

PRIMER NOTE

Cross-species amplification of microsatellite loci in aphids: assessment and application

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Abstract

Despite the relative ease of isolating microsatellites, their development still requires substantial inputs of time, money and expertise. For this reason there is considerable interest in using existing microsatellites on species from which markers were not cloned. We tested cross-species amplification of 48 existing aphid loci in species of the following genera: Aphidinae: Aphidini: *Aphis* and *Rhopalosiphum*; Aphidinae: Macrosiphini: *Acyrtosiphum*, *Brevicoryne*, *Diuraphis*, *Illinoia*, *Macrosiphoniella*, *Macrosiphum*, *Metopeurum*, *Metapolophium*, *Myzus*, *Phorodon*, *Sitobion* and *Uroleucon* and Neuquenaphidinae: *Neuquenaphis*. Our results show cross-species application of known microsatellite loci is a highly promising source of codominant markers for population genetic and evolutionary studies in aphids.

Keywords: Aphidini, cross-priming, Macrosiphini, microsatellite, Neuquenaphidinae, X-linked

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Microsatellites have revolutionized aphid population biology (Wilson *et al.* 2003). They have been widely applied in population genetic studies both at the scale of a country (e.g. Sunnucks *et al.* 1996; Simon *et al.* 1999; Wilson *et al.* 1999, 2002; Llewellyn *et al.* 2003; Papura *et al.* 2003) and more recently to study metapopulation structure within fields (e.g. Haack *et al.* 2000; Massonnet *et al.* 2002b). In aphids, microsatellites are currently the only codominant genetic markers that are sufficiently polymorphic to identify clones and clonal lineages (e.g. Wilson *et al.* 2003), the occurrence of sexual reproduction (e.g. Sunnucks *et al.* 1997; Papura *et al.* 2003), and evolution by mutation in asexual

lineages (e.g. Wilson *et al.* 1999, 2003). Microsatellites and their flanking sequences, in conjunction with mitochondrial markers, have also been useful in elucidating the mechanisms by which obligately parthenogenetic aphid lineages could arise (Delmotte *et al.* 2001, 2002, 2003).

Microsatellites have now been isolated from a wide range of aphid species. These include: *Sitobion miscanthi* (Sunnucks *et al.* 1996; Wilson *et al.* 1997; Simon *et al.* 1999), *Sitobion avenae* (Simon *et al.* 1999), *Aphis gossypii* (Vanlerberghe-Masutti *et al.* 1999), *Pemphigus bursarius* (Miller *et al.* 2000), *Pemphigus spyrothecae* (Johnson *et al.* 2000), *Myzus persicae* (Sloane *et al.* 2001), *Rhopalosiphum padi* (Simon *et al.* 2001), *Macrosiphoniella tanacetaria* (Massonnet *et al.* 2001), *Metopeurum fuscoviride* (Massonnet *et al.* 2002a), and *Dysaphis plantaginea* (Harvey *et al.* 2003). Additionally, we provide previously unpublished primer sequences for another 21 aphid microsatellite loci, 14 of which were isolated from

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Sitobion miscanthi, three from *Sitobion avenae* and four from *Myzus persicae* (Table 1).

Despite the relative ease of cloning microsatellite loci from aphids (cf. e.g. avian species; Zane *et al.* 2002), microsatellite

development still requires a skilled molecular biologist, and a considerable investment of time and resources on the part of the researcher. Thus, using loci already developed in a related species may provide a cost-effective alternative

Table 1 Characteristics of microsatellite loci isolated from *Sitobion miscanthi* (*Sm*), *Sitobion avenae* (*Sav*) and *Myzus persicae* (*Mp*). Locus name, core repeat in sequenced clone, n genotypes = number of genotypes over which allelic diversity (n alleles) and observed heterozygosity (H_O) were calculated, primer names and sequences. Size, is the range of allele sizes of PCR fragments in base pairs observed across the genotypes for which allelic diversity and H_O are reported. PCR prg, PCR amplification details for amplification of loci in cloned species, see Appendix S1 for details of *S. miscanthi* and *M. persicae* PCR programs. For the *S. avenae* loci this table lists the annealing temperature of each locus and details of PCR cycling are described in Appendix S1. For loci cloned from *Sitobion miscanthi*, number of alleles and H_O is calculated for a subset of Australian and New Zealand functionally parthenogenetic *Sitobion* aphids (data largely from Wilson *et al.* 1999). For loci cloned from *Sitobion avenae*, number of alleles and H_O are calculated for a subset of *S. avenae* individuals from Western France (data compiled from Simon *et al.* 1999; Haack *et al.* 2000; Papura *et al.* 2003). For loci cloned from *Myzus persicae*, number of alleles and H_O are reported from Wilson *et al.* (2002). *X-linked locus; †Autosomal locus; ‡Requires 2× as much primer for good amplification

