

Revision of the Japanese Species of the Aphid Genus *Hamamelistes* (Hemiptera, Aphididae, Hormaphidinae) Based on the Mitochondrial DNA Sequence Data

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Abstract. Aphids of the genus *Hamamelistes* host-alternate between *Hamamelis* (the primary host) and *Betula* (the secondary host). The taxonomy of the Japanese species has been in a mess. Eight different names have been used for them, and no combination between the primary- and secondary-host generations has been established. By sequencing their mitochondrial COII genes, we made it clear that three species occur in Japan: *Hamamelistes miyabei* (Matsumura) on *Hamamelis japonica* and *Betula maximowicziana*, *Hamamelistes kagamii* (Monzen) on *H. japonica* and *B. grossa*, and *Hamamelistes betulinus* (Horvath) on *H. japonica*, *B. platyphylla*, *B. davurica* and probably also on *B. ermanii*. The life cycles of the three species are reviewed, and synonyms are listed under the valid names.

Key words: Aphid, *Betula*, gall, *Hamamelis*, *Hamamelistes*, mitochondrial DNA, molecular taxonomy.

Introduction

The aphid tribe Hormaphidini (Hormaphidinae) consists of only two genera, *Hormaphis* and *Hamamelistes*. Species of both genera basically migrate between *Hamamelis*, their primary host, and *Betula*, their secondary hosts. While *Betula* is widely distributed in the Holarctic region, *Hamamelis* is disjunctly distributed in eastern Asia (China and Japan) and eastern North America (Wen & Shi, 1999). The genus *Hormaphis* contains one Eurasian species (*H. betulae*) and two North American species (*H. cornu* & *H. hamamelidis*), whose life cycles are now well known (Pergande, 1901; von Dohlen & Gill, 1989; von Dohlen & Stoetzel, 1991; Aoki & Kurosu, 1991). The genus *Hamamelistes* contains one North American species (*H. spinosus*)¹ and a few Eurasian species (Blackman & Eastop, 1994). Pergande (1901) showed that *H. spinosus*, a North American species, migrates between *Hamamelis virginiana* and *Betula*

nigra. It took him more than 20 years to confirm the host alternation. The taxonomy of Eurasian species has been badly confused. The primary-host generations of Eurasian species have hitherto been recorded only from the Japanese witchhazel, *Hamamelis japonica*. Galls of two types have been found on *H. japonica*, and the aphids have been referred to as *Hamamelistes miyabei* and *H. kagamii*. On the secondary host, *Betula* spp., at least two distinct species occur, but they have been reported under four species names (*H. betulinus*, *shirakabae*, *gibberi* & *cristafoliae*), one subspecies name (*H. betulinus makabae*) and one race name (*H. gibberi* biological race *grossae*). No combination between the primary-host and the secondary-host generations has been proposed except Mordvilko's (1935) erroneous union between *H. betulinus* and *H. miyabei*. The confusion of taxonomy is in part due to the fact that the aphids are not very distinct in morphology from each other (Blackman & Eastop, 1994). In addition, it is not easy to carry out a transfer experiment from *Hamamelis* to *Betula* or vice versa because of their two-year life cycles. In either case, a researcher has to wait for more than half a year to know whether the transfer experiment is successful or not.

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¹ There is another anholocyclic "species" on *Betula* in North America, which is closely related to *H. spinosus* (von Dohlen, unpubl.).

To determine how many species of *Hamamelistes* occur on *Hamamelis* and *Betula* in Japan, and to establish the combination between the generations on the primary and secondary hosts, we sampled aphids from both hosts and sequenced their mitochondrial DNA. As will be shown, there occur three host-alternating species in Japan.

Materials and Methods

1. General account of the life cycle

The following account of the life cycle of the genus *Hamamelistes* is mainly based on Pergande's (1901) and von Dohlen's (1991) work on *H. spinosus*, but it also applies to the Japanese species mentioned in this paper.

