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Hybridization between Whiptail Lizards in Texas: *Aspidoscelis laredoensis* and *A. gularis*, with Notes on Reproduction of a Hybrid

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ABSTRACT

Karyotypes and allozyme data for 32 genetic loci overwhelmingly support the conclusion that *Aspidoscelis laredoensis* is a diploid all-female species that had a hybrid origin between *A. gularis* x *A. sexlineatus*. Comparisons of allozymes in individuals representing three mother-to-daughter generations raised in the laboratory suggest that they reproduce by parthenogenetic cloning. In addition to two previously described morphotypes (pattern classes A and B) that occur in southern Texas, we report the existence of three all-female clonal lineages based on allozymes. Individuals of at least one of these lineages occasionally hybridize in nature with males of *A. gularis*, producing viable and healthy triploid offspring that can grow to adulthood, one of which herself produced an offspring in the laboratory and could have represented a new, clonal triploid species. The possibility exists that cloned offspring of triploid hybrids are present in South Texas and/or northern Mexico, awaiting discovery. These would represent a new species that would appear to be very similar to *A. laredoensis*.

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INTRODUCTION

Aspidoscelis laredoensis, the Laredo striped whiptail lizard, is a unisexual (all-female) species that occurs mostly along or in the vicinity of the Rio Grande in southern Texas and adjacent northern Mexico (McKinney et al., 1973; Walker, 1987; Walker et al., 1989a, 1989b, 2001, 2016). As in other unisexual species of whiptail lizards, this one had a hybrid origin. In the case of *A. laredoensis*, the bisexual *Aspidoscelis gularis* and *Aspidoscelis sexlineatus* were the progenitors (McKinney et al., 1973; Bickham et al., 1976; Dessauer and Cole, 1989), and for specimens examined to date, the female progenitor was a representative of *A. gularis* (Wright et al., 1983). Two morphological pattern classes, A and B, of *A. laredoensis* are known, differing most conspicuously in color pattern, some mean scale counts, and histocompatibilty (Walker, 1987; Abuhteba et al., 2001).

Preliminary observations suggest that occasionally some *A. laredoensis* undergo backcross hybridization with *A. gularis*, which can result in triploid hybrid offspring, although genetic data on the hybrids are somewhat limited (Walker et al., 1989a, 1989b, 1991). For the present paper, we have compared higher-resolution karyotypes and the first large allozyme dataset of representative triploid hybrids and their parental ancestors, and we address the following questions: (1) do the newly developed genetic data confirm the reported hybrid origin of *A. laredoensis*; (2) does *A. laredoensis* reproduce by parthenogenetic cloning; (3) are there more than two forms or clones of *A. laredoensis*; (4) does *A. laredoensis* occasionally backcross with *A. gularis* producing triploid hybrids; and (5) is there potential for the triploids to clone themselves and establish a new triploid parthenogenetic species?

We follow Reeder et al. (2002) in using 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.

MATERIALS AND METHODS

Specimens

Samples of relevant lizards were collected at various localities in their respective geographic ranges (see appendix, Specimens Examined), as follows: *A. laredoensis* pattern class A from nature, *N* = 24; laboratory-cloned *A. laredoensis* pattern class A, *N* = 14; *A. laredoensis* pattern class B, *N* = 3; natural hybrids of *A. laredoensis* A x *A. gularis*, *N* = 4; laboratory offspring from a triploid natural hybrid, *N* = 1; *A. gularis*, *N* = 11; and *A. sexlineatus*, *N* = 18.

Laboratory Maintenance of Lizards

Individuals were maintained in a laboratory colony at the American Museum of Natural History (AMNH) by our usual methods (Cole and Townsend, 1977; Townsend, 1979; Townsend and Cole, 1985). Note, however, that we did experience some problems in raising captive whiptail lizards (Porter et al., 1994).

Karyotypes

We used our standard methods (Cole, 1979) for preparing giemsa-stained chromosomes of whiptail lizards and describing karyotypes (sodium citrate cell suspension, methanol and glacial acetic acid fixation, flame-drying on slides). A total of 138 cells at mitotic metaphase were examined from the following lizards: *A. laredoensis* pattern class A ($N = 20$ cells, including cells from two F_1 laboratory offspring); natural hybrids of *A. laredoensis* × *A. gularis* ($N = 16$ cells); *A. gularis* ($N = 37$ cells); and *A. sexlineatus* ($N = 65$ cells). Specimens examined are listed in the appendix.

Allozymes

We analyzed allozymes of 32 gene loci, based on phenotypes of tissue protein activities on starch gels following electrophoresis (following Harris and Hopkinson, 1976; Murphy et al., 1996; and Dessauer et al., 2000, specifically for whiptail lizards). The following 52 lizards were examined: *A. laredoensis* pattern class A ($N = 38$ specimens, including 13 specimens of F_1 and F_2 generation offspring cloned in the laboratory); *A. laredoensis* pattern class B ($N = 3$ specimens); natural hybrids of *A. laredoensis* pattern class A × *A. gularis* ($N = 4$ specimens); laboratory offspring of a natural hybrid of *A. laredoensis* pattern class A × *A. gularis* ($N = 1$ specimen); *A. gularis* ($N = 3$ specimens in addition to the one studied by Dessauer and Cole, 1989); and *A. sexlineatus* ($N = 3$ specimens in addition to the one studied by Dessauer and Cole, 1989). Specimens examined are listed in the appendix.

