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Parallelism in secondary loss of sex from a heterogonic life cycle on different host plants in the *Andricus mukaigawae* complex (Hymenoptera: Cynipidae), with taxonomic notes

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Abstract

The *Andricus mukaigawae* complex consists of bivoltine heterogonic (= cyclically parthenogenetic) and univoltine thelytokous (parthenogenetic) populations. The bivoltine heterogonic populations are divided into *A. mukaigawae* ($2n=12$), which produces bur-shaped unisexual galls (producing only asexual females) on *Quercus aliena*, *Q. mongolica*, and *Q. serrata*; and *A. kashiwaphilus* ($2n=10$), which produces flower-shaped unisexual galls on *Q. dentata*. The univoltine thelytokous populations have to date been treated as one species, *A. targionii* (s. lat.), but the population on *Q. aliena* produces bur-shaped galls and that on *Q. dentata* produces flower-shaped galls. I investigated the karyotype of the population of *A. targionii* (s. lat.) on *Q. dentata*. This population had the same karyotype as that of *A. kashiwaphilus*. The karyotype and shape of galls indicate that *A. targionii* (s. lat.) on *Q. dentata* is derived from *A. kashiwaphilus*, and that on *Q. aliena* is derived from *A. mukaigawae* through the parallel deletion of the bisexual (sexually reproducing) generation on different host plants. Since *A. targionii* (s. lat.) is thus shown to be polyphyletic, the name *A. targionii* (s. str.) should be applied to the univoltine thelytokous population on *Q. aliena*, and the univoltine thelytokous population on *Q. dentata* should be identified as *A. pseudoflos* comb. n., judging from the original descriptions.

Keywords: Gall, heterogony, host plant, karyotype, parallelism, sex

Introduction

Heterogony, or cyclical parthenogenesis, is of interest to evolutionary biologists because it is considered significant for understanding the balance between costs and benefits of sex (Williams 1975; Maynard Smith 1978; Bell 1982). Heterogony is known to occur in seven groups of animals, the Rotifera, Cladocera, Digenea, Aphidoidea, Cecidomyiidae, Micromalthidae, and Cynipidae (Hebert 1987; Suomalainen et al. 1987). A strict regularity of unisexual and bisexual generations is a characteristic of cynipid heterogony (Hebert 1987; Suomalainen et al. 1987). Among the Cynipidae, heterogony occurs in the Cynipini (oak gallwasps) and the Pediapidini (one gall-former on *Acer* and a small number

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of other species whose life cycles are unknown), and is considered to be a possible synapomorphy of the two tribes (Liljeblad and Ronquist 1998). Thelytoky appears to be induced by *Wolbachia* infection in two other cynipid tribes, the Aylacini (herb gallers) and the Diplolepidini (rose gallers) (Plantard et al. 1998, 1999), but heterogony in the Cynipini is not induced by *Wolbachia* (Rokas et al. 2001, 2002; Abe and Miura 2002). Secondary loss of sex from a heterogonic life cycle has been known to occur in some species of the Cynipini (Stone et al. 2002), but *Wolbachia* was not detected by standard screening procedures in permanently thelytokous wasps of an oak gallwasp, the *Andricus mukaigawae* complex (Abe and Miura 2002).

The *A. mukaigawae* complex consists of bivoltine heterogonic and univoltine thelytokous populations on *Quercus* spp., and adults of the unisexual generation of these populations are scarcely distinguishable from each other on the basis of morphology (Abe 1986). The life cycles of these populations are as follows (Abe 1986). The bisexual galls of the bivoltine heterogonic populations are produced on edges and midribs of leaves, and after copulation in spring the female adults emerging from the galls deposit their eggs in immature axillary buds. In summer, unisexual bud galls appear singly, and unisexual females emerging from the galls oviposit into mature axillary buds in winter. In the univoltine thelytokous populations, the unisexual galls appear on leaf edges, midribs, petioles, and elongating shoots soon after bud burst in spring. The female adults emerge from these galls and lay eggs in mature axillary buds in winter.

Even if the univoltine thelytokous population of the *A. mukaigawae* complex on *Q. dentata* is reared in a warm area, it does not produce bisexual galls but produces unisexual galls (Abe 1986). The univoltine thelytokous life cycle is considered to have derived from the bivoltine heterogonic life cycle with a deletion of the bisexual generation (Abe 1986). The deletion of sex appears to be caused by a failure of the genetic regulatory switch that switches from unisexuality to bisexuality (Abe 1986). The failure of the switch does not seem to be induced by *Wolbachia* infection, because *Wolbachia* was not detected in the univoltine thelytokous wasps (Abe and Miura 2002).