The 1st-instar fundatrix of *Hamamelistes* hatches in late spring or early summer and transforms a bud of *Hamamelis* into a pouch gall. She becomes an apterous adult that produces 2nd-generation aphids in the gall. The offspring all become alates and migrate to the secondary host, *Betula*. The 1st-instar nymphs produced by the alates are coccidiform (oval and flattened) with long stylets, and settle on twigs of the birch, but do not grow until the following spring. In early spring the overwintered nymphs become sessile apterous adults and produce many nymphs of the 2nd generation on the birch, which crawl to the underside of unfolding leaves and transform the leaves into blister-like galls. The 2nd-generation nymphs become apterous adults. The apterous adults on the leaf produce "normal" nymphs that grow either to apterous adults like those of the 2nd generation or to alates,

and also may produce coccidiform nymphs that overwinter on the birch. The alates are sexuparae that fly to *Hamamelis* and produce 1st-instar sexuals on the leaves. The sexuals mature and lay eggs, which do not hatch until the following year. In some locations, anholocyclic ("incomplete") derivative life cycles exist, in which alates on birch are secondary migrants that fly to other trees of *Betula*, and produce coccidiform nymphs that hibernate there. In both types of life cycles, the aphids could persist indefinitely on *Betula* without returning to *Hamamelis*.

2. Materials for DNA sequencing

Aphids from *Hamamelis*: Spiny galls of *Hamamelistes miyabei* and irregular pouch galls of *H. kagamii* were found on *Hamamelis japonica* at the Shomaru Pass, Saitama Pref., and Masutomi, Yamanashi Pref., Japan. Some aphids in the galls were deposited in nearly pure ethanol for DNA extraction and the remaining aphids were preserved in 80% ethanol for voucher specimens. All galls of *H. miyabei* we found were formed at the position of lateral leaf buds. On the other hand, while some galls of *H. kagamii* were formed on lateral buds, some were on flower buds. We sampled aphids from both gall types to determine whether these galls were formed by a single species, or two. At Temmabayashi, Aomori Pref., northern Japan, we found another type of galls formed on *Hamamelis japonica* at the position of flower buds, which were similar to those of *H. kagamii* but differed from the latter in having more ramified projections. We also sampled aphids from these galls. In addition, a sample of *Hamamelistes spinosus* was collected from *Hamam-*

Table 1. Insect materials used for DNA extraction.

Sample no.	Species	Host	Part	Locality	Date	Accession no.
12	<i>H. miyabei</i>	<i>H. japonica</i>	leaf bud gall	Masutomi	17 Jul. 1998	AF328771
8	<i>H. kagamii</i>	<i>H. japonica</i>	flower bud gall	Masutomi	17 Jul. 1998	AF328772
6	<i>H. kagamii</i>	<i>H. japonica</i>	leaf bud gall	Shomaru Pass	8 Jul. 1999	AF328773
7	<i>H. kagamii</i>	<i>H. japonica</i>	flower bud gall	Shomaru Pass	8 Jul. 1999	AF328774
4	<i>H. sp. A</i>	<i>H. japonica</i>	flower bud gall	Temmabayashi	7 Aug. 1998	AF328775
15	<i>H. spinosus</i>	<i>H. virginiana</i>	flower bud gall	Washington, DC	May 1993	AF328783
9	<i>H. cristifoliae</i>	<i>B. maximowicziana</i>	twig*	Sapporo	5 Sep. 1998	AF328776
10	<i>H. cristifoliae</i>	<i>B. maximowicziana</i>	leaf gall	Mt. Akagi	25 May 1999	AF328777
11	<i>H. cristifoliae</i>	<i>B. maximowicziana</i>	leaf gall	Sapporo	15 June 1999	AF328778
5	<i>H. gibberi</i> biol. race <i>grossae</i>	<i>B. grossa</i>	leaf blister gall	Sanjonoyu	20 May 1999	AF328779
1	<i>H. betulinus</i>	<i>B. platyphylla</i>	leaf blister gall	Okutamako	20 May 1999	AF328780
2	<i>H. betulinus</i>	<i>B. platyphylla</i>	leaf blister gall	Sapporo	15 June 1999	AF328781
3	<i>H. sp. B</i>	<i>B. davurica</i>	leaf blister gall	Masutomi	17 Jul. 1998	AF328782

*Coccidiform 1st-instar nymphs

elis virginiana in the U.S.A.

Aphids from *Betula*: Aphids of *Hamamelistes* were sampled from the following *Betula* species in Japan: *B. maximowicziana*, *B. platyphylla*, *B. davurica* and *B. grossa*.

