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Comparative Meristic Variability in Whiptail Lizards (Teiidae, *Aspidoscelis*): Samples of Parthenogenetic *A. tesselata* Versus Samples of Sexually Reproducing *A. sexlineata*, *A. marmorata*, and *A. gularis septemvittata*

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ABSTRACT

Is it correct, as is often assumed, that the clonal form of inheritance in parthenogenetic lizards results in less variability than occurs with genetic recombination in their sexually reproducing (gonochoristic) relatives? We tested this hypothesis by comparing morphological variability in samples of parthenogenetic *Aspidoscelis tesselata* and several gonochoristic species of whiptail lizards. To control for environmental factors that might differentially affect embryonic development of morphological characters, we compared samples obtained from the same or geographically adjacent localities. In addition, we compared apparently "uniclonal" and multiclonal samples from each of two color-pattern classes (C and E) of *A. tesselata*.

For univariate meristic characters, parthenogenetic *A. tesselata* matched the variability of a sympatric gonochoristic species in 11 of 20 comparisons, had lower variability in six comparisons, and was more variable in three. For multivariate characters derived from principal components analyses (PCA), the relative meristic variability of samples of *A. tesselata* could not

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be predicted by its reproductive mode, color-pattern class, apparent "uniclonal" or multiclonal state, or geographic location.

In addition, we compared *A. tesselata*, *A. sexlineata*, *A. marmorata*, and *A. gularis septemvittata* in a single PCA, with the latter two species representing the two ancestral taxa from which *A. tesselata* was derived through hybridization. Once again, relative variability of *A. tesselata* was not always predictable based on its reproductive mode. It had greater variability than *A. sexlineata*, equivalent variability with *A. gularis septemvittata*, and less variability than *A. marmorata*.

DEDICATION

It is with great pleasure that we dedicate this work to two North American herpetologists who were pioneers in recognizing that some species of whiptail lizards are unisexual, which challenged everything they had learned about reproduction of tetrapods. These two scientists were also among the first to provide comparative analyses of variation involving *Aspidoscelis tesselata*, wondering whether it would have less variation than gonochoristic species. One was T. Paul Maslin (deceased), University of Colorado, in whose memory we make this dedication, and the other is Richard G. Zweifel, American Museum of Natural History, who is retired and living in Portal, Arizona.

Zweifel, on October 10, 1958, wrote to colleagues and announced that I.S. Darevsky (1958) had reported probable parthenogenesis in some Armenian lacertid lizards, indicating that this might explain samples of whiptail lizards from North America that lacked males (Lowe, 1993). Later, in Duellman and Zweifel (1962), Zweifel reported that several species of *Aspidoscelis* are all-female species, and they might be parthenogenetic; however, at that time, Duellman did not believe the material on all-female populations that Zweifel put in their paper (personal communication from Duellman to C.J.C.). In addition, Zweifel (1965) analyzed comparative morphological variation in lizards, including *A. tesselata*, to see if samples were less variable than samples of gonochoristic species. We know that study had been underway since the late 1950s, because Zweifel took C.J.C. as an undergraduate student assistant to one of his New Mexico study sites in 1960 while discussing emerging thoughts about parthenogenesis in whiptail lizards.

Maslin (1962) first reported that some species of *Aspidoscelis*, including *A. tesselata*, are all-female species. He then used skin grafting experiments to test whether individuals might be genetically identical (Maslin, 1967), and contributed a seminal position paper on taxonomic problems in parthenogenetic vertebrates, in which he also discussed relative variability and reproductive mode (Maslin, 1968).

INTRODUCTION

A fundamental problem in vertebrate biology is how sexual and parthenogenetic modes of reproduction can each maintain ecologically successful species in nature (White, 1973), as seen in lizards of the genus *Aspidoscelis*. With genetic recombination present in the former and absent in the latter, among clonal lizards (Cuellar, 1971; Lutes et al., 2010), one would expect fundamental differences in evolution of genetically based phenotypic variation. In clonal forms, evolution would be based only on natural selection acting on mutation products, whereas both

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mutation and genetic recombination in gonochoristic forms should produce considerably more genetic and phenotypic variation for exposure to natural selection. The word *bisexual* has often been used to refer to sexually reproducing species, but it has also been widely used to signify hermaphrodites. Therefore, we use the term *gonochoristic* to refer to sexually reproducing species (Tomlinson, 1968).

We used pattern classes C and E of *Aspidoscelis tesselata* (Zweifel, 1965; Walker et al., 1997; Cordes and Walker, 2006) as our parthenogenetic comparators because they include tokogenetic arrays that illustrate evolutionary changes in meristic characters and life history characteristics of clonal lizards (Taylor et al., 2003, 2005). The term *tokogenetic array* (or simply *array*) is used sensu Frost and Hillis (1990) to refer to the pattern of mother-daughter relationships in parthenogenetic lizards. Our samples of *A. tesselata* represent arrays that have genotypic information known from electrophoretic analyses of protein phenotypes. Rationale for selection of gonochoristic species and samples to provide a "common garden" approach for the statistical comparisons is explained in Materials and Methods.

The application of statistics to meristic variation in *Aspidoscelis* was introduced as a tool for resolving species boundaries among members of a sympatric assemblage of five species in New Mexico (Lowe and Zweifel, 1952; Lowe, 1993). It is of historical interest that three of those five species were not recognized as parthenogenetic at the time, i.e., parthenogenesis was not suggested by external morphology. One of those parthenogens was *A. tesselata*, the first teiid lizard suspected of being unisexual (Minton, 1958 [1959]; Maslin, 1962; Duellman and Zweifel, 1962) and one of two parthenogenetic lizards whose meristic variability was initially compared to a gonochoristic congener (Taylor, 1965; Zweifel, 1965).

Aspidoscelis tesselata originated from a hybridization event between a female of *A. marmorata* and a male of *A. gularis septemvittata* (Neaves, 1969; Parker and Selander, 1976; Brown and Wright, 1979; Dessauer and Cole, 1989; Dessauer et al., 1996). Current evidence suggests that there was a single origin (Maslin, 1967; Taylor et al., 1997, 2005; Cordes and Walker, 2003, 2006), and there is a clonal mode of inheritance (Dessauer and Cole, 1986; Taylor et al., 2003). With these possibilities in mind, early initiatives to elucidate relative phenotypic variability between parthenogenetic and gonochoristic congeners were followed by three comprehensive investigations of genotypic and phenotypic variation in *A. tesselata, A. marmorata*, and *A. gularis septemvittata* (Parker and Selander, 1976; Parker, 1979a, 1979b). In Parker (1979a), color-pattern classes (sensu Zweifel, 1965) and genotypic variation (Parker and Selander, 1976) were used to classify *A. tesselata* into uniclonal or multiclonal categories for comparisons of phenotypic variability with gonochoristic *A. tigris* (including *A. marmorata* sensu Hendricks and Dixon, 1986). As hypothesized by Parker (1979a), meristic variability increased through the sequence: uniclonal *A. tesselata* < multiclonal *A. tesselata* < *A. tigris*.

When Parker's studies were conducted, the name *A. tesselata* was used for both diploid and triploid entities, the latter containing an *A. sexlineata* genome from its *A. tesselata* × *A. sexlineata* origin (Neaves, 1969; Neaves and Gerald, 1969; Parker and Selander, 1976; Dessauer and Cole, 1989). As a consequence of that taxonomy, inclusion of triploid individuals in the sample of "multiclonal" *A. tesselata* from Higbee, Colorado (Parker, 1979a; Walker et al., 1995), inflated

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meristic variability of Parker's multiclonal category (Taylor, personal obs.). It was not until triploid entities were removed from *A. tesselata* and described as *A. neotesselata* that the name *A. tesselata* was reconciled with evolutionary history (Walker et al., 1997).

In the present study, we used multivariate statistics to summarize phenotypic variability. Specifically, we used principal components analyses to describe patterns of meristic variability in *A. tesselata*, as presently understood: (1) among "uniclonal" and multiclonal arrays of two color-pattern classes of *A. tesselata*, (2) between each of four geographically disjunct arrays of *A. tesselata* and a sympatric gonochoristic species, and (3) among *A. tesselata*, its progenitors, *A. marmorata* and *A. gularis septemvittata*, and *A. sexlineata*.

