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ASPIDOSCELIS TIGRIS SEPTENTRIONALIS (BURGER, 1950), PLATEAU TIGER WHIPTAIL, IN THE WESTERN UNITED STATES: INDIVIDUAL, ONTOGENETIC, AND GEOGRAPHIC VARIATION IN COLOR PATTERN

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***Abstract*.—No diurnal reptilian species is more characteristic of North American desert habitats and adjacent arid areas than *Aspidoscelis tigris* (Tiger Whiptail). It is widely distributed in northern Mexico, the western United States, and islands east and west of Baja California, occurring in desert, woodland, chaparral, and even grassland communities. Within the vast range of this taxon, which is defined by a unique combination of morphological, karyotypic, and biochemical characters, there are many different color patterns previously used in part to delineate subspecies. Nonetheless, detailed descriptions of variation in color patterns in systematic and morphological studies of continental populations of *A. tigris* typically have been lacking, and treatment of this subject has been relegated to a few general statements. Recently, we observed that samples from populations separated by > 500 km in Mohave County, Arizona, and San Juan County, New Mexico, presently allocated to *A. tigris septentrionalis* (Plateau Tiger Whiptail), were characterized by strikingly different color patterns throughout ontogeny. Thus, we devised a formalized system for capturing and expressing the details of these ensembles of color pattern (i.e., referenced herein as strongly contrasted in Mohave County compared with faded [= weakly] contrasted in San Juan County) to understand the nature of the observed variation and its relevance to the currently recognized subspecies. Discovery of these divergent populations also indicated that a single widely distributed taxon may include distinctive regional components that are separately worthy of evaluation for conservation status.**

Key Words.—Arizona; contrasted dorsal patterns; faded dorsal patterns; lizards; New Mexico

INTRODUCTION

Aspidoscelis tigris (Baird, 1852), Tiger Whiptail, sensu Walker and Maslin (1981), occurs in desert and semi-desert habitats within a vast area of North America including the western United States, northern Mexico, Baja California, and islands east and west of the Baja península. Within its preferred open-structured habitats, it is typically ubiquitous, abundant, and wary. Collections of this species from continental sites constitute among the largest reptile holdings in virtually all herpetological collections in the western United States (e.g., California Academy of Sciences, University of Colorado Museum of Natural History, University of Arizona Museum of Natural History, Museum of Southwestern Biology of University of New Mexico, and Texas Cooperative Wildlife Collection of Texas A&M University). Nevertheless, many questions remain to be answered before a reliable taxonomy for the *A. tigris* complex, including *A. marmorata*, is possible (Walker and Maslin 1981; Hendricks and Dixon 1986; Dessauer and Cole 1991; Taylor and Buschman 1993; Dessauer et al. 2000). The primary basis of the uncertainty is daunting variation in dorsal and ventral color patterns that may be variously categorized as individual, ontogenetic, sexually dimorphic, ecotypic, and/or geographic (see Walker and Maslin 1965; Hendricks and Dixon 1986; Wright 1993; Dessauer et al. 2000; Taylor 2003). In fact, localized populations are known in this complex that possess such striking variation in color patterns as to warrant consideration of application of conservation measures (e.g., San Juan County faded variant reported herein).

An especially problematic group of continental populations of *A. tigris* is currently allocated to *A. t. septentrionalis* (Burger, 1950), Plateau Tiger Whiptail, type locality Una, Garfield County, western Colorado (Burger 1950). This name (see de Queiroz and Reeder 2012) is currently used for populations of highly variable, diurnal, terrestrial, heliothermic lizards in peripheral and adjacent areas of the Great Basin Desert in four of the western United States of northern Arizona, southern Utah, western Colorado, and northwestern New Mexico (see map figures in Pianka 1970; Taylor and Buschman 1993; Dessauer et al. 2000). Taylor (1988) reported that *A. tigris tigris* (Great Basin Whiptail) and

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A. t. septentrionalis are conspecific, initially basing the opinion on field observations of intermediate color patterns among lizards from a geographic area between their ranges, and subsequently on multivariate analyses of four meristic characters. Thus, gene exchange was indicated within a zone of intergradation situated "…east of the Beaver Dam and Virgin Mountains in southwestern Utah and northwestern Arizona." Accordingly, evidence of intergradation was observed "…for sample sites 950–1000 m in elevation, where [there was] a mixture of community elements from both Mohave Desertscrub and Great Basin Desertscrub…" (Taylor 1988).

Identifiable primarily on the basis of geographic provenance and to a lesser extent on color pattern characters, *A. t. septentrionalis* has been the focus of several studies pertaining to genetics (Dessauer et al. 2000), reproduction (Taylor et al. 1992), meristic variation (Taylor 1988; Taylor and Buschman 1993), and taxonomic relationships (Taylor 1988; Taylor and Buschman 1993). Nevertheless, detailed analyses of color patterns, which were not included within the scope of any of those studies, are needed to reconcile variation within the subspecies to presently understood taxonomic boundaries. Although Taylor and Buschman (1993) studied SVL and seven meristic characters in 664 specimens in samples from 17 demes in Arizona (n = 7 samples), Utah (n = 4), Colorado (n = 4), and New Mexico (n = 2) referred to *A. t. septentrionalis*, they provided only a few general statements on color pattern. Instead, they concentrated on multivariate analyses of meristic characters, from which it was concluded that a diagnosis of the subspecies was not possible.

Two of us (BKS and JEC) independently launched field expeditions to obtain samples of *A. t. septentrionalis* and other continental members of the *A. tigris* group and two of us (JMW and GJM) conducted subsequent laboratory investigations to bridge some of the gaps in knowledge of variation in color pattern and meristic characters apparent in other studies of populations referred to Plateau Tiger Whiptail (e. g., Taylor 1988; Taylor and Buschman 1993; Dessauer et al. 2000). Herein, we describe ontogenetic, individual, and geographic variation in color pattern and present analyses of meristic characters in *A. t. septentrionalis* from several areas, with emphasis on a sample from Mohave County, Arizona, and one from San Juan County, New Mexico, to determine if the taxon is in fact diagnosable. We recognize that the subspecies concept is controversial (e.g., Sullivan 2009; Sullivan et al. 2014); indeed, among the present authors there is a diversity of perspectives as to the use and epistemological rationale for subspecies. While we adopt the currently accepted taxonomy of subspecies for *A. tigris* (Crother et al. 2012; de Queiroz and Reeder 2012), we accept that these may represent pattern classes, and leave aside further discussion of the evolutionary status of these entities.

