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Secondary Monoecy of the Gall Aphid *Thecabius populimonilis* (Homoptera)

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Abstract Galls of the aphid *Thecabius populimonilis* were sampled from cottonwoods in Colorado, Utah and Arizona to investigate its life cycles. Both a monoecious and a heteroecious series of generations were found to occur in Colorado. First-instar nymphs deposited by emigrants were very similar to those of the sexuparous generation produced on the primary host, especially in having a characteristic set of wax plates on the abdominal tergites. This corroborated the generation-packing hypothesis that the monoecious series of generations was secondarily derived from the heteroecious series through the packing of the sexuparous generation into the gall. Further studies will be necessary to determine whether aphids exhibiting the two life cycles belong to the same or different species.

Key words: aphid; gall; host alternation; life cycle; *Populus*; *Thecabius*.

Introduction

Most species of the gall-forming aphid subfamilies Pemphiginae and Hormaphidinae have heteroecious (host-alternating) life cycles. They migrate between (woody) primary hostplants, on which they form galls, and (mainly herbaceous) secondary hostplants. Monoecious (non-host-alternating) life cycles on the primary host (with sex) occur only sporadically among them (Blackman &

EASTOP, 1994), suggesting that most of these monoecious life cycles have been secondarily derived from heteroecious life cycles. The minority of monoecious life cycles may be due in part to the fact that evolution from heteroecy to monoecy on the primary host is not an easy process for gall-forming aphids. The "generation-packing (GP)" model by AOKI and KUROSU (1986, 1988) is an attempt to explain how such evolution occurred.

According to the GP model, a monoecious life cycle will result, if emigrants (alates migrating from the primary host to the secondary host) lay nymphs in the gall instead of on the secondary host, and if the nymphs grow to alate sexuparae. (It is also assumed that the emigrants later lose wings and become apterae.) If this happens in one of those related species whose primary-host generations are well differentiated from the secondary-host generations in morphology, the sexuparous generation of the monoecious species will resemble the secondary-host generations of the related species, rather than the gall generation of the own species. AOKI and KUROSU (1986, 1988) showed that this is true for *Pemphigus spyrothecae* PASSERINI and *P. monophagus* MAXSON.

Thecabius populimonilis (RILEY) is an allegedly monoecious species on the cottonwood *Populus angustifolia* (RILEY & MONELL, 1879; GILLETTE, 1913). The taxonomic position of this species has not yet been definitely settled. RILEY and MONELL (1879) and PATCH (1913) placed the species in the genus *Pemphigus*, but later authors transferred it to the genus *Thecabius* (GILLETTE, 1913; GILLETTE & PALMER, 1934; HARPER, 1959; BLACKMAN & EASTOP, 1994) or *Parathecabius* (SMITH, 1974). Although the species differs from the other species of the three genera in that more than two gall-forming generations occur on the primary host, there is little doubt that it belongs to the clade *Pemphigus*+*Parathecabius*+*Thecabius*. The heteroecious species belonging to the clade, as well as species of *Pachypappa* and its related genera, produce, on the secondary host, apterae and nymphs which have a characteristic set of wax plates on the third to seventh abdominal tergites. Each wax plate consists of small, roundish cells, each of which has a kernel-like dark spot (ZWÖLFER, 1957). This type of wax plates never appears on aphids of the primary-host generations of heteroecious species (AOKI & KUROSU, 1986). We can therefore safely conclude that the monoecious life cycle of *Thecabius populimonilis* was secondarily derived from a heteroecious life cycle if the sexuparous generation shows this type of wax plates. One purpose of this paper is to examine whether this is the case.