On the basis of the life cycles, Abe (1986) divided the *A. mukaigawae* complex into bivoltine heterogonic *A. mukaigawae* (Mukaigawa, 1913) (s. lat.) and univoltine thelytokous *A. targionii* Kieffer, 1903. Two host races were recognized in *A. mukaigawae* (s. lat.), as judged from differences in ovipositional preference, gall-forming ability, and shape of the unisexual gall (Abe 1988). Later, the allochronic isolation between the two host races of the bisexual generation was demonstrated in the field (Abe 1991). Examination of the chromosomes of unisexual females revealed that the two races had different karyotypes ($2n=10$ and $2n=12$) (Abe 1998). The karyotype was uniform within each race, and no structural heterozygosity of chromosomes occurred in individuals from localities where the two races coexist (Abe 1998). Thus, the two races were regarded as distinct species (Abe 1998). On the basis of the original description and illustration, the name *Andricus mukaigawae* (s. str.) was applied to the race that produces bur-shaped unisexual galls on *Q. aliena*, *Q. mongolica*, and *Q. serrata*. The other race, which produces flower-shaped unisexual galls on *Q. dentata*, was described as *A. kashiwaphilus* Abe, 1998. The two shapes of the unisexual gall are ascribable not to differences in host plant species but to those between the insects themselves, because *A. mukaigawae* (s. str.) can produce galls also on *Q. dentata* and the bur-shaped galls co-existed with the flower-shaped galls on the branches of *Q. dentata* (Abe 1988). The close relationship between *A. mukaigawae* (s. str.) and *A. kashiwaphilus* was confirmed by Rokas et al. (2003) on the basis of data from a fragment of the mitochondrial cytochrome *b* gene from 62 oak gallwasp species, including those two species.

Andricus targionii was described from an individual that emerged from the bur-shaped gall on the leaf midrib of *Q. aliena* in Shensi, China (Kieffer 1903). The gall position shows that this species is univoltine and thelytokous (Abe 1986). The bur-shaped unisexual gall illustrated by Kieffer (1903) resembles the unisexual gall produced by *A. mukaigawae* (s. str.) on *Q. aliena*, *Q. mongolica*, and *Q. serrata*. On *Q. dentata*, *A. targionii* (s. lat.) and the unisexual generation of *A. kashiwaphilus* produce flower-shaped galls. The two shapes of the unisexual gall indicate a parallel change in life cycle from bivoltine heterogony to univoltine thelytoky in the *A. mukaigawae* complex on different host plants. If the deletion of the bisexual generation occurred independently on different host plants, *A. targionii* (s. lat.) would be polyphyletic. If so, it should be divided into two species: one producing bur-shaped galls on *Q. aliena* and the other producing flower-shaped galls on *Q. dentata*.

The present study tested the hypothesis that the deletion of the bisexual generation occurred in parallel on different host plants in the *A. mukaigawae* complex from the karyotype of *A. targionii* (s. lat.) on *Q. dentata*. If the karyotype of *A. targionii* (s. lat.) on *Q. dentata* is similar to that of *A. kashiwaphilus*, but not to that of *A. mukaigawae* (s. str.), the hypothesis stands. On the basis of the inferred phylogenetic relationships, taxonomic treatments of the *A. mukaigawae* complex are discussed.

Material and methods

I collected a total of 161 specimens of *A. targionii* (s. lat.) on *Q. dentata* from six localities in Japan (Figure 1; Table I). Using an air-drying method (Imai et al. 1988), I prepared the brains of prepupae or the ovaries of pupal specimens for chromosomal examination (for

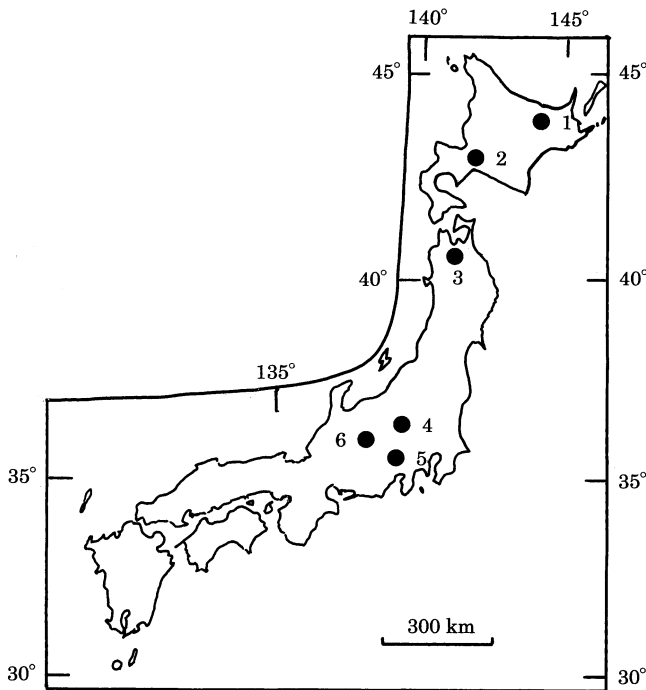


Figure 1. *Andricus targionii* (s. lat.) populations on *Quercus dentata* used for the present chromosome study. 1, Kitami; 2, Minami-chitose; 3, Aomori; 4, Mt Haruna; 5, Lake Yamanaka; 6, Lake Shirakaba.

