
RARE SYNTOPY OF THE DIPLOID PARTHENOGENETIC LIZARD (*ASPIDOSCELIS LAREDOENSIS* B) AND BOTH GONOCHORISTIC PROGENITORS (*A. GULARIS* AND *A. SEXLINEATA*) IN TEXAS, USA

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Abstract.—We surveyed several sites in Dimmit County, Texas, and provide the first records for *Aspidoscelis laredoensis* (Laredo Striped Whiptail) clonal complex B therein. Site D-5 (= Texas FM 2644 West), about 31 km (straight line distance) east of the Rio Grande in chronically disturbed habitat bordering Texas FM Hwy 2644, is the most distant point from the river known for this hybrid-derived diploid parthenogenetic lizard. It is also the only site in the range of clonal complex B, which includes certain border areas of Texas and the Mexican states Coahuila and Tamaulipas, where large numbers of *A. laredoensis* B have been observed in syntopy with substantial numbers of its gonochoristic progenitors, *A. gularis* (Texas Spotted Whiptail) and *A. sexlineata* (Six-lined Racerunner). *Aspidoscelis gularis* is the only whiptail species present at all of the other five sites in Dimmit County featured herein, with no other congener at D-1 (= Carrizo Springs) and D-2 (= Valley Wells), with *A. laredoensis* clonal complex A at D-3 (= Catarina), and with *A. sexlineata* at D-4 (= Texas FM 2644 East) and D-6 (= Chaparral Wildlife Management Area). Dimmit County is crucial to understanding regional relationships of *A. laredoensis* A and B, *A. gularis*, and *A. sexlineata* because it encompasses an area in which all except *A. gularis* exist at some aspect of their biogeographical limits. Different search strategies employed at D-5 often changed the number of individuals of each whiptail species observed owing to subtle aspects of habitat partitioning related to soil type and diversity and density of vegetation. We also report a rare hybrid of *A. laredoensis* B x *A. gularis* from site D-5.

Key Words.—evolution; parthenogenesis; preferred habitats; racerunners; syntopy; Texas lizards; whiptail lizards

INTRODUCTION

The *Aspidoscelis* (= *Cnemidophorus*) *laredoensis* (Laredo Striped Whiptail) subgroup of diploid cloned-hybrid parthenogenetic lizards has a composite geographic range consisting of a sinuous distribution area that follows parts of both sides of the Rio Grande trenchment from the binational sister cities Del Rio/Acuña, southeast to within a few km of the Gulf of Mexico, and limited areas away from the river in Dimmit, La Salle, and Starr counties, Texas (Walker 1987a, b; Walker et al. 1990, 2004; Paulissen et al. 2001). The two clonal complexes are designated *A. laredoensis* A, equivalent to the species described by McKinney et al. (1973) and discussed by Walker (1987a), and *A. laredoensis* B, discovered in the 1980s (Walker 1987b). They are characterized by differences in geographic distributions (Walker 1987b; Walker et al. 1990, 2004; Paulissen and Walker 1998; Paulissen et al. 2001), color patterns (Walker 1987b), meristic characters (Walker et al. 1989), genes controlling histoincompatibility responses (Abuhteba et al. 2000, 2001), and allozymes (Parker et al. 1989). These divergent characteristics reflect the mode of origin of clonal complex A (McKinney et al. 1973; Bickham et al.

1976; Wright et al. 1983) and B (Parker et al. 1989; Abuhteba et al. 2001) of asexual *A. laredoensis* through separate hybridization events involving the sexual species *A. gularis* (Texas Spotted Whiptail) and *A. sexlineata* (Six-lined Racerunner). Individuals of both clonal complexes of *A. laredoensis* and the two gonochoristic progenitor species are diurnal, widely foraging, ground-dwelling forms that feed on insects and other arthropods located by sight and olfaction (Paulissen et al. 1992). Any syntopic combination of these asexual clonal complexes and their gonochoristic progenitors present compelling opportunities for assessment of morphological and ecological consequences of their unique evolutionary histories.

During extensive field research on the subgroup from 1984 through 2012, we located every site in Texas and México known for *A. laredoensis* B (Walker 1987b; Walker et al. 1990; Paulissen et al. 2001; Cordes and Walker 2011). With the exception of its presence in Dimmit County, Texas, which was the basis of this study, all of these sites were located within 10 km of the Rio Grande in the Mexican border states Coahuila (five sites) and Tamaulipas (six), and the northwest to southeast Texas border counties Val Verde (two), Kinney (one), Maverick (three), Webb (four), Zapata

