Herpetological Conservation and Biology 7(2): 227–248
Submitted: 25 January 2012; Accepted: 30 July 2012; Published: 10 September 2012.

MICHELLE'S LIZARD: IDENTITY, RELATIONSHIPS, AND ECOLOGICAL STATUS OF AN ARRAY OF PARTHENOGENETIC LIZARDS (GENUS *ASPIDOSCELIS*: SQUAMATA: TEIIDAE) IN COLORADO, USA

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Abstract.*—Using a shared photograph, we identified a lizard captured by a young naturalist in 1995 in La Junta, Otero County, Colorado, USA, to either triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata*) or diploid parthenogenetic Common Checkered Whiptail (*A. tesselata*). On 12 August 1997, LJL located the species in question near the original La Junta location. The parthenogenetic species at La Junta represents a new pattern class, *A. neotesselata* D, identity and distinctiveness of which were verified by both univariate and multivariate statistics. We used other triploid lizards from sites ~100 km apart (i.e., *A. neotesselata* D from La Junta and *A. neotesselata* A from Pueblo, Pueblo County, Colorado) to verify skin histocompatibility, indicating that each group was derived from the same hybridization event. We also identified a tetraploid hybrid of *A. neotesselata* x *A. sexlineata viridis* from La Junta. Of the several small patches of habitat that support *A. neotesselata* D and Prairie Racerunner (*A. sexlineata viridis*) at La Junta, only a few are elevated above the flood zone of the adjacent Arkansas River. An unusual characteristic of flat parts of La Junta involves the life cycle of Kochia (*Kochia scoparia*). This tall-growing annual constitutes ~100% of the vegetative structure on these flats from germination in the spring until die-off in the fall/winter. Searches to increase the known range of *A. neotesselata* D beyond 1 km of La Junta were unsuccessful. We regard the La Junta array of *A. neotesselata* D as a naturally occurring peripheral isolate.

Key Words.—Aspidoscelis; ecology; evolution; flood disturbance; Kochia; parthenogenesis

INTRODUCTION

As nine-year old Michelle Keefer and her mother Sue emerged from a local restaurant (37.987804°N, 103.537873°W) on 15 June 1995 in La Junta, Otero County, Colorado, USA, Michelle captured a juvenile whiptail lizard (family Teiidae) on a paved parking lot. The animal was carried to the family residence near Las Animas ~30 km east of La Junta where it was photographed by Sue Keefer before it escaped. Believing that the mysterious lizard discovered through serendipity by his daughter could be of biological significance, the photograph was passed among the authors for opinions on the identity of the animal (Fig. 1). As a result, LJL visually verified the presence of the species at a second site in La Junta, near the Arkansas River, on 12 August 1997 (Figs. 2–3). News of that discovery stimulated JMW to initiate field research on what the authors hypothesized was a previously overlooked and established extralimital array (i.e., group of asexual parthenogenetic individuals) of one of the two hybrid-derived species (triploid Colorado Checkered Whiptail, *Aspidoscelis neotesselata* or diploid Common Checkered Whiptail, *A. tesselata*) of all-female lizards in southeastern Colorado (Fig. 4) based on Walker et al. (1995, 1997). From 1997–2009, we sought to evaluate the biological significance of the surprising presence of this array of all-female lizards in a radically altered, perpetually disturbed, highly vulnerable, and readily accessible ecological setting on private property in the central area of the city of La Junta near the Arkansas River (Fig. 5). We undertook to answer these questions: (1) which species and pattern class in the *A. tesselata* complex is represented there; (2) was the array descended from naturally occurring or introduced ancestors; (3) is it disjunct from other members of the complex; (4) is there evidence of hybridization between normally parthenogenetic individuals and males of the syntopic gonochoristic paternal progenitor, Prairie Racerunner (*A. sexlineata viridis*); and (5) is the La Junta array threatened by natural and/or human perturbations?

FIGURE 1. Photograph of the first individual of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata* pattern class D) discovered; a second year juvenile shown in a terrarium. It was captured 15 June 1995 by Michelle Keefer on a paved parking lot at a Pizza Hut Restaurant (37.987804ºN, 103.537873ºW) at 402 E First Street, south of the Arkansas River, La Junta, Otero County, Colorado, USA. (Photographed by Sue Keefer).

FIGURE 3. Photograph of habitat elevated above the flood zone of the Arkansas River consisting of a jumble of concrete blocks, sandy/loamy soil, and thick Kochia (*Kochia scoparia*) where North Street from Colorado Hwy. 109 enters the northeastern edge of La Junta-BNSF, La Junta, Otero County, Colorado, USA. Both triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata* pattern class D) and gonochoristic Prairie Racerunner (*Aspidoscelis sexlineata viridis*) were observed here during most visits to the site from 1997–2009. (Photographed by Lauren J. Livo).

FIGURE 2. Photograph of first individual triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata* pattern class D) observed at the northeastern edge of La Junta-BNSF (37.990555ºN, 103.533291ºW), south of the Arkansas River, La Junta, Otero County, Colorado, USA.. This was a second year juvenile found 12 August 1997. (Photographed by Lauren J. Livo).

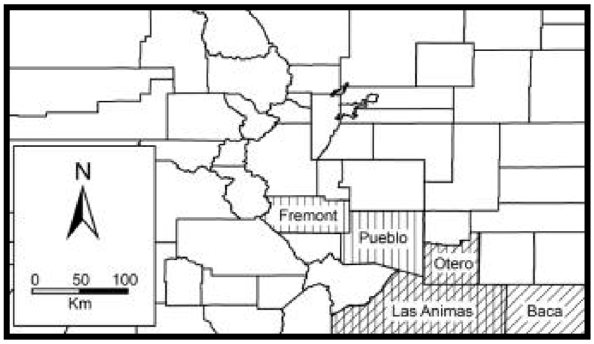

FIGURE 4. Map of the state of Colorado, USA, showing counties with sites inhabited by diploid parthenogenetic Common Checkered Whiptail (*Aspidoscelis tesselata*; angled hatching), those with sites inhabited by triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata*; vertical hatching), and those with sites inhabited by both species (cross hatching).

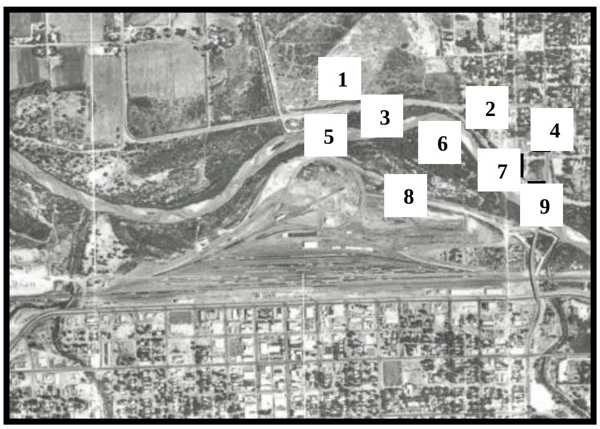

FIGURE 5. Satellite image of the Burlington Northern and Santa Fe inactive railway complex (= La Junta-BNSF) inhabited by triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata* pattern class D) and gonochoristic Prairie Racerunner (*Aspidoscelis sexlineata viridis*), immediately south of the Arkansas River in La Junta, Otero County, Colorado, USA. From top to bottom are: 1, Church Road; 2, searched habitat; 3, wetland in floodplain; 4, suburban area; 5, remnants of turning circle for trains where no lizards were observed; 6, part of site not used by whiptail species in 1997–1999; 7, another part of the site potentially central to presence of both species; 8, prime lizard habitat; and 9, Colorado Hwy 109. (Image copied from Google Earth [e.g. © 2011 Google]; numbers added by James M. Walker).

MATERIALS AND METHODS

Genus, complex, species, pattern classes, and SSAR common names.—*Aspidoscelis* was resurrected from the synonymy of the genus *Cnemidophorus*, found to be paraphyletic by Reeder et al. (2002), for whiptail lizards exclusive of members of the *C. lemniscatus* group (*sensu* Burt 1931) in South and Central America. Of the three species in the parthenogenetic *A. tesselata* complex (Walker et al. 1990, 1995, 1997; Cordes and Walker 2006) two of them inhabit parts of southeastern Colorado. Diploid (typically 2n = 46) *A. tesselata* is distributed from the Mexican state Chihuahua northward into Texas, New Mexico, Oklahoma, and some canyonland parts of Baca, Las Animas, and Otero counties, Colorado (Zweifel 1965; Parker and Selander1976; Walker et al. 1997; Fig. 4). Triploid (typically 3n = 69) *A. neotesselata* is endemic to southeastern Colorado in a variety of habitats in parts of Fremont, Las Animas, Otero, and Pueblo counties (Fig. 4), and it occurs with its maternal progenitor *A. tesselata* at some sites in Otero and Las Animas counties (Parker and Selander 1976; Walker et al. 1995, 1997; Walker and Cordes 1998; Taylor et al. 2006a).

We chose not to lead in implementing the use of plural common names for the taxa of *Aspidoscelis* as recommended for all animal species by de Queiroz (2011), using instead forms of common names recommended in the checklist of the Society for the Study of Amphibians and Reptiles by Crother et al. (2008). We also circumvented use of the term population in favor of array for a local group of individuals that is representative of a parthenogenetic species of *Aspidoscelis*. We refer to a mosaic of arrays of individuals of the same species of *Aspidoscelis*, characterized by similar dorsal color schemes in contiguous geographic areas in southeastern Colorado, as pattern classes, each designated by an upper case letter following the species epithet (*sensu* Zweifel 1965; Walker et al. 1997; Cordes and Walker 2006). Included are allopatric pattern classes A, B, C, and D (newly identified herein) in *A. neotesselata* (e.g., as in Fig. 6), and C and D in *A. tesselata* which are syntopic in the vicinity of Higbee, Otero County (Table 1).

Sampling and samples compared.—We collected specimens of parthenogenetic *A. neotesselata* and gonochoristic *A. sexlineata viridis* from La Junta under authority of state permits in 1997–2009 on an inactive, but publically accessible, property of Burlington Northern and Santa Fe Railway Company (= La Junta-BNSF; see Figs. 5–7), and adjacent areas. The distinctive configuration of the La Junta-BNSF site and points of significance therein, located between the south side of the Arkansas River and First Street, is depicted in the satellite image in Fig. 5. We discovered parthenogenetic lizards at La Junta-BNSF on 12 August 1997 through visual identification (Figs. 2–3; Appendix 1) ~580 m north-northeast of where Michelle Keefer fortuitously captured the juvenile in 1995 (Fig. 1).

To determine the specific identity (*A. neotesselata* versus *A. tesselata* C) and pattern class of parthenogenetic lizards in La Junta, we compared the array to the following samples (codes based on Walker and Cordes 1998): La Junta-BNSF, Otero County (*A. sexlineata viridis*); Higbee-Ninemile Valley = Higbee-

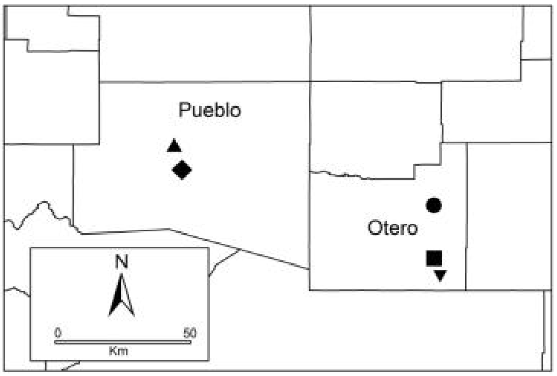

FIGURE 6. Map showing sites in southeastern Colorado, USA, from which we obtained samples of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata*) [La Junta-BNSF (●); Pueblo-NC (▲); Lime-SCR (♦); Higbee-VCT (■)], diploid parthenogenetic Common Checkered Whiptail (*Aspidoscelis tesselata*) [Higbee-NV (▼)], and gonochoristic Prairie Racerunner (*Aspidoscelis sexlineata viridis*) [La Junta-BNSF (●)].

NV, Otero County (*A. tesselata* C); Higbee-Vogel Canyon Trailhead = Higbee-VCT, Otero County (*A. neotesselata* B); Higbee-Vogel Canyon = Higbee-VC, Otero County (*A. tesselata* C and *A. neotesselata* B); Pueblo-Nature Center = Pueblo-NC, Pueblo County (*A. neotesselata* A); and Lime-St. Charles River = Lime-SCR, Pueblo County (*A. neotesselata* C; Table 1). We did not consider use of specimens of *A. tesselata* pattern class D from Higbee‑VC, Higbee-VCT, and Higbee-NV to be relevant to this study (see photographs in Walker et al. 1997). The specimens examined for use in various analyses (Appendices 1–6) are from the following collections: American Museum of Natural History (AMNH); Regis University (RU); University of Arkansas Department of Zoology (UADZ); and University of Colorado Museum of Natural History (UCM).

