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## COLOR PATTERN AND BODY SIZE VARIATION IN LIVE *ASPIDOSCELIS COSTATUS COSTATUS* (SQUAMATA: TEIIDAE) FROM A PROTECTED ENCLAVE IN SOUTHERN MEXICO

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**Abstract.**—Whiptail lizards in the *sexlineatus* species group (genus *Aspidoscelis*) in North America represent some of the most challenging patterns of variation in the North American herpetofauna. The range of color patterns in these populations is based on individual, ontogenetic, sexual, seasonal, and/or geographic variation. We studied representatives of a population of Western Mexico Whiptail (*A. costatus costatus*) from a protected private enclave of approximately 0.27 ha in the municipality and city of Ixtapan de la Sal, Estado de México, México. We captured 50 lizards in 2016 and 24 in 2018, most of which we photographed *ex situ* and a few *in situ*. These photographs revealed that a variety of age/size related dorsal and ventral patterns were consistently present. Males progressed through five stages of dorsal pattern changes from pale stripes, dark intervening fields, no spots to spots, and diverse pale configurations set in a black ground color. Females in this population showed similar changes but did not lose striping as they grew. Ontogenetic changes in ventral color patterns were also apparent, with males becoming more colorful than females. The adaptive significance of extensive color pattern variation in this urban population of *A. c. costatus* warrants further study.

**Key Words.**—adaptive significance; Balsas Basin Whiptail; body size; dorsal coloration; Mexican lizards; ontogeny; spots; stripes; ventral coloration

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### INTRODUCTION

Individual, ontogenetic, sexual, and geographic variation in color patterns in the Teiid lizard genus *Cnemidophorus* (Squamata: Teiidae), endemic to the Americas, had been a characterization challenge for over a century prior to the seminal publications of Zweifel (1959), Duellman and Wellman (1960), and Duellman and Zweifel (1962). These authors provided a framework for understanding and describing variation in complex color patterns in whiptail lizards wherein the marked diversity had resulted in much confusion, and little previous success, in resolving species boundaries (e.g., Burt 1931; Smith 1949; Burger 1950). More recently, much of that troublesome variation was relegated to the genus *Aspidoscelis*. Based on a combination of morphological, karyotypic, electrophoretic, and genetic data, *Aspidoscelis* was resurrected from the synonymy of the genus *Cnemidophorus* to partly resolve paraphyly therein (Reeder et al. 2002). Thus, *Aspidoscelis*, as redefined, accommodated all taxa of whiptail lizards in North and Central America, except those temporarily retained in the *Cnemidophorus lemniscatus* species group, pending the revisions offered by Harvey et al. (2012), McCranie and Hedges (2013), and Tucker et al. (2016).

Pertaining to resurrection of *Aspidoscelis* from the synonymy of *Cnemidophorus* (Reeder et al. 2002), the resulting nomenclature has been subject to confusion. We base the specific epithets of certain species of *Aspidoscelis* referenced in this report on Steyskal (1971), a publication long overlooked by researchers of whiptail lizards until Tucker et al. (2016) reiterated the International Commission on Zoological Nomenclature (ICZN) basis for treating *Aspidoscelis* as being of masculine rather than feminine sex. Consequently, in Appendix D of Tucker et al. (2016), it was indicated that names with the suffix -a (e.g., *alpina*, *costata*, *griseocephala*, *septemvittata*, *stictogramma*), as recommended for *Aspidoscelis* by Reeder et al. (2002), should be returned to the suffix -us (e.g., *alpinus*, *griseocephalus*, *costatus*, *septemvittatus*, *stictogrammus*).

Systematic treatment of diversity in the *Aspidoscelis* *deppii* (Duellman and Wellman 1960; Grismer 1999; Taylor and Walker 2014a,b), *A. cozumelus* (Fritts 1969; Taylor and Cooley 1995; Taylor et al. 2014), *A. sexlineatus* (Zweifel 1959; Duellman and Zweifel 1962; Walker 1981a,b; Walker et al. 2018), *A. tessellatus* (Walker et al. 1995, 1997; Cordes and Walker 2006), and *A. tigris* species groups (Walker and Maslin 1981; Hendricks and Dixon 1986) formerly in the

genus *Cnemidophorus* (Burt 1931), and reallocated to *Aspidoscelis* (Reeder et al. 2002), has been an ongoing problem that has only grown over time (Barley et al. 2019). In fact, none of the species groups in *Aspidoscelis* has escaped systematic chaos resulting primarily from confusing color pattern variation. The complexity of color pattern variation and its taxonomic implications in the speciose *A. sexlineatus* group, however, is especially noteworthy among reptilian complexes in the North American herpetofauna, and that in particular includes the uncertain taxonomic treatment of *A. c. costatus* and other included subspecies (Burt 1931; Smith 1949; Zweifel 1959; Duellman and Zweifel 1962; Reeder et al. 2002).

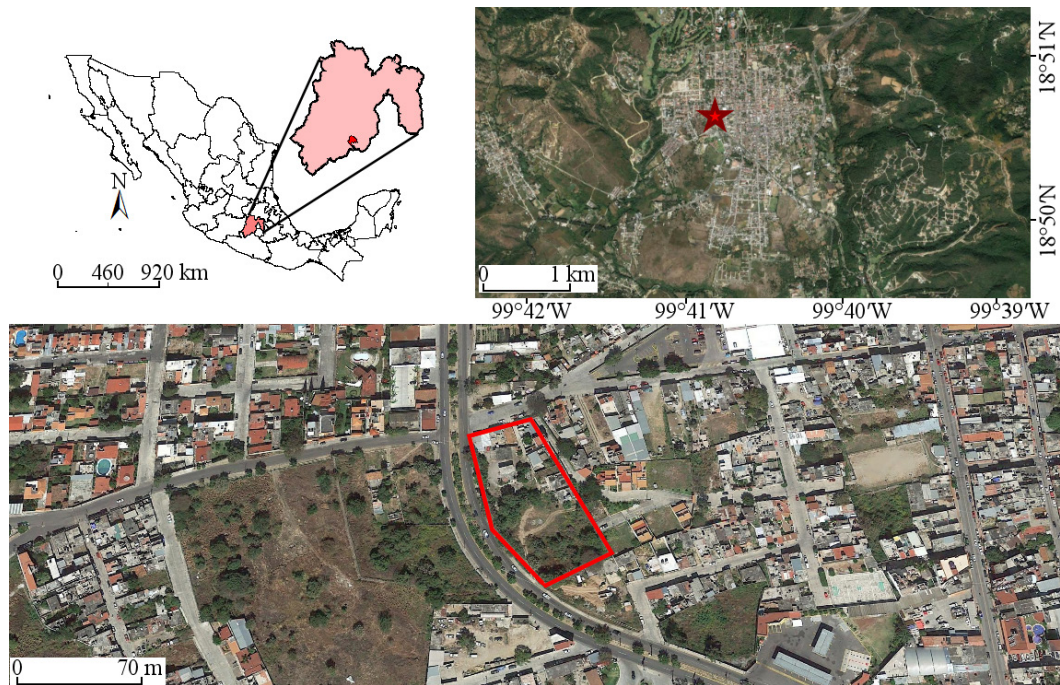
*Aspidoscelis costatus*, commonly called Western México Whiptail, was recognized as a problematic complex within the *A. sexlineatus* species group by Reeder et al. (2002), a conundrum that has remained unresolved (Barley et al. 2019). The choice of names used by Zweifel (1959) in the comprehensive study of morphological variation in the polytypic *costatus* complex exemplified problems stemming from misinterpretation of color pattern variation in whiptail lizards. For example, Zweifel (1959) acceded to the identification by Smith (1949) of the presently accepted holotype of *C. c. costatus* as that of *C. s. sackii* (= *C. s. sacki*), which was actually shown to have resulted from confusion regarding its dorsal color pattern. Duellman and Zweifel (1962), however, identified the type specimen in question as that of *C. c. costatus* and reallocated numerous populations previously treated as *C. sacki* (*sensu* Zweifel 1959) from Guerrero, Morelos, México, and Puebla in southern México, as well as from other Mexican states, to that taxon. Duellman and Zweifel (1962) then transferred all taxa to *C. costatus*, which had been treated as subspecies of *Cnemidophorus sacki* by Zweifel (1959) and Duellman (1960). Reeder et al. (2002) could not conclusively resolve the species status of *A. c. costatus* based on morphological and genetic data with respect to what they treated as polytypic *A. burti* (see Walker and Cordes 2011), polytypic *A. gularis* (see Walker 1981a,b; Walker et al. 2001), and we add monotypic *A. alpinus* (see Walker 1980). Each of these comprised a widely distributed complex of populations with complicated ontogenies of color pattern. As such, the species is presently considered to consist of multiple subspecies including *A. c. costatus*, *A. costatus barrancarum* (= *barrancorum*), *A. costatus griseocephalus*, *A. costatus huico*, *A. costatus mazatlanensis*, *A. costatus nigrigularis*, *A. costatus occidentalis*, and *A. costatus zweifeli* (Zweifel 1959; Duellman and Zweifel 1962; Walker 1980), but see Wright (1993) and Barley et al. (2019). All eight provisionally recognized subspecies of *A. costatus* are endemic to México (i.e., in parts of the