MATERIALS AND METHODS

Taxonomy, Pattern Classes, and Geographical Relationships

We assessed variability in meristic characters in representatives of the *sexlineata*, *tigris*, and *tesselata* species groups (Lowe et al., 1970) in the recently revived genus *Aspidoscelis* (Reeder et al., 2002) of North and Central America, using four samples of *A. tesselata* as parthenogenetic comparators. *Aspidoscelis tesselata* is distributed as disjunct arrays over an 1100 km latitudinal range from northern Chihuahua, Mexico, northward through areas in western Texas, much of New Mexico, and extreme western Oklahoma, with its northern limit in southeastern Colorado, United States. Throughout its range, three color-pattern classes (i.e., variants C, D, and E) are syntopic or sympatric with each other and/or different combinations of four gonochoristic congeners (i.e., *A. gularis*, *A. inornata*, *A. marmorata*, and *A. sexlineata*) and six hybrid-derived parthenogenetic congeners (*A. dixoni* [2n], *A. exsanguis* [3n], *A. neomexicana* [2n], *A. neotesselata* [3n], *A. uniparens* [3n], and *A. velox* [3n]). In southeastern Colorado, northeastern New Mexico, and western Oklahoma, *A. sexlineata* is the only gonochoristic species with which *A. tesselata* is syntopic. *Aspidoscelis sexlineata* is the most widely distributed member of the *A. sexlineata* species group ranging from coastal Tamaulipas, Mexico, into the United States and north to Michigan, and from the foothills of the Rocky Mountains in Colorado and the High Plains of New Mexico to the Atlantic Coast (Wright, 1993: map; Conant and Collins, 1998: map; Pérez-Ramos et al, 2010). As previously noted, this taxon, with three subspecies, is allopatric to parthenogenetic congeners except near the Rio Grande Valley of Texas, and along the western periphery of its range. For comparisons of variability between *A. tesselata* C and *A. sexlineata viridis*, which hybridized in the past and produced *A. neotesselata* in southeastern Colorado (Parker and Selander, 1976), we used samples of *A. tesselata* from the canyonlands of Otero County, Colorado, and the high plains of San Miguel County, New Mexico (appendix 1).

In northern Chihuahua, southwestern Trans-Pecos Texas, and southern New Mexico, either syntopic or parapatric associations of *A. tesselata* and its maternal progenitor *A. marmorata* can be commonly observed; however, associations of the latter and *A. sexlineata* have not been reported. The *A. tigris* species group occurs in western North America, usually at low elevations in arid and semiarid environs (Dessauer et al, 2000). Although the overall range of the group includes much of the combined areas of the Great Basin, Mohave, Sonoran, and Chihuahuan des-

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erts in Mexico and the United States, these lizards also occur in semidesert areas and on islands in the Gulf of California and eastern Pacific Ocean (Wright, 1993 map; Dessauer et al., 2000: map). Whether the name *A. tigris* should be applied as a single species (Wright, 1993, 1994) or as a complex of closely related species (Walker and Maslin, 1981; Grismer, 1999) has remained controversial, and the question is relevant to this study. *Aspidoscelis marmorata* is the sister group of other North American representatives of *A. tigris* and is relatively distantly related to these entities (Reeder et al., 2002).We use the name *A. marmorata* (sensu Hendricks and Dixon, 1986: map) rather than *A. tigris* (sensu Wright, 1994: map; Dessauer et al., 2000: map; Taylor et al., 2001). However, contra Hendricks and Dixon (1986), we did not use subspecific designations for *A. marmorata* for our samples from Chaves and Sierra counties, New Mexico, for comparisons with samples of *A. tesselata* E from the same counties (appendix 1).

A single, local site of syntopy (in Presidio County, Texas) has been reported for *A. tesselata* and its paternal progenitor *A. gularis septemvittata* (Scudday, 1973), the third and largest gonochoristic form used in our analyses. It is part of a complex of striped-spotted lizards with a vast distribution area in many states in Mexico in the central plateau south to Mexico (state), and eastern coastal lowlands south to Tamaulipas and Veracruz states, respectively, then from Jalisco to the eastern gulf coast. The name *septemvittata* remains at the center of controversy, the question being whether it be used as the name of a species (Wright, 1993, 1994; Forstner et al., 1998) or the name of a subspecies (Walker, 1981a, 1981b; Walker et al., 2001; Reeder et al., 2002). In this report, we use the name *A. gularis septemvittata* for the paternal progenitor of *A. tesselata* with a distribution encompassing parts of northern Mexico (i.e., northeastern Chihuahua and adjacent Coahuila) and the Big Bend region of Texas (i.e., mostly in Brewster and Presidio counties; Walker, 1981a, 1981b ; Walker et al., 2000, 2001). Our representative sample of *A. g. septemvittata* is from the topographically complex Chinati Mountains region of Presidio County (appendix 1), where it is occasionally found in syntopy with some combination of two gonochoristic species (i.e., *A. inornata* and *A. marmorata*) and three parthenogenetic species (i.e., *A. dixoni*, *A. exsanguis*, and at one site with *A. tesselata;* see Scudday, 1973).

Samples

For the first four of the five following geographic areas, local samples of *A. tesselata* were compared with syntopic or adjacent samples of gonochoristic congeners. Comparing samples from geographically and ecologically identical or similar environmental regimes was intended to control at least in part for the influence of the environment on embryonic development of morphological characters, aiming for a "common garden" approach. The five geographic areas sampled for our study are: **(1)** Purgatoire River Valley and associated canyonlands, Otero County, Colorado: *A. tesselata* C (pattern class C), "uniclonal" (no allelic variation found at 21 nuclear gene loci, but we use quotation marks because there could have been clonal variation at loci that were not examined: Parker and Selander, 1976)—compared to *A. sexlineata* from assorted sites in Baca, Las Animas, Otero, and Pueblo Counties, southeastern Colorado; **(2)** Arroyo del Macho, Chaves County, New Mexico: *A. tesselata* E (pattern class E), "uniclonal" (based on absence of variation at 34 nuclear gene loci; Taylor et al., 2001, 2003)—compared to *A. marmorata* from this

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locality and a nearby site; **(3)** Conchas Lake, San Miguel County, New Mexico: *A. tesselata* C, multiclonal based on variation at glucose-6-phosphate isomerase (GPI) and muscle esterase (EST2) loci as determined from independent analyses of 21 nuclear gene loci by Parker and Selander (1976) and 34 nuclear gene loci by Dessauer and Cole (Taylor et al., 2003) plus variation at aconitase hydratase (sACOH) and mannose-6-phosphate isomerase (MPI) loci discovered by Dessauer and Cole (Taylor et al., 2003)—compared to *A. sexlineata* from a nearby site; **(4)** vicinity of Engle, Sierra County, New Mexico: *A. tesselata* E, multiclonal based on variation at GPI and leucyl-alanine peptidase (PEP) loci (Parker and Selander, 1976)—compared to *A. marmorata* from the same site; and **(5)** Presidio County, Texas: *A. gularis septemvittata*, paternal progenitor of *A. tesselata*—compared to pooled samples of the other three taxa.

Individual specimens were collected as they were encountered. See appendix 1 for specific localities and specimen identities including genotypic variation.

Meristic Characters

We used five meristic characters with proven effectiveness in elucidating patterns of phenotypic variation in *Aspidoscelis*: GAB: number of granular dorsal scales in a single row around midbody; 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 included all scales in and anterior to the suture line between the third and fourth supraoculars; Maslin and Walker, 1973); FP: sum of femoral pores on both thighs; SDL: number of subdigital lamellae on the fourth toe of the right foot (unless damaged, in which case the left one was used).

Statistical Procedures

Analytical and statistical routines were performed with software from NCSS 2007 (Hintze, 2007), SPSS 17 (SPSS, 2008), and SYSTAT 13 (SYSTAT, 2011). We used principal components analysis (PCA) to determine patterns of meristic variability. PCA is a multivariate technique (McGarigal et al., 2000) that uses variance/covariance relationships among variables (e.g., GAB, FP, COS, LSG, and SDL) to produce new, uncorrelated variables (principal components) that are linear compounds of the original meristic character scores and coefficients factored to concentrate as much of the original variation as possible in the first principal component. The second principal component conserves as much of the remaining variation as possible, down through the remaining components. Although the number of components produced in a PCA equals the number of original characters factored, we selected the first two principal components for interpretation because they summarized at least 85% of the variation in each analysis.

Because all characters were measured on the same scale (discrete counts of scales and femoral pores), we used variance/covariance matrices to obtain coefficients used to compute component scores. A variance/covariance matrix retains the relative variances of original characters, so that characters with larger variances are given greater weight in developing the principal components (Neff and Marcus, 1980). Specimens are not preassigned to taxon, tokogenetic array, genotype, or reproductive category in PCA; therefore, all individuals in a PCA are treated

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as a single sample for deriving principal component scores. We coupled PC1 and PC2 scores to specific specimens, post hoc, to provide statistical and graphical information on the variability of specific samples. Statistical data (e.g., descriptive statistics in table 1) and all analyses are based only on specimens with complete data.

