Distribution of bisexual and unisexual species in the aphid genus *Colopha* Monell (Aphididae: Eriosomatinae), with the description of a new species in Japan

MASAKAZU SANO & SHIN-ICHI AKIMOTO

*Systematic Entomology, Department of Ecology and Systematics, Graduate School of Agriculture, Hokkaido University, Sapporo, Japan

(Accepted 25 December 2003)

Abstract
Aphids of the genus *Colopha* are represented by three bisexual and three unisexual species. The bisexual species are associated with two *Ulmus* species that are most closely related, being distributed disjunctively in Europe and eastern North America on the host plants. A new unisexual species of *Colopha*, collected from *Setaria chondrachne* (Poaceae) in Japan, is described under the name *Colopha setaricola* sp. nov. The distribution of the three unisexual species is discussed in relation to aphid-plant associations and historical changes in the distribution of the host plants. It is suggested that these unisexual species have persisted on the secondary hosts through parthenogenetic reproduction since the extinction of the primary host plants, *Ulmus* species section *Blepharocarpus*. Therefore, the unisexual species in *Colopha* exemplify Mordvilko’s hypothesis that unisexual species on the secondary host plants have remained as relics in the region where the primary host was once distributed but then became extinct.

Keywords: Parthenogenesis, biogeography, Beringia, disjunct distribution, gall, Ulmus, relics

Introduction
Aphids of the Eriosomatine and Hormaphidine are typically gall formers on broad-leaved deciduous trees and highly specific to their host plants (Blackman and Eastop 2000). Biogeographic evidence suggests that their host associations have a long history tracing back to the early Tertiary (Akimoto 1985; Moran 1989). Throughout the Tertiary and Quaternary, hardwood taxa drastically shifted their distributional ranges depending on global climatic changes, which have resulted in the disjunctive distributions of some taxa, for example in East Asia and eastern North America (Pielou 1979; Tiffney 1985a; Wen 1999). Hardwood trees adapted to mild climates are known to have survived glacial epochs in some fragmented refuges and expanded their distribution to the north in interglacial epochs, with the retreat and expansion of their distribution having been repeated during the
Quaternary (Haffer 1982; Hewitt 1999; Davis and Shaw 2001). The distribution of gall-forming aphids is exclusively dependent on the distribution of their host plants. Thus, for an understanding of the present distributions of aphids, it is necessary to consider past changes in the distributions of their hosts.

Most eriosomatine and hormaphidine aphids are host-alternating between the primary host on which the sexual phase occurs, broad-leaved deciduous trees, and the secondary host, mainly herbaceous plants. However, some species include local populations that have persisted on the secondary host parthenogenetically (Moran 1991), and a few species are wholly parthenogenetic on historically secondary hosts. Mordvilko (1935) presented the hypothesis that permanently parthenogenetic aphid species are relics that have been left on the secondary host since the primary host became extinct. In fact, during the late Tertiary and Quaternary, a number of hardwood species became extinct from local regions (Tiffney 1985b). If Mordvilko’s hypothesis is true, the distributional ranges of parthenogenetic (unisexual) species should be included in the past ranges of the primary host plants. This hypothesis has been criticized because unisexual populations can expand their ranges through dispersal between secondary hosts (e.g. Hille Ris Lambers 1970). However, for aphid species that lack alate migrants between secondary hosts, this hypothesis deserves to be tested.

The genus Colopha Monell (Aphididae, Eriosomatinae, Eriosomatini) is a small aphid group with five described species (Remaudière G and Remaudière M 1997; Barbagallo 2002), which are distributed in Eurasia or North America. This genus consists of three bisexual species, C. compressa, C. graminis and C. ulmicola, and two unisexual species, C. hispanica and C. kansugei. The bisexual species induce closed, cock’s comb-shaped galls on Ulmus spp. and host-alternate between Ulmus and Poaceae or Cyperaceae (Blackman and Eastop 1994, 2000), while the unisexual species reproduce parthenogenetically on Cyperaceae (Akimoto 1985; Nieto Nafria and Mier Durante 1987). This genus is readily recognized by a well-developed setal socket at the ventro-anterior position of fore tarsi in adult exules (Akimoto 1985). The presence of unisexual species and their distribution pattern make this genus a candidate for testing Mordvilko’s hypothesis.

An aphid species collected on Setaria chondrachne (Poaceae) in Takao, Tokyo in 1985 had the characters of the genus Colopha but did not correspond to any known Colopha species. More specimens of this species were recently collected from the same host-plant in two localities of central Japan. We here describe this species formally based on first instar and adult exules and sexuparae. We then examine the validity of Mordvilko’s hypothesis in relation to aphid-plant associations in Colopha and historical changes in the distribution of the host plants.

**Description**

*Colopha setaricola* sp. nov.

Measurements are indicated as ranges and means (in parentheses), based on five individuals from each of the three localities. Drawings are based on materials from one locality, from which the holotype was collected. The holotype and some paratypes are deposited in Systematic Entomology, Hokkaido University, Sapporo, Japan and other paratypes in the National Science Museum, Tokyo, Japan; Departamento de Biología Animal, Universidad de León, León, Spain; and the Natural History Museum, London, UK.
First instar exule

Body (Figures 1, 2) elliptical, 0.64–0.75 (0.70) mm long, 0.37–0.41 (0.40) times as wide as long, with distinct wax gland plates and sclerotized bands scattered over.