MATERIALS AND METHODS

Analyses of genetic relationships, based on mtDNA obtained from specimens of *A. t. punctilinealis* (Sonoran Tiger Whiptail), *A. t. marmorata* (= *A. m. marmorata*; Western Marbled Whiptail), *A. t. septentrionalis* (Plateau Tiger Whiptail), *A. t. tigris* (Great Basin Whiptail), and intergrades between certain of these taxa collected by JEC and BKS, are deferred to a subsequent paper with other collaborators. We based the use of the foregoing scientific and common names on the checklist by the Society for the Study of Amphibians and Reptiles (de Queiroz and Reeder 2012). For this report we analyzed dorsal and ventral patterns using the formalized terminology (Table 1) for characters in *A. t. septentrionalis* collected from Utah, Arizona, and New Mexico (Figs. 1–2, 4) by JEC in 2012–2014, and deposited in the University of Arkansas Department of Zoology (UADZ) collection. We also examined specimens and photographs from Utah and Arizona obtained by BKS (Fig. 3) and maintained in his personal collection and archives pending deposition in the Arizona State University (ASU) vertebrate collection in 2016. Digital photographs of the dorsum and ventrum of specimens of *A. t. septentrionalis* from south of the Grand Canyon in Coconino County, Arizona, were made by GJM in 2014 during a visit to the American Museum of Natural History (AMNH).

Specimens and characters studied.—We used only the specimens collected by JEC in 2012–2014 from Arizona, New Mexico, and Utah to assess, describe, and quantify individual and ontogenetic variation in color pattern (Tables 1 and 3) and variation in six meristic characters (Table 2). Those samples were also used and discussed in the following section to determine the mean and range of variation of granular scales between the paravertebral stripes at midbody (PV) and the mean and range of variation in percentage of the granular scales around midbody located between the paravertebral stripes (PV/GAB × 100) as used in studies of the *A. sexlineata* species group by Duellman and Zweifel (1962), Walker (1981a, b), Walker et al. (2009), and Walker and Cordes (2011).

Analysis.—We used calipers to measure the SVL of each preserved specimen of *A. t. septentrionalis* to the nearest mm and spring scales to obtain the mass to 0.1 g prior to preservation. We statistically analyzed the three UADZ samples of *A. t. septentrionalis* representing contrasted and faded dorsal patterns from the aforementioned states (Table 2) using data files processed on an institutional PC with University of

TABLE 1. Qualitative characters pertaining to variation in scutellation and color pattern in samples of specimens of *Aspidoscelis tigris septentrionalis* from Arizona, Colorado, New Mexico, and Utah, USA, based on Burt (1931), Duellman and Zweifel (1962), Walker et al. (2009), and Walker and Cordes (2011).

Character	Descriptive Statement
Anterior Extent of Circumorbital Scales	Scales medial to right and left supraoculars, extending anteriorly to variable positions opposite the supraoculars
Size of Mesoptychial Scales	Small (i.e., not enlarged) scales at/near the edge of the gular fold
Size of Postantebrachial Scales	Granular scales on the posterior aspect of forearm
Number of Preanal Scales	Condition of one (rarely) or two (usually) large preanal scales anterior to the cloacal slit
Dorsal Cephalic Surface	Color and pattern of the dorsal surface of the head, including 4–4 supraoculars
Lateral Cephalic Surfaces	Color and pattern of the sides of head anterior and ventral to the orbits
Pale Colored Lateral Stripes	Stripe on each side of body (from ventral to orbit posteriorly to hindlimb), which is often fragmented
Pale Colored Dorsolateral Stripes	Stripe on each side of body superior to lateral stripe (from cephalic superciliary scales posteriorly to base of tail)
Pale Colored Paravertebral Stripes	Stripe on each side superior to dorsolateral stripe (from cephalic parietal scales posteriorly onto proximal part of tail)
Pale Colored Vertebral Stripe	Stripe (= absent, partial, distinct, indistinct, complete, or interrupted) between the paravertebral stripes (from interparietal scale to base of tail)
Dark Colored Lower Lateral Fields	Longitudinal field on each side between lateralmost row of ventral scales and lateral stripe (paler in hue than more dorsal fields)
Dark Colored Upper Lateral Fields	Longitudinal field on each side between lateral and dorsolateral stripes
Dark Colored Dorsolateral Fields	Longitudinal field on each side between dorsolateral and paravertebral stripes
Dark Colored Vertebral Field	Longitudinal field between paravertebral stripes longitudinally divided by vertebral stripe when present
Pale Colored Supernumerary Lines	Lines or longitudinal alignments of spots and/or expanded portions of bars in the dark fields
Dorsal Spots	Rounded pale colored areas in certain of the fields expressed as absent, incipient, or moderately distinct
Dorsal Bars	Elongate pale colored areas, arranged vertically on the sides or transversely on the dorsum, between the stripes
Dorsal Aspect of Forelimbs	Pattern of pale colored markings on dark colored dorsal surfaces of forelimbs
Dorsal Aspect of Hindlimbs	Pattern of pale colored markings on dark colored dorsal surfaces of hindlimbs
Color Pattern of Tail	Color variation of dorsal, lateral, and ventral aspects of tail
Coloration of Ventral Surfaces	Ventral color pattern of throat, chest, abdomen, and limbs

Arkansas licensed JMP software (Version 10; SAS Institute, Inc., Cary, North Carolina, 2012). We used ANOVA and quantiles to generate a sample mean ± one standard error and range of variation for each meristic character and ratio analyzed. We compared the resulting three sample means for each character for significant differences ($\alpha = 0.05$) using Tukey-Kramer HSD tests in JMP. Significantly different means were identified in a Connecting Letters Report (CLR) for each character provided by the analysis (Table 2).

***Historical perspective*.—**We used the report by Taylor and Buschman (1993) on range-wide meristic variation and preliminary assessment of color patterns in *A. t. septentrionalis* as the context for the design of this study. To evaluate use of meristic data for defining *A. t. septentrionalis*, we extracted the low and high means ± SE from Table 1 of Taylor and Buschman (1993) for each of seven characters analyzed among 17 samples from Arizona, Colorado, New Mexico, and Utah (see Table 2 herein). Their Sample 1 had the low mean for two characters (COS and LSOG = LSG herein) and the high mean for two characters (GIBPT = OR and SDLl = SDL). Sample 15 had the high mean for three characters (GAB, FP, and LSG) Other samples contributing more than one low or high mean for characters was 13 (low GAB and high COS) and 11 (low SDL and high GS). It was noteworthy (see Taylor and Buschman 1993, Fig. 1) that most of the preceding samples were from areas that marked the known range limits for *A. t. septentrionalis* (e.g., Sample 1 to the south from Navajo County, Arizona; Sample 11 to the west from Mohave County, Arizona; and Sample 15 to the northwest from Emery County, Utah). As a further indication of the meristic distinctiveness of Sample 1 (Taylor and Buschman 1993), 13 of 14 specimens (92.9%) with complete data for all characters were classified to correct a priori group by a canonical variate analysis (CVA). However, not all peripheral groups were meristically distinct; for Sample 17 from the northern range limits in Colorado only 10.5% of specimens were correctly classified to a priori group by a CVA. We used new samples of *A. t. septentrionalis*, one from Mohave County, Arizona, and one from San Juan County, New Mexico, to test for

