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Karyotypes of the North American Parthenogenetic Whiptail Lizard *Aspidoscelis velox*, and Return of *Aspidoscelis innotatus* to the Synonymy of *A. velox* (Reptilia: Squamata: Teiidae)

CHARLES J. COLE,[1] JAMES E. CORDES,[2] AND JAMES M. WALKER[3]

ABSTRACT

Aspidoscelis velox is a triploid parthenogenetic species with clonal inheritance. We studied karyotypes of population samples representing diverse localities from much of its range. All specimens were triploids, but six different karyotypes were found with small differences among them, apparently resulting from chromosomal mutations that occurred after the origin of the species. As in other parthenogens, karyotypes and allozymes reveal variant clones in *A. velox*, but we do not recommend naming any of these genetic lineages as separate species. Specimens from the vicinity of Kanab, Kane County, Utah, have been treated by other herpetologists as a separate but morphologically similar species, *Aspidoscelis innotatus*, based on the assumption that they represented a diploid species. That assumption, made without any genetic evidence of ploidy, was recently based on evidence of histoincompatibility among certain population samples, but that could have been caused by factors other than ploidy (e.g., mutations at histocompatibility loci). We have examined specimens from Kane County, Utah, and all individuals were triploids similar to other population samples of *A. velox* from Arizona and New Mexico.

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INTRODUCTION

Aspidoscelis velox (Springer, 1928), the plateau striped whiptail lizard, occurs in the southwestern United States, in northern Arizona, northern New Mexico, southwestern Colorado, and southern Utah (Duellman and Zweifel, 1962, fig. 10; Maslin and Secoy, 1986). This is a unisexual (all-female) parthenogenetic species that reproduces by cloning unfertilized eggs, and individuals previously karyotyped and/or for which ploidy was indicated by allozymes, were all triploids (Pennock, 1965; Neaves, 1969; Dessauer and Cole, 1989).

Aspidoscelis velox was originally described as *Cnemidophorus gularis velox* (Springer, 1928), based on three specimens from Oraibi, Navajo County, Arizona, and one from Pueblo Bonito, San Juan County, New Mexico. As discussed by Lowe (1955), the history of the name *C. velox* is complex, but involves Burger's (1950) assignment of specimens from the vicinity of Kanab, Kane County, Utah, to a new subspecies that he named *Cnemidophorus sackii innotatus*. Lowe (1955) also correctly recognized *Cnemidophorus velox* as a full species, and he considered *C. sackii innotatus* to be a synonym of *C. velox*.

The name *Cnemidophorus innotatus* was resurrected by Wright (1993), based on Orlando Cuellar's observations on skin grafts. Cuellar (1977) and Cuellar and Wright (1992) had demonstrated that individuals of *A. velox* from Utah were histoincompatible with certain individuals from Colorado and New Mexico. Citing Maslin's (1967) results showing that similar-looking diploid and triploid parthenogenetic species of *Aspidoscelis* were histoincompatible, Cuellar and Wright (1992) suggested that the histoincompatibility observed in *A. velox* resulted from different ploidy levels in the populations, which would indicate they represented different species. Consequently, Wright (1993) concluded that the specimens from Utah represented a diploid parthenogenetic species, for which he resurrected the name *Cnemidophorus innotatus*. This action was taken without data on the ploidy level of the specimens from Utah, even though histoincompatibility can occur among parthenogenetic individuals of the same ploidy (e.g., owing to postformational mutations at histocompatibility loci).

Following Reeder et al. (2002), we use the resurrected name *Aspidoscelis* for the genus of North American whiptail lizards that were previously referred to *Cnemidophorus*. We follow Tucker et al. (2016) in using masculine suffixes for specific epithets.

In this paper we present karyotype data and discuss the ploidy level of specimens of *Aspidoscelis velox* from Arizona, New Mexico, and Utah. Representatives of specimens examined in this study are shown in figure 1.