3. DNA sequencing

The samples from which DNA was extracted are listed in Table 1. For each sample, total DNA was prepared from one or a few aphids from the same gall, by a protein salting-out method (Sunnucks & Hales, 1996). The mitochondrial cytochrome oxidase II gene was amplified by PCR with primers 2993+ (Stern, 1994) and A3772 ("Eva") (Normark, 1996). We sequenced 757 nucleotides of this region with an ABI 377 automated sequencer. Pairwise, absolute distances were calculated with PAUP* (version 4.0b4a; Swofford, 1998). The sequence data can be obtained from C.D.V.D. or from Gen Bank (accessions AF 328771-83).

4. Other materials and field observations

The collection data of other aphid materials and the date and place of our field observations will be described in the section for each species. Many aphids from the samples were boiled in 10% KOH solution, stained with Evans' blue or acid fuchsin, and mounted in balsam, and the slide-mounted specimens were examined under a light microscope. In particular, we measured the width of the 2nd segment of a hind tarsus at the middle and the length of the longer seta on the 1st segment to the nearest 0.002 mm for 23 gall-living 1st-instar nymphs collected from *Betula grossa*, 20 from *B. platyphylla*, six from *B. davurica*, and six from *B. ermanii*.

Results and Discussion

An absolute distance matrix based on the mtCOII gene sequences among 13 samples is shown in Table 2. The samples of Japanese *Hamamelistes* species formed three distinct groups: 1) *Hamamelistes miyabei* and *H. cristafoliae*, 2) *H. kagamii* and *H. gibberi* biological race *grossae*, and 3) *H. sp. A*, *H. betulinus* and *H. sp. B*. Within each group, there was found no or only one nucleotide substitution. There is no doubt that the samples contained three distinct species, whose nomenclature and biology are treated below:

1. *Hamamelistes miyabei* (Matsumura)

Mansakia miyabei Matsumura, 1917 [original description]; Monzen, 1929 [redescription], 1954 [short redescription]; Sorin, 1977 [brief comment, photo of gall, and the illustration of the antenna of alate and the coccidiform nymph].

Hamamelistes betulinus miyabei: Mordvilko, 1935 [proposal of the combination].

Hamamelistes miyabei: Blackman & Eastop, 1994 [brief comment]; Kurosu & Aoki, 1991 [brief comment on gall-cleaning behavior]; Yukawa & Masuda, 1996 [photo of gall].

Hamamelistes cristafoliae Monzen, 1954 [original description]; Blackman & Eastop, 1994 [brief comment]; Akimoto *et al.*, 1996 [defensive behavior and life cycle on *Betula*].

Mansakia betulina makabae Inouye, 1963 [original description].

Gall on *Hamamelis*

The gall of *Hamamelistes miyabei* on *Hamamelis japonica* (Fig. 1A) is similar to that of the North

Table 2. Distance matrix of pairwise, absolute substitution differences in the mitochondrial COII gene (757 bases) for 13 samples of *Hamamelistes* spp.

Sample no.	1	2	3	4	5	6	7	8	9	10	11	12	15
1. <i>betulinus</i>	—												
2. <i>betulinus</i>	0	—											
3. sp. B	1	1	—										
4. sp. A	0	0	1	—									
5. <i>grossae</i>	20	20	19	20	—								
6. <i>kagamii</i>	19	19	18	19	1	—							
7. <i>kagamii</i>	19	19	18	19	1	0	—						
8. <i>kagamii</i>	19	19	18	19	1	0	0	—					
9. <i>cristafoliae</i>	46	46	47	46	44	45	45	45	—				
10. <i>cristafoliae</i>	46	46	47	46	44	45	45	45	0	—			
11. <i>cristafoliae</i>	46	46	47	46	44	45	45	45	0	0	—		
12. <i>miyabei</i>	46	46	47	46	44	45	45	45	0	0	0	—	
15. <i>spinus</i>	58	58	59	58	56	57	57	57	58	58	58	58	—