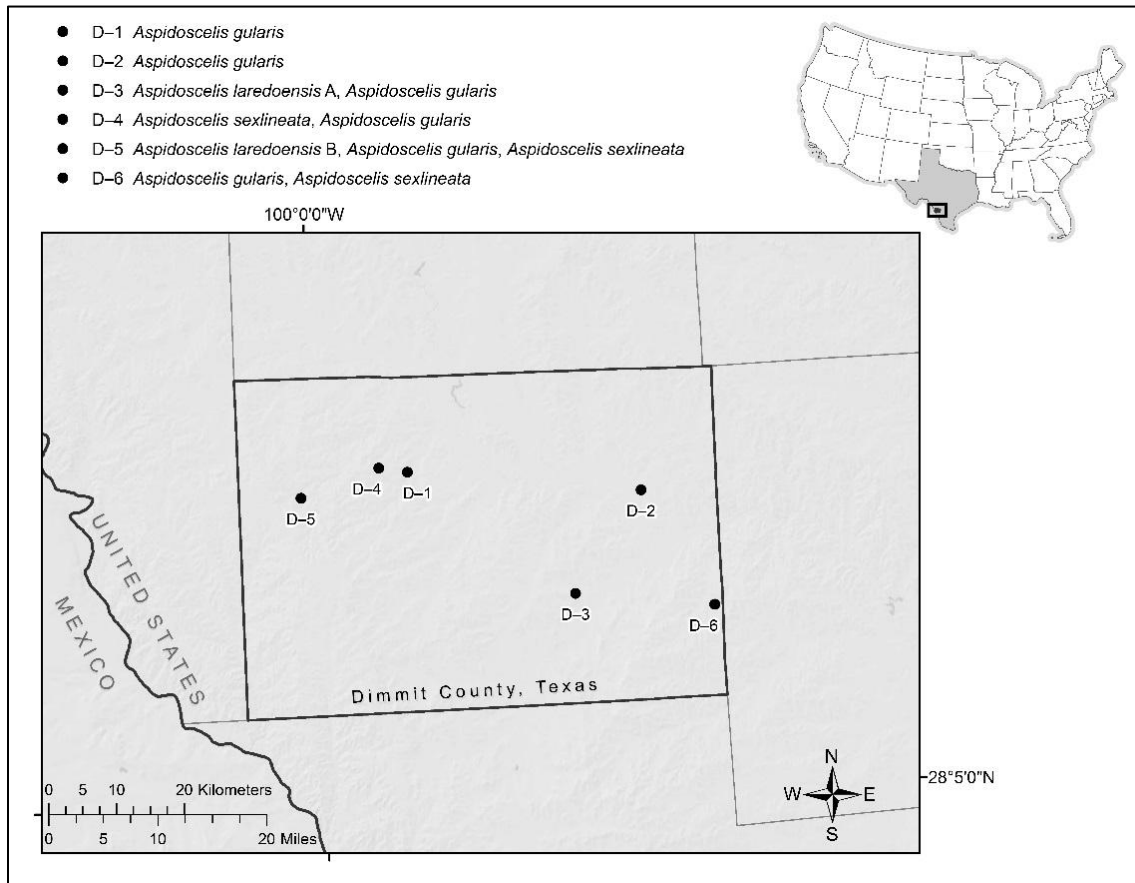


FIGURE 1. Outline map of Dimmit County, Texas, USA, showing proximity to Rio Grande and spatial relationships of various guilds of whiptail lizards (genus *Aspidoscelis*) at six study sites: D-1 (Carrizo Springs); D-2 (Valley Wells); D-3 (Catarina), D-4 (Texas FM 2644 East); D-5 (Texas FM 2644 West); and D-6 (Chaparral Wildlife Management Area). Above the map, species are listed in order of abundance at each site. (Created by Hanna Ford).

(zero), Starr (three), Hidalgo (five), and Cameron (three). We also discovered a hiatus in the range of *A. laredoensis* B that extends about 225 km along the Rio Grande from extreme western Webb County and through most of the county and all of Zapata County to southern Starr County (Walker 1987b, Walker et al. 1990, 2004; Paulissen et al. 2001). We not only repeatedly searched for this parthenogen over many years within the hiatus, which is inhabited by *A. laredoensis* A and/or *A. gularis*, but also continued in attempts to extend the known range of the form to away from the immediate vicinity of the Rio Grande in Texas and México.

Walker et al. (2001; map) provided the first records of syntopy between the two clonal complexes of *A. laredoensis* and both of their gonochoristic progenitors at sites located along Texas FM 1472 in northwestern Webb County. While *A. gularis* occurs throughout the entire range of both clonal complexes of *A. laredoensis* and is frequently syntopic with them, *A. sexlineata* and *A. laredoensis* have largely mutually exclusive geographic ranges between northwestern Webb County

and Cameron County, the latter which borders the Gulf of Mexico. The area described lacks obvious geographical barriers to whiptail lizard dispersal. That *A. sexlineata* has dispersed to South Padre Island, Cameron County, Texas (Perez-Ramos et al. 2010), but is not known to occur near the Rio Grande in Texas, is especially puzzling. Extensive field work, however, has led to discovery of the site in Dimmit County, which borders Webb County to the south, where *A. laredoensis* B, *A. gularis*, and *A. sexlineata* are abundantly syntopic in one small area. The significance of this is that the chronically disturbed site is the most distant one from the Rio Grande inhabited by this clonal complex of whiptail lizards discovered to date. It also represents one of only four sites where we have found morphological evidence of hybridization between *A. laredoensis* B and *A. gularis* (see Walker et al. 1991). We also compared this site with others in Dimmit County that support different combinations of whiptail lizards even though they are separated from each other by relatively short distances (Fig. 1; Table 1).

TABLE 1. Whiptail lizard guilds (genus *Aspidoscelis*) observed at six sites in Dimmit County, Texas, USA; included are number of visits to each site (NA = not applicable to D-6) and species listed in order of relative abundance from left (high) to right (low) based on collection totals (in parentheses). Species are listed by order of their relative abundance (number) and the literature source is given except for D-5 reported herein.

Site	Coordinates	Visits	Species
D-1; Carrizo Springs	28.517912°N 99.859079°W	1	<i>Aspidoscelis gularis</i> (1); Walker (1987b)
D-2; Valley Wells	28.480819°N 99.509209°W	1	<i>A. gularis</i> (13); Walker et al. (2004)
D-3; Catarina	28.347567°N 99.614690°W	11	<i>A. laredoensis</i> A (80), <i>A. gularis</i> (24); Walker et al. (2004)
D-4; Texas FM 2644 East	28.524995°N 99.901650°W	3	<i>A. sexlineata</i> (25), <i>A. gularis</i> (9); Walker et al. (2004)
D-5; Texas FM 2644 West	28.48944°N 100.02056°W	21	<i>A. laredoensis</i> B (53), <i>A. gularis</i> (23), <i>A. sexlineata</i> (16)
D-6; Chaparral Wildlife Area	28.324716°N 99.406704°W	NA	<i>A. gularis</i> (1,147), <i>A. sexlineata</i> (18); Ruthven et al. (1999)