RESULTS AND DISCUSSION

Color Patterns of the Lizards

Aspidoscelis laredoensis pattern class A (fig. 1) is distinguished (according to McKinney et al., 1973: 362), by having a

> single, narrow, cream or white-colored vertebral stripe and distinct paravertebral, dorsolateral, and lateral stripes with a dark green or greenish-brown background color between the stripes. Small faded or indistinct spots are usually found between the lateral and dorsolateral stripes on the posterior one-third to one-half of the body. Similar spots are also occasionally found posteriorly between the paravertebral and dorsolateral stripes. The dorsal surface of the hind legs has a semireticulated pattern of cream-colored irregular lines. The entire venter is immaculate white (but females larger than 78 mm snout-vent length often have a suffusion of blue on the sides of the belly and throat (Paulissen, 2000). The tail is greenish-brown on top and the dorsolateral stripes extend out about one-third the length of the tail. The ventral surface of the tail is light tan.

Aspidoscelis laredoensis pattern class B is distinguished most easily from A in having two irregular and thinly divided light vertebral stripes instead of one sharply defined one (Walker, 1987).

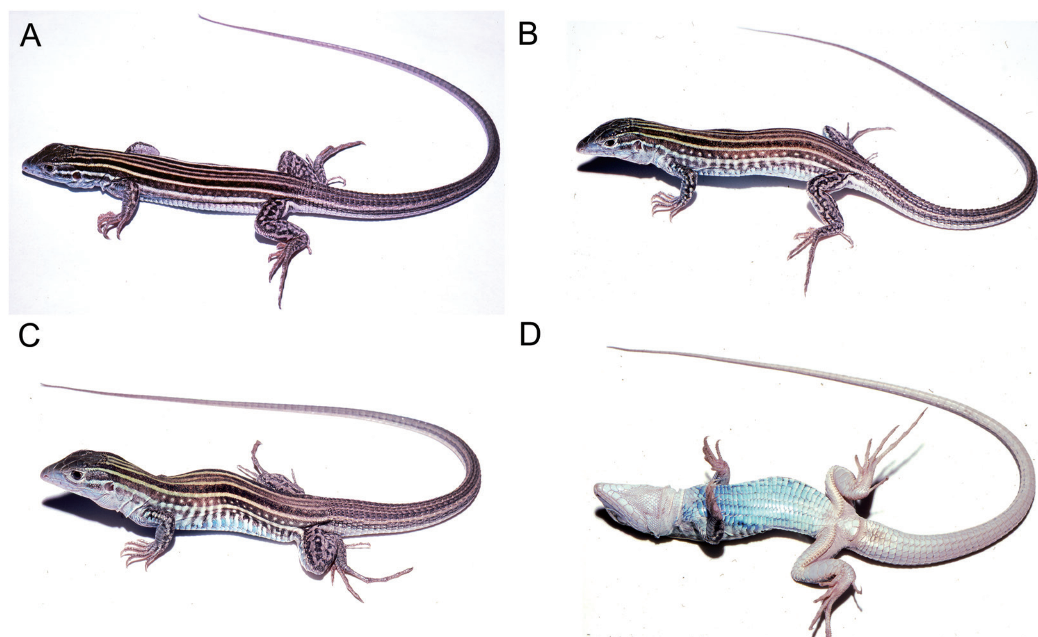

FIGURE 1. Representatives of the diploid parthenogenetic *Aspidoscelis laredoensis* pattern class A and natural triploid hybrids between *A. laredoensis* pattern class A × *A. gularis*. **A.** *A. laredoensis*, female, AMNH R-126892; snout-vent length (SVL), 72 mm. **B.** Hybrid female, AMNH R-148419; SVL, 82 mm. **C, D.** Hybrid male, AMNH R-148416; SVL, 76 mm.

Natural hybrids between *A. laredoensis* pattern class A × *A. gularis* (fig. 1) were reported to be very similar to *A. laredoensis* pattern class A, but with more distinct spots in the upper lateral dark fields, a less distinct vertebral stripe, a pinkish-red throat (as in *A. gularis*) and a faint iridescent pinkish tinge under the tail (which is intermediate to the parents), as well as some other subtle coloration differences (Walker et al., 1989b). The differences are subtle enough to the untrained eye that the best way to identify a hybrid is when it happens to be a male that looks like the all-female *A. laredoensis* pattern class A. In the present study, we have confirmed with genetic data that lizards identified in the field as probable hybrids actually were hybrids. Yet the general similarity of female hybrids to *A. laredoensis* suggests that female hybrids may be more easily overlooked in nature than male hybrids, and clones of these females may also be somewhat easily overlooked, especially by untrained eyes.

Less frequently encountered natural hybrids between *A. laredoensis* pattern class B × *A. gularis* were also reported to be most similar to the maternal rather than paternal parent (Walker et al., 1991), but we did not do any genetic analyses on such specimens for this report.

