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Phylogeny, Evolution and Biogeography of Gall-Forming Aphids (Insecta: Homoptera): A Case Study from the Eriosomatini

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ABSTRACT

Gall-forming aphids are highly specific to their host plants, and speciation in galling aphids has proceeded in association with a single species or species group of host plants (primary host). This study firstly aims to revise the associations between galling aphids and their host plants by focusing on historical changes in the distribution of host plants. Aphids of the Eriosomatinae are typically associated with the primary and secondary host plants and alternate host plants seasonally, with sexual reproduction on the primary host plant. However, some species are not host-alternating and are wholly parthenogenetic on the secondary host plant. This study secondly aims to test the possibility of long-term persistence of an aphid species by means of parthenogenesis (relict hypothesis). The eriosomatine genus *Colopha* is a small aphid group represented by three sexual and three asexual species. The sexual species are associated with two *Ulmus* sister species distributed disjunctly in Europe and eastern North America. In East Asia, an asexual species, *Colopha kansugei*, is distributed widely on the secondary host. This study tested whether the relict hypothesis is applicable to *C. kansugei* by comparing DNA sequences. A high rate of substitution (3.4% at the maximum) was found in the mitochondrial COI sequence between local populations. Available evidence suggests that *Colopha kansugei* has persisted on the secondary host plant through parthenogenesis, probably following the local extinction of the primary host. Use of molecular techniques might possibly detect much more ancient species among parthenogenetic aphids with disjunct distributions.

Keywords: Asexual, Host alternation, Disjunct distribution, Refuge, Relict

INTRODUCTION

Gall-forming insects, as parasites to plants, are monophagous and highly specific to their host plants. Gall-forming insects have shared an evolutionary history with their host plants, and their life cycles and distribution ranges have been constrained by the host plants. Biogeographic evidence suggests that the associations between gall-forming aphids and their host plants have a long history that traces back to the early Tertiary [1–2]. Throughout the Ter-

tiary and Quaternary, hardwood taxa drastically shifted their distributional ranges depending on global climatic changes, which has resulted in the disjunct distributions of some hardwood taxa in, for example, East Asia and eastern North America [3–5]. Hardwood trees adapted to mild climates are known to have survived glacial episodes in some fragmented refuges and expanded their distribution to the north in interglacial episodes, with the retreat and expansion of their distribution having been repeated during the Quaternary [6–8]. Because the dis-

tribution of gall-forming insects is exclusively affected by the distribution of the host plants, it is necessary to consider past changes in the distributions of the host plants for an understanding of the present distributions of gall-forming insects.

The general pattern in the speciation of gall-forming insects is that a specific clade of gall-forming insects has diversified in association with a specific clade of host plants. Although this phenomenon is likely to be interpreted from the viewpoints of host-parasite coevolution, the most marked pattern is not cospeciation between host plants and insects but accelerated diversification of galling insects on a single plant species. There are a number of examples in which several closely related species of gall-forming insects are associated with the same host species and often coexist on the same host individuals [9–14]. Among gall-forming aphids, examples include *Eriosoma* on *Ulmus* [15], *Pemphigus* on *Populus* [16], Fordinae on *Pistacia* [14, 17], *Tuberocephalus* on *Prunus* [18] and *Nipponaphis* on *Distylium* [19]. This study provides more detailed information about the phylogeny, distribution pattern and host relationship of gall-forming aphids of the Eriosomatini (Aphidoidea: Eriosomatinae) by focusing on historical changes in the host plants of the family Ulmaceae.

