

The strawberry aphid complex, *Chaetosiphon (Pentatrichopus) spp.* (Hemiptera: Aphididae): taxonomic significance of variations in karyotype, chaetotaxy and morphology

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Abstract

Holocyclic populations of aphids of the *Chaetosiphon (Pentatrichopus) fragaefolii* (Cockerell) group from *Fragaria* in British Columbia were found to have a homozygous $2n = 12$ female karyotype, whereas samples from predominantly anholocyclic populations in Oregon, California, England and New Zealand have 13, 14, 15 or 17 chromosomes showing various degrees of structural heterozygosity. The 17-chromosome form is a morphologically recognizable taxon, *C. jacobi* Hille Ris Lambers. The other karyotypes apparently represent a series of parthenogenetic lineages derived from the $2n = 12$ holocyclic form and carrying one, two or three autosome dissociations. The North American populations showed no correlation between karyotype and the number of submarginal setae, a character previously used in attempts to differentiate taxa within this species complex in western North America. Submarginal setal number varied greatly within and between clones and tended to increase in successive generations from the fundatrix, confirming that this character varies both genetically and seasonally and has little taxonomic value. Populations of the *fragaefolii* group from *Rosa* spp. in North America have a shorter rostrum than those from *Fragaria*. The name *C. thomasi* Hille Ris Lambers is assigned to this rose-feeding species, which is holocyclic on *R. rugosa* in British Columbia and colonizes *Potentilla* spp. (but apparently not *P. anserina*) as alternative hosts. Old World populations on *Fragaria*, presumably originating from North America, have longer siphunculi than North American populations of *fragaefolii* and few or no submarginal setae; these differences are probably due to founder effects. Both Old and New World populations of *fragaefolii* use *P. anserina* as an alternative host-plant.

Introduction

Aphids of *Chaetosiphon* subgenus *Pentatrichopus* are important as vectors of strawberry viruses in many parts of the world. Distinct species of this group occur on *Rosa* and *Potentilla*, but the complex of species associated with *Fragaria* is a long-standing taxonomic problem, particularly in North America where four strawberry-feeding species are recognized (Schaefers, 1960). *C. minor* (Forbes) in eastern North America, and *C. jacobi* Hille Ris Lambers in the west, are reasonably distinct forms found only on *Fragaria* species, but the other two nominal taxa, *fragaefolii* (Cockerell) and *thomasi* Hille Ris

Lambers, occur sympatrically, colonize species of *Rosa*, *Potentilla* and *Fragaria*, and are distinguished from each other only by the number of submarginal setae on the first four abdominal tergites.

Schaeffers (1960) made a detailed study of the variation in this character in Californian populations of *C. fragaefolii/thomasi*. He found a bimodal distribution of submarginal setal number in one field population, and progeny in laboratory clones tended to inherit high or low setal numbers from their mothers. However, this character varied widely within as well as between clones and could not be used to allocate many individual specimens to either *fragaefolii* or *thomasi*. Richards (1963) thought there was only one species, explaining the variation in terms of differing degrees of neotenic development. Crock & Shanks (1983) supported this view when they showed that a single laboratory clone could 'switch', using the criterion of submarginal setal number, from *fragaefolii*- to *thomasi*-type aphids and back again in the course of three generations.

Outside North America, introduced populations of *Chaetosiphon* on *Fragaria* generally have few or no submarginal setae and have therefore generally been regarded as *fragaefolii*.

In this paper, we report variation in the karyotype of members of *Chaetosiphon* subgenus *Pentatrachopus*, which may help to interpret relationships within this group. We report further on the variation in chaetotaxy in different clones of the *fragaefolii* group. We also demonstrate morphological differences between rose- and strawberry-feeding populations in North America, and between Old World and New World populations on *Fragaria*.

Materials and methods

Thirty-eight samples of populations of the *C. fragaefolii/thomasi* group were examined cytologically. Of these, 19 originated from overwintered eggs (14 from cultivated *Fragaria* and 5 from *R. rugosa*) in British Columbia, while the remainder were from presumed anholocyclic populations on commercial strawberry varieties in Oregon (14), California (1), England (1) and New Zealand (1), and on *R. multiflora* in New Zealand (2). A clone of *C. jacobi* from California, one sample of *C. minor* from Ontario, two samples of *C. tetraerhodum* (Walker) (both from England) and one of *C. coreanum* (Paik) (from Japan) were also karyotyped.

The aphids were fixed in 3 parts methanol:1 part glacial acetic acid and chromosome preparations made according to Blackman (1980). After dissecting out the embryos for karyotyping, whole-mount slide preparations were made of their mothers for morphological study. Selected prometaphase chromosome sets were photographed. Negatives were projected onto graph paper and the outlines of the chromosomes traced for measurement of relative lengths. Relative lengths of individual chromosomes were expressed as percentages of the summed lengths of all chromosomes of the set.