As will be mentioned below, GILLETTE (1913) showed that a monoecious series of generations occurs in *T. populimonilis* in Colorado. However, LANGE (1943) briefly remarked that the species is heteroecious in California, and that *Salix* sp. is a secondary host (the roots are infested with the aphids). If true, then it will follow that the species has both monoecious and heteroecious life cycles, and we will be able to compare the sexuparous generation produced on the primary host with the secondary-host generation within a single species. This prompted us to study *T. populimonilis.*

Previously Known Life Cycles

GILLETTE (1913) studied *T. populimonilis* in Colorado. The life cycle elucidated by him is summarized as follows (see Fig. 1): The fundatrix appears in June and forms an almond-shaped gall on a leaf of a young tree of *Populus angustifolia.* She produces 1st-instar nymphs in the gall. The 1st-instar nymphs leave the maternal gall and each of them forms a similar gall on newly-developed leaves. Many galls are formed on a leaf, and they look just like beads. The nymphs grow either to large apterae which are light cinnamon brown in color (referred here to as "large apterae") or to alates. The large apterae then produce 1st-instar nymphs like their own, which disperse to other leaves and form galls. GILLETTE (1913) was not able to adequately explain the function of the alates. He suggested that they might fly to other trees of *P. angustifolia* (but see BLACKMAN & EASTOP, 1994). Note that early in the season each aphid forms a gall. Later in the season, from August on, orange-colored apterae (referred to as "late-summer apterae"), which are much smaller than large apterae, appear. They produce, in the gall, 1st-instar nymphs of the sexuparous generation. In contrast with the nymphs produced by the fundatrix and by large apterae, they remain in the maternal gall until they become adult winged sexuparae. The sexuparae produce males and oviparous females, which mate and deposit overwintering eggs.

On the other hand, LANGE (1943) showed few data supporting his hypothesis that the species is heteroecious in California. He found apterous aphids (including wingpadded nymphs) of presumed *T. populimonilis* from roots of *Salix* sp. along the banks of the Arroyo Seco River in Monterey County. He also found galls of *T. populimonilis* on *Populus* spp. at Gonzales, which is not far from the Arroyo Seco locality. No description of the root aphids was given in his paper.

Materials and Methods

Many galls of *T. populimonilis* were sampled from a few small trees of *Populus angustifolia* at Pine (Colorado, 6900 ft. alt.) and at Deckers (Co., 6600 ft. alt.) on 26 August 1994, and along Little Thumpson Creek (Co., 7800 ft. alt.) on 31 August 1994. They were immediately submerged in 80% ethanol. Many galls were also found on a few small trees of *P. angustifolia* near Jacks Cabin (Co., 8400 ft. alt.) on 29 August 1994, but owing to heavy predation and parasitism only 20 galls with live aphids (referred to as "live galls") were

