

## PERMANENT GENETIC RESOURCES

# Thirteen polymorphic microsatellite DNA loci from whiptails of the genus *Aspidoscelis* (Teiidae: Squamata) and related cnemidophorine lizards

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## Abstract

We describe polymerase chain reaction primers and amplification conditions for 13 microsatellite DNA loci isolated from two bisexual species of whiptail lizards *Aspidoscelis costata huico* and *Aspidoscelis inornata*. Primers were tested on either 16 or 48 individuals of *A. c. huico* and/or 26 individuals of *A. inornata*. Ten of the 13 primers were also tested against a panel of 31 additional whiptail taxa. We detected three to nine alleles per locus in *A. c. huico* and four to 19 alleles per locus in *A. inornata*, with observed heterozygosity ranging from 0.60 to 0.87 and from 0.15 to 1.00, respectively. These primers will be an important resource for surveys of genetic variation in these lizards.

**Keywords:** *Ameiva*, *Aspidoscelis*, *Cnemidophorus*, lizard, microsatellite, PCR primers, SSR, STR, teiid, whiptail

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Teiid whiptail lizards (whiptails) of the genus *Aspidoscelis* occur throughout much of North and Central America. They are particularly abundant and diverse in the arid lands of the southwest USA and Mexico (Reeder *et al.* 2002). Their biology (e.g. Winne & Keck 2004; Woolley *et al.* 2004; Cooper *et al.* 2005; Paulissen *et al.* 2006), population genetics (Rosenblum 2006), and systematic biology (e.g. Walker *et al.* 2001; Reeder *et al.* 2002; Cordes & Walker 2006) have been extensively studied. Whiptails are of particular interest to biologists because of the presence of many unisexual (parthenogenetic) complexes within *Aspidoscelis* and other closely related whiptail genera (Reeder *et al.* 2002). Although these microsatellite loci are not the first published for whiptails (see Rowe *et al.* 2002), those previously published are from a taxon (*Cnemidophorus vanzoi*) that is more closely related to Neotropical *Ameiva*

than to *Aspidoscelis* (Reeder *et al.* 2002). Here, we describe 13 polymorphic microsatellite loci (five dinucleotides, one trinucleotide, six tetranucleotides and one mixed di/tetranucleotide) that were isolated from the DNA of *Aspidoscelis costata huico* and *Aspidoscelis inornata*. These markers will be useful for assessing intraspecific genetic variation (especially genetic and clonal diversity within unisexual species), investigating metapopulations and assigning parentage in mating system studies. Microsatellite loci also have the potential to provide new insights involving introgression and hybridization among the numerous species complexes within *Aspidoscelis* (e.g. *A. burtti/costata*, *A. gularis*, *A. inornata* and *A. tigris* complexes).

To develop the primers in *A. inornata*, we extracted genomic DNA from liver tissue using DNeasy Kits (QIAGEN) and used the enrichment technique of Glenn & Schable (2005) to isolate and sequence microsatellite-containing DNA fragments. DNA from one individual was digested with *RsaI* (New England Biolabs) to generate

