AMERICAN MUSEUM NOVITATES

Number 3849, 20 pp. February 4, 2016

Morphological Variation in a Unisexual Whiptail Lizard (*Aspidoscelis exsanguis*) and One of Its Bisexual Parental Species (*Aspidoscelis inornata*) (Reptilia: Squamata: Teiidae): Is the Clonal Species Less Variable?

CHARLES J. COLE,[1] HARRY L. TAYLOR,[1, 2] AND CAROL R. TOWNSEND[1]

ABSTRACT

Two clonal lineages, each comprising multiple generations of unisexual *A. exsanguis*, were produced in the laboratory from two lizards that were collected at the same locality in the field. Based on 10 meristic and four additional characters, we assessed morphological scores and relative variation as follows: (1) between the two laboratory lineages; (2) between these lineages pooled and samples of *A. exsanguis* and the bisexual (gonochoristic) *A. inornata* from the field; and (3) between field samples of the clonal lizards and *A. inornata* from a nearby locality. The two lineages differed significantly in the means and variances of two univariate characters and the two most informative multivariate characters. Contrary to expectations, the pooled sample of cloned laboratory lineages of *A. exsanguis* were as variable as the bisexual species in all 10 univariate characters and four important multivariate characters.

INTRODUCTION

Individuals of all-female species of whiptail lizards (genus *Aspidoscelis*) reproduce by parthenogenetic cloning (Lutes et al., 2010). This preserves the high levels of heterozygosity that result from their hybrid origins (reviewed by Reeder et al., 2002) and explains their very low levels of variation in genetic characters, such as allozymes (e.g., Neaves, 1969; Parker and Selander, 1976;

[1] Division of Vertebrate Zoology (Herpetology), American Museum of Natural History.
[2] Department of Biology, Regis University, Denver, Colorado.

 ISSN 0003-0082

Dessauer and Cole, 1986; Taylor et al., 2015) and microsatellite DNA (Lutes et al., 2011). Nonlethal mutations can produce new or derived lineages of parthenogens, as they are cloned, so multiple clonal lineages can occur in populations of unisexual whiptail lizards (Parker and Selander, 1976; Dessauer and Cole, 1989; Lutes et al., 2011). Different clones can also result from separate original F_1 hybrid zygotes (e.g., Cole and Dessauer, 1993; Lutes et al., 2011).

Considering the clonal inheritance, one might expect to find comparatively little variation in morphological characters of unisexual versus bisexual species. For example, if a parthenogenetic female has a count of 70 epidermal scales or granules around the middle of the body, 17 epidermal femoral pores on the right thigh, and 30 epidermal subdigital lamellae on the left fourth toe, is it likely that her offspring will have the same scale counts? Alternatively, if there is variation in such characters in parthenogens, is it less than what occurs in bisexual (gonochoristic) species, including ancestors of the clonal forms? For the variation that does exist within a clone, to what might this be attributed? Taylor et al. (2012) found surprising variation in a clonal species (*Aspidoscelis tesselata*) compared with three bisexual species, including its two progenitor relatives, based on population samples collected in the field. However, comparative variation within clonal lineages represented by multiple generations of known heritage has not been studied in detail, although data for two lineages of *Aspidoscelis neavesi* were presented by Cole et al. (2014) (discussed below).

Here we compare variation in 14 morphological characters representing each of two clonal lineages of parthenogenetic *Aspidoscelis exsanguis* that were produced in the laboratory. The two lineages stemmed from different P_1 females, but both were collected at the same locality in the field. These P_1 females are AMNH R-109468 and AMNH R-113352. The specimens represent the F_1–F_7 generations of the AMNH R-109468 lineage and the F_1–F_3 generations of the AMNH R-113352 lineage. Representatives of these lineages, including some of the same individuals, were used to document parthenogenetic reproduction (Hardy and Cole, 1981) and clonal inheritance (Dessauer and Cole, 1986) in unisexual whiptail lizards, so we know that these phenomena pertain to these specimens. We also studied variation in a population sample of *A. exsanguis* from the same locality in nature where the P_1 females were obtained, comparing this with variation in the two laboratory lineages pooled (assuming that there are pooled lineages in the field sample) and with variation in a bisexual species, *Aspidoscelis inornata* from a nearby locality, as this is one of the bisexual ancestors of *A. exsanguis*. Finally, we compared variation in only the field samples of *A. exsanguis* and *A. inornata* and briefly discuss possible morphological effects of the laboratory environment, although none was found.

MATERIALS AND METHODS

Morphological Characters

The characters analyzed with multivariate statistics are discrete counts of epidermal scales and pores in the skin. The characters and their abbreviations are described in appendix 1, along with snout-vent length. Additional characters are described in the text where they are discussed.

Specimens Examined

All specimens are at the American Museum of Natural History (AMNH), and they are listed in appendix 2. As all the specimens of *A. exsanguis* are females, we examined only females of *A. inornata* also, although these characters are not known to be sexually dimorphic in these lizards.

Laboratory Maintenance of Reproducing Lizards

Lizards in laboratory colonies were maintained at the AMNH as described by Townsend (1979) and Townsend and Cole (1985). Following oviposition, eggs were removed from the cage and allowed to develop at room temperature.

Statistics

Statistical procedures and tests were performed with SPSS© and NCSS© software. We used a modified Levene test (recommended by Conover et al. [1981] and available in NCSS©) to check for significant pairwise differences in sample variances. For sample pairs with heterogeneous variances, we used relative size of standard deviations to identify the sample with significantly greater variation. Depending on number of samples compared, we used either *t*-tests or one-way ANOVAs to test for significant differences in character means. If significant differences were indicated by ANOVAs, the specifically different samples were identified with Tukey multiple-comparison tests.

All specimens were scored for 10 univariate meristic characters (appendix 1), and specimens with complete data for the 10 characters formed the base data for the multivariate comparisons. For each comparison, the subgroup of original samples used was treated as a single sample in a principal components analysis (PCA), and meristic variation for that subgroup was captured in the 10 principal components derived from that analysis. Because all characters were recorded on the same scale (discrete counts of epidermal scales and femoral pores), we used the variance/covariance matrix to obtain the coefficients used to compute component scores. A variance/covariance matrix retains the relative variances of the original characters, so that characters with larger variances are given greater weight in developing the principal components (Neff and Marcus, 1980).

Following Jombart et al. (2010), we used either a discriminate function analysis (DFA) or a canonical variate analysis (CVA) of the principal components (as new variables) to determine similarities and significant differences among the original samples included in the comparisons. Principal components were included stepwise in a DFA or CVA model if *F*-to-enter probabilities were < 0.05 and did not exceed 0.10 when other components were included.