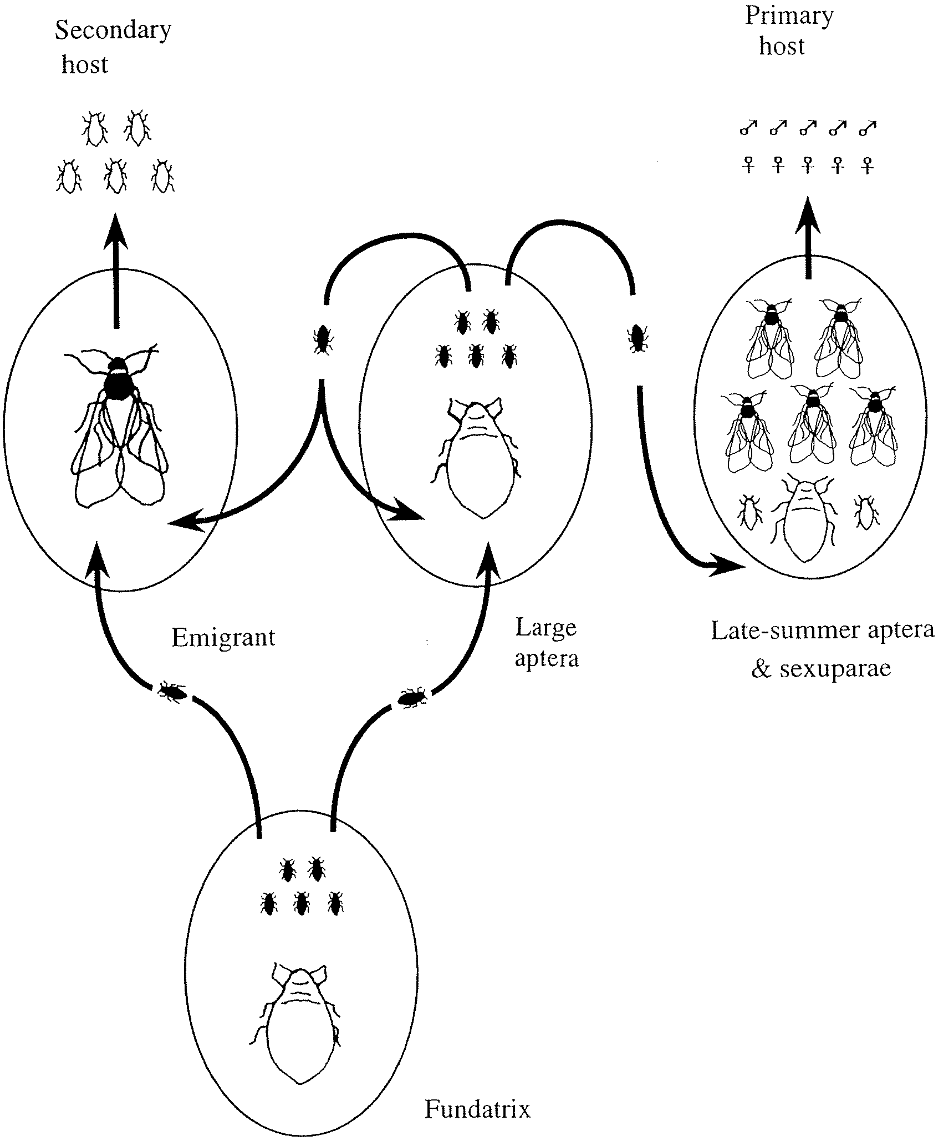

Fig. 1. Life cycle of *Thecabius populimonilis*. Small aphids indicated by black are 1st-instar gall-formers, and those indicated by white are 1st-instar nymphs to be sexuparae and 1st-instar nymphs of the secondary-host generation. The GP hypothesis predicts similarity between the last two (see text). It is not shown in the figure but assumed that alate sexuparae are also produced on the secondary host and fly to the primary host. Late-summer apterae may produce some 1st-instar gall formers in addition to nymphs to be sexuparae.

collected.

We sampled a total of 423 live galls of *T. populimonilis* from several trees of *Populus fremontii* at Patagonia, Santa Cruz County, Arizona, 10 times from 6 August 1991 to 2 November 1991. Additional 123 live galls were collected from *P. fremontii* at Patagonia on 3 September 1994, and at Modera, Pima County, Arizona, on 21 July 1991 and on 4 September 1994. We also sampled a total of 87 live galls of *T. populimonilis* from *P. angustifolia* in Utah: at City Creek Canyon, Salt Lake City, on 14 June 1993, 16 July, 20 July and 1 August 1992, at Red Butte Canyon, Salt Lake City, on 8 July 1992, at Lamb's Canyon, Wasatch Mountains, on 8 July 1992, and at Beaver Creek near Kamas, Unita Mountains, on 11 August 1992.

They were dissected to examine whether sexuparae are produced on the primary host. Three non-sexuparous alates collected near Jacks Cabin and 21 collected at Patagonia were confined in glass vials to obtain their 1st-instar offspring.

Almost all adult sexuparae (164 in total) contained in undamaged galls were dissected to investigate sex ratio. Female embryos were much larger than male embryos, and thereby they could be easily sexed. Twenty female embryos and 20 male embryos were placed on slide glasses and the length and width were quickly measured under a light microscope. Fourteen non-sexuparous alates collected in Utah were also dissected to count the number of embryos.

