Copeia, 1998(2), pp. 354–366

Genetic Variation, Species Status, and Phylogenetic Relationships in Rose-Bellied Lizards (*Variabilis* Group) of the Genus *Sceloporus* (Squamata: Phrynosomatidae)

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We investigated species boundaries and phylogenetic relationships in the *Sceloporus variabilis* group, using multilocus isozyme characters. Forty-one genetic markers were screened in a sample of 238 lizards from 47 localities, representing eight ingroup species. Thirty-four loci were variable within or between taxa. Morphologically well-defined species (*S. chrysostictus, S. cozumelae,* and *S. parvus*) were strongly and unambiguously differentiated genetically. Within *S. variabilis, S. v. marmoratus,* high-elevation populations of *S. v. variabilis* (from Hidalgo, Queretaro and San Luis Potosi), low-elevation populations of *S. v. variabilis,* and *S. v. olloporus,* were each recognized as full species. Low-elevation populations of *S. v. variabilis* were only slightly divergent from *S. v. teapensis* and were retained as conspecific. Two different methods of parsimony analysis recovered trees with the following structure: (*S. parvus* (*S. chrysostictus* (*S. cozumelae* + *S. variabilis* species-group))). A FREQPARS analysis recovered a different topology.

Investigamos el límite entre especies y las relaciones filogenéticas en el grupo *Sceloporus variabilis,* utilizando isoenzimas con multiples loci. Se revisaron 41 marcadores genéticos en una muestra de 238 lagartijas de 47 localidades, las cuales representaban 8 especies. Treinta y cuatro loci fueron variables inter e intra especificamente. Las especies distinguibles morfologicamente, también resultaron estar fuertemente diferenciadas geneticamente (*S. chrysostictus, S. cozumelae* y *S. parvus*). Entre las subespecies de *S. variabilis, S. v. marmoratus,* poblaciones de *S. v. variabilis* de tierras altas (en Hidalgo, Querétaro y San Luis Potosí), poblaciones de *S. v. variabilis* de tierras bajas, y *S. v. olloporus,* se reconocen como especies diferentes. Las poblaciones de tierras bajas de *S. v. variabilis* fueron solo ligeramente divergentes de *S. v. teapensis,* por lo que se retuvieron como entidades conespecíficas. Dos análisis diferentes de parsimonia resultan en arboles con la siguiente topología: (*S. parvus* (*S. chrysostictus* (*S. cozumelae* + especies del grupo *S. variabilis*))). Un análisis con FREQPARS, arroja una topología diferente.

THE lizard genus *Sceloporus* is one of the most conspicuous and widely distributed in North America. The radiation is comprised of at least 70 species that offer numerous advantages as models for ecological and evolutionary studies (Sites et al., 1992). However, addressing questions in comparative biology by using a model group requires well-defined species and well-corroborated hypotheses of relationships within the group (Brooks and McLennan, 1991; Harvey and Pagel, 1991).

Smith (1939) partitioned *Sceloporus* into two "radiations": one with small scales and body size, and another with large scales and large body size. The *S. variabilis* species group and seven other species groups were assigned to the small-scaled, small-bodied radiation. The *S. variabilis* group, as defined by Smith (1937, 1939), included five species: *S. couchii, S. cozumelae, S. parvus, S. teapensis,* and *S. variabilis.* Smith proposed that presence of a postfemoral dermal pocket, small lateral-body scales, 36–83 (minimum-maximum) dorsal scales, smooth ventral and preanal scales, granular posterior thigh surface scales, and presence of two canthals were diagnostic for the group.

Larsen and Tanner (1974, 1975), using a set of characters that included cranial osteology, karyology, behavior, and zoogeography considered the *S. variabilis* group to include three species: *S. cozumelae, S. variabilis,* and *S. teapensis. Sceloporus chrysostictus* was hypothesized to be the sister taxon to this assemblage. The other members of Smith's original *variabilis* group where placed in the genus *Lysoptychus* Cope, resurrected by Larsen and Tanner.

Hall (1973, 1983), inferred relationships in *Sceloporus* based on chromosome data and considered the *S. variabilis* group to include *S. cozumelae, S. teapensis,* and *S. variabilis,* with this assemblage being closely related to the monotypic *S. chrysostictus* group. Hall defined the (*S. chry-*

sostictus group + *S. variabilis* group) clade on the basis of general similarity in morphology. Cole (1971, 1978) documented the presence of a secondary constriction (the nucleolar-organizing region, or NOR) close to the centromere in one of the longest pair of microchromosomes and the absence of such a constriction in the second pair of macrochromosomes in both the *S. chrysostictus* and *S. variabilis* groups, supporting the notion that both shared a common ancestor. On the basis of this arrangement of the NOR position, Cole added *S. couchii* back into the *S. variabilis* group (Sites et al., 1992).

Based on molecular and morphological data, Reeder and Wiens (1996) reassessed these relationships and also recovered a monophyletic clade consisting of the *S. variabilis* group plus *S. chrysostictus*. Although their study included many of the relevant taxa in the *S. variabilis* group, their geographic sampling was inadequate to test alternative interpretations of species boundaries proposed by Sites and Dixon (1982) and Smith et al. (1993).

Sites and Dixon (1982), based on a multivariate study of morphology, concurred with Cole (1978) that *S. "teapensis"* should be a subspecies of *S. variabilis*. They also synonymized *S. variabilis olloporus* with *S. variabilis* on the basis of overlapping femoral pore counts. Smith et al. (1993) investigated geographic variation in 12 morphological characters among subspecies of *S. variabilis*. They recognized *S. smithi* and *S. teapensis* as full species, and resurrected the subspecies *S. v. olloporus*. With this new arrangement, *S. variabilis* was composed of three subspecies: *S. v. variabilis*, *S. v. marmoratus*, and *S. v. olloporus*. The geographic range of *S. teapensis*, as recognized by Smith et al. (1993), split populations of *S. v. variabilis* into three allopatric groups (Fig. 1).

In this paper, we employ multilocus isozyme electrophoresis (Selander et al., 1971; Murphy et al., 1996) to summarize patterns of genetic variability and test species boundaries for *S. variabilis*, particularly with regard to the issue of species status for *S. teapensis* relative to *S. v. variabilis*. For these and other species previously included in the *variabilis* group, we also present a phylogenetic hypothesis based on isozyme markers.

Materials and Methods

A total of 235 specimens representative of taxa in the *S. variabilis* group was collected from 47 localities (Fig. 1) in Mexico, during the summers of 1992 and 1993. Localities, sample sizes, and vouchers are listed in Materials Examined.