MATERIALS AND METHODS

We used previously published methods (with colchicine, hypotonic citrate, and flame drying) for preparing and studying standard, giemsa-stained chromosomes and for reference to chromosome morphology (Cole, 1979). We examined cells at mitotic metaphase from bone marrow of 40 lizards representing 16 population samples from three states (see appendix 1, Specimens Examined).

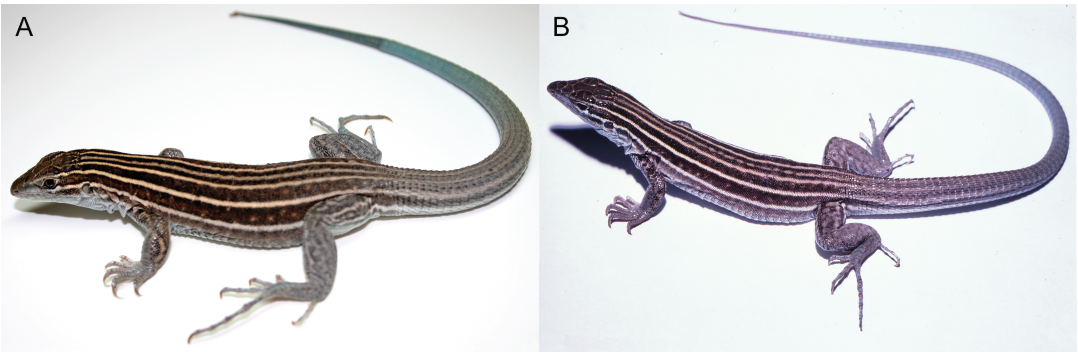

FIGURE 1. Representatives of two population samples of *Aspidoscelis velox*. **A.** Adult female from Kane County, Utah, AMNH R-178713, previously referred to *A. innotatus*; snout-vent length = 84 mm. This individual had karyotype K1. **B.** Adult female from Sandoval County, New Mexico, AMNH R-127247; snout-vent length = 78 mm. This individual had karyotype K4.

RESULTS

Six different karyotypes (K1–K6), all triploid or modified triploids, were observed among the 40 specimens of *A. velox* examined. The modified triploids all had the same basic chromosomal components as the original triploid condition, but apparently with postformational modifications (i.e., in generations following origin of the species) resulting from apparent nonlethal chromosome mutations as described below. Four of the karyotypic variants involved clearly resolved differences among the largest macrochromosomes, which are illustrated. Two variants involved small chromosomes, and we do not take the space here to illustrate additional whole karyotypes to make the minor point once again that such variants are commonly found in parthenogens (see Discussion).

K1 (fig. 2A): This is the original unmodified triploid karyotype, which resulted from the two basic hybridization events that produced *A. velox* (see Reeder et al., 2002). The diploid bisexual ancestors, a female *A. burti stictogrammus* (= *A. stictogrammus*) or *A. costatus barrancorum* (= *A. barrancarum*), and two males of *A. inornatus* (in two steps of hybridization from one generation to the next), are all members of the *sexlineatus* species group of *Aspidoscelis* (see Lowe et al., 1970a). Consequently, the unmodified triploid karyotype of *A. velox* consists of three haploid complements of chromosomes of the *sexlineatus* group (fig. 2A). Following the terminology of Lowe et al. (1970a, 1970b), the haploid state of the *sexlineatus* group consists of 23 chromosomes. There is 1 Set I (large biarmed) chromosome that is metacentric with a somewhat elongate subterminal secondary constriction on one arm (the nucleolar organizer region; Ward and Cole, 1986; Porter et al., in press). There are 12 Set II (smaller and basically uniarmed) chromosomes, of which the largest is clearly subtelocentric, the others telocentric or nearly so. There are 10 Set III (very small) microchromosomes, a few of which usually appear biarmed in the clearest cells. Consequently, the haploid karyotypic formula is referred to as $n = 23$, with 1 + 12 + 10 chromosomes, the diploid state is $2n = 46$, with 2 + 24 + 20, and the triploid state is $3n = 69$, with 3 + 36 + 30 (fig. 2A). This karyotype has the widest geographic distribution of all the karyotypes we found in *A. velox*. It was seen in 18 specimens from widespread localities, as follows: Apache County, Arizona; Gila County, Arizona; Mohave County, Arizona; two sites in Yavapai County, Arizona; and Kane County, Utah (see appendix 1, Specimens Examined).