Karyotypes

Karyotype of *Aspidoscelis laredoensis*: As this species resulted from hybridization between two diploid bisexual species, *A. gularis* and *A. sexlineatus*, it has a haploid genome from each parental species (Bickham et al., 1976). Consequently, it is a diploid species that

has two very similar haploid sets of chromosomes that represent those of the *sexlineatus* group of species (Lowe et al., 1970a). Following the chromosome terminology of Lowe et al. (1970a, 1970b) and Cole (1979), the haploid karyotype consists of 23 chromosomes as follows. There is 1 Set I biarmed chromosome (large, essentially metacentric, with a subterminal secondary constriction on one arm, which is the nucleolar-organizing region; Ward and Cole, 1986; Porter et al., 2019) + 12 Set II chromosomes (smaller, with most being uniarmed or nearly so), the largest of which is clearly subtelocentric + 10 Set III (very small) microchromosomes, of which a few appear to be biarmed in the clearest cells. *Aspidoscelis sexlineatus* differs from the other species in this species group in that the fourth largest pair of Set II consists of clearly biarmed subtelocentric chromosomes, and *A. laredoensis* has one of these chromosomes in this position (fig. 2), as expected. A comparison of the karyotypes of *A. gularis, A. sexlineatus,* and *A. laredoensis* was illustrated well by Bickham et al. (1976). However, they stated that the tenth largest pair of Set II chromosomes in *A. sexlineatus* is also clearly subtelocentric, although C.J.C. suggests that the centromere position on that pair appears to vary from cell to cell to the extent that it is not so distinctive among the other Set II chromosomes.

Karyotype of *A. laredoensis* x *A. gularis* Hybrids: Chromosomes of hybrids between *A. laredoensis* × *A. gularis* were reported by Walker et al. (1989b, 1991), but morphology of the chromosomes lacked clarity and the chromosome counts varied from 65 to 71 among the cells examined. Nevertheless, the number of chromosomes approximated $3n = 69$, which would be expected if an ovum of *A. laredoensis* were to be fertilized by a spermatozoon of *A. gularis*. For the present study, living lizards suspected to be natural hybrids were sent to the AMNH for karyotype work, and they proved to be such hybrids, with $3n = 69$ chromosomes (fig. 2). The presence of only one of the fourth largest Set II chromosomes being subtelocentric is consistent with the one in *A. sexlineatus* and *A. laredoensis*, and its absence in the third genome of the hybrid is consistent with fertilization having been by a male of *A. gularis*.

Allozymes of the Species and Hybrids from Nature

Allozymes of 15 gene loci were reported by McKinney et al. (1973) for *A. laredoensis* pattern class A. Although only four loci expressed heterozygosity in *A. laredoensis*, the alleles that they reported were consistent with one haploid set of genes from *A. gularis* and one from *A. sexlineatus*, and this was consistent with the other 11 loci having one and the same allele shared in the homozygous state in all the species studied. Here we add to the previously published data (McKinney et al., 1973; Dessauer and Cole, 1989) and report on allozymes representing 32 gene loci for *A. laredoensis* pattern class A (= LARA), *A. laredoensis* pattern class B (LARB), *A. gularis* (GUL), *A. sexlineatus* (SEX), LARA × GUL triploid hybrids (L × G), and one offspring produced in the laboratory (L × G2) by one of these hybrids. For the 32 loci studied, 14 were especially informative because they exhibited variation in comparisons of the taxa, hybrids, and other individuals compared, while 18 loci had one and the same allele present in the homozygous state in all specimens examined (table 1).

