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Authors: MANNING, GLENN J., COLE, CHARLES J., DESSAUER, HERBERT C., and WALKER, JAMES M.

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Hybridization Between Parthenogenetic Lizards (*Aspidoscelis neomexicana*) and Gonochoristic Lizards (*Aspidoscelis sexlineata viridis*) in New Mexico: Ecological, Morphological, Cytological, and Molecular Context

GLENN J. MANNING,[1] CHARLES J. COLE,[2] HERBERT C. DESSAUER,[3] AND JAMES M. WALKER[4]

CONTENTS

[1] Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701 (gmannin@uark.edu).
[2] Division of Vertebrate Zoology (Herpetology), American Museum of Natural History (cole@amnh.org).
[3] Division of Vertebrate Zoology (Herpetology), American Museum of Natural History; Department of Biochemistry and Molecular Biology, Louisiana State University Medical Center, New Orleans, LA 70112.
[4] Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701 (jmwalker@uark.edu).

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ABSTRACT

Whiptail lizard guilds consisting of different combinations of parthenogenetic *Aspidoscelis exsanguis*, *Aspidoscelis neomexicana*, and *Aspidoscelis tesselata* pattern classes C and D and gonochoristic *Aspidoscelis sexlineata viridis* inhabit numerous sites in the immediate vicinity of Conchas Lake, San Miguel County, New Mexico. Based on morphological identification by other workers of specimens collected in 1978, *A. neomexicana* was the species most recently added to the list of whiptail lizards known to occur at Conchas Lake, about 190 km east of its main distribution area in the Rio Grande Valley. We sampled guilds consisting of *A. neomexicana* and its congeners at Conchas Lake from 2000 through 2003. In 2002 we also collected specimens of what appeared to be another tokogenetic array of *A. neomexicana* east of the Rio Grande Valley in syntopy with *A. tesselata* E and *A. sexlineata viridis* at Fort Sumner, De Baca County, New Mexico. Comparison of karyotypes revealed that individuals of *A. tesselata* and those assigned by their discoverers to *A. neomexicana* from Conchas Lake and Fort Sumner have identical diploid karyotypes ($2n = 46$) that include diagnostic haploid complements of chromosomes derived from independent hybridizations between species in the *tigris* and *sexlineata* species groups. Consequently, we used electrophoretic data for 23 gene loci, of which the sMDH, sMDHP, sIDH, ESTD, PEPA, PEPB, ADA, MPI, GPI, and PGM2 loci were definitive, to further validate the hypothesis that the disjunct groups of putative *A. neomexicana* in eastern New Mexico had been correctly identified. The specimens analyzed electrophoretically also indicated that the Conchas Lake clone of *A. neomexicana* is identical to the most widely distributed clone of the species in the Rio Grande Valley of New Mexico and that the Fort Sumner clone possessed a distinctive allele.

We describe the habitat for *A. neomexicana* at Conchas Lake at three sites north of the Canadian River and two sites south of the river. Two of the sites north of the Canadian River were studied as examples of guilds that did not include *A. sexlineata viridis*. The latter species was observed with *A. neomexicana*, *A. tesselata*, and *A. exsanguis* at one site north of the Canadian River and two sites south of the river. At Fort Sumner, we studied *A. neomexicana* at two sites where it was syntopic with *A. tesselata* E and *A. sexlineata viridis*.

We identified 15 lizards from three sites at Conchas Lake as hybrids of *A. neomexicana* × *A. sexlineata viridis*. Most of these hybrids were found in either patchy or weedy chronically disturbed habitats in which the parental forms were forced into unusually close syntopic relationships. Hybrids between these parental forms were collected in each year from 2000–2003 and represented a minimum of four and a maximum of five generations.

Although hybrids of *A. neomexicana* × *A. sexlineata viridis* were characterized by distinctive color patterns, all were rather similar to maternal parent *A. neomexicana*, but with modifications resulting from the genetic contribution of its paternal parent *A. sexlineata viridis*. All specimens identified as hybrids by color pattern also possessed meristic characters that distinguished them from both parental forms. Univariate and multivariate analyses of scutellation also revealed evidence of the genetic effects of the parental species on the hybrids.

One live hybrid male of *A. neomexicana* × *A. sexlineata viridis* was collected at Conchas Lake. The hybrid (American Museum of Natural History R-151739) was a triploid ($3n = 69$) including the complete diploid complement of *A. neomexicana* (= *A. tigris marmorata* × *A. inornata*) plus a second haploid complement of *sexlineata* group chromosomes. Karyotypically, in all details this triploid appeared to be an F_1 hybrid of *A. neomexicana* × *A. sexlineata viridis*. This confirmed hybrid possessed a similar array of color pattern and scutellation characters observed in the other individuals of presumptive *A. neomexicana* × *A. sexlineata viridis* from Conchas Lake. Of the 23 allozyme loci analyzed, 9 showed no allelic variation among the individuals of the parental taxa and the hybrid examined; however, 12 loci were particularly informative for identifying the hybrid and its parental species. For most of these loci, the suspected hybrid (based on morphology and triploid karyotype) had electrophoretic banding patterns consistent with a triploid bearing a combination of alleles that included the two found in diploid *A. neomexicana* plus a third allele from the local *A. sexlineata viridis*. This is consistent with a cloned *A. neomexicana* ovum having been fertilized by a haploid *A. sexlineata viridis* spermatozoan.

We present the first evidence of perennial hybridization in *Aspidoscelis* between a parthenogen and a species other than a progenitor. However, we found no evidence that occasional

hybridization between *A. neomexicana* and *A. sexlineata viridis* has had a significant negative effect on either of these species at Conchas Lake.

INTRODUCTION

Complex geographic and physiographic features similar to those exploited in the impoundment of Conchas Lake have also formed terrestrial habitats that support diverse communities of diurnal ground-dwelling lizards (Teiidae: *Aspidoscelis* Fitzinger, 1843) in San Miguel County, New Mexico. A combination of three cloned hybrid all-female species (*Aspidoscelis exsanguis*, *Aspidoscelis neomexicana*, and *Aspidoscelis tesselata* pattern classes C and D) and one gonochoristic species (*Aspidoscelis sexlineata viridis*) occur in the variety of habitats in the immediate vicinity of Conchas Lake. The most recently discovered of these populations, identified as *Cnemidophorus neomexicanus* (= *A. neomexicana*) on the basis of morphology by Leuck et al. (1981), was separated by a hiatus of about 190 km from the nearest record known at that time for the species in the Rio Grande Valley at San Pedro, Sandoval County, New Mexico. Based on zoogeographic considerations and fieldwork conducted at Conchas Lake by students of whiptail lizards such as J.W. Wright (Wright and Lowe, 1967, 1968; Wright, 1971; Tanner, 1975; Densmore et al., 1989), E.D. Parker, Jr. (Parker and Selander, 1984), and CJC (Cole et al., 1988) that did not reveal the presence of *A. neomexicana* there prior to 1978, Cole et al. (1988), Degenhardt et al. (1996), and Persons and Wright (1999) agreed with the stated opinion of Leuck et al. (1981) that its occurrence in San Miguel County probably resulted from introduction by humans. Recently, disjunct populations identified as *A. neomexicana* have also been reported in Petrified Forest National Park in the Rio Puerco Valley, Apache County, Arizona, by Persons and Wright (1999) and in Fort Sumner in the Pecos River Valley, De Baca County, New Mexico, by Taylor (2002). Not unlike the discovery of this species at Conchas Lake, confirmation of its presence in Fort Sumner by Taylor (2002) was preceded by the field studies of other investigators including E.D. Parker, Jr. (Parker and Selander, 1984) and JMW (Taylor et al., 1997), who found only *A. sexlineata viridis* and *A. tesselata* in the city. At present, *A. neomexicana* (mostly limited to the Rio Grande Valley except for a few disjunct groups) is known to be syntopic with *A. sexlineata viridis* (limited in New Mexico to the eastern part of the state) only at Conchas Lake (Walker et al., 1990, 1992) and Fort Sumner (this study).

Aspidoscelis neomexicana is an obligate parthenogenetic species of cloned descent from one or a few hybrids of *A. tigris marmorata* ♀ × *A. inornata* ♂ (Lowe and Wright, 1966a, 1966b; Neaves, 1969; Cuellar, 1977; Brown and Wright, 1979; Parker and Selander, 1984; Cole et al., 1988; Densmore et al., 1989). Nevertheless, at several sites along the Rio Grande in New Mexico, an unusual interruption in parthenogenetic reproduction occurs when occasional insemination of females of *A. neomexicana* by males of its paternal progenitor *A. inornata* produces hybrids (Axtell, 1966; Taylor and Medica, 1966; Wright and Lowe, 1967; Christiansen and Ladman, 1968; Christiansen et al., 1971; Cuellar and McKinney, 1976; Taylor and Walker, 1996). Also, hybrids of *A. neomexicana* × *A. tigris* have been reported from Hidalgo and Grant counties, New Mexico (Dessauer et al., 2000). The apparently sterile hybrids of *A. neomexicana* × *A. inornata* reported to date have included both allotriploid females and males; the two reported hybrids of *A. neomexicana* × *A. tigris* were sterile allotriploid females. Walker et al. (1990) also described one hybrid male and mentioned a putative hybrid female of *A. neomexicana* × *A. sexlineata viridis* from Conchas Lake. That report stimulated GJM to undertake an intensive field study in 2000–2003 to understand ecological and morphological aspects of hybridization between these species. Subsequently, the study was expanded to a collaboration among the present authors to include cytological and molecular aspects of hybridization between *A. neomexicana* and *A. sexlineata viridis*.

We have determined that the species com-

position and local distribution of *Aspidoscelis* guilds at Conchas Lake reflect site- specific ecological characteristics largely resulting from human activities. During the study, the most widely distributed species at Conchas Lake were *A. neomexicana* and *A. tesselata* C, whereas the forms with more restricted local distributions were *A. sexlineata viridis*, *A. exsanguis*, and *A. tesselata* D. In our 2002–2003 investigation of the recently discovered populations of *A. neomexicana* in Fort Sumner (Taylor, 2002), the species was observed in syntopy with both *A. tesselata* E and *A. sexlineata viridis* at each site. At Conchas Lake and Fort Sumner, we observed that some individuals of each of the all-female species of *Aspidoscelis* present came into contact with males of *A. sexlineata viridis* during their normal activities. However, offspring resulting from occasional inseminations of normally parthenogenetic females of *A. neomexicana* by males of *A. sexlineata viridis* were the only products of hybridization that we found in the two areas.

Maslin et al. (1958), Wright and Lowe (1967), Taylor and Walker (1996), and Walker (1997) have contributed to the controversy involving the genealogy of the lectotype of *Cnemidophorus perplexus* Baird and Girard, 1853, for which no genetic data exist. Based on morphology, Wright and Lowe (1967) concluded that this type specimen is a hybrid female of *C. neomexicanus* × *C. inornatus* (= *A. neomexicana* × *A. inornata*), whereas Maslin et al. (1958), Taylor and Walker (1996), and Walker (1997) inferred that this type is merely an unusually large individual of *C. neomexicanus* (= *A. neomexicana*). This case convincingly shows that opinions can vary on whether certain female specimens resembling *A. neomexicana* in color pattern and scutellation are unusual individuals of this species or hybrids between it and a gonochoristic species.

Ideally, then, all of the putative hybrids of *A. neomexicana* × *A. sexlineata viridis* reported herein would have been accompanied by genetic data verifying their parentage. Unfortunately, because of their extreme wariness, only 1 of 13 putative hybrids from the vicinity of the South Recreation Area at Conchas Lake could be obtained alive for subsequent karyotypic and electrophoretic analyses. Nevertheless, we join Walker et al. (1989, 1990, 1994, 2000), and Taylor et al. (2001) in the opinion that it becomes possible to use subtle morphological characters to identify hybrids between an all-female and gonochoristic species of *Aspidoscelis* lacking genetic data, particularly when compared with additional specimens having genetic data.

This collaboration focused on obtaining ecological (GJM and JMW), morphological (GJM and JMW), karyotypic (CJC), and electrophoretic (CJC and HCD) data forming the biological context within which to answer the following questions: (1) Are the specimens from Conchas Lake and Fort Sumner that appeared to be *A. neomexicana* really this species or are they something else, such as a variant of *A. tesselata* or a new species? (2) Are the specimens from Conchas Lake and Fort Sumner that appear to be *A. neomexicana* representatives of the same clone? (3) Are the apparent hybrids of *A. neomexicana* × *A. sexlineata viridis* (N = 15) from Conchas Lake really that, that is, triploids with genomes from three ancestral gonochoristic taxa (*A. neomexicana* [= *A. tigris marmorata* × *A. inornata*] × *A. sexlineata viridis*)? (4) How do the protein genotypes for a hybrid compare with its parental species? (5) Is the presence of the hybrid genome accompanied by a unique combination of features of color pattern compared to variation in the parental species? (6) What patterns of univariate and multivariate morphological variation can be discerned in hybrids of *A. neomexicana* × *A. sexlineata viridis* in comparison to their parental species? (7) What are the reproductive consequences of the hybrid genome? (8) What ecological conditions facilitate hybridization between *A. neomexicana* and *A. sexlineata viridis* at Conchas Lake?

MATERIALS AND METHODS

Taxonomic Treatment and Pattern Class Designations

We followed Reeder et al. (2002) in using the recently resurrected generic name *Aspidoscelis* for the North and Central American parthenogenetic and gonochoristic species of whiptail lizards in the *cozumela*, *deppei*, *sex-*

lineata, *tesselata*, and *tigris* species groups recently partitioned from *Cnemidophorus* to partially resolve paraphyly in that genus. Spellings of the names *neomexicana*, *sexlineata*, and *tesselata* reflect the femine gender of *Aspidoscelis* (Reeder et al., 2002). We reference the two color pattern variants of *A. tesselata* at Conchas Lake as C (sensu Zweifel, 1965) and D (sensu Zweifel, 1965; Taylor et al., 1996) as a compromise position preferred by GJM and JMW pending further study (Manning and Walker, unpubl.) of the statistically based C-E redesignation of C by Taylor et al. (2003).

Study Sites at Conchas Lake and Fort Sumner

Conchas Lake is an Army Corps of Engineers impoundment. Land joining the north shore of the Conchas River arm and the west shore of the Canadian River arm of the lake are parts of private ranches, as are parts of the south and east shores. Conchas Lake State Park comprises the disjunct North, Central, and South Recreation areas, which are surrounded by either Corps or private lands (fig. 1). Although state and federal officials permitted access to *Aspidoscelis* study sites at Conchas Lake in 2000–2003, private land owners in the area did not. The latter limitation prevented GJM from searching for additional groups of *A. neomexicana* on the east shore of the Canadian River part of Conchas Lake and south along the river.

We assigned a code to sites inhabited by *A. neomexicana* at Conchas Lake consistent with those used by Walker et al. (1992: fig. 1) and we assigned a name to each site (this study; table 1, fig. 1). Each code was based on CL (= Conchas Lake) and the numerical order of the date of discovery of *A. neomexicana* at the site (* denotes that *A. neomexicana* × *A. sexlineata viridis* hybrids also have been collected at the site). Three sites north of the Canadian River (South of Clabberhill Ranch [CL-1*], Cove Campground [CL-13], and North of Canadian River [CL-4]) and two sites south of the river (East of Conchas Lake Levee [CL-5*] and South Recreation Area [CL-2*]) were relevant to this study (table 1). Site CL-5* included two ecological components, and CL-2* included five components (table 1). We did not observe *A. sexlineata viridis* at CL-13 and CL-4; however, these sites were included because assessment of the biological significance of hybridization between *A. neomexicana* and *A. sexlineata viridis* should be evaluated in the context of the extent of syntopy between these species in the larger Conchas Lake area. Straight-line distances between sites and components at Conchas Lake are given in kilometers in table 2.

The sites referenced for *A. neomexicana* in De Baca County included FS-1 (Fort Sumner–De Baca County Landfill) adjacent to the suburbs of Fort Sumner and FS-2 (Fort Sumner–Railroad Depot) within the city. Both De Baca County and City of Fort Sumner officials with jurisdiction over these areas facilitated this study in 2002 and 2003 by allowing access to *Aspidoscelis* study sites.

Field Studies at Conchas Lake and Fort Sumner

On 12 July 1988, JMW and J.E. Cordes visited the Valley–plateau-hill Component (CL-5VPH*) at East of Conchas Lake Levee (CL-5*) to acquire individuals of *A. tesselata* pattern classes C and D for skin histocompatibility experiments (Cordes and Walker, 2003). Among the 62 specimens collected on this date were one individual of *A. neomexicana* and one apparent *A. neomexicana* × *A. sexlineata viridis* hybrid (Walker et al, 1990). Subsequently, JMW and colleagues returned to the lake to study

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Fig. 1. Map from Maptech (vers. 5.03. 2001. Amesbury, MD) showing distribution of study sites for *Aspidoscelis* at Conchas Lake, San Miguel County, New Mexico: South of Clabberhill Ranch (CL-1* = 1), Cove Campground (CL-13 = 13), North of Canadian River (CL-4 = 4), East of Conchas Lake Levee (CL-5* = 5), and South Recreation Area (CL-2* = 2). Hybrids of *A. neomexicana* × *A. sexlineata viridis* have been collected at sites numbered from north to south 1, 5, and 2 in order of their discovery.