Variances of the five meristic characters and two multivariate characters (PC1 and PC2) did not differ significantly between the two sexes for our samples of *Aspidoscelis sexlineata*, *A. marmorata*, and *A. gularis septemvittata* (appendix 2), permitting us to pool sexes for analyses.

Although there were significant differences among sample means, variances were independent of means (GAB, $P = 0.84$; FP, $P = 0.67$; COS, $P = 0.30$; LSG, $P = 0.07$; SDL, $P = 0.27$; PC1, $P = 0.54$; PC2, $P = 0.30$). Therefore, we used untransformed data for our comparisons of variability (Sokal and Rohlf, 1981). We used a modified Levene test (Hintze, 2007; recommended by Conover et al., 1981) to determine whether character variances were significantly different between paired samples from the four sampling localities and among pooled samples of the four taxa. Most formal tests for homogeneity of sample variances are too strict because they also assess for normality (Tabachnick and Fidell, 2001). The modified Levene test is an exception and provides robust testing even with departures from normal distributions (Conover et al., 1981; Tabachnick and Fidell, 2001).

RESULTS

Univariate Comparisons of Variability

With five meristic characters and four groups for comparison, *Aspidoscelis tesselata* and sympatric gonochoristic species expressed the same level of meristic variability in 11 of the 20 univariate comparisons, and a gonochoristic species was more variable in six comparisons. *Aspidoscelis tesselata* was more variable than the gonochoristic species in only three comparisons, all involving pattern class C from the two northern localities (table 1). In one comparison, "uniclonal" *Aspidoscelis tesselata* C was more variable in COS than *A. sexlineata* from southeastern Colorado, but the same taxa from Conchas, New Mexico, had equivalent variances for COS, indicating geographical variation in variability. For the second and third comparisons, *A. tesselata* C was more variable in LSG and GAB than *A. sexlineata* from Conchas, New Mexico. This high GAB variability in Conchas *A. tesselata* has been temporally consistent, i.e., no difference between our sample ($N = 30$) collected in 2000, a sample ($N = 21$) collected in 1958 (Zweifel, 1965: table 3; $F_{20,29} = 1.859$; $P = 0.15$), and a sample of genotyped specimens ($N = 21$) collected in 1963 and 1978 (appendix 1; $F_{20,29} = 1.170$; $P = 0.69$). Although the GAB variance superficially appeared to be larger in "uniclonal" *A. tesselata* E than *A. marmorata* from Arroyo del Macho, the difference was not significant.

Comparisons of Multivariate Variability among Tokogenetic Arrays of *A. tesselata*

Only two meristic characters (GAB and LSG) contributed significantly to the principal components model, with PC1 and PC2 summarizing 86.3% of univariate variation (table 2).

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TABLE 1. Descriptive statistics of meristic characters and snout-vent length (SVL) in samples[a] of parthenogenetic *Aspidoscelis tesselata* and Three Gonochoristic Congeners: *A. sexlineata*, *A. marmorata*, and *A. gularis septemvittata.*

First line: mean ± SE; second line: SD and (range of variation). Significantly larger variances (SDs) are in **boldface**.

Locality[b] and Groups[c]	Characters[d]					
	GAB	FP	COS	LSG	SDL	SVL
Colorado						
TESS C	90.2 ± 0.40	41.2 ± 0.36	17.5 ± 0.46	37.5 ± 0.69	36.3 ± 0.18	82.8 ± 2.7
N = 31	2.2 (86–95)	2.0 (37–45)	**2.6** (13–24)	3.9 (32–49)	1.0 (34–38)	15.2 (57–106)
SEX	75.5 ± 0.97	31.5 ± 0.34	6.3 ± 0.25	18.0 ± 0.72	26.0 ± 0.25	63.9 ± 1.2
N = 31	**5.4** (65–86)	1.9 (28–35)	1.4 (4–9)	4.0 (12–25)	1.4 (23–29)	6.8 (40–74)
Conchas, NM						
TESS C	91.1 ± 1.21	41.0 ± 0.35	18.1 ± 0.31	40.1 ± 0.95	36.6 ± 0.23	81.0 ± 2.1
N = 30	**6.6** (81–104)	1.9 (37–44)	1.7 (14–21)	**5.2** (31–52)	1.3 (35–40)	11.4 (65–96)
SEX	73.4 ± 0.71	29.6 ± 0.38	7.4 ± 0.38	19.0 ± 0.62	25.8 ± 0.28	57.4 ± 1.0
N = 31	4.0 (65–83)	2.1 (26–35)	2.1 (4–12)	3.5 (14–31)	1.6 (22–28)	5.6 (48–67)
Macho, NM						
TESS E	93.6 ± 1.0	41.4 ± 0.30	18.0 ± 0.24	35.0 ± 0.77	37.0 ± 0.23	89.2 ± 1.6
N = 38	6.2 (87–109)	1.8 (37–46)	1.5 (14–20)	4.8 (23–45)	1.4 (35–42)	10.0 (59–109)
MARM	91.5 ± 0.84	45.4 ± 0.47	19.3 ± 0.66	41.8 ± 2.0	32.2 ± 0.35	78.2 ± 1.4
N = 29	4.5 (84–101)	2.5 (41–50)	**3.6** (12–28)	**10.8** (24–65)	1.9 (26–36)	7.6 (63–92)
Engle, NM						
TESS E	97.9 ± 0.43	44.4 ± 0.26	20.3 ± 0.34	35.3 ± 0.81	38.7 ± 0.23	86.2 ± 1.3
N = 30	2.3 (92–104)	1.4 (41–47)	1.9 (15–24)	4.5 (30–48)	1.3 (36–40)	6.9 (68–99)
MARM	94.0 ± 0.97	45.9 ± 0.44	24.4 ± 0.46	45.3 ± 1.6	33.0 ± 0.27	81.4 ± 1.4
N = 33	**5.5** (83–105)	**2.6** (40–51)	2.6 (18–31)	**9.3** (30–63)	1.6 (30–37)	7.9 (67–97)
Presidio, TX						
SEP	87.0 ± 0.75	37.3 ± 0.42	13.2 ± 0.30	30.1 ± 0.93	32.2 ± 0.31	89.1 ± 2.4
N = 40	4.8 (77–96)	2.7 (33–42)	1.9 (10–18)	5.9 (19–49)	1.9 (28–37)	15.4 (69–114)

[a]Samples comprise only specimens with complete data, i.e., those used in principal component analyses.

[b]Sampling localities (see appendix 1 for specifics): Colorado (southeastern Colorado); Conchas, NM (vicinity of Conchas Lake, San Miguel County, New Mexico); Macho, NM (Arroyo del Macho, Chaves County, New Mexico); Engle, NM (vicinity of Engle, Sierra County, New Mexico); Presidio, TX (Presidio County, Texas).

[c]Groups compared were TESS C (*Aspidoscelis tesselata* pattern class C), SEX (*A. sexlineata*), TESS E (*A. tesselata* pattern class E), MARM (*A. marmorata*), and SEP (*A. gularis septemvittata*). See appendix 1 for sample compositions.

[d]Characters: GAB, number of granular dorsal scales around midbody; FP, total number of femoral pores on both thighs; COS, total number of circumorbital scales; LSG, total number of lateral supraocular granules; SDL, number of subdigital lamellae on fourth toe of one foot (right was chosen unless damaged); SVL body length (mm) from snout to vent. See Materials and Methods for details.

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The pattern of variation resolved itself as two pairs of samples, each pair having similar distributions of principal component scores (fig. 1).

Colorado *A. tesselata* C ("uniclonal") and Engle *A. tesselata* E (multiclonal) was the less variable pair of samples, and Conchas *A. tesselata* C (multiclonal) and Macho *A. tesselata* E ("uniclonal") was the more variable pair, with their 95% confidence ellipses stretched by variation in GAB and LSG (fig. 1). Equivalent variability between Conchas *A. tesselata* C and Macho *A. tesselata* E and higher variability between these two arrays and the other two was verified statistically (table 3). As noted previously, *A. tesselata* C was more variable than *A. sexlineata* for COS in Colorado, but COS was not a meaningful contributor to the pattern of meristic variation across the four samples of *A. tesselata* (table 2).