Eyes with three ommatidia and, in the space surrounded by them, with about 15 small sclerotized tubercles. Antennae (Figure 3) five-segmented, 0.145–0.170 (0.157) mm long, 0.20–0.24 (0.22) times as long as body, 1.02–1.21 (1.13) times the length of hind femorotrochanter. Antennal segments I–III smooth, segments IV and V spinulose. Antennal setae sparse; setal arrangement on each segment as follows: I 3 (one of which is feeble), II 2, III 0, IV 4, and V 2 + 5. Primary rhinarium surrounded by cilia in a single row, with a circular opening, from which a semi-transparent tonguelet projects. Tonguelet on segment IV small and furcated, that on segment V extending apically like a horn. Some accessory rhinaria present close to primary one, surrounded by cilia in a single row, without a tonguelet. Rostrum reaching abdominal segment IV or V. Ultimate segment (Figure 4) spinulose, with two pairs of accessory setae, 0.075–0.88 (0.82) mm long, 0.55–0.63 (0.59) times the length of hind femorotrochanter.

Femorotrochanter slender, slightly spinulose along hind margin, 0.129–0.145 (0.139) mm long in hind legs. Tibia shorter than femorotrochanter, spinulose, 0.105–0.121 (0.116) mm long in hind legs. Tarsus (Figure 5) spinulose, with six pairs of setae; two pairs dorsally, two pairs ventrally, one pair laterally, and one pair on empodium. In fore legs one of the two dorso-apical setae capitate and longer, but in middle and hind legs the two setae capitate and equal in length. Empodial setae simple, exceeding the point of claws. Hind claws 0.022–0.026 (0.024) mm long, 0.43–0.51 (0.48) times tarsal length.

Wax gland plates (Figure 6) circular or elliptical, consisting of one or two central fields and circumferential cells. Central field microscopically bright, with a broad blackish rim, usually larger than circumferential cells. Circumferential cells with minute blackish points scattered over, surrounding the central field(s) in a single layer. Head (Figures 1, 2) with

Figures 1–6. First instar exule of *C. setaricola*. (1) Body in dorsal view. (2) Body in ventral view. (3) Antenna in ventral view. (4) Ultimate rostral segment. (5) Hind tarsus. (6) Wax gland plate on pleural position of abdominal tergite IV. Scale bar: 0.2 mm (1, 2); 0.1 mm (3); 0.05 mm (4–6).
five pairs of wax gland plates; on the dorsum one pair medio-posteriorly and one pair latero-posteriorly; on the frons one pair; on the ventrum one pair medio-anteriorly and one pair latero-facially. Prothorax with one dorso-spinal pair of wax gland plate and one ventro-lateral pair. Meso- and metathorax and abdominal segments I–VI each with three pairs at dorso-spinal, dorso-pleural and ventro-lateral positions. Abdominal segment VII with one dorso-lateral and one ventro-lateral pairs. Lateral pair rather located on the dorsal side on anterior segments, especially on thorax.

Body setae all simple and short. Head (Figures 1, 2) with eight pairs of setae; on the dorsum one pair outside medio-posterior wax gland plates, one pair outside latero-posterior wax gland plates, one pair laterally just above antennal bases, and one pair medio-anteriorly; on the frons one pair; on the ventrum three pairs facially. Pronotum with two spinal pairs of setae and two lateral pairs. Meso- and metanotum each with one spinal, one pleural and two lateral pairs. Abdominal tergites I–VI each with three pairs at spinal, pleural and lateral positions. Abdominal tergite VII with one spinal and one lateral pair. Abdominal tergite VIII with one pleural pair. Cauda with two setae. Abdominal sternite VIII with four setae.

Abdominal segments I–VI each with one pair of sclerotized bands, on which spinal and pleural setae, and spinal and pleural wax gland plates are situated. Abdominal segments VII and VIII sclerotized dorsally.

Adult exule

Body elliptical, tapering posteriorly, 1.42–1.93 (1.69) mm long, 0.60–0.79 (0.69) times as wide as long, with distinct wax gland plates scattered over.

Eyes with about 10 ommatidia, without small sclerotized tubercles in the space surrounded by them. Arrangement of cephalic setae and wax gland plates (Figure 7) as in the first instar exule, but some wax gland plates rudimentary or absent. Rostrum short, reaching a little beyond fore coxae. Antennae (Figure 8) six-segmented with the division between segments III and IV sometimes incomplete, or rarely five-segmented with segment III completely fused with IV, 0.198–0.251 (0.223) mm long, 0.12–0.16 (0.13) times as long as body, 0.89–1.15 (0.98) times the length of hind femorotrochanter. Primary rhinarium not transversely extended, surrounded by cilia in a single row, with a circular opening, from which a semi-transparent tonguelet projects. Some accessory rhinaria present on segment VI. Antennal setae short and scarce; their arrangement as follows, I 2–3 (one of which is feeble), II 2, III 0–1, IV 0, V 4, and VI 2+–5. Ultimate segment (Figure 9) slightly spinulose, 0.070–0.093 (0.081) mm long, 0.32–0.38 (0.35) times as long as hind femorotrochanter, with two pairs of accessory setae.