For each comparison, we checked each sample (a priori group) for multivariate outliers by evaluating D^2 distances (based on the original a priori groups) from each specimen to the centroid of the remaining cases in that group (provided as output by SPSS). Specimens with D^2 values exceeding a critical chi-square value at $P = 0.001$ and degrees of freedom defined by the number of principal components included in the CVA model would be identified as outliers and removed from the definitive analyses (Tabachnick and Fidell, 2013). However, there were no multivariate outliers identified in the multivariate comparisons of this study.

TABLE 1. Descriptive statistics for samples of two laboratory lineages of clonal *Aspidoscelis exsanguis* and scores for their two P_1 individuals from nature. For each character, first row: mean ± 1 SE (samples sharing the same capital letter in a row are not significantly different at $\alpha = 0.05$); second row: standard deviation (samples with different lower case letters in a row have significantly different variances for that character); third row: range and (sample size). Characters are described in appendix 1. Sample details are provided in appendix 2. For characters with (u), sample size was maximized by using the count from the right side of the body, except on individuals where that was not available, the left side was used.

Character	Lineages			
	AMNH 109468	P1 109468	P1 113352	AMNH 113352
PC1	-0.5 ± 0.11 A 0.56 a -1.3 to 0.6 (28)	---	---	1.0 ± 0.26 B 0.96 b -0.9 to 2.5 (14)
PC6	0.2 ± 0.20 A 1.04 a -2.0 to 2.7 (28)	---	---	-0.4 ± 0.22 A 0.82 a -1.5 to 1.0 (14)
DF1	-0.8 ± 0.14 A 0.76 a -2.3 to 0.9 (28)	---	---	1.6 ± 0.37 B 1.37 b -0.8 to 3.5 (14)
GAB	68.7 ± 0.35 A 2.37 a 65–74 (46)	69	76	74.8 ± 1.03 B 4.12 b 66–82 (16)
PSC	15.4 ± 0.34 A 2.18 a 11–22 (41)	18	---	14.9 ± 0.44 A 1.77 a 13–19 (16)
GUL	16.7 ± 0.27 A 1.70 a 14–20 (39)	22	21	17.3 ± 0.40 A 1.58 a 15–21 (16)
TBS	19.6 ± 0.25 A 1.68 a 17–24 (46)	25	21	19.1 ± 0.46 A 1.84 a 16–22 (16)
LSG(u)	15.3 ± 0.30 A 2.02 a 11–22 (45)	13	13	16.1 ± 0.38 A 1.50 a 14–19 (16)
SDL-F(u)	13.6 ± 0.16 A 1.07 a 12–16 (46)	15	15	13.4 ± 0.20 A 0.81 a 12–15 (16)
SDL-T(u)	29.5 ± 0.21 A 1.32 a 27–34 (41)	30	30	28.7 ± 0.22 A 0.82 a 27–30 (14)
FP(u)	16.8 ± 0.14 A 0.92 a 15–19 (46)	17	18	16.5 ± 0.22 A 0.89 a 15–18 (16)
COS(u)	4.5 ± 0.12 A 0.78 a 3–6 (46)	4	4	4.0± 0.16 B 0.63 b 3–5 (16)
SPV	5.4 ± 0.10 A 0.69 a 3–7 (46)	6	5	5.8 ± 0.14 A 0.58 a 5–7 (16)

TABLE 2. Correlations between characters and either principal components (PCs) or discriminant function 1 (DF1) from multivariate analyses of two laboratory lineages of clonal *Aspidoscelis exsanguis*. Univariate characters are described in appendix 1, and sample details are provided in appendix 2. Principal components are those selected by the DFA model as having discrimination value.

Principal components analysis	Characters	PC1	PC6
	GAB	0.992	0.008
	PSC	-0.346	0.246
	GUL	0.170	-0.211
	TBS	-0.269	-0.244
	LSG(u)	0.487	0.127
	SDL-F(u)	0.273	0.208
	SDL-T(u)	-0.094	0.696
	FP(u)	-0.073	0.673
	COS(u)	0.018	0.001
	SPV	0.396	-0.053
Eigenvalues		21.121	1.851
Proportion of variation		55.5%	4.9%

Discriminant function analysis	Characters	DF1
	PC1	0.851
	PC6	-0.253
Eigenvalue		1.357
Proportion of intergroup variation		100%

RESULTS AND DISCUSSION

Statistical Comparisons of Two Cloned Lineages

Here we address three related questions: (1) are the two field-collected P_1 females alike in quantitative expressions of morphological characters; (2) do all specimens in a cloned lineage resemble each other and the founder of the lineage in scores of the morphological characters; and (3) are there significant differences in morphological characters and the extent of their variation between two laboratory lineages cloned from the same natural population?

Note that the two P_1 females were similar or identical in most characters except GAB and TBS (table 1) and there was a range of data for all characters, not consistent uniformity. In some characters (GUL, TBS, LSG(u)), a P_1 female had scores that were outside the range

TABLE 3. Classification of specimens in two laboratory lineages of clonal *Aspidoscelis exsanguis* by discriminant function analysis. A priori groups are in columns, and rows show number of individuals assigned to each group by the discriminant function model (table 2). Overall classification success was 88.1% for original grouped specimens and 85.7% for jackknifed specimens. Lineages are described in appendix 2.

Jackknifed classification	*N*	Lineage AMNH 109468	Lineage AMNH 113352
Lineage AMNH 109468	28	25 (89.3%)	3 (10.7%)
Lineage AMNH 113352	14	3 (21.4%)	11 (78.6%)
Original grouped specimens	*N*	Lineage AMNH 109468	Lineage AMNH 113352
Lineage AMNH 109468	28	26 (92.9%)	2 (7.1%)
Lineage AMNH 113352	14	3 (21.4%)	11 (78.6%)

of variation observed in her cloned derivatives (table 1). For univariate comparisons, the lineage from AMNH R-109468 included 39–46 specimens and that from AMNH R-113352 included 14–16 (table 1), depending on the number of characters that could not be scored owing to physical damage. The lineages differed significantly in two of the 10 meristic characters (GAB and COS(u); table 1), but not in TBS. Considering the differences between the P_1 females in GAB (table 1), these two lineages may represent two different clones from the natural population.

Aspidoscelis neavesi is the only other clonal whiptail for which data can be compared for individuals of two different laboratory lineages, and the same characters were studied for those lizards (Cole et al., 2014: 10, table 2). Interestingly, the maternal parent for *A. neavesi* was an *A. exsanguis*, and the observed range for all characters studied in *A. neavesi* was similar to that of the *A. exsanguis* reported here also. The two lineages of *A. neavesi* differed significantly in two characters, SPV and FP, although the actual differences were small (Cole et al., 2014). Nevertheless, the founders of those lineages were females from different F_1 hybrid zygotes of *A. exsanguis* × *A. inornata* (Lutes et al., 2011).