Statistical treatments.—We used SPSS Statistics 17 software for statistical routines including canonical variate analyses (CVA; SPSS 2008), a multivariate technique that can determine how well pre-identified (*a priori*) groups can be discriminated based on information in a particular set of characters (Tabachnick and Fidell 2001). We employed a step-wise character selection procedure for each CVA, with characters incorporated into a model if *F*-probabilities did not exceed 0.05 when other characters were entered (see Tables 3–11). Characters were retained in the model if probabilities did not change to exceed 0.10 when other characters were added. We tested univariate means for significant differences using ANOVA, and specific differences ($\alpha = 0.05$) among samples were revealed by *post hoc* multiple comparison tests (Tukey HSD used for characters with

FIGURE 7. Photographs of three habitat components of the La Junta-BNSF site occupied by one or both of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata* pattern class D = *A. n.* D) and gonochoristic Prairie Racerunner (*Aspidoscelis sexlineata viridis*). A: looking east along dirt/gravel road (extending under Colorado Hwy 109) bordered by thick annual growths of Kochia (*Kochia scoparia*) forming prime habitat for both whiptail lizard species in 1997–1999, but subject to periodic flooding. B: looking west along North Street (extending from Colorado Hwy 109 into the site) bordered by mixture of grasses/forbs forming marginal habitat for *A. n.* D, but above the flood zone. C: looking east along an abandoned railroad spur on a levee (at west end of La Junta-BNSF) with mixture of shrubs/grasses/forbs forming prime habitat for *A. n.* D, but above the floodplain of the Arkansas River on the left and narrow wetland with Common Reed (*Phragmites australis)* on the right. (Photographed by James M. Walker).

TABLE 1. Species and pattern classes either present (P; color-shaded) or absent (unshaded) at each of the coded sites, arranged west to east, from which we examined or referenced specimens of *Aspidoscelis* in southeastern Colorado, USA.

Site Code	*A. n.* A (3n) ♀♀	*A. n.* B (3n) ♀♀	*A. n.* C (3n) ♀♀	*A. n.* D (3n) ♀♀	*A. t.* C (2n) ♀♀	*A. t.* D (2n) ♀♀	*A. s. v.* ♀♂
Pueblo-NC	P						
Pueblo-CD		P					P
Lime-SCR			P				P
La Junta-BNSF				P			P
Higbee-VCT		P				P	P
Higbee-VC		P			P	P	P
Higbee-NV		P			P	P	P

homogeneous variances and Tamhane's T-2 used for characters with heterogeneous variances).

Basic color patterns.—We use standard terminology with reference to the dorsal color patterns in *A. neotesselata* and *A. tesselata* in southeastern Colorado,

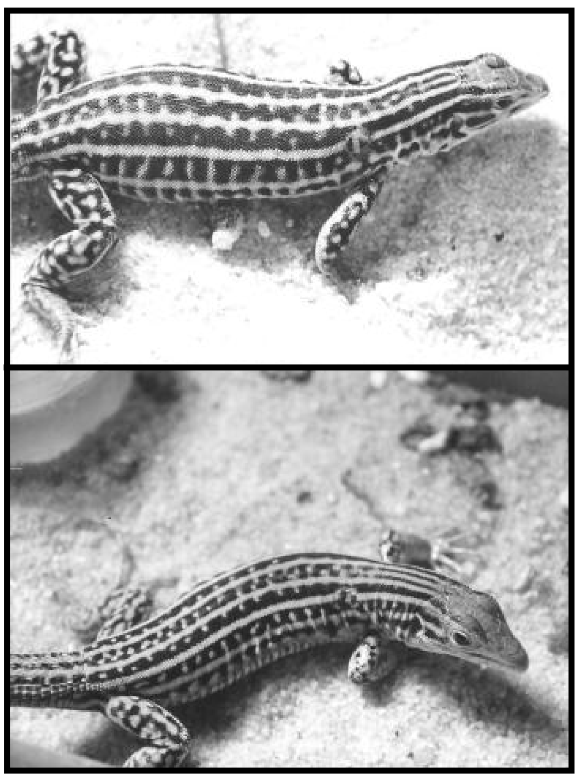

FIGURE 8. Photographs of individuals of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata*) captured by HLT and JMW and used in the laboratory by JEC in histocompatibility experiments (note accepted circular graft in second stripe dorsal to right forelimb of each lizard). Top: UADZ 6218 (pattern class D) from La Junta-BNSF (graft accepted 328 days). Bottom: UADZ 6222 (pattern class A) from Pueblo-NC (graft accepted 278 days). (Photographed by James E. Cordes).

which is discussed in reference to numerous photographs in Walker et al. (1995, 1997). To summarize, juveniles and adults in both species have a black ground color giving way to gray/tan near the ventral scales (Figs. 1–2, and 8). There are six pale longitudinal primary stripes (= fixed in position) arranged in three bilateral pairs (ventral to dorsal): the laterals, dorsolaterals, and paravertebrals. A partial, complete, broken (= fragmented), unbroken (= complete), or zigzag vertebral line is present between the paravertebral stripes (Fig. 8). The intervening black areas between the stripes include the bilateral lower and upper lateral fields ventral and dorsal, respectively, to the lateral stripes, the dorsolateral fields between the dorsolateral and paravertebral stripes, and the vertebral field between the paravertebral stripes. Rounded light-colored areas in the dorsal pattern are termed spots; light areas perpendicular to stripes are termed bars (Fig. 8). The color pattern of gonochoristic *A. sexlineata viridis* includes three bilateral pairs of primary stripes, named as in the *A. tesselata* complex, a vertebral stripe of variable expression, and intervening fields devoid of spots and bars.

Characters analyzed.—Scutellation characters (terminology after Burt 1931; Smith 1946; Walker 1981a, b) analyzed in samples of *Aspidoscelis* included: GAB, granules (= scales) at midbody counted from the right outer row of ventral scales over the body to the left outer row of ventrals; OR, dorsal granules longitudinally from the occipitals to the first row of caudals; PV, granules between the paravertebral stripes at midbody; FP, femoral pores on the ventral aspect of each thigh (summed from both sides); SDL, subdigital lamellae on the longest toe of the left pes; COS, circumorbital scales between the supraoculars and median cephalic scales (summed); LSG, lateral supraocular granules between the supraoculars and superciliary scales anterior to junction between third and fourth supraoculars (summed); MS, enlarged mesoptychial scales at the edge of the gular fold; and ILS, interlabial scales (summed).

TABLE 2. Aspects of dorsal color pattern used to distinguish triploid Colorado Checkered Whiptail (*Aspidoscelis neotesselata* D) from Common Checkered Whiptail (*Aspidoscelis tesselata* C) in southeastern Colorado, USA.

Aspect of Dorsal Pattern	*Aspidoscelis neotesselata* D (3n) La Junta-BNSF	*Aspidoscelis tesselata* C (2n) Higbee-NV
Pattern on posterior surface of thigh	Gray-white stripe/slash on black	Irregular gray-white spots on black
Primary dorsal Stripes	Three pairs- relatively straight	Three pairs-somewhat irregular
Light colored pattern in vertebral field	Dash, partial stripe, or linear spots	Zigzag vertebral “stripe”
Lateral stripe complete or not	Few if any interruptions	Interruptions common
Vertical bars between stripes	Low number present	Extensive barring between stripes
Fields and stripes on base of tail	Distinctly apparent on tail	Not apparent on tail (spots present)

Color pattern characters quantitatively analyzed in juvenile specimens (SVL 37–55 mm, n = 48) of triploid parthenogenetic *A. neotesselata* (see Appendix 3), in addition to the PV previously described, included: PV/GAB x 100, percentage of the granules around midbody between the paravertebral stripes at midbody;D L, granules between the dorsolateral stripes at midbody; DL/GAB x 100, percentage of the granules around midbody between the dorsolateral stripes at midbody; VS/VF x 100, percentage of the vertebral field between the paravertebrals occupied by the vertebral line from interparietal to its first interruption; VF, stripe fragments/spots in the vertebral field from occiput to rump; SPUL, spots in the left upper lateral field; SPLL, spots in the left lower lateral field; CONL, constrictions along the length of the left lateral stripe; and CONPV, constrictions along the length of the left paravertebral stripe. Color pattern characters quantitatively analyzed in adult specimens (SVL 73–106 mm, n = 46) of *A. neotesselata* (see Appendix 4), in addition to the PV, PV/GAB, DL, DL/GAB, VS/VF, VF, SPUL, and SPLL, included: SPDL, spots in the left dorsolateral field; BLL, bars in the left lower lateral field; and ILL, interruptions in the left lateral stripe.

Histocompatibility experiments.—We conducted three sets of experiments using reciprocal skin grafts to assess genetic relationships of the La Junta-BNSF array of parthenogenetic lizards (Appendix 6). One of us (JEC) used techniques for skin-grafting and laboratory maintenance of lizards described by Cordes and Walker (2003, 2006) and Taylor et al. (2005). Set 1 allografts were exchanged between an adult from La Junta-BNSF (UADZ 6218) and one of its suspected closest relatives from Pueblo-NC (UADZ 6222) captured by HLT and JMW in June 1998. Set 2 allografts were exchanged between two adults lizards from La Junta-BNSF (UADZ 7770–7771) captured by GJM in August 2004. Set 3 xenografts were exchanged between two lizards from La Junta-BNSF (UADZ 7770–7771) and two individuals of *A. tesselata* C from Sumner Lake State Park, De Baca County, New Mexico (RU 0079–0080) captured by HLT in July 2003.

Ploidy levels.—We became familiar with the color pattern and/or scutellation characters useful in distinguishing both allopatric and syntopic arrays of superficially similar, and occasionally syntopic, diploid *A. tesselata* C and triploid *A. neotesselata* B (see figures and data in Walker et al. 1995, 1997) using specimens collected by E. D. Parker, Jr. at Higbee-VC and Higbee-NV (see Appendix 5). Ploidy levels in these specimens had been determined by electrophoretic analyses of proteins (Parker and Selander 1976).

RESULTS

Specific identity of the La Junta array of all-female lizards.—We identified parthenogenetic lizards in the La Junta-BNSF and Higbee-NV samples to different species based on differences in color pattern in all ontogenetic stages. Our *A. tesselata* reference was from ~ 30 km south of La Junta, the nearest site for *A. tesselata* C (Fig. 6). Lizards from La Junta-BNSF (Figs. 1–2, 8) represent triploid *A. neotesselata* based on the set of aspects of dorsal pattern (e.g., character of stripes on body, line on posterior part of each thigh, and stripes/fields on base of tail) summarized in detail in Table 2. Lizards from Higbee-NV (Fig. 6) near the Purgatoire River represent diploid *A. tesselata* C based on the set of aspects of dorsal pattern (e.g., character of stripes on body, spots on posterior part of each thigh, and scattered spots on base of tail) summarized in detail in Table 2. The foregoing distinguishing features in color patterns of La Junta-BNSF and Higbee-NV lizards were congruent with significant differences between eight of nine meristic characters compared in Table 3. In addition, the multivariate distinctiveness of the La Junta-BNSF and Higbee-NV samples was evident in the plot of CV scores for specimens grouped by qualitative features of color pattern (Fig. 9; Tables 4–5). Plots for the two samples were widely separated on the CV1 axis, and there were

TABLE 3. Univariate comparisons of nine meristic characters of scutellation, CV1, and CV2 in four pattern classes of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata* = *A. n.*) (D from La Junta-BNSF, Otero County; A from Pueblo-NC, Pueblo County; B from Higbee-VCT, Otero County; C from Lime-SCR, Pueblo County); one pattern class of diploid parthenogenetic Common Checkered Whiptail (*Aspidoscelis tesselata* = *A. t.*) (C from Higbee-NV, Otero County); and one sample of gonochoristic Prairie Racerunner (*Aspidoscelis sexlineata viridis* = *A. s. v.*) (from La Junta-BNSF). Characters include: GAB, granular scales around midbody; OR, scales from the occipital scales to the base of tail; PV, scales between paravertebral stripes at midbody; FP, femoral pores summed; SDL, subdigital lamellae of left longest toe; COS, circumorbital scales summed; LSG, lateral supraocular scales summed; MS, mesoptychial scales; ILS, interlabial scales summed; and CV, canonical variate (see text for details). Numbers are means ± SE with range and (n) beneath; two means are significantly different if they do not share a common superscripted letter.