For studies of chaetotaxy, 50 fundatrices originating as eggs or first-instar nymphs from a commercial strawberry field (cv. Totem) in Abbotsford, British Columbia, were caged individually on isolated plants of an alpine strawberry (*Fragaria vesca semperflorens*). After they had produced 10–15 progeny, the adult fundatrices were preserved and mounted for microscopical examination to determine the numbers of submarginal setae. Five clones started from fundatrices with totals of 0, 1, 2, 5 and 6 submarginal setae on abdominal tergites 1–4 were each maintained for five generations in controlled conditions (15–17°C, 16-h photoperiod with light intensity 70 μE per m^2 per sec). The submarginal setae of a sample from each clone were counted in each generation.

For morphometric study, adult aphids were mounted in Canada balsam after maceration, dehydration and clearing by Martin's method (Blackman & Eastop, 1984, p. 376). Body length was measured from the centre of the frons (excluding antennal tubercles) to the end of the abdomen (excluding cauda). The last segment of the rostrum (i.e. the combined segments 4 and 5) was measured from its base to the tips of the distal sensory papillae.

Results

Karyotypes of holocyclic populations of the C. fragaefolii group

Aphids of the *fragaefolii* group overwinter as eggs on both *Rosa* and *Fragaria* in British Columbia. In spring 1985, 14 samples were collected either as eggs or fundatrices from *Fragaria* and five from *Rosa*. One individual fundatrix, or one of its progeny, was karyotyped from each sample. All had $2n = 12$, and appeared structurally homozygous with six pairs of chromosomes (Figs 1a & 2A). The longest chromosome pair were more condensed in prophase than the other five pairs and often had terminal associations with nucleoli; by analogy with numerous other aphid species, these are assumed to be the X chromosomes, although this can only be fully confirmed when male karyotypes have been seen.

Mean relative lengths of chromosomes in prometaphase nuclei of samples from the holocyclic populations on *Fragaria* and *Rosa* are compared in Table I. It is impossible to test the data critically because of the accumulated errors involved in the measuring, ranking and pairing procedure, but the length relationships of the chromosomes of aphids

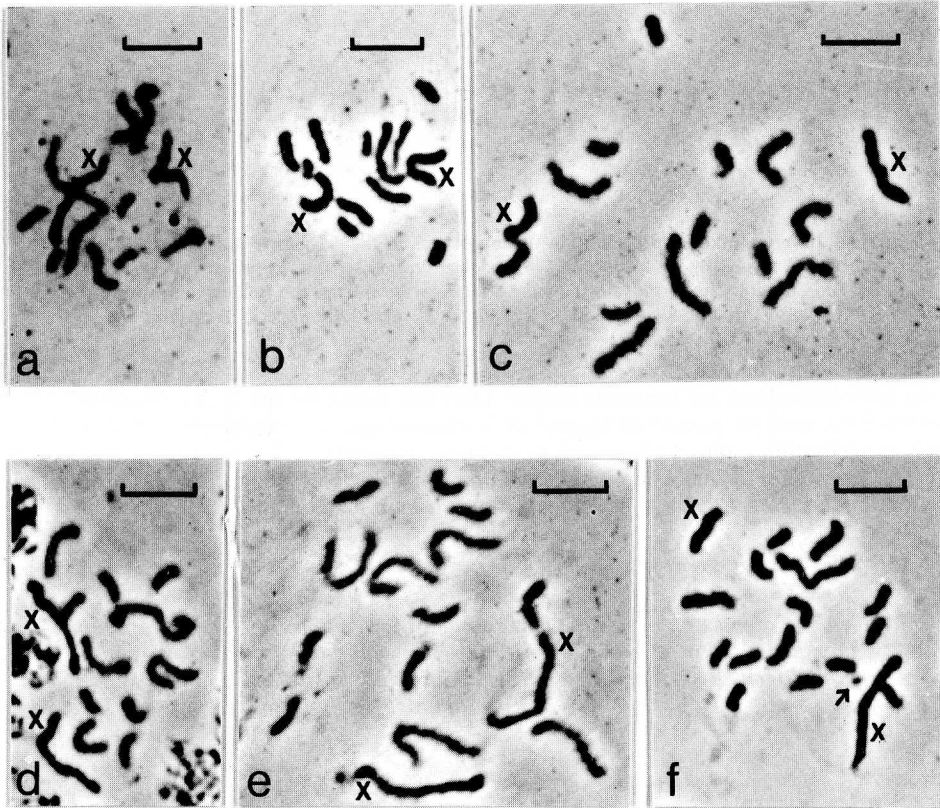


Fig. 1.—Somatic cell prometaphase chromosome sets from embryos of *Chaetosiphon fragaefolii* group virginoparae from western North America; a, $2n = 12$ holocyclic form from British Columbia; b, 13-chromosome (8l,5s) form from Oregon; c, 14-chromosome (8l,6s) form from Oregon; d, 13-chromosome (7l,6s) form from Oregon; e, 14-chromosome (7l,7s) form from Oregon; f, *Chaetosiphon jacobi*, with 17 chromosomes, from California (satellite arrowed). (Putative X chromosomes are marked 'X'. Scale bar represents $5 \mu\text{m}$.)