FIGURE 1. Variation in dorsal and ventral color patterns of *Aspidoscelis tigris septentrionalis* (Plateau Tiger Whiptail): Frame 1 (left), UADZ 9245 (♂ 84 mm SVL) from Kane County, Utah; Frames 2 and 3 (middle two), L, UADZ 9466 (♂ 100 mm SVL) from Mohave County, Arizona, and R, UADZ 9479 (♂ 100 mm SVL) from San Juan County, New Mexico; Frame 4 (right), L, UADZ 9460 (♀59 mm SVL) from Mohave County and M, UADZ 9487 (♂ 56 mm SVL) and R, UADZ 9488 (♀ 58 mm SVL) from San Juan County. (Photographed by James M. Walker).

congruence between strongly contrasted and faded dorsal patterns, respectively, and variation in six meristic characters (Table 2).

Pertaining to the 17 geographic samples analyzed by Taylor and Buschman (1993), "…three generalized classes of adult color pattern…" were recognized including P (= pale, faded pattern lacking sharp contrast between pale stripes and dark fields), T (= faded posteriorly, sharp contrast between stripes and fields only to midbody then faded), and D (= dark, sharp contrast between stripes and fields from head to base of tail). Only Sample 1 among the 17 samples included a single color pattern class that being P. All other samples from west of the Colorado River in Arizona, including Sample 11, comprised color pattern classes T and D, though their proportional representations were not given by the authors. We could not consistently apply the P, T, and D pattern designations of Taylor and Buschman (1993) because it was not possible to determine the extent to which they were based on individual, ecotypic,

FIGURE 2. Variation in dorsal color patterns of *Aspidoscelis tigris septentrionalis* (Plateau Tiger Whiptail): Frame 1 (left), UADZ 9548 (♀ 57 mm SVL), UADZ 9547 (♀ 64 mm SVL), UADZ 9545 (♀ 74 mm SVL), UADZ 9546 (♀ 83 mm SVL) ontogenetic series from San Juan County, Utah; Frame 2 (middle), UADZ 9473 (♀ 85 mm SVL) , UADZ 9454 (♀ 87 mm SVL), UADZ 9540 (♀ 87 mm SVL) individual variation from Mohave County, Arizona; Frame 3 (right), UADZ 9494 (♀ 80 mm SVL) and UADZ 9483 (♀ 77 mm SVL) individual variation from San Juan County, New Mexico. (Photographed by James M. Walker).

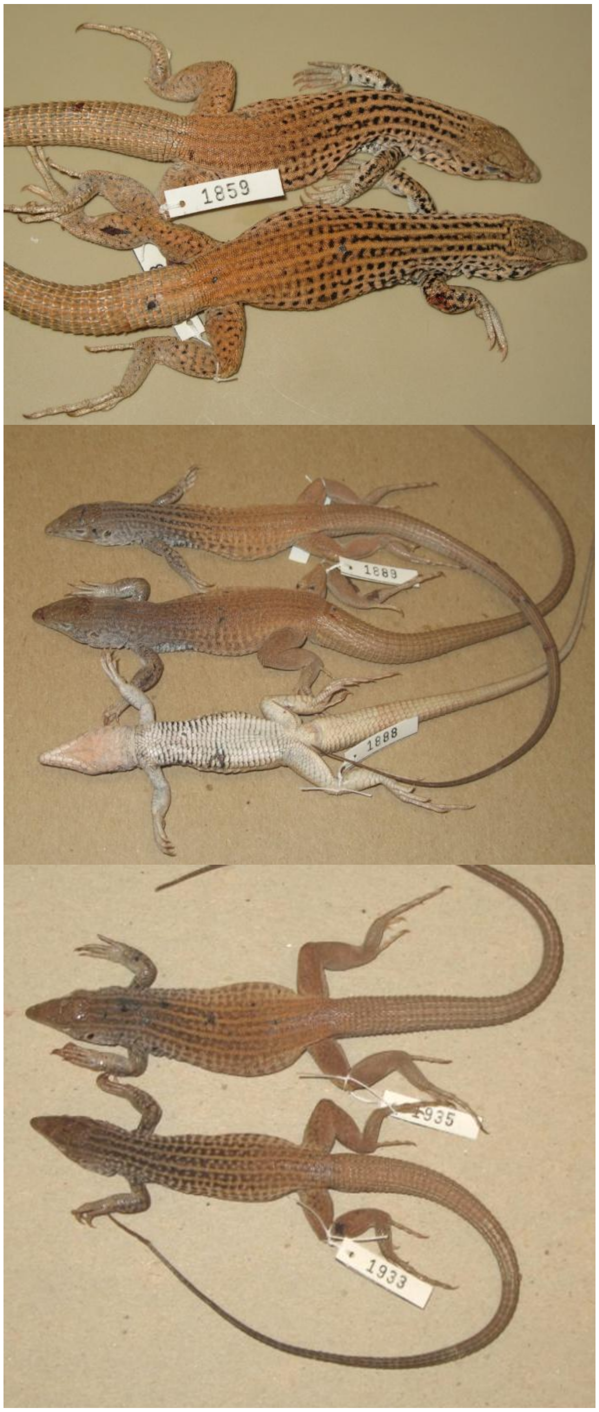

FIGURE 3. Variation in dorsal and ventral patterns in adults of *Aspidoscelis tigris septentrionalis* (Plateau Tiger Whiptail). Frame 1 (top), BKS 1858–1859 from Coconino County, Arizona; Frame 2 (middle), BKS 1888–1890, and Frame 3 (bottom), BKS 1933, 1935 both from Navajo County, Arizona. (Photographed by Brian K. Sullivan).

ontogenetic, and/or geographic variation. Thus, for this report we use the designations contrasted patterns for black ground color and pale dorsal markings (e.g., sample from Mohave County, Arizona) and faded patterns for blended dusky ground color and pale dorsal markings (e.g., sample from San Juan County, New Mexico).