states of Chihuahua, Jalisco, Sonora, Sinaloa, Nayarit, Michoacán, Morelos, Guerrero, Puebla, Tlaxcala, Oaxaca, and México) spanning both temperate and tropical habitats (Zweifel 1959; Duellman 1960; Maslin and Secoy 1986; Reeder et al. 2002; Barley et al. 2019). According to Wilson et al. (2013), *A. costatus* scores a medium (11) environmental vulnerability score principally due to its restricted distribution.

We studied numerous aspects of the dorsal and ventral color patterns and attendant variation in body size of gonochoristic *A. c. costatus* (Balsas Basin Whiptail), primarily based on live lizards from a restricted urban area in Ixtapan de la Sal, Estado de México, México. The results have resolved a major gap in our knowledge about color variation of this taxon (*sensu* Reeder et al. 2002) by extending knowledge beyond the preliminary notes on color patterns and snout-vent lengths (SVL) of preserved specimens of the taxon presented by Zweifel (1959), who used the name *C. s. sacki* (*sensu* Smith 1949). The objectives of this research were to provide the most extensive analyses possible to understand the complexities of size, dorsal color patterns, and ventral color patterns based on ontogenetic and sexual variation in the vulnerable local population of *A. c. costatus* (*sensu* Duellman and Zweifel 1962) on a private estate in the municipality and city of Ixtapan de la Sal, Estado de México, México. This should enable subsequent workers to consider the adaptive significance of extensive color pattern variation in this protected urban population of *A. c. costatus*.

## MATERIALS AND METHODS

**Study site.**—We examined live lizards captured from an isolated area (2,700 m<sup>2</sup>) at an urban site (= private estate) in Estado de México, México (Figs. 1 and 2), within the city and municipality of Ixtapan de la Sal (18°50'34.5"N, 99°40'51.8"W; WGS84; elevation 1,800 m). The study site was entirely surrounded by unsuitable habitat for whiptail lizards. The two first authors live-captured and subsequently released all lizards used in the study. We made captures either by using drift fences during whiptail lizard activity periods spanning about 1000–1700 Central Daylight Savings Time (CDST) on 27 May 2016 (end of dry season—start of rainy season, n = 50) and 1000–1200 CDST on 29 June 2018 (rainy season, n = 24) or by turning rocks. The release of lizards was a major concession to conservation of this vulnerable population at a restricted site in a densely populated urban area (Figs. 1 and 2). The study site for *A. c. costatus* at Ixtapan de la Sal comprised parts of the estate grounds of a human habitation, the owners of which have maintained as much naturalistic surroundings for privacy and conservation purposes as feasible within a densely



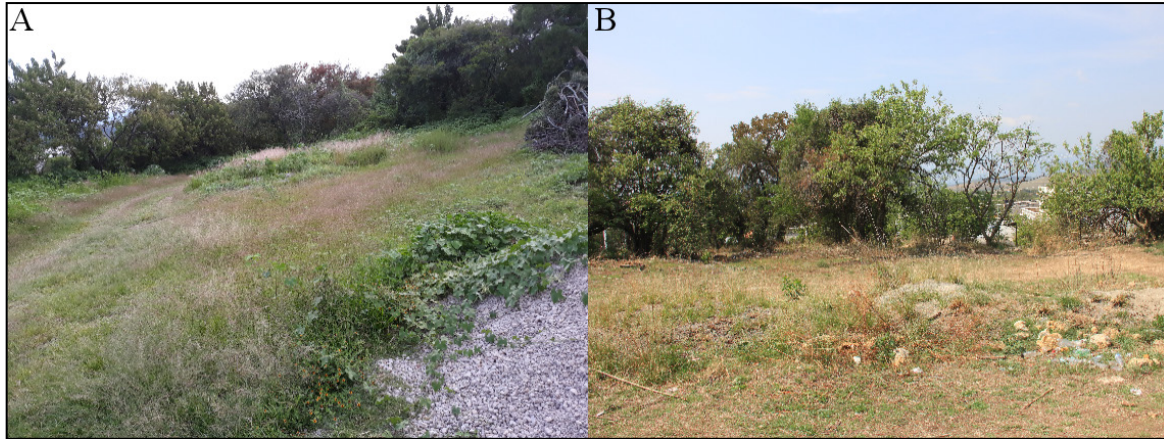
**FIGURE 1.** Estado de México (top left panel), the urban matrix of Ixtapan de la Sal (top right panel), and the surroundings of the outlined study area (bottom panel) where Balsas Basin Whiptail (*Aspidoscelis c. costatus*) was sampled in the insular-like urban site. (Images taken from: Google Earth).

populated urban matrix (Figs. 1 and 2). The first author first observed *A. c. costatus* at the site in 2012 on and near a sidewalk bordering the property (Figs. 1 and 2), and he initially sampled the population 20 March 2015. This site has a well-marked seasonality with patches of either completely exposed or relatively exposed mixtures of sandy and limestone rubble substrate amongst grasses and forbs (Fig. 2). Examples of vegetation at the site (which did not provide optimal habitat for lizards, per se) included an introduced South American tree species of the genus *Jacaranda* and introduced landscape ornamental shrubs mainly of the family Cupressaceae. A wide variety of grasses and herbaceous annual and perennial plant species were also present at the site bordering sidewalks, driveways, and small limestone barrens in intermittently sunlit areas provided optimal lizard habitat (Fig. 2). During the rainy season, the general habitat was denser and greener than in the dry season, when the vegetation was browner and less dense (Fig. 2), as documented previously in studies with other populations involving seasonal changes in the dorsal coloration related with the microhabitats in *A. c. costatus* (Hernández-Gallegos and Domínguez-Vega 2012). This urban enclave of *A. c. costatus* habitat was surrounded by human habitations and associated surroundings on three sides and by a street and sidewalk on the fourth side (Fig. 1), along which were rocks used as retreats by *A. c. costatus*. The numbers of lizards we captured and released at the site 27 May 2016 ( $n = 50$ ) and 29 June 2018 ( $n = 24$ ) were

indicative that *A. c. costatus* has maintained unusually high densities at this insular site since its discovery. We observed no other species of *Aspidoscelis* at the Ixtapan de la Sal study site; however, the area is the habitat of other herpetofauna taxa including frogs (*Eleutherodactylus*) and other lizards (*Sceloporus* and *Urosaurus*).

**Analyses of body characteristics in *Aspidoscelis c. costatus*.**—We determined the sex of whiptail lizards captured in 2016 by external characteristics (e.g., Ashton 2003), and we measured their SVL to the nearest 1 mm using a ruler. We released the 2018 captures after measuring SVL and tail lengths (i.e., original plus regenerated portion if applicable) to the nearest 1 mm, weighing to 0.5 g (using a 60 g spring scale), and photographing lizards. We photographed lizards using a standard distance (30 cm) and camera flash to ensure uniformity, *ex situ* prior to release, but we photographed several large adults *in situ*. Based on previous studies, we determined that adult females were  $\geq 68$  mm SVL, juvenile females were 46–67 mm SVL, hatchling females were  $\leq 45$  mm SVL, adult males were  $\geq 67$  mm SVL, juvenile males were 46–66 mm SVL, and hatchling males were  $\leq 45$  mm SVL (Rubio-Blanco 2007; Granados-González et al. 2013).