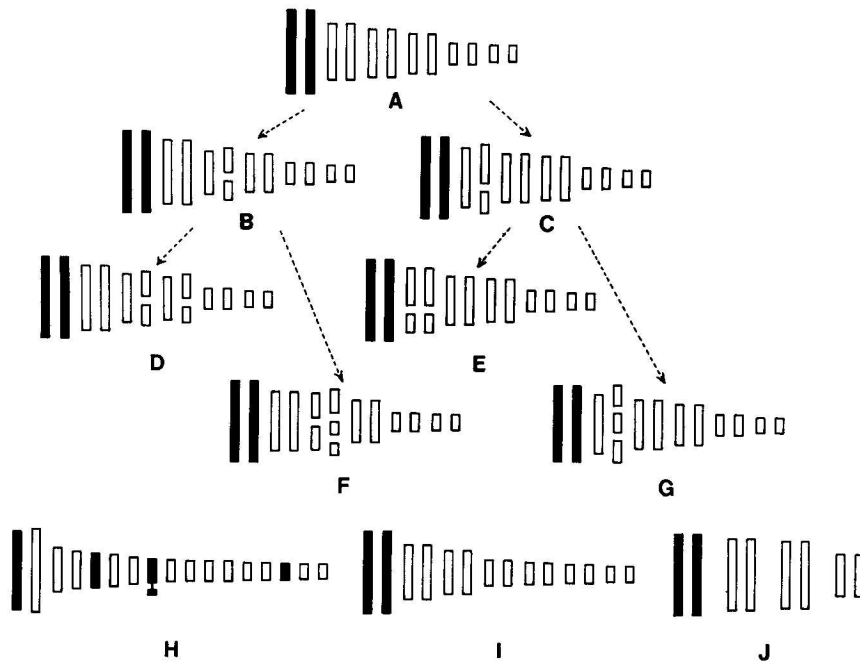


Fig. 2.—Idiogrammatic representation of karyotypes in the *Chaetosiphon fragaefolii* group (putative X chromatin is black); A, holocyclic, $2n = 12$ from *Rosa* or *Fragaria*; B–G, presumed anholocyclic forms and their possible derivation from the holocyclic form by one, two or three dissociations; H, *C. jacobi*; I, *C. tetraerhodum*; J, *C. coreanum*.

from both host-plants are generally similar. Only the values for the X chromosomes differ significantly, and the measured lengths of X chromosomes are particularly unreliable as their condensation is out of phase with that of the autosomes.

The karyotype of one sample of *C. minor*, which is holocyclic on *Fragaria* in eastern North America, was also $2n = 12$ and appeared structurally homozygous.

TABLE I. Comparison of mean relative lengths of chromosomes, pairing presumed homologues, in the prometaphase nuclei of embryos of fundatrices and fundatrigeniae of *Chaetosiphon fragaefolii* group from *Rosa* and *Fragaria* in British Columbia

Number of nuclei measured		<i>Rosa</i>		<i>Fragaria</i>	
		8		20	
Mean relative length	X	Mean	s.e.	Mean	s.e.
		A1	10.43	0.33	11.28
A2	8.88	0.23	9.26	0.15	
A3	7.73	0.14	7.53	0.18	
A4	3.73	0.31	4.01	0.07	
A5	3.01	0.18	3.30	0.09	

Only the X chromosomes differ significantly between host-plants ($P < 0.05$).

Karyotypes of anholocyclic populations of the C. fragaefolii group

Aphids of the *C. fragaefolii* group overwinter parthenogenetically in most parts of the world where they are of economic importance as pests of strawberry. None of the samples examined from presumed anholocyclic populations on cultivated *Fragaria* in Oregon and California, USA, had the 'normal' diploid $2n = 12$ karyotype. On the contrary, they showed varying degrees of structural heterozygosity (Figs 1*b-e* & 2*B-G*). Relative length data are again impossible to test statistically in any meaningful way, but by comparing the different karyotypes with each other and with the $2n = 12$ form it is possible to arrange the chromosomal elements according to a 'best fit' hypothesis in each case, based on the assumption that one or two dissociations of one or both autosomes of pairs 1, 2 and 3 have occurred (Table II & Fig. 2). No evidence was found of involvement of the X chromosome pair in any of these changes.

