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Natural hybridisation between *Aphis grossulariae* and *Aphis schneideri*: morphological evidence (Sternorrhyncha: Aphididae)

RIMANTAS RAKAUSKAS

Department of Zoology, Vilnius University, Čiurlionio 21/27, LT 2009 Vilnius, Lithuania; e-mail: rimantas.rakauskas@gf.vu.lt

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Abstract. Morphometric analysis of 176 natural samples of *A. grossulariae* Kaltenbach, 1843 and *A. schneideri* (Börner, 1940) was performed, using 308 alate and 750 apterous viviparous females from 25 countries altogether. Morphologically intermediate specimens of presumably hybrid origin were noticed in 63 (35.79%) samples, comprising 12.67% of all apterous and 4.87% of all alate viviparae studied. 31 sample originating from 11 countries had 50% or more intermediate specimens of one or both morphs. "Rich" samples (having 4 or more specimens of the same morph) with the prevailing numbers of hybrid morphotypes were from the Netherlands, Russia (Moscow and Stavropol regions), Moldova, Turkey (Ankara) and Tajikistan (Dushanbe). Present data are discussed in the context of possible natural hybridisation between *A. grossulariae* and *A. schneideri* (see also Rakauskas, 1999a, 1999b). Canonical discrimination functions are being advocated as more powerful tools for separating between the two species when compared with single morphological characters or ratios commonly used in the keys.

INTRODUCTION

The possibility of hybridising and producing viable and fertile progeny is an important feature of biparental species, being emphasized by the reproductive species definitions, including the biological (e.g. Mayr, 1982; Dobzhansky, 1970) and recognition species concepts (Paterson, 1993). Various isolating mechanisms usually prevent natural hybridisation between "good" species in nature. Therefore, hybridisation studies might supply important information on the taxonomic status of the forms involved in a complex (Müller, 1985; Shaposhnikov, 1987; Guldemond, 1990; etc.).

Palaearctic species of the genus *Aphis* L. inhabiting currants [*A. grossulariae* Kaltenbach, 1843, *A. triglochinis* Theobald, 1926, and *A. schneideri* (Börner, 1940)] have been reported as capable of interspecific hybridisation under experimental conditions (Rakauskas, 1999a, 1999b, 2000; Turčinavičienė, 2000). Experimental crosses normally reproduced by means of parthenogenesis, and fertile bisexual generations appeared in some cases. When pondering whether currant inhabiting *Aphis* species are capable also of natural hybridisation, morphometric methods can provide certain information. Namely, 26% of experimental *A. grossulariae* × *A. schneideri* hybrid clones appeared to be morphologically intermediate between the parental species (Rakauskas, 1999a). Such intermediate hybrid morphotypes can be easily detected in nature thus supporting the idea of natural hybridisation of both species.

The aim of this work was to perform morphometric analysis of *Aphis grossulariae* and *A. schneideri* samples from various collections seeking for the natural hybrid morphotypes having intermediate morphological characters.

MATERIAL AND METHODS

Morphometric data have been extracted from specimens labelled as *A. schneideri* and *A. grossulariae* in various public and private collections in 1987–2001. Currant specimens in the collection of Natural History Museum (London) that have been labelled by D. Hille Ris Lambers as new species *Aphis szelegiewiczi* and *Aphis subepilobii* respectively (unpublished *nomina nuda*), have been also analysed. Only currant morphs of *A. grossulariae* [collected on currants and gooseberries (*Ribes* spp.)] were used. 176 samples comprising 308 alate and 750 apterous viviparous females from 25 countries have been studied altogether (Table 1, Fig. 1). The whole list of analysed samples is available from the author on the request.