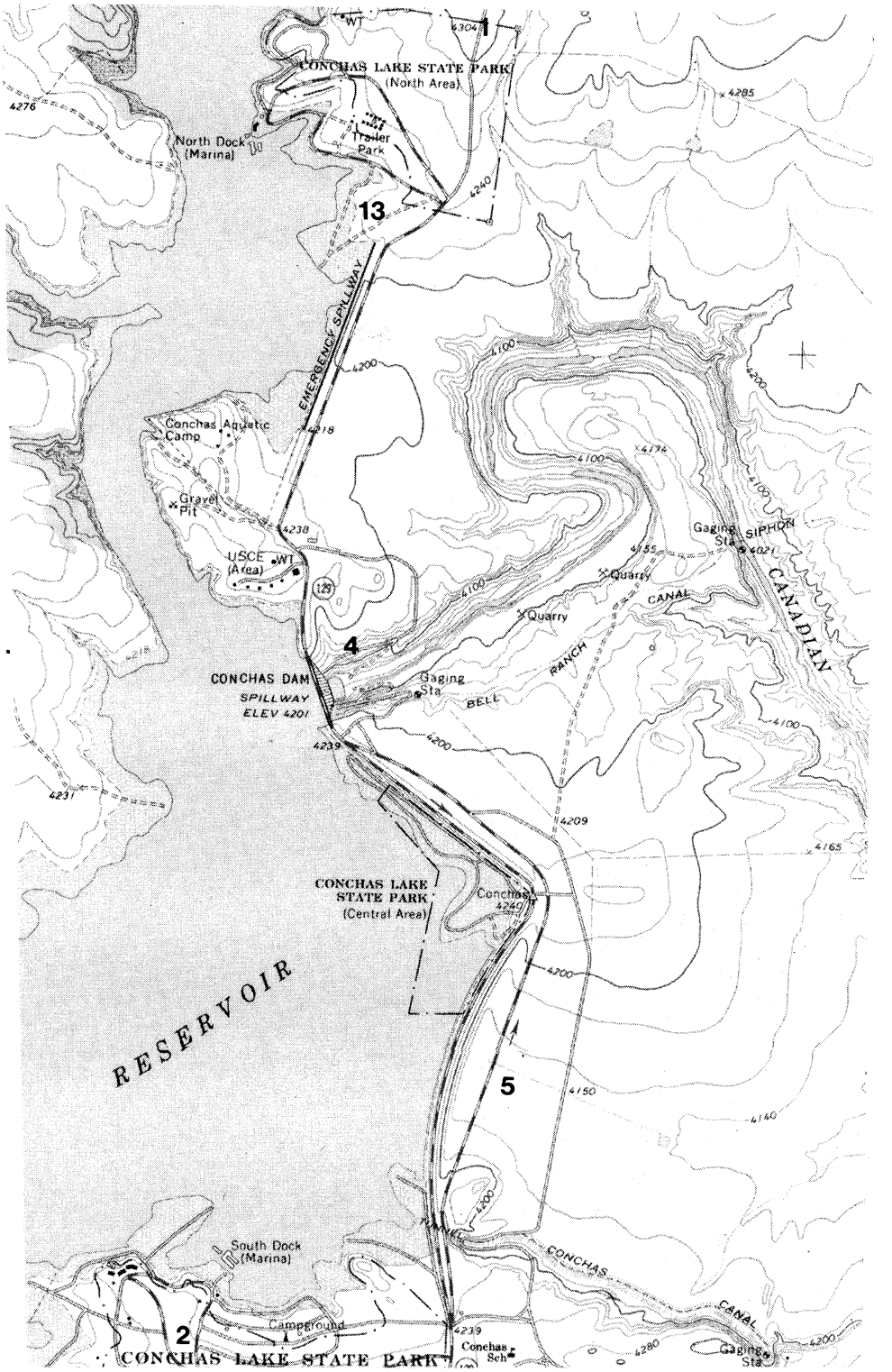

TABLE 1

Study Sites and Their Components, Date of Discovery and Discoverers of *Aspidoscelis neomexicana*, and Species of *Aspidoscelis* Known to Occur at Each Site Listed in Order of Their Inferred Abundance Based on Collecting Records

Site code (and name); Date of discovery and discoverers of *Aspidoscelis neomexicana* at site Codes and names of habitat components, if designated Composition of *Aspidoscelis* guild at site or component
CL-1*[a] (South of Clabberhill Ranch); 22 July 1978 by B.E. Leuck et al. No components designated *A. neomexicana*, *A. tesselata* C, *A. exsanguis*, *A. sexlineata viridis*
CL-13 (Cove Campground); 22 June 2000 by G.J. Manning No components designated *A. neomexicana*, *A. tesselata* C
CL-4 (North of Canadian River); 8 July 1988 by B.E. Leuck et al. No components designated *A. tesselata* C, *A. neomexicana*, *A. exsanguis*
CL-5* (East of Conchas Lake Levee); 12 July 1988 by J.M. Walker and J.E. Cordes CL-5V (Valley Component [= V]); 14 June 2000 by G.J. Manning *A. sexlineata viridis*, *A. tesselata* C, *A. tesselata* D, *A. neomexicana* CL-5VPH* (Valley-plateau-hill Component [= VPH]); 12 July 1988 by J.M. Walker and J.E. Cordes *A. tesselata* C, *A. neomexicana*, *A. sexlineata viridis*, *A. tesselata* D
CL-2* (South Recreation Area); 7 July 1979 by B.E. Leuck et al. CL-2C* (South Campground Component [= C]); 28 May 1990 by C.J. Cole et al. *A. neomexicana*, *A. sexlineata viridis*, *A. tesselata* C, *A. tesselata* D CL-2G (Group Shelter Component [= G]); 23 June 2000 by G.J. Manning *A. neomexicana*, *A. sexlineata viridis*, *A. exsanguis* CL-2H* (Hill Component [= H]); 19 June 2000 by G.J. Manning *A. neomexicana*, *A. sexlineata viridis* CL-2J* (Juniper Campground Component [= J]); 14 June 2000 by G.J. Manning *A. neomexicana*, *A. sexlineata viridis*, *A. tesselata* C, *A. tesselata* D CL-2L* (Lodge Component [= L]); 15 June 2000 by G.J. Manning *A. neomexicana*, *A. sexlineata viridis*, *A. tesselata* D, *A. tesselata* C, *A. exsanguis*
FS-1 (Fort Sumner-De Baca County Landfill); 9 June 2002 by H.L. Taylor No components designated *A. sexlineata viridis*, *A. neomexicana*, *A. tesselata* E
FS-2 (Fort Sumner-Railroad Depot); 12 July 2002 by G.J. Manning No components designated *A. neomexicana*, *A. sexlineata viridis*, *A. tesselata* E

[a]Sites or components marked by an asterisk (*) were sources of hybrids of *Aspidoscelis neomexicana* × *A. sexlineata viridis*.

A. neomexicana and to seek additional hybrids on 12 August 1988, 3 August 1989, 7 June 1990, and 15 July 1997. These visits resulted in discovery of *A. neomexicana* at only two sites north of the Canadian River (e.g., CL-4) where *A. sexlineata viridis* was not observed. Visits to the South Recreation Area by CJC on 22–23 May 1976, 28–29 May 1978, 19 July 1981, and 28 May 1990 produced only one *A. neomexicana* in 1990, but no hybrids. More recently, GJM conducted fieldwork at Conchas Lake on 12–15 and 17–23 June 2000, 6–15 June 2001, 17–18 and 20–21 August 2001, 5–9 June 2002, and 12–13 August 2003 specifically to locate syntopic associations of *A. neomexi-*

TABLE 2
Computer-Generated Straight-Line Distances in Kilometers Between *Aspidoscelis* Study Sites and Their Ecological Components at Conchas Lake, San Miguel County, New Mexico

	Sites and Components									
	CL-1*	CL-13	CL-4	CL-5V	CL-5VPH*	CL-2C*	CL-2G	CL-2H*	CL-2J*	CL-2L*
CL-1*		0.884	2.899	4.041	5.150	5.908	5.674	5.850	5.714	5.775
CL-13			2.082	3.471	4.413	5.062	4.908	4.992	4.840	4.874
CL-4				1.985	2.395	3.044	2.864	3.015	2.854	2.916
CL-5V					1.724	2.962	2.414	3.072	3.220	3.205
CL-5VPH*						1.241	0.705	1.398	1.692	1.644
CL-2C*							0.619	0.250	0.613	0.654
CL-2G								0.809	1.127	1.172
CL-2H*									0.369	0.431
CL-2J*										0.082

cana and *A. sexlineata viridis*, and to search for hybrids between the two species.

Upon learning of the discovery of *A. neomexicana* at Fort Sumner (H.L. Taylor, personal commun.; Taylor, 2002), GJM visited the city to study the species on 12–14 July 2002, 20–23 June 2003, and 15–17 August 2003. Also, a sample of *A. neomexicana* was collected at our request by J. Hobart at Fort Sumner on 25 July 2002.

Sampling Methods at Conchas Lake and Fort Sumner

On 12 July 1988, JMW and J.E. Cordes sampled the *Aspidoscelis* guild at East of Conchas Lake Levee (CL-5*), technically outside of Conchas Lake State Park, using BB air guns with permission of personnel of the Corps of Engineers. This method resulted in collection of about 40% of the *A. sexlineata viridis*, 60% of the *A. tesselata* C and D, the only *A. neomexicana*, and the only *A. neomexicana* × *A. sexlineata viridis* seen and identified on that date. On 12 August 1988 additional *A. tesselata* C and D and the only individual of *A. sexlineata viridis* observed were collected using the same method. Thereafter, sampling at Conchas Lake involved use of large rubber bands to collect whiptail lizards. Unlike the less wary species *A. exsanguis* and *A. tesselata* C and D, which could be collected more often than not with rubberbands, about 75–80% of individuals of *A. neomexicana* and *A. sexlineata viridis* evaded collection, especially when only one investigator was involved. At Fort Sumner, *A. neomexicana* and *A. sexlineata viridis* were also very difficult to collect with rubberbands. In fact, our inability to collect most of the individuals of *A. neomexicana* and *A. sexlineata viridis* observed, and presumably those of *A. neomexicana* × *A. sexlineata viridis*, was the most significant limiting factor encountered in our studies at Conchas Lake and Fort Sumner.

To understand the presence and relative abundance of each species of *Aspidoscelis* at study sites in both areas, GJM counted the whiptail lizards encountered that were either identified to species or noted as unidentified *Aspidoscelis*, but not collected, on each date. We also attempted to identify the habitat features affecting the composition of *Aspidoscelis* guilds and those that appeared to facilitate interbreeding between *A. neomexicana* and *A. sexlineata viridis*.

The live-captured lizards used in this study (one *A. neomexicana* from Conchas Lake and one from Fort Sumner and one hybrid male *A. neomexicana* × *A. sexlineata viridis* from Conchas Lake) were obtained with difficulty by GJM. The live lizards were transported from New Mexico by him and subsequently shipped to CJC for color photography, karyotyping, and dispensation of tissues to HCD for electrophoretic analysis.

Specimens of *Aspidoscelis* referenced in this report (appendices 1–8) bear numbers representing the American Museum of Natural History (AMNH), University of Arkan-

sas Department of Zoology (UADZ), Los Angeles County Museum (LACM), University of New Mexico Museum of Southwestern Biology (MSB), and Oklahoma Museum of Natural History (OMNH).

Internal Examination of Hybrids and Parental Species

We did not conduct internal examination of two specimens of *A. neomexicana*, LACM 128281 from Conchas Lake (appendix 1) and MSB 65617 from Fort Sumner (appendix 6). All other lizards listed in the appendices were examined internally for the purposes of sex determination and assessment of reproductive status.

Estimation of the Year of Hatching of Hybrids and Their Maternal Progenitor

We used the graphic method devised by JMW (Taylor et al., 2001) to depict inferences pertaining to the number of generations of hybrids of *A. neomexicana* × *A. sexlineata viridis* represented in our 2000–2003 collections from the South Recreation Area. Estimation of the age of a lizard at the time of collection was based on its snout–vent length.

Analyses of Color Patterns in Hybrids and Parental Species

At Conchas Lake, *A. exsanguis*, *A. neomexicana*, *A. sexlineata viridis*, and *A. tesselata* C and D have distinctive color patterns from hatchling through adulthood. At Fort Sumner, *A. neomexicana*, *A. sexlineata viridis*, and *A. tesselata* pattern class E also have distinctive color patterns throughout ontogeny. The differences among these species are based on variation in the following components: ground color, the dark dorsal pigmentation surrounding all of the pale colored components; lateral, dorsolateral, and paravertebral primary stripes and the middorsal or vertebral stripe(s), the longitudinally arrayed series of pale-colored granules extending the length of the body; fields, the dark longitudinal zones of ground color between the light stripes; bars, the elongate areas of pale pigment in the fields situated at right angles to the stripes; and spots, the rounded to irregularly shaped areas of pale-colored granules in the fields and on the stripes. Dorsal tail coloration also differs among the forms of *Aspidoscelis* at Conchas Lake and Fort Sumner, as does ventral coloration to a lesser extent. We initially identified all hybrids reported herein on the basis of unusual combinations of certain of the aforementioned features of color pattern.

Analyses of Scutellation in Hybrids and Parental Species

We studied meristic characters (i.e., scutellation) in selected samples of *Aspidoscelis* to confirm the identities of suspected hybrids of *A. neomexicana* × *A. sexlineata viridis* and to assess the morphological relationship of hybrids to the parental species and to *A. tesselata* C.

For each specimen, we noted the anterior extent of the left and right circumorbital scale series (complete, to junction of 2nd and 3rd supraocular scales, to a point opposite 3rd supraoculars, etc.), size of the mesoptychial scales bordering the edge of the gular fold (small, greatly enlarged, or enlarged), size of the postantebrachial scales on the posterior surface of each forelimb (granular, slightly enlarged, or enlarged), and condition of the preanal scales (one or two).

We made counts of a suite of meristic variables on each specimen used in univariate and multivariate comparisons. These characters included: GAB, granules (= scales) around midbody; OR, granules from occiput to rump; PV, granules separating the paravertebral stripes at midbody; FP, sum of the left and right femoral pores; SDL, number of subdigital lamellae on the fourth toe of the left foot; COS, sum of the left and right circumorbital scales medial to the supraocular scales; LSG, sum of the left and right lateral supraocular granules; MS, number of enlarged mesoptychial scales in the transverse row bordering the gular fold (count not possible in *A. neomexicana* because of lack of scale enlargement); and ILS, sum of the left and right interlabial scales.

Several authors have employed multivariate statistics to compare *Aspidoscelis* hybrids with their candidate parental species (Walker et al., 1994, 2000; Taylor and Walker, 1996; Walker, 1997; Taylor et al., 2001; and see

Cole et al., 1988, for a species of hybrid origin). We used desktop PC based software (JMP 5.0.1.2, SAS Institute) in accordance with the JMP users' manual (SAS 2002) to perform principal component (PC) and canonical variate (CV) analyses. We used three groups of lizards from CL-2* identified on the basis of color pattern and variation in the size of the mesoptychial scales and anterior extent of circumorbital scale series (see Results) as *A. neomexicana* × *A. sexlineata viridis* ($N = 13$), *A. neomexicana* ($N = 49$), and *A. sexlineata viridis* ($N = 26$). Initially, we were compelled to consider the possibility that the Conchas Lake form identified by Leuck et al. (1981) and Walker et al. (1990, 1992) as an enigmatic disjunct group of *A. neomexicana* was possibly a new clone of *A. tesselata*, in which case this species would be the maternal parent of the hybrids. This reasoning accounted for the inclusion of *A. tesselata* C from CL-5* ($N = 26$ specimens with complete data) in both the CV and PC procedures. In addition, specimen UADZ 7448 from site CL-2* resembled juveniles of *A. tesselata* C in certain features of color pattern, raising the alternative possibility that two types of hybrids were present in samples from the site.

We followed Cole et al., (1988), Taylor and Walker (1996), and Taylor et al. (2001) in using a PC analysis to provide an unbiased multivariate comparison to results obtained from the CV analysis. Specimens are not allocated to a priori groups in the PC procedure, which was based on the correlation matrix generated from the eight meristic variables examined in each specimen (GAB, OR, PV, FP, SDL, COS, LSG, and ILS). Factors with eigenvalues greater than 1.0 were selected for interpretation in the PC model.

We used a CV analysis based on the covariation among counts of the above meristic variables to generate scores for plotting on two CV axes. This resulted in a graphic portrayal of the multivariate relationships between the four samples of *Aspidoscelis* from Conchas Lake chosen for the analysis. Mahalanobis distance (D^2) was used to compare the patterns of meristic variation among the a priori groups in the CV analysis.

Equations generated in the CV and PC procedures were employed to obtain scores for two specimens, in addition to UADZ 7448, not assigned to a priori groups. They included UADZ 3272 (= AMNH 144085) from CL-5*, identified using univariate analyses and color pattern as an *A. neomexicana* × *A sexlineata viridis* hybrid male by Walker et al. (1990), and an unusual female specimen collected by B.E. Leuck at CL-1* (OMNH 35109). The scores of these individuals were plotted to show their group affinities in the PC and CV graphics.

Analyses of Karyotypes in Hybrids and Parental Species

We used previously published methods for preparing and studying standard giemsa-stained chromosomes from bone marrow cells (Cole, 1979). In addition to examining karyotypes of *A. neomexicana* previously published (see Lowe and Wright, 1966a; Dessauer and Cole, 1984; Cole et al., 1988), for this report we examined 16 cells at miotic metaphase from three apparent *A. neomexicana* (two from Conchas Lake and one from Fort Sumner) and 10 cells from an apparent male hybrid of *A. neomexicana* × *A. sexlineata viridis* from Conchas Lake. In addition, we examined 24 cells from five specimens of *A. sexlineata viridis* (four from Conchas Lake and one from Colorado) for this report.

Analyses of Allozymes in Hybrids and Parental Species

New electrophoretic data for 23 gene loci are provided, based on the same four specimens mentioned above as karyotyped for this paper (three *A. neomexicana* and the apparent hybrid; see appendices 2, 5, and 7). We selected the loci that are most informative for addressing the questions involved, including the loci that are diagnostic for *A. neomexicana* from other localities (Cole et al., 1988), with which comparisons are also made here. It was not necessary to examine proteins from additional specimens of *A. sexlineata viridis* for this report (see Dessauer and Cole, 1984, 1989, and unpubl.; Cole et al., 1988); our most recent dataset for *A. sexlineata viridis* from throughout its range includes 30 individuals.

Methodology for preparation of tissue homogenates, conducting electrophoresis, lo-

calizing specific proteins, and scoring gel phenotypes in the context of gene products followed Harris and Hopkinson (1976), Murphy et al. (1996), and particularly for North American lizards of the genus *Aspidoscelis*, Dessauer et al. (2000). For each locus, alleles are designated in alphabetical order according to decreasing anodal migration of their allozymes. For multilocus enzymes, loci are listed numerically in order of decreasing anodal migration of their isozymes.

RESULTS

Aspidoscelis at Site CL-1* (South of Clabberhill Ranch)

The first of the four lizards used by Leuck et al. (1981) to voucher the presence of *A. neomexicana* at Conchas Lake (LACM 128281) was collected in 1978 ''near the entrance to the Clabber Hill [= Clabberhill] Ranch'' (about 500 m south of the ranch gate; Leuck, personal commun.; Walker et al., 1992 [CL-1 on map]; fig. 1 this study). This specimen and an apparent hybrid female of *A. neomexicana* × *A. sexlineata viridis* (OMNH 35109), *A. exsanguis*, and *A. tesselata* (Leuck, personal commun.) were found in habitat described by Leuck et al. (1981) as ''open Juniper-grassland on sandstone substrate.''

The part of site CL-1* investigated by GJM in 2000–2003, about 500 m northwest of the point of origin of Leuck's specimens, marked the known distributional limit of *A. neomexicana* north of the Canadian River and provided the only known site of syntopy between *A. neomexicana* and *A. sexlineata viridis* north of the river in San Miguel County, New Mexico. Here, sandy mesquite-invaded grassland (preferred by *A. sexlineata viridis*, foreground in fig. 2) merges with a hilly area with junipers (preferred by *A. neomexicana*, background in fig. 2). In four visits to CL-1* in 2000–2003, GJM collected 14 *A. neomexicana*, two *A. exanguis*, two *A. tesselata* C, and observed two *A. sexlineata viridis* (appendix 1). We hypothesized that the lack of a disturbed transition zone between the grassland and hill components at South of Clabberhill Ranch (fig. 2) had minimized syntopic interactions and the likelihood of hybridization between *A. neomexicana* and *A. sexlineata viridis* here. The only putative hybrid from CL-1* remains OMNH 35109 collected by B.E. Leuck and colleagues in 1978.

Aspidoscelis at Site CL-13 (Cove Campground)

Aspidoscelis neomexicana was abundant at Cove Campground (tables 1, 2), the source of specimen AMNH R-151740 used in our karyotypic and electrophoretic analyses. Site CL-13 consisted of a relatively open-structured assemblage of grasses, weeds, and scattered mesquites (fig. 2). Flat topography, periodic mowing, and use by humans constituted the primary nonclimatic modifiers of habitat structure at CL-13. In three visits to the site, GJM collected 12 *A. neomexicana* and five *A. tesselata* C (appendix 2). This enclave of *Aspidoscelis* habitat, like most that we sampled north of the Canadian River, was temporally inhabited only by parthenogenetic species to the exclusion of *A. sexlineata viridis*.

Aspidoscelis at Site CL-4 (North of Canadian River)

Site CL-4 is located on the north side of the Canadian River near the dam (tables 1–3; fig. 1; appendix 3). It extends from the hilltop east of a parking lot to a bench ele-

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Fig. 2. Habitats located north of the Canadian River and east of Conchas Lake, San Miguel County, New Mexico. **Top.** Looking north–northwest at the transition from relatively stable mesquite-grassland (foreground) to juniper-dotted hills (background) at South of Clabberhill Ranch (CL-1*) from which individuals of *Aspidoscelis neomexicana*, *A. tesselata* C, *A. exsanguis*, *A. sexlineata viridis*, and *A. neomexicana* × *A. sexlineata viridis* have been collected. **Bottom.** Looking south-southwest at degraded mesquite-grassland at Cove Campground (CL-13) from which individuals of *Aspidoscelis neomexicana* (including AMNH R-151740 used in karyotypic and electrophoretic analyses in this study) and *A. tesselata* C have been collected.

Fig. 3. A relatively stable topographically and ecologically complex area located north of the Canadian River and east of Conchas Lake Dam as viewed from the south side of the river, San Miguel County, New Mexico. North of Canadian River (CL-4); V near middle shows the area with open-structured mesquite, grasses-weeds, and junipers along an unpaved road on the upper bench near a precipice from which individuals of *Aspidoscelis neomexicana*, *A. tesselata* C, and *A. exsanguis*, but not *A. sexlineata viridis* or *A. tesselata* D, have been collected; lower V shows bench near the river with dense mesquite, grasses, and weeds in which only individuals of *A. neomexicana* have been observed. The presence of *Aspidoscelis neomexicana* along the rocky precipice at CL-4, from which it flees into the boulders below when threatened, makes this site the most unusual known to us for the species throughout its range.

vated above the Canadian River, then about 500 m to the east. At North of Canadian River, we observed whiptail lizards on the hilltop, the steep south-facing hillside, the upper bench with an unpaved road and a precipice, the smaller bench at the base of the precipice, and in the roughlands area to the east of the upper bench (fig. 3). Plants at the site included combinations of grasses and other herbaceous vegetation, cacti, mesquites, and a few junipers in a gravelly and rocky substrate.

