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Congruent Patterns of Genetic and Morphological Variation in the Parthenogenetic Lizard *Aspidoscelis tesselata* (Squamata: Teiidae) and the Origins of Color Pattern Classes and Genotypic Clones in Eastern New Mexico

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CONTENTS

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ABSTRACT

Aspidoscelis tesselata exhibits significant clonal diversity despite its recent origin (from hybridization between *A. tigris marmorata* and *A. gularis septemvittata*) and its parthenogenetic mode of reproduction. Two hypotheses have been advanced to explain the derivation of its genetic and morphological variation: (1) separate parthenogenetic lineages derived from several different F_1 hybrid zygotes, and (2) postformational mutations occurring in a parthenogenetic lineage derived from a single F_1 hybrid zygote. We evaluated these competing hypotheses with evidence from skin transplant studies, protein electrophoresis, multivariate analyses of morphological characters, and geographic distributions of pertinent groups. Starting with the clonal diversity at Conchas Lake State Park, San Miguel County, New Mexico, we expanded the study to include populations at Sumner Lake State Park and Fort Sumner (De Baca County), Puerto de Luna (Guadalupe County), and Arroyo del Macho and Roswell (Chaves County). This enabled us to resolve origins of color pattern classes and genotypic clones in eastern New Mexico. We used pattern class designations C-E and E-C to signify that elements of both pattern classes were expressed in populations at Conchas Lake and Arroyo del Macho.

The two pattern classes at Conchas Lake (C-E and D) had the same F_1 hybrid karyotype ($2n = 46$), with haploid sets of 23 chromosomes characteristic of each progenitor species of *A. tesselata*. Clonal variation was found at 4 of the 35 gene loci examined electrophoretically: GPI (glucose-6-phosphate isomerase), EST2 (a muscle esterase), sACOH (aconitase hydratase), and MPI (mannose-6-phosphate isomerase). The strong congruence between genotype and morphological variation facilitated the characterization of three morphological subgroups of C-E. Although these subgroups lacked individually distinctive color patterns, they were discriminated effectively in canonical variate analyses based on scalation characters and a priori groups of known genotype.

Nine individuals of Conchas C-E and four individuals of Conchas D have histocompatibility data from a recent skin transplant study (Cordes and Walker, 2003). The subgroup identities of the C-E specimens document histocompatibility among the three morphological subgroups of C-E and between each subgroup and representatives of pattern class D. This evidence, together with Maslin's (1967) report of histocompatibility between pattern classes C and E, suggests that all color pattern classes, morphological subgroups, and genotypic clones of *A. tesselata* can be traced back to a single ancestral F_1 hybrid zygote.

A pair of pale broken lines in the middorsal region distinguishes pattern class D from the other pattern classes. However, Conchas ID shared the GPI −100/−96, EST2 100/96 genotype with Conchas IC-E, and individuals of these pattern classes were very similar in multivariate meristic characters. Sumner D expressed the same type of relationship, resembling the syntopic population of Sumner C rather than the other population of D. In addition, certain individuals of Sumner C had partially divided (D-like) vertebral lines—additional evidence that Sumner C was ancestral to Sumner D. We conclude that pattern class New Mexico D is polyphyletic, having originated twice from different individuals of C-E and C in the vicinities of Conchas and Sumner Lakes.

The northern position of pattern classes C and C-E in the range of *A. tesselata* is consistent with recent colonizations by individuals from more southerly populations. A candidate source population, based on its extensive color pattern and meristic variation, is E-C at Arroyo del Macho. The strong morphological resemblance of several northern populations to Macho E-C rather than to either syntopic clones or geographically proximate populations of other pattern classes supports this possibility. Evidence from geographic distributions, patterns of genotypic and meristic variation, and histocompatibility identifies postformational mutations as the likely basis for the genetic and morphological variation found in *A. tesselata*. This variation also includes different life-history characteristics between pattern classes C and E at Sumner Lake State Park.

The name *tesselata* is presently associated indirectly with pattern class C through the neotype of *A. tesselata*. The neotype is a specimen of Colorado D, a derivative of pattern class C. With respect to pattern classes E-C, E, and other southern variants, taxonomic restructuring would confront mosaic patterns of genotypic, phenotypic, and geographic variation—patterns expected from random mutations in clonally reproducing species. *Aspidoscelis tesselata* has exploited a variety of ecological opportunities despite the constraints of clonal inheritance. Postformational mutations in the generalized genotype acquired from its progenitor species may have contributed to its ecological success.

INTRODUCTION

Reeder et al. (2002) presented evidence that North American lizards previously assigned to the genus *Cnemidophorus* represent a monophyletic group, leaving South American species in possession of the generic name in a separate clade. This necessitated resurrecting the generic name *Aspidoscelis* for North American species. Therefore, the present paper involves an interpretation of the evolutionary history of the diploid parthenogenetic species *Aspidoscelis tesselata* in eastern New Mexico, the species formerly allocated to *Cnemidophorus tesselatus*.

Aspidoscelis tesselata is an excellent species for assessing the evolutionary potential of a parthenogenetic vertebrate. Its attributes include a broad latitudinal distribution, well-marked genotypic and phenotypic variation, and histocompatibility evidence that evolutionary divergence began with a single basal parthenogenetic individual (Maslin, 1967; Cordes and Walker, 2003). Of additional evolutionary interest, *Aspidoscelis tesselata* participated in the origin of a new species. Although hybridization between *A. tesselata* and *A. tigris marmorata* produced sterile triploid hybrids (Taylor et al., 2001), the triploid species *A. neotesselata* (Walker et al., 1997a) originated from an *A. tesselata* × *A. sexlineata* hybridization (Parker and Selander, 1976; Densmore et al., 1989; Dessauer and Cole, 1989). Equally intriguing is the possibility that a new parthenogenetic species could result from genetic changes (divergence) in an established parthenogenetic species (Echelle, 1990; Taylor and Cooley, 1995a, 1995b; Manríquez-Morán et al., 2000; Schmitz et al., 2001). In addition to this possibility, we investigated the origin of color pattern classes and the pattern of divergence that has occurred in *A. tesselata* from eastern New Mexico.

Aspidoscelis tesselata originated recently (Densmore et al., 1989; Reeder et al., 2002) from hybridization between a female *A. tigris marmorata* and a male *A. gularis septemvittata* (Neaves, 1969; Parker and Selander, 1976; Dessauer and Cole, 1989; Dessauer et al., 1996). Despite its clonal pattern of inheritance (Dessauer and Cole, 1986), *A. tesselata* is ecologically successful based on a geographic range that includes parts of Chihuahua, Mexico (Zweifel, 1965), Texas (Dixon, 2000), New Mexico (Degenhardt et al., 1996), Oklahoma (Webb, 1970), and Colorado (Hammerson, 1999), and its presence in various assemblages of bisexual and parthenogenetic congeners (Cuellar, 1979; Taylor et al., 2000, 2001). Based on its extensive latitudinal distribution, *Aspidoscelis tesselata* might have inherited an advantageous generalized genotype from its two progenitor species (Taylor et al., 2001). This ecological success has occurred despite the absence of genetic recombination. Price (1992) and Price et al. (1993) provide a contrasting interpretation of ''success'' in *A. tesselata*.

Morphological variation in *A. tesselata* includes four color pattern classes (Zweifel, 1965; Taylor et al., 1996) integrated into the currently understood phylogenetic history of *A. tesselata* by Walker et al. (1997a). Another diploid pattern class (F), included in *A. tesselata* by Zweifel (1965), was described as *A. dixoni* by Scudday (1973), and Densmore et al. (1989) presented mitochondrial DNA evidence that *A. dixoni* and *A. tesselata* may have originated from independent hybridizations.

Color pattern differences among pattern classes C, Colorado D, New Mexico D, and E were used to discover local examples of ecological (Walker et al., 1997b) and life-history (Taylor et al., 1997, 2000) differences between sympatric clones. However, we expose (below) complications in using color pattern classes C and E as simple descriptors of regional patterns of geographic variation.

Our study is rooted in the important pioneering investigations of Zweifel (1965), Maslin (1967), Parker and Selander (1976), and Parker (1979). Zweifel (1965) set the stage for future research by recognizing that a few color pattern classes could accommodate the previously undecipherable morphological variation in *A. tesselata*. He was then able to describe *A. tesselata* from Conchas Lake as comprising two color pattern classes (C and D) and document the remarkable meristic variation in Conchas C. The magnitude of this morphological variation was unexpected because it challenged the intuitive expectation that parthenogenetic reproduction

constrains phenotypic variability. With great acuity, Zweifel (1965) predicted that Conchas C might consist of several clones, and electrophoretic analyses of proteins by Parker and Selander (1976) confirmed this prediction. Parker (1979) then demonstrated congruence between meristic and genotypic variation, thereby providing genetic markers (clones IC, VIC, and VIIIC) for morphological subgroups of Conchas C. These clones appeared to have combinations of alleles that were polymorphic in their bisexual ancestors. Therefore, Parker and Selander (1976), Parker (1979), and Parker et al. (1989) argued that several independent hybridizations were responsible for the genetic and morphological variation in Conchas C. However, Maslin (1967) revealed histocompatibility between pattern classes C and E, implying that the genealogies of different pattern classes converged on a single parthenogenetic progenitor.

The purpose of the present study was to (1) reconcile patterns of genotypic and morphological variation for clones of *A. tesselata* at Conchas Lake and different color pattern classes from eastern New Mexico, (2) reassess the multiple hybridization hypothesis to explain variation among these groups, (3) evaluate evidence that the genetic and morphological variation in *A. tesselata* was generated by postformational mutation, and (4) determine if divergent clones deserve formal taxonomic recognition.

MATERIALS AND METHODS

Morphological Analyses

In a departure from all previous studies, we use new pattern class designations to flag color pattern ambiguities in *A. tesselata* at Conchas Lake State Park and Arroyo del Macho. The results of a discriminant analysis (DA) justified two pattern class designations. Using Zweifel's (1965) pattern class designations, the DA model was based on samples of pattern class ''C'' from Conchas Lake and pattern class ''E'' from Arroyo del Macho as the a priori groups (fig. 1). These specimens met body size criteria (see below) that removed ontogenetic variation from the three color pattern characters used in the DA (table 1). The DA model, with standardized discriminant functions of 1.308 for L-breaks, −0.519 for DL-breaks, and −0.380 for PV-breaks, classified 26 of 100 specimens of Conchas ''C'' as Macho ''E'' and 14 of 37 specimens of Macho ''E'' as Conchas ''C''. Despite misclassified individuals and a weak eigenvalue (0.113), the two groups differed significantly in discriminant function scores ($t_{135} = -3.912$; $P < 0.0005$). Therefore, we used two new pattern class designations: C-E for the Conchas Lake non-Ds, and E-C for the form at Arroyo del Macho. The first letter signifies the pattern class identity of this population in previous studies; the second letter emphasizes that this population contains a range of color pattern variation that includes individuals with color pattern features of this second pattern class. Additional evidence of color pattern ambiguities in these two groups is presented in other sections of the paper.

With the addition of two new color pattern designations, our study was based on five color pattern classes of *A. tesselata* from six localities. The focal samples comprised pattern classes C-E ($N = 135$) and D ($N = 51$) from Conchas Lake State Park (fig. 1). These samples included 34 specimens (21 C-E, 13 D) with protein phenotypes identified electrophoretically by Parker and Selander (1976) and H.C.D. and C.J.C. (this study) and 13 specimens (9 C-E, 4 D) used in skin transplant experiments by Cordes and Walker (2003). Two additional groups of samples were included to determine patterns of evolutionary divergence. The first group consisted of pattern classes E and E-C with electrophoretic data from Fort Sumner ($N = 11$), Roswell ($N = 10$), and Arroyo del Macho ($N = 10$). The second group comprised samples lacking electrophoretic data. These were (1) pattern class C ($N = 47$), pattern class E ($N = 47$), and pattern class D ($N = 5$) from Sumner Lake State Park (approximately 90 linear km south of the Conchas Lake localities), (2) pattern class E ($N = 25$) from Puerto de Luna (approximately 34 linear km northwest of the Sumner Lake collecting sites), (3) pattern class E ($N = 5$) from Fort Sumner (approximately 18 linear km southeast of Sumner Lake), and (4) pattern class E-C ($N = 31$) from Arroyo del Macho (approximately 105 linear km south of Sumner Lake). The geographic relationships of sam-

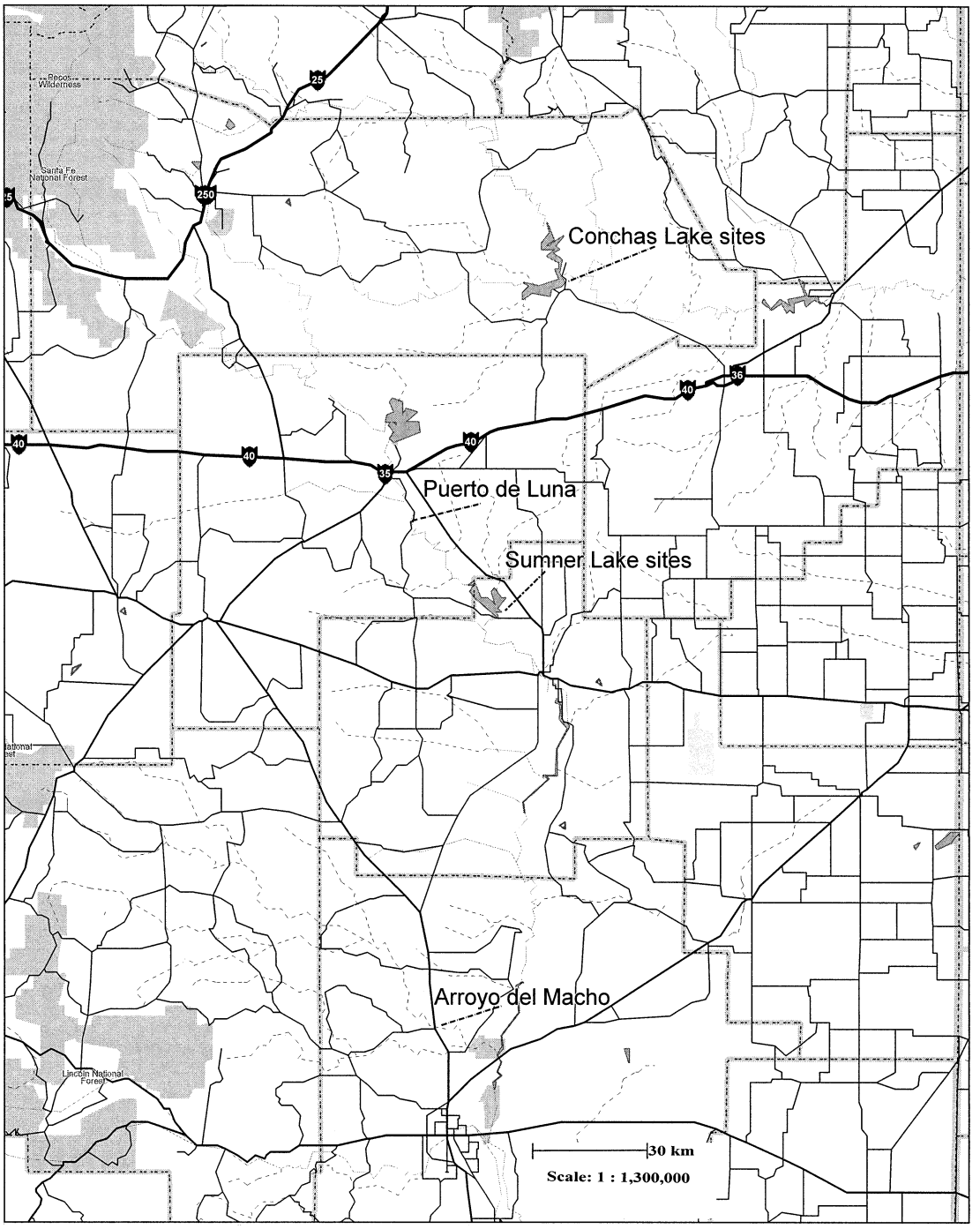


Fig. 1. Geographic relationships among four northern collecting localities of *Aspidoscelis tesselata* of color pattern classes C, New Mexico D, and E and convenience classes C-E and E-C. Color patterns found at the four sites are (1) Conchas Lake State Park: C-E and New Mexico D; (2) Sumner Lake State Park: C, New Mexico D, and E; (3) Puerto de Luna: E; and (4) Arroyo del Macho: E-C.

TABLE 1
Meristic Characters (and SVL) Used in Analyses of Morphological Variation in *Aspidoscelis tesselata* from the Locations Studied

Character abbreviation	Description
GAB	Number of granular dorsal scales in a single row around midbody. There are eight longitudinal rows of enlarged scales making up the ventral body surface. The third ventral row on either side of the mid-sagittal line terminates anteriorly in the axillary region. The 15th ventral scale posterior to this terminus established the point for beginning the GAB count.
COS	Bilateral total of circumorbital scales as standardized by Wright and Lowe (1967).
LSG	Sum of lateral supraocular granules on both sides of the head. These granular scales are located between the supraoculars and superciliary scales, and the count includes all scales anterior to the suture line between the third and fourth supraoculars.
FP	Sum of femoral pores on both thighs.
GS	Number of granular gular scales bordering the medial edges of the eight anterior sublabials (four on each side, or their subdivisions) and the posterior mental.
PSC	Sum of all scales, including occipitals, contacting the outer perimeter of parietal and interparietal scales.
L-breaks	Total number of interruptions by black pigment of the lateral pale stripes.
DL-breaks	Total number of interruptions by black pigment of the dorsolateral pale stripes.
PV-breaks	Total number of interruptions by black pigment of the paravertebral pale stripes.
SDL-T4	Number of subdigital lamellae on the fourth toe of one foot (right was chosen unless damaged).
SVL	Length of body from tip of snout to posterior edge of preanal scales (in mm).

pling localities are shown in figure 1, and specific information on samples and sampling localities is provided in appendix 1.

We shortened frequent references to genotypic clones (GPI and EST2 loci) and affiliated pattern class as follows: Conchas IC-E (Roman numerals indicate that the genotype is known) and 1C-E (Arabic numerals refer to morphological subgroups corresponding to a priori groups of known genotype); VIC-E and 6C-E; VIIIC-E and 8C-E. We also combined abbreviated names of collecting localities and pattern class designations to refer to various groups (Conchas D; Sumner C, D, and E; Luna E; Macho E-C).

Each specimen was scored for 10 meristic characters representing seven scalation features and three color pattern features (tables 1, 2), the latter involving the number of breaks (disruptions by transverse black bars) in the lateral, dorsolateral, and paravertebral pale stripes. A traditional character (SDL-T4 in tables 1 and 2) was omitted from multivariate analyses to maintain consistency and comparability across different color pattern classes, genotypic clones, and morphological subgroups. We excluded this character because certain individuals in critical samples (those with protein phenotypes and those used for skin transplants) had damaged or missing 4th toes on both feet.