Typical morphological features of both species were taken from clonal specimens. Clones that were holocyclic facultatively heteroecious between *Ribes* spp. and Onagraceae herbs (13 clones, 105 apterae and 100 alatae altogether) were taken as typical *A. grossulariae.* Holocyclic monoecious on *Ribes* spp. clones were taken as typical *A. schneideri.* (17 clones, 113 apterae and 102 alatae altogether). These clones were originally started from Polish and Lithuanian material. The entire list of typical clones and their detailed morphometric data are published (Rakauskas, 1993, 1998). These data were used for obtaining key characters and canonical discrimination function values typical for *A. schneideri* and *A. grossulariae.*

Two methods were used for the morphological identification of museum specimens. First, the identification was attempted using key characters (Rakauskas, 1998). For example, apterous viviparous females having ratio siphon length: longest hair on third antennal segment length exceeding 7 were identified as *A. grossulariae*. Specimens having the same ratio smaller than 6.6 were taken as *A. schneideri.* Ratio values from 6.61 to 6.99 were recognised as intermediate.

Second method was canonical variates analysis, a method that has proved very useful in distinguishing closely related aphid species (e.g., Blackman, 1987, 1992). Morphometric data of the above mentioned typical *A. schneideri* and *A. grossulariae* clones (30 morphological characters, the entire list published in Rakauskas, 1998) were used for calculating canonical discrimi-