Table I. Chromosome numbers in *Andricus targionii* (s. lat.) on *Quercus dentata*.

Locality	Date of collection	No. of individuals observed	Chromosome number ($2n$)
Kitami	11 August 1993	7	10
Minami-chitose	10 August 1993	36	10
Aomori	8 August 1993	19	10
Mt Haruna	5 August 1992	19	10
Lake Yamanaka	5 September 1998	61	10
Lake Shirakaba	6 September 1998	19	10

details see Abe (1998)). The karyotypes were classified into the categories defined by Levan et al. (1964).

Results

The karyotype was composed of five pairs of metacentrics in all specimens observed (Figure 2; Table I). There was no geographical variation of karyotype.

Discussion

Phylogenetic relationships

The present results support the hypothesis that the deletion of the bisexual generation has occurred in parallel on different host plants in the *A. mukaigawae* complex (Figure 3). As described in a previous paper (Abe 1998), the karyotype of unisexual females of *A. mukaigawae* (s. str.) on *Q. aliena*, *Q. serrata*, and *Q. mongolica* var. *grosserrata* is composed of four pairs of metacentrics, a pair of acrocentrics, and a pair of subtelocentrics; and that of *A. kashiwaphilus* on *Q. dentata* is composed of five pairs of metacentrics. The flower-shaped unisexual gall and the same karyotype indicate that *A. targionii* (s. lat.) on *Q. dentata* originated from *A. kashiwaphilus* through the deletion of the bisexual generation. Also, the bur-shaped unisexual gall indicates that *A. targionii* (s. lat.) on *Q. aliena* originated similarly from *A. mukaigawae* (s. str.), but further study is needed to examine the karyotype of *A. targionii* (s. lat.) on *Q. aliena*.

Taxonomic treatment

The present results and the shape of the gall indicate that *A. targionii* (s. lat.) is polyphyletic: *A. targionii* (s. lat.) on *Q. aliena* arose from *A. mukaigawae* (s. str.), and that on *Q. dentata* arose from *A. kashiwaphilus* through the secondary loss of sex (Figure 3). Each of the two populations of *A. targionii* (s. lat.) is closely associated with different host plant species, and thus occupies a different niche. Moreover, they are adequately



Figure 2. Representative karyotype of *Andricus targionii* (s. lat.) on *Quercus dentata*, Kitami. Scale bar: 10 μ m.

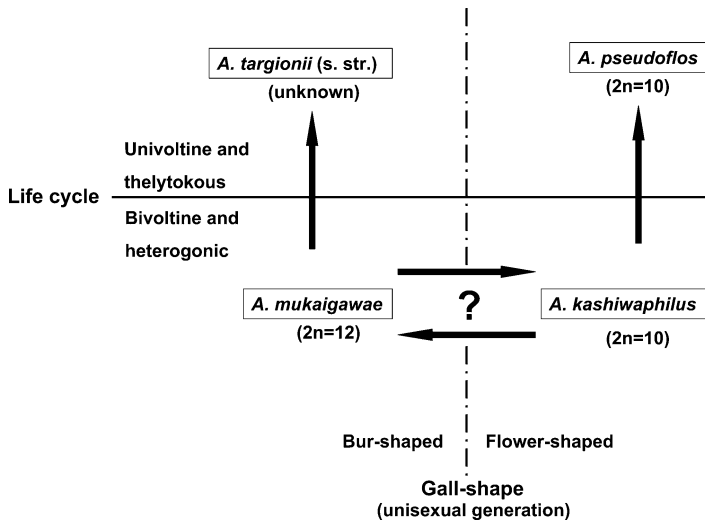


Figure 3. The life cycles, gall shape of unisexual generation, and suggested changes in the *Andricus mukaigawae* complex.

distinguishable from each other by the shape of gall. Thus, I consider that the naming of each host-associated population as species is reasonable (Table II).

