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Hybridisation between *Aphis grossulariae* and *Aphis schneideri* (Sternorrhyncha: Aphididae): An experimental approach

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Abstract. *A. schneideri* and *A. grossulariae* clones from southern Poland produced fertile hybrid eggs under experimental conditions. Established hybrid clones expressed normal parthenogenetic reproduction but bisexual generations were not obtained, though a few sexuales developed in some cases. Morphological features of *A. schneideri* and host-specificity of *A. grossulariae* tended to dominate in the majority of hybrid clones. Independent inheritance of the studied morphological characters and host specificity can therefore be presumed.

Present results do not exclude the possibility of natural hybridisation of studied aphid species. Natural crosses might cause taxonomic and currant pest management problems.

INTRODUCTION

"A species is a dynamic system capable of self-regulation. The complicated structure of species, and the ability of clones and populations to adapt rapidly…are the basis of species dynamics of aphids" (Shaposhnikov, 1987b: 423). This can result in the appearance of complexes of sympatric closely related forms causing taxonomic and pest management problems and extremely interesting from the point of view of speciation analysis (Müller, 1985; Shaposhnikov, 1987a; Mackenzie & Guldemond, 1994). Careful biosystematic analysis can result in describing sibling species inside "good" species (Guldemond, 1990b; etc.), or joining together other "good" species. Hybridisation experiments might supply important information on the taxonomic status of the forms involved in the complex, although aphid crossing experiments are rather complicated, due to the reasons summarized in the review of Hales et al. (1997).

Aphis grossulariae Kaltenbach, 1843 and *Aphis schneideri* (Börner, 1940) are well-known pests of currants and gooseberries. *A. schneideri* is known to be monoecious holocyclic on *Ribes* spp., whilst *A. grossulariae* is holocyclic heteroecious between *Ribes* spp. and Onagraceae, mainly *Epilobium* spp. (Stroyan, 1984; Blackman & Eastop, 1984; Heie, 1986). Some authors refer to *A. grossulariae* as being monoecious holocyclic on *Ribes* spp. (Gusynina, 1963; Savzdarg & Ponomareva, 1978). One of the possible explanations concerns diagnostic problems (Stroyan, 1984: 104; Blackman & Eastop, 1984: 234). There may be another possibility: hybridisation of species resulting in the appearance of monoecious holocyclic clones possessing morphological features of *A. grossulariae*. This would be possible if certain morphological features and host plant specificity and/or life cycle mode are inherited independently. It was noted by Guldemond (1990a), that host plant specificity in the aphid genus *Cryptomyzus* might be controlled by only few genes, and host alternation monofactorially. Briggs (1965) has also reported single gene control of the ability to colonize raspberry varieties by the aphid *Amphorophora rubi* (Kaltenbach).

The hybridisation between *Aphis schneideri* and *A. grossulariae* might be possible for the following reasons: distribution areas of both species are broadly overlapping; they are sympatric species. Bisexual reproduction of both species occurs on similar winter hosts – various wild and cultivated currants and gooseberries. The seasonal phenology of bisexual reproduction is similar in both species, at least in populations of southern Poland and Lithuania (Table 1). Furthermore, both species have the same chromosome number (Turčinavičienė et al., 1997).

The aim of this work was to study the possibilities of hybridisation between *A. grossulariae* and *A. schneideri* under experimental conditions.

MATERIAL AND METHODS

Five clones of *A. grossulariae* and four clones of *A. schneideri* originating from southern Poland were used for interspecific crossing experiments in Katowice (southern Poland) in 1987, each clone starting from a single fundatrix or fundatrigenia (Table 2). Seven *A. grossulariae* × *A. schneideri* and nineteen reciprocal crossings were tried. Ten oviparae and one male of the alternative species were isolated in muslin branch tip cages on currant bushes for each cross. Hybrid eggs were obtained from sixteen crosses (Table 3). Intraspecific interclonal and intraclonal crosses were also performed. Eggs were subsequently transferred (together with fragments of shoots on which they were deposited) to Vilnius (Lithuania) and maintained in field conditions throughout the winter. This was performed by attaching the fragments of the shoots containing hybrid eggs to the appropriate tip shoots of the field grown black currant bushes (mid-ripening variety "Derliai"). Hatched larvae had the opportunity of crawling to bursting buds and continuing their development. Hatching larvae were counted daily, as were mature fundatrices. Certain fundatrices were isolated separately in branch tip muslin cages, initiating hybrid clones for subsequent morphological analysis and host specificity tests. Thus thirty hybrid clones were started and propagated throughout 1988 in Vil-

TABLE 1. Dates of first observation and peak appearance of oviparae, males and overwintering eggs of *A. schneideri* and *A. grossulariae* in Vilnius (Lithuania) and Katowice (southern Poland).

