
MORPHOLOGICAL VARIATION, HABITAT, AND CONSERVATION STATUS OF PARTHENOGENETIC *ASPIDOSCELIS TESSELATUS* PATTERN CLASS C IN THE CANYONLANDS OF SOUTHEASTERN COLORADO, USA

JAMES M. WALKER¹, CHAD E. MONTGOMERY^{2,4}, JAMES E. CORDES³, AND MADELYN J. MANGAN²

¹Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701, USA

²Department of Biology, Truman State University, Kirksville, Missouri 63501, USA

³Division of Sciences and Mathematics, Louisiana State University, Eunice, Louisiana 70535, USA

⁴Correspondent: chadmont@truman.edu

Abstract.—We studied an array of diploid parthenogenetic *Aspidoscelis tessellatus* (Common Checkered Whiptail) at Carrizo Canyon Picnic Area (CCPA) in the Comanche National Grassland, Baca County, Colorado, USA. The CCPA locale represents the southeastern-most site in Colorado where adults of this species have been studied in the field and adequately sampled for laboratory analyses. We used dorsal color patterns and meristic characters in five juveniles and 13 adults collected in May 2017 from canyon rim habitat at CCPA to confirm their identities as *A. tessellatus* rather than the phenotypically similar triploid parthenogenetic species *A. neotesselatus* (Colorado Checkered Whiptail). Comparison of the CCPA specimens to samples of *A. tessellatus* from Ninemile Valley of the Purgatoire River in Otero County (n = 99), Colorado, collected from valley floor habitat, and Cottonwood Creek in Baca County (n = 15), Colorado, collected from juniper dominated habitat, revealed significant meristic ($P = 0.05$) and color pattern differences among the three arrays of pattern class C of the species. *Aspidoscelis tessellatus* in syntopy with *A. sexlineatus viridis* (Prairie Racerunner) at CCPA reflected the availability of narrow zones of gravelly to rocky ecotonal habitats bordering the east and west sides of the canyon, preferred by the former species, and contiguous Sand Sage Prairie habitats, preferred by the latter species. We considered it unlikely that foreseeable anthropogenic causations other than climate change would threaten the habitation of either *A. tessellatus* or *A. sexlineatus viridis* at CCPA, an area regulated by restrictive federal and state strictures and private land-use practices.

Key Words.—body size; color pattern; Comanche National Grassland; macrohabitat use; meristic characters; whiptail lizard

INTRODUCTION

The genus *Aspidoscelis* (Squamata: Teiidae) is represented by three species of whiptail lizards in southeastern Colorado, USA: gonochoristic *Aspidoscelis sexlineatus viridis* (Prairie Racerunner); diploid parthenogenetic *A. tessellatus* (Common Checkered Whiptail); and triploid parthenogenetic *A. neotesselatus* (Colorado Checkered Whiptail). Two distinct variants of *A. tessellatus* occur in the area, dorsal pattern classes C and D, which are only known to be syntopic at several sites of a few hectares in Ninemile Valley of the Purgatoire River near Higbee, Otero County, with each pattern class being strongly numerically dominant at different sites (Walker and Cordes 1998; Walker et al. 1997, 1998). Elsewhere in parts of Otero, Bent, Las Animas, and Baca counties in extreme southeastern Colorado (Fig. 1) only one pattern class of *A. tessellatus* is present at each site known for the species (Zweifel 1965; Walker et al. 1997, 1998; Martin et al. 2015; Taylor et al. 2017). Range-wide, including parts of Colorado, Oklahoma, New Mexico,

and Texas, USA, and Chihuahua, Mexico, *A. tessellatus* has been of noteworthy historical significance in the conformation (Maslin 1962, 1966, 1971; Zweifel 1965) of suspected (Tinkle 1959) parthenogenesis in the genus *Cnemidophorus* (= *Aspidoscelis* in part).

A complicating factor in studies of *A. tessellatus* pattern class C in southeastern Colorado is distinguishing it from phenotypically similar triploid *A. neotesselatus* pattern class B with which it is syntopic in varying proportions enumerated for some sites in Otero and Las Animas counties (Walker et al. 1995, 1997, 1998; Walker and Cordes 1998; Taylor et al. 2006a). Significantly, only in southeastern Colorado is there a triploid parthenogenetic species (*A. neotesselatus*) that has an extant, as well as syntopic, diploid maternal progenitor (*A. tessellatus*) in addition to an extant paternal progenitor (*A. sexlineatus viridis*; Parker and Selander 1976; Walker et al. 1995, 1997). Thus, the distributional relationships and ecologies of these lizard species are of special interest based on: 1) their uniquely interrelated evolutionary histories (*A. neotesselatus* originated in southeastern Colorado through hybridization between a

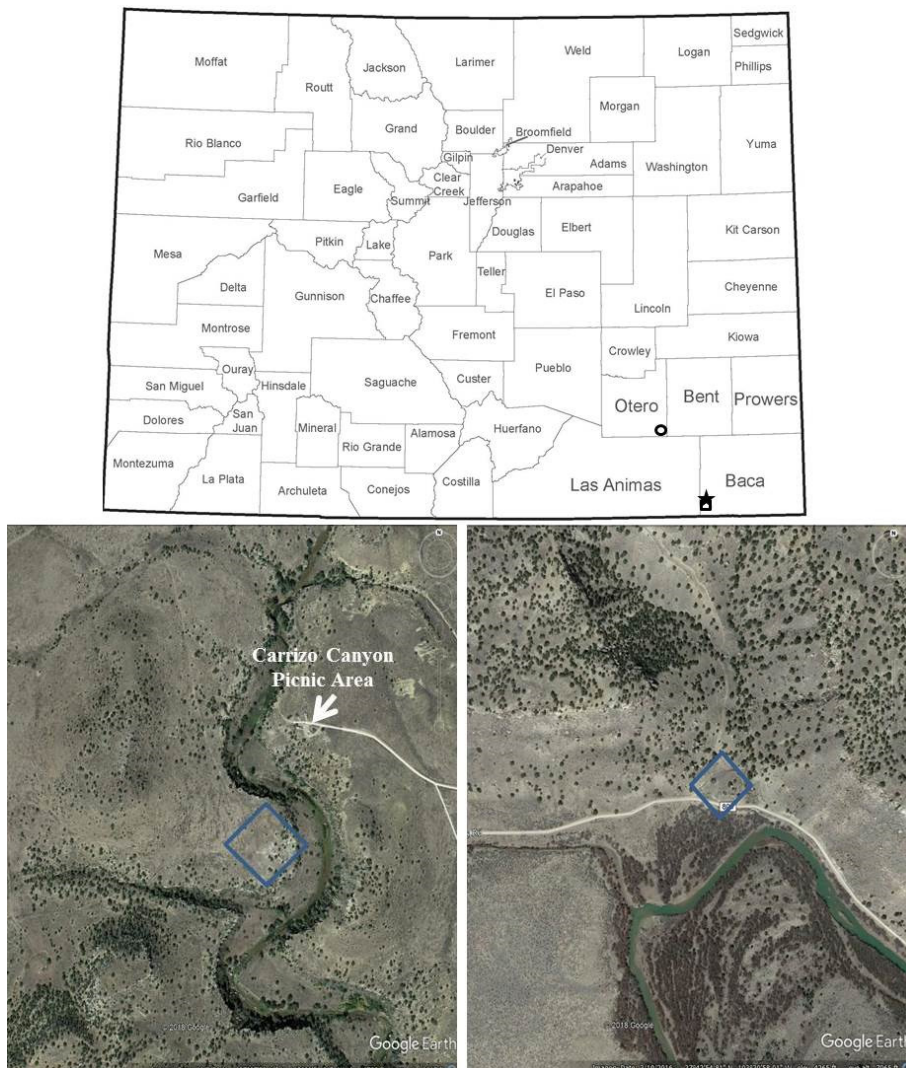


FIGURE 1. Map (A) of the state of Colorado, USA, of which the southeastern quadrant comprises contiguous counties among which Colorado Checkered Whiptail (*Aspidoscelis neotesselatus*) has been reported from sites in Teller, El Paso, Fremont, Pueblo, Otero and Las Animas, Common Checkered Whiptail (*A. tessellatus*) has been reported from sites in Otero and Las Animas. Carrizo Canyon Picnic Area (CCPA) is indicated by a star on the map, Cottonwood Creek is indicated by a square (partially obscured by CCPA star), and Ninemile Valley is indicated by a circle. Bottom left aerial image depicts the area of the CCPA, with the main focus of this study of *A. tessellatus* C marked by diamond symbol southwest of the picnic area and west of Carrizo Canyon (carved by East Carrizo Creek) in the Comanche National Grassland, Baca County, Colorado. Bottom right aerial image depicts the area in Ninemile Valley, marked by diamond symbol, situated 11.5–12.5 km southwest of Colorado Highway 109 on road 804, Otero County, Colorado, from which the sample of *A. tessellatus* C was collected over many years.