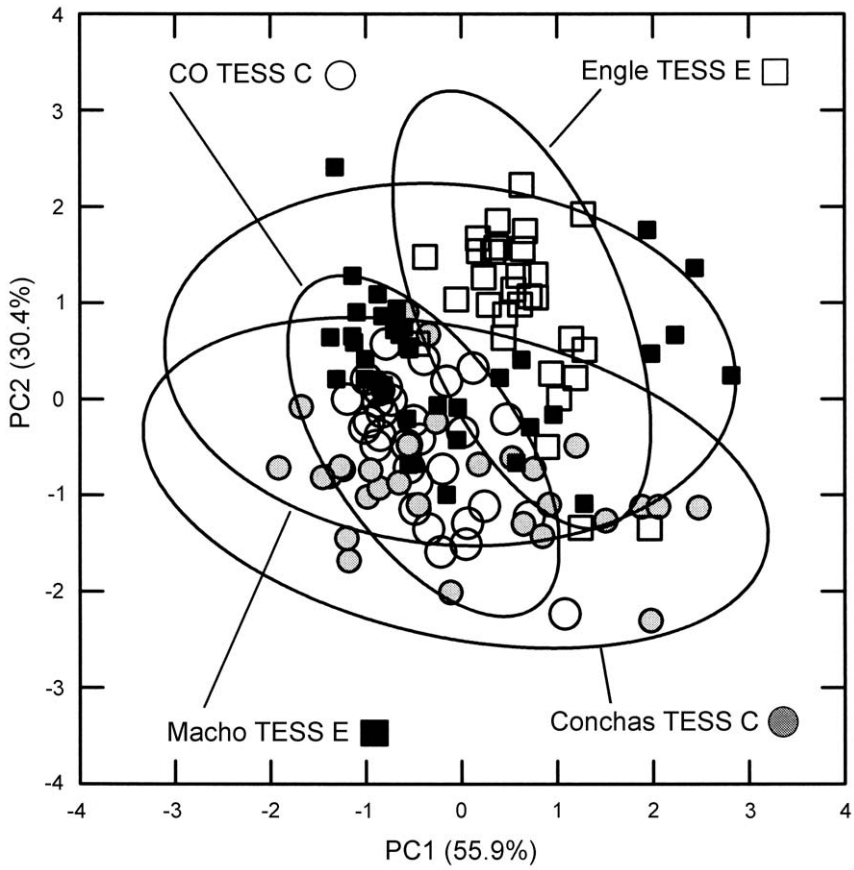

FIGURE 1. Pattern of meristic variation among four tokogenetic arrays of *Aspidoscelis tesselata* depicted by the projection of principal component scores on PC1 and PC2 axes: southeastern Colorado, $N = 31$ (○); Conchas, New Mexico, $N = 30$ (●); Engle, New Mexico, $N = 30$ (□); and Macho, New Mexico, $N = 38$ (■). Percentages represent the proportion of meristic variation summarized by each principal component, and ellipses define the 95% confidence limits for score distributions.

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TABLE 2. Loadings (correlations between meristic characters and principal components) from a principal components analysis of 129 lizards.

Species	Characters	PC1 loadings	PC2 loadings
Aspidoscelis tesselata	GAB	0.762	0.560
	FP	0.055	0.083
	COS	0.049	0.013
	LSG	0.400	-0.935
	SDL	0.023	0.058
Eigenvalues		38.4	20.9
Total meristic variation explained		55.9%	30.4%

TABLE 3. Comparisons of meristic variability (summarized by principal components) among samples of two color pattern classes of parthenogenetic *Aspidoscelis tesselata.*

Standard deviations are listed in group sequence. Groups in **boldface** have significantly greater variances (SDs).

Groups		Standard deviations			Variances different?	
Colorado C and **Conchas C**	$N = 31$ and $N = 30$	PC1	0.54	1.24	Yes	$P < 0.001$
		PC2	0.68	0.65	No	$P = 0.52$
Colorado C and Engle E	$N = 31$ and $N = 30$	PC1	0.54	0.51	No	$P = 0.68$
		PC2	0.68	0.87	No	$P = 0.50$
Colorado C and **Macho E**	$N = 31$ and $N = 38$	PC1	0.54	1.15	Yes	$P = 0.02$
		PC2	0.68	0.73	No	$P = 0.84$
Conchas C and Engle E	$N = 30$ and $N = 30$	PC1	1.24	0.51	Yes	$P < 0.001$
		PC2	0.65	0.87	No	$P = 0.24$
Conchas C and Macho E	$N = 30$ and $N = 38$	PC1	1.24	1.15	No	$P = 0.35$
		PC2	0.65	0.73	No	$P = 0.40$
Engle E and **Macho E**	$N = 30$ and $N = 38$	PC1	0.51	1.15	Yes	$P = 0.01$
		PC2	0.87	0.73	No	$P = 0.60$

The pattern of variability was as follows: ["uniclonal" Colorado *A. tesselata* C = multiclonal Engle *A. tesselata* E] < [multiclonal Conchas *A. tesselata* C = "uniclonal" Macho *A. tesselata* E] (fig. 1). The pattern of variability demonstrated that these "uniclonal" and multiclonal categories were not helpful in explaining patterns of meristic variability, and that relative variability could not be predicted by color-pattern class.

Multivariate Comparisons of Variability between *A. tesselata* Pattern Classes C and E and Sympatric Gonochoristic Congeners

Comparisons of *A. tesselata* C and *A. sexlineata*

Representative specimens are shown in figure 2. Over 91% of the variation was summarized by PC1, with all five meristic characters making significant contributions in each of the Colorado, and Conchas, New Mexico, comparisons (table 4, note large loadings). Separation of individuals into

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TABLE 4. Loadings (correlations between meristic characters[a] and principal components) from four principal components analyses.

Groups compared	Characters	PC1 loadings	PC2 loadings
SE Colorado: *A. tesselata* C ("uniclonal")	GAB	-0.935	0.340
and *A. sexlineata*	FP	-0.936	0.009
	COS	-0.960	-0.020
	LSG	-0.972	-0.209
	SDL	-0.944	0.017
Eigenvalues		251.3	13.2
Total meristic variation explained by component		91.1%	4.8%
Conchas, NM: *A. tesselata* C (multiclonal)	GAB	-0.952	-0.293
and *A. sexlineata*	FP	-0.913	0.276
	COS	-0.932	0.269
	LSG	-0.985	0.047
	SDL	-0.938	0.230
Eigenvalues		313.3	16.5
Total meristic variation explained by component		91.7%	4.8%
Macho, NM: *A. tesselata* E ("uniclonal")	GAB	0.502	-0.852
and *A. marmorata*	FP	0.592	0.137
	COS	0.656	0.053
	LSG	0.983	0.160
	SDL	-0.122	-0.695
Eigenvalues		85.3	28.7
Total meristic variation explained by component		66.2%	22.2%
Engle, NM: *A. tesselata* E (multiclonal)	GAB	-0.059	-0.969
and *A. marmorata*	FP	0.173	0.010
	COS	0.540	0.345
	LSG	0.994	-0.082
	SDL	-0.563	-0.590
Eigenvalues		85.0	26.2
Total meristic variation explained by component		67.1%	20.7%

[a]Characters: GAB, number of granular dorsal scales around midbody; FP, total number of femoral pores on both thighs; COS, total number of circumorbital scales; LSG, total number of lateral supraocular granules; SDL, number of subdigital lamellae on fourth toe of one foot (right was chosen unless damaged). See Materials and Methods for details.

two nonoverlapping clusters (fig. 3) reflects pronounced meristic differences between *A. tesselata* and *A. sexlineata*, with little or no overlap between ranges of variation for each character (table 1).

In Colorado, variability in PC1 was essentially the same for *Aspidoscelis tesselata* C and *A. sexlineata*, but *A. sexlineata* was more variable for PC2 (table 5). Although 95% confidence ellipses differ in size (fig. 3A), the critical feature is the spread of PC1 scores projected on the

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PC1 axis, as more than 90% of the variability is explained there, and this is similar for the two species. In contrast, *A. tesselata* C from Conchas was significantly more variable than *A. sexlineata* in both PC1 and PC2 (fig. 3B; table 5).

Comparisons of *A. tesselata* E and *A. marmorata*

Representative specimens are shown in figure 4 (A–D). The pattern of variation between *A. tesselata* E and *A. marmorata* was fundamentally different than was found for *A. tesselata* C and *A. sexlineata*. The greater meristic resemblance between *A. tesselata* E and *A. marmorata* (table 1) required both PC1 and PC2 to summarize more than 85% of the original variation (table 4). This probably results from the greater amount of genetic information shared between *A. tesselata* and *A. marmorata*, its maternal progenitor species.