MATERIALS AND METHODS

Study areas.—Based on the USA Census Bureau, Dimmit County, Texas, USA, has an area of 3,455 km², of which only 7.8 km² (0.27%) is water. The southwestern corner of this rectangular-shaped county is about 4 km Straight Line Distance (SLD) from the Rio Grande through the narrow westernmost extension of Webb County (Fig 1). We visited Dimmit County to study whiptail lizards on > 30 d between 1984 and 2005 after discovering the disjunct array of *A. laredoensis* A at Catarina in 1986. Many sites in the county were searched for species other than the ubiquitous *A. gularis* (Tables 1 and 2). However, parts of most visits included stops at either vicinity of Catarina (i.e., 28.347567°N, 99.614690°W) where parthenogenetic *A. laredoensis* A and gonochoristic *A. gularis* are syntopic (Walker 1987a,b; Walker et al. 2004) or at sites along Texas FM 2644 (i.e., 28.48944°N, 100.02056°W, = about 16 km SLD southwest of the county seat Carrizo Springs, = about 14.6 km SLD southwest of the junction with US Hwy 277, and = about 31 km SLD east of the Rio Grande) to study syntopic relationships among parthenogenetic *A. laredoensis* B and its gonochoristic progenitors *A. gularis*, and *A. sexlineata* in chronically disturbed habitat (Tables 1–3).

Geographically, Texas FM 2644 is a frequently used corridor for humans entering Texas from México. Consequently, a major determinant of lizard habitat structure and abundance at the study site near the highway involves techniques used in immigration enforcement by personnel of the US Border Patrol. Along the paved highway in sandy areas, it employs various types of objects (i.e., pieces of chain link fence, large tires, and rakers) pulled behind vehicles to maintain approximately 4-m wide vegetation-free lanes

of deep sandy soil on the sides of the highway (Figs. 2 and 3; Table 4). These dragged lanes readily reveal human footprints and the tracks of lizards (Fig. 2). The north side of the road between the western Dimmit County boundary and US Hwy 277 is not subject to this treatment in most places, but long stretches of the south side are dragged many times a year during both mornings and afternoons. The premise is that humans attempting to avoid detection will walk in the sandy lanes rather than the Sandbur (*Cenchrus incertus*) infested untreated roadsides/ditches. An incidental aspect of this activity is the extensive use of the lanes by large numbers of lizards of three species of *Aspidoscelis* and one species of *Holbrookia*.

Data analyzed.—We use the appellation D-5 (= Dimmit County site 5 = Texas FM 2644 West) in reference to the study site emphasized herein based on the system of codes used by Walker (1987a, b; Walker et al. 1990, 2001, 2004) for other sites inhabited by whiptail lizards in the county (e.g., Chaparral Wildlife Management Area [D-6, new code], FM 2644 East [D-4], Catarina [D-3], Valley Wells [D-2], and Carrizo Springs [D-1]; Table 1). Data from the literature referenced herein are based on specimens of *Aspidoscelis* reported on by Walker et al. (2001, 2004). Newly reported data herein are based on 93 specimens of *A. laredoensis* B, *A. gularis*, and *A. sexlineata* collected at D-5 between 2000 and 2005 (Tables 1–3). We made all collections by using large rubber bands, noosing, excavation, air guns, and/or .22 caliber pistols with dust shot, which were authorized by permits from Texas Parks and Wildlife Department to either JEC or MAP. Some lizards survived capture and were used in skin histocompatibility experiments, detailed results of which are not included in this report. We assigned each dead and live lizard a number in the University of Arkansas

TABLE 2. Comparison of collecting results at three sites in Dimmit County, Texas, USA (Fig. 1), at the most distant sites from the Rio Grande known for the two clonal complexes of diploid parthenogenetic *Aspidoscelis laredoensis* (D-3 [= Catarina] from 1986–1996 by an average of three collectors and D-5 [= Texas FM 2644 West] from 2000–2005 by an average of one collector, and a westernmost Texas site for *A. sexlineata* (D-4 [= Texas FM 2644 East]).

Site (Visits/Results)	<i>A. laredoensis</i> A	<i>A. laredoensis</i> B	<i>A. gularis</i>	<i>A. sexlineata</i>
D-3 (1986–1996)				
Collected/Observed	80/210 (38.1%)	Not Present	24/44 (54.5%)	Not Present
Per visit by three	7.3 (2–23)		2.2 (1–10)	
Visits none collected	0		4	
D-5 (2000–2005)				
Collected/Estimated	Not Present	53/176 (30.1%)	24/120 (20%)	16/80 (20%)
Per visit by one		2.5 (1–14)	1.1 (1–4)	0.8 (1–3)
Visits none collected		4	6	9
D-4 (1989–1999)				
Collected/Estimated	Not Present	Not Present	9/18 (50%)	25/50 (50%)
Per visit by three			3.0 (1–5)	8.3 (1–16)
Visits none collected			0	0

Department of Zoology (UADZ) collection maintained by JMW. Preserved specimens with an attached number were fixed in 10% formalin and permanently stored in 70% ethanol.