Femorotrochanter tapering apically, slightly spinulose along posterior margin, 0.198–0.250 (0.229) mm long in hind legs. Tibia shorter than femorotrochanter. Fore tarsus (Figure 10) short, 0.033–0.046 (0.040) mm long, ventro-apically with a large prominent setal socket, whose seta is stout and shorter than the points of claws, about 0.015 mm long. Middle and hind tarsi (Figure 11) rather long, 0.038–0.55 (0.048) mm long and 0.045–0.063 (0.056) mm long, respectively, without a well-developed setal socket. Arrangement of setae on tarsi as in the first instar exule, but lacking an empodial pair.

Wax gland plates (Figure 12) as in the first instar exule, but central fields weakly rimmed as in circumferential cells with rough blackish points scattered over and sometimes not distinguishable from circumferential cells. Arrangement of wax gland plates as in the first instar exule. Body setae short, as long as the diameter of wax gland plates, arranged in a
transverse row. Cornicles absent. Genital plate (Figure 13) consisting of two lobes, altogether with 10–17 setae, two of which are much stouter and longer and situated at the centre of each lobe. Anal plate (Figure 13) with slightly lifting three lobes, with 11–18 setae and 5–9 feeble setae, the latter of which are scattered along anterior margin of a depression surrounded by three lobes. Cauda with two setae.

**Sexupara**

Materials from the two localities included males and bisexual females in the abdomen, suggesting that they are sexuparae, not alate exules.

Body 1.56–2.16 (1.91) mm long, without wax gland plates or sclerotized bands on abdomen.

Antennae (Figure 14) six-segmented. Antennal segment III the longest, as long as segments IV, V and VI combined, 0.23–0.28 (0.25) mm long. Segment IV a little longer than segment V, but shorter than segments V and VI combined, 0.085–0.11 (0.097) mm long. Segment V a little longer than segment VI, 0.078–0.090 (0.83) mm long. Segment VI slightly spinulose, 0.065–0.083 (0.74) mm long. Antennal setae short, as long as basal width of segment III, arrangement of which as follows; II 2, III 1–6, IV 0–1, V 4, and VI 2+4–5. Secondary rhinaria microscopically represented as bright lines, present on segments III–VI. Those on segments III–V covering usually about half the circumference from the ventral side; some rhinaria much shorter. Secondary rhinarium on segment VI short and rudimentary. Primary rhinarium on segment V not ciliated, without an opening, always connected with the apical secondary rhinarium. Primary rhinarium on segment VI slightly ciliated with a semi-transparent tonguelet, often connected with the apical

---

**Figures 7–13.** Adult exule of *C. setaricola*. (7) Antenna in ventral view. (8) Head in dorsal view. (9) Ultimate rostral segment. (10) Fore tarsus in posterior view. (11) Hind tarsus. (12) Wax gland plates. (13) Genital and anal plates. Scale bar: 0.2 mm (8, 13); 0.1 mm (7, 12); 0.05 mm (9–11).
secondary rhinarium, which is more irregular in shape and sometimes thicker than other secondary ones. Some accessory rhinaria present dorsally on segment VI. Antennal segments III, IV, V, and VI with 12–18, 3–6, 3–5, and 1–3 secondary rhinaria, respectively. Head (Figure 15) dorsally with five pairs of minute setae; one pair medio-posteriorly, one pair latero-posteriorly, one pair medio-anteriorly, one pair latero-posteriorly and one pair frontally. Rostrum short, a little exceeding fore coxae. Ultimate segment (Figure 16) slender, spinulose, with three to five accessory setae, 0.088–0.11 (0.094) mm long, 0.83–1.02 (0.90) times as long as the second segment of hind tarsus.

Hind femorotrochanter 0.41–0.49 (0.46) mm long. Second segment of tarsi with transverse rows of spinules. Empodial pair of setae simple, reaching the points of claws. Second segment of hind tarsus 0.099–0.115 (0.105) mm long, with 10–11 setae, two of which are on empodium.

Cornicles absent. Cauda with two to six setae. Genital plate (Figure 17) depressed in the middle, forming two lobes, altogether with 20–26 setae mainly scattered on lobes. Anal plate (Figure 17) with 17–25 setae. Fore wings with once-branched media. Hind wings with two oblique veins.

Type materials
Holotype: one adult exule, Takao, Hachioji, Tokyo Met., 23 November 1985, ex *Setaria chondrachne* (on the aerial parts), S. Takagi leg. Paratypes: 26 first instar exules, eight adult exules and 10 sexuparae, same data as in holotype; 22 first instar exules, 13 adult exules and 24 sexuparae, Fukiage-gyoen, the Imperial Palace, Tokyo Met., 7 November 2001, ex *S. chondrachne* (on the lamina), Y. Matsumoto leg; 12 first instar exules and six adult exules, Morito-gawa River, Hayama, Kanagawa Pref., 10 November 2002, ex *S. chondrachne* (on the spike and under the leaf), M. Sano leg.
Distribution

Japan (central Honshū).