Body length (snout–vent length = SVL) was measured to the nearest millimeter with digital calipers. Significant relationships were found between color pattern characters and SVL in composite samples of pattern classes C and C-E ($N = 173$) and E and E-C ($N = 112$). These relationships were between L-breaks and SVL in C + C-E ($P = 0.003$) and between L-breaks and SVL ($P = 0.016$) and PV-breaks and SVL ($P = 0.001$) in E + E-C. Using specimens >66 mm SVL for pattern classes C, C-E, and D and >69 mm SVL for pattern classes E and E-C removed ontogenetic variation from the definitive samples ($P = 0.08$ and $P = 0.62$ for the regressions of L-breaks on SVL, and $P = 0.18$ for the regression of PV-breaks on SVL).

Three morphological subgroups of pattern class C-E were identified from a canonical variate analysis (CVA) of 21 individuals of known genotype, using the three GPI, EST2 genotypes as a priori groups. These subgroups, corresponding to genotypic clones,

TABLE 2

Descriptive Statistics of Morphological Characters Among the Color Pattern Classes and Morphological Subgroups of *Aspidoscelis tesselata* from the Locations Studied

(To eliminate ontogenetic variation in color pattern characters, individuals were chosen that exceeded 66 mm SVL for pattern classes C, C–E, and D and 69 mm SVL for pattern classes E and E–C. Mean ± SE, sample size, and range limits are shown for each sample.)

	Collecting locality								
	Conchas Lake State Park				Sumner Lake State Park			Puerto de Luna	Arroyo del Macho
Character[a]	Con 1C-E	Con 6C-E	Con 8C-E	Con D	Sum C	Sum D	Sum E	Luna E	Macho E-C
GAB	85.4 ± 0.29	97.4 ± 0.68	87.8 ± 0.70	85.5 ± 0.48	92.1 ± 0.44	92.4 ± 0.93	98.4 ± 0.55	96.4 ± 0.63	93.5 ± 1.05
	58, 81–90	25, 91–104	17, 83–94	32, 81–90	45, 86–99	5, 89–94	34, 91–105	16, 91–100	36, 87–109
COS	18.9 ± 0.22	17.6 ± 0.26	16.4 ± 0.48	18.1 ± 0.25	16.5 ± 0.37	17.4 ± 0.68	19.0 ± 0.25	22.8 ± 0.62	18.0 ± 0.24
	58, 13–22	25, 14–19	17, 14–20	32, 15–21	45, 13–25	5, 15–19	34, 15–24	16, 19–26	37, 14–20
LSG	37.3 ± 0.34	42.9 ± 0.92	35.4 ± 0.80	37.8 ± 0.49	39.7 ± 0.57	41.2 ± 1.93	37.4 ± 0.89	42.9 ± 1.04	34.6 ± 0.75
	58, 31–43	25, 32–52	17, 31–44	32, 33–44	45, 33–47	5, 36–48	34, 26–53	16, 35–51	37, 23–45
FP	41.8 ± 0.20	41.4 ± 0.30	39.0 ± 0.34	40.1 ± 0.30	40.9 ± 0.25	41.2 ± 0.74	42.6 ± 0.29	40.1 ± 0.32	41.3 ± 0.30
	58, 38–45	25, 37–44	17, 37–41	32, 36–43	45, 36–44	5, 39–43	34, 39–46	16, 38–42	37, 37–46
GS	19.5 ± 0.17	19.8 ± 0.24	19.8 ± 0.42	19.2 ± 0.18	20.0 ± 0.19	20.6 ± 0.51	21.0 ± 0.26	22.3 ± 0.37	19.4 ± 0.28
	58, 16–23	25, 18–23	17, 17–24	32, 18–21	45, 17–23	5, 19–22	34, 16–24	16, 19–25	36, 16–23
PSC	20.6 ± 0.13	19.7 ± 0.30	21.5 ± 0.38	19.9 ± 0.26	21.1 ± 0.19	20.2 ± 0.49	20.1 ± 0.25	22.1 ± 0.34	21.3 ± 0.25
	58, 19–23	25, 17–22	17, 19–25	32, 18–22	45, 18–24	5, 19–21	34, 15–22	16, 20–24	37, 18–24
L-breaks	7.4 ± 0.71	10.4 ± 1.40	8.7 ± 1.44	6.8 ± 0.81	3.5 ± 0.32	3.0 ± 0.71	21.5 ± 0.92	11.8 ± 1.75	11.9 ± 0.98
	58, 0–20	25, 2–27	17, 1–21	32, 0–20	45, 0–9	5, 1–5	33, 8–31	16, 1–24	37, 2–26
DL-breaks	2.9 ± 0.36	5.0 ± 0.89	1.5 ± 0.41	2.1 ± 0.40	1.6 ± 0.19	1.8 ± 0.20	10.7 ± 0.94	4.1 ± 0.89	3.4 ± 0.87
	58, 0–13	25, 0–17	17, 0–5	32, 0–10	45, 0–6	5, 1–2	32, 2–23	16, 0–13	37, 0–19
PV-breaks	7.1 ± 0.45	7.9 ± 0.76	8.0 ± 0.93	6.0 ± 0.51	3.6 ± 0.35	5.0 ± 1.05	12.7 ± 1.10	6.4 ± 1.38	7.3 ± 0.82
	58, 1–19	25, 2–18	17, 2–19	32, 1–12	45, 0–11	5, 3–9	32, 0–25	16, 0–18	37, 2–22
SDL-T4	36.8 ± 0.15	37.0 ± 0.23	36.1 ± 0.30	36.8 ± 0.16	36.6 ± 0.20	36.2 ± 0.37	36.5 ± 0.17	37.7 ± 0.33	37.1 ± 0.23
	57, 35–40	25, 35–40	17, 35–38	32, 35–39	45, 34–40	5, 35–37	34, 35–39	16, 36–40	37, 35–42
SVL	79.0 ± 1.02	82.0 ± 1.71	80.1 ± 2.39	82.3 ± 1.70	85.4 ± 1.62	84.0 ± 5.45	84.6 ± 0.98	80.6 ± 2.55	90.7 ± 1.25
	58, 67–95	25, 67–96	17, 68–95	32, 67–98	45, 68–100	5, 70–97	34, 70–92	16, 70–97	37, 71–109

[a]The characters are as follows: GAB, number of granules (scales) around midbody; COS, number of circumorbital scales; LSG, number of lateral supraocular granules; FP, number of femoral pores; GS, number of gular scales; PSC, number of scales contacting the outer perimeter of parietal and interparietal scales; L-breaks, number of interruptions of the lateral stripes; DL-breaks, number of interruptions of the dorsolateral stripes; PV-breaks, number of interruptions of the paravertebral stripes; SDL-T4, number of subdigital lamellae on fourth toe of one foot; SVL, snout–vent length. Methods for standardizing certain characters are provided in table 1.

were then used as a priori groups to assign individuals of C-E lacking electrophoretic data to morphological subgroup. The pattern of meristic variation among the morphological subgroups was then depicted by a definitive CVA, with subgroup assignments used to define a priori groups. The same procedure was used to assign the skin transplant specimens of Cordes and Walker (2003) to morphological subgroup and show their patterns of variation.

Nine meristic characters (table 1) were used in most analyses. Exceptions included CVAs based only on color pattern characters and those used for skin transplant specimens. We excluded characters based on DL-breaks and PV-breaks from the latter because the dorsolateral and paravertebral stripes had been used as transplantation sites, and the integrity of the pattern was compromised in these specimens. Only specimens with complete data were included in each analysis. Specific procedures are detailed in the appropriate sections of Results and Discussion.

To facilitate comparisons, a symmetric dissimilarity matrix of Mahalanobis distances (D^2) between group means was used to construct an additive tree depicting the morphological similarities and differences among the various groups. The D^2 values were obtained from BMDP program 5M, Linear and Quadratic Discriminant Analysis, accessed via SYSTAT 10.2. Additive trees are directed graphs with paths (sums of horizontal branch lengths) representing relative distances between entities. This procedure, in conjunction with ordination (de Queiroz and Good, 1997), is more appropriate than hierarchical clustering for illustrating patterns of divergence from similarity/dissimilarity data (Sattath and Tversky, 1977; Wilkinson et al., 1996; de Queiroz, 1998). For example, intracluster branches (representing specific groups) can vary in length on an additive tree but not on trees generated by hierarchical joining techniques. Therefore, additive trees provide information on differences among intracluster groups in addition to intercluster groups. Additive trees are not intended as phylogenetic reconstructions, but clonal divergence manifested in quantitative meristic differences should be evident.

Electrophoretic Analyses

Two of the 21 presumptive protein loci assayed with horizontal starch gel electrophoresis by Parker and Selander (1976), Pgi (= GPI, glucose-6-phosphate isomerase) and Est-2 (= EST2, a muscle esterase), and 4 of the 31 presumptive protein loci assayed by H.C.D. and C.J.C. (GPI, EST2, aconitase hydratase [sACOH], and mannose-6-phosphate isomerase [MPI]) revealed clonal differences in the Conchas Lake samples. Parker and Selander (1976) designated alleles at each locus according to migration of their allozymes relative to the most common allele (''100'' for anodally migrating proteins and ''−100'' for cathodally migrating proteins) found in *A. tigris marmorata*. Clonal designations from Parker (1979) use a combination of multilocus electrophoretic genotype (Roman numerals I–XIII) and pattern class (B = *A. neotesselata*; C, D, and E = *A tesselata*; F = *A. dixoni*). All available specimens of pattern classes C (= C-E here) and D analyzed by Parker and Selander (1976) and Parker (1979) were rescored for meristic characters and combined with AMNH specimens with known GPI and EST2 genotypes from Conchas Lake to represent the foundation for the present study: 10 individuals of clone IC-E (GPI −100/−96, EST2 100/96), 7 individuals of clone VIC-E (GPI −99/−96, EST2 100/96), 4 individuals of clone VIIIC-E (GPI −100/−96, EST2 96/96), and 10 individuals of clone ID (GPI −100/−96, EST2 100/96). Unfortunately, the three individuals of clone VIIC (GPI −99/−96, EST2 96/96) described by Parker (1979) have been lost and were thus unavailable for reanalysis.

New electrophoretic data for 31 gene loci have been provided by H.C.D. and C.J.C. (table 3), based on more recently collected AMNH specimens (see appendix 1). These loci include 17 of the 21 analyzed by Parker and Selander (1976). Methodology followed Harris and Hopkinson (1976), Murphy et al. (1996), and, particularly for North American lizards of the genus *Aspidoscelis*, Dessauer et al. (2000). For each locus, alleles are designated in alphabetical order according to decreasing anodal migration of their allozymes. For multilocus enzymes, loci are listed nu-

TABLE 3

Genotypes at 31 Gene Loci[a] in Clones[b] of *Aspidoscelis tesselata* of Pattern Classes C–E and D from Conchas Lake State Park Compared with Pattern Class E–C from Arroyo del Macho

(See Taylor et al., 2001.)

Locus	TESC-E (N = 3)	TESC-E (N = 2)	TESC-E (N = 2)	TESD (N = 2)	TESE-C (N = 11)
Oxidoreductases					
ADH	ab	ab	ab	ab	ab
G3PDH	aa	aa	aa	aa	aa
IDDH	aa	aa	aa	aa	aa
LDH1	ab	ab	ab	ab	ab
LDH2	aa	aa	aa	aa	aa
sMDH	ab	ab	ab	ab	ab
mMDH	aa	aa	aa	aa	aa
sMDHP	ab	ab	ab	ab	ab
sIDH	bb	bb	bb	bb	bb
mIDH	aa	aa	aa	aa	aa
sSOD	ab	ab	ab	ab	ab
mSOD	aa	aa	aa	aa	aa
Transferases					
sAAT	ab	ab	ab	ab	ab
mAAT	ab	ab	ab	ab	ab
CK1	aa	aa	aa	aa	aa
AK	aa	aa	aa	aa	aa
Hydrolases					
ESTD	bb	bb	bb	bb	bb
EST2[c]	bc	bc	bc	bc	bc
PEPA	cd	cd	cd	cd	cd
PEPB	bb	bb	bb	bb	bb
PEPD	cc	cc	cc	cc	cc
PEPE	aa	aa	aa	aa	aa
ADA	ac	ac	ac	ac	ac
Lyase					
sACOH	**ac**	bc	bc	bc	bc
Isomerases					
MPI	**ac**	**ac**	ab	**ac**	ab
GPI[c]	ac	ac	**ab**	ac	ac
PGM2	ab	ab	ab	ab	ab
PGM3	ab	ab	ab	ab	ab
Blood proteins					
TF[c]	bb	bb	bb	bb	bb
ALB	ab	ab	ab	ab	ab
HB	aa	aa	aa	aa	aa

[a]Abbreviations for loci are as follows: ADH, alcohol dehydrogenase; G3PDH, glycerol-3-phosphate dehydrogenase; IDDH, L-iditol dehydrogenase; LDH, L-lactate dehydrogenase; MDH, malate dehydrogenase; MDHP, malate enzyme; IDH, isocitrate dehydrogenase; SOD, superoxide dismutase; AAT, aspartate aminotransferase; CK, creatine kinase; AK, adenylate kinase; EST, esterase; PEP, peptidase; ADA, adenosine deaminase; ACOH, aconitase hydratase; MPI, mannose-6-phosphate isomerase; GPI, glucose-6-phosphate isomerase; PGM, phosphoglucomutase; TF, transferrin; ALB, albumin; and HB, hemoglobin; s, cytosolic enzyme; m, mitochondrial enzyme. For loci at which no a- or b-allele is shown, these occurred in other samples or in closely related taxa that are not included in this paper.

[b]Distinctive alleles (not found in pattern class E-C) that characterize different clones of pattern classes C-E and D are in an enlarged, boldface type and involve only three loci: sACOH, MPI, and GPI.

[c]This table consists of new data determined by H.C.D. and C.J.C. For EST2, all lizards were heterozygotes, thus consistent with the common clone designated by Parker and Selander (1976) and Parker (1979) as 100/96. For GPI, the ac genotype is the same as the common clone designated as −100/−96 for Pgi by Parker and Selander (1976) and Parker (1979), whereas our ab genotype is their −99/−96 genotype. As we only recently recognized the subtle differences in GPI, the ac genotype we report here is the same as the ab genotype reported by Taylor et al. (2001).

merically in order of decreasing anodal migration of their isozymes.

Karyotypic Analysis

We used previously published methods for preparing and studying standard, giemsa-stained chromosomes (Cole, 1979). We examined 38 cells at mitotic metaphase from bone marrow of four females of pattern class C-E and three individuals of pattern class D of *A. tesselata* from Conchas Lake State Park, San Miguel County, New Mexico (see appendix 1).

RESULTS AND DISCUSSION

Color Pattern Features of Pattern Classes Are Inherited Clonally

Partitioning of morphological variation in *A. tesselata* traditionally begins with an assignment of individuals to color pattern class. Therefore, it is important to know that fundamental elements of color pattern are transferred clonally from mothers to daughters. Dessauer and Cole (1986) established this fact for pattern classes C-E and D from Conchas Lake State Park, but not all individuals documenting this clonal inheritance were specified. The evidence included three adults of pattern class C-E from Conchas Lake that produced eggs in the *Aspidoscelis* colony at the American Museum of Natural History. The nine hatchlings derived from these clutches were all non-D in pattern class; that is, they lacked the paired, broken vertebral lines that characterize pattern class D throughout ontogeny. Similarly, two representatives of pattern class D from Conchas Lake produced eight hatchlings from two clutches of eggs; all had the characteristic color pattern of New Mexico D. All sets of hatchlings and their mothers are identified in appendix 1.

Karyotypes Are Consistent with Hybrid Origin

To date, two clearly resolved diploid karyotypes have been published for *Aspidoscelis tesselata*. Dessauer and Cole (1989: 57, fig. 8A) depict one from an individual of pattern class D from Conchas Lake State Park, and Taylor et al. (2001: 24, fig. 10A) depict one from an individual of pattern class E-C from Arroyo del Macho. These two karyotypes are identical, and as discussed in detail by Taylor et al. (2001), the karyotypes illustrated are identical to the expectations for F_1 hybrids from *A. tigris marmorata* × *A. gularis septemvittata* (a haploid set of chromosomes from each; $2n = 46$). A variant karyotypic clone was found at Arroyo del Macho (also pattern class E-C) in which the X-chromosome originally inherited from *A. tigris marmorata* was apparently fissioned at the centromere to become two smaller telocentric chromosomes ($2n = 47$).

For the present study, we determined the karyotypes of four specimens of *A. tesselata* pattern class C-E and three specimens of pattern class D from Conchas Lake State Park. All individuals had the typical F_1 hybrid karyotype ($2n = 46$) with the original, unfissioned X-chromosome from *A. tigris*.

Genotypic Differences Within Pattern Class C-E from Conchas Lake

Parker and Selander Analyses: Allozyme variation at 21 gene loci was reported in a range-wide study of *A. tesselata* (including the triploid *A. neotesselata*) by Parker and Selander (1976), who identified processes that could account for the patterns of genotypic variation detected (Parker, 1979; Parker et al., 1989). The three representatives of clone VIIC have been lost and cannot be reanalyzed morphologically for canonical variate analysis. Clone VIIC shares the −99/−96 GPI genotype with clone VIC and the 96/96 EST2 genotype with clone VIIIC (Parker, 1979). One individual of clone VIIC was similar to clones IC-E, VIIIC-E, and ID for the nine meristic characters scored by Parker (1979), while the other two individuals were similar to clone VIC-E in having significantly higher counts for LCOF (left circumorbital scales in contact with frontal scale), GAB (granules around midbody at the level of the 20th ventral scale row, as scored by Parker, 1979), L3 (number of lamellae on the 3rd toe of the left hindfoot), and SAT (number of scales around the tail at the level of the 15th caudal scale row). Thus, eight of the nine individuals of clones VIC-E and VIIC-E, marked by the GPI −99/−96 ge-

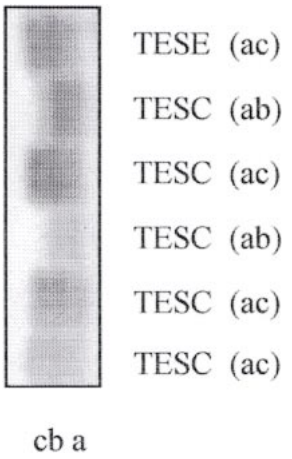


Fig. 2. Electrophoretic phenotypes of GPI, a dimeric enzyme, from erythrocyte hemolysates of six specimens of *Aspidoscelis*. Letters below gel identify allozymes based on alleles present (table 3), and the genotype of each lizard is listed on the right. Note the very slight difference in migration between the products of the b-allele versus c-allele. Lanes for individual lizards are labeled beside their patterns on the gel as follows: TESC, *A. tesselata* of pattern class C-E from Conchas Lake State Park, New Mexico; and TESE, *A. tesselata* of pattern class E from Sandoval County, New Mexico. Anode is to the right.