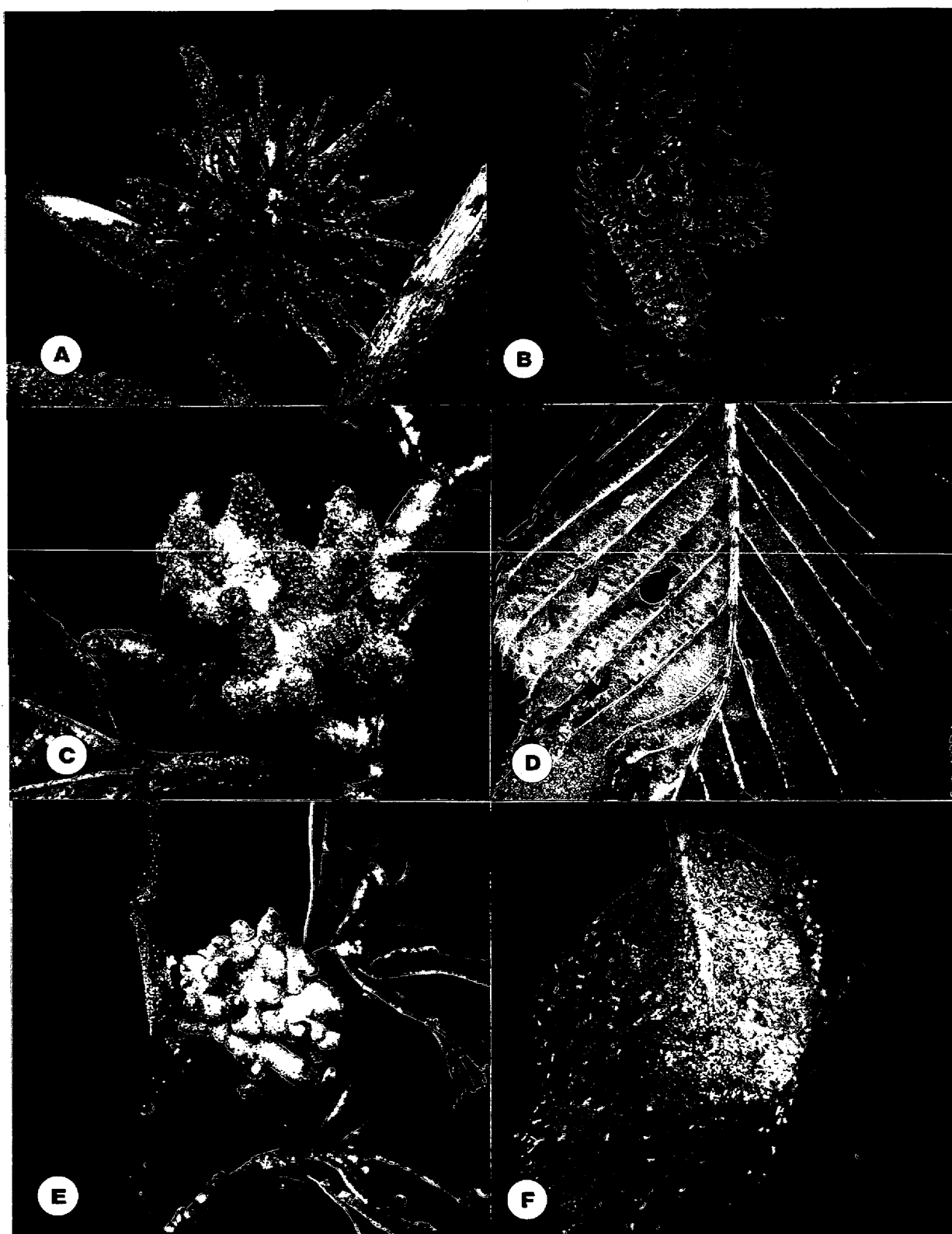


Fig. 1. Galls of *Hamamelistes* species: A, spiny gall of *H. miyabei* on *Hamamelis japonica*; B, cockscomb-like gall of *H. miyabei* on *Betula maximowicziana*; C, irregular pouch-like gall of *H. kagamii* on *H. japonica*; D, blister-like gall of *H. kagamii* on *B. grossa* (from underside); E, coral-like gall of *H. betulinus* on *H. japonica*; F, blister-like gall of *H. betulinus* on *B. platyphylla* (from underside).