**Analyses of dorsal and ventral color patterns.**—Most stages of dorsal and ventral color pattern development were represented among the individuals (including



**FIGURE 2.** (A) The mixed habitat components of trees, shrubs, forbs, grasses, and exposed substrate during the rainy season on a property with a human habitation that supported Balsas Basin Whiptail, *Aspidoscelis c. costatus*. (Photographed by Aldo Gómez-Benitez). (B) The same property showing the dry season in the insular-like urban site in municipality and city of Ixtapan de la Sal, Estado de México, México. (Photographed by Oswaldo Hernández-Gallegos).

both years 2016 and 2018) of *A. c. costatus* examined from Ixtapan de la Sal, Estado de México, México (Appendices 1–3). We used images of the dorsal and ventral patterns of the 2018 captives and data on color patterns (stripes, spots in dark fields and coloration) obtained by the first author. We synthesized the general framework for analyses of color pattern variation in *A. c. costatus* from studies by Burt (1931), Zweifel (1959), Duellman and Wellman (1960), and Duellman and Zweifel (1962), and modeled the study based on more recent studies of species such as *A. alpinus* in México (Walker 1980), *A. gularis* in México and the U.S. (Walker 1981a, b), *A. stictogrammus* in México and the U.S. (Walker and Cordes 2011), and *A. uniparens* in México (Walker et al. 2018)

We used standard terminology for dorsal color pattern components (i.e., longitudinal pale-colored stripes, dark-colored longitudinal fields, variously shaped pale-colored markings, and scales; Appendix 1) synthesized from studies by Burt (1931), Zweifel (1959), Duellman and Zweifel (1962), and Walker (1981a,b). These publications also analyzed ventral color patterns with reference to throat, chest, abdomen, limb, and tail colorations. Herein, we introduce the appellation Virtual Components based on the observation that distinct pale-hued stripes apparent in juvenile and young adult males of *A. c. costatus* were not readily apparent to the unaided eye in fully metamorphosed males but were often discernible as effects of photographic enlargement.

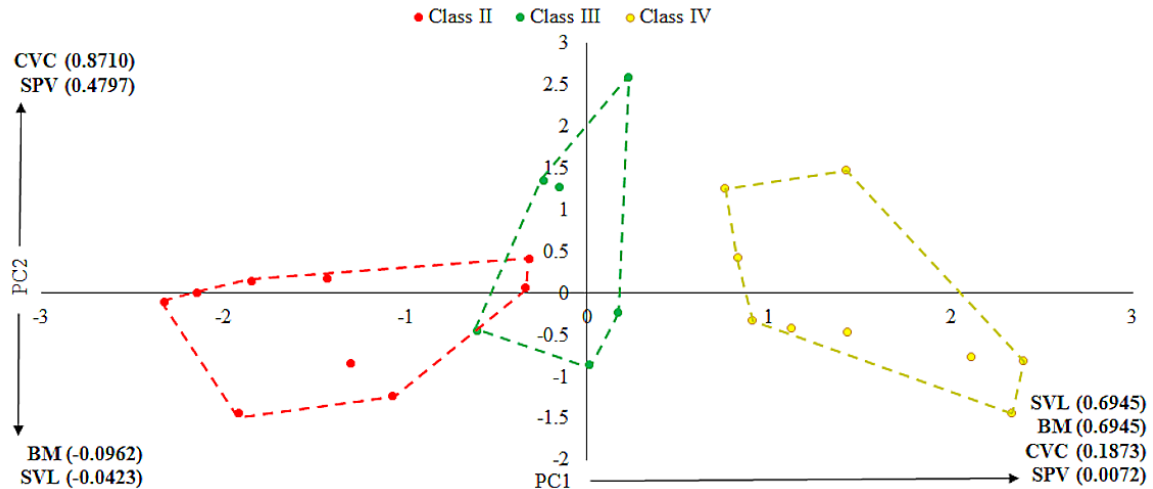
We quantified two aspects of scutellation: SPV, the scales transversely separating the paravertebral stripes, and CVC, count of contacts of vertebral configuration with paravertebral stripes in *A. c. costatus* in 2018 males ( $n = 12$ ) and females ( $n = 12$ ). We also measured SVL and body weight from UCM 8580, 8582–8583, 8626–8632, 8634–8638, 8641–8644, 8646, 8649–8660 collected by

others from several sites in Estado de Morelos listed by locality by Walker (1980). The Morelos sample also included one small lizard (UCM 8660) for which we could not determine its sex; however, we assumed its SVL of 31 mm was representative of the approximate hatchling size for the taxon. We could not describe CVC for the Morelos sample.

**Statistical analyses.**—We conducted a Principal Components Analysis on a correlation matrix using SVL, weight, PV, and CVC to determine if dorsal-color pattern classes could be visually separated. Employing the same variables above, a MANOVA was conducted to assess differences between pattern classes. We used Statgraphics Centurion software version 18.1.01. for analysis. Our results were significant if  $P \leq 0.05$ .

## RESULTS

**Dorsal color pattern in *Aspidoscelis c. costatus*.**—Size-related characteristics had the highest loadings on principal component 1, for which the convex hulls for the Ixtapan 2018 lizards separated. The PCA shows three pattern classes (Fig. 3), and these classes differed significantly (Wilks'  $\lambda = 0.1304$ ,  $F = 7.960$ ,  $P < 0.001$ ). Five live female *A. c. costatus* (Fig. 4) and four live males (Fig. 5) captured in June 2018 were characterized by a dorsal pattern of pale-hued longitudinal stripes and a complex highly variable pale-hued linear middorsal configuration, all sharply bordered by mostly black fields, presence of green-hued developing spots particularly posteriorly in the dorsolateral fields, and an indistinctly striped brown-hued tail (i.e., equivalent to pattern class II of Zweifel 1959). Details of the patterns in these individuals comprised three primary stripes on each side of the body including: a white lateral,



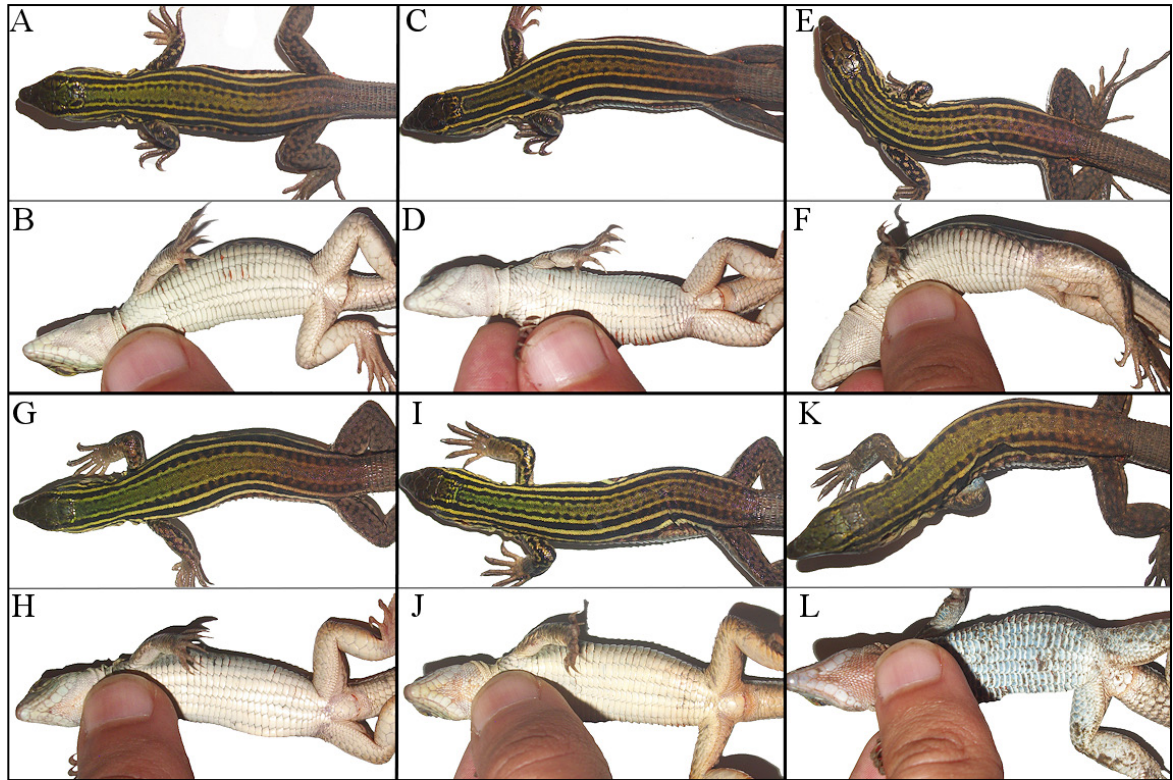
**FIGURE 3.** Principal Components Analysis for dorsal color pattern in Balsas Basin Whiptail (*Aspidoscelis c. costatus*) from Ixtapan de la Sal, Estado de México, México, based on the loading of SVL and weight (characteristics related to size) in principal component 1 (PC1), and the dispersion of data (note that convex hulls are separated) that analysis lends support to three pattern classes as Burt (1931), Zweifel (1959), Duellman and Zweifel (1962), and Walker (1981a, b) synthesized. The first two principal components accounted for 75.27% of the variability of the data.