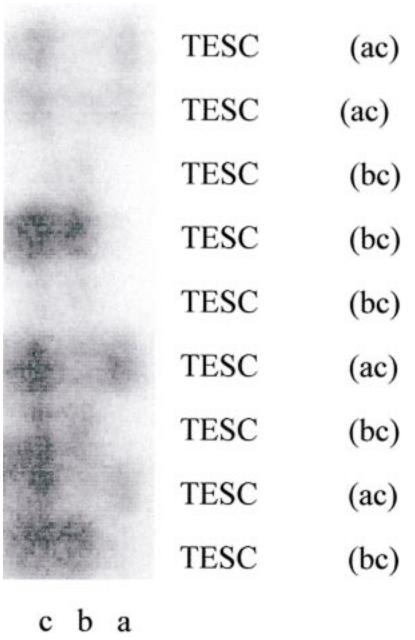


Fig. 3. Electrophoretic phenotypes of sACOH, a monomeric enzyme, from liver homogenates of nine specimens of *A. tesselata* of pattern class C-E from Conchas Lake State Park, New Mexico. Letters below gel identify allozymes based on alleles present (table 3), and the genotype of each lizard is listed on the right. Lanes for individual lizards are labeled beside their patterns on the gel. Anode is to the right.

notype (Parker, 1979, table 2: 1153), were morphologically divergent from clones marked by GPI −100/−96. Although clone VIIC is apparently rare, some of its representatives may have been included in our morphological subgroups. However, we are confident that the patterns of variation have not been distorted because clone VIIC is not distinctive in meristic variation (Parker, 1979).

DESSAUER AND COLE ANALYSES: Seven specimens of pattern class C-E and two of pattern class D from Conchas Lake State Park were assessed at 31 gene loci (table 3). As was found previously (Parker and Selander, 1976), GPI genotypes of −100/−96 (IC-E) and −99/−96 (VIC-E) were present (ac and ab for GPI, respectively, in table 3; fig. 2), but all nine individuals were apparently heterozygous for the EST2 alleles (bc for EST2 in table 3, presumably the same as Parker and Selander's 100/96). Note, however, that the gene products revealed at EST2 may not actually represent only one gene locus, as they do with reasonable certainty for the other loci tested. In addition, genotypic variation was detected at two other loci (table 3; sACOH, fig. 3, and MPI, fig. 4), neither of which was included in the Parker and Selander (1976) analyses. This additional genotypic variation included genotypes bc and ac at the sACOH locus and genotypes ac and ab at the MPI locus. These genotypic designations denote the relative migration distances in electrophoretic gels, with the alphabetical sequence of letters representing decreasing anodal migration.

A review of all of the electrophoretic data presented for *A. tesselata* of pattern classes C, C-E, E-C, E, and New Mexico D by Parker and Selander (1976), Dessauer and Cole (1986, 1989), Taylor et al. (2001), table 3, and additional unpublished data of H.C.D. and C.J.C. reveals that data are now available for a total of 34 clearly identified gene loci

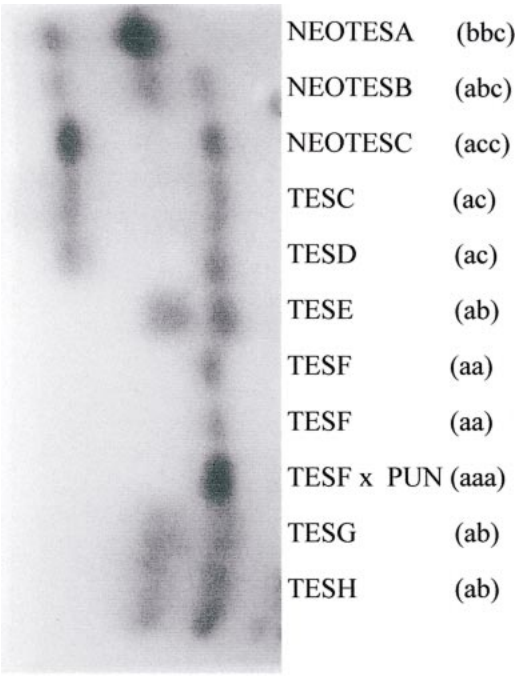


Fig. 4. Electrophoretic phenotypes of MPI, a monomeric enzyme, from liver homogenates of 11 specimens of *Aspidoscelis*. Letters below gel identify allozymes based on alleles present (table 3), and the genotype of each lizard is listed on the right. Lanes for individual lizards are labeled beside their patterns on the gel (with genotype) as follows: NEOTESA, B, and C, different pattern classes of the triploid *A. neotesselata* from Colorado; TESC and D, *A. tesselata* of pattern classes C-E and D from Conchas Lake State Park, New Mexico; TESE, *A. tesselata* of pattern class E-C from Arroyo del Macho, New Mexico; TESF, *A. dixoni* from New Mexico; TESF × PUN, triploid hybrid of *A. dixoni* × *A. tigris punctilinealis* from New Mexico; and TESG and H, *A. dixoni* of two pattern classes from Texas. Anode is to the right.

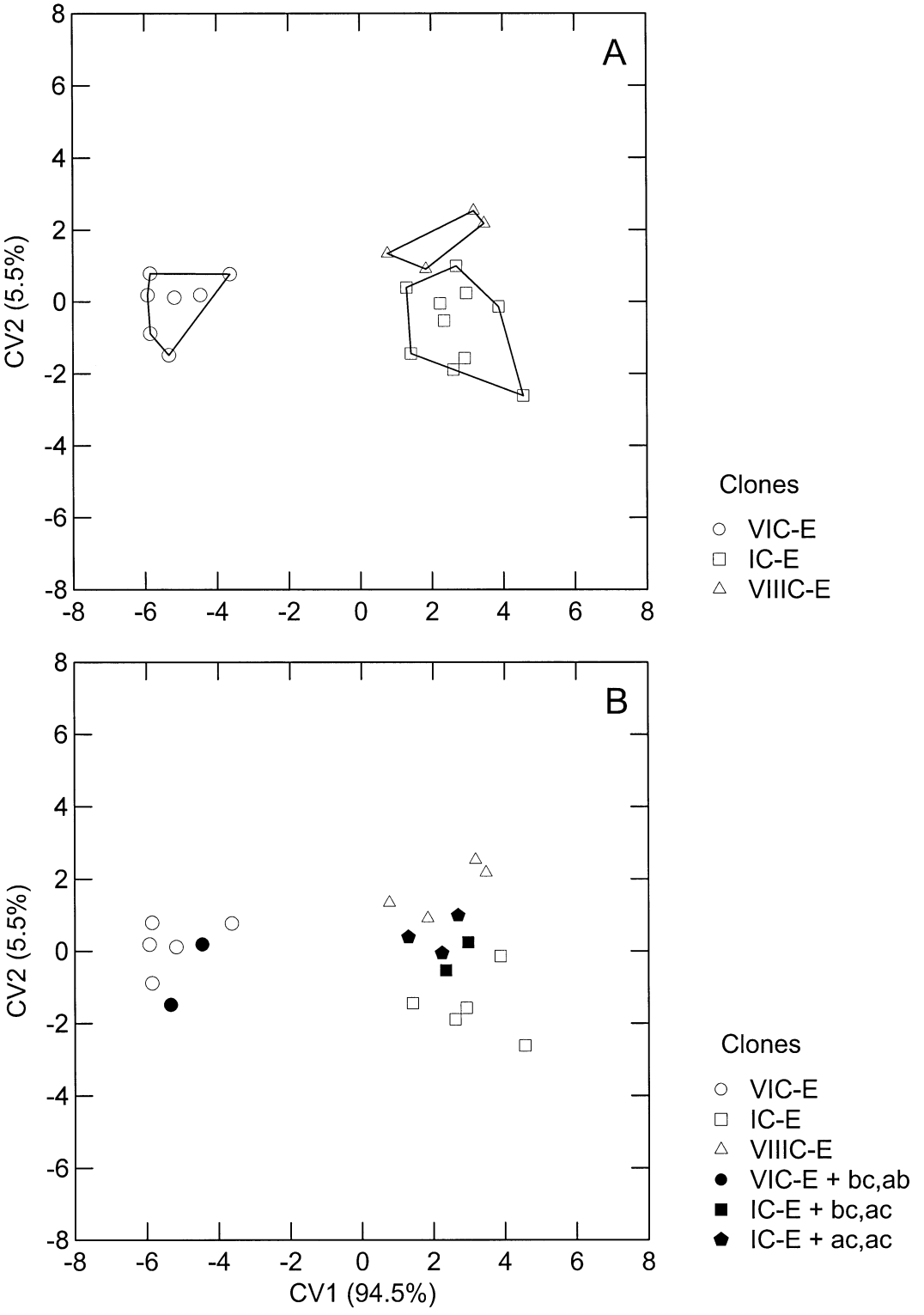
(excluding the questionable EST2) for which comparisons have also been made with the bisexual parental taxa, *A. tigris marmorata* and *A. gularis septemvittata*. Heterozygosity is fixed and very high, at 47% of these loci, in the parthenogenetic *A. tesselata*, whereas it averages 5% for bisexual species of *Aspidoscelis* (Parker and Selander, 1976; Dessauer and Cole, 1989). As initially pointed out by Parker and Selander (1976), the generality remains that for all loci the combination of alleles found in *A. tesselata* is a combination that could be found in an F_1 hybrid derived from *A. tigris marmorata* × *A. gularis septemvittata*, with very few exceptions in variant clones (e.g., sACOH and MPI). Furthermore, the allele combinations present in individuals of pattern classes C, C-E, New Mexico D, E, and E-C typically are identical or nearly identical to each other for each locus.

Congruence Between External Morphology and Genetic Markers in Pattern Class C-E From Conchas Lake State Park

Three subgroups of pattern class C-E at Conchas Lake are morphologically congruent with GPI, EST2, sACOH, and MPI genotypes (fig. 5). These subgroups were characterized by a canonical variate analysis of meristic characters, using the 21 specimens with known GPI and EST2 genotypes (Parker's [1979] clonal identities) as three a priori groups: clone IC-E (GPI −100/−96, EST2 100/96), clone VIIIC-E (GPI −100/−96, EST2 96/96), and clone VIC-E (GPI −99/−96, EST2 100/96). We included the three color pattern characters in the CVA after first regressing each character on SVL and demonstrating an absence of ontogenetic variation in the a priori groups (L-breaks: $r^2 = 0.10$, $P = 0.17$; DL-breaks: $r^2 < 0.0005$, $P = 0.98$; PV-breaks: $r^2 = 0.07$, $P = 0.24$). The CVA model (table 4) had an overall classification success of 90%, with the misclassifications being 2 of 10 individuals of clone IC-E classified to clone VIIIC-E (which we identify below as a likely mutational derivative of clone IC-E).

Patterns of Variation Among Morphological Subgroups of Pattern Class C-E and Pattern Class D From Conchas Lake State Park

Samples of known genotype (clones IC-E, $N = 10$; VIC-E, $N = 7$; VIIIC-E, $N = 4$) were used as a priori groups in a CVA to assign to morphological subgroup those specimens of Conchas C-E with unknown genotypes but having complete meristic data ($N = 79$). Arabic numerals designated subgroups (1C-E, 6C-E, and 8C-E) correspond-



ing to genotypic clones (IC-E, VIC-E, and VIIIC-E). The CVA assigned 48 individuals to 1C-E, 18 to 6C-E, and 13 to 8C-E. The assignment CVA was followed by a second CVA (table 5), using subgroups 1C-E, 6C-E, and 8C-E as the a priori groups. This CVA had a classification success of 96%, which was reflected in the clear delineation of subgroups in the ordination of canonical variate scores (fig. 6A). Three misclassifications were made among the 79 specimens—one individual of 6C-E assigned to 8C-E and two individuals of 1C-E, one assigned to each of subgroups 6C-E and 8C-E. Another CVA (table 6) substantiated that none of the subgroups (1C-E, 6C-E, and 8C-E) had a distinctive color pattern (fig. 6B). The classification success was only 42%, and each morphological subgroup contained individuals with C-like and E-like color pattern features (figs. 7, 13).

To determine the morphological subgroup most closely resembled by Conchas D, a CVA (table 7) was based on a priori groups composed of morphological subgroups 1C-E, 6C-E, 8C-E, and pattern class D. Although Parker and Selander (1976) reported single representatives of clones VID and VIIID from Conchas Lake, the voucher specimen for clone VIIID (EDP 842) was reidentified as a representative of pattern class C by Walker et al. (1997a) and clone VIIIC-E (this study). The voucher specimen for clone VID (EDP 846) is missing. However, Parker (1979) determined that it was morphologically similar to individuals of clone ID. Our sample of ID comprises 21 specimens, including the 9 specimens analyzed electrophoretically by Parker and Selander (1976) and Parker (1979) and 1 specimen (EDP 835) identified as a representative of clone IC in those publications. Walker et al. (1997a) assigned the latter specimen to pattern class D, and we concur, but these differences of opinion are expected to arise when visually classifying specimens with ambiguous color patterns. Eleven specimens of Conchas D analyzed electrophoretically by H.C.D. and C.J.C. were identical to clone IC-E for all loci tested and thus represented clone ID. Although it appears that clonal variation in pattern class D is limited, we use the more general designation of D for this a priori group.

Color pattern differences between Conchas C-E and Conchas D are centered in the vertebral field, where a pair of fragmented vertebral lines distinguishes the latter (figs. 7, 8). This distinctive color pattern difference belies the fact that clones ID and IC-E are identical to each other in electrophoretic characters, and Conchas D and morphological subgroup1C-E are nearly identical in multivariate morphological characters (fig. 9A, B).

TABLE 4
Discriminant Functions Used to Distinguish Genotypically Different Groups of *Aspidoscelis tesselata* of Pattern Class C–E from the Vicinity of Conchas Lake, San Miguel County, New Mexico

Character[a]	CV1	CV2
GAB	−1.215	0.202
L-breaks	0.826	0.284
LSG	−0.340	0.008
DL-breaks	0.089	−0.975
PV-breaks	−0.321	0.668
COS	0.471	−0.522
FP	−0.213	−0.411
PSC	0.046	0.299
GS	0.043	−0.265
Eigenvalue	15.626	0.915
Total explained variation	94.5%	5.5%

[a] Characters are defined in table 1.

←

Fig. 5. **A.** Pattern of multivariate morphological variation among 21 individuals of *Aspidoscelis tesselata* of pattern class C-E with genotypic data from Conchas Lake State Park, San Miguel County, New Mexico. Fourteen of these specimens were used by Parker and Selander (1976) to identify, from GPI and EST2 genotypes, clones IC-E, VIC-E, and VIIIC-E. **B.** Open symbols denote Parker and Selander specimens shown in part A and solid symbols identify the seven AMNH specimens in part A with known GPI, EST2, sACOH (given first), and MPI (given second) genotypes. Canonical variate scores were derived from a canonical variate analysis (table 4) using nine meristic characters.

TABLE 5
Discriminant Functions Used to Distinguish Three Morphological Subgroups of Pattern Class C–E of *Aspidoscelis tesselata* from the Vicinity of Conchas Lake, San Miguel County, New Mexico

Character[a]	CV1	CV2
GAB	−0.959	−0.067
COS	0.537	−0.311
PV-breaks	0.118	0.052
GS	0.111	0.097
L-breaks	0.079	0.059
FP	0.310	−0.790
PSC	0.025	0.477
DL-breaks	0.186	−0.310
LSG	−0.212	−0.186
Eigenvalue	4.284	1.188
Total explained variation	78.3%	21.7%

[a] Characters are defined in table 1.

Histocompatibility Among Morphological Subgroups of Pattern Class C-E and Pattern Class D

Cordes and Walker (2003) documented histocompatibility among the nine individuals of Conchas C-E tested. We determined the morphological subgroup membership of each specimen by using CVA and individuals of known genotype (10 representatives of IC-E, 7 of VIC-E, and 4 of VIIIC-E) as a priori groups. The CVA model assigned three individuals to 1C-E, two to 6C-E, and four to 8C-E. A follow-up CVA (table 8) used these assignments to depict the pattern of morphological variation and skin exchanges among the nine specimens. In addition to two color pattern characters disrupted by skin transplants, the PSC character did not meet the minimum tolerance criterion of the CVA model and was also omitted from the analysis. Despite the reduced number of characters, the classification success was 100% within each of the three morphological subgroups: 1C-E transplants, 6C-E transplants, and 8C-E transplants. Reciprocal skin transplants had been made (and accepted) among representatives of all three morphological subgroups (fig. 10A).

Cordes and Walker (2003) also demonstrated unequivocal histocompatibility between all lizards of pattern classes C-E and D tested. A CVA (table 9), using morphological subgroups of C-E and representatives of pattern class D as a priori groups, revealed the pattern of morphological variation among the four groups, and substantiated that reciprocal skin transplants had been made between representatives of each morphological subgroup (1C-E, 6C-E, and 8C-E) and pattern class D (fig. 10B).

Patterns of Morphological Variation Among Pattern Classes C, D, and E from Sumner Lake State Park

Different color pattern classes of *A. tesselata* coexist at three localities—near the historic townsite of Higbee, Colorado, and in the vicinities of Conchas and Sumner Lakes, New Mexico. These assemblages provide valuable information on phenotypic divergence because shared environments increase the likelihood that their phenotypic differences have a genetic basis. The Sumner Lake assemblage was particularly important because this is the only locality known where pattern class E coexists with pattern classes C and D (Taylor et al., 1997). This assemblage facilitated the resolution of more inclusive patterns of morphological variation in *A. tesselata* from eastern New Mexico.

A CVA (table 10) was used to determine the morphological distinctiveness of the Sumner Lake pattern classes C (N = 45), D

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Fig. 6. Pattern of multivariate morphological variation in three morphological subgroups of *Aspidoscelis tesselata* of pattern class C-E (1C-E, N = 48; 6C-E, N = 18; and 8C-E, N = 13) from the vicinity of Conchas Lake State Park, San Miguel County, New Mexico. Samples of specimens of known genotype were used as a priori groups to make the original subgroup assignments; specimens used to make the assignments were omitted from the definitive CVA. **A.** Distributions derived from a CVA using nine meristic characters summarized in table 5. **B.** Distributions derived from a CVA of three color pattern characters summarized in table 6.