American *Hamamelistes spinosus* both in appearance and structure (cf. Pergande, 1901). The gall has many spine-like hairs on the surface. The wall is thick and the cavity is spherical. When the gall matures, an ostiole opens at the base, through which alates escape and honeydew is pushed out of the gall. All galls we found were formed at the position of lateral leaf buds, unlike *H. spinosus*, which transforms flower buds into the spiny galls.

Gall on *Betula*

The gall of *H. miyabei* on *Betula maximowicziana* (Fig. 1B) can easily be distinguished from those of the other species on other birches. The leaf infested with the aphids is distinctly protruded on the upper surface, and the galls look like cockscombs. The surfaces of the galls have irregular spine-like projections and are very rough.

Life cycle on *Hamamelis*

At the Shomaru Pass, we found sexuparae and yellowish sexuals on the underside of leaves on 14 and 21 May 1987 and 25 May 1990, orange-colored 1st-instar fundatrices on lateral buds on 7 and 14 May 1987, and a few incipient galls on lateral buds on 21 and 28 May 1987. However, it is uncertain whether these aphids and galls were of this species or of the next. Identifiable young galls of *H. miyabei* were found on lateral buds at the Shomaru Pass on 17 and 24 June 1987 and 23 June 1988. Larger, yet unopened galls were found at the Shomaru Pass on 3 July 1984 and 8 July 1999. All 2nd-generation aphids become alates. Galls containing alates were found at the Shomaru Pass on 25 July 1983, 14 August 1991, 15 August 1992 and 18 September 1989, at Mt. Sammaiwa, Tochigi Pref., on 7 August 1983, at Kuriyama, Tochigi Pref., on 26 September 2000, and at the Botanical Gardens of Hokkaido University, Sapporo, Hokkaido, on 10 August 1997.

Life cycle on *Betula*

On *Betula maximowicziana*, overwintered 1st-generation apterae and young cockscomb-like galls were found at Shintoku, eastern Hokkaido, in late May (Akimoto *et al.*, 1996). We also found young galls without alates at Sapporo, Hokkaido, on 15 June 1999 and at Mt. Akagi, Gumma Pref., on 25 May 1999 (Table 1). Apterae of the 2nd generation produce both 1st-instar nymphs to be alates or apterae and coccidiform 1st-instar nymphs to be the 1st-generation apterae on *Betula* (Akimoto *et al.*, 1996). Akimoto *et al.* (1996) collected four galls containing

alates at Sapporo in early August and found that all alates they examined contained coccidiform embryos in their abdomens. They thought that this meant the lack of sexual reproduction. However, we examined alates from galls on *B. maximowicziana* collected at Arakawamura, Saitama Pref., on 16 June 1997, and found that all alates contained sexual embryos. It is therefore possible that alates produced early in the season are sexuparae, while those produced late in the season are secondary migrants (i.e., alates that migrate to another tree of the secondary host). Judging from the date of the appearance of sexuparae on *Betula* and the date of gall formation on *Hamamelis* in Saitama Pref., the fundatrix probably hatches the next year; i.e., the species has a two-year life cycle.

Secondary host

Betula maximowicziana is the only known secondary host of *H. miyabei*. We transferred alates from galls of the species on *Hamamelis* to trees of *Betula platyphylla* four times (in 1989, 1991, 1992 & 1997). A few coccidiform 1st-instar nymphs settled on the twigs but no galls were formed on the trees the following spring.

Behavior of aphids on *Hamamelis*

Out of the gall on *Hamamelis japonica* wax-coated honeydew is pushed through the ostiole resembling toothpaste appearing out of a tube. We observed small nymphs, probably of the 1st instar, pushing thread-like honeydew by their backs at the exit (at the Shomaru Pass on 25 July 1983). A nymph also pushed a cast-off skin out of the gall (at the Shomaru Pass on 19 August 1983). We also cut off the upper part of a gall, and observed cleaning behavior from above (at the Shomaru Pass on 2 August 1984). A 4th-instar (wingpadded) nymph was pushing a mass of honeydew with its back.

Behavior of aphids on *Betula*

Normal 1st-instar nymphs produced in the gall on *Betula maximowicziana* are known to play a defensive role against predators (Akimoto *et al.*, 1996).