Most individuals of *A. neomexicana* collected and observed at CL-4 were found in a zone of about 10 m in width bordering about 100 m of the rocky precipice of the upper bench (fig. 3). Most of these lizards were found within 5 m of the edge of the precipice in the most unusual habitat known to us for *A. neomexicana*. In the first visit to CL-4 in 1988, JMW found only *A. exsanguis* and *A. tesselata* C on the hilltop and hillside. The part of the site preferred by *A. neomexicana* was not located until B.E. Leuck informed him that she had observed the species along the precipice earlier in 1988. In four out of six visits to the precipice and bench in 2000 and 2001, GJM collected four *A. neomexicana*, seven *A. exsanguis*, and seven *A. tesselata* C (table 3, appendix 3). We doubt that *A. sexlineata viridis* could become established at topographically complex CL-4. Surprisingly, *A. tesselata* D was not observed at CL-4, but was collected on the opposite side of the river.

Aspidoscelis at Site CL-5* (East of Conchas Lake Levee)

The first New Mexico whiptail (UADZ 3235 = AMNH 148599) and hybrid male *A.*

TABLE 3

***Aspidoscelis* Lizards Observed and Collected at Conchas Lake in an Area of No Contact Between Parthenogens and *A. sexlineata viridis*, CL-4 (North of Canadian River), North Side of Conchas Dam Below Picnic Area Overlooking Canadian River, 1220–1243 m, San Miguel County, New Mexico, by JMW and Associates (1988–1990, 1997) and GJM, JMW, and J.T. Briggler (2000–2001)**

	A.n.		*A.s.*		A.h.		*A.e.*		*A.t.* C		*A.t.* D		UI
	O	C	O	C	O	C	O	C	O	C	O	C	O
12 August 1988	—	0	—	0	—	0	—	1	—	1	—	0	—
12 August 1989	—	3	—	0	—	0	—	0	—	6	—	0	—
7 June 1990	—	2	—	0	—	0	—	4	—	13	—	0	—
15 July 1997	—	4	—	0	—	0	—	0	—	2	—	0	—
Subtotal	—	9	—	0	—	0	—	5	—	22	—	0	—
12 June 2000	9	3	0	0	0	0	0	6	7	3	0	0	4
15 June 2000	9	0	0	0	0	0	0	1	2	0	0	0	7
18 June 2000	0	0	0	0	0	0	0	0	1	0	0	0	0
6 June 2001	14	0	0	0	0	0	2	0	0	4	0	0	1
9 June 2001	1	0	0	0	0	0	1	0	0	0	0	0	0
17 August 2001	4	1	0	0	0	0	0	0	0	0	0	0	0
Subtotal	37	4	0	0	0	0	3	7	10	7	0	0	12

Abbreviations: *A.n., A. neomexicana* ♀♀; *A.s., A. sexlineata viridis* ♀♂; A.h., *A. neomexicana* × *A. sexlineata viridis*; *A.e., A. exsanguis* ♀♀; *A.t.* C or D, *A. tesselata* C or D ♀♀; O, observed and not collected; C, collected; UI, unknown identity; —, no data.

neomexicana × *A. sexlineata viridis* (UADZ 3272 = AMNH 144085) from CL-5* were discovered at the Valley-plateau-hill component (CL-5VPH*) by JMW and J.E. Cordes in July 1988 (Walker et al., 1990). A thorough search of this component a month later in August 1988 (Walker et al., 1992) revealed no additional hybrids or individuals of *A. neomexicana*. The 1988 studies at CL-5VPH* at East of Conchas Lake Levee resulted in observation of a greater than 60:1 ratio of each of *A. sexlineata viridis* and *A. tesselata* to *A. neomexicana*. These results led Walker et al. (1990, 1992) to state that previous collectors working at CL-5* easily could have overlooked *A. neomexicana* based on its scarcity at the site in 1988.

Ecological characteristics of the three levels comprising the CL-5VPH* component at the south end of East of Conchas Lake Levee (fig. 4) remain essentially as described by Walker et al. (1990, 1992). At CL-5VPH* (tables 1, 4; appendix 4; fig. 4), away from the base of the plateau, the relative abundance of *A. neomexicana*, *A. tesselata* C and D, and *A. sexlineata viridis* are presently similar to levels observed in 1988 (Walker et al., 1992). However, recent observations by GJM indicate that both *A. neomexicana* and *A. sexlineata viridis* are now more numerous in the immediate vicinity of the middle-level manmade plateau than recorded in 1988. In five visits to CL-5VPH* in 2000–2002, GJM collected five *A. neomexicana*, four *A. sexlineata viridis*, 17 *A. tesselata* C, two *A. tesselata* D, and no hybrids.

We refer to the topographically less complex Valley component (across the levee from the Central Campground of Conchas Lake State Park) designated East of Conchas Lake Levee as CL-5V (table 1; fig. 4; appendix 4). This is a relatively stable sandy mesquite-grassland with very few *A. neomexicana* and with large numbers of *A. sexlineata viridis*. In five visits to CL-5V in 2000–2002, GJM collected two *A. neomexicana*, 17 *A. sexlineata viridis*, five *A. tesselata* C, two *A. tesselata* D, and no hybrids.

Aspidoscelis at Site CL-2* (South Recreation Area)

The first report of *A. neomexicana* south of the Canadian River and Conchas Lake was

TABLE 4

***Aspidoscelis* Lizards Observed and Collected at Conchas Lake, CL-5* (East of Conchas Lake Levee), at Both Ecological Components in the Vicinity of 2–3 km South of Conchas Dam, or East of the South End of the Levee, Along New Mexico Highway 129, 1258–1274 m, San Miguel County, New Mexico, by JMW and J.E. Cordes (1988) and GJM and J.T. Briggler (2000–2002)**

	A.n.		*A.s.*		A.h.		*A.e.*		*A.t.* C		*A.t.* D		UI
	O	C	O	C	O	C	O	C	O	C	O	C	O
12 July 1988	—	1	—	26	—	1	—	0	—	27	—	7	—
12 August 1988	—	0	—	1	—	0	—	0	—	11	—	4	—
Subtotal	—	1	—	27	—	1	—	0	—	38	—	11	—
13 June 2000	0	0	1	0	0	0	0	0	4	2	0	0	2
14 June 2000	0	0	1	1	0	0	0	0	1	1	0	0	1
8 June 2001	0	0	1	2	0	0	0	0	5	1	1	0	0
10 June 2001	1	1	16	9	0	0	0	0	2	3	1	0	4
11 June 2001	14	0	12	1	0	0	0	0	4	2	1	1	12
17 August 2001	4	0	0	1	0	0	0	0	0	0	0	0	0
18 August 2001	2	3	1	2	0	0	0	0	0	8	0	1	1
21 August 2001	0	0	0	1	0	0	0	0	0	0	0	0	0
8 June 2002	3	2	1	0	0	0	0	0	3	5	1	0	1
9 June 2002	3	1	8	4	0	0	0	0	1	0	1	2	7
Subtotal	27	7	41	21	0	0	0	0	20	22	5	4	28

Abbreviations: *A.n., A. neomexicana* ♀♀; *A.s., A. sexlineata viridis* ♀♂; A.h., *A. neomexicana* × *A. sexlineata viridis*; *A.e., A. exsanguis* ♀♀; *A.t.* C or D, *A. tesselata* C or D ♀♀; O, observed and not collected; C, collected; UI, unknown identity; —, no data.

based on specimen OMNH 35110 collected "ca. 1.25 km SSE of the town of Conchas [= Hooverville]" in 1979 (Leuck et al. 1981). This record is within the area designated as site CL-2* (Walker et al., 1992), which we here redefine to include five ecological components located in and near the South Recreation Area (tables 1, 2, 5; fig. 1; appendix 5).

Seven visits to CL-2C*, the South Campground component at CL-2* (fig. 5), by CJC in 1976–1990 resulted in collection of numerous specimens of *A. sexlineata viridis*, *A. tesselata* C, and *A. tesselata* D. However, it was not until the last visit to CL-2C* in 1990 that an individual of *A. neomexicana* was obtained by CJC (appendix 5). More recently, GJM found that *A. neomexicana* is now the most abundant species at the part of CL-2C* that is along a row of trees bordered by large blocks of rock among grasses and other herbaceous vegetation (fig. 5). In five out of eight visits in 2000–2003, he obtained 14 *A. neomexicana*, six *A. sexlineata viridis*, two *A. exsanguis*, two *A. tesselata* C, two *A. tesselata* D, and one male and two female hybrids of *A. neomexicana* × *A. sexlineata viridis* (appendix 5). We inferred that hybrid-

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Fig. 4. Habitats found south of the Canadian River at East of Conchas Lake Levee (CL-5*), San Miguel County, New Mexico. **Top.** Looking north–northwest at relatively stable mesquite-grassland at the Valley Component (CL-5V) from which individuals of *Aspidoscelis neomexicana*, *A. tesselata* C and D, and *A. sexlineata viridis* have been collected (*A. exsanguis* was not observed at either component at this site from 1988 to 2002). **Bottom.** Looking south–southwest at the topographically and ecologically complex (foreground to background) Valley-plateau-hill Component (CL-5VPH*) from which individuals of *Aspidoscelis neomexicana*, *A. tesselata* C and D, *A. sexlineata viridis*, and *A. neomexicana* × *A. sexlineata viridis* have been collected.

TABLE 5

***Aspidoscelis* Lizards Observed and Collected at Conchas Lake, CL-2* (South Recreation Area), at All Ecological Components in and Near the South Recreation Area, 1279–1310 m, San Miguel County, New Mexico, by CJC and C.R. Townsend (1976, 1978, 1981, 1990) and GJM and J.T. Briggler (2000–2003)**

	A.n.		*A.s.*		*A.*h.		*A.e.*		*A.t.* C		*A.t.* D		UI
	O	C	O	C	O	C	O	C	O	C	O	C	O
22–23 May 1976	—	0	—	7	—	0	—	0	—	2	—	5	—
28 May 1978	—	0	—	0	—	0	—	0	—	1	—	0	—
28–29 May 1978	—	0	—	0	—	0	—	0	—	3	—	4	—
29 May 1978	—	0	—	1	—	0	—	0	—	0	—	0	—
19 July 1981	—	0	—	6	—	0	—	0	—	0	—	0	—
28 May 1990	—	1	—	0	—	0	—	0	—	5	—	1	—
Subtotal	—	1	—	14	—	0	—	0	—	11	—	10	—
12 June 2000	0	0	0	0	0	0	0	0	0	0	0	0	2
14 June 2000	0	0	0	0	0	0	0	0	0	0	0	0	6
19 June 2000	17	1	7	3	0	2	1	0	3	1	0	0	18
23 June 2000	16	1	4	0	0	0	0	0	0	0	0	0	3
6 June 2001	7	1	2	1	0	0	0	0	0	0	0	0	2
8 June 2001	10	0	4	1	0	0	0	0	0	0	0	0	10
11 June 2001	1	0	0	0	0	0	0	0	0	0	0	0	2
14 June 2001	2	1	1	1	0	0	0	0	0	0	0	0	2
15 June 2001	25	1	4	2	0	1	0	0	0	0	0	0	1
17 August 2001	21	10	1	1	0	3	0	0	0	0	0	0	0
18 August 2001	8	2	0	0	0	0	0	0	0	1	0	0	0
20 August 2001	0	1	0	0	0	0	0	1	0	0	0	1	0
6 June 2002	22	0	1	0	0	4	1	3	0	0	0	1	4
7 June 2002	11	6	0	0	0	2	0	0	1	1	0	1	1
12 August 2003	13	13	0	2	0	0	0	0	2	6	0	0	0
13 August 2003	19	11	0	2	0	1	0	0	0	1	0	1	0
Subtotal	172	48	24	13	0	13	2	4	6	10	0	4	51

Abbreviations: *A.n.*, *A. neomexicana* ♀♀; *A.s.*, *A. sexlineata viridis* ♀♂; *A.* h., *A. neomexicana* × *A. sexlineata viridis*; *A.e.*, *A. exsanguis* ♀♀; *A.t.* C or D, *A. tesselata* C or D ♀♀; O, observed and not collected; C, collected; UI, unknown identity; and —, no data.

ization between these species occurred as they utilized the base of the rock-line for foraging, burrowing, and escape, behaviors that would presumably result in many interspecific encounters.

Immediately west of the paved road leading to the South Campground is CL-2H*, the Hill component of CL-2*, consisting of a hilltop and an east-facing hillside with modified mesquite and juniper grassland (including many clumps of yucca) in sandy soil (fig. 6). In 2000–2003, GJM found numerous *A. neomexicana* and a few *A. sexlineata viridis* on the hillside, as well as three male and four

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Fig. 5. Habitats modified by the activities of man south of Conchas Lake in South Recreation Area (CL-2*), San Miguel County, New Mexico. **Top.** Looking east at fragmented grass-weed associations along and among boulders and trees at the South Campground Component (CL-2C*) from which individuals of *Aspidoscelis neomexicana*, *A. tesselata* C and D, *A. sexlineata viridis*, and *A. neomexicana* × *A. sexlineata viridis* have been collected. **Bottom.** A south–southeast view of the mesquite-grass-weed association at the Hill Component (CL2H*) from which individuals of *Aspidoscelis neomexicana*, *A. tesselata* D, *A. sexlineata viridis*, and *A. neomexicana* × *A. sexlineata viridis* have been collected.

Fig. 6. An example of extreme habitat degradation resulting from the activities of man south of Conchas Lake in South Recreation Area (CL-2*), San Miguel County, New Mexico. Looking northeast across the Juniper Campground Component (CL-2J*) from which individuals of *Aspidoscelis neomexicana*, *A. tesselata* C and D, *A. exsanguis*, *A. sexlineata viridis*, and *A. neomexicana* × *A. sexlineata viridis* (including AMNH R-151739 used in karyotypic and electrophoretic analyses in this study) have been collected.

female hybrids of *A. neomexicana* × *A. sexlineata viridis*. Hybrids constituted 47.1% of the 17 *Aspidoscelis* collected on the hillside, including the only four lizards collected on 6 June 2002 (appendix 5). In four visits to CL-2H*, GJM also collected nine *A. neomexicana* and one *A. sexlineata viridis*.

Approximately 1 km northwest of the South Campground is CL-2J*, the Juniper Campground component of CL-2*, consisting of fragmented sandy mesquite and juniper grassland in a small heavily used recreation area (fig. 6). Clearly, *A. neomexicana* was much more abundant than *A. sexlineata viridis* in this component from which two hybrid males, including AMNH 151739 used in karyotypic and electrophoretic analyses, were collected on 7 June 2002. In three out of six visits to this component in 2001–2003, GJM also collected 20 *A. neomexicana*, two *A. sexlineata viridis*, six *A. tesselata* C, and one *A. tesselata* D.

The Lodge component (CL-2L*) is slightly elevated above the Juniper Campground

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Fig. 7. Habitats at Fort Sumner, De Baca County, New Mexico, inhabited by *Aspidoscelis* lizards. **Top.** Looking north along a roadside (cedar trees on the left form the border of a cemetery) with a grass-weed association (left of fence row) near the Fort Sumner–De Baca County Landfill (FS-1) from which individuals of *Aspidoscelis neomexicana*, *A. tesselata* E, and *A. sexlineata viridis* have been collected. **Bottom.** Looking south, near view of a patch of mesquite-grassland habitat at Fort Sumner–Railroad Depot (FS-2) from which individuals of *Aspidoscelis neomexicana* (including AMNH R-151741 used in karyotypic and electrophoretic analyses in this study), *A. tesselata* E, and *A. sexlineata viridis* have been collected.

component of CL-2*, and it consisted of a mowed grass-forbs association. Most of the lizards present at CL-2L* were *A. neomexicana*. In four visits to this component in 2000, 2001, and 2003, GJM also collected four *A. neomexicana*, two *A. sexlineata viridis*, one *A. exsanguis*, two *A. tesselata* C, one *A. tesselata* D, and one female hybrid *A. neomexicana* × *A. sexlineata viridis*.

Aspidoscelis at Two Fort Sumner Sites

The first specimen of *A. neomexicana* reported from the Pecos River drainage in De Baca County was collected on 9 June 2002 at FS-1, Fort Sumner-De Baca County Landfill (table 1; fig. 7; appendix 6) in the suburbs of Fort Sumner (Taylor, 2002). Subsequently, in three visits to FS-1 in 2002 and 2003, a site consisting of frequently altered patches of roadside weeds, mounds of earth, and debris (fig. 7), GJM found syntopic associations of *A. neomexicana*, *A. sexlineata viridis*, and *A. tesselata* E. Both E. D. Parker (personal commun.) and JMW collected and observed only *A. sexlineata viridis* and *A. tesselata* E at FS-1 in 1973 and 1996–1998, respectively.

At FS-2, Fort Sumner-Railroad Depot, consisting of the railroad right-of-way and a bordering mesquite association (fig. 7), GJM found a large number of *A. neomexicana* including AMNH R-151741 used in karyotypic and electrophoretic analyses (appendix 7). In five visits to the Fort Sumner-Railroad Depot in 2002 and 2003, he observed syntopic associations of *A. neomexicana*, *A. sexlineata viridis*, and *A. tesselata* E.

Habitat Structure as an Extrinsic Facilitator of Hybridization Between *A. neomexicana* and *A. sexlineata viridis*

At Conchas Lake, we observed syntopy between *A. neomexicana* and *A. sexlineata viridis* in about 70% of the area known to be inhabited by this parthenogen south of the Canadian River (CL-2* and CL-5*), but in only about 5% of the area known to be inhabited by this parthenogen north of the river (CL-1*). The 15 hybrids collected at Conchas Lake indicated that neither behavioral nor cytogenetic differences are perfect barriers to hybridization between *A. neomexicana* and *A. sexlineata viridis*.

Previous studies have identified two types of plant assemblages as being among the extrinsic factors that promote hybridization between certain parthenogenetic and gonochoristic species of *Aspidoscelis* by increasing contacts between the members of the syntopic assemblages (table 6). These include ecotonal settings (e.g., *A. neomexicana* × *A. tigris marmorata* in New Mexico, Dessauer et al. 2000; *A. tesselata* × *A. tigris marmorata* in New Mexico, Taylor et al., 2001) and weedy habitats resulting from human disturbances (e.g., *A. neomexicana* × *A. inornata* in New Mexico, Christiansen et al., 1971; *A. laredoensis* × *A. gularis* in Texas and México, Walker et al., 1989). Consistent with these observations is our finding that all of the hybrids of *A. neomexicana* × *A. sexlineata viridis* obtained in 2000–2003 from the South Recreation Area ($N = 13$) were found in either altered weedy assemblages or fragmented habitats (i.e., CL-2C*, CL-2H*, CL-2J*, and CL-2L*) resulting from human activities (figs. 5, 6).