APHIDS AND HOST PLANTS

Aphid Life Cycle and Mordvilko's Hypothesis

Aphids of the Eriosomatini are associated with two kinds of plants (primary and secondary hosts) that are distantly related and they seasonally alternate host plants between the primary host, broad-leaved deciduous trees, and the secondary host, mainly herbaceous plants. Most species of eriosomatine aphids consist of sexual and asexual strains. Sexual strains are host-alternating between the primary and secondary host plants, with sexual reproduction on the primary host and asexual reproduction on the secondary host. In contrast, asexual strains persist on the secondary host and reproduce parthenogenetically all year round. In a local population, obligatorily or facultatively asexual strains often coexist with sexual strains on the secondary host [20, 21], and the proportion of asexual strains varies depending on the environmental conditions. Obligatorily asexual populations are sometimes distributed beyond the ranges of the primary host plant. A few species are wholly parthenogenetic on the secondary hosts. Mordvilko [22] hypothesized that asexual strains will be distributed outside the range of the

primary host if sexual strains became extinct together with local extinction of the primary host due to cold and arid climates but if asexual strains survived *in situ* on the secondary host. This hypothesis is based on the prediction that secondary host plants, herbaceous and grass species, may be much more cold-tolerant than primary hosts, hardwood species. Mordvilko [22] illustrated this theory with *Tetraneura rubra* (= *T. caerulescens*) that is found on the secondary host in Egypt, where the primary host (*Ulmus* spp.) does not occur at present. If Mordvilko's hypothesis is true, asexual populations may have reproduced parthenogenetically over a long period of time since the extinction of the primary host. In another example, based on molecular phylogeny, von Dohlen et al. [23] inferred that an American *Hamamelistes* species has lasted on the secondary host by means of parthenogenesis for 2–4 million years.

Some authors [e.g., 20, 24] have criticized Mordvilko's hypothesis on the ground that asexual strains can expand their range by alate migration beyond the range of the primary host where sexual and asexual strains coexist. Several eriosomatine species can disperse over a long distance by means of alate exules that fly from secondary host to secondary host. If this criticism is true, the origins of asexual populations should be more recent events than Mordvilko's hypothesis predicts. The present study makes use of fossil records of the host plants and molecular phylogenetic analysis to evaluate whether or not Mordvilko's hypothesis is true for the origin of some asexual species.

Phylogeny and Biogeography of Ulmaceae

Gall-forming aphids of the Eriosomatini are associated with the genera *Ulmus* and *Zelkova* (Ulmaceae; Ulmoideae) as primary hosts. The ancestors of *Ulmus* and *Zelkova* originated in the Cretaceous, and in the early Tertiary the elements of the genera were distributed widely in higher latitudes of the Northern Hemisphere around the arctic zone. Ancestors of *Ulmus* and *Zelkova* contributed to the so-called Arcto-Tertiary flora that existed in the early Tertiary. Fossil records suggest that with climatic deterioration after the mid Miocene, the distribution of *Ulmus* and *Zelkova* gradually shifted southwards, and that the elements survived glacial episodes in some mild refuges, including eastern and western North America, East Asia, the eastern and northwestern Himalaya, the Caucasus, and southern Europe [6]. The present study is based on the present and past distribution of *Zelkova* and the main clades of

Ulmus, and on a molecular phylogeny of *Ulmus* [25].

The genus *Zelkova*, including 5 extant species, is currently distributed disjunctly in East Asia, West Asia (around the Black Sea), Crete and Sicily (Fig. 1), but the fossil record shows that trees of this genus were distributed widely in Eurasia and North America across Beringia during the mid Tertiary. Fossils of *Zelkova* leaves have been found in sediments from Oregon, North America [26]. The present distribution of *Zelkova* corresponds to Quaternary refuges, suggesting that local extinction of *Zelkova* species has occurred frequently outside the refuges.

The genus *Ulmus*, including 18 extant species, has been divided into five sections. The section *Blepharocarpus* is composed only of two species, *U. americana* and *U. laevis*. Molecular phylogeny reveals that these two *Ulmus* species are most closely related to each other [25], but they are distributed disjunctly in central Europe (*U. laevis*) and in eastern North America (*U. americana*) (Fig. 2). This distribution pattern suggests that the elements of *Blepharocarpus* have become extinct in Asia and in western North America. *Ulmus parvifolia* and its re-

lated species, characterized by autumnal blooming, occur from southern East Asia to Southeast Asia (Fig. 1). This clade includes evergreen elements and is adapted to moist and warm climates. Molecular phylogeny shows that this clade had branched off the other clades early on [25] and had become restricted to areas around refuges in the Quaternary.