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fragments of manageable size. We ligated the fragments to double stranded SuperSNX24 linkers (forward 5'-GTT-TAAGGCCTAGCTAGCAGAATC-3', reverse 5'-GATTCT-GCTAGCTAGGCCTTAAACAAA-3') before hybridizing microsatellite-containing fragments to biotinylated oligonucleotide repeat probes. Probes were captured with magnetic streptavidin beads (Dynal) and unhybridized DNA was discarded. We performed two rounds of enrichment with the following oligonucleotide probes: (TG)<sub>12</sub> (AG)<sub>12</sub> (AAG)<sub>8</sub> (ATC)<sub>8</sub> (AAC)<sub>8</sub> (AAT)<sub>12</sub> (ACT)<sub>12</sub> (AAAC)<sub>6</sub> (AAAG)<sub>6</sub> (AATC)<sub>6</sub> (AATG)<sub>6</sub> (ACCT)<sub>6</sub> (ACAG)<sub>6</sub> (ACTC)<sub>6</sub> (ACTG)<sub>6</sub> (AAAT)<sub>8</sub> (AACT)<sub>8</sub> (AAGT)<sub>8</sub> (ACAT)<sub>8</sub> (AGAT)<sub>8</sub> (AACC)<sub>5</sub> (AACG)<sub>5</sub> (AAGC)<sub>5</sub> (AAGG)<sub>5</sub> and (ATCC)<sub>5</sub>. Enriched DNA was recovered and amplified using the SuperSNX24 forward primer in a polymerase chain reaction (PCR) as follows: 10 mM Tris-HCl pH 8.3, 50 mM KCl, 2.0 mM MgCl<sub>2</sub>, 25.0 µg/mL BSA, 0.5 µM SuperSNX24 forward primer, and 0.5 U JumpStart *Taq* DNA polymerase (Sigma). We ligated this PCR product into pCR2.1-TOPO vector (Invitrogen), inserted it into One Shot Top10 Chemically Competent *Escherichia coli* cells (Invitrogen), and screened for successful insertion using the β-galactosidase gene along with materials and protocols provided by a TOPO TA cloning kit (Invitrogen). We amplified inserts from positive colonies using M13 primers and sequenced with Big Dye (version 2.0 or 3.1, Applied Biosystems) chemistry and an ABI PRISM 377–96 or ABI PRISM 3130xl automated sequencer. We edited sequences with SEQUENCHER 4.2 (GeneCodes) and used EPHEMERIS 1.0 (available at [www.uga.edu/srel/DNA\\_Lab/programs.htm](http://www.uga.edu/srel/DNA_Lab/programs.htm)) to search the sequences for microsatellites. We designed PCR primer pairs using OLIGO 6.67 (Molecular Biology Insights). One primer of each pair was modified with a tag at the 5' end (either 5'-GGAAACAGCTATGACCATG-3' or 5'-CAGTCGGGCGTCATCA-3') allowing the binding of a fluorescently labelled oligonucleotide to the PCR product for detection of polymorphism on an ABI PRISM 3130xl genetic analyser (cf. Boutin-Ganache *et al.* 2001).

Primers were optimized using eight individuals, which included *Aspidoscelis velox*, *A. tigris* and *A. inornata*. Variable loci were then screened against a larger array of *Aspidoscelis* species. PCRs were performed in 25-µL volumes with an Eppendorf Mastercycler Gradient thermal cycler. Concentrations of the reagents were 10 mM Tris-HCl pH 8.3, 50 mM KCl, 1.5–2.0 mM MgCl<sub>2</sub>, 25.0 µg/mL BSA, 0.4 µM unlabelled primer, 0.04 µM tag-labelled primer, 0.36 µM dye-labelled primer (HEX or 6-FAM), 0.15 mM dNTPs, 0.25 U JumpStart *Taq* DNA Polymerase (Sigma), and 30–50 ng DNA template. With the directly labelled primer (Acos5), both forward and reverse primers were at final concentration of 0.2 µM. Primers were optimized with two different touchdown PCR thermal cycling programmes, which test a range of annealing temperatures (i.e. 65–55 °C or 55–45 °C). Programmes consisted of five cycles of 96 °C for 20 s, the highest annealing temperature for 30 s, and 72 °C for 1 min

followed by 21 cycles of 30 s of 96 °C, highest annealing temperature minus 0.5 °C each cycle for 30 s, and 72 °C for 1 min; and finally, 10 cycles of 96 °C for 30 s, the lowest annealing temperature for 30 s, and 72 °C for 1 min. We sized products with Naurox ladder (DeWoody *et al.* 2004), to which GTTT was added to the 5' end of unlabelled primers, and with GENEMAPPER 4.0 software (Applied Biosystems) on an ABI PRISM 3130xl genetic analyser.