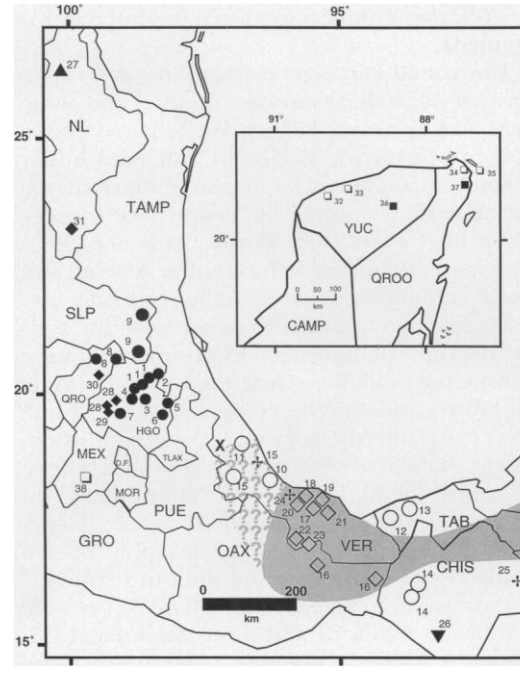

Fig. 1. Collection localities for *Sceloporus variabilis*. Numbers of individual localities and names of political units are given in Materials Examined. Symbols identify the following: *S. v. variabilis* (high-elevation sites)—solid circles; *S. v. variabilis* (low-elevation sites)—open circles; *S. v. marmoratus*—solid triangle; *S. v. olloporus*—inverted solid triangle; *S. v. teapensis*—open diamonds; *S. parvus*—solid diamonds; and *S. bicanthalis*—open square. Crosses (plus signs) show collecting localities characterized by transitional samples: localities 15 and 24—*S. v. variabilis* × *S. v. teapensis*; locality 25—*S. v. variabilis* × *S.v. olloporus*. "X" marks northernmost locality for *S. v. teapensis* (of fig. 6 of Smith et al. 1993). Shaded "?" identifies the possible range of *S. v. teapensis* if it is extended to the northernmost locality. Inset: collecting localities for *S. chrysostictus* (solid squares) and *S. cozumelae* (open squares).

Localities that were represented by only one or a few specimens were grouped together by geographic proximity if they were fixed for or shared the same alleles. These aggregate samples are identified by superscripts in Materials Examined and are plotted in Figure 1. Specimens were assigned to taxon by using identification keys in Smith and Taylor (1950). Three individuals of *S. bicanthalis* were included as an outgroup.

Various tissues (heart, liver, stomach, intestine, kidney, and skeletal muscle) were removed from freshly killed specimens, preserved in liquid nitrogen, and stored at −70 C. Voucher specimens were preserved using standard methods and deposited in Mexico's National Univer-

sity (catalog numbers are listed in Materials Examined).

Horizontal starch-gel electrophoresis was performed on skeletal muscle, intestine and stomach, and liver and kidney. We followed protocols in Murphy et al. (1996) and used buffer systems in combinations to resolve more charge variation than resolved by "single pass" electrophoresis (Coyne, 1982; Barbadilla et al., 1996). Enzymes, putative gene loci, buffer systems, and tissue combinations are listed in Appendix 1.

We inferred individual genotypes on the basis of isozyme phenotypes. Electromorphs were considered homologous if they had the same mobility in side-by-side comparisons on all buffers that resolved any given locus. Those of different mobilities were registered as different alleles by using alphabetic designations based on decreasing mobility (cathode to anode). Genotypes per individual for all polymorphic loci are available upon request from the third author.

Data were analyzed using BIOSYS-1, release 1.7 (D. L. Swofford and R. B. Selander, 1981, unpubl.). Genetic distances (Nei, 1978) were clustered using the UPGMA algorithm (Sneath and Sokal, 1973). The matrix of genetic distances used in the UPGMA clustering is available upon request from the third author.

Following suggestions of Sites and Crandall (1997), we defined empirical criteria we considered necessary to support species recognition and then applied them to address status of populations in the *S. variabilis* complex. We stress the advantages of identifying characters in a concordant geographic framework (Avise and Ball, 1990; Mallet, 1995) to distinguish populations that may be isolated only ephemerally (O'Hara, 1993) from those that have been isolated long enough for unlinked characters to coalesce within the same collection of reproductively connected populations (Baum and Donoghue, 1995). Specifically, our criterion for species recognition is that two or more characters (morphological features, nuclear genetic markers, or any combination of these) should diagnose the same set of geographic populations, that is, unique character states should be shared among samples, although not necessarily present at 100% frequency.

Cladistic analysis employed branch-and-bound searches with PAUP, version 3.1.1 (D. L. Swofford, 1993, unpubl.), using all informative loci, including those that are polymorphic within and among populations. We first employed the most conservative loci, that is, those showing little or no intraspecific polymorphism (23 total). Characters (individual loci) were coded by assigning alternative states to unique combinations of electromorphs. This approach captures information based on presence of unique electromorphs (Crother et al., 1992). We then used the step matrix method (Mabee and Humphries, 1993) to accommodate highly polymorphic loci. This approach permitted use of all loci showing inter- and/or intraspecific variability (34 total). Individual loci were again designated as characters, but electromorph frequencies were transformed to Manhattan distances, which then served as the weighted values of the step matrix (Wiens, 1995). This approach incorporates frequency information and permits use of multistate characters (McGuire, 1996). The step matrix is available from the third author upon request. Both coding methods are subject to limitations of sampling error associated with small sample sizes (Baverstock and Moritz, 1996). A third analysis was performed based on the FREQPARS program (Swofford and Berlocher, 1987). Support for internal nodes on cladograms was evaluated by bootstrap proportions (Felsenstein, 1985).

Results

Patterns of isozyme variability.—Seven of 41 genetic loci assayed were monomorphic in all samples: *Ck-A, Fba-1, Gtdh-A, M-Aat-A, M-Mdh-A, S-Mdh-A,* and *Pk-A.* The remaining loci were polymorphic either within or among samples (Appendix 2). Mean number of alleles per locus (A) varied from 1.0 (*S. v. olloporus*) to 2.0 (*S. v. variabilis,* high-land); direct-count, median heterozygosity (H) ranged from 0.044 (*S. v. olloporus*) to 0.218 (*S. v. variabilis,* high-land). Data on individual genotypes by locality are available upon request from the third author.