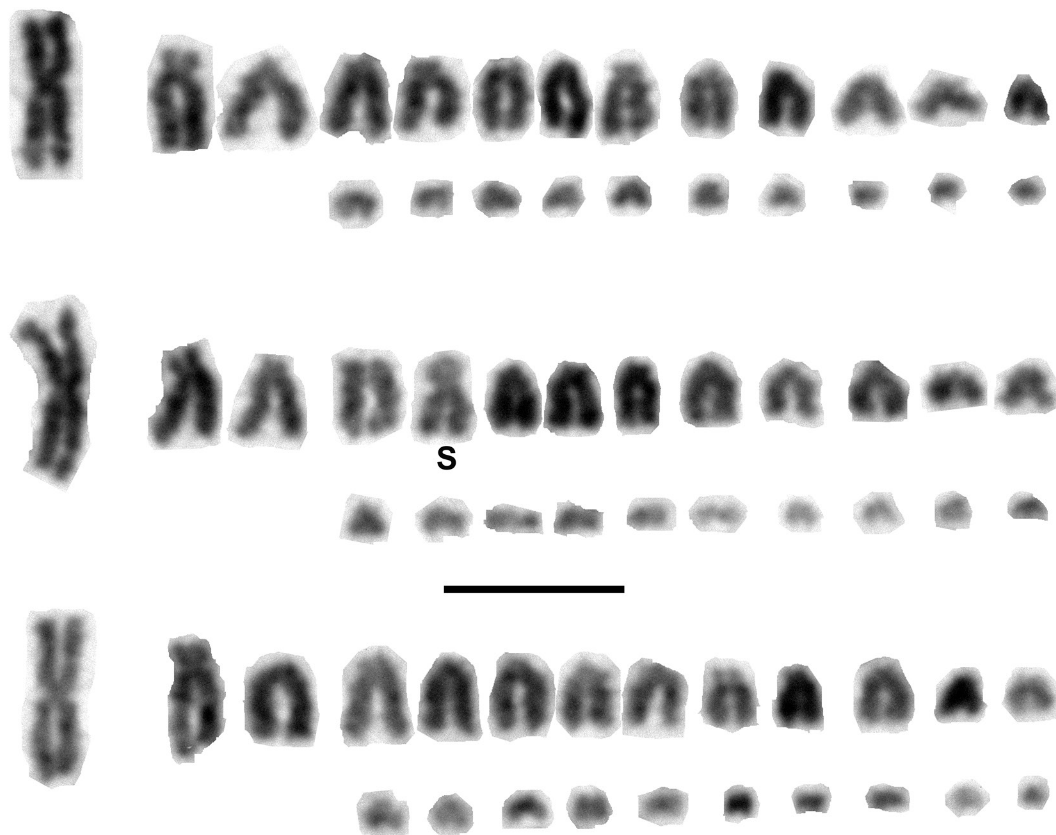

FIGURE 2. Karyotype of a triploid hybrid between *Aspidoscelis laredoensis* pattern class A × *A. gularis* (AMNH R-148416), with the chromosomes arranged in six rows representing the haploid complements in its genealogy. **Upper two rows.** Haploid set of chromosomes as found in *A. gularis*. **Middle two rows.** Haploid set of chromosomes as found in *A. sexlineatus* (S indicates the medium-sized submetacentric to subtelocentric chromosome that characterizes this species). The total of the upper and middle two rows represent the diploid karyotype of the parthenogenetic *A. laredoensis*. **Lower two rows.** The second haploid set of chromosomes as found in *A. gularis*, received in the recent hybridization event. Scale bar = 10 microns.

Allozymes of *A. laredoensis* Pattern Class A (LARA): For 36 of 38 specimens examined, including 13 F_1 and F_2 offspring produced in the laboratory colony, all alleles present were identical at all 32 loci (table 1), including 12 loci that had alleles fixed in the heterozygous state. This is consistent with the conclusion that LARA reproduces by parthenogenetic cloning. In addition, for all loci, the alleles present in LARA were consistent with its genome consisting of one haploid set of genes inherited from *A. gularis* (GUL) and one set inherited from *A. sexlineatus* (SEX). It is particularly pertinent that for five loci where *A. gularis* and *A. sexlineatus* were found to consistently have different alleles from each other (sMDHP, sSOD, PEPA, PEPB, and PGM2), one allele from GUL and one from SEX was present in *A. laredoensis*. This is consistent with the conclusion that LARA had a hybrid origin that involved *A. gularis* × *A. sexlineatus*. Finally, the two specimens of LARA (LARA2) that differed from the other LARA

TABLE 1. Genotypes[a] at 32 gene loci[b] in samples of *Aspidoscelis*.[c] Variant alleles (differing from those in LARA) are in bold.

Locus	LARA	LARA2	LARB	L × G	L × G2	GUL	SEX
Oxidoreductases							
ADH	BB	BB	BB	BBB	–	B/A	B/A
IDDH	AA	AA	AA	–	–	AA	B/A
sMDH	AB	AB	AB	ABB	ABB	B/A	AA
sMDHP	AB	AB	AB	ABB	–	BB	AA
sIDH	AB	AB	AB	ABB	–	B/A	AA
sSOD	BC	BC	BC	–	–	BB	CC
Hydrolases							
ESTD	BC	B**B**	BC	BBC	BBC	BB	A/C/B
PEPA	AC	AC	AC	ACC	ACC	B/C	AA
PEPB	BC	BC	B**D**	BBC	BBC	BB	C/D
PEPD	AC	AC	**B**C	ABC	–	C/B/A	D/C/B
Lyase							
sACOH	AB	AB	AB	AAB	–	B/A	B/C/D/A
Isomerases							
PGM2	AB	AB	AB	ABB	–	BB	AA
PGM3	BC	BC	BC	BBC	–	B/C	C/B/D
Blood protein							
TF	BC	BC	–	BBC	BBC	BB	C/A/B/D

[a] Alleles are designated in alphabetical order according to decreasing anodal migration of their allozymes. Locus abbreviations and methods follow Harris and Hopkinson (1976), Murphy et al. (1996), and Dessauer et al. (2000). For multilocus systems, loci are numbered in order of decreasing anodal migration of their isozymes; s, cytosolic enzyme; m, mitochondrial enzyme. Where two or more alleles are shown for GUL or SEX (e.g., B/A), alleles are listed from the most frequently to the least frequently observed. If no A-allele is shown for a locus (e.g., sSOD), it was observed in other lizards of species not included in this study.

[b] Abbreviations for loci: ADH, alcohol dehydrogenase; IDDH, L-iditol dehydrogenase; MDH, malate dehydrogenase; MDHP, malate enzyme; IDH, isocitrate dehydrogenase; SOD, superoxide dismutase; EST, esterase; PEP, peptidase; ACOH, aconitase hydratase; PGM, phosphoglucomutase; and TF, transferrin. The following 18 loci were also tested but not listed in the body of the table because all individuals shared the same allele in the homozygous state: G3PDH, glycerol-3-phosphate dehydrogenase; LDH1 and LDH2, L-lactate dehydrogenase; mMDH; PGDH, phosphogluconate dehydrogenase; G6PDH, glucose-6-phosphate dehydrogenase; mIDH; mSOD; s and mAAT, aspartate aminotransferase; CK1 and 2, creatine kinase; AK, adenylate kinase; ADA, adenosine deaminase; MPI, mannose-6-phosphate isomerase; GPI, glucose-6-phosphate isomerase; PGM1; and HB, hemoglobin.