female of *A. tessellatus* C and a male of *A. sexlineatus viridis*; Parker and Selander 1976); 2) the restricted and patchy distribution of *A. tessellatus* in the state in which it occurs in only a fraction of each of the aforementioned four counties owing to habitat specificity (Zweifel 1965; Walker et al. 1997; Alvarez et al. 2017); and 3) the endemic status of *A. neotesselatus* in which it has a patchy habitat-limited natural distribution in parts of Fremont, El Paso, Pueblo, Teller, Otero, and Las Animas counties in southeastern Colorado (Walker et al. 1997; Walker 2012; Taylor et al. 2015a; Alvarez et al. 2017).

Important details of the distributional relationships and evolution of *A. tessellatus* C and D and *A. neotesselatus* A, B, and D in southeastern Colorado have continued to be added to the literature. These new records have supplemented the summaries provided by Zweifel (1965), Walker et al. (1997, 1998), and Walker and Cordes (1998), albeit irregularly owing to the difficulty in accessing the complex topography in remote and/or militarily restricted areas in the canyonlands hypothetically inhabited by one or both of these parthenogenetic species (Table 1). Significantly,

Herpetological Conservation and Biology

TABLE 1. Summary of important publications relevant to the evolution, distribution, and systematic relationships of Colorado Checkered Whiptail, *Aspidoscelis neotesselatus* (*A. n.*), Common Checkered Whiptail, *A. tessellatus* (*A. t.*), and Prairie Racerunner, *A. sexlineatus viridis* (*A. s. v.*), in southeastern Colorado, USA, beginning with the seminal publication by Zweifel (1965).

Publication	Coverage in southeastern Colorado
Zweifel (1965)	Range-wide designations of pattern classes <i>A. t.</i> A–F; presently only <i>A. t.</i> C–E are included in the species.
Parker and Selander (1976)	Range-wide genetic (electrophoretic) assessment of pattern classes <i>A. t.</i> A–F; presently only <i>A. t.</i> C–E are included in the species.
Walker et al. (1990)	Hybridization of <i>A. t. C</i> x <i>A. s. v.</i> and <i>A. n. B</i> (then undescribed) x <i>A. s. v.</i> in Ninemile Valley near Higbee, Otero Co.
Walker et al. (1994)	Hybridization of <i>A. t. C</i> x <i>A. s. v.</i> in Ninemile Valley near Higbee, Otero Co.
Walker et al. (1995)	Morphological identification of diploid and triploid arrays in communities in Ninemile Valley near Higbee, Otero Co.
Walker et al. (1997)	Combinations of <i>A. n. B</i> (new species), <i>A. t. C</i> , <i>A. t. D</i> , and/or <i>A. s. v.</i> in whiptail lizard communities near Higbee, Otero Co.
Mackessy (1998)	<i>A. n.</i> , <i>A. t.</i> , and <i>A. s. v.</i> in the herpetofauna of Comanche National Grassland, southeastern Colorado.
Cordes and Walker (2003)	Histocompatibility of <i>A. t. C</i> and <i>A. t. D</i> from Conchas Lake, San Miguel Co., New Mexico, relevant to origin of pattern classes.
Walker and Cordes (2003)	Report of an unusual variant of <i>A. t.</i> from Conchas Lake, San Miguel Co., New Mexico, relevant to origin of pattern classes.
Taylor et al. (2006a)	<i>A. n. B</i> , <i>A. t. C</i> , and <i>A. s. v.</i> in and near Lockwood Canyon, Piñon Canyon Maneuver Site, Las Animas Co.
Taylor et al. (2006b)	<i>A. n. B</i> and <i>A. s. v.</i> near Pueblo Chemical Depot, Pueblo Co.
Newby et al. (2011)	First record for <i>A. t. D</i> in Las Animas Co.
Weaver et al. (2011)	<i>A. n. B</i> established in Grant Co., Washington State, resulting from anthropogenic causation.
Walker (2012)	<i>A. n. A</i> in fragmented habitat in Valco Ponds Wildlife Area, City of Pueblo, Pueblo Co.
Walker et al. (2012)	<i>A. n. D</i> (new pattern class) and <i>A. s. v.</i> in La Junta, Otero Co., compared with <i>A. n. C</i> and <i>A. n. A, B</i> , and <i>C</i> .
Martin et al. (2015)	First record for <i>A. t. D</i> in Bent Co.; Hammerson's (1999) record for <i>A. t.</i> in the county is unverifiable.
Taylor et al. (2015b)	Genetic (electrophoresis and karyology) and morphological comparisons of <i>A. n. A, B, C, D</i> in southeastern Colorado.
Taylor et al. (2015a)	First plotted records of <i>A. n. A</i> in Teller and El Paso counties, and possibility of <i>A. n. D</i> in El Paso Co.
Taylor et al. (2016)	New record for <i>A. n. B</i> in Otero Co.
Alvarez et al. (2017)	Climate models for distributions of <i>A. n.</i> and <i>A. t.</i> in 2050 and 2070, including southeastern Colorado.
Taylor et al. (2017)	New record for <i>A. t. C</i> in Otero Co.
Walker et al. (here)	<i>A. t. C</i> presence and <i>A. s. v.</i> at Carrizo Canyon Picnic Area, Baca Co.

certain of these reports have only recently verified the presence of *A. tessellatus* D in Las Animas County (Newby et al. 2011) and Bent County (Martin et al. 2015), *A. neotesselatus* D in Otero County (Walker et al. 2012), *A. neotesselatus* A in Teller and El Paso counties (Taylor et al. 2015a), *A. neotesselatus* B in Pueblo County (Taylor et al. 2006b), and possibly *A. neotesselatus* D in El Paso County (Taylor et al. 2006b). The impact of global climate change on distribution estimates for *A. neotesselatus* and *A. tessellatus* projected for 2050 and 2070 indirectly emphasized the importance of documentation of the current status of these species at the periphery of their present geographic distributions (Alvarez et al. 2017).

To further elucidate the known distribution of species of *Aspidoscelis* in Colorado, we investigated a site at the

southeastern extent of the distribution of *A. tessellatus* in the state. *Aspidoscelis tessellatus* and *A. sexlineatus viridis* were known from this site based on observations in 2009 (Lauren J. Livo, pers. comm.) and 2013 (pers. obs.). Herein, we report on the identity, variation (morphology, color patterns, and snout vent lengths), habitat preferences, and conservation status of an array of parthenogenetic lizards in syntopy with *A. sexlineatus viridis* in the vicinity of the state and federally controlled Carrizo Canyon Picnic Area (CCPA), Baca County (Fig. 1). We considered discovery of the CCPA array of *A. tessellatus* to be highly significant because numerous attempts by the authors, and others, to locate this species in Baca County, Colorado, and adjacent Cimarron County, Oklahoma, since 1988 had been largely unsuccessful.