The species *S. chrysostictus* (samples 36–37), *S. cozumelae* (samples 32–35), and *S. parvus* (samples 28–31), as well as the outgroup taxon *S. bicanthalis* (sample 38) are distinguishable from each other and from all populations of *S. variabilis* by fixed electromorphs at several loci (Appendix 2). *Sceloporus cozumelae, S. parvus,* and all samples of *S. variabilis* shared electromorphs *Pnp-A*(a) and *Tpi-A*(a) to the exclusion of *S. chrysostictus.* Within *S. variabilis,* all samples were fixed or nearly fixed for several electromorphs absent from other ingroup taxa. Diagnostic electromorphs for (*S. variabilis* + *S. cozumelae*) included *Glydh*(a) and *S-Aat-A*(a); electromorphs *Ak-A*(a) and α-*Man-A*(a,b) were diagnostic for all nominate samples of *S. variabilis,* and *S-Mdhp-A*(a) was diagnostic for all nominate samples of *S. variabilis* except *S. v. marmoratus* (Appendix 2). Samples of *S. variabilis* also shared a polymorphism [*Adh-A*(b)] absent in

other taxa. The subspecies *S. v. marmoratus* (sample 27) is distinguished by the fixed or nearly fixed electromorphs *Gpi-A*(b) and *Iddh*(c), whereas *S. v. olloporus* (sample 26) is distinguished by the fixed electromorphs α-*Man-A*(b) and *Pep-F*(b) (Appendix 2). The two groups of *S. v. variabilis* [high- (samples 1–9) and low-elevation (samples 10–14)], and *S. v. teapensis* (samples 16–23) shared the following electromorphs (either as fixed or polymorphic characters): *Fbp*(b), *Pgdh*(b), and "*Uk*"(a,b). The low-elevation populations of *S. v. variabilis* and *S. v. teapensis* shared electromorphs *M-Acoh-A*(c) and *Pep-*?(d), and the high- and low-elevation populations of *S. v. variabilis* were distinguished from each other by nearly fixed differences between electromorphs at the *Ldh-A* and *Ldh-B* loci and major differences in electromorph frequencies at *Iddh-A*, α-*Man-A*, *Pep-A*, and *Pep-*? (Appendix 2).

Because of the unexpected divergence between high- and low-elevation samples of *S. v. variabilis*, we examined the three morphological characters found by Smith et al. (1993) to be highly variable in the *S. variabilis* complex: number of dorsal scales; number of sacral dorsal scale rows; and total number of femoral pores. We compared these counts from 78 lizards (37 from high-elevation sites, and 41 from low-elevation sites). High-elevation lizards had a mean of 59.6 dorsal scales (range 54–65), with means of 10.8 (range 10–12) and 25.3 (range 22–29) for sacral dorsal scales rows and femoral pores, respectively. Low-elevation lizards had means and ranges for these same characters of 54.5 (47–61), 9.7 (9–12), and 24.0 (20–27), respectively. A Statistical Analysis Systems *t*-test (vers. 6, SAS Institute, Inc., 1989, unpubl.) showed that means for all counts were significantly higher in high-elevation populations: dorsal scales ($t = 6.44$, df = 76, $P < 0.01$), sacral dorsal scales ($t = 6.8$, df = 76, $P < 0.01$), and femoral pores ($t = 2.91$, df = 73, $P < 0.01$).

Patterns of genetic divergence.—Genetic identity values varied from 0.019 (samples 34 vs 35) to 1.0 (samples 20 vs 22); genetic distances ranged from 0.0 (samples 20 vs 22) to 1.443 (samples 37 *vs* 29). UPGMA cluster analysis (available upon request from the third author) clearly separated *S. chrysostictus* and *S. cozumelae* from each other and from a cluster including *S. cozumelae* and the *S. variabilis* complex. Within this cluster, *S. cozumelae* is most distinct, followed by *S. v. marmoratus*, the high-elevation samples of *S. v. variabilis*, then *S. v. olloporus*, and the most nested cluster that includes all low-elevation samples of *S. v. variabilis* and all samples of *S. v. teapensis*.

Terminal taxa.—Eight clusters of samples defined by UPGMA analyis were used as terminal taxa for phylogenetic analyses. We reduced the number of terminal taxa to decrease search times in phylogenetic analyses. Based on patterns of isozyme and/or morphological variation, three samples appeared to represent either hybrid or integrade populations. These samples included #15 (*S. v. variabilis* × *S. v. teapensis*), #24 (same combination), and #25 (*S. v. olloporus* × *S. v. variabilis*). These samples were not included in phylogenetic analyses.

Phylogenetic relationships.—The data matrix for 23 conservative loci for the eight terminal taxa is given in Table 1. The two most-parsimonious trees (65 steps) differed in relationships among *S. v. marmoratus, S. v. olloporus,* and *S. cozumelae.* Topologies relative to these three species in the two trees were: (*cozumelae* ((*v. marmoratus* + *v. olloporus*) (*v. teapensis* (*v. variabilis*-low + *v. variabilis*-high)))); and (*v. marmoratus* (*v. olloporus* (*cozumelae* (*v. teapensis* (*v. variabilis*-low + *v. variabilis*-high))))). The strict consensus topology is shown in Figure 2A.

A branch-and-bound search of a Manhattan distance step matrix for all 34 polymorphic loci (available upon request from the third author) resolved a single most-parsimonious tree (7362 steps) with a topology (Fig. 2B) concordant with the strict consensus tree derived from parsimony analysis of conserved electromorphs: *S. parvus* was basal and sister to the clade (*S. chrysostictus* (*S. cozumelae* + *S. variabilis*)). The topology of the step matrix tree differs from both of the unweighted parsimony trees with respect to placement of *S. v. marmoratus*: (*S. v. olloporus* (*S. v. teapensis* (*S. v. variabilis*-low (*S. v. variabilis*-high + *S. v. marmoratus*)))).

A FREQPARS-generated topology (143 steps, available from the third author upon request) differed substantially from those produced via parsimony analysis: (*S. v. olloporus* (*S. v. marmoratus* (*S. parvus* (*S. cozumelae* (*S. v. variabilis*-high (*S. chrysostictus* (*S. v. teapensis* + *S. v. variabilis*-low)))))))). This topology rendered *S. variabilis* paraphyletic with respect to other, well-defined ingroup taxa. This result may be attributed in part to the fact that FREQPARS has no provision for implementing efficient tree search algorithms (Berlocher and Swofford, 1997) and often recovers suboptimal trees (Wiens, 1995). If this were the cause of the discrepancy observed in our results, we would expect FREQPARS to perhaps perform better when con-

TABLE 1. INPUT CHARACTER MATRIX EMPLOYED IN MAXIMUM-PARSIMONY ANALYSIS OF NINE TERMINAL TAXA. Taxa are represented by two lines in the matrix: the top line is the character state; the bottom line is the electromorph composition at each locus. Characters are: 1 = *Pgm-A*, 2 = *Mpi-A*, 3 = *Idh*-2, 4 = *Idh*-1, 5 = *Pep-D*(PAP), 6 = *Ddh-A*, 7 = *S-Acoh-A*, 8 = *Glydh*, 9 = *Pgdh*, 10 = *G3pdh-A*^{2}, 11 = *Ak-A*, 12 = *Adh*, 13 = *Ada*, 14 = *S-Mdhp-A*, 15 = α-*Man-A*, 16 = *S-Aat-A*, 17 = "*Udh*", 18 = *Gpi-A*, 19 = *Ldh-B*, 20 = *Ldh-A*, 21 = *Pep-*?(LA), 22 = *Iddh*, 23 = *Fbp*.