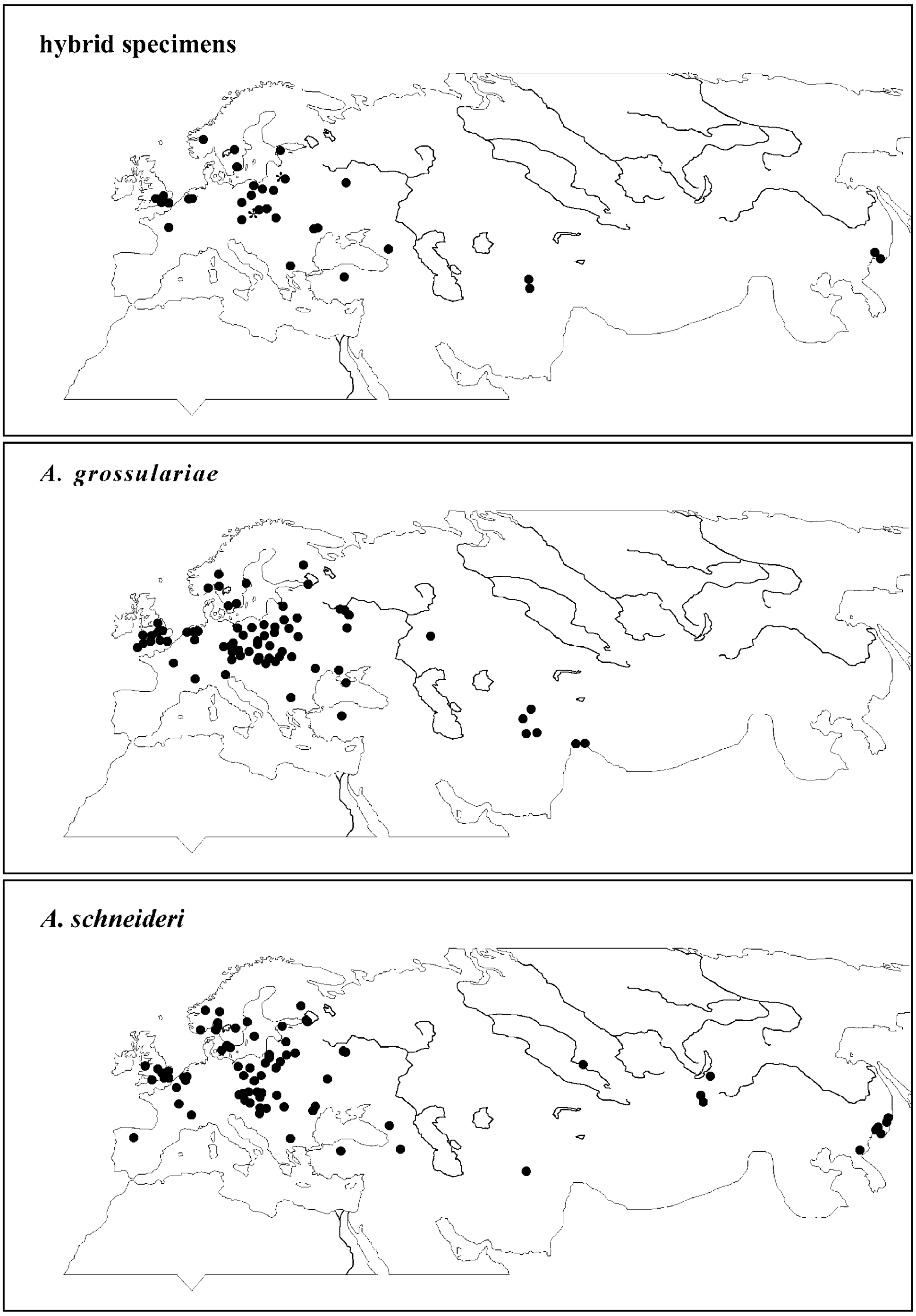

Fig. 1. Sampling places of *A. schneideri*, *A. grossulariae* (both from *Ribes* spp. and summer hosts) and hybrid specimens. Localities, where experimental hybrid clones were received (Rakauskas, 1999a, 1999b), are marked with the asterisks.

nation 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, 2000, Vol. III, Chapter 2). The list of variables used when calculating CDF for every morph (with the respective constants and variable coefficients) is presented in Table 2. The obtained CDF values were subsequently counted for every museal specimen of respective morph. Scatterplot of the CDF individual values of apterous viviparous females from 12 samples representing eight countries is presented in Fig. 2, respective box and whisker plot of the same samples - in Fig. 3. Information on the morphological features of apterous and alate viviparous females was summarized, an example being presented in Table 3.

All calculations were done using the STATSOFT statistical package STATISTICA for WINDOWS 5.5 (StatSoft, 2000).

RESULTS AND DISCUSSION

63 samples out of 176 (35.79%) had one or more morphologically intermediate specimens, 95 apterous viviparous females (12.67% of all analysed apterae) and 15 alate viviparous females (4.87%) among them. These samples originated from 15 countries (Table 1, Fig. 1). 31 sample had 50% or more intermediate specimens of one

TABLE 1. Aphid material used in this study showing the numbers of analysed samples, alate and apterous viviparous females (% of intermediate specimens or samples having intermediate specimens).

Country	No of analysed (% of intermediate specimens):		
	samples	alatae	apterae
Armenia	1 (0)		1
Belgium	1 (0)	2	3
Bielorus	1 (0)		3
Bulgaria	2 (50.0)	2 (0)	11 (18.2)
Czech Republic	14 (28.6)	22 (4.5)	78 (7.7)
Danmark	1 (0)	1	
England	11 (45.5)	23 (13.0)	62 (8.1)
Estonia	1 (100.0)	2 (0)	4 (25.0)
Finland	1 (100.0)	10 (40.0)	10 (40.0)
France	4 (25.0)	6 (0)	4 (50.0)
Kazakhstan	1 (0)		8
Latvia	3 (0)	3	9
Lithuania	36 (25.0)	121 (0)	76 (22.4)
Moldova	11 (54.6)	22 (0)	46 (23.9)
Mongolia	2 (0)		13
Netherlands	6 (33.3)	2 (0)	30 (13.3)
Norway	7 (42.9)	4 (50.0)	14 (21.4)
Poland	27 (33.3)	25 (4.0)	158 (7.6)
Russia (Buryatya)	1 (0)		7
Russia (Eur. Part)	9 (22.2)	21 (0)	23 (34.8)
Russia (Far East)	6 (66.7)	15 (6.7)	37 (13.5)
Slovakia	8 (50.0)	3 (0)	54 (7.4)
Spain	1 (0)	2	5
Sweden	8 (50.0)	2 (0)	29 (13.8)
Tajikistan	8 (87.5)	15 (33.3)	48 (18.8)
Turkey	1 (100)	4 (50.0)	4 (75.0)
Ukraine	4 (0)	1	13
Altogether	176 (35.79)	308 (4.87)	750 (12.67)

TABLE 2. Canonical discrimination functions (CDF) constants and coefficients for the discrimination between apterous and alate viviparous females of *A. schneideri* and *A. grossulariae*.