NOMENCLATURE UPDATE

The generic name *Aspidoscelis* Fitzinger 1843, resurrected from synonymy by Reeder et al. (2002) to partially resolve paraphyly in *Cnemidophorus* Wagler 1830, is technically of masculine rather than feminine gender (Steyskal 1971 summarized by Tucker et al. 2016). Therefore, we used the scientific epithets *A. sexlineatus viridis*, *A. neotesselatus*, and *A. tessellatus*, rather than *A. sexlineata viridis*, *A. neotesselata*, and *A. tessellata* as incorrectly emended by Reeder et al. (2002). Unfortunately, Crother (2017), in the latest checklist of the amphibians and reptiles of North America north of Mexico, did not change the nomenclature of lizards of the genus *Aspidoscelis* from the emendations of Reeder et al. (2002). We accept, however, common names based on the SSAR checklist, which herein were not preceded by an article.

We used an upper-case letter to represent a distinctive dorsal pattern class (= variant) of either diploid parthenogenetic *A. tessellatus* (i.e., C or D) or triploid parthenogenetic *A. neotesselatus* (i.e., A, B, C, or D) in southeastern Colorado based on a convention introduced by Zweifel (1965). In a range-wide study of *Cnemidophorus* (= *Aspidoscelis*) *tessellatus*, which included two subsequently described parthenogenetic species, Zweifel (1965) applied the letters A–F to a hypothesized phylogenetic series of mostly allopatric variants, except for actual syntopy between pattern classes C and D in restricted areas of San Miguel County, New Mexico, USA (e.g., Parker and Selander 1976; Cordes and Walker 2003), and Otero County, Colorado (e.g., Parker and Selander 1976; Walker et al. 1997). The genetics of color pattern classes in *Aspidoscelis* have been published by Parker and Selander (1976) and Taylor et al. (2003, 2015b); discussions of the origins of color pattern classes have been offered by Abuhteba et al. (2000) and Cordes and Walker (2003).

Scudday (1973) described Zweifel's pattern class F as diploid *Cnemidophorus* (*Aspidoscelis*) *dixoni* consisting of pattern classes A and B, to which Walker et al. (1994) added pattern class C. Walker et al. (1997), based in part on studies by Parker and Selander (1976) and Walker et al. (1995), described Zweifel's pattern classes A and B as triploid *Cnemidophorus* (*Aspidoscelis*) *neotesselatus* and recognized new pattern class C. Subsequently, Walker et al. (2012) also recognized *A. neotesselatus* D. Taylor et al. (2015a,b, 2016, 2017) have also used pattern class designations in studies of *A. tessellatus* and *A. neotesselatus*, as did Cole et al. (2007) in a study of *A. dixoni*. In each of diploid parthenogenetic *A. dixoni* (A–C) and *A. tessellatus* (C–E) and triploid parthenogenetic *A. neotesselatus* (A–D), the designations represent the chronological sequence in which they were applied; each pattern class in each

species is both intraspecifically and interspecifically distinct. The barrier to recognition of each intraspecific pattern class as a species is philosophical; based on existing evidence (Cordes and Walker 2006; Taylor et al. 2015b), they are post-formational arrays rather than products of separate interspecific hybrid events; however, we retain *A. dixoni* as a distinct species with pattern classes A–C (*sensu* Cordes and Walker, 2006; Cole et al. 2007), rather than as a variant of *A. tessellatus* (*sensu* Crother et al. 2017). We avoided use of the term population for local groups of a parthenogenetic species because of its usual association with males and females of a gonochoristic species. Instead, we refer to a local group of parthenogenetic females as an array.

MATERIALS AND METHODS

Study area.—We conducted the study on specimens of *A. tessellatus* C (Figs. 2–3) collected from 16–21 May 2017 in the vicinity of Carrizo Canyon Picnic Area (CCPA), which is located within the Comanche National Grassland in southwestern Baca County, Colorado (Fig. 1). The canyon (37°07'58.97"N, 103°00'59.07"W; WGS84; elevation 1,457 m) was carved by a permanent stream, East Carrizo Creek. Extending from both the east and west, canyon rims were ecotonal habitats that graded into Sand Sage Prairie. Weather station data from Kim, Colorado, reported a maximum temperature of 20.6° C, a mean temperature of 12.8° C, and 1.24 cm precipitation during the field study.

Additional specimens analyzed.—We included specimens of *A. tessellatus* C (Fig. 4), but not syntopic and distinctive *A. tessellatus* D, from Ninemile Valley of the Purgatoire River (n = 99), Otero County, Colorado, from the University of Arkansas Department of Zoology (UADZ), University of Colorado Museum of Natural History (UCM), and Regis University (RU) collections. We also included specimens of *A. tessellatus* C from Cottonwood Creek (n = 15), extreme western Baca County, Colorado, from the UCM for body size, meristic, and color pattern comparisons (Table 2). To access geographic variation, we compared the sample of *A. tessellatus* C from CCPA with samples of *A. tessellatus* C from Cottonwood Creek, approximately 5.0 km southwest of CCPA and Ninemile Valley, approximately 125.0 km northwest of CCPA.

Data collection.—We captured *A. tessellatus* C and *A. sexlineatus viridis* opportunistically at CCPA while searching suitable habitat on foot. We captured specimens by hand after uncovering them while dormant under natural cover objects, or by noose. Following capture, we measured snout-vent length (SVL; \pm 1.0 mm SE); however, SVL was later recorded

Herpetological Conservation and Biology

TABLE 2. Statistical comparisons of 10 meristic characters and a ratio in three samples of diploid *Aspidoscelis tessellatus* C (Common Checkered Whiptail) from sites in Otero and Baca counties in southeastern Colorado, USA, from the following collections: Truman State University (TSU); University of Arkansas Department of Zoology (UADZ); University of Colorado Museum (UCM); and Regis University (RU). Numbers are means \pm 1 standard error above and range of variation and number of specimens beneath; different superscript letters for means for a character indicate significant differences ($P < 0.05$) as determined by these commands in JMP (Quartiles, Means/Kruskal-Wallis, and Mann-Whitney).