Sampling locality	Year	Species/No. of clones observed	Oviparae		Males		Eggs	
			First	Peak	First	Peak	First	Peak
Vilnius	1978	*schneideri*/2	08.15	08.29	08.29	no data	no data	no data
		grossulariae/5	08.15	09.01	no data	no data	08.29	09.14
	1979	*grossulariae*/2	09.08	no data	09.07	09.16	09.14	10.01
	1980	*schneideri*/5	09.10	09.12	09.03	09.20	09.29	10.04
	1983	*grossulariae*/3	08.29	09.08	no data	no data	08.29	09.08
	1985	*schneideri*/1	09.18	no data	09.24	no data	09.24	no data
		grossulariae/1	09.11	no data	no data	no data	no data	no data
	1988	*schneideri*/1	08.31	no data	08.31	no data	10.04	no data
		grossulariae/4	no data	no data	08.31	09.15	10.04	no data
Katowice	1987	*schneideri*/5	09.01	09.14	09.01	09.10	09.01	09.20
		grossulariae/5	09.01	09.15	08.25	09.07	09.16	10.05

nius. The list of clones is presented in Tables 4 and 5; rearing methods were the same as described earlier (Rakauskas, 1993).

The fundatrix and twenty specimens (when available) of the main morphs (alatae and apterae from winter and summer hosts) of each hybrid clone were mounted in Faure-Berlese fluid on microscope slides for morphological analysis. Two methods were used for the morphological identification of hybrid clones. Firstly, the identification was tried using common key characters (Rakauskas, 1998). Secondly, canonical variates analysis, a method that has proved very useful in distinquishing closely related aphid species (Blackman, 1992; etc.), was applied. Morphometric data of pure *A. schneideri* and *A. grossulariae* clones from Lithuania and Poland were used for calculating canonical discrimination functions (CDF) for every morph. Variables to be used in the CDF were selected on the basis of their discriminatory power: those having the smallest partial Wilks' Lambda were taken when calculating CDF for every morph (for details see StatSoft, 1995, Chapter 2). List of variables used for calculating CDF for every morph is presented in Table 6. Wider information on the aphid material used has been already published (Rakauskas, 1998). The obtained CDF values were subsequently counted for every hybrid specimen of every morph, and standard box and whisker plot procedure was applied for morphological determination of various morphs of every hybrid clone. Examples illustrating the morphological identification procedure of the alate currant-inhabiting viviparous females are presented in Fig. 1 (using the key characters) and Fig. 2 (exploiting the CDF). Every morph of each hybrid clone was treated as having morphology of particular species if the range of the studied character or CDF values in that morph was covered by the range of the same character of that particular species. Thus, alate viviparous females (currant morph) of the hybrid clone gs12 were determined as having morphology of *A. schneideri* both by means of key characters (Fig. 1) and CDF values (Fig. 2). The hybrid clone morph was treated as tending morphologically to particular species if the 25–75% box area of the studied character or CDF value of that morph was covered or overlapped by the range of that particular species. For example, alate viviparous females (currant morphs) of hybrid clones gs1, gs5-11, gs13 were determined by means of key characters as tending morphologically to *A. schneideri* (Fig. 1). The hybrid morph was treated as morphologically intermediate if the 25–75% box area of the studied character or CDF value of that morph was in between the ranges of both species, or overlapped by the ranges of both species to a similar extent. This way, alate viviparous females (currant morphs) of hybrid clones gs1–3, gs6, gs10, gs13 were determined by means of CDF as having intermediate morphology between *A. schneideri* and *A. grossulariae* (Fig. 2).

Graphical data for other morphs of all hybrid clones (similar to those presented in Figs 1–2 for alate viviparous females) are available from the author upon request. Morphological identification of fundatrices was different, because only one fundatrix of every clone was available. Scatterplot analysis procedure was performed in this case, an example being presented in Fig. 3. In total, five morphs of every hybrid clone were evaluated morphologically by means of key characters and CDF. Thus, ten evaluations (two per every morph) concerning morphology of

TABLE 2. *A. grossulariae* and *A. schneideri* clones used for the crossing experiments in Katowice (Poland) in 1987 (c. v. – cultivated variety).