Host plant

*Setaria chondrachne* (Poaceae). This species forms colonies on the aerial parts of the secondary host, and the colonies are densely covered with a large amount of wax (Figure 18). Primary host plant unknown.

Remarks

Adult exules of *C. setaricola* can be distinguished from those of other *Colopha* species in the antennae, eyes and wax gland plates. *C. setaricola* has usually six-segmented antennae, while other species have four- or five-segmented antennae. *C. setaricola* has eyes consisting of about 10 ommatidia, while other species have only three ommatidia. In *C. setaricola* the wax gland plates have a central field that is weakly rimmed as in circumferential cells, while in other *Colopha* species wax gland plates have a conspicuously rimmed central field.

First instar exules of *C. setaricola* can be distinguished from those of *C. kansugei*, the only species described for this stage, by the abdomen, tarsi and ultimate rostral segment; *C. setaricola* has sclerotized bands on abdominal tergites I–VII, while *C. kansugei* has abdomen not sclerotized; the ultimate rostral segment of *C. setaricola* is densely spinulose, while that of *C. kansugei* is very slightly spinulose; *C. setaricola* has symmetrical claws and symmetrical dorso-apical setae on middle and hind tarsi, while *C. kansugei* has asymmetrical claws and asymmetrical dorso-apical setae on middle and hind tarsi.

Figure 18. A colony of *Colopha setaricola* on *Setaria chondrachne*. (Photographed in Fukiage-gyoen, the Imperial Palace, Tokyo, Japan; courtesy of Y. Matsumoto.)
Life cycle

It is likely that this species reproduces parthenogenetically on the secondary host plants, although sexuparae are produced in autumn. No alate exules have been found. Despite our extensive survey and a long history of galling aphid studies in Japan (Matsumura 1917; Monzen 1929; Shinji 1941, 1944; Yukawa and Masuda 1996), no galls of Colopha species have been found on Ulmus spp. or Zelkova serrata.

Distribution and host plants of other Colopha species

Approximate distributional ranges of six Colopha species are illustrated in Figure 19, and the primary and secondary host species for six Colopha species are tabulated in Table I.

C. compressa is widely distributed in continental Europe ranging from southern Scandinavia to the north of the Pyrenees and Alps, and east to Turkey and the European former USSR. In these regions, mainly Ulmus laevis, occasionally U. minor (=campestris and foliacea), U. glabra (=scabra) and U. celtidea are reported as the primary host species. In contrast to the primary hosts, the secondary host species of C. compressa are Carex spp. (Cyperaceae), rarely Eriophorum (Cyperaceae), and grass species. C. graminis and C. ulmicola are distributed in North America, and the primary host species are mainly U. americana, occasionally U. rubra. The secondary host species of C. graminis and C. ulmicola are some grass species.

C. hispanica is found in northern Spain, and its primary host species is Scirpus holoschoenus (Cyperaceae). C. kansugei is found in East Asia, and its secondary host species are Carex lenta and Carex brunnea (Cyperaceae). C. setaricola sp. nov. is found in central Japan, and its secondary host species is Setaria chondrachne (Poaceae).

Figure 19. Approximate distributional ranges of six Colopha species. Plain and dotted areas indicate the range of bisexual and unisexual species, respectively.

Table I. The primary and secondary host species for six Colopha species

| Colopha species (distribution) | The primary host species | The secondary host species |
|-------------------------------|--------------------------|---------------------------|
| C. compressa (Europe)         | Ulmus laevis, occasionally U. minor, U. glabra and U. celtidea | Carex spp. (Cyperaceae), rarely Eriophorum (Cyperaceae), and grass species |
| C. graminis (North America)  | U. americana, and occasionally U. rubra | Some grass species |
| C. ulmicola (North America)  | U. americana, and occasionally U. rubra | Some grass species |
| C. hispanica (northern Spain) | –                         | Scirpus holoschoenus (Cyperaceae) |
| C. kansugei (East Asia)       | –                         | Carex lenta and Carex brunnea (Cyperaceae) |
| C. setaricola sp. nov. (central Japan) | –                           | Setaria chondrachne (Poaceae) |
hosts (Börner 1952; Tuatay and Remaudière 1964; Shaposhnikov 1967; Szelegiwicz 1968; Rupais 1969; Achremowicz 1972; Heie 1980). There are a few reports from U. minor in Spain and Italy (Remaudière et al. 1986; Roberti 1990–91; Barbagallo and Patti 1994) where no U. laevis is distributed (Tutin 1964). Only unisexual populations are reported from Britain and Iceland (Hille Ris Lambers 1955; Stroyan 1964, 1976). C. compressa infests roots of Carex spp. as the secondary host (Börner 1952; Shaposhnikov 1967; Szelegiwicz 1968; Heie 1980), with exceptional records of Eriophorum (Stroyan 1964) and grass species (Shaposhnikov 1967).