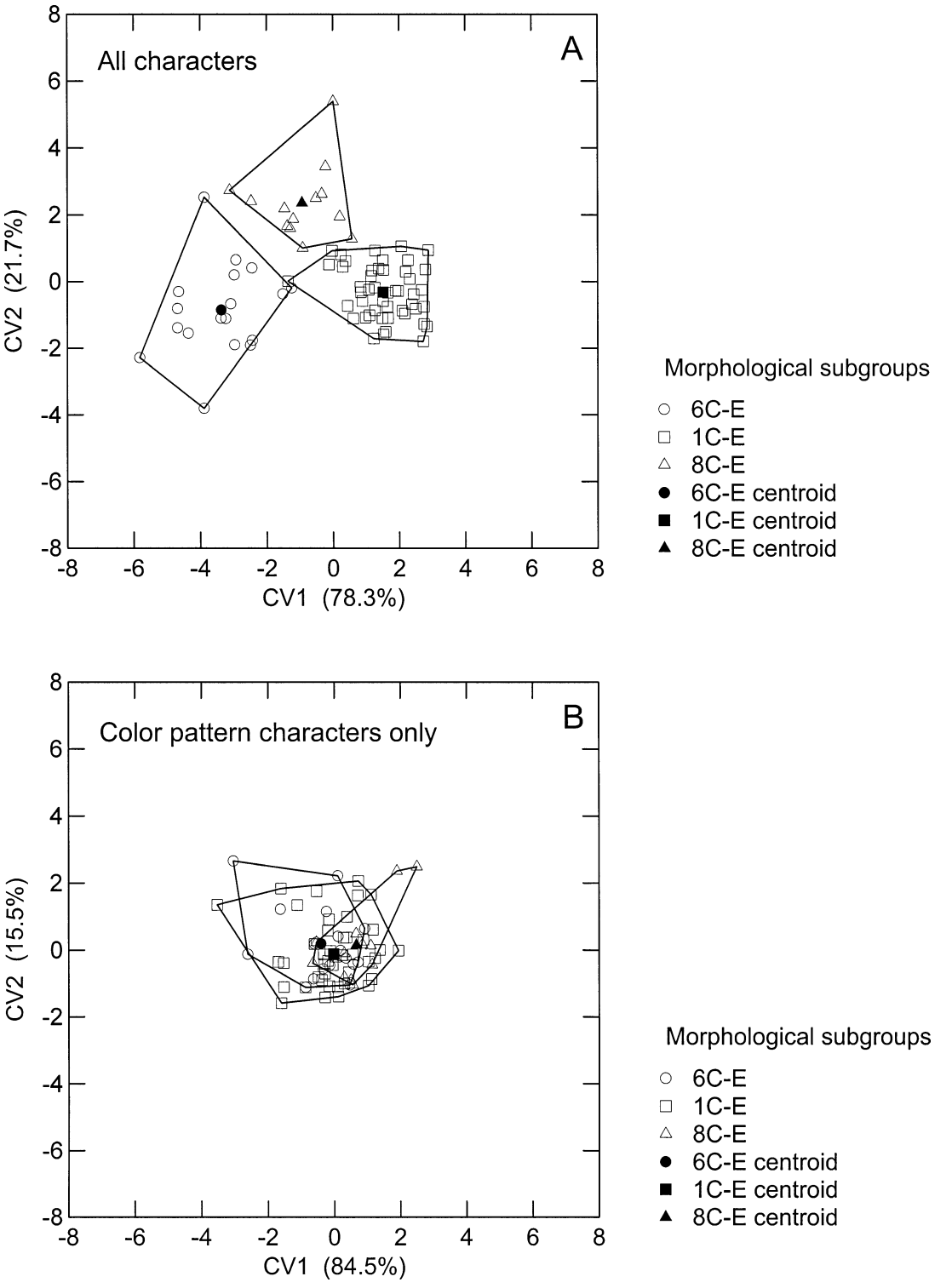

TABLE 6
Discriminant Functions Used to Determine If Three Morphological Subgroups of *Aspidoscelis tesselata* of Pattern Class C–E from the Vicinity of Conchas Lake, San Miguel County, New Mexico, Could be Distinguished by Color Pattern Characters

Character[a]	CV1	CV2
DL-breaks	−1.288	−0.205
PV-breaks	0.312	−0.254
L-breaks	0.531	1.146
Eigenvalue	0.114	0.021
Total explained variation	84.5%	15.5%

[a] Characters are defined in table 1.

(N = 5), and E (N = 32). Individuals were assigned to a priori group by visual assessment of color pattern. The CVA gave an overall classification success of only 79%; however, except for 1 of 32 individuals of pattern class E misclassified to pattern class C, the other misclassifications were between pattern classes C and D (15 of 45 Sumner C assigned to Sumner D and 1 of 5 Sumner D assigned to Sumner C). The high number of misclassifications between C and D emphasizes the meristic similarity of these two groups.

TABLE 7
Discriminant Functions Used to Distinguish Three Morphological Subgroups of *Aspidoscelis tesselata* of Pattern Class C–E and Pattern Class D from the Vicinity of Conchas Lake, San Miguel County, New Mexico

Character[a]	CV1	CV2
GAB	−0.982	0.030
LSG	−0.262	−0.048
L-breaks	0.072	0.044
GS	0.092	−0.056
FP	0.143	−0.792
COS	0.356	−0.518
PSC	0.042	0.387
DL-breaks	0.188	−0.441
PV-breaks	−0.016	0.165
Eigenvalue	3.643	0.911
Total explained variation	76.1%	19.0%

[a] Characters are defined in table 1.

The pattern of variation at Sumner Lake is a contrast between the meristic similarity of pattern classes C and D and the pronounced difference between these classes and Sumner E (fig. 11). Most individuals of Sumner E and Sumner C can be distinguished by visual inspection of the dorsal color pattern (e.g., Taylor et al., 1997: 864, fig. 1). However, a few individuals require subjective decisions regarding the degree of lateral barring (typically less extensive in C, more extensive in E) and the pale vertebral line (typically present and relatively intact in C and absent or broken extensively in E). For example, certain individuals of Sumner E have a relatively prominent vertebral line, thereby combining a C-like feature with an E-like, disrupted lateral stripe (e.g., RU 9743 shown in fig. 12A, B). The reverse combination also occurs; for example, RU 9507 (fig. 12D) was previously assigned to pattern class E because of its disrupted vertebral field (Taylor et al., 1997, 2000). However, a CVA classified this individual as pattern class C (P = 0.90), with the assignment being influenced by the low number of stripe disruptions: 4 L-breaks, 0 DL-breaks, and 6 PV-breaks (fig. 12E). In addition, certain individuals of Sumner C expressed unusual, partially divided vertebral lines, some just below the threshold of development seen in pattern class D from this locality (e.g., RU 9710 and 9725 shown in fig. 8B, C). As another example of confounding color pattern elements, certain individuals of Colorado D had partially divided, but essentially single, vertebral lines (Taylor et al., 1996, fig. 1C, D: 256).

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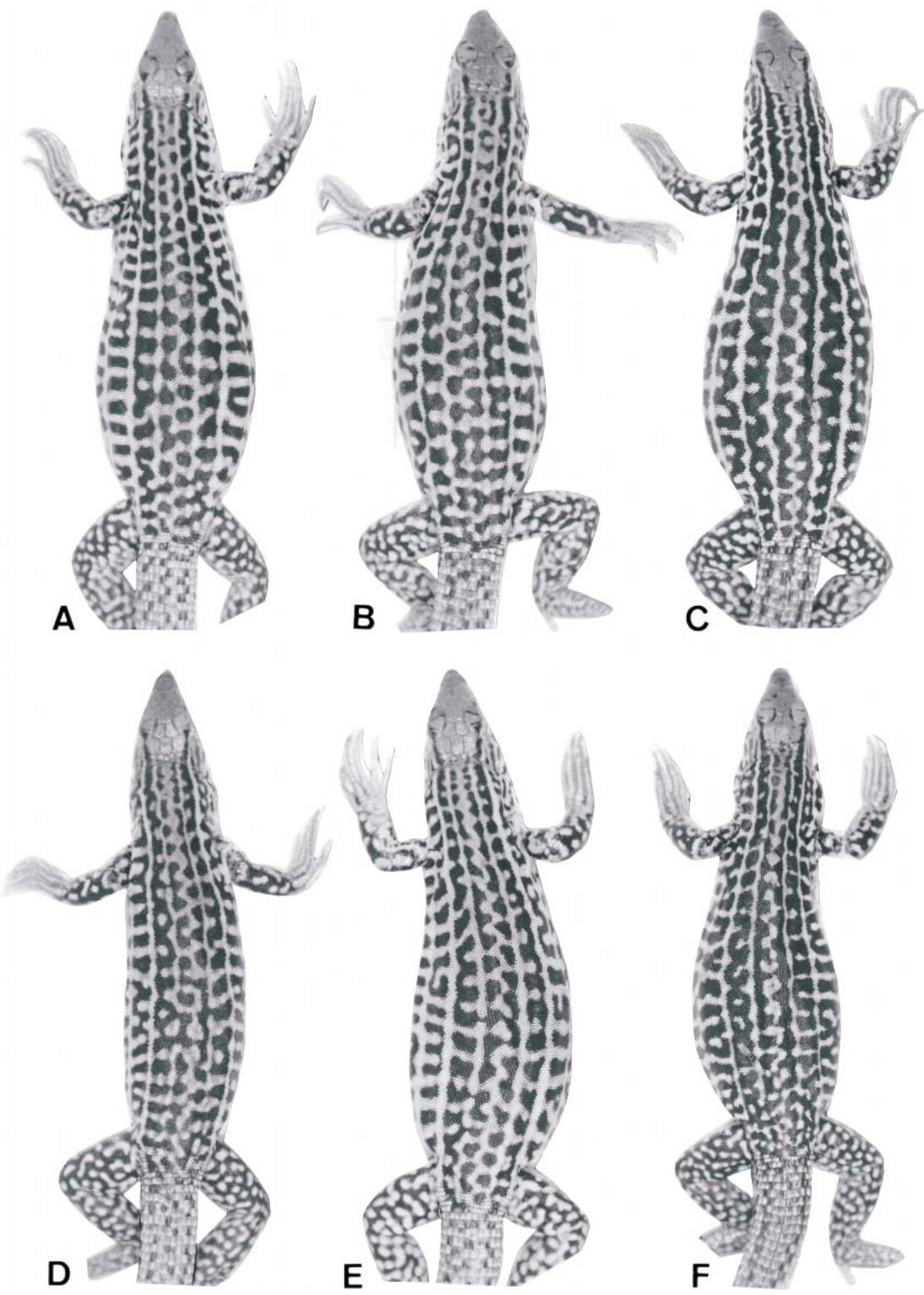
Fig. 7. Color pattern variation in *Aspidoscelis tesselata* of pattern class C-E from the vicinity of Conchas Lake State Park, San Miguel County, New Mexico. Morphological subgroup 6C-E: **A** (RU 0002, 93 mm SVL); **B** (RU 0029, 96 mm SVL); morphological subgroup 1C-E: **C** (RU 0013, 95 mm SVL); **D** (RU 0030, 89 mm SVL); **E** (RU 0021, 95 mm SVL); morphological subgroup 8C-E: **F** (RU 0027, 86 mm SVL).



Comparison of Pattern Classes C, C-E, E, and E-C from Eastern New Mexico

It appears likely that pattern classes C and C-E were derived from an ancestral pattern class, such as E or E-C. These are logical ancestral candidates because only populations presently allocated to pattern class E are sympatric with the progenitor species of *A. tesselata*. Therefore, if E or E-C are older pattern classes, their lineages should have accrued more mutations than those of pattern classes C, C-E, and D. This possibility manifests itself in the color pattern variation found within and among groups traditionally assigned to pattern class E. A preview of this variation is provided by Walker et al. (1997a: 240, fig. 4). Color pattern variation is expected because clonal reproduction of selectively neutral, genetically modified phenotypes should include color pattern features. This would be evidenced by significant differences in color pattern characters between geographically proximate populations of the same pattern class. As an example, the degree of lateral stripe disruption (L-breaks) was the principal character used by Zweifel (1965) to distinguish pattern classes C and E. Our sample of Luna E was not only significantly different in L-breaks from Sumner C (as expected), it also differed from Sumner E ($P < 0.0005$ for each comparison), although these samples came from sites separated by only 34 km. Paradoxically, there was no significant difference in L-breaks between Luna E and each morphological subgroup of Conchas C-E ($F_{3,139} = 2.225$; $P = 0.09$).

We summarized color pattern variation by a CVA of color pattern characters (table 11), with samples of Conchas 1C-E (+D), 6C-E, and 8C-E, Sumner C (+D), Sumner E, Luna E, and Macho E-C serving as a priori groups. Because of insignificant multivariate differences between Sumner D and Sumner C and between Conchas D and Conchas 1C-E, each of these pairs was pooled for this (and the following) analysis. The pattern of variation was a tight cluster of C-like individuals, a loose cluster of E-like individuals, and broad distributions of 1C-E, 6C-E, 8C-E, and Macho E-C individuals across both C-like and E-like clusters (fig. 13A).

We next used the seven a priori groups from the previous analysis in a CVA (table 12) to depict a comprehensive (color pattern and scalation characters) pattern of morphological variation. The inclusion of scalation characters enhanced the separation of Sumner E and Luna E from the other groups, with Conchas 6C-E and Macho E-C being distinguished, as before, by the breadth of their morphological variation (fig. 13B). We simplified this two-dimensional pattern to one dimension by an additive tree phenogram (fig. 14) constructed from a symmetric matrix of Mahalanobis D^2 distances between sample centroids (table 13). Note that the resemblance of Sumner D was with syntopic Sumner C (distance of 9.4) rather than with Conchas D (distance of 15.2), with smaller values reflecting greater similarity. The same pattern exists at Conchas Lake, where Conchas D was most similar to syntopic Conchas 1C-E (distance of 10.0) with which it shares the same GPI, EST2 genotype. Disregarding the Conchas D derivative, Conchas 1C-E and 8C-E were morphologically most similar to Sumner C (fig. 14).

Certain patterns of geographic variation suggest that a population resembling Macho E-C played an important role in the colonization of northern habitats by *A. tesselata*. One example involves the three populations identified historically as pattern class E. Despite the short geographic distance between the Sumner Lake and Puerto de Luna sites (fig. 1), Sumner E and Luna E resembled Macho E-C more closely than they resem-

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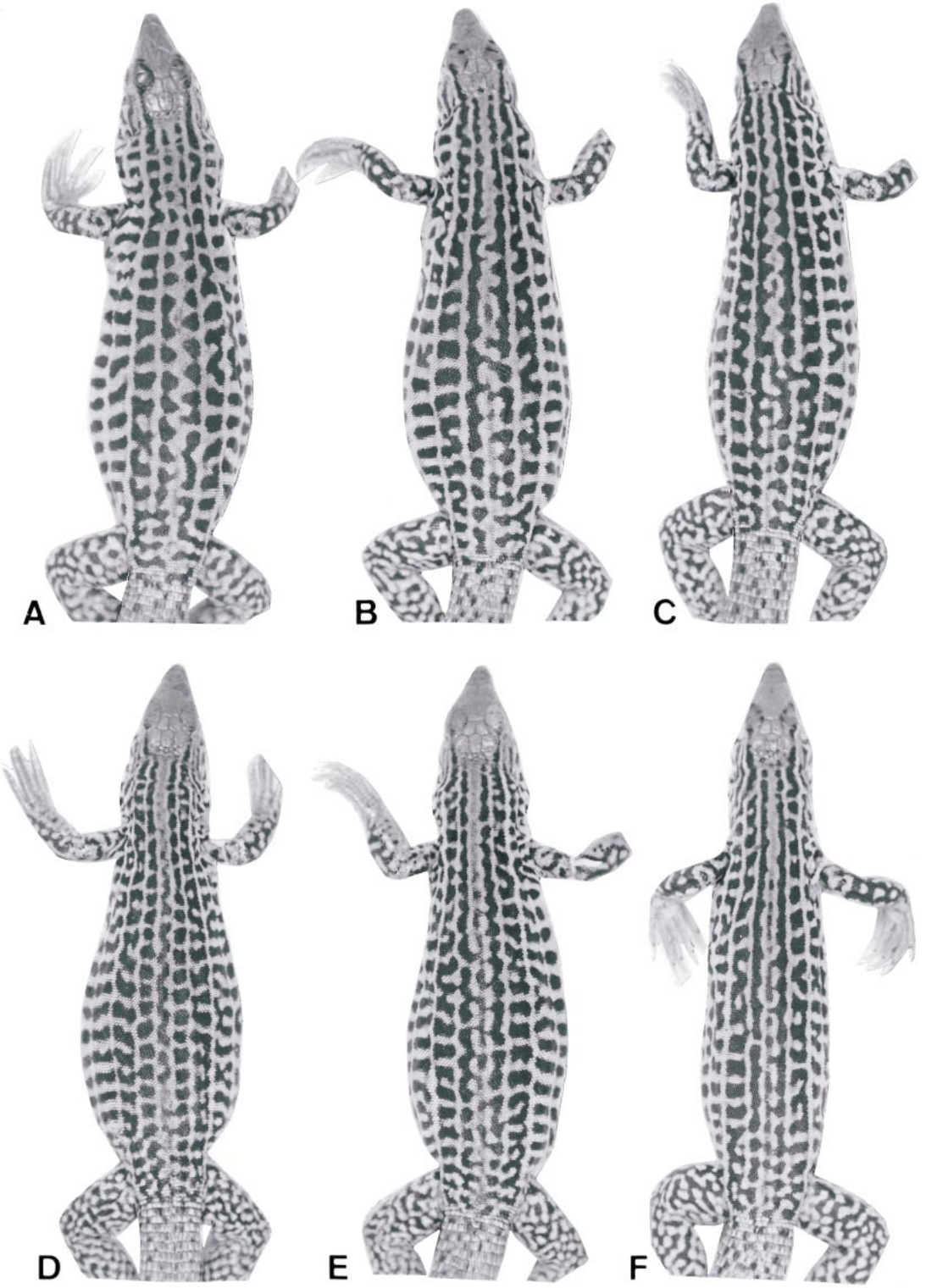
Fig. 8. Color pattern variation in *Aspidoscelis tesselata* of pattern classes C and D from the vicinity of Sumner Lake State Park, De Baca County, New Mexico, and pattern class D from the vicinity of Conchas Lake State Park, San Miguel County, New Mexico. Sumner C: **A** (RU 9711, 97 mm SVL); **B** (RU 9710, 97 mm SVL); **C** (RU 9725, 93 mm SVL); Conchas D: **D** (RU 0004, 95 mm SVL); **E** (RU 0043, 98 mm SVL); Sumner D: **F** (RU 9632, 97 mm SVL). Note the partial doubling of the vertebral stripe in individuals B and C (double vertebral lines being a characteristic of pattern class D).



bled each other (additive tree distances of 17.0 for Sumner E–Macho E-C; 19.4 for Luna E–Macho E-C; 30.2 for Sumner E–Luna E). In addition, Sumner C and the three morphological subgroups of Conchas C-E were also more similar to Macho E-C than to either of the geographically proximate populations of pattern class E. In fact, as the E-C designation suggests, certain individuals at Arroyo del Macho are C-like, with relatively intact pale stripes and vertebral lines (see Taylor et al., 2001: 16, fig. 4C, F, and compare these two specimens of pattern class E-C to representatives of pattern class C illustrated in Walker et al., 1997a: 239, fig. 3). Another example linking Macho E-C to northern groups was the strong morphological resemblance of Conchas 6C-E to Macho E-C rather than to syntopic clones of Conchas 1C-E and 8C-E (fig. 14).