RESULTS

***Meristic variation*.—**We compared 24 specimens of *A. t. septentrionalis* with contrasted dorsal patterns from Mohave County, Arizona, with a sample of 25 specimens with faded dorsal patterns from San Juan County, New Mexico to assess the relationship between extremes in color pattern and variation in six meristic characters (Table 2). No significant differences between the respective distinctive color patterns represented by the samples from Arizona (contrasted dorsal pattern) and New Mexico (faded dorsal patterns) for GAB (HSD, P = 0.985), SDL (HSD, P = 0.308), or COS (HSD, P = 0.816) characters (CLR). However, significant, though non-diagnostic, differences were present (CLR) among means for OR (HSD, P = 0.019), FP (HSD, P < 0.001), and LSG (HSD, P = 0.011) characters (Table 2). All means except for OR (lower) and FP (lower) for the San Juan County sample were within the ranges of means for the same characters for 17 samples of *A. t. septentrionalis* reported by Taylor and Buschman (1993).

Statistical evaluation of two aspects of the dorsal patterns of 24 specimens from Mohave County and 25 from San Juan County did not reveal significant differences in the number of granular scales (i.e., spacing) between the paravertebral stripes at midbody (PV = 6.0 ± SE 0.17, range 5–8 versus 6.2 ± SE 0.17, range 5–8; HSD, P = 0.986) and percentage of the granular scales around midbody located between the paravertebral stripes at midbody (PV/GAB × 100 = 7.5 ± 0.23, range 5.7–9.6 versus PV/GAB = 7.6 ± 0.22, range 5.6–10.0; HSD, P = 0.999), respectively. In summary, the divergent patterns that characterized samples from Mohave County and San Juan County could not be distinguished by significant, though non-diagnostic, difference in three meristic characters.

***Contrasted dorsal patterns (Mohave County, Arizona)*.—**Color pattern data for 24 specimens of *A. t. septentrionalis* revealed retention of four primary dorsolateral and paravertebral stripes, which were ontogenetically modified in adults by coalescence with spots/bars, and the remnants of two interrupted laterals. Only three specimens (12.5%) had a vertebral stripe, whereas five (20.8%) had a partial vertebral, and 16 (66.7%) lacked the stripe. Only three specimens (12.5%) lacked supernumerary lines (SNL) in the dark fields between the primary stripes. Twenty-one specimens (87.5%) had one SNL on each side between the lateral and dorsolateral stripes (position two), whereas three (12.5%) had those plus an additional SNL

FIGURE 4. Individual variation in dorsal color pattern of two live adults of *Aspidoscelis tigris septentrionalis* (Plateau Tiger Whiptail). Frame 1 (left), UADZ 9241; Frame 2 (middle), close up of UADZ 9241; and Frame 3 (right), UADZ 9242 both from Aztec, San Juan County, New Mexico. (Photographed by James E. Cordes).

on each side between the dorsolateral and paravertebral (position three). Side-by-side comparisons of adults revealed striking individual differences in the details of dorsal patterns (Fig. 2, Frame 2). Nevertheless, 18 (75%) were characterized by strongly contrasting patterns over the entire dorsum, whereas only six (25%) had faded patterns on the posterior aspect of the dorsum.

Ontogenetic variation in the sample was apparent. The dorsal pattern of a second summer juvenile female (UADZ 9460; Fig. 1, Frame 4-L) with a SVL of 59 mm, tail length of 206 mm, and mass of 6.4 g included a gray head with faint dusky black mottling. Unlike adults, little dusky black was present in the ground color of the body owing to predominance of gray dorsal pattern elements including the six primary stripes (i.e., interrupted laterals and continuous dorsolaterals and paravertebrals), SNL-like arrays (i.e., in fields in positions one through three; Table 1), rounded spots/dots, and elongate/vertical (laterally)/horizontal (dorsally) bars. Similarly, the dusky black ground color of the limbs was reduced by numerous gray reticulations/mottling/spotting. The tail was medium gray with white scale keels, and it lacked posterior extensions of the primary stripes. The resulting ensemble in juvenile UADZ 9460 was that of a dominantly gray-hued dorsal pattern which was in stark contrast to the pattern described for juveniles of *A. t. punctilinealis* (Sonoran Tiger Whiptail) from Gila and Maricopa counties, Arizona, with largely unmarked black upper lateral and dorsolateral fields (positions two and three) and striped proximal fourth of the tail (Walker and Sullivan 2014). Ventrally, UADZ 9460 was gray with the slightest indication of dusky black markings on the sides of the throat.

Sexual dimorphism in the color pattern was most apparent in the ventral pattern of specimens from Mohave County, in which males differed only slightly from females. Males exhibited variable numbers of black spots on gray throats (Fig. 1, Frame 3-L), whereas females lacked spots, had a spot here or there, or had vague dusky bands. However, both sexes exhibited a semblance of a checkered pattern of gray and black on the chest and abdomen, though it was more pronounced in adult males.

The complexity of the contrasted adult color pattern ensemble was apparent in the largest among 24 specimens from Mohave County, an adult male (UADZ 9466; Fig. 1, Frame 2-Left) with a SVL of 100 mm, complete tail of 341 mm, and mass of 28.5 g. Dorsally, the head was gray-tan with scattered irregular black blotches. The ground color of the dorsum was black within which the gray-tan pattern elements comprised the primary stripes, SNL, rounded spots, and vertical (laterally)/horizontal (dorsally) bars (see Table 1). There was no diminution of contrast in the pattern resulting from either anterior or posterior fading of the dark ground color to blend with the pale pattern elements (Fig. 1, Frame 2-L). The black ground color of the forelimbs formed a reticular pattern within the extensive distribution of gray markings, and the same obtained for the hindlimbs with gray mottling. The base of the tail was gray-tan with numerous black spots; however, a banded pattern was apparent on the proximal 40% of the tail resulting from the dusky black edges and gray-white keels of the scales in the caudal whorls (Fig. 1, Frame 2-L).

Additional details of the dorsal color pattern in UADZ 9466 included the ontogenetically modified pairs of primary stripes of which the paravertebrals extended continuously from the occipital region of the head to the base of the tail, the dorsolaterals extended continuously from the posterior edges of the parietal scales to within a few mm of the base of the tail, and remnants of the laterals with the numerous interruptions by black ground

TABLE 2. Low mean (LM), high mean (HM), and difference in means divided by the low mean (DM/LM) for seven characters examined by Taylor and Buschmann (1993) in 664 specimens in their samples 1–17 from Arizona, Colorado, New Mexico, and Utah identified to *Aspidoscelis* (= *Cnemidophorus*) *tigris septentrionalis*, and the means for six characters we examined in samples from Mohave County in Arizona (MAZ) and San Juan counties in New Mexico (SJNM) and Utah (SJUT). Shown for LM and HM are the mean ± SE and sample number for each in parentheses, the range of values for the character and the sample size for the range, and the value and percentage in parentheses for DM/LM. The means for our samples have the same notations as for the LM or HM values except that each mean ± SE is followed by a letter; only means for a character with all different letters are significantly different (P = 0.05).