Many aphids from the samples were heated in 10% KOH solution, stained with Evans' blue, and mounted in balsam. Some were mounted in gum-chloral without being stained. These slide-mounted specimens were examined under a differential interference microscope. In particular, late-summer apterae were carefully mounted to know whether their embryos would be of the sexuparous 1st-instar nymph or of the gall-former. However, most late-summer apterae had already laid all their offspring, and we were able to examine only 23 embryos in 15 late-summer apterae.

Results

1. Galls collected in Utah and Arizona, and near Jacks Cabin

All live galls collected in Utah and Arizona and near Jacks Cabin, Colorado, contained either a single aphid or a large apterous adult (or a fundatrix) with her 1st-instar offspring. No gall was found containing more than one non-1st-instar aphid. The morphology of the 1st-instar offspring (Fig. 2A) accorded with that of 1st-instar cast-off skins found in the galls occupied by a single aphid.

Alates were found from galls collected at Patagonia and Modera from 18 August to 2 November, those collected in Utah from 8 July to 11 August, and those collected near Jacks Cabin. All (63) alates contained rostrate embryos. The number of embryos for 14 alates collected in Utah was 56.21±4.01 (mean ±SE) (range 27–80). Four galls containing a fundatrix with her 1st-instar offspring were collected in Utah on 14 June. No sexuparae or late-summer apterae were found.

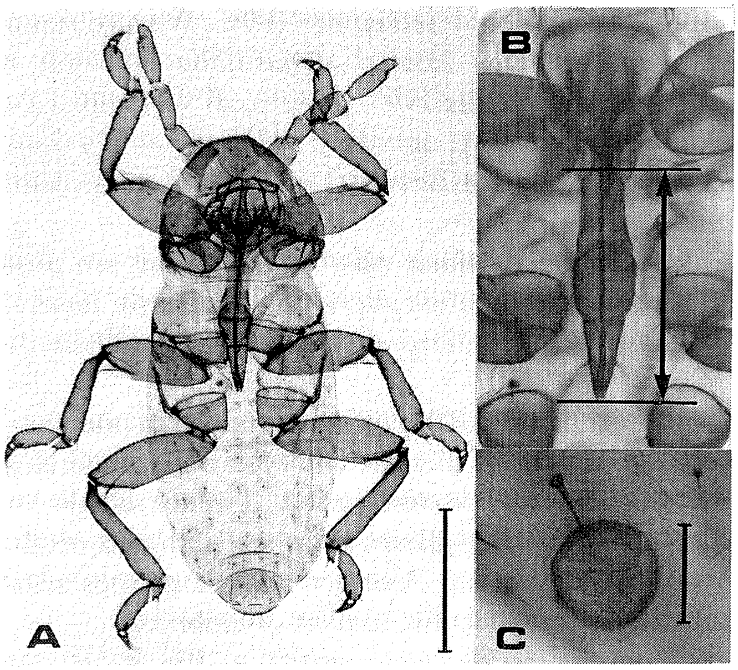

Fig. 2. A, First-instar gall-former; B, rostrum of another individual, defining the length of the apical three segments; C, an abdominal wax plate of late-summer aptera. Scales: 0.2 mm (A) and 0.04 mm (C).

2. *Galls collected in Colorado (except near Jacks Cabin)*

Galls collected at Pine and Deckers and along Little Thumpson Creek were heavily damaged by predators including immatures of a chamaemyiid, a syrphid, an anthocorid and a tortricid. Of 332 galls sampled, 47.3% were damaged by them, and 68.8% of the damaged galls contained a chamaemyiid larva.

