tergites I–VII and though rarely even on

1) In the figures of the present paper, the apical part of the ultimate rostral segment is drawn schematically.

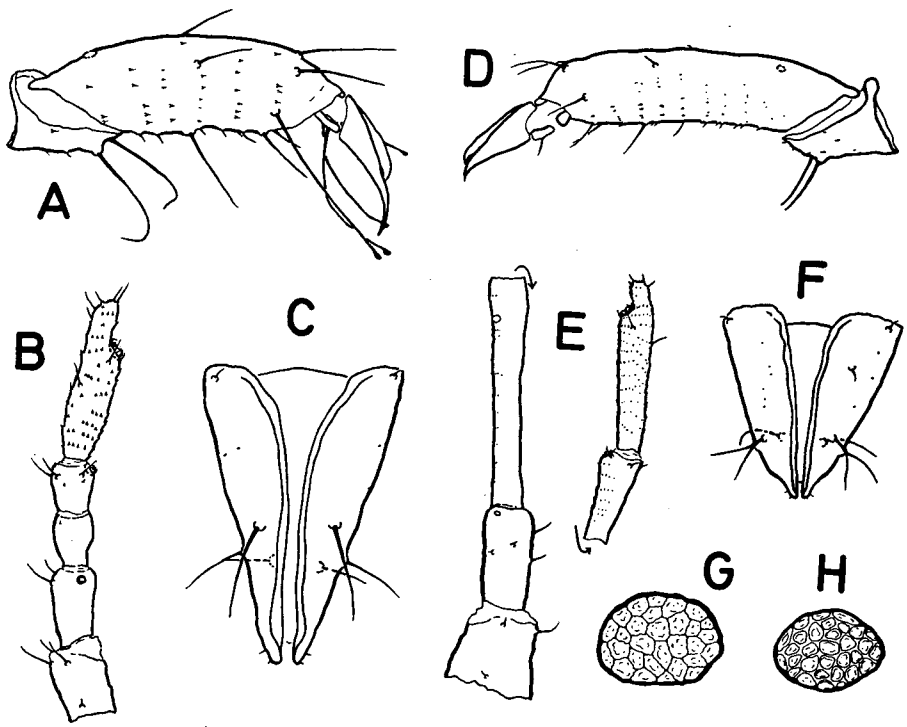

Fig. 1. *Pemphigus orientalis* fundatrix. First instar larva: A, hind tarsus; B, antenna; C, ultimate rostral segment. Adult: D, hind tarsus; E, antenna; F, ultimate rostral segment, G & H, abdominal wax gland plate.

abdominal tergite VIII, marginal ones on thoracic tergites I–III and abdominal tergites I–VII, and pleural ones on thoracic tergites II and III (rarely only on III) and abdominal tergites I–VI, in addition to small accessory wax gland plates sometimes appearing irregularly. Tergites with a number of setae, some of the setae long and stout, and possibly primary; the longest one on abdominal tergite III *ca.* 0.030–0.040 mm., that on abdominal tergite VIII *ca.* 0.042–0.055 mm. Cornicle absent. Cauda with 2–5 setae. Two gonapophyses present, with 2–9 setae between them. Genital plate with 20–31 setae.

Measurements of 9 specimens in mm. Ultimate rostral segment 0.112 (0.105–0.120); 2nd segment of hind tarsus 0.194 (0.165–0.220).

Emigrant. First instar larva with capitate empodial setae, whereas 2nd to last instar larvae and adult with pointed empodial setae.

Emigrant 1st instar larva (Fig. 2, A–E).

Description is mainly based on 10 specimens, of which 5 were collected from some primary galls on *Populus maximowiczii* (Sapporo, Hokkaidô; 15 vi 1972) and the other five from some secondary galls on *Populus maximowiczii* (Sapporo, Hokkaidô; 23 vi 1973).

General colour in life yellowish. Head without wax gland plate. Antenna (Fig. 2, D) 5-segmented; number of setae on each segment as follows: I: 4 (rarely 3), II: 2, III: 0, IV: 3 (rarely 4), V: 2+5; the longest seta on V (except terminal setae) *ca.* 0.020–0.025 mm.; primary rhinarium ciliate, on IV *ca.* 0.005–0.010 mm. and on V *ca.* 0.010–0.015 mm. in axial length; III, IV and V spinose. Ultimate rostral segment (Fig. 2, E) faintly spinose, without accessory seta. Thoracic tergites I–III each with 4 pairs of setae. Prothoracic tergite often with a pair of small spinal wax gland plates. Tarsi (Fig. 2, C) 2-segmented, spinose; 1st segment with a pair of setae, which are *ca.* 0.040–0.048 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 1 pair+2–4, ventrally 1 pair+2–4, laterally 1 pair+0–2, and 1 pair on empodium, the empodial setae long, extending beyond the apices of claws, capitate, the others all pointed, the dorsoapical setae clearly longer than the ventroapical setae. Abdominal tergites I–VI each with 3 pairs of setae, the longest one on tergite III *ca.* 0.012–0.020 mm.; abdominal tergite VII with 2 pairs of setae; abdominal tergite VIII with a pair of setae, the longer one *ca.* 0.015–0.023 mm.; cauda with a pair of setae; anal plate with 2 pairs of setae. Abdominal wax gland plates as in Fig. 2, B, their distribution (Fig. 2, A) is as follows: spinal ones on tergites I–VII, pleural ones on tergites I–VI, and marginal ones on tergites I–VII; the spinal ones on tergites III–VII and the pleural ones on tergites III–VI large in size, each composed of a large number of facets, the others small in size, with fewer facets. Cornicle absent.

Measurements of 10 specimens in mm. Body 0.69 (0.63–0.74); antennal segments (I–V): 0.049 (0.045–0.053), 0.053 (0.050–0.055), 0.071 (0.067–0.078), 0.056 (0.050–0.060), 0.125 (0.117–0.130); ultimate rostral segment 0.090 (0.085–0.095); 2nd segment of hind tarsus 0.116 (0.110–0.123).

Emigrant adult (Fig. 2, F–H).

Description is mainly based on 10 specimens from secondary galls on *Populus maximowiczii*. Measurements of certain parts and collection data in Table 7.

Head rarely with small wax gland plates. Antenna (flagellum: Fig. 2, H) 6-segmented; IV–VI weakly imbricated; V with 3 setae at apex, the longest seta *ca.* 0.015–0.023 mm., often with 1 or 2 additional setae at middle, the basal articular diameter *ca.* 0.017–0.023 mm.; VI with 2 setae at apical 1/4, 5 setae at apex, and sometimes a seta at basal 1/3; secondary rhinaria present on III–VI, very slender, mostly encircling *ca.* 1/2 the segment; primary rhinaria fringed with cilia which are often furcated; that on VI apparently encircling *ca.* 2/3–3/4 the segment, *ca.* 0.015–0.023 mm. in axial length; that on V often united with secondary rhinarium to form an irregular, partially ciliate, united rhinarium, *ca.* 0.015–0.025 mm. in axial length. Ultimate rostral segment (Fig. 2, F) faintly spinose, with a few accessory setae. Mesothorax and metathorax with spinal wax gland plates. Fore wing with simple media. Tarsi spinose: 1st segment usually with 1–3 accessory setae and a spine-like seta between primary setae, the spine-like seta sometimes absent on mid and hind leg; the longest dorsal seta (except apical setae) on hind 2nd segment *ca.* 0.015–0.025 mm. Abdominal wax gland plates of normal type (Fig. 9, F) rather numerous, occurring irregularly on tergites I–VIII, partially out of longitudinal rows. Abdomen also with other reduced wax gland plates (?) (Fig. 2, G), each plate with a seta, as follows: tergites III–VI each with 4, tergite VII with 2, tergites I and II with some. Similar

plates yet without seta on tergites I–VII near the marginal wax gland plates. Cornicle absent. Abdominal tergite VIII with 2–4 setae. Cauda with 2 or 3 setae. Genital plate with 15–26 setae.

Measurements in mm. Ultimate rostral segment (in 9 specimens) 0.113 (0.105–0.125); 2nd segment of hind tarsus (in 10 specimens) 0.249 (0.215–0.260).

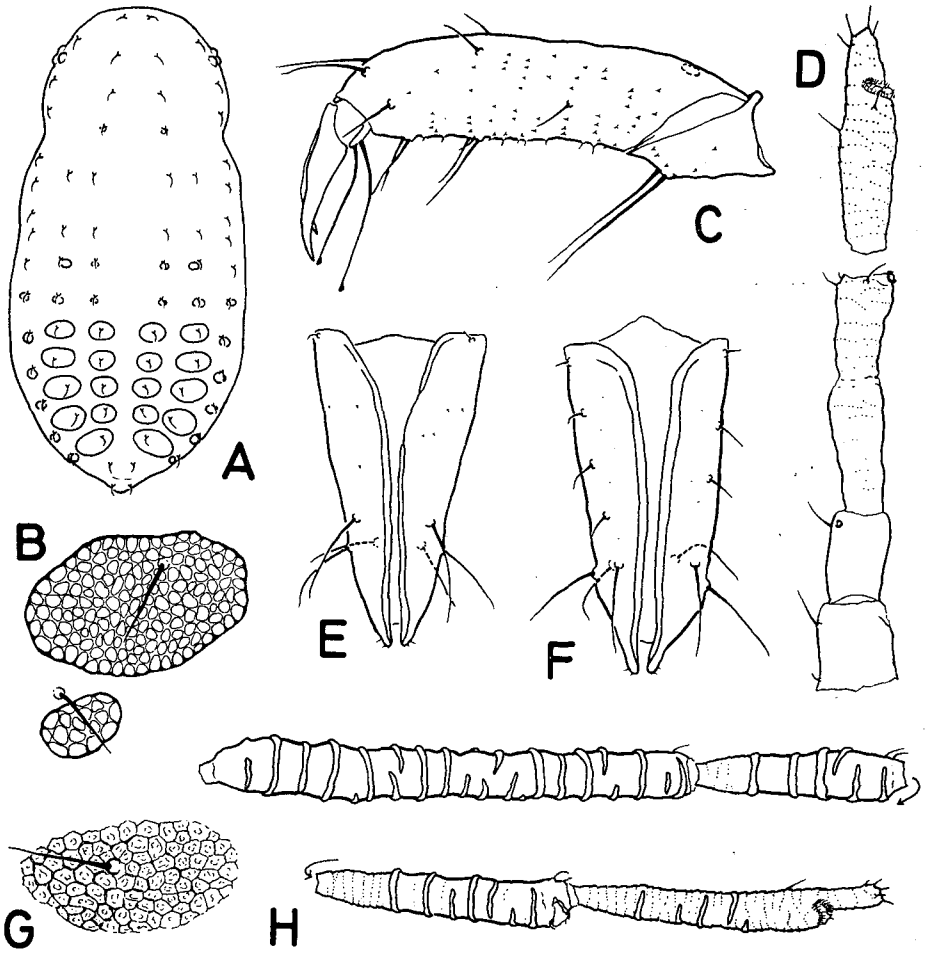

Fig. 2. *Pemphigus orientalis* emigrant. First instar larva: A, distributional pattern of wax gland plates; B, abdominal wax gland plate; C, hind tarsus; D, antenna; E, ultimate rostral segment. Adult: F, ultimate rostral segment; G, reduced wax gland plate (?); H, flagellum.

Exule 1st instar larva (3rd generation) (Fig. 3, A–C).

Description is mainly based on 10 specimens deposited by emigrants (Sapporo, Hokkaidô; 6 & 7, vii 1973).

Antenna (Fig. 3, C) 5-segmented; number of setae on each segment as follows: I: 4, II: 2 or 3 (usually 2), III: 0, IV: 3, V: 2+5; the longest seta on V (except

terminal setae) *ca.* 0.015–0.023 mm.; primary rhinaria ciliate, on IV *ca.* 0.007–0.010 mm. and on V *ca.* 0.012–0.015 mm. in axial length; membraneous neck between IV and V not remarkable. Ultimate rostral segment (Fig. 3, A) faintly spinose, sometimes with an accessory seta. Tarsi (Fig. 3, B) 2-segmented, spinose; 1st segment with a pair of pointed setae, which are *ca.* 0.030–0.038 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 1 pair+2–5, ventrally 1 pair+2–4, laterally 1 pair+0–2, and 1 pair on empodium, all these setae pointed, the empodial setae *ca.* 0.010–0.015 mm. in maximum length on hind tarsus. Abdominal tergites I–VI each with 3 pairs of setae, the longest one on tergite III *ca.* 0.015–0.018 mm.; abdominal tergite VII with 2 pairs of setae; abdominal tergite VIII with a pair of setae, the longer one *ca.* 0.017–0.020 mm.; cauda with a pair of setae; anal plate with 2 pairs of setae. Abdominal wax gland plates composed of many separated facets with a "Zentralkern", their distribution is as follows: spinal ones on tergites III–VII, pleural ones on tergites III–VI. Cornicle absent.

Measurements of 10 specimens in mm. Body 0.70 (0.66–0.75); antennal segments (I–V): 0.056 (0.052–0.060), 0.060 (0.057–0.063), 0.070 (0.067–0.075), 0.056 (0.052–0.060), 0.113 (0.110–0.118); ultimate rostral segment 0.096 (0.092–0.100); 2nd segment of hind tarsus 0.115 (0.112–0.120).

Exule 1st instar larva from secondary host.

Eight exule 1st instar larvae collected from *Ranunculus quelpaertensis* (Morioka, Iwate Pref.; 11 viii 1973) were examined. They are slightly different from the materials of the 3rd generation in the following morphological characters:

Antenna: II often with 3 setae; primary rhinarium on V *ca.* 0.012–0.018 mm. in axial length; the longest seta on V *ca.* 0.015–0.018 mm. Ultimate rostral segment with 1 or 2 accessory setae. The setae on hind 1st tarsal segment *ca.* 0.027–0.038 mm. in maximum length. The longest seta on abdominal tergite III *ca.* 0.012–0.018 mm.

Measurements of 8 specimens in mm. Body (in 4 specimens) 0.75–0.86; antennal segments (I–V): 0.054 (0.050–0.060), 0.061 (0.055–0.068), 0.073 (0.057–0.078), 0.060 (0.055–0.063), 0.114 (0.102–0.123); ultimate rostral segment 0.095 (0.085–0.100); 2nd segment of hind tarsus 0.115 (0.110–0.120).

Apterous exule adult (Fig. 3, D & E).

Description is mainly based on 10 specimens collected from *Ranunculus quelpaertensis*. Measurements of certain parts and collection data in Table 8.

Head with a number of indistinct wax gland plates. Antenna (apical segments: Fig. 3, D) distinctly 6-segmented, the articulations all functional; V with 3 setae at apex and 1–3 setae at middle; VI with 5 (rarely 6) setae at apex, 2 or 3 (usually 2) setae at apical 1/3 and rarely with a seta at basal 1/3–1/2; primary rhinaria distinctly ciliate, on V *ca.* 0.012–0.015 mm. and on VI *ca.* 0.015–0.020 mm. in axial length. Ultimate rostral segment (Fig. 3, E) spinose, with 3–6 accessory setae. Tarsi 2-segmented, spinose; 1st segment with a pair of long primary setae and 0–3 secondary setae, the fore leg always and the middle leg usually also with a short spine-like seta between the primary setae. Form and distribution of abdominal wax gland plates as in the 1st instar larva. Cauda rather obtuse-angled triangular in outline, with a pair of setae. Two gonapophyses, and 2–5 setae

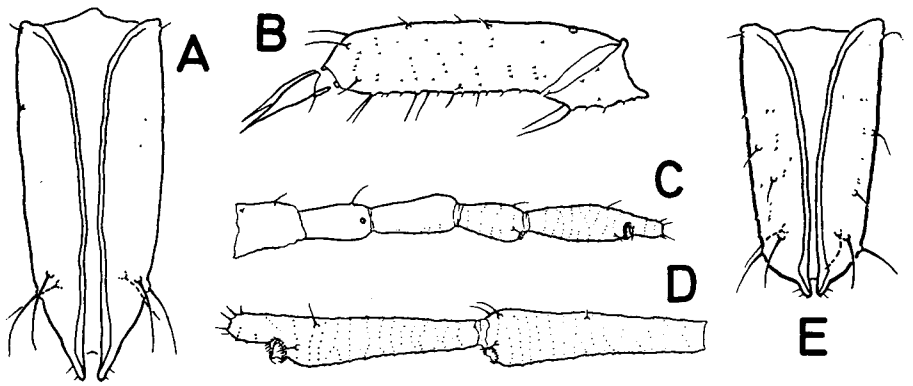

Fig. 3. *Pemphigus orientalis* exule. First instar larva: A, ultimate rostral segment; B, hind tarsus; C, antenna. Apterous adult: D, two apical segments of antenna; E, ultimate rostral segment.

between them. Genital plate with 21–28 setae.

Measurements of 10 specimens in mm. Ultimate rostral segment 0.125 (0.112–0.135); 2nd segment of hind tarsus 0.237 (0.220–0.265).

Gall. Primary gall (Pl. II, A) made of marginal part of leaf of *Populus maximowiczii* folded on underside, the folded part, *ca.* 12–15 mm. in length, with the neighbouring region becoming red; secondary gall (Pl. II, B) made of young leaf of *Populus maximowiczii* rolled or folded under, usually becoming red.

Host. Primary host: *Populus maximowiczii, Populus suaveolens* (in Ussuri and in Kamchatka, after Mordvilko 1935), *Populus laurifolia* (in Mongolia, after Holman and Szelegiewicz 1972); secondary host: *Ranunculus japonicus* (after Shinji 1944), *Ranunculus quelpaertensis, Ranunculus ternatus* (after Essig and Kuwana 1918), *Ranunculus vernyi* (in Korea, after Paik 1972).

Distribution. Mongolia (after Holman and Szelegiewicz 1972), Kamchatka (after Mordvilko 1935); Ussuri (after Mordvilko 1935); Japan: Hokkaidô, Honshû, Kyûshû (after Shinji 1922); Korea (after Paik 1972).

Biological notes. Fundatrix lives in primary gall. First instar larva of the next generation leaves the gall to make secondary gall. All of the 2nd generation insects then become winged and emigrate to secondary hosts.[1] The collection dates for various stages of the galls at Sapporo and Jôzankei (near Sapporo) are as follows: primary gall with fundatrix 2nd instar larva: 20 & 25 v 1973; primary gall with fundatrix adult: 4, 11, 15, 18 & 27 vi 1972, 18 vii 1972, 30 vi 1973, 5, 9 & 18 vii 1973; secondary gall without emigrant adult: 3 vii 1972, 18, 23 & 30 vi 1973; secondary gall with emigrant adult: 5, 8, 9, 18 & 20 vii 1973. I have found this aphid mainly on young riverside trees of *Populus maximowiczii*.

Discussion. Shinji (1922) described "*Pemphigus ranunculi*" (homonymous with *P. ranunculi* Kaltenbach and *P. ranunculi* Davidson), and later he (1941) transferred it to *Prociphilus*. The type specimens are lost. Judging from his descriptions, however, it is very similar to the exule form of *Pemphigus affinis*.

1) In *Pemphigus affinis*, Börner and Heinze (1957) reported the presence of the apterous fundatrigenia, but I could not find that morph in *orientalis*.

In the summer of 1973 I collected apterous exules of *Pemphigus* from *Ranunculus quelpaertensis* at Morioka and its suburbs, and found that their characters agree with his descriptions. Having examined the 1st instar larvae from Morioka, I could not find any reliable difference between them and the 1st instar larvae laid by emigrants of *orientalis* collected at Sapporo. It is probable that *ranunculi* Shinji is the exule form of *orientalis*.

The type locality of *ranunculi* Shinji is Miyakonojô (Kyûshû). Shinji (1941) adds certain other localities, some of which are clearly beyond the range of the primary host, *Populus maximowiczii* (see Fig. 4). If he is right, it is suggested that an anholocyclic sequence occurs at least locally in this species.

The present materials slightly differ from the European *Pemphigus affinis* described by Zwölfer (1957) in the following aspects: (1) in fundatrix adult abdominal tergite VII with 2 pairs of wax gland plates; (2) wax gland plates in emigrant 1st instar larva less developed; (3) cornicle absent in emigrant adult.

Fig. 4. Distribution of exule form of *Pemphigus orientalis* (after Shinji 1941) and *Populus maximowiczii* (after Kurata 1971). o: locality of *"ranunculi"* Shinji, x: type locality of *"ranunculi"* Shinji, •: locality of *Populus maximowiczii*.