We included all 10 univariate characters in a PCA to initiate multivariate comparisons (table 2). Samples for PCA and DFA were reduced to 28 specimens of the AMNH R-109468 lineage and 14 of the AMNH R-113352 lineage because 20 individuals had damage to at least one character. We used the 10 principal components, generated in the PCA, as potential candidate variables for DFA of the two lineages. Two of the 10 principal components (PC1 and PC6) were selected by the stepwise selection criteria (Materials and Methods) for inclusion in the DFA model (table 2).

The two lineages differed significantly in PC1 and discriminant function 1 (DF1; table 1), and the Wilks' lambda value of 0.424 (P <0.0001) suggested that differences between the two lineages were responsible for approximately 58% of the variation. This variation was sufficient to classify more than 85% of the specimens to the correct a priori group (table 3). In relative variation, as depicted by standard deviations, lineage AMNH R-113352 was significantly more variable than lineage AMNH R-109468 in GAB, PC1, and DF1, and lineage AMNH R-109468 was more variable in COS (table 1).

TABLE 4. Descriptive statistics for field samples of clonal *A. exsanguis* and bisexual *A. inornata* and a pooled sample of two laboratory lineages of clonal *Aspidoscelis exsanguis*. For each character, first row: mean ± 1 SE (samples sharing the same capital letter in a row are not significantly different at α = 0.05); second row: standard deviation (for each row, samples sharing the same lower case letter do not differ significantly in variance); third row: range and (sample size). Characters are described in appendix 1. Sample details are provided in appendix 2. For characters with (u), sample size was maximized by using the count from the right side of the body, except on individuals where that was not available, the left side was used.

Character	Sample		
	Field *A. exsanguis*	Lab *A. exsanguis*	Field *A. inornata*
PC1	0.3 ± 0.09 A 0.33 a -0.2 to 0.8 (13)	0.5 ± 0.11 A 0.71 b -0.4 to 2.4 (42)	-1.3 ± 0.14 B 0.60 ab -2.5 to -0.6 (19)
PC2	0.1 ± 0.18 AB 0.65 a -0.7 to 1.2 (13)	0.2 ± 0.15 B 0.98 a -1.6 to 2.1 (42)	-0.6 ± 0.24 A 1.04 a -2.2 to 1.8 (19)
CV1	1.5 ± 0.22 A 0.79 a 0.2 to 2.7 (13)	2.1 ± 0.15 A 0.95 a 0.0 to 3.6 (42)	-5.6 ± 0.28 B 1.22 a -8.7 to -3.8 (19)
CV2	0.7 ± 0.31 A 1.12 a -0.9 to 2.3 (13)	-0.2 ± 0.16 B 1.0 a -1.9 to 3.0 (42)	0.0 ± 0.20 AB 0.88 a -1.5 to 1.7 (19)
GAB	70.0 ± 0.58 A 2.55 a 65–76 (19)	70.3 ± 0.50 A 3.94 a 65–82 (62)	61.4 ± 0.70 B 3.59 a 55–68 (26)
LSG(u)	14.7 ± 0.35 A 1.49 a 12–17 (18)	15.5 ± 0.25 A 1.92 a 11–22 (61)	11.2 ± 0.58 B 2.86 a 7–20 (24)
SPV	5.6 ± 0.14 A 0.60 a 4–6 (19)	5.5 ± 0.08 A 0.67 ab 3–7 (62)	9.8 ± 0.22 B 1.12 b 8–12 (26)
TBS	19.0 ± 0.63 A 2.73 a 15–25 (19)	19.4 ± 0.22 A 1.72 b 16–24 (62)	16.9 ± 0.37 B 1.88 ab 13–20 (26)
GUL	17.7 ± 0.44 A 1.87 a 15–22 (18)	16.9 ± 0.23 A 1.67 a 14–21 (55)	17.2 ± 0.39 A 1.85 a 15–23 (22)
PSC	15.7 ± 0.35 A 1.33 a 14–18 (14)	15.2 ± 0.27 A 2.06 a 11–22 (57)	15.7 ± 0.37 A 1.68 a 11–18 (21)
SDL-T(u)	29.8 ± 0.24 A 1.03 a 28–32 (19)	29.3 ± 0.17 A 1.26 a 27–34 (55)	27.9 ± 0.26 B 1.34 a 25–30 (26)
SDL-F(u)	14.4 ± 0.20 A 0.90 a 13–16 (19)	13.5 ± 0.13 B 1.00 a 12–16 (62)	14.3 ± 0.19 A 0.94 a 13–16 (25)
FP(u)	17.1 ± 0.19 A 0.81 a 16–18 (19)	16.7 ± 0.12 A 0.92 a 15–19 (62)	15.3 ± 0.25 B 1.28 a 13–18 (26)
COS(u)	4.7 ± 0.14 A 0.58 a 4–6 (18)	4.4 ± 0.10 A 0.77 a 3–6 (62)	4.3 ± 0.19 A 0.94 a 3–6 (25)