PC1 and PC2 summarized similar proportions of meristic variation in each pair of samples, but certain characters important to the summaries differed between them. Both LSG and COS were important contributors to PC1 for each of the Engle and Arroyo del Macho comparisons,

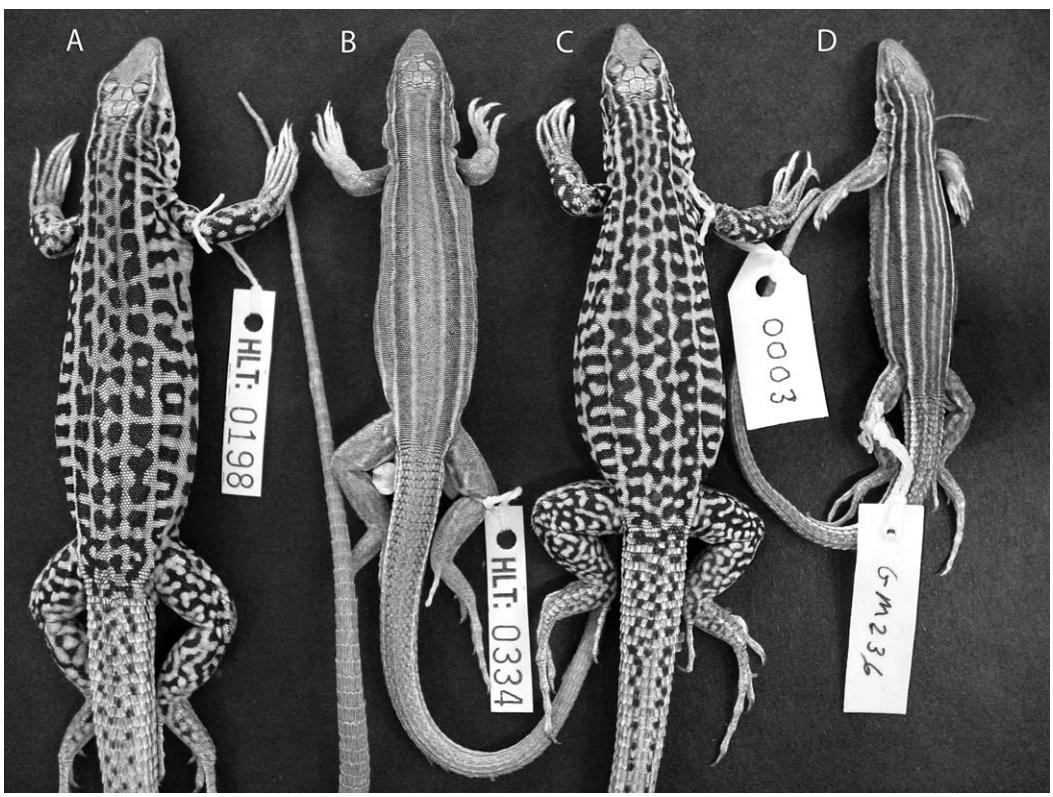

FIGURE 2. Representative specimens used in this study. Southeastern Colorado: **A**. *Aspidoscelis tesselata* C (RU 0198; 93 mm SVL); **B**. *A. sexlineata* (RU 0334; ♂, 71 mm SVL). Conchas Lake, New Mexico: **C**. *A. tesselata* C (RU 0003; 86 mm SVL); **D**. *A. sexlineata* (GM 236 [UADZ 7405]; ♀, 61 mm SVL).

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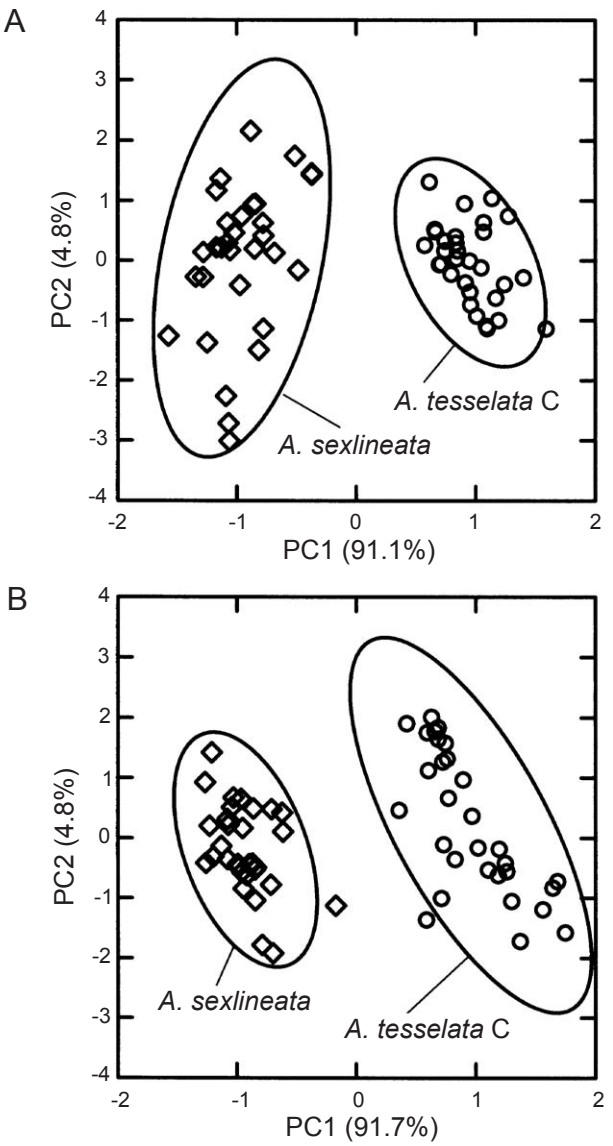

FIGURE 3. Pattern of meristic variation between parthenogenetic *Aspidoscelis tesselata* C (◯) and gonochoristic *A. sexlineata* (◊): **A**. southeastern Colorado (N = 31 for each sample); **B**. Conchas Lake, New Mexico (N = 30 and N = 31, respectively). Percentages represent the proportion of meristic variation summarized by each principal component, and ellipses define the 95% confidence limits for score distributions.

with SDL also being important for Engle and FP and GAB for Macho. PC2 summarized variation in GAB and SDL for both pairs of samples, with COS making a lesser contribution to the Engle sample (table 4).

The close meristic resemblance among individuals of *A. tesselata* and *A. marmorata* at each locality was illustrated graphically by extensive overlap of 95% confidence ellipses for PC score distributions (fig. 5). *Aspidoscelis marmorata* was more variable in PC1 at Arroyo del Macho and in both PC1 and PC2 at Engle (table 5; fig. 5).

Of the four pairs of parthenogenetic and gonochoristic samples, the Conchas pair was the only one in which *A. tesselata* was clearly more variable than its companion gonochoristic species.

Multivariate Comparisons of Variability Among *A. tesselata*, *A. sexlineata*, *A. marmorata* and *A. gularis septemvittata*

Representative specimens are shown in figures 2 and 4. All five meristic characters made important contributions to variation summarized by PC1, while SDL, GAB, and LSG also contributed to the smaller percentage of variation summarized by PC2. Because of the close genetic relationship among *A. tesselata* and its progenitor species, it took both components to summarize more than 85% of univariate variation (table 6). As gauged by 95% confidence ellipses (fig. 6), *A. tesselata* and *A. gularis septemvittata* (its paternal progenitor) were similar in meristic variability and intermediate to the lower variability of *A. sexlineata* and higher vari-

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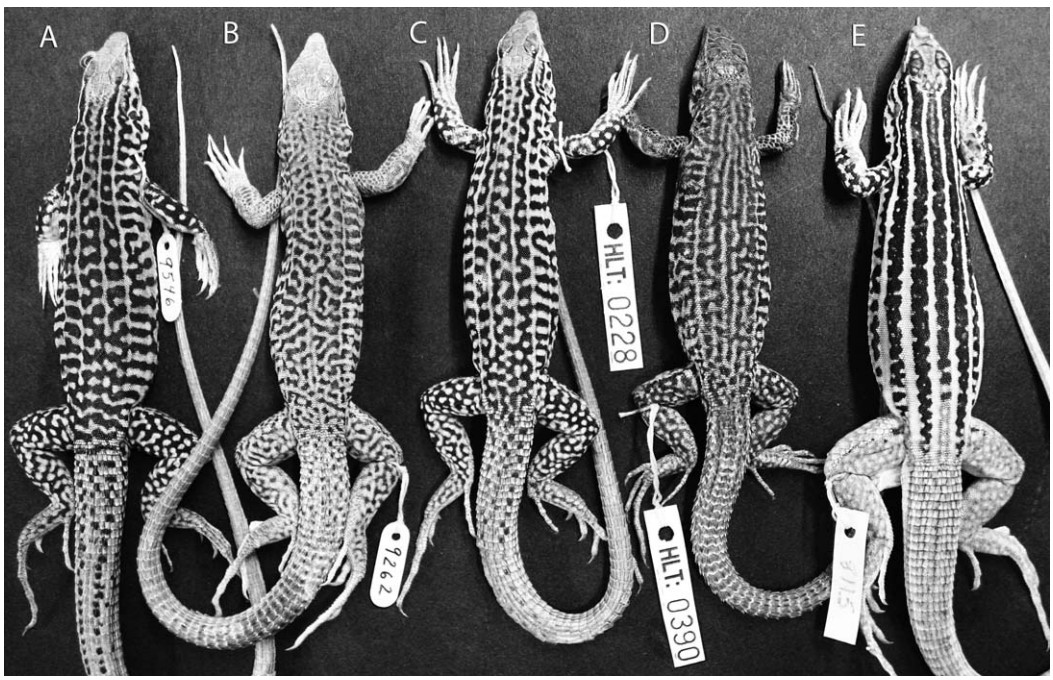

FIGURE 4. Representative specimens used in this study. Engle, New Mexico: **A**. *Aspidoscelis tesselata* E (RU 9546; 87 mm SVL); **B**. *A. marmorata* (RU 9262; ♀, 84 mm SVL). Arroyo del Macho, New Mexico: **C**. *A. tesselata* E (RU 0228; 84 mm SVL); **D**. *A. marmorata* (RU 0390; ♀, 79 mm SVL). Presidio County, Texas: **E**. *A. gularis septemvittata* (UADZ 8115; ♂, 90 mm SVL).