irregular in outline on the head and relatively straight-margined on the body, from a pale circle surrounding the ear opening to the hind limb where it angled onto the anterior surface of the thigh; a pale yellow to yellow-green dorsolateral, irregular on the head and relatively straight-margined on the body, from beneath the orbit onto the base of the tail. They also show an evenly (e.g., Fig. 4E) to unevenly margined (e.g., Fig. 4G) yellow paravertebral (Appendix 2) from the suprascapular scales superior to the orbits to the base of the tail. From the occipital region of the head to the base of the tail were green to green-yellow components of a vertebral configuration consisting of either one or perhaps two poorly defined and highly irregularly margined lines with lateral extensions in contact with both right and left paravertebral stripes (Figs. 4 and 5; Appendix 2).

Also apparent in the dorsal pattern on each side of the body in each individual was a dusky black lower lateral field ventral to the lateral stripe, a black upper lateral field dorsal to the lateral stripe, and a black dorsolateral field dorsal to the dorsolateral stripe, devoid of distinct spots. Barely visible, however, are indications of developing (= incipient) spots that were present within the last few millimeters of the upper lateral and dorsolateral fields. These were the first discernable indications of ontogenetic changes in the subspecies (i.e., pattern class II of Zweifel 1959; herein Figs. 4A, C, E, G, I and 5A, C, E, G). The forelimbs were black with green-tan spotting and mottling, the hind limbs were similarly patterned dorsally though with a yellow-tan line on the posterior surface of each thigh. The dorsal aspect of the tail was dark brown with barely discernible striping (Figs. 4A, C, E, G, I and 5A, C, E, G).

Four live female *A. c. costatus* (Figs. 4K and 6) and two live males (Fig. 5I, K) captured in June 2018 possessed a different pattern of stripes, spots, and bars (i.e., pattern class III of Zweifel 1959), and had undergone a moderate amount of ontogenetic modifications. The six primary stripes (i.e., consistently present and relatively invariable paired laterals, dorsolaterals, and paravertebrals) and the secondary vertebral configuration (i.e., highly variable) were intact and distinct in these individuals. The black to dusky lower lateral fields (ventral to the lateral stripes), black upper lateral fields (dorsal to the lateral stripes), and black dorsolateral fields (dorsal to the dorsolateral stripes), however, had developed a linear series of essentially equally spaced green-tan cross-bars and spots, many of which were in contact with the stripes (Figs. 4K and 6A, C, E). The vertebral configuration was more individually variable than were the primary stripes. Also apparent were developing dot-like spots on the dorsal aspects of the hind limbs.

Three live female *A. c. costatus* (Fig. 5) and six live males (Fig. 7) captured in June 2018 possessed a third pattern of equally apparent stripes, spots, and bars (i.e., pattern class IV of Zweifel 1959). In the largest three of 12 females from 2018, the ubiquity of the spots and bars, along with the stripes of diminished ubiquity, had resulted in the black ground color appearing as essentially rectangular island-like remnants, particularly in the position of the dorsolateral fields. In fact, the primary stripes had been partly to largely replaced near the base of the tail in these females, and each of them had dot-like pale-hued markings on the hind limbs, and there was a lack of stripes on the tail. Interestingly, the largest of the 12 females (Fig. 6K) had the most distinct

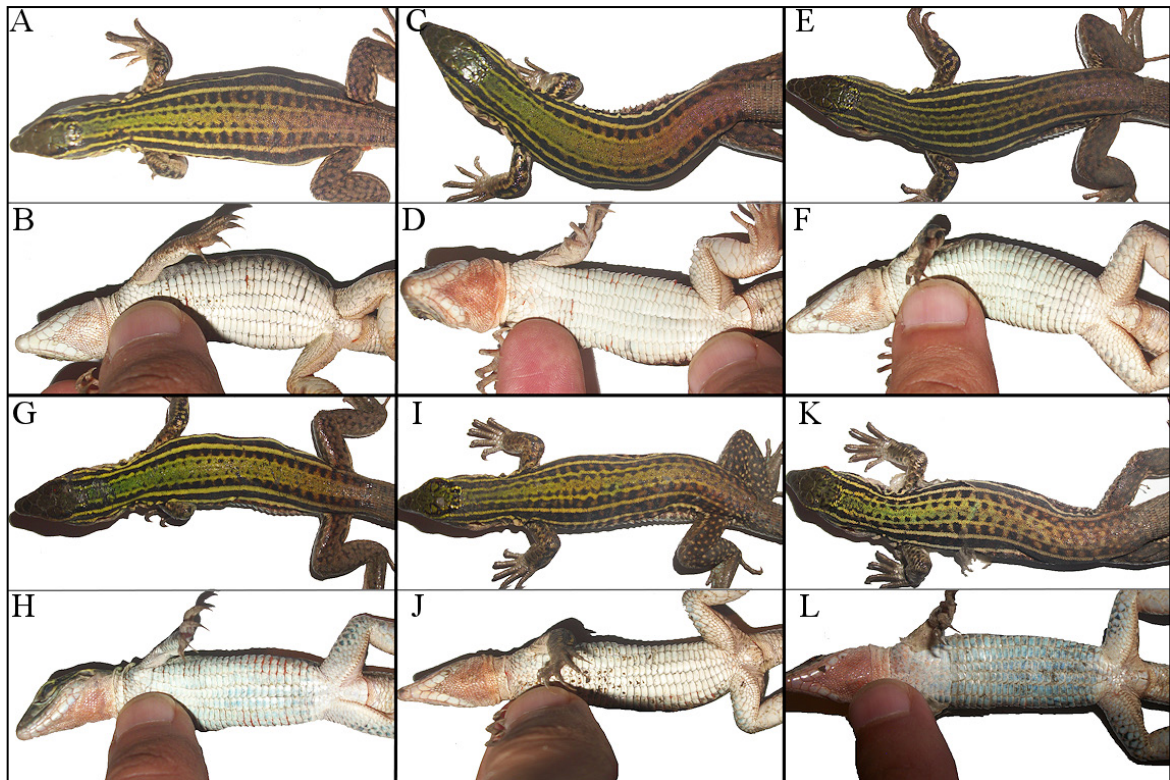


**FIGURE 4.** Dorsal and ventral view and pattern class (PC; dorsal, Roman numeral; ventral, Arabic numeral) of five live juvenile and one adult female of Balsas Basin Whiptail (*Aspidoscelis c. costatus*) captured and released 29 June 2018 from municipality and city of Ixtapan de la Sal, Estado de México, México. (A-B) PC II-1, 59 mm SVL. (C-D) PC II-1, 65 mm SVL. (E-F) PC II-1, 67 mm SVL. (G-H) PC II-1, 69 mm SVL. (I-J) PC II-1, 70 mm SVL. (K-L) PC III-3, 80 mm SVL. (Photographed by Aldo Gómez-Benitez).

stripes, though each of the three largest females exhibited evidence of a black band developing in the positions of the upper lateral field on each side of the body. In each of the largest six of the 12 males from 2018, the integrity of the primary stripes was compromised by spots and bars either anteriorly near the head (Fig. 7K), posteriorly near the tail (Fig. 7C, E, G, I, K) or both ends of the body (Fig. 7A). The dorsal surfaces of the hind limbs had pale-hued dot-like markings, and there was a lack of evidence of stripes on the tail.