All (175) undamaged galls contained a small, orange-colored, late-summer aptera and/or aphids of the sexuparous generation (alate sexuparae or sexuparae-to-be). Twenty-six of the undamaged galls contained adult sexuparae. Fourteen undamaged galls contained no late-summer aptera; 12 of them contained 2–12 alate sexuparae, and the remaining two contained several 4th-instar nymphs. There is little doubt that the late-summer aptera had died and had fallen off these galls. One, two and 17 of the undamaged galls collected at Pine, at Deckers and along Little Thumpson Creek, respectively, contained an immature late-summer aptera, and the youngest immature was 2nd-instar (collected along Little Thumpson Creek). No undamaged gall contained more than one (non-1st-instar) late-summer aptera, indicating that each gall is formed by a single individual. Sixty seven galls contained a late-summer aptera with her offspring which included neither adults nor 1st-instar nymphs. Because it is likely that from such a gall no alate had yet escaped and that the aptera had already ceased larviposition, the number of nymphs in it probably indicates the exact brood size.

The average number±SE of offspring for these galls was 12.61±0.29 (range 8–21).

3. *Morphology of 1st-instar nymphs and late-summer apterae*

A) First-instar nymphs produced by large apterae (Fig. 2A). The following description is based on 10 well-mounted specimens collected in Utah on 14 June 1993 and 19 June 1986. Body 0.60–0.68 (mean 0.65) mm long, without wax plates. Legs dusky. Rostrum not extending beyond hind coxae, the apical 3 segments together (defined in Fig. 2B) 0.160–0.184 (0.171) mm long; ultimate rostral segment conical, 0.060–0.070 (0.066) mm long. Hind femorotrochanter 0.168–0.188 (0.178) mm long. Empodial setae capitate, extending beyond the apices of claws. Abdominal tergites with sclerites around setae, without cornicles.

There is no doubt that nymphs of this type are gall-formers (referred to as "1st-instar gall-formers" or simply as "gall-formers") and become large apterae, non-sexuparous alates and late-summer apterae. Wax plates (see Fig. 2C) appear after the first molt. The morphology of cast-off skins found in galls containing a late-summer aptera also accorded with that of the nymphs.

B) First-instar nymphs deposited by non-sexuparous alates (Fig. 3A).

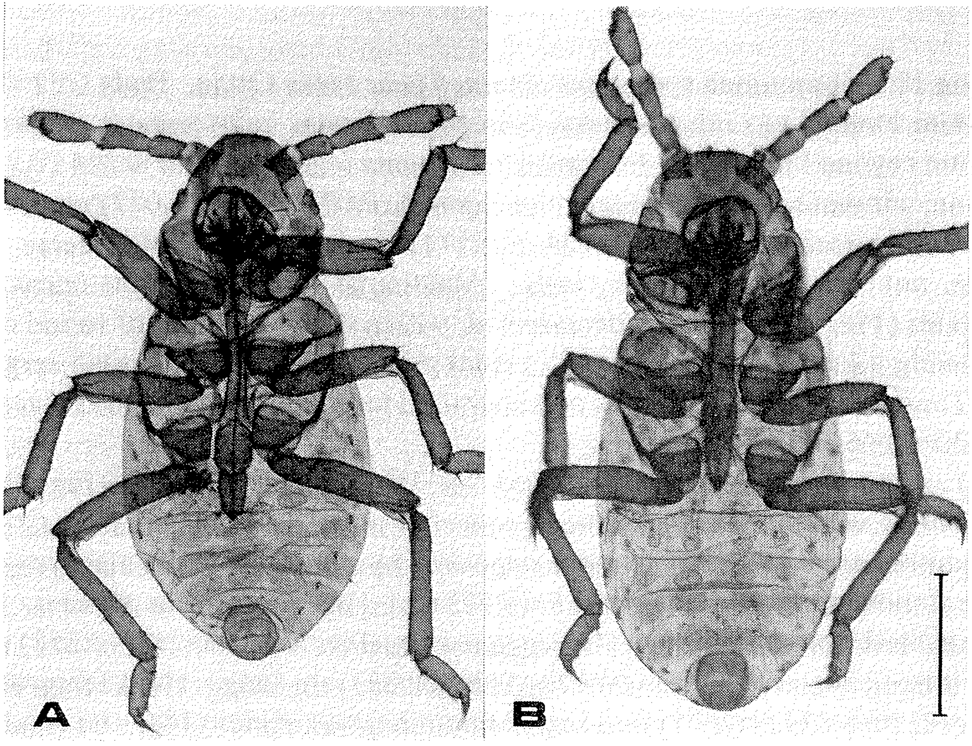

Fig. 3. First-instar nymph deposited by emigrant (A) and 1st-instar sexupara produced in gall (B). Scale: 0.2 mm.