Morphological Character	Ninemile Valley, Otero County UADZ, UCM, RU	Cottonwood Creek, Baca County UCM	Carrizo Canyon, Baca County TSU = UADZ	F Statistics, Probability
Granules (Scales) Around Midbody (GAB)	90.9 \pm 0.29 ^B 86–98 (99)	94.3 \pm 0.68 ^A 9–100 (15)	94.8 \pm 0.62 ^A 88–105 (18)	$\chi^2 = 28.98$, $P = < 0.001$
Granules Occiput to Rump (OR)	190.9 \pm 0.52 ^B 176–207 (99)	204.8 \pm 1.34 ^A 196–203 (15)	206.6 \pm 1.22 ^A 195–220 (18)	$\chi^2 = 66.49$, $P = < 0.001$
Granules Between Paravertebral Stripes (GPV)	10.5 \pm 0.09 ^B 9–12 (99)	11.7 \pm 0.22 ^A 10–14 (15)	11.4 \pm 0.20 ^A 11–12 (18)	$\chi^2 = 35.44$, $P = < 0.001$
Percentage of Granules Between/Around (GPV/GAB)	11.3 \pm 0.09 ^B 9.5–13.3 (99)	12.4 \pm 0.24 ^A 10.4–14.1 (15)	12.1 \pm 0.21 ^A 10.5–13.6 (18)	$\chi^2 = 17.91$, $P < 0.001$
Combined (l & r) Femoral Pores (FP)	41.4 \pm 0.17 ^B 37–45 (99)	44.5 \pm 0.44 ^A 41–48 (15)	43.6 \pm 0.40 ^A 39–47 (18)	$\chi^2 = 40.46$, $P = < 0.001$
Subdigital Lamellae Fourth Digit of 1 Pes (SDL)	37.3 \pm 0.11 ^A 35–41 (99)	37.5 \pm 0.29 ^A 36–40 (15)	36.1 \pm 0.23 ^B 34–38 (18)	$\chi^2 = 16.38$, $P = < 0.001$
Combined Circumorbital Scales (COS)	17.4 \pm 0.19 ^B 13–22 (99)	18.5 \pm 0.50 ^{AB} 15–22 (15)	19.2 \pm 0.46 ^A 16–22 (18)	$\chi^2 = 14.29$, $P = < 0.001$
Combined Lateral Supraocular Scales (LSG)	35.3 \pm 0.26 ^B 30–43 (99)	35.5 \pm 0.66 ^{AB} 31–42 (15)	37.3 \pm 0.60 ^A 34–43 (18)	$\chi^2 = 9.47$, $P = 0.009$
Enlarged Mesoptychial Scales (MS)	12.4 \pm 0.13 ^B 9–16 (99)	14.3 \pm 0.34 ^A 12–16 (15)	12.4 \pm 0.27 ^B 11–15 (18)	$\chi^2 = 22.22$, $P = < 0.001$
Combined Interlabial Scales (ILS)	38.6 \pm 0.44 ^A 29–48 (99)	39.5 \pm 1.06 ^A 35–44 (15)	40.8 \pm 0.97 ^A 36–51 (18)	$\chi^2 = 3.65$, $P = 0.162$
Combined Supraocular Scales (SO)	8.1 \pm 0.04 ^B 8–10 (99)	8.9 \pm 0.17 ^A 8–10 (15)	8.3 \pm 0.10 ^B 8–11 (18)	$\chi^2 = 48.29$, $P = < 0.001$



FIGURE 2. Right side of an individual of Common Checkered Whiptail, *Aspidoscelis tessellatus* (released), from May 2013 from along western rim of Carrizo Canyon, Comanche National Grassland, Baca County, Colorado, USA. The individual shows a distinct pale-colored lateral and dorsolateral stripes though showing some interruptions (= breaks) on the neck, pale-colored vertical bars extending from the lateral stripe into the lower and upper lateral fields, and bars forming in posterior aspect of dorsolateral field. All are characters of *A. tessellatus* C rather than of *A. neotessellatus* B. (Photographed by Michael I. Kelrick).



FIGURE 3. Dorsum of an individual of Common Checkered Whiptail, *Aspidoscelis tessellatus* (released), from May 2013 from along western rim of Carrizo Canyon, Comanche National Grassland, Baca County, Colorado, USA. The individual shows a distinct pale-colored dorsolateral and paravertebral stripes, zig-zag vertebral stripe with extensions to paravertebral stripes, vague indications of pale stripes and dark fields on the tail, and bars forming in the dorsolateral fields. All are characters of *A. tessellatus* C rather than *A. neotessellatus* B. (Photographed by Michael I. Kelrick).

from preserved specimens for comparisons among samples. We euthanized lizards with an overdose of 20% benzocaine (Orajel™, Church & Dwight Co., Inc., Ewing, New Jersey, USA) and preserved them in 10% formalin for inclusion in the UADZ collection.

We used body size data to estimate age class, including young of year (YOY), and to clarify ontogenetic variation in color pattern. We used age class estimation to represent monthly distributions of age classes. We documented meristic characters previously used in part or in total by Duellman and Zweifel (1962), Zweifel (1965) and Walker et al. (1995, 1997) in comparative studies of the *A. tessellatus* complex (Table 2). The meristic characters we analyzed included granules (=

scales) around midbody (GAB); granules from occiput to rump counted along the middorsal region (OR); granules counted between the paravertebral stripes at midbody (GPV); percentage of the granules around midbody situated between the paravertebral stripes at the same level (GPV/GAB x 100); combined number (right and left) of femoral pores (FP) counted on each thigh; subdigital lamellae counted on the ventral aspect of the longest toe of the left pes (SDL); combined number of circumorbital scales counted between the supraocular and median head scales (COS); combined number of lateral supraocular granules counted anteriorly from the third supraocular sutures (LSG); number of enlarged mesoptychial scales counted in the row bordering



FIGURE 4. An individual *Aspidoscelis tessellatus* C (released) from May 2012 from near David Canyon Road (37.758611°N, 103.588888°W), Otero County, Colorado, USA, with a dorsal pattern characteristic of lizards in the sample of the species from Ninemile Valley of the Purgatoire River, Otero County, Colorado. (Photographed by Anthony J. Wilmes).

the edge of the gular fold (MS); combined number of interlabial scales counted between the chin shields and upper labial scales (ILS); and combined number of supraocular scales assessed superior to the eyes (SO).

Data analysis.—Adult body size data were normally distributed and homoscedastic for each population. We used ANOVA to compare adult body size in *A. tessellatus* C (> 60.0 mm SVL) between specimens from Ninemile Valley and CCPA (the Cottonwood Creek sample was deleted from this analysis due to lack of adults from this site). As most meristic characters were not normally distributed for at least one population, we used separate Kruskal-Wallis tests, with Mann-Whitney post-hoc comparisons, to compare each meristic character among the three sites with a Bonferroni correction that reduced $\alpha = 0.0045$ for each analysis. In addition, we used Discriminant Function Analysis to compare meristic characters among Ninemile Valley, Cottonwood Creek, and CCPA samples to determine the degree of separation among the parthenogenetic arrays. As the first canonical score was not normally distributed, we used a Kruskal-Wallis test with post-hoc Mann-Whitney tests to compare the two canonical scores among sites. We used JMP© 7.0 (SAS Institute Inc., Cary, North Carolina, USA) for statistical analysis, with $\alpha = 0.05$. We present means with \pm one standard error.

RESULTS

Body size and age classes in *Aspidoscelis tessellatus* C.—We analyzed 18 *A. tessellatus* C, including 13 adults and five juveniles from CCPA during May 2017. There was no significant difference in adult SVL between CCPA ($89. \pm 2.56$ mm, $n = 13$) and Ninemile Valley (89.2 ± 1.1 mm, $n = 72$; $F_{1,83} = 0.791$, $P = 0.377$). We analyzed 15 YOY (37–44 mm SVL) collected from Cottonwood Creek and 21 YOY (38–50 mm SVL) and five adults (83–91 mm SVL) from Ninemile Valley in September of 1960 and 1989, respectively, with all included adults collected at the beginning of September. Activity of adults of *A. tessellatus* C sharply decreased in August and ceased altogether by early September, although YOY were intermittently active into early October. The five juveniles (49–53 mm SVL) we collected in May 2017 at CCPA likely hatched during late summer 2016, and probably were inactive from approximately mid-October 2016 to early May of 2017. As indicated by low temperatures during the study period, whiptail lizard activity was limited in May 2017 at CCPA.

Color patterns in *Aspidoscelis tessellatus* C.—Five juvenile lizards (49–53 mm SVL; mean = 51.0 mm) from CCPA possessed gray-white longitudinal components on each side of the body, a vestigial ventrolateral stripe

from the angle of the jaw to the forelimb, an irregularly margined lateral stripe with several narrow anterior interruptions (= breaks) from the postorbital area onto the anterior aspect of the thigh, an irregular dorsolateral stripe from the superciliary scales to well onto the tail, and a less irregular paravertebral stripe from the occipital region to well onto the tail. A vertebral stripe with an exaggerated zig-zag profile was also present in the black vertebral field of each juvenile specimen, though the angular aspects of the profiles were neither well developed nor in lateral contact with the paravertebral stripes. Incipient (= developing) pale vertical bars were apparent extending dorsally and ventrally from each lateral stripe into the black upper and dusky lower lateral fields, respectively, and incipient (= developing) spots were apparent in the black dorsolateral fields. The forelimbs and hindlimbs were black with distinct gray-white spots, but spots rather than a line were present on the posterior aspects of the thighs.