A population of *C. fragaefolii* group aphids on *R. multiflora* in New Zealand had 14 chromosomes and resembled in karyotype the 14-chromosome form from the strawberries at Howell Prairie, Oregon (perhaps homozygous for a dissociation of the autosome 1 pair; karyotype E in Fig. 2); but this population had a consistently shorter terminal antennal process than North American populations on *Fragaria* and may have evolved in association

TABLE II. Mean relative lengths of chromosomes in prometaphase nuclei of embryos of *Chaetosiphon fragaefolii* group, comparing the holocyclic $2n = 12$ form with karyotypes of six anholocyclic forms (see text and Fig. 2)

Chromosome	Holocyclic form ($2n = 12$)	Anholocyclic forms					
		B (71,6s)	C (81,5s)	D (61,8s)	E (81,6s)	F (61,9s)	G (71,7s)
X	15.08	15.45	15.00	14.66	14.35	15.44	13.95
	15.08	15.45	15.00	14.66	14.35	15.44	13.95
A1	11.04	11.91	10.99	12.12	7.29	10.80	11.22
	11.04	11.91	6.97 +4.20	12.12	+3.57	10.80	3.82
					7.29 +3.57		
A2	9.15	8.00	8.96	8.68	9.33	4.73	9.24
	9.15	4.40 +3.66	8.96	4.70 +3.62	9.33	+4.33 4.47 +2.63 +2.04	9.24
A3	7.59	7.28	7.86	7.96	8.02	7.76	7.58
	7.59	7.28	7.86	4.34 +2.89	8.02	7.76	7.58
A4	3.93	4.05	3.82	3.80	4.08	3.57	4.03
	3.93	4.05	3.82	3.80	4.08	3.57	4.03
A5	3.21	3.21	3.16	3.25	3.35	3.30	3.71
	3.21	3.21	3.16	3.25	3.35	3.30	3.71
No. of samples examined	19	1	6	1	1	1	3
No. of nuclei measured	14	1	9	1	1	4	11

Letters A-G refer to the karyotypes illustrated in Fig. 2.

l = 'long' chromosome, greater than 7% of total length; s = 'short' chromosome, less than 5% of total length.

with *R. multiflora*. A strawberry-feeding population in New Zealand had 13 chromosomes (like karyotype B in Fig. 2).

In England, oviparae and males may occur in small numbers in the autumn, but Dicker (1952) concluded that sexual reproduction was unlikely to play a significant part in the life cycle. A population collected in 1982 on *Fragaria* at Kew, England, had 14 chromosomes, but of a different karyotype to the 14-chromosome form in North America, having six long and eight short chromosomes (Fig. 2D); relative length data for chromosomes of the single cell measured were best explained in terms of a dissociation in one member of each of chromosome pairs A2 and A3, but a homozygous A2 dissociation was another possibility, in which case the karyotype would be very like that of *C. tetraerhodum* (Fig. 2I).

C. jacobi is found only in western North America on wild, thin-leaved *Fragaria* species and appears totally anholocyclic, no males having been found (Schaefer, 1960). A sample of *C. jacobi* from California had 17 chromosomes in somatic cell nuclei with a high degree of structural heterozygosity, such that it is impossible to speculate on the homologies of particular chromosomes with those of *C. fragaefolii*, except for one apparently unaltered X chromosome (Figs 1f & 2H). The other X chromosome has possibly dissociated into three parts, the longest of these having acquired a small satellite. However, a more complex arrangement involving translocation of X chromosomal and autosomal chromatin cannot be ruled out.

Karyotypes of other Chaetosiphon (Pentatrachopus) species

C. tetraerhodum, a widely distributed aphid on roses, has $2n = 14$, with eight short autosomes (Fig. 2I). Relative length data suggest that autosome pairs 4 and 5 of *tetraerhodum* could be equivalent to autosome pair 2 of *fragaefolii*, although such comparisons between species should be treated circumspectly. A sample of *C. coreanum*, which is holocyclic on *Rosa* in Japan, had $2n = 8$ with no short autosomes (Fig. 2J).

Chaetotaxy

Variation in relation to karyotype.—The number of submarginal setae on abdominal segments 1–4 was not correlated with karyotype (Table III). There was considerable variation within and between samples of all North American karyotypes, and with large

TABLE III. Total numbers of submarginal setae on abdominal segments 1–4 in North American apterae of the Chaetosiphon fragaefolii group, in relation to karyotype