Species	Locus	Repeat	n alleles	n genotype	H_O	Primers (5'–3')	Size	PCR prg	GenBank Accession no.
<i>Sm</i>	S9	(AC) ₁₁	7	13	0.23	F: GCTCGTGGCTATCGTTTGTG R: ATCCGTGTGTGTGCGCGTAG	146–162	PMS1	AY349958
<i>Sm</i>	S10	(AC) ₁₆	9	12	1.00	F: TCTTCTCTATACACCTATAAAC R: TTATGCTAATCTCACAATAC	86–120	PMS2*‡	AY349959
<i>Sm</i>	S12	(CA) ₈ impure	1	12	0.00	F: TTCGGTATAAATAGTGGCGTG R: GGCGATGGCGACTAAAC	87	PMS1	AY349957
<i>Sm</i>	S16b	(CA) ₁₄	12	13	0.69	F: ATAAAACAAGAGCAATTCC R: GTAAAAGTAAAGGTTCCACG	166–206	AMS1†	AY349960
<i>Sm</i>	S17b	(CA) ₁₁ TA(CA) ₈ C(TA) ₇	8	11	0.55	F: TTCCTGGCTTCATTTCCGGTCCG R: CGTCGCGTTAGTGAACCGTG	182–227	PMS1*	AY349961
<i>Sm</i>	S19	(CA) ₃₀	15	13	1.00	F: GCGCATTTGTGTAGCGAGC R: CAAACATGTTATGTCAACAATAC	96–179	PMS1†	AY349962
<i>Sm</i>	S23	(GA) ₁₄	7	13	0.69	F: GGTCGAGAGCATTCATTAGG R: CGTCGTTGTCAATTGTCGTCG	122–156	PMS1†	AY349963
<i>Sm</i>	S24	(CA) ₂₀	9	12	0.83	F: CCCGACCCCGTCCATTCAAA R: CCTCCACCCTACTTTTCACTCC	167–218	AMS1/PMS1†	AY349964
<i>Sm</i>	S25	impure mixed tri.	2	12	0.17	F: TATAGGCTCGTTCGCGGTTG R: TTGATTTGACACGCCACGACC	129–140	AMS1	AY349965
<i>Sm</i>	S30	(CA) ₁₃	4	13	0.23	F: CCGACATAAAACACACCCAG R: GTTTTGCCTCCTCCCTC	163–175	AMS1/PMS1†	AY349966
<i>Sm</i>	S35	(TA) ₅	1	13	0.00	F: CATAGAAGAAAAAGAGGGTAAGC R: GGGATAAATAAGAAAAAAGTCCG	106	PMS1	AY349967
<i>Sm</i>	S43ii	(CA) ₁₁ + (T) ₁₀	4	12	0.75	F: GATATTTATATTACATGCGCG R: GGTGGTCCGGTTTACG	225–231	PMS2*	AY349968
<i>Sm</i>	S45	(AT) ₆	6	11	0.09	F: CCATATACACGCAACAC R: GCCACCAACCTACCG	134–147	PMS1	AY349969
<i>Sm</i>	S49	(CA) ₂₆	10	11	0.73	F: CGCATTTAGGAGTTTCGAC R: CATGTGCAGTGGAGCAGGAA	91–164	PMS1*	AY349970
<i>Sav</i>	S3.R	(AT) ₆ ~(CA) ₁₄	5	75	0.51	F: CATCCGAGCGGTGGAATG R: CATTTCGTATCATTTTGCTACATG	337–369	66 °C	AY352644
<i>Sav</i>	S3.43	(ATT) ₇ ~(TG) ₁₀ ~(TG) ₆	4	10	0.74	F: GGCGAGACCCCTAAAATCC R: GAGATACTCTTTTCGTCGTTAAACC	185–188	62 °C	AY352642
<i>Sav</i>	S5.L	(TG) ₁₀	4	75	0.80	F: GGACGACTCGTTAGTATAGGTGG R: CTATCTCTACCGTTTCGAATCG	223–229	56 °C	AY352643
<i>Mp</i>	myz2	impure (GA) ₃₀	6	53	0.58	F: TGGCGAGAGAGAAGACCTGC R: TCGGAAGACAGAGACATCGAGA	177–207	PMS1†	AY429659
<i>Mp</i>	myz3	(GA) ₁₈	5	53	0.35	F: GGTGTCCTCGTTATGATTATG R: ATTCTTTTCCCGCAGTTTAC	111–125	PMS2*	AY429660
<i>Mp</i>	myz9	impure (GA) ₅₃	7	53	0.60	F: AACCTCACCTCGTGGAGTTTCG R: CTGGATGTGTGGGGTGC	204–238	AMS1†	AY429661
<i>Mp</i>	myz25	(AG) ₂₄	3	53	0.52	F: AACCCATCTCACTCGTCAGCC R: GAATCTGGAGAGCGGTTAATGC	119–126	AMS1*	AY429662