Character	La Junta-BNSF *A. n.* D (3n)	Pueblo-NC *A. n.* A (3n)	Higbee-VCT *A. n.* B (3n)	Lime-SCR *A. n.* C (3n)	Higbee-NV *A. t.* C (2n)	La Junta-BNSF *A. s. v.*
GAB	77.0 ± 0.30^{A} 73–84 (61)	82.8 ± 0.52^{B} 74–104 (74)	85.4 ± 0.67^{C} 80–100 (29)	86.1 ± 0.38^{C} 80–92 (48)	90.8 ± 0.25^{D} 86–98 (88)	78.3 ± 1.01^{A} 71–89 (19)
OR	182.7 ± 0.60^{A} 167–193 (61)	193.4 ± 0.71^{B} 177–208 (74)	198.1 ± 1.05^{C} 190-218 (29)	188.8 ± 0.64^{D} 178–197 (48)	191.2 ± 0.50^{AD} 181–207 (88)	192.2 ± 2.91^{ABCD} 170–214 (19)
PV	6.7 ± 0.12^{A} 5–9 (61)	7.2 ± 0.16^{A} 5–14 (74)	10.8 ± 0.15^{BD} 9–12 (29)	9.1 ± 0.13^{BC} 8–11 (48)	10.3 ± 0.09^{D} 9–12 (88)	9.3 ± 0.28^{C} 7–12 (19)
FP	39.4 ± 0.19^{A} 35–43 (61)	38.0 ± 0.19^{B} 33–43 (73)	39.8 ± 0.32^{A} 36–43 (29)	37.7 ± 0.26^{B} 34–42 (48)	41.3 ± 0.17^{C} 37–45 (87)	31.2 ± 0.47^{D} 28–36 (19)
SDL	33.4 ± 0.16^{A} 28–35 (61)	34.6 ± 0.18^{B} 30–38 (71)	35.3 ± 0.27^{B} 32–39 (29)	34.4 ± 0.18^{B} 32–37 (48)	37.4 ± 0.12^{C} 35–41 (88)	26.7 ± 0.40^{D} 25–31 (19)
COS	12.8 ± 0.18^{A} 9–16 (60)	11.4 ± 0.20^{B} 8–17 (74)	13.6 ± 0.51^{AC} 11–26 (29)	15.4 ± 0.37^{C} 10–22 (47)	17.4 ± 0.21^{D} 13–22 (88)	6.6 ± 0.39^{E} 4–9 (19)
LSG	17.6 ± 0.23^{A} 13–23 (60)	22.4 ± 0.32^{B} 16–29 (74)	22.5 ± 0.50^{B} 17–27 (29)	21.0 ± 0.35^{B} 15–28 (48)	35.3 ± 0.26^{C} 30–43 (88)	20.6 ± 1.37^{AB} 11–38 (19)
MS	13.4 ± 0.11^{A} 11–15 (61)	13.9 ± 0.15^{A} 11–17 (74)	13.2 ± 0.27^{AB} 11–16 (29)	13.5 ± 0.14^{A} 11–15 (48)	12.7 ± 0.12^{BC} 10–16 (88)	13.5 ± 0.28^{AC} 11–15 (19)
ILS	31.3 ± 0.42^{A} 24–39 (60)	33.2 ± 0.82^{A} 19–62 (74)	40.3 ± 1.95^{B} 26–67 (29)	40.1 ± 1.00^{B} 28–55 (47)	38.7 ± 0.47^{B} 29–48 (88)	19.0 ± 0.73^{C} 14–26 (19)
CV1	-2.79 ± 0.10^{A} -4.7 to -1.3 (60)	-1.80 ± 0.12^{B} -4.1–0.60 (70)	0.05 ± 0.20^{C} -1.6–3.8 (29)	-0.54 ± 0.16^{C} -2.7–1.9 (47)	5.2 ± 0.09^{D} 3.2–7.4 (87)	-6.9 ± 0.41^{E} -9.9 to -3.01 (19)
CV2	2.17 ± 0.10^{A} -0.004–3.6 (60)	0.18 ± 0.12^{B} -4.3–2.6 (70)	-0.06 ± 0.18^{B} -2.2–2.1 (29)	0.60 ± 0.14^{B} -1.9–2.7 (47)	-0.73 ± 0.10^{C} -2.9–2.2 (87)	-5.7 ± 0.38^{D} -10.6 to -3.8 (19)

no misclassified individuals between the samples of *A. neotesselata* from La Junta-BNSF and *A. tesselata* C from Higbee-NV (Fig. 9; Table 5).

Intraspecific affinities of the La Junta array.—We identified lizards in the samples from La Junta-BNSF and Higbee-VCT (the nearest site for *A. neotesselata* B at ~24 km south of La Junta; Fig. 6) to different pattern classes of *A. neotesselata* based on divergent dorsal color schemes in all available lizards. Specimens from Higbee-VCT represented *A. neotesselata* B based on seven dorsal stripes or their remnants throughout ontogeny, numerous bars between the stripes, and the lateral stripes interrupted by extensive barring (see photographs in Walker et al. 1995, 1997). Postformational divergence in the color patterns of La Junta-BNSF and Higbee-VCT lizards was congruent with significant differences between the samples in six (GAB, OR, PV, SDL, LSG, and ILS) of nine meristic characters (Table 3). The lower range of variation (5–9) in the La Junta-BNSF and higher range (9–12) in the Higbee-VCT samples for the PV character were correlated with the six-striped pattern in the former and seven-striped pattern in the latter. The multivariate meristic distinctiveness of the two samples is apparent in the plots of CV scores for specimens in six *a priori* groups identified by qualitative features of color pattern (Fig. 9; Tables 4–5). Means of both CV1 and CV2 were significantly different between La Junta-BNSF and Higbee-VCT samples (Table 3). There were no misclassified specimens between the two samples (Fig. 9, Table 5).

***Recognition of a new pattern class of* Aspidoscelis neotesselata.**—We compared the La Junta-BNSF sample to samples from Lime-SCR (nearest site for *A. neotesselata* C at ~17 km south of Pueblo and ~96 km west of La Junta; Fig. 6), and Pueblo-NC (nearest

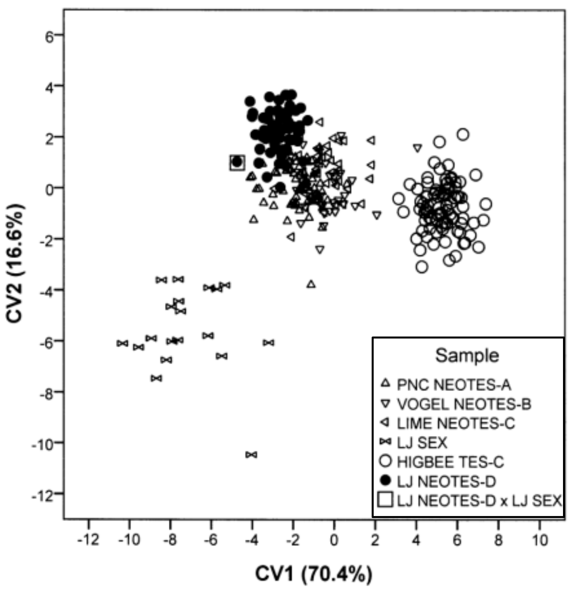

FIGURE 9. Morphological relationships expressed by the distribution of canonical variate scores derived from a canonical variate analysis of 10 meristic characters for 312 specimens of three species of *Aspidoscelis* from Pueblo (Pueblo-NC and Lime-SCR) and Otero (La Junta-BNSF, Higbee-VCT and Higbee-NV) counties, Colorado, USA. Included are specimens of pattern classes A, B, C, and D (first recognized herein) of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata*), pattern class C of diploid parthenogenetic Common Checkered Whiptail (*Aspidoscelis tesselata*), and gonochoristic Prairie Racerunner (*Aspidoscelis sexlineata viridis*). Percentages represent the proportion of explained meristic variation accounted for by canonical variates, CV1 and CV2.

site for *A. neotesselata* A at Pueblo ~103 km west of La Junta) for qualitative features of color pattern, univariate and multivariate comparisons of juvenile and adult color patterns, and univariate and multivariate comparisons of

TABLE 4. Loadings (correlations between meristic characters and canonical variates) from a canonical variate analysis based on 10 meristic characters of scutellation and six a priori groups of whiptail lizards: four pattern classes of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata*; 60 specimens of D from La Junta-BNSF, Otero County; 70 of A from Pueblo-NC, Pueblo County; 29 of B from Higbee-VCT, Otero County; 47 of C from Lime-SCR, Pueblo County); one pattern class of diploid parthenogenetic Common Ckeckered Whiptail (*Aspidoscelis tesselata*; 87 of C from Higbee-NV, Otero County); and one sample of gonochoristic Prairie Racerunner (*Aspidoscelis sexlineata viridis*; 19 from La Junta-BNSF). Abbreviations are the same as in Table 3, except SO (supraocular scales summed).

Character	CV1 Loadings	CV2 Loadings
GAB	0.380	-0.237
OR	0.043	-0.237
PV	0.272	-0.459
FP	0.332	0.414
LSDL	0.468	0.371
COS	0.375	0.205
LSG	0.611	-0.501
MS	-0.087	0.046
ILS	0.184	0.174
SO	-0.009	0.058
Eigenvalues	13.435	3.170
Proportion of discrimination accounted for by CV	70.4%	16.6%

variation in scutellation. Pattern class B was excluded from the analysis based on findings presented in the preceding section. The univariate comparison of 10 color pattern variables among juveniles of the samples (Table 6) revealed that La Junta-BNSF lizards differed significantly from Lime-SCR lizards in six characters

TABLE 5. Classification based on a canonical variate analysis of 10 characters of scutellation for specimens in six *a priori* groups of whiptail lizards: four pattern classes of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata* = *A. n.*): D from La Junta-BNSF, Otero County; A from Pueblo-NC, Pueblo County; B from Higbee-VCT, Otero County; C from Lime-SCR, Pueblo County; one pattern class of diploid parthenogenetic Common Checkered Whiptail (*Aspidoscelis tesselata* = *A. t.*): C from Higbee-NV, Otero County; and one sample of gonochoristic *Aspidoscelis sexlineata viridis* = *A. s. v.* from La Junta-BNSF, grouped on the basis of qualitative features of color pattern; color-shading indicates misclassified individuals.

A priori Group	La Junta-BNSF *A. n.* D (3n)	Higbee-VCT *A. n.* B (3n)	Lime-SCR *A. n.* C (3n)	Pueblo-NC *A. n.* A (3n)	Higbee-NV *A. t.* C (2n)	La Junta-BNSF *A. s. v.*
La Junta-BNSF *A. n.* D	58	0	1	1	0	0
Higbee-VCT *A. n.* B	0	27	1	1	0	0
Lime-SCR *A. n.* C	0	2	41	4	0	0
Pueblo-NC *A. n.* A	4	1	7	58	0	0
Higbee-NV *A. t.* C	0	0	0	0	87	0
La Junta-BNSF *A. s. v.*	0	0	0	0	0	19

TABLE 6. Univariate comparisons of 10 characters of color pattern, CV1, and CV2 in three pattern classes of young-of-year of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata* = *A. n.*) (D from La Junta-BNSF, Otero County; A from Pueblo-NC, Pueblo County; C from Lime-SCR, Pueblo County) grouped on the basis of qualitative features of color pattern. Characters include: PV, granular scales between paravertebral stripes at midbody; PV/GAB x 100, percentage of the scales around midbody between paravertebral stripes at midbody; DL, scales between the dorsolateral stripes at midbody; DL/GAB x 100, percentage of the scales around midbody between dorsolateral stripes at midbody; VS/VF x 100, percentage of the vertebral field between paravertebrals occupied by the vertebral line from interparietal to its first interruption; VF, stripe fragments/spots in vertebral field from occiput to rump; SPUL, spots in left upper lateral field; SPLL, spots in left lower lateral field; CONL, constrictions along the length of the left lateral stripe; CONPV, constrictions along the length of the left paravertebral stripe; and CV, canonical variate (see text for details). Numbers are mean ± SE with range and (N) beneath; two means are significantly different if they do not share a common superscripted letter.