Taxa	Characters																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
S. bicantha	a	f	c	b	f	a	b	c	o	a	b	a	b	c	c	c	a	c	d	d	g	a	a
	AA	AB	CC	BB	AB	AA	BB	CC	DE	AA	BB	AA	BB	CC	CC	CC	AA	CC	DD	DD	AC	AA	AA
S. chrysosti	d	c	a	a	g	c	f	c	a	c	b	a	b	g	e	d	b	a	c	c	c	a	a
	DD	CC	AA	AA	AC	CC	AB	CC	AA	CC	BB	AA	BB	AC	EE	DD	BB	AA	CC	CC	CC	AA	AA
S. cozumelae	g	b	a	a	z	c	a	a	a	b	b	a	a	e	e	f	s	a	f	a	g	g	a
	AC	BB	AA	AA	ABCD	CC	AA	AA	AA	BB	BB	AA	AA	EE	EE	AB	ACD	AA	AB	AA	AC	AC	AA
S. parvus	c	a	c	b	z	p	b	m	y	q	c	a	b	d	d	b	a	a	a	a	m	f	a
	CC	AA	CC	BB	ABCD	ABC	BB	CD	CDE	ABD	CC	AA	BB	DD	DD	BB	AA	AA	AA	AA	CD	AB	AA
S. v. marmor	f	a	a	a	a	f	f	f	a	b	f	f	a	b	a	a	a	b	b	b	g	c	a
	AB	AA	AA	AA	AA	AB	AB	AB	AA	BB	AB	AB	AA	BB	AA	AA	AA	BB	BB	BB	AC	CC	AA
S. v. ollopo	a	a	a	a	a	a	a	a	a	b	a	f	a	f	b	a	a	a	a	a	c	a	a
	AA	AA	AA	AA	AA	AA	AA	AA	AA	BB	AA	AB	AA	AB	BB	AA	AA	AA	AA	AA	CC	AA	AA
S. v. teapen	a	g	f	f	a	a	a	f	p	b	a	f	a	f	p	f	a	a	f	f	m	f	p
	AA	AC	AB	AB	AA	AA	AA	AB	ABC	BB	AA	AB	AA	AB	ABC	AB	AA	AA	AB	AB	CD	AB	ABC
S. v. v. low	a	a	f	a	a	f	a	a	f	b	a	f	a	p	f	f	f	f	f	a	s	g	p
	AA	AA	AB	AA	AA	AB	AA	AA	AB	BB	AA	AB	AA	ABC	AB	AB	AB	AB	AB	AA	ACD	AC	ABC
S. v. v. high	p	a	f	a	f	a	a	a	f	f	a	f	f	p	p	f	g	a	p	p	p	g	p
	ABC	AA	AB	AA	AB	AA	AA	AA	AB	AB	AA	AB	AB	ABC	ABC	AB	AC	AA	ABC	ABC	ABC	AC	ABC

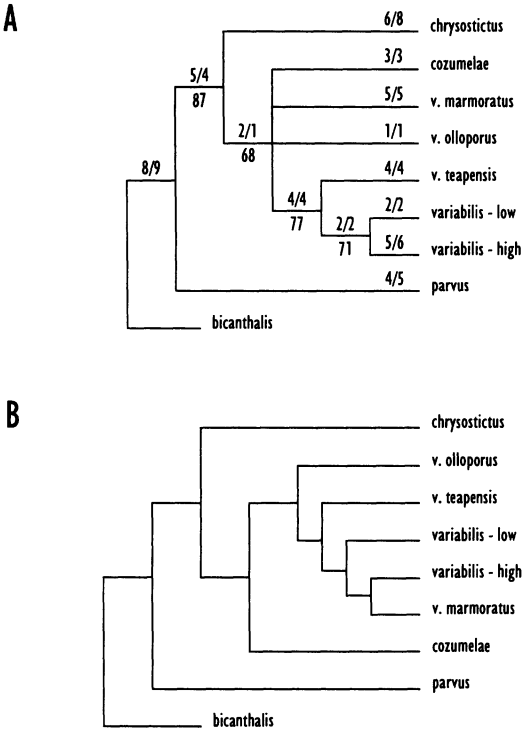

Fig. 2. (A) Strict consensus of two most-parsimonious hypotheses of relationships among samples of the *Sceloporus variabilis* group (65 steps, CI = 0.844, RI = 0.677, RC = 0.572). Values above branches represent total number of synapomorphies/number of uniquely derived synapomorphies. Numbers below branches are bootstrap proportions (1000 replications). (B) Single most-parsimonious tree derived from branch-and-bound analysis of a Manhattan distance step matrix for all loci; tree length is 7362 steps.

strained to one of the topologies depicted in Figure 2. However, when FREQPARS analyses were repeated using the constraint topologies represented in Figure 2A and Figure 2B, FREQPARS trees had total lengths of 152 and 164, respectively. Some of the samples used in this study are small, and this may bias a FREQPARS analysis, but sampling error is expected to be smaller for frequency data than for fixed characters (Swofford and Berlocher, 1987).

Discussion

Sceloporus chrysostictus, S. parvus, and to a lesser extent, *S. cozumelae* are characterized by multiple fixed allozymes at several loci. Within *S. variabilis,* both *S. v. marmoratus* (sample 27) and *S. v. olloporus* (sample 26) are differentiated by a number of electromorph frequencies, suggesting that both have been isolated for an amount of time sufficient for presumably independent characters to coalesce. On the basis of a number of conservative species concepts (Davis and Nixon, 1992; Mallet, 1995; Sites and Crandall, 1997), we believe that both warrant recognition as full species.

High-elevation samples of *S. v. variabilis* from the western Sierra Madre Occidental in Hidalgo, Querétaro, and San Luis Potosí (localities 1–9) grouped together based on similar electromorph frequencies at seven loci, two of which [*Ldh-A*(b), and *Ldh-B*(b)] were close to fixation. Four other electromorphs [*Iddh*(a,c), and "*Udh*"(a,c)] in the high-elevation samples were rare or absent in other samples of *S. variabilis.* Although Sites and Dixon (1982) showed that populations in this region (their samples 7 and 8) were divergent morphologically, neither they nor Smith et al. (1993) examined much material from this area. Patterns of variation in high- versus low-elevation samples of *S. v. variabilis* strongly suggest that the high-elevation samples represent a distinct species and that further morphological and genetic studies in this part of the species range would be productive.