Acronym/Description	LM	HM	DM/LM	MAZ	SJNM	SJUT
GAB: Granular scales (= granules) around midbody	77.4 ± 1.11 (13) 67–89 (20)	82.9 ± 0.70 (15) 75–92 (39)	5.5 (7.1%)	80.8 ± 0.90^{A} 73–88 (24)	81.0 ± 0.88^{A} 68–89 (25)	81.0 ± 1.80^{A} 76–84 (6)
GIPBT = OR: Granules from occipital scales to base of tail	164.3 ± 1.53 (8) 145–179 (35)	176.2 ± 1.39 (1) 164–191 (23)	11.9 (7.2%)	170.3 ± 1.62^{A} 154–191 (24)	163.9 ± 1.59^{B} 148–175 (25)	169.5 ± 3.25^{AB} 161–174 (6)
FP: Total of right and left femoral pores	39.6 ± 0.37 (7) 33–44 (44)	43.5 ± 0.36 (15) 39–50 (40)	3.9 (9.8%)	41.7 ± 0.45^{A} 36–46 (24)	38.8 ± 0.44^{B} 35–43 (25)	40.7 ± 0.90^{AB} 40–42 (6)
SDL1 = SDL: Left fourth toe subdigdital lamellae	29.8 ± 0.24 (11) 27–34 (35)	34.7 ± 0.37 (1) 31–38 (23)	4.9 (16.4%)	30.9 ± 0.29^{A} 28–33 (24)	31.5 ± 0.29^{A} 30–34 (25)	32.3 ± 0.58^{A} 30–34 (6)
COS; Total of right and left circumorbital scales	13.5 ± 0.42 (1) 9–18 (23)	17.4 ± 0.76 (13) 13–24 (20)	3.9 (28.9%)	17.1 ± 0.55^{A} 10–21 (24)	16.5 ± 0.54^{A} 12–24 (25)	16.3 ± 1.10^{A} 14–20 (6)
LSOG = LSG: Total of right and left lateral supraocular granules	22.7 ± 0.74 (1) 17–29 (24)	41.7 ± 1.04 (15) 30–60 (39)	19.0 (83.7%)	33.3 ± 1.06^{A} 24–44 (24)	28.8 ± 1.03^{B} 18–43 (25)	34.0 ± 2.12^{AB} 28–42 (6)
GS: Total of right and left gular scales	20.6 ± 0.48 (3) 14–26 (36)	24.3 ± 0.38 (11) 19–28 (37)	3.7 (17.9%)	---	---	---

color were only intermittently apparent from the postaxillary regions to the hindlimbs. No evidence of a secondary (i.e., vertebral) stripe was present in UADZ 9466, though anterior spots and posterior bars in the vertebral field were coalesced with the paravertebral stripes. Indistinct SNL-like arrays, partly composed of connected spots and expanded parts of bars, were present between the primary stripes on each side of the body in the respective lower lateral field (position one) and in the upper lateral field (position two), but they were not present in the dorsolateral field (position three). Ontogenetic modifications of the primary stripes and SNL were apparent resulting from their coalescence with rounded gray-tan spots, some of which were isolated in the fields, and the profusion of vertical/horizontal bars, some of which extended from stripe to stripe producing rectangular areas of black ground color.

Ventrally, the largest male of *A. t. septentrionalis* from Mohave County UADZ 9466 (Fig. 1, Frame 3-L) exhibited the maximum development of melanism of all specimens examined. The throat and gular fold were gray with transversely arranged patches of black scales. The ventral aspects of the forelimbs were gray with several patches of black scales, and the scales of the hindlimbs were gray some with dusky black edges. The chest and abdomen were gray with numerous partly black scales forming a semblance of a black and gray checker distribution. The midventral aspect of the tail was gray-white, lateral to which it was gray with the semicircular dusky black extensions from the previously described dorsal bands.

Faded patterns (San Juan County, New Mexico).—Faded dorsal patterns characterized 25 specimens of *A. t. septentrionalis* from northwestern New Mexico (Table 3). All retained four faintly visible ontogenetically modified dorsolateral and paravertebral stripes by fusion with spots/bars/loss of definition posteriorly, and two interrupted laterals. Also present in 20 specimens (80.0%) was a partial or complete vertebral, whereas five (20.0%) lacked the stripe. Only one of these specimens (4.0%) lacked evidence of SNL in the dark colored fields. Eight specimens (32.0%) had one SNL in the upper lateral field on each side (position two), whereas 17 (68.0%) had those plus an additional SNL in the dorsolateral field on each side (position three).

We assessed ontogenetic variation and sexual dimorphism in the sample comprising six second-year subadults (24.0%) 56–66 mm SVL and 19 adults (76.0%). Dorsally, the overall appearance of the color patterns of the subadults (Fig. 1, Frame 4-M and R) was slightly darker than in adults, though moderately faded. Frame 4-L versus M and R (Fig. 1), juveniles from Mohave and San Juan counties were similar, except that four of the latter subadults had a complete vertebral stripe and two had a partial vertebral stripe. Also, five had SNL in dark field positions two and three and one had SNL only in position two (Table 1). All had faded

Table 3. Comparison of color pattern characters in samples of *Aspidoscelis tigris septentrionalis* from Mohave County (n = 24), Arizona, and San Juan County (n = 25), New Mexico, USA (juveniles and adults combined).

Color Pattern Character	Mohave Co. Number (%)	San Juan Co. Number (%)
Status of Lateral Stripe		
Interrupted by Black Ground Color Forming Lateral Barring	24 (100%)	25 (100%)
Primary Stripes and Vertebral		
Six Primary Stripes and No Vertebral	16 (66.7%)	1 (4.0%)
Six Primary Stripes and Partial Vertebral	0	4 (16.0%)
Six Primary Stripes and Linear Alignment of Vertebral Spots	5 (20.8%)	4 (16.0%)
Six Primary Stripes and Complete Vertebral	3 (12.5%)	16 (84.0%)
Supernumerary Lines Within Dark Colored Fields		
Supernumerary Lines in Lower Lateral Fields (Position 1)	1 (4.2%)	0
Supernumerary Lines in Upper Lateral Fields (Position 2)	21 (87.5%)	23 (96.0%)
Supernumerary Lines in Dorsolateral Fields (Position 3)	3 (12.5%)	16 (84.0%)
No Supernumerary Lines in Fields	3 (12.5%)	1 (4.0%)
Contrast Between Ground Color and Dorsal Pattern Elements		
Extensive or Partial Blending of Pattern Components and Ground Color	6 (25.0%)	24 (96.0%)
Blending of Pattern Components and Ground Color Lacking	18 (75.0%)	1 (4.0%)
Ventral Pattern		
Numerous Black Markings on Throat, Chest, and Abdomen	6 ♂ (25.0%)	0 (00.0%)
Black Markings Few to Lacking	18 ♀ (75.0%)	25 ♀♂ (100%)

dorsal patterns (= reduced contrast between ground color and stripes, lines, spots, and bars). Ventrally, the juveniles were gray with vague dusky marking limited to the sides of the throat.