Character	La Junta-BNSF *A. n.* D (3n)	Pueblo-NC *A. n.* A (3n)	Lime-SCR *A. n.* C (3n)
PV	7.2 ± 0.16^{B} 6–8 (21)	7.8 ± 0.48^{B} 6–14 (16)	9.1 ± 0.28^{A} 8–10 (11)
PV/GAB	9.2 ± 0.21^{B} 7.6–10.9 (21)	9.1 ± 0.38^{B} 7.5–13.4 (16)	10.5 ± 0.28^{A} 9.0–11.9 (11)
DL	24.6 ± 0.21^{B} 23–27 (21)	26.1 ± 0.61^{A} 24–34 (16)	27.5 ± 0.31^{A} 25–29 (11)
DL/GAB	31.7 ± 0.23^{A} 29.6–33.7 (21)	31.0 ± 0.31^{A} 29.9–32.9 (16)	31.9 ± 0.46^{A} 29.4–35.0 (11)
VS/VF	26.0 ± 1.22^{A} 15.6–35.4 (21)	18.2 ± 1.52^{B} 8.6–29.2 (16)	21.9 ± 2.02^{A} 11.6–34.4 (11)
VF	12.0 ± 0.61^{B} 7–19 (21)	12.4 ± 1.61^{B} 3–27 (16)	18.1 ± 0.84^{A} 13–23 (11)
SPUL	19.7 ± 1.12^{A} 2–28 (21)	19.4 ± 0.38^{A} 17–21 (16)	19.1 ± 0.68^{A} 16–23 (11)
SPLL	15.3 ± 0.54^{B} 9–19 (21)	17.1 ± 0.24^{A} 15–18 (16)	15.2 ± 0.44^{B} 14–18 (11)
CONL	12.8 ± 0.90^{B} 3–20 (21)	19.0 ± 0.34^{A} 16–22 (16)	18.6 ± 0.43^{A} 16–21 (11)
CONPV	14.8 ± 0.67^{B} 9–19 (21)	19.7 ± 0.56^{A} 16–24 (16)	21.0 ± 0.47^{A} 18–23 (11)
CV1	-1.44 ± 0.28^{C} -3.72–0.90 (21)	0.74 ± 0.17^{B} -0.63–1.81 (16)	1.68 ± 0.20^{A} 0.72–2.77 (11)
CV2	-0.19 ± 0.26^{B} -2.82–1.40 (21)	0.86 ± 0.23^{A} -1.18–2.31 (16)	-0.87 ± 0.16^{B} -1.63 to -0.06 (11)

PV, PV/GAB, DL, VF, CONL, and CONPV) and from Pueblo-NC in five characters (DL, VS/VF, SPLL, CONL, and CONPV). Significant differences in different univariate characters among the three samples made it worthwhile to apply a canonical variate analysis (CVA) of color pattern variables for a composite perspective of sample differences (Table 7; Fig. 10). Only seven of 48 specimens (14.6%) were misclassified, of which three La Junta-BNSF specimens were classified to Pueblo-NC and one to Lime-SCR (Table 8). Because of ontogenetic variation in color pattern, we used a different set of 10 characters to compare La Junta-BNSF adults with those from Lime-SCR and Pueblo-NC. The La Junta-BNSF sample differed from Lime-SCR in PV, PV/GAB, Dl, VS/VF, SPDL, SPUL, BLL, and LI, and from Pueblo-NC in PV, SPDL, SPUL, and BLL (Table 9). As was found for juveniles, two new characters (CV1 and CV2) derived from the CVA (Table 10) were useful in simplifying the underlying pattern of sample differences (Fig. 11). Only three of 46 specimens (6.5%) were misclassified by the CVA model; the single misclassified La Junta-BNSF specimen was classified to Pueblo-NC (Table 11).

In a univariate comparison of scutellation characters, the La Junta-BNSF array differed significantly from *A. neotesselata* C at Lime-SCR in all meristic variables except the MS (Table 3). Not surprisingly, our CVA of scutellation characters (Table 4) revealed that the two arrays were well-differentiated, with single individuals from La Junta-BNSF being misclassified to the Lime-SCR and Pueblo-NC samples (Table 5).

The remaining issue to be resolved was whether the La Junta-BNSF and Pueblo-NC sample differences in scutellation (they are significantly different in GAB, OR, FP, SDL, COS, LSG) and juvenile and adult color patterns identify them as different pattern classes of *A. neotesselata*. In addition to the univariate and multivariate distinctiveness of lizards in the La Junta-BNSF sample, we found that when mixed with Pueblo-NC specimens in the same storage containers, 100% could be correctly sorted without recourse to other laboratory or field data. This could be accomplished by observing either the ventral coloration or dorsal pattern of a lizard. Those from La Junta-BNSF retained a gray-blue to distinctly blue coloration in the central thoracic area and lateral abdominal rows of ventral scales, while Pueblo-NC lizards retained an off-white to cream-white coloration in these regions. Dorsally, La Junta-BNSF lizards were characterized by a reduction in the number of spots and bars in the lower lateral, upper lateral, and dorsolateral fields, darker stripe colors, and distinctly blue (juveniles) to gray-blue tail (adults). Thus, we will henceforth refer to the La Junta-BNSF array as *A. neotesselata* pattern class D.

Origin of the La Junta array of* Aspidoscelis neotesselata *D.—On 2 July 1998, JEC excised patches of integument from similar positions on the anterior parts of adult lizards from La Junta-BNSF (UADZ 6218) captured on 29 June 1998 and from Pueblo-NC (UADZ 6222) captured on 30 June 1998 (Fig. 6). The patches were exchanged between the lizards to cover the wounds made by the respective excisions with the length of stripe in each patch oriented at a right angle to the dorsolateral stripe of the recipient. It was evident within

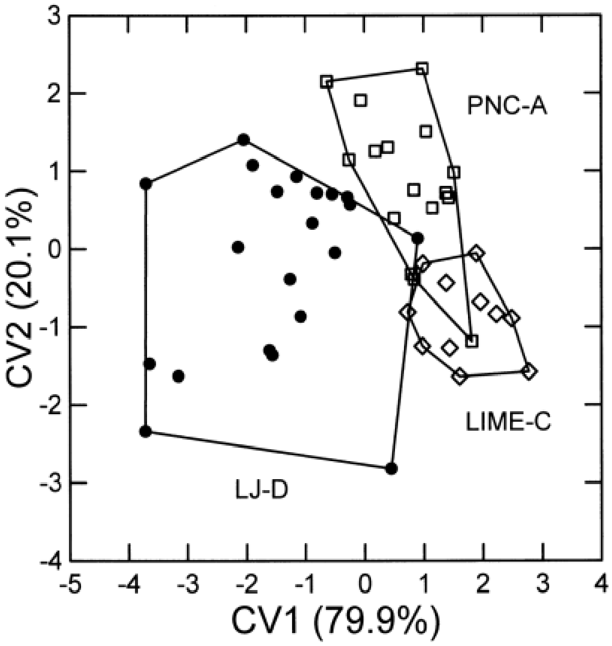

FIGURE 10. Color pattern distinctiveness expressed by the distribution of canonical variate scores derived from a canonical variate analysis of four meristic characters for 48 juvenile specimens of *Aspidoscelis* from Pueblo (Pueblo-NC and Lime-SCR) and Otero (La Junta-BNSF) counties, Colorado, USA. Included are specimens of pattern classes A, C, and D (first recognized herein) of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata*). Percentages represent the proportion of explained meristic variation accounted for by canonical variates, CV1 and CV2.

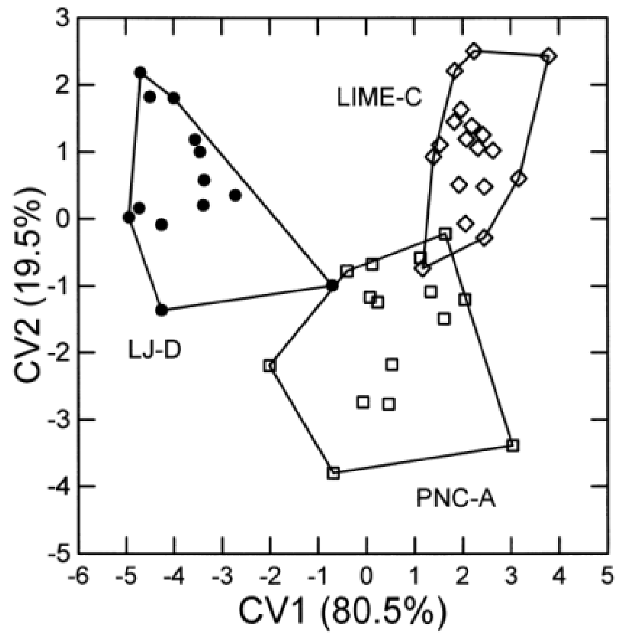

FIGURE 11. Color pattern distinctiveness expressed by the distribution of canonical variate scores derived from a canonical variate analysis of four meristic characters for 46 adult specimens of *Aspidoscelis* from Pueblo (Pueblo-NC and Lime-SCR) and Otero (La Junta-BNSF) counties, Colorado, USA. Included are specimens of pattern classes A, C, and D (first recognized herein) of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata*). Percentages represent the proportion of explained meristic variation accounted for by canonical variates, CV1 and CV2.

three weeks that the grafts were growing on the recipients (Fig. 8). Both UADZ 6218 from La Junta-BNSF and UADZ 6222 from Pueblo-NC, sites ~103 km apart, retained the viable donated grafts until their deaths on 26 May 1999 (sacrificed after 332 days of captivity) and 6 April 1999 (died after 281 days of captivity). The histocompatibility experiments did not hamper the overall conditions of the lizards as indicated by laboratory clutch production (e.g., UADZ 6218 laid clutches of three eggs on 15 August 1998 and four eggs on 22 December 1998, 12 February 1999, and 19 May 1999; UADZ 6222 laid a clutch of three eggs on 14 January 1999).

Capture of UADZ 7770–7771 at La Junta-BNSF permitted us to exchange reciprocal allografts between individuals of *A. neotesselata* D from the same site on 8 October 2004; both lizards accepted the grafts and retained them until they were sacrificed after 180 days. These two sets of reciprocal graft exchange experiments indicated that the two females from geographically distant sites and two females from the same site had the histocompatibility responses that would be expected between identical twins, indicating that all were the descendants of the same *A. tesselata* x *A. sexlineata* fertilization event. The third set of reciprocal graft exchanges involving two UADZ lizards from La Junta-BNSF and two RU lizards from Sumner Lake State Park, New Mexico, resulted in acceptance of the graft from RU 0080 by UADZ 7770 and from RU 0079 by UADZ 7771 and rejection of the graft from UADZ 7770 by RU 0080 and from UADZ 7771 by RU 0079.

Interspecific hybridization.—The first lizard obtained by JMW at La Junta-BNSF on 20 August 1997, in color pattern and meristic variables, is unlike any other specimen of either *A. neotesselata* D or *A. sexlineata viridis* subsequently obtained at the site. Support for the hypothesis that UADZ 6014 is a tetraploid (4n = 92) hybrid female of triploid *A. neotesselata* D x *A. sexlineata viridis* is indicated by the following observations: it was collected in a roadside patch of habitat occupied by both species; it has lower GAB, OR, and FP counts than any of the several hundred specimens of *A. neotesselata* examined to date, it has a distinctive color pattern of straight stripes, reduced spotting, and an unusually distinctive blue tail (in life) unlike all *A.*

Table 7. Loadings (correlations between meristic characters and canonical variates) from a canonical variate analysis based on four color pattern characters and three *a priori* groups of juvenile *Aspidoscelis neotesselata*: (21 specimens of D from La Junta-BNSF, Otero County; 16 of A from Pueblo-NC, Pueblo County; 11 of C from Lime-SCR, Pueblo County). Abbreviations are the same for included characters as in Table 6.

Character	CV1 Loadings	CV2 Loadings
VF	0.321	-0.573
SLL	0.128	0.672
CONL	0.734	0.467
CONPV	0.810	0.139
Eigenvalues	1.859	0.466
Proportion of discrimination accounted for by CV	79.9%	20.1%

Table 8. Classification based on a canonical variate analysis of four color pattern characters (CONPV, CONL, VF, SLL) for 48 juvenile specimens in three *a priori* groups = pattern classes of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata* = *A. n.*) (D from La Junta-BNSF, Otero County; A from Pueblo-NC, Pueblo County; and C Lime-SCR, Pueblo County) grouped on the basis of qualitative features of color pattern. See text for characters indicated by abbreviations; color-shading indicates misclassified individuals.

A Priori Group	La Junta-BNSF *A. n.* D (3n)	Pueblo-NC *A. n.* A (3n)	Lime-SCR *A. n.* C (3n)
La Junta-BNSF (*A. n.* D)	17	3	1
Pueblo-NC (*A. n.* A)	0	13	3
Lime-SCR (*A. n.* C)	0	0	11

neotesselata examined. A plot of its CV scores revealed that it shared the same CV scores as an individual of La Junta-BNSF *A. neotesselata* D (Fig. 9). However, we consider the alternative explanation that UADZ 6014 is an "outlier" specimen of *A. neotesselata* D to be untenable for these reasons: the observed correlation between hybrid origin and lower GAB, OR, and FP scores compared to the range of variation for the maternal parent and the presence of color pattern characters trending toward the paternal parent, but not identical to it.