*C. hispanica* is unisexual, recorded from northern Spain and endophytic inside the stems of Scirpus holoschoenus (Nieto Nafria and Mier Durante 1987).

*C. kansugei* is know as an anholocyclic (unisexual) species, having a wide range stretching from Nepal through China to south-western Japan (Akimoto 1985) and south to northern Thailand (Sano and Akimoto unpublished). This species is associated with *Carex lenta* in Japan (Moritsu 1983; Matsumoto 1999, 2000) and *Carex brunnea* in Taiwan (Takahashi 1937). A record from Carex morrowii by Uye (1924) is doubtful, because at the time of the record several species of Carex were confused under the name of Carex morrowii; *C. kansugei* has not been found from *Carex morrowii* (Matsumoto 1999, 2000).

*C. graminis* and *C. ulmicola* are holocyclic (bisexual) and widely distributed in North America (Smith and Parron 1978; Blackman and Eastop 1994). Both species are collected mainly from *U. americana*, and occasionally from *U. rubra (= fulva*) as the primary host, and from the roots of some grass species as the secondary host (Patch 1910; Hottes and Frison 1931; Gillette and Palmer 1934; Knowlton 1983; Smith 1985).

**Discussion**

*Mordvilko’s hypothesis*

Most host-alternating species of eriosomatine and hormaphidine aphids are able to persist on the secondary host parthenogenetically all year round. Obligatorily or facultatively unisexual strains may often coexist with bisexual strains on the secondary host (Bodenheimer and Swirski 1957; Moran 1991). Obligatorily unisexual populations are sometimes distributed beyond the ranges of the primary host plant, as shown in *C. compressa*. A few species consist of unisexual populations alone, as in *C. setaricola*. Mordvilko (1935) hypothesized that unisexual strains would be distributed outside the range of the primary host if bisexual strains became extinct due to local extinction of the primary host in cold and arid climates but unisexual strains survived on the more cold-tolerant secondary host. Mordvilko (1935) 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, unisexual populations may have reproduced parthenogenetically over a long period of time since the extinction of the primary host. Based on molecular phylogeny, for example, von Dohlen et al. (2002) inferred that a unisexual North American *Hamamelistes* species has persisted on the secondary host for 2–4 million years.

Several eriosomatine and hormaphidine species can migrate over a long distance through dispersal of alate exules that fly from secondary host to secondary host. Some authors (e.g. Bodenheimer and Swirski 1957; Hille Ris Lambers 1970) criticized Mordvilko’s hypothesis on the grounds that unisexual strains can expand their range by alate migration beyond the range of the primary host where bisexual and unisexual strains coexist. If this criticism is true, the origins of unisexual populations should be more recent events than Mordvilko’s
hypothesis predicts. Whether Mordvilko’s hypothesis is applicable to the origin of two East Asian unisexual species, *C. setaricola* and *C. kansugei*, is evaluated by invoking fossil records of the host plants.

**Disjunctive distribution and Land Bridge**

The bisexual species *C. compressa*, *C. graminis* and *C. ulmicola* are mostly recorded from *Ulmus laevis* or *U. americana*, with occasional records from other *Ulmus* species (Table 1). A recent study based on molecular phylogeny indicates that *U. laevis* and *U. americana* are sister species, comprising the section *Blepharocarpus* (Wiegrefe et al. 1994), distributed disjunctively in Europe (*U. laevis*) and eastern North America (*U. americana*) (Tutin 1964; Bate-Smith and Richens 1973; Sherman-Broyles et al. 1997). Disjunctions between East Asia and eastern or western North America are more common patterns of intercontinental distribution in temperate biota, so the distribution pattern of this section requires explanation. Intercontinental disjunctions have usually been explained by ancestral, continuous distribution across the Bering Land Bridge or the Atlantic Land Bridge and subsequent separation and isolation into two continents. The Bering Land Bridge that connected East Asia and North America was inhabited by deciduous broad-leaved trees from the Eocene to Middle Miocene, whereas the Atlantic Land Bridge that connected Europe and eastern North America was available for dispersion of temperate biota from the Paleocene to the Early Eocene (reviewed by Pielou 1979; Wen 1999; Sanmartín et al. 2001).

The fossils of *Ulmus* fruits that provide diagnostic characters for the genus are traceable back to the sediment of the Eocene in western North America and the Oligocene in East Asia (Manchester 1989). Fossil leaves of *Ulmus* are recorded from the sediment of the Eocene in Japan (Endo 1968; Tanai 1972) although fossil records without fruits are less reliable for identification. In Europe, although a number of fossil records of *Ulmus* fruits and leaves have been documented, none of them is found before the middle Oligocene (Manchester 1989). Dispersion of *Ulmus* through the Atlantic Land Bridge would predict much older records of *Ulmus* fossils in Europe. Temperate broad-leaved deciduous forests had expanded from East Asia to western North America through the Beringia by the Middle Miocene, with the same species found both from Asia and from Alaska, such as *Ulmus newberryi* and *Zelkova oregontiana* (Wolfe and Leopold 1967). These lines of evidence are consistent with the hypothesis of the dispersion of *Blepharocarpus* across the Bering Land Bridge rather than across the Atlantic Land Bridge. If this hypothesis is true, the section *Blepharocarpus* may have had a continuous and extensive distribution from Eurasia to North America.