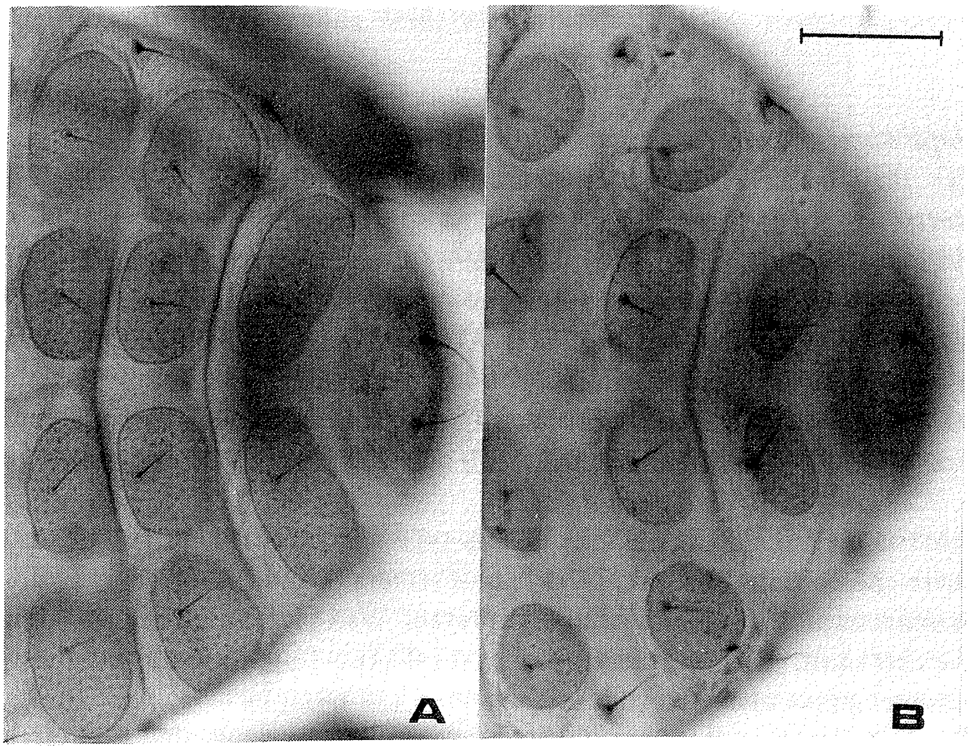

Fig. 4. Abdominal wax plates of 1st-instar nymph deposited by emigrant (A) and of 1st-instar sexupara produced in gall (B). Scale: 0.05 mm.

Based on 10 well-mounted specimens obtained near Jacks Cabin. Body 0.72–0.79 (0.74) mm long. Legs not so dusky as in the 1st-instar gall-formers. Rostrum extending beyond hind coxae, the apical 3 segments together 0.280–0.304 (0.292) mm long; ultimate rostral segment not conical, 0.074–0.080 (0.077) mm long. Hind femorotrochanter 0.208–0.224 (0.217) mm long. Empodial setae not capitate, not reaching apices of claws. Abdominal tergites without cornicles. Wax plates (Fig. 4A) distinctly demarcated, with a seta, composed of round cells each having a kernel-like dark spot; a spinal pair of rows on abdominal tergites III–VII and a pleural pair of rows on abdominal tergites III–VI; pleural plate on III 0.030–0.046 (0.041) mm wide.