to microsatellite isolation and development in a species of interest. Cross-species amplification is only effective if primer sequences are conserved between species. Generally the number of loci amplifying tends to decrease with increasing divergence between species (Moore *et al.* 1991; Peakall *et al.* 1998), although extreme conservation of loci has also been reported (Schlötterer *et al.* 1991; FitzSimmons *et al.* 1995; Rico *et al.* 1996; Scott *et al.* 2003). For this reason we have investigated, in a range of nontarget species, the potential for cross-species amplification of 48 aphid microsatellite loci, isolated from five target species (Supplementary material Table S1). Three of these target species belong to the tribe Macrosiphini: *Myzus persicae* (10 loci), *Sitobion*

avenae (four loci) and *Sitobion miscanthi* (18 loci) and two to the tribe Aphidini: *Aphis gossypii* (eight loci) and *Rhopalosiphum padi* (eight loci). The materials and methods used for cross-species amplification tests are detailed in the Appendix S1.

We found that amplification success in species belonging to the same genus as the target species was high, in the order of 80% (e.g. *Sitobion*, Table 2), whereas amplification success in noncongeners of the same tribe was lower (e.g. for non-*Sitobion* of the Macrosiphini, 59% of tested loci amplified, Table 2). Surprisingly, of the small total number of loci tested outside the subfamily from which they were isolated, 35% amplified successfully (Tables 2 and 3). These results overall suggest that time and money invested

Table 2 Application of microsatellite loci cloned from *Sitobion avenae*, *Aphis gossypii*, *Rhopalosiphum padi* and *Myzus persicae* to species in tribes Aphidini and Macrosiphini of subfamily Aphidinae and two species of the subfamily Neuquenaphidinae. See Supplementary material for the source of primer sequences of each of the microsatellite loci listed in this table and assay description. +, amplification; ++, amplification and see Supplementary material Table S2 for details of polymorphism assessment; ?, equivocal; -, failed amplification; (blank cell), untested