Karyotype (see Fig. 2)	Morph	Number of individuals	Mean no. of submarginal setae	Range
A ($2n = 12$ from <i>Fragaria</i>)	Fundatrix	4	4.25	0–8
	Fundatrigenia	11	7.73	3–8
A ($2n = 12$ from <i>Rosa</i>)	Fundatrix	6	2.17	0–5
	Fundatrigenia	4	6.75	6–7
B (7l,6s)	Virginopara	5	6.00	4–8
C (8l,5s)	Virginopara	16	5.69	2–8
E (8l,6s)	Virginopara	3	7.66	7–8
F (6l,9s)	Virginopara	48	4.52	0–8
G (7l,7s)	Virginopara (lab. clone)	4	8.00	—
	Virginopara (field)	23	0.13	0–2

enough samples the complete range from nil to eight submarginal setae could probably have been found for each karyotype. Holocyclic populations collected in spring from both *Rosa* and *Fragaria* showed similar variation, although the karyotyped fundatrices tended to have fewer submarginal setae than subsequent generations. Out of 23 specimens from a clone with karyotype G (seven long, seven short) maintained by R. H. Converse at Corvallis, Oregon, 21 had no submarginal setae, the others having one and two submarginals respectively; whereas four field-collected individuals with this karyotype had the full complement of eight submarginals.

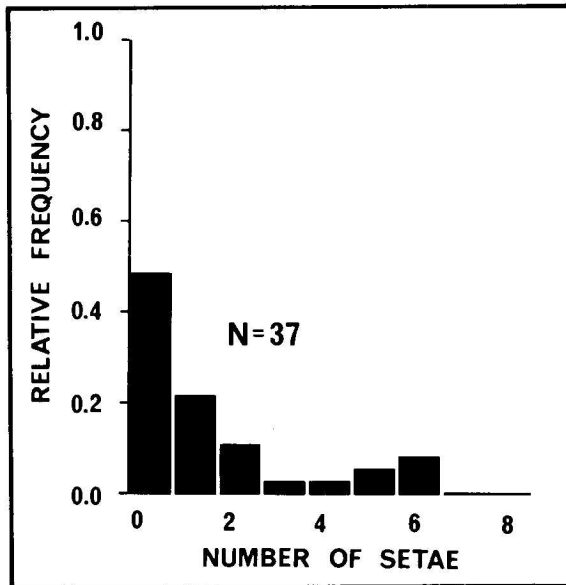


Fig. 3.—Relative frequencies of submarginal setae of field-collected fundatrices of *Chaetosiphon fragaefolii*.

Variation in relation to age of clone.—Of the 50 fundatrices isolated in order to study chaetotaxy, 37 survived to the adult stage. Nearly 50% of these had no submarginal setae and none had more than six (Fig. 3). The first generation of adults from fundatrices with no submarginal setae had individuals with a complete range of setal numbers, and none of the 78 aphids of the fifth generation had fewer than two submarginals (Fig. 4). Clones started from fundatrices with five or six submarginals consisted almost entirely of individuals with eight submarginals by the fourth generation (Fig. 5). The general trend of increased numbers of submarginals by the fourth and fifth generations was observed in all clones. The higher the number of submarginal setae on the fundatrix the more numerous were individuals with submarginals in all five generations and the fewer the generations needed to achieve the full complement.