Distribution area of* Aspidoscelis neotesselata *D.— Prior to the historic flood in May 1999, knowledge of the distribution of *A. neotesselata* D in La Junta had progressed as follows: initial discovery was made at a restaurant parking lot at 402 E First Street on 15 June 1995 by Michelle Keefer, first observed/photographed at La Junta-BNSF between First Street and the Arkansas River on 12 August 1997 by LJL, and first observed/

Table 9. Univariate comparisons of 10 characters of color pattern, CV1, and CV2 in adults of three pattern classes of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata* = *A. n.*) (D from La Junta-BNSF, Otero County; A from Pueblo-NC, Pueblo County; C from Lime-SCR, Pueblo County) grouped on the basis of qualitative features of color pattern. Characters include: PV, granular scales between paravertebral stripes at midbody; PV/GAB, percentage of the scales around midbody between paravertebral stripes at midbody; DL, scales between the dorsolateral stripes at midbody; DL/GAB x 100, percentage of the scales around midbody between dorsolateral stripes at midbody; VS/VF X 100, percentage of the vertebral field between paravertebrals occupied by the vertebral line from interparietal to its first interruption; VF, stripe fragments/spots in vertebral field from occiput to rump; SPDL, spots in the left dorsolateral field; SPUL, spots in left upper lateral field; BLL, bars in the left lower lateral field; ILL, interruptions in the left lateral stripe; and CV, canonical variate (see text for details). Numbers are mean ± SE with range and (n) beneath; two means are significantly different if they do not share a common superscripted letter.

Character	La Junta-BNSF *A. n.* D (3n)	Pueblo-NC *A. n.* A (3n)	Lime-SCR *A. n.* C (3n)
PV	6.3 ± 0.17^{C} 5–7 (13)	7.3 ± 0.35^{B} 6–10 (15)	8.6 ± 0.16^{A} 8–10 (18)
PV/GAB	8.1 ± 0.22^{B} 6.5–9.2 (13)	8.9 ± 0.32^{B} 7.3–11.2 (15)	10.0 ± 0.19^{A} 9.0–11.7 (18)
DL	24.8 ± 0.28^{B} 23–27 (13)	25.9 ± 0.44^{B} 23–29 (15)	27.6 ± 0.25^{A} 26–30 (18)
DL/GAB	31.7 ± 0.34^{A} 29.8–33.7 (13)	31.7 ± 0.33^{A} 29.7–33.7 (15)	31.9 ± 0.23^{A} 30.2–34.0 (18)
VS/VF	22.3 ± 2.96^{B} 7.4–46.7 (13)	26.9 ± 2.48^{B} 10.4–39.6 (15)	40.6 ± 2.56^{A} 25.3–68.1 (18)
VF	10.2 ± 0.70^{A} 5–13 (13)	11.4 ± 0.86^{A} 5–17 (15)	8.6 ± 1.05^{A} 2–18 (18)
SPDL	15.2 ± 0.53^{C} 12–19 (13)	20.9 ± 1.05^{B} 14–28 (15)	26.9 ± 0.68^{A} 22–31 (18)
SPUL	20.5 ± 0.57^{C} 17–24 (13)	22.5 ± 0.42^{B} 20–25 (15)	25.6 ± 0.41^{A} 23–29 (18)
BLL	5.7 ± 0.90^{B} 3–14 (13)	16.4 ± 0.72^{A} 13–24 (15)	16.2 ± 0.27^{A} 14–18 (18)
ILL	0.7 ± 0.17^{B} 0–2 (21)	2.5 ± 0.87^{B} 0–10 (15)	5.0 ± 0.80^{A} 0–13 (18)
CV1	-3.73 ± 0.31^{C} -4.93 to -0.70 (13)	0.60 ± 0.32^{B} -2.01–3.03 (15)	2.19 ± 0.14^{A} 1.17–3.79 (18)
CV2	0.53 ± 0.29^{A} -1.36–2.18 (13)	-1.70 ± 0.28^{B} -3.80 to -0.22 (15)	1.04 ± 0.21^{A} -0.73–2.50 (18)

collected in various parts of La Junta-BNSF on 20 August 1997 by JMW (Fig. 5; Appendix 1). Subsequently, *A. neotesselata* D was observed/collected near the entrance road to La Junta-BNSF in the summer of 1999 by JMW indicating that some whiptails had either survived or had been unaffected by the flood.

No whiptail lizards were observed in 1999 by JMW at 10.6 km east of La Junta (straight line distance [SLD]) in the area of historic Bent's Old Fort on the north side of the Arkansas River. Also, only *A. sexlineata viridis* was

TABLE 10. Loadings (correlations between meristic characters and canonical variates) from a canonical variate analysis based on four characters and three *a priori* groups of adult *Aspidoscelis neotesselata*: (13 specimens of D from La Junta-BNSF, Otero County; 15 of A from Pueblo-NC, Pueblo County; 18 of C from Lime-SCR, Pueblo County). Abbreviations are the same as in the preceding table.

Character	CV1 Loadings	CV2 Loadings
PV	0.388	0.269
SPUL	0.438	0.372
SPDL	0.608	0.360
BLL	0.789	-0.495
Eigenvalues	6.355	1.541
Proportion of discrimination accounted for by CV	80.5%	19.5%

TABLE 11. Classification based on a canonical variate analysis of four characters (BLL, SPDL, PV, SPUL) of color pattern for 46 specimens of adults in three *a priori* groups = pattern classes of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata* = *A. n.*) (D from La Junta-BNSF, Otero County; A from Pueblo-NC, Pueblo County; and C from Lime-SCR, Pueblo County) grouped on the basis of qualitative features of color pattern. See text for characters indicated by abbreviations; color-shading indicates misclassified individuals.

A Priori Group	La Junta-BNSF *A. n.* D (3n)	Pueblo-NC *A. n.* A (3n)	Lime-SCR *A. n.* C (3n)
La Junta-BNSF (*A. n.* D)	12	1	0
Pueblo-NC (*A. n.* A)	0	14	1
Lime-SCR (*A. n.* C)	0	1	17

observed in 1999 by SK and JMW on the south side of John Martin Reservoir on the Arkansas River at 50.6 km E of La Junta (SLD). Similarly, JMW observed only *A. sexlineata viridis* during visits to the Lyon Canal several blocks north of La Junta-BNSF. A report to JMW from personnel at the office of the Comanche National Grassland indicated that workers had observed spotted whiptail lizards near Anderson Arroyo in southwestern La Junta; however, lizards were not found on several visits to that area. Numerous attempts by JMW to locate *A. neotesselata* between La Junta and the following areas known to be inhabited by different pattern classes of the species were also unsuccessful: Vogel Canyon Trailhead to the south-southwest via Colorado Hwy 109; Iron Springs to the southwest via U. S. Hwy 330; and Pueblo to the east by U. S. Hwy 50. Measurements (SLD) using Google Earth that clarify the position and size dimensions of the La Junta-BNSF distribution area for *A. neotesselata* D are: east-west from the junction of unpaved North Street/ Colorado Hwy 109 to an inactive circular train turning component, 700 m; variation in north-south widths of parts with patches of habitat inhabited by whiptail lizards, 100–150 m; North Street entrance to the point of collection of first individual of *A. neotesselata* D at the Pizza Hut, 580 m; slope from Colorado Hwy 109 to flats of La Junta-BNSF, 120 m; and shortest distance from a part of La Junta-BNSF inhabited by lizards to Arkansas River, 45 m (see Figs. 3, 5).

An estimated 75% of La Junta-BNSF is unsuitable for whiptail lizards, examples being a west end narrow strip of persistent wetlands with Common Reed (*Phragmites australis*), centrally located catch basins surrounded by stands of annual Kochia (*Kochia scoparia*), southeastern grassy area formerly littered with derelict appliances, a southwestern poorly drained area with stunted vegetation and the inactive circular train turning area (Fig. 5). Interspersed among the aforementioned areas not used whiptail lizards are disconnected patches of habitat where lizards predictably could be observed, examples being disclimax vegetation consisting mostly of grasses/forbs in gravelly/rocky soil along the sides of the sloped part of the North Street entrance to the site (Fig. 7B), an elevated railroad spur/levee with grasses/forbs/shrubs with a jumble of rocky debris at the west end (Fig. 7C), and a growth of Kochia around a slightly elevated jumble of concrete blocks at the base of the slope of the entrance road (Fig. 3). All patches of habitat where both species were observed in the floodplain of La Junta-BNSF were characterized by sandy/loamy/gravelly soil with pure stands of Kochia that grow to > 2.0 m in height and > 1.0 m in diameter (Figs. 3, 7A). The combined area of the several patches occupied by lizards in 1997–2002 did not exceed 2 ha in dry periods (e.g., fall of 1998 and summer of 2002) or more than 1 ha (e.g., early summer of 1999) to 1.5 ha in wet years (e. g. fall of 1997).

The most severe catastrophic flood event in the La Junta area since 5 May 1955 occurred on 2 May 1999 when the Arkansas River crested at 4.74 m (http://water.weather.gov/ahps2/crests.php?wfo=pub&gage=lxhc2). During the 1999 flood, the rising Arkansas River at 45–80 m north of La Junta-BNSF (Fig. 3, 5) spilled across the site and contributed to First Street, the main east to west thoroughfare of La Junta, becoming a canal several feet deep. The flood also inundated the area near Pizza Hut where *A. neotesselata* D was discovered in June 1995. Four topographical features (previously listed as stable components) totaling less than 1.5 ha, based on the pattern of visible hydraulic erosion, likely served as refugia for some individuals of *A. neotesselata* D and *A. sexlineata viridis* during the flood. These included the 120 m long part of North St. that sloped from Hwy 109 to the flat area (Fig. 5), the slightly elevated 20 x 35 m area with the jumble of concrete blocks on the north side of the street as it entered the flats (Fig. 3), the gravelly/rocky abandoned railroad spur/earthen levee of 4–7 m in width and elevated 2–3 m above the north side of the street and 2–3 m above the floodplain of the Arkansas River (Fig. 7C), and a sloping dirt/gravel Kochia-bordered road passing under the highway bridge (Fig. 5, 7A).

DISCUSSION

Aspidoscelis neotesselata, *a hybrid-derived triploid species.*—Based on data for the world herpetofauna in Sites et al. (2011), triploid *A. neotesselata* would be among 9,004 species of lizards and snakes, 5,486 species of lizards, and one of only ~40 independent origins of a vertebrate obligate parthenogenetic species. The evolutionary progression that produced the array of *A. neotesselata* D at La Junta-BNSF began thousands of years ago in the Chihuahuan Desert in either southern Trans-Pecos Texas or northern Chihuahua State, Mexico. There, a single hybrid (Cordes and Walker 2006) of *A. tigris marmorata* x *A. gularis septemvittata* (Wright and Lowe 1967; Parker and Selander 1976; Dessauer and Cole 1989) was the founder of diploid parthenogenetic *A. tesselata*. In thousands of generations its descendants became the all-female species of *Aspidoscelis* with the largest latitudinal range, and a biogeographic newcomer to the herpetofauna of southeastern Colorado. Today, > 90% of the ~1000 km latitudinal range of *A. tesselata* is north of the present day range of the paternal progenitor Big Bend Spotted Whiptail (*A. gularis septemvittata*) in Texas and > 50% of its range is north of the present day range of the maternal progenitor Western Marbled Whiptail (*A. tigris marmorata* = *A. marmorata marmorata*) in New Mexico.

The second stage in the evolution of *A. neotesselata* occurred in or near the Purgatoire River Valley, in the general area of one of the largest dinosaur track sites in the world, only 30–50 km south-southwest of La Junta in either Otero or Las Animas counties (Taylor et al. 2006a) where a single hybrid (James Cordes and James Walker, unpubl. data) of *A. tesselata* x *A. sexlineata viridis* (Wright and Lowe 1967; Parker and Selander 1976; Dessauer and Cole 1989) was the founder of the species. Today, only *A. neotesselata* among the seven triploid species of *Aspidoscelis* has extant maternal and paternal progenitors, and is syntopic with both of them at some sites (Walker et al. 1997; Walker and Cordes 1998; Taylor et al. 2006a). Hybrids between *A. tesselata* and its maternal progenitor (i.e., *A. tigris marmorata*) are sterile (Taylor et al. 2001). However, hybridity (i.e., addition of the genome from *A. sexlineata viridis*) coincidental with parthenogenetic capability preadapted *A. neotesselata* (Taylor et al. 2006a) for coexistence with both of its progenitors in the canyonlands of Las Animas and Otero counties, and also allowed it to spread into habitats that are extralimital to the adaptive potential of *A. tesselata* (e.g., at La Junta-BNSF, Pueblo-NC, and Lime-SCR; Fig. 6; Table 12; Appendix 7). Some sites inhabited by *A. neotesselata* in Fremont, Pueblo, and Otero counties are situated at higher elevations along the montane foothills/canyonlands/Great Plains ecotones in which *A. sexlineata viridis* is also present, but not *A. tesselata* C (Hammerson 1999). That *A. neotesselata* has made no further inroads into the lower elevations of the Great Plains than to La Junta to the northeast is in part based on the absence of accessible habitats with rocky/gravelly soil and open-structured shrubby vegetation.