Species	Sampling locality	Sampling date	Host plant	Subsequent clone No.
A. grossulariae	Katowice	05.12.1987	red currant c. v.	B1
	Katowice	05.12.1987	*Ribes aureum* Pursh.	E1
	Katowice	05.12.1987	*Ribes aureum* Pursh.	E2
	Katowice	05.12.1987	*Ribes aureum* Pursh.	F1
	Katowice	05.23.1987	gooseberry c. v.	F2
A. schneideri	Zabierzow, Krakow distr.	05.21.1987	*Ribes aureum* Pursh.	B2
	Katowice	05.12.1987	black currant c. v.	C1
	Katowice	05.12.1987	black currant c. v.	D1
	Jurkow, Kielce distr.	05.30.1987	black currant c. v.	D2

TABLE 3. *A. schneideri* and *A. grossulariae* successful crossings, with information on the amount of live (black shining) eggs obtained, hatching and maturation success of fundatrices (Fx) and subsequent hybrid clone No.

Crossing (♀ × ♂)	Maternal and paternal clones		No. of eggs	Hatching success		Fx maturation success (%)	Subsequent hybrid clone No.
	Females	Males		No.	%		
A. grossulariae × *A. schneideri*	B1	C1	40	14	35	100	gs1–4
	E1	C1	54	8	14.8	100	gs5–8
	F1	D1	8	6	75	100	gs9–11
	F2	B2	21	12	57.1	16.7*	gs12–13
A. schneideri × *A. grossulariae*	B2	B1	39	31	79.5	35.5	sg1–3
	B2	E2	8	5	62.5	100	not cloned
	C1	B1	9	5	55.6	100	not cloned
	C1	F2	9	6	66.7	100	not cloned
	D1	E2	8	2	25	100	not cloned
	D1	F2	11	6	54.5	100	not cloned
	D1	F1	7	5	71.4	100	sg4–6
	D1	E1	2	1	50	100	sg7
	D2	F2	14	10	71.4	100	sg8–11
	D2	E2	30	12	40	83.3	sg12–15
	D2	F1	28	11	39.3	81.8	sg16–19
	D2	E1	33	21	63.6	100	not cloned

* Parasitoid invasion.

every hybrid clone were received. Every hybrid clone was afterwards summarized as having certain overall morphological features on the basis of these ten evaluations. For example, hybrid clone gs1 (Table 4) had 5 of 10 evaluations as being morphologically intermediate, and two pairs of evaluations [fundatrices and apterous viviparous females from *Epilobium* (aptII)] were alternative. Thus, in overall determination, this hybrid clone was treated as having intermediate morphology between *A. grossulariae* and *A. schneideri*. Following the same procedure, hybrid clone gs2 was also determined as morphologically intermediate, gs3 as tending morphologically to *A. grossulariae,* gs4 – as real *A. grossulariae*, gs5 – as tending morphologically to *A. schneideri*, and so on (Tables 4–5). Discussion of morphological characters elswhere in this paper concerns the overall morphological determination of the clone, unless otherwise mentioned.

All calculations were done using the STATSOFT statistical package STATISTICA for WINDOWS 5.1 (StatSoft, 1995).

Host specificity and life cycle analysis of every hybrid clone were performed as described earlier (Rakauskas, 1993). Potted *Epilobium adenocaulon* plants were tested as potential summer hosts for every clone. Transfers of alate females were repeated (if first transfers were unsuccessful) at weekly intervals until this morph was no longer available. Groups of five migrants were used for every transfer test. That was one of the reasons for insufficient numbers of certain morphs used for morphological analysis in some clones (e.g. lack of alate viviparae from currants in clones gs4, gs7, sg6 and sg7). When only few winged viviparae were obtained, they all were used for transfer experiments.

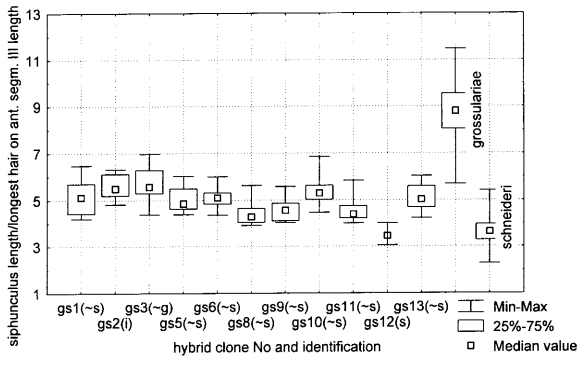

Fig. 1. Box and whisker plot of the ratio siphunculus length/longest hair on ant. segm. III length for the alate viviparous females of *A. grossulariae* and *A. schneideri* and *grossulariae* × *schneideri* hybrid clones (currant morphs).