Mordvilko (1935) gave a subspecific status to the Far Eastern form of *"Thecabius affinis"* based on the following two observations:

> "Nach Mittelsibirien dringt von Osten die *P.* [*Populus*] *suaveolens* vor, die bis Nischneudinsk und Kansk vordringt. Im Ussurigebiet lebt auf *Populus suaveolens* und *P. maximowiczii* eine schwach abweichende Form, die man *Th. affinis orientalis* nennen kann. Ihre Gallen gleichen denjenigen, welche *Th. affinis* in Europa hervorruft; doch fehlten sie vollständig bei Wladiwostock auf jungen angepflanzten *Populus nigra*, was wohl dadurch zu erklären ist, dass der ussurische *Thecabius* auf diese Pappeln nicht hinübergehen kann.
>
> "In einem der Dörfer (Jazyl, unweit von Sluzk, Gouv. Minsk) wuchsen im Garten neben dem Hause zwei *Populus pyramidalis*. In Sommer des Jahres 1910 und hernach 1919 habe ich auf ihnen die Gallen folgender Arten der Pemphigea gefunden: *Thecabius affinis* Kalt., *Pemphigus bursarius* Tullgr. (*pyriformis* Licht.), *P. filaginis* Boyer de F. und einige andere. Auf dem fast neberan wachsenden *Populus laurifolia* waren nur Gallen von *P. borealis* Tullgr."

Most of the gall-making pemphigine species have their primary host range associated with peculiar poplar species groups, and it is not rare that one species is restricted within a single poplar section (e.g. see Lange 1965). The primary hosts of the European *Pemphigus affinis* are *Populus nigra*, *P. italica*, *P. pyramidalis* and *P. monilifera* (after Börner 1952, Börner and Heinze 1957, Börner and Schilder 1931, van der Goot 1915, Ilharco 1973, Lampel 1960, Patch 1938, Shaposhnikov 1964,

Zwölfer 1957), all of which belong to the section *Aigeiros* (according to Fernald 1950, etc.). Those of the East Asian form are *Populus maximowiczii, P. suaveolens* and *P. laurifolia,* all of which belong to the section *Tacamahaka* (according to Sargent 1917). These facts suggest a distinct difference in primary host preference between the two forms. For this reason I give tentatively a full species status to the East Asian form. However, it is unknown whether there is a distinct gap in their distribution depending upon their secondary host plants. Furthermore, the North American *Pemphigus populiconduplifolius,* which is very closely related to both forms, shows the wide primary host range. After Gillete (1914), Maxon and Knowlton (1929), Patch (1913 & 1938), Palmer (1952) and Harper (1966), the primary hosts of *populiconduplifolius* are *Populus balsamifera, P. deltoides, P. monilifera, P. occidentalis, P. sargenti* and *P. trichocarpa,* which practically cover the whole range of primary host differences at the section level found between *affinis* and *orientalis.* It is very interesting whether a local population of *populiconduplifolius* can cause galls both on *Aigeiros* and on *Tacamahaka.* Though Harper (1966) says that "*affinis* and *populiconduplifolius* may be synonymous", three species, i.e. *affinis, orientalis* and *populiconduplifolius,* may be better accepted until helpful information has been available.

In this paper, these three closely related species are lumped together as "*affinis* group". The characteristics of this group is briefly given below:

Affinis group of *Pemphigus.* A Holarctic group. Life cycle obligatory-heteroecious with paracycle and anholocycle; 1 generation of fundatrigenia except in *affinis,* which sometimes has more than one generation. Alate morph of exule known. Primary hosts are *Populus* species belonging to the sections *Aigeiros* and *Tacamahaka;* secondary hosts are *Ranunculus* species. Fundatrix and fundatrigenia live in the respective galls separately. Primary gall is made of leaf margin folded beneath; secondary gall a roll of folded young leaf. Fundatrix 1st instar larva: Thoracic and abdominal tergites not extensively sclerotized; antenna 5-segmented, but segments III and IV with a non-functional articulation; fore femur normal in size; empodial setae and lateroapical setae on 2nd tarsal segment capitate, setae on 1st tarsal segment pointed. Fundatrix adult: Head with wax gland plates; antenna 5-segmented, the articulations all functional. Second generation 1st instar larva: Antenna 5-segmented; empodial setae long and capitate. Emigrant adult: Secondary rhinaria on antennal segments III–VI, very narrow, without cilia; processus terminalis long and slender; abdominal pleural wax gland plates; a short spine-like seta between primary setae on 1st tarsal segment. Exule 1st instar larva: Antenna 5-segmented; empodial setae comparatively short. Exule adult: Head with wax gland plates; antenna 6-segmented, the articulations all functional.

I have examined the apterous exule adult of *affinis* determined by Dr. D. Hille Ris Lambers in addition to the present material of *orientalis.* The above description of *affinis* group are partly based on Palmer (1952) and Zwölfer (1957).

Pemphigus latisensoria (Hori) n. comb.

Thecabius latisensoria Hori 1938: 121.

Fundatrix adult (Fig. 5, A–D).

Description is based on one specimen collected from a primary gall on *Populus maximowiczii* (Sapporo, Hokkaidô, 27 vii 1973).

Head and part of prothorax sclerotized. Head on the left half with 3 wax gland plates, of which the largest one is 0.095 mm. in largest diameter; on the right none. Antenna (Fig. 5, B) distinctly 5-segmented, the articulations all functional, and segment III with an abortive division; number of setae on each segment as follows (left/right): I: 3(4?)/4(5?), II: 7/7, III: 4/2, IV: 3/3, V: 1+5/2+5; the longest seta on V (except terminal setae) 0.025 mm.; III the longest, wider than IV, and IV clearly wider than V; primary rhinaria ciliate, on left IV 0.018 mm. and on left V 0.013 mm. in axial length. Ultimate rostral segment (Fig. 5, D) acute, conical with rather straight sides, without accessory seta and spine. Femora very wide. Tarsi (Fig. 5, A) 2-segmented, spinose ventrally; 1st segment with a pair of setae, which are 0.025 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium, all these setae pointed, the empodial setae *ca.* 0.007–0.010 mm. on hind tarsus. Thoracic and abdominal wax gland plates (Fig. 5, C) with irregular facets rather appressed together, their distribution is as follows: spinal ones on thoracic tergites I–III and abdominal tergites I–VII, pleural ones on thoracic tergites II and III and abdominal tergites I–VI, and marginal ones on thoracic tergites I–III and abdominal tergites I–VI. Tergites with many setae, some of the setae long and stout, and possibly primary, the longest one on abdominal tergite III 0.060 mm. Cornicle absent.

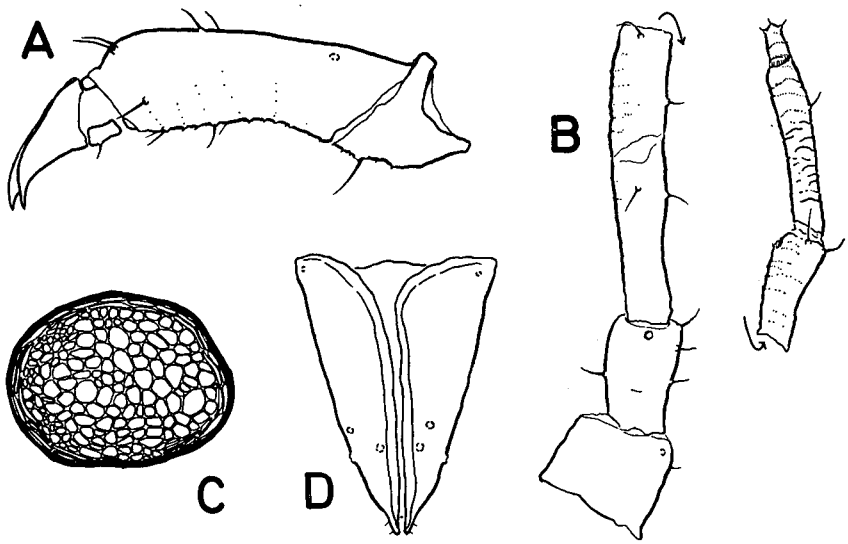

Fig. 5. *Pemphigus latisensoria* fundatrix. Adult: A, hind tarsus; B, antenna; C, abdominal wax gland plate; D, ultimate rostral segment.

Measurements in mm. Body 4.56; left antennal segments (I–V): 0.130, 0.140, 0.330, 0.125, 0.250; ultimate rostral segment 0.160; 2nd segment of left hind tarsus 0.190.

Second generation 1st instar larva.

Description is based on some embryos remaining in the body of fundatrix.

Antenna 4-segmented; in one specimen the number of setae on left antennal segment is as follows: I: 4, II: 2, III: 3, IV: 2+5; primary rhinaria ciliate; III and IV spinose. Ultimate rostral segment 0.100 mm. in length (in one specimen). Tarsi 2-segmented, spinose; 1st segment with a pair of setae; setal distribution on 2nd segment as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium, the empodial setae long, extending beyond the apices of claws, capitate, the others all pointed, the dorsoapical setae clearly longer than ventroapical setae. Abdominal wax gland plates visible, but the distributional pattern can not be made out on the basis of the present material.

Emigrant adult (Fig. 6, A–C).

Description is mainly based on 10 specimens collected from some secondary galls on *Populus maximowiczii*. Measurements of certain parts and collection data in Table 9.

Head with a pair of spinal wax gland plates or with traces of them. Antenna (flagellum: Fig. 6, C) 6-segmented; V with 3 (rarely 4) setae at apex, of which the longest one is *ca.* 0.022–0.028 mm., the basal articular diameter *ca.* 0.022–0.028 mm.; VI with 2 setae about apical 1/4, with 5 setae at apex; secondary rhinaria found along whole of segments III–V and basal part of VI, broad, distinctly wider than interrhinarial distances, spanning nearly the entire circumference of the segment when complete, but often broken (especially on III); primary rhinarium on V similar to secondary rhinaria, but partially and irregularly fringed with cilia which are often furcated, *ca.* 0.030–0.048 mm. in axial length; primary rhinarium on VI of normal type, encircling *ca.* 1/2 the segment, fringed with cilia which are often furcated, *ca.* 0.017–0.025 mm. in axial length; processus terminalis rather long, somewhat imbricated. Ultimate rostral segment (Fig. 6, A) sometimes with an accessory seta. Mesothorax and metathorax with a pair of spinal wax gland plates. Fore wing with simple media. Tarsi 2-segmented, spinose; 1st segment with 1 or 2 (usually 2) accessory setae, the fore leg also with a spine-like seta between primary setae; the longest dorsal seta (except apical setae) on hind 2nd segment *ca.* 0.027–0.040 mm., empodial setae *ca.* 0.012–0.018 mm. in maximum length on hind tarsus. Abdominal wax gland plates (Fig. 6, B) often irregular in shape, not only pigmented around, but also pigmented inside faintly, so that looking somewhat dusky, their distribution is as follows: spinal ones on tergites I–VIII, marginal ones on tergites I–VII, and pleural ones on tergites I–VII and irregular in distribution. Abdomen with other sclerotized plates, which look dusky in mounted specimens and lack seta: spinal ones on tergites I–VII, marginal ones on tergites I–VII, and pleural ones on tergites I–VI. Cornicle present, but not strongly sclerotized. Abdominal tergite VIII with 3–5 setae. Cauda with 2 or 3 setae. Genital plate with 33–39 setae.

Measurements in mm. Ultimate rostral segment (in 8 specimens) 0.143

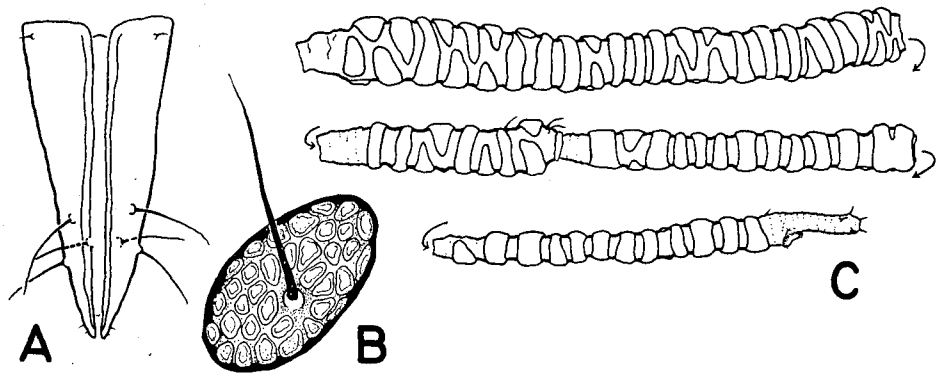

Fig. 6. *Pemphigus latisensoria* emigrant. Adult: A, ultimate rostral segment; B, abdominal wax gland plate; C, flagellum.

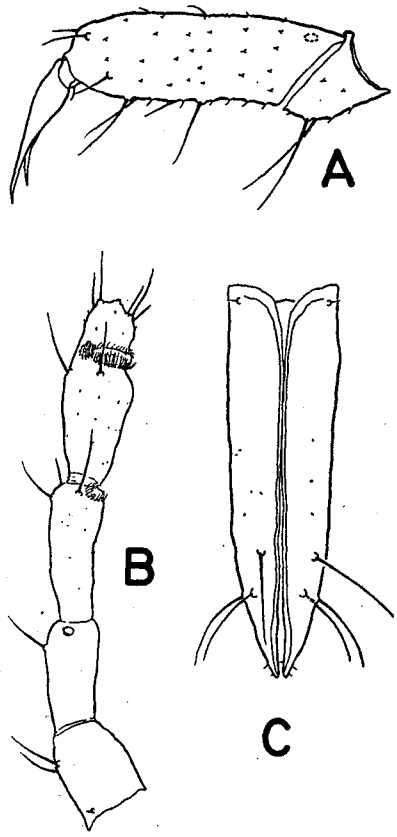

Fig. 7. *Pemphigus latisensoria* exule. First instar larva: A, hind tarsus; B, antenna; C, ultimate rostral segment.

(0.140–0.145); 2nd segment of hind tarsus (in 10 specimens) 0.281 (0.270–0.290).

Exule 1st instar larva from emigrant (Fig. 7, A–C).

Description is mainly based on 10 specimens deposited by emigrants (Sapporo, Hokkaidô; 27 vii 1973).

Antenna (Fig. 7, B) 4-segmented; number of setae on each segment as follows: I: 4, II: 2, III: 3, IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.032–0.038 mm.; primary rhinaria ciliate, on III *ca.* 0.007–0.013 mm. and on IV *ca.* 0.012–0.018 mm. in axial length; III and IV faintly spinose. Ultimate rostral segment (Fig. 7, C) faintly spinose, without accessory seta. Tarsi (Fig. 7, A) 2-segmented, spinose; 1st segment with a pair of pointed setae, which are *ca.* 0.035–0.040 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium, all these setae pointed, the empodial setae very short, on hind tarsus *ca.* 0.002–0.005 mm. in maximum length. Abdominal tergites I–VI each with 3 pairs of setae, the longest one on tergite III

ca. 0.015–0.020 mm.; abdominal tergite VII with 2 pairs of setae; abdominal tergite VIII with a pair of setae, the longer one *ca.* 0.015–0.020 mm.; cauda with a pair of setae; anal plate with 2 pairs of setae. Abdominal wax gland plates composed of many separated facets with a "Zentralkern", their distribution is as follows: spinal ones on tergites III–VII, and pleural ones on tergites III–VI.

Measurements of 10 specimens in mm. Body 0.63 (0.61–0.67); antennal segments (I–IV): 0.057 (0.052–0.063), 0.062 (0.060–0.065), 0.083 (0.080–0.085), 0.109 (0.102–0.113); ultimate rostral segment 0.106 (0.102–0.108); 2nd segment of hind tarsus 0.080 (0.077–0.083).

Gall. Primary gall (Pl. II, C): A rather slender swelling, open beneath, *ca.* 23 mm. in length and *ca.* 6 mm. in height. The general colour in life unknown, but probably yellowish. Secondary gall (Pl. II, D): The leaf affected is folded lengthwise along the midrib and the margins are applied together at the ventral surface. The greater part of the leaf is swollen into a large sac or pocket. Colour yellowish green, not turning red.

Host. Primary host: *Populus maximowiczii*; secondary host: unknown.

Distribution. Saghalien (after Hori 1938); Japan: Hokkaidô.

Discussion. The poplar gall shown in Pl. II, D is one of galls found on a tree growing by the Toyohira River in Sapporo on July, 26th & 27th, 1973. From the galls many alate viviparae and the nymphs were obtained, and their morphological characters agree well with Hori's (1938) original description of *Thecabius latisensoria.* Many leaves on a spray of *Populus maximowiczii* were infested by the aphids, and on a basal leaf of the spray was found another type of gall (Pl. II, C), which contained a dead fundatrix. From the former type of gall no fundatrix was obtained, and Hori (1938) gives no information as to the fundatrix of *latisensoria.* On the other hand, the North American "folded-leaf balsam aphid", *Pemphigus gravicornis,* (after Patch 1913 and Palmer 1952) and the European *Pemphigus lysimachiae* (after Börner 1916) make two kinds of galls corresponding to the two types of the present material. This suggests that the fundatrix found is that of *latisensoria.*

Hori (1938) says that "in the shape of the gall it [*latisensoria*] resembles *Th. populi-monilis* (Riley)", and expresses it as "bead-like" gall as Riley (1879) does in *populimonilis.* However, his photograph is too obscure to see whether it is really a bead-like one and like Riley's figure. His statement may mislead the reader to the idea that *latisensoria* is closely related to *populimonilis,* and even is a monoecious species like the latter. However, these species are in reality not so closely related. The present species is clearly heteroecious because the 1st instar larva laid by the alate vivipara is of exule type and similar to exule 1st instar larva of *lysimachiae* described by Zwölfer (1957).

This species resembles *Pemphigus lysimachiae.* In my comparing the present specimens with Dutch specimens of emigrant adults determined by Dr. D. Hille Ris Lambers as *lysimachiae,* and judging from Stroyan's (1964) redescriptions of the latter species, the former is distinguished from the latter in the following aspects of emigrant adult. (1) Generally large, e.g., flagellar segments together 1.53–1.63 mm. in length (0.87–1.00 mm. in *lysimachiae*). (2) Secondary rhinaria numerous, e.g. on segment III 33–43 (17–21), when counting each part of a broken rhinarium as a unit. (3) Abdominal wax gland plates well developed,

spinal ones occurring on tergites I-VIII (usually absent on tergites IV–VI) and pleural ones occurring on tergites I–VII irregular, small, yet not inconspicuous (inconspicuous). (4) Abdomen with local sclerotizations, which look dusky in mounted specimen (without such sclerotizations). This species also resembles *Pemphigus gravicornis*, but differs from the latter in the presence of a number of secondary rhinaria on antennal segment VI of the emigrant adult.

Pemphigus latisensoria, P. lysimachiae and *P. gravicornis* are closely related to each other, and in this paper they are lumped together to form "*lysimachiae* group" as follows:

Lysimachiae group of *Pemphigus*. A Holarctic group. Life cycle heteroecious with paracycle; apterous fundatrigenia unknown. Primary hosts are *Populus* species belonging to the sections *Aigeiros* and *Tacamahaka*; secondary hosts are *Lysimachia* species. Fundatrix and fundatrigenia live in the respective galls separately. Primary gall more or less as in Pl. II, C, secondary gall more or less as in Pl. II, D. Fundatrix adult: Head sometimes with wax gland plates; antenna 5-segmented, the articulations all functional; femora very wide. Second generation 1st instar larva: Antenna 4-segmented; empodial setae long and capitate. Emigrant adult: Secondary rhinaria numerous, broad, their widths clearly larger than interrhinarial distances; processus terminalis long and slender; fore 1st tarsal segment with a short spine-like seta between primary setae; abdomen at least sometimes with pleural wax gland plates and local sclerotizations. Exule 1st instar larva: Antenna 4-segmented; ultimate rostral segment rather long; empodial setae very short. Apterous exule adult: Antenna 5- or 6-segmented.

I have examined the exule adult of *lysimachiae* determined by Dr. D. Hille Ris Lambers in addition to the present material of *latisensoria*. The above description of the *lysimachiae* group are partly based on Börner (1916), Palmer (1952), Patch (1913), Stroyan (1964) and Zwölfer (1957).

Pemphigus microsetosus n. sp.