References to dorsal color pattern in *A. laredoensis* B and progenitor species followed the nomenclature of Burt (1931), Duellman and Zweifel (1962), and Walker (1981a, b) for the pale colored longitudinal stripes (i.e., laterals, dorsolaterals, paravertebrals, and vertebral[s]), intervening longitudinal dark fields (lower laterals, upper laterals, dorsolaterals, and vertebral), spots (rounded light-colored areas in fields and on stripes if present), and bars (vertical to horizontal light areas perpendicular

to the stripes). We used preserved snout vent length (SVL) data and body mass (BM) data obtained prior to fixation of specimens of the three species from the site of syntopy in Dimmit County. We did not use lizards from D-5 with tails lost during collection for analyses of the relationship between SVL and BM in *A. laredoensis* B, *A. gularis*, and *A. sexlineata*. We analyzed 11 meristic characters and a ratio (terminology based on Burt 1931; Smith 1946; Walker 1981b; Table 5) including (1) granules (= scales) at midbody from the right outer row of ventral scales over the body to the left outer row of ventral scales (GAB), (2) dorsal granules longitudinally from the occipital scales to the first row of



FIGURE 2. Far view looking west at D-5 (Texas FM 2644 West; 28.48944°N, 100.02056°W) in Dimmit County, Texas, USA, showing the low-growth band between the paved highway and sandy vegetation-free lane (note footprints) regularly dragged by the US Border Patrol, and the narrow strip of habitat between the lane and fence from which *Aspidoscelis laredoensis* B, *A. gularis*, and *A. sexlineata* were collected 2000–2005. (Photographed by James E. Cordes).



FIGURE 3. Near view looking west at D-5 (Texas FM 2644 West; 28.48944°N, 100.02056°W) in Dimmit County, Texas, USA, showing the vegetation-free sandy lane regularly dragged by personnel of the US Border Patrol (note large tire for this purpose on sand to upper right) and vegetational components (mesquite, cactus, yucca, Buffelgrass, *Cenchrus ciliaris*, and forbs) on both sides of the fence line inhabited by *Aspidoscelis laredoensis* B, *A. gularis*, and *A. sexlineata* 2000–2005. (Photographed by James E. Cordes).

TABLE 3. Specimens of *Aspidoscelis laredoensis* B (A/B), *A. gularis* (Ag), *A. sexlineata* (As), hybrids (H), and total (T) collected during 21 visits between 2000 and 2005 to D-5 (Texas FM 2644 West; 28.48944°N, 100.02056°W) at about 14.6 km W from jet with US 277, Dimmit County, Texas, USA.

Date	A/B	Ag	As	H	T	Specimens Collected
23 March 2000	1	0	1	0	2	<i>A. l. B</i> (UADZ 6854); <i>A. s.</i> (released)
24 May 2000	1	2	1	0	4	<i>A. l. B</i> (UADZ 6679); <i>A. g.</i> (UADZ 6681–6682); <i>A. s.</i> (UADZ 6680)
24 June 2000	3	0	1	0	4	<i>A. l. B</i> (UADZ 6814–6816); <i>A. s.</i> (UADZ 6817)
9 August 2000	1	2	0	0	3	<i>A. l. B</i> (UADZ 6861); <i>A. g.</i> (UADZ 6862–6863)
31 May 2001	0	1	1	0	2	<i>A. g.</i> (UADZ 6878); <i>A. s.</i> (UADZ 6877)
6 June 2001	0	2	2	0	4	<i>A. g.</i> (UADZ 6890–6891); <i>A. s.</i> (UADZ 6888–6889)
7 June 2001	1	0	0	0	1	<i>A. l. B</i> (UADZ 6892)
1 July 2001	0	0	3	0	3	<i>A. s.</i> (UADZ 6896–6898)
14 July 2001	1	2	1	0	4	<i>A. l. B</i> (UADZ 6959); <i>A. g.</i> (UADZ 6956–6957); <i>A. s.</i> (UADZ 6958)
15 July 2001	2	0	1	0	3	<i>A. l. B</i> (UADZ 6961–6962); <i>A. s.</i> (UADZ 6960)
2 August 2001	4	1	0	0	5	<i>A. l. B</i> (UADZ 6977–6980); <i>A. g.</i> (UADZ 6981)
3 August 2001	2	0	0	0	2	<i>A. l. B</i> (UADZ 6982–6983)
11 July 2002	3	1	0	0	4	<i>A. l. B</i> (UADZ 7033–7035); <i>A. g.</i> (UADZ 7036)
12 July 2002	2	1	2	0	5	<i>A. l. B</i> (UADZ 7040, 7042); <i>A. g.</i> (UADZ 7039); <i>A. s.</i> (UADZ 7037–7038)
5 June 2003	3	2	0	0	5	<i>A. l. B</i> (UADZ 7141–7143); <i>A. g.</i> (UADZ 7140, 7144)
6 June 2003	5	4	1	0	10	<i>A. l. B</i> (UADZ 7145–7149); <i>A. g.</i> (UADZ 7150, 7152–7154); <i>A. s.</i> (UADZ 7151)
14 June 2004	6	0	0	1	7	<i>A. l. B</i> (UADZ 7241–7246); <i>A. l. B</i> x <i>A. g.</i> (UADZ 7247)
5 June 2005	14	2	1	0	17	<i>A. l. B</i> (UADZ 7826, 7828, 7830, 7832–7842); <i>A. g.</i> (UADZ 7827, 7831); <i>A. s.</i> (UADZ 7829)
6 June 2005	2	1	1	0	4	<i>A. l. B</i> (UADZ 7844, 7846); <i>A. g.</i> (UADZ 7845); <i>A. s.</i> (UADZ 7843)
23 July 2005	0	1	0	0	1	<i>A. g.</i> (UADZ 7970)
12 August 2005	2	1	0	0	3	<i>A. l. B</i> (UADZ 8030, 8032); <i>A. g.</i> (UADZ 8031)
Total All Visits	53	23	16	1	93	<i>A. l. B</i> ; <i>A. g.</i> ; <i>A. s.</i> ; <i>A. l. B</i> x <i>A. g.</i>

caudals (OR), (3) percentage of GAB/OR \times 100, (4) granules between the paravertebral stripes at midbody (PV), (5) percentage of granules around midbody between paravertebral stripes (PV/GAB \times 100), (6) femoral pores summed from both sides (FP), (7) arbitrarily only subdigital lamellae of the longest toe of the left pes (SDL), (8) circumorbital scales of both sides summed (COS), (9) lateral supraocular granules of both sides summed (LSG), (10) enlarged scales in the first or second row bordering the posterior gular fold (MS), (11) interlabial scales of both sides summed (ILS), and (12) supraocular scales separately on each side of the head (SO). Scutellation characters qualitatively referenced include (1) anterior extent of the circumorbital scale series between the supraocular and median head scales, (2) size of the postantibrachial scales on the posterior part of each lower arm, and (3) size of the mesoptychial scales bordering the edge of the posterior gular fold. We

determined the sex of each specimen via inspection of femoral pores, scales posterior to the cloacal opening, and/or internal sex organs.