None of the 12 adult males *A. c. costatus* from 2018 had ontogenetically attained a dorsal pattern matching the description of Zweifel's (1959) pattern class V (i.e., entirely lacking more than remnants of the primary stripes). Thus, we included two males of 106 mm and 110 mm SVL from Ixtapan de la Sal to depict pattern class V and one hatchling for pattern class I (31 mm; Fig. 8), which we captured and released in 2016. These adults represent examples of dorsal patterns in the subspecies dominated by complex arrays of pale-hued dorsal components including spots, bars, annuli, and disruptive camouflage-like arrays rather than stripes (Fig. 8). Also, a distinctive feature of these dorsal patterns was the presence of a black band-like zone of ground color in the approximate position of the upper

lateral field on each side of the body, which is diagnostic in the color pattern of *A. c. costatus*. Dorsal and ventral to this black band on each side of the body were only isolated areas of the black ground color resulting from the extensive distribution of brown-tan components of various shapes; however, in the largest adults the anterior half of the dorsum was essentially brown with very little evidence of the black ground color, a description that also applied to the vertebral region. Such individuals also had irregularly shaped brown-tan lateral bars. Overall, the appearance of the dorsum could be best described as presenting a camouflage-like pattern as in Figs. 4–8. Also, present were distinctly spotted hind limbs and a brown tail as in Figs. 4–8. Based on the June 2018 sample of 12 males and 12 females of *A. c. costatus* from Ixtapan de la Sal, Estado de México, color pattern classes I–IV (*sensu* Zweifel 1959) in females and males were approximated have the following SVLs: (1) class I (31–55 mm SVL,  $n = 2$ , based on the hatchling from Estado de Morelos and the 2019 Ixtapan hatchling); (2) class II (59–72 mm SVL,  $n = 6$ ); (3) class III (72–80 mm SVL,  $n = 9$ ); (4) class IV (91–106 mm SVL,  $n = 9$ ); and (5) class V (106, 110 mm SVL,  $n = 2$  based on May 2016 specimens; Fig. 9).



**FIGURE 5.** Dorsal and ventral view and pattern class (PC; dorsal, Roman numeral; ventral, Arabic numeral) of six live adult males of Balsas Basin Whiptail (*Aspidoscelis c. costatus*) captured and released 29 June 2018 from municipality and city of Ixtapan de la Sal, Estado de México, México. (A-B) PC II-2, 72 mm SVL. (C-D) PC II-2, 80 mm SVL. (E-F) PC II-2, 80 mm SVL. (G-H) PC II-2, 81 mm SVL. (I-J) PC III-2, 83 mm SVL. (K-L) PC III-4, 88 mm SVL. (Photographed by Aldo Gómez-Benitez).

**Ventral color pattern in *Aspidoscelis c. costatus*.**—

The ventral color patterns in female *A. c. costatus* ( $n = 12$ ) in the 2018 Ixtapan de la Sal sample (Appendix 1) proceeded from essentially plain cream-white with a pinkish tinge in juveniles and small adults (e.g., Fig. 4) through several stages to become a complex array of colors in adult females to involve the chin (= pink to red gular region), chest (= mixed light and very dark blue thoracic region), abdomen (= mixed light and dark blue abdominal region), and pelvis (mixed red and blue hind limbs, cloacal area, and base of tail; e.g., Fig. 6). Although there were no juveniles among the males in the 2018 sample ( $n = 12$ ), a similar sequence of stages (Appendix 1) was indicated in the development of the ventral pattern based on young males (Fig. 5B). The gular coloration in males of intermediate sizes continued to intensify before development of changes in more posterior areas (Fig. 5D, F, H, J, and L). Complete metamorphosis of the ventral pattern was evident only in the largest males (Fig. 7).

**Summary of dorsal color pattern in *Aspidoscelis c. costatus*.**—We analyzed 15 photographs of lizards both subsequently released and *in situ* from 2016 representing the color pattern developmental stages of each sex. We

used these photographs to construct the description of each developmental stage: (1) stripes and no spots (two males 45 and 51 mm SVL, one female 53 mm SVL); (2) stripes with spots only starting to form in the posterior aspect of certain fields between stripes (three males 70–90 mm SVL, one female 66 mm SVL); (3) stripes and a profusion of distinct spots and bars (two males 61 and 91 mm SVL, three females 91–104 mm SVL); and (4) without stripes (three males 90–110 mm SVL, no completely unstriped females were observed). We analyzed photographs of all 24 lizards we captured in 2018 representing developmental stages of dorsal color patterns in each sex (12 males, 12 females). We used these photographs to construct the description of each developmental stage in 2018: (1) stripes with spots only starting to form in the posterior aspects of certain fields between stripes (five females of 59–70 mm SVL and four males 72–81 mm SVL); (2) stripes and a profusion of distinct spots and bars (four females 80–86 mm SVL and two males 83–88 mm SVL); and (3) spots and bars more prevalent than stripes (three females 97–98 mm SVL and six males 95–106 mm SVL). In Appendix 3 we have summarized sources of color pattern variation in *A. c. costatus* from Ixtapan de la Sal (i.e., individual, ontogenetic, and sexual).