Taxonomic notes and nomenclature

Since the name *H. miyabei* predates *H. cristifoliae* and *H. betulina makabae*, the latter two are junior synonyms of the former name.

2. *Hamamelistes kagamii* (Monzen)

Mansakia kagamii Monzen, 1929 [original description]; Monzen, 1954 [redescription]; Sorin, 1977

[brief comment and illustration of the gall and the head and antenna of alate].

Hamamelistes kagamii: Blackman & Eastop, 1994 [brief comment]; Kurosu & Aoki, 1991 [brief comment on gall-cleaning behavior].

Hamamelistes gibberi biological race *grossae* Monzen, 1954 [original description]; Blackman & Eastop, 1994 [brief comment].

Gall on *Hamamelis*

Hamamelistes kagamii forms a pouch-like gall with a number of conical projections, which are usually simple and not ramified (Fig. 1C). The wall is thin. When the gall matures, it opens at various parts: usually at the base and/or the tips of some of the projections. *H. kagamii* transforms both lateral and flower buds into the galls.

Gall on *Betula*

The leaf of *Betula grossa* infested with the aphids is more or less protruded on the upper surface, exhibiting blisters (Fig. 1D). The aphids can be easily seen from the underside.

Life cycle on *Hamamelis*

At the Shomaru Pass, identifiable young galls of *H. kagamii* were found formed on lateral buds on 17 June 1987 and 23 June 1988, on flower buds on 24 June 1987, on both lateral and flower buds on 26 June 1989. Larger, yet unopened galls were found at the Shomaru Pass on 3 July 1984 and 8 July 1999. All the 2nd-generation aphids become alates. Opened galls containing alates were found at Masutomi, Yamanashi Pref., on 17 July 1998, at the Matsuhime Pass, Yamanashi Pref., on 26 July 1999, at Mt. Sammaiwa, Tochigi Pref., on 7 August 1983, and at the Shomaru Pass on 18 September 1989.

Life cycle on *Betula*

Blisters-like galls on *Betula grossa* were found at Sanjonoyu, Yamanashi Pref., on 20 May 1999, 7 June 1997 and 30 June 1996. Those collected on 20 May and 7 June contained alates that were sexuparae. Coccidiform 1st-instar nymphs were found in galls collected on 7 and 30 June. They were undoubtedly produced by apterae, because some apterae contained coccidiform embryos. On 7 June we found coccidiform 1st-instar nymphs and a dead overwintered aptera on a lignified twig. Secondary migrants have not been found. Judging from the date of the appearance of sexuparae on *Betula* in Yamanashi Pref. and the date of gall formation on *Hamamelis* in Saitama

Pref., the species probably has a two-year life cycle.

Secondary host

Betula grossa is probably the only secondary host of *Hamamelistes kagamii*. When a twig of *B. grossa* is broken, it smells noticeably of methyl salicylate (Kitamura & Murata, 1979; Watanabe, 1995), which might serve a defensive function against phytophagous insects in general. We transferred more than 200 alates from galls of *H. kagamii* on *Hamamelis* collected at Masutomi to a tree of *Betula platyphylla* at Niiza, Saitama Pref., in July 1998, but no galls were formed on the tree the following spring.

Taxonomic notes and nomenclature

The galls of *Hamamelistes kagamii* are rather commonly found on *Hamamelis japonica* in the mountainous regions of Saitama and Yamanashi Prefs. The galls of the species are similar to those of the next species, but can be distinguished from the latter by fewer projections. However, the gall-living aphids resemble those of the next species and we have failed to find good morphological characters to distinguish between them. Because of the similarity, there remains some doubt about the nomenclature adopted here. The type specimen of *Hamamelistes kagamii* was probably lost, and the photo of its galls shown in Monzen (1929, his fig. 31) is quite obscure. We propose that the name *H. kagamii* should be adopted for this species because this requires the least nomenclatorial change.

The normal 1st-instar nymphs produced in the gall on *Betula* can be distinguished from those of the next species by the longer setae on the first tarsal segment of the hind leg. In all 23 specimens of *H. kagamii*, the longer seta on the 1st segment was longer than the width of the 2nd segment. The setae were 0.024–0.042 mm (mean 0.033 mm) long, and the 2nd segments were 0.020–0.026 mm (mean 0.023 mm) wide. In all 26 specimens of the next species collected from *B. platyphylla* and *B. davurica*, the longer seta was shorter than the width of the 2nd segment. The setae were 0.012–0.020 mm (mean 0.017 mm) long, and the 2nd segments were 0.022–0.026 mm (mean 0.024 mm) wide.