Certain consequences of asexuality in species of the *A. tesselata* complex have been experimentally revealed, and a general paradigm established. Acceptance of reciprocal grafts by parthenogenetic lizards with the same ploidy levels (i.e., histocompatibility) indicates that they represent descendants from the same interspecific hybridization event (Cuellar 1976, 1977; Abuhteba et al. 2000; Cordes and Walker 2003, 2006). Rejection of reciprocal grafts by parthenogenetic lizards of an array with the same ploidy (i.e., histoincompatibility) indicates that they represent different interspecific hybridization events, an exception being when only random individuals of an array have accumulated mutations among genes affecting immunogical responses (Abuhteba et al. 2000, 2001). Individuals of gonochoristic species reject reciprocal grafts (Maslin 1967; Cuellar and Smart 1977). Maslin (1967) also found that triploid lizards in the *A. tesselata* complex accept grafts from diploid individuals in the complex. For example, we found that diploid *A. tesselata* from Sumner Lake that accepted reciprocal grafts (Taylor et al. 2005) rejected the grafts of triploid *A. neotesselata* from La Junta–BNSF (see Maslin 1967; this study).

Aspidoscelis neotesselata, *a composite of four pattern classes.*—*Aspidoscelis neotesselata* comprises a minimum of four distinctive regional color pattern classes, each of which could be recognized as a parthenogenetic species based on diagnosability and an allopatric distribution area. Each of pattern classes A, B, C, and D (sensu Zweifel 1965; Walker et al. 1995, 1997, this study) is identifiable by stable characters (e.g., dorsal color pattern schemes, quantitative characters of color pattern in juveniles and adults, and scutellation). The extent of the distinctiveness of the pattern classes is further indicated by the remarkable multivariate classification success of juveniles (Table 8) in view of the tendency of closely related *Aspidoscelis* juveniles not to have well-differentiated color patterns (Duellman and Zweifel 1962).

A postformational mode of origin of the four color pattern classes in *A. neotesselata* is supported by results of our histocompatibility experiments (e.g., mutual acceptance of reciprocal grafts in A and D from widely separated localities). All together, these entities comprise a large amount of phenotypic variation relative to the small geographic range of the species, obligate parthenogenetic reproduction, and recent origin

Table 12. Variation among the five sites in southeastern Colorado inhabited by various combinations of species and pattern classes of parthenogenetic and gonochoristic *Aspidoscelis* lizards. L = location; H = habitat description; N ≈ number of lizards present; R = risk of lizards to extirpation or other negative impacts.

Local Site and Species Present, Followed by Descriptors	
Pueblo-NC (Pueblo County)‑*Aspidoscelis neotesselata* A	
L	Near trails and roads in the public Nature and Raptor Center of Pueblo, and immediate environs on the north side of Arkansas River in Pueblo
H	Narrow riparian forested area bordered by steep hills; sandy/loamy/gravelly soil; grasses/forbs/shrubs
N	Dozens of individuals of *A. neotesselata* A typically observed during visits to site, *A. sexlineata viridis* not present
R	Low to negligible susceptibility of lizards to impacts by perpetual human presence and proximity to river
Lime-SCR (Pueblo County)‑*Aspidoscelis neotesselata* C; *Aspidoscelis sexlineata viridis*	
L	Immediate vicinity of abandoned Lime townsite on west side of St. Charles River; access problematic
H	Sandy/loamy/gravelly soil dominated by localized trees, Rabbitbrush (*Chrysothamnus nauseosus),* and Skunkbush *(Rhus trilobata)*
N	Numerous individuals of *A. neotesselata* C typically observed during visits to site, *A. sexlineata viridis* only present peripheral to site
R	Low susceptibility of lizards to impacts by proximity of river and occasional presence of humans and cattle
La Junta-BNSF (Otero County)‑*Aspidoscelis neotesselata* D; *Aspidoscelis sexlineata viridis*	
L	Burlington Northern & Santa Fe Railway Company rail yard on south side of Arkansas River and other property on north side of river in La Junta
H	Main part of site on south side of river with rocky/gravelly soil; elevated roadside and rail spur/levee with grasses/forbs; flats with Kochia,
N	As many as 20+ to 30+ individuals of *A. neotesselata* D observed on three selected dates; 5+ to 10+ *A. sexlineata viridis* observed on those dates
R	High susceptibility of lizards to catastrophic flooding (e.g., May 1999) and destructive human activities; extirpation of both species possible
Higbee-VCT (Otero County)‑*Aspidoscelis neotesselata* B; *Aspidoscelis tesselata* D; *Aspidoscelis sexlineata viridis*	
L	Juniper-dominated campground and large contiguous area of arroyos and canyons with public access trails in Comanche National Grassland
H	Rock surfaces and intervening areas of rocky/gravelly/sandy soil from campground into the extensive canyonlands
N	*A. sexlineata viridis* moderately abundant in sandy areas; but only zero to seven *A. neotesselata* B and *A. tesselata* D observed per visit in rocky areas
R	No apparent susceptibility of lizards to impacts from frequent human presence and some cattle grazing; but possibility of flash flooding in arroyos
Higbee-NV (Otero County)‑*Aspidoscelis neotesselata* B; *Aspidoscelis tesselata* C and D; *Aspidoscelis sexlineata viridis*	
L	Ninemile Valley of the Purgatoire River on private property in the vicinity of abandoned Higbee townsite; access problematic
H	Rocky/gravelly soil along grassy roadsides; sandy/loamy soil in grassy Greasewood (*Sarcobatus vermiculatus*) flats; fall growth of Kochia
N	*A. tesselata* C abundant, *A. tesselata* D and *A. sexlineata viridis* moderate abundance, and *A. neotesselata* B rare (see Walker and Cordes 1998)
R	Low to moderate susceptibility of lizards to impacts from natural or human causes because of large size of site

of the *A. neotesselata* complex (Parker and Selander 1976; Walker et al. 1995, 1997; Taylor et al. 2006a). Geographically, each of these entities represents a set of adaptations that underlie different ecologies typical of subspecies or species. Consequently, lumping of these variants under a single binomial, with or without informal pattern class designations, obscures biodiversity and complicates formation of meaningful conservation strategies for regional variants. For example, the continued existence of *A. neotesselata* D at La Junta-BNSF on private property seems unlikely without a state-sanctioned management plan, formation of which could be elusive if its status remains that of a local array of threatened asexual lizards rather than a threatened taxon.

Aspidoscelis neotesselata*, a mosaic of asexual arrays*.—Each pattern class of *A. neotesselata* and *A. tesselata* comprises local arrays of asexual individuals with attributes and potentials (e.g., relative abundance, dispersion of individuals, and susceptibility to habitat changes) that exist apart from the sexual plexus that integrates members of all gonochoristic species (Table 12). At Higbee-VCT (Table 12; Appendix 2), a peripheral canyonlands continuum for *A. neotesselata* B and the closest known site to La Junta-BNSF for the species, we found that individuals of B were widely dispersed and difficult to locate. This dispersion pattern for lizards was apparent in many visits to Higbee-VCT from 1993–2012, with the result that only two or three individuals of B per trip were typically obtained/observed. However, that *A. neotesselata* B is threatened by either natural or human actions is contradicted by its distribution through vast areas of the canyonlands of Las Animas, Pueblo, and Otero counties.

In comparison to the minimally disturbed climax plant associations and apparent scarcity of *A. neotesselata* B at Higbee-VCT, many aspects of the occupancy of La Junta-BNSF by *A. neotesselata* D are different. There, it has persisted in a clumped dispersion in patches of suitable habitat in greater abundance per unit of area from 1997–2009 in an urban environment despite perpetual disturbances and occasional catastrophic flooding (Table 12). Ecologically, La Junta‑BNSF is the only site for *A. neotesselata* known to us where trees and/or shrubs are of no significance to habitat structure, and where there is a complete change in vegetative structure in most parts of the site from fall to spring as a result of winter die-off of annual Kochia.

Is the array of *A. neotesselata* D at La Junta-BNSF an undocumented anthropogenic introduction, as reported for *A. neomexicana* in Utah by Oliver and Wright (2007) and *A. neotesselata* in Washington State by Weaver et al. (2011)? Reasons to seriously consider this possibility are that the La Junta-BNSF array is apparently disjunct from all other arrays of the species and is established in an inactive rail yard near perpetual east-west rail traffic that frequently stops in the city. An appropriate test as to whether the La Junta-BNSF array of *A. neotesselata* D was an anthropogenic introduction or is a naturally occurring derivative of either pattern class A or B will be determination of its presence or absence near the Arkansas River between La Junta-BNSF and Pueblo Chemical Depot (Pueblo-CD) ~78 km to the west (Table 1, Appendix 7) where the species was reported by Taylor et al. (2006b). Logically, sites inhabited by *A. neotesselata* should be expected at several intermediate areas near the river if the species spread to La Junta-BNSF by slow penetration from the west; however, efforts by JMW to locate sites with the species in that area from 1997–1999 were largely thwarted by lack of access to the Arkansas River.

That *A. neotesselata* D is not convincingly an adventive includes the following points. The lack of evidence of contiguity between sites known for the other pattern classes is far from unusual. For *A. neotesselata* A, it is ~25 km between the westernmost record at Pueblo Reservoir and the record to the west at Florence, and then ~12 km west to the record west of Cañon City. The site for the species nearest to La Junta-BNSF is ~24 km to the southwest at Higbee-VCT. Also, it does not seem likely that the descendants of lizards introduced to La Junta could now be divergent enough from all other arrays of the species as to be recognizable as a distinct pattern class.

Vicissitudes of whiptail lizard existence at La Junta-BNSF.—Since 1997, the La Junta-BNSF array of *A. neotesselata* D and deme of *A. sexlineata viridis* have persisted at La Junta-BNSF following a catastrophic flood from the Arkansas River in May 1999, several smaller floods in more recent years, ongoing commercial and noncommercial trash-dumping, frequent vehicular traffic, a massive removal of derelict appliances from a southeastern section, road-grading, and mowing of vegetation. Flooding on the north side of the river also inundated most, if not all, of the area where both *A. neotesselata* D and *A. sexlineata viridis* were subsequently collected in August 2009 (Fig. 5).

That during dry periods lizards use parts of the site subject to inundation during wet periods was substantiated by JMW on 5 September 1998 when > 20 mostly young-of-the-year *A. neotesselata* were observed throughout stands of Kochia in and around the empty east catch basin, which was filled to over-flowing the previous August. Although JMW observed few individuals of *A. neotesselata* D and *A. sexlineata* at La Junta-BNSF during several post-flood visits in 1999, GJM counted 24 mostly second-year non-reproductive individuals of *A. neotesselata* D on 13 June 2002, indicating that the species had continued to prosper at the site following the flood. Some of these lizards were located adjacent to the east and south sides of the Colorado Hwy 109 Bridge where JMW had not previously observed lizards (Fig. 5).

The part of the La Junta-BNSF site dominated by Kochia is unlike any other *Aspidoscelis* habitat that we have observed. As lizards emerge from hibernation in late April or early May there is no living vegetation until the Kochia seeds germinate and the vegetational structure begins to slowly develop anew. In one instance, a small area at the west end with a thick stand of Kochia inhabited by several *A. neotesselata* one year was completely devoid of vegetation and lizards the next year, indicating that dispersion of lizards onsite is dynamic.

We noted several threats to lizards at La Junta-BNSF that could annually exceed the damage done by periodic collecting. During the study, the roadside stands of Kochia were periodically mowed by workers which placed both species of *Aspidoscelis* at risk under the wheels and blades of heavy machinery, in addition to complete destruction of swaths of habitat. Fortunately, the topography of La Junta-BNSF limited mowing to relatively level roadsides. Aside from fluctuations in the weather (e. g., destructive effects of flooding and inhibition of Kochia growth by drought), there is another formidable natural threat to lizards at the site. In mid-May 1999, LJL observed a Western Coachwhip (*Coluber flagellum testaceus*), an efficient whiptail lizard predator, and a Plains Garter Snake (*Thamnophis radix*) at La Junta-BNSF.

Acknowledgments.—Without Michelle Keefer's interest in natural history at an early age, and her mother's encouragement of those interests, the capture of a juvenile of *Aspidoscelis neotesselata* D near the Pizza Hut on E First Street on 15 June 1995 in La Junta, Otero County, Colorado, USA, would not have happened. We are eternally grateful to Michelle and Sue Keefer for initiating the chain of events that culminated in this study. Specimens from Colorado in the AMNH, RU, UCM, and UADZ collections were obtained under the authority of permits provided by the Colorado Division of Wildlife to JEC (HP 256), CEM (HP 950), and HLT (HP 772), and specimens in the RU collection from New Mexico were obtained based on a permit from the New Mexico Department of Game and Fish to HLT (1905). We are grateful to curators at the AMNH and UCM for cataloging specimens collected by HLT during field work supported by Summer Research Grants from Regis University. Personnel of the Burlington Northern and Santa Fe Railway Company allowed free access to property on both sides of North Street (i.e., the La Junta-BNSF study site). In August 2009, Anthony Wilmes and Laura Garey, Truman State University, were the first to discover *Aspidoscelis neotesselata* D on the north side of the Arkansas River across from La Junta-BNSF. Over the years, specimens, allozyme data, and locality records provided by E. D. Parker, Jr. were invaluable in our studies of the *Aspidoscelis tesselata* complex of parthenogenetic whiptail lizards.