The low-elevation samples of *S. v. variabilis* also are distinct, differing from other samples by near-fixation of a *Pep*-?(c) electromorph in all but one sample and by fixed or high frequency electromorphs at α-*Man-A*(a) and *Ldh-A*(a). The genetic similarity of disjunct, low-elevation samples in coastal Veracruz, coastal Tabasco, and the Central Depression of Chiapas is concordant with morphological similarity among these samples (Smith et al., 1993).

Patterns of isozyme variation are thus interpreted to indicate species-level distinction for *S. v. marmoratus, S. v. olloporus,* high-elevation samples of *S. v. variabilis,* and low-elevation samples of *S. v. variabilis.* Our interpretations should be tested further by sampling additional localities, especially for *S. v. marmoratus* and *S. v. olloporus.*

The taxonomic confusion regarding the status of *S. v. teapensis* may stem in part from the distribution of these populations relative to the low-elevation populations of *S. v. variabilis* (Fig. 1). An examination of the most detailed distribution map published to date (fig. 6 in Smith et al., 1993) reveals a complex pattern in which the range of *S. v. teapensis* splits *S. v. variabilis* into three allopatric populations. Further, the southernmost of the isolates of *S. v. variabilis* (the Chiapas-Oaxaca-Guatemala enclave of Smith et al., 1993), separates *S. smithi* to the west from *S. v. olloporus* to the east. This patchwork distribution is further compounded by cases of sympatry and/or hybridization between the following pairs of taxa: *S. v. variabilis* × *S. v. teapensis* (several sites in southern Veracruz); *S. v. tea-*

pensis × *S. v. olloporus* (western Guatemala); *S. v. variabilis* × *S. v. olloporus* (southeastern Guatemala); and *S. v. teapensis* × *S. smithi* (two cases of sympatry in which individuals of one taxon are recorded from well within the range of the other, and a third possible example of hybridization, all in Oaxaca; see fig. 6 in Smith et al., 1993).

Our sampling was centered on addressing the question of species status of *S. v. teapensis* relative to parapatric, low-elevation populations of *S. v. variabilis*. Samples of *S. v. teapensis* were the least differentiated genetically in our study, yet Smith et al. (1993) were able to diagnose most of their samples of *S. v. teapensis* on the basis of external morphology. Sites and Dixon (1982) and Smith et al. (1993) have shown that samples assigned to *S. v. teapensis* typically possess low dorsal scale counts, low nuchal and sacral dorsal scale rows, and relatively enlarged groin scales. Smith et al. (1993), however, stressed that distinction between *S. v. teapensis* and *S. v. variabilis* blurred where their ranges overlapped in southern Veracruz. Several instances of presumed sympatry between the two are recorded, and the range of morphological variation in these instances suggests that hybridization has occurred repeatedly at many of these localities (Smith et al., 1993, 1995). Understanding the interactions between these taxa may require collecting similar to the effort needed to map the distribution of chromosome races of the *S. grammicus* complex in one small part of its range (Arévalo et al., 1991, 1993; Sites et al., 1993). If such studies eventually demonstrate hybridization characterized by limited introgession of nuclear genetic and morphological characters, then species status for *S. v. teapensis* would be strongly supported. However, if such interactions result in introgression of genetic and or morphological characters to the extent that a bimodal distribution of diagnostic characters is lost (Mallet, 1995), conspecificity would be inferred. In our opinion, the evidence for species status for *S. v. teapensis* is equivocal, and rather than substituting one taxonomic uncertainty for another, we retain the trinomial for this taxon.

Two of the three phylogenetic analyses produced the topology (*S. parvus* (*S. chrysostictus* (*S. cozumelae, S. marmoratus, S. olloporus* (*S. v. teapensis* (*S. v. variabilis*-low + *S. v. variabilis*-high))))). Use of conservative loci alone did not resolve the position of *S. marmoratus* within the *S. variabilis* complex; whereas the topology derived from a Manhattan distance matrix was (*S. parvus* (*S. chrysostictus* (*S. cozumelae* (*S. olloporus* (*S. v. teapensis* (*S. variabilis*-low (*S. variabilis*-high + *S. marmoratus*)))))))). With the exception of *S. marmoratus*, these topologies are not in conflict, and are likely similar because of the influence of the 23 conservative loci. Predominance of fixed electromorphs (values of 1.00 in the step matrix) may override polymorphic loci and contribute more to tree structure. A study of mitochondrial DNA sequences in progress will permit a statistical test of the alternative positions for *S. marmoratus*.

Materials Examined

Specimens used in the study are listed by locality, sample size, and catalog number. Vouchers are deposited in the Museo de Zoología, Facultad de Ciencias (MZFC), at the National University (Universidad Nacional Autónoma de México, UNAM) of Mexico. Superscripts for a locality identify sites that were pooled as single samples for analyses; these are the numbers plotted in Figure 1.

Sceloporus variabilis variabilis.—HIDALGO: (1) 5.3 km E Tlanchinol (Arroyo de Aplantazol)[1]; n = 5 [5330(2), 6059 (3)]; (2) Temapa[1]; n = 3 (6064); (3) Calnali[1]; n = 1 (6066); (4) Olotla[1]; n = 3 (6070); (5) San Pedro Huazatlingo[2]; n = 3 (5556, 6074, 6075); (6) Sietla[3]; n = 3 [5412(2), 5555]; (7) Lago Atezca[4]; n = 1 (5332); (8) San Bartolo Tutotepec[5]; n = 2 (6067); (9) 4 km E Tenango de Doria[6]; n = 2 (5331); (10) Tolantongo[7]; n = 2 (6072–73); QUERETARO: (11) Concá[8]; n = 6 (5369); (12) Acatitlán de Zaragoza[8]; n = 1 (5370); SAN LUIS POTOSI: (13) 6 km N Ciudad Valles[9]; n = 4 [5374, 5375(2), 5376]; (14) Xilitlilla[9]; n = 1 (5557); VERACRUZ: (15) Alvarado[10]; n = 10 [5552(5), 5558(4), 5809]; (16) 1 km E El Copital[11]; n = 2 (5802); (21) Playa Mocambo[15]; n = 13 [5483(9), 5484(4)]; (22) 3 km ENE Coscomatepec (Jumapa River)[15]; n = 1 (5129); TABASCO: (17) Sánchez Magallanes[12]; n = 7 (5792); (18) 20 km ESE Sánchez Magallanes[13]; n = 3 (5793); CHIAPAS: (19) km 25, federal hwy 190 (El Chorreadero)[14]; n = 4 (5553); (20) Mirador "La Coyota" (Cañón del Sumidero)[14]; n = 1 (5554).