Fundatrix. First instar larva differs from adult in many respects, whereas 2nd to last instar larvae are similar to adult in general.

Fundatrix 1st instar larva (Fig. 8, A & B).

Description is based on one moult (syntype) left in gall on *Populus maximowiczii* (Jôzankei, Hokkaidô; 8 vii 1973).

The whole tergites and appendages strongly sclerotized as in *Epipemphigus niisimae*. Body 0.77 mm. in length, without visible wax gland plate. Third to last segments of left antenna and 2nd to last segments of right one missing; I (left) 0.050 mm. in length, II 0.055 mm. in length; number of setae on each segment as follows (left/right): I: 4/4, II: 2. Ultimate rostral segment (Fig. 8, B) 0.123 mm. in length, without accessory seta. Number of setae on each thoracic tergite as follows (left/right): I: 4/5, II: 4/4, III: 4/4. Fore femur not enlarged, i.e. fore femorotrochanteric length (right) 0.208 mm., while hind one (right) 0.238 mm. Tarsi (Fig. 8, A) 2-segmented, with some spines ventrally; 1st segment with a pair of long pointed setae, which are *ca.* 0.038 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 1 pair+2, ventrally

4–6 (left fore 4; right fore missing; left mid 6; right mid 4; left hind 5; right hind 5), laterally 1 pair, and 1 pair on empodium, the empodial setae bent and capitate, extending beyond the apices of claws, the lateral setae long, less capitate than empodial setae, 2nd segment of hind tarsus (right) 0.103 mm. in length. Abdominal tergites II, III and V–VIII each with 3 pairs of setae, the longest seta on tergite III 0.033 mm., that on tergite VIII 0.038 mm.; abdominal tergites I and IV each with 7 setae; cauda with a pair of setae; anal plate with 3 pairs of setae. Cornicle absent.

Fundatrix adult (Fig. 8, C–F).

Description is based on 6 specimens (syntypes) collected from galls on *Populus maximowiczii*. Measurements of certain parts and collection data in Table 10.

General colour in life yellowish green. Head without wax gland plate. Antenna (Fig. 8, E) 5-segmented, the articulations all functional, segment III sometimes with an abortive division; number of setae on each segment as follows: I: 4, II: 2–5, III: 0–2, IV: 3, V: 2+5; the longest seta on V (except terminal setae) *ca.* 0.017–0.025 mm.; III the longest, about as wide as IV, IV somewhat wider than V; primary rhinaria distinctly ciliate, on IV *ca.* 0.012–0.015 mm. and on V *ca.* 0.017–0.028 mm. in axial length. Ultimate rostral segment (Fig. 8, D)

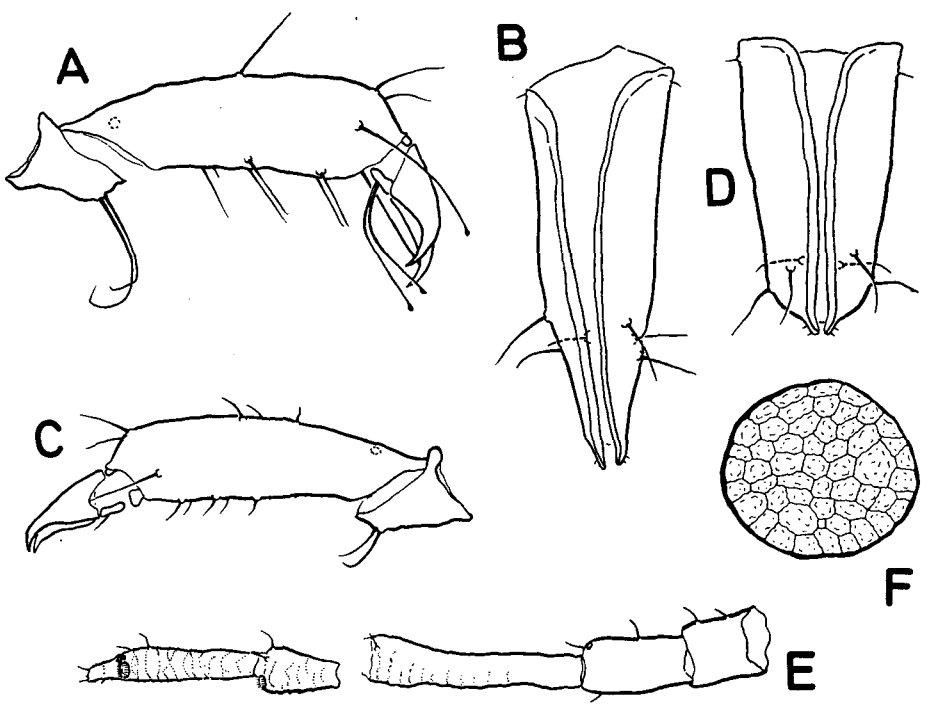

Fig. 8. *Pemphigus microsetosus* fundatrix. First instar larva: A, hind tarsus; B, ultimate rostral segment. Adult: C, hind tarsus; D, ultimate rostral segment; E, antenna; F, abdominal wax gland plate.

sometimes faintly spinose, without accessory seta. Tarsi (Fig. 8, C) 2-segmented; 1st segment with a few minute spines along distal margin, with a pair of setae, which are *ca.* 0.025–0.030 mm. in maximum length on hind tarsus; 2nd segment with a few minute spines ventrally, empodial setae *ca.* 0.017–0.025 mm. in maximum length on hind tarsus. Thoracic and abdominal wax gland plates (Fig. 8, F) each composed of tightly appressed polygonal facets; their distribution is as follows: spinal ones on thoracic tergites I–III and abdominal tergites I–VI, but often disappearing on thoracic tergite I, marginal ones on thoracic tergites I–III and abdominal tergites I–VI, and pleural ones on thoracic tergites II and III and abdominal tergites I–VI. Tergites with a number of setae; some of the setae rather long and possibly primary, the longest one on abdominal tergite III *ca.* 0.032–0.048 mm., and that on tergite VIII *ca.* 0.040–0.050 mm. Cornicle absent. Cauda with 6–8 setae. Genital plate with 23–31 setae.

Measurements of 6 specimens in mm. Ultimate rostral segment 0.146 (0.142–0.150); 2nd segment of hind tarsus 0.190 (0.180–0.200).

Emigrant 1st instar larva (Fig. 9, A–E).

Description is mainly based on 10 specimens (syntypes) collected from a closed pouch gall on *Populus maximowiczii* (Sapporo, Hokkaidô; 2 vii 1973).

General colour in life yellowish. Head and thorax without wax gland plate. Antenna (Fig. 9, E) 4-segmented; number of setae on each segment as follows: I: 4, II: 2 (rarely 1 ?), III: 3, IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.017–0.020 mm.; primary rhinaria ciliate, on III *ca.* 0.007–0.010 mm. and on IV *ca.* 0.015–0.018 mm. in axial length; III and IV spinose. Ultimate rostral segment (Fig. 9, D) hardly spinose, without accessory seta. Thoracic tergites I–III each with 4 pairs of setae. Tarsi (Fig. 9, C) 2-segmented; 1st segment faintly spinose apically, with a pair of setae, which are *ca.* 0.030–0.038 mm. in maximum length on hind tarsus; 2nd segment spinose ventrally, its setal distribution is as follows: dorsally 1 pair+2, ventrally 1 pair+2–4, laterally 1 pair, and 1 pair on empodium, all these setae pointed, the empodial setae *ca.* 0.005–0.008 mm. in maximum length on hind tarsus, dorsoapical setae about as long as ventroapical setae. Abdominal tergites I-VI each with 3 pairs of setae, the longest one on tergite III *ca.* 0.022–0.028 mm.; abdominal tergite VII with 2 pairs of setae; abdominal tergite VIII with a pair of setae, the longer one *ca.* 0.025–0.035 mm.; cauda with a pair of setae; anal plate with 2 pairs of setae. Abdominal wax gland plates as in Fig. 9, B, their distribution (Fig. 9, A) is as follows: spinal ones on tergites III–VI, and pleural ones on tergites III–VI, the pleural one on tergite VI sometimes reduced in size. Cornicle present.

Measurements of 10 specimens in mm. Body 0.75 (0.70–0.80); antennal segments (I–IV): 0.051 (0.047–0.053), 0.060 (0.057–0.063), 0.096 (0.087–0.100), 0.115 (0.107–0.123); ultimate rostral segment 0.118 (0.112–0.125); 2nd segment of hind tarsus 0.105 (0.097–0.113).

Emigrant adult (Fig. 9, F–H).

Description is mainly based on 10 specimens (syntypes) collected from galls on *Populus maximowiczii*. Measurements of certain parts and collection data in Table 11.

Head without wax gland plate. Antenna (flagellum: Fig. 9, H) 6-segmented; IV–VI imbricated; V with 3 setae at apex, of which the longest one is *ca.* 0.022–0.028 mm., and with 1–5 setae on about middle, the basal articular diameter *ca.* 0.015–0.018 mm.; VI with 2 setae at about apical 1/3 and 6 (rarely 5 ?) setae at apex; secondary rhinaria on III, IV and rarely on V near the primary rhinarium, rather slit-like and their widths clearly smaller than interrhinarial distances; primary rhinarium on V partially ciliate, *ca.* 0.020–0.028 mm. in axial length; primary rhinarium on VI of normal type, encircling *ca.* 1/2–2/3 the segment, fringed with cilia, *ca.* 0.020–0.025 mm. in axial length; processus terminalis rather long. Ultimate rostral segment (Fig. 9, G) without secondary seta. Mesothorax and metathorax with a pair of spinal wax gland plates. Fore wing with a simple media. Tarsi 2-segmented, spinose; 1st segment with 1 or 2 (usually 2) secondary setae and a pair of spine-like secondary setae between primary setae; the longest dorsal seta (except apical setae) on hind 2nd segment *ca.* 0.025–0.030 mm. Abdominal wax

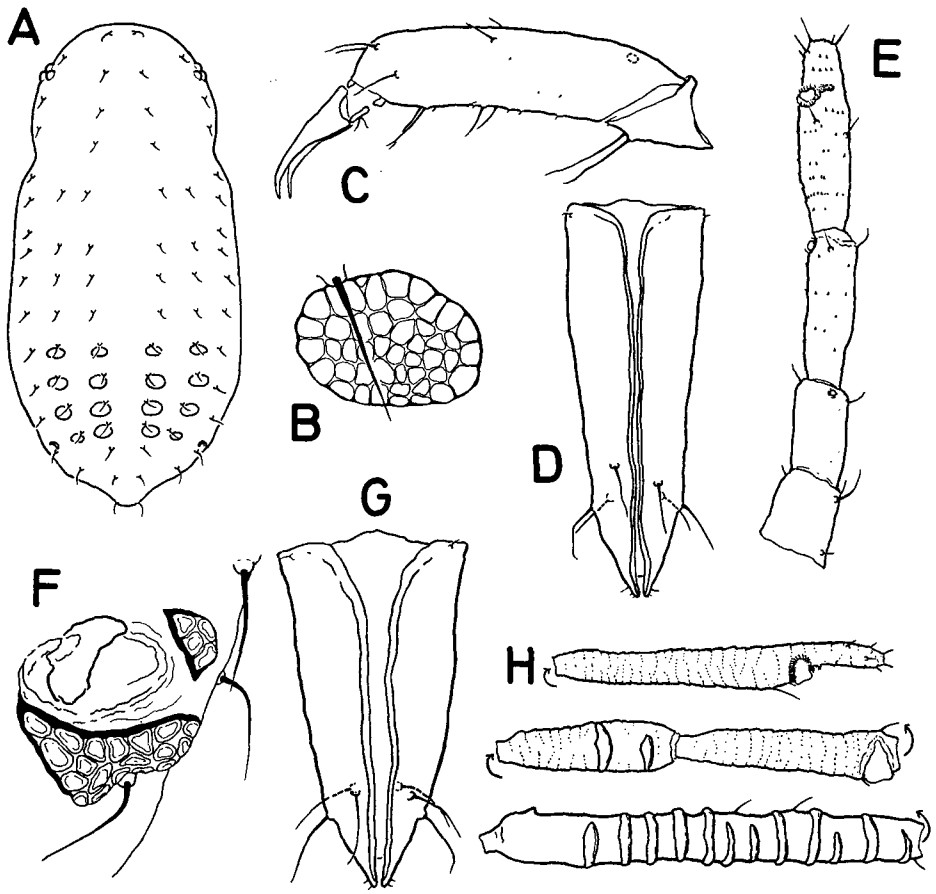

Fig. 9. *Pemphigus microsetosus* emigrant. First instar larva: A, distributional pattern of wax gland plates; B, abdominal wax gland plate; C, hind tarsus; D, ultimate rostral segment; E, antenna. Adult: F, cornicle and abdominal wax gland plates; G, ultimate rostral segment; H, flagellum.

gland plates (Fig. 9, F) of normal type, their distribution is as follows: spinal ones on tergites I–VII and rarely also on tergite VIII, but often disappearing on tergite VI, marginal ones on tergites I–VII, and pleural ones, always small, on tergites I–III sporadically. Abdomen often with other net-like weak sclerotizations (or reduced wax gland plates ?) which lack seta. Cornicle as in Fig. 9, F. Abdominal tergite VIII with 3–5 setae. Cauda with 4–6 setae. Genital plate with 26–30 setae.

Measurements in mm. Ultimate rostral segment (in 7 specimens) 0.136 (0.130–0.143); 2nd segment of hind tarsus (in 10 specimens) 0.261 (0.250–0.270).

Exule 1st instar larva (3rd generation) (Fig. 10, A–C).

Description is mainly based on 10 specimens (syntypes) deposited by emigrants (Sapporo, Hokkaidô; 27 vii 1973).

Antenna (Fig. 10, B) 4-segmented; number of setae on each segment as follows: I: 4, II: 2, III: 3, IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.030–0.033 mm.; primary rhinaria ciliate, on III *ca.* 0.010–0.013 mm. and on IV *ca.* 0.015–0.018 mm. in axial length; membraneous neck between III and IV somewhat remarkable in some specimens, but not so in others. Ultimate rostral segment (Fig. 10, C) faintly spinose, without accessory seta. Tarsi (Fig. 10, A) 2-segmented, spinose; 1st segment with a pair of pointed setae, which are *ca.* 0.037–0.043 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 1 pair+2, ventrally 1 pair+3–5 (usually+2 pairs), laterally 1 pair, and 1 pair on empodium, all these setae pointed, the empodial setae very short, on hind tarsus at most *ca.* 0.005 mm. in length. Abdominal tergites I–VI each with 3 pairs of setae, the longest one on tergite III *ca.* 0.017–0.023 mm.; abdominal tergite VII with 2 pairs of setae; abdominal tergite VIII with a pair of setae, the longer one *ca.* 0.022–0.028 mm.; cauda with a pair of setae; anal plate with 4–6 (usually 2 pairs of) setae. Abdominal wax gland plates composed of many separated facets with a "Zentralkern", their distribution is as follows: spinal ones on tergites III–VII, and pleural ones on tergites III–VI.

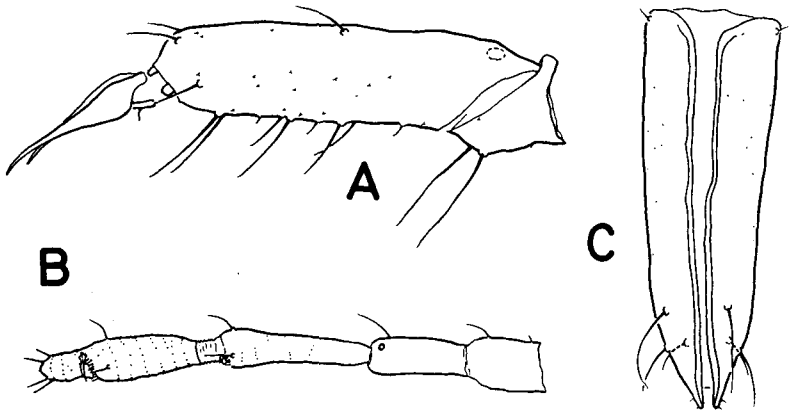

Fig. 10. *Pemphigus microsetosus* exule. First instar larva: A, hind tarsus; B, antenna; C, ultimate rostral segment.

Measurements of 10 specimens in mm. Body 0.80 (0.76–0.85); antennal segments (I–IV): 0.062 (0.057–0.065), 0.086 (0.080–0.093), 0.126 (0.120–0.130), 0.133 (0.130–0.143); ultimate rostral segment 0.127 (0.120–0.133); 2nd segment of hind tarsus (in 9 specimens) 0.106 (0.100–0.110).

Gall. A closed pouch gall on the leaf of *Populus maximowiczii*. Early one with a petiole, occurring on and concolorous with the nerve (Pl. III. A). As time goes on, the gall grows huge to take in the whole leaf, and several holes are made, through which emigrants escape. After all uninfested leaves of the poplar have fallen, the lignified galls still remain on the tree.

Host. Primary host: *Populus maximowiczii*; secondary host unknown.

Distribution. Japan: Hokkaidô.

Biological notes. All fundatrigeniae become emigrants. The collection dates for two stages of galls at Sapporo and Jôzankei are as follows: gall with fundatrix adult but without emigrant adult: 2, 8, 9, 16 & 18 vii 1973; gall with fundatrix and emigrant adult: 26 & 27 vii 1973.

Discussion. This species is very peculiar in having the combination of the following characters: gall closed; in fundatrix 1st instar larva, the whole tergite strongly sclerotized; in fundatrix adult, antenna 5-segmented, wax gland plates composed of appressed polygonal facets; in emigrant adult, 1st tarsal segment with a pair of spine-like setae between primary setae, abdominal tergite VIII usually without wax gland plate; in exule 1st instar larva, antenna 4-segmented, antennal segment III very long, empodial setae very short. The exule 1st instar larva of the present species is similar to that of *"Parathecabius" stammeri* described by Zwölfer (1957). But the latter species lives anholocyclically on *Lysimachia*, and the true relationship between them is still obscure.

Pemphigus saliciradicis (Börner)

Parathecabius saliciradicis Börner 1950: 18.
Pemphigus salicicola Hille Ris Lambers 1952: 31.
Pemphigus saliciradicis: Stroyan 1964: 65 & 1972: 75.

Exule 1st instar larva (Fig. 11, A–C).

Description is mainly based on 10 specimens collected from roots of *Salix* sp. (Sapporo, Hokkaidô; 8 vi 1973).

Antenna (Fig. 11, C) 4-segmented, number of setae on each segment as follows: I: 4, II: 2–3 (mostly 2), III: 3, IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.025–0.030 mm.; primary rhinaria distinctly ciliate, on III *ca.* 0.007–0.013 mm. and on IV *ca.* 0.012–0.018 mm. in axial length; III and IV spinose. Ultimate rostral segment (Fig. 11, B) short, spinose, without accessory seta. Tarsi (Fig. 11, A) 2-segmented, spinose; 1st segment with a pair of setae, which are *ca.* 0.035–0.038 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium, all these setae pointed, the empodial setae *ca.* 0.010–0.013 mm. in maximum length on hind tarsus. Abdominal tergites I–VI each with 3 pairs of

setae, the longest one on tergite III *ca.* 0.015–0.018 mm.; abdominal tergite VII with 2 pairs of setae; abdominal tergite VIII with a pair of setae, the longer one *ca.* 0.015–0.018 mm.; cauda with a pair of setae; anal plate with 2 pairs of setae. Abdominal wax gland plates composed of many separated facets with a "Zentralkern", their distribution is as follows: spinal ones on tergites III–VII, and pleural ones on tergites III–VI. Cornicle absent.

Measurements of 10 specimens in mm. Body 0.75 (0.70–0.83); antennal segments (I–IV): 0.054 (0.052–0.058), 0.055 (0.052–0.058), 0.075 (0.070–0.083), 0.094 (0.085–0.100); ultimate rostral segment 0.077 (0.070–0.083); 2nd segment of hind tarsus 0.086 (0.080–0.095).

Apterous exule adult (Fig. 11, D & E).

Description is mainly based on 10 specimens. Measurements of certain parts and collection data in Table 12.