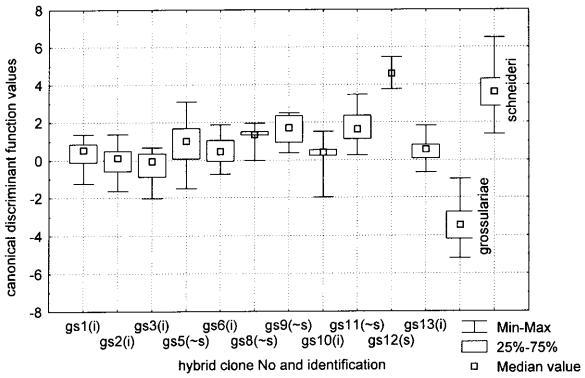

Fig. 2. Box and whisker plot of canonical discriminant function values for the alate viviparous females of *A. grossulariae* and *A. schneideri*, and hybrid clones *grossulariae* × *schneideri* (currant morphs).

TABLE 4. Morphological and biological features of the experimental hybrid clones (*A. grossulariae* × *A. schneideri*) showing the possibility to colonize *Epilobium adenocaulon* as a summer host (+, normal propagation on *Epilobium*; ±, poor propagation; –, no propagation), morphological pecularities of different morphs of each clone (fx – fundatrix; apt, al – apterae and alatae from currants; aptII, alII – apterae and alatae from *Epilobium*; s, → s – morphology as in *A. schneideri* or tending to it; g, → g – morphology as in *A. grossulariae* or tending to it; i – intermediate morphological features; n – morph not obtained; 0 – morph obtained, but not measured) when performing identification by common key characters (Key) or by means of canonical discriminant function (CDF, further explained in material and methods), and the overall morphology of the clone (Summary). Figures in Morph/No. column – number of analysed specimens of respective morph.

Clone No.	*Epilobium* acceptance	Life cycle mode	Morphology			
			Morph/No.	Key	CDF	Summary
gs1	+	heteroecious	fx /1	→ s	g	i
			apt /5	i	i	
			al /12	→ s	i	
			aptII /18	→ g	→ s	
			alII /6	i	i	
gs2	+	heteroecious	fx /1	→ s	i	i
			apt /2	→ g	i	
			al /12	i	i	
			aptII /4	→ g	i	
			alII /6	→ g	→ g	
gs3	+	heteroecious	fx /1	g	g	→ g
			apt /11	→ g	i	
			al /19	→ g	i	
			aptII /19	i	i	
			alII /6	→ g	→ g	
gs4	+	heteroecious	fx /1	g	g	g
			apt /0	0	0	
			al /0	0	0	
			aptII /21	g	g	
			alII /14	g	g	
gs5	–	monoecious	fx /1	i	i	→ s
			apt /15	→ s	→ s	
			al /19	→ s	→ s	
			aptII /n	n	n	
			alII /n	n	n	
gs6	+	heteroecious	fx /0	0	0	i
			apt /16	→ s	i	
			al /16	→ s	i	
			aptII /11	→ g	→ g	
			alII /9	→ g	→ g	
gs7	+	heteroecious	fx /1	g	g	g
			apt /0	0	0	
			al /0	0	0	
			aptII /23	g	g	
			alII /20	g	g	
gs8	±	heteroecious ?	fx /1	s	i	→ s
			apt /8	→ s	i	
			al /5	→ s	→ s	
			aptII /0	0	0	
			alII /n	n	n	
gs9	+	heteroecious	fx /1	→ s	i	→ s
			apt /10	→ s	→ s	
			al /7	→ s	→ s	
			aptII /10	→ s	→ g	
			alII /12	s	→ s	
gs10	+	heteroecious	fx /1	s	i	→ s
			apt /10	→ g	→ s	
			al /10	→ s	i	
			aptII /14	→ s	→ s	
			alII /0	0	0	
gs11	+	heteroecious	fx /1	s	i	→ s
			apt /3	→ s	→ s	
			al /10	→ s	→ s	
			aptII /20	s	→ s	
			alII /9	s	→ s	
gs12	–	monoecious	fx /1	i	→ g	s
			apt /15	s	s	
			al /4	s	s	
			aptII /n	n	n	
			alII /n	n	n	
gs13	+	heteroecious	fx /1	→ s	→ s	→ s
			apt /10	→ g	→ s	
			al /14	→ s	i	
			aptII /8	→ s	i	
			alII /n	n	n	

RESULTS

It seems obvious that *A. schneideri* and *A. grossulariae* are capable of hybridising under experimental conditions. Obtained clones were true hybrids, because of their intermediate morphology, at least in some of hybrid clones. Information on the secondary host specificity and morphological features of hybrid clones is presented in Tables 4 and 5. The results can be summarized as follows.