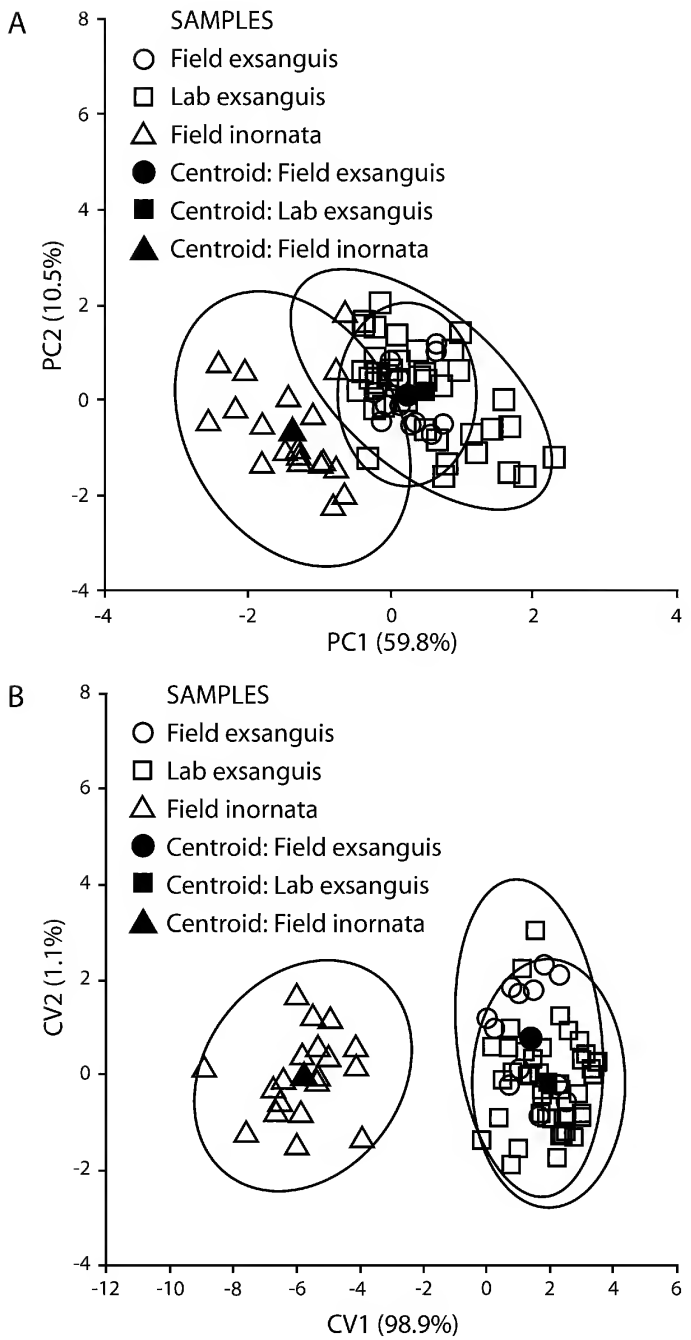

FIGURE 1. Scatterplots from multivariate statistical analyses. Ellipses define the 95% confidence limits of score distributions. **A.** Principal component scores of 14 field *A. exsanguis*, 42 laboratory *A. exsanguis* of two lineages pooled, and 19 field *A. inornata*. Axis percentages reflect variance explained by PC1 and PC2 (table 5). **B.** Canonical variate scores of the same specimens as in A. Axis percentages are relative contributions of CV1 and CV2 to the discrimination (table 5).

Comparisons of Unisexual *A. exsanguis*, Bisexual *A. inornata*, and Two Lineages of *A. exsanguis*

In univariate and multivariate statistical comparisons of field samples of unisexual *A. exsanguis*, bisexual *A. inornata*, and a pooled sample of two laboratory lineages of *A. exsanguis,* we address three related questions: (1) does the field sample of clonal *A. exsanguis* differ from the sample of pooled laboratory lineages of this species; (2) is the field sample of *A. exsanguis* less variable than the field sample of *A. inornata*; and (3) is the pooled sample of the two laboratory lineages of *A. exsanguis* less variable than either or both the field samples of *A. exsanguis* and *A. inornata*? For these comparisons, we pooled the data for the two laboratory lineages of *A. exsanguis* because the field sample of this species must have included more than one lineage.

In univariate comparisons of 10 meristic characters, the only difference between the sample of field *A. exsanguis* and the pooled clones of laboratory *A. exsanguis* was in SDL-F(u), although this character did not differ between the field samples of *A. exsanguis* and *A. inornata* (table 4). There were significant differences in the means of seven of the 10 univariate characters among the three samples and there was a considerable range of variation for each character in each sample. Six of the significant differences were interspecific.

Thirty-three specimens had one or more damaged characters, thereby precluding use of those individuals in the multivariate analyses. We used all 10 univariate characters in the PCA model, and seven of the 10 principal components generated were selected by stepwise selection criteria as having value in discriminating the three a priori groups (table 5). Field-caught and laboratory *A. exsanguis* both differed significantly from field *A. inornata* (but not from each other) in PC1 and CV1, laboratory *A. exsanguis* differed significantly from field *A. inornata* but not field *A. exsanguis* in PC2, and laboratory *A. exsanguis* differed significantly from field *A. exsanguis* but not field *A. inornata* in CV2 (table 4). These results are visually depicted in figure 1. A Wilks' lambda value of 0.071 for the combination of CV1 + CV2 in the CVA model (table 5) suggested that differences among the three a priori groups were responsible for approximately 93% of the variation. Classification success of specimens from the original a priori groups was 78.4%. All 19 specimens of *A. inornata* were classified correctly, but 7 of the 13 specimens of field *A. exsanguis* were classified to laboratory *A. exsanguis*, and 12 of 42 specimens of laboratory *A. exsanguis* were classified to field *A. exsanguis.*

In variation of univariate characters, significant differences among the three samples were found with SPV and TBS (table 4). For SPV, field *A. inornata* was more variable than field *A. exsanguis* ($P = 0.02$) but not laboratory *A. exsanguis.* For TBS, field *A. exsanguis* was more variable than laboratory *A. exsanguis* ($P = 0.001$) but the variation in *A. inornata* was not different from either sample of *A. exsanguis.* For multivariate characters, laboratory *A. exsanguis* expressed greater variation than field *A. exsanguis* for PC1 ($P = 0.02$) but was similar to *A. inornata* (table 4; fig. 1). The same relative degree of variability was expressed by all three groups for PC2, CV1, and CV2 (table 4; fig. 1); i.e., the sexual *A. inornata* was not more variable than the clonal *A. exsanguis* in these characters.

TABLE 5. Correlations between characters and either principal components (PC) or canonical variates (CV) of field samples of *A. exsanguis* and *A. inornata* and a pooled sample of two laboratory lineages of clonal *Aspidoscelis exsanguis*. Univariate characters are described in appendix 1, and sample details are provided in appendix 2. Principal components are those selected by the CVA model as having discrimination value.

Principal components analysis	Characters	PC1	PC2	PC3	PC4	PC5	PC6	PC7
	GAB	0.979	-0.198	0.036	-0.031	-0.015	-0.006	0.001
	LSG(u)	0.698	0.484	-0.431	0.171	0.048	-0.232	0.085
	SPV	-0.647	-0.501	-0.123	-0.146	-0.229	-0.271	0.360
	TBS	0.350	0.527	0.699	-0.069	-0.292	-0.094	0.114
	GUL	-0.054	-0.220	0.038	0.874	-0.402	0.090	-0.091
	PSC	-0.226	-0.245	0.540	0.381	0.579	-0.328	0.088
	SDL-T(u)	0.408	0.260	0.039	0.109	0.321	0.592	0.461
	SDL-F(u)	-0.107	-0.203	-0.225	0.280	-0.146	0.277	0.607
	FP(u)	0.498	0.240	0.136	0.119	0.292	0.297	-0.094
	COS(u)	0.128	0.027	0.055	0.145	0.042	0.259	0.222
Eigenvalues		34.566	6.064	5.261	3.555	2.746	2.121	1.555
Proportion of variation		59.8%	10.5%	9.1%	6.2%	4.8%	3.7%	2.7%