[c] Abbreviations for species and individuals (column headers): LARA, *A. laredoensis* pattern class A (the second column for LARA, LARA2, is for two specimens that differed from the others at ESTD (AMNH R-147484 and 147485); LARB, *A. laredoensis* pattern class B; L × G, natural hybrids between *A. laredoensis* pattern class A × *A. gularis*; L x G2, a single laboratory offspring (AMNH R-148422) of one of the hybrids (AMNH R-148415); GUL, *A. gularis*; and SEX, *A. sexlineatus*. See appendix for details on the specimens examined.

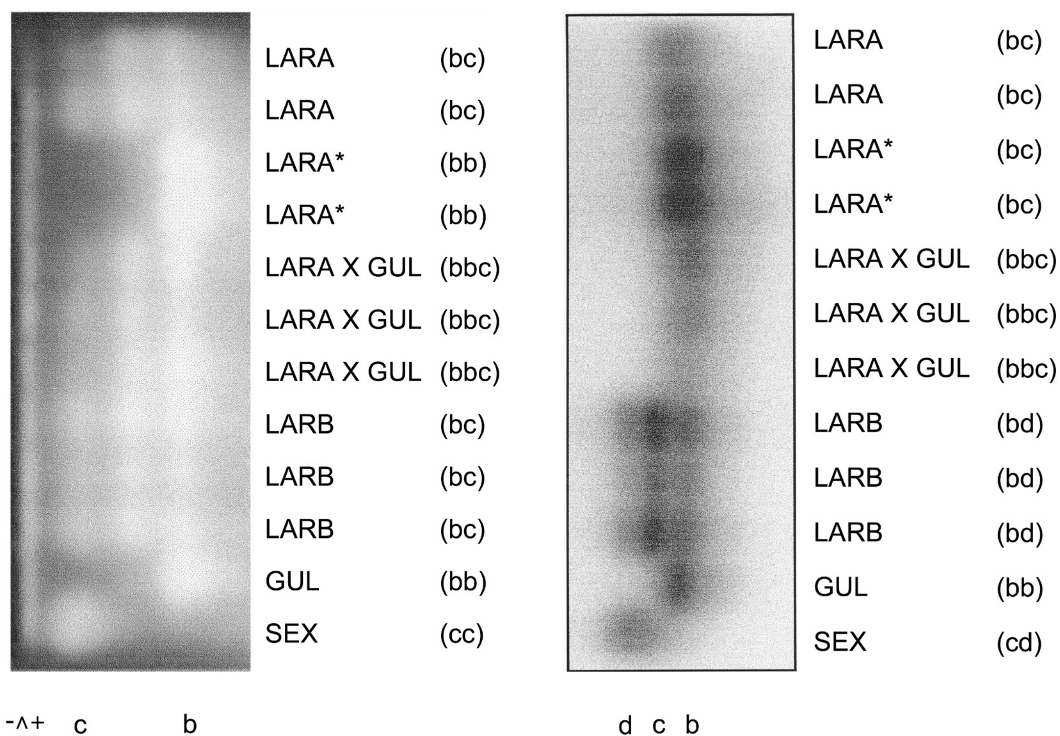

FIGURE 3. Electrophoretic phenotypes of 12 lizards. **Left.** EST-D, a dimeric enzyme. **Right.** PEP-B, a dimeric enzyme. For each photograph, letters below the gel identify allozymes based on alleles present (table 1). Lanes for individual lizards are labeled beside the gel (with genotype), as follows: LARA, *A. laredoensis* pattern class A; LARA*, variants of LARA for EST-D that were identical to all the other specimens of LARA at all other loci (e.g., PEP-B); LARA X GUL, natural hybrid of *A. laredoensis* × *A. gularis*; LARB, *A. laredoensis* pattern class B; GUL, *A. gularis*; SEX, *A. sexlineatus*. Anode is to the right; arrow indicates position of sample application for EST-D.

were distinctive at only the ESTD locus (table 1; fig. 3). The source of this difference is not known, as it could have resulted from either a mutation or gene conversion within LARA or from a separate hybrid zygote, as the B-allele occurs in both GUL and SEX.

Allozymes of *A. laredoensis* Pattern Class B (LARB): The three specimens examined had the same alleles present as each other at all 31 loci examined (TF was not examined on these), and they differed from LARA at only two loci (PEPB, PEPD; table 1; figs. 3, 4). The combination of alleles at these two loci is consistent with the suggestion that LARB may have originated from GUL × SEX but possibly from a separate hybrid zygote from the one(s) that produced LARA (see also Abuhteba et al., 2001).