The section of *Ulmus* with the largest species diversity is *Madocarpus*, the elements of which are currently very common and distributed continuously and widely over Eurasia from Europe to northern East Asia (Fig. 3). One element of this section occurs in eastern North America. The wide and continuous distribution of *Madocarpus* suggests that this clade rapidly expanded its range northwards from refuges after the last glacial maximum both in Europe and in Asia; *Madocarpus* is thus considered to be the most cold-tolerant among clades of *Ulmus*. The elements of this section are very similar to one another, without clear morphological discontinuities.

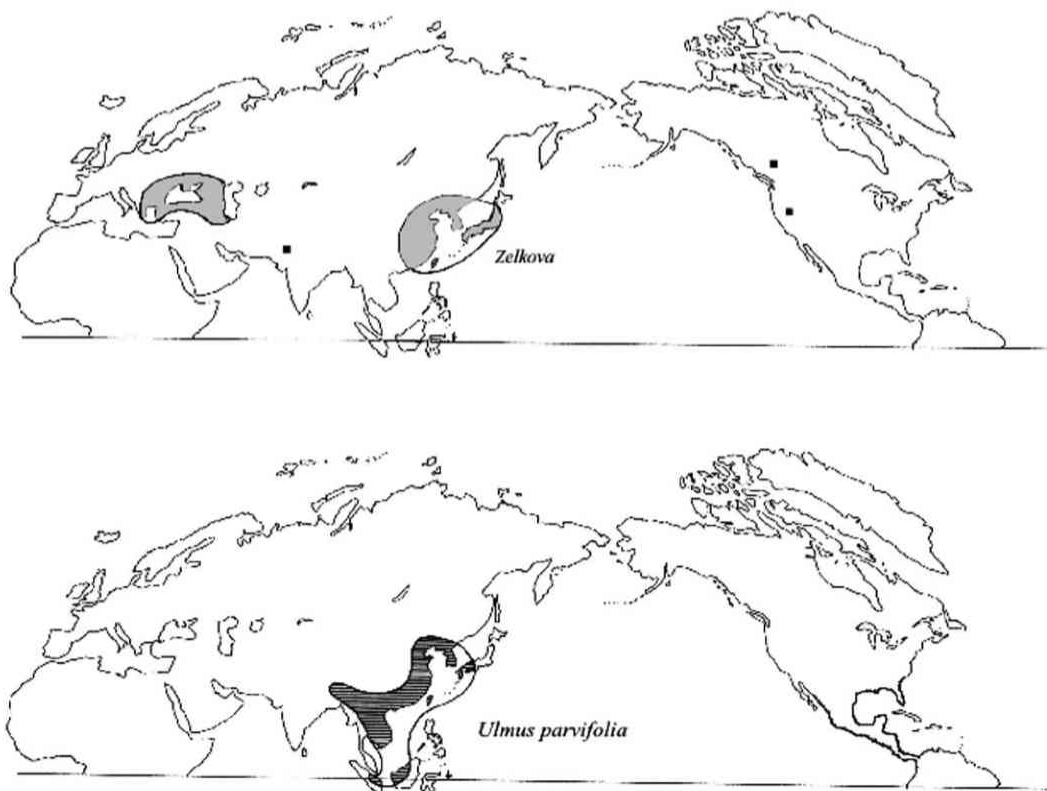


Fig. 1 Distribution of the genus *Zelkova* (above) and of the *parvifolia* group of *Ulmus* (below). Filled squares in the upper figure indicate the collection records of a parthenogenetic aphid species, *Ghariesia polunini*.