The original description and illustration of the gall by Kieffer (1903) show that the name *A. targionii* (s. str.) should be applied to the univoltine thelytokous species on *Q. aliena* in China. The univoltine thelytokous species on *Q. dentata* was described by Monzen (1954) as *Cynips pseudoflos*. According to Monzen’s (1954) description, this species is univoltine and thelytokous, and produces flower-shaped galls on twigs and midribs of *Q. dentata*. *C. pseudoflos* was synonymized with *A. targionii* (s. lat.) by Abe (1986), but I raise it to separate species status and transfer it to the genus *Andricus* here.

***Andricus targionii* Kieffer (s. str.)**

Judging from the inferred phylogenetic relationships, the name *A. targionii* (s. str.) should be applied to the univoltine thelytokous species of the *A. mukaigawae* complex on *Q. aliena* in China. Abe (1986) regarded the populations on *Q. liaotungensis*, *Q. mongolica*, and *Q. dentata* in Shenyang, China, as members of *A. targionii* (s. lat.). Since clustered flower-shaped galls appear on *Q. dentata* in spring when bud burst occurs (Weih 1965), I regard

Table II. Recognized species and key features in the *Andricus mukaigawae* complex.

Species	Life cycle	Gall shape of unisexual generation	Chromosome number (2n)	Host plants
<i>A. targionii</i> s. str.	Univoltine and thelytokous	Bur-shaped	Unknown	<i>Q. aliena</i>
<i>A. mukaigawae</i>	Heterogonic	Bur-shaped	12	<i>Q. aliena</i> , <i>Q. mongolica</i> , <i>Q. serrata</i>
<i>A. pseudoflos</i>	Univoltine and thelytokous	Flower-shaped	10	<i>Q. dentata</i>
<i>A. kashiwaphilus</i>	Heterogonic	Flower-shaped	10	<i>Q. dentata</i>

the population on *Q. dentata* as *A. pseudoflos*. The life cycles of the populations on *Q. liaotungensis* and *Q. mongolica* should be clarified, because the appearance time and position of bur-shaped galls are not mentioned in Weih (1965). Abe (1986) regarded the population on *Q. mongolica* in the far east of Russia (Kovalev 1965) as a member of *A. targionii* (s. lat.), but the life cycle of this population should be clarified.

Andricus pseudoflos (Monzen, 1954) comb. n.

Cynips pseudoflos Monzen 1954, p 25.

Adleria pseudoflos: Kovalev 1965.

Andricus targionii: Abe 1986.

The examined specimens of *A. targionii* (s. lat.) collected from *Q. dentata* by Abe (1986) are identified as *A. pseudoflos*.

Lectotype designation

I examined the type specimens of *A. pseudoflos* kept in the Entomological Laboratory, Kyushu University. One, labelled “*Cynips pseudoflos* Monzen, Okunakayama, Dec. 1953” is hereby designated as the lectotype, and labelled as such in order to fix the status of this specimen as the sole name-bearing type of this species. Left flagellar segments, all legs, and metasoma are lost in the lectotype. The other three specimens, labelled “Okunakayama, Dec. 1953, Suzuki leg.”, have been labelled by me as paralectotypes. Okunakayama is located in northern Iwate Prefecture, Japan.

Secondary loss of sex from heterogonic life cycle

Secondary loss of the bisexual generation from a heterogonic life cycle is known to have occurred in some groups of heterogonic animals (Hebert 1987). Among oak gallwasps, a univoltine thelytokous life cycle occurs also in *Plagiotrochus suberi* Weld, *A. quadrilineatus* Hartig, and *Dryocosmus kuriphilus* Yasumatsu. As reviewed by Melika and Abrahamson (2002), *P. suberi* is heterogonic in Europe, but the introduced population in the USA is univoltine and thelytokous. Folliot (1964) revealed that unisexual females of *A. quadrilineatus* produce both bisexual and unisexual generations. Yasumatsu (1951) described a univoltine thelytokous species, *D. kuriphilus*, which is a serious pest of chestnut trees in Japan. Although this species has been studied by many applied entomologists, a candidate for the ancestral heterogonic species has not been found. In the *A. mukaigawae* complex, I consider that secondary loss of sex occurred in parallel on different host plants (Figure 3). Whether or not such a loss occurred on the same host plant species more than once could be resolved by using molecular markers.

In another heterogonic insect group, aphids, transition from heterogony to permanent thelytoky appears to have occurred frequently (Moran 1992). Structural difference in karyotype between thelytokous and the extant heterogonic relatives are revealed in some aphids (Blackman 1980). In many animals and plants, permanent thelytoky is accompanied by polyploidy (Suomalainen et al. 1987), but change in ploidy level has not been detected in such aphids. In the present study, no structural difference was found in karyotype between bivoltine heterogonic *A. kashiwaphilus* and univoltine thelytokous *A. pseudoflos*. The phenotypic potential for the bisexual generation of *A. kashiwaphilus* may have been retained in the genome of *A. pseudoflos*.

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