Canonical variate analysis	Characters	CV1	CV2
	PC1	0.370	-0.119
	PC2	0.111	-0.050
	PC3	0.048	-0.038
	PC4	0.038	0.629
	PC5	0.065	0.179
	PC6	0.043	0.579
	PC7	-0.087	0.424
Eigenvalue		11.449	0.126
Proportion of intergroup variation		98.9%	1.1%

TABLE 6. Descriptive statistics for field samples of clonal *Aspidoscelis exsanguis* and bisexual *A. inornata*. For each character, first row: mean ± 1 SE (samples sharing the same capital letter in a row are not significantly different at $\alpha = 0.05$); second row: standard deviation (samples with different lower case letters in a row have significantly different variances for that character); third row: range and (sample size). Characters are described in appendix 1. Sample details are provided in appendix 2. For characters with (u), sample size was maximized by using the count from the right side of the body, except on individuals where that was not available, the left side was used.

Character	Species	
	A. exsanguis	*A. inornata*
PC1	1.0 ± 0.09 A 0.34 a 0.5 to 1.5 (13)	-0.7 ± 0.14 B 0.60 a -1.9 to 0.2 (19)
PC2	-0.1 ± 0.21 A 0.75 a -1.1 to 1.8 (13)	0.1 ± 0.26 A 1.16 a -2.0 to 2.6 (19)
DF1	4.2 ± 0.23 A 0.83 a 2.8 to 5.2 (13)	-2.9 ± 0.25 B 1.10 a -5.1 to -0.3 (19)
GAB	70.0 ± 0.58 A 2.55 a 65–76 (19)	61.4 ± 0.70 B 3.59 a 55–68 (26)
SPV	5.6 ± 0.14 A 0.60 a 4–6 (19)	9.8 ± 0.22 B 1.12 b 8–12 (26)
FP(u)	17.1 ± 0.19 A 0.81 a 16–18 (19)	15.3 ± 0.25 B 1.28 a 13–18 (26)
LSG(u)	14.7 ± 0.35 A 1.49 a 12–17 (18)	11.2 ± 0.58 B 2.86 a 7–20 (24)
SDL-T(u)	29.8 ± 0.24 A 1.03 a 28–32 (19)	27.9 ± 0.26 B 1.34 a 25–30 (26)
TBS	19.0 ± 0.63 A 2.73 a 15–25 (19)	16.9 ± 0.37 B 1.88 a 13–20 (26)
GUL	17.7 ± 0.44 A 1.87 a 15–22 (18)	17.2 ± 0.39 A 1.85 a 15–23 (22)
PSC	15.7 ± 0.35 A 1.33 a 14–18 (14)	15.7 ± 0.37 A 1.68 a 11–18 (21)
SDL-F(u)	14.4 ± 0.20 A 0.90 a 13–16 (19)	14.3 ± 0.19 A 0.94 a 13–16 (25)
COS(u)	4.7 ± 0.14 A 0.58 a 4–6 (18)	4.3 ± 0.19 A 0.94 a 3–6 (25)

Comparisons of Field Samples of *A. exsanguis* and *A. inornata*

Is it possible that aspects of the laboratory environment (e.g., temperature during egg incubation) have biased variation of morphological characters in the specimens of the laboratory lineages? As a check on this possibility, we repeated the comparisons here but included only the specimens obtained in the field (although we realize that differing environmental factors at the two localities might have affected development of the characters).

The field samples of *A. exsanguis* and *A. inornata* differed significantly in 6 of 10 univariate meristic characters (table 6), but we included all 10 characters in a PCA to obtain principal components to use as characters in a discriminate function analysis (table 7). Samples included in the PCA and DFA were reduced to 13 specimens of *A. exsanguis* and 19 of *A. inornata* because 13 individuals had damage to one or more characters. Six of the 10 principal components were selected by stepwise selection criteria (Materials and Methods) for inclusion in the DFA to discriminate the two samples (table 7).

The two species differed significantly in principal component 1 (PC1) and discriminant function 1 (DF1; table 6), and a Wilks' lambda value of 0.073 ($P < 0.0001$) suggested that interspecific differences were responsible for approximately 93% of the variation. There were no misclassifications among the 32 specimens. Only one character, SPV, had a significant interspecific difference in variance, with *A. inornata* being more variable than *A. exsanguis* (table 6).

Variation in Additional Characters

Our focus above has been on scalation characters that normally vary in *Aspidoscelis*, both from individual to individual within species and often with different ranges of variation from species to species and character to character. There are also scalation characters that are essentially invariant within groups of closely related species, so much so that they characterize members of species groups and genera of teiids. For example, all species of the *sexlineata* species group of *Aspidoscelis*, which includes both *A. exsanguis* and *A. inornata*, normally have 2 frontoparietal scales, 3 parietal scales, and 4 supraocular scales (each side) on the head (Lowe et al., 1970), and all species of the genus *Aspidoscelis* normally have 8 rows of large ventral scutes across midbody (Reeder et al., 2002). At higher levels of taxonomy, there are many scale characters that are taxonomically useful because they are essentially invariant within families but different from family to family. Consequently, it appears as if development of certain scale characters is canalized, while many are not, and we know nothing about the evolutionary significance of this. The following observations pertain to four characters that usually are thought of as essentially invariant.

Postantebrachial Scales on Forearm: the typical condition in *A. exsanguis* is for these scales (Duellman and Zweifel, 1962) to be enlarged and angular in shape, and this was the condition in all specimens examined, including 46 of the AMNH R-109468 lineage, 16 of the AMNH R-113352 lineage, and 19 of the field sample. The typical condition in *A. inornata* is for these scales to be smaller although somewhat enlarged, and this was the condition in all specimens examined, including 26 of the field sample.

TABLE 7. Correlations between characters and either principal components (PC) or discriminant function 1 (DF1) from multivariate analyses of field samples of clonal *Aspidoscelis exsanguis* and gonochoristic *A. inornata*. Univariate characters are described in appendix 1, and sample details for these analyses are provided in appendix 2. Principal components are those selected as having discrimination value by the DFA model.