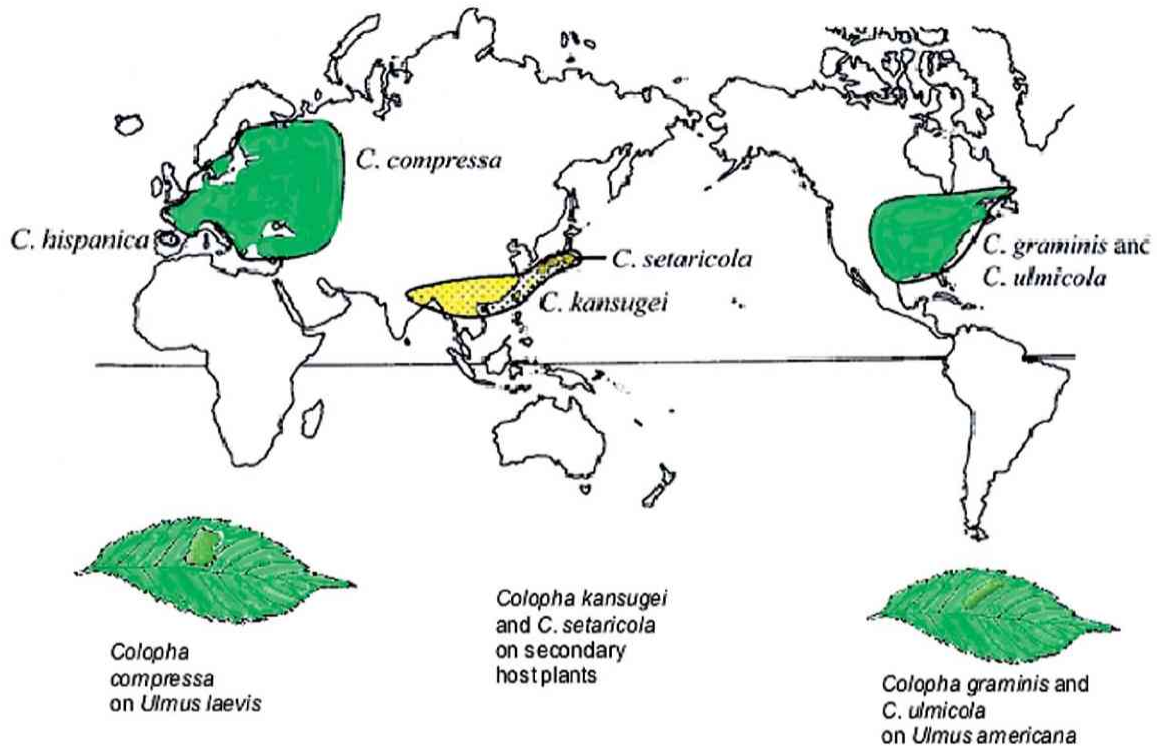


Fig. 2 The distribution ranges of *Ulmus* section *Blepharocarpus* (*Ulmus laevis* and *U. americana*; green areas) and the associated gall-forming aphids, the genus *Colopha*. No elements of *Blepharocarpus* are distributed in East Asia, but parthenogenetic species *Colopha kansugei* and *C. setaricola* are distributed on the secondary hosts, *Carex lenta* and *Setaria chondrachne*, respectively, there (yellow area). Another parthenogenetic species *Colopha hispanica* is distributed in Spain.