A. grossulariae × *A. schneideri* crossings $\left(\frac{\text{morphology}}{\text{life cycle mode}}\right)$:

$3\,\frac{gross.\&\rightarrow gross.}{\text{heteroec.}} : 3\,\frac{\text{interm.}}{\text{heteroec.}} : 4\,\frac{\rightarrow schneid.}{\text{heteroec.}} : 1\,\frac{\rightarrow schneid.}{\text{heteroec.?}} : 2\,\frac{schneid.\&\rightarrow schneid.}{\text{monoec.}}$

A. schneideri × *A. grossulariae* crossings:

$1\,\frac{\rightarrow schneid.}{\text{monoec.}} : 9\,\frac{\rightarrow schneid.}{\text{heteroec.}} : 2\,\frac{\text{interm.}}{\text{heteroec.}} : 1\,\frac{\text{interm.}}{\text{heteroec.?}} : 2\,\frac{\text{interm.}}{\text{monoec.}} : 1\,\frac{gross.}{\text{heteroec.}} : 3\,\frac{schneid.\&?}{?}$

Independent inheritance of studied morphological features and host plant specificity can be supposed based on the fact that, in *A. grossulariae* × *A. schneideri* crossings, out of ten *Epilobium*-inhabiting hybrid clones (host specificity mode of *A. grossulariae*) only 3 possessed also morphological features of *A. grossulariae*, or were similar

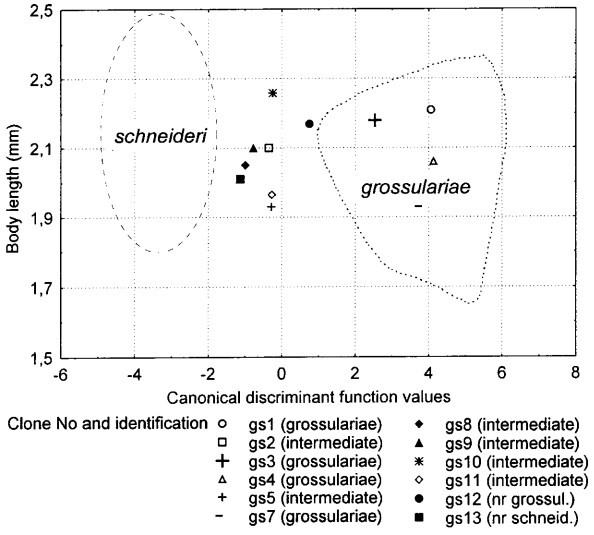

Fig. 3. Scatterplot of canonical discriminant function values plotted against the body length of hybrid fundatrices (*A. grossulariae* × *A. schneideri* crossing) showing the distribution of the same values in *A. grossulariae* and *A. schneideri* fundatrices.

to it. Other clones tended morphologically to *A. schneideri* (4 clones), or were intermediate between both species (3 clones). In reciprocal crossings, out of 12 heteroecious clones only one had morphological features of *A. grossulariae*, whilst others tended morphologically to *A. schneideri* (9 clones) or possessed intermediate morphology (2 clones).

TABLE 5. Morphological and biological features of the experimental hybrid clones (*A. schneideri* × *A. grossulariae*). Abbreviations as in Table 4.

Clone No.	*Epilobium* acceptance	Life cycle mode	Morphology			
			Morph/No.	Key	CDF	Summary
sg1	+	heteroecious	fx /1	s	→ s	→ s
			apt /7	→ s	i	
			al /20	→ s	→ s	
			aptII /13	→ s	i	
			alII /2	i	i	
sg2	+	heteroecious	fx /1	s	→ g	i
			apt /4	→ s	i	
			al /7	→ s	i	
			aptII /13	→ s	i	
			alII /n	n	n	
sg3	+	heteroecious	fx /1	s	s	i
			apt /8	g & s	g & s	
			al /14	g & s	g & s	
			aptII /13	g	g	
			alII /2			
sg4	–	monoecious	fx /1	i	i	i
			apt /18	→ g	i	
			al /8	→ s	→ s	
			aptII /n	n	n	
			alII /n	n	n	
sg5	–	monoecious	fx /1	→ s	→ s	→ s
			apt /19	→ s	i	
			al /15	→ s	→ s	
			aptII /n	n	n	
			alII /n	n	n	
sg6	±	heteroecious ?	fx /1	→ s	→ s	i
			apt /10	→ g	i	
			al /0	0	0	
			aptII /0	0	0	
			alII /n	n	n	
sg7	–	monoecious	fx /1	s	0	i
			apt /7	→ g	i	
			al /0	0	0	
			aptII /n	n	n	
			alII /n	n	n	
sg8	+	heteroecious	fx /1	s	s	→ s
			apt /20	→ g	i	
			al /20	→ s	→ s	
			aptII /0	0	0	
			alII /0	0	0	
sg9	+	heteroecious	fx /1	g	g	g
			apt /20	g	g	
			al /6	g	g	
			aptII /9	g	g	
			alII /2	g	g	
sg10	+	heteroecious	fx /1	s	s	→ s
			apt /12	→ s	→ s	
			al /5	→ s	→ s	
			aptII /16	s	i	
			alII /14	s	→ s	
sg11	+	heteroecious	fx /1	s	→ s	→ s
			apt /15	→ g	i	
			al /3	→ s	→ s	
			aptII /20	→ s	i	
			alII /8	→ s	i	
sg12	+	heteroecious	fx /1	s	s	→ s
			apt /11	→ s	i	
			al /18	→ s	→ s	
			aptII /20	→ s	→ g	
			alII /6	s	→ s	
sg15	+	heteroecious	fx /1	s	s	→ s
			apt /12	i	i	
			al /4	→ s	→ s	
			aptII /21	→ s	i	
			alII /19	s	→ s	
sg16	+	heteroecious	fx /1	s	s	→ s
			apt /11	→ s	→ s	
			al /21	→ s	→ s	
			aptII /12	s	→ s	
			alII /2	s	s	
sg17	?	?	fx /1	s	s	s
			apt /n	n	n	
			al /n	n	n	
			aptII /n	n	n	
			alII /n	n	n	
sg18	+	heteroecious	fx /0	0	0	→ s
			apt /13	→ s	→ s	
			al /14	→ s	→ s	
			aptII /5	→ s	→ s	
			alII /n	n	n	
sg19	+	heteroecious	fx /1	→ s	i	→ s
			apt /12	i	→ s	
			al /20	→ s	→ s	
			aptII /21	s	i	
			alII /6	s	→ s	