Head often with wax gland plates, which are at times rudimentary. Antenna (apical segments: Fig. 11, D) 5- or 6-segmented, but in the latter case segments III and IV with a non-functional articulation; primary rhinaria distinctly ciliate, on penultimate segment *ca.* 0.010–0.013 mm. and on ultimate segment *ca.* 0.012–0.015 mm. in axial length. Ultimate rostral segment (Fig. 11, E) short, abruptly and bluntly rounded at apex, rarely with some accessory setae. First tarsal segment faintly spinose, with a pair of spine-like short stout primary setae, on the fore leg also with a thinner spine-like seta between primary setae. Second tarsal segment spinose ventrally, often with some secondary setae. Form and distribution of abdominal wax gland plates as in the 1st instar larva, but those on tergite III reduced in size and often disappearing. Abdominal tergite VIII with 5–6 setae. Cauda with a pair of setae. Gonapophyses hardly sclerotized. Gential plate with 19–27 setae.

Measurements of 10 specimens in mm. Ultimate rostral segment 0.098 (0.092–0.103); 2nd segment of hind tarsus 0.162 (0.142–0.180).

Alate exule (or virgino-sexupara) (Fig. 11, F–H).

Description is based on 6 specimens. Measurements of certain parts and collection data in Table 13.

Head without wax gland plate. Antenna (flagellum: Fig. 11, H) 6-segmented; secondary rhinaria on III, IV, and rarely also on V, rather slit-like, without cilia; primary rhinaria small, distinctly ciliate, on V *ca.* 0.015–0.018 mm. and on VI *ca.* 0.015–0.018 mm. in axial length; V weakly imbricated, with 3 setae at apex, of which the longest one is *ca.* 0.017–0.020 mm., and rarely with a seta at middle, the basal articular diameter *ca.* 0.015–0.020 mm.; VI somewhat imbricated, with 2 setae at middle and 5 setae at apex. Ultimate rostral segment (Fig. 11, F) short, rather bluntly-rounded, often with a few accessory setae. Thoracic tergites often with spinal wax gland plates. Fore wing with simple media. Tarsi spinose; 1st segment with 0–3 accessory setae in addition to a pair of long primary setae, on the fore leg also with a short spine-like seta between primary setae; the longest dorsal seta (except apical setae) on hind 2nd segment *ca.* 0.015–0.018 mm. Abdominal wax gland plates of normal type as follows: marginal ones oval, on tergites I–VII; spinal ones usually rather transverse, often fragmentary on tergites

I–V, on tergite VIII strongly transverse and united mesially to form the largest one. Abdomen with other reduced wax gland plates (?) with a seta (Fig. 11, G), which partially look dusky, but are not pigmented around, as follows: submarginal ones on tergites III–VI, and pleural ones on tergites III–VII. Cornicle absent. Abdominal tergite VIII with 6–8 setae. Cauda with 2 or 3 setae. Genital plate with 16–19 setae.

Measurements of 6 specimens in mm. Ultimate rostral segment 0.102 (0.097–0.105); 2nd segment of hind tarsus 0.210 (0.205–0.215).

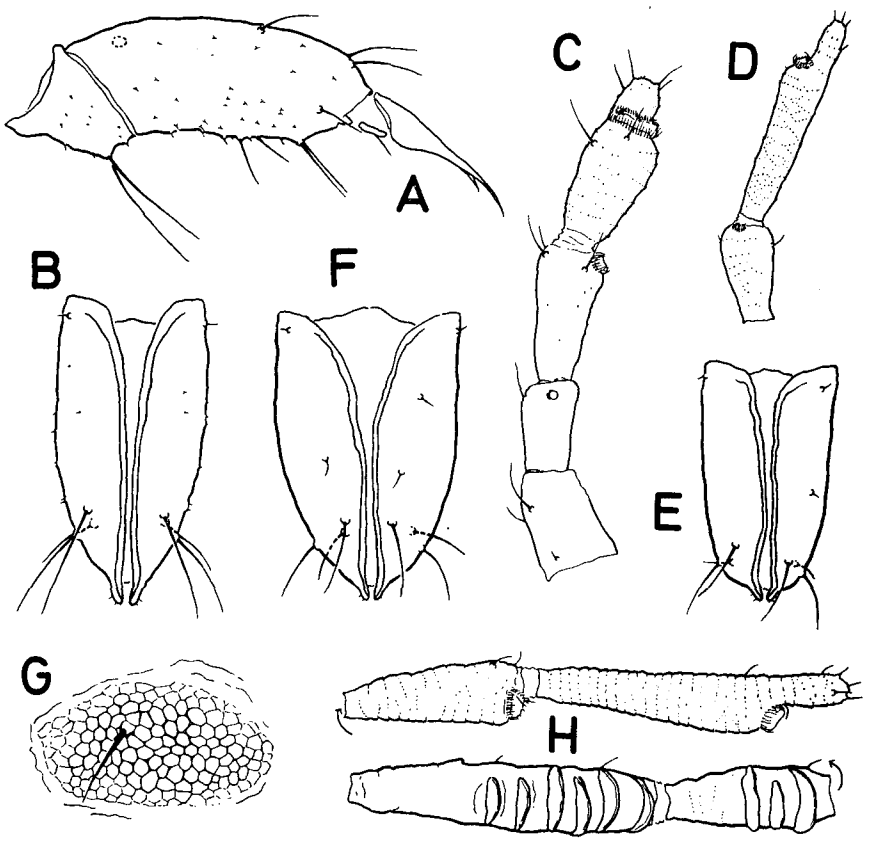

Fig. 11. *Pemphigus saliciradicis*. Exule 1st instar larva: A, hind tarsus; B, ultimate rostral segment; C, antenna. Apterous exule adult: D, apical segments of antenna; E, ultimate rostral segment. Alate exule (or virgino-sexupara): F, ultimate rostral segment; G, reduced wax gland plate (?); H, flagellum.

Host. Secondary host: *Salix* sp., *Salix fragilis* (England, after Stroyan 1964), *Salix herbacea* (Greenland, after Hille Ris Lambers 1952), *Salix polaris* (East Alps, after Börner 1950), "Grass roots" (Greenland, after Hille Ris Lambers 1952).

Distribution. Japan: Hokkaidô; England (after Stroyan 1964); East Alps (after Börner 1950); Greenland (after Hille Ris Lambers 1952).

Discussion. Exules of a *Pemphigus* species were found colonizing on the roots

of *Salix* growing by the Toyohira River in Sapporo on May 27th, and June 3rd and 8th, 1973, accompanied by neither alate morph nor alatoid larva. On September 20th, 1973, I found a large colony of this aphid with some alatoid larvae mingled under a stone (host undeterminable) by the river near Jôzankei. On October 3rd, 1973, I collected 6 alate viviparae from the same colony, but on October 8th, 1973, neither alate morph nor alatoid larva. Having examined the embryos of these alate viviparae, I found that three of them were virgines, containing embryos all rostrate, and that the others were virgino-sexuparae, containing both rostrate and arostrate embryos (see Table 13). The absence of the true sexupara suggests that primary host is not included in the life cycle of this aphid.

As I could not find any reliable difference in the apterous exule adults between the Japanese and European forms (specimens examined of the European form: 3 apterous exule adults from Switzerland determined by Dr. D. Hille Ris Lambers as *saliciradicis*), I tentatively identify the Japanese form with *Pemphigus saliciradicis*, which is characterized by having "extremely bluntly-rounded apical rostral joint" in the apterous exule adult. However, the Japanese form is different in producing the alate morph. Lange (1965) records "*Pemphigus*-like aphids" from California which "undoubtedly belong to the same group as two already described species – *P. salicicola* H.R.L. from Greenland, and *Parathecabius salici-radicis* Börner from the East Alps". After him this North American form produces sexuparae in fall, and in this respect it differs from both the European form and Japanese form. Whether primary host is included in its life cycle or not, the American form holds a typical (or primitive) pattern of life cycle on secondary host. It is obvious that the pattern of life cycle of Japanese form and also that of European one are derivable from such one as the American form shows. The trend toward the elimination of sexupara might have been developed in two different ways: one is the suppression of producing alate morph, and the other is the replacement of sexupara by alate exule. The European form should exhibit a result in the former way, while the Japanese form probably in both the ways. The virgino-sexupara in Pemphigidae is an abnormal or less adaptive morph in the sense that her progeny partly can not propagate themselves on either of primary and secondary hosts. Therefore its occurrence in the Japanese form can be considered as a transitional phase. As far as I know, the occurrence of alate exule has hitherto been unknown in *Pemphigus* except in the *affinis* group. It may be an important character in considering the phylogeny of this species.

Pemphigus dorocola Matsumura

Pemphigus dorocola Matsumura 1917: 84.
Pemphigus borealis: Takahashi 1920: 196 & 1923: 150.
Pemphigus dorocola: Hori and Oshima 1924: 5; Monzen 1929a: 34 & 1929b: 361; Börner and Schilder 1931: 650; Hori 1938: 124; Shinji 1941: 1073 (partim), & 1944: 111 & 557; Paik 1972: 604.
Pemphigus bursarius: Tao 1970: 139 (partim).

Fundatrix. First instar larva differs from adult in many respects, whereas 2nd to last instar larvae are similar to adult in general.

Fundatrix 1st instar larva (Fig. 12, A–D).

Description is based on 2 specimens: one, with skin of 2nd instar larva inside, was collected from an early gall on *Populus maximowiczii* (Sapporo, Hokkaidô; 25 v 1973), the other was collected as a moult from a gall on *Populus maximowiczii* (Sapporo, Hokkaidô; 12 vi 1973).

General colour in life orange. Body without visible wax gland plate. Thoracic and abdominal tergites not sclerotized except for small regions each with 1 or 2 setae (1 on abdominal tergites I–VII) (Fig. 12, D). Antenna (Fig. 12, C) 4-segmented; number of setae on each segment as follows: I: 3–4, II: 2, III: 3, IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.020–0.025 mm.; primary rhinaria ciliate, on III *ca.* 0.008 mm. and on IV *ca.* 0.010 mm. in axial length; IV distinctly, III faintly spinose. Ultimate rostral segment (Fig. 12, B) without accessory seta. Thoracic tergites I–III each with 4 pairs of setae. Hind femur larger than fore one. Tarsi (Fig. 12, A) 2-segmented, not or very faintly spinose; 1st segment with a pair of long pointed setae, which are *ca.* 0.035 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium, the empodial setae long, extending beyond the apices of claws, bent and capitate, the lateral setae also long but less capitate than the empodial setae. Abdominal tergites I–VII each with 3 pairs of setae, the longest one on tergite III *ca.* 0.017–0.020 mm.; abdominal tergite VIII with 2 pairs of setae, the longest one *ca.* 0.020–0.035 mm.; cauda sclerotized, with a pair of setae; anal plate with 3 pairs of setae. Cornicle absent.

Measurements of 2 specimens in mm. Body (in 1 specimen) 0.71; antennal segments (I–IV): 0.035–0.038, 0.033, 0.032–0.035, 0.062–0.065; ultimate rostral segment 0.072–0.078; 2nd segment of hind tarsus 0.067–0.073; fore femorotrochanter 0.135–0.150; hind femorotrochanter 0.162–0.208.

Fundatrix adult (Fig. 12, E–H).

Description is based on 6 specimens collected from galls on *Populus maximowiczii*. Measurements of certain parts and collection data in Table 14.

General colour in life green. Head and sides of prothorax sclerotized. Head rarely with a wax gland plate. Antenna (Fig. 12, F) 4-segmented, the articulations all functional, and segment III often with an abortive division; number of setae on each segment as follows: I: 4 or 5, II: 2, III: 3, IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.012–0.020 mm.; III the longest, clearly wider than IV; primary rhinaria ciliate, on III *ca.* 0.013 mm. and on IV *ca.* 0.015–0.018 mm. in axial length. Ultimate rostral segment (Fig. 12, G) sometimes faintly spinose, without secondary seta. Tarsi 2-segmented; 1st segment without spine, with a pair of setae, which are *ca.* 0.015–0.025 mm. in maximum length on hind tarsus; 2nd segment faintly spinose ventrally, sometimes with a secondary seta ventrally, empodial setae *ca.* 0.012–0.015 mm. in maximum length on hind tarsus. Thoracic and abdominal wax gland plates as in Fig. 12, H, their distribution is as follows: spinal ones on thoracic tergites I–III and abdominal tergites I–VII (in one specimen an additional small one on tergite VIII), marginal ones on thoracic tergites I–III and abdominal tergites I–VII; and pleural ones on thoracic tergites II and III and abdominal tergites I–VI; accessory small wax

gland plates rarely on abdominal tergites. Tergites with a number of setae; some of the setae long and rather stout, and possibly primary, the longest one on abdominal tergite VIII *ca.* 0.040–0.050 mm. Cornicle absent. Cauda with 8–14 setae. Two gonapophyses, and a few setae between them. Genital plate with 20–26 setae.

Measurements of 6 specimens in mm. Ultimate rostral segment 0.113 (0.100–0.120); 2nd segment of hind tarsus 0.161 (0.150–0.190).

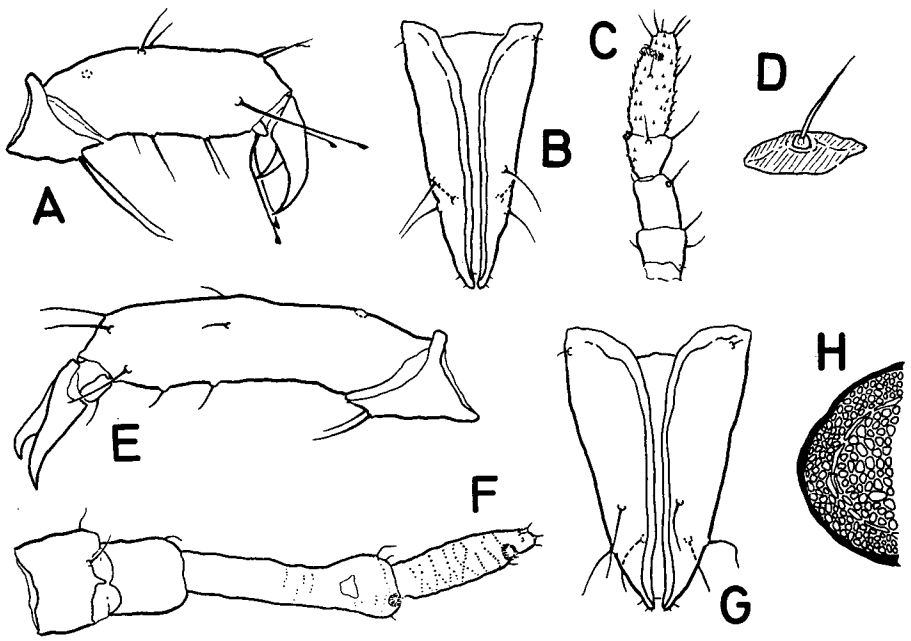

Fig. 12. *Pemphigus dorocola* fundatrix. First instar larva: A, hind tarsus; B, ultimate rostral segment; C, antenna; D, abdominal tergal seta. Adult: E, hind tarsus; F, antenna; G, ultimate rostral segment; H, abdominal wax gland plate.

Emigrant. First instar larva with capitate empodial setae, whereas 2nd to last instar larvae and adult with pointed empodial setae.

Emigrant 1st instar larva (Fig. 13, A–F).

Description is based on 9 specimens collected from a twig gall of *Populus maximowiczii* (Sapporo, Hokkaidô; 12 vi 1973).

General colour in life pale. Head and thorax without wax gland plate. Antenna (Fig. 13, D) 4-segmented; number of setae on each segment as follows: I: 4, II: 2, III: 3, IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.007–0.010 mm.; primary rhinaria ciliate, on III *ca.* 0.007–0.010 mm. and on IV *ca.* 0.010–0.015 mm. in axial length; IV spinose. Ultimate rostral segment (Fig. 13, F) without accessory seta. Thoracic tergites I–III each with 4 pairs of setae. Tarsi (Fig. 13, E) 2-segmented, faintly spinose; 1st segment with a pair of setae, which are *ca.* 0.030–0.035 mm. in maximum length on hind tarsus; setal distribution on

2nd segment as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium, the empodial setae long, extending beyond the apices of claws, and capitate, the others all pointed, the dorsoapical setae longer than the ventroapical setae. Abdominal tergites I–VI each with 3 pairs of setae, the longest one on tergite III *ca.* 0.025–0.030 mm.; abdominal tergite VII with 3 or 4 (usually 2 pairs of) setae; abdominal tergite VIII with a pair of setae, the longer one *ca.* 0.032–0.043 mm.; cauda with a pair of setae; anal plate with 3–5 setae. Abdomen with wax gland plates as follows (see Fig. 13, A): spinal ones composed of small facets on tergites III–VII; pleural ones (Fig. 13, C) similar to spinal ones on tergites III–VI; marginal ones (Fig. 13, B) composed of comparatively large facets on tergites I–VII, indistinct and sometimes disappearing on tergites I and II. Cornicle present.

Measurements of 9 specimens in mm. Body (in 8 specimens) 0.71 (0.62–0.79); antennal segments (I–IV): 0.051 (0.047–0.055), 0.048 (0.042–0.053), 0.071 (0.067–0.078), 0.101 (0.095–0.105); ultimate rostral segment 0.083 (0.080–0.088); 2nd segment of hind tarsus 0.089 (0.085–0.093).

Emigrant adult (Fig. 13, G & H).

Description is mainly based on 10 specimens collected from galls on *Populus maximowiczii*. Measurements of certain parts and collection data in Table 15.

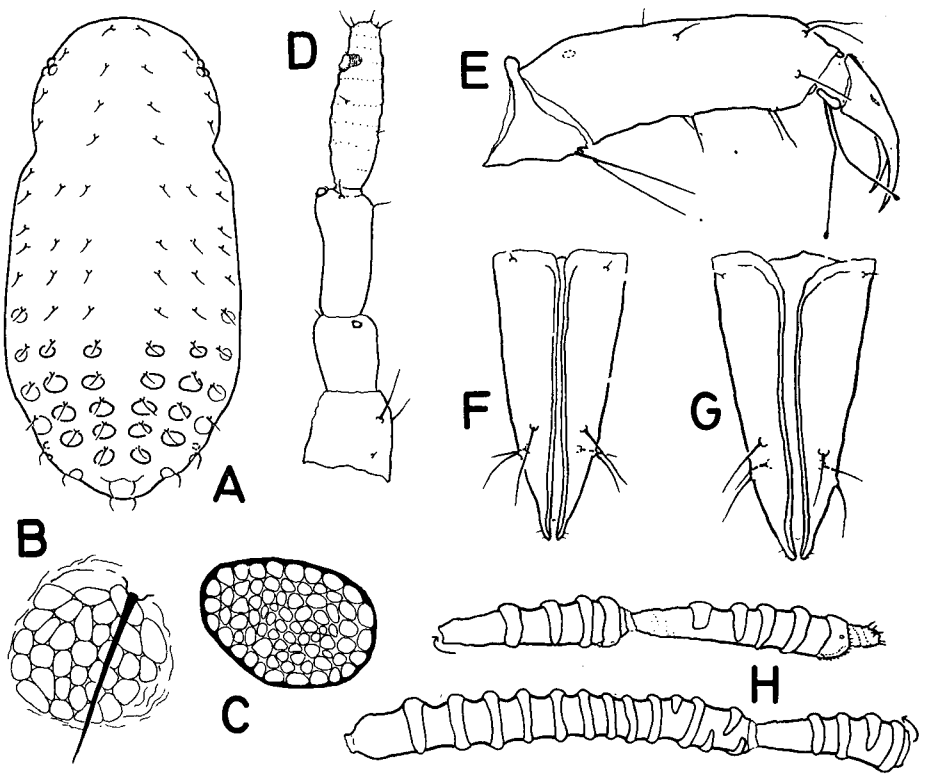

Fig. 13. *Pemphigus dorocola* emigrant. First instar larva: A, distributional pattern of wax gland plates; B & C, abdominal wax gland plate; D, antenna; E, hind tarsus; F, ultimate rostral segment. Adult: G, ultimate rostral segment; H, flagellum.

Head without wax gland plate. Antenna (flagellum: Fig. 13, H.) 6-segmented; V with 3 setae at apex, of which the longest one is *ca.* 0.010–0.015 mm., the basal articular diameter *ca.* 0.012–0.020 mm.; VI with 5 setae at apex; secondary rhinaria on III–VI, extending at most a little more than half the circumference of antennae; primary rhinaria distinctly larger than normal secondary rhinaria, irregular in outline, on VI distinctly fringed with cilia, *ca.* 0.022–0.033 mm. in axial length, and on V usually only partially fringed with cilia, *ca.* 0.017–0.028 mm. in axial length; processus terminalis short, stout and imbricated. Ultimate rostral segment (Fig. 13, G) without secondary seta. Metathorax with a pair of spinal wax gland plates. Fore wing with a simple media. Tarsi 2-segmented; 1st segment rarely with some secondary setae; the longest dorsal seta (except apical setae) on hind 2nd segment *ca.* 0.012–0.015 mm. Abdominal wax gland plates of normal type, their distribution is as follows: spinal ones on tergites I–VI and VIII (rarely also on VII), and marginal ones on tergites I and VII (rarely also on II–VI). Cornicle is present as a mere ring. Abdominal tergite VIII with 2–4 setae. Cauda with 2–4 setae. Genital plate with 21–28 setae.