Characters	Morphs, with respective CDF coefficients and constants	
	apterae	alatae
Length of the basal part of ant. segm. VI	54,5585	38,8096
Length of the siphunculus	–21,2972	–24,4958
Length of the ant. segm. III	–21,8691	
Length of the longest hair on ant. segm. III	215,282	175,4556
No of hairs on cauda	0,1829	
Maximum width of ant. segm. III	93,3679	
Length of the processus terminalis		–18,4035
No of rhinaria on ant. segm. V		0,3754
Constant	–9,3189	–1,8396
CDF values for *A. schneideri*	3 – 7.7	0.8 – 6.4
CDF values for *A. grossulariae*	–2 – –7.3	–1.4 – –6.4

or both morphs (Table 3). These were from 11 countries, Russian Far East, Subcaucasus and Moscow regions among them. Relatively numerous samples (with 4 or more specimens of the same morph) having prevailing numbers of hybrid morphotypes were only six (Table 3). They originated from Russian Subcaucasus (Stavropol area, Kislovodsk, No. 1271 509, abbreviated as "ki"), Moldova (Karmanovo, No. 1943, "m1"), Moscow region (No. 167, "mo"), the Netherlands (Wageningen, "ne"), Tajikistan (Dushanbe, 89–45, "ta"), Turkey (Ankara, sample No. 3834, "tu"). This information advocates the possibility of natural hybridisation occuring sporadically in different parts of the *A. grossulariae* and *A. schneideri* distribution area. It must be noted that just 26% of experimental *A. grossulariae* × *A. schneideri* hybrid clones were morphologically intermediate between the parental species (Rakauskas, 1999a). Other hybrid clones were

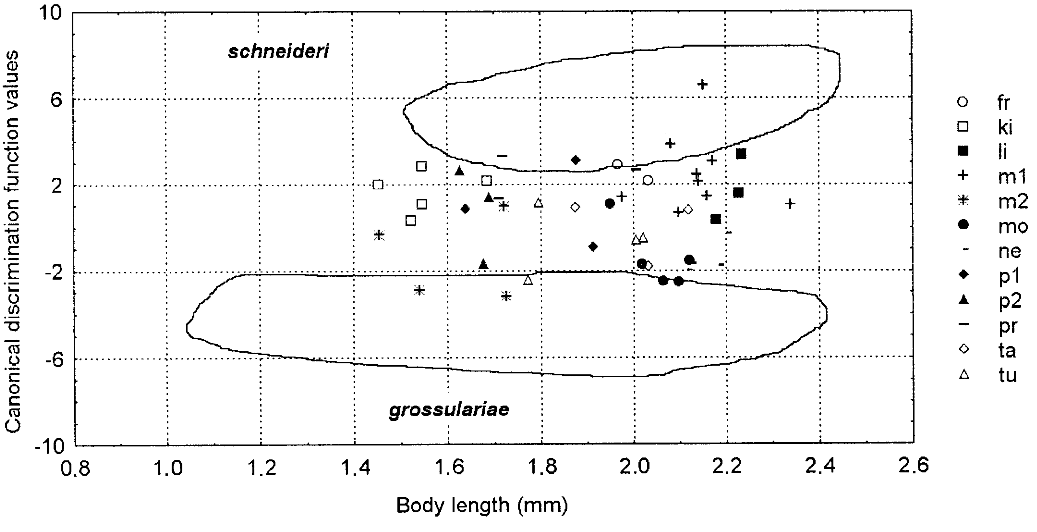

Fig. 2. Scatterplot of the canonical discrimination function individual values plotted against the body length of the apterous viviparous females (sample abbreviations as in Table 3) showing the distribution of respective values in *A. grossulariae* (N = 105) and *A. schneideri* (N = 113).

Table 3. Samples having 50% and more specimens with intermediate morphological characters of one or both morphs when estimated by means of the common key characters (Rakauskas, 1998) or the CDF (wider explained in Material and methods). Rich samples with the prevailing hybrid morphotypes are in bold.