Principal components analysis	Characters	PC1	PC3	PC4	PC5	PC6	PC7
	GAB	0.965	-0.183	0.0	0.080	-0.025	-0.003
	SPV	-0.723	-0.225	-0.213	0.527	0.235	0.004
	FP(u)	0.702	0.052	0.166	-0.049	-0.146	0.498
	LSG(u)	0.654	0.207	-0.109	0.069	0.153	0.062
	SDL-T(u)	0.709	-0.063	0.286	-0.174	0.195	-0.459
	TBS	0.427	0.696	-0.287	-0.030	0.080	-0.046
	GUL	0.032	0.607	0.705	0.345	-0.070	0.019
	PSC	-0.023	-0.177	0.310	-0.305	0.674	0.254
	SDL-F(u)	0.011	-0.112	0.281	0.122	0.418	-0.320
	COS(u)	0.391	-0.065	0.093	-0.149	0.259	0.036
Eigenvalues		31.944	6.233	3.283	2.294	2.023	1.290
Proportion of variation		56.3%	11.0%	5.8%	4.0%	3.6%	2.3%

Discriminant function analysis	Characters	DF1
	PC1	0.482
	PC3	0.035
	PC4	0.046
	PC5	-0.092
	PC6	-0.044
	PC7	0.037
Eigenvalue		12.723
Proportion of intergroup variation		100%

TABLE 8. Condition of enlarged ventral preanal scales in samples of two laboratory lineages of clonal *Aspidoscelis exsanguis* and a field sample each of *A. exsanguis* and gonochoristic *A. inornata*. Both P_1 field females had Type I.

Condition	Lineage of R-109468	Lineage of R-113352	Field *A. exsanguis*	Field *A. inornata*
Type I	24 (52%)	11 (69%)	12 (63%)	16 (62%)
Type II	1 (2%)	0 (0%)	0 (0%)	4 (15%)
Type III	21 (46%)	5 (31%)	7 (37%)	6 (23%)

Mesoptychial Scales Across Throat: These scales are on the anterior edge of the posterior gular fold on the throat. The typical condition in *A. exsanguis* is for these scales to be abruptly larger than the scales in the fold, rather large, and angular in shape, and this was the condition in all specimens examined, including 46 of the AMNH R-109468 lineage, 16 of the AMNH R-113352 lineage, and 19 of the field sample. The typical condition in *A. inornata* is for these scales to be somewhat enlarged and slightly angular in shape as compared to *A. exsanguis*, and this was the condition in all specimens examined, including 26 of the field sample.

Enlarged Ventral Scutes across Belly: On each specimen examined, these scales were counted in several places posterior to midbody. As is typical for the genus, nearly every specimen of *A. exsanguis* consistently had 8, including 44 of the AMNH R-109468 lineage, 16 of the AMNH R-113352 lineage, and 19 of the field sample. For one specimen of the R-109468 lineage (AMNH R-134888) the number of rows was reduced to 7 posterior to midbody, and for another individual the character could not be scored. Also, for 8 specimens (50%) in the R-113352 lineage, there were additional atypical enlarged ventrolateral scales beside the lateralmost ventral scute. For *A. inornata*, all 26 specimens in the field sample consistently had 8 rows, but AMNH R-131062 had additional atypical enlarged ventrolateral scales beside the lateralmost ventral scute.

Enlarged Ventral Preanal Scales: These scales were recorded as occurring in one of three conditions. In Type I there are 3 enlarged scales, 2 bordering the vent and 1 anterior to these. In Type II there are 2 enlarged scales, 1 bordering the vent and 1 anterior to it. Most specimens of *Aspidoscelis* have one or the other of these conditions. However, specimens with a different pattern of preanal scalation were scored in a catchall alternative called Type III. There was considerable variation in this character (table 8), although more than 50% of the four samples (the two laboratory lineages and two field samples) had Type I, but more than 20% of each sample had Type III. Type II was more common in *A. inornata* than *A. exsanguis*.

Did the Laboratory Environment Affect Morphological Characters?

It has been documented for various species of reptiles that environmental factors can affect the development of certain morphological characters, including some scale counts and certain important features such as sex determination (e.g., Fox, 1948; Osgood, 1978; Bull and Vogt, 1979; and Andrews et al., 2000). Consequently, we considered whether the laboratory environment affected development of some of the characters studied.

TABLE 9. Egg clutch and hatchling statistics for samples of two lineages of *Aspidoscelis exsanguis*. For each character, first row: mean ± 1 SE (samples sharing the same capital letter in a row are not significantly different at α = 0.05); second row: standard deviation (samples with different lower case letters in a row have significantly different variances for that character); third row: range and (sample size).Characters are described in the text; sample details are provided in appendix 2.

Character	Lineage	
	AMNH 109468	AMNH 113352
Egg weight at laying	0.78 ± 0.02 A 0.09 a 0.7 to 1.0 (33)	0.66 ± 0.03 B 0.09 a 0.6 to 0.8 (8)
Number of days to hatching	70.3 ± 1.07 A 7.23 a 58–84 (46)	74.6 ± 2.19 A 8.75 a 62–82 (16)
Weight at hatching	0.83 ± 0.02 A 0.11 a 0.6–1.0 (43)	0.77 ± 0.03 A 0.14 a 0.6–1.1 (16)
SVL at hatching	32.7 ± 0.21 A 1.35 a 30–35 (43)	30.8 ± 0.50 B 2.01 a 28–35 (16)

When a clutch was laid, we weighed it and divided by the number of eggs to estimate the weight of one egg in that clutch. Because eggs were incubated at room temperature, which varied, we recorded the number of days to hatching as a proxy for temperature. Finally, upon hatching, we recorded the weight and SVL of the hatchlings (table 9). Because GAB was the scale character with the widest range of variation, we compared that character with these life history variables. We used specimens having complete data for both lineages (AMNH R-109468 lineage $N = 30$; AMNH R-113352 lineage $N = 8$) in multiple regression analyses and regression of GAB on number of days to hatching, using data for the two lineages both separated and pooled (to increase sample size). No clear relationships were found.

SUMMARY AND CONCLUSIONS

For the characters we examined, there is no general pattern that shows clonal *A. exsanguis* as less variable than bisexual *A. inornata*. All meristic characters had a range of variation in the two laboratory lineages compared, not a fixed condition from individual to individual (table 1).

The two lineages of *A. exsanguis* cloned in the laboratory from field females collected at the same locality differed in 2 out of 10 meristic characters (GAB and COS(u); table 1). This is consistent with the theory that a population sample of a parthenogenetic species can consist of more than one clone, although we do not know whether the cause of these meristic differences is based on differences in DNA. This is consistent also with two laboratory clones of *A. neavesi* differing in 2 out of the same 10 characters (SPV and FP; Cole et al., 2014), and the

clutches of *A. neavesi* were also all incubated at one temperature (28° C), in this case at the Stowers Institute for Medical Research (D.P. Baumann, personal commun.). In general, the standard errors of the univariate variation of the 10 characters were similar in the *A. exsanguis* reported here and the *A. neavesi* reported by Cole et al. (2014), except that the standard errors were clearly higher in GAB, SDL-F(u), GUL, and PSC in the lineage of AMNH R-113352 reported here, which is the smallest sample.