It might be concluded that heteroecy dominates against monoecy in this group of aphids. In *A. grossulariae* × *A. schneideri* crosses there were 10 heteroecious clones, 1 possibly heteroecious, 2 monoecious. In reciprocal crossings the ratio was 12 heteroecious : 1 possibly heteroecious : 3 monoecious : 3 unknown. Guldemond (1990b) has reported both domination and recessivity of host alternation against monoecy in different host races of currant aphid *Cryptomyzus galeopsidis* (Kaltenbach). Our data do not support the information on the extranuclear inheritance of heteroecy in aphids, as reported by Dahl (1968) for *Myzus cerasi* (F.).

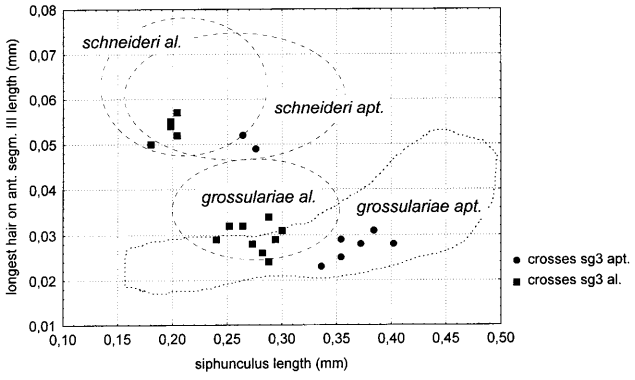

Fig. 4. Scatterplot of two morphological characters of apterous and alate viviparous females of hybrid clone sg3 showing the distribution of respective characters for pure *A. schneideri* and *A. grossulariae* clones.

TABLE 6. Morphological characters exploited for calculating canonical discriminant functions for the discrimination between the respective morphs of *A. schneideri* and *A. grossulariae*. Abbreviations as in Table 4.

Characters	Morphs				
	fx	apt	al	aptII	alII
Siphunculus length	+	+	+	+	+
Hind tibia length	+				
Ant. segm. III length	+				+
Longest hair on ant. segm. III length	+	+	+	+	+
No. of additional hairs on ultimate rostral segment	+				
Length of the basal part of ant. segm. VI		+	+		
No. of hairs on cauda		+			
No. of secondary rhinaria on ant. segm. IV					+
No. of secondary rhinaria on ant. segm. V			+		
Length of the second segment of hind tarsus				+	+

Morphological features of *A. schneideri* seem to dominate against *A. grossulariae* morphology. Thus, in *A. grossulariae* × *A. schneideri* crosses there were 7 clones tending morphologically to *A. schneideri*, 3 clones tending morphologically to *A. grossulariae*, and 3 intermediate clones. In reciprocal crosses the ratio was respectively 11 *A. schneideri* : 1 *A. grossulariae* : 5 intermediate and 2 unknown. The dominance was not absolute: only 2 clones (one in *A. grossulariae* × *A. schneideri* crossings and one in reciprocal) had "pure" morphological features of *A. schneideri*, others were more or less similar to it. That can be explained by the polygenic inheritance of analysed morphological features, already noted by Müller (1976) for *Aulacorthum solani* (Kaltenbach).