Label data	Abbr.	No of apt/al	No of intermediate apt/al	
			key	CDF
England – Oxford, 1954.6.23, 1380, *R. gordonianum*, *A. grossulariae*	en	6/2	0/0	2/1
France - La Varenne, 1986.5.24, 14911, *R. rubrum*, *A. schneideri*	fr	2/0	0	2
Kislovodsk - Russia, 1947.6.27, 1271 509, *R. nigrum*, *A. grossulariae*	**ki**	**5/0**	**0**	**5**
Kondara - Tajikistan, 1972.5.28, 13851, *R. aureum*, *A. grossulariae*	ko	9/1	0/0	3/1
Kondara - Tajikistan, 1972.5.28, 13850, *R. nigrum*, *A. grossulariae*	ko1	6/4	0/2	0/2
Lithuania – Vilnius, 1983.5.10, Rr1, *R. rubrum*, *A. schneideri*	li	3/12	1/0	2/0
Lithuania – Vilnius, 1997.7.18, 97-163g, *R. carpathicum*, undetermined	li1	4/0	0	2
Lithuania – Vilnius, 1997.7.30, 97-196g, *R. triste*, undetermined	li2	8/0	0	4
Lithuania - Vilnius, 1983.5.31, EG2, *R. uva - crispa*, *A. schneideri*	li3	2/1	0/0	2/0
Lozovyj, Primorskij kraj - Russia, 1978.6.7, 1810, *R. nigrum*, *A. schneideri*	lo	2/1	0/0	1/0
Moldova – Karmanovo, 1967.5.29, 1943, *R. nigrum*, *A. schneideri*	**m1**	**10/8**	**2/0**	**6/0**
Moldova.-.Kishinev, 1962.6.8, 963, gooseberry, *A. grossulariae*	m2	4/0	1	2
Moldova – Kishinev, 1958.6.19, 10, *R. nigrum*, *A. grossulariae*	m3	6/0	1	3
Moldova – Kishinev, 1977.6.22, 3464, *R. nigrum*, *A. schneideri*	m4	2/0	0	1
Moldova.-.Kishinev, 1962.5.31, 923, *R. nigrum*, *A. schneideri*	m5	4/1	0/0	2/0
Moscow region, Luzhki – Russia, 1967.6.30, 167, *R. uva – crispa*, *A. schneideri*	**mo**	**5/0**	**1**	**4**
Netherlands – Wageningen, 1961.6.19, *R. grossularia*, *A. grossulariae*	**ne**	**4/0**	**0**	**3**
Netherlands – Randwijk, 1962.7.6, *R. rubrum*, *A. schneideri*	ne1	2/0	0	1
Norway - Hurum Buskerud, 1953.6.16, III 3-4, *Ribes* x cult. , *A. schneideri*	no	0/4	0	2
Poland – Palacza, 1964.6.10, *R. aureum*, *A. schneideri*	p	1/0	1	1
Poland – Dolistowo, 1978.6.20, *R. nigrum*, *A. schneideri*	p1	3/1	2/0	2/0
Poland - Starogard Gdanski, 1963.7.10, *R. rubrum*, *A. grossulariae*	p2	3/0	0	3
Poland – Olsztyn, 1963.7.4, *R. aureum*, *A. schneideri*	p3	1/0	0	1
Poland - Tarnawce Przemysl, 1965.6.27, *R. rubrum*, undetermined	p4	2/0	0	1
Poland – Warszawa, 1962.6.15, *R. nigrum*, *A. schneideri*	p5	1/1	0/0	0/1
Primorskij kraj - Anisimovka, Russia, 1982.9.29, 5283, *R. triste*, *A. grossulariae*	pr	3/0	0	2
Sweden – Växjo, 1975.6.15, 2767:9, *R. aureum*, *A. grossulariae*	sw	2/2	0/0	1/0
Sweden –Örebro, 1987.7.15, 5318:11, *R. alpinum*, *A. schneideri*	sw1	2/0	0	1
Tajikistan – Dushanbe, 1989.5.8, 89-45, *R. aureum*, *A. grossulariae*	**ta**	**5/0**	**2**	**3**
Tajikistan – Dushanbe, 1972.5.23, 13802, *R. saxatilis*, *A. grossulariae*	ta1	3/2	0/0	0/1
Turkey – Ankara, 1966.6.28, 3834, *Ribes* sp., *A. grossulariae*	**tu**	**4/4**	**0/0**	**3/2**