**Origin of Colopha and unisexuality**

Gall-forming aphids are highly host specific (Eastop 1973; Wool 1984). The three bisexual species form closed, cock's comb-shaped galls (Blackman and Eastop 1994, 2000) on *Ulmus* species of *Blepharocarpus*. This gall shape and the morphology of fore tarsi in exules are peculiar to *Colopha* among eriosomatine aphids, suggesting that *Colopha* is monophyletic. If the speciation and diversification of *Colopha* species have proceeded in association with this section of *Ulmus*, the origin of *Colopha* can trace back prior to the Middle Miocene when the section *Blepharocarpus* is considered to have expanded in Asia.
and North America through the Bering Land Bridge. The ancestral stock of *Colopha* may have had an extensive distribution on this section of *Ulmus*, resulting in the present disjunctive distribution.

Two unisexual species, *C. setaricola* and *C. kansugei*, are distributed in East Asia where no *Ulmus* species of the section *Blepharocarpus* are present. However, fossils of this section were found from the Tertiary flora of Japan and Kazakhstan (Grudzinskaya 1967). Furthermore, Tanai (1961) pointed out that the fossil *U. appendiculata* from the Neogene sediment in Japan closely resembles the extant *U. americana*. Thus, the ancestors of *C. setaricola* and *C. kansugei* may have formed galls on the ancestors of *Blepharocarpus*, which have probably become extinct from East Asia. The ranges of *C. setaricola* and *C. kansugei*, stretching from Nepal to south-western Japan (Figure 19), are included in the area that functioned as a refuge for temperate biota during the glacial epochs (Haffer 1982). Unisexual populations of *C. setaricola* and *C. kansugei* may have survived on the secondary host as relics in East Asia since the extinction of the primary host.

*C. hispanica* is distributed in northern Spain where no *U. laevis* occurs naturally (Tutin 1964). The Iberian Peninsula is known to have been one of the refuges for temperate biota during the glacial epochs (Haffer 1982; Taberlet et al. 1998; Hewitt 1999). Therefore, it is also possible that *C. hispanica* has survived in the refuge after the local extinction of the primary host.

There is no sound evidence that a unisexual species was derived from another unisexual species, but it is conceivable that unisexual populations were genetically differentiated among local regions during the expansion of the range to the extent that the morphology of a local unisexual population is recognized as a distinct species. If this were true, the most recent ancestors of *C. setaricola* and *C. kansugei* may not have been gall-formers. But this would require the production of alate exules, by which unisexual populations of, for example, *C. compressa* may have expanded the distribution to East Asia. However, alate exules have not been reported for *C. setaricola* nor for most populations of *C. kansugei* except for the Nepalese population (Akimoto 1985). Therefore, it is most likely that *C. setaricola* and *C. kansugei* originated in East Asia.

The distributional ranges of the three unisexual species of *Colopha* are outside the present range of the section *Blepharocarpus*. However, the disjunctive distribution of *Blepharocarpus* suggests that the elements have become extinct in several localities including the present ranges of the unisexual species. Therefore, it is concluded that the origins and present distributional pattern of the unisexual species are consistent with Mordvilko’s hypothesis. Many fossil species of *Ulmus* that are now extinct are reported from the Neogene flora of Japan (Tanai 1961). If the section *Blepharocarpus* has become extinct from East Asia since the Neogene, *C. setaricola* and *C. kansugei* would have a history of parthenogenesis of more than 1.6 million years.

**Acknowledgements**

We thank M. Suwa and K. Yoshizawa for their many valuable comments on the manuscript, and S. Takagi and Y. Matsumoto for their kind offer of the materials. We also thank Y. Matsumoto for helping with taking the photograph, and Y. Suzuki and Y. Matsumoto for their assistance with the senior author’s collection in Kanagawa Prefecture. This research is supported in part by a 21st-Century COE Programme on “Neo-Science of Natural History” (Programme Leader: Hisatake Okada) at Hokkaido University financed by the Ministry of Education, Culture, Sports, Science and Technology, Japan.
References

Achremowicz J. 1972. Mszyce (Homoptera, Aphidoidea) Niziny Wielkopolsko-kujawskiej II. Fragm Faunistica 18:1–32.

Akimoto S. 1985. Taxonomic study on gall aphids, Colepho, Paracolopha and Kaltenbachia (Aphidoidea: Pemphigidae) in East Asia, with special reference to their origins and distributional patterns. Insecta Matsumurana New Ser 31:1–79.

Barbagallo S. 2002. Zelkovaphis trinacriae, a new Eriosomatine aphid genus and species living on Zelkova in Sicily (Rhyynchota: Aphididae). Boll Zool Agrar Bachicolt Ser II 34:281–301.

Barbagallo S, Patti I. 1994. Appunti faunistici sugli Apidi (Homoptera Aphidoidea) dell’Italia nord-orientale. Boll Zool Agrar Bachicolt Ser II 26:59–114.