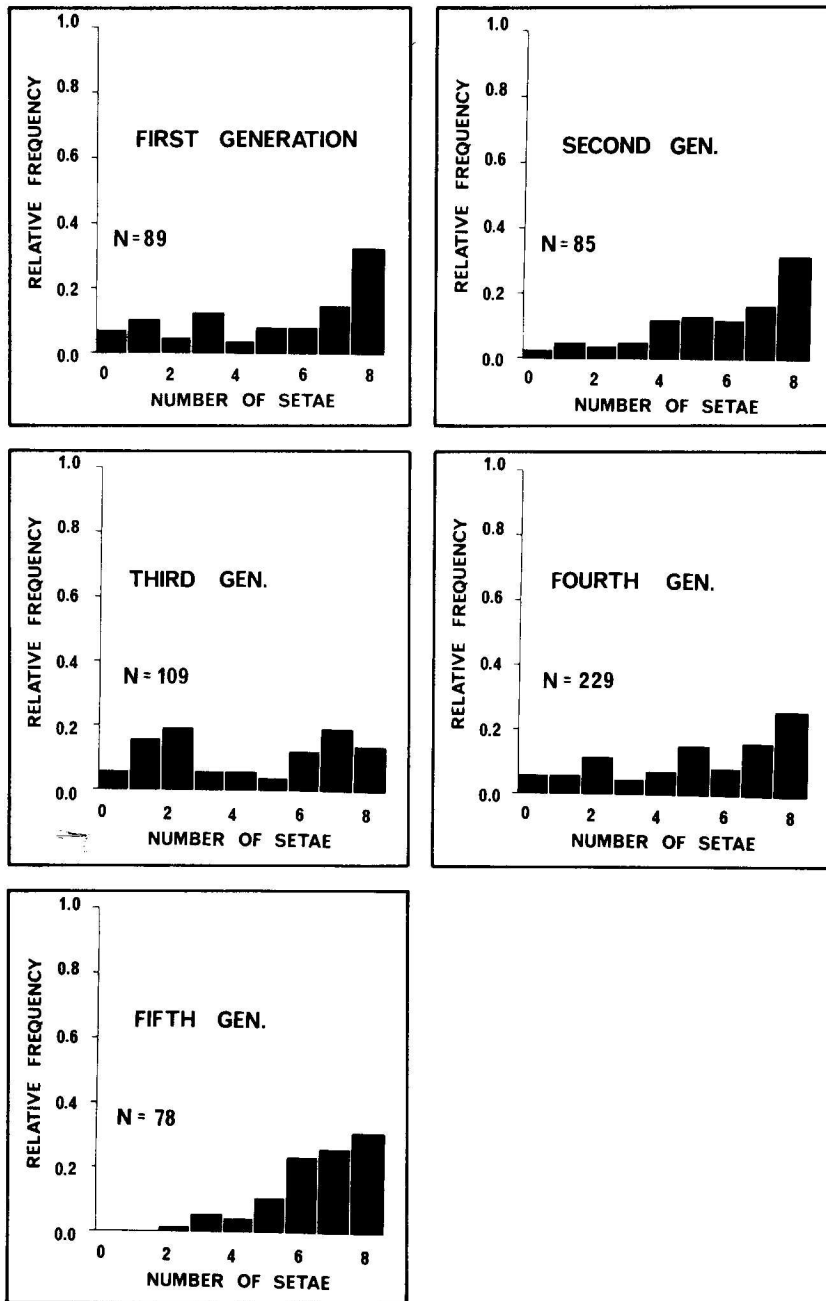


Fig. 4.—Relative frequencies of submarginal setae of five successive generations of apterous virginoparae of *Chaetosiphon fragaefolii* originating from 18 fundatrices with no submarginals.