Primer pairs for *A. c. huico* were developed following a different protocol. DNeasy kits (QIAGEN) were used to extract genomic DNA from blood samples from lizards from the Isla Isabel, México. One microgram of DNA pooled from 10 unrelated adults (5 males and 5 females) was digested with *Mbo*I (Promega) and ligated to 600 ng of annealed *Sau*LA and *Sau*LB linkers (Armour *et al.* 1994) with 3 U of T4 DNA ligase, 1× ligase buffer (Promega) [10 mM Tris-HCl (pH 7.8), 10 mM MgCl<sub>2</sub>, 5 mM DTT, 1 mM ATP] in a 50-µL volume. Two microlitres of the ligation product were amplified in each of four 50-µL PCRs containing 1× Bionline buffer [16 mM (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub>, 67 mM Tris-HCl (pH 8.8), 0.01% Tween 20], 0.01 mM dNTP, 2.0 mM MgCl<sub>2</sub>, 20 pmol of *Sau*LA linker and 0.2 U *BioTaq* (Bionline) at 72 °C for 2 min, 94 °C for 3 min then 20 cycles of 94 °C for 30 s, 57 °C for 30 s and 72 °C for 1.5 min and a final elongation step of 5 min at 72 °C in a PTC-100 thermocycler (MJ Research). Enrichment for CA repeats was carried out as in Muniz *et al.* (2003) except that we used only a single round of enrichment and the amplification product was hybridized to the nylon membrane at 42 °C. The linkers were removed by digestion with *Mbo*I and the DNA purified also as in Muniz *et al.* (2003). The purified fragments were then ligated into 'Ready-to-go' *Bam*HI digested pUC18 (Pharmacia) following manufacturer's protocol. After transformation in Epicurian XL1 Blue MRF' supercompetent cells (Stratagene) and plating onto Luria-Bertani agar plates with 50 µg/mL ampicillin, the colonies were screened with (CA)<sub>24</sub> oligonucleotides end-labelled with [<sup>32</sup>P] dATP (T4 Polynucleotide kinase RTG kit, Pharmacia). We identified 51 positive colonies out of 460 screened, extracted plasmid DNA from these with Eppendorf Perfectprep plasmid kits, amplified inserts with M13 primers and sequenced to determine insert length. Colonies with inserts 300–500 bp were preserved and sequenced on an ABI PRISM 377 sequencer. Four sequences included suitable repetitive sequences and flanking regions. Primers for these sequences were designed using PRIMER 3 (Rozen & Skaletsky 2000).

PCR conditions were optimized using genomic DNA from two *A. c. huico* individuals. Reactions for the *A. c. huico* primers were performed in 20-µL volumes containing 10 mM Tris-HCl pH 8.4, 50 mM KCl, 0.5–2.5 mM MgCl<sub>2</sub>, 0.5 pmol forward primer, 0.5 pmol reverse primer, 0.10 mM dNTPs, 0.7 U of *Taq* DNA polymerase (Life Technologies do Brazil Ltd), and 25 ng DNA template, on a PTC-100 thermo-cycler (MJ Research). PCR annealing temperatures

**Table 1** Four PCR primer pairs are characterized in *Aspidoscelis costata huico* against one population of 48 individuals (loci Acos2, Acos3 and Acos5) and in 16 individuals (locus Acos6) from Isla Isabel, Nayarit, México. An additional nine primer pairs are characterized in *Aspidoscelis inornata* against two populations of  $\geq 11$  individuals from White Sands National Monument and the Jornada Experimental Range in New Mexico, USA. Locus Acos5 is genotyped against both data sets. 'Pigtail' tags and tags for universal fluorescent primer binding (e.g. M13 or CAG) are in italics;  $T_a$  corresponds to highest annealing temperature in a thermal cycling programme; dye is either the fluorescent label or silver nitrate stain (SN);  $k$  is number of alleles; allele size range includes the CAG or M13 universal primers if present (see main text for sequences);  $H_O$  and  $H_E$  are observed and expected heterozygosities; \* indicates loci are not in HWE after Bonferroni correction