Thirteen adult females (81–98 mm SVL) from CCPA had dorsal patterns consistent with the descriptions of Zweifel (1965) and Walker et al. (1997) for *A. tessellatus* C. Each specimen possessed a black dorsal ground color on the limbs and body except for the dusky gray-black lower lateral fields, a pair of vestigial ventrolateral stripes, three pairs of irregularly margined gray-white primary stripes (= laterals, dorsolaterals, and paravertebrals), a zigzag gray-tan vertebral configuration (= secondary stripe) between the paravertebral stripes, spots and/or bars either between the stripes or merging with them, irregular gray-white spots rather than a line on the posterior aspect of each thigh, and evidence of longitudinal extensions of the dorsolateral and paravertebral stripes and intervening fields on the base of the tail (Figs. 2–3). Though each juvenile *A. tessellatus* C from CCPA had a vertebral stripe configuration that was irregularly margined that did not contact the paravertebral stripes by lateral extensions, ontogenetic changes in all 13 adult lizards had resulted in coalescence (= contact) of lateral extensions of the vertebral with each of the paravertebrals (range of total contacts, 14–35; mean = 24.0). Among the adults of *A. tessellatus* C, the vertebral stripe configuration had no breaks in three specimens, one break in six, two breaks in three, and five breaks in one (range, 0–5; mean = 1.3). The ontogenetically modified left lateral stripe was discernable in all 13 adults though they had been modified by coalescence with spots and vertical bars. Breaks (interruptions by black ground color) in the left lateral stripe numbered 2–9 (mean = 4.5).

Analysis of univariate meristic characters in *Aspidoscelis tessellatus* C.—Comparisons of the Cottonwood Creek, Ninemile Valley, and CCPA samples of *A. tessellatus* C revealed significant differences (P

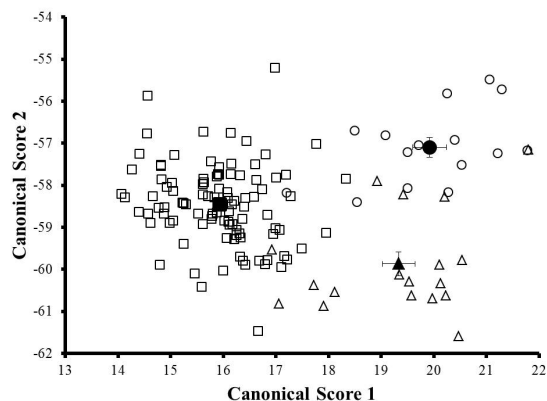


FIGURE 5. Relationship between the second canonical score and the first canonical score for individuals of *Aspidoscelis tessellatus* C from three arrays in southeastern Colorado, USA: triangles = Carrizo Canyon Picnic Area (CCPA); squares = Ninemile Valley; circles = Cottonwood Creek; closed symbols = means for the respective arrays; and error bars = represent one standard error (error bars may be hidden by symbol).

< 0.005) in nine of the 11 meristic characters (Table 2). Cottonwood Creek and CCPA samples were not significantly different in eight of 11 meristic characters, while the Ninemile Valley sample was significantly different from CCPA in eight of 11 characters and Cottonwood Creek samples in seven of 11 characters (Table 2). Somewhat surprisingly due to their close proximity, the Cottonwood Creek and CCPA samples were significantly different in three of 11 meristic characters. Comparison of the CCPA and Ninemile Valley samples revealed significant differences in GAB, OR, PV, PV/GAB, FP, SDL, COS, and LSG (Table 2). Of these, significantly higher means existed for all characters for CCPA except for SDL. Also, comparisons of the Cottonwood Creek and Ninemile Valley samples revealed significant differences in GAB, OR, PV, PV/GAB, FP, MS, and SO, with higher mean values at Cottonwood Creek for all values (Table 2).

Analysis of multivariate meristic characters in *Aspidoscelis tessellatus* C.—Comparisons of the Cottonwood Creek, Ninemile Valley, and CCPA samples of *A. tessellatus* C revealed that the first canonical score (CS1) accounted for 84.1% of the variation in meristic characters, with PV having a strongly positive loading and PV/GAB having a strongly negative loading (Table 3). There was a significant difference in CS1 among sites ($H = 70.67$, $df = 2$, $P < 0.001$; Fig. 5). The Ninemile Valley sample had a significantly lower CS1 than both Cottonwood Creek and CCPA samples, which were not significantly different from each other ($W = 1.890$, $df = 1$, $P = 0.170$). There was also a significant difference in CS2 among sites ($H = 37.35$, $df = 2$, $P < 0.001$). The

TABLE 3. Character loadings and percentage of total variance explained for the first two canonical (Can) scores from a Discriminate Function Analysis of samples of diploid *Aspidoscelis tessellatus* C (Common Checkered Whiptail) from sites in Otero (Ninemile Valley) and Baca (Cottonwood Creek and Carrizo Canyon Picnic Area) counties in southeastern Colorado, USA.

Character	Can 1	Can 2
Granules (Scales) Around Midbody	-0.225	-0.748
Granules Occiputto Rump	0.120	-0.080
Granules Between Paravertebral Stripes	3.296	6.717
Percent of Granules Between/Around	-2.867	-5.984
Combined Femoral Pores	0.197	0.060
Subdigital Lamellae Fourth Digit of Left Pes	-0.129	0.315
Combined Circumorbital Scales	0.036	-0.014
Combined Lateral Supraocular Scales	0.009	-0.101
Enlarged Mesoptychial Scales	0.162	0.405
Combined Interlabial Scales	0.010	-0.045
Combined Supraocular Scales	0.664	1.186
Total Variance	84.14	15.86

Cottonwood Creek sample was significantly greater than the Ninemile Valley sample ($W = 20.07$, $df = 1$, $P < 0.001$), which was significantly greater than the CCPA sample ($W = 18.09$, $df = 1$, $P < 0.001$).

Discriminant Function Analysis correctly predicted 72.2% (13/18) of individuals from CCPA, with 22.2% (four of 18) incorrectly predicted to be from Cottonwood Creek and 5.6% (one of 18) incorrectly predicted to be from Ninemile Valley. Discriminant Function Analysis correctly predicted 86.6% (13 of 15) of the Cottonwood Creek sample, with 6.7% (one of 15) incorrectly predicted to be from each of Ninemile Valley and CCPA. Discriminant Function Analysis correctly predicted 96.0% (95 of 99) of the Ninemile Valley sample, with 2.0% (two of 99) incorrectly classified as each of Cottonwood Creek and CCPA.

Habitat and activity in *Aspidoscelis tessellatus* C.—

We searched for whiptail lizards on the east and west sides of Carrizo Canyon, as well as in the riparian zone in the canyon along East Carrizo Creek (Fig. 6). Based on observations by us in May 2013, and May and July 2017, *A. tessellatus* was most abundant along the west rim, was not observed in the riparian zone, and was less abundant than *A. sexlineatus viridis* near the eastern rim. Except for a few areas on the eastern rim that marginally duplicated components of substrate (i.e., boulders, rock surfaces, and rocky/gravelly soil) and vegetation (i.e., junipers) more typical of the west side, the immediate vicinity of the picnic area was Sand Sage Prairie, prime habitat for *A. sexlineatus viridis*. We also observed the latter species in the sandy/grassy corridor in the canyon.