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HARRY L. TAYLOR is Professor Emeritus, recently retired after 45 years in the Biology Department, Regis University, Denver, Colorado, and a Research Associate in the Department of Herpetology, American Museum of Natural History, New York. He obtained a B.S. degree from Northeast Missouri State College (now Truman State University), Kirksville, Missouri, and M.A. and Ph.D. degrees from the University of Colorado, Boulder, where he and J. M. Walker became hooked on whiptail lizards under the tutelage of T. P. Maslin. Once hooked, you stay caught; research has been conducted, almost exclusively, on geographic variation, patterns of evolution, life-history strategies, and ecological relationships in parthenogenetic and sexually reproducing lizards of the genus *Aspidoscelis*. (Photographed by Patty Boulware)

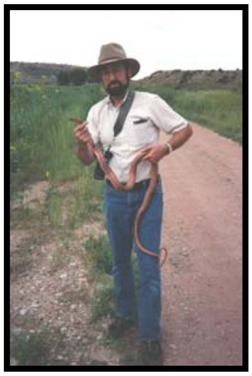
GLENN J. MANNING is an Assistant Professor in Biology at the University of Arkansas at Monticello. Glenn received his B.S. in Biochemistry and Biology from Kansas State University, where he studied pectinases in the Rice Weevil (*Sitophilus oryzae*). After receiving his B.S., he attended the University of Arkansas to study whiptail lizards in Eastern New Mexico for his Ph.D. (Photographed by Jim Brewer)

JAMES E. CORDES is Professor of Biology at Louisiana State University Eunice, Eunice, Louisiana, USA. Jim received his B.S and M.S. degrees from Texas State University and Ph.D. from the University of Arkansas. He has been the recipient of six Endowed Professorships funded by Opelousas General Hospital and awarded by LSU Eunice to study the genetic relationships of parthenogenetic teiid lizards through skin-graft histocompatibility. Since 1984, Jim has been involved in > 70 field expeditions to Mexico, Arizona, Colorado, New Mexico, Oklahoma, and Texas to secure live parthenogenetic whiptail lizards for laboratory experiments and preserved voucher specimens of numerous species for ecological and systematic studies. He is author of > 80 publications on lizards in the genus *Aspidoscelis.* (Photographed by Lyndsey Nacole Schexnayder)

CHAD E. MONTGOMERY is Assistant Professor in Biology at Truman State University, which is also where he received his B.S. in Biology. Chad received his M.A. thesis degree from the University of Northern Colorado, where he studied clinal variation in Texas Horned Lizard (*Phrynosoma cornutum*). After receiving his M.A., he attended the University of Arkansas to study the effects of foraging mode on life history in *Agkistrodon contortrix* (Copperhead) and *Crotalus horridus* (Timber Rattlesnake) for his Ph.D. Chad currently conducts research in Central America, including a project examining body size variation in *Boa constrictor* (Boa Constrictor) on islands off of the north coast of Honduras. (Photographed by John Iverson)

LAUREN J. LIVO started catching horned lizards (genus *Phrynosoma*) and box turtles (genus *Terrapene*) as a preschooler and never stopped. She earned a B.A. from the University of Colorado at Boulder in 1973 and an M.A. from the University of Colorado at Denver in 1981. Her doctoral research on Boreal Toads (*Anaxyrus boreas*) was supported by the Colorado Division of Wildlife. After receiving her Ph.D. from the University of Colorado at Boulder in 1999, she remained at CU as a postdoctoral research associate, studying the effects of the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) on Boreal Toads (*Anaxyrus boreas*) and other amphibians, both in the laboratory and in the field. Currently she is completing a photographic guide to Colorado's amphibians, to be published by Colorado Parks and Wildlife that includes eggs, tadpoles and metamorphs. (Photographed by Steve Wilcox)

STEVE KEEFER is a 1981 graduate of Colorado State University with a BS in Wildlife Biology. From 1974 until 1986 he held a number of positions in wildlife including: the Kansas Biological Survey, USFWS Denver Research Station and National Wildlife Labs, USFS Intermountain Range and Forest Research Station, Natal Parks Board, and a private hunting and fishing ranch. They involved small mammal, breeding bird, and aquatic invertebrate surveys, performing post mortems on specimens, and preparing research specimens. Twice he was the team leader for small mammal surveys. Since 1986 he has been a District Wildlife Manager for the Colorado Division of Wildlife, now Colorado Parks and Wildlife. This position involves law enforcement, education, wildlife monitoring, habitat management, making management decisions, and sometimes being involved in research projects. The research projects have included developing base line species surveys, and assisting the USFWS with Black-footed Ferret (*Mustela nigripes*) reintroduction research. Steve is a life-long outdoorsman, hunter, fisherman, and boater. He has also been involved in search and rescue, Boy Scouts, 4-H, and other youth and educational programs. (Photographed by Sue Keefer)



CHARLES W. LOEFFLER, a graduate of Colorado State University, started his career with the Colorado Division of Wildlife in 1972 as a District Wildlife Manager. In 1977 he was appointed as the first Regional Nongame Wildlife Biologist in Colorado, and worked on a wide variety of management and recovery projects for nongame and endangered species in southeastern Colorado, including the initiation of reptile and amphibian surveys on State Wildlife Areas, and organizing and training volunteers to assist with Boreal Toad *(Anaxyrus boreas)* survey work. From 1996 to 2002, he was responsible for all Colorado Division of Wildlife management projects involving reptiles, amphibians, mollusks, and crustaceans in the State of Colorado, including chairing the Boreal Toad recovery team for Colorado, Wyoming and New Mexico. Charles retired from the Colorado Division of Wildlife in 2002. (Photographed by Lauren J. Livo)

MICHELLE KEEFER, who captured the first *Aspidoscelis neotesselata* D in 1995 in La Junta, Otero County, Colorado, USA, shown at age nine. (Photographed by Sue Keefer)

APPENDIX 1. Chronology of records documenting the extent of the known area inhabited by triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata* D) in La Junta, Otero County, Colorado, USA.

First Capture of Triploid *Aspidoscelis neotesselata* D at La Junta (By Michelle Keefer)
Colorado: Otero County: City of La Junta, Pizza Hut Restaurant parking lot at 402 E First Street (S of Arkansas River), 37.987804°N, 103.537873°W, 1239 m [15June 1995 (Vouchered by photograph of second-year individual in a terrarium by Sue Keefer)].

First Observation of Triploid *Aspidoscelis neotesselata* D at La Junta-BNSF West of CO Hwy. 109 (By LJL)
Colorado: Otero County: City of La Junta, 0.12 km W of Colorado Hwy. 109, near unpaved North Street on property of Burlington Northern and Santa Fe Railway Company (S of Arkansas River), 37.990555°N, 103.533291°W, 1237 m [12 August 1997 (Vouchered by photographs of lizards in situ by LJL)].

First Collection of Triploid *Aspidoscelis neotesselata* D from La Junta-BNSF West of CO Hwy. 109 (By JMW)
Colorado: Otero County: City of La Junta, W of Colorado Hwy. 109 on both sides of unpaved North Street through property of Burlington Northern and Santa Fe Railway Company (S of Arkansas River), 37.990555°N, 103.533291°W, 1236 m [20 August 1997 (UADZ 6009–6012, 6014–6020, N = 11)].

First Collection of Triploid *Aspidoscelis neotesselata* D from La Junta-BNSF East of CO Hwy. 109 (By GJM)
Colorado: Otero County: City of La Junta, opposite (east) side Colorado Hwy. 109 from property of Burlington Northern and Santa Fe Railway Company (S of Arkansas River), 37.989660°N, 103.531906°W, 1236 m [8 August 2004 (among UADZ 7766–7773, N = 8)].

First Collection of Triploid *Aspidoscelis neotesselata* D from North of Arkansas River (By Students of CEM)
Colorado: Otero County: City of La Junta, W of Colorado Hwy. 109 (N of Arkansas River), 37.991281°N, 103.531746°W, 1235 m [6 August 2009 (UADZ 8843–8844, N = 2)].

APPENDIX 2. Specimens of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata*), diploid parthenogenetic Common Checkered Whiptail (*Aspidoscelis tesselata*), and gonochoristic Prairie Racerunner (*Aspidoscelis sexlineata viridis*) from the AMNH, RU, UADZ, and UCM collections used as sources of data for Tables 1–7 and Figs. 9–11).

Specimens of Triploid *Aspidoscelis neotesselata* A from Pueblo-NC (n = 82)
Colorado: Pueblo County: City of Pueblo, Nature and Raptor Center of Pueblo, I.6 km W of Pueblo Blvd. on 11th Street (N of Arkansas River), 38.268843°N, 104.679512°W, 1439 m [9 August 1990 (UADZ 4294–4315, n = 22); 15 September 1990 (UCM 56251, n = 1); 22 September 1990 (UCM 56252–56266, n = 15); 18 June 1991 (UCM 57192–57207, n = 16); 15 July 1991 (UCM 57208–57212, UADZ 4489–4504, n = 21); 1 July 1993 (UADZ 5014–5017, n = 4); 30 June 1998 (UADZ 6221–6223, n = 3)].

Specimens of Triploid *Aspidoscelis neotesselata* B from Higbee-VCT (n = 31)
Colorado: Otero County: vicinity of abandoned Higbee townsite, Comanche National Grassland, Vogel Canyon Picnic Area and Trailhead, 22.3 km S of La Junta by Colorado Hwy. 109 to 802, then 2.24 km W, then 2.4 km S to picnic area and trailhead, 37.769947°N, 103.512749°W, 1338 m [8 June 1993 (UCM 57214, n = 1); 9 June 1993 (UCM 57215–57216, n = 2); 10 June 1993 (UCM 57217–57218, n = 2); 30 June 1993 (UADZ 5007–5009, n = 3); 16 August 1993 (UADZ 5149, n = 1); 6 July 1994 (UADZ 5576, n = 1); 6 September 1998 (UADZ 6341, n = 1); 22 May 1999 (AMNH 146596, n = 1); 23 May 1999 (AMNH 146597–146598, n = 2); 1 July 1999 (UADZ 6558–6559, n = 2); 3 July 2000 (UADZ–JMW 1176–1177, 1179, 1184, n = 4); 4 July 2000 (UADZ 1183, n = 1): 7 June 2001 (UADZ 8035, 8042, 8045, 8046, 8049, n = 5); 9 August 2009 (UADZ 8862–8864, 8866, 8871, n = 5)].

Specimens of Triploid *Aspidoscelis neotesselata* C from Lime-SCR (n = 62)
Colorado: Pueblo County: Lime, 17.4 km S Pueblo, then 2.1 km E of Interstate Hwy, 25 on Lane 25, then 300 m to abandoned Lime town site and St Charles River, 38.148201°N, 104.624471°W, 1515 m [20 June 1963 (UCM 21572–21573, n = 2); 6 June 1990 (UADZ 4131–4154, 4156–4157, n = 26); 9 August 1990 (UADZ 4279–4293, n = 15); 15 September 1990 (UCM 56240–56245, n = 6); 22 September 1990 (UCM 56246–56250, n = 5); 3 June 1999 (UADZ 7222–7226, n = 5); 21 May 1999 (AMNH 146593–146595, n = 3)].

Specimens of Triploid *Aspidoscelis neotesselata* D from La Junta-BNSF (n = 79)
Colorado: Otero County: City of La Junta, W of Colorado Hwy. 109 (N of Arkansas River), 37.991281°N, 103.531746°W, 1235 m [6 August 2009 (UADZ 8843–8844, n = 2)].

Colorado: Otero County: City of La Junta, W of Colorado Hwy. 109 on both sides of unpaved North Street through property of Burlington Northern and Santa Fe Railway Company (S of Arkansas River), 37.990555°N, 103.533291°W, 1237 m [20 August 1997 (UADZ 6009–6012, 6014–6020, n = 11); 18 June 1998 (RU 98083–98084, n = 2); 29 June 1998 (UADZ 6217–6218, n = 2); 1 July 1998 (UADZ 6231, n = 1); 27 July 1998 (UADZ 6273–6279, n = 7); 28 July 1998 (UADZ 6283–6288, n = 6); 5 September 1998 (UADZ 6319–6334, n = 16); 6 September 1998 (UADZ 6346, n = 1); 29 June 1999 (UADZ 6541–6543, n = 3); 1 July 1999 UADZ 6553, n = 1); 13 June 2002 (UADZ 7220, n = 1); 8 August 2004 (UADZ 7766–7773, n = 8); 18 August 2007 (uncatalogued, n = 4); 7 August 2009 (UADZ 8849–8856, n = 8)].