Allozymes of Triploid Natural Hybrids between *A. laredoensis* Pattern Class A × *A. gularis* (L × G): The four specimens examined were identical to each other at the 30 loci examined (IDDH and sSOD were not examined on these; table 1; figs 3, 4). For each locus, the alleles present were consistent with a triploid hybrid genome consisting of the two haploid sets of genes commonly found in LARA plus one haploid set inherited from *A. gularis* (GUL). It is interesting that all four hybrids had the same triploid genome, although *A. gularis* showed

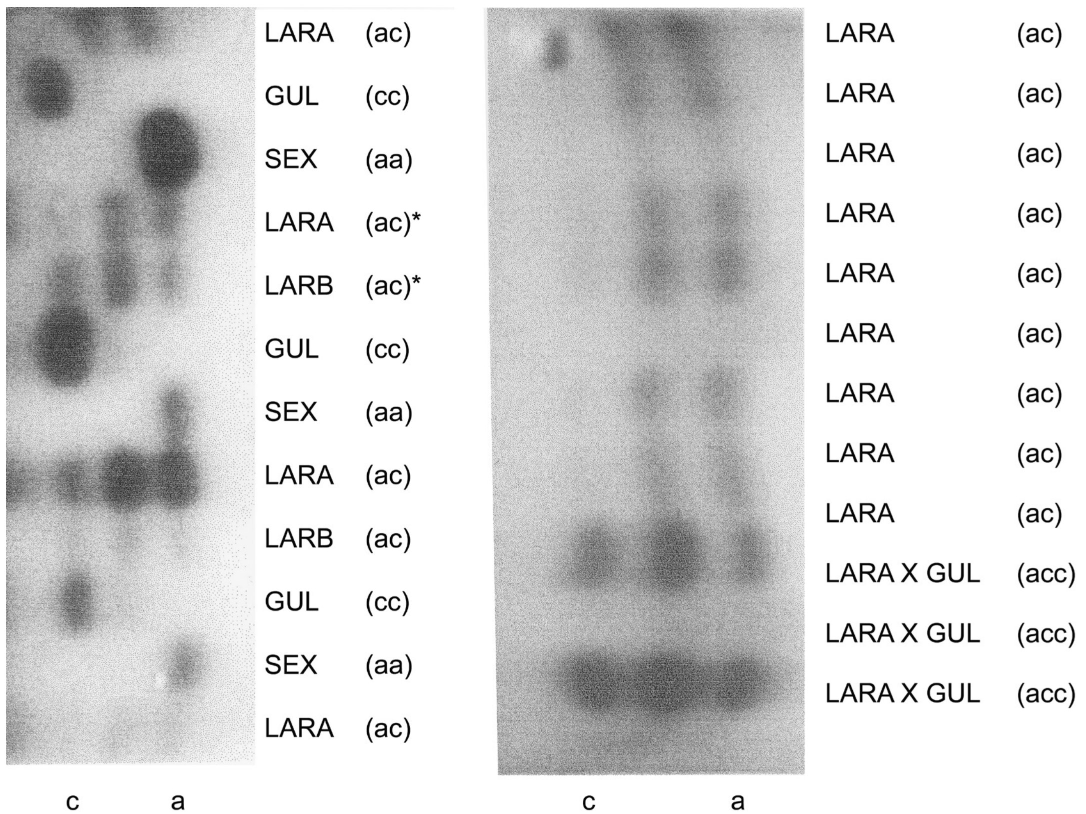

FIGURE 4. Electrophoretic phenotypes of the dimeric enzyme PEP-A for 12 different lizards (a total of 24) on each of two gels. Letters and labeling are as in figure 3, except that here the asterisk is to note that activity of the A- or C-allele in the diploid LARA or LARB is present but under-expressed.

allelic variation at seven loci, so different hybrids from separate fertilization events could easily have had nonidentical genomes at the loci we tested. The four hybrids consisted of two males and two females, so we are reasonably certain that at least three separate zygotes were involved (one for each male, and one for a female, which might or might not have cloned herself).

Allozymes of an Offspring Produced by a Natural Hybrid L × G in the Laboratory: One of the natural triploid hybrids produced an offspring in the laboratory (see appendix, Specimens Examined). We refer to this laboratory offspring as L × G2. We could examine only 19 loci of this small lizard (L × G2), including five of the most informative ones that showed variation among the species and specimens compared (table 1). At all loci examined, this individual was identical to its mother, suggesting that she had cloned the offspring. Unfortunately, this offspring died of unknown causes on the day of hatching in the laboratory.

The taxonomic norm among unisexual whiptail lizards is to treat F_1 hybrids as simply unnamed hybrid individuals having parents of two species, but to treat cloned offspring of hybrids as representing new species, regardless of the number of F_1 hybrids that might have cloned lineages (e.g., Cole et al., 2014, 2017). As this apparently cloned offspring died on the day of hatching, and none others like it are known, we will not name a species here. However,

the origin of this individual is very suggestive. If one F_1 hybrid cloned herself in the laboratory, how many might be cloning themselves in nature? In the future, as more females of apparent hybrids between *A. laredoensis* × *A. gularis* are found, the intriguing question will be whether these individuals are additional F_1 hybrids or cloned individuals representing a new, un-named triploid species.