Status of Pattern Class New Mexico D

Each group of pattern class D, including Colorado D (Taylor et al., 1996), resembled a sympatric group of pattern class C or C-E rather than pattern class D from other localities. This suggests that pattern class D was either derived by mutation from its companion population of pattern class C or C-E or that shared environments caused developmental convergence of meristic variation between the two pattern classes at each site of sympatry. Evidence from the Sumner Lake pattern classes indicates that the environmental alternative is unlikely. Despite shared habitats and activity periods, Sumner E is meristically distinct from Sumner C and Sumner D. Therefore, syntopy does not ensure morphological similarity, and the close meristic resemblance between Sumner C and Sumner D is more likely based on genetic similarities between ancestral (C) and derived (D) clones. Because the sampling procedure involved collecting individuals as they were encountered, the ratio of 47 C : 47 E : 5 D collected in 1995–1997 should approximate the relative numbers of each pattern class at Sumner Lake. Although pattern class D is polyphyletic in the sense of having originated several times from different individuals of pattern classes C and C-E, the proportion of its representatives at each locality does increase latitudinally from south to north: Sumner Lake (47 C : 5 D = 10%), Conchas Lake (126 C-E : 33 D = 21%), and Higbee (96 C : 79 D = 45%, Taylor et al., 1996). This trend could reflect different times of origin, different levels of success in different habitats, or both.

Zweifel (1965) discerned that pattern class C was distributed as a series of allopatric populations, whereas pattern class D was always sympatric with pattern class C. Because of significant meristic differences between pattern class D from Higbee and Conchas Lake, Zweifel also hypothesized that pattern class D had originated twice from representatives of pattern class C. Multivariate morphological evidence supports this hypothesis (Taylor et al., 1996). Based on identical genotypes for GPI, EST2, sACOH, and MPI and meristic similarities, we now identify Conchas clone IC-E as the likely progenitor of Conchas D and provide morphological evidence that Sumner D was similarly derived from Sumner C (fig. 14). Pattern class D is atavistic in the expression of broken, double vertebral lines—a color pattern feature of many individuals of *A. tigris marmorata*, the maternal progenitor species of *A. tesselata*.

MODEL 1 FOR ORIGINS: MULTIPLE HYBRIDIZATIONS EXPLAIN THE VARIATION IN *ASPIDOSCELIS TESSELATA* IN EASTERN NEW MEXICO

The only published evidence to explain the genetic and morphological variation in *A.*

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Fig. 9. Pattern of multivariate morphological variation in *Aspidoscelis tesselata* of subgroups 6C-E (N = 25), 1C-E (N = 58), 8C-E (N = 17), and pattern class D (N = 32) from Conchas Lake State Park, San Miguel County, New Mexico. Samples of specimens of known genotype were used as a priori groups to assign representatives of pattern class C-E to morphological subgroup. **A.** Distributions derived from a CVA using nine meristic characters (table 7). **B.** Centroids (means) of the distributions shown in part A.

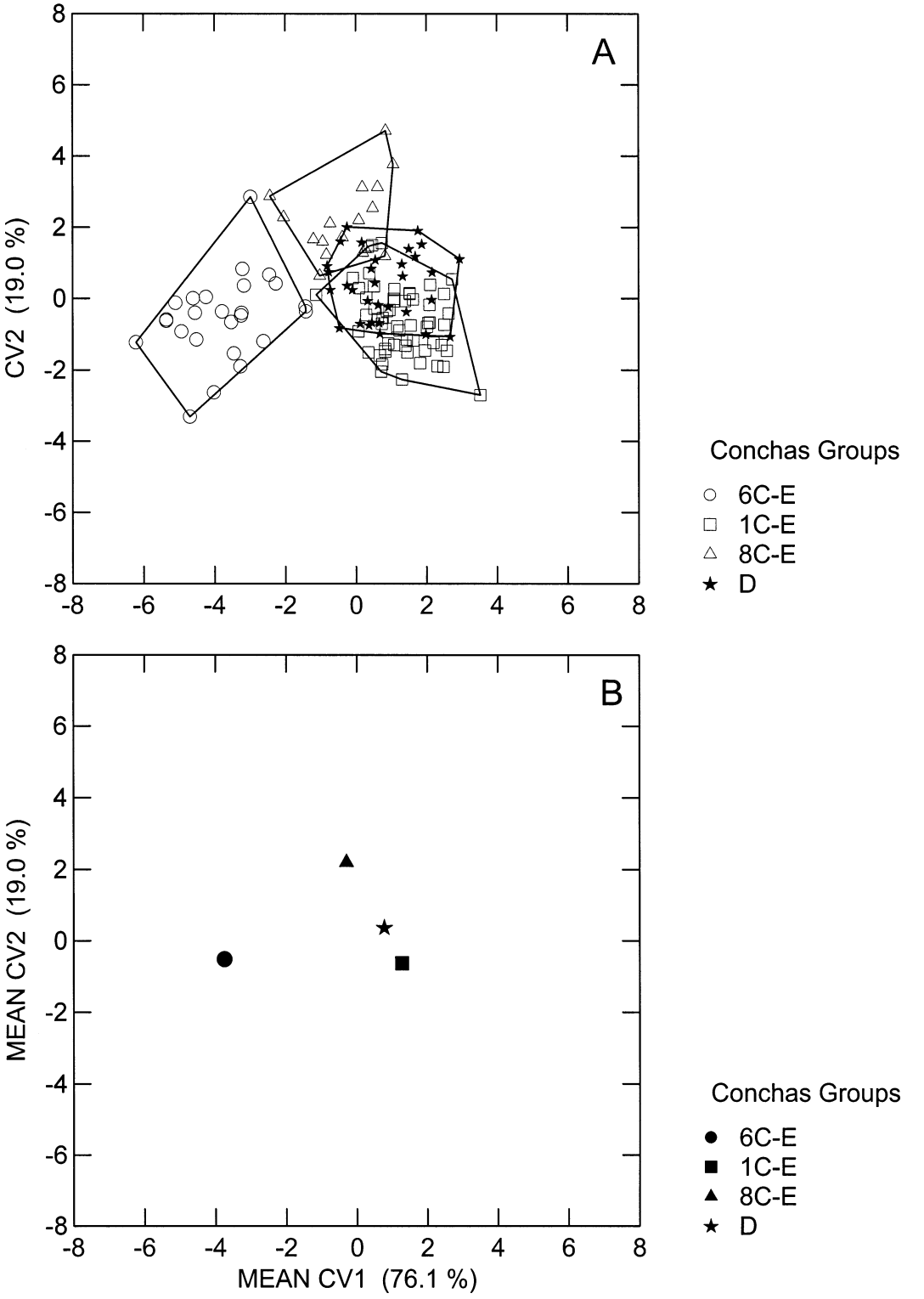

TABLE 8
Discriminant Functions Used in a CVA to Depict the Pattern of Morphological Variation Among Skin Transplant Specimens of *Aspidoscelis tesselata* of Pattern Class C–E from the Vicinity of Conchas Lake, San Miguel County, New Mexico

Character[a]	CV1	CV2
GAB	−2.780	−0.514
FP	2.255	−0.990
GS	2.208	−0.404
LSG	1.652	−0.591
L-breaks	1.097	0.147
COS	−0.950	−0.510
Eigenvalue	16.947	2.636
Total explained variation	86.5%	13.5%

[a] Characters are defined in table 1.

tesselata from Conchas Lake is detailed in Parker (1979) and Parker et al. (1989). This hypothesis is based on allele combinations in *A. tesselata* being consistent with multiple hybridizations having taken place between its bisexual parental ancestors. Taken by itself, the allozyme diversity in the Conchas assemblage could have been generated by multiple origins since there is no association between genotypes at the variable loci, and all four combinations of genotypes were detected in pattern class C-E (GPI −100/−96, EST2 100/96; GPI −100/−96, EST2 96/96; GPI −99/−96, EST2 100/96; GPI −99/−96, EST2 96/96). For example, both the GPI −99 and −100 alleles appeared to be present in *A. gularis septemvittata*, and different hybrid combinations could occur even within one clutch of eggs resulting from a single mating between representatives of *A. tigris marmorata* with a GPI −96/−96 genotype and *A. gularis septemvittata* having a GPI −100/−99 genotype. This would also be compatible with the morphological distinctiveness of the clones marked by GPI −99/−96 (Parker et al., 1989). The variation at EST2 is more problematical for this hypothesis. Because the 96-allele of EST2 was apparent only in *A. gularis septemvittata* and not in *A. tigris marmorata*, the origin of the EST2 96/96 genotype in the different GPI clones would require gene conversion (Hillis et al., 1991) or convergent mutation from the original F_1 hybrid genotype, EST2 100/96. However, if *A. tigris marmorata* previously had the 96-allele of EST2, or has it in low frequency or at localities not yet tested, then these genotypes could also have been produced by different hybrid combinations of parental gametes.

One problem with this model is biogeographical—the necessity of a historical northward displacement of the current, geographically restricted sympatry between the two progenitor species. Could the former range of *A. gularis septemvittata* have extended farther north and overlapped that of *A. tigris marmorata* more extensively than it does today in southwestern Texas (Parker and Selander, 1976)? If so, hybridization could then have taken place closer to the present ranges of color pattern classes C, C-E, and D. Although the northernmost population of *A. tigris marmorata* in the Pecos River drainage (vicinity of Arroyo del Macho) is reasonably close to the Sumner Lake pattern classes, the northernmost population of *A. gularis septemvittata* is close to Deer Mountain, Hudspeth County, Texas (Dixon, 2000). These populations are separated by approximately 400 linear km, and the Pecos River corridor is occupied by an intervening population of the more ecologically flexible *A. gularis gularis* (Degenhardt et al., 1996: 217). A recent range shift of this magnitude is doubtful, and it is also unlikely to have taken place through the range of *A. gularis*

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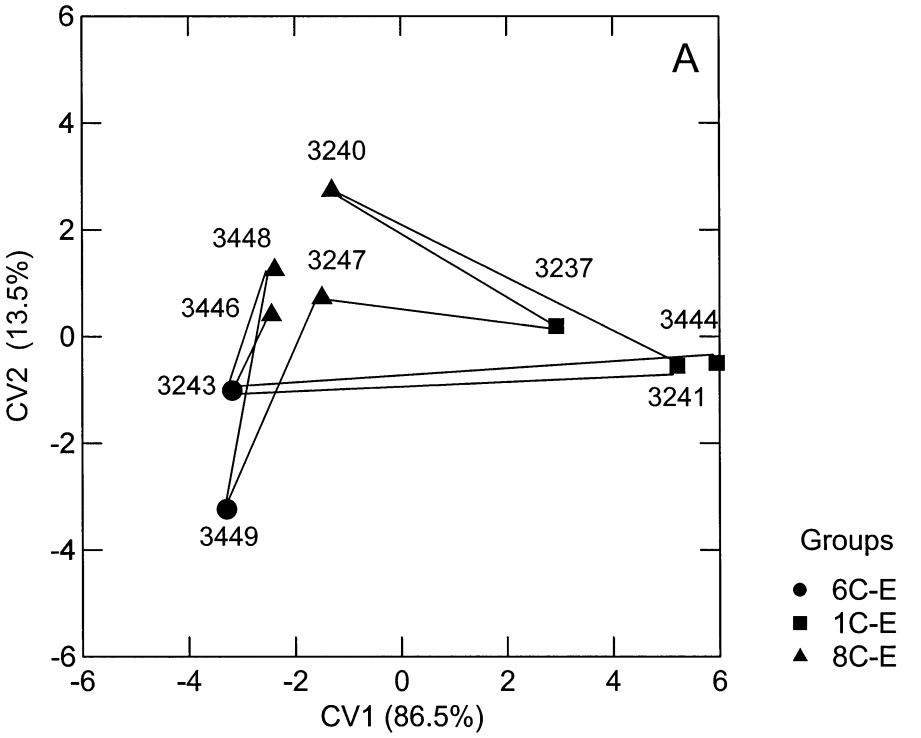
Fig. 10. Multivariate morphological variation among skin transplant specimens of *Aspidoscelis tesselata* from Conchas Lake State Park, San Miguel County, New Mexico. Numbers are University of Arkansas, Department of Zoology (UADZ) accession numbers; lines identify reciprocal skin exchanges. Separate CVAs were run for each depiction (tables 8, 9). **A.** Transplants between individuals of three morphological subgroups of pattern class C-E. **B.** Transplants between representatives of three morphological subgroups of pattern class C-E and New Mexico D.



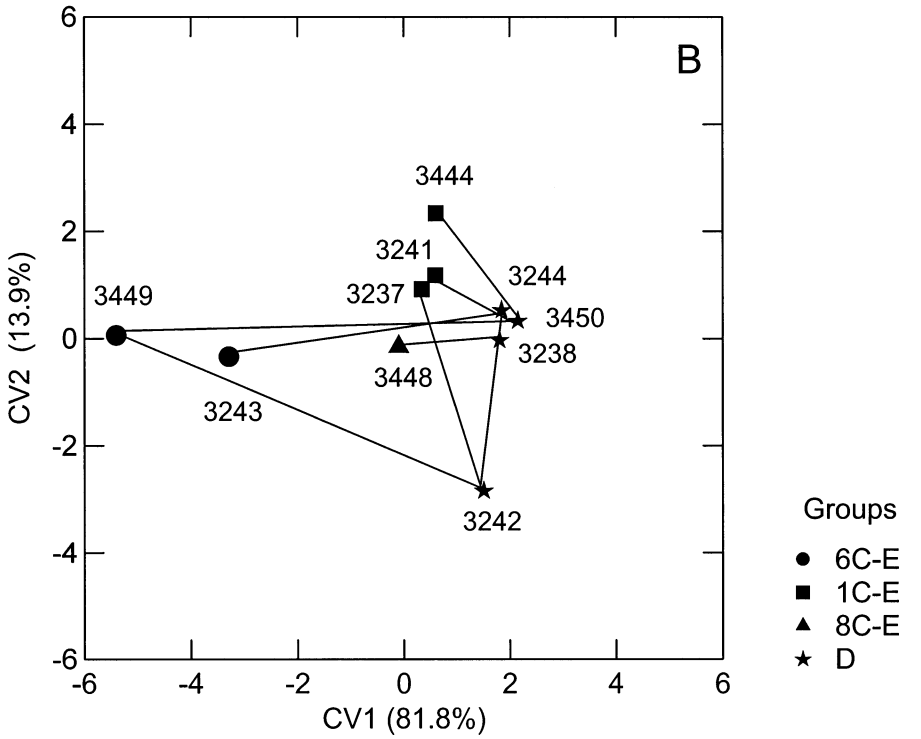


TABLE 9

Discriminant Functions Used in a CVA to Depict the Morphological Affinities of Skin Transplant Specimens of *Aspidoscelis tesselata* of Pattern Classes C–E and D from the Vicinity of Conchas Lake, San Miguel County, New Mexico

Character[a]	CV1	CV2
PSC	−1.394	−0.237
LSG	−1.061	0.297
COS	0.993	0.160
L-breaks	0.763	0.541
GAB	−0.645	−0.364
FP	−0.265	0.990
GS	−0.071	0.427
Eigenvalue	6.931	1.064
Total explained variation	81.4%	12.5%

[a] Characters are defined in table 1.

TABLE 10

Discriminant Functions Used to Distinguish *Aspidoscelis tesselata* of Pattern Classes C, New Mexico D, and E from Sumner Lake State Park, De Baca County, New Mexico

Character[a]	CV1	CV2
L-breaks	0.897	0.299
GAB	0.268	0.327
PV-breaks	−0.238	−0.671
PSC	−0.152	0.645
COS	−0.028	−0.483
LSG	−0.185	−0.288
DL-breaks	0.191	0.094
FP	0.279	−0.185
GS	0.122	−0.074
Eigenvalue	7.203	0.078
Total explained variation	98.9%	1.1%

[a] Characters are defined in table 1.

gularis without leaving evidence of intergradation.

MODEL 2 FOR ORIGINS: POSTFORMATIONAL MUTATIONS EXPLAIN THE EVOLUTION OF *ASPIDOSCELIS TESSELATA* IN EASTERN NEW MEXICO

One purpose of this study was to evaluate an alternative hypothesis to explain the source and pattern of genetic and morphological variation in *A. tesselata* from eastern New Mexico. This hypothesis posits that the morphological diversity in *A. tesselata* is based on postformational genetic divergence (i.e., after establishment of parthenogenesis) following the origin of *A. tesselata* from a single F_1 hybrid zygote (Taylor et al., 1996; Walker et al., 1997b: 167, fig. 1; Taylor et al., 2000).

This model is tied to three premises. The first assumes that histocompatibility among different individuals of *Aspidoscelis tesselata* reflects a single origin from one ancestral zygote. Although the genetic mechanism responsible for the immune response in *Aspidoscelis* has not been identified from extensive transplant experimentation (Cuellar and Smart, 1979), a rationale for interpreting histocompatibility as evidence of identical sets of histocompatibility alleles was provided by Cuellar (1976, 1977b), following Maslin (1967). This rationale was used to explain histocompatibility among parthenogenetic individuals of *A. cozumela* and *A. maslini* (Hernandez-Gallegos et al., 1998). It was also used as evidence that two clones of *A. laredoensis* had been derived from separate zygotes (Abuhteba et al., 2000). Conversely, histoincompatibility evidence for separate hybridizations would be subject to error if mutations in histocompatibility alleles had occurred in clones derived from the same F_1 hybrid zygote. Possible examples of such individuals are identified in *A. laredoensis* by Abuhteba et al. (2000).