Conversely, the components of site CL-5* (East of Conchas Lake Levee) represented examples of vegetational assemblages that have remained relatively stable during the past 25 years and are apparently mostly devoid of extrinsic facilitators of hybridization between *A. neomexicana* and *A. sexlineata viridis* (fig. 5). Numerous visits to CL-5* by GJM in 2000–2002 did not add to the one hybrid male obtained at the site by JMW and J.E. Cordes in 1988. Although recent collecting data indicate that *A. neomexicana* has increased its numbers on the small plateau at the south end of CL-5VPH* since 1988, there is no evidence that it has become more abundant in the valley below, where there has remained a large number of *A. sexlineata viridis*. The topographic and vegetational complexity of the Valley-plateau-hill Component at CL-5* essentially resulted in localized syntopy between *A. neomexicana* and *A. sexlineata viridis*. We found it possible to increase the number of encounters with each of the species present at CL-5* by searching different parts of the site; the mosaic distributions of mesquite with growths of grasses were more productive for *A. tesselata* C and

TABLE 6

Comparison of Five Aspects of Natural History Pertaining to Four Examples of Hybridization Between Parthenogenetic and Gonochoristic Species of *Aspidoscelis* in New Mexico

Hybridizing species (site of hybridization in New Mexico)	Position of site relative to the distribution of each hybridizing species	Habitat structure (presence or absence of distinctive types of habitats)	Determinants of habitat structure	Relative numbers of parental species at site of hybridization	Frequency of production of hybrids
Example 1 (this study)					
Aspidoscelis neomexicana × *A. sexlineata viridis* (Conchas Lake, San Miguel County)	Near periphery of geographic distributions of both species in New Mexico	Habitat separation not a factor in reducing species interactions	Disturbed vegetation structure resulting directly from activities of man	Many more *A. neomexicana* present at site than *A. sexlineata viridis*	Evidence of perennial production of hybrids (fig. 8)
Example 2 (Taylor and Walker, 1996)					
Aspidoscelis neomexicana × *A. inornata* (Albuquerque, Bernalillo County)	Well within the geographic distributions of both species in New Mexico	Habitat separation not a factor in reducing species interactions in urban enclave	Disturbed vegetation structure resulting directly from activities of man	Many more *A. neomexicana* present at site than *A. inornata*	Evidence of perennial production of hybrids
Example 3 (Dessauer et al., 2000)					
Aspidoscelis neomexicana × *A. tigris* (Grant and Hidalgo Counties)	At periphery of geographic distribution of parthenogenetic species	Ecotone between microhabitats reduces species interactions	Intermingling of mesquite-creosote communities resulting from desertification	Many more *A. tigris* at site than *A. neomexicana*	Hybridization extremely rare
Example 4 (Taylor et al., 2001)					
Aspidoscelis tesselata × *A. tigris* (Arroyo del Macho, Chaves County)	Near periphery of geographic distributions of both species in New Mexico	Preferred habitat of *A. tigris* is a factor in reducing species interactions	Intermingling of mesquite-creosote communities resulting from desertification	Many more *A. tesselata* at site than *A. tigris*	Evidence of perennial production of hybrids

D, exposed grassy areas with widely scattered mesquite for *A. sexlineata viridis*, and the plateau for *A. neomexicana*. We seldom observed *A. tesselata* and *A. neomexicana* at CL-5VPH* in the grassy exposed areas lacking shrubs; however, we did observe occasional individuals of *A. sexlineata viridis* in the mesquite with *A. tesselata* and, rarely, on the small plateau with *A. neomexicana*.

The Hill component, the source of 7 of 13 hybrids collected in South Recreation Area in 2000–2003, is of special interest. We observed an ensemble of ecological factors that appeared to facilitate hybridization between *A. neomexicana* and *A. sexlineata viridis* at CL-2H*. Here, we observed an occasional individual of *A. sexlineata viridis* in a 50 × 80 m zone of open-structured disturbed vegetation that contained about 10 times as many females of *A. neomexicana*. Habitat separation between the hybridizing species was not apparent at CL-2H*, and thus the few males of *A. sexlineata viridis* in the zone of syntopy would likely have had many en-

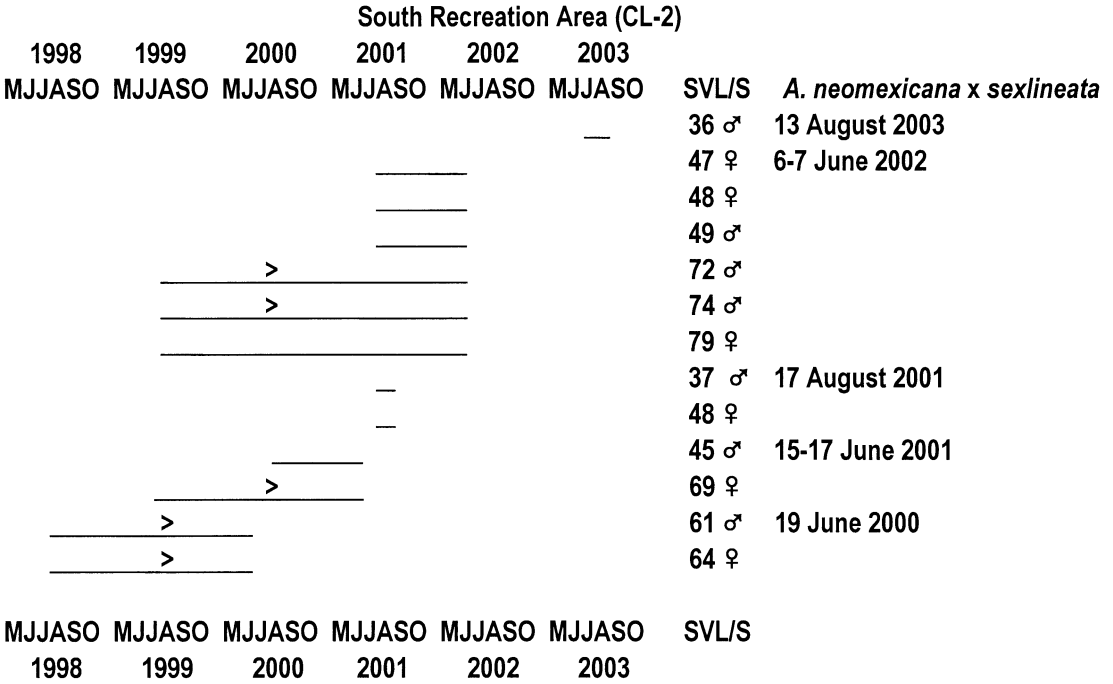


Fig. 8. Four or five generations represented by specimens of *Aspidoscelis neomexicana* × *A. sexlineata viridis* from South Recreation Area (CL-2*), Conchas Lake, San Miguel County, New Mexico, inferred from date of collection and snout–vent length (mm). Some lizards are active at the site from May to October (MJJASO) each year; horizontal line representing each lizard extends from the inferred year and month of hatching to the actual year and month of collection (> = younger or older age uncertain).

counters with females of *A. neomexicana*. Obviously, some of these contacts had produced the seven hybrids collected at the component in 2000–2002. Also, it is possible that the absence of other species at CL-2H* removed the potential for deflecting encounters between the hybridizing species.

Perennial Production of *A. neomexicana* × *A. sexlineata viridis* Hybrids at Conchas Lake

Using SVL data and date of collection for 13 hybrids from CL-2*, we determined that they represented a minimum of four and a maximum of five generations (depending upon acceptance of either a conservative or a liberal estimate of the ages of six adult hybrids depicted in fig. 8). Although perennial hybridization between *A. neomexicana* and *A. sexlineata viridis* is indicated for the South Recreation Area as a whole (figs. 5, 6), this is not to say that collection of hybrids here necessarily can be accomplished on demand. Indeed, results from visits to CL-2* by GJM on 12 and 13 August 2003 to collect additional hybrids indicated that previous successes in obtaining hybrids were a matter of serendipity. Of the *neomexicana*-like lizards collected in 2003 at the South Recreation Area, only 1 was a hybrid (from the Campground component) and 24 were *A. neomexicana*.

Aspidoscelis neomexicana and *A. tesselata* possess indistinguishable hybrid-derived kar-

yotypes consisting of a set of chromosomes from a member of the *tigris* species group (*A. tigris marmorata* for both) and a set from a member of the *sexlineata* species group (*A. inornata* for the former and *A. gularis septemvittata* for the latter). None of the areas of syntopy between *A. tesselata* and *A. sexlineata viridis* investigated at Conchas Lake included both the absence of habitat structural integrity and large numbers of the parthenogen mixed with small numbers of the gonochoristic form. However, close contacts between these species affording opportunities for hybridization were observed at the CL-5VPH* component at East of Conchas Lake Levee. Based on the lack of hybrids of *A. tesselata* and *A. sexlineata viridis* in our collections from this and other sites in the area, we infer that there are intrinsic barriers to hybridization between these species (i.e., body size differential, behavior, and/or cytogenetic factors) that outweigh extrinsic facilitators of hybridization. Nevertheless, such a hybrid (*A. tesselata* ♀ × *A. sexlineata viridis* ♂) was the ancestor of *A. neotesselata* (Neaves, 1969; Parker and Selander, 1976; Dessauer and Cole, 1989) and one was reported from Higbee, Otero County, Colorado, by Walker et al. (1994).

Sex Ratio of Hybrids Based on Internal Organs

In male specimens sexed by internal examinations, we could not identify a lizard from CL-5* and seven from CL-2* to *A. sexlineata viridis*, the only gonochoristic species of *Aspidoscelis* at Conchas Lake, because of unusual color pattern and scutellation characters. Subsequently, we identified these eight males (three adults and five juveniles) and six unusual females (three adults and three juveniles also examined internally) from Conchas Lake that resembled the males in external anatomy as hybrids of *A. neomexicana* × *A. sexlineata viridis*. A seventh female, OMNH 35109 sexed based on external anatomy, contributed to an overall sex ratio of eight males and seven females for hybrids obtained at Conchas Lake.

Color Pattern in Male Hybrids and Parental Species

Pertaining to an unusual male from CL-5* collected in 1988, Walker et al. (1990) stated that ''Sharp discontinuities in color pattern distinguish *Cnemidophorus neomexicanus* and *C. sexlineatus* at all ontogenetic stages of development. Thus, the presence of male reproductive structures in a lizard with color pattern features characteristic of all-female *C. neomexicanus*, and never present in male *C. sexlineatus*, was the basis of our hypothesizing that UADZ 3272 [= AMNH 144085] is a hybrid, which would be triploid.'' Further study of the color pattern of AMNH 144085 (SVL 67 mm) compared with specimens of the parental species obtained at CL-5* in 2000–2002 have reinforced the hypothesis that the AMNH specimen is a male of *A. neomexicana* × *A. sexlineata viridis*. Characters relevant to this conclusion were summarized and illustrated by Walker et al. (1990: table 1, fig. 1).

We used a male lizard captured alive (AMNH R-151739, 74 mm SVL from CL-2J*, figs. 9B, 12A) in karyotypic and electrophoretic analyses to genetically verify its hybrid genealogy. It differed from all available specimens of *A. neomexicana* and *A. sexlineata viridis* in the following features: (1) anterior 50% of the vertebral and paravertebral stripes relatively straight; (2) posterior 50% of vertebral stripe intermittently wavy and fragmented; (3) upper lateral and dorsolateral fields a very dark hue of brown; (4) spot formation in the dorsolateral fields not evident anteriorly and arrested at the earliest discernable stage posteriorly; (5) spot formation in the lower and upper lateral fields arrested at intermediate stages; and (6) sides of the head, anterior surfaces of the forelimbs, and ventral surfaces of the body a conspicuous pastel blue (now faded in alcohol). The other adult hybrid males, UADZ 7344 (SVL 61 mm from CL-2H*, fig. 12E) and UADZ 7553 (SVL 72 mm from CL-2H*, fig. 12C), possessed the same color hues described for AMNH R-151739. However, the waviness of the vertebral stripe and presence of distinct spots in the upper lateral fields in UADZ 7344 more closely resembled individuals of *A. neomexicana* of similar size than either of the other two adult hybrid males. We were also able to easily sort the four juvenile hybrid males from CL-2* from specimens of *A. neomexicana* of similar size based on these features: UADZ 7700 (SVL

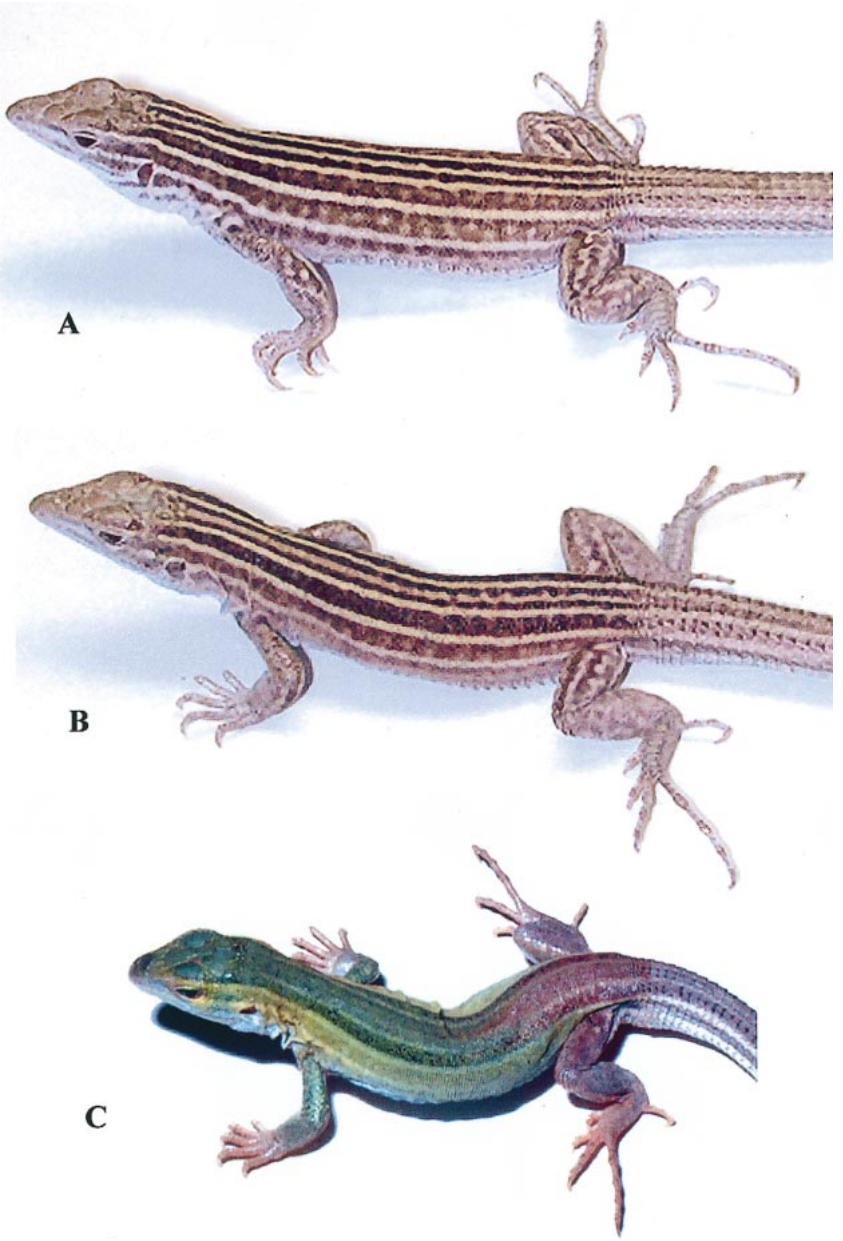


Fig. 9. Life colors in three lizards used in genetic studies. **A.** Diploid *Aspidoscelis neomexicana* adult female, AMNH R-151740, SVL 72 mm, Cove Campground (CL-13), Conchas Lake, San Miguel County, New Mexico. **B.** Triploid *Aspidoscelis neomexicana* × *A. sexlineata viridis* hybrid male, AMNH R-151739, SVL 74 mm, from South Recreation Area (CL-2*), Conchas Lake, San Miguel County, New Mexico. **C.** Diploid *A. sexlineata viridis* adult male, AMNH R-108142, SVL 69 mm, from Kiowa County, Colorado.

36 mm from CL-2J*, not illustrated), UADZ 7561 (SVL 49 mm from CL-2J*, fig. 13A), and UADZ 7452 (SVL 37 mm from CL-2H*, fig. 13D) by their obviously straighter stripes and lack of distinct spots in any of the dark fields, and UADZ 7448 (SVL 45 mm from CL-2H*, fig. 13E) by its straighter primary stripes, intermittently fragmented vertebral stripe, and indistinct spots in the upper lateral fields. In alcohol, UADZ 7448 closely resembled juveniles of *A. tesselata* C in the fragmented vertebral stripe and darkly hued fields; however, in life its dark brown rather than black fields and its intense blue tail color identified the individual as *A. neomexicana* × *A. sexlineata viridis*.

Color Pattern in Female Hybrids and Parental Species

With the exception of probable hybrid OMNH 35109 from CL-1*, all specimens examined from north of the Canadian River at Conchas Lake represent *A. neomexicana*, *A. sexlineata viridis*, *A. exsanguis*, or *A. tesselata* C based on distinctive color patterns. Beth E. Leuck (personal commun.) considered the unique color pattern of OMNH 35109 collected alive in 1978 to be indicative of a hybrid origin. Although Leuck made the live lizard available to J.W. Wright for karyotyping, that did not occur. Our examination of the preserved specimen revealed it to be darkened, presumably by formalin; however, a superb color slide of the dorsal color pattern of the live lizard was made available to us by B.E. Leuck (represented in fig. 10).

We compared OMNH 35109 with a pooled sample of 37 *A. neomexicana* (e.g., fig. 11A) from sites north of the Canadian River (CL-1*, CL-13, and CL-4) that included a minimum of four year classes (SVL 36–80 mm). Each specimen in the pooled sample had the dorsal pattern (spots and wavy stripes) and ventral coloration typical of this parthenogenetic species except for UADZ 7532 (SVL 38 mm) from CL-1*, which had a black-pigmented throat unlike any other individual of *A. neomexicana* known to us from throughout its range. However, we did not consider UADZ 7532 to be a hybrid based on its total ensemble of color pattern and scutellation characters. Conversely, we found OMNH 35109 to be quite unlike all adult females in the pooled sample, and it seemed appropriate to embrace B.E. Leuck's hypothesis of an *A. neomexicana* × *A. sexlineata viridis* genealogy for the individual.

Fig. 10. Unusual dorsal pattern in OMNH 35109, a putative hybrid female, SVL 69 mm, of *Aspidoscelis neomexicana* × *A. sexlineata viridis* from South of Clabberhill Ranch (CL-1*), Conchas Lake, San Miguel County, New Mexico.

The alternative hypothesis that this unusual specimen (OMNH 35109; SVL 69 mm; fig. 10) is merely an ''outlier'' of *A. neomexicana* based on an aberrant dorsal color pattern, as verified in the case of AMNH 125547 from Hidalgo County, New Mexico, by Dessauer and Cole (1989), is not supported by its ventral color pattern and results from univariate and multivariate analyses of scutellation. In life, ONMH 35109 was characterized by (1) unspotted brown fields, (2) lateral stripes represented by a longitudinal array of lichenoid components, (3) dorsolateral and paravertebral stripes with unusually wavy edges, (4) vertebral stripe of extreme waviness (interrupted anteriorly and with extensions that touch the paravertebral stripes), (5) indistinctly patterned gray-tan-brown hindlimbs, (6) a gray-tan tail, and (7) sky blue ventral surfaces.