We used the following commands in JMP v. 11 (SAS Institute, Cary, North Carolina) to establish ranges of variation (Quantiles) and means \pm 1 SE for each univariate meristic character, SVL for each sex, and population sample. We used ANOVA to compare characters among species. We also used JMP 11 to determine the relationship between SVL and BM. For overall models that were statistically significant ($\alpha = 0.05$), we used Tukey HSD to determine which means differed from the others.

RESULTS

Whiptail lizards at D-5.—*Aspidoscelis laredoensis* B was initially collected by MAP on 23 March 2000 at

TABLE 4. Historical and habitat characteristics of three sites (D-5 [= Texas FM 2644 West], D-4 [= Texas FM 2644 East], and D-3 [Catarina]) in Dimmit County, Texas, USA, that supported differently structured guilds of whiptail lizards (genus *Aspidoscelis*) listed in order of abundance from left to right.

Historical and Habitat Characteristics	(D-5) <i>A. laredoensis</i> B, <i>A. gularis</i> , <i>A. sexlineata</i>	(D-4) <i>A. sexlineata</i> , <i>A. gularis</i>	(D-3) <i>A. laredoensis</i> A, <i>A. gularis</i>
Discovery (visits)	23 March 2000 (21)	13 May 1988 (3)	26 April 1986 (13)
Location	1 km along paved highway	along south side of paved highway	horse pasture E of US Hwy 83
Distance from the Rio Grande (GPS)	31.0 km (28.48944°N, 100.02056°W)	42.6 km (28.524995°N, 99.901650°W)	50.5 km (28.347567°N, 99.614690°W)
Nature of habitat	Altered and unstable	Altered and relatively unstable	Altered and unstable
Type of disturbance	Dragging, mowing, grazing, trampling, brush removal	Grazing, trampling, brush removal, access road maintenance	Grazing, trampling, brush removal, road maintenance
Habitat components	Mowed roadside, dragged area, fence	Heavily grazed ranch land, roads for ranch vehicles	Horse pasture, roadsides, vacant lots
Principal plants in whiptail habitat	Mesquite, cacti, yucca, buffelgrass, forbs	Large stands of cacti, mesquite, buffelgrass, forbs	Mesquite, cacti, (pasture), then buffelgrass/forbs
Soil type	Sandy and exposed	Sandy and exposed	Sandy and exposed

D-5, a site selected for investigation based on habitat characteristics that seemed conducive to the presence of *A. sexlineata*, then known only from D-4 in the area (Table 1). Unexpected discovery of *A. laredoensis* B at this most distant site from the Rio Grande (about 31 km SLD) known for the parthenogen prompted JEC to make many additional visits to D-5, ranging from 2–3 h in length, through 12 August 2005 (Tables 1–4). During 21 visits, we obtained 53 (57.0%) specimens of *A. laredoensis* B, 23 (24.7%) of *A. gularis*, 16 (17.2%) of *A. sexlineata*, and one (1.1%) putative hybrid of *A. laredoensis* B \times *A. gularis* for use in histocompatibility, morphological, and reproductive analyses. We obtained specimens of *A. laredoensis* B (Table 3) during 17 (81.0%) of 21 visits, *A. gularis* during 14 (66.7%) visits, *A. sexlineata* during 12 (57.1%) visits, and all three species during only six (28.6%) visits. Based on counts of the number of each species observed versus those collected (Table 2) during each visit, *A. laredoensis* B was the most abundant whiptail species at the site as a whole between 2000 and 2005. We estimated that about 30% of *A. laredoensis* B and about 20% of *A. gularis* and *A. sexlineata* observed were collected at the site (Table 2). We were never able to obtain more than three individuals of *A. sexlineata* and four of *A. gularis* in a single trip to D-5; on 24 May 2000 only one of > 20 individuals of the former species could be collected because of their successful escape behaviors. In fact, we found that individuals of both of the two gonochoristic species were less susceptible to capture by any one of the aforementioned techniques employed because of their response to a collector.

Preliminary evidence of whiptail lizard habitat partitioning at D-5.—We visually identified three habitat components at D-5 (Table 4). Between paved Texas FM 2644 and the dragged lane on each side at D-5 was an approximately 3-m wide sloping band of mowed open-structured low-growing grasses and forbs. A collector walking in the dragged zone on the south side would occasionally flush individuals of *A. sexlineata*, which either bolted several meters through the vegetation bordering the road or into a nearby burrow (about 20% collected), whereas individuals of *A. gularis* often fled across the highway (about 20% collected). We did not observe *A. laredoensis* B in this part of D-5. On the opposite side of the dragged area, both sides of the sandy fence line provided the habitat components most extensively used by whiptails at the site. The open structure of the vegetation, in addition to the clumps of introduced Buffelgrass (*Cenchrus ciliaris*), included forbs, a few mesquite (*Prosopis* sp.) shrubs/trees interspersed with sparsely distributed clumps of prickly pear (*Opuntia* sp.), and yucca (*Yucca* sp.). This was the microhabitat at D-5 that supported most of the individuals of parthenogenetic *A. laredoensis* B observed or collected and gonochoristic *A. gularis*, but relatively few individuals of gonochoristic *A. sexlineata*, which preferred the grassy patches at the site. It was possible to maximize sightings of *A. laredoensis* B and *A. gularis* by concentrating on the low hill on the west end of D-5, whereas *A. sexlineata* was the prevalent whiptail at the lower, more grassy east end.