Locus accession no.	Primer sequence (5'-3')	$T_a$ (°C)	Dye	Repeat motif	Allele size range (bp)	Locality	Sample size	$k$	$H_O$	$H_E$
Acos2 EF367111	F: CCTGAAGAGGATGCATTCAA R: TGGAAATAGTTTTCCGAAGTGC	61	SN	(CA) <sub>7</sub>	186–202	IINMX	48	5	0.65	0.66
Acos3 EF367112	F: GACGGAATGATTGCCPTTGT R: AATCTGGGGTTTTCCGTCT	61	SN	(CA) <sub>17</sub>	241–265	IINMX	48	8	0.60*	0.72
Acos5 DQ910543	F: CGAGTGAAGGCTGGAAAAC R: CCTATCCTGATGAATAGCACTGA	55	PET	(GT) <sub>15</sub>	173–187	JLTER	13	4	0.85	0.68
—	—	61	SN	—	166–170	IINMX	48	3	0.65	0.47
Acos6 EF408839	F: CAGCAACCTCCCAAATAAGC R: GGCTTCTCTGAAAAGGCAAAA	65	SN	(CT) <sub>11</sub> (CA) <sub>17</sub>	128–138	IINMX	16	3	0.56	0.58
Ai5013 DQ910537	F: CAG-AAATTAATGTGCAGCACTAT R: GTTGGCAGTTTTTCAGCTAAG	55	NED	(ATAG) <sub>25</sub>	249–373	JLTER	12	19	0.83	0.94
Ai5033 EF367108	F: AATGATGTTTGAATTAGAT R: M13-TCCGTATTTTCAGCATAGT	55	NED	(GGAT) <sub>24</sub>	171–329	JLTER	11	14	0.82	0.92
Ai5035 EF441867	F: CAG-AAATTGTGGAGAAAAC R: GTTTCATTTCTTGTAGCTTTAGTC	55	NED	(AGAT) <sub>26</sub> (ACAG) <sub>12</sub>	314–423	JLTER	13	13	1.00	0.88
Ai5037 DQ910538	F: CAG-TTCATTTTATATGCTGTAA R: GTTTCATGAAGATTTCCAAATACT	55	NED	(GATA) <sub>16</sub> ... (GATA) <sub>16</sub>	253–427	JLTER	12	17	0.67*	0.93
Ai5042 EF367109	F: GTTCTGAACCCCAAAAATATC R: CAG-TGCAAAATTAAGGCTACTT	55	NED	(TGA) <sub>23</sub>	132–201	JLTER	13	13	0.69	0.89
Ai5043 EF441868	F: GTTAAAAAGAAAAGGAAGAACTAA R: CAG-TGAGACAAGTTGGGTAGA	65	6-FAM	(ACAG) <sub>30</sub> (AGAT) <sub>30</sub>	221–342	JLTER	13	14	0.69*	0.91
Ai5057 DQ910539	F: AGATGAAGCTAAAGGTAATC R: CAG-GCTATGTTTCTAAATATGT	55	6-FAM	(GT) <sub>12</sub> (ATGT) <sub>12</sub> (GT) <sub>6</sub> (ATGT) <sub>17</sub>	232–256	JLTER	11	5	0.91	0.64
Ai5062 EF367107	F: GTTGTGCATTC AATGATGTATT R: CAG-GCTTTGCTCAGTGTAACT	55	NED	(AGAT) <sub>30</sub> ... (TTCA) <sub>14</sub>	233–341	JLTER	13	12	0.15*	0.89
Ai5071 EF367110	F: GTTCTCCCAATTTTCTACAT R: CAG-TTGCATATGTGAAGTAAAGTAT	55	NED	(TG) <sub>10</sub> (AG) <sub>13</sub>	249–265	JLTER	10	6	0.40	0.75
						WSNM	13	4	0.38	0.64

were tested in pairs (e.g. 54 °C and 55 °C), with the programme consisting of one cycle of 94 °C for 5 min, followed by 10 cycles of 94 °C for 30 s, the highest annealing temperature for 40 s, and 72 °C for 40 s, then 20 cycles of 94 °C for 30 s, the lowest annealing temperature for 40 s, and 72 °C for 40 s, and, finally, a step of 72 °C for 5 min. We sized products with 10-bp ladder (Invitrogen) on 6% polyacrylamide gels at 1.6 kV for 3–5 h, and stained gels with 0.001% AgNO<sub>3</sub>.

To assess polymorphism, we genotyped 48 *A. c. huico* for loci Acos2, Acos3 and Acos5, 16 *A. c. huico* for Acos6, and 26 *A. inornata* for the 'Ai' series primers (as well as Acos5). We also genotyped 31 additional cnemidophorine (whiptail) lizard taxa, with a primary focus on bisexual *Aspidoscelis* (including representatives of the *A. tigris*, *A. deppii* and *A. sexlineata* species groups). The 13 primer pairs and amplification results for *A. c. huico*/*A. inornata* are summarized in Table 1. Observed and expected heterozygosities were calculated for each locus with GENALEX version

6.0 (Peakall & Smouse 2006). We used GENEPOP version 3.5 (web interface) to test for deviations from Hardy–Weinberg equilibrium (HWE) and for evidence of genotypic linkage disequilibrium. BLAST searches of cloned sequences yielded no significant hits.

We detected three to nine alleles per locus in *A. c. huico* and four to 19 alleles per locus in *A. inornata*, with observed heterozygosity ranging from 0.60 to 0.87 and from 0.15 to 1.00, respectively. There was no evidence of linkage among our loci. Expectations of HWE deviated in Acos3, Ai5033, Ai5035, Ai5037, Ai5042, Ai5043, Ai5062 and Ai5071 after Bonferroni correction in at least one of the three populations investigated (see Table 1). For the 'Ai' series loci, both populations were collected in regions that may represent hybrid zones of either *A. i. ilanuras*/*A. i. gypsi* at the White Sands National Monument (WSNM) or *A. i. ilanuras*/*A. i. heptagramma* at the Jornada Experimental Range (JER) (Wright & Lowe 1993). Additionally, the program STRUCTURAMA (Huelsenbeck *et al.* Submitted) assigns individuals