The ecotone between the western rim of Carrizo Canyon and prairie where we located *A. tessellatus* 15–19 May 2013 and 16–21 May 2017 occurred into the Carrizo Canyon from the picnic area, south along



the east side of Carrizo Creek, crossed the stream, and scaled a sloping bedrock formation to the western rim. In the study period in 2017, daily temperature conditions were mostly suboptimal for whiptail lizard surface activity; however, in the transition zone of up to 35 m in width between canyon rim and prairie, the substrate was strewn with numerous flat slabs of rock. Between 16–21 May 2017, we found several individuals of *A. tessellatus* C per day under the flat rocks in the transition zone. This zone (Fig. 6) also supported scattered juniper and pinyon pine trees and sparse growths of grasses and forbs. The substrate of coarse well-drained soil was strewn with flat rocks and patches of bedrock and boulders. The availability of this habitat was the basis for the presence of the parthenogenetic whiptail species, but it was suboptimal for the small gonochoristic species.

DISCUSSION

***Aspidoscelis tessellatus* C at CCPA.**—Body size, color pattern, and meristic characters of *A. tessellatus* from CCPA were generally within the limits previously described for the species and specifically for pattern class C (Walker et al. 1995, 1997). Based on meristic characters, the CCPA population was more similar to the Cottonwood Creek array than the more geographically distant Ninemile Valley array. East Carrizo Creek is a tributary to Cottonwood Creek, with relatively contiguous habitat between the two sites, making historical dispersal between these arrays more likely. Ninemile Valley is more geographically distant and separated by large swaths of inhospitable habitat, reducing the likelihood of current dispersal between Ninemile Valley and either Cottonwood Creek or CCPA.

***Life history of Aspidoscelis tessellatus* C at CCPA.**—Hatchlings of *A. tessellatus* C appear in late summer (i.e., mid-August to early September) and could remain active intermittently until October, long after other age classes have retired for the activity cycle as indicated by the Cottonwood Creek and Ninemile Valley samples of juveniles. Juveniles from the previous fall then re-emerged from overwintering refugia in the following spring. Juvenile *A. tessellatus* C grew upwards of 20.0 mm SVL in their second activity cycle, with growth slowing after the onset of first reproduction in the third activity cycle. This growth pattern resulted in the

FIGURE 6. Habitat of whiptails (top) from July 2017 from along western rim of Carrizo Canyon, Comanche National Grassland, Baca County, Colorado, USA, showing pinyon pine trees, juniper trees, boulders, numerous flat rocks, coarse gravelly to rocky soil, and sparse groundcover of grasses and forbs; a constellation of habitat components permitting the presence of many *Aspidoscelis tessellatus* C and few Prairie Racerunner, *A. sexlineatus viridis*. Habitat (middle) from July 2017 from along east side of the creek in Carrizo Canyon, Comanche National Grassland, Baca County, Colorado, showing riparian complex of sandy soil and tall grasses, habitat components, which support *Aspidoscelis sexlineatus viridis* but not *A. tessellatus* C. Habitat (bottom) from July 2017 from near Carrizo Canyon, Comanche National Grassland (east of the picnic area), Baca County, Colorado, showing components of sand sage habitat that permits presence of many individuals of *Aspidoscelis sexlineatus viridis*, but no individuals of *A. tessellatus* C. (Photographed by James E. Cordes).

array at Ninemile Valley, and we hypothesize at CCPA, comprising individuals of up to five activity cycles of life (Taylor et al. 1999). All 13 adults of *A. tessellatus* C from CCPA had large postcoelomic fat bodies, indicating insufficient mobilization of fat reserves to yolk ovarian follicles by May 2017.

***Aspidoscelis tessellatus* in Baca County.**—The juniper woodland macrohabitat occupied by *A. tessellatus* C at CCPA was more similar to that observed for the pattern class at Cottonwood Creek, than that for the arrays of *A. tessellatus* C sampled in Ninemile Valley of the Purgatoire River, which mainly inhabited greasewood flats (Walker and Cordes 1998; Walker et al. 1995, 1997, 1998). Daily weather conditions during the study period in May were mostly suboptimal for whiptail surface activity, although, based on weather data for the area, intermittent suitable weather conditions had occurred prior to the sampling period, which would have allowed *A. tessellatus* C to emerge from overwintering refugia. This pattern has also been observed in various years in Ninemile Valley, with whiptail lizard activity being unpredictable as a result of the vicissitudes of climatic conditions until well into June (pers. obs.).

The vicinity of CCPA in Baca County is the most southeasterly canyonland area yet discovered for the diploid parthenogenetic *A. tessellatus* in Colorado. All whiptail lizard specimens we examined from Baca County were either *A. tessellatus* C or *A. sexlineatus viridis*. The habitat requirements observed for the two species at CCPA, namely that *A. tessellatus* C, which is much more restricted to rock strewn canyon edges, and *A. sexlineatus viridis*, which is associated with open and mixed prairie, have been widely observed elsewhere where the species are locally sympatric. Nevertheless, numerous searches for *A. tessellatus* we have made in the past in the areas of CCPA and/or Cottonwood Creek in Baca County and neighboring Cimarron County, Oklahoma, have failed. Conversely, similar searches have been invariably successful in Ninemile Valley, Otero County. Although gonochoristic *A. sexlineatus* is known from many sites in Baca County (Mackessy 1988; Hammerson 1999), relatively few voucher specimens for the parthenogenetic species are known (Walker et al. 1997). The disparity in the occupancy by the two species reflects the fact that most areas inhabited by whiptail lizards in Baca County are of prairie derivation, which are far more extensive than the narrow canyonlands within our study area. Interestingly, we know of no specimens of *A. tessellatus* C from the area crossed by a straight line of approximately 125 km from south of Ninemile Valley of the Purgatoire River near Higbee, Otero County, through Las Animas county to CCPA in Baca County. All specimens from various sites in the

vicinity of this line in Otero and Las Animas counties are either diploid parthenogenetic *A. tessellatus* pattern Class D or triploid parthenogenetic *A. neotessellatus* pattern class B (unpubl. data).

***Aspidoscelis tessellatus*.**—The northern termini of the geographic range of *A. tessellatus* are in southeastern Colorado (Zweifel 1965; Parker and Selander 1976; Walker et al. 1997; Martin et al. 2015; Taylor et al. 2017) and the southern termini of its range are approximately 1,100 km to the south associated with the valley of the Rio Conchos and some of its tributaries in Chihuahua State, Mexico (Smith et al. 1963; Zweifel 1965; Parker and Selander 1976; Walker et al. 1997). Our studies have shown that across most of the range of *A. tessellatus* (e.g., Potter, Armstrong, Randall, Brisco, Reeves, Crane, Upton, Brewster, Culberson, and Presidio counties in Texas; Guadalupe, De Baca, San Miguel, Quay, and Chaves counties in New Mexico; and in parts of Chihuahua), the species was relatively abundant and easily observed. That cannot be said of our experiences in Bent and Baca counties, Colorado, and Cimarron County, Oklahoma, however. It remains a haunting enigma that the CCPA sample of *A. tessellatus* C used in this study was obtained by searching for inactive lizards. The present study emphasizes that the species can be locally abundant, but that suitable habitats in Baca County exist in a patchy occurrence and that its activity pattern is enigmatic. Continued survey efforts are necessary to thoroughly document the extent of the range of *A. tessellatus* and *A. neotessellatus* in southeastern Colorado in light of the potential for loss of suitable habitat due to ongoing global climate change (Alvarez et al. 2017). In particular, emphasis should be placed on determining the distribution of each pattern class of *A. tessellatus* and *A. neotessellatus* to investigate dispersal and occupancy of these evolutionarily significant arrays.

SPECIMENS EXAMINED

***Aspidoscelis tessellatus* C from Carrizo Canyon Picnic Area (n = 18).** Colorado: Baca County: vicinity of Carrizo Canyon Picnic Area, Comanche National Grassland, along western rim of canyon WGS84 37°07'58.97"N, 103°00'59.07"W, 1,457 m (16–21 May 2017, UADZ 9701–9718, n = 18).