Although histocompatibility genetics in lizards is poorly understood, the demonstration of histocompatibility for different color pattern classes of *A. tesselata* by Maslin (1967) and Cordes and Walker (2003) is a compelling argument for this model. If we assume that similar genetic systems are responsible for histocompatibility in lizards and humans, then the genetic variation at the sACOH and MPI loci (table 3) is consistent with evidence that the clonal diversity at Conchas Lake State Park originated from a single F_1 hybrid zygote. There are two sACOH genotypes (bc and ac) in *A. tesselata* at Conchas Lake. The origin of two of the three alleles can be accounted for because the c-allele is found in *A. tigris marmorata*, and the b-allele is found in *A. gularis septemvit-*

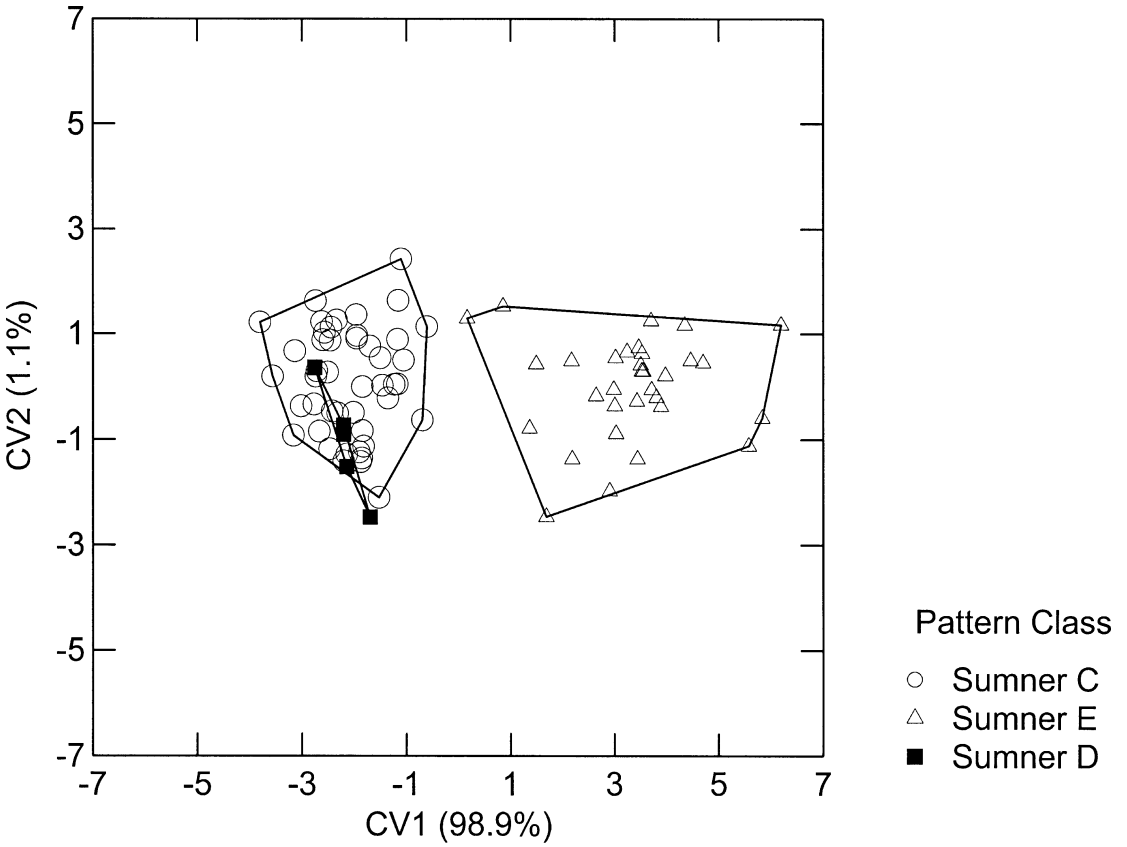
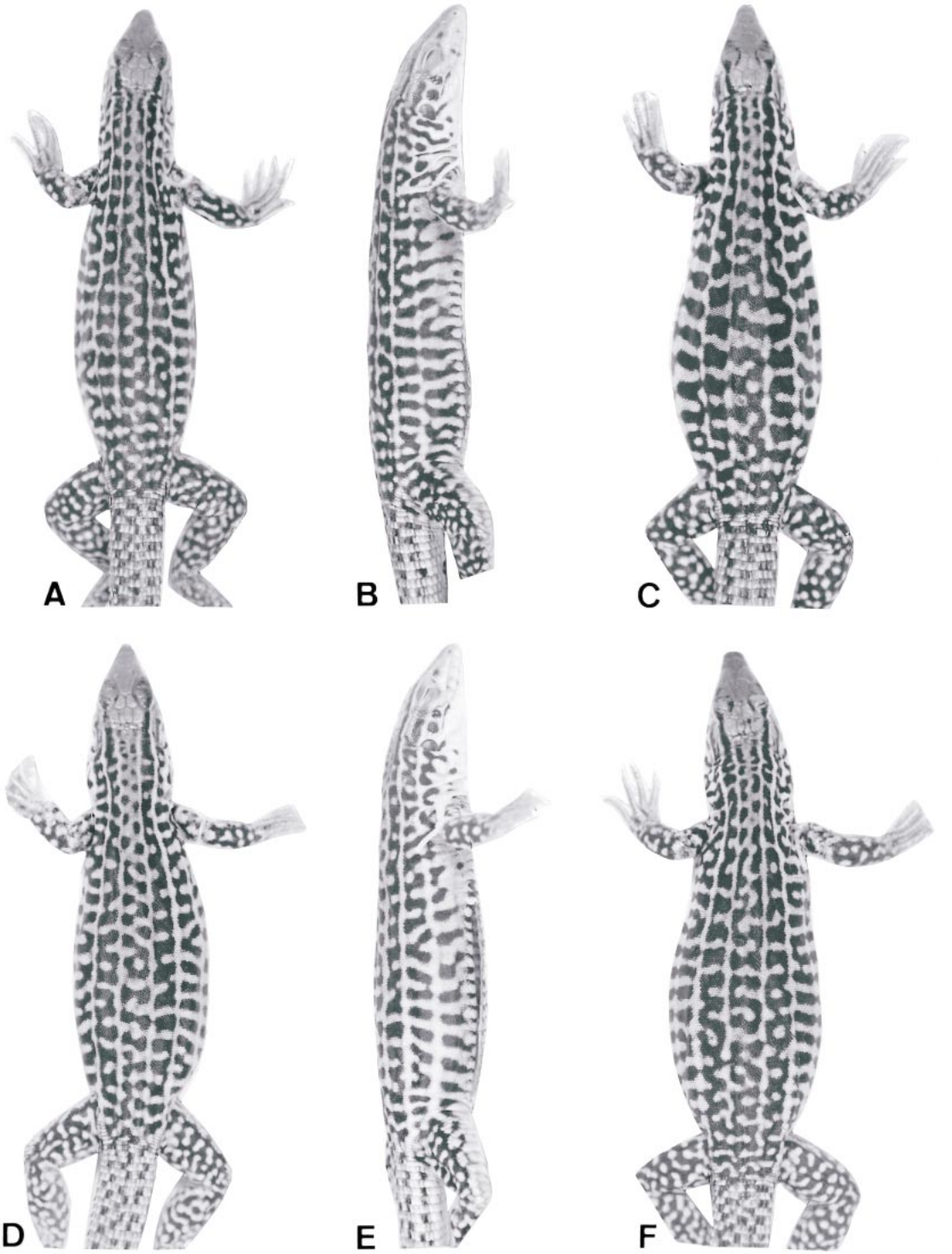


Fig. 11. Pattern of multivariate morphological variation among *Aspidoscelis tesselata* of pattern classes C ($N = 44$), E ($N = 32$), and New Mexico D ($N = 5$) from the vicinity of Sumner Lake State Park, De Baca County, New Mexico. Canonical variate scores were derived from a canonical variate analysis using meristic characters identified in table 10.

tata (the two progenitor species of *A. tesselata*, Neaves, 1969; Parker and Selander, 1976; Dessauer and Cole, 1989; Dessauer et al., 1996). The common genotype bc occurs in lizards of pattern classes C, D, E, and E-C, and clone VIC-E, and genotype ac is found only in certain individuals of clones IC-E and VIIIC-E. The a-allele has not been found in either bisexual progenitor taxon. The a-allele apparently does occur (with the b-allele) in *A. gularis gularis* (a close relative of *A. g. septemvittata*) and *A. sexlineata* (Dessauer and Cole, unpubl. data), so it is possible that the a-allele exists, undiscovered, in some extant population of *A. g. septemvittata*.

The same argument can be made from the MPI alleles, with genotypes ab and ac found in *A. tesselata* from Conchas Lake. Again, two of the three alleles could have come from the progenitor taxa; the a-allele is found in *A. tigris marmorata*, the b-allele is found in *A. gularis septemvittata*, but the c-allele has not been found in either progenitor taxon. The c-allele apparently does occur (with the b-allele) in *A. gularis gularis* (Dessauer and Cole, unpubl. data) so it too might also occur in some populations of A. g. *septemvittata*. Therefore, if genotypic diversity at the sACOH and MPI loci were acquired from different alleles in separate fertilizations, it would require three separate F_1 hybrid zygotes from *A. tigris marmorata* (sACOH c-, MPI a-) $\times$ *A. gularis* (sACOH ab, MPI: bc) to generate the three sACOH, MPI clones at Conchas Lake (bc ab; bc ac; ac ac). Because



different combinations of histocompatibility alleles would be expected in each zygote (Maslin, 1967; Cuellar and Smart, 1979), skin graft rejection would then be expected between individuals within subgroups 1C-E (bc ac and ac ac) and 8C-E (bc ac and ac ac) and between individuals in these subgroups and those in 6C-E (bc ab). A test of this hypothesis was provided by the reciprocal skin exchanges among all morphological subgroups (fig. 10A). The complete lack of skin graft rejection is cause for rejecting the multiple hybridizations hypothesis.

The alternative hypothesis posits that this genotypic diversity resulted from point mutations at each of the two loci after the parthenogenetic lineage had been established. The putative ancestral sACOH, MPI genotype (bc ab) characterizes pattern class E-C from Arroyo del Macho and clone VIC-E from Conchas Lake. The alternative sACOH, MPI genotypes (bc ac and ac ac), both in clones IC-E and VIIIC-E, could be accounted for by a single mutation at each locus. Samples from other localities were not assessed for sACOH and MPI genotypes.

The second premise assumes that evolutionary patterns in *A. tesselata* can be inferred from patterns of genotypic and morphological variation. Densmore et al. (1989) concluded, from the low level of sequence divergence in mtDNA, that *A. tesselata* had originated very recently. The same conclusion had been reached by Parker and Selander (1976) based on the relatively low genotypic variation found throughout the range of this species. In addition, *A. tesselata* lacks a mechanism (sexual reproduction) for internal cohesion of variation (Dessauer and Cole, 1986). Therefore, if *A. tesselata* originated from a single hybridization event (one F_1 zygote), spontaneous mutation would produce a pattern of mosaic divergence into various clones.

TABLE 11

Discriminant Functions, Derived from Color Pattern Characters, Used to Distinguish *Aspidoscelis tesselata* of Pattern Classes C–E (Three Morphological Subgroups) from Conchas Lake State Park, San Miguel County; Pattern Classes C and E from Sumner Lake State Park, De Baca County; Pattern Class E from Puerto de Luna, Guadalupe County; and Pattern Class E–C from Arroyo del Macho, Chaves County, All in New Mexico

(Samples of pattern class D have been pooled with samples of putative local ancestral groups 1C–E and Sumner C for this analysis.)

Character[a]	CV1	CV2
L-breaks	0.850	0.533
DL-breaks	0.274	−1.370
PV-breaks	−0.066	0.879
Eigenvalue	1.035	0.155
Total explained variation	83.6%	12.5%

[a] Characters are defined in table 1.

The third premise is based on the correspondence between meristic and genotypic variation identified in Parker (1979) and this study. We assume that genotypes of untested groups can be inferred from either geographic proximity or morphological resemblance to groups of known genotype. For example, although genetic information was not available for pattern class E from Sumner Lake, the GPI, EST2 genotypes are known for pattern class E from Fort Sumner, only 18 linear km southeast of the Sumner Lake sampling localities. All individuals from Fort Sumner (N = 11) belonged to genotypic clone VIE (GPI −99/−96 [Parker and Selander, 1976: 798, table 5] and EST2 100/96 [Parker and

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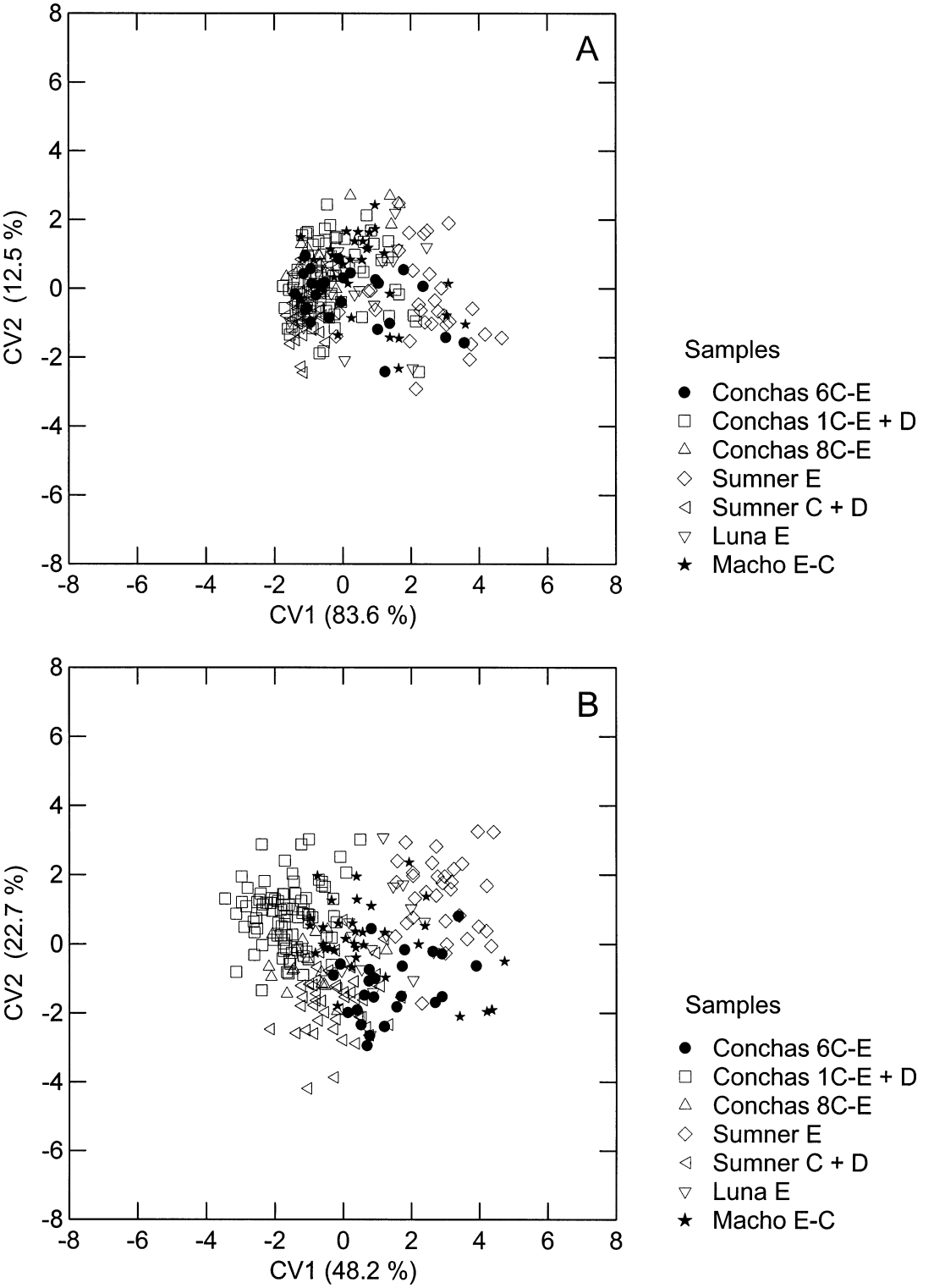
Fig. 12. Color pattern variation in *Aspidoscelis tesselata* of pattern classes C and E from the vicinity of Sumner Lake State Park, De Baca County, New Mexico, and Puerto de Luna, Guadalupe County, New Mexico. Sumner E: **A** and **B** (RU 9743, 92 mm SVL) and **C** (RU 9748, 87 mm SVL); Sumner C: **D** and **E** (RU 9507, 89 mm SVL) (based on a visual assessment of the disrupted vertebral stripe, RU 9507 had been previously assigned to pattern class E. However, a CVA classified this individual as a pattern class C, with the relatively uninterrupted lateral stripe being important in this assignment.); Luna E: **F** (RU 0054, 95 mm SVL).



Selander, 1976: 797, table 4]). The Pecos River drainage provides a habitat corridor between Fort Sumner and Sumner Lake, and the general historical pattern of colonization of suitable habitats by *A. tesselata* has been from south to north (Parker and Selander, 1976). In addition, Parker and Selander (1976) found GPI variation within individual pattern classes at only two widely separated localities—Conchas Lake, in the Canadian River drainage, and the south end of Elephant Butte Reservoir and Engle vicinity, both in the Rio Grande drainage. The geographically restricted nature of genotypic variation in *A. tesselata* makes it likely that pattern class E at Sumner Lake State Park and Fort Sumner share the same GPI −99/−96 genotype. This GPI genotype also characterizes clone VIC-E from Conchas Lake. Differences in the EST2 genotype have been found only in C-E from the Conchas Lake vicinity.

We also lack genetic data for Sumner C, but we surmise that Sumner C and Sumner E have different GPI genotypes because of their pronounced morphological differences (table 2; figs. 12, 13). Therefore, the genotype for Sumner C was inferred from its morphological resemblance to another group. Morphologically, Conchas 1C-E and 8C-E (both GPI −100/−96) most closely resemble Sumner C, and Sumner C most closely resembles Macho E-C (GPI −100/−96) (fig. 14). This chain of resemblance suggests that Sumner C is also GPI −100/−96, which is the most common GPI genotype in this species (Parker and Selander, 1976).

Divergence in *A. tesselata* from Eastern New Mexico

Biogeographical Perspective: The ancestral pattern class in *A. tesselata* can be inferred from the geographic distributions of its color pattern classes and progenitor species *A. tigris marmorata* and *A. gularis septemvittata*. Pattern class E (sensu Zweifel, 1965) is the only pattern class that contacts the two progenitor species, with contact restricted to a few sites in northeastern Chihuahua, Mexico, and southwestern Texas (Scudday, 1973; Scudday and Dixon, 1973; Parker and Selander, 1976). The present geographic range of pattern class E (sensu Zweifel, 1965) extends northward from Trans-Pecos Texas, with the Rio Grande and Pecos River drainages being the principal dispersal routes (Cuellar, 1977a, fig. 3: 841). Pattern

TABLE 12

Discriminant Functions, Derived from Scalation and Color Pattern Characters, Used to Distinguish *Aspidoscelis tesselata* Pattern Classes C–E (Three Morphological Subgroups) from Conchas Lake State Park, San Miguel County; Pattern Classes C and E from Sumner Lake State Park, De Baca County; Pattern Class E from Puerto de Luna, Guadalupe County; and Pattern Class E–C from Arroyo del Macho, Chaves County, all in New Mexico

(Samples of pattern class D have been pooled with samples of putative local ancestral groups 1C–E and Sumner C for this analysis.)

Character[a]	CV1	CV2
GAB	0.870	−0.513
PV-breaks	−0.186	0.031
GS	0.116	−0.009
COS	−0.054	0.566
FP	0.107	0.403
L-breaks	0.277	0.512
LSG	−0.260	−0.379
DL-breaks	0.249	0.266
PSC	−0.011	−0.123
Eigenvalue	2.399	1.130
Total explained variation	48.2%	22.7%

[a] Characters are defined in table 1.

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Fig. 13. Patterns of multivariate variation among *Aspidoscelis tesselata* of morphological subgroups 1C-E and Conchas D ($N = 90$), 6C-E ($N = 25$), and 8C-E ($N = 17$) from the vicinity of Conchas Lake, San Miguel County; pattern classes C and D ($N = 50$) and E ($N = 32$) from the vicinity of Sumner Lake State Park, De Baca County; pattern class E from Puerto de Luna, Guadalupe County ($N = 16$); and pattern class E-C from Arroyo del Macho, Chaves County ($N = 36$), all from New Mexico. **A.** Canonical variate scores derived from a CVA of three color pattern characters identified in table 11. **B.** Canonical variate scores derived from a CVA using nine meristic characters identified in table 12.