Bate-Smith EC, Richens RH. 1973. Flavonoid chemistry and taxonomy in Ulmus. Biochem Syst 1:141–146.

Blackman RL, Eastop VF. 1994. Aphids on the world’s trees: an identification and information guide. Wallingford: CAB International. 1004 p.

Blackman RL, Eastop VF. 2000. Aphids on the world’s crops: an identification and information guide. 2nd ed., Chichester: John Wiley & Sons. 466 p.

Bodenheimer FS, Swirski E. 1957. The Aphidoidea of the Middle East. Jerusalem: The Weizmann Science Press of Israel. 378 p.

Börner C. 1952. Europae centralis Aphides: die Blattläuse Mitteleuropas: Namen, Synonyme, Wirtspflanzen, Generationszyklen. Mitt Thüring Bot Ges 3:1–488.

Davis MB, Shaw GR. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292:673–679.

Eastop VF. 1973. Deductions from the present day host plants of aphids and related insects. In: van Emden HF, editor. Insect/plant relationships. London: Blackwell Scientific Publications. p 157–178.

Endo S. 1968. The flora from the Eocene Woodwardia Formation, Ishikari Coal Field, Hokkaido, Japan. Bull Natl Sci Mus 11:411–449, Plates 1–26.

Gillette CP, Palmer MA. 1934. The Aphidae of Colorado: part III. Ann Entomol Soc Am 27:133–255.

Grudzinskaya IA. 1967. Ulmaceae and reasons for distinguishing Celtidoideae as a separate family Celtidaceae Link. Bot Zh 52:1723–1749, (Rus with Eng summary).

Haffer J. 1982. General aspects of the refuge theory. In: Prance GT, editor. Biological diversification in the tropics. New York: Columbia University Press. p 6–24.

Heie OE. 1980. The Aphidoidea (Hemiptera) of Fennoscandia and Denmark I: general part, the families Mindaridae, Hormaphididae, Thelaxidae, Ameerciidae, and Pemphigidae. Klimpenborg: Scandinavian Science Press. 236 p.

Hewitt GM. 1999. Post-glacial re-colonization of European biota. Biol J Linn Soc 68:87–112.

Hille Ris Lambers D. 1955. Hemiptera 2: Aphididae. In: Fröbrikkson A, Tuxen SL, editors. The zoology of Iceland. Copenhagen: Einar Munksgaard. p 1–29.

Hille Ris Lambers D. 1970. A study of Tetramena Hartig, 1841 (Homoptera, Aphididae), with descriptions of a new subgenus and new species. Boll Zool Agrar Bachicolt Ser II 9:21–101.

Hottes FC, Frison TH. 1931. The plant lice, or Aphididae, of Illinois. Ill Nat Hist Surv Bull 19:121–447.

Knowelton GF. 1983. Aphids of Utah. Utah State Univ Res Bull 509:i–iii, 1–155.

Manchester SR. 1989. Systematics and fossil history of the Ulmaceae. In: Crane PR, Blackmore S, editors. Evolution, systematics, and fossil history of the Hamamelidaceae. Volume 2, “Higher” Hamamelidaceae. London: Oxford Science Publications. p 221–251.

Matsumoto Y. 1999. Aphids of Chiba prefecture. In, Biological Society of Chiba Prefecture, Fauna of Chiba prefecture. Tokyo: Bun-ichi Sogo Shuppan. p 288–299, (Jpn).

Matsumoto Y. 2000. Aphids (Insecta, Homoptera, Sternorrhyncha) of the Imperial Palace, Tokyo, Japan. Mem Natl Sci Mus 36:83–98, (Jpn with Eng summary).

Matsumura S. 1917. Synopsis of the Pemphigidae of Japan. In, Nawa Entomological Laboratory, A collection of essays for Mr. Yasusi Nawa. Gifu: Nawa Entomological Laboratory. p 39–94, Plates 10–13.

Monzen K. 1929. Studies on some gall producing aphids and their galls. Saito Ho-on Kai Monogr 1:1–80, Plates 1–17.

Moran NA. 1989. A 48-million-year-old aphid-host plant association and complex life cycle: biogeographic evidence. Science 245:173–175.

Moran NA. 1991. Phenotype fixation and genotypic diversity in the complex life cycle of the aphid Pemphigus beta. Evolution 45:957–970.