Measurements of 10 specimens in mm. Ultimate rostral segment 0.091 (0.085–0.093); 2nd segment of hind tarsus 0.203 (0.185–0.210).

Exule 1st instar larva (3rd generation) (Fig. 14, A–C).

Description is mainly based on 10 specimens deposited by emigrants (Sapporo, Hokkaidô; 20 ix 1973).

Antenna (Fig. 14, C) 4-segmented; number of setae on each segment as follows: I: 3–4 (usually 4), II: 2, III: 3, IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.020–0.025 mm.; primary rhinaria ciliate, on III *ca.* 0.010–0.013 mm., and on IV *ca.* 0.012–0.018 mm. in axial length; IV spinose, III faintly spinose; membraneous neck between III and IV not remarkable. Ultimate rostral segment (Fig. 14, A) faintly spinose, without accessory seta. Tarsi (Fig. 14, B) 2-segmented, faintly spinose; 1st segment with a pair of pointed setae, which are *ca.* 0.027–0.033

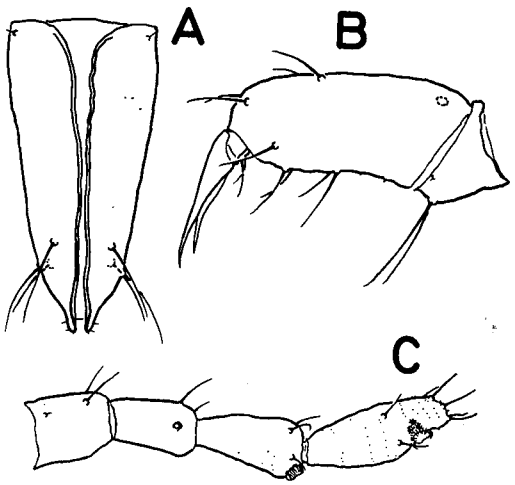

Fig. 14. *Pemphigus dorocola* exule. First instar larva: A, ultimate rostral segment; B, hind tarsus; C, antenna.

mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium, all these setae pointed, the empodial setae *ca.* 0.012–0.015 mm. in maximum length on hind tarsus. Abdominal tergites I–VI each with 3 pairs of setae, the longest one on tergite III *ca.* 0.013 mm.; abdominal tergite VII with 2 pairs of setae; abdominal tergite VIII with a pair of setae, the longer one *ca.* 0.015 mm.; cauda with a pair of setae; anal plate with 2 pairs of setae. Abdominal wax gland plates composed of many separated facets with a "Zentralkern", their distribution is as follows: spinal ones on tergites III–VII, and pleural ones on tergites III–VI.

Measurements of 10 specimens in mm. Body 0.57 (0.55–0.61); antennal segments (I–IV): 0.047 (0.042–0.050), 0.054 (0.052–0.058), 0.063 (0.057–0.070), 0.087 (0.082–0.090); ultimate rostral segment 0.086 (0.085–0.088); 2nd segment of hind tarsus 0.065 (0.062–0.068).

Gall (Pl. III, B). An open pouch gall on the twig of *Populus maximowiczii*, with a transverse split at apex through which emigrants escape, concolorous with the young twig at first and then turning somewhat reddish. After all leaves of the poplar have fallen, the lignified twig galls still remain.

Host. Primary host: *Populus maximowiczii* (=*Populus balsamifera* in Matsumura 1917, and Higuchi and Miyazaki 1969); secondary host unknown.[1)]

Distribution. Japan: Hokkaidô, Honshû (after Monzen 1929a, etc.); Korea (after Paik 1972).

Biological notes. All fundatrigeniae become emigrants. The collection dates for various stages of the galls at Sapporo and Jôzankei are as follows: gall with fundatrix 1st instar larva: 25 v 1973; gall with fundatrix larva: 3 vi 1973; gall with fundatrix adult but without emigrant adult: 18 & 20 vi 1972, 12 vi 1973, 23 vi 1973; gall with emigrant adult: 26, 28, 29 & 30 vii 1972, 12 & 22 ix 1972, 3 & 7 x 1972, xi 1972, 5 & 9 vii 1973, 20 ix 1973. This species has a very long emigratory period, and it is suggested that the fundatrix lives very long, for I collected a gall with a living fundatrix on October 7th, 1972.

Discussion. There are three described species which resemble this species: *Pemphigus borealis* Tullgren 1909 (after Tullgren 1925, primary host is *Populus laurifolia*), *Pemphigus mordwilkoi* Cholodkovsky 1912 (from Himalaya, ex *Populus ciliata*) and *Pemphigus nainitalensis* Cholodkovsky 1912 (from Himalaya, ex *Populus ciliata*). Takahashi (1920) proposes the union of *dorocola* and *borealis*. However, Hori (1938) says that the former "may be easily distinguished from the latter by the structure of the gall and the size of the body". The figures of the *borealis* gall given by Tullgren (1909 & 1925) are very similar to the *dorocola* gall. In addition to this, judging from my own data, the body size is not a reliable character in distinguishing the two forms. Though the possibility can not be excluded that all these four are even specifically identical, the form inhabiting Japan and Korea is here treated under the name *dorocola*.

Shinji (1941, fig. 523) gives a photograph of the gall of "*dorocola*", but it undoubtedly belongs to *matsumurai*. Tao (1970) proposes the union of *dorocola*

1) Though Shinji (1944) says that this species emigrates to the subterranean parts of *Agrimonia pilosa*, *Plantago asiatica*, etc., he does not show any reliable datum. Higuchi and Miyazaki (1969) follow him.

and *bursarius*, but the latter is a leaf petiole gall-maker.

Pemphigus matsumurai Monzen

Pemphigus matsumurai Monzen 1927: 8.
Pemphigus matsumurai: Monzen 1929a: 32 & 1929b: 361; Hori 1938: 126 (partim).
Pemphigus borealis: Hori 1929: pl. 2.
Pemphiginus (?) *matsumurai*: Börner and Schilder 1931: 654.
Pemphigus dorocola: Shinji 1941: 1073 (partim).
Pemphigus niisimae: Shinji 1941: 1075 (partim), & 1944: 111 & 556 (partim).

Fundatrix. First instar larva differs from adult in many respects, whereas 2nd to last instar larvae are similar to adult in general.

Fundatrix 1st instar larva (Pl. I, A; Fig. 15, A–C).

Description is based on 10 specimens (including moults) collected from galls on *Populus maximowiczii* (Sapporo, Hokkaidô; 20–31, v 1973).

General colour in life except for sclerotized parts yellowish, slightly covered with wax, yet without visible wax gland plate. Thoracic and abdominal tergites extensively yet not wholly sclerotized (Pl. I, A). Antenna (Fig. 15, B) 4-segmented; number of setae on each segment as follows: I: 4, II: 3–4 (usually 3), III: 3, IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.020–0.023 mm.; primary rhinaria distinctly ciliate, on III *ca.* 0.008 mm. and on IV *ca.* 0.012–0.015 mm. in axial length; III and IV spinose. Ultimate rostral segment (Fig. 15, C) long, without accessory seta. Thoracic tergites I–III each with 4 pairs of setae. Fore femur not enlarged. Tarsi (Fig. 15, A) 2-segmented, spinose; 1st segment with a pair of long pointed setae, which are *ca.* 0.032–0.040 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium, the empodial setae long, extending far beyond the apices of claws, bent and capitate, but the lateral setae pointed. Abdominal tergites I–VII each with 3 pairs of setae, the longest one on tergite III *ca.* 0.015–0.020 mm.; abdominal tergite VIII with 2 pairs of setae, the longest one *ca.* 0.027–0.033 mm.; cauda with a pair of setae; anal plate with 3 pairs of setae. Cornicle absent.

Measurements of 10 specimens in mm. Body (in 7 specimens) 0.76 (0.60–0.84); antennal segments (I–IV): 0.037 (0.035–0.040), 0.043 (0.040–0.048), 0.039 (0.037–0.043), 0.075 (0.067–0.078); ultimate rostral segment (in 9 specimens) 0.118 (0.112–0.120); 2nd segment of hind tarsus (in 9 specimens) 0.081 (0.077–0.085).

Fundatrix adult (Fig. 15, D–G).

Description is based on 10 specimens collected from galls on *Populus maximowiczii*. Measurements of certain parts and collection data in Table 16.

General colour in life green. Head rarely with a wax gland plate. Antenna (Fig. 15, E) 4-segmented, the articulations all functional, segment III with an abortive division; number of setae on each segment as follows: I: 4, II: 2–5, III: 3, IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.012–0.015 mm.; III the longest, wider than IV; primary rhinarium on III indistinctly ciliate, *ca.* 0.012–

0.018 mm. in axial length; primary rhinarium on IV distinctly ciliate, *ca.* 0.017–0.023 mm. in axial length. Ultimate rostral segment (Fig. 15, F) hardly spinose, without secondary seta. Prothorax weakly sclerotized. Tarsi (Fig. 15, D) 2-segmented, faintly spinose ventrally; 1st segment with a pair of setae, which are *ca.* 0.020–0.025 mm. in maximum length on hind tarsus; 2nd segment at times with a secondary seta ventrally, empodial setae *ca.* 0.017–0.025 mm. in maximum length on hind tarsus. Thoracic and abdominal wax gland plates as in Fig. 15, G, comparatively small and rather indistinct, their distribution is as follows: spinal ones on thoracic tergites I–III and abdominal tergites I–VII, and sometimes also on abdominal tergite VIII, marginal ones on thoracic tergites I–III and abdominal tergites I–VII, and pleural ones on thoracic tergites II and III (at times absent ?) and abdominal tergites I–VI. Tergites with a number of setae; some of the setae rather long, and possibly primary; the longest one on abdominal tergite III *ca.* 0.027–0.038 mm. and that on abdominal tergite VIII *ca.* 0.040–0.048 mm. Cornicle absent. Cauda with 2–5 setae. Genital plate with 24–36 setae.

Measurements of 10 specimens in mm. Ultimate rostral segment 0.132 (0.115–0.143); 2nd segment of hind tarsus 0.149 (0.135–0.185).

Emigrant 1st instar larva (Fig. 16, A–E).

Description is mainly based on 10 specimens collected from a closed pouch gall on *Populus maximowiczii* (Sapporo, Hokkaidô; 18 vi 1973).

General colour in life pale. Head and thorax without wax gland plate.

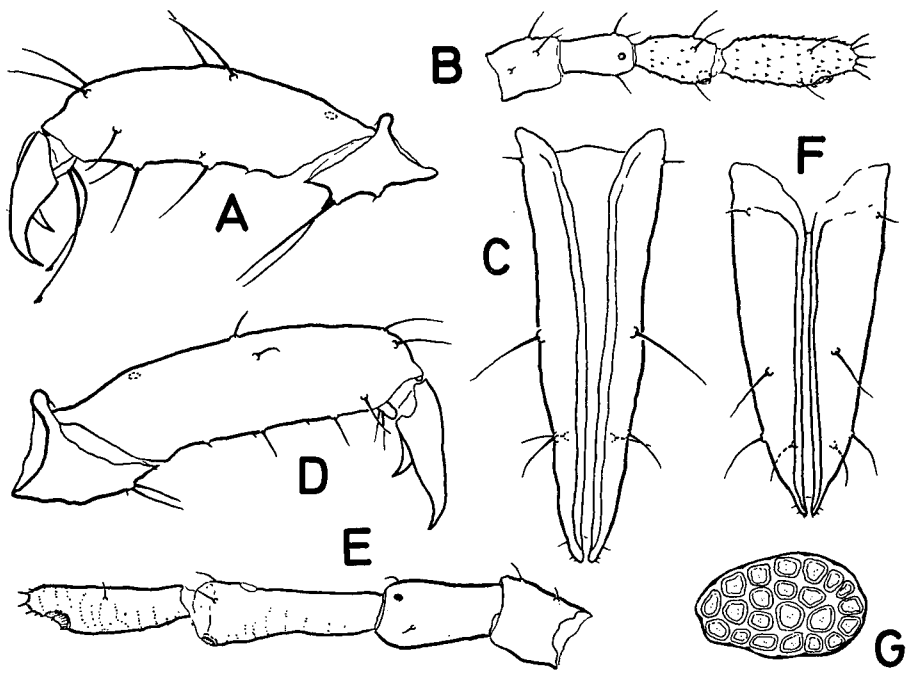

Fig. 15. *Pemphigus matsumurai*, fundatrix. First instar larva: A, hind tarsus; B, antenna; C, ultimate rostral segment. Adult: D, hind tarsus; E, antenna; F, ultimate rostral segment; G, abdominal wax gland plate.

Antenna (Fig. 16, D) 4-segmented; number of setae on each segment as follows: I: 4, II: 2 (rarely 1?), III: 2 or 3 (usually 3), IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.012–0.015 mm.; primary rhinaria ciliate, on III *ca.* 0.005–0.008 mm. and on IV *ca.* 0.012–0.018 mm. in axial length; IV weakly and III faintly imbricated. Ultimate rostral segment (Fig. 16, E) without accessory seta. Thoracic tergites I–III each with 4 pairs of setae. Tarsi (Fig. 16, C) 2-segmented, spinose; 1st segment with a pair of setae, which are *ca.* 0.017–0.023 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium, all these setae pointed, the empodial setae *ca.* 0.012–0.018 mm. in maximum length on hind tarsus. Abdominal tergites I–VI each with 3 pairs of setae, the longest one on tergite III *ca.* 0.013 mm.; abdominal tergite VII with 2 pairs of setae; abdominal tergite VIII with 3 or 4 (usually 2 pairs of) setae, the longest one *ca.* 0.015–0.020 mm.; cauda with a pair of setae; anal plate with 4–6 setae. Abdomen with wax gland plates (Fig. 16, B) as follows (see Fig. 16, A): spinal ones on tergites III–VII, and pleural ones on tergites III–VI; but on tergite III reduced in size and indistinct. Cornicle absent.

Measurements of 10 specimens in mm. Body 0.85 (0.78–0.92); antennal segments (I–IV): 0.045 (0.045–0.048), 0.047 (0.042–0.050), 0.077 (0.072–0.080), 0.086 (0.082–0.088); ultimate rostral segment 0.111 (0.105–0.115); 2nd segment of hind tarsus 0.091 (0.087–0.098).

Emigrant adult (Fig. 16, F–H).

Description is mainly based on 10 specimens collected from galls on *Populus maximowiczii*. Measurements of certain parts and collection data in Table 17.

Head without wax gland plate. Antenna (flagellum: Fig. 16, G) 6-segmented; VI somewhat imbricate, without secondary rhinarium, with 2 setae at apical 1/3 and 5 setae at apex; V with 3 setae at apex, of which the longest one is *ca.* 0.012–0.018 mm., and rarely with a seta at middle, the basal articular diameter *ca.* 0.015–0.020 mm.; secondary rhinaria on III–V, more or less normal in type, but generally less extensively encircling antenna and more irregular than in *P. dorocola*; primary rhinarium on VI fringed with cilia which are often furcated, apparently encircling *ca.* 1/2 the segment, *ca.* 0.022–0.025 mm. in axial length, that on V united with secondary rhinarium to form an irregular, partially ciliate enlarged rhinarium, *ca.* 0.017–0.028 mm. in axial length. Ultimate rostral segment (Fig. 16, F) spinose, long and acute. Metathorax with a pair of spinal wax gland plates. Fore wing with simple media. Tarsi spinose; 1st segment sometimes with 1 or 2 accessory setae, without short spine-like seta between primary setae; the longest dorsal seta (except apical setae) on hind 2nd segment *ca.* 0.017–0.025 mm. Abdomen with wax gland plates of normal type as follows: marginal ones oval, on tergites I–VII; no pleural ones; spinal ones mostly rather transverse, often fragmented or indistinct on tergites I–VII, on tergite VIII united mesially to form the largest one. Abdomen sometimes with other reduced wax gland plates (?) (Fig. 16, H) on posterior segments. Cornicle absent. Abdominal tergite VIII with 5–8 setae. Cauda with 2–5 setae. Genital plate with 30–44 setae.

Measurements of 10 specimens in mm. Ultimate rostral segment 0.124 (0.115–0.138); 2nd segment of hind tarsus 0.228 (0.205–0.250).

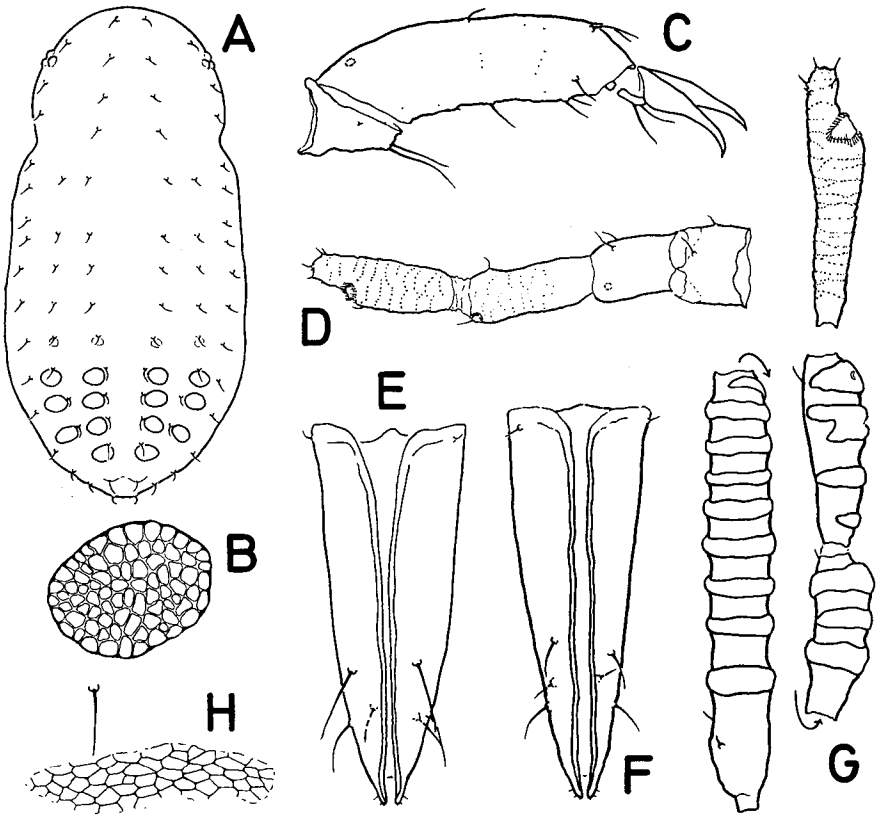

Fig. 16. *Pemphigus matsumurai* emigrant. First instar larva: A, distributional pattern of wax gland plates; B, abdominal wax gland plate; C, hind tarsus; D, antenna; E, ultimate rostral segment. Adult: F, ultimate rostral segment, G, flagellum; H, reduced wax gland plate (?).

Exule 1st instar larva (3rd generation) (Fig. 17, A–C).

Description is based on 10 specimens deposited by emigrants (Jôzankei, Hokkaidô; 9 vii 1973).

Antenna (Fig. 17, C) 4-segmented; number of setae on each segment as follows: I: 4, II: 2 or 3 (usually 2), III: 3, IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.020–0.023 mm.; primary rhinaria ciliate, on III *ca.* 0.010–0.013 mm. and on IV *ca.* 0.017–0.023 mm. in axial length; IV spinose, III faintly spinose; membraneous neck between III and IV not remarkable. Ultimate rostral segment (Fig. 17, B) without accessory seta. Tarsi (Fig. 17, A) 2-segmented, faintly spinose; 1st segment with a pair of pointed setae, which are *ca.* 0.025–0.028 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium, all these setae pointed, the empodial setae *ca.* 0.015–0.018 mm. in maximum length on hind tarsus. Abdominal tergites I–VI each with 3 pairs of setae, the longest one on tergite III *ca.* 0.015–0.018 mm.; abdominal tergite VII with 2 pairs of setae; abdominal tergite VIII with 1 or 2 (usually 2) pairs of setae, the longest one *ca.* 0.015–0.020 mm.; cauda with a pair of setae; anal plate with 4 or 5 setae.