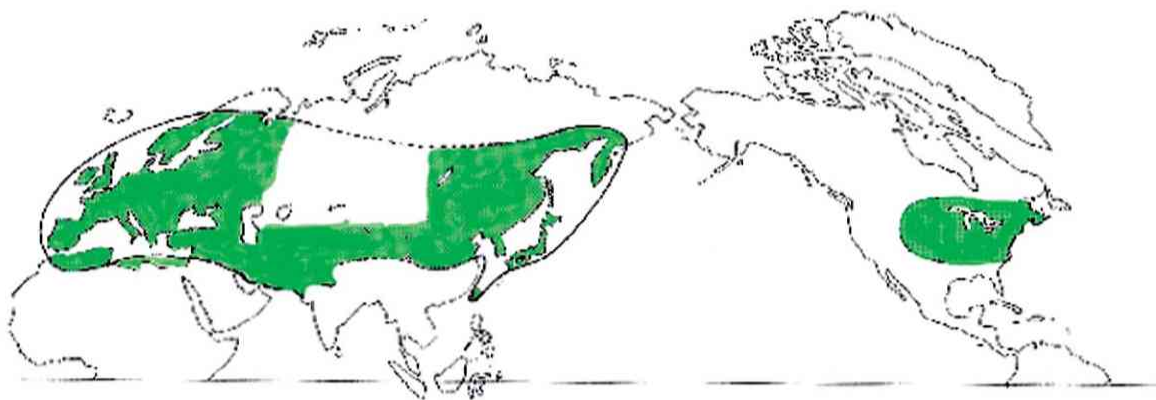


Fig. 3 The distribution ranges of *Ulmus* section *Madocarpus*.

DIVERSITY AND BIOGEOGRAPHY OF ERIOSOMATINI

The number of species, distribution ranges, and host relationships of the Eriosomatinae are summarized in Table 1. The Eriosomatini is composed of two large and many small genera. *Eriosoma* and *Tetraneura* are large genera with more than 30 species

each. These genera are mainly associated with the *Ulmus* section *Madocarpus* as the primary hosts, and, as genera, are distributed widely over Eurasia (and in North America, *Eriosoma*). On the other hand, three genera closely related to *Eriosoma* (*Aphidunguis*, *Schizoneurata* and *Schizoneurella*) are all monotypic and associated with *U. parvifolia* and *U. villosa*, both of which are adapted to warm climates.

Table 1 Genera of the Eriosomatinae and their distribution and host plants.

Genus	#species*	Distribution	Primary host**	Type of gall
<i>Eriosoma</i>	32(1)	Eurasia-N America	<i>U. Madocarpus</i>	leaf roll, open
<i>E. yangi</i>	1	East Asia	<i>Ulmus parvifolia</i>	leaf roll, open
<i>Aphidounguis</i>	1	East Asia	<i>Ulmus parvifolia</i>	leaf roll, open
<i>Schizoneurata</i>	1(1)	Southern N America	SH	—
<i>Schizoneurella</i>	1	Eastern Himalaya	<i>Ulmus villosa</i>	leaf roll, open
<i>Tetraneura</i>	32(?)	Eurasia	<i>U. Madocarpus</i>	pouch, closed
<i>Kaltenbachiella</i>	8(1)	Eurasia-N America	<i>U. Madocarpus</i>	pouch, closed
<i>Colopha</i>	6(3)	Eurasia-N America	<i>U. Blepharocarpus</i>	pouch, closed
<i>Paracolopha</i>	2(1)	East Asia	<i>Zelkova</i>	pouch, closed
<i>Colophina</i>	4(2)	East Asia	<i>Zelkova</i>	pouch, open
<i>Byrsocrioptoides</i>	2	West Asia	<i>Zelkova</i>	leaf roll, open
<i>Hemipodaphis</i>	3(1)	East Asia-West Asia	<i>Zelkova</i>	leaf roll, open
<i>Ghariesia</i>	1(1)	Himalaya-N America	SH	—

* the total number of species in a genus, with the number of parthenogenetic species found only on the secondary hosts in parenthesis.

** *U. Ulmus*; SH, recorded from secondary hosts.

Schizoneurata is from the secondary host in Florida, North America, and the primary host is unknown. This pattern of species diversity is likely to reflect historical changes in the distributional area of the host plant. It may be hypothesized that the three monotypic genera, *Aphidounguis*, *Schizoneurata* and *Schizoneurella*, represent survivors of ancestral stocks which had a large species diversity before Quaternary glaciation, during which most of the elements became extinct together with the primary host. The low species diversity of galling aphids and their restricted distribution could be explained by assuming a large-scale extinction of ancestral host groups adapted to warm climates during glacial episodes. A similar pattern is found in *Tetraneura* and its allied genera. *Tetraneura* is another large genus, and its sister genus *Paracolopha* is associated with *Zelkova* and represented by only two species. *Zelkova* now has a disjunct and restricted distribution, so, as mentioned above, most local populations of *Zelkova* species may have become extinct since the late Tertiary. Such local extinction of host plants may have been responsible for limited species diversity in aphid genera associated with *Zelkova*, i.e., *Colophina*, *Byrsocryptoides* and *Hemipodaphis*.