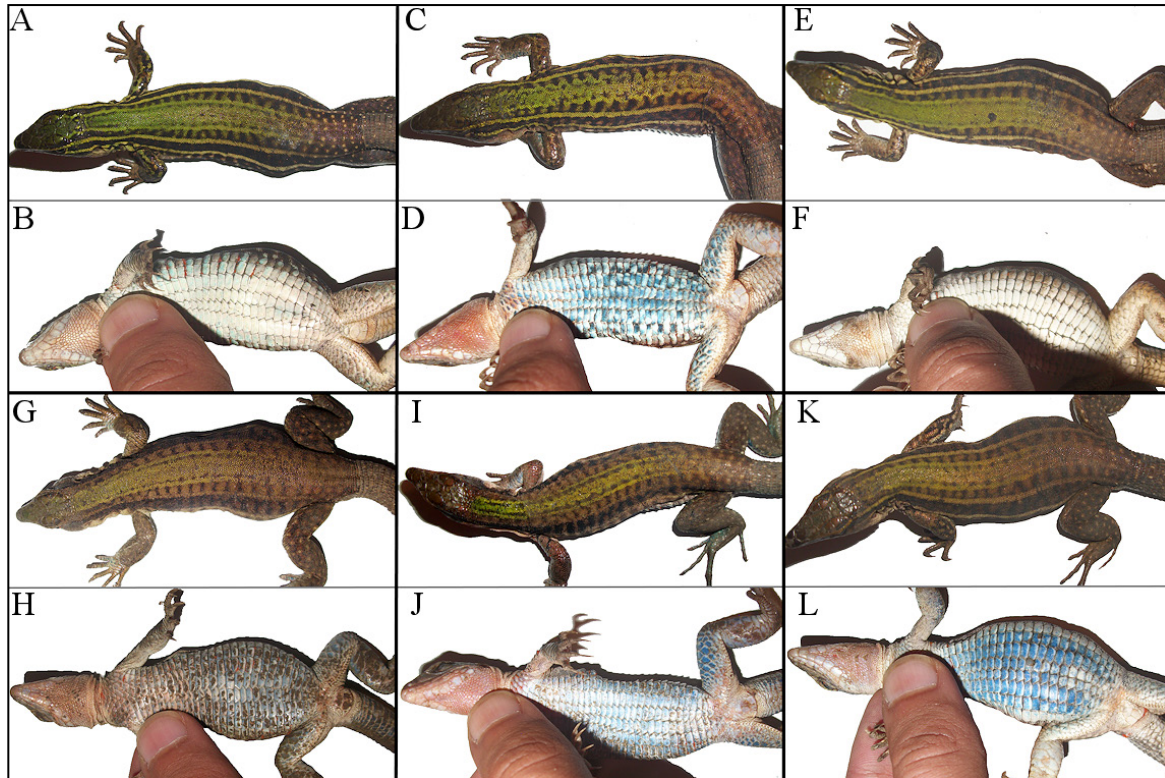


FIGURE 6. Dorsal and ventral view and pattern class (PC; dorsal, Roman numeral; ventral, Arabic numeral) of six live adult females of Balsas Basin Whiptail (*Aspidoscelis c. costatus*) captured and released 29 June 2018 from municipality and city of Ixtapan de la Sal, Estado de México, México. (A-B) PC III-2, 84 mm SVL. (C-D) PC III-2, 85 mm SVL. (E-F) PC III-2, 86 mm SVL. (G-H) PC IV-4, 91 mm SVL. (I-J) PC IV-3, 97 mm SVL. (K-L) PC IV-3, 98 mm SVL. (Photographed by Aldo Gómez-Benitez).

## DISCUSSION

We have studied large samples of nine relevant taxa with complicated color schemes (Appendix 4). The smallest individuals of *A. c. costatus* captured at Ixtapan de la Sal, though diagnostic in their middorsal configurations, exemplified the basic hatchling to early juvenile dorsal pattern observed in a number of species and subspecies in the *A. sexlineatus* group (*sensu* Burt 1931; Lowe et al. 1970; Duellman and Zweifel 1962; Degenhardt et al. 1996) including *A. burti* (*sensu* Walker and Cordes 2011), *A. gularis* (*sensu* Walker 1981a,b; Walker et al. 2001), *A. septemvittatus* (Walker *sensu* 1981a,b), *A. scalaris* (*sensu* Walker 1981a,b), and *A. alpinus* (*sensu* Walker 1980). From a basic dorsal pattern of pale-hued stripes, intervening dark-hued fields, and absence of distinct spots, there develops a myriad of dorsal patterns that are diagnostic of an as yet undetermined number of species and subspecies (see Barley et al. 2019).

The hatchling bearing the museum number UCM 8660 that we used in our study was among 13 specimens of *A. c. costatus* (UCM 8649–8660) collected 18 August 1956 from Morelos. Although the sample was initially catalogued as *Cnemidophorus sackii gigas* based on a

misinterpretation of color pattern (*sensu* Smith 1949), it was re-identified by Walker (1980) to *C. c. costatus* (= *A. costata costata* based on Reeder et al. 2002 and *A. c. costatus* based on Tucker et al. 2016) following reinterpretation of color pattern coupled with analyses of meristic characters. Color pattern ontogenetic variation must be considered in lizard diagnosis to avoid species determination errors. Our work provides all metamorphic stages in color pattern of *A. c. costatus* that could be used in species determination. Nevertheless, we suggest to always include meristic traits in diagnosis due to all the sources of color pattern variation present in the genus.

Color pattern variation in *A. c. costatus* from Ixtapan de la Sal derives from individual, ontogenetic, and sexual sources. As noted by Hawlena et al. (2006), non-reproductive related changes in color pattern has been received very little attention. Hernández-Gallegos and Domínguez-Vega (2012) have recorded the first known instance of a correlation between seasonal changes in habitat and the dorsal coloration of *A. c. costatus* based on 95 individuals from the city and municipality of Tonatico (18°45'N, 99°13'W; WGS84; elevation 1,500–1,600 m). Lizards were collected at Tonatico from February to October 2007 during the rainy season (n =



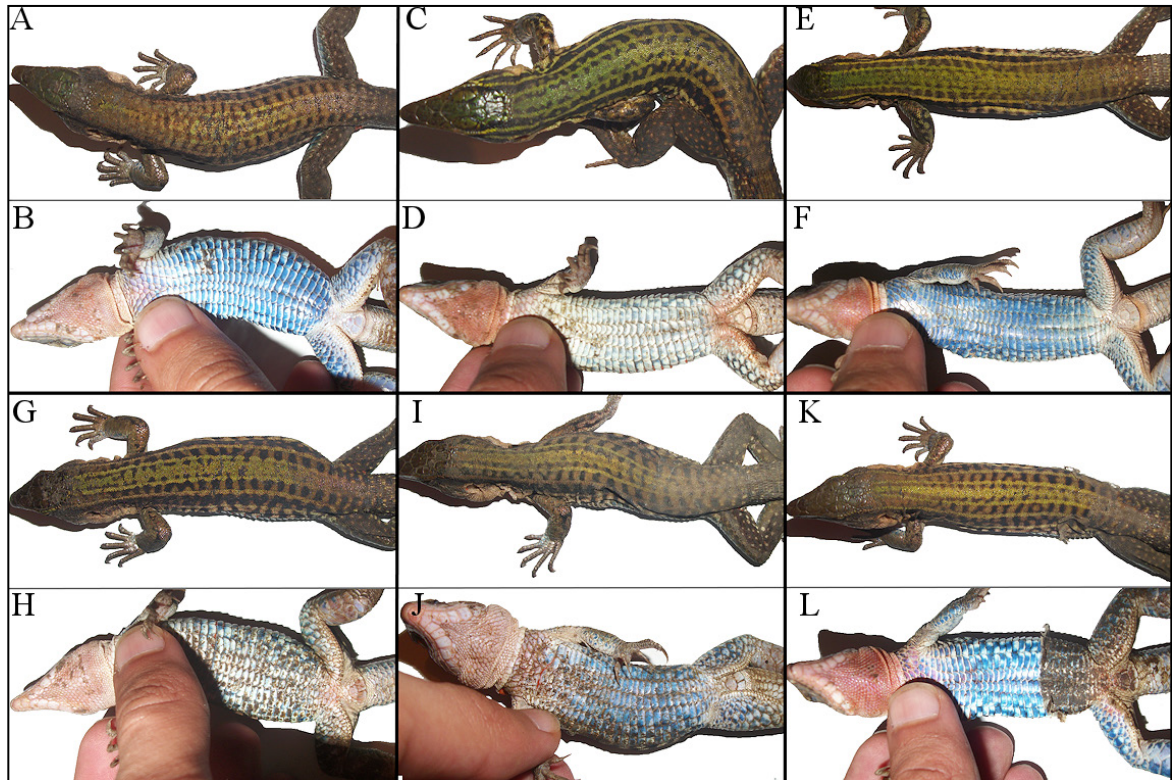


FIGURE 7. Dorsal and ventral view and pattern class (PC; dorsal, Roman numeral; ventral, Arabic numeral) of six live adult males of Balsas Basin Whiptail (*Aspidoscelis c. costatus*) captured and released 29 June 2018 from municipality and city of Ixtapan de la Sal, Estado de México, México. (A-B) PC IV-4, 95 mm SVL. (C-D) PC IV-4, 96 mm SVL. (E-F) PC IV-4, 99 mm SVL. (G-H) PC IV-4, 105 mm SVL. (I-J) PC IV-4, 105 mm SVL. (K-L) PC IV-4, 106 mm SVL. (Photographed by Aldo Gómez-Benitez).

42), which typically extended from mid-June to mid-September, and the other lizards were collected during the dry season ( $n = 53$ ), which typically included other parts of the year. They observed that survivorship in *A. c. costatus* at Tonatico was likely enhanced in the dry season by a habitat-matching brownish dorsal coloration and in the rainy season by development of a vegetation-matching greenish dorsal coloration.