The adult color patterns among 25 specimens from San Juan County manifested the loss of contrast between the ground color and pale pattern elements well beyond that recorded for class P in Sample 1 of Taylor and Buschman (1993, Fig. 2 Top Left). The pattern, exemplified in the largest adult male in the sample, UADZ 9479 (Fig. 1, Frame 2-R) with a SVL of 100 mm, original proximal part of tail of 87 mm, regenerated part of tail of 158 mm, and mass of 24.7 g, consisted of a faded ensemble reminiscent of the reduced contrast between fields and stripes of *A. inornata gypsi* (Little White Whiptail) from the White Sands of Otero County, New Mexico (Wright and Lowe 1993; Rosenblum and Harmon 2011). Dorsally, the head of UADZ 9479 was gray. The black ground color of the limbs was about 95% obscured by gray spots or mottling or reticulations. Except for the sides of the body and anterior part of the middorsal area showing small rectangular remnants of the black ground color between the gray vertical/horizontal bars, primary stripes, and SNL, the dorsum was gray. The tail was gray, unbanded, and had caudal scales with white-tipped keels. Ventrally, the throat and mesoptychium were gray with few small black spots, whereas the chest and abdomen were gray with the scattered black-edged scales limited to the sides of the body (Fig. 1, Frame 3-R).

Details of the dorsal color pattern in UADZ 9479 included ontogenetically modified pairs of primary stripes that were difficult to discern. Only the paravertebrals and dorsolaterals were visible as unbroken elements on the anterior part of the body, albeit coalesced with spots and bars. Interrupted lateral stripes and SNL were only vaguely apparent. Evidence of a wavy band-like vertebral stripe was present, though it was difficult to discern between the paravertebral stripes on the posterior part of the body. Connected spots forming SNL-like arrays were present between the primary stripes on each side in the respective lower lateral field between the lateral stripe and ventral scales (position one) and in the upper lateral field between the lateral stripe and dorsolateral stripe (position two), but they were not present in the dorsolateral field between the dorsolateral and paravertebral stripe (position three). Ontogenetic modifications of the primary stripes and SNL were apparent as a result of their coalescence (= fusion) with many of the rounded gray-tan spots, some of which were isolated in the fields, and the profusion of vertical/horizontal bars, some of which extended from stripe to stripe producing small rectangular areas of black ground color.

Referred populations (Utah, New Mexico, and Arizona).—Specimens from selected sites in Utah, New Mexico, and Arizona indicated need for further studies of color pattern variation in *A. t. septentrionalis*. During many visits to Coral Pink Sands State Park, Kane County, Utah, UADZ 9245 (♂ 84 mm SVL) was the

TABLE 4. Diagnostic characters of *Aspidoscelis tigris tigris* (Great Basin Whiptail) and *Aspidoscelis tigris septentrionalis* (Plateau Tiger Whiptail).

Character of Color Pattern	*Aspidoscelis tigris tigris*	*Aspidoscelis tigris septentrionalis*
Primary Stripes	four (Paired paravertebrals and dorsolaterals)	six (Paired paravertebrals, dorsolaterals, fragmented laterals)
Secondary Stripe (= Vertebral)	None	Absent or rare, but present in southern San Juan County, NM
Supernumerary Lines	None	Present in one or all of positions 1–3 between primary stripes
Contrast of Fields and Pale Elements	Moderately strong	Typically some or extensive fading
General Hue of Dorsal Scheme	Two-toned blue-gray and checkered	Two–toned and often with orange posterior hue
Pattern of Base of Tail	Numerous spots	Unspotted
Pattern of Gular Region (= Throat)	Gray reticulum	Irregular spots to no spots
Pattern of Chest and Abdomen	Gray to presence of a few scattered partially black scales	Gray to presence of numerous scattered partially black scales

only specimen of *A. tigris* observed by JEC, though triploid parthenogenetic *A. velox* was abundant in the park. UADZ 9245 differed from all other specimens examined in having paravertebral and dorsolateral stripes only to midbody where they were fragmented, linear series of spots rather than SNLin the fields, medium rather than low contrast between ground color and pattern components, and conspicuously barred sides (Fig. 1, Frame 1). The specimen could not be allocated to *A. t. tigris*; we hypothesized that it represented an ecotype of *A. t. septentrionalis* in marginal habitat provided by the coral pink sand dunes. Four specimens from the west side of the San Juan River in western San Juan County, Utah, comprised an ontogenetic series of second year and older females of 57, 64, 74, and 83 mm SVL, which exhibited dorsal pattern components that differed from the previously described specimen (UADZ 9545–9548; Fig. 2, Frame 1). They lacked both a complete vertebral stripes and faded dorsal patterns, being unlike the faded patterns observed among specimens in the sample of 25 specimens from south of Aztec in adjacent San Juan County, New Mexico. In fact, two adult lizards (UADZ 9241–9242) from Aztec in the county captured alive by JEC had dorsal patterns (Fig. 4) more similar to the adjacent Utah sample (i.e., UADZ 9545–9548) than to lizards with faded dorsal patterns from farther south in San Juan County, New Mexico.

Taylor and Buschman (1993) stressed the multivariate meristic distinctiveness of their Sample 1, identified as an outlier of *A. t. septentrionalis* from Navajo County, northeastern Arizona (8.0 km north of Winslow on Leupp Road [University of Colorado Museum 54707–54731, n = 25]). It was the only one of 17 samples from Arizona, Colorado, New Mexico, and Utah, that comprised a single dorsal color pattern class that they designated P (i.e., faded). We also examined specimens from 8.0 km north of Winslow (BKS 1888–1890, 1931–1935, n = 8), and agree that the population was properly allocated to *A. t. septentrionalis* by Taylor and Buschman (1993). We concluded that, based on variation in specimens such as BKS 1889–1890 (Fig. 3, Frame 2) and BKS 1935 (Fig. 3, Frame 3), the dorsal patterns among individuals in the population at large would vary in being either entirely faded or faded with an orange hue only on the posterior half of the body and would either include a vertebral stripe or not, but all would be expected to have SNL, fragmented lateral stripes, essentially unmarked gray-tan hindlimbs, a gray-tan tail without bands, and gray ventral surfaces with either little or no black, which are characters identifying *A. t. septentrionalis*.