Abdominal wax gland plates composed of many separated facets with a "Zentralkern", their distribution is as follows: spinal ones on tergites III–VII, and pleural ones on tergites III–VI.

Measurements of 10 specimens in mm. Body 0.64 (0.61–0.69); antennal segments (I–IV): 0.041 (0.037–0.043), 0.048 (0.045–0.053), 0.051 (0.047–0.053), 0.086 (0.082–0.088); ultimate rostral segment 0.109 (0.105–0.110); 2nd segment of hind tarsus 0.075 (0.072–0.078).

Gall (Pl. III, C). A globular, closed gall on the upper base of midrib of leaf of *Populus maximowiczii*, generally concolorous with the leaf petiole or somewhat more reddish. When the gall ripens, the surface is split and emigrants escape through these secondary openings.

Host. Primary host: *Populus maximowiczii*; secondary host unknown. Monzen (1929a) says that "this species never produces its gall on the imported poplar such as *Populus nigra* and *Populus monilifera*."

Distribution. Japan: Hokkaidô, Honshû (after Monzen 1929a, etc.).

Biological notes. All fundatrigeniae become emigrants. The collection dates for various stages of galls at Sapporo and Jôzankei are as follows: gall with fundatrix 1st instar larva: 15 & 25 v 1973; gall with fundatrix larva: 20, 25 & 31 v 1973, 3, 8 & 12 vi 1973; gall with fundatrix adult but without emigrant adult: 11, 15, 18 & 27 vi 1972, 12, 18 & 23 vi 1973; gall with fundatrix and emigrant adult: 20 vi 1972, 3 & 4 vii 1972, 30 vi 1973, 2, 5, 6 & 9 vii 1973.

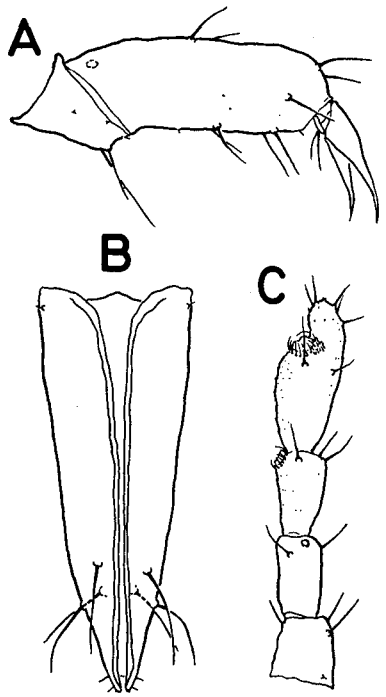

Fig. 17. *Pemphigus matsumurai* exule. First instar larva: A, hind tarsus; B, ultimate rostral segment; C, antenna.

Discussion. Surprisingly, Shinji (1941 & 1944) proposes the union of *matsumurai* and *niisimae*. In his earlier paper (1941) he describes "*dorocola*", of which the antenna (p. 1073, fig. 522) is surely of *dorocola* here understood, but the photograph of the galls (p. 1074, fig. 523, partim) is, as already mentioned, clearly of *matsumurai*. In his later paper (1944), he gives a photograph of the gall of "*niisimae*" (p. 111, fig. 202), but it is also clearly of *matsumurai*; furthermore, his figure of the alate vivipara of "*niisimae*" (p. 555, fig. 93) is not of a Pemphigine but of an Eriosomatine. Hori (1938) and Paik (1972) give descriptions of sexuparae of "*matsumurai*", but I do not see whether their identifications are right.

The position of this species is still obscure. Börner and Schilder (1931) place this species in *Pemphiginus* (type-species: *Pemphigus populi*) with a question mark. *Pemphiginus*, comprising the two European species *populi* and

vesicarius, is treated by Roberti (1938, as a genus), Börner (1952, as a subgenus of *Pemphigus*), Börner and Heinze (1957, as a subgenus of *Pemphigus*) and Stroyan (1957, as a subgenus of *Pemphigus*)[1] and characterized as follows: fundatrix and fundatrigenia live in a closed gall; in fundatrix adult, antenna 4-segmented, wax gland plates comparatively small in size; in emigrant adult, cornicle absent, antennal segment VI without secondary rhinarium. Though the present species has these characters in common with the European species, it is open to doubt whether they are really phylogenetically related to one another. As the fundatrix 1st instar larva of this species is rather peculiar in having pointed 2nd tarsal lateroapical setae and extensively sclerotized tergites, a comparison of this stage between them may give a clue to their phylogeny.

Epipemphigus niisimae (Matsumura) n. comb.

Pemphigus niisimae Matsumura 1917: 85.
Pemphigus niisimae: Hori and Oshima 1924: 5; Monzen 1929a: 35 & 1929b: 360; Hori 1929: pl. 2 & 1938: 128; Börner and Schilder 1931: 653; Mordvilko 1935: 79; Shinji 1941: 1075 (partim), & 1944: 111 & 556 (partim); Börner and Heinze 1957: 653.
Pemphigus filaginis: Tao 1970: 138 (partim).

Fundatrix. Three galls of this species each containing a young fundatrix adult and 4 moults were found; therefore, it is inferred that the fundatrix moults four times. First instar larva differs from adult in many respects, whereas 2nd to 4th instar larvae are similar to adult in general.

Fundatrix 1st instar larva (Pl. I, B; Fig. 18, A–C).

Description is mainly based on 10 specimens collected from galls on *Populus maximowiczii* (Sapporo, Hokkaidô; 13 v 1973).

General colour in life black, with wax filaments at apex of abdomen, yet without visible wax gland plate. The whole tergites and appendages strongly sclerotized (Pl. I, B). Antenna (Fig. 18, B) 4-segmented; number of setae on each segment as follows: I: 3 or 4 (usually 4), II: 2 or 3, III: 3, IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.022–0.030 mm.; primary rhinaria not or scarcely ciliate, on III *ca.* 0.007–0.013 mm. and on IV *ca.* 0.015–0.020 mm. in axial length; IV with many spines. Ultimate rostral segment (Fig. 18, C) without accessory seta. Thoracic tergites I–III each with 4 pairs of setae. Fore femur enlarged, larger than hind one, with the ratio of fore femorotrochanteric length to hind one 1.02–1.13. Tarsi (Fig. 18, A) 2-segmented, without spine; 1st segment with a pair of long spatulate setae, which are *ca.* 0.037–0.040 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium, the lateral setae long and capitate, the empodial setae long, extending far beyond the apices of claws, bent and capitate. Abdominal tergites I–VII each with 3 pairs of setae, the longest one on tergite III *ca.* 0.022–0.028 mm.; abdominal tergite VIII with 2 or 3 pairs of setae; cauda with a pair of setae; anal plate with 3 pairs of setae. Cornicle absent.

Measurements of 10 specimens in mm. Body 0.76 (0.64–0.83); antennal

1) He does not refer to *vesicarius*.

segments (I–IV): 0.043 (0.040–0.048), 0.043 (0.037–0.048), 0.038 (0.032–0.043), 0.061 (0.057–0.065); ultimate rostral segment 0.080 (0.075–0.088); 2nd segment of hind tarsus (in 9 specimens) 0.060 (0.055–0.065); fore femorotrochanter 0.182 (0.157–0.198); hind femorotrochanter 0.169 (0.147–0.183).

Fundatrix adult (Fig. 18, D–F).

Description is based on 10 specimens collected from galls on *Populus maximowiczii*. Measurements of certain parts and collection data in Table 18.

Body without wax gland plate. Antenna (Fig. 18, E) 4-segmented, the articulations all functional; number of setae on each segment as follows: I: 4, II: 2 or 3, III: 3 or 4 (usually 3), IV: 2 (rarely 3)+5; the longest seta on IV (except terminal setae) *ca.* 0.022–0.030 mm.; III the longest, about as wide as IV; primary rhinaria ciliate, on III *ca.* 0.012–0.020 mm. and on IV *ca.* 0.015–0.030 mm. in axial length. Ultimate rostral segment (Fig. 18, F) without secondary setae. Thorax often with local sclerotizations besides lateral part of prothorax always sclerotized. Tarsi (Fig. 18, D) faintly spinose ventrally; 1st segment with a pair of pointed setae, which are *ca.* 0.025–0.035 mm. in maximum length on hind tarsus; 2nd segment comparatively short, without secondary seta, all of the primary setae pointed, the empodial setae *ca.* 0.012–0.020 mm. in maximum length on hind tarsus. Tergites with 2 kinds of setae; long thick setae regularly arranged almost as in the manner of the dorsal setae of the 1st instar larva, the longest one on abdominal tergite III

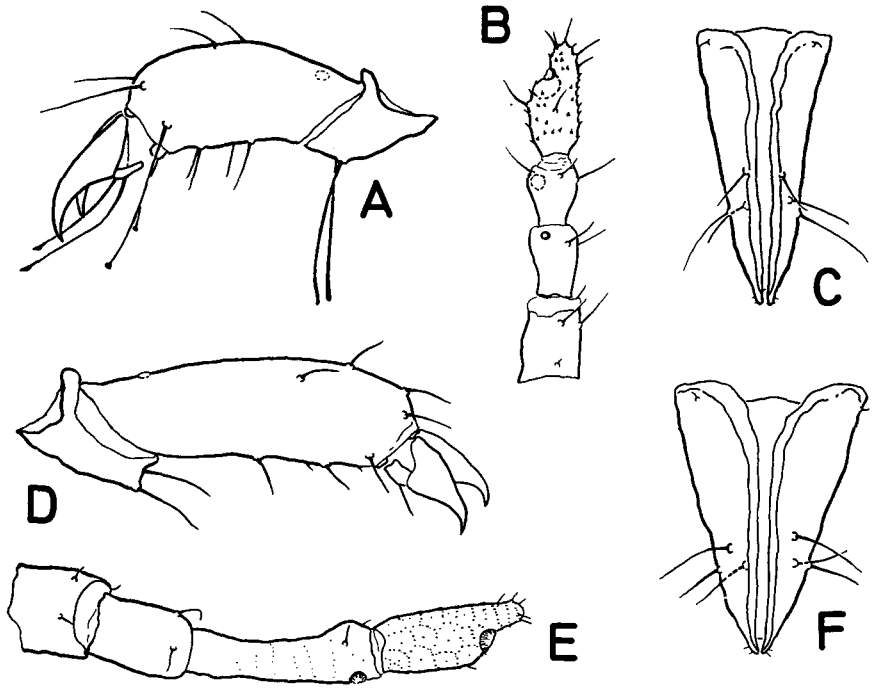

Fig. 18. *Epipemphigus niisimae* fundatrix. First instar larva: A, hind tarsus; B, antenna; C, ultimate rostral segment. Adult: D, hind tarsus; E, antenna; F, ultimate rostral segment.

ca. 0.052–0.085 mm. and that on abdominal tergite VIII *ca.* 0.057–0.080 mm.; short thin setae rather numerous, scattered irregularly. Cornicle absent. Cauda with 3–6 setae. Genital plate with 22–31 setae.

Measurements in mm. Ultimate rostral segment (in 9 specimens) 0.098 (0.090–0.105); 2nd segment of hind tarsus (in 10 specimens) 0.117 (0.105–0.130).

Emigrant 1st instar larva (Fig. 19, A–E).

Description is mainly based on 10 specimens collected from galls on *Populus maximowiczii* (Sapporo, Hokkaidô; 31 v 1973).

Antenna (Fig. 19, C) 4-segmented; number of setae on each segment as follows: I: 4, II: 2 or 3 (usually 3), III: 3 (rarely 4), IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.022–0.028 mm.; primary rhinaria ciliate, on III *ca.* 0.010–0.013 mm. and on IV *ca.* 0.015–0.018 mm. in axial length; IV spinose. Ultimate rostral segment (Fig. 19, D) without spine, rarely with an accessory seta. Tarsi (fore tarsus: Fig. 19, E) without spine; 1st segment with a pair of pointed setae, which are *ca.* 0.025–0.030 mm. in maximum length on hind tarsus; setal distribution on 2nd segment as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium, the empodial setae very variable in length, on hind tarsus 0.007–0.023 mm. in length, with longer one often capitate and reaching the apex of claw, the lateral setae often long and sometimes even capitate, the others pointed. Tergal setae on abdominal segments I–VII each usually within a somewhat sclerotized plate. Abdominal tergites I–VI each with 3 pairs of setae, the longest one on tergite III *ca.* 0.030–0.043 mm.; abdominal tergite VII with 4 or 5 setae; abdominal tergite VIII with 2 or 3 setae, the longest one *ca.* 0.025–0.038 mm.; cauda with 2 or 3 setae; anal plate with 4–6 setae. Wax gland plates as in Fig. 19, B, their distribution is as follows (see Fig. 19, A): spinal ones on abdominal tergites III–VII, and pleural ones on abdominal tergites III–VI, but spinal ones on tergites III and VII often disappearing. Cornicle present.

Measurements of 10 specimens in mm. Body 0.75 (0.66–0.81); antennal segments (I–IV): 0.049 (0.045–0.053), 0.047 (0.045–0.050), 0.068 (0.065–0.070), 0.087 (0.082–0.090); ultimate rostral segment 0.084 (0.080–0.090); 2nd segment of hind tarsus 0.080 (0.075–0.085).

Emigrant adult (Fig. 19, F & G).

Description is mainly based on 10 specimens collected from galls on *Populus maximowiczii*. Measurements of certain parts and collection data in Table 19.

Head without wax gland plate. Antenna (flagellum: Fig. 19, G) 6-segmented; V weakly imbricated, without secondary rhinarium, with 3 or 4 (usually 3) setae at apex, of which the longest one is *ca.* 0.022–0.025 mm., the basal articular diameter *ca.* 0.015–0.020 mm.; VI somewhat imbricated with 1(?) or 2 setae at middle and 5 setae at apex; secondary rhinaria on III and IV, with a wide, minutely ciliated rim; primary rhinaria large, fringed with long, often furcated or dendritic cilia, without distinct rim, that on V comparatively regular in shape, apparently encircling *ca.* 2/3 the segment, and *ca.* 0.017–0.025 mm. in axial length, that on VI larger than that on V, apparently encircling *ca.* 2/3–3/4 the segment, and *ca.* 0.027–0.040 mm. in axial length. Ultimate rostral segment (Fig. 19, F) acute, conical with rather straight sides, spinose, without accessory seta. Thorax often

with spinal wax gland plates. Fore wing with simple media. Tarsi spinose, 1st segment usually with 2 secondary setae, without spine-like seta between primary setae. Abdomen with wax gland plates of normal type as follows: marginal ones oval, on tergites I–VII; no pleural ones; spinal ones mostly rather transverse, often fragmented on tergites I–VII, on tergite VIII strongly transverse and united mesially into the largest one often somewhat broadly pigmented around. Cornicle present, sclerotized semicircularly, not forming an entire ring. Abdominal tergite VIII sometimes with local weakly sclerotized areas, with 2–5 setae. Cauda with 4–7 setae. Genital plate with 28–41 setae.

Measurements of 10 specimens in mm. Ultimate rostral segment 0.080 (0.077–0.083); 2nd segment of hind tarsus 0.181 (0.165–0.195).

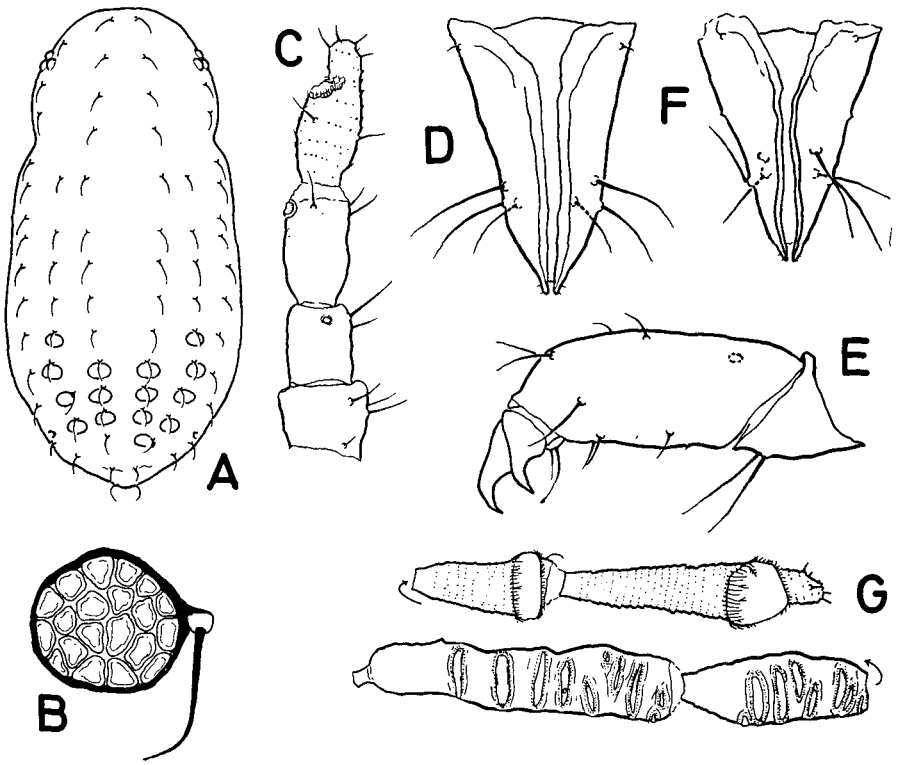

Fig. 19. *Epipemphigus niisimae* emigrant. First instar larva: A, distributional pattern of wax gland plates; B, abdominal wax gland plate; C, antenna; D, ultimate rostral segment; E, fore tarsus. Adult: F, ultimate rostral segment; G, flagellum.

Exule 1st instar larva (3rd generation) (Fig. 20, A–C).

Description is mainly based on 10 specimens deposited by emigrants (Sapporo, Hokkaidô; 25 vi, and, 5 vii, 1973).

Antenna (Fig. 20, C) 4-segmented; setal number on each segment as follows: I: 4, II: 2–4 (usually 3), III: 3, IV: 2+5; the longest seta on IV (except terminal setae) *ca.* 0.017–0.020 mm. in length; primary rhinaria ciliate, on III *ca.* 0.007–0.010 mm. and on IV *ca.* 0.012–0.015 mm. in axial length; IV spinose, III faintly

spinose; membraneous neck between III and IV comparatively remarkable. Ultimate rostral segment (Fig. 20, B) short, without accessory seta. Tarsi (Fig. 20, A) 2-segmented; 1st segment faintly spinose, with a pair of pointed setae, which are *ca.* 0.017–0.023 mm. in maximum length on hind tarsus; 2nd segment spinose, its setal distribution is as follows: dorsally 2 pairs, ventrally 2 pairs, laterally 1 pair, and 1 pair on empodium, all these setae pointed, the empodial setae *ca.* 0.007–0.010 mm. in maximum length on hind tarsus. Abdominal tergites I–VI each with 3 pairs of setae, the longest one on tergite III *ca.* 0.010–0.015 mm.; abdominal tergite VII with 2 pairs of setae; abdominal tergite VIII with a pair of setae, the longer one *ca.* 0.007–0.013 mm.; cauda with a pair of setae; anal plate with 2 pairs of setae. Abdominal wax gland plates composed of many separated facets with a "Zentralkern", their distribution is as follows: spinal ones on tergites III–VII, and pleural ones on tergites III–VI.

Measurements of 10 specimens in mm. Body 0.52 (0.48–0.57); antennal segments (I–IV): 0.037 (0.035–0.040), 0.047 (0.042–0.050), 0.046 (0.042–0.048), 0.076 (0.072–0.080); ultimate rostral segment 0.063 (0.060–0.065); 2nd segment of hind tarsus 0.055 (0.050–0.058).

Gall (Pl. III, D). A cockscomb-like, loosely closed gall on the leaf of *Populus maximowiczii*, usually along the midrib, with a longitudinal primary split at the underside through which emigrants escape; general colour yellow to crimson red. A detailed description is given by Monzen (1929a).

Host. Primary host: *Populus maximowiczii* (=*Populus balsamifera* in Matsumura 1917, and in Higuchi and Miyazaki 1969), *Populus suaveolens* (in Ussuri, after Mordvilko 1935); secondary host unknown.[1)]

Distribution. Ussuri (after Mordvilko 1935); Japan: Hokkaidô, Honshû (after Monzen 1929a, etc.).