TABLE 13

Pairwise Mahalanobis Distances (D^2) Among Centroids of Canonical Variate Scores for Samples of *Aspidoscelis tesselata* 6C–E, 1C–E, 8C–E, and Pattern Class D from the Vicinity of Conchas Lake State Park, San Miguel County; Pattern Classes C, D, and E from Sumner Lake State Park, De Baca County; Pattern Class E from Puerto de Luna, Guadalupe County; and Pattern Class E–C from Arroyo del Macho, Chaves County, all in New Mexico

(This dissimilarity matrix was used to construct figure 14.)

	6C-E	1C-E	8C-E	Sumner E	Sumner C	Luna E	Macho E-C	Conchas D	Sumner D
6C-E	0.00								
1C-E	16.00	0.00							
8C-E	12.92	8.47	0.00						
Sumner E	11.70	20.56	23.75	0.00					
Sumner C	5.47	10.22	5.95	19.40	0.00				
Luna E	16.54	19.95	19.07	19.49	16.86	0.00			
Macho E-C	7.52	9.64	6.70	9.07	6.44	14.07	0.00		
Conchas D	13.02	2.11	5.02	24.07	7.58	19.24	9.55	0.00	
Sumner D	5.30	7.94	7.72	19.92	1.44	16.31	9.03	5.81	0.00

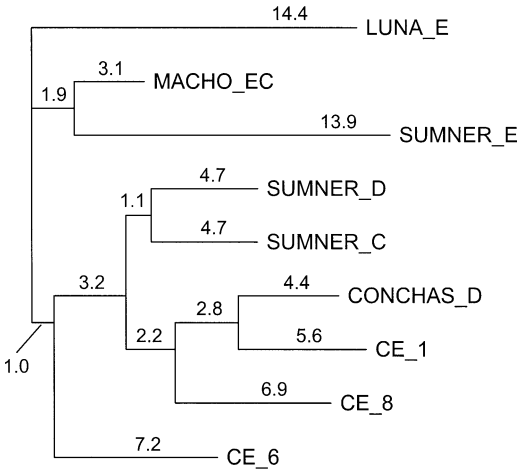

Fig. 14. Additive tree (phenogram), based on Mahalanobis D^2 distances (table 13), depicting meristic resemblance among nine groups of *Aspidoscelis tesselata*. Distances (similarities) between groups are computed by adding lengths of nodes between groups of interest. Terminal nodes represent the nine groups, and internal nodes represent horizontal distances between clusters. As an interpretation example, the resemblance between Conchas 6C-E and Conchas 1C-E is 7.2 + 3.2 + 2.2 + 2.8 + 5.6 = 21.0, while the resemblance between Conchas 6C-E and Macho E-C is 7.2 + 1.0 + 1.9 + 3.1 = 13.2.

classes C and D are first encountered near the northern range boundary of pattern class E, at Sumner Lake State Park, De Baca County, New Mexico (Taylor et al., 1997). Historically, the range of pattern class E extended north to Santa Rosa Lake (named Los Esteros Reservoir when constructed), Guadalupe County, New Mexico (documented by specimens in the Museum of Southwestern Biology), but this population was evidently extirpated when the reservoir basin filled (Brown, 1980; J. Applegarth, personal commun.). We have not seen representatives of *A. tesselata* at Santa Rosa Lake State Park during several recent visits to this locality, although J. M. Walker discovered in 1996 the population at Puerto de Luna, approximately 13.5 km southeast of Santa Rosa.

Scattered populations of pattern class C are found northeast of Sumner Lake in parts of northeastern New Mexico, northwestern Texas, southeastern Colorado, and southwestern Oklahoma (Zweifel, 1965). Therefore, the relatively abrupt latitudinal shift from pattern class E to pattern class C may be related to mutations that preadapted pattern class C to the shorter growing seasons in the northern part of the range. The south-

ern range boundary of pattern class C (and D) at Sumner Lake is separated from sympatric populations of the two bisexual progenitor species by approximately 520 linear km (Scudday, 1973; Scudday and Dixon, 1973). Because pattern classes E-C and E are geographically interposed between the ranges of the bisexual progenitor species and pattern classes C, C-E, and D, pattern classes E-C and E are ancestral pattern class candidates. The E-C alternative is particularly appealing because of the breadth of its color pattern variation, although color pattern variants could also originate, similar to pattern class D, by mutation within established groups.

MORPHOLOGICAL PERSPECTIVE: Most individuals of *A. tesselata* can be assigned to color pattern class because of quasi-binary color pattern characters (Zweifel, 1965; Taylor et al., 1996; Walker et al., 1997a). Double, fragmented vertebral lines distinguish most representatives of pattern class D from pattern classes C, C-E, E, and E-C, and the presence (Colorado D) or absence (New Mexico D) of supernumerary pale stripes distinguishes most individuals of the D-pattern classes (Taylor et al., 1996). Individuals of Colorado D lacking supernumerary stripes or having essentially intact vertebral lines are occasionally produced (Zweifel, 1965: 4, fig. 2D; Walker et al., 1997a: 238, fig. 2C).

Because of the distinctive color pattern of New Mexico D, the assignment of individuals to this pattern class is generally straightforward. However, it is easy to demonstrate the reduced level of distinctiveness in Conchas C-E and Macho E-C. Because the three morphological subgroups at Conchas Lake were most similar to either Sumner C (1C-E and 8C-E) or Macho E-C (6C-E), samples of Sumner C and Macho E-C were used as a priori groups in three discriminant analyses (DAs). Specimens of a different subgroup (1C-E, 6C-E, or 8C-E) were included as unclassified in each DA for classification to a priori group. The standardized discriminant functions (eigenvalue of 1.156) were 1.146 for L-breaks, −0.607 for DL-breaks, and 0.212 for PV-breaks. Classification success for the a priori groups was 96% for Sumner C (43 of 45 specimens assigned correctly) but only 73% for Macho E-C; 10 of 37 individuals were identified as belonging to Sumner C! With respect to the subgroups of pattern class C-E from Conchas Lake, the assignments were (1) subgroup 1C: 36 individuals to Sumner C and 22 to Macho E-C, (2) subgroup 6C: 12 individuals to Sumner C and 13 to Macho E-C, and (3) subgroup 8C-E: 8 individuals to Sumner C and 9 to Macho E-C. This quantifies what is evident upon visual inspection of Conchas Lake and Arroyo del Macho samples—use of pattern class C and E is misleading and oversimplifies color pattern variation in these populations.

For example, the form at Arroyo del Macho (Macho E-C) was referred to pattern class E by Zweifel (1965: 43), but differences were noted by Taylor et al. (2001). The mix and range of color pattern expressions in Macho E-C were illustrated by a DA, using the samples of Sumner E and Sumner C as a priori groups. These samples are appropriate representatives of pattern classes C and E because of their high level of morphological distinctiveness (fig. 11). Individuals of Macho E-C were entered as unclassified for assignment to group. Because of the strong divergence between color patterns E and C at Sumner Lake, this model had a relatively high eigenvalue of 5.680, with standardized discriminant functions of 1.079 for L-breaks, 0.091 for DL-breaks, and −0.254 for PV-breaks. There were few misclassifications in the a priori groups; 94% (30 of 32) of Sumner E and 100% (45 of 45) of Sumner C were classified correctly. However, 21 of 37 individuals of Macho E-C were classified as Sumner C, with the remaining 16 classified as Sumner E. Although some populations of pattern class E lack evidence of a lateral stripe, Macho E-C has color pattern elements of both progenitor species—lateral barring from *A. tigris marmorata* and a lateral stripe from *A. gularis septemvittata*. The breadth of color pattern variation in Macho E-C is sufficient (fig. 13A) to have established the color pattern themes exhibited by the disjunct groups in northeastern New Mexico.

GENETIC PERSPECTIVE: Ideally, a description of the evolutionary history of *A. tesselata* would emerge from an initial understanding of the processes generating the genetic and morphological variability in this clonally diverse species. Unfortunately, the

genetic bases of color pattern features and scalation differences are unknown, although there is evidence that elements of both are cloned (Dessauer and Cole, 1986; this study).

Nevertheless, Densmore et al. (1989) provide mtDNA evidence that pattern classes C, D, and E share one hybridization event in their past. This conclusion is consistent with the results of histocompatibility experiments (Maslin, 1967; Cordes and Walker, 2003). Therefore, if a single F_1 hybrid represented the origin of *A. tesselata*, its subsequent divergence into genetic and morphological clones should have a plausible explanation. As background information, genotype −100/−96 is the most common and widespread of the GPI alternatives (Parker and Selander, 1976); therefore, it is the logical candidate for the ancestral combination of alleles. Genotype GPI −100/−96 characterizes populations at Roswell (IE), Arroyo del Macho (IE-C), and Conchas Lake (IC-E and VIIIC-E). The presumed derivative, GPI −99/−96, is found at Fort Sumner (VIE) and Conchas Lake (VIC-E).

The simplest fit of biogeographical, morphological, and genotypic data is provided by a model in which the origin and establishment of derived color pattern classes and GPI clones followed a general south-to-north range expansion by colonists of GPI −100/−96. Clone VIC-E from Conchas Lake shares the GPI −99/−96 genotype with VIE from Fort Sumner, yet the morphological affiliations of both Conchas VIC-E and the Sumner Lake population of pattern class E are with clone IE-C from Arroyo del Macho. The mosaic nature of variation in different character systems (color pattern, scalation, proteins, karyotypes) is consistent with random mutations occurring after the establishment of parthenogenesis in *A. tesselata*.

We discussed above two competing hypotheses to explain the origin of variation in *Aspidoscelis tesselata*. Variation stemmed either (1) from different F_1 hybrid zygotes (separate fertilizations, whether involving the same individual parents and egg clutch or not), or (2) from mutations that occurred after parthenogenesis was established. The hypothesis of multiple fertilization events is favored by the fact that there are individuals of different color pattern classes (C, D, E) of *A. tesselata* with vertebral dark field patterns that can be matched by color pattern variation in *A. tigris marmorata*, and that certain variant alleles detected by protein electrophoresis appear to exist as polymorphisms in the ancestral bisexual taxa. However, the genetic differences in these character states may be due to simple mutations or gene conversions that can occur more than once, and they may be reversible. In addition, it is possible that what appears on a gel to be the same allele product representing different lizards could actually be different allele products having the same migration characteristics in the gel.

We are impressed by the data produced by Maslin (1967) and Cordes and Walker (2003) demonstrating reciprocal histocompatibility among lizards of pattern classes C and E and among the genotypic clones of pattern class C-E and pattern class New Mexico D, respectively. If, as in humans, the histocompatibility genes of *Aspidoscelis* involve multiple loci with many independently assorting alleles (more than 50 alleles for one locus in humans; Gebhardt, 1996), this would suggest that *A. tesselata* originated from a single F_1 zygote. The rejection of skin transplants among 15 individuals from one population of bisexual *A. tigris* is consistent with the assumption that lizards derived from different zygotes are histoincompatible (Cuellar and Smart, 1977).

Deficiencies of the Pattern Class C and E Designations

The distinction between pattern classes C and E is essentially unambiguous at Sumner Lake, once color pattern ontogeny has been completed; for example, a CVA (table 11, fig. 13A) based on three color pattern characters classified all individuals correctly to two groups, C + D or E. Nevertheless, Zweifel (1965) provided examples that challenged the range-wide operationalism of pattern class E. This evidence included samples of pattern class E from disjunct sites in the Rio Grande drainage of New Mexico containing specimens with an intact lateral stripe (a characteristic of pattern class C). Zweifel (1965) also noted the unpredictable distribution of such variants in the geographic

range of pattern class E. Therefore, a dilemma exists for all who actually use color pattern criteria (rather than sampling locality) as the basis of color pattern assignments. Abandoning pattern class C and E designations for divergent groups such as those at Sumner Lake is unnecessary. However, it is misleading to refer to the non-D lizards at Conchas Lake as representing pattern class C or to the form at Arroyo del Macho as representing pattern class E. These populations comprise individuals with variable expressions of C and E color pattern elements and do not represent syntopic assemblages of two distinct pattern classes.

Taxonomic Interpretation

Small multivariate differences and shared habitats between Sumner C and Sumner D suggest that these pattern classes represent the same biological entity. This is also true for Conchas C-E and Conchas D, with the color patterns at each locality reflecting ancestral (C and C-E) and derived (D) states. Therefore, New Mexico D is polyphyletic, having originated at least twice from different individuals in pattern classes C and C-E. Giving formal recognition to either group of New Mexico D is unwarranted.

It is also apparent that the same species is represented by the three clones of pattern class C-E from the Conchas Lake vicinity. Although Conchas 1C-E, 6C-E, and 8C-E are genotypically and meristically distinctive, all three express the same color pattern variation, an example of the mosaicism expected in clonal divergence. The three clones also appear to be ecologically equivalent based on sampling conducted (June 6–June 9, 2000) in one roadside habitat. The sample contained 27 individuals exceeding 66 mm SVL, a size used in this study to exclude incompletely developed color pattern characters from the statistical analyses. Of the 27 specimens, 11 had been classified to 1C-E, 10 to 6C-E, and 6 to 8C-E. Sampling variation can account for these numerical differences (Chi-square = 1.556; $P = 0.46$), indicating an absence of ecological segregation in this mesquite-dominated habitat.

Among the groups studied, the most compelling case for postformational speciation involves pattern classes C and E at Sumner Lake State Park. Besides color pattern differences, they are significantly different in meristic characters, mean body size (SVL) of reproductively mature individuals, and life-history characteristics. Sumner C and Sumner E occur at equivalent densities although Sumner C is larger than Sumner E and produces larger clutches. Compensation is apparently achieved by certain individuals of Sumner E beginning reproduction in their second year, with Sumner C delaying reproduction to year three (Taylor et al., 1997, 2000). Sumner Lake State Park is of considerable interest as a natural experiment because it represents an area where pattern classes E and C reach their northern and southern range limits, respectively. Do Sumner C and Sumner E reflect a postformational speciation event, with independent trajectories established by the separation of a tokogenetic clone vector (Wiley and Mayden, 2000) or tokogenetic array (Frost and Hillis, 1990) into two such entities? If so, a taxonomic decision regarding pattern class C is moot. The name *A. tesselata* is associated, through the selection of a neotype by Walker et al. (1997a), with Colorado D from Higbee. Therefore, unless Colorado D can be shown to represent a different biological entity (Walker et al., 1997b), pattern class C will continue to share the name *A. tesselata* with its Colorado D derivative.

Groups such as Conchas C-E and Macho E-C demonstrate the discordance of color pattern features and geographic range boundaries between entities traditionally regarded as pattern classes C and E. These two groups exemplify the challenges that mosaic patterns of genetic and phenotypic variation impose on the range-wide utility of color pattern classes and on the formal taxonomic recognition of pattern class ''E'' and its variants. The alternative to taxonomic restructuring is not without merit—a perspective of *A. tesselata* as a single species, conceptually important for demonstrating the effectiveness of a generalized genotype (Taylor et al., 2001), and subsequent random mutations, to meet evolutionary challenges in a parthenogenetic entity of recent origin.

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REFERENCES

Abuhteba, R.M., J.M. Walker, and J.E. Cordes. 2000. Genetic homogeneity based on skin histocompatibility and the evolution and systematics of parthenogenetic *Cnemidophorus laredoensis* (Sauria: Teiidae). Canadian Journal of Zoology 78: 895–904.

Brown, T.L. 1980. Now you see it, now you don't: herping at Los Esteros Reservoir. New Mexico Herpetological Society Newsletter 17(3): 1.

Cole, C.J. 1979. Chromosome inheritance in parthenogenetic lizards and evolution of allopolyploidy in reptiles. Journal of Heredity 70: 95–102.

Cordes, J.E., and J.M. Walker. 2003. Skin histocompatibility between syntopic pattern classes C and D of parthenogenetic *Cnemidophorus tesselatus* in New Mexico. Journal of Herpetology 37: 185–188.

Cuellar, O. 1976. Intraclonal histocompatibility in a parthenogenetic lizard: evidence of genetic homogeneity. Science 193: 150–153.

Cuellar, O. 1977a. Animal parthenogenesis: a new evolutionary–ecological model is needed. Science 197: 837–843.

Cuellar, O. 1977b. Genetic homogeneity and speciation in the parthenogenetic lizards *Cnemidophorus velox* and *C. neomexicanus*: evidence from intraspecific histocompatibility. Evolution 31: 24–31.

Cuellar, O. 1979. On the ecology of coexistence in parthenogenetic and bisexual lizards of the genus *Cnemidophorus*. American Zoologist 19: 773–786.

Cuellar, O., and C. Smart. 1977. Analysis of histoincompatibility in a natural population of the bisexual whiptail lizard *Cnemidophorus tigris*. Transplantation 24: 127–133.

Cuellar, O., and C. Smart. 1979. On the genetics of transplantation in the lizard *Cnemidophorus tigris*. Immunogenetics 8: 109–118.

Degenhardt, W.G., C.W. Painter, and A.H. Price. 1996. Amphibians and reptiles of New Mexico. Albuquerque, NM: University of New Mexico Press.

Densmore, III, L.D., J.W. Wright, and W.M. Brown. 1989. Mitochondrial-DNA analyses and the origin and relative age of parthenogenetic lizards (genus *Cnemidophorus*). II. *C. neomexicanus* and the *C. tesselatus* complex. Evolution 43: 943–957.

de Queiroz, K. 1998. The general lineage concept

of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendation. *In* D.J. Howard and S.H. Berlocher (editors), Endless forms: species and speciation: 57–75. Oxford, England: Oxford University Press.

de Queiroz, K., and D.A. Good. 1997. Phenetic clustering in biology: a critique. The Quarterly Review of Biology 72: 3–30.

Dessauer, H.C., and C.J. Cole. 1986. Clonal inheritance in parthenogenetic whiptail lizards: biochemical evidence. Journal of Heredity 77: 8–12.

Dessauer, H.C., and C.J. Cole. 1989. Diversity between and within nominal forms of unisexual teiid lizards. *In* R.M. Dawley and J.P. Bogart (editors), Evolution and ecology of unisexual vertebrates: 49–71. Albany, NY: New York State Museum Bulletin 466.

Dessauer, H.C., C.J. Cole, and C.R. Townsend. 2000. Hybridization among western whiptail lizards (*Cnemidophorus tigris*) in southwestern New Mexico: population genetics, morphology, and ecology in three contact zones. Bulletin American Museum Natural History 246: 1–148.

Dessauer, H.C., T.W. Reeder, C.J. Cole, and A. Knight. 1996. Rapid screening of DNA diversity using dot-blot technology and allele-specific oligonucleotides: maternity of hybrids and unisexual clones of hybrid origin (lizards, *Cnemidophorus*). Molecular Phylogenetics and Evolution 6: 366–372.

Dixon, J.R. 2000. Amphibians and reptiles of Texas, 2nd ed. College Station, TX: Texas A&M University Press.

Echelle, A.A. 1990. Nomenclature and non-Mendelian (''clonal'') vertebrates. Systematic Zoology 39: 70–78.

Frost, D.R., and D.M. Hillis. 1990. Species in concept and practice: herpetological applications. Herpetologica 46: 87–104.