3. *Hamamelistes betulinus* (Horvath)

Tetraxis betulinus Horvath, 1896 [original description].

Hamamelistes shirakabae (nec Monzen, 1927): Monzen, 1929 [description], 1934 (in part) [redescription and life cycle on *Betula*], 1954 (in part) [redescription].

Hamamelistes gibberi Monzen, 1954 (s. str.) [original description]; Blackman & Eastop, 1994 [brief comment].

Hamamelistes kagamii: Yukawa & Masuda, 1996 [photo of gall].

Hamamelistes betulinus: Blackman, 1986 [karyotype]; Blackman & Eastop, 1994 [brief comment].

Gall on *Hamamelis*

The gall of *Hamamelistes betulinus* is similar to that of *H. kagamii*, but the gall looks like a coral because the projections are well ramified (Fig. 1E). Exit holes open at the tips of projections. All galls we found were formed at the position of flower buds. *H. betulinus* transforms flower buds into the coral-like galls. A gall shown in Yukawa & Masuda (1996, their fig. C-290b) is not of *H. kagamii* but of *H. betulinus*.

Gall on *Betula*

Hamamelistes betulinus causes blister-like galls on leaves of various birches including *Betula platyphylla* (Fig. 1F) and *B. davurica*. The galls resemble those of *H. kagamii* on *B. grossa*.

Life cycle on *Hamamelis*

Many galls of *H. betulinus* were collected at Tem-mabayashi on 7 August 1998. Some of the galls contained alates. We also found a few galls containing alates at the Botanical Gardens of Hokkaido University, Sapporo, on 23 August 1995.

On 6, 9, 11, 18 and 19 May 1990 many sexuparae of *H. betulinus* emerged from galls on *Betula platyphylla* found in Kumagaya and Niiza were transferred to small trees of *Hamamelis japonica* planted in Niiza. Some of the sexuparae soon larviposited on the underside of leaves, and yellowish immature sexuals were found on the leaves along the veins or walking on the twigs. On 20 May we observed at least two pairs of sexuals in copulation on twigs. We also found sexuals in crevices in the bark. Many eggs were found attached to twigs and trunks on 26 May, when we still found yellowish sexuals. The eggs were pale green in color, but some of them were darker. However, no galls were formed within the year or the next. This is probably because the trees were small and had no flower buds.

Life cycle on *Betula*

Blister-like galls of *H. betulinus* are commonly found on leaves of *Betula platyphylla* in Japan. In Kumagaya, Saitama Pref., we found coccidiform apterae at the base of winter buds that were just

unfolding on 27 March 1990 and 29 March 2000. On the undersides of new leaves there were many 1st-instar nymphs of the 2nd generation. Galls with alate sexuparae were found in Niiza, Saitama Pref., on 5 May 1990, in Kumagaya on 7 and 17 May 1990 and 18 May 1996, in Kiyosato, Nagano Pref., on 16 June 1996, in Iida, Nagano Pref., on 12 and 16 June 1996, and in Sapporo on 15 June 1999. Apterae with coccidiform embryos and/or coccidiform 1st-instar nymphs were detected from galls as early as 7 May (1990) in Kumagaya and 15 June (1999) in Sapporo, and found in all galls collected thereafter. Alates containing coccidiform embryos (i.e., secondary migrants) were found from galls on *B. ermanii* on 21 August (see below).

Secondary host

The main secondary host of *H. betulinus* is *Betula platyphylla* in Japan. The aphids collected from *Betula davurica* were found belonging to the same species (Table 2). *H. betulinus* also feeds on *B. ermanii* (see below) and, outside Japan, on *B. pendula*, *B. pubescens* and *B. verrucosa* (Heie, 1980; Blackman & Eastop, 1994).