Comparing standard deviations, the lineage of AMNH R-113352 was more variable than the lineage of AMNH R-109468 in GAB, PC1, and DF1, but the lineage of AMNH R-109468 was more variable in COS(u).

In univariate comparisons of 10 meristic characters of the field *A. exsanguis* versus the two laboratory lineages of *A. exsanguis* pooled, the only significant difference was in SDL-F(u) (table 4), but this character did not differ between the field *A. exsanguis* and *A. inornata*. Interestingly, this character did not differ between the two lineages (table 1) and the two characters that did differ between the lineages (GAB and COS) were not significantly different in this comparison (table 4). In multivariate characters, PC1 and CV1 of the field and laboratory *A. exsanguis* differed from *A. inornata* but not from each other; PC2 of laboratory *A. exsanguis* differed from *A. inornata* but not from field *A. exsanguis*; and CV2 differed between the field versus pooled laboratory lineages of *A. exsanguis* (table 4), but neither sample of *A. exsanguis* differed from *A. inornata* in this character. It appears as if samples of parthenogens collected in the field may be pooled samples of different clones, for which the distinctions may be concealed within the overall sample.

Clonal laboratory *A. exsanguis* was not less variable than bisexual *A. inornata* in any of the 10 univariate characters (table 4). In univariate comparisons, only SPV and TBS showed significant differences in variation. For TBS, field *A. exsanguis* was more variable than laboratory *A. exsanguis*, but neither sample differed from *A. inornata* in variation in this character. For SPV, bisexual *A. inornata* was more variable than the field *A. exsanguis* but not more so than the sample of two pooled laboratory clones (table 4). In multivariate comparisons of variation among these samples, the only difference was that the pooled lineages of cloned laboratory *A. exsanguis* showed greater variation in PC1 than the field sample of this species, but the variability of *A. inornata* was similar to both samples of *A. exsanguis* in this character. There were no differences in variation between *A. exsanguis* and *A. inornata* in PC2, CV1, and CV2 (table 4). The absence of differences in variability of the multivariate characters was also exhibited in comparing the field samples of *A. exsanguis* versus field samples of *A. inornata* (compare tables 4 and 6). In univariate comparisons of the field samples only, SPV was the only character that showed a difference in variation, which was higher in *A. inornata* than in *A. exsanguis* (table 6).

With respect to additional characters (e.g., number of enlarged ventral scutes across the belly), it would be interesting to know why (canalization?) certain characters are essentially invariant from individual to individual, whether members of the same lineage or not. Also, while many characters vary, the range of observed variation appears to be constrained to some extent, and the amount of the observed range also varies from character to character. In any event, we have no clear evidence that the laboratory environment affected development of the characters we studied.

ACKNOWLEDGMENTS

Fieldwork in New Mexico was based at the Southwestern Research Station (SWRS, Portal, AZ), with significant assistance from the director at that time, Wade C. Sherbrooke, and various volunteer assistants, including Jeffrey A. Cole. William C. Miller, Jr., and his son, Chet, of Rodeo and Post Office Canyon, Peloncillo Mountains, Hidalgo County, New Mexico, provided important advice and kept our field vehicle in top condition throughout our fieldwork. Charlie Painter and others in the New Mexico Department of Game and Fish provided the permits necessary for this research.

In the laboratory at the AMNH, Margaret G. Arnold, Colleen C. Coogan, Phil Damiani, David Dickey, George W. Foley, Sarah Heady, Mary Ellen Holden, and José P.O. Rosado provided important care for the animals in the lizard colony and curated the collections.

We also thank Peter E. Baumann, Robert L. Bezy, and William B. Neaves for providing thoughtful comments on an earlier version of the manuscript. This research was supported in part by the National Science Foundation (grant BSR-8105454 to C.J.C.). When necessary, the AMNH bridged the gap in funding, thanks largely to Michael J. Novacek.

REFERENCES

Andrews, R.M., T. Mathies, and D.A. Warner. 2000. Effect of incubation temperature on morphology, growth, and survival of juvenile *Sceloporus undulatus*. Herpetological Monographs 14: 420–431.

Bull, J.J., and R.C. Vogt. 1979. Temperature-dependent sex determination in turtles. Science 206: 1186–1188.

Cole, C.J., and H.C. Dessauer. 1993. Unisexual and bisexual whiptail lizards of the *Cnemidophorus lemniscatus* complex (Squamata: Teiidae) of the Guiana Region, South America, with descriptions of new species. American Museum Novitates 3081: 1–30.

Cole, C.J., H.C. Dessauer, and G.F. Barrowclough. 1988. Hybrid origin of a unisexual species of whiptail lizard, *Cnemidophorus neomexicanus*, in western North America: new evidence and a review. American Museum Novitates 2905: 1–38.

Cole, C.J., L.M. Hardy, H.C. Dessauer, H.L. Taylor, and C.R. Townsend. 2010. Laboratory hybridization among North American whiptail lizards, including *Aspidoscelis inornata arizonae* × *A. tigris marmorata* (Squamata: Teiidae), ancestors of unisexual clones in nature. American Museum Novitates 3698: 1–43.

Cole, C.J., H.L. Taylor, D.P. Baumann, and P. Baumann. 2014. Neaves' whiptail lizard: the first known tetraploid parthenogenetic tetrapod (Reptilia: Squamata: Teiidae). Breviora 539: 1–19.

Conover, W.J., M.E. Johnson, and M.M. Johnson. 1981. A comparative study of tests for homogeneity of variance, with applications to the Outer Continental Shelf bidding data. Technometrics 23: 351–361.

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. New York State Museum Bulletin 466: 49–71.

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 of the American Museum of Natural History 246: 1–148.

Duellman, W.E., and R.G. Zweifel. 1962. A synopsis of the lizards of the *sexlineatus* group (genus *Cnemidophorus*). Bulletin of the American Museum of Natural History 123 (3): 155–210.

Fox, W. 1948. Effects of temperature on development of scutellation in the garter snake, *Thamnophis elegans atratus*. Copeia 1948: 252–262.

Hardy, L.M., and C.J. Cole. 1981. Parthenogenetic reproduction in lizards: histological evidence. Journal of Morphology 170: 215–237.

Jombart, T., S. Devillard, and F. Balloux. 2010. Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genetics 11: art. 94. [approximately15 pp.]

Lowe, C.H., J.W. Wright, C.J. Cole, and R.L. Bezy. 1970. Chromosomes and evolution of the species groups of *Cnemidophorus* (Reptilia: Teiidae). Systematic Zoology 19: 128–141.