***Aspidoscelis sexlineatus viridis* from Carrizo Canyon Picnic Area (n = 3).** Colorado: Baca County: vicinity of Carrizo Canyon Picnic Area, Comanche National Grassland, along western rim of canyon WGS84 37°07'58.97"N, 103°00'59.07"W, 1,457 m (16–21 May 2017, UADZ 9719–9721, n = 3).

***Aspidoscelis tessellatus* C from Cottonwood Creek (n = 15).** Colorado: Baca County: 24 km south, 20 km west of Pritchett (1 September 1960, UCM 14813, 14814, n = 2; 2 September 1960 UCM 14816–14823, 14825–14829, n = 13).

***Aspidoscelis tessellatus* C from Ninemile Valley of the Purgatoire River (n = 99).** Colorado: Otero County: Ninemile Valley of the Purgatoire River, Southwest of Colorado Highway 109 on road 804, datum WGS84 37.717819°N, 103.515303°W (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; 3 July 2004, RU 0122, n = 1; 5 July 2004, RU 0130–0131, n = 2; 14 June 2005, HLT 164, n = 1; 15 June 2005, RU 0167, n = 1).

Acknowledgments.—We extend thanks to Tanner Bandy, Laurel Bonebrake, Lauren Dierkes, Jake Friehbohle, Alyssa Johnson, Sarah Lamprecht, Samuel Leone, Kelly Lovera, Carolyn Mann, and Natalie Wronkiewicz, who are all undergraduate students at Truman State University, for assistance in the field. The field course was supported by Truman State University. All research was conducted in accordance with Truman State University Institutional Animal Care and Use Committee guidelines. Colorado Parks and Wildlife, Department of Natural Resources, Division of Wildlife provided Scientific Collecting License 17HP2376 to CEM. We thank Lauren J. Livo for providing her observations on whiptail lizards at Carrizo Canyon Picnic Area from 2009. We also acknowledge personnel from the University of Colorado Museum and Harry L. Taylor from Regis University for providing loans of specimens from Cottonwood Creek and Ninemile Valley in their care. Figure 1 was prepared by James Walker and Chad Montgomery and Figure 5 was prepared by Chad Montgomery.

LITERATURE CITED

- Abuhteba, R.M., J.M. Walker, and J.E. Cordes. 2000. Genetic homogeneity based on skin histocompatibility and the evolution and systematics of parthenogenetic *Cnemidophorus laredoensis* (Sauria: Teiidae). *Canadian Journal of Zoology* 78:895–904.
- Alvarez, G., E.A.L. Salas, N.M. Harings, and K.G. Boykin. 2017. Projections of future suitable bioclimatic conditions of parthenogenetic whiptails. *Climate* 5(2) 34; <https://doi.org/10.3390/cli5020034>.
- Cole, C.J., C.W. Painter, H.C. Dessauer, and H.L. Taylor. 2007. Hybridization between the endangered unisexual Gray-checked Whiptail Lizard (*Aspidoscelis dixonii*) and the bisexual Western Whiptail Lizard (*Aspidoscelis tigris*) in southwestern New Mexico. *American Museum Novitates* 3555:1–31.
- Cordes, J.E., and J.M. Walker. 2003. Skin histocompatibility between syntopic pattern classes C and D of parthenogenetic *Cnemidophorus tessellatus* in New Mexico. *Journal of Herpetology* 37:185–188.
- Cordes, J.E., and J.M. Walker. 2006. Evolutionary and systematic implications of histocompatibility among parthenogenetic teiid lizards: three color pattern classes of *Aspidoscelis dixonii* and one of *Aspidoscelis tessellata*. *Copeia* 2006:14–26.
- Crother, B.I. (Committee Chair). 2017. Scientific and Standard English Names of Amphibians and Reptiles of North America North of Mexico, with Comments Regarding Confidence in our Understanding. 8th Edition. Moriarty, J.J. (Ed.). *Herpetological Circular* 43, Society for the Study of Amphibians and Reptiles, Topeka, Kansas, USA.
- Duellman, W.E., and R.G. Zweifel. 1962. A synopsis of the lizards of the *sexlineatus* group (genus *Cnemidophorus*). *Bulletin American Museum of Natural History* 123:155–210.
- Fitzinger, L.J. 1843, *Systema Reptilium*. Volume 1. Braumüller & Seidel, Vienna:Vindobonae, Austria. 106 p.
- Hammerson, G.A. 1999. *Amphibians and Reptiles in Colorado*. 2nd Edition. University Press of Colorado, Niwot, Colorado, USA.
- Mackessy, S.P. 1998. A survey of the herpetofauna of the Comanche National Grasslands in southeastern Colorado. U.S. Department of Agriculture, Forest Service, Jamestown, North Dakota, USA. 61 p.
- Martin, D.J., L.E.R. Martin, D. Wojnowski, and B.A. Fisher. 2015. Geographic distribution. *Aspidoscelis tessellata* (Common Checkered Whiptail). *Herpetological Review* 46:568.
- Maslin, T.P. 1962. All-female species of the lizard genus *Cnemidophorus*, Teiidae. *Science* 135:212–213.
- Maslin, T.P. 1966. The sex of hatchlings of five apparently unisexual species of whiptail lizards (*Cnemidophorus*, Teiidae). *American Midland Naturalist* 75:369–378.
- Maslin, T.P. 1971. Conclusive evidence of parthenogenesis in three species of *Cnemidophorus* (Teiidae). *Copeia* 1971:156–158.
- Newby, J.L., J. Boling, J. Estes, L.K. Garey, A.M. Grelle, J. Hasken, R. McKee, A. Wilmes, C.E.