**Table 2** Ten PCR primer pairs tested against 33 whiptail lizard taxa. '+' indicates presence of amplification product, '0' indicates no amplification, 'n' is the minimum number of individuals genotyped for each locus. PCR conditions are the same as those reported in Table 1

Taxon	Acos5	Ai5013	Ai5033	Ai5035	Ai5037	Ai5042	Ai5043	Ai5057	Ai5062	Ai5071
<i>Aspidoscelis angusticeps</i> * n = 1	+	0	+	0	+	+	0	+	+	+
<i>A. burti burti</i> * n = 1	+	0	+	+	0	+	+	+	+	+
<i>A. b. stictogramma</i> * n = 2	+	+	+	+	0	0	+	0	+	+
<i>A. b. xanthanota</i> * n = 1	+	0	+	+	0	0	+	0	+	+
<i>A. costata costata</i> * n = 1	+	+	+	+	0	+	+	+	+	+
<i>A. c. barrancorum</i> * n = 3	+	0	+	0	+	+	0	0	+	+
<i>A. c. grisceophala</i> * n = 4	+	0	+	0	0	+	0	0	0	+
<i>A. c. huico</i> * n = 1	+	+	+	0	0	+	0	0	+	+
<i>A. c. nigrigularis</i> * n = 1	+	+	+	+	0	0	+	+	+	+
<i>A. c. zwiefeli</i> * n = 2	+	+	+	+	+	+	+	+	+	+
<i>A. gularis gularis</i> * n = 2	+	+	+	+	+	+	+	+	+	+
<i>A. g. scalaris</i> * n = 2	0	+	+	+	+	+	0	+	+	+
<i>A. hyperythra</i> ‡ n = 1	+	+	+	+	+	+	0	+	+	+
<i>A. inornata arizonae</i> * n = 1	+	+	+	+	+	+	+	+	+	+
<i>A. i. gypsi</i> * n = 17	+	+	+	+	+	+	+	+	+	+
<i>A. i. heptogramma</i> * n = 1	+	+	+	+	+	+	+	+	+	+
<i>A. i. llanuras</i> * n = 14	+	+	+	+	+	+	+	+	+	+
<i>A. marmorata</i> † n = 1	+	+	0	+	+	+	+	+	+	+
<i>A. mexicana</i> * n = 2	+	+	+	+	+	+	+	0	+	+
<i>A. montague</i> * n = 2	+	+	+	+	+	+	0	+	+	+
<i>A. parviosocia</i> * n = 1	+	+	+	+	+	0	0	+	+	+
<i>A. sacki gigias</i> * n = 1	+	0	+	+	0	+	0	0	+	+
<i>A. s. sacki</i> * n = 2	+	+	+	+	+	+	0	+	+	+
<i>A. tigris tigris</i> † n = 2	+	+	0	0	+	+	+	+	+	+
<i>A. t. maxima</i> † n = 1	+	+	0	0	+	0	0	+	+	+
<i>A. uniparens (unisexual)</i> n = 11	+	+	+	+	+	+	+	+	+	+
<i>A. velox (unisexual)</i> n = 1	+	+	+	+	0	+	+	+	+	+
<i>Ameiva ameiva</i> n = 1	0	+	0	0	0	0	0	0	0	0
<i>Cnemidophorus' lemniscatus</i> n = 2	0	0	0	0	0	+	0	0	0	0
<i>Kentropyx altamazonica</i> n = 1	0	0	0	0	0	0	0	0	0	0
<i>K. calcarata</i> n = 1	0	0	0	0	0	0	0	0	0	0
<i>K. striata</i> n = 1	0	0	0	0	0	+	0	0	0	0
<i>Tupinambis teguixin</i> n = 1	+	0	0	0	0	0	0	0	0	0

\**Aspidoscelis sexlineata* group; †*Aspidoscelis tigris* group; ‡*Aspidoscelis deppii* group.

from the same locality (i.e. individuals within WSNM or JER) to different populations. Thus, neither population appears to be panmictic, and future studies will formally assess whether deviations from HWE result from hybridization among genetically distinct subspecies. Our screen of these loci against 31 whiptail taxa suggests they amplify best within the *A. sexlineata* and *A. tigris* species groups (Table 2). In many instances, we were only able to screen against one or two individuals; thus, those loci that did not appear to amplify in some taxa may still be informative. To conclude, these highly polymorphic microsatellite markers will likely prove valuable for future population genetic research in whiptails.

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