C) First-instar nymphs produced by late-summer apterae (Fig. 3B). Based on 10 well-mounted specimens collected along Little Thumpson Creek. Very similar to the 1st-instar nymphs deposited by non-sexuparous alates except for the following: Body 0.74–0.83 (0.78) mm long. Rostrum shorter, just reaching hind coxae, the apical 3 segments together 0.236–0.260 (0.252) mm long; ultimate rostral segment 0.078–0.086 (0.083) mm long. Hind femorotrochanter 0.196–0.224 (0.207) mm long. Abdominal wax plates (Fig. 4B) smaller; pleural plate on tergite III 0.012–0.024 (0.019) mm wide.

Wax plates of the same type appear until the final molt.

D) Late-summer apterae. Based on 10 well-mounted specimens collected at Deckers and along Little Thumpson Creek. Body 1.51–1.92 (1.68) mm long. Hind femorotrochanter 0.35–0.45 (0.40) mm long. Wax plates (Fig. 1C) composed of polygonal cells without central kernel-like structure, appearing on head, all thoracic tergites and 1st to 8th abdominal tergites. Rostrum reaching middle coxae. Cornicle absent.

4. *Embryos remaining in late-summer apterae*

Of 23 embryos in 15 late-summer apterae examined, 17 were of the sexuparous 1st-instar nymph and the remaining six were of the gall-former. It was easy to discriminate between the two, because the former had short, normal empodial setae while the latter had long, capitate empodial setae (Section 3). One aptera contained embryos of both types.

We found two undamaged galls in which an adult late-summer aptera coexisted with her offspring and one or two 1st-instar gall-formers. It is not certain whether these 1st-instar gall-formers were born in the gall or invaders (see the next section).

5. *Dead 1st-instar gall-formers*

We noticed that galls of *T. populimonilis* sampled at Pine and Deckers and along Little Thumpson Creek often contained a dead 1st-instar gall-former. Of 59 undamaged galls collected from a heavily infested tree along Little Thumpson Creek, 33 or 55.9% contained one dead 1st-instar gall-former or more (up to nine). The average number for the 59 galls was 1.15. This suggests that lethal fighting occurs between 1st-instar gall-formers of *T. populimonilis.* Lethal fighting is known to occur among 1st-instar fundatrices of the gall aphid *Epipemphigus niisimae* (MATSUMURA) (AOKI & MAKINO, 1982) and among non-fundatrix gall-formers of *Smynthurodes betae* WESTWOOD (INBAR, in prep.). In the latter case, INBAR (in prep.) showed that the adult gall owner can kill 1st-instar invaders.

6. *Sex ratio*

The overall numerical sex ratio (no. of male embryos/no. of embryos) was 0.47. The mean length and width (in mm) of 20 male embryos were 0.55 and 0.25, respectively, and of 20 female embryos 0.79 and 0.42. Assuming the embryos to be prolate ellipsoids, the volume ratio was approximately 1 : 4.03. The investment ratio calculated from the volume ratio was 0.18. This female-biased sex ratio suggests the occurrence of a strong local mate competition (HAMILTON, 1967). The number of male embryos in a sexupara was 4.37±1.48 (mean±SD) (range 1–8), while that of female embryos was 4.95±1.55 (1–9). Since the C.V. of the former (34%) is not smaller than that of the latter (31%), the result does not accord with the prediction from YAMAGUCHI's (1985) ESS model that the number of males is constant. Only one gall (collected at Pine) contained sexuparae with a constant number of male embryos (10 sexuparae with 4 males).