Whiptail lizards at D-4.—On 13 May 1988, prior to discovery of D-5, we ventured into ranchland (Texas FM 2644 East = D-4) to search for *A. laredoensis* A or B,

TABLE 5. Comparison of univariate characters for samples of *Aspidoscelis laredoensis* B (*A. l. B*), *A. gularis* (*A. g.*), *A. sexlineata* (*A. s.*), and the hybrid between *A. laredoensis* B and *A. gularis* (Hybrid 7247) from site D-5 (Texas FM 2644 West; 28.48944°N, 100.02056°W) at about 14.6 km W from junction with US 277, Dimmit County, Texas. Characters include: GAB, granular scales around midbody; OR, scales from the occipital scales to the base of tail; GAB/OR × 100, percentage of granules around midbody to granules from occipital scales to base of tail; PV, scales between paravertebral stripes at midbody; PV/GAB × 100, percentage of granules around midbody between paravertebral stripes; FP, femoral pores summed; SDL, subdigital lamellae of left longest toe; COS, circumorbital scales summed; LSG, lateral supraocular scales summed; MS, mesoptychial scales; ILS, interlabial scales summed; SVL, snout vent length; BM, body mass, Adj r^2 , adjusted r^2 for the linear regression of clutch size on SVL; and CS, clutch size. Numbers are mean ± SE (first row) and range and sample size (second row). Only means for each character followed by all different letters are significantly different at $P < 0.05$ (Tukey HSD).

Character	<i>A. l. B</i> ♀♀+	<i>A. g.</i> ♀♂	<i>A. s.</i> ♀♂	<i>F, P</i> Statistics	Hybrid 7247
GAB	86.7 ± 0.59 ^B 82–93 (43)	91.6 ± 0.89 ^A 86–107 (19)	78.4 ± 1.00 ^C 70–88 (15)	$F_{2,74} = 48.94, P < 0.001$	82
OR	212.7 ± 1.13 ^B 202–224 (43)	227.9 ± 1.70 ^A 208–245 (19)	198.7 ± 1.91 ^C 180–223 (15)	$F_{2,74} = 66.24, P < 0.001$	215
GAB/OR	40.7 ± 0.29 ^A 38.3–43.7 (43)	40.2 ± 0.43 ^A 36.6–44.2 (19)	39.5 ± 0.48 ^A 35.7–46.9 (15)	$F_{2,74} = 2.73, P = 0.071$	38.1
PV	15.1 ± 0.22 ^A 11–17 (43)	15.6 ± 0.33 ^A 13–19 (19)	9.0 ± 0.37 ^B 6–12 (15)	$F_{2,74} = 114.99, P < 0.001$	11
PV/GAB	17.4 ± 0.26 ^A 12.1–20.7 (43)	17.0 ± 0.39 ^A 13.1–21.6 (19)	11.4 ± 0.44 ^B 8–15.2 (15)	$F_{2,74} = 76.26, P < 0.001$	13.4
FP	33.9 ± 0.17 ^A 32–36 (43)	32.6 ± 0.45 ^B 30–38 (19)	30.6 ± 0.65 ^C 25–35 (15)	$F_{2,74} = 21.244, P < 0.001$	34
SDL	31.3 ± 0.12 ^A 30–34 (43)	29.7 ± 0.42 ^B 27–35 (19)	30.1 ± 0.51 ^B 26–33 (15)	$F_{2,74} = 8.74, P = 0.004$	33
COS	10.2 ± 0.15 ^B 8–12 (43)	12.8 ± 0.75 ^A 9–24 (19)	8.7 ± 0.27 ^B 7–11 (15)	$F_{2,74} = 24.39, P < 0.001$	13
LSG	27.0 ± 0.49 ^A 22–35 (43)	27.5 ± 1.47 ^A 18–43 (19)	25.9 ± 1.67 ^A 17–37 (15)	$F_{2,74} = 0.437, P = 0.647$	28
MS	14.4 ± 0.17 ^A 12–17 (43)	13.4 ± 0.33 ^B 11–17 (19)	12.7 ± 0.36 ^B 10–15 (15)	$F_{2,74} = 12.39, P < 0.001$	14
ILS	23.7 ± 0.92 ^{A,B} 10–38 (43)	27.6 ± 1.15 ^A 19–37 (19)	22.6 ± 0.86 ^B 18–32 (15)	$F_{2,74} = 4.52, P = 0.014$	27
SVL	73.2 ± 0.84 ^A 64–81 (30)	73.5 ± 1.16 ^A 63–85 (16)	67.7 ± 1.14 ^B 61–73 (15)	$F_{2,58} = 8.17, P = 0.007$	72
BM	9.3 ± 0.42 ^A 5.5–13.5 (22)	10.1 ± 0.60 ^A 5.9–14.2 (11)	6.9 ± 0.53 ^B 5.2–8.4 (14)	$F_{2,44} = 9.43, P = 0.004$	8.6
CS	2.4 ± 0.17 ^B 1–5 (25)	3.8 ± 0.37 ^A 3–5 (5)	2.0 ± 0.00 ^B 2 (5)	$F_{2,32} = 7.60, P = 0.020$	
ADJ r^2	0.639 $P < 0.001$	0.764 $P < 0.001$	0.448 $P = 0.005$	— —	

only to find a large number *A. sexlineata*, but only a token representation of *A. gularis*. Three visits to D-4, the only site previously known for *A. sexlineata* in western Dimmit County (Walker et al. 2004), resulted in collection of 25 and nine specimens of *A. sexlineata* and

A. gularis, respectively. Although this site is only 7.8 km SLD east of D-5 (Texas FM 2644 West) where we eventually discovered *A. laredoensis* B, it comprised very different habitat by comparison. In fact, D-4 included ecological components ideal for *A. sexlineata*;

we searched an approximately 2.03 ha area with ample exposed sandy soil, pervasive introduced Buffelgrass, large patches of prickly pear, and scattered mesquite trees (Table 4).