The link between great species diversity of *Tetraneura* and *Eriosoma* and a wide and continuous distribution of their *Madocarpus* host plants seems highly plausible. By being associated with host plants that are cold- and arid-tolerant, *Tetraneura* and *Eriosoma* may have evaded extinction, and this may be a reason for their large species diversity.

One *Eriosoma* species, *Eriosoma yangi*, is exceptionally associated with *Ulmus parvifolia*. The association with *Ulmus parvifolia* in *Eriosoma* may be ancestral (ancestral host plant, with a subsequent host shift to *Madocarpus*) or derived (host shift from *Madocarpus* to *U. parvifolia*). The peculiar morphology of *Eriosoma yangi* seems to point to the possibility of an ancestral association with *Ulmus parvifolia*.

The hypotheses presented here can partly be tested by constructing a molecular phylogeny of Eriosomatinae. If these hypotheses are true, each monotypic genus should have branched off the main branch of the phylogeny early on, and these genera, as a whole, should constitute a paraphyletic group. In contrast, species of *Tetraneura* and *Eriosoma* should have diverged rapidly since the late Tertiary, and each of the genera should constitute a monophyletic taxon.

DISJUNCT DISTRIBUTION AND RELICT APHIDS

Possible Examples

The genus *Ghariesia* is monotypic, and *G. polunini* has been recorded from *Carex* spp., originally secondary hosts, at a high elevation of more than 3000 m at three localities: the Himalayan region and two mountainous sites in California, North America (Fig. 1). Based on a morphological comparison, Hille Ris Lambers [27] concluded that the Himalayan and American populations belong to the

same species. The primary host of *Ghariesia* is not known. It is a puzzle to understand this long-distance disjunct distribution at high altitude. Mordvilko's hypothesis may explain this distributional pattern. This hypothesis would propose that during the mid Tertiary this aphid species had expanded its distribution from Eurasia to North America across Beringia, together with an unknown host plant of Ulmaceae. After the extinction of the primary host, *Ghariesia* may have been left on the secondary host at refuges on different continents and may have persisted as a relict. If this hypothesis is true, *Ghariesia polunini* may have originated before the mid Tertiary (at least 12 my ago) when Beringia was covered with deciduous forest for the last time [3]. If this hypothesis is true, a molecular genetic analysis should reveal great genetic differentiation between the Himalayan and California populations.

The genus *Colopha* induces closed-pouch galls on leaves of *Ulmus* species of the section *Blepharocarpus*, that is, *Colopha compressa* on *Ulmus laevis* and *Colopha graminis* and *C. ulmicola* on *Ulmus americana* (Fig. 2). These sexual species are distributed disjunctly in North America and in central Europe, together with the host plants of *Blepharocarpus*. This distribution pattern suggests that the origin of the genus *Colopha* can be traced back to mid Tertiary (at least 12 my ago) for the reason already discussed. In contrast, three parthenogenetic species of *Colopha* are distributed outside the present distribution ranges of *Blepharocarpus*: *Colopha kansugei* and *C. setaricola* in East Asia and *C. hispanica* in Spain (Fig. 2). The origin of these parthenogenetic

species could be explained if the primary hosts, *Ulmus* species of *Blepharocarpus*, became extinct from the ranges of these species and if they have persisted on the secondary hosts while maintaining morphological stasis [28]. This hypothesis predicts that there should be large genetic differentiation between local populations or between clones because the asexual species have accumulated genetic changes without genetic recombination since the extinction of the primary hosts. This prediction can be tested by comparing DNA sequences between local populations of an asexual species.