Gebhardt, B.M. 1996. The major histocompatibility complex and transplantation. *In* W.A. Volk, B.M. Gebhardt, M.-L. Hammarskjold, and R.J. Kadner (editors), Essentials of medical microbiology, 5th ed.: 121–135. Philadelphia, PA: Lippincott–Raven.

Hammerson, G.A. 1999. Amphibians and reptiles in Colorado, 2nd ed. Niwot, CO: University Press of Colorado.

Harris, H., and D.A. Hopkinson. 1976. Handbook of enzyme electrophoresis in human genetics. Amsterdam: North-Holland.

Hernandez-Gallegos, O., N. Manriquez-Moran, F.R. Mendez, M. Villagran, and O. Cuellar. 1998. Histocompatibility in parthenogenetic lizards of the *Cnemidophorus cozumela* complex from the Yucatan Peninsula of Mexico. Biogeographica 74: 117–124.

Hillis, D.M., C. Moritz, C.A. Porter, and R.J. Baker. 1991. Evidence for biased gene conversion in concerted evolution of ribosomal DNA. Science 251: 308–310.

Manríquez-Morán, N.L., M. Villagrán-Santa Cruz, and F.R. Méndez-de la Cruz. 2000. Origin and evolution of the parthenogenetic lizards, *Cnemidophorus maslini* and *C. cozumela*. Journal of Herpetology 34: 634–637.

Maslin, T.P. 1967. Skin grafting in the bisexual teiid lizard *Cnemidophorus sexlineatus* and in the unisexual *C. tesselatus*. Journal of Experimental Zoology 166: 137–150.

Murphy, R.W., J.W. Sites, Jr., D.G. Buth, and C.H. Haufler. 1996. Proteins: isozyme electrophoresis. *In* D.M. Hillis, C. Moritz, and B.K. Mable (editors), Molecular systematics, 2nd ed.: 51–120. Sunderland, MA: Sinauer.

Neaves, W.B. 1969. Adenosine deaminase phenotypes among sexual and parthenogenetic lizards in the genus *Cnemidophorus* (Teiidae). Journal of Experimental Zoology 171: 175–183.

Parker, E.D., Jr. 1979. Phenotypic consequences of parthenogenesis in *Cnemidophorus* lizards. I. Variability in parthenogenetic and sexual populations. Evolution 33: 1150–1166.

Parker, E.D., Jr., and R.K. Selander. 1976. The organization of genetic diversity in the parthenogenetic lizard *Cnemidophorus tesselatus*. Genetics 84: 791–805.

Parker, E.D., Jr., J.M. Walker, and M.A. Paulissen. 1989. Clonal diversity in *Cnemidophorus*: ecological and morphological consequences. *In* R. Dawley and J.P. Bogart (editors), Evolution and ecology of unisexual vertebrates: 72–86. Albany, NY: New York State Museum Bulletin 466.

Price, A.H. 1992. Comparative behavior in lizards of the genus *Cnemidophorus* (Teiidae), with comments on the evolution of parthenogenesis in reptiles. Copeia 1992: 323–331.

Price, A.H., J.L. LaPointe, and J.W. Atmar. 1993. The ecology and evolutionary implications of competition and parthenogenesis in *Cnemidophorus*. *In* J.W. Wright and L.J. Vitt (editors), Biology of whiptail lizards (genus *Cnemidophorus*): 371–410. Norman, OK: Oklahoma Museum of Natural History.

Reeder, T.W., C.J. Cole, and H.C. Dessauer. 2002. Phylogenetic relationships of whiptail lizards of the genus *Cnemidophorus* (Squamata: Teiidae): a test of monophyly, reevaluation of karyotypic evolution, and review of hybrid origins. American Museum Novitates 3365: 1–61.

Sattath, S., and A. Tversky. 1977. Additive similarity trees. Psychometrika 42: 319–345.

Schmitz, A., M. Vences, S. Weitkus, T. Ziegler, and W. Böhme. 2001. Recent maternal divergence of the parthenogenetic lizard *Leiolepis guentherpetersi* from *L. guttata*: molecular evidence (Reptilia: Squamata: Agamidae). Zoologische Abhandlungen Staatliches Museum für Tierkunde Dresden 51: 355–360.

Scudday, J.F. 1973. A new species of lizard of the *Cnemidophorus tesselatus* group from Texas. Journal of Herpetology 7: 363–371.

Scudday, J.F., and J.R. Dixon. 1973. Diet and feeding behavior of teiid lizards from Trans-Pecos, Texas. Southwestern Naturalist 18: 279–289.

Taylor, H.L., and C.R. Cooley. 1995a. A multivariate analysis of morphological variation among parthenogenetic teiid lizards of the *Cnemidophorus cozumela* complex. Herpetologica 51: 67–76.

Taylor, H.L., and C.R. Cooley. 1995b. Patterns of meristic variation among parthenogenetic teiid lizards (genus *Cnemidophorus*) of the Yucatán Peninsula and their progenitor species, *C. angusticeps* and *C. deppei*. Journal of Herpetology 29: 583–592.

Taylor, H.L., J.M. Walker, and J.E. Cordes. 1996. Systematic implications of morphologically distinct populations of parthenogenetic whiptail lizards: *Cnemidophorus tesselatus* pattern class D. Herpetologica 52: 254–262.

Taylor, H.L., J.M. Walker, and J.E. Cordes. 1997. Reproductive characteristics and body size in the parthenogenetic teiid lizard *Cnemidophorus tesselatus*: comparison of sympatric color pattern classes C and E in De Baca County, New Mexico. Copeia 1997: 863–868.

Taylor, H.L., J.M. Walker, and J.E. Cordes. 2000. Ecological patterns of body-size and clutch-size variation in the parthenogenetic teiid lizard *Cnemidophorus tesselatus*. Herpetologica 56: 45–54.

Taylor, H.L., C.J. Cole, L.M. Hardy, H.C. Dessauer, C.R. Townsend, J.M. Walker, and J.E. Cordes. 2001. Natural hybridization between the teiid lizards *Cnemidophorus tesselatus* (parthenogenetic) and *C. tigris marmoratus* (bisexual): assessment of evolutionary alternatives. American Museum Novitates 3345: 1–64.

Walker, J.M., H.L. Taylor, and J.E. Cordes. 1995. Parthenogenetic *Cnemidophorus tesselatus* complex at Higbee, Colorado: resolution of 30 years of controversy. Copeia 1995: 650–658.

Walker, J.M., J.E. Cordes, and H.L. Taylor. 1997a. Parthenogenetic *Cnemidophorus tesselatus* complex (Sauria: Teiidae): a neotype for diploid *C. tesselatus* (Say, 1823), redescription of the taxon, and description of a new triploid species. Herpetologica 53: 233–259.

Walker, J.M., H.L. Taylor, J.E. Cordes, and M.A. Paulissen. 1997b [1998]. Distributional relationships and community assemblages of three members of the parthenogenetic *Cnemidophorus tesselatus* complex and *C. sexlineatus* (Squamata: Teiidae) at Higbee, Otero County, Colorado. Herpetological Natural History 5: 165–174.

Webb, R.G. 1970. Reptiles of Oklahoma. Norman, OK: University of Oklahoma Press.

Wiley, E.O., and R.L. Mayden. 2000. The evolutionary species concept. *In* Q.D. Wheeler and R. Meier (editors), Species concepts and phylogenetic theory: a debate: 70–89. New York, NY: Columbia University Press.

Wilkinson, L., G. Blank, and C. Gruber. 1996. Desktop data analysis with SYSTAT. Upper Saddle River, NJ: Prentice Hall.

Wright, J.W., and C.H. Lowe. 1967. Hybridization in nature between parthenogenetic and bisexual species of whiptail lizards (genus *Cnemidophorus*). American Museum Novitates 2286: 1–36.

Zweifel, R.G. 1965. Variation in and distribution of the unisexual lizard, *Cnemidophorus tesselatus*. American Museum Novitates 2235: 1–49.

APPENDIX 1

Specimens Examined

Specimens are referred to by their individual catalog numbers and initials of their repositories as follows: AMNH (American Museum of Natural History), UADZ (University of Arkansas Department of Zoology [EDP = specimens collected by E.D. Parker, Jr.; GM = UADZ specimens collected by Glenn J. Manning]); RU (Regis University Department of Biology). Individuals classified by CVA to morphological subgroup of pattern class C-E are identified by designations 1C-E, 6C-E, and 8C-E and individuals karyotyped for this paper with (k). Specimens lacking subgroup designations did not meet the minimum SVL criterion for inclusion in the CVA used to assign individuals to subgroup.

Aspidoscelis tesselata (Pattern Class C-E) with Electrophoretic Data: New Mexico, San Miguel County, around picnic tables south of Conchas Dam: clone IC-E: UADZ 5418, 5419, 5421–5423 (= EDP 836, 837, 839–841); clone

VIC-E: UADZ 5415–5417, 5426, 5427 (= EDP 830, 831, 834, 845, 849); clone VIIIC-E: UADZ 5420, 5424, 5425, 5428 (= EDP 838, 842 [842 was identified as a pattern class D in Parker and Selander, 1976; Parker, 1979; and Parker et al., 1989], 844, 850. Conchas Lake at South State Park campground: clone VIC-E and sACOH (bc), MPI (ab): AMNH R-136875, R-136878 (k); clone IC-E and sACOH (bc), MPI (ac): AMNH R-123029, R-136877; clone IC-E and sACOH (ac), MPI (ac): AMNH R-123033 (k), R-136876, R-136879.

ASPIDOSCELIS TESSELATA (PATTERN CLASS C-E), LAB HATCHLINGS WITH ELECTROPHORETIC DATA: AMNH R-123026 (from egg produced by R-123025), R-123035 (from egg produced by R-123033).

ASPIDOSCELIS TESSELATA (PATTERN CLASS C-E), LAB HATCHLINGS LACKING ELECTROPHORETIC DATA: AMNH R-123027, R-123028 (from eggs produced by R-123025), R-123030–123032 (from eggs produced by R-123029), R-123034, R-123036 (from eggs produced by R-123033).

ASPIDOSCELIS TESSELATA (PATTERN CLASS C-E), SKIN TRANSPLANT SPECIMENS: New Mexico, San Miguel County, 3 km south of Conchas Dam or east of south end of levee, along east side Hwy 129 (Hwy 433): morphological subgroup 6C-E: UADZ 3243, 3449; morphological subgroup 1C-E: UADZ 3237, 3241, 3444; morphological subgroup 8C-E: UADZ 3240, 3246, 3247, 3448.

ASPIDOSCELIS TESSELATA (PATTERN CLASS C–E) LACKING ELECTROPHORETIC DATA: New Mexico, San Miguel County. Along Army Corps of Engineer road east of and paralleling Hwy 433 (the entrance road to Conchas Lake State Park), approximately 1 km from the junction of this road and Hwy 433 (east of the entrance to Central Recreation Area): RU 0001 (8C-E), 0002 (6C-E), 0003 (6C-E), 0008 (8C-E), 0009 (6C-E), 0010 (8C-E), 0011 (1C-E), 0012 (6C-E), 0013 (1C-E), 0014 (1C-E), 0015 (6C-E), 0016, 0017 (8C-E), 0018 (1C-E), 0019 (6C-E), 0020 (1C-E), 0021 (1C-E), 0022 (1C-E), 0027 (8C-E), 0028 (1C-E), 0029 (6C-E), 0030 (1C-E), 0031 (6C-E), 0032 (6C-E), 0033 (8C-E), 0037, 0038 (6C-E), 0039 (1C-E), 0040 (6C-E), 0041 (1C-E). North side Canadian River, 200–300 m below dam: GM 110 (1C-E), 111 (1C-E), 112 (1C-E); south side Canadian River, near one-way road into park, below dam: GM 113, 114; south side Canadian River, plateau above river: GM 116 (8C-E); south side Canadian River, parking lot below dam: GM 119, 120 (1C-E); south side of Canadian River, South Recreation Area: GM 129; Central Recreation Area fronting lake: GM 136 (6C-E), 137 (1C-E), 138, 139; north side Canadian River, north of Park Office and North Recreation Area near Boy Scout camp: GM 142, 143 (1C-E), 145 (1C-E), 146 (1C-E); north side of Canadian River, near (below) North Recreation Area: GM 147; north side of Canadian River, near (above) North Recreation Area: GM 152 (1C-E). Conchas Lake at South State Park campground: EDP UADZ 843 (1C-E), 844 (1C-E), 848; UADZ 3214, 3215 (1C-E), 3217, 3218 (1C-E), 3219 (6C-E), 3220 (6C-E), 3221, 3222 (1C-E), 3223 (8C-E), 3224 (1C-E), 3226 1C-E), 3227 (6C-E), 3229, 3231 (6C-E), 3232 (1C-E), 3233 (1C-E), 3234 (1C-E), 3236, 3239 (1C-E), 3245 (8C-E), 3432 (8C-E), 3433, 3434 (1C-E), 3435 (6C-E), 3437, 3438 (1C-E), 3439 (1C-E), 3442, 3443 (1C-E), 3744 (1C-E), 3745 (1C-E), 3746 (1C-E), 3747 (1C-E), 3748 (1C-E), 3749 (1C-E), 4158 (1C-E), 4159 (1C-E), 4160, 4161, 4162 (1C-E), 4163–4167, 4168 (1C-E), 4169 (1C-E), 4170 (1C-E). South State Park campground: AMNH R-119545 (8C-E), R-123025 (6C-E; k), R-123050 (6C-E), R-123051 (8C-E; k).

ASPIDOSCELIS TESSELATA (PATTERN CLASS C) LACKING ELECTROPHORETIC DATA: New Mexico, De Baca County, Sumner Lake State Park, Westside Campground area: RU 9507, 9651; terrace on west side Pecos River via road south of Hwy 203 to West River Picnic area, then on flats north of unimproved road providing access to area to the west: RU 9735; east side of Pecos River and Sumner Lake from arroyo on south side of Hwy 203 (southwest of the road to Eastside Campground), then 5.0 km north of Hwy 203 along road to Eastside Campground and continuing east and north to primitive area: RU 9518, 9521, 9533–9537, 9539–9541, 9602–9604, 9608–9611, 9614, 9615, 9626, 9627, 9629, 9630, 9633, 9637, 9638, 9640–9642, 9647, 9709–9712, 9725–9729, 9737–9740, 9745, 9746.

ASPIDOSCELIS TESSELATA (PATTERN CLASS D) WITH ELECTROPHORETIC DATA: New Mexico, San Miguel County, Conchas Lake State Park, around picnic tables south of Conchas Dam: clone ID: UADZ 5404–5414 (= EDP 826–829, 832, 833, 835 [835 was identified as a pattern class C in Parker and Selander, 1976 and Parker, 1979], 843, 846–848). Conchas Lake at South State Park campground: clone sACOH (bc), MPI (ac): AMNH R-123042, R-136880.

ASPIDOSCELIS TESSELATA (PATTERN CLASS D), LAB HATCHLINGS WITH ELECTROPHORETIC DATA: AMNH R-123038 (from egg produced by R-123037) R-123043, R-123044 (from eggs produced by R-123042).

ASPIDOSCELIS TESSELATA (PATTERN CLASS D), LAB HATCHLINGS LACKING ELECTROPHORETIC DATA: AMNH R-123039–R123041 (from eggs produced by R-123037); AMNH R-123045, R-123046 (from eggs produced by R-123042).

ASPIDOSCELIS TESSELATA (PATTERN CLASS D), SKIN TRANSPLANT SPECIMENS: New Mexico, San Miguel County, 3 km south of Conchas Dam or east of south end of levee, along east side of Hwy 129 (Hwy 433): UADZ 3238, 3242, 3244, 3450.

ASPIDOSCELIS TESSELATA (PATTERN CLASS D) LACKING ELECTROPHORETIC DATA: New Mexico, San Miguel County. Along Army Corps of Engineer road east of and paralleling Hwy 433 (the entrance road to Conchas Lake State Park), approximately 1 km from the junction of this road and Hwy 433 (east of the entrance to Central Recreation Area): RU 0004–0007, 0023–0026, 0034–0036, 0042–0046. South side of Canadian River, 200–300 m below spillway, very close to river: GM 121, 122, 141. South of Canadian River Central Recreation Area of park, fronting lake: GM 134. South State Park campground: AMNH R-114236 (k), R-114237 (k), R-119546, R-123037 (k), R-123042, R-123047–123049, R-123052. New Mexico, De Baca County, Sumner Lake State Park, east side of Pecos River and Sumner Lake from arroyo on south side of Hwy 203 (southwest of the road to Eastside Campground), then 5.0 km north of Hwy 203 along road to Eastside Campground and continuing east and north to primitive area: RU 9517, 9612, 9632, 9741; terrace on west side Pecos River via road south of Hwy 203 to West River Picnic area, then on flats north of unimproved road providing access to area to the west: UADZ 5744.

ASPIDOSCELIS TESSELATA (PATTERN CLASS E) WITH ELECTROPHORETIC DATA: New Mexico, De Baca County, Fort Sumner city dump: EDP 309–319. New Mexico, Chaves County, Roswell city dump: EDP 631–640.

ASPIDOSCELIS TESSELATA (PATTERN CLASS E) LACKING ELECTROPHORETIC DATA: New Mexico, De Baca County. Sumner Lake State Park, Westside Campground area: RU 9508–9516, 9519, 9520, 9616; terrace on west side Pecos River via road south of Hwy 203 to West River Picnic area, then on flats north of unimproved road providing access to area to the west: RU 9605, 9736; east side of Pecos River and Sumner Lake from arroyo on south side of Hwy 203 (southwest of the road to Eastside Campground), then 5.0 km north of Hwy 203 along road to Eastside Campground and continuing east and north to primitive area: RU 9522, 9523, 9538, 9542, 9543, 9601, 9605, 9613, 9625, 9628, 9631, 9634, 9635, 9639, 9643–9646, 9648, 9713–9716, 9730–9732, 9742–9744, 9747–9750. Fort Sumner, east end of Hwy 60–84 bypass at base of elevated railroad grade and in adjacent mesquite assemblage: UADZ 5688–5690, 5699. Fort Sumner, at Hwy 60–84 bypass, in mesquite at entrance to city dump (Parker and Selander [1976] collecting site): UADZ 6308. New Mexico, Guadalupe County, south along sandy road, southeastern edge of Puerto de Luna: RU 0048–0073.

ASPIDOSCELIS TESSELATA (PATTERN CLASS E-C) WITH ELECTROPHORETIC DATA: New Mexico, Chaves County, north side Arroyo del Macho, 22 km north on Hwy 285 from junction with Hwy 70 north of Roswell, New Mexico, then 0.8 km east on Eden Valley Road: AMNH R-145142–145144, 146629, 146630 (laboratory hatchling; offspring of either AMNH R-146629 or 146631), 146631–146633, 146636, 146638, 146639.

ASPIDOSCELIS TESSELATA (PATTERN CLASS E-C) LACKING ELECTROPHORETIC DATA: New Mexico, Chaves County, north side Arroyo del Macho, 22 km north on Hwy 285 from junction with Hwy 70 north of Roswell, New Mexico, then 0.8 km east on Eden Valley Road: AMNH R-146612–146628, R-146634, R-146635, R-146637, R-146640–146649, R-147547.

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