We identified three adult and three juvenile hybrid females of *A. neomexicana* × *A. sexlineata viridis* from CL-2* (South Recreation Area). Among the adults, UADZ 7554 is an

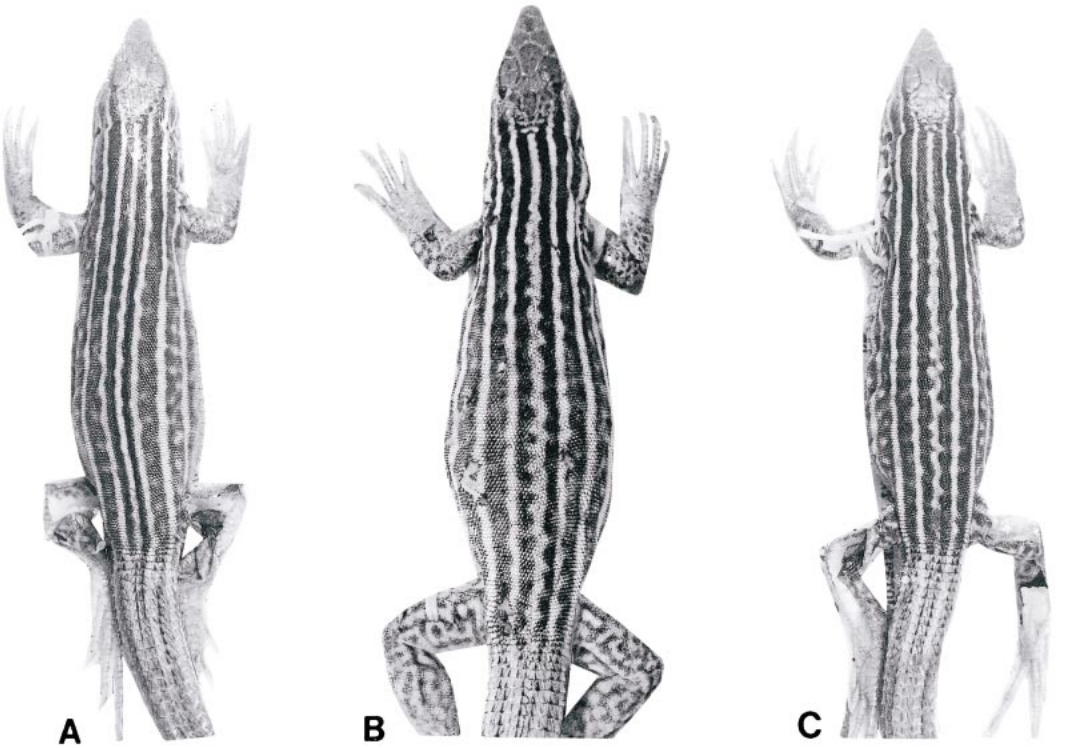
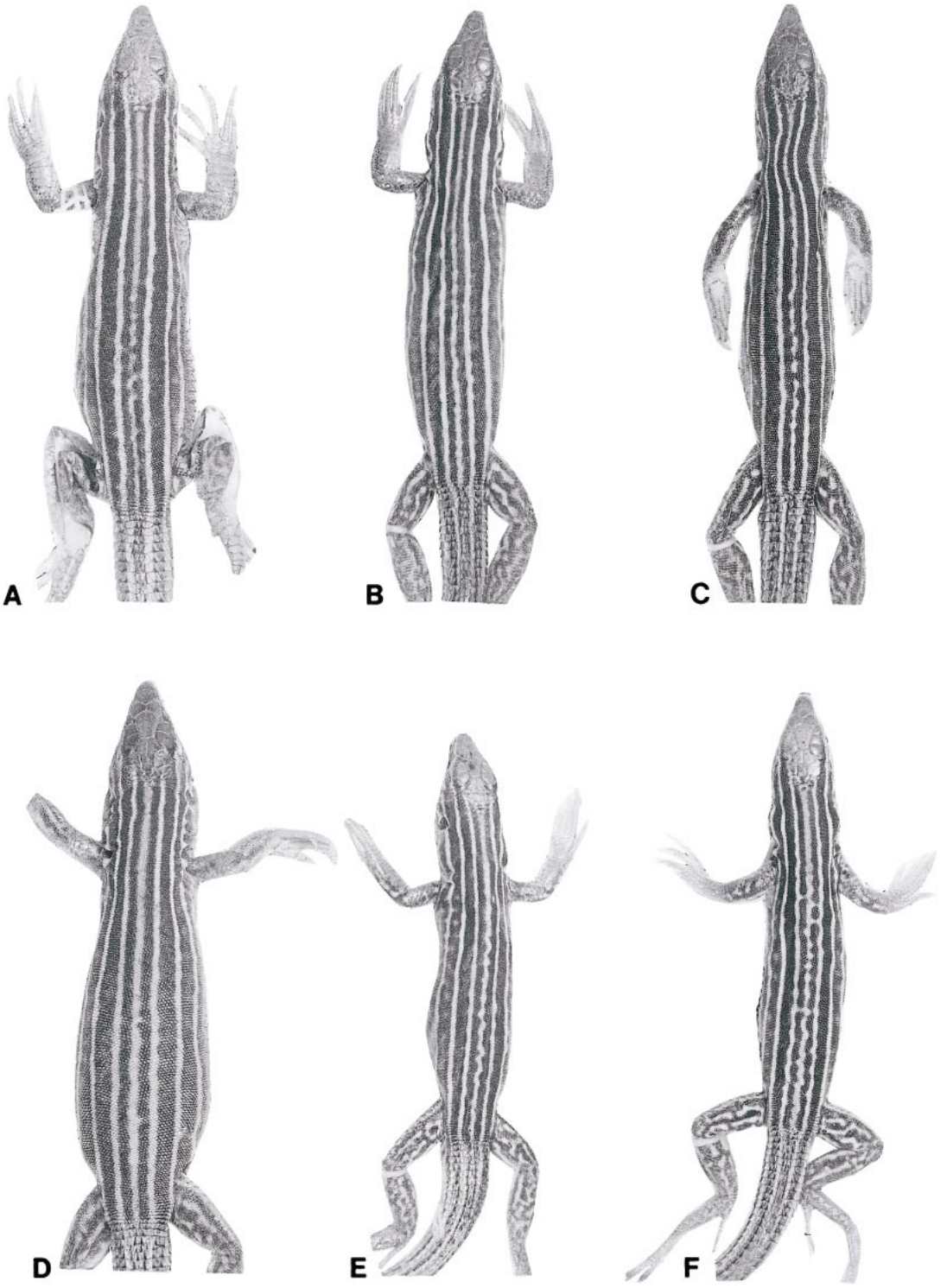


Fig. 11. Adult specimens of *Aspidoscelis neomexicana* of special significance. **A.** AMNH R-151740 ♀, SVL 73 mm, from Cove Campground (CL-13), Conchas Lake, San Miguel County, New Mexico, used in karyotypic and electrophoretic analyses in this study. **B.** MSB 65617 ♀, SVL 79 mm, from Fort Sumner–De Baca County Landfill (FS-1), Fort Sumner, De Baca County, New Mexico; first reported specimen of the species from the county (Taylor, 2002). **C.** AMNH R-151741 ♀, SVL 73 mm, from Fort Sumner–Railroad Depot (FS-2), Fort Sumner, De Baca County, New Mexico, used in karyotypic and electrophoretic analyses in this study.

unusually large female (SVL 79 mm from CL-2H*, fig. 12D) with a color pattern that is intermediate between the parental forms. It has (1) straight stripes on the anterior 50% of the body, (2) gray-brown fields, (3) only the faintest indication of spot formation in the fields, and (4) gray-blue ventral surfaces. Hybrid female UADZ 7445 (SVL 69 mm from CL-2L*, fig. 12B) has slightly more distinct spots than does UADZ 7554 (fig. 12D), and it has a greater overall resemblance to *A. neomexicana* in the character of the stripes. The most distinctive feature of hybrid female UADZ 7349 (SVL 64 mm from CL-2C*, fig. 12F) involved the waviness and interconnections of the paravertebral and vertebral stripes and distinct spots in the upper lateral fields. Three juvenile females (UADZ 7561, SVL 49 mm from CL-2J*, fig. 13A; UADZ 7555, SVL 47 mm

→

Fig. 12. Adult *Aspidoscelis neomexicana* × *A. sexlineata viridis* hybrids from components of the South Recreation Area (CL-2*), Conchas Lake, San Miguel County, New Mexico. **A.** AMNH R-151739 ♂, CL-2J*, SVL 74 mm. **B.** UADZ 7445 ♀, CL-2L*, SVL 69 mm. **C.** UADZ 7553 ♂, CL-2H*, SVL 72 mm. **D.** UADZ 7554 ♀, CL-2H*, SVL 79 mm. **E.** UADZ 7344 ♂, CL-2H*, SVL 61 mm. **F.** UADZ 7349 ♀, CL-2C*, SVL 64 mm.



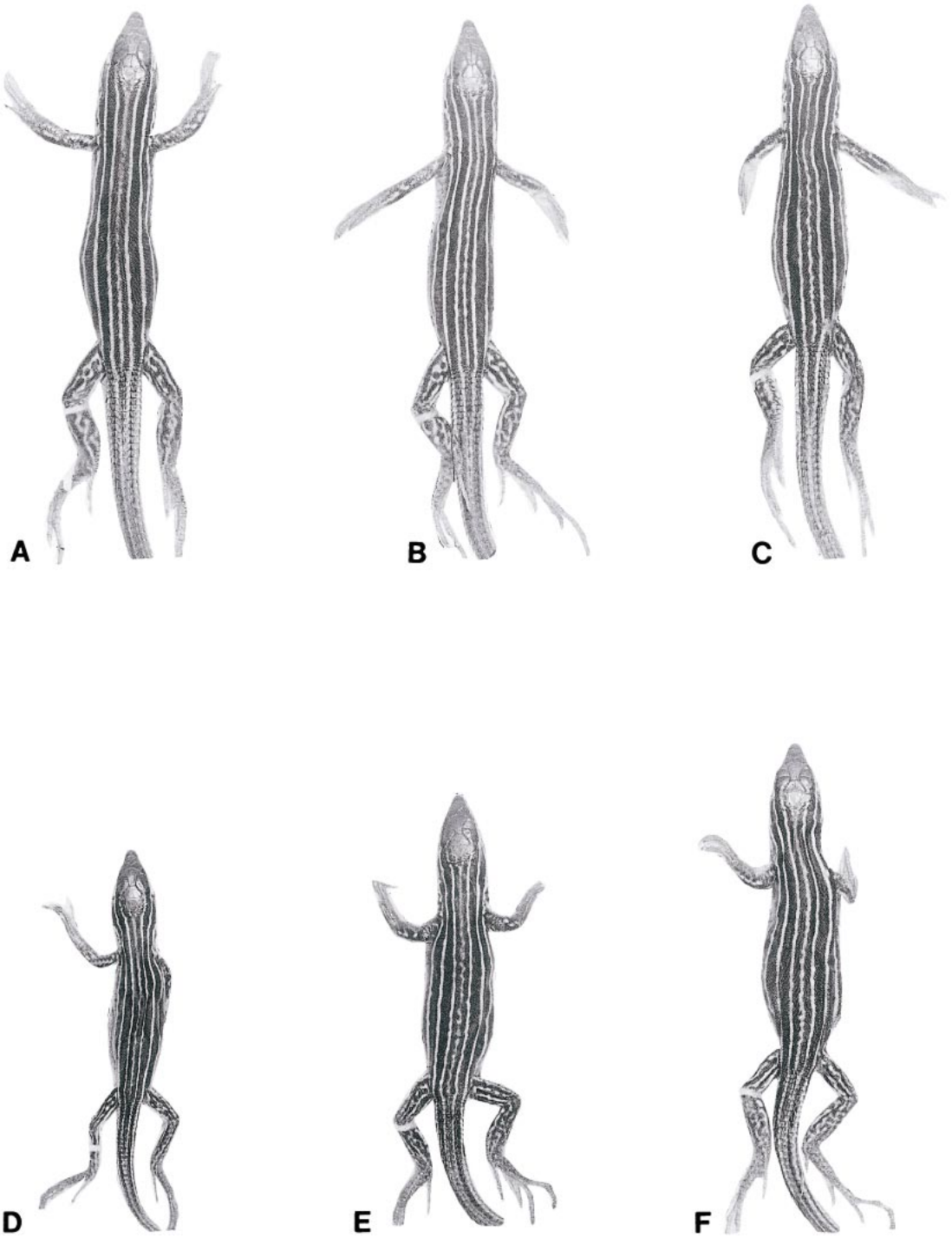


Fig. 13. Subadult *Aspidoscelis neomexicana* × *A. sexlineata viridis* hybrids from components of the South Recreation Area (CL-2*), Conchas Lake, San Miguel County, New Mexico. **A.** UADZ 7561 ♂, CL-2J*, SVL 49 mm. **B.** UADZ 7556 ♀, CL-2H*, SVL 49 mm. **C.** UADZ 7555 ♀, CL-2H*, SVL 47 mm. **D.** UADZ 7452 ♂, CL-2H*, SVL 37 mm. **E.** UADZ 7448 ♂, CL-2H*, SVL 45 mm. **F.** UADZ 7455 ♀, CL-2C*, SVL 48 mm.

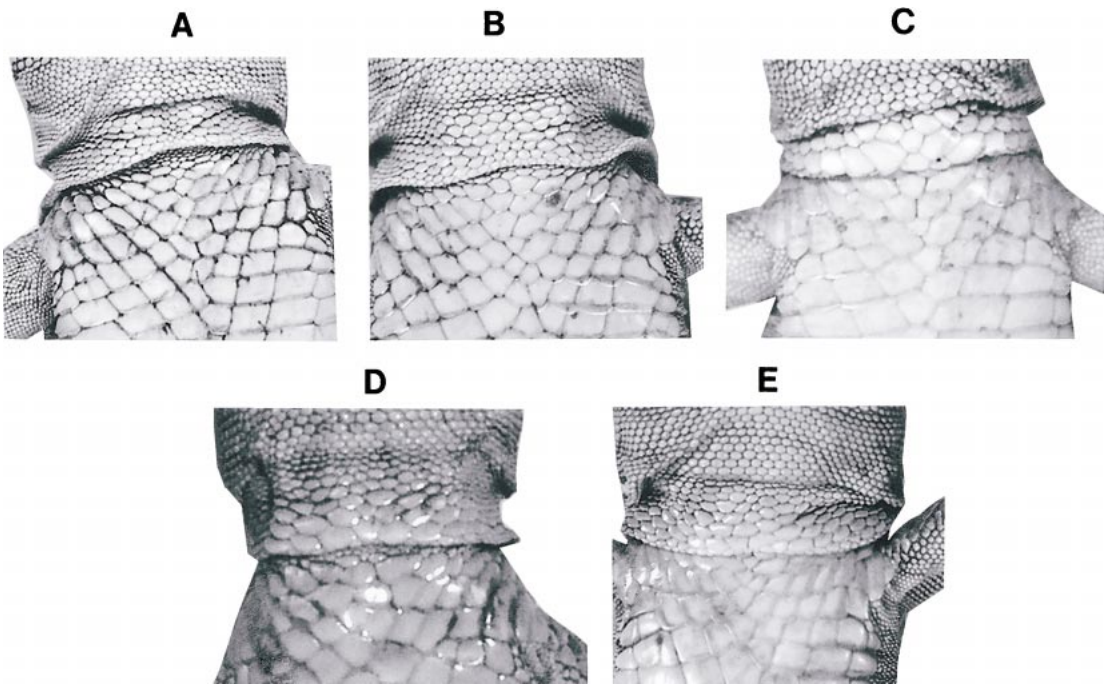


Fig. 14. Comparison of mesoptychial scale size in parental forms and their hybrids. **A.** UADZ 7318 ♀, SVL 80 mm, small scales in *Aspidoscelis neomexicana*. **B.** UADZ 7464 ♀, SVL 68 mm, small scales in *A. neomexicana*. **C.** UADZ 7396 ♀, SVL 63 mm, greatly enlarged scales in *A. sexlineata viridis*. **D.** UADZ 7553 ♂, SVL 72 mm, enlarged scales in *A. neomexicana* × *A. sexlineata viridis*. **E.** UADZ 7554 ♀, SVL 79 mm, enlarged scales in *A. neomexicana* × *A. sexlineata viridis*.

from CL-2H*, fig. 13C; UADZ 7455, SVL 48 mm from CL-2C*, fig. 13F) were initially sorted from juveniles of *A. neomexicana* on the straightness of their paravertebral stripes and unusual vertebral stripes.

Univariate Analyses of Scutellation in Hybrids and Parental Species

In 96 specimens of *A. neomexicana* from five sites at Conchas Lake (CL-1*, CL-13, CL-4, CL-5*, and CL-2*), the first several transverse rows of scales anterior to the edge of the gular fold were very small and there were no groups of countable enlarged mesoptychials (the scales along the edge of the gular fold, fig. 14A, B), with the size of the scales being completely diagnostic compared with *A. sexlineata viridis* (fig. 14C). In 49 *A. sexlineata viridis* from Conchas Lake (CL-5* and CL-2*) the mesoptychial scales were arrayed in three subtly different patterns: (1) a transverse row of very small scales preceded by a row of abruptly enlarged scales, (2) more than four small scales intermittently appearing between the posterior edges of enlarged scales, and (3) only one to three small scales along the gular fold between the posterior edges of enlarged scales (fig. 14C). In the eight hybrid males and seven hybrid females from Conchas Lake the mesoptychial scales closely resembled conditions 1 and 2 described for *A. sexlineata viridis* except for being slightly smaller; they differed from *A. neomexicana* in their much larger size and distinctive arrangement (fig. 14D, E).

All individuals of *A. neomexicana* had circumorbital series that extended farther anteriorly than in *A. sexlineata viridis*; the two species could be distinguished on this character alone. Variation for circumorbital series in specimens of *A. neomexicana* from five sites at Conchas Lake is summarized in table 7. Among specimens of *A. neomexicana* the circumorbital scale series were complete on both sides of the head in 47/96 (49.0%), complete on only the left side in 12/96

TABLE 7

Variation in Three Characters of Scutellation in *Aspidoscelis neomexicana* from sites CL-1*, CL-13, CL-4, CL-5*, and CL-2*, *A. neomexicana* × *A. sexlineata viridis* (= hybrids) from CL-5* and CL-2*, and *A. sexlineata viridis* from CL-5* and CL-2* at Conchas Lake, San Miguel County, New Mexico

		COS				MS		PA	
Taxon, site	*N*	LC-RC	LC-RI	LI-RC	LI-RI	S	L	1	2
A. neomexicana									
CL-1*	14	7[a]	0	1	6	14	0	5	9
		50.0%	0%	7.1%	42.9%	100%	0%	35.7%	64.3%
CL-13	12	8	1	0	3	12	0	7	5
		66.7%	8.3%	0%	25.0%	100%	0%	58.3%	41.7%
CL-4	12	8	3	0	1	12	0	8	4
		66.7%	25.0%	0%	8.3%	100%	0%	66.7%	33.3%
CL-5*	8	2	1	0	5	8	0	7	1
		25.0%	12.5%	0%	62.5%	100%	0%	87.5%	12.5%
CL-2*	50	22	7	2	19	50	0	35	15
		44.0%	14.0%	4.0%	38.0%	100%	0%	70.0%	30.0%
Total	96	47	12	3	34	96	0	62	34
		49.0%	12.5%	3.1%	35.4%	100%	0%	64.6%	35.4%
Aspidoscelis hybrids									
CL-5*, CL-2*	14	0	0	0	14	0	14	10	4
		0%	0%	0%	100%	0%	100%	71.4%	28.6%
A. sexlineata viridis									
CL-5*, CL-2*	49	0	0	0	49	0	49	1	48
		0%	0%	0%	100%	0%	100%	2.0%	98.0%

Abbreviations: COS, circumorbital scale series (C, complete; I, incomplete; L, left; R, right); MS, mesoptychial scales small and not countable (S) or large and countable (L); and PA, 1 or 2 preanal scales.

[a]Number of specimens with percentages listed below.

(12.5%), complete on only the right side in 3/96 (3.1%), and incomplete on both sides in 34/96 (35.4%). Among 49 individuals of *A. sexlineata viridis* from Conchas Lake (CL-5* and CL-2*) the circumorbital scale series extended as far anteriorly as the middle of the third supraocular scales in only one specimen; the series terminated more posteriorly either near the middle of the fourth supraocular scales or at the suture between the third and fourth supraoculars in the other specimens. All hybrid males had incomplete circumorbital scale series that resembled individuals of *A. neomexicana* with incomplete series rather than resembling *A. sexlineata viridis* with short series (tables 7–10).

Variation for the one (N = 62, 64.6%) or two (N = 34, 35.4%) preanal scale character states in specimens of *A. neomexicana* from five sites at Conchas Lake are summarized in table 7 (= suture patterns of Dessauer and Cole, 1989; they reported one female with one preanal from Sandoval County that produced two neonates with one scale and two neonates with two scales). In *A. sexlineata viridis* there were two preanal scales immediately anterior to the vent in 48/49 specimens from CL-5* and CL-2*; the other specimen had one preanal scale. Fourteen hybrids from CL-5* and CL-2* resembled *A. neomexicana* in usually having one preanal scale (N = 10, 71.4%) rather than two (N = 4, 28.6%) scales (table 7).

In summary, all male and female hybrids of *A. neomexicana* × *A. sexlineata viridis* possessed enlarged mesoptychial scales (fig. 14C, D) and incomplete circumorbital series along with color patterns that resembled the

maternal parent (figs. 9, 11–13). We reexamined all specimens with incomplete circumorbital series and small mesoptychial scales and there were no changes in our conclusion that all were examples of *A. neomexicana* rather than some being cryptic hybrids.