Mordvilko A. 1935. Die Blattläuse mit unvollständigem Generationszyklus und ihre Entstehung. Ergeb Fortschr Zool 8:36–328.
Moritsu M. 1983. Aphids of Japan in colors. Tokyo: Zenkoku Nóson Kyóiku Kyókai. 545 p. (Jpn).
Nieto Nafría JM, Mier Durante MP. 1987. Colopha hispanica sp. n. (Homoptera: Aphidoidea: Pemphigidae): an unusual endophytic aphid living inside the stems of Scirpus holoschoenus (Cyperaceae). Syst Entomol 12:221–230.
Patch EM. 1910. Gall aphids of the elm. Maine Agric Exp Stn Bull 181:193–240, Figures 126–197.
Pielou EC. 1979. Biogeography. New York: Wiley-Interscience. 351 p.
Remaudière G, Nieto Nafría JM, Mier Durante MP. 1986. Nuevas aportaciones al conocimiento de la fauna española de pulgones (Hom. Aphidoidea). Bol Asoc Esp Entomol 10:313–333.
Remaudière G, Remaudière M. 1997. Catalogue des Aphididae du monde. Paris: Institut National de la Recherche Agronomique. 473 p.
Robert D. 1990–91. Gli Afidi d’Italia (Homoptera-Aphidoidea). Entomologica 25/26:3–387.
Rupais A. 1969. Atlas of the Baltic dendrofilous plantlice. Riga: Publishing House Zinátne. 364 p, (Rus).
Sanmartín I, Enghoff H, Ronquist F. 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. Biol J Linn Soc 73:345–390.
Shaposhnikov GKh. 1967. Suborder Aphidinea. In: Bei-Bienko GYa, editor. Keys to the insects of the European USSR. Volume 1, Jerusalem: Israel Program for Scientific Translations. p 616–799.
Sherman-Broyles SL, Barker WT, Schulz LM. 1997. Ulmaceae Mirbel. In, Flora of North America Editorial Committee, Flora of North America north of Mexico. Volume 3, Magnoliophyta: Magnoliidae and Hamamelidae, Oxford: Oxford University Press. p 368–375.
Shinji O. 1941. Monograph of Japanese Aphididae. Tokyo: Shûkyôsya Shoin. 1215 p, 8 plates. (Jpn).
Shinji O. 1944. Galls and gall insects. Tokyo: Shunyodo. p 580 p, 3 plates. (Jpn).
Smith CF. 1985. Pemphiginae in North America. In: Szélégiewicz H, editor. Evolution and biosystematics of aphids. Warszaw: Zakład Narodowy Im. Ossolińsckich Wyawnictwo. p 277–302.
Smith CF, Parron CS. 1978. An annotated list of Aphididae (Homoptera) of North America. N C Agric Exp Stn Tech Bull 255:i–viii, 1–428.
Stroyan HLG. 1964. Notes on hitherto unrecorded or overlooked British aphid species. Trans R Entomol Soc Lond 116:29–72.
Stroyan HLG. 1976. A supplement to the Scottish aphid fauna. Glasg Nat 19:235–258.
Szelégiewicz H. 1968. Mszyce Aphidoidea. Warszaw: Państwowe Wydawnictwo Naukowe. p 316 p, 1 map.
Taberlet P, Fumagalli L, Wust-Saussy A-G, Cosson J-F. 1998. Comparative phylogeography and postglacial colonization routes in Europe. Mol Ecol 7:453–464.
Takahashi R. 1937. Some Aphididae from South China and Hainan (Homoptera), II. Lingnan Sci J 16:199–208.
Tanai T. 1961. Neogene floral change in Japan. J Fac Sci Hokkaido Univ Ser IV Geol Mineral 10:119–398, Plates 1–32.
Tanai T. 1972. Tertiary history of vegetation in Japan. In: Graham A, editor. Floristics and paleofloristics of Asia and eastern North America. Amsterdam: Elsevier Publishing Co. p 235–255.
Tiffney BH. 1985a. Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. J Arnold Arbor 66:73–94.
Tiffney BH. 1985b. The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere. J Arnold Arbor 66:243–273.
Tuatay N, Remaudière G. 1964. Première contribution au catalogue des Aphididae (Hom.) de la Turquie. Rev Pathol Veg Entomol Agric Fr 43:243–278.
Tutin TG. 1964. Ulmus L. In: Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA, editors. Flora Europaea. Volume 1, Lycopodiaceae to Platanaceae, Cambridge: Cambridge University Press. p 65.
Uye T. 1924. New species of Aphididae and Pemphigidae. Insect World 28:408–411. (Jpn).
von Dohlen CD, Kurosu U, Aoki S. 2002. Phylogenetics and evolution of the eastern Asian–eastern North America disjunct aphid tribe, Hormaphidini (Hemiptera: Aphididae). Mol Phylogenet Evol 23:257–267.
Wen J. 1999. Evolution of eastern Asian and eastern North American disjunct distributions in flowering plants. Annu Rev Ecol Syst 30:421–455.
Wiegrefe SJ, Sytsma KJ, Guries RP. 1994. Phylogeny of elms (Ulmus, Ulmaceae): molecular evidence for a sectional classification. Syst Bot 19:590–612.
Wolfe JA, Leopold EB. 1967. Neogene and early Quaternary vegetation of northwestern North America and northeastern Asia. In: Hopkins DM, editor. The Bering Land Bridge. Stanford (CA): Stanford University Press. p 193–206.
Wool D. 1984. Gall-forming aphids. In: Ananthakrishnan TN, editor. Biology of gall insects. London: Edward Arnold. p 11–58.
Yukawa J, Masuda H. 1996. Insect and mite galls of Japan in colors. Tokyo: Zenkoku Nóson Kyóiku Kyókai. 826 p. (Jpn with Eng explanation for colour plates).