Sceloporus variabilis teapensis.—OAXACA: (23) Santa María Chimalapa[16]; n = 1 (4750); (24) Santiago Jalajui[16]; n = 3 (5420–21, 5451); VERACRUZ: (25) Catemaco[17]; n = 10 (5819); (26) Estación de Biología "Los Tuxtlas"[18]; n = 6 [5816(2), 5817, 5818(3)]; (27) Monte Pío[19]; n = 3 (5818); (28) Vertiente E Volcán San Martín[20]; n = 9 (5486); (29) 7 km NE Coyame[21]; n = 10 [5508(9), 5510]; (30) Estación FFCC Achotal[22]; n = 4 (5510); (31) Estación FFCC Oja-

pa[23]; n = 4 (5511); (32) Punta Arenas[24]; n = 12 [5487(2), 5488, 5489(2), 5490(7)]; (33) Paraje Petates[25]; n = 12 [5549(2), 5550(2), 5559(8)].

Sceloporus variabilis olloporus.—CHIAPAS: (34) 7 Cigarros, km 110 Carretera 200[26]; n = 1 (5551).

Sceloporus variabilis marmoratus.—NUEVO LEON: entre km 20–20.5 carretera 6 (Candela-Sabinas Hidalgo)[27]; n = 7 [5465, 5466(6)].

Sceloporus parvus.—HIDALGO: (36) jct. to San Cristóbal (3.5 km SE Tolantongo)[28]; n = 2 (6062–63); (37) 10 km S Tolantongo[28]; n = 11 [6060(5), 6061(6)]; (38) Santuario Mapheté[29]; n = 2 (5364, 5403); QUERETARO: (39) Mesa de León[30]; n = 1 (6056); (40) 10 km NE San Antonio Peña Nevada[31]; n = 2 (5344).

Sceloporus cozumelae.—YUCATAN: (41) Puerto Sisal[32]; n = 17 [5485(8), 5506(9)]; (42) Puerto Progreso[33]; n = 10 (5507); QUINTANA ROO: (43) Punta Sam[34]; n = 10 (5544); (44) Isla Mujeres[35]; n = 14 (5794).

Sceloporus chrysostictus.—YUCATAN: (45) Pisté[36]; n = 3 (5512); QUINTANA ROO: (46) 8 km W Cancún (rd to Tulum)[37]; n = 3 [5513(2), 5573].

Sceloporus bicanthalis.—MEXICO: Nevado de Toluca[38]; n = 3 (5762).

Acknowledgments

For support in different stages of this paper, the authors thank D. G. Mink, D. S. Rogers, Y. Hortelano, E. Martínez-Solís, I. Goyenechea, E. Hernández-García, M. Mancilla, J. Archie, C. Rodríguez, W. Schmidt, A. Loeza, A. Nieto Montes de Oca, A. Rendón, G. Santos, G. Escalona, H. Ruiz, H. M. Smith, J. J. Wiens, J. McGuire, K. Crandall, J. Fetzner, E. Arellano, F. González J. Sites, I. Vargas, L. León, G. Pérez, D. Harris, E. Linder, M. Benabib, and K. Kjer. Research was financed by a National Science Foundation grant to OF-V and JWS (DEB 91-19091) and DGAPA IN203493 to J. Llorente and OF-V. OF-V thanks members of the Zoology Department at Brigham Young University for facilities to finish the research. Parts of this paper were presented by FM-Q to fulfill requirements for master's degree at Facultad de Ciencias, UNAM, México.

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APPENDIX 1. STAIN AND ELECTROPHORETIC CONDITIONS USED IN THE STUDY. Enzyme names, EC numbers, and locus abbreviations follow recommendations of the International Union of Biochemistry (1984). Tissues are as follows: S = stomach and intestine, L = liver and kidney, and M = skeletal muscle.

Enzyme	EC Number	Locus	Tissue	Buffer[a]
Aconitate hydratase	4.2.1.3	*M-Acoh-A*	L	A
		S-Acoh-A	L	A
Adenylate kinase	2.7.4.3	*Ak-A*	M	A
Adenosine deaminase	3.5.4.4	*Ada*	S	B
Alcohol dehydrogenase	1.1.1.1	*Adh*	L	A
Aspartate aminotransferase	2.6.1.1	*M-Aat-A*	L	A, D
		S-Aat-A	L	A, D
Creatine kinase	2.7.3.2	*Ck-A*	S	A, B, C, D
Dihydrolipoamide dehydrogenase	1.8.1.4	*Ddh-A*	L	B, D
Fructose-biphosphate aldolase	4.1.2.13	*Fba-1*	L	B
Fructose-biphosphatase	3.1.3.11	*Fbp*	M	A
Glucose-6-phosphate isomerase	5.3.1.9	*Gpi-A*	S	A, D
α-Glucosidase	3.2.1.20	α-*Glus-1*	L	A
β-Glucosidase	3.2.1.21	β-*Glus-1*	S	A
β-Glucuronidase	3.2.1.31	β-*Glur-1*	L	B
Glutamate dehydrogenase	1.4.1.2	*Gtdh-A*	L	B, D
Glycerate dehydrogenase	1.1.1.29	*Glydh*	L	A
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3pdh-A*[1]	M	A
		G3pdh-A[2]	M	A
"Unidentified" dehydrogenase	—	"*Udh*"	M	A
L-iditol dehydrogenase	1.1.1.14	*Iddh*	L	A
Isocitrate dehydrogenase	1.1.1.42	*Idh-1*	L	A
		Idh-2	L	A
L-lactate dehydrogenase	1.1.1.27	*Ldh-A*	L	B
		Ldh-B	L	B
Malate dehydrogenase	1.1.1.37	*M-Mdh-A*	L	A
		S-Mdh-A	L	A
α-Mannosidase	3.2.1.24	α*Man-A*	L	B
Peptidases	3.4.–.–			
glycyl-L-leucine		*Pep-A*(GL)	S	A, C
L-leucylglycylglycine		*Pep-B*(LGG)	S	A, C
L-leucyl-L-leucyl-L-leucine		*Pep-F*(LLL)	S	A, B, C
L-phenylalanyl-L-proline		*Pep-D*(PAP)	S	C
L-leucyl-L-alanyne		*Pep-?*(LA)	M	B
Phosphoglucomutase	5.4.2.2	*Pgm-A*	L	B, D
"Unidentified kinase"	—	"*Uk*"	L	B, D
Phosphogluconate dehydrogenase	1.1.1.44	*Pgdh*	L	A
Purine-nucleoside phosphorylase	2.4.2.1	*Pnp-A*	S	B
Pyruvate kinase	2.7.1.40	*Pk-A*	M	A
Triose-phosphate isomerase	5.3.1.1	*Tpi-A*	S	A, B

[a] A: Starch gel, Tris-citrate, pH 8.0, ~10 h at 75 mA; B: Starch gel, Tris-citrate III, pH 8.3, ~10 h at 75 mA; C: Starch gel, Poulik discontinuous, pH 8.7, ~12 h at 200 v; D: Cellulose acetate gel, Tris-maleate, pH 7.8 ~30 min at 75 mA. (Starch gels were prepared following Murphy et al., 1996; cellulose acetate gels following Richardson et al., 1986).