Biological notes. All fundatrigeniae become emigrants. The collection dates for various stages of galls at Sapporo and Jôzankei are as follows: gall with fundatrix 1st instar larva: 13 & 15 v 1973; gall with fundatrix larva: 13, 15, 20, 25 & 31 v 1973; gall with fundatrix adult but without emigrant adult: 11 & 15 vi 1972, 31 v

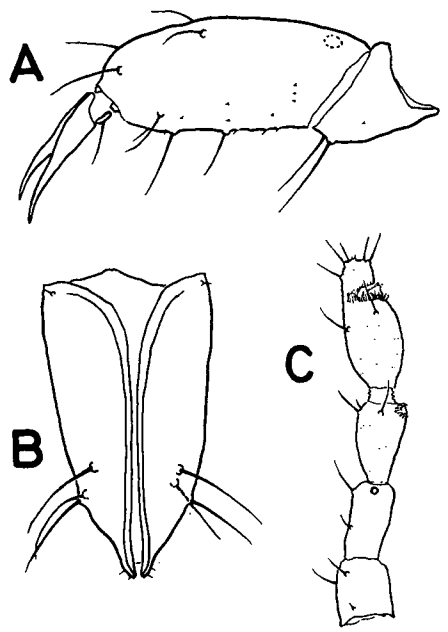

Fig. 20. *Epipemphigus niisimae* exule. First instar larva: A, hind tarsus; B, ultimate rostral segment; C, antenna.

1) Shinji (1941 & 1944) says that this species emigrates to the subterranean parts of *Agrimonia pilosa*, *Bidens tripartita*, *Fatoua villosa* and *Larix leptolepis*. However, these records are open to doubt, for he confounds *niisimae* and *matsumurai*, and for he does not give any description of the exule morph. Higuchi and Miyazaki (1969) follow him. Paik (1972) gives a description of *niisimae* on *Agrimonia pilosa*, but I do not see whether his identification is right.

1973, 12 vi 1973; gall with fundatrix and emigrant adult: 16, 18, 20 & 27 vi 1972, 2 vii 1972, 18, 23, 24 & 25 vi 1973, 5 & 8 vii 1973.

On June 16th, 1972, at Hokkaidô Forest Experiment Station, Bibai, Hokkaidô, I found a number of galls of *niisimae* on *Populus maximowiczii*, but I could not find any gall on adjacent trees of *Populus nigra* and *Populus alba*.

Discussion. The monotypic genus *Epipemphigus* was erected by Hille Ris Lambers (1966a) as a separation from *Pemphigus* in order to accept *Pemphigus imaicus* Cholodkovsky 1912. Recently he kindly sent me a slide[1] containing emigrant last instar larvae and emigrant adults of *imaicus*. On the basis of my comparison and also on his (1966a) redescription of *imaicus*, *niisimae* and *imaicus* are distinguished in the emigrant characters given in Table 20. They are closely related and can be lumped together to form a small group. The morphological gap between this group and other *Pemphigus* species is remarkable; therefore, it is reasonable to give it a generic status. The diagnosis of the genus *Epipemphigus* is given as follows:

Genus *Epipemphigus* Hille Ris Lambers 1966a

Type-species: *Epipemphigus imaicus* (Cholodkovsky 1912).

Known from Asia. Life cycle obligatory-heteroecious; with 1 generation of fundatrigenia. Primary hosts are *Populus* species belonging to the section *Tacamahaka*; secondary hosts unknown. Gall with a primary split beneath, cockscomb- or sausage-like in shape, occurring on upper side of the leaf, with fundatrix and fundatrigenia living together. Fundatrix 1st instar larva (based on *niisimae*): Body strongly sclerotized; antenna 4-segmented; fore femur enlarged; empodial setae and lateroapical setae on 2nd tarsal segment capitate, setae on 1st tarsal segment spatulate. Fundatrix adult: Body without wax gland plate; antenna 4-segmented, the articulations all functional, segment III at least sometimes with an abortive division. Emigrant 1st instar larva: Antenna 4-segmented, number of apical setae on segment IV 5 in *niisimae* and 8–10 in *imaicus*; empodial setae pointed, but in *niisimae* sometimes capitate; abdomen with some wax gland plates. Emigrant adult: Atennal segment VI without secondary rhinarium, secondary rhinaria distinctly ciliate, primary rhinarium on segment VI large, number of apical setae on segment VI 5 in *niisimae* and 8–10 in *imaicus*; ultimate rostral segment short, acute and conical; thorax often with wax gland plates; fore wing with a simple media; 1st tarsal segment without spine-like seta; abdomen without row of pleural wax gland plates. Exule 1st instar larva: Antenna 4-segmented; ultimate rostral segment short; empodial setae rather short.

As Hille Ris Lambers (1966a) already points out, this genus has two important characters which may suggest its close relationship to *Pachypappa*: one character is the absence of wax gland plate in fundatrix adult; the other is, in the emigrant adult, secondary rhinarium ciliation. On the other hand, it shows a number of characters in common with certain species of *Pemphigus* (e.g. *dorocola* and *matsumurai*). According to Börner and Heinze (1957) *Pachypappa* differs from *Epipemphigus* and these species of *Pemphigus* at least by lacking the following characters: in fundatrix adult, 4-segmented antenna, in emigrant adult, simple media; in exule 1st instar larva, short empodial setae. The correct position of

1) Labelled "*Epipemphigus imaicus* Chol./2nd gen./Det. D.H.R.L./N. Pakistan/Pl. *Populus ciliata*/Loc. Murrae/Date 29. V. '68/Leg. Ghani/969".

Epipemphigus could not be decided until a careful comparison with *Pachypappa* and other Börner's (1952) Pachypappini is carried out.

General consideration

On the 1st instar larva

The fundatrix 1st instar larva is peculiar in many respects. It has well-sclerotized tergites and well-developed setae, whereas the succeeding instars have membraneous tergites and less developed setae. As already mentioned, the fundatrix 1st instar larvae hatch from the eggs overwintering in bark crevices and migrate to leaves or shoots to produce a peculiar gall, within which the succeeding instars grow. It is obvious that these morphological differences are associated with the habitat differences between them, the sclerotized tergites probably playing a protective role in the 1st instar.

The emigrant 1st instar larvae of *orientalis*, *latisensoria* and *dorocola* always have long and capitate empodial setae, while those of *microsetosus* and *matsumurai* short and pointed ones. In *niisimae*, the empodial setae are usually short and pointed, but sometimes long and even capitate. The capitate empodial seta is associated with more or less peculiar types of the emigrant 1st instar larva. In *orientalis* and *latisensoria*, the emigrant 1st instar larva emigrates from the leaf bearing the primary gall to another leaf to make the secondary gall. It is probable that capitate empodial seta has some function in migration. The fact that the second to last instar larvae and the adult lack this character and that all of the fundatrix 1st instar larvae here described have capitate empodial setae support this assumption. But in *dorocola* the meaning of the character is still obscure. The occasional appearance of the capitate empodial seta in *niisimae* may be interpreted as a sort of reversion to the state of fundatrix 1st instar larva.

The exule 1st instar larva is similar to the adult in general respects. At least in the 3rd generation, the 1st instar larva should be active in order to search for a suitable place on its secondary host plant. Lange (1965) briefly mentions the wind dispersal of the 1st instar larva in a certain anholocyclic population.

On Thecabius, Parathecabius and Pemphigus

The genus *Parathecabius* is erected by Börner (1950) to accept *lysimachiae* (type-species), *saliciradicis* and *cerastii*, and it is distinguished by him from the *affinis* group or *Thecabius* on account of the 4-segmented antenna with short processus terminalis in the exule 1st instar larva. But he does not refer to the difference between it and the other *Pemphigus* species. He might think that the former could be distinguished from the latter by the presence of emigration in the 2nd generation 1st instar larva. Hille Ris Lambers (1952) points out a strong similarity between *saliciradicis* (=*salicicola*) and the *Pemphigus* species in the apterous exule. Stroyan (1964), then, excludes *saliciradicis* and *cerastii* from *Parathecabius*, in which he includes *auriculae*, *glebae*, *pseudoauriculae* and *stammeri*, which are, except *glebae* without host record, associated with Primulaceae for secondary hosts; he looks upon it as a subgenus of *Pemphigus* opposed to *Thecabius*. He characterizes the subgenus *Parathecabius* as follows: 1) Associated with

Primulaceae for secondary hosts; 2) Emigrating in the 1st instar larva of the 2nd generation; 3) With secondary rhinaria narrow and slit-like, and with abdomen at least sometimes pigmented locally in the sexupara. He says that "this combination of characters seems to provide a justification for the retention of *Parathecabius* as a subgenus". However, as to the 2nd of these characters not all of the speices referred by him to *Parathecabius* have been established. Zwölfer (1957), who lumps *lysimachiae* and *stammeri* in *Parathecabius*, comments as follows: "da hier die fundatrigenen Formen nur teilweise bekannt sind (und zum Teil vielleicht endgültig in Verlust gerieten), kann eine sichere Aussage über eine etwaige polyphyletische Entstehung der Gattung nicht gemacht werden." Smith (1971) finds on *Lysimachia* the exule form of *Mordvilkoja vagabunda*, which lacks the second character. Judging from his description, the exule 1st instar larva is similar to that of *latisensoria* and that of *microsetosus*, especially in having very short empodial setae. This suggests that *Parathecabius* in Stroyan's (1964) sense may be untenable. These problems will be solved with the increase of our knowledge about the relationships among *lysimachiae* group, *microsetosus* and *Mordvilkoja vagabunda*.

On the other hand, *lysimachiae* group has often been lumped together with *affinis* group in opposition to the other *Pemphigus* species, e.g. by Shaposhnikov (1964) and by Palmer (1958). They may stress the common presence of two characters: 1) with 5-segmented antenna in fundatrix adult; and 2) emigrating in the 2nd generation 1st instar larva. However, the common presence of the first character possibly means nothing more than an agreement in primitiveness; such an antenna is also found in *microsetosus* and in other Pemphiginae. As to the second character, convergence or parallelism may also be adopted for explanation. It is reasonable to think that both *lysimachiae* group and *affinis* group evolved from heteroecious species with non-emigratory 2nd generation 1st instar larva. However, it seems to me improbable that the two have a very recent common ancestor, which emigrated in the 1st instar of the 2nd generation. The position of *lysimachiae* group proposed by Stroyan (1964), I think, is more appropriate, because the 4-segmented antenna of the exule 1st instar larva is held in common throughout. But, this character is rather universal in Pemphiginae, and therefore not a strong evidence. As both the morphological and the ecological gaps between *affinis* group and other *Pemphigus* species are not so large, it seems to me reasonable to lump them together in a single genus. Needless to say, this is merely a compromise in the present state of our knowledge.

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TABLES

Table 1. Comparison of main characters of fundatrix 1st instar larva among *Pemphigus orientalis*, *P. microsetosus*, *P. dorocola*, *P. matsumurai* and *Epipemphigus niisimae*.

Feature \ Species	*orientalis*	*microsetosus*	*dorocola*	*matsumurai*	*niisimae*
Antenna	5-segmented	?	4-segmented	4-segmented	4-segmented
Thoracic and abdominal tergites	only partially sclerotized	wholly sclerotized	only partially sclerotized	extensively but not wholly sclerotized	wholly sclerotized
Fore femur	not enlarged	not enlarged	not enlarged	not enlarged	enlarged
Setae on 1st tarsal segment	pointed	pointed	pointed	pointed	spatulate
Lateroapical setae on 2nd tarsal segment	capitate	capitate	capitate	pointed	capitate
Initial infesting part	leaf blade near margin (underside)	nerve (underside)	shoot	basal part of main nerve (underside)	leaf blade (underside)

Table 2. Comparison of main characters of fundatrix adult among *Pemphigus orientalis*, *P. latisensoria*, *P. microsetosus*, *P. dorocola*, *P. matsumurai* and *Epipemphigus niisimae*.

Feature \ Species	*orientalis*	*latisensoria*	*microsetosus*	*dorocola*	*matsumurai*	*niisimae*
Antenna	5-segmented	5-segmented, III with an abortive division	5-segmented, III sometimes with an abortive division	4-segmented, III often with an abortive division	4-segmented, III often with an abortive division	4-segmented
Femora	not enlarged	enlarged	not enlarged	not enlarged	not enlarged	not enlarged
Abdominal wax gland plates	usually with separated facets, but on posterior segments often with facets appressed together	with irregular facets rather appressed together	with polygonal facets appressed together	with separated facets	comparatively small in size, with separated facets	absent

Table 3. Comparison of main characters of emigrant 1st instar larva among *Pemphigus orientalis*, *P. latisensoria*, *P. microsetosus*, *P. dorocola*, *P. matsumurai* and *Epipemphigus niisimae*.

Species / Features	*orientalis*	*latisensoria*	*microsetosus*	*dorocola*	*matsumurai*	*niisimae*
Antenna	5-segmented	4-segmented	4-segmented	4-segmented	4-segmented	4-segmented
Cornicle	absent	?	present	present	absent	present
Empodial setae	long and capitate	long and capitate	short and pointed	long and capitate	short and pointed	usually pointed but sometimes capitate
Emigration	present	present	absent	absent	absent	absent
Galls	open	open	closed	open	closed	loosely closed

Table 4. Comparison of main characters of emigrant adult among *Pemphigus orientalis*, *P. latisensoria*, *P. microsetosus*, *P. dorocola*, *P. matsumurai* and *Epipemphigus nissimae*.

Species / Feature	*orientalis*	*latisensoria*	*microsetosus*	*dorocola*	*matsumurai*	*niisimae*
Processus terminalis	long, slender	long, slender	long, slender	short, stout	short, stout	short, stout
Secondary rhinaria	on antennal segments III–VI, very narrow, without cilia	on antennal segments III–VI, broad, without cilia	on antennal segments III & IV, and sometimes on segment V, somewhat narrow, slit-like, without cilia	on antennal segments III–VI, with average width, without cilia	on antennal segments III–V, with average width, without cilia	on antennal segments III & IV, slit-like, ciliate
Spine-like seta between 1st tarsal primary setae	single, always present on fore leg, sometimes absent on mid and hind legs	single, present on fore leg	double, present on all legs	absent	absent	absent
Abdominal pleural wax gland plates	present	present	present	absent	absent	absent
Cornicle	absent	present	present	present	absent	present

Table 5. Comparison of main characters of exule 1st instar larva among *Pemphigus orientalis*, *P. latisensoria*, *P. microsetosus*, *P. saliciradicis*, *P. dorocola*, *P. matsumurai* and *Epipemphigus niisimae*.

Feature \ Species	*orientalis*	*latisensoria*	*microsetosus*	*saliciradicis*	*dorocola*	*matsumurai*	*niisimae*
Antenna	5-segmented	4-segmented	4-segmented	4-segmented	4-segmented	4-segmented	4-segmented
Ratio of ultimate antennal segment length to penultimate one	1.84-2.20	1.23-1.38	1.00-1.13	1.17-1.36	1.21-1.46	1.61-1.79	1.52-1.78
Maximum length of empodial seta on hind tarsus (mm.)	0.010-0.015	0.002-0.005	0.002(?)-0.005	0.010-0.013	0.012-0.015	0.015-0.018	0.007-0.010
Ultimate rostral segment length (mm.)	0.085-0.100	0.102-0.108	0.120-0.133	0.070-0.083	0.085-0.088	0.105-0.110	0.060-0.065
Host	*Ranunculus* (usually on aerial parts)	?	?	*Salix* (on root)	?	?	?

Table 6. Measurements of *Pemphigus orientalis* fundatrix adult.

Indiv.	BL	AL	Ant.					SW3T
			I	II	III	IV	V	
1	3.56	0.790	0.110	0.115	0.280	0.105	0.180	0.078
2	3.56	0.810	0.110	0.125	0.270	0.110	0.195	0.060
3	3.69	0.740	0.110	0.125	0.225	0.105	0.175	0.098
4	3.88	0.905	0.115	0.140	0.310	0.120	0.220	0.075
5	3.56	0.945	0.115	0.135	0.325	0.145	0.225	0.065
6	3.81	0.965	0.120	0.140	0.330	0.145	0.230	0.073
7	4.13	0.795	0.110	0.125	0.265	0.110	0.185	0.068
8	3.56	0.780	0.105	0.115	0.255	0.110	0.195	0.070
9	4.13	0.870	0.120	0.140	0.300	0.120	0.190	0.063

Individual 1: Sapporo, Hokkaidô, 30 vi 1973; 2 & 3: Sapporo, 5 vii 1973; 4–6: Sapporo, 4 vi 1972; 7–9: Sapporo, 15 vi 1972. BL: length of body (mm.); AL: length of antenna (mm.); Ant.: length of antennal segment (mm.); SW3T: maximum length of spinal wax gland plates on 3rd abdominal tergite (mm.).

Table 7. Measurements of *Pemphigus orientalis* emigrant adult.

Indiv.	BL	FL	Ant.				SRN (l/r)			
			III	IV	V	VI	III	IV	V	VI
1	2.12	1.210	0.475	0.205	0.255	0.230+0.045	22/23	9/7	9/9	5/6
2	2.24	1.180	0.465	0.185	0.250	0.235+0.045	17/25	8/8	8/9	5/7
3	2.12	1.205	0.475	0.190	0.250	0.250+0.040	24/23	9/7	9/9	5/4
4	2.28	1.235	0.495	0.200	0.255	0.240+0.045	25/24	7/7	9/7	6/6
5	2.28	1.245	0.495	0.205	0.260	0.240+0.045	22/21	9/8	11/11	6/7
6	?	1.160	0.465	0.190	0.230	0.235+0.040	25/22	8/7	7/7	6/5
7	2.04	1.175	0.465	0.200	0.255	0.220+0.035	26/25	8/7	10/9	5/6
8	2.16	1.165	0.475	0.195	0.240	0.215+0.040	23/21	7/7	8/7	5/7
9	2.04	1.045	0.420	0.165	0.205	0.210+0.045	19/20	6/5	8/6	5/4
10	2.32	1.140	0.450	0.185	0.240	0.220+0.045	22/22	6/8	9/7	4/5

Individual 1–5: Jôzankei, Hokkaidô, 9 vii 1973; 6–10: Sapporo, Hokkaidô, 5 vii 1973. BL: length of body (mm.); FL: length of flagellum (mm.); Ant.: length of antennal segment (mm.); SRN (l/r): number of secondary rhinaria on antennal segment (left/right).

Table 8. Measurements of *Pemphigus orientalis* apterous exule adult.

Indiv.	BL	AL	Ant.						HTb	SW3T
			I	II	III	IV	V	VI		
1	2.08	1.025	0.100	0.145	0.270	0.115	0.175	0.175+0.045	0.73	0.195
2	2.16	1.195	0.110	0.155	0.355	0.140	0.205	0.195+0.035	0.81	0.170
3	2.12	1.225	0.105	0.170	0.345	0.160	0.200	0.200+0.045	0.81	0.178
4	1.96	1.050	0.110	0.145	0.290	0.115	0.165	0.175+0.050	0.76	0.150
5	2.28	1.060	1.110	0.145	0.285	0.125	0.175	0.175+0.045	0.71	0.180
6	1.88	0.975	0.095	0.130	0.245	0.110	0.170	0.175+0.050	0.63	0.140
7	1.96	0.920	0.100	0.125	0.225	0.110	0.155	0.160+0.045	0.62	0.138
8	2.04	1.040	0.100	0.135	0.280	0.135	0.185	0.170+0.035	0.66	0.153
9	1.96	1.000	0.105	0.135	0.260	0.115	0.170	0.170+0.045	0.70	0.165
10	1.96	0.950	0.095	0.125	0.245	0.120	0.165	0.160+0.040	0.64	0.133

Individual 1–4: Tsunagi, Iwate Pref., 13 viii 1973; 5–10: Morioka, Iwate Pref., 11 viii 1973. BL: length of body (mm.); AL: length of antenna (mm.); Ant.: length of antennal segment (mm.); HTb: length of hind tibia (mm.); SW3T: maximum length of spinal wax gland on 3rd abdominal tergite (mm.).

Table 9. Measurements of *Pemphigus latisensoria* emigrant adult.