DISCUSSION

Members of the *A. tigris* species group (sensu Walker and Maslin 1969) share a distinctive karyotype (Lowe et al. 1970) and the following unique combination of characters of scalation: granular postantebrachial scales on the posterior aspect of each forearm, small mesoptychial scales bordering the edge of the gular fold, usually four right and four left supraocular scales, and typically two enlarged preanal scales (Table 4). Nevertheless, content of the *A. tigris* group has remained controversial. Wright (1993) considered the group to comprise a single polytypic species, including *A. tigris septentrionalis*, and synonymized many long recognized insular and continental populations. Walker and Maslin (1981) conceived of the group as comprising a continental species with two insular populations (i.e., *A. maxima*), a polytypic species with both continental and insular subspecies (i.e., *A. tigris*), and numerous insular species in the Gulf of California (i.e., *A. bacata*, *A. cana*, *A. catalinensis*, *A. celeripes*, *A. estebanensis*, and *A. martyris*). Apart from that controversy and the ongoing debate on recognition of subspecies per se (see comments in Sullivan 2009; Sullivan et al. 2014), we provide the bases for a diagnosis for Plateau Tiger Whiptail (*A. t. septentrionalis*, Burger, 1950) sensu Taylor and Buschman (1993), Reeder et al. (2002), and de Queiroz and Reeder (2012). We concur with Taylor and Buschman (1993) that *A. t. tigris* (type locality restricted to Salt Lake City, Salt Lake County, Utah) and *A. t. septentrionalis* (type locality Una, Garfield County, Colorado) are not diagnosable taxonomic entities based strictly on morphology (i.e., scutellation, meristic characters, and body size). However, this study has revealed that the taxa are diagnosable based on color patterns of both subadults and adults, despite the opinion of Taylor and Buschman (1993) that such was not possible pending a range-wide study of variation in the nominal subspecies. More appropriate standards for their distinctness entail proof that they maintain their taxonomic identities on the respective sides of a zone of intergradation with *A. t. tigris* in northwestern Arizona as detailed by Taylor (1988), and that that all specimens of *A. t. septentrionalis* examined by Taylor and Buschman (1993; e.g., Fig. 2) and in this study are distinguishable from topotypic and near topotypic specimens of the nominal subspecies.

Walker and Maslin (1969, 1981) reported that young-of-the-year and subadult color patterns and subsequent ontogenetic patterns of development thereof are useful in defining taxonomic boundaries, and are potentially of adaptive significance, in taxa of the *A. tigris* species group (Walker and Maslin 1969). Moreover, ontogenetic loss of some or all stripes is likewise not uncommon in the *A. sexlineata* species group (Duellman and Zweifel 1962; Walker 1981a, b; Walker and Cordes 2011), and should be included in diagnoses of such taxa in both species groups. Nevertheless, ontogeny as a source of taxonomically significant color pattern variation was not addressed in the comprehensive study of *A. t. septentrionalis* by Taylor and Buschman (1993) involving 664 specimens, concentrating instead on multivariate analyses of meristic data. Our analyses of six meristic characters in newly acquired samples of this taxon further underscored the futility of that approach to diagnosing either *A. t. septentrionalis* or any other continental subspecies of *A. tigris* because meristic and color pattern characters vary independently. Taylor (1988) analyzed intergradation between *A. t. tigris* and *A. t. septentrionalis* in northwestern Arizona using meristic data, but did not give attention to juveniles perhaps because the characters of color pattern used required lizards of adult sizes in the range of 74−101 mm SVL. Similarly, Dessauer et al. (2000) studied intergradation (= hybridization) between *A. t. punctilinealis* and *A. t. marmorata* (= *A. m. marmorata*; de Queiroz and Reeder 2012) in Hidalgo County, southwestern New Mexico, using samples comprising lizards of 62−97 mm SVL. In a recent study of *A. t. punctilinealis*, Walker and Sullivan (2014) used samples spanning 38−106 mm SVL, which revealed striking differences of taxonomic significance between young-of-the-year, subadults, and adults of that subspecies compared with *A. t. septentrionalis*.

Analyses of subadults of *A. t. septentrionalis* from three geographic areas; northwestern Arizona, northwestern New Mexico, and southeastern Utah revealed similarities among them including low contrast between pale pattern components and slightly darker fields, presence of supernumerary lines (SNL) between the primary stripes, and virtual absence of black markings in the ventral pattern. We found SNL to be diagnostic of *A. t. septentrionalis*, though presence of them was not reported by Taylor and Buschman (1993). However, adults from the same areas in the three states differed in extent of contrast between pale and dark dorsal components and ventral patterns, presumably representing adaptation to regional conditions. For example, only 12.5% of adults from Arizona possessed a vertebral stripe, compared with 84.0% with the stripe present in lizards from New Mexico, indicating that these character states would have also been present in the respective subadults had larger samples been available.

There is precedent for our use of color pattern to diagnose adults of *A. t. septentrionalis* as such characters were used to distinguish *A. t. septentrionalis* versus *A. t. tigris* in northwestern Arizona by Taylor (1988; p. 179), *A. t. punctilinealis* versus *A. t. tigris* in southwestern Arizona by Taylor (1990; p. 449), and *A. t. punctilinealis* versus *A. t. marmorata* in southwestern New Mexico by Dessauer et al. (2000; p. 79). To summarize, adults of *A. t. septentrionalis* differ from other subspecies in having this unique combination of characters: a gray venter with few to no black markings over most of distribution area except in large males from Mohave County, Arizona, supernumerary lines in some dark fields, consistent absence of a vertebral stripe except in southern San Juan County, New Mexico, and presence of various degrees of blended hues of dorsal pattern components the extreme of which characterizes lizards from southern San Juan County, New Mexico. The striking uniformity in color pattern of populations of *A. t. septentrionalis* across much of the Colorado Plateau may represent a mere pattern class, rather than indicating species level divergence from other currently recognized subspecies of *A. tigris*. The genetic relationships of populations represented by the UADZ and BKS specimens (see Appendix 1) referenced herein are being investigated using various DNA analyses by collaborators. In particular, it will be of interest to determine if the boldly contrasting dorsal and ventral patterns of the population of *A. t. septentrionalis* in Mohave County, Arizona, and the faded dorsal and ventral patterns of populations in

San Juan County, New Mexico, are correlated with detectable genetic divergence.

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APPENDIX 1. Specimens referenced in this study were from the following collections: American Museum of Natural History (AMNH); Brian K. Sullivan (BKS); University of Arkansas Department of Zoology (UADZ); and University of Michigan Museum of Zoology (UMMZ).