Taxonomic notes and nomenclature

Monzen (1954) described *Hamamelistes gibberi* based on specimens from *Betula ermanii*. Not only Monzen (1954) but also Akimoto *et al.* (1996) mentioned that the apterous adults of *H. gibberi* can be distinguished from those of the other species in having pore-like cornicles. However, we ascertained that *H. betulinus* (and also *H. kagamii*) produces both apterae with cornicles and apterae without cornicles in the birch gall. This is because the overwintered apterae produce 1st-instar nymphs without cornicles, which probably become apterae without cornicles. In the gall, these 2nd-generation apterae produce 1st-instar nymphs with cornicles, which probably become apterae with cornicles or alates with cornicles. We therefore consider *H. gibberi* to be the same as the species on *B. platyphylla*. Although we have not examined DNA from aphids on *B. ermanii*, the morphology of six 1st-instar nymphs collected from *B. ermanii* at the Mugikusa Pass, Nagano Pref., on 21 August 1981, accorded well with the 1st-instar nymphs from *B. platyphylla* and *B. davurica*. The longer setae on the 1st segment of the hind tarsus were 0.016–0.020 mm (mean 0.019 mm) and the 2nd segments were 0.024 mm wide. We think that the species utilizes a wide range of *Betula* species for secondary hostplants, although it is possible that aphids on *B.*

ermanii represent a recently derived, anholocyclic population.

Monzen (1927) described "*Hamamelistes*" *shirakabae* based on specimens collected from leaves of *B. platyphylla* ('Shirakaba' means *B. platyphylla*) at Morioka, Iwate Pref., on 10 September 1926. Because he wrote (in Japanese) that the aphids live on the underside of a leaf but cause no deformity of the leaf, and that the hind wing of the alate has two oblique veins with a common stalk, there is no doubt that the species is not of *Hamamelistes* but of *Hormaphis*. We regard the name *Hamamelistes shirakabae* as a synonym of *Hormaphis betulae* (Mordvilko). Monzen later brought about much confusion in taxonomy by applying the name "*Hamamelistes shirakabae*" to a true *Hamamelistes* species on *Betula platyphylla* (Monzen, 1929, 1934, 1954). He first mentioned that the alates of *H. shirakabae* have "inconspicuous" cornicles (Monzen, 1929). He later added that while the "summer alate form [has] cornicles [which are] small, brownish circles", the "autumn alate form" has no cornicles (Monzen, 1934), or that the "alate viviparous female (migrant on the leaf of *Betula* in June) [has] cornicles small [and] not distinct", but the "autumn alate form (on the leaf of *Betula* in September)" has not (Monzen, 1954). We have found no alates of *Hamamelistes* without cornicles (or with "inconspicuous" cornicles) from *B. platyphylla*. Because Monzen (1929, 1934, 1954) refers to no other *Hamamelistes* species on *B. platyphylla*, and the aphids we are treating here are of the commonest *Hamamelistes* species on *Betula* in Japan, the two are likely to belong to the same species. Monzen's record of alates without cornicles may have been a simple mistake due to his confusion of *Hamamelistes* with *Hormaphis*.

Here we adopt the name *H. betulinus* for the species. The name has hitherto been applied to the anholocyclic population on birch (*B. pendula*, *B. pubescens* & *B. verrucosa*) from Europe to eastern Asia (Heie, 1980; Blackman & Eastop, 1994). Both Heie (1980) and Blackman & Eastop (1994) mentioned that the apterous adults in galls have no cornicles. It remains to be confirmed whether all apterous adults in galls of the anholocyclic population lack cornicles. If the European anholocyclic population turns out to be a different species, then the name *H. gibberi* will be adopted for the Japanese population.

Acknowledgments

We thank the following persons for their help in collecting materials used for the study: Shiho Arai,

Osamu Furuta, Tadashi Ishikawa, Arata Ishizuka, Junichiro Kaneko, Keiichi Matsumoto, Kouichi Matsumoto, Yoshiyuki Matsumoto, Nancy Moran, Junko Narukawa, Shuhei Niitsu, Larry Smith, Koji Toyoda and Shigeshi Usuba. This study was in part supported by a National Science Foundation grant (DEB-9807076) to C.D.v.D. and by a grant from the Nakayama Foundation for Human Science.

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- (*Original was not seen.)

(Received October 30, 2000; Accepted December 4, 2000)