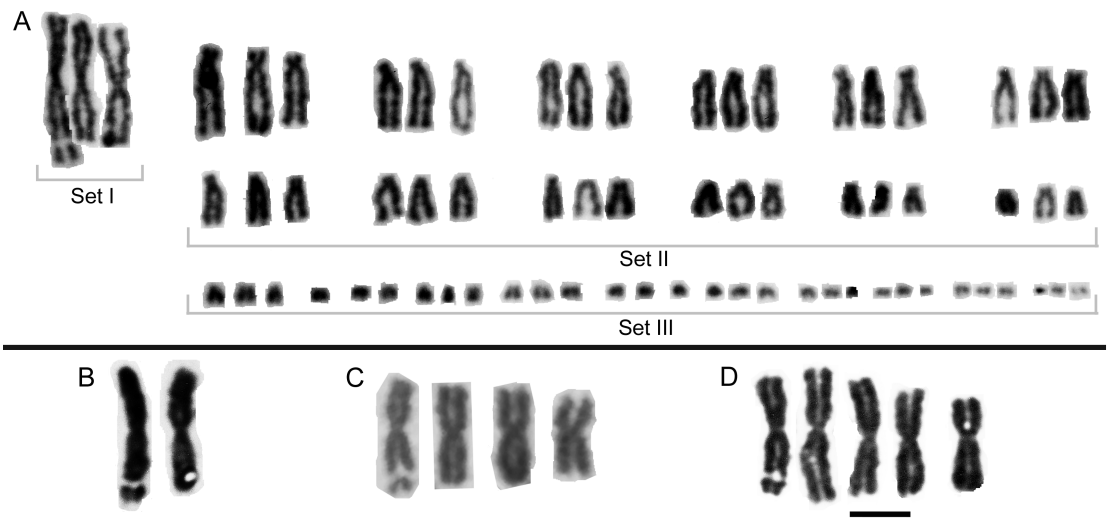

FIGURE 2. Chromosomes of four individuals of the triploid *Aspidoscelis velox*. **A.** The original unmodified karyotype (K1), with 3 + 36 + 30 = 69 chromosomes; from UAZ 18743. **B.** The Set I macrochromosomes of karyotype K2, in which one of the original Set I metacentrics apparently underwent centric fission, resulting in 2 + 38 + 30 = 70 chromosomes; from UAZ 21647. **C.** The Set I macrochromosomes of karyotype K3, in which two of the Set II chromosomes apparently had undergone centric fusion, resulting in 4 + 34 + 30 = 68 chromosomes; from AMNH R-128317. **D.** The Set I macrochromosomes of karyotypes K4–K6, in which another pair of Set II chromosomes apparently underwent centric fusion, resulting in 5 + 32 + 30 = 67 chromosomes in K4, followed by additional modifications in K5 and K6 (not illustrated; see text); from AMNH R-115954. Note that there is only one clear secondary constriction (NOR) in each, subterminal on one arm of a Set I metacentric chromosome. Scale bar represents 10 microns.

K2 (fig. 2B): This karyotype is identical to K1 except that one of the Set I metacentric macrochromosomes appears to be missing, apparently having undergone centric fission. Consequently, there are only two Set I chromosomes and what was the third apparently is represented by the additional two Set II chromosomes (so it was not actually missing, but reconfigured). The karyotypic formula is $3n = 70$, with 2 + 38 + 30. We found this karyotype in five specimens from Coconino County, Arizona, and Gila County, Arizona (see Specimens Examined).

K3 (fig. 2C): This karyotype is identical to K1 except that two of the Set II subtelocentric or telocentric chromosomes have apparently undergone centric fusion. Consequently, there are four large Set I chromosomes (instead of three) and the extra one represents the two fewer Set II chromosomes that were apparently involved in the fusion. The karyotypic formula is $3n = 68$, with 4 + 34 + 30. We found this karyotype in three specimens from Lyman Lake State Park, Apache County, Arizona (see Specimens Examined), where this modified karyotype and the original unmodified one (K1) occur in syntopy.