APPENDIX 2. ELECTROMORPH FREQUENCIES FOR 34 LOCI FROM 38 SAMPLES OF THE *Sceloporus variabilis* COMPLEX. Taxa are identified by the following abbreviations: SVV-HE = *S. v. variabilis* (high-elevation); SVV-LE = *S. v. variabilis* (low-elevation); SVT = *S. v. teapensis*; SVO = *S. v. olloporus*; SVM = *S. v. marmoratus*; SPS = *S. parvus*; SCZ = *S. cozumelae*; SCR = *S. chrysostictus*; SBI = *S. bicanthalis*; SVV × SVT = *S. v. variabilis* × *S. v. teapensis*; SVV × SVO = *S. v. variabilis* × *S. v. olloporus*. Numbers in parentheses indicate either the total number of localities for each taxon, or the localities for hybrid populations as given in Materials Examined section.

Locus	Allele	SVV-HE (n = 9)	SVV-LE (n = 5)	SVT (n = 8)	SVO (n = 1)	SVM (n = 1)	SPS (n = 4)	SCZ (n = 2)	SCR (n = 2)	SBI (n = 1)	SVV-SVT (#15)	SVV × SVT (#24)	SVV × SVO (#25)
Pep-A	a	0.51	0.81	0.99	1.00	1.00	0.81	0.99	0.58	0.00	0.67	1.00	1.00
	b	0.35	0.06	0.00	0.00	0.00	0.19	0.01	0.42	0.00	0.29	0.00	0.00
	c	0.14	0.13	0.01	0.00	0.00	0.00	0.00	0.00	1.00	0.04	0.00	0.00
Pep-B	a	0.89	0.84	0.98	1.00	0.50	0.32	0.92	0.00	0.50	1.00	1.00	1.00
	b	0.04	0.08	0.00	0.00	0.50	0.68	0.06	1.00	0.50	0.00	0.00	0.00
	c	0.07	0.08	0.02	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00
Pep-D	a	0.97	1.00	1.00	1.00	1.00	0.77	0.97	0.38	0.67	1.00	1.00	1.00
	b	0.03	0.00	0.00	0.00	0.00	0.04	0.01	0.00	0.33	0.00	0.00	0.00
	c	0.00	0.00	0.00	0.00	0.00	0.13	0.01	0.62	0.00	0.00	0.00	0.00
	d	0.00	0.00	0.00	0.00	0.00	0.06	0.01	0.00	0.00	0.00	0.00	0.00
Pep-F	a	0.97	0.96	1.00	0.00	0.93	0.64	0.99	0.88	0.00	0.96	1.00	0.46
	b	0.03	0.04	0.00	1.00	0.07	0.36	0.01	0.12	1.00	0.00	0.00	0.29
	c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.25
Pep-?	a	0.56	0.00	0.00	0.00	0.14	0.00	0.01	0.00	0.17	0.07	0.00	0.00
	b	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	c	0.38	0.88	0.03	1.00	0.86	0.12	0.99	1.00	0.83	0.00	0.00	0.58
	d	0.00	0.12	0.97	0.00	0.00	0.88	0.00	0.00	0.00	0.93	1.00	0.42
Gpi-A	a	1.00	0.95	1.00	1.00	0.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00
	b	0.00	0.05	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
β-*Glus*-1	a	0.67	0.66	0.82	1.00	1.00	0.83	0.83	0.00	1.00	0.45	0.59	0.67
	b	0.33	0.34	0.18	0.00	0.00	0.17	0.16	1.00	0.00	0.41	0.41	0.33
	c	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.14	0.00	0.00
Tpi-A	a	0.77	0.81	1.00	0.50	0.43	0.81	0.89	0.00	0.00	0.69	1.00	0.78
	b	0.18	0.10	0.00	0.50	0.57	0.19	0.03	0.00	0.00	0.00	0.00	0.05
	c	0.05	0.09	0.00	0.00	0.00	0.00	0.08	1.00	1.00	0.31	0.00	0.17
Ada	a	0.94	1.00	1.00	1.00	1.00	0.00	1.00	0.00	0.00	1.00	1.00	1.00
	b	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	c	0.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00	1.00	0.00	0.00	0.00
Pnp-A	a	0.92	0.96	0.82	1.00	1.00	1.00	1.00	0.00	0.00	0.54	0.73	1.00
	b	0.02	0.02	0.18	0.00	0.00	0.00	0.00	1.00	1.00	0.46	0.27	0.00
	c	0.06	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ak-A	a	1.00	1.00	1.00	1.00	0.93	0.00	0.00	0.00	0.00	1.00	1.00	1.00
	b	0.00	0.00	0.00	0.00	0.07	0.00	1.00	1.00	1.00	0.00	0.00	0.00
	c	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
G3pdh-A[1]	a	1.00	1.00	0.98	1.00	0.64	0.06	1.00	0.42	1.00	1.00	1.00	0.96
	b	0.00	0.00	0.02	0.00	0.36	0.94	0.00	0.00	0.00	0.00	0.00	0.00
	c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.58	0.00	0.00	0.00	0.04
G3pdh-A[2]	a	0.03	0.00	0.00	0.00	0.00	0.84	0.00	0.00	1.00	0.00	0.00	0.00
	b	0.97	1.00	1.00	1.00	1.00	0.12	1.00	0.00	0.00	1.00	1.00	1.00
	c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
	d	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00
"*Udh*"	a	0.70	0.99	1.00	1.00	1.00	1.00	0.87	0.00	1.00	1.00	0.29	1.00
	b	0.00	0.01	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.71	0.00
	c	0.30	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00
	d	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00

APPENDIX 2. CONTINUED.