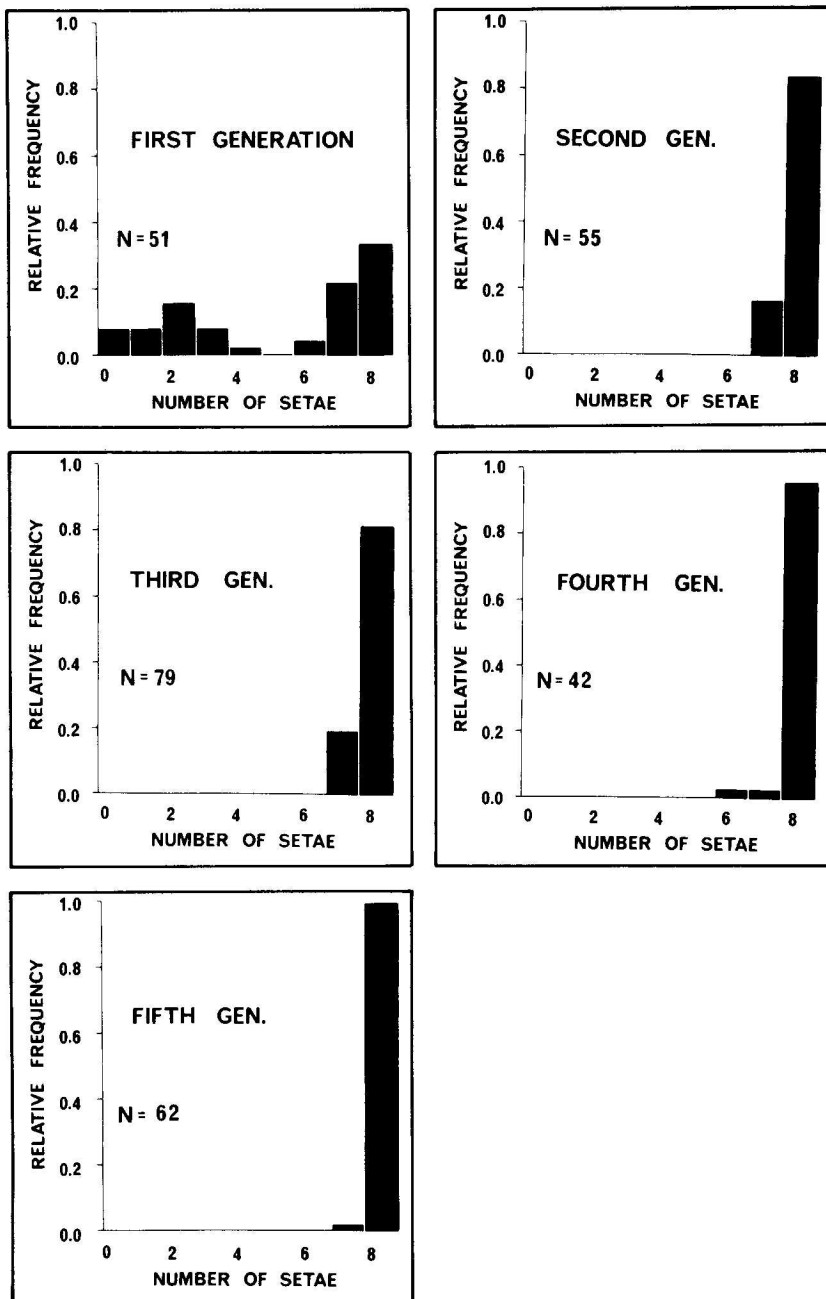


Fig. 5.—Relative frequencies of submarginal setae of five successive generations of apterous virginoparae of *Chaetosiphon fragaefolii* originating from fundatrices with 5-6 submarginals.

Morphometrics

A preliminary morphological study of the karyotyped samples failed to reveal any characters by which the different anholocyclic karyotypes in western North America might be distinguished from each other, or from the holocyclic $2n = 12$ form of *Fragaria*. However, the single karyotyped individual from England differed from all the North American populations in having longer siphunculi relative to the third antennal segment. Examination of material in the British Museum (Natural History) (BMNH) collection showed that 88% of apterae from *Fragaria* in Europe, the Middle East and New Zealand had siphunculi more than 1.1 times longer than antennal segment III, whereas this ratio was less than 1.1 in 92% of North American specimens.

Fundatrices developing from eggs on *Fragaria* in British Columbia were clearly distinct from those which had overwintered as eggs on *R. rugosa*. The *Fragaria* fundatrices differed little in their morphology from the next and later generations or from individuals of anholocyclic populations on *Fragaria*, whereas the *Rosa* fundatrices were more typically fundatriciform, being larger and broader-bodied with a short processus terminalis (1.67–2.73 times longer than base of last antennal segment, in comparison to 3.40–4.44 times in fundatrices from *Fragaria*).

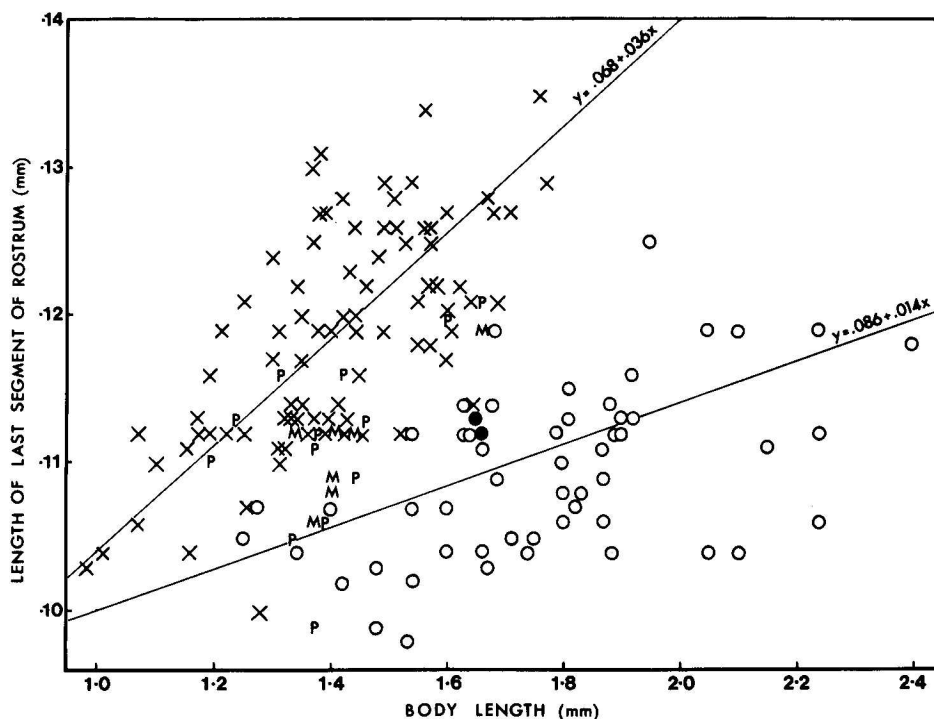


Fig. 6.—Plot of the length of the last segment of the rostrum against body length for apterous virginoparae of the *Chaetosiphon fragaefolii* group from North America. (X, from *Fragaria* spp.; O, from *Rosa* spp.; M, from *R. multiflora* in New Zealand; P, from *Potentilla* spp.; ●, co-types of *thomasi*.)

The aphids from *Rosa* also had a shorter rostrum than those from *Fragaria*. Examination of apterae of North American populations of the *fragaefolii* group in the BMNH collection showed that the relationship between body length and length of last rostral segment was consistently different for specimens from these two host-plants (Fig. 6). Some of the specimens from *Potentilla*, including all those from *P. anserina*, had the

longer rostrum of the *Fragaria*-feeding form, but others, including the two available syntypes of *thomasi*, had a rostrum length similar to that of the *Rosa*-feeding form.