CONCLUSIONS

Our results, based on improved data, support prior suggestions regarding *A. laredoensis* and its relatives and suggest new possibilities to be investigated by future investigators:

1. *Aspidoscelis laredoensis* is a diploid parthenogenetic species that had a hybrid origin between *A. gularis* × *A. sexlineatus*.
2. Three all-female clonal lineages, based on allozymes, are known to exist in southern Texas.
3. Individuals of at least one of these clones occasionally hybridize with males of *A. gularis*, producing viable and healthy triploid offspring that can grow to adulthood.
4. The possibility exists that one or more of these hybrids could establish a new triploid parthenogenetic species in southern Texas or adjacent northern Mexico.

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REFERENCES

Abuhteba, R.M., J.M. Walker, and J.E. Cordes. 2001. Histoincompatibility between clonal complexes A and B of parthenogenetic *Cnemidophorus laredoensis*: evidence of separate hybrid origins. Copeia 2001: 262–266.

Bickham, J.W., C.O. McKinney, and M.F. Mathews. 1976. Karyotypes of the parthenogenetic whiptail lizard *Cnemidophorus laredoensis* and its presumed parental species (Sauria: Teiidae). Herpetologica 32: 395–399.

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

Cole, C.J., and C.R. Townsend. 1977. Parthenogenetic reptiles: new subjects for laboratory research. Experientia 33: 285–289.

Cole, C.J., H.L. Taylor, D.P. Baumann, and P. Baumann. 2014. Neaves' whiptail lizard: the first known tetraploid parthenogenetic tetrapod (Reptilia: Squamata: Teiidae). Breviora 539: 1–19.

Cole, C.J., et al. 2017. The second known tetraploid species of parthenogenetic tetrapod (Reptilia: Squamata: Teiidae): description, reproduction, comparisons with ancestral taxa, and origins of multiple clones. Bulletin of the Museum of Comparative Zoology 161: 285–321.

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.

Dessauer, H.C., C.J. Cole, and C.R. Townsend. 2000. Hybridization among western whiptail lizards (*Cnemidophorus tigris*) in southwestern New Mexico: population genetics, morphology, and ecology in three contact zones. Bulletin of the American Museum of Natural History 246: 1–148.

Harris, H., and D.A. Hopkinson. 1976. Handbook of enzyme electrophoresis in human genetics. Amsterdam: North-Holland.

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.

McKinney, C.O., F.R. Kay, and R.A. Anderson. 1973. A new all-female species of the genus *Cnemidophorus*. Herpetologica 29: 361–366.

Murphy, R.W., J.W. Sites, Jr., D.G. Buth, and C.H. Haufler. 1996. Proteins: isozyme electrophoresis. *In* D.M. Hillis, C. Moritz, and B.K. Mable (editors), Molecular systematics, 2nd ed.: 51–120. Sunderland, MA: Sinauer.

Paulissen, M.A. 2000 ("1999"). Life history and drought tolerance of the parthenogenetic whiptail lizard *Cnemidophorus laredoensis* (Teiidae). Herpetological Natural History 7: 41–57.

Porter, C., O.G. Ward, C.J. Cole, and R.J. Baker. 2019. 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 Publication Number 71: 805–818.

Porter, W.P., C.J. Cole, and C.R. Townsend. 1994. Captive maintenance and lineage senescense in parthenogenetic lizards (family Teiidae). *In* J.B. Murphy, K. Adler, and J.T. Collins (editors), Captive management and conservation of amphibians and reptiles (Contributions in Herpetology 11): 91–98. Ithaca, NY: Society for the Study of Amphibians and Reptiles.

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.

Townsend, C.R. 1979. Establishment and maintenance of colonies of parthenogenetic whiptail lizards. International Zoo Yearbook 19: 80–86.

Townsend, C.R., and C.J. Cole. 1985. Additional notes on requirements of captive whiptail lizards (*Cnemidophorus*) with emphasis on ultraviolet radiation. Zoo Biology 4: 49–55.

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.

Walker, J.M. 1987. Distribution and habitat of a new major clone of a parthenogenetic whiptail lizard (genus *Cnemidophorus*) in Texas and Mexico. Texas Journal of Science 39: 313–334.

Walker, J.M., W.C. Guest, J.E. Cordes, and M.A. Paulissen. 1989a. Morphological and chromosomal evidence of hybridization between all-female *Cnemidophorus laredoensis* and gonochoristic *Cnemidophorus gularis*. Copeia 1989: 1059–1064.

Walker, J.M., J.E. Cordes, and M.A. Paulissen. 1989b. Hybrids of two parthenogenetic clonal complexes and a gonochoristic species of *Cnemidophorus*, and the relationship of hybridization to habitat characteristics. Journal of Herpetology 23: 119–130.

Walker, J.M., R.M. Abuhteba, and J.E. Cordes. 1991. Morphological and experimental verification of hybridization between all-female *Cnemidophorus laredoensis* B and gonochoristic *Cnemidophorus gularis* (Squamata: Teiidae). Herpetologica 47: 152–164.

Walker, J.M., J.E. Cordes, R.M. Abuhteba, and M.A. Paulissen. 2001. Syntopy between clonal complexes A and B of parthenogenetic *Cnemidophorus laredoensis* and both of their gonochoristic progenitors. American Midland Naturalist 145: 397–401.

Walker, J.M., J.E. Cordes, and M.A. Paulissen. 2016. Rare syntopy of the diploid parthenogenetic lizard (*Aspidoscelis laredoensis* B) and both gonochoristic progenitors (*A. gularis* and *A. sexlineata*) in Texas, USA. Herpetological Conservation and Biology 11: 29–39.