Complex ontogenetic variation in the dorsal pattern of *A. c. costatus* is typical for all populations of this polytypic species (Zweifel 1959; Duellman and Zweifel 1962), as well as in many other species in the *A. sexlineatus* group (Duellman and Zweifel 1962; Walker 1980; 1981a,b; Walker and Cordes 2011). We found that ontogenetic change in color pattern occurs in the urban studied population just as in wild populations (based on Zweifel 1959), denoting no relationship between ontogenetic change in dorsal color pattern and the habitat conditions. We suggest that the myriad of dorsal pattern variants in populations of *A. c. costatus* may not be discernable per se to either predators or potential mates because a population always contains males and females representing all stages of color patterns, thus the adaptive value of the general pattern type is not compromised by individual variation. Some authors,

however, suggest that the striped body is correlated with foraging strategies and movements; striped lizards being active foragers and more mobile than lizards with cryptic patterns (Ortolan 1999; Hawlena et al. 2006; Halperin et al. 2016). Nevertheless, the adaptive significance of ontogenetic variation in the dorsal and ventral color patterns of *A. c. costatus* remains somewhat enigmatic.

*Acknowledgments.*—We thank the Delgado family for permission to capture and release individuals of *Aspidoscelis c. costatus* on their property (i.e., the study site). Accolades are due to Justin L. Rheubert for useful comments on a first draft of our manuscript, and J. E. Cordes for assistance of many categories. Students at the Universidad Autónoma del Estado de México, Daniel Sánchez-Manjarrez, Edgar Vásquez-Alcántara, Orlando Suárez-Rodríguez, Ailed Pérez-Pérez, and Ana E. López-Moreno, helped us during sampling. Heather Bateman and Brian Sullivan of Arizona State University, Phoenix, USA, kindly responded to our requests for assistance during this project. We also acknowledge the following curators and individuals who facilitated examinations of comparative material in the previously identified collections: Julio Alberto Lemos-Espinal (LEUBIPRO); Hobart M. Smith (UCM,

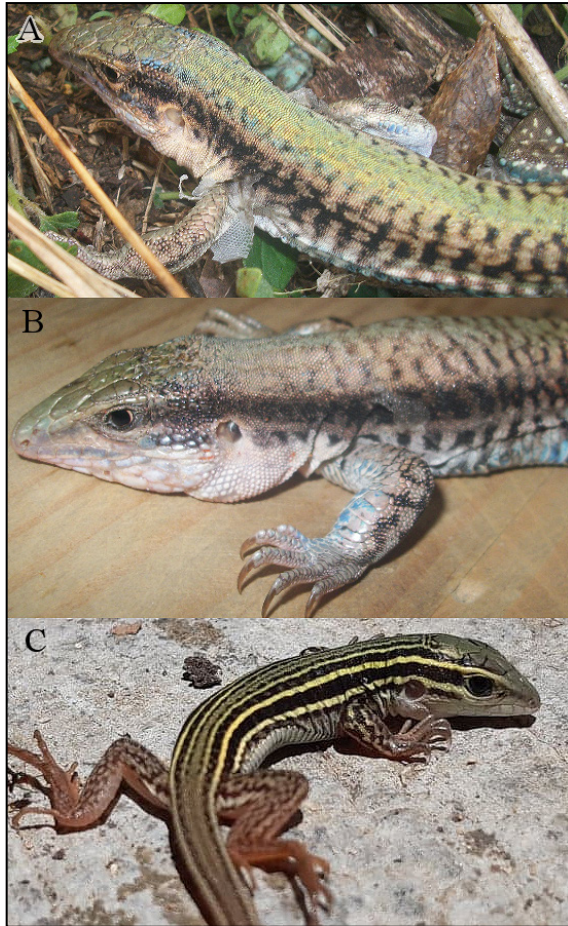


FIGURE 8. Two male Balsas Basin Whiptail (*Aspidoscelis c. costatus*) with complete ontogenetic development of dorsal patterns from the 2016 sample and a hatchling sighted in 2019 from the municipality and city of Ixtapan de la Sal, Estado de México, México. (A) PC V-4, 106 mm SVL. (B) PC V-4, 110 mm SVL. (C) PC I-1, 31 mm SVL. (Photographed by Aldo Gómez-Benitez).

deceased); Laurie J. Vitt (OMNH); Paul T. Maslin (UCM, deceased); James R. Dixon (TCWC, deceased); Robert C. Drewes (CAS); Christopher J. Raxworthy (AMNH); Greg Pauly (LACM), and Gerald G. Raun (TNHC). The Mexican government provided Scientific Collector Permit SEMANART FAUT-0186.

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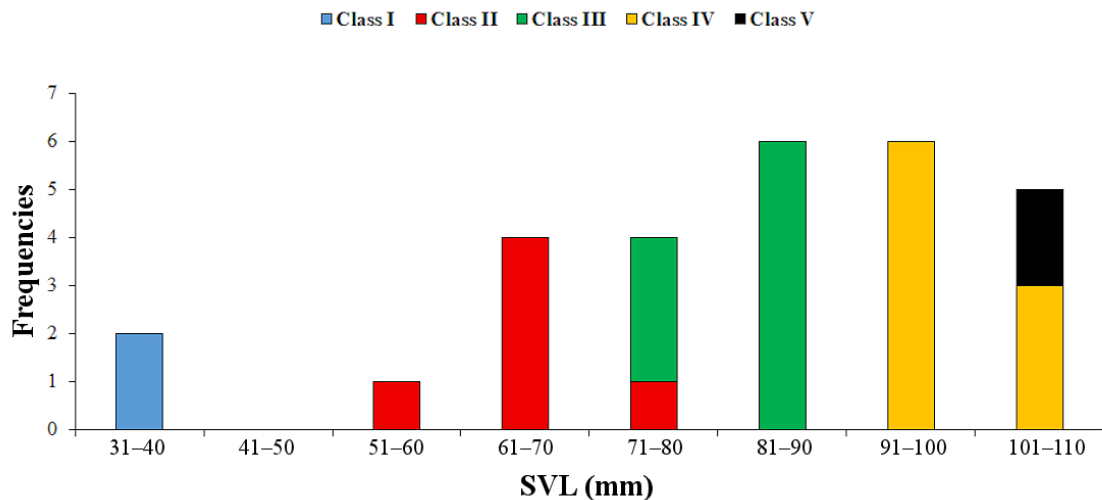
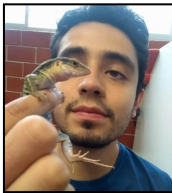


FIGURE 9. Frequencies of the dorsal color pattern class (*sensu* Zweifel 1959) of Balsas Basin Whiptail (*Aspidoscelis c. costatus*) individuals from Ixtapan de la Sal, Estado de México, México captured on June 2018 and two males from May 2016 and a hatchling from Estado de Morelos. Relative frequencies within the dorsal color pattern classes are: I (0.07), II (0.21), III (0.32), IV (0.32), and V (0.07).

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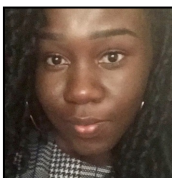
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## Herpetological Conservation and Biology

**APPENDIX 1.** Aspects of dorsal and ventral color pattern, size, and scutellation analyzed in specimens of gonochoristic Balsas Basin Whiptail (*Aspidoscelis c. costatus*) from the municipality and city of Ixtapan de la Sal, Estado de México, México.