Species	Locus	Aphidinae											Neuquenaphidinae	
		Aphidini			Macrosiphini								Ne	Ns
		Ac	Ag	Rp	Ap	Dn	Mt	Md	Mf	Mp	Sav	Ut		
<i>Sitobion avenae</i>	S4.Σ	-	+	-	+	++	++	+	++	+	+	-	-	-
	S5.L	-	+	-	++	-	-	+	-	-	+	-	-	?
	S3.R	-	+	-	-	-	-	-	-	-	+	-	-	-
<i>Aphis gossypii</i>	S3.43	+	+	-	+	-	+	-	-	+	-	+	-	-
	A.go 24		+	-	-	-	-	-	++	-	-	-	-	-
	A.go 53		+	-	-	-	-	-	-	-	-	-	-	-
	A.go 59		+	-	-	-	-	-	++	-	-	-	-	-
	A.go 66		+	-	+	-	++	-	++	-	+	++	-	-
	A.go 69	+	+	-	+	-	-	-	-	-	-	-	-	-
	A.go 84		+	-	-	-	-	-	-	-	-	-	-	-
	A.go 89	+	+	+	+	-	-	-	-	-	-	-	-	-
	A.go 126	+	+	-	-	-	-	-	-	-	-	-	-	-
<i>Rhopalosiphum padi</i>	R5.10	+	+	+	+	-	+	++	+	++	+	++	-	-
	R2.73	+	+	+	-	-	-	-	-	-	-	-	-	-
	R3.171	-	-	+	+	-	-	-	-	-	-	-	-	-
	R5.29b	+	+	+	+	-	++	+	++	+	+	-	-	-
	R1.35	-	+	+	-	-	+	-	-	-	-	+	-	-
	R6.3	-	-	+	-	-	-	-	-	-	-	-	-	-
	R5.138		+	+	+	-	-	+	-	+	-	-	-	-
	R5.50		+	+	+	-	-	+	-	-	+	-	-	-
	<i>Myzus persicae</i>	M35	+	+	-	-	-	-	-	-	+	-	-	-
M37		+	+	-	-	-	-	-	-	+	-	-	-	-
M40		+	+	-	+	-	++	+	++	+	+	++	-	-
M49		-	+	-	-	-	-	-	-	+	-	-	-	++
M55		+	+	-	-	-	++	-	-	+	-	-	-	-
M62		+	+	-	+	-	-	+	-	+	-	-	++	++
M63				-	-	-	-	-	+	-	-	++	++	++
M77		-	-	-	-	-	-	-	-	+	+	-	++	++
M86		-	-	-	-	-	-	-	-	+	-	-	-	-
M107			-	-	-	-	-	-	+	-	-	-	-	

Species key: Ac, *Aphis craccivora*; Ag, *Aphis gossypii*; Rp, *Rhopalosiphum padi*; Ap, *Acyrtosiphon pisum*; Dn, *Diuraphis noxia*; Mt, *Macrosiphoniella tanacetaria*; Md, *Metopolophium dirhodum*; Mf, *Metopeurum fuscoviride*; Mp, *Myzus persicae*; Sav, *Sitobion avenae*; Ut, *Uroleucon tanacetii*; Ne, *Neuquenaphis edwardsi*; Ns, *Neuquenaphis staryi*.

Table 3 Application of microsatellite loci cloned from *Sitobion miscanthi* to species in tribes Aphidini and Macrosiphini of subfamily Aphidinae and one species of subfamily Neuquenaphidinae. See Supplementary material for the source of primer sequences of each of the microsatellite loci listed in this table and assay description. +, amplification, ++, amplification and see Supplementary material Table S2 for details of polymorphism assessment; ?, equivocal; –, failed amplification; (blank cell), untested

Locus	Aphidinae																											Neuquenaphidinae									
	Aphidini			Macrosiphini																																	
	Ac	Ag	Rp	Ap	Bb	Dn	Ia	Mt	Ma	Me	Mr	Mf	Md	Mef	Mya	Myn	Myp	Ph	Sak	Sav	Sb	Sf	Si	Sm	Snf	Sp	Srh		Sru	Sw	Sfs	Ua	Ufu	Ufo	Ut	Ns	
Sm10	-	-	+	++		++	-	-	+	+	+	++	+	+			-	+	+	++	-	++	+	+	++	+	-	?	-	+	+	-	-	-	?		
Sm11	-	-	+	++	+	++	-	++	+	+	-	-	+	+			+	?	+	++	-	++	+	+	++	-	-	+	-	+	-	+	+	++	++		
Sm12	-	-	?	+		++		-	-			-	+				-		+	++		-	+	-										-	-		
Sm17	-	+	?			-	+	-	+	+	+	-	+	+			-	-	+	++	+	++	+	+	++	-	+	+	+	+	+	+	+	++	?		
S9							++					++					-		-				+	++										-			
S10				++								+					-		++				+	++													
S12	-	-					-					-	+				-	+	+				+	+											-		
S16b	+	+	++			++	++					++	+			++	++	++	+		++		+	++											++		
S17b	+	+	++	++		++	++					++	+			++	++	++	+		++		+	++												-	
S19	-	+					-					-	-				-	-		++			+	++												-	
S23	+	+	+	++		++	++					++	+		++	++	++	+		+			+	++												++	
S24	+	+	+	++			++					++	+				++	+		+			+	++												++	
S25	-	+	-	++			++					++	+				-	-		+			+	+												-	
S30	-	+	+	++			++					-	+				-	+		+			+	++												++	
S35	-	+	-	++			-					-	+				-	-		+			+	++												-	
S43ii						-														++			+	++													
S45	-	-					-					-											+	-													
S49	-	-	+			++	-					-	+				-	-		++			+	++												-	