Lutes, A., W.B. Neaves, D.P. Baumann, W. Wiegraebe, and P. Baumann. 2010. Sister chromosome pairing maintains heterozygosity in parthenogenetic lizards. Nature 464: 283–286.

Lutes, A., D.P. Baumann, W.B. Neaves, and P. Baumann. 2011. Laboratory synthesis of an independently reproducing vertebrate species. Proceedings of the National Academy of Sciences of the United States of America 108: 9910–9915.

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

Neff, N.A., and L.F. Marcus. 1980. A survey of multivariate methods for systematics. New York: American Museum of Natural History.

Osgood, D.W. 1978. Effects of temperature on the development of meristic characters in *Natrix fasciata*. Copeia 1978: 33–47.

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

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.

Tabachnick, B.G., and L.S. Fidell. 2013. Using multivariate statistics. 6th ed. Upper Saddle River, NJ: Pearson Education, Inc.

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.

Taylor, H.L., C.J. Cole, G.J. Manning, J.E. Cordes, and J.M. Walker. 2012. 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*. American Museum Novitates 3744: 1–24.

Taylor, H.L., J.M. Walker, C.J. Cole, and H.C. Dessauer. 2015. Morphological divergence and genetic variation in the triploid parthenogenetic teiid lizard, *Aspidoscelis neotesselata*. Journal of Herpetology 49: 491–501.

Townsend, C.R. 1979. Establishment and maintenance of colonies of parthenogenetic whiptail lizards. International Zoo Yearbook 19: 80–86.

Townsend, C.R., and C.J. Cole. 1985. Additional notes on requirements of captive whiptail lizards (*Cnemidophorus*), with emphasis on ultraviolet radiation. Zoo Biology 4: 49–55.

Walker, J.M., H.L. Taylor, and T.P. Maslin. 1966. Evidence for specific recognition of the San Esteban whiptail lizard (*Cnemidophorus estebanensis*). Copeia 1966: 498–505.

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.

APPENDIX 1

Character Abbreviations

Abbreviations for morphological characters examined are listed below. Any character abbreviation followed by (u) indicates that it is a paired character and the count used is from one side of the body (unilateral; the right side, but the left side if the right could not be counted, as in table 1). This maximizes sample size, and the paired characters used this way normally do not show asymmetry in *Aspidoscelis*, including hybrids (e.g., Dessauer et al., 2000: 99–101). If a paired character is not followed by (u), the total of both sides is presented.

COS(u), number of circumorbital semicircle scales (following Wright and Lowe, 1967, using the count from the right side of the head, but left side if right could not be counted).

FP(u), number of femoral pores on right leg, but left leg if right could not be counted.

GAB, number of dorsal scales (granules) around midbody, following Wright and Lowe (1967).

GUL, number of gular scales, following Cole et al. (1988).

LSG(u), number of lateral supraocular granules (on right side of head, whether in one or two rows, but left side if right could not be counted) between the supraoculars and superciliaries, counting forward from an imaginary line extended from the suture between the third and fourth supraoculars toward the superciliaries, following Walker et al. (1966).

PSC, total number of scales in contact with outer perimeter of parietal and interparietal scales, following Cole et al. (2010).

SDL-F(u), number of subdigital lamellae on the right fourth finger, but using the left finger if the right could not be counted, following Taylor et al. (2001).

SDL-T(u), number of subdigital lamellae on the right fourth toe, but using the left toe if the right could not be counted, following Cole et al. (1988).

SPV, number of granules (scales) between the paravertebral light stripes at midbody, following Wright and Lowe (1967).

SVL, snout-vent (body) length, in mm.

TBS, number of enlarged dorsal scales around dorsal aspect of base of tail; the count is made while holding the hind legs at the hip perpendicular to the body and counting on an imaginary line along the posterior edges of the legs, but not including lateral granules on the tail.

APPENDIX 2

Specimens Examined

All specimens are in the herpetological collections of the AMNH. The P_1 parent of each laboratory lineage of *A. exsanguis* is listed with the field sample.

Laboratory Lineage of *A. exsanguis* AMNH R-109468: F_1 generation (AMNH R-113359); F_2 generation (AMNH R-115990–115992, R-122852–122854, and R-122856); F_3 generation (AMNH R-122863, R-122865–122867, R-122888–122889, and R-122895–122897); F_4 generation (AMNH R-122879–122881, R-122883, R-122913–122914, R-122916, and R-122929); F_5 generation (AMNH R-122918–122919, R-122921–122922, R-134875, and R-134884); F_6 generation (AMNH R-134879 and R-134888–134894); F_7 generation (AMNH R-134895–134901).

Laboratory Lineage of *A. exsanguis* AMNH R-113352: F_1 generation (AMNH R-113356); F_2 generation (AMNH R-115978–115982, R-115987, R-122843–122847, and R-122849–122850); F_3 generation (AMNH R-122899–122900).

Field *A. exsanguis*: The sample was accumulated over many years during which time several collectors visited the site and noted the locality slightly differently from time to time. Nevertheless, all of the following specimens were collected at one and the same place. NEW MEXICO: Hidalgo County; Clanton Draw, Peloncillo Mountains, 1700 m elev. (AMNH R-84751 and R-84754); 4.8 km W, 12.1 km N Cloverdale (AMNH R-109350, R-109468, R-113352, and R-115993); Clanton Canyon, 4.8 km W and 12.1 km N (linear) Cloverdale, 1700 m elev. (AMNH R-114148–114151); Clanton Canyon, Peloncillo Mountains, 4.8 km W, 12.1 km N Cloverdale (AMNH R-119513–119518, and R-119520–119522).

Field *A. inornata*: The sample was accumulated over many years along a stretch of 1.1 km of highway in desert-grassland. Only females, which are the specimens cited below, were used for the study. NEW MEXICO: Hidalgo County; 26.9 km (by US hwy 70) NW Lordsburg, 1340 m elev. (AMNH R-131061–131064, R-114192–114194, R-114197–114199, R-114200–114202, R-114204, and R-114211); 27.2 km (by US hwy 70) NW Lordsburg, 1310 m elev. (AMNH R-120669–120670); 27.5 km (by US hwy 70) NW Lordsburg, 1325 m elev. (AMNH R-114206); 27.7 km (by US hwy 70) NW Lordsburg (AMNH R-120656, R-125538, R-125542, and R-131065); 28 km (by US hwy 70) NW Lordsburg, 1310 m elev. (AMNH R-112840, R-114185–114186, and R-114188).

All issues of *Novitates* and *Bulletin* are available on the web (http://digitallibrary.amnh.org/dspace). Order printed copies on the web from:
http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html

or via standard mail from:
American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).