Univariate comparisons were quantitatively extended to eight meristic characters and the PV/GAB ratio in the pooled samples of *A. neomexicana*, *A. sexlineata viridis*, and *A. neomexicana* × *A. sexlineata viridis* hybrids (excluding OMNH 35109 from CL-1*) from Conchas Lake. The OR character was not significantly different among any of the three samples. The GAB, PV/GAB, SDL, COS, and LSG characters differed significantly among all samples. The sample of hybrids differed from *A. neomexicana* in the GAB, PV, SDL, COS, and LSG and from *A. sexlineata viridis* in the GAB, FP, SDL, COS, LSG, and ILS (PV/GAB not included in table 9). Means for the sample of hybrids were intermediate to the parental forms in the LSG, COS, FP, SDL, PV, and PV/GAB, higher than both parental forms in the OR and ILS, and lower than both parental forms in the GAB (table 9). The low variability that we hypothesized for parthenogenetic *A. neomexicana* as a consequence of clonal reproduction and the high variability expected in *A. sexlineata viridis* as a result of gonochoristic reproduction were confirmed by three aspects of the univariate statistics. First, COV values for *A. neomexicana* were lower for each character than the COV values for *A. sexlineata viridis* (tables 8, 9). The sample of hybrids was intermediate to the parental species in COV values for more than half of the characters, but not in the ILS, GAB, FP, and PV/GAB. Second, ranges of variation for the OR, GAB, FP, and SDL in *A. sexlineata viridis* were about twice those for the same characters in both *A. neomexicana* and the hybrids. Third, we used the Shapiro-Wilk W Test of Normality for data dispersions by variable to identify normal (N) and not normal (NN) distributions for the following characters in each pooled sample (table 9): *A. neomexicana* (N, OR and ILS; NN, GAB, PV, FP, SDL, COS, and LSG); *A. neomexicana* × *A. sexlineata viridis* (N, GAB, OR, FP, SDL, LSG, and ILS; NN, PV and COS; and *A. sexlineata viridis* (N, GAB, OR, LSG, and ILS; NN, PV, FP, SDL, and COS). The relationship between parthenogenetic reproduction and NN data dispersions in *A. neomexicana* is reflected in a preponderance of characters with narrow ranges of variation and leptokurtic distribution yet the hybrids had mostly N data dispersions. The NN distributions for several characters in *A. sexlineata viridis* reflect wide ranges of variation and curves with positive or negative skews.

We also conducted a by-site comparison of eight meristic variables and a ratio for five samples of *A. neomexicana* (CL-1*, CL-13, and CL-4 located north of Canadian River; CL-5* and CL-2* located south of river), two samples of *A. sexlineata viridis* (CL-5* and CL-2*), and male and female hybrids (CL-5* and CL-2*) (table 10). There were no significant intraspecific differences for any pair of means among the samples of either *A. neomexicana* or *A. sexlineata viridis*, and no sexual dimorphism was apparent between male and female hybrids. The ranges of differences among means for nine variables in five samples of *A. neomexicana* followed by two of *A. sexlineata viridis* are: GAB, 1.4 and 1.9; OR, 4.5 and 7.0; PV, 0.9 and 0.8; PV/GAB, 1.0 and 0.8; FP, 1.0 and 0.3; SDL, 0.9 and 0.3; COS, 1.3 and 0.5; LSG, 2.8 and 2.4; and ILS, 4.4 and 3.0. The COS mean for the sample of *A. neomexicana* from CL-2* ($N = 49$) obscures variation, which was discussed previously. In fact, specimens collected in 2003 at this site necessitated reevaluation of our seemingly robust hypothesis that specimens from CL-5* ($N = 1$) and CL-2 ($N = 13$) collected in 1988–2002 with color patterns similar to *A. neomexicana*, incomplete circumorbital scale series on both sides of the head, and enlarged mesoptychial scales along or near the edge of the gular fold represented *A. neomexicana* × *A. sexlineata viridis* hybrids. The sample of specimens of *A. neomexicana* from CL-2* collected prior to 2003 ($N = 26$) included 15 specimens with complete circumorbital series on both sides, four with complete series on only the left side, and seven with incomplete series on both sides, all with typical color patterns and small mesoptychial scales. The sample of the species obtained in 2003 ($N = 25$) included 7 specimens with complete circumorbital series on both sides, 2 with com-

TABLE 8

Comparisons of Coefficients of Variation in Three Sets of Parental Species and their Hybrids (genus *Aspidoscelis*) from Sites in New Mexico (Data for set 1 from this Study, each SD and COV for set 2 calculated from Taylor and Walker [1996], COV for set 3 calculated from Taylor et al. [2001])

	Maternal Parent (*N*)	Hybrids (*N*)	Paternal Parent (*N*)
	SD/M × 100 = COV	SD/M × 100 = COV	SD/M × 100 = COV
Set 1	*A. neomexicana* (96)	*A.n.* × *A.s.* (14)	*A. sexlineata* (48)
GAB	1.99/76.0 = 2.62	2.69/69.7 = 3.86	5.06/73.4 = 6.89
Set 2	*A. neomexicana* (30)	*A.n.* × *A.i.* (13)	*A. inornata* (50)
GAB	1.69/74.6 = 2.27	1.69/64.0 = 2.64	3.18/61.5 = 5.17
Set 3	*A. tesselata* (39)	*A.t.* × *A.t.* (20)	*A. tigris* (28)
GAB	6.12/93.5 = 6.55	4.47/84.8 = 5.27	4.55/91.4 = 4.98
Set 1	*A. neomexicana* (96)	*A.n.* × *A.s.* (14)	*A. sexlineata* (49)
FP	1.23/36.9 = 3.33	1.07/35.9 = 2.98	1.94/29.1 = 6.67
Set 2	*A. neomexicana* (30)	*A.n.* × *A.i.* (13)	*A. inornata* (50)
FP	1.75/37.2 = 4.70	1.72/37.5 = 4.59	1.90/33.6 = 5.65
Set 3	*A. tesselata* (39)	*A.t.* × *A.t.* (20)	*A. tigris* (28)
FP	1.76/41.4 = 4.25	1.97/44.8 = 4.40	2.35/45.4 = 5.18
Set 1	*A. neomexicana* (96)	*A.n.* × *A.s.* (14)	*A. sexlineata* (49)
SDL	1.13/31.7 = 3.56	1.17/31.0 = 3.77	1.29/26.6 = 4.85
Set 2	*A. neomexicana* (30)	*A.n.* × *A.i.* (13)	*A. inornata* (50)
SDL	1.20/31.9 = 3.76	1.04/32.3 = 3.22	1.27/27.9 = 4.55
Set 3	*A. tesselata* (39)	*A.t.* × *A.t.* (20)	*A. tigris* (28)
SDL	1.43/37.0 = 3.86	1.43/36.8 = 3.89	1.84/32.2 = 5.71
Set 1	*A. neomexicana* (96)	*A.n.* × *A.s.* (14)	*A. sexlineata* (48)
COS	2.38/19.3 = 12.33	3.06/14.1 = 21.70	1.83/7.1 = 25.77
Set 2	*A. neomexicana* (30)	*A.n.* × *A.i.* (13)	*A. inornata* (50)
COS	2.68/19.6 = 13.67	2.77/18.0 = 15.39	1.48/9.6 = 15.42
Set 3	*A. tesselata* (39)	*A.t.* × *A.t.* (20)	*A. tigris* (28)
COS	1.51/18.0 = 8.39	2.77/19.9 = 13.92	3.44/19.3 = 17.82
Set 1	*A. neomexicana* (96)	*A.n.* × *A.s.* (14)	*A. sexlineata* (47)
LSG	3.39/36.7 = 9.23	3.45/29.9 = 11.54	4.32/18.3 = 23.61
Set 2	*A. neomexicana* (30)	*A.n.* × *A.i.* (13)	*A. inornata* (50)
LSG	3.71/40.3 = 9.21	5.36/34.2 = 15.67	6.15/28.6 = 21.50
Set 3	*A. tesselata* (39)	*A.t.* × *A.t.* (20)	*A. tigris* (28)
LSG	4.74/34.8 = 13.62	5.86/40.3 = 14.54	12.21/42.0 = 29.07

Abbreviations: GAB, granules (scales) around midbody; FP, femoral pores; SDL, subdigital lamellae; COS, circumorbital scales; and LSG, lateral supraocular granules.

plete series on only the left side, 2 with complete series on only the right side, and 14 with incomplete series on both sides. We were compelled to reexamine each specimen in the 2003 sample of *A. neomexicana* from CL-2* to determine if some of the individuals with incomplete circumorbital series were actually hybrids. This analysis resulted in identification of one probable hybrid (presence of incomplete circumorbital series on both sides and large mesoptychial scales) among the 25 specimens, with all other specimens having mesoptychial scales and color patterns typical of *A. neomexicana*.

Multivariate Analysis of Scutellation In Hybrids and Parental Species

Principal Components Analysis (PCA): The PCA revealed that the first two principal components represented a remarkably high 78.3% of the variation included in the eight characters of scutellation (GAB, OR, PV, FP, SDL, COS, LSG, and ILS) used in this multivariate analysis of samples of *A. neomexicana*, *A. neomexicana* × *A. sexlineata viridis*, *A. sexlineata viridis*, and *A. tesselata* from Conchas Lake. Significant differences among all sample scores for the first principal component (employing these variables as univariate characters) were noted; however, not all scores were significantly different for the second principal component. Comparison of component loadings (table 11) to characters with nonsignificant differences between hybrids and one of the parental species (table 9) indicated that the first principal component reflected similarities of hybrids to *A. neomexicana* in number of femoral pores. The second principal component reflected similarities of hybrids to *A. neomexicana* in number of interlabial scales and to *A. sexlineata viridis* in number of granules separating the paravertebral stripes.

The multivariate pattern of variation was depicted in an ordination of principal components scores on the first two axes (fig. 15). There was some overlap in PCA scores representing both of the parental species and the hybrids, but no overlap between those scores and *A. tesselata*, based on the 95% confidence limits. This pattern is consistent with the assumption of a hybrid origin for the specimens involving the maternal parental species *A. neomexicana* and paternal parental species *A. sexlineata viridis*.

Canonical Variate (CV) Analysis: We used a linear CV analysis based on the same characters of scutellation used in the PCA to further assess the multivariate relationships of four a priori groups, the *A. neomexicana* × *A. sexlineata viridis* hybrids and their possible parental species *A. neomexicana*, *A. tesselata*, and *A. sexlineata viridis*. The CV analysis not only assigned each specimen to its predicted a priori group, but the plots of CV scores for each species on standardized discriminant axes were widely separated (fig. 16). All putative hybrids from CL-2* were also assigned to predicted a priori group, and the plot of CV scores for these individuals added weight to our conclusion that all of them represented the morphologically intermediate progeny of *A. neomexicana* females that had been inseminated by *A. sexlineata viridis* males and that they were, as expected, morphologically closer to their maternal parent (fig. 16). The CV scores generated for two additional putative hybrids, from sites CL-1* (OMNH 35109) and CL-5* (AMNH 144085), were contained within the 95% ellipse for the hybrids from CL-2*. The first two canonical variates explained 95.9% of the variation (table 11).

Mehalanobis distances (D^2) among centroids of the four a priori groups provided a quantitative measure of multivariate resemblance among hybrids and the other species analyzed (table 12). The hybrids were closer to *A. neomexicana* ($D^2 = 25.9$, 2 of 3 sets of shared chromosomes) than to *A. sexlineata viridis* ($D^2 = 68.1$, 1 set of shared chromosomes). In comparison, the D^2 value between *A. neomexicana* and *A. sexlineata* that share no chromosomes was 101.6. Hybrids OMNH 35109 and AMNH 144085 had D^2 values comparable to that of the 13 hybrids from CL-2*.

Karyotypes of a Hybrid and Parental Species

Clearly resolved karyotypes of the allodiploid *A. neomexicana* have been published previously and are consistent with its hybrid origin involving *A. tigris marmorata* × *A. inornata* (Lowe and Wright, 1966a; Parker and Selander, 1984; Cole et al., 1988). *Aspidoscelis tigris marmorata* and *A. inornata* belong to the *tigris* and *sexlineata* species groups, respectively (Lowe et al., 1970; Reeder et al., 2002). Each species group has a diagnostically distinct karyotype (Lowe et al., 1970).

The *A. tigris marmorata* complement ($n = 23$) consists of 3 large Set I biarmed macrochromosomes + 8 smaller Set II biarmed intermediate-sized macrochromosomes + 12 Set III microchromosomes. The second largest chromosome in Set I of *A. tigris* has a dotlike satellite on the end of one arm, which

TABLE 9

Comparisons of Pooled Samples of *Aspidoscelis neomexicana* (*A.n.*, sites CL-1*, CL-13, CL-4, CL-5*, CL-2*), *A. neomexicana* × *A. sexlineata viridis* (*A.h.*, sites CL-5*, CL-2*), and *A. sexlineata viridis* (*A.s.*, sites CL-5*, CL-2*) from Conchas Lake, San Miguel County, New Mexico

Taxon	*N*	Mean ± SE	G[a]	COV	ND[b]	Range and dispersion of variation
						Granules (scales) from occiput to rump
						150 159 167 168 169 171 172 173 176 177 178 179 180 181 182 183 184
A.n.	96	185.0 ± 0.44	A	2.37	Y	– – – – – – 1 – 1 – 4 3 4 5 11 8 8
A.h.	14	187.8 ± 2.03	A	4.04	Y	– – – – – – – – – 1 – – 1 1 1 – 2
A.s.	46	181.4 ± 1.49	A	5.57	Y	1 1 1 2 1 1 1 2 1 3 3 1 3 2 1 2 2
						185 186 187 188 189 190 191 192 193 194 195 196 197 199 200 204
						10 7 7 6 4 5 3 5 1 2 1 – – – – –
						– 1 – 1 1 2 – – – 1 – – – – 1 1
						– 1 2 5 – 3 1 – – 1 2 1 1 1 – –
						Lateral supraocular granules
						6 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
A.n.	96	36.7 ± 0.35	A	9.23	N	– – – – – – – – – – – – – – – – – 3 2 2 1
A.h.	14	29.9 ± 0.92	B	11.54	Y	– – – – – – – – – – – – – 1 1 – 2 1 1 2 1
A.s.	47	18.3 ± 0.63	C	23.61	Y	1 1 – 3 8 6 2 7 3 3 3 4 1 1 1 2 – – – – –
						32 33 34 35 36 37 38 39 40 41 42 43
						3 4 4 9 15 12 10 14 7 3 5 2
						1 1 2 1 – – – – – – – –
						1 – – – – – – – – – – –
						Interlabial scales
						12 13 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 34 35 36 37 49
A.n.	96	23.1 ± 0.39	AB	16.45	N	– 1 – 1 4 3 5 6 13 11 9 11 16 3 2 5 2 1 1 1 1 – –
A.h.	14	25.0 ± 0.82	A	12.24	Y	– – – – – – – 1 1 3 – – 1 4 – 2 2 – – – – – –
A.s.	49	21.7 ± 0.93	B	30.23	N	1 2 1 5 3 2 10 5 2 – 2 1 2 4 – 3 3 1 – – – 1 1
						Granules around midbody
						62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 81 82 83
A.n.	96	76.0 ± 0.20	A	2.62	N	– – – – – – – – – – 2 8 18 12 10 21 16 7 1 1 – –
A.h.	14	69.7 ± 0.72	C	3.86	Y	– – – – 1 3 1 2 2 1 1 1 2 – – – – – – – – – –
A.s.	48	73.4 ± 0.73	B	6.89	Y	1 – – 2 3 3 1 – 4 1 4 4 3 3 6 2 4 3 1 – 1 2

TABLE 9
(Continued)

Taxon	*N*	Mean ± SE	G[a]	COV	ND[b]	Range and dispersion of variation																				
						Circumorbital scales																				
						4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
A.n.	96	19.3 ± 0.24	A	12.33	N	–	–	–	–	–	–	–	–	–	2	1	3	8	11	9	9	17	20	12	3	1
A.h.	14	14.1 ± 0.82	B	21.70	N	–	–	–	–	–	–	1	–	3	4	2	1	1	–	–	–	1	1	–	–	–
A.s.	48	7.1 ± 0.26	C	25.77	N	5	3	12	9	8	5	5	1	–	–	–	–	–	–	–	–	–	–	–	–	–
						Femoral pores																				
						24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39					
A.n.	96	36.9 ± 0.13	A	3.33	N	–	–	–	–	–	–	–	–	–	–	3	9	22	32	20	10					
A.h.	14	35.9 ± 0.29	A	2.98	Y	–	–	–	–	–	–	–	–	–	–	1	4	5	3	1	–					
A.s.	49	29.1 ± 0.28	B	6.67	N	1	–	3	1	12	16	8	3	2	1	1	1	–	–	–	–					
						Subdigital lamellae																				
						23	24	25	26	27	28	29	30	31	32	33	34									
A.n.	96	31.7 ± 0.12	A	3.56	N	–	–	–	–	–	–	–	15	32	19	27	3									
A.h.	14	31.0 ± 0.31	B	3.77	Y	–	–	–	–	–	–	1	4	5	2	2	–									
A.s.	49	26.6 ± 0.18	C	4.85	N	1	–	7	17	14	8	1	–	1	–	–	–									
						Paravertebral granules																				
						7	8	9	10	11	12	13	14													
A.n.	96	12.4 ± 0.09	A	7.10	N	–	–	–	3	12	34	42	5													
A.h.	14	9.6 ± 0.34	B	13.23	N	–	2	6	3	1	2	–	–													
A.s.	49	9.5 ± 0.19	B	14.10	N	3	10	10	14	9	3	–	–													

[a]Means marked by the same letter are not different at $P = 0.05$.
[b]For normal distributions, Y indicates yes and N indicates no.

TABLE 10

Data (mean ± SE, Range) for Eight Characters of Scutellation and a Ratio in Samples of *Aspidoscelis neomexicana*, *A. sexlineata viridis*, and *A. tesselata* C Compared to Data for Hydrids of *A. neomexicana* × *A. sexlineata viridis* from Sites at Conchas Lake, San Miguel County, New Mexico

	A. neomexicana					*A. sexlinata viridis*		*A. tesselata* C
Character	CL-1* $N = 14$	CL-13 $N = 12$	CL-4 $N = 12$	CL-5* $N = 8$	CL-2* $N = 50$	CL-5* (*N*)	CL-2* $N = 24$	CL-5* (*N*)
GAB	76.2 ± 0.54 73–79	75.4 ± 0.56 73–79	75.0 ± 0.58 72–78	75.9 ± 0.64 73–78	76.4 ± 0.27 73–81	72.4 ± 0.85 65–79 (24)	74.3 ± 1.17 62–83	90.7 ± 0.93 81–102 (30)
OR	184.5 ± 1.05 178–192	182.0 ± 0.83 178–187	182.7 ± 0.89 176–188	185.1 ± 2.29 172–192	186.5 ± 0.58 178–195	185.5 ± 1.83 169–199 (22)	178.5 ± 2.25 150–197	195.3 ± 1.31 185–212 (29)
PV	12.1 ± 0.27 10–13	12.3 ± 0.18 11–13	11.7 ± 0.21 11–13	12.5 ± 0.27 11–13	12.6 ± 0.13 10–14	9.1 ± 0.25 7–12 (25)	9.9 ± 0.27 7–12	11.9 ± 0.16 10–13 (30)
PV/GAB (× 100)	15.9 ± 0.30 13.5–17.3	16.2 ± 0.21 14.6–17.5	15.4 ± 0.33 14.1–18.0	16.5 ± 0.33 14.7–17.9	16.4 ± 0.15 13.4–18.4	12.6 ± 0.36 10.0–15.7 (24)	13.4 ± 0.26 10.2–15.4	13.0 ± 0.21 10.7–16.0 (30)
FP	37.2 ± 0.28 35–39	37.2 ± 0.24 36–38	37.6 ± 0.24 36–39	36.9 ± 0.35 36–39	36.6 ± 0.19 34–39	28.5 ± 0.29 26–32 (25)	29.8 ± 0.45 24–35	41.5 ± 0.27 38–44 (30)
SDL	31.1 ± 0.25 30–33	32.0 ± 0.30 30–33	31.6 ± 0.24 31–33	31.1 ± 0.44 30–33	31.9 ± 0.17 30–34	26.4 ± 0.29 23–28 (22)	26.7 ± 0.27 25–31	37.0 ± 0.20 35–39 (29)
COS	18.5 ± 0.49 16–22	19.8 ± 0.65 16–23	19.2 ± 0.62 14–22	18.9 ± 0.52 17–21	19.3 ± 0.39 13–24	7.4 ± 0.31 5–10 (24)	6.9 ± 0.43 4–11	17.8 ± 0.36 13–20 (29)
LSG	34.9 ± 0.76 28–38	36.3 ± 1.46 28–43	35.7 ± 0.76 30–38	35.8 ± 1.31 28–39	37.7 ± 0.41 29–42	19.6 ± 0.99 14–32 (22)	17.2 ± 0.77 6–25	36.4 ± 0.67 31–47 (29)
ILS	22.6 ± 0.86 17–28	21.3 ± 1.15 13–29	25.7 ± 1.34 20–35	23.5 ± 1.45 18–30	22.9 ± 0.48 16–36	20.2 ± 0.86 13–30 (35)	23.2 ± 1.65 12–49	35.5 ± 0.81 22–43 (30)

TABLE 10
(Continued)

	UADZ (7) and AMNH (1) Individuals of *A.n.* × *A.s.* ♂ by Site								UADZ (6) and OMNH (1) Individuals of *A.n.* × *A.s.* ♀ by Site						
	CL-2*							CL-5*	CL-2*						CL-1*
	7344	7448	7452	7553	7561	7570	7700	144085	7349	7445	7455	7554	7555	7556	35109
GAB	72	74	70	69	67	74	71	70	67	67	66	68	69	73	66
OR	189	200	177	188	180	194	190	184	182	190	184	181	184	204	157
PV	12	9	11	8	9	10	9	12	9	8	10	9	10	9	10
PV/GAB	16.6	12.1	15.7	11.5	13.4	13.5	12.7	17.1	13.4	11.9	15.1	13.2	14.5	12.3	15.1
FP	37	36	36	36	37	35	37	36	38	36	35	35	34	35	36
SDL	31	33	29	32	30	30	31	33	31	31	32	31	30	30	30
COS	20	13	13	21	12	13	10	12	12	13	14	15	13	16	11
LSG	30	27	28	36	29	34	25	27	24	32	31	30	34	33	36
ILS	29	26	26	21	20	25	28	22	22	26	29	26	28	28	36

Abbreviations: GAB, granules (scales) around midbody; OR, granules from occiput to rump; PV, granules between the paravertebral stripes; FP, femoral Pores; SDL, subdigital lamellae; COS, circumorbital scales; LSG, lateral supraocular granules; ILS, interlabial scales; and PV/GAB, paravertebral granules/granules around midbody (× 100).