Species key: Ac, *Aphis craccivora*; Ag, *Aphis gossypii*; Rp, *Rhopalosiphum padi*; Ap, *Acyrtosiphon pisum*; Bb, *Brevicoryne brassicae*; Dn, *Diuraphis noxia*; Ia, *Illinoia azalea*; Mt, *Macrosiphoniella tanacetaria*; Ma, *Macrosiphum albifrons*; Me, *Macrosiphum euphorbiae*; Mr, *Macrosiphum rosae*; Mf, *Metopeurum fuscoviride*; Md, *Metopolophium dirhodum*; Mef, *Metopolophium festucae*; Mya, *Myzus antirrhinii*; Myn, *Myzus nicotianae*; Myp, *Myzus persicae*; Ph, *Phorodon humuli*; Sak, *Sitobion akebiae*; Sav, *Sitobion avenae*; Sb, *Sitobion blackmani*; Sf, *Sitobion fragariae*; Si, *Sitobion ibariae*; Sm, *Sitobion miscanthi*; Snf, *Sitobion near fragariae*; Sp, *Sitobion pauliani*; Srh, *Sitobion rhamni*; Sru, *Sitobion rubiophila*; Sw, *Sitobion walkeri*; Sfs, *Sitobion from smilax*; Ua, *Uroleucon adenophorae*; Ufu, *Uroleucon fuchuensis*; Ufo, *Uroleucon formosanum*; Ut, *Uroleucon tanacetii*; Ns, *Neuquenaphis staryi*.

in investigating the cross-species amplification of microsatellite loci in nontarget species may be well spent. However, our more extensive cross-species amplification data (Supplementary material Table S2) indicate that allelic diversity can be very low in nontarget species compared with target species (see especially data for *Macrosiphoniella tanacetaria*, *Metopeurum fuscoviride* and *Uroleucon tanacetii*). In cases where levels of allelic diversity are extremely low, the usefulness of these loci is greatly limited and workers should consider isolating microsatellite loci in their species of interest. Further caution needs to be used in utilizing microsatellite loci in nontarget species by investigating the occurrence of null alleles, as detected for example in *S. fragariae* samples amplified with microsatellite primers designed from *S. miscanthi* sequences (Sunnucks *et al.* 1997).

Sitobion miscanthi loci, S10, S17b, S49 and S43ii are X-linked in *S. miscanthi* (Wilson 2000) and locus Sm11 is X-linked in *Sitobion* near *fragariae* (Wilson *et al.* 1997). We have confirmed the X-linkage of loci S10, S17b and S49 in *Sitobion* near *fragariae*, loci Sm11, S10, S17b and S49 in *S. avenae* and locus Sm11 and S17b in *R. padi*. Loci Sm11, S10 and S17b are X-linked in *A. pisum* (Caillaud *et al.* 2002). Finally, locus S17b is also X-linked in *M. persicae* (Sloane *et al.* 2001). It is worth noting that whilst the X-linkage of these loci has not been confirmed in species other than those listed above, many of these X-linked loci have been shown to cross-amplify in many species (Table 2). These include: Sm11, which has amplified in 22/33 species including the taxonomically distant species, *Neuquenaphis staryi*; S10, which has amplified in 5/6 species in which it has been tested; S17b, which has amplified in 15/16 species; and S49, which has amplified in 6/13 species. Overall, X-linked loci amplified in 71% of tests compared with 51% amplification of all loci tested (autosomal, X-linked and those of unknown location). The X-chromosomes are the largest chromosome pair in most aphid species, accounting for over 25% of the genome (e.g. Wilson *et al.* 1997). These data suggest that X-linked loci may be more conserved in aphids than autosomal loci. Finally, because X-linkage of loci is easily determined in cyclically parthenogenetic aphids, we encourage researchers to investigate the chromosomal location of their markers using the simple diagnostic test described in Wilson *et al.* (1997).

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Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/MEN/MEN584/MEN584sm.htm>

Appendix S1. Supplementary information.

Table S1. Source of microsatellite primer sequences for each of the loci used in the cross-species amplification study.

Table S2. Detailed cross-species amplification data for fourteen non-target species.

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