Structure as Referenced	Description of Structure
Pale-Hued Paired Primary Laterals	Essentially straight stripe on each side dorsal to the lateral row of ventral scales
Pale-Hued Paired Primary Dorsolaterals	Essentially straight stripe on each side dorsal to the lateral stripe
Pale-Hued Paired Primary Paravertebrals	Essentially irregular stripe on each side dorsal to the dorsolateral stripe
Pale-Hued Vertebral Configuration	Single or double-lined configuration, band like or not, with lateral extensions
Dark-Hued Paired Lower Lateral Fields	Dusky black field on each side ventral to the lateral stripe
Dark-Hued Paired Upper Lateral Fields	Black field on each side dorsal to the lateral stripe
Dark-Hued Paired Dorsolateral Fields	Black field on each side dorsal to the dorsolateral stripe
Dark-Hued Single Vertebral Field	Black field between the paravertebral stripes from occiput to base of tail
Pale-Hued Spots	Rounded areas in either fields or encroaching onto stripes and on limbs
Pale-Hued Bars	Narrow elongate elongated rectangles in fields, in contact with stripes or not
Pale-hued irregular configurations	Endlessly variable areas surrounded by ground color
Suffusion of coloration	Stain-like shading of color overlying ground color
SPV = Scales Between Paravertebrals	Granular scales between paravertebral stripes at midbody
CVC = Contacts of Vertebral Configuration	Contacts of vertebral configuration extensions with paravertebral stripes
Throat = Gular Coloration	Subject to sexual dimorphism and ontogenetic variation
Chest = Thoracic Coloration	Subject to sexual dimorphism and ontogenetic variation
Abdominal = Belly Coloration	Subject to sexual dimorphism and ontogenetic variation
Tail = Ventral Caudal Coloration	Subject to sexual dimorphism and ontogenetic variation
SVL = Snout to Vent Length to mm	Snout to vent length to nearest mm from tip of snout to cloacal slit
Dorsal Pattern Class I modified; Zweifel (1959)	Lines (= stripes), dark fields, no spots
Dorsal Pattern Class II modified; Zweifel (1959)	Stripes, incipient spots (pale-hued areas) in upper lateral and dorsolateral fields
Dorsal Pattern Class III modified; Zweifel (1959)	Stripes, distinct pale-hued spots in upper lateral and dorsolateral fields
Dorsal Pattern Class IV modified; Zweifel (1959)	Stripes and pale-hued spots and bars equally obvious
Dorsal Pattern Class V modified; Zweifel (1959)	Stripes absent or only remnants present, replaced by a variety of configurations
Ventral Pattern Class 1 here proposed	Cream gular, thoracic, abdominal, and pelvic regions
Ventral Pattern Class 2 here proposed	As above except pink to red gular region which is also present in classes 3 and 4
Ventral Pattern Class 3 here proposed	Light to medium blue thoracic to abdominal regions; red and blue pelvic region
Ventral Pattern Class 4 here proposed	Increased intensity of coloration of gular, thoracic, abdominal, and pelvic regions

**APPENDIX 2.** Data for females and males of Balsas Basin Whiptail (*Aspidoscelis c. costatus*) captured 29 June 2018 from municipality and city of Ixtapan de la Sal, Estado de México, México. Abbreviations are S-CPC = sex-color pattern class; SVL = snout vent length to 1 mm; TL = tail length to 1 mm; BM = body mass to 0.5 g; SPV = count of scales between paravertebral stripes at midbody; CVC = count of contacts of vertebral configuration with paravertebral stripes; GSVC = general structure of vertebral configuration; TVC (single or double even partly) = type of vertebral configurations; coloration (C = cream, P = Pink, R = red, B = blue); TH = throat; CH = chest; AB = abdominal; VC = ventral caudal; PV = paravertebral stripes normal and relatively straight (N), stripes very irregular (I), or stripes fragmented (F); DC = either green (G) or brown coloration of pale-hued dorsal components subject to seasonal variation .

S-CPC	SVL	TL	WT	PVS	CVC	GSVC	TVC	TH	CH	AB	VC	PV	DC
1 F-II-1	59	135	7.0	14	44	Serrate	Double	C	C	C	C	N	G
2 F-II-1	65	139	8.0	15	35	Serrate	Double	CB	CB	C	P	N	G
3 F-II-1	67	141	10.5	13	33	Serrate	Double	C	CB	C	P	N	G
4 F-II-1	69	157	10.5	14	50	Band	Double	C	CB	CO	P	I	G
5 F-II-1	70	154	11.0	16	27	Serrate	Double	CP	CB	CO	P	N	G
6 F-III-3	80	185	19.0	16	50	Band	Single	R	B	B	CP	I	G
7 F-III-2	84	170	21.0	17	38	Band	Double	R	C	CB	P	I	G
8 F-III-3	85	163	22.5	14	46	Zigzag	Single	R	CB	CB	P	F	G
9 F-III-2	86	160	21.0	18	50	Band	Double	C	C	CO	O	F	G
10 F-IV-4	91	123R	25.0	16	50	Band	Double	R	RB	RB	B	F	G
11 F-IV-3	97	161	26.0	16	36	Serrate	Double	R	B	B	RB	F	G
12 F-IV-3	98	170	31.0	17	44	Serrate	Double	R	B	B	CB	F	G
1 M-II-2	72	151	12.0	13	44	Serrate	Double	R	CB	CO	C	F	G
2 M-II-2	80	198	19.5	15	45	Band	Double	CR	CB	CB	C	F	G
3 M-II-2	80	140R	18.0	15	16	Zigzag	Double	R	CB	CB	CP	I	G
4 M-II-2	81	152R	17.0	14	50	Zigzag	Double	R	CB	CB	CB	F	G
5 M-III-2	83	185	18.0	15	30	Zigzag	Double	R	CB	CB	CP	F	G
6 M-III-4	88	224	21.5	14	35	Zigzag	Double	R	RB	RB	RB	F	G
7 M-IV-4	95	197	33.5	14	44	Zigzag	Double	R	CB	CB	CB	F	G
8 M-IV-4	96	190	28.5	14	44	Zigzag	Double	R	RB	RB	RB	F	G
9 M-IV-4	99	178R	23.0	14	45	Serrate	Double	R	CB	CB	RB	F	G
10 M-IV-4	105	233RR	41.0	14	40	Serrate	Single	R	CP	RB	RB	F	G
11 M-IV-4	105	252	37.0	14	40	Serrate	Double	R	RB	B	RB	F	G
12 M-IV-4	106	231	39.5	13	40	Serrate	Single	R	CB	B	B	F	G

**APPENDIX 3.** Sources of variation contributing to the color pattern of Balsas Basin Whiptail (*Aspidoscelis c. costatus*) captured from municipality and city of Ixtapan de la Sal, Estado de México, Mexico (unless otherwise noted observations based entirely on this study). The abbreviation SVL = snout-vent length.

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1. Individual Variation in Juveniles of < 67 mm SVL in males and < 73 mm SVL in females
  2. Striping pattern on sides of head
  3. Secondary configuration in vertebral field between primary paravertebral stripes
  4. Individual Variation in Adults of > 67 mm SVL in males and > 73 mm SVL in females
    - 4.1. Distribution of spots and bars
  5. Configuration of pattern elements surrounded by black ground color
  6. Ontogenetic Variation
  7. Juveniles striped and entirely lack spots
  8. Young adults with patterns of stripes and incipient spots
    - 8.1. Mid-range adults have patterns of stripes and spots/bars of approximately equal intensity
    - 8.2. Large adults have patterns dominated by spots and other shaped dorsal configurations
  9. Seasonal Variation Primarily in Adults (Hernández-Gallegos and Domínguez-Vega 2012)
    - 9.1. Development of green-hued dorsal coloration corresponding with rainy season
    - 9.2. Development of brownish-hued coloration corresponding with dry season
  10. Sexual dimorphism
    - 10.1. Stripes completely replaced by spots and other configurations in large adult males
    - 10.2. Parts of stripes retained in large adult females
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**APPENDIX 4.** Studied samples of relevant taxa with complicated color schemes (in the indicated museum collections) to contextualize the uniqueness of color pattern variation in *Aspidoscelis c. costatus*.

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- Aspidoscelis alpinus* (University of Colorado Museum = UCM)
- A. burti* [*sensu* Walker and Cordes 2011 (UCM and University of Arkansas Department of Zoology = UADZ)]
- A. gularis* [including *A. scalaris* and *A. septemvittatus* (UCM, UADZ, and Texas Natural History Collection = TNHC; Texas Cooperative Wildlife Collection = TCWC)]
- A. costatus barrancarum* (Laboratorio de Ecología, Unidad de Biotecnología y Prototipos = LEUBIPRO; American Museum of Natural History = AMNH)
- A. costatus griseocephalus* (California Academy of Sciences = CAS; Los Angeles County Museum = LACM)
- A. costatus huico* (CAS)
- A. costatus nigrigularis* (CAS)
- A. costatus occidentalis* (CAS, UCM)
- A. stictogrammus* (*sensu* Burger 1950; UADZ, LEUBIPRO, University of Oklahoma Museum of Natural History = OMNH).
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