Test for the Relict Hypothesis

The relict hypothesis was tested using *Colopha kansugei* collected at several localities in East Asia. This species is appropriate for this test because it is common, with a wide distribution range from western Japan to Nepal. Extraction of template DNA from aphid samples, amplification of a 700 bp fragment of the mitochondrial COI gene by PCR, and sequencing are based on Yoshizawa and Johnson [29]. Detailed results are presented elsewhere, and only a synopsis of the results is mentioned here. The relict hypothesis predicts considerable genetic divergence among local parthenogenetic populations of a relict species such as *C. kansugei*. In contrast, the hypothesis predicts less genetic divergence in a species that has been broadly distributed through dispersal by alates. *Tetraneura nigriabdominalis* is broadly distributed over the same range as the ancestral population of *C. kansugei*. Thus, this study compares geographic variation in COI sequences between *C.*

Table 2 Percentage genetic distances (uncorrected p distances) between local populations of *Colopha kansugei* in 700 bp of mitochondrial COI. 1–11, *C. kansugei*; 12, *C. setaricola*. 1 and 5, Chiba prefecture; 2 and 3, Kanagawa prefecture; 6, Fukuoka prefecture; 7–9, Nansei Islands; 10, Wakayama prefecture; 11, Chiangmai, Thailand.

	1	2	3	4	5	6	7	8	9	10	11
1 Tateyama											
2 Hayama	0.143										
3 Yokohama	0.286	0.143									
4 Tokyo	0.714	0.571	0.429								
5 Kashiwa	0.143	0	0.143	0.571							
6 Fukuoka	0.286	0.143	0.286	0.714	0.143						
7 Okinawa	0.286	0.143	0.286	0.714	0.143	0					
8 Ishigaki	1	0.857	1	1.429	0.857	0.714	0.714				
9 Iriomote	0.429	0.286	0.429	0.857	0.286	0.143	0.143	0.857			
10 Kii	2.143	2	2.143	2.571	2	2.143	2.143	2	2.286		
11 Thai	3.286	3.143	3.286	3.429	3.143	3.286	3.286	3.143	3.429	1.143	
12 <i>C. setar</i>	10.71	10.57	10.71	10.29	10.57	10.71	10.71	11.43	10.86	11.86	12

kansugei and *T. nigriabdominalis*.

Large genetic differentiation in the sequence of mitochondrial COI was found between some local populations of *C. kansugei* (Table 2). In particular, the Kii peninsular population differed considerably from other Japanese populations at a level of 2% or more sequence divergence. The Thailand population differed from most of the Japanese populations at more than 3%. A clock for arthropod mtDNA indicates rates of pairwise divergence of about 2% per my for taxa that diverged less than about 3 mya [30–32]. This estimation suggests the Kii and other Japanese populations diverged about 1 mya.

Molecular phylogenies based on the neighbor-joining method and the parsimony method revealed that the Thai population and the Kii population constituted a clade, while the other populations constituted another clade. There were no remarkable differences in morphology between populations of *C. kansugei*. It is difficult to explain the present distribution of the Thai-Kii clade on the basis of geological changes, but there is a possibility that the Kii population represents an ancestral clone that branched off the main clade early on. In sexually reproducing species, this kind of genetic differentiation is unlikely because of interbreeding between neighboring local populations. However, asexual species could maintain ancestral clones in vicinity to the distribution of derived clones. This pattern of genetic differentiation in *C. kansugei* contrasted sharply with the differentiation between populations of *Tetraneura nigriabdominalis*, which is widely distributed from East Asia to Europe on *Ulmus* species of the section *Madocarpus*. The European population of *T. nigriabdominalis* differed from the Hokkaido population by only 0.429% (700 bp), which is roughly equivalent to the differentiation among the Honshu populations of *Colopha kansugei* except for the Kii population. This comparison suggests that *C. kansugei* has continued parthenogenetic reproduction for a long time after the extinction of the primary host, so that a large genetic change has accumulated among local populations. This result is consistent with the relict hypothesis.

The evolutionary history of gall-forming aphids is highly constrained by host plants, and ancestral aphid species or ancestral clones may sometimes have survived the Quaternary if their host plants have persisted in refuges. By estimating the phylogeny and by synthesizing geological, biogeographical and phylogenetic information, we can perhaps understand the general pattern of evolution in gall-forming aphids.

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