Colorado: Otero County: City of La Junta, 0.48 km W of Colorado Hwy. 109 on unpaved North Street through property of Burlington Northern and Santa Fe Railway Company on an elevated abandoned railroad spur/levee (S of Arkansas River), 37.992655°N, 103.539723°W, 1236 m [28 July 1998 (UADZ 6289–6294, n = 6)].

Specimen of Tetraploid *Aspidoscelis neotesselata* D x *Aspidoscelis sexlineata viridis* from La Junta-BNSF (n = 1)
Colorado: Otero County: City of La Junta, 0.48 km W Colorado Hwy. 109 on the south side of unpaved North Street through property of Burlington Northern and Santa Fe Railway Company (south of Arkansas River), 37.990555°N, 103.533291°W, 1237 m [20 August 1997 (UADZ 6013)].

Specimens of Diploid *Aspidoscelis tesselata* C from Higbee-NV (n = 95)
Colorado: Otero County: Higbee, Ninemile Valley of the Purgatoire River, 11.5–13.0 km SW of Colorado Hwy. 109 on road 804, 37.717819ºN, 103.515303ºW, 1383 m [9 July 1988 (UADZ 3150, 3155–3156, 3159–3160, 3167, 3170, 3174, 3176, n = 9); 10 July 1988 (UADZ 3182, 3184–3185, 3187–3188, 3193-3195, 3198–3199, 3203–3204, n = 12); 11 August 1988 (UADZ 3409–3412, 3414–3423, 3426–3428, n = 17); 1 August 1989 (UADZ 3710–3713, n = 4); 2 September 1989 (UCM 56116, n = 1); 3 September 1989 (UCM 56117–56123, n = 7); 4 September 1989 (UCM 56126–56132, n = 7); 16 September 1989 (UCM 56138–56142, n = 5); 17 September 1989 (UCM 56148–56155, n = 8); 4 June 1990 (UADZ 4088–4090, 4092–4094, 4097, n = 7); 5 June 1990 (UADZ 4104–4106, 4108–4109, 4111–4113, 4115–4119, 4122, n = 14); 10 August 1990 [UADZ 4323–4325, n = 3)]; 29 May 1993 (UADZ 5000, n = 1)].

Specimens of *Aspidoscelis sexlineata viridis* from La Junta-BNSF (n = 19)
Colorado: Otero County: City of La Junta, W of Colorado Hwy. 109 (N side of Arkansas River), 37.991281ºN, 103.531746ºW, 1236 m [6 August 2009 (UADZ 8845–8848, n = 4)].

Colorado: Otero County: City of La Junta, W of Colorado Hwy. 109 on both sides of unpaved North Street through property of Burlington Northern and Santa Fe Railway Company (S of Arkansas River), 37.990555ºN, 103.533291ºW, 1237 m [20 August 1997 (UADZ 6014, n = 1); 29 June 1998 (UADZ 6219–6220, 6230, n = 3), 27 July 1998 (UADZ 6268–6272, n = 5); 28 July 1998 (UADZ 6282, n = 1); 5 September 1998 (UADZ 6335–6338, n = 4); 6 September 1998 (UADZ 6345, n = 1)].

APPENDIX 3. Specimens used as source of data for analyses of color pattern in 48 juveniles of three pattern classes of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata*).

Juveniles of Triploid *Aspidoscelis neotesselata* A from Pueblo-NC (SVL 41–52 mm, n = 16)
Colorado: Pueblo County: City of Pueblo, Nature and Raptor Center of Pueblo, I.6 km W of Pueblo Blvd. on 11th Street (N of Arkansas River), 38.268843ºN, 104.679512ºW, 1439 m [15 September 1990 (UCM 56251, n = 1); 22 September 1990 (UCM 56252–56266, n = 15)].

Juveniles of Triploid *Aspidoscelis neotesselata* C from Lime-SCR (41–53 mm, n = 11)
Colorado: Pueblo County: Lime, 17.4 km S Pueblo, then 2.1 km E of Interstate Hwy, 25 on Lane 25, then 300 m to abandoned Lime town site and St. Charles River, 38.148201ºN, 104.624471ºW, 1515 m [15 September 1990 (UCM 56240–56245, n = 6); 22 September 1990 (UCM 56246–56250, n = 5)].

Juveniles of Triploid *Aspidoscelis neotesselata* D from La Junta-BNSF (37–55 mm, n = 21)
Colorado: Otero County: City of La Junta, W of Colorado Hwy. 109 on both sides of unpaved North Street through property of Burlington Northern and Santa Fe Railway Company (S of Arkansas River), 37.990555ºN, 103.533291ºW, 1237 m [20 August 1997 (UADZ 6015–6019, n = 5); 29 June 1998 (UADZ 6217, n = 1); 5 September 1998 (UADZ 6319–6323, 6325–6330, 6332–6334, n = 14); 6 September 1998 (UADZ 6346, n = 1)].

APPENDIX 4. Specimens used as source of data for analyses of color pattern in 46 adults of three pattern classes of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata*).

Adults of Triploid *Aspidoscelis neotesselata* A from Pueblo-NC (SVL 73–91 mm, n = 15)
Colorado: Pueblo County: City of Pueblo, Nature and Raptor Center of Pueblo, I.6 km W of Pueblo Blvd. on 11th Street (N of Arkansas River), 38.268843ºN, 104.679512ºW, 1439 m [18 June 1991 (UCM 57192–57195, 57197–57207, n = 15)].

Adults of Triploid *Aspidoscelis neotesselata* C from Lime-SCR (SVL 75–106 mm, n = 18)
Colorado: Pueblo County: Lime, 17.4 km S Pueblo, then 2.1 km E of Interstate Hwy. 25 on Lane 25, then 300 m to abandoned Lime town site and St. Charles River, 38.148201ºN, 104.624471ºW, 1515 m [6 June 1990 (UADZ 4131–4132, 4134–4136, 4138–4143, 4145–4150, 4154, n = 18)].

Adults of Triploid *Aspidoscelis neotesselata* D from La Junta-BNSF (SVL 78–92 mm, n = 13)
Colorado: Otero County: City of La Junta, W of Colorado Hwy. 109 on both sides of unpaved North Street through property of Burlington Northern and Santa Fe Railway Company (S of Arkansas River), 37.990555ºN, 103.533291ºW, 1237 m [20 August 1997 (UADZ 6009, 6020, n = 2); 18 June 1998 (RU 98083–98084, n = 2); 27 July 1998 (UADZ 6273–6274, 6276, n = 3); 28 July 1998 (UADZ 6283–6285, n = 3); 5 September 1998 (UADZ 6321, 6331, n = 2)].

Colorado: Otero County: City of La Junta, 0.48 km W Colorado Hwy. 109 on unpaved North Street through property of Burlington Northern and Santa Fe Railway Company, (S of Arkansas River) on an elevated abandoned railroad spur, 37.992655ºN, 103.539723ºW, 1236 m [28 July 1998 (UADZ 6294, n = 1)].

APPENDIX 5. Specimens collected by E. D. Parker, Jr. from the vicinity of the abandoned Higbee townsite with ploidy levels determined by electrophoresis (Parker and Selander 1976), initially used by Walker et al. (1995, 1997) to distinguish samples of diploid parthenogenetic Common Checkered Whiptail (*Aspidoscelis tesselata* from superficially similar triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata*).

Specimen of Diploid *Aspidoscelis tesselata* C from Higbee-VC (n = 1)
Colorado: Otero County: Higbee, Ninemile Valley of the Purgatoire River, 1.6 km S of Higbee School (= vicinity of entrance of Vogel Canyon, 4.3 km SW of Colorado Hwy. 109) on road 804 [15 July 1973 (UADZ 3936, n = 1)].

Specimens of Diploid *Aspidoscelis tesselata* C from Higbee-NV (n = 2)
Colorado: Otero County: Higbee, Ninemile Valley of the Purgatoire River, 11.5–13.0 km SW of Colorado Hwy. 109 on road 804, 37.717819ºN, 103.515303ºW, 1383 m [12 August 1973 (UADZ 3937–3938, n = 2)].

Specimens of Triploid *Aspidoscelis neotesselata* B from Higbee-VC (n = 9)
Colorado: Otero County: Higbee, Ninemile Valley of the Purgatoire River, 1.6 km S of Higbee School (= vicinity of entrance of Vogel Canyon, 4.3 km SW of Colorado Hwy. 109) on road 804 [15 July 1973 (UADZ 3927–3935, n = 9)].

Specimen of Tetraploid *Aspidoscelis neotesselata* B x *Aspidoscelis sexlineata viridis* from Higbee-VC (n = 1)
Colorado: Otero County: Higbee, Ninemile Valley of the Purgatoire River, 1.6 km S of Higbee School (= vicinity of entrance of Vogel Canyon, 4.3 km SW of Colorado Hwy. 109) on road 804 [15 July 1973 (UADZ 3926, n = 1)].

APPENDIX 6. Specimens of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata*) and diploid parthenogenetic Common Checkered Whiptail (*Aspidoscelis tesselata*) used in histocompatibility experiments.

Triploid *Aspidoscelis neotesselata* A from Pueblo-NC (n = 1)
Colorado: Pueblo County: City of Pueblo, Nature and Raptor Center of Pueblo, I.6 km W of Pueblo Blvd. on 11th Street (N of Arkansas River), 38.268843ºN, 104.679512ºW, 1439 m [30 June 1998 (UADZ 6222, n = 1)].

Triploid *Aspidoscelis neotesselata* D from La Junta-BNSF (n = 3)
Colorado: Otero County: City of La Junta, W of Colorado Hwy. 109 on both sides of unpaved North Street through property of Burlington Northern and Santa Fe Railway Company (S of Arkansas River), 37.990555ºN, 103.533291ºW, 1237 m [29 June 1998 (UADZ 6218, n = 1); 8 August 2004 (UADZ 7770–7771, n = 2)].

Diploid *Aspidoscelis tesselata* C from De Baca County, New Mexico (n = 2)
New Mexico: De Baca County: Sumner Lake State Park, E of Sumner Lake on Eastside Campground Road and Beaver Shore Road, 34.604957ºN, 104.377208ºW, 1309 m [19 July 2003 (RU 0079–0080, n = 2)].

APPENDIX 7. Summary of GPS and elevation data from Google Earth for points/sites of significance to this study of triploid parthenogenetic Colorado Checkered Whiptail (*Aspidoscelis neotesselata* = *A. n.*) and diploid parthenogenetic Common Checkered Whiptail (*Aspidoscelis tesselata* = *A. t.*) in southeastern Colorado, USA.

La Junta Pizza Hut Restaurant (parking lot; capture of first *A. n.* D in city in 1995)	37.987804ºN, 103.537873ºW	1239 m
La Junta-BNSF (W of jct. of North St./CO Hwy. 109; first *A. n.* D observed in 1997)	37.990555ºN, 103.533291ºW	1237 m
La Junta-BNSF (W of jct. of North St./CO Hwy. 109; first A. n. D collected in 1997)	37.990555°N, 103.533291°W	1237 m
La Junta-BNSF (Road under CO Hwy. 109 bridge; flood prone habitat for *A. n.* D)	37.990218ºN, 103.532850ºW	1236 m
La Junta-BNSF (Area of removal of debris; no whiptails observed here)	37.989497ºN, 103.534201ºW	1237 m
La Junta-BNSF (West end rail spur/levee; habitat above flood zone for *A. n.* D)	37.992655ºN, 103.539723ºW	1236 m
La Junta-BNSF (E of CO Hwy. 109 bridge; first *A. n.* D collected in 2004)	37.989660ºN, 103.531906ºW	1236 m
La Junta-BNSF (N of CO Hwy. 109 bridge; first *A. n.* D collected in 2009)	37.991281ºN, 103.531746ºW	1235 m
Higbee-VCT (Campground at canyonlands/plains ecotone; source of *A. n.* B)	37.769947ºN, 103.512749ºW	1338 m
Higbee-NV (Purgatoire River canyonlands/flats ecotone; source of *A. t.* C)	37.717819ºN, 103.515303ºW	1383 m
Lime-SCR (West of St Charles River at abandoned Lime townsite; source of *A. n.* C)	38.148201ºN, 104.624471ºW	1515 m
Pueblo-NC (Within and adjacent to Raptor and Nature Center; source of *A. n.* A)	38.268843ºN, 104.679512ºW	1439 m
Pueblo-CD (Near Pueblo Chemical Depot; source of referenced *A. n.* B)	38.270083ºN, 104.353221ºW	1417 m
Sumner Lake, NM (East side of lake; source of *A. t.* New Mexico C)	34.604957ºN, 104.377208ºW	1309 m