Locus	Allele	SVV-HE (n = 9)	SVV-LE (n = 5)	SVT (n = 8)	SVO (n = 1)	SVM (n = 1)	SPS (n = 4)	SCZ (n = 2)	SCR (n = 2)	SBI (n = 1)	SVV-SVT (#15)	SVV × SVT (#24)	SVV × SVO (#25)
Fbp	a	0.86	0.95	0.97	1.00	1.00	1.00	1.00	1.00	1.00	0.89	0.96	1.00
	b	0.10	0.05	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00
	c	0.04	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00
Pgdh	a	0.97	0.93	0.90	1.00	1.00	0.00	1.00	1.00	0.00	1.00	0.75	0.50
	b	0.03	0.07	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	c	0.00	0.00	0.08	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.25	0.50
	d	0.00	0.00	0.00	0.00	0.00	0.68	0.00	0.00	0.50	0.00	0.00	0.00
	e	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.50	0.00	0.00	0.00
Adh	a	0.85	0.66	0.83	0.50	0.90	1.00	1.00	1.00	1.00	0.96	0.92	0.77
	b	0.15	0.34	0.17	0.50	0.10	0.00	0.00	0.00	0.00	0.04	0.08	0.23
Iddh	a	0.48	0.92	0.88	1.00	0.00	0.50	0.98	1.00	1.00	1.00	0.75	1.00
	b	0.00	0.00	0.12	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.25	0.00
	c	0.52	0.08	0.00	0.00	1.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00
Glydh	a	1.00	1.00	0.98	1.00	0.83	0.00	1.00	0.00	0.00	1.00	1.00	1.00
	b	0.00	0.00	0.02	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	c	0.00	0.00	0.00	0.00	0.00	0.43	0.00	1.00	1.00	0.00	0.00	0.00
	d	0.00	0.00	0.00	0.00	0.00	0.57	0.00	0.00	0.00	0.00	0.00	0.00
M-Acoh-A	a	0.77	0.88	0.54	1.00	0.86	0.98	0.71	0.00	0.33	0.50	0.38	0.84
	b	0.23	0.11	0.03	0.00	0.14	0.02	0.26	0.83	0.00	0.36	0.33	0.08
	c	0.00	0.01	0.41	0.00	0.00	0.00	0.00	0.00	0.67	0.14	0.29	0.08
	d	0.00	0.00	0.02	0.00	0.00	0.00	0.03	0.17	0.00	0.00	0.00	0.00
S-Acoh-A	a	1.00	1.00	1.00	1.00	0.83	0.00	1.00	0.92	0.00	1.00	1.00	1.00
	b	0.00	0.00	0.00	0.00	0.17	1.00	0.00	0.08	1.00	0.00	0.00	0.00
S-Aat-A	a	0.99	1.00	0.97	1.00	1.00	0.00	0.45	0.00	0.00	0.89	0.92	0.92
	b	0.01	0.00	0.03	0.00	0.00	1.00	0.55	0.00	0.00	0.11	0.08	0.08
	c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	d	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
Ddh-A	a	1.00	1.00	1.00	1.00	0.93	0.53	0.00	0.00	1.00	0.96	1.00	1.00
	b	0.00	0.00	0.00	0.00	0.07	0.41	0.00	0.00	0.00	0.04	0.00	0.00
	c	0.00	0.00	0.00	0.00	0.00	0.06	1.00	1.00	0.00	0.00	0.00	0.00
β-*Glur*-1	a	0.45	0.20	0.60	1.00	1.00	0.49	0.85	1.00	0.00	0.89	0.64	0.72
	b	0.40	0.42	0.40	0.00	0.00	0.00	0.01	0.00	0.00	0.11	0.14	0.17
	c	0.15	0.18	0.00	0.00	0.00	0.51	0.14	0.00	1.00	0.00	0.22	0.11
	d	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
α-*Man-A*	a	0.44	1.00	0.79	0.00	1.00	0.00	0.00	0.00	0.00	0.96	1.00	0.00
	b	0.42	0.00	0.11	1.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	1.00
	c	0.14	0.00	0.10	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	d	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
	e	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00
Ldh-A	a	0.03	1.00	0.99	1.00	0.00	1.00	1.00	0.00	0.00	1.00	1.00	1.00
	b	0.94	0.00	0.01	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	c	0.03	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
	d	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Ldh-B	a	0.03	0.91	0.95	1.00	0.00	1.00	0.61	0.00	0.00	0.93	1.00	1.00
	b	0.92	0.09	0.05	0.00	1.00	0.00	0.39	0.00	0.00	0.07	0.00	0.00
	c	0.05	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
	d	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
α-*Glus*-1	a	0.51	0.67	0.51	1.00	0.57	0.84	0.77	0.67	0.33	0.29	0.67	1.00
	b	0.45	0.30	0.27	0.00	0.43	0.12	0.02	0.17	0.33	0.67	0.21	0.00
	c	0.04	0.03	0.22	0.00	0.00	0.04	0.21	0.16	0.33	0.04	0.12	0.00

APPENDIX 2. CONTINUED.

Locus	Allele	SVV-HE (n = 9)	SVV-LE (n = 5)	SVT (n = 8)	SVO (n = 1)	SVM (n = 1)	SPS (n = 4)	SCZ (n = 2)	SCR (n = 2)	SBI (n = 1)	SVV-SVT (#15)	SVV × SVT (#24)	SVV × SVO (#25)
Idh-1	a	1.00	1.00	0.99	1.00	1.00	0.00	1.00	1.00	0.00	1.00	1.00	1.00
	b	0.00	0.00	0.01	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00	0.00
Idh-2	a	0.96	1.00	0.95	1.00	1.00	0.00	1.00	1.00	0.00	0.93	1.00	1.00
	b	0.04	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00
	c	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.00	0.00
S-Mdhp-A	a	0.80	0.67	0.36	0.50	0.00	0.00	0.00	0.38	0.00	0.89	0.00	0.00
	b	0.19	0.33	0.64	0.50	1.00	0.00	0.00	0.00	0.00	0.04	1.00	0.96
	c	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.62	1.00	0.07	0.00	0.00
	d	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.04
	e	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Mpi-A	a	1.00	1.00	0.97	1.00	1.00	1.00	0.00	0.00	0.67	1.00	0.67	1.00
	b	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.33	0.00	0.33	0.00
	c	0.00	0.00	0.03	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
Pgm-A	a	0.97	1.00	1.00	1.00	0.50	0.00	0.98	0.00	1.00	1.00	1.00	0.96
	b	0.02	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.04
	c	0.01	0.00	0.00	0.00	0.00	1.00	0.02	0.00	0.00	0.00	0.00	0.00
	d	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
"*Uk*"	a	0.82	0.74	0.52	0.00	0.00	0.00	0.85	0.00	0.00	1.00	0.00	0.00
	b	0.18	0.26	0.03	0.00	0.00	0.00	0.11	1.00	1.00	0.00	0.00	0.00
	c	0.00	0.00	0.44	0.00	0.00	1.00	0.04	0.00	0.00	0.00	1.00	0.00
	d	0.00	0.00	0.01	1.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.83
	e	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.17
Average number of alleles per locus		2.0	1.6	1.4	1.0	1.1	1.4	1.1	1.2	1.2	1.1	1.2	1.1
Average heterozygosity per locus (direct count), H		0.218	0.150	0.133	0.044	0.088	0.165	0.099	0.079	0.081	0.088	0.096	0.074