morphologically similar to one or another parental species. Cases, when specimens of two species are present in the same sample, can be also explained by means of hybridogenesis: morphological splitting inside the hybrid clones has been reported for experimental crosses *A. grossulariae* × *A. schneideri* (Rakauskas, 1999a) and *A. grossulariae* × *A. triglochinis* (Turčinavičienė, 2000). In present study there appeared 11 samples (6.21% of all studied) having specimens of two species. This figure, together with the above mentioned 63 samples (35.59%) having intermediate morphotypes supports the idea of the natural hybridisation between *A. schneideri* and *A. grossulariae*. Nevertheless, further studies are needed to confirm this: DNA analysis of pure and hybrid clones (e.g. microsatellites and mitochondrial DNA techniques, see Hales et al., 1997; Sunnucks et al., 1997) would help to evaluate the degree of introgression between natural populations of these species. Natural isolating mechanisms such as sex pheromone specificity, circadian rhythm of sex pheromone release, and other aspects of possible natural specific mate recognition system should be also studied (Guldemond et al., 1994; Guldemond & Dixon, 1994; Thieme & Dixon, 1996).

Morphological features of different morphs did not coincide within the same sample. For example, 6 out of 10 apterae in Moldova (Karmanovo, No. 1943, “m1”) sample appeared to be morphologically intermediate, whilst all 8 alatae of this sample had morphology of A. schneideri (when estimated by CDF). Similar situation was also in samples ko1, li, sw, ta1 (Table 3). The only opposite example is a sample from Turkey (Ankara, 3834, “tu”), in which 3 (out of 4) apterae and 2 (of 4) alatae had intermediate morphology when evaluated by means of CDF. Noticeable, that evaluation results were

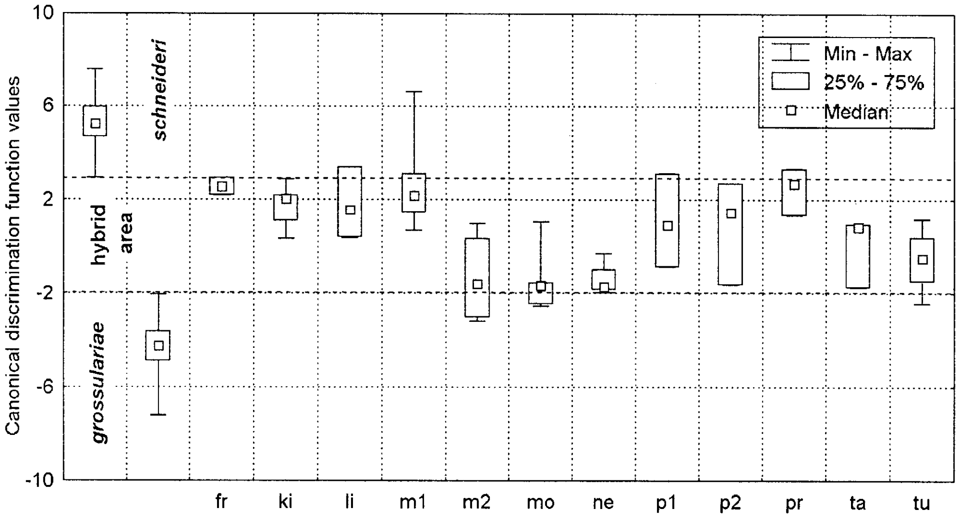

Fig. 3. Box and whisker plot of canonical discrimination function values for the apterous viviparous females of *A. grossulariae* (N = 105) and *A. schneideri* (N = 113) and museum samples (sample abbreviations as in Table 3).

different when using key characters and CDF. In the above mentioned sample from Ankara the key characters showed all specimens being "good" species, whilst 5 (of 8) specimens appeared to be intermediates when estimated by means of CDF. Evaluation results when using different methods coincided only in 4 samples out of 31 presented in Table 3. This is due to the reduced discriminatory power of the key character when compared with CDF. The "gap" between *A. grossulariae* and *A. schneideri* when estimated by the CDF comprises 5 units (from –2 till + 3, Table 2) when compared with 0.4 (6.6 till 7) that is supported by the key ratio (Rakauskas, 1998). Respective gaps for the alate viviparous females are even more narrow: 2.2 when using CDF and 0 for the key ratio. That is, alatae of *A. grossulariae* have the ratio siphon length/longest hair on ant. segm. III length more than 5.5, whilst those of *A. schneideri* less than 5.5 (Rakauskas, 1998). It can be concluded here that the CDF is more reliable for the identification of the currant inhabiting *Aphis* species when compared with the common key characters. This has been already shown for the identification of the *Dysaphis chaerophyllina - brachycyclica* complex (Stekolshchikov & Lobanov, 1990) and *Myzus persicae* group (Blackman, 1987).