It is interesting that "similar" crossings gave different results. For example, hybrid clones gs1–4, obtained from *A. grossulariae* (maternal clone B1) × *A. schneideri* (paternal clone C1) crossing, were 2 heteroecious with intermediate morphology, 1 heteroecious with *A. grossulariae* morphology, and 1 heteroecious with morphology near *A. grossulariae*. That is, all four hybrid clones tended clearly to *A. grossulariae*. Another three hybrid clones (gs9–11), also from *A. grossulariae* (but maternal clone F1) × *A. schneideri* (paternal clone D1) crossing, were heteroecious, but morphologically tended to *A. schneideri*. These differences might be explained by the differences in genotypes of the maternal and paternal clones, and by the polygenic inheritance of morphological features under analysis. Another interesting result: hybrid clones possessing "pure" morphological and life cycle features of *A. grossulariae* (gs4, gs7, sg9) were not related to any certain maternal or paternal clones. There was only one hybrid clone having "pure" morphological and life cycle features of *A. schneideri* in *A. grossulariae* × *A. schneideri* crossings scheme (gs12), and no such hybrid clones were obtained in reciprocal crossings.

A result that might be due to the modifying effect of the host plant was observed in hybrid clone gs6. That is, apterae and alatae on currants expressed morphological similarities with *A. schneideri*, but respective morphs on *Epilobium* morphologically tended to *A. grossulariae*. Generally, all hybrid clones, independently of their morphology, when feeding on *Epilobium*, released higher numbers of specimens having 5-segmented antennae, that is more characteristic to *A. grossulariae* than to *A. schneideri*. The influence of host plant on the diagnostic morphological characters has been reported by Shaposhnikov (1981) in the aphid genus *Dysaphis*.

In hybrid clone sg3, apterae and alatae from currants were distinctly separated morphologically into two groups: some were identical with *A. schneideri*, others with *A. grossulariae* (Fig. 4). The fundatrix of this clone morphologically was *A. schneideri*, whereas morphs from *Epilobium* had morphological features of *A. grossulariae*. A similar phenomenon was previously noted when cloning pure *A. schneideri* lineages in Katowice in 1987: in clone D1 subclone cultivated on red currants, there appeared some specimens which morphologically resembled *A. grossulariae* (Rakauskas, unpubl.). Müller (1969) reported on the mixed morphological features in fundatrices of a hybrid *Myzus myosotidis* × *M. persicae*, but I did not find any information on the morphological splitting inside the same hybrid clone.

None of the hybrid clones succeeded in completing their entire life cycle and it was therefore impossible to perform backcrossing experiments. Oviparae were produced in only one clone, gs2 (5 individuals). A few immature oviparae also appeared in clones gs9 and gs11, but they did not finish their development due to frosts. One male was produced by clone gs9. Five eggs were obtained from clone gs2, oviparae mated with the male of *A. schneideri*, but nothing hatched from them in 1989. No males or oviparae were produced in any other hybrid clones. It might be concluded that there exist certain postzygotic isolating mechanisms between the species under analysis resulting in reduced possibilities of bisexual reproduction. It can only be clearly stated that hybrid clones were viable enough and reproduced successfully parthenogenetically.

Oviparae were produced on *Epilobium* in October in clone gs11. Males were absent, so bisexual reproduction did not occur. Nevertheless, this fact supports the idea of Guldemond (1990a) on the possibility of sympatric speciation in aphids through the production of oviparae on new hosts.

DISCUSSION AND CONCLUSIONS

A. schneideri and *A. grossulariae* clones from southern Poland are able to produce fertile hybrid eggs under experimental conditions. Established hybrid clones expressed normal parthenogenetic reproduction, but bisexual generations were not obtained, though a few sexuales developed in some cases. Nevertheless, it remains unclear whether the failure of bisexual reproduction in hybrid clones was due to the reduced potential of crosses for sexual reproduction or caused by other reasons (modified rearing conditions, inappropriate host plants, or weather conditions), because severely reduced possibilities for bisexual reproduction were observed in 1988 also in pure clones of *A. schneideri* and *A. grossulariae*, transferred from Katowice to Vilnius. Only one interclonal hybrid clone of *A. grossulariae* (out of 5 propagated) succeeded in producing bisexual generation, but no eggs were laid. No males or oviparae appeared in three intraclonal hybrid clones of *A. schneideri*. This might be explained by clonal differences at the time of switching from parthenogenetic to bisexual reproduction, as documented for the aphid *Rhopalosiphum padi* (L.) (Simon et al., 1996). Clones from southern Poland might have different switching mode to the clones of eastern Lithuania, because of different conditions.