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., C. Spolsky, and W.M. Brown. 1983. The origin of the parthenogenetic lizard *Cnemidophorus laredoensis* inferred from mitochondrial DNA analysis. Herpetologica 39: 410–416.

APPENDIX

Specimens Examined

Specimens are cited by their individual catalog numbers. The initials for their respective museum collections are as follows: AMNH, American Museum of Natural History; UAZ, University of Arizona Museum of Natural History. All the specimens are from the United States unless specified otherwise. The lowercase letters following the catalog number for each specimen indicates the type of data used, as follows: a, allozymes; k, karyotype.

Aspidoscelis gularis

Texas: Cameron County: along the Rio Grande, 0.4 km W small town of El Ranchito (AMNH R-147466, a). Hidalgo County: 1.5 km S town of Los Ebanos (AMNH R-147468 and 147469, both a). Reeves County: junction of TX Hwy 17 and US Hwy 290, 4.6 mi E Balmorhea (UAZ 18542, 18961, and 30268, all k); 5.2 mi E Balmorhea (UAZ 18558 and 18974, both k). Tarrant County: 2.4 mi W jct US Hwy 377 and Benbrook-Aledo Rd (AMNH R-122821, k). Travis County: Municipal Golf Course, Austin (Lake Austin and Exposition Drive) (UAZ 28247, k). MEXICO: *San Luis Potosi*: 2.8 mi (by rd) S Charcas (about 67 mi [linear] N San Luis Potosi) (AMNH R-106555, k).

Aspidoscelis laredoensis Pattern Class A

Texas: Hidalgo County: 1.5 km S town of Los Ebanos (AMNH R-147482 and 147483 and 147485–147487, all a); edge of field along Rio Grande, immediately SW Bentsen Rio Grande Valley State Park

(AMNH R-147475–147481, all a). Webb County: along US Hwy 83 at 1 mi S Chacon Creek in SE Laredo (AMNH R-126891, 126892 [also k], 135052, 135068 [also k], 135075 [also k], 135080, all a). Zapata County: 3.6 mi (by US Hwy 83) N San Ygnacio (AMNH R-126889, 126890, 135049, and 135056, all a).

Aspidoscelis laredoensis Pattern Class A, ESTD Allozyme Variant

Texas: Hidalgo County: 1.5 km S town of Los Ebanos (AMNH R-147484 and 147485, both a).

Aspidoscelis laredoensis Pattern Class A Cloned Laboratory Offspring

F_1 generation offspring (AMNH R-135058, a) of AMNH R-135056 (a; locality given above). F_1 generation offspring (AMNH R-135061, a) of AMNH R-135060 (k; same locality as given for AMNH R-135056 above). F_2 generation offspring (AMNH R-135063, 135066, 135067, all a) of AMNH R-135061 (a; genealogy given above). F_1 generation offspring (AMNH R-135069, a; R-135070, k; R-135072, a) of AMNH R-135068 (a, k; locality given above). F_1 generation offspring (AMNH R-135081–R-135083, all a) of AMNH R-135080 (a; locality given above). F_2 generation offspring (AMNH R-135084, a) of AMNH R-135081 (a; genealogy given above). F_2 generation offspring (AMNH R-135086 and 135087, both a) of AMNH R-135085 (neither a nor k; offspring of AMNH R-135081 (a; genealogy given above).

Aspidoscelis laredoensis Pattern Class B

Texas: Cameron County: along the Rio Grande, 0.4 km W small town of El Ranchito (AMNH R-147488, a). Hidalgo County: 1.5 km S town of Los Ebanos (AMNH R-147489 and 147490, both a).

Natural Hybrids of *A. laredoensis* Pattern Class A × *A. gularis*

Texas: Hidalgo County: Bentsen-Rio Grande Valley State Park, S of city of Mission (AMNH R-148415, a; AMNH R-148416 and 148417, both a, k; AMNH R-148418, a).

F_1 Laboratory Offspring of a Natural Hybrid of *A. laredoensis* Pattern Class A × *A. gularis*

AMNH R-148422 [a], F_1 generation offspring of AMNH R-148415 (see above).

Aspidoscelis sexlineatus

Colorado: Kiowa County: 9.4 mi N Eads at Rush Creek (AMNH R-108142, k). Pueblo County: Vertrees Ranch, vicinity of Undercliffe (=Doyle), ca. 18 mi (linear) SE Pueblo (UAZ 18502, 18517, 18978, and 18979, all k); Huerfano River bridge on Doyle Rd, 18.6 mi (by rd) S Avondale (AMNH R-131122, k). *Florida*: Dade County: US Hwy 27, 8.8 mi NW Hialeah (UAZ 18739, k). *Maryland*: Calvert County: Flag Pond, 4.4 mi SE St. Leonard (UAZ 18559 and 18977, both k). *New Mexico*: Mora County: 1.9 mi by rd) W Shoemaker (UAZ 18738 and 18755, both k); San Miguel County: Conchas Lake, at South State Park Campground (AMNH R-114231 and 114233–114235, all k). *Texas*: Brooks County: edge of US Hwy 281, at 3.5 km W small town of Encino (AMNH R-147491–147493, all a).

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