Material from the Natural History Museum (London) that D. Hille Ris Lambers designated as *A. szelegiewiczii* sp. n. and *A. subepilobii* sp. n. (unpublished *nomina nuda*) appeared to be morphologically similar to *A. schneideri* (Fig. 4). *A. szelegiewiczii* is a sample of 5 apterous viviparous females and one alatiforma that H. Szelegiewicz has collected in Ulaan Bataar (Mongolia) on July 30, 1963 from *Ribes diacanthum*. *A. subepilobii* comprises two samples from Norway that C. Stenseth has collected in Vestergate Grimstad (AAY) on August 14, 1968 (3 apterae) and Ås on October 2, 1958 (2 apterae and 1 alatiforma), both samples from *Ribes alpinum*.

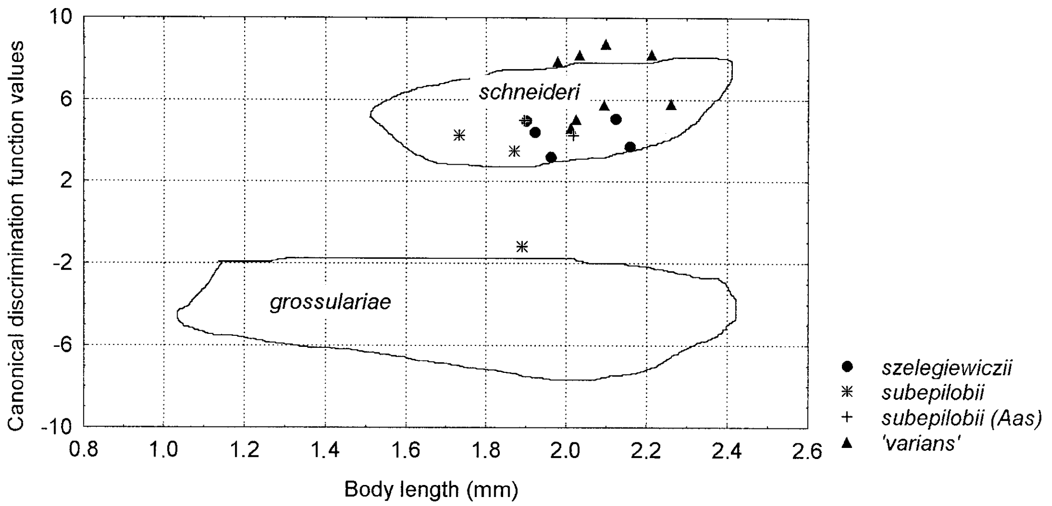

Fig. 4. Scatterplot of the canonical discrimination function individual values plotted against the body length of apterous viviparous females of the new species of D. Hille Ris Lambers and *A. varians* Hille Ris Lambers nec Patch showing the distribution of respective values in *A. grossulariae* (N = 105) and *A. schneideri* (N = 113).

Apterous viviparous females of both "new species" have CDF values typical for *A. schneideri*, except one specimen from Vestergate Grimstad that is in hybrid area closer to *A. grossulariae*. It is also evident from Fig. 4 that apterous viviparous females of *A. varians* sensu Hille Ris Lambers nec Patch (coll. H. Szelegiewicz, Mongolia: Ulaan Bataar, July 30, 1963, R. diacanthum, 6 apterae; Culuud, August 16, 1965, R. nigrum, 2 apterae, 20 oviparae, 2 males) are morphologically identical with *A. schneideri*. It is remarkable that oviparae from Culuud have very few scent plagues on their hind tibiae, and males are apterous, that are characterics of *A. schneideri* (Rakauskas, 1998).

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