Body size and clutch size of whiptail lizards from D-5.—The mean SVL of adult whiptail lizards from D-5 differed significantly ($F_{2,58} = 8.18$, $P = 0.007$), and *A. sexlineata* (67.7 ± 1.14 mm) had the significantly smallest mean (Tukey HSD, $P < 0.05$) and smallest maximum SVL (72 mm) of the three syntopic species (Table 4). Similarly, the mean BM of adult whiptail lizards from D-5 differed significantly ($F_{2,44} = 9.43$, $P < 0.001$), and *A. sexlineata* (6.9 ± 0.53 mm) had the significantly smallest mean (Tukey HSD, $P < 0.05$) and smallest maximum BM (8.4 g) of the three syntopic species (Table 4). It also had the significantly smallest mean clutch size (CS = 2.0; $F_{2,32} = 7.60$, $P < 0.001$). Although *A. laredoensis* B and *A. gularis* were significantly larger (Tukey HSD, $P < 0.05$) than *A. sexlineata* in these size parameters (Table 5), they did not differ significantly from each other in mean SVL (73.3 ± 0.84 and 73.5 ± 1.16 mm, respectively) and mean BM (9.3 ± 0.42 and 10.1 ± 0.60 g, respectively). However, in comparison to *A. laredoensis* B, the data revealed larger maximum SVL (85 versus 81 mm), maximum BM (14.2 versus 13.5 g), and mean CS (3.8 versus 2.5 eggs) for *A. gularis*. There was a positive relationship between SVL and BM for *A. laredoensis* B ($F_{1,20} = 38.09$, $r^2 = 0.656$), *A. sexlineata* ($F_{1,12} = 11.55$, $r^2 = 0.500$), and *A. gularis* ($F_{1,9} = 33.39$, $r^2 = 0.788$).

Color pattern in specimens from D-5.—We used color pattern to field-identify lizards and to sort



FIGURE 4. Adult of *Aspidoscelis laredoensis* B (UADZ 7246) from D-5 (Texas FM 2644 West; 28.48944°N, 100.02056°W) in Dimmit County, Texas, USA, photographed in captivity at Louisiana State University, Eunice, during use in histocompatibility experiments (James Cordes and James Walker, unpubl. data). (Photographed by James E. Cordes).

specimens into samples in the laboratory. Those with six unbroken primary stripes (i.e., paired laterals, dorsolaterals, and paravertebrals), a vertebral stripe of variable expression, unspotted dorsum (i.e., the most telling character), blue to blue-gray tail, and white to pale blue venter were obviously specimens of *A. sexlineata*. Those with three pairs of primary stripes and a vertebral band resembling two closely applied lines, spotted/barred lower lateral fields, linearly spotted upper lateral fields, green-tan tail (Fig. 4), and white to dark blue venter were identified to *A. laredoensis* B. Those with three pairs of primary stripes and one or two vertebral stripes, brown fields, profusion of dorsal spots, reddish distal part of tail, pink-red throat (both sexes), and purple/black thoracic suffusion (males) were identified to *A. gularis*. One specimen with a color pattern intermediate to *A. laredoensis* B and *A. gularis* was identified as a hybrid of the two species.

Scutellation and meristic characters in specimens from D-5.—Specimens from D-5 possessed one of three character states pertaining to size of postantibrachial scales: essentially granular (*A. sexlineata*); moderately enlarged and essentially hexagonal (*A. laredoensis* B); and enlarged and plate-like (*A. gularis*). Each of the species had enlarged mesoptychial scales bordering the gular fold; however, only *A. sexlineata* typically had a few small scales preceding the enlarged scales at the center of the fold and the scales were noticeably larger in *A. laredoensis* B. In *A. sexlineata* and *A. laredoensis* B the circumorbital scales series on each side of the head extended anteriorly only to the division between the third and fourth supraocular scales (13 of 15 = 86.7% versus 30 of 38 = 78.9%, respectively), whereas the series typically extended more anteriorly to the midpoints of the third supraocular scales or beyond in *A. gularis* (15 of 20 = 75%).

For 11 of 12 univariate characters (excluding the SO) based on specimens of the three species from site D-5, means for GAB/OR and LSG showed no significant differences among the three species (Table 5). Means for GAB, OR, and FP were significantly different for all three species: *A. sexlineata* (lowest for all three); *A. laredoensis* B (intermediate for GAB and OR; highest for FP); and *A. gularis* (highest for GAB and OR; intermediate for FP). Means for PV and PV/GAB were not significantly different between *A. laredoensis* B and *A. gularis*, but both were significantly different from *A. sexlineata* in both characters (Table 5). Means for SDL and MS were not significantly different between *A. gularis* and *A. sexlineata*, but both were significantly different from *A. laredoensis* B in both characters (Table 5). For the COS, *A. laredoensis* B and *A. sexlineata* were not different, though both were different from *A. gularis* in the character; for the ILS *A. laredoensis* B did not differ from its progenitor species, though both of the

latter differed from each other. Data for the SO (not included in Table 5) indicate that the 4L/4R character state obtains in all specimens of *A. laredoensis* B (n = 27) and *A. gularis* (n = 19), though not in *A. sexlineata* (11 of 15 = 73.3%).