Discussion

The *C. fragaefolii* group seems to provide a very good example of two main features of aphid chromosomal evolution (Blackman, 1980); (i) dissociations and fusions, particularly the former, appear to play a dominant part as mechanisms of reorganization of the karyotype, and (ii) such changes are most frequently observed in anholocyclic populations. The situation in *Chaetosiphon* (*Pentatrachopus*) closely resembles that in the related group *Myzus* (*Nectarosiphon*), which also has a basic diploid $2n = 12$ karyotype and a number of anholocyclic forms with varying degrees of structural heterozygosity (Blackman, 1980). *M. dianthicola* Hille Ris Lambers, an anholocyclic, morphologically distinct form on carnations, is the equivalent in that group to *C. jacobi*, possibly representing an old, permanently parthenogenetic line that has diverged significantly from the ancestral, diploid, holocyclic parent species.

Thus it appears that the different karyotypes in the *C. fragaefolii* group represent a series of anholocyclic lines derived, in some cases independently and in other cases perhaps in sequence, from an originally homozygous $2n = 12$ karyotype. Probably other karyotypes remain to be discovered in anholocyclic populations of this group in western North America and elsewhere. Apparently similar karyotypes may have arisen independently; for example, the karyotype of the New Zealand form on *Fragaria* resembles that of the 13-chromosome (eight long, five short) form in Oregon, USA, but the New Zealand population has relatively longer siphunculi like the 14-chromosome (six long, eight short) form in England and other Old World populations.

The present results provide further confirmation that differences in the numbers of submarginal setae do not provide a valid basis for separating the North American populations of the *fragaefolii* complex on strawberry into two taxa, *fragaefolii* and *thomasi*. This character varies between clones, and also seasonally, depending on the number of generations from the fundatrix.

The biological properties and karyotypes of all the forms now recognized in the *C. fragaefolii* group are summarized in Table IV. Present evidence indicates that populations on cultivated strawberries in western North America should all be assigned to *fragaefolii* but that a series of clones co-exist in anholocyclic populations of this species, recognizable

TABLE IV. *Constituents of the Chaetosiphon fragaefolii complex*

Host-plant	Locality	Submarginal setae	Karyotype ($2n$)	Life cycle	Available name
<i>Fragaria</i> (incl. c.v.)	Eastern N. America	Absent	12	Holocyclic	<i>minor</i>
<i>Fragaria</i> (not on c.v.)	Western N. America	0-8	17	Anholocyclic	<i>jacobi</i>
<i>Fragaria</i>	Old World, widespread	0-1	13(8l,5s) 14(6l,8s)	Mainly anholocyclic	<i>fragariae</i>
<i>Fragaria</i>	N. America	0-8	12	Holocyclic	<i>fragaefolii</i>
<i>Fragaria</i>	N. America	0-8	13(8l,5s) 13(7l,6s) 14(7l,7s) 14(8l,6s) 15(6l,9s)	?All anholocyclic	<i>fragaefolii</i>
<i>Rosa rugosa</i>	Western N. America	0-8	12	Holocyclic	<i>thomasi</i>
<i>Rosa multiflora</i>	New Zealand	0-2	14(8l,6s)	Unknown	None
<i>Rosa fendleri</i>	Colorado, Utah	0-8	Unknown	Unknown	None

by karyotype and possibly, with more work, by biological, electrophoretic or morphometric differences.

It could be argued that the Old World *fragaefolii* populations with long siphunculi and few or no submarginal setae should be regarded as a distinct taxon, for which the Theobald name *fragariae* is already available. However, these populations presumably originated as introductions from part of the far more variable gene pool of *fragaefolii* in North (or South) America, and the differences are most probably due to founder effects.

Both Old and New World populations of *C. fragaefolii* utilize *Potentilla anserina* as an alternative host-plant.

We propose that the name *thomasi* is applicable to the aphid with the short rostrum which is holocyclic on *R. rugosa* in British Columbia and occurs elsewhere in North America on both wild and cultivated roses. Rostrum length on its own is not a reliable character for species separation, as it can be modified within a species according to the food-plant (e.g. Shaposhnikov, 1985). However, the distinctive morphology of the fundatrices on *R. rugosa* is indicative of species status.

Besides feeding on *Rosa*, *C. thomasi* occurs on various *Potentilla* species but has not so far been recorded from *P. anserina*. The syntypes of *thomasi* were collected from *P. monspeliensis*.

The aphids feeding on *R. multiflora* in New Zealand, and a form with distinct alatae on *R. fendleri* in Utah and Colorado, may represent two additional rose-feeding taxa.

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