TABLE 5. Comparisons of meristic variability (summarized by principal components) between two color pattern classes of parthenogenetic *Aspidoscelis tesselata* and sexually reproducing congeners.

Standard deviations are ordered by taxon sequence. Groups with significantly greater variances (SDs) are in **boldface**.

Sampling site(s)	Comparison	N	Standard deviations			Variances different?	
Colorado	TESS C and **SEX**	31 and 31	PC1	0.24	0.28	No	$P = 0.48$
			PC2	0.66	1.26	Yes	$P = 0.03$
Conchas, NM	**TESS C** and SEX	30 and 31	PC1	0.38	0.23	Yes	$P = 0.01$
			PC2	1.19	0.74	Yes	$P = 0.004$
Macho, NM	TESS E and **MAR**	38 and 29	PC1	0.65	1.22	Yes	$P = 0.003$
			PC2	0.95	0.70	No	$P = 0.59$
Engle, NM	TESS E and **MAR**	30 and 33	PC1	0.48	0.97	Yes	$P < 0.001$
			PC2	0.44	1.14	Yes	$P < 0.001$

ability of *A. marmorata*. The ordination of PC scores revealed an apparent intermediate position of *A. tesselata* to its progenitor species, *A. marmorata* and *A. gularis septemvittata* (fig. 6), although there is extensive overlap among the three of them (this intermediate position is clearly depicted by a canonical variate analysis in Walker et al., 2000; fig. 2). The pattern of variability (table 7) was as follows: *A. marmorata*, maternal progenitor of *A. tesselata*, was more

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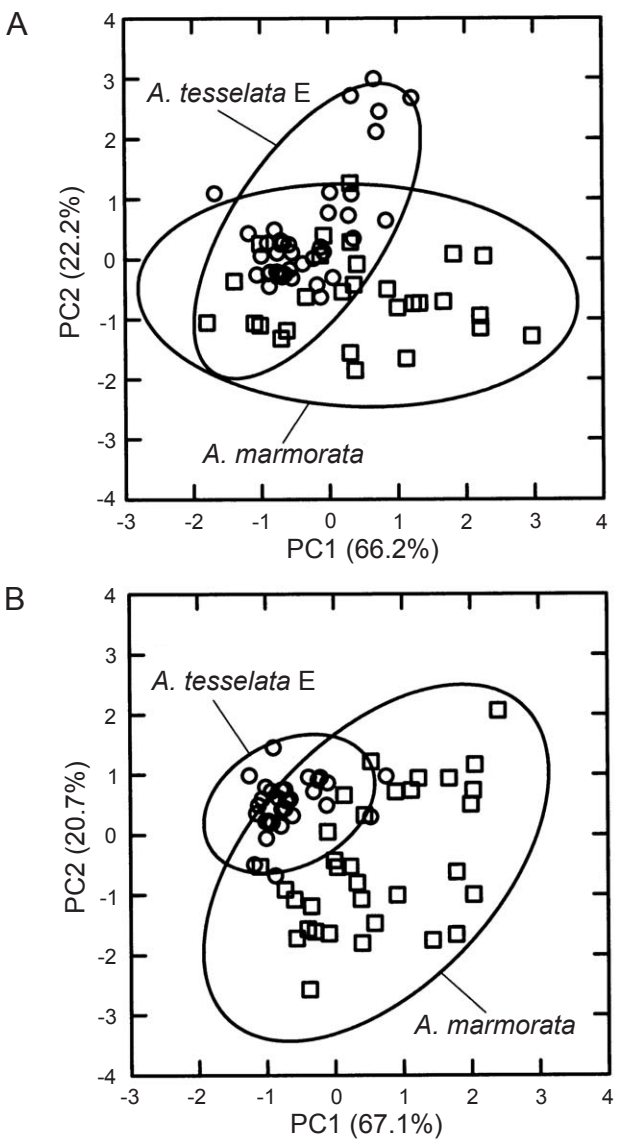

FIGURE 5. Pattern of meristic variation between parthenogenetic *Aspidoscelis tesselata* E (○) and gonochoristic *A. marmorata* (□) depicted by the projection of principal component scores on PC1 and PC2 axes: **A**. Arroyo del Macho, Chaves County, New Mexico (N = 38 and N = 29, respectively); **B**. vicinity of Engle, Sierra County, New Mexico (N = 30 and N = 33, respectively). Percentages represent the proportion of meristic variation summarized by each principal component, and ellipses define the 95% confidence limits for score distributions.

variable than the other three taxa, while *A. tesselata* was more variable than *A. sexlineata* and equivalent in variability to *A. gularis septemvittata*, its paternal progenitor.

DISCUSSION

This study addressed four major questions: (1) Are there individual meristic characters in which *A. tesselata* is more variable than a sympatric gonochoristic species? We found two examples. One was COS, which in *A. tesselata* C was more variable than *A. sexlineata* in southeastern Colorado, but any significant contribution of COS to multivariate variation disappeared in a PCA of all four samples of *A. tesselata*. The best example involves high variability in Conchas *A. tesselata*, for GAB (Zweifel, 1965) and GAB and LSG (Parker, 1979a; Taylor et al. (2003).

Zweifel (1965) noted the high GAB variance in *A. tesselata* C from Conchas, and it was sufficiently unusual that he hypothesized that this particular population might be genotypically multiclonal. This prediction was confirmed by the discovery of genotypic variation at glucose-6-phosphate isomerase (GPI) and muscle esterase (EST2) loci (Parker and Selander, 1976), which enabled Parker (1979a) to discover congruence between meristic variability and genotypic variation at the GPI locus. Subsequently, Dessauer and Cole discovered additional variation at sACOH and MPI loci in Conchas *A. tesselata* C and confirmed genotypic variation at the GPI locus (Taylor et al., 2003). The sACOH and MPI genotypes are available for samples

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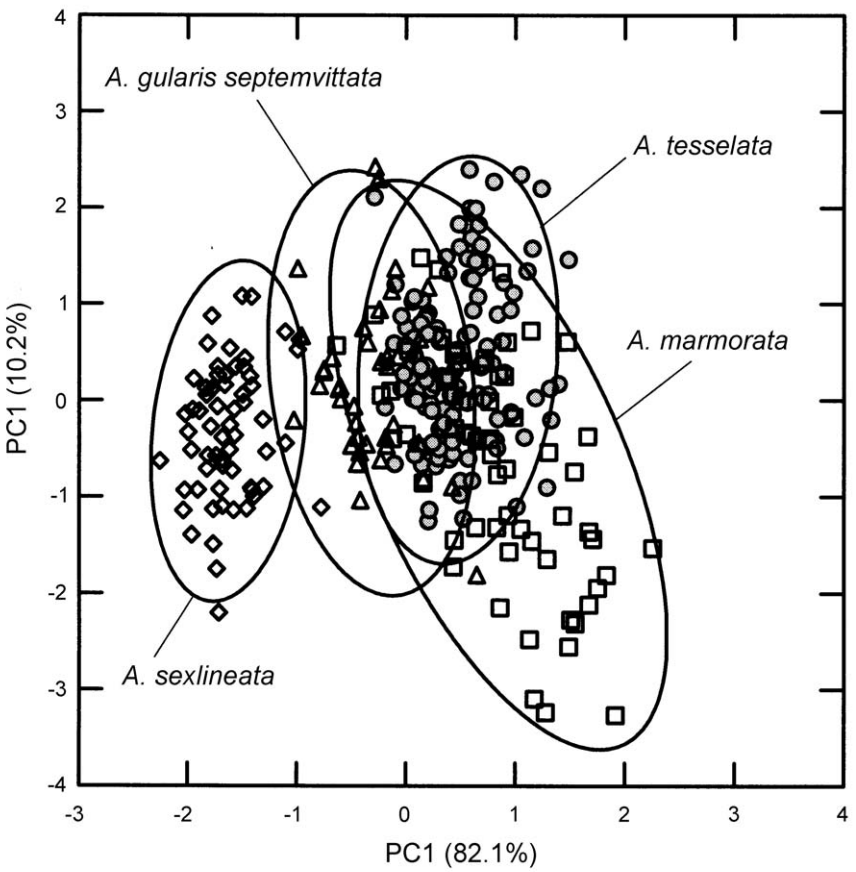