- Montgomery, M.I. Kelrick, and J.M. Walker. 2011. Pattern class D of parthenogenetic *Aspidoscelis tessellata* (Sauria: Teiidae) in Las Animas County, Colorado. *Southwestern Naturalist* 56:128–130.
- Parker, E.D., Jr., and R.K. Selander. 1976. The organization of genetic diversity in the parthenogenetic lizard *Cnemidophorus tessellatus*. *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* 2002:1–61.
- Scudday, J.F. 1973. A new species of lizard of the *Cnemidophorus tessellatus* group from Texas. *Journal of Herpetology* 7:363–371.
- Smith, H.M., K.L. Williams, and E.O. Moll 1963. Herpetological explorations on the Rio Conchos, Chihuahua, Mexico. *Herpetologica* 19:205–215.
- Steyskal, G.C. 1971. On the grammar of names formed with *-scelus*, *-sceles*, *-scelis*, etc. *Proceedings Biological Society of Washington* 84:7–11.
- Taylor, H.L., C.J. Cole, H.C. Dessauer, and E.D. Parker, Jr. 2003. Congruent patterns of genetic and morphological variation in the parthenogenetic lizard *Aspidoscelis tessellata* (Squamata: Teiidae) and the origins of color pattern classes and genotypic clones in eastern New Mexico. *American Museum Novitates* 3424:1–40.
- Taylor, H.L., B.A. Droll, and J.M. Walker. 2006a. Proximate causes of a phylogenetic constraint on clutch size in parthenogenetic *Aspidoscelis neotesselata* (Squamata: Teiidae) and range expansion opportunities provided by hybridity. *Journal of Herpetology* 40:294–304.
- Taylor, H.L., L.J. Livo, D.J. Martin, W.R. Maynard, A. Estep, R. Clawges, D. Roth, J. Kellner, and T. Jackson. 2015a. New northern distribution records for pattern classes A, B, and D of *Aspidoscelis neotesselata* (Colorado Checkered Whiptail) in Colorado, and biogeographic sources of northern colonists. *Herpetological Review* 46:312–319.
- Taylor, H.L., R. J. Rondeau, and J. Sovell. 2006b. Alternative ontogenetic pathways to color pattern class B in a newly discovered population of parthenogenetic *Aspidoscelis neotesselata* (Squamata: Teiidae). *Herpetological Review* 37:40–44.
- Taylor, H.L., J.M. Walker, C.J. Cole, and H.C. Dessauer. 2015b. Morphological divergence and genetic variation in the triploid parthenogenetic teiid lizard, *Aspidoscelis neotesselata*. *Journal of Herpetology* 49:491–501.
- Taylor, H.L., J.M. Walker, and J.E. Cordes. 1999. Monthly distributions of size classes and reproductive status in *Cnemidophorus tessellatus* (Sauria: Teiidae) from southeastern Colorado. *Herpetological Review* 30:205–207.
- Taylor, H.L., A.J. Wilmes, L.K. Garey, C.E. Montgomery, L.J. Livo, and J.M. Walker. 2016. Rare color-pattern misfits in indigenous arrays of parthenogenetic *Aspidoscelis neotesselata* (Colorado Checkered Whiptail). *Herpetological Review* 47:561–568.
- Taylor, H.L., A.J. Wilmes, C.E. Montgomery, L.J. Livo, and J.M. Walker. 2017. Recent northward range expansion of the parthenogenetic lizard *Aspidoscelis tessellatus* in Colorado and the distributional enigma posed by pattern-classes C and D at the northern range periphery. *Southwestern Naturalist* 62:179–186.
- Tinkle, D.W. 1959. Observations on the lizards *Cnemidophorus tigris*, *Cnemidophorus tessellatus* (sic), and *Crotaphytus wislizeni*. *Southwestern Naturalist* 4:195–200.
- Tucker, D.B., G. R. Colli, L.G. Giugliano, S.B. Hedges, C.R. Hendry, E.M. Lemmon, A.R. Lemmon, J.W. Sites Jr., and R.A. Pyron. 2016. Methodological congruence in phylogenomic analyses with morphological support for teiid lizards (Sauria: Teiidae). *Molecular Phylogenetics and Evolution* 103:75–84.
- Wagler, J.G. 1830. *Natürliches System der Amphibien: mit vorangehender Classification der Säugethiere und Vögel: ein Beitrag zur vergleichenden Zoologie*. J.G. Cotta. Munich, Germany.
- Walker, J.M. 2012. *Aspidoscelis neotesselata* (Colorado Checkered Whiptail). Natural history notes. Fragmented habitat. *Herpetological Review* 43:478–479.
- Walker, J.M., and J.E. Cordes. 1998. Parthenogenetic *Cnemidophorus tessellatus* complex (Squamata: Teiidae) at Higbee, Otero County, Colorado: research between 1950 and 1998. *Bulletin Chicago Herpetological Society* 33:75–84.
- Walker, J.M., and J.E. Cordes. 2003. Can parthenogenetic *Cnemidophorus tessellatus* (Sauria: Teiidae) occasionally produce offspring markedly different from the mother? *Southwestern Naturalist* 48:126–129.
- Walker, J.M., J.E. Cordes, and H.L. Taylor. 1997. Parthenogenetic *Cnemidophorus tessellatus* complex (Sauria: Teiidae): a neotype for diploid *C. tessellatus* (Say, 1823), redescription of the taxon, and description of a new triploid species. *Herpetologica* 53:233–259.
- Walker, J.M., E.D. Parker, Jr., H.L. Taylor, J.E. Cordes, and R.M. Abuhteba. 1990. Hybridization between all-female *Cnemidophorus tessellatus* and gonochoristic

Herpetological Conservation and Biology

- Cnemidophorus sexlineatus*. Journal of Herpetology 24:388–396.
- Walker, J.M., H.L. Taylor, and J.E. Cordes. 1994. Hybrid *Cnemidophorus* (Sauria: Teiidae) in Ninemile Valley of the Purgatoire River, Colorado. Southwestern Naturalist 39:235–240.
- Walker, J.M., H.L. Taylor, and J.E. Cordes. 1995. Parthenogenetic *Cnemidophorus tessellatus* complex at Higbee, Colorado: resolution of 30 years of controversy. Copeia 1995:650–658.
- Walker, J.M., H.L. Taylor, J.E. Cordes, and M.A. Paulissen. 1998. Distributional relationships and community assemblages of three members of the parthenogenetic *Cnemidophorus tessellatus* complex and *C. sexlineatus* (Squamata: Teiidae) at Higbee, Otero County, Colorado. Herpetological Natural History 5:165–174.
- Walker, J.M., H.L. Taylor, G.J. Manning, J.E. Cordes, C.E. Montgomery, L.J. Livo, S. Keefer, and C. Loeffler. 2012. Michelle's lizard: identity, relationships, and ecological status of an array of parthenogenetic lizards (genus *Aspidozelis*: Squamata: Teiidae) in Colorado. Herpetological Conservation and Biology 7:227–248.
- Weaver, R.E., A.P. O'Connor, J.L. Wallace, J.M. King, and J.M. Walker. 2011. Discovery of the parthenogenetic Colorado Checkered Whiptail, *Aspidozelis neotesselata* (Squamata: Teiidae), in Washington State. Northwestern Naturalist 92:233–236.
- Zweifel, R.G. 1965. Variation in and distribution of the unisexual lizard, *Cnemidophorus tessellatus*. American Museum Novitates 2235:1–49.



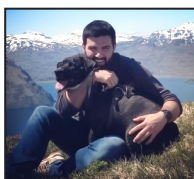
JAMES M. WALKER is Professor of Biological Sciences, University of Arkansas, Fayetteville, Arkansas, USA. Since earning B.S. and M.S. degrees from Louisiana Tech University, Ruston, USA, and a Ph.D. from the University of Colorado, Boulder, USA, he has taught and conducted research at the University of Arkansas (1965–present) and collaborated with numerous scientists on the biology and systematics of whiptail lizards (genera *Aspidozelis* and *Cnemidophorus*: Family Teiidae). His graduate students have completed theses and dissertations on a variety of amphibian and reptile species. (Photographed by James M. Walker, Jr.).



CHAD E. MONTGOMERY is an Associate Professor in Biology at Truman State University, Kirksville, Missouri, USA, which is also where he received his B.S. in Biology. Chad received his M.A. thesis degree from the University of Northern Colorado, Greeley, USA, where he studied clinal variation in Texas Horned Lizard (*Phrynosoma cornutum*). After receiving his M.A., he attended the University of Arkansas, Fayetteville, USA, to study the effects of foraging mode on life history in Copperheads (*Agkistrodon contortrix*) and Timber Rattlesnakes (*Crotalus horridus*) for his Ph.D. Chad currently conducts research in Central America, including projects on Ctenosaura and Boa Constrictors (*Boa imperator*) on islands off of the north coast of Honduras. (Photographed by John Iverson).



JAMES E. CORDES is Professor of Biology at Louisiana State University (LSU), Eunice, Louisiana, USA. Jim received his B.S. and M.S. degrees from Texas State University, San Marcos, USA, and Ph.D. from the University of Arkansas, Fayetteville, USA. He has been the recipient of seven 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 > 85 field expeditions to Mexico, Arizona, Colorado, New Mexico, Oklahoma, Texas, and Utah to collect 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 *Aspidozelis* (Whiptail Lizards). (Photographed by Lyndsey Nacole Schexnayder).



MADelyn J. MANGAN completed her undergraduate and M.S. degrees in biology at Truman State University, Kirksville, Missouri, USA, where she studied how environmental factors influence activity of the Lone Star Tick (*Amblyomma americanum*) throughout its life cycle. She has strong interests in vector ecology and conservation, and currently works with Global Vision International to promote more sustainable and humane ecotourism for Asian Elephants (*Elephas maximus*) in northern Thailand. (Photographed by Alex Santos).