Indiv.	BL	FL	Ant.				SRN (1/r)			
			III	IV	V	VI	III	IV	V	VI
1	3.28	1.59	0.60	0.25	0.33	0.35+0.06	36/36	11/10	10/12	11/12
2	3.12	1.60	0.60	0.25	0.35	0.34+0.06	39/43	11/12	13/11	11/10
3	3.28	1.55	0.57	0.23	0.35	0.35+0.05	38/35	10/10	13/13	10/13
4	3.36	1.60	0.59	0.26	0.33	0.36+0.06	34/34	12/11	12/13	11/11
5	3.32	1.54	0.57	0.25	0.33	0.33+0.06	37/39	11/10	14/14	9/14
6	3.24	1.57	0.59	0.26	0.32	0.34+0.06	41/39	11/12	14/14	11/12
7	3.16	1.53	0.57	0.23	0.33	0.34+0.06	34/36	11/13	14/15	13/11
8	3.16	1.54	0.58	0.24	0.33	0.34+0.05	35/37	11/13	14/13	12/12
9	3.48	1.54	0.56	0.25	0.33	0.34+0.06	33/36	13/13	14/12	10/14
10	3.48	1.63	0.62	0.25	0.35	0.35+0.06	38/36	13/11	13/12	12/12

Individual 1: Sapporo, Hokkaidô, 27 vii 1973; 2–10: Sapporo, 26 vii 1973. BL: length of body (mm.); FL: length of flagellum (mm.); Ant.: length of antennal segment (mm.); SRN (1/r): number of secondary rhinaria on antennal segment (left/right).

Table 10. Measurements of *Pemphigus microsetosus* fundatrix adult.

Indiv.	BL	AL	Ant.					SW3T
			I	II	III	IV	V	
1	3.44	0.755	0.105	0.125	0.235	0.095	0.195	0.075
2	3.69	0.665	0.090	0.110	0.200	0.095	0.170	0.068
3	3.06	0.785	0.110	0.120	0.230	0.120	0.205	0.073
4	3.06	0.755	0.095	0.120	0.235	0.105	0.200	0.088
5	3.19	0.780	0.105	0.120	0.250	0.110	0.195	0.065
6	2.75	0.705	0.090	0.115	0.215	0.095	0.190	0.065

Individual 1: Sapporo, Hokkaidô, vii 1973; 2–5: Jôzankei, Hokkaidô, 8 vii 1973; 6: Sapporo, 2 vii 1973. BL: length of body (mm.); AL: length of antenna (mm.); Ant.: length of antennal segment (mm.); SW3T: maximum length of spinal wax gland plates on 3rd abdominal tergite (mm.).

Table 11. Measurements of *Pemphigus microsetosus* emigrant adult.

Indiv.	BL	FL	Ant.				SRN (l/r)		
			III	IV	V	VI	III	IV	V
1	2.44	0.830	0.295	0.140	0.160	0.185+0.050	12/11	2/3	0/0
2	2.36	0.860	0.310	0.145	0.160	0.195+0.050	14/12	3/2	0/0
3	2.44	0.830	0.305	0.130	0.160	0.185+0.050	13/12	3/3	0/0
4	2.24	0.855	0.315	0.140	0.160	0.190+0.050	13/11	3/2	0/0
5	2.16	0.830	0.300	0.135	0.160	0.185+0.050	13/11	2/2	1/0
6	2.28	0.830	0.305	0.140	0.150	0.185+0.050	14/13	2/3	0/0
7	2.44	0.815	0.310	0.125	0.145	0.185+0.050	12/10	2/2	0/0
8	2.32	0.870	0.325	0.135	0.160	0.200+0.050	11/12	2/2	1/0
9	2.24	0.835	0.305	0.135	0.150	0.195+0.050	11/14	3/3	0/0
10	?	0.825	0.315	0.125	0.150	0.180+0.055	14/12	3/2	0/0

Individual 1–6: Sapporo, Hokkaidô, 26 vii 1973; 7–10: Sapporo, 27 vii 1973. BL: length of body (mm.); FL: length of flagellum (mm.); Ant.: length of antennal segment (mm.); SRN (l/r): number of secondary rhinaria on antennal segment (left/right).

Table 12. Measurements of *Pemphigus saliciradicis* apterous exule adult.

Indiv.	BL	AL	Ant.						HTb	SW3T
			I	II	III	IV	V	VI		
1	2.28	0.555	0.075	0.095	0.093	0.068	0.070	0.120+0.035	0.61	0.080
2	2.32	0.635	0.080	0.100	0.118	0.065	0.098	0.143+0.033	0.69	0.123
3	1.96	0.533	0.075	0.088	0.085	0.063	0.070	0.120+0.033	0.58	0.083
4	2.20	0.575	0.080	0.093	0.095	0.063	0.080	0.138+0.028	0.62	0.090
5	2.28	0.558	0.078	0.095	0.098	0.060	0.070	0.128+0.030	0.59	0.093
6	?	0.508	0.075	0.083	0.083	0.053	0.063	0.115+0.038	0.55	0.070
7	2.04	0.563	0.078	0.100	0.098	0.058	0.075	0.120+0.035	0.55	0.040
8	2.00	0.473	0.065	0.080	0.118		0.063	0.115+0.033	0.46	—
9	1.92	0.495	0.070	0.085	0.125		0.068	0.113+0.035	0.49	—
10	1.96	0.468	0.068	0.083	0.113		0.063	0.113+0.030	0.48	—

Individual 1–5: Sapporo, Hokkaidô, 8 vi 1973, ex *Salix* sp.; 6–10: Jôzankei, Hokkaidô, 20 ix 1973. BL: length of body (mm.); AL: length of antenna (mm.); Ant.: length of antennal segment (mm.); HTb: length of hind tibia (mm.); SW3T: maximum length of spinal wax gland plates on 3rd abdominal tergite (mm.).

Table 13. Measurements of *Pemphigus saliciradicis* alate viviparae.

Indiv.	BL	FL	Ant.				SRN (1/r)			EN (e/s)
			III	IV	V	VI	III	IV	V	
1	2.20	0.585	0.175	0.110	0.100	0.160+0.040	7/6	3/3	0/0	6/0
2	2.36	0.650	0.205	0.120	0.120	0.165+0.040	8/7	4/4	0/0	6/0
3	2.16	0.605	0.190	0.115	0.115	0.145+0.040	7/6	3/5	1/1	6/0
4	2.36	0.615	0.185	0.110	0.115	0.165+0.040	6/7	3/4	0/0	3/3
5	2.20	0.575	0.175	0.105	0.105	0.155+0.035	6/7	2/2	0/0	4/3
6	2.32	0.600	0.190	0.105	0.115	0.150+0.040	7/6	4/3	0/0	4/1

Individual 1–6: Jôzankei, Hokkaidô, 3 x 1973. BL: length of body (mm.); FL: length of flagellum (mm.); Ant.: length of antennal segment (mm.); SRN (1/r): number of secondary rhinaria on antennal segment (left/right); EN (e/s): number of embryos (exule/sexuale).

Table 14. Measurements of *Pemphigus dorocola* fundatrix adult.

Indiv.	BL	AL	Ant.				SW3T
			I	II	III	IV	
1	2.88	0.560	0.075	0.105	0.235	0.145	0.123
2	2.44	0.470	0.065	0.075	0.200	0.130	0.113
3	3.00	0.550	0.085	0.085	0.235	0.145	0.120
4	3.38	0.555	0.085	0.095	0.235	0.140	0.168
5	3.50	0.580	0.080	0.090	0.260	0.150	0.143
6	3.38	0.525	0.075	0.095	0.225	0.130	0.100

Individual 1: Sapporo, Hokkaidô, 12 vi 1973; 2: Sapporo, 18 vi 1972; 3: Sapporo, 23 vi 1973; 4: Sapporo, 5 vii 1973; 5: Jôzankei, Hokkaidô, 9 vii 1973; 6: Sapporo, 7 x 1972. BL: length of body (mm.); AL: length of antenna (mm.); Ant.: length of antennal segment (mm.); SW3T: maximum length of spinal wax gland plates on 3rd abdominal tergite (mm.).

Table 15. Measurements of *Pemphigus dorocola* emigrant adult.

Indiv.	BL	FL	Ant.				SRN (l/r)			
			III	IV	V	VI	III	IV	V	VI
1	1.88	0.790	0.315	0.120	0.150	0.180+0.025	16/15	4/5	4/4	4/4
2	2.04	0.765	0.315	0.115	0.145	0.170+0.020	16/14	5/4	3/3	4/4
3	1.96	0.830	0.340	0.130	0.155	0.175+0.030	15/16	4/4	4/3	3/4
4	2.24	0.800	0.300	0.120	0.160	0.190+0.030	13/14	4/5	4/5	6/6
5	2.24	0.745	0.285	0.115	0.145	0.175+0.025	13/15	4/6	5/4	6/5
6	2.28	0.745	0.280	0.110	0.145	0.185+0.025	13/13	5/5	4/4	5/6
7	2.32	0.790	0.300	0.120	0.150	0.190+0.030	13/14	5/5	4/4	5/5
8	2.32	0.780	0.300	0.120	0.150	0.185+0.025	13/13	5/4	4/5	5/4
9	2.32	0.795	0.300	0.130	0.145	0.185+0.030	14/12	5/5	4/5	5/5
10	2.08	0.740	0.300	0.115	0.130	0.170+0.025	14/13	5/4	4/4	6/5

Individual 1–3: Sapporo, Hokkaidô, 30 viii 1972; 4–10: Sapporo, 7 x 1972. BL: length of body (mm.); FL: length of flagellum (mm.); Ant.: length of antennal segment (mm.); SRN (l/r): number of secondary rhinaria on antennal segment (left/right).

Table 16. Measurements of *Pemphigus matsumurai* fundatrix adult.

Indiv.	BL	AL	Ant.				SW3T
			I	II	III	IV	
1	2.64	0.458	00.78	0.100	0.148	0.133	0.060
2	2.52	0.405	0.068	0.085	0.128	0.125	0.065
3	2.76	0.420	0.070	0.090	0.133	0.128	0.068
4	2.36	0.425	0.068	0.098	0.133	0.128	0.053
5	2.80	0.485	0.075	0.093	0.185	0.133	?
6	2.52	0.475	0.073	0.108	0.155	0.140	?
7	3.24	0.545	0.083	0.108	0.200	0.155	?
8	2.88	0.460	0.078	0.103	0.155	0.125	0.070
9	2.44	0.478	0.078	0.100	0.163	0.138	0.050
10	2.64	0.458	0.070	0.098	1.160	0.130	0.055

Individual 1 & 2: Sapporo, Hokkaidô, 11 vi 1972; 3 & 4: Sapporo, 12 vi 1973; 5 & 6: Sapporo, 18 vi 1973; 7–10: Sapporo, 23 vi 1973. BL: length of body (mm.); AL: length of antenna (mm.); Ant.: length of antennal segment (mm.); SW3T: maximum length of spinal wax gland plates on 3rd abdominal tergite (mm.).

Table 17. Measurements of *Pemphigus matsumurai* emigrant adult.

Indiv.	BL	FL	Ant.				SRN (l/r)		
			III	IV	V	VI	III	IV	V
1	2.64	0.760	0.325	0.120	0.135	0.155+0.025	13/11	4/4	3/2
2	2.00	0.695	0.290	0.110	0.125	0.145+0.025	10/12	4/3	3/3
3	2.16	0.715	0.325	0.100	0.125	0.140+0.025	11/9	2/3	3/3
4	2.40	0.695	0.295	0.100	0.125	0.150+0.025	12/10	3/4	3/2
5	1.96	0.610	0.245	0.090	0.115	0.135+0.025	10/10	3/3	3/3
6	2.28	0.750	0.300	0.130	0.135	0.160+0.025	10/10	3/5	4/3
7	2.40	0.755	0.315	0.130	0.130	0.155+0.025	11/11	4/4	2/2
8	2.40	0.750	0.315	0.120	0.130	0.160+0.025	13/11	4/4	2/4
9	2.04	0.660	0.270	0.110	0.120	0.135+0.025	12/8	3/4	2/3
10	1.76	0.635	0.250	0.105	0.115	0.140+0.025	12/10	3/4	2/3

Individual 1–10: Sapporo, Hokkaidô, 4 vii 1972. BL: length of body (mm.); FL: length of flagellum (mm.); Ant.: length of antennal segment (mm.); SRN (l/r): number of secondary rhinaria on antennal segment (left/right).

Table 18. Measurements of *Epipemphigus niisimae* fundatrix adult.

Indiv.	BL	AL	Ant.			
			I	II	III	IV
1	2.52	0.428	0.080	0.083	0.150	0.115
2	2.68	0.418	0.080	0.083	0.130	0.125
3	2.68	0.408	0.080	0.083	0.128	0.118
4	2.28	0.380	0.073	0.075	0.125	0.108
5	2.24	0.363	0.078	0.075	0.105	0.105
6	2.52	0.413	0.078	0.083	0.135	0.118
7	2.20	0.385	0.075	0.075	0.118	0.118
8	2.20	0.385	0.075	0.073	0.125	0.113
9	2.32	0.418	0.075	0.078	0.158	0.108
10	2.12	0.410	0.070	0.070	0.153	0.118

Individual 1: Sapporo, Hokkaidô, 31 v 1973; 2–5: Sapporo, 11 vi 1972; 6–8: Sapporo, 2 vii 1972; 9 & 10: Sapporo, 26 v 1972. BL: length of body (mm.); AL: length of antenna (mm.); Ant.: length of antennal segment (mm.).

Table 19. Measurements of *Epipemphigus niisimae* emigrant adult.

Indiv.	BL	FL	Ant.				SRN (1/r)	
			III	IV	V	VI	III	IV
1	2.40	0.650	0.230	0.115	0.115	0.150+0.040	13/10	4/5
2	2.36	0.640	0.225	0.130	0.100	0.150+0.035	12/10	4/8
3	2.28	0.590	0.200	0.110	0.095	0.150+0.035	12/8(9?)	4/4
4	2.32	0.650	0.220	0.130	0.110	0.160+0.030	8/8	6(7?)/5
5	2.32	0.620	0.195	0.125	0.110	0.160+0.030	8/8	5/3
6	2.28	0.620	0.205	0.125	0.100	0.155+0.035	9/10	6/5
7	2.12	0.665	0.225	0.135	0.115	0.160+0.030	7/8	3/4
8	2.16	0.605	0.200	0.115	0.100	0.150+0.040	13/11	5/5
9	2.28	0.640	0.215	0.140	0.095	0.155+0.035	11/9	6/4
10	2.16	0.595	0.210	0.125	0.090	0.140+0.030	9/7	6/5

Individual 1–3: Sapporo, Hokkaidô, vi 1972; 4–8: Sapporo, 20 vi 1972; 9 & 10: Sapporo, 27 vi 1972. BL: length of body (mm.); FL: length of flagellum (mm.): Ant.: length of antennal segment (mm.); SRN (1/r): number of secondary rhinaria on antennal segment (left/right).

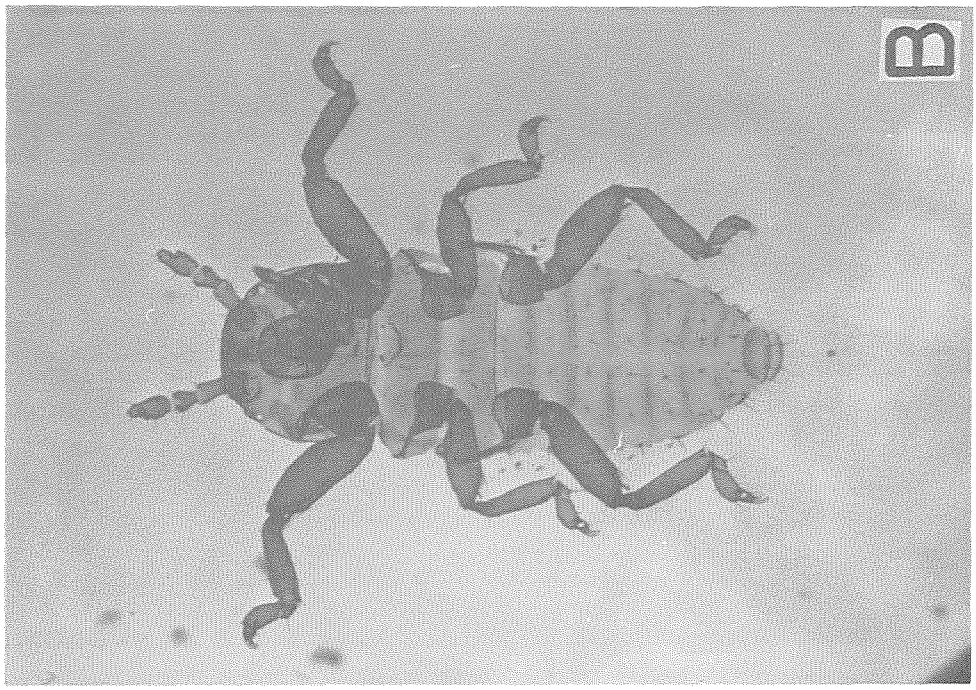
Table 20. Comparison of main characters between *Epipemphigus niisimae* and *Ep. imaicus*.

niisimae	*imaicus*
Emigrant 1st instar larva	
Processus terminalis with 5 setae near apex.	Processus terminalis with 8–10 setae near apex.
Empodial setae sometimes capitate.	Empodial setae always pointed.
Emigrant adult	
Secondary rhinarium always absent on antennal segment V; primary rhinarium on antennal segment V regular in shape.	Secondary rhinaria often present on antennal segment V; primary rhinarium on antennal segment V very irregular in shape.
Processus terminalis with 5 setae near apex.	Processus terminalis with 8–10 setae near apex.
Ultimate rostral segment with rather straight sides.	Ultimate rostral segment with rather convex sides.
Cornicle sclerotized semicircularly.	Cornicle invisible.

PLATES

Plate I

Fig. 21. Fundatrix 1st instar larva.
A: *Pemphigus matsumurai*.
B: *Epipemphigus niisimae*.


B

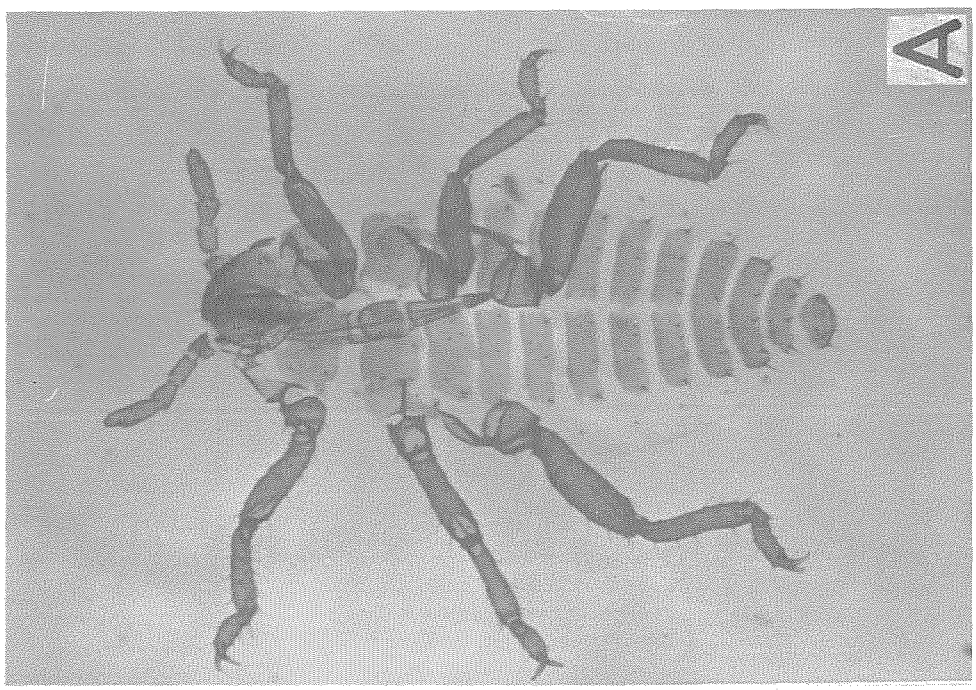

A

Plate II

Fig. 22. Gall.
A: *Pemphigus orientalis* (primary gall).
B: Ditto (secondary gall).
C: *Pemphigus latisensoria* (primary gall).
D: Ditto (secondary gall).

A
B
C
D

Plate III

Fig. 23. Gall.
A: *Pemphigus microsetosus.*
B: *Pemphigus dorocola.*
C: *Pemphigus matsumurai.*
D: *Epipemphigus niisimae.*

C
D
A
B