K4 (fig. 2D): This karyotype is identical to K3 except that two more of the Set II subtelocentric or telocentric chromosomes have apparently undergone centric fusion. Consequently, there are five large Set I chromosomes and two more fewer Set II chromosomes, apparently those represented in the fusion. The karyotypic formula is $3n = 67$, with 5 + 32 + 30. The fifth

largest Set I chromosome is a little smaller than the others of Set I, and appears somewhat submetacentric in most cells. We found this karyotype in five specimens from Cibola County, New Mexico and Sandoval County, New Mexico (see Specimens Examined).

K5: This karyotype is identical to K4 except that there is one extra Set III microchromosome of unknown origin (duplication?), or $3n = 68$, with 5 + 32 + 31. We found this karyotype in five specimens from McKinley County, New Mexico and Sandoval County, New Mexico (see Specimens Examined). In addition, for one specimen from the vicinity of Meteor Crater, Coconino County, Arizona (AMNH R-136826) and one from Moenkopi Wash, Navajo County, Arizona (AMNH R-136820), the same five Set I chromosomes were observed but the details of their Set II and Set III chromosomes could not be resolved.

K6: This karyotype is identical to K5 except that there is one fewer Set II subtelocentric or telocentric chromosome of unknown cause, or $3n = 67$, with 5 + 31 + 31. We found this karyotype in two specimens from Navajo County, Arizona; one was collected in the field, the other was a laboratory offspring from a different female (see Specimens Examined).

DISCUSSION

The present study shows that samples of *A. velox*-like lizards from the vicinity of Kanab, Kane County, Utah, are not diploids, as they were assumed to be by Wright (1993). They are triploids and possess the same karyotype (K1) that was most commonly observed in specimens of *A. velox* from Arizona. These results are consistent with measurements of nuclei of erythrocytes of *velox*-like lizards from Arizona, New Mexico, and Utah, including individuals from near Kanab, Kane County, Utah, suggesting that all individuals were triploid (unpublished data, Trevor B. Persons, personal commun.). Consequently, we now relegate the name *Aspidoscelis innotatus* back into the synonymy of *A. velox*.

The variation in karyotypes of *A. velox* is not surprising, as analysis of genetic characters (e.g., karyotypes and allozymes) in diverse populations of unisexual whiptails often reveals considerable clonal variation (e.g., Lowe, et al., 1970b; Cole, 1979; Dessauer and Cole, 1989; Taylor et al., 2001; Cole et al., 2007; Taylor et al., 2018, 2019). This is no surprise, as the genes and chromosomes of unisexual species should be prone to the same kind of mutations that occur in bisexual species. However, in unisexual species, individuals with such mutations can be the founders of new clones, if the mutations are not lethal. What is interesting in this respect, however, especially for karyotypes, is that such variation is rarely or never observed in samples of bisexual species (C.J.C., personal obs.), probably because sublethal mutations are eliminated by sexual reproduction. In unisexual species, if such mutations are not lethal, they may survive, accumulate, and diversify further, through many generations of clonal reproduction.

It is possible that all the variant karyotypes observed in *A. velox* resulted from postformational chromosome mutations (i.e., which occurred after the origin of the species). Although each of the variants may have originated in a single historical genetic event, thus constituting separate lineages, we do not consider these lineages to be separate species. In our view, none of the variants we have observed warrant being named as anything other than *A. velox*.

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REFERENCES

Burger, W.L. 1950. New, revived, and reallocated names for North American whiptailed lizards, genus *Cnemidophorus*. Chicago Academy of Sciences, Natural History Miscellanea 65: 1–9.

Cole, C.J. 1979. Chromosome inheritance in parthenogenetic lizards and evolution of allopolyploidy in reptiles. Journal of Heredity 70: 95–102.