Present results raise the question on the possibility of natural hybridisation between *A. schneideri* and *A. grossulariae*. Experimental crossing procedure may circumvent certain prezygotic isolating mechanisms, as has already been shown for the aphid genera *Dysaphis* (Shaposhnikov, 1981, 1987a, b), *Cryptomyzus* (Guldemond et al., 1994; Guldemond & Dixon, 1994) and *Aphis fabae* Scopoli (Thieme & Dixon, 1996). To clear the matter, natural isolating mechanisms between *A. schneideri* and *A. grossulariae* need to be studied, especially sex pheromone specificity, circadian rhythm of sex pheromone release and male activity, and other aspects of possible natural specific mate recognition systems of the studied species. Crossing experiments need to be repeated with clones from other parts of the species distribution area, because possibilities to produce hybrids may differ in different populations (Hewitt, 1990). Wide scale morphological analysis of the material from different parts of the distribution area of both species might result in discovering specimens of intermediate, hybrid-like morphology. Detailed biosystematic studies of *A. popovi* Mordvilko (described from currants in Yakutiya, see Rakauskas, 1996) and *A. octotuberculata* Mamontova [described from currants in Ukraine by Mamontova (1955), later synonymized with *A. schneideri* by Eastop & Hille Ris Lambers (1976)] would also be of value. The question of natural hybridisation between *A. schneideri* and *A. grossulariae* is important not only in a taxonomic context, but also due to practical needs of currant pest management.

Morphological features of hybrid clones varied from typical *A. schneideri* through intermediate characters to typical *A. grossulariae* (Tables 4, 5). Morphological features of *A. schneideri* tended to dominate, although intermediate morphologically between *A. schneideri* and *A. grossulariae* hybrid clones were the most numerous, thus supporting the idea of polygenic inheritance of the key morphological characters. In hybrid clone sg3, the bimodal distribution of morphological characters in apterae and alatae (currant morphs) was present: some of the specimens were identical with *A. schneideri*, others with *A. grossulariae* (Fig. 4). One of the possible explanations for these results is the contamination of the clone, that can never be absolutely excluded even if "aphid-proof" cages are used. Nevertheless, it is rather unlikely in the case of hybrid clone sg3, because the morphological splitting was detected from the first generation of fundatrigeniae, after the maturation of the first born progeny of fundatrix. These aphids were grown separately from their mother, so the contamination would have been easily detected. Another possible explanation is the modifying effect of environmental conditions on key morphological features in *A. schneideri* and *A. grossulariae*.

The majority of hybrid clones, 22 of 28 tested, accepted *Epilobium adenocaulon* as summer host, thus supporting the domination of host alternation against monoecy in this group. Only two hybrid clones appeared to have intermediate host preferences between *A. grossulariae* and *A. schneideri*, which may suggest monogenic control of this character.

Life cycle mode was inherited independently from morphological features. Thirteen hybrid clones, morphologically similar to *A. schneideri*, were also able to use *Epilobium adenocaulon* as summer host, which is characteristic of *A. grossulariae*. Three hybrid clones (gs4, gs7 in *A. grossulariae* × *A. schneideri* crosses and sg9 in reciprocal crosses) had "pure" morphological and life-cycle features of *A. grossulariae*, and one hybrid clone (gs12) – of *A. schneideri*. Fundatrix of clone gs12 was intermediate morphologically (Table 4), supporting the idea of the possible contamination of this hybrid clone. Due to the reasons presented above, the probability of contamination is rather low. Contamination is an especially unlikely explanation when considering clones gs4, gs7, sg9 (also "pure" hybrid clones), because all morphs of these clones were *A. grossulariae*-like. Another possible explanation is that, despite the polygenic control of the studied morphological characters, the gene combination resulting in "pure" morphology of one of the maternal/paternal species may not be impossible. The same holds for the life-cycle features, especially having in mind that host alternation in aphids might be controlled monofactorially (Guldemond, 1990a). Concerning "pure" hybrid clones gs4 and gs7, the phenomenon of certain maternal influences can also be involved when trying to explain their "purity", e.g. action of maternal genes (for wider explanation see Lewin, 1996: 1141–1179). It might also be explained by means of gynogenesis – when male germ cell acts just to stimulate development of the egg, but makes no genetic contribution to the resulting individual (Ham & Veomett, 1980: 605).

Present results do not support the hypothesis that clones monoecious holocyclic on currants (which is characteris-

tic of *A. schneideri*) similar morphologically to *A. grossulariae* may appear due to the hybridisation between the species. No such clones were obtained experimentally. Nevertheless, natural crosses (if possible) might cause taxonomic and currant pest management problems.

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