FIGURE 6. Pattern of meristic variation among *Aspidoscelis tesselata*, $N = 129$ (●); *A. sexlineata*, $N = 62$ (◊); A. *marmorata*, $N = 62$ (□); and *A. gularis septemvittata*, $N = 40$ (Δ), depicted by the projection of principal component scores on PC1 and PC2 axes. Percentages represent the proportion of meristic variation summarized by each principal component, and ellipses define the 95% confidence limits for score distributions.

of *A. tesselata* from Conchas, and Macho, New Mexico, but not for samples from southeastern Colorado, and Engle, New Mexico. High meristic variation associated with the presence of GPI ac and GPI ab genotypes at Conchas (Parker, 1979a; Taylor et al., 2003) was mirrored by the presence of MPI ac and MPI ab genotypes at that locality (Taylor et al., 2003: fig. 5). In addition, *A. tesselata* E from Arroyo del Macho matched the high GAB and LSG variances seen in *A. tesselata* C from Conchas, although there was no allelic variation observed at GPI, EST2, sACOH, or MPI among the 11 individuals of *A. tesselata* E tested from Macho. However, this fact was somewhat obscured by having *A. marmorata*, rather than *A. sexlineata*, as the local gonochoristic comparator at Arroyo del Macho.

Although EST2 variation was also present at Conchas Lake, GAB variation was not correlated with variation at the EST2 locus. Of the genotyped specimens from Conchas (appendix

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TABLE 6. Loadings (correlations between meristic characters[a] and principal components) from a principal components analysis of 293 lizards.

Species	Characters	PC1 loadings	PC2 loadings
A. tesselata, *A. sexlineata*,	GAB	0.906	0.376
A. marmorata, and	FP	0.894	0.124
A. gularis septemvittata	COS	0.906	-0.009
	LSG	0.932	-0.351
	SDL	0.770	0.378
Eigenvalues		237.8	29.5
Total meristic variation explained		82.1%	10.2%

[a]Characters: GAB, number of granular dorsal scales around midbody; FP, total number of femoral pores on both thighs; COS, total number of circumorbital scales; LSG, total number of lateral supraocular granules; SDL, number of subdigital lamellae on fourth toe of one foot (right was chosen unless damaged). See Materials and Methods for details.

TABLE 7. Comparisons of meristic variability (summarized by principal components) between parthenogenetic *Aspidoscelis tesselata* and sexually reproducing *A. sexlineata*, *A. marmorata*, and *A. gularis septemvittata*.

Standard deviations are ordered by taxon sequence. Groups with significantly greater variances (SDs) are in **boldface**.

Samples	N		Standard deviations		Variances different?	
TESS and SEX	129 and 62	PC1	0.37	0.28	Yes	$P = 0.008$
		PC2	0.85	0.70	No	$P = 0.127$
TESS and **MAR**	129 and 62	PC1	0.37	0.61	Yes	$P < 0.001$
		PC2	0.85	1.17	Yes	$P = 0.003$
TESS and SEP	129 and 40	PC1	0.37	0.37	No	$P = 0.74$
		PC2	0.85	0.85	No	$P = 0.72$
SEX and **MAR**	62 and 62	PC1	0.28	0.61	Yes	$P < 0.001$
		PC2	0.70	1.17	Yes	$P < 0.001$
SEX and SEP	62 and 40	PC1	0.28	0.37	No	$P = 0.08$
		PC2	0.70	0.85	No	$P = 0.39$
MAR and SEP	62 and 40	PC1	0.61	0.37	Yes	$P = 0.003$
		PC2	1.17	0.85	Yes	$P = 0.02$

1), 10 were GPI ac EST2 bc and four were GPI ac EST2 bb. There was no significant difference between these two groups in either mean GAB (85.3 vs. 86.0; $t_{12} = 0.591$, $P = 0.56$) or GAB variances (SDs = 2.0 for each sample, $L = 0$, $P = 1$).

(2) Do multiclonal arrays of *A. tesselata* express greater meristic variability than "uniclonal" arrays? We did not find consistent differences in meristic variability between either color-pattern classes or "uniclonal" and multiclonal categories. There was equivalent variability between (a)

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"uniclonal" Colorado *A. tesselata* C and multiclonal Engle *A. tesselata* E and (b) "uniclonal" Macho *A. tesselata* E and multiclonal Conchas *A. tesselata* C. Samples from Arroyo del Macho and Conchas Lake were more variable than samples from southeastern Colorado and Engle. Allelic variation in GPI and MPI at Conchas can be explained by postformational mutations of structural genes; these alleles are equally functional (Dessauer and Cole, 1984). While increased variability of GAB and LSG characters is congruent with genotypic variation at GPI and MPI loci in some instances (Parker, 1979a; Taylor et al., 2003), we lack evidence that the isomerase products of these loci are involved in developmental processes affecting meristic variation. In addition to genetic and environmental interactions, there are various possible genetic and epigenetic mechanisms that might increase phenotypic variability by affecting gene expression (e.g., see Cole, 1980; Kearney et al., 2009: 463), but none of these has yet been demonstrated to be contributors to phenotypic variation within tokogenetic arrays of lizards.

(3) Are differences in meristic variability between *A. tesselata* and sympatric gonochoristic species congruent with reproductive mode? This was not predictable. Gonochoristic *A. marmorata* was more variable in PC1 and PC2 than multiclonal *A. tesselata* E from Engle and for only PC1 in "uniclonal" *A. tesselata* E from Macho. The variability of *Aspidoscelis tesselata* exceeded that of gonochoristic *A. sexlineata* from Conchas Lake, but this was not the case for samples from southeastern Colorado.

(4) How does *A. tesselata* rank on a scale of relative meristic variability with gonochoristic *A. sexlineata*, *A. marmorata*, and *A. gularis septemvittata*? We are in agreement with Parker (1979a) that *A. marmorata* is more variable than *A. tesselata*, and *A. marmorata* is also more variable than the other two gonochoristic species examined. However, for pooled samples, the meristic variability of *A. tesselata* exceeded that of *A. sexlineata* and was equivalent to that of *A. gularis septemvittata*. *Aspidoscelis tesselata* comprises collections of independent tokogenetic arrays, each with the potential to evolve by accumulating different combinations of random mutations. This means that the relative meristic variability of a particular tokogenetic array may not be predictable by reproductive mode, color-pattern class, or geographic location. This was confirmed by the present study.

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toire River, southeastern Colorado. I thank the U.S. Army for permission to collect specimens of *A. sexlineata* on the Pueblo Chemical Depot, access coordinated by K. M. Canestorp, U.S. Fish and Wildlife Service, and on the Piñon Canyon Maneuver Site, coordinated by Richard Bunn, Directorate of Environmental Compliance and Management (DECAM). Thanks to C. Cooley for assistance in collecting samples in 1992 from the Engle locality, New Mexico. Regis Summer Faculty Research Grants supported fieldwork for this project.

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Appendix 1
Sampling Localities and Specimens in This Study
Coordinates based on WGS84 datum.