Cole, C.J., C.W. Painter, H.C. Dessauer, and H.L. Taylor. 2007. Hybridization between the endangered unisexual gray-checkered whiptail lizard (*Aspidoscelis dixoni*) and the bisexual western whiptail lizard (*Aspidoscelis tigris*) in southwestern New Mexico. American Museum Novitates 3555: 1–31.

Cuellar, O. 1977. Genetic homogeneity and speciation in the parthenogenetic lizards *Cnemidophorus velox* and *C. neomexicanus*: evidence from intraspecific histocompatibility. Evolution 31: 24–31.

Cuellar, O., and J.W. Wright. 1992. Isogenicity in the unisexual lizard *Cnemidophorus velox*. Comptesé Rendus des Séances de la Société de Biogéographie 68: 157–160.

Dessauer, H.C., and C.J. Cole. 1989. Diversity between and within nominal forms of unisexual teiid lizards. *In* R.M. Dawley and J.P. Bogart (editors), Evolution and ecology of unisexual vertebrates. New York State Museum Bulletin 466: 49–71.

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

Lowe, C.H., Jr. 1955. A new species of whiptailed lizard (genus *Cnemidophorus*) from the Colorado Plateau of Arizona, New Mexico, Colorado, and Utah. Breviora 47: 1–9.

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

Lowe, C.H., J.W. Wright, C.J. Cole, and R.L. Bezy. 1970b. Natural hybridization between the teiid lizards *Cnemidophorus sonorae* (parthenogenetic) and *Cnemidophorus tigris* (bisexual). Systematic Zoology 19: 114–127.

Maslin, T.P. 1967. Skin grafting in the bisexual teiid lizard *Cnemidophorus sexlineatus* and in the unisexual *C. tesselatus*. Journal of Experimental Zoology 166: 137–149.

Maslin, T.P., and D.M. Secoy. 1986. A checklist of the lizard genus *Cnemidophorus* (Teiidae). University of Colorado Museum, Contributions in Zoology 1: 1–60.

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

Pennock, L.A. 1965. Triploidy in parthenogenetic species of the teiid lizard, genus *Cnemidophorus*. Science 149: 539–540.

Porter, C.A., O.G. Ward, C.J. Cole, and R.J. Baker. In press. Distribution and expression of ribosomal DNA in the composite genomes of unisexual lizards of hybrid origin (genus *Aspidoscelis*). *In* R.D. Bradley, H.H. Genoways, D.J. Schmidly, and L.C. Bradley (editors), From field to laboratory: a memorial volume in honor of Robert J. Baker. Museum of Texas Tech University, Lubbock, Special Publications 71: xi + 1–911.

Reeder, T.W., C.J. Cole, and H.C. Dessauer. 2002. Phylogenetic relationships of whiptail lizards of the genus *Cnemidophorus* (Squamata: Teiidae): a test of monophyly, reevaluation of karyotypic evolution, and review of hybrid origins. American Museum Novitates 3365: 1–61.

Springer, S. 1928. An annotated list of the lizards of Lee's Ferry, Arizona. Copeia 169: 100–104.

Taylor, H.L., et al. 2001. Natural hybridization between the teiid lizards *Cnemidophorus tesselatus* (parthenogenetic) and *C. tigris marmoratus* (bisexual): assessment of evolutionary alternatives. American Museum Novitates 3345: 1–64.

Taylor, H.L., C.J. Cole, and C.R. Townsend. 2018. Relegation of *Aspidoscelis flagellicaudus* to the synonymy of the parthenogenetic teiid lizard *A. sonorae* based on morphological evidence and a review of relevant genetic data. Herpetological Review 49: 636–653.

Taylor, H.L., C.J. Cole, and C.R. Townsend. 2019. Patterns of multivariate meristic variation, color-pattern variation, and a review of genetic variation in the North American parthenogenetic teiid lizard *Aspidoscelis exsanguis*. Herpetological Review 50: 263–271.

Tucker, D.B., et al. 2016. Methodological congruence in phylogenomic analyses with morphological support for teiid lizards (Sauria: Teiidae). Molecular Phylogenetics and Evolution 103: 75–84.