DISCUSSION

Local aspects of a guild of asexual and sexual congeners.—We found areas adjacent to the dragged zones at D-5, perhaps more related to availability of exposed sandy soil and adjacent open structure of vegetation than mechanical disturbance per se, to support larger concentrations of lizards than the undragged less sandy areas, with the former becoming intricately crisscrossed with tail tracks soon after an application. Because of the open structure of the habitat at D-5, it was typically difficult to approach individuals of each of *A. laredoensis* B, *A. gularis*, and *A. sexlineata* close enough to either observe their activities or collect them. The specimens upon which this study was based required extensive effort over many years to obtain (i.e., only 4.4 lizards/trip). However, a rough estimate of local abundance of species at the site was possible because most lizards that escaped could be field identified as *A. laredoensis* B (most abundant), *A. gularis* (intermediate in abundance), or *A. sexlineata* (least abundant) based on previously discussed distinctive color patterns if lizards could be observed even momentarily. In hand, it was always immediately apparent, except for the hybrid, which species had been collected owing to dorsal and ventral color patterns. Analyses of color patterns, size data, and meristic characters indicated that *A. laredoensis* B phenotypically resembled *A. gularis* more closely than it resembled *A. sexlineata*, notwithstanding the fact that it is a diploid cloned hybrid derivative with one genome from each species.

Site D-5, a peripheral component in the zoogeographical whole.—Our > 25 y of field investigations in Texas and the adjacent Mexican states of Coahuila, Nuevo León, and Tamaulipas have identified Dimmit County as a uniquely significant area in understanding the zoogeographic relationships of clonal complexes A and B of diploid parthenogenetic *A. laredoensis* and gonochoristic progenitors, *A. gularis* and *A. sexlineata*. Much of Dimmit County provides habitat, mostly grazed range lands, road corridors, and adjacent areas, which support one or more species of whiptail lizards. We compared guilds of *Aspidoscelis* present at six sites in Dimmit County. Predictably, based on its extensive range covering parts of Texas, New Mexico, and Mexico, *A. gularis* was the euryoecious whiptail in the county as shown by its presence at all six sites and, based on observations of its

great abundance at many additional sites, its range was county wide. However, *A. laredoensis* A was the numerically dominant species in syntopy with *A. gularis* at D-3 (Catarina) in chronically disturbed sandy habitats (e.g., horse pasture and sandy roadsides), which were less optimal for the latter (Walker et al. 2004). It remains the only site in Dimmit County, and most distant point from the Rio Grande (Walker 1987a, b), known for this parthenogenetic clonal complex (Walker et al. 1990, 2004; Paulissen and Walker 1998; Paulissen et al. 2001). Based on extensive pitfall trapping data (Ruthven et al. 1999), only locally restricted *A. sexlineata* and ubiquitous *A. gularis* are present in D-6, the 6, 156 ha Chaparral Wildlife Management Area, which is partly in Dimmit County (i.e., about 21 km ESE of D-5). Moreover, our numerous attempts to locate *A. laredoensis* A between Catarina, and Artesia Wells and Encinal in La Salle County, and the distribution area of the species in the Rio Grande Valley have been unsuccessful.

***Aspidoscelis laredoensis* A and B, independently evolving entities.**—Perhaps no observations could more persuasively emphasize the different distributional capabilities and biogeographical histories of clonal complexes A and B of *A. laredoensis* than the presence of the former at one known site in eastern Dimmit County and latter at one known site in the western part of the county. It is noteworthy that both A and B coexist with *A. gularis* and *A. sexlineata* in neighboring northwestern Webb County at site W-15 to the south and with *A. sexlineata* at site W-19; however, only six individuals of Six-lined Racerunner have been collected in many visits to those sites (see Walker et al. 2001). It is probable that *A. sexlineata* has a more or less continuous distribution between western Webb County sites and Dimmit County sites D-4 (i.e., Texas FM 2644 East) and D-5 (i.e., Texas FM 2644 West) about 40 km to the northwest through the Carrizo Sand Formation (Geologic Atlas of Texas: Crystal City-Eagle Pass Sheet). Based on collecting data for the period 2000–2005, *A. laredoensis* B successfully coexists with large numbers of its gonochoristic progenitor species *A. gularis* and *A. sexlineata*, and the phrynosomatid species *Holbrookia maculata* (Lesser Earless Lizard), at D-5 in a sandy chronically disturbed roadside setting where the intricacies of habitat partitioning/niche utilization remain to be fully explored.

This example of coexistence between a parthenogenetic species and both of its progenitor species does not seem consistent with Wright and Lowe's (1968) hypothesis that unisexual species of *Cnemidophorus* (= *Aspidoscelis sensu*; Reeder et al. 2002) are expected to thrive mostly in areas unsuitable for gonochoristic species. The *A. laredoensis* clonal

complexes typically coexist with *A. gularis* (Paulissen et al. 1992) even though their diet and microhabitat usage overlap extensively and the potential for competition is high (Paulissen 2001). What was unusual in this case was the syntopy between *A. laredoensis* B and its other gonochoristic progenitor *A. sexlineata*. Unlike the generalist *A. gularis*, the ecological requirements of *A. laredoensis* B and *A. sexlineata* appear to be very narrow, so much so that few sites have the combination of ecological conditions and geographic proximity to source populations that enable both *A. laredoensis* B and *A. sexlineata* to disperse to and survive in the same place. Site D-5 is the one such site and to date is the only one we have found during our extensive field work in south Texas and northern México where *A. sexlineata* is similar in abundance to one of the clonal complexes of *A. laredoensis*.

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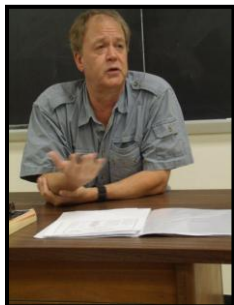
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