Southeastern Colorado Samples

Otero County: *Aspidoscelis tesselata* C: Ninemile Valley of the Purgatoire River, 11.5–13.0 km SW Colorado Hwy. 109, on road 804; UTM 13S 630854E, 4175545N: Regis University (RU) 0122, 0125, 0127, 0130, 0131, 0164, 0167; Purgatoire Canyon of the Purgatoire River, accessed from Withers Canyon (this site is approximately 6.5 km SW of the Ninemile Valley collecting locality.); UTM 13S 626757E, 4169176N: RU 0077, 0084, 0169, 0170, 0198, 0199, 02006–02008, 02015, 02016, 02082–02085; Withers Canyon Trailhead to Purgatoire Canyon; UTM 13S 626030E, 4169132N: RU 0172, 02010, 02013, 02014, 02019–02022, 02089. *Aspidoscelis sexlineata*. Vogel Canyon Picnic Grounds; UTM 13S 631004E, 4181319N: RU 0117, 0128, 0129; Purgatoire Canyon accessed from Withers Canyon; UTM 13S 626757E, 4169176N: RU 02004, 02005, 02017, 02087, 02088, RU 0173, 0200; Withers Canyon Trailhead to Purgatoire Canyon; UTM 13S 626030E, 4169132N: RU 02018, 02024, RU 0078; Lockwood Canyon; UTM 13S 602968E, 4150335N: RU 0151; Rourke Road; UTM 13S 629191E, 4179916N: RU 0332; Off Hwy. 109; UTM 13S 633315E, 4182719N: RU 0334. **Pueblo County:** *Aspidoscelis sexlineata*: Pueblo Chemical Depot, Chico Creek, UTM 13S 554856E, 4236332N: RU 0007–0010, 0015–0017, 0023, 0024, 0075, 0137, 0138; Lime town-site; UTM 13S 532904E, 4222325N; RU 0052. **Baca County:** *Aspidoscelis sexlineata*: County road north of Carrizo Creek; UTM 13S 672499E, 4107475N: RU 9282. **Las Animas County:** *Aspidoscelis sexlineata*: slope NW Cottonwood Creek; UTM 13S 669753E, 4112069N: RU 953.

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Conchas Lake, New Mexico, Samples

San Miguel County: *Aspidoscelis tesselata* C: along Army Corps of Engineers 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; UTM 13S 574628E, 3916332N. RU 0001–0003, 0008–0022, 0027–0033, 0037–0041. *A. sexlineata*: vicinity of South Campground, Conchas Lake State Park (component CL-2 of Manning et al., 2005). University of Arkansas Department of Zoology (UADZ) 7343, 7346, 7348, 7351, 7356, 7375, 7379, 7381, 7382, 7391–7396, 7399, 7401, 7402, 7405, 7409, 7413, 7414, 7443, 7444, 7447, 7577, 7578, 7582, 7584, 7674, 7692. *Aspidoscelis tesselata* C with electrophoretic data: around picnic tables south of Conchas Dam: **Clone GPI ac, EST2 bc**: UADZ 5418, 5419, 5421–5423 (= EDP 836, 837, 839–841), 5420, 5424, 5425, 5428; **Clone GPI ac EST2 bb**: 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); **Clone GPI ab, EST2 bc**: UADZ 5415–5417, 5426, 5427 (= EDP 830, 831, 834, 845, 849); Conchas Lake at South State Park campground: **Clone GPI ab, MPI (ab)**, **EST2 bc, sACOH (bc)**: AMNH R-136875, R-136878; **Clone GPI ac, MPI (ac)**, **EST2 bc, sACOH (bc)**: AMNH R-123029, R-136877; **Clone GPI ac, MPI (ac)**, **EST2 bc, sACOH (ac),**: AMNH R-123033, R-136876, R-136879.

Arroyo del Macho, New Mexico, Samples

Chaves County: N side Arroyo del Macho; UTM 13S 541582E, 3723117N; approximately 22 km N on Hwy. U.S. 285 from junction with Hwy. U.S. 70 N of Roswell, New Mexico, then 0.8 km E on Eden Valley Road. *Aspidoscelis tesselata* E: RU 96053, 96054, 97155, 97157, 97159, 97161–97165, 97167, 97169–97171, 97173, 97175, 97176, 98020–98025, 98034–98037, 98041, 98043–98048, 98050, 99004, 99007, 99009 (American Museum of Natural History [AMNH] R-145142–145144, 146612–146629, 146631–146639, 146641–146647, 146649). *Aspidoscelis marmorata*: RU 98028, 98029, 98046, 98047 (AMNH R-146650–146653), RU 0228; approximately 1.6 km W Pecos River, north side of Hwy. U.S. 70, approximately 16.1 km east of Hwy. U.S. 285 and U.S. 70 interchange; UTM 13S 556511E, 3713689N. *Aspidoscelis marmorata*: RU 98051, 98052, 98055, 98057–98060, 98062–98076 (AMNH R-146654, 146655, 146658, 146660–146663, 146665–146679); RU 0366, 0389, 0390.

Vicinity of Engle, New Mexico, Samples

Sierra County: Approximately 14 km S Engle on County road A013, then 1.3 km W on county road A038; UTM 13S 310293E, 36593783N. *Aspidoscelis tesselata* E: RU 9234–9259, 9271–9277, 9544–9559, RU 0378. *A. marmorata*: RU 9242–9253, 9260–9270, RU 0379–0388.

Presidio County, Texas, Sample

Aspidoscelis gularis septemvittata. Mesquite Ranch, San Antonio Canyon, Campo Nuevo: University of Arkansas Department of Zoology (UADZ) 4420 (American Museum of Natural History [AMNH] 147594; 1.0 km N Campo Nuevo: UADZ 4362, 4396, 4406 (AMNH 147595–147597; 3.2 km N Campo Nuevo: UADZ 4351, 4353, 4355–4358, 4363, 4369, 4370, 4373, 4434, 4435, 4440 (AMNH 147581–147592, 147594; 3.3 km N Campo Nuevo: UADZ 4372, 4395, 4402 (AMNH 147598–147600); 3.4 km N Campo Nuevo: UADZ 4371, 4393, 4394, 4438 (AMNH 147601–147604); 4.2 km N Campo Nuevo: UADZ 4361 (AMNH 147605); 1.5 km W Campo Nuevo: UADZ 4364, 4365 (AMNH 147606, 147607); Pelillos Canyon, 0.3 km S Campo Nuevo: UADZ 4381, 4386 (AMNH 147608, 147609); boundary Mesquite Ranch and Rancho Chaa, 6.3 km E Mesquite Ranch proper: UADZ 4413–4416, 4423, 4430–4432 (AMNH 147610–147617); 3.8 km S head of Pelillos Canyon, 4.1 km S Campo Nuevo: UADZ 4421, 4424, 4441 (AMNH 147618–147620); near road to Upper San Antonio Canyon: UADZ 5293; upper San Antonio Canyon: UADZ 8115.

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Appendix 2

Evidence for Absence of Sexual Dimorphism in Meristic Variability

The modified Levene test was used to test for homogeneous sample variances.

Southeastern Colorado

Aspidoscelis sexlineata viridis (*N* = 20 males; 10 females)

GAB (*L* = 0.0478, *P* = 0.83); FP (*L* = 0.3530, *P* = 0.56); COS (*L* = 1.6779, *P* = 0.21); LSG (*L* = 0.1699, *P* = 0.68); SDL (*L* = 0.0, *P* = 1.0); PC1 (*L* = 0.6603, *P* = 0.42); PC2 (*L* = 0.6033, *P* = 0.44).

Conchas Lake, New Mexico

Aspidoscelis sexlineata viridis (*N* = 17 males; 14 females)

GAB (*L* = 0.2709, *P* = 0.61); FP (*L* = 0.0096, *P* = 0.92); COS (*L* = 0.8526, *P* = 0.36); LSG (*L* = 0.3993, *P* = 0.53); SDL (*L* = 0.9891, *P* = 0.33); PC1 (*L* = 0.1017, *P* = 0.75); PC2 (*L* = 0.1841, *P* = 0.67).

Arroyo del Macho, New Mexico

Aspidoscelis marmorata (N = 19 males; 10 females)

GAB (*L* = 0.0125, *P* = 0.91); FP (*L* = 0.9490, *P* = 0.34); COS (*L* = 0.2596, *P* = 0.61); LSG (*L* = 0.0450, *P* = 0.83); SDL (*L* = 0.0101, *P* = 0.92); PC1 (*L* = 0.1587, *P* = 0.69); PC2 (*L* = 0.2837, *P* = 0.60).

Vicinity of Engle, New Mexico

Aspidoscelis marmorata (*N* = 19 males; 14 females)

GAB (*L* = 0.0011, *P* = 0.97); FP (*L* = 1.3294, *P* = 0.26); COS (*L* = 0.0419, *P* = 0.84); LSG (*L* = 0.0024, *P* = 0.96); SDL (*L* = 0.0696, *P* = 0.79); PC1 (*L* = 0.0037, *P* = 0.95); PC2 (*L* = 0.5983, *P* = 0.44).

Presidio County, Texas

Aspidoscelis gularis septemvittata (*N* = 25 males; 15 females)

GAB (*L* = 0.1541, *P* = 0.70; FP (*L* = 1.7674, *P* = 0.19); COS (*L* = 2.8899, *P* = 0.10); LSG (*L* = 1.9421, *P* = 0.17); SDL (*L* = 0.5726, *P* = 0.45); PC1 (*L* = 0.2509, *P* = 0.62); PC2 (*L* = 1.4781, *P* = 0.23).

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