Ward, O.G., and C.J. Cole. 1986. Nucleolar dominance in diploid and triploid parthenogenetic lizards of hybrid origin. Cytogenetics and Cell Genetics 42: 177–182.

Wright, J.W. 1993. Evolution of the lizards of the genus *Cnemidophorus*. *In* J.W. Wright and L.J. Vitt (editors), Biology of whiptail lizards (genus *Cnemidophorus*). Norman, OK: Oklahoma Museum of Natural History.

APPENDIX 1

Specimens Examined

The 40 specimens are individually cataloged in the herpetological collections of the American Museum of Natural History (AMNH) or the University of Arizona Museum of Natural History (UAZ). They are listed below sequenced according to the karyotype (K1–K6) that they possessed.

K1 Specimens. *Arizona*: Apache County; Lyman Lake State Park, 17.3 mi (by US Hwy 180) N Springerville, 6100 ft. elev. (AMNH R-128319). *Arizona*: Gila County; vicinity of Rose Creek

Campground, Sierra Ancha Mountains, 41.5 mi (by US Hwy 60, AZ Hwy 88, and AZ Hwy 288) NNW Globe, 5450 ft. elev. (AMNH R-128308–128310 and 128312–128313). *Arizona*: Mohave County; Cottonwood Mountains, 0.9 mi (by Willows Ranch Rd) NE Hwy I-40 ca. 37 mi by I-40 E Kingman, 4850 ft. elev. (AMNH R-127241). *Arizona*: Yavapai County; 24.5 mi (by Williamson Valley Rd) NNW Prescott, then 6.7 mi W (by rd to Camp Wood), 4850 ft. elev. (AMNH R-128322–128323). *Arizona*: Yavapai County; 5.6 mi by rd S Simmons, Williamson Valley, 4650 ft. elev. (UAZ 18729 and 18743). *Utah*: Kane County; Coral Pink Sands State Park (AMNH R-178707–178713).

K2 Specimens. *Arizona*: Coconino County; Grasshopper Point Recreation Site, 2 mi (by US Hwy 89A) N Sedona, 4900 ft. elev. (AMNH R-127236). *Arizona*: Gila County; Pinal Mountains, old CCC camp, 5 mi (linear) SSW Globe, 4700 ft. elev. (AMNH R-127229). *Arizona*: Gila County; Pinal Mountains, Russell Gulch, jct Madera and Signal Peaks Rds, 5800 ft. elev. (UAZ 21647, 21716, and 21721).

K3 Specimens. *Arizona*: Apache County; Lyman Lake State Park, 17.3 mi. (by US Hwy 180) N Springerville, 6100 ft. elev. (AMNH R-128315–128317).

K4 Specimens. *New Mexico*: Cibola County; Sandoval Canyon, ca 1.5 mi W Cañoncito (AMNH R-136839–136840). *New Mexico*: Sandoval County; along the Rio Grande, 1.1 mi (by rd) NE San Felipe Pueblo, 5300 ft. elev. (AMNH R-127247–127249).

K5 Specimens. *Arizona*: Coconino County; 4 mi N Meteor Crater (AMNH R-136826). *Arizona*: Navajo County; Moenkopi Wash, Indian Hwy 41 (=4), 12.0 mi SE jct with US Hwy 160 (SE Black Mesa; AMNH R-136820). *New Mexico*: McKinley County; 19.5 mi (by US Hwy 666) N Gallup (AMNH R-136853 and 136855). *New Mexico*: Sandoval County; Rio Grande crossing and Cochiti Dam, 3.3 mi (by NM Hwy 22) N Peña Blanca (AMNH R-114252 and 114254–114255).

K6 Specimens. *Arizona*: Navajo County; 7.8 mi N Snowflake (by dirt rd to Woodruff along Silver Creek), 5500 ft. elev. (AMNH R-109407). Also, an offspring of AMNH R-115952, a female from *Arizona*: Navajo County; 7.9 mi. N Snowflake (by dirt rd to Woodruff along Silver Creek), then 0.4 mi W, 5500 ft. elev. (AMNH R-115954).

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