TABLE 11

Factor Loadings for Two Principal Components and Two Canonical Variates Derived from Meristic Variation Among Individuals of *Aspidoscelis neomexicana*, *A. sexlineata viridis*, *A. tesselata* C, and *A. neomexicana* × *A. sexlineata viridis* from Conchas Lake, San Miguel County, New Mexico

Character[a]	PC1	PC2	CV1	CV2
GAB	0.344	0.383	−0.006	−0.224
OR	0.344	0.254	−0.004	0.024
PV	0.285	−0.429	0.197	0.404
FP	0.420	0.046	0.311	−0.047
SDL	0.416	0.082	0.444	−0.253
COS	0.359	−0.440	0.108	0.065
LSG	0.387	−0.338	0.146	0.161
ILS	0.273	0.536	−0.055	−0.044
Eigenvalue	4.751	1.466	19.919	5.306
Total explained variation	59.39%	18.32%	73.74%	20.18%

[a]See table 10 for abbreviations.

is often difficult to see, and the third largest chromosome is the sex chromosome (Cole et al., 1969; Bull, 1978) of which the X-chromosome is recognizable in the karotype of *A. neomexicana*. The complement from *A. inornata* (n = 23) consists of only one large Set I metacentric macrochromosome (with a subterminal secondary constriction on one arm followed by an elongate satellite) + 12 smaller Set II intermediate-sized telocentric or subtelocentric macrochromosomes + 10 Set III microchromosomes. The sex chromosomes of *A. inornata* are not morphologically recognizable. The secondary constrictions on the Set I chromosomes of both *A. tigris* and *A. inornata* are the nucleolar organizer regions (Ward and Cole, 1986).

As expected, the three putative representatives of *A. neomexicana* (AMNH R-136881, R-151740 from Conchas Lake, and R-151741 from Fort Sumner) had a diploid karyotype consisting of one normal *tigris* group haploid complement and one normal *sexlineata* group haploid complement of chromosomes, or $2n$ = 46. Consequently, karyotypes are consistent with the assumption that these specimens are correctly identified as *A. neomexicana* from both localities. However, the karyotype is not diagnostic, as the karyotype of *A. tesselata* from Conchas Lake is identical (Dessauer and Cole, 1989: 57). Nevertheless, the proteins do confirm the identity of these *A. neomexicana* (see below). In addition, the five *A. sexlineata viridis* examined all had the normal *sexlineata* group karyotype, and each had a distinctive subtelocentric pair of Set II chromosomes that characterizes this species (Bickham et al., 1976), although CJC's data suggest that there is only one of these distinctive Set II pairs (about the fourth largest Set II pair), instead of two as reported by Bickham et al. (1976).

The suspected hybrid male (AMNH R-151739) from Conchas Lake was a triploid having $3n$ = 69 chromosomes, including the full diploid karyotype of *A. neomexicana* plus a second haploid complement of *sexlineata* group chromosomes (fig. 17). In all details of the karyotype, this triploid appeared to be an F_1 hybrid of *A. neomexicana* × *A. sexlineata viridis*. In addition, the karyotype was identical to that of the laboratory-produced hybrid of *A. neomexicana* × *A. sexlineata* reported by Dessauer and Cole (1984). Based on the morphology of this karyotyped individual, we infer that five additional males (AMNH 144085, GM [at UADZ] 128, 279, 412, 430) from Conchas Lake with color patterns largely resembling *A. neomexicana* are also F_1 hybrids between these species.

Allozymes of a Hybrid and Parental Species

Based on genotypes detected at 23 loci, we obtained evidence bearing on the following questions: (1) Were the specimens of sus-

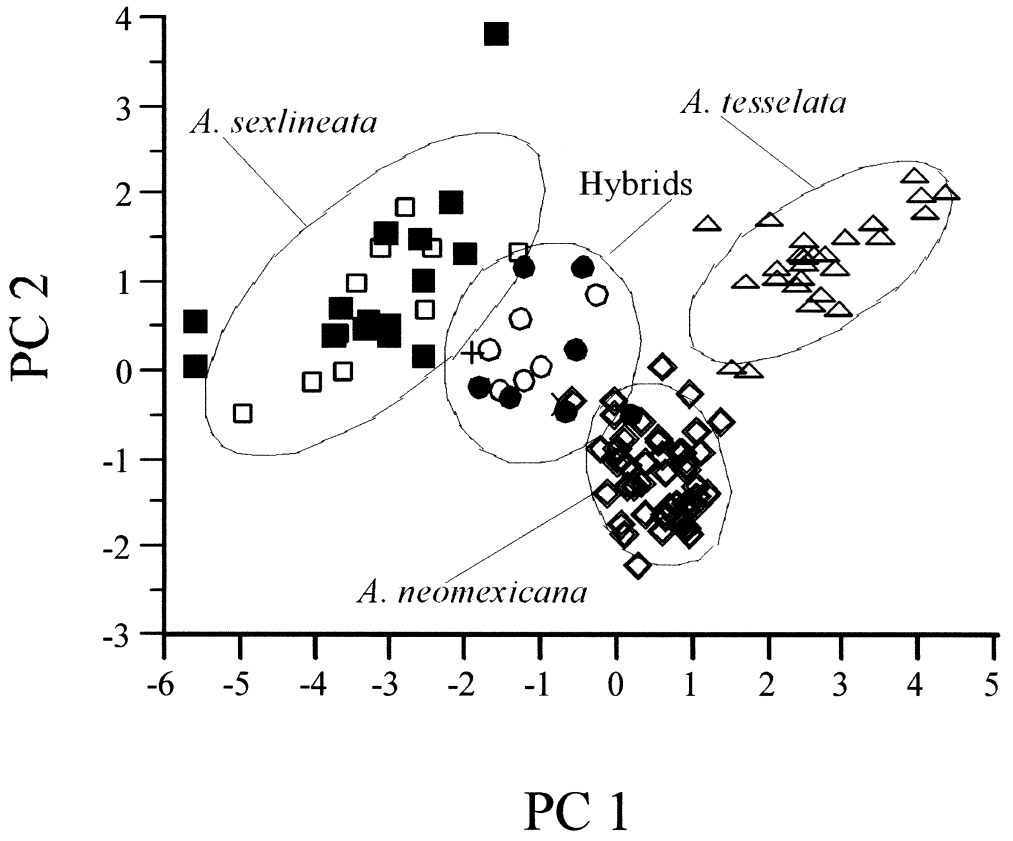


Fig. 15. Pattern of morphological variation expressed by the distribution of scores on the first two principal components extracted from a correlation matrix of eight meristic characters for 49 *A. neomexicana* (◊), 26 *A. sexlineata viridis* (■ = ♂ and □ = ♀), 13 *A. neomexicana* × *A. sexlineata viridis* (● = ♂ and ○ = ♀), AMNH 144085 = UADZ 3272 (×, assigned to the hybrid group as indicated by Walker et al., 1990), OMNH 35109 (+, assigned to the hybrid group as suspected by B.E. Leuck), and 26 *A. tesselata* C (△) from Conchas Lake, San Miguel County, New Mexico. Ellipses represent the 95% confidence limits of each group.

pected *A. neomexicana* from Conchas Lake (AMNH R-136881, R-151740) and Fort Sumner (AMNH R-151741) actually this species and not something else similar to that, such as a new color pattern class of *A. tesselata*? (2) Was the suspected hybrid (AMNH R-151739) actually that? (3) Was the male parent of the hybrid a representative of *A. sexlineata viridis*?

The two *A. neomexicana* examined from Conchas Lake and Fort Sumner had identical genotypes at each of the 23 loci (table 13), except for one allele in the lizard from Fort Sumner. Twelve or 13 loci (52–56%) had alleles in the heterozygous state, attesting to the ultimate origin of this taxon from a hybridization event (*A. tigris marmorata* ♀ × *A. inornata* ♂). In addition, the specimen from Conchas Lake appeared to be identical (all loci, all alleles) to specimens of the most common and most widely distributed clone of *A. neomexicana* from elsewhere in its geographic range (table 13; Cole et al., 1988). In particular, the two orphan alleles known to characterize *A. neomexicana* from other localities appeared to be present in the specimens from both Conchas Lake and Fort Sumner. These are the very distinctive d-allele at ESTD (fig. 18) and c-allele at PEPB (also normally found in *A. sexlineata viridis*; table 13; appendix 8; Cole et al., 1988).

The specimen of *A. neomexicana* from

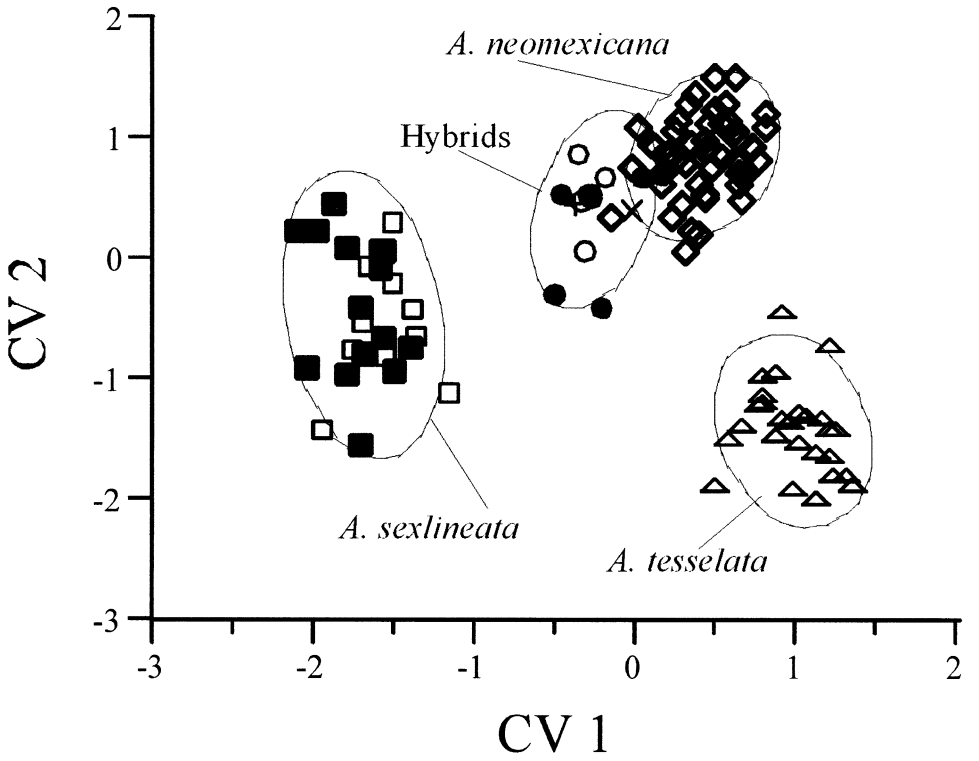


Fig. 16. Pattern of morphological distinctiveness expressed by the distribution of canonical variate scores derived from a linear canonical variate analysis of eight meristic characters in 49 *A. neomexicana* (◊), 26 *A. sexlineata viridis* (■ = ♂ and □ = ♀), 13 *A. neomexicana* × *A. sexlineata viridis* (● = ♂ and ○ = ♀), AMNH 144085 = UADZ 3272 (×, assigned to the hybrid group as indicated by Walker et al., 1990), OMNH 35109 (+, assigned to the hybrid group as suspected by B.E. Leuck), and 26 *A. tesselata* C (△) from Conchas Lake, San Miguel County, New Mexico. Ellipses represent the 95% confidence limits of each group.

Fort Sumner was identical to the one from Conchas Lake, excepting one allele. It differed only by possessing one b-allele at sMDH (heterozygous ab, fig. 18). It would be interesting to compare this b-allele with the variant sMDH allele found by Parker and Selander (1984) to occur infrequently in *A. neomexicana* in the vicinity of Engle, Sierra County, New Mexico.

Normally, *A. neomexicana* and *A. tesselata* (including those from Conchas Lake) differ at the following 10 loci among those examined for this report: sMDH, sMDHP, sIDH, ESTD, PEPA, PEPB, ADA, MPI, GPI, and PGM2 (Dessauer and Cole, 1989, and unpubl.). Clearly (table 13), the new specimens we examined for the present report that appeared to be *A. neomexicana* are correctly identified as representing that taxon and are not a new clone of *A. tesselata* (table 13).

Of the 23 loci analyzed (table 13), 9 showed no allelic variation among the individuals of each taxon and the hybrid examined (the same alleles were shared universally), but 12 loci were particularly informative for identifying the hybrid and its parental species. For nearly each of these loci, the suspected hybrid (based on morphology and triploid karyotype) had electrophoretic banding patterns consistent with a triploid bearing a combination of alleles that included the two found in the diploid *A. neomexicana* plus a third allele from the local *A. sexlineata viridis*. This is consistent with a cloned *neomexicana* ovum having been fertilized by a haploid *sexlineata* spermatozoan (table 13).

The presence of the *sexlineata* allele in the

TABLE 12
Mean Mahalanobis Distances (D^2) Among Centroids of Four a priori Groups Compared with the Number of Haploid Genomes Shared Between Pairs of a priori Groups Used in a CV Analysis

	A. neomexicana	*A. sexlineata*	Hybrids	*A. tesselata* C
A. neomexicana	—			
A. sexlineata	112.3 (0/2)[a]	—		
A.n. × *A.s.*	28.2 (2/3)	63.6 (1/3)	—	
AMNH 144085	19.6 (2/3)	72.4 (1/3)	—	52.7 (1/3)
OMNH 35109	52.1 (2/3)	75.1 (1/3)	—	96.0 (1/3)
A. tesselata C	45.3 (1/2)	156.8 (0/2)	66.3 (1/3)	—

[a]Chromosome set shared/chromosome set possessed.

hybrid was detected at most loci based on allele dosage effects on band densities (isozyme activities) in electrophoretic phenotypes. For example, at PEPA, specimens of the diploid *A. neomexicana*, which are heterozygotes (ac), show a three-banded pattern. The hybrid shows the same three bands, but the relative band densities differ from those of *neomexicana*. Phenotypes (gel patterns) predicted for the ac genotype of this dimeric enzyme by the expansion of $(a + c)^2$, which equals $a^2 + 2ac + c^2$, consist of three isozymes with a ratio of activities (band densities on gels) approximating 1:2:1, as observed for *neomexicana* (fig. 18). The phenotype predicted for the aac genotype, pre-

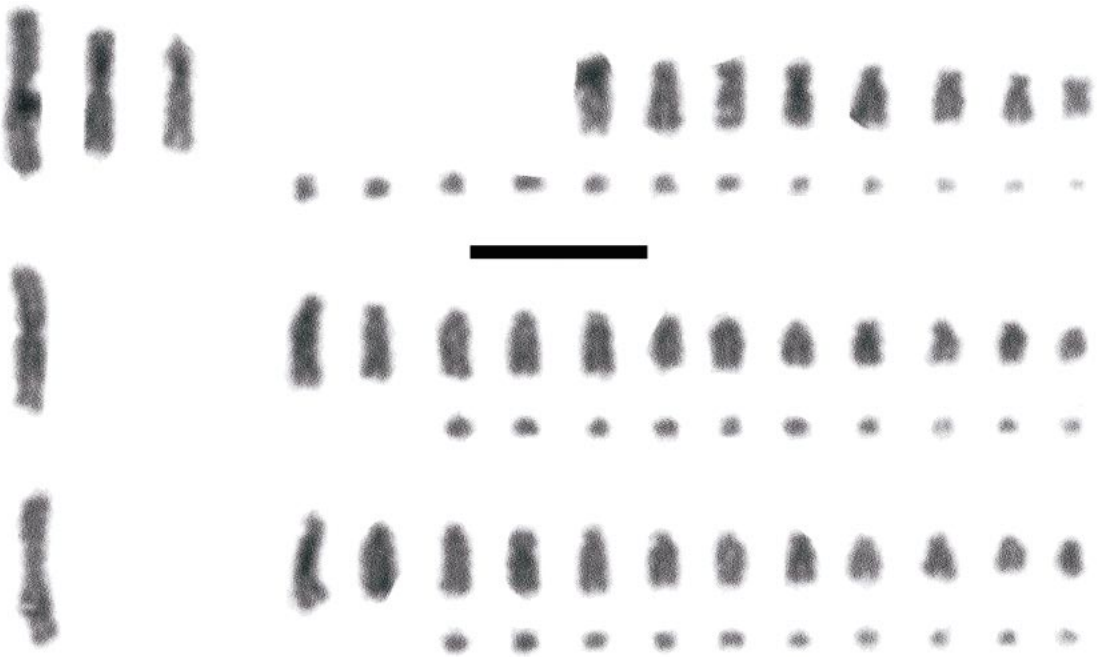


Fig. 17. Karyotype of a triploid whiptail lizard (AMNH R-151739; 3*n* = 69) from Conchas Lake, San Miguel County, New Mexico. This is a hybrid between *A. neomexicana* × *A. sexlineata viridis*. The three haploid genomes (two rows of chromosomes each) are arranged to illustrate ancestry of the hybrid, as follows: *A. tigris marmorata* (top) × *A. inornata* (middle), which were inherited from the diploid maternal parent of the hybrid (*A. neomexicana*), and *A. sexlineata viridis* (bottom), from the paternal parent. Bar = 10 μm.