Aspidoscelis tigris septentrionalis (Burger, 1950)

Arizona: Mohave County: Coral Springs access road (= Hancock Road) called County Hwy. 237 in Arizona (unpaved), 3.2 km S of Utah/Arizona border that is 36.2 km S of jct. Coral Springs access road and US Hwy. 89; 12S 333546E, 4093661N, elev. 1598 m ±7 m [10 July 2013 (UADZ 9345, n = 1)]; 3.12 km S of Utah/Arizona border on Hancock road that becomes a dirt road in Arizona; 12S 333537E, 4093652N, elev. 1608 m [3 June 2014 (UADZ 9453–9457, n = 5); 4 June 2014 (UADZ 9458–9468, n = 11); 5 June 2014 (UADZ 9469–9470, n = 2); 11 July 2014 (UADZ 9530–9533, n = 4); 12 July 2014 (UADZ 9540–9541, n = 2)]; 68.8 km SW of Fredonia, Hurricane Cliffs, turn W off AZ Hwy. 389 onto Hwy. 5 (unpaved Cane Bed Road) and travel 59.5 km; 12S 314432E, 4046259N, elev. 1645 m [5 June 2014 (UADZ 9471, n = 1)]; roadside turnout/overlook off AZ Hwy. 389 NW of Pipe Springs, 0.48 km S of jct. of Yellowstone Road and AZ Hwy. 389; 12S 329414E, 4084833N, elev. 1575 m ± 2 m WAAS [6 June 2014 (UADZ 9473, n = 1)].

Arizona: Coconino County: State Road 89A, 8.0 km W of Marble Canyon; 12S 436144E, 4067540N) [14 May 2007 (BKS 1858–1860, n = 3); 15 May 1861–1865, n = 5)]; State Road 89A, 35.2 km W of Marble Canyon at Wildlife Refuge Road; 12S 415520E, 4062178N [15 May 2007 (BKS 1866–1871, n = 6)]; State Road 89, 57.6 km N of I-40, Babbitt Ranch; 12S 455286E 3952345N [25 May 2005 (BKS 1624–1626, n = 3); 26 May 2005 (BKS 1628–1629, n = 2)]; State Road 89, 57.6 km N of I-40, Babbitt Ranch; 12S 456516E 3952299N [17 July 2006 (BKS 1421, n = 1)]; State Road 89, 57.6 km N of I-40; Babbitt Ranch; 12S 455345E 3952335N [25 May 2005 (BKS 1630–1631, n = 2)]; 6.9 km (by Arizona Hwy. 264) SE of Moenkopi [17 June 1990 (AMNH R-136802–136812, n = 11)]; Salt Trail Canyon, Little Colorado River, 9.6 km upriver from the confluence with the Colorado River [3 May 1990 (AMNH R-136813, n = 1); 19 July 1990 (R-136814–136816, n = 3)].

Arizona: Navajo County: IR 71, 8.0 km N of Winslow, west of Little Colorado River; 12S, 528695E, 3887097N [25 May 2007 (BKS 1888–1890, n = 3)]; IR 114.4 km N of Winslow, east side toward Little Colorado River; 12S, 528573E, 3887096N [5 June May 2008 (BKS 1931–1935, n = 5)].

Arizona: Apache County: Many Farms [22 June 1990 (AMNH R-136796–136800, n = 5)];

Utah: Washington County: Zion National Forest, The Subway – left fork of North Creek Trailhead; 12S 308749E, 4122854N, 1119 m [12 July 2013 (UADZ 9349, 1 tail only, n = 2)]. **Utah: Kane County:** Coral Pink Sand Dunes State Park. 2nd bldg., from Hwy.; 12S 36003E, 4112249N, elev. 1689 m [2 June 2013 (UADZ 9245, n = 1)].

Utah: San Juan County: Bluff, Mokee Motel, 12S 626907E, 4127016N, elev. 1315 m [9 July 24 (UADZ 9519, n = 1)]; Mexican Hat, Canyonlands Motel Room 9, dry sedimentation ponds above motel; 12S 601093E, 4112246N, elev. 1308 m [14 July 2014 (UADZ 9542, n = 1)]; 41.44 km W of jct. US Hwy. 191 and US Hwy. 160 on 191 where it crosses San Juan River, 0.12 km SW of crossing, west bank of San Juan River; 12S 622276E, 4124233N, elev. 1295 m [17 July 2014 (UADZ 9545–9548, n = 4).

New Mexico: San Juan County: Town of Aztec, 0.24 km S of NM Hwy. 550 on NM Hwy. 173; 36.83504°N, 107.97661°W, elev. 1745 ± 8 m WAAS [16 July 2012 (UADZ 9140–9141, n = 2)]; 0.96 km N jct. San Juan County Hwys. 7500 and 8860 on NM Hwy. 371 new site; 12S 754418E, 4009679N [9 June 2014 (UADZ 9478–9479, n = 2); 2.56 N of jct. county roads 7500 and 8860 off NM Hwy. 371, mile marker 64 [10 June 2014 (UADZ 9480–9488, n = 9)]; mile marker 64 at 102.4 km N of I-40 on NM Hwy. 371; 12S 753703E, 4010494N, elev. 1823 m, 20.5 km S of first *A. inornata* site on NM Hwy. 371, (San Juan Co. begins at mile marker 48) [11 June 2014 (UADZ 9494–9495, n = 2); 10 August 2014 (UADZ 9574, n = 1]; NM Hwy. 371, 101.6 km N jct. I-40 and NM Hwy. 371, San Juan County, New Mexico; 12S 753916E, 4010352N, elev. 1838 m [6 July 2014 (UADZ 9503, n = 1); 7 July 2014 (UADZ 9509–9513, n = 5)]; NM Hwy. 371 at 105.6 km N of jct. I-40 and NM 371; 12 S 750775 E, 4011418N, elev. 1799 m [10 August 2014 (UADZ 9572–9573, n = 2)]; NM Hwy. 371, 100.8–103.2 km N jct. I-40 and NM Hwy. 371; 12S 754091E, 4010185 [11–12 August 2014 (UADZ 9576, 9584–9585, n = 3)].

Aspidoscelis tigris tigris (Baird, 1852)

Utah: Millard County: sand sage flats 20.8 km W of Fillmore [13 July 1931 (UMMZ 70536a–e, n = 5)].
Utah: Tooele County: Windover [21 July 1930 (UMMZ 69449, n = 1)].
Utah: Salt Lake County: E of Sandy, elev. 1524 m [9 July 1924 (UMMZ 59718, 59724, n = 3)].