Discussion

1. Heteroecious life cycle

All live galls collected in Arizona and Utah and near Jacks Cabin, Colorado, contained a large aptera (or a fundatrix) with her 1st-instar offspring or an alate or an immature. The alates contained rostrate embryos. The 1st-instar nymphs (Fig. 3A) laid by the alates showed morphology typical of the secondary-host generation of *Pemphigus.* They closely resembled 1st-instar nymphs of *Pemphigus saliciradicis* (BÖRNER) collected from roots of *Salix* sp. in Japan in the shape of the ultimate rostral segment, tarsi and antennae (see AOKI, 1975). This confirmed LANGE's (1943) assertion that *T. populimonilis* is a host-alternating species, but whether *Salix* spp. are really its secondary hosts remains to be demonstrated through, say, a transfer experiment.

Near Jacks Cabin and at Patagonia, alate emigrants were collected even near the end of season (on 29 August near Jacks Cabin and on 2 November at Patagonia). It is quite unlikely that offspring of these emigrants would return to the cottonwood within the season. Hibernation on the secondary host therefore probably occurs.

2. Monoecious life cycle

Galls collected at Pine and Deckers and along Little Thumpson Creek, on the other hand, contained many aphids of the sexuparous generation. This confirmed GILLETTE's (1913) observations in general, although his suggestion that alates produced early in the season fly to other cottonwoods is untenable. He also suggests that late-summer apterae may produce some gall-forming 1st-instar aphids. We confirmed this suggestion. However, how frequently this occurs remains to be investigated.

3. Secondary monoecy of T. populimonilis

As described before, the 1st-instar nymphs produced by late-summer apterae closely resembled those deposited by emigrants (Fig. 3). Both had a set of wax plates characteristic of the secondary-host generation (Fig. 4). This close resemblance corroborated the generation-packing hypothesis that the monoecious life cycle of *T. populimonilis* was derived from the heteroecious life cycle through the packing of the sexuparous generation into the gall (see Introduction). The GP hypothesis can explain why sexuparous 1st-instar nymphs (sexuparae-to-be) remain in their maternal gall and do not form galls by themselves as 1st-instar nymphs produced by large apterae do. They do not have the ability to induce galls because they *were* of the secondary-host generation when the life cycle was obligately host-alternating. An alternative hypothesis may be that sexuparous 1st-instar nymphs do not form galls because new leaves are not available for gall formation. However, GILLETTE (1913) observed that some new galls were formed when sexuparous 1st-instar nymphs were being produced. (*T. populimonilis* prefers young trees which continue to develop shoots until autumn.) In addition, we found that at least some late-summer apterae produce sexuparous 1st-instar nymphs and gall-formers at the same time. This hypothesis is therefore unlikely.

The GP hypothesis implies that late-summer apterae were transformed from emigrants. It follows that this transformation entailed a great (ca. 3/4) reduction in the number of embryos. Gall-living sexuparous 1st-instar nymphs have also been modified to some extent; the rostrum has been shortened, presumably as an adaptation to the gall life.

In order to explain the production of gall-formers by late-summer apterae, we need an auxiliary hypothesis that late-summer apterae later acquired the ability to produce some gall-formers in addition to sexuparous 1st-instar nymphs. Such a mutation seems not rare among aphids (see AOKI & KUROSU, 1986). AOKI and KUROSU (1986) introduced a similar auxiliary hypothesis to explain the evolution of monoecy in *Pemphigus spyrothecae.*

4. Is Thecabius populimonilis a single species?

A defect of the present study is our failure to determine whether single clones of *T. populimonilis* in Colorado can produce both emigrants and sexuparae. GILLETTE (1913) thought that they do, but one suspects that he observed two species: a heteroecious and a monoecious species. Here we argue that gene flow between the monoecious and heteroecious series of generations probably occurs, on an admittedly tenuous ground. If gene flow did not occur, then the sex ratio of monoecious populations would become an ESS, as in the monoecious aphid *Pemphigus spyrothecae*, where the number of males in a sexupara is almost always two (FOSTER & BENTON, 1992). The fact that the number of males is not constant in *T. populimonilis* suggests that some sexuparae from the secondary host may join the sex ratio game (cf. KUROSU & AOKI, 1991). Further studies of genetic markers in these aphids could test this hypothesis.

Acknowledgments

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