TABLE 13

Genotypes or Alleles[a] at 23 Gene Loci[b] in Samples of *Aspidoscelis neomexicana*, *A. neomexicana* × *A. sexlineata viridis*, and *A. sexlineata viridis*

	A. neomexicana			*A.n.* × *A.s.*	*A. sexlineata viridis*
Locus	Cole et al. (1988)	FS-2	CL-13	CL-2*	
Oxidoreductases					
G3PDH	w	w	w	w	w
IDDH	w	w	w	w	w,a+
LDH1	ab	ab	ab	abb	b
LDH2	w	w	w	w	w
sMDH	aa	ab	aa	aaa	a
mMDH	w	w	w	w	w
sMDHP	w	w	w	w	w
sIDH	ab	ab	ab	aab	a
mIDH	w	w	w	w	w
sSOD	ab	ab	ab	abb	b
mSOD	w	w	w	w	w
Transferases					
sAAT	ab	ab	ab	abb	b,a
mAAT	ab	ab	ab	aab	a,b
Hydrolases					
ESTD	bd	bd	bd	abd	c,a,b
PEPA[c]	ac	ac	ac	aac	b,a
PEPB	ac	ac	ac	acc	c,b,d
ADA	ab	ab	ab	abb	b,a
Isomerases					
MPI	ab	ab	ab	abb	b
GPI	w	w	w	w	w
PGM2	—	aa	aa	aaa	a
Blood proteins					
TF[d]	bc	bc	bc	abc	c,a,b
PREALB	ac	ac	ac	abc	c,a,b
HB	w	w	w	w	w

[a]Alleles only are presented for *A. sexlineata viridis* (*A.s.*). If one allele is given, all specimens were homozygous for that allele. If two or more alleles are given, the first listed are the highest frequencies. For *A. neomexicana* (*A.n.*, FS-2 [Fort Sumner–Railroad Depot], CL-13 [Cove Campground]), the common clone is shown along with the only variant observed from Fort Sumner (sMDH); their genotypes are presented. Genotypes are presented for the hybrid also.

[b]Alleles are designated in alphabetical order according to decreasing anodal migration of their allozymes. For multilocus enzymes, loci are numbered in order of decreasing anodal migration of their isozymes. Abbreviations and methods follow Harris and Hopkinson (1976), Murphy et al. (1996), and Dessauer et al. (2000); s = cytosolic enzyme; m = mitochondrial enzyme. Abbreviations for loci are as follows: G3PDH, glycerol-3-phosphate dehydrogenase; IDDH, l-iditol dehydrogenase; LDH, l-lactate dehydrogenase; MDH, malate dehydrogenase; MDHP, malate enzyme; IDH, isocitrate dehydrogenase; SOD, superoxide dismutase; AAT, aspartate aminotransferase; EST, esterase; PEP, peptidase; ADA, adenosine deaminase; MPI, mannose-6-phosphate isomerase; GPI, glucose-6-phosphate isomerase; PGM, phosphoglucomutase; TF, transferrin; PREALB, prealbumin; and HB, hemoglobin.

[c]We have not observed the a-allele at PEPA in specimens of *A. sexlineata*, only the b-allele. The extra a-allele in the hybrid, however, indicates that it occurred in the paternal parent, for which all other alleles in the hybrid are consistent with *A. sexlineata viridis*.

[d]To date, for *A. sexlineata viridis* we have found the a-allele at TF only in individuals from New Mexico and Colorado as a local polymorphism. In this instance, the hybrid analyzed inherited the a-allele.

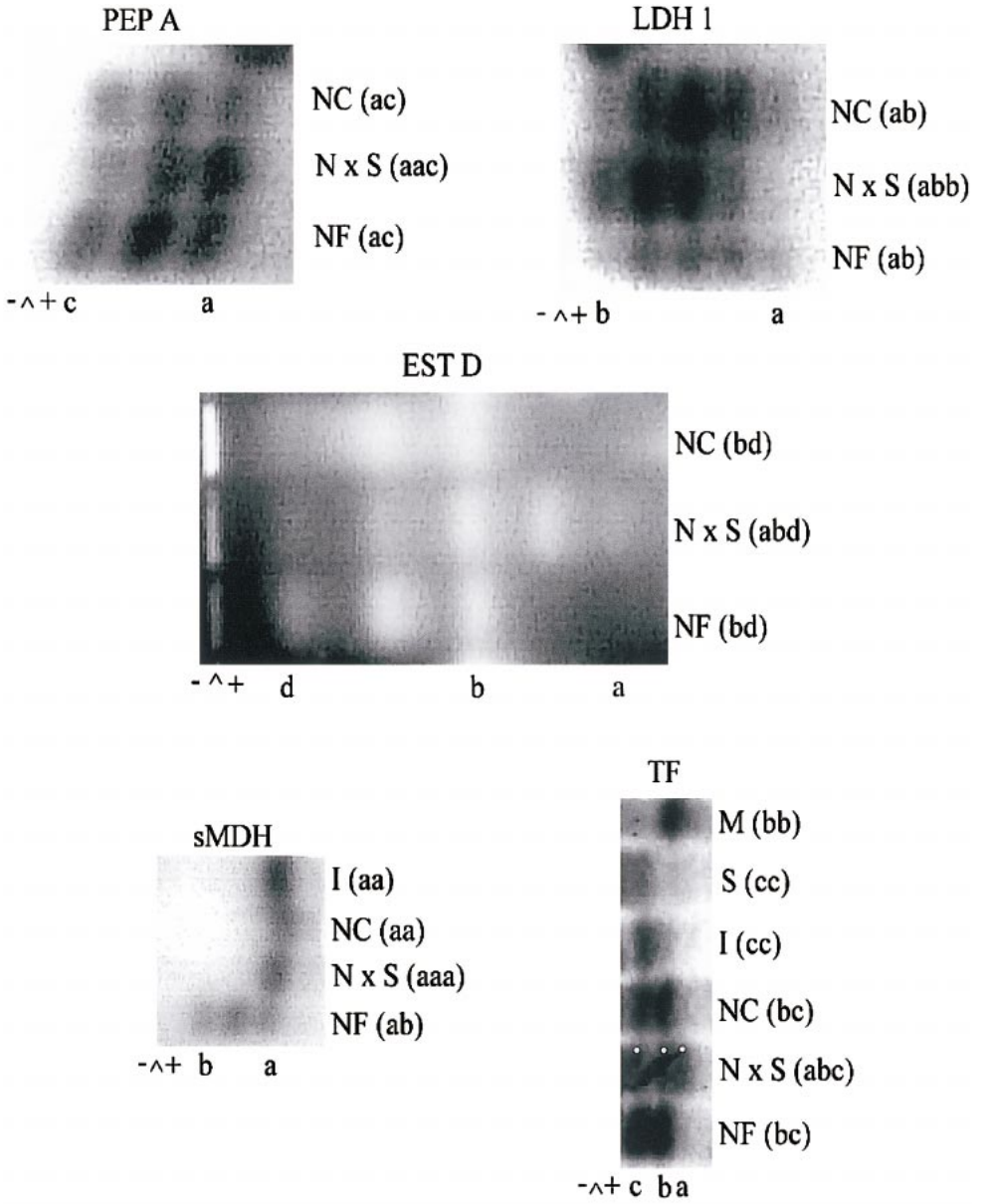


Fig. 18. Electrophoretic phenotypes of five proteins as expressed on separate gels. **PEPA,** a dimeric enzyme, for three lizards. **LDH1,** a tetrameric enzyme, for three lizards. **ESTD,** a dimeric enzyme, for three lizards. **sMDH,** a dimeric enzyme, for four lizards. **TF,** a monomeric enzyme, for six lizards; white dots mark the three isozymes from the hybrid. Letters below gel identify allozymes based on alleles present (table 13). Lanes for individual lizards are labeled beside the gel (with genotype) as follows: I, *A. inornata*; M, *A. tigris marmorata*; N, *A. neomexicana*; NC, *A. neomexicana* from Conchas Lake; NF, *A. neomexicana* from Fort Sumner; N × S, the hybrid; S, *A. sexlineata viridis*. Anode is to the right, ^ indicates relative position of sample applications.

dicted by the expansion of $(2a + c)^2$, which equals $4a^2 + 4ac + c^2$, consists of the same three isozymes but with a ratio of activities approximating 4:4:1, as observed in the triploid hybrid (fig. 18). Consequently, *neomexicana* and the hybrid had three-banded patterns for PEPA, but the ratio of the band densities differed between them. For *A. sexlineata viridis*, the b-allele is the most common one at PEPA (table 13; Cole et al., 1988), so the second a-allele found in the hybrid indicates that the a-allele occurs rarely in *A. sexlineata viridis*.

Similarly, LDH1 showed the same bands of isozymes in *A. neomexicana* and the hybrid, but there were differences in the band densities owing to the extra b-allele in the triploid contributed by *A. sexlineata viridis*. LDH1 is a tetrameric enzyme for which *neomexicana* is heterozygous (ab). The phenotype expected for the ab genotype of *A. neomexicana*, predicted by the expansion of $(a + b)^4 = a^4 + 4a^3b + 6a^2b^2 + 4ab^3 + b^4$, is for five isozymes with a ratio of activities approximating 1:4:6:4:1 (fig. 18). The phenotype predicted for the abb triploid genotype of the hybrid, predicted by the expansion of $(a + 2b)^4 = a^4 + 8a^3b + 24a^2b^2 + 32ab^3 + 16\ b^4$, shows the same five isozymes but correspondingly different band-densities, as expected (fig. 18).

Banding patterns for TF and ESTD, however, involved differences in both the number of isozymes and the band densities present in *A. neomexicana* versus the hybrid. TF is a monomeric enzyme, so the bc genotype of *neomexicana* shows two more-or-less equally dense bands (fig. 18). However, the abc triploid genotype of the hybrid shows three bands (fig. 18), and the a-allele at TF is one that is common in specimens of *A. sexlineata viridis* from New Mexico and Colorado. At ESTD, a dimeric enzyme, specimens of the diploid *A. neomexicana*, which are heterozygotes (bd), show a three-banded pattern. However, the hybrid shows a five-banded pattern. Phenotypes predicted for the bd genotype of this dimeric enzyme by the expansion of $(b + d)^2$, which equals $b^2 + 2bd + d^2$, consist of three isozymes with a ratio of activities approximating 1:2:1, although the b-band is more active than the d-band in *neomexicana* (fig. 18). The phenotype predicted for the abd genotype, predicted by the expansion of $(a + b + d)^2$, which equals $a^2 + 2ab + b^2 + 2ad + 2bd + d^2$, consists of six isozymes with a ratio of activities approximating 1:2:1:2:2:1. Five bands were resolved presumably because the b^2 and 2ad isozymes have the same migration rate and were superimposed on the gel (fig. 18), and band densities still reflect the greater expression of the b-allele, as in *A. neomexicana*.

DISCUSSION

Biochemical genetic data for one lizard from Fort Sumner (AMNH R-151741) and one from Conchas Lake (AMNH R-136881) verified that the isolated groups from which they were collected were correctly identified to *A. neomexicana* based on morphology in the respective reports of their discovery by Leuck et al. (1981) and Taylor (2002). The data indicated that Conchas Lake *A. neomexicana* belongs to the most widely distributed clone of the species in New Mexico (Parker and Selander, 1984; Cole et al., 1988), and that the Fort Sumner population contains a variant sMDH allele which may be the same one found by Parker and Selander (1984) in some individuals of the species from the vicinity of Engle, Sierra County, New Mexico.

Aspidoscelis neomexicana comprises the cloned descendants from hybrid event(s) between one or more females and males, respectively, of the divergent taxa *A. tigris marmorata* and *A. inornata* (Lowe and Wright, 1966b; Parker and Selander, 1984; Cole et al., 1988; Densmore et al., 1989). Although the gonochoristic progenitors of *A. neomexicana* still occur in syntopy at numerous sites in desert-grassland communities in Texas and New Mexico, there have been no reports of contemporary F_1 hybrids between moderately large-bodied *A. tigris* and small-bodied *A. inornata* (Cole et al., 1988). It is possible that a single hybrid female (i.e., the first *A. neomexicana*) founded the tokogenetic array known to occur over most of the range of the species, which comprises a single allozyme clone (Parker and Selander, 1984; Cole et al., 1988) of mutually histocompatible individuals (Cuellar, 1977; Cordes et al., 1990). Moreover, it is likely that the two additional allozyme clones of *A. neo-*

mexicana (Cole et al., 1988) were produced from the original clone by mutation or recombination. That the New Mexico Whiptail is a successful parthenogenetic species despite its low clonal diversity is evidenced by both ecological and zoogeographic data (Axtell, 1966; Wright and Lowe, 1968; Cole et al., 1988; Cordes et al., 1989).

There are at least three historical obstacles to formation of new all-female species of *Aspidoscelis* from hybridizing species. First, the production of hybrids between gonochoristic species of *Aspidoscelis*, exclusive of instances of secondary intergradation which some authors have referred to as hybridization, is so rare that none has been identified to date. Second, there is no evidence of parthenogenetic capability in any of the many F_1 hybrids between a parthenogenetic and a gonochoristic species that have been described in the literature, indicating that few hybrids are capable of founding tokogenetic arrays. Third, the odds would seem to be insurmountable against establishment of a new hybrid-derived parthenogenetic species in competition with both of its parental forms and other syntopic congeners. Nevertheless, in the case of *A. neomexicana* the parthenogenetic descendants of the original hybrid female (i.e., the first few generations) somehow overcame these odds and became established at a site inhabited by *A. tigris marmorata* and *A. inornata*. One model to account for the success of the early generations of this ''general purpose'' genotype that has spread to inhabit most of the range of *A. neomexicana* was outlined by Dessauer and Cole (1989: 52): ''. . . an ability of one clone of *C. neomexicanus* to tolerate different local habitats may have prevented its immediate extinction following its hybrid origin in desert-grassland: 'gallery forests along the Rio Grande could have had an important role in the survival of this nascent species of instantaneous hybrid origin, by providing sites for parthenogenetic hybrids to reproduce with minimal interference from the ancestral males of both species, which generally avoid the gallery forests' (Cole et al., 1988, p. 35).'' Today, sites inhabited by this parthenogen are mostly associated with the Rio Grande and some of its tributaries and adjacent playas in New Mexico and Texas (Axtell, 1966; Wright and Lowe, 1968; Cuellar, 1977; Cordes et al., 1989). In time, *A. neomexicana* became integrated into diverse guilds of whiptail lizards (e.g., those at Conchas Lake and Fort Sumner) consisting of variable combinations from among three gonochoristic species (*A. tigris marmorata*, *A. inornata*, and *A. sexlineata viridis*) and four parthenogenetic species (*A. exsanguis*, *A. tesselata*, *A. uniparens*, and *A. velox*) (table 1).

Several investigations have focused on the biological significance of perennial hybridization between a normally parthenogenetic species and one of its progenitors: *A. laredoensis* ♀ × *A. gularis gularis* ♂ (Walker et al., 1989; Paulissen et al., 1992; Walker et al., 2004) and *A. tesselata* ♀ × *A. tigris marmorata* ♂ (Taylor et al., 2001). These studies reported no indication that interspecific hybridization has had a substantial biological impact on any of the species involved. Moreover, the observations that *A. laredoensis*, *A. neomexicana*, and *A. tesselata* have all progressed to the final stage in the evolution of a hybrid-derived parthengenetic species of *Aspidoscelis* as allodiploids, namely ''capture of a habitat'' (Wright and Lowe, 1968), constitute a priori evidence of their avoidance of destabilizing hybridization with their gonochoristic progenitors during the first few generations of the ''establishment stage''.

Discovery of natural hybrids of *A. neomexicana* × *A. sexlineata viridis* at Conchas Lake in five different years between 1988 and 2003 represents the first evidence of perennial hybridization between a parthenoform and a gonochoristic species other than one of its progenitors. Although *A. neomexicana* and *A. sexlineata viridis* hybridize at CL-2* at a frequency approaching that reported for *A. neomexicana* and *A. inornata* (Christiansen et al., 1971) and *A. tesselata* and *A. tigris marmorata* (Taylor et al., 2001), these examples of ''occasional hybridization'', similar to some cases described by Mayr (1963) for gonochoristic species, apparently have had no significant negative biological consequences on the species involved. At Conchas Lake, this conclusion was based on annual observations of large numbers of juveniles of *A. neomexicana* in 2000–2003 by GJM at all sites and ecological components where *A. neomexicana* was

found in syntopy with *A. sexlineata viridis*. Although *A. neomexicana* and its much larger maternal progenitor *A. tigris marmorata* may well have existed in syntopy at various sites for thousands of years, it appears that hybridization between these species remains quite rare as only two of their hybrids, both sterile females, have been reported (Dessauer et al., 2000). Both of these hybrids were detected during electrophoretic analyses of hundreds of specimens of *A. tigris* from Hidalgo and Grant Counties with which the hybrids had been confused at the time of collection based on locally variable color patterns. Conversely, the substantial number of sites from which hybrids between *A. neomexicana* and its smaller paternal progenitor *A. inornata* have been reported (Axtell, 1966; Taylor and Medica, 1966; Wright and Lowe, 1967; Christiansen and Ladman, 1968; Christiansen et al., 1971; Cuellar and McKinney, 1976; Taylor and Walker, 1996) indicates that these species have engaged in a low frequency of hybridization for countless generations without apparent genetic consequences to either species and without formation of a new allotriploid species.

The disjunct populations of *A neomexicana* at Fort Sumner and Conchas Lake raise perplexing questions: Do they represent introductions by humans, zoogeographic relicts, or naturally occurring peripheral groups (contiguous or not with the principal range of the species)? Even the coauthors of this report have not been of one mind on the mode of origin of *A. neomexicana* at Conchas Lake. If it was introduced to the area as hypothesized by Leuck et al. (1981), Cole et al. (1988), Densmore et al. (1989), and Persons and Wright (1999), then the potential for hybridization with *A. sexlineata viridis* in San Miguel County is very recent, involving only 15–30 years. The basis of earlier dates is that the species was not included in a large sample of whiptail lizards collected there by E.D. Parker [personal commun.] in 1973; the basis of later dates is the 1988 collection of the hybrid reported by Walker et al. (1990). If *A. neomexicana* is naturally occurring in the area as others have hypothesized (Walker et al., 1990, 1992; Taylor, 2002), then the potential for hybridization with *A. sexlineata viridis* in San Miguel County has continued over many generations. Both sides of the argument pertaining to the hypothesis of a human introduction of *A. neomexicana* at Conchas Lake are summarized in table 14. Two points based on observations that postdate the initial discovery of the species at Conchas Lake seem particularly relevant to the debate. First, it seems unlikely that the complex distribution pattern of the species in evidence at sites both north (e.g., CL-1* and CL-4) and south (e.g., CL-5* and CL-2*) of the river and lake as early as 1979, following its initial discovery in 1978 (Leuck et al., 1981), could have developed from either accidental or purposeful human point releases. Second, the recent discovery of the species in Fort Sumner, De Baca County, New Mexico partially bridged a previously supposed hiatus between Conchas Lake and the Rio Grande Valley (Taylor, 2002).

Evolution of a new triploid species from an *A. neomexicana* × *A. sexlineata viridis* hybrid is an intriguing possibility. As previously noted, the karyotypes of *A. tesselata* (*A. tigris marmorata* × *A. gularis septemvittata*) and *A. neomexicana* (*A. tigris marmorata* × *A. inornata*) at Conchas Lake are not diagnostic, with each species having one haploid complement from a member of the *tigris* species group and one from a member of the *sexlineata* species group (Cole et al., 1988: 22, fig. 7; Dessauer and Cole, 1989: 57, fig. 17). That is not to say that the two species are not readily distinguishable on the basis of allozymes and/or morphology. That the potential existed for incorporation of the basic diploid *neomexicana* or *tesselata* chromosome complement into a triploid karyotype with a complement from a third species is verified by the existence of *A. neotesselata*. That this potential was not realized for thousands of years until *A. tesselata* had spread from its presumed site(s) of origin in southern Texas or northern Mexico to the northern periphery of its range near Higbee, Otero County, Colorado, and that one or more hybridizations between *A. tesselata* × *A. sexlineata viridis* resulted in *A. neotesselata* are noteworthy. Moreover, the existence of *A. neotesselata*, which inhabits a restricted range in a four-county area of Colorado, suggests that a single chromosome complement from *A. tigris* can be incorporated into the

TABLE 14

Evaluation of the Hypothesis of a Human Introduction for *Aspidoscelis neomexicana* at Conchas Lake, San Miguel County, New Mexico

Hypothesis (authors favoring [**AF**] or not favoring [**ANF**] it) Observations favoring hypothesis (**OF**) Observations not favoring hypothesis (**ONF**)
Human Introduction (**AF**: Leuck et al., 1981; Cole et al., 1988; Densmore et al. 1989; Persons and Wright, 1999. **ANF**: Walker et al., 1990, 1992; Taylor, 2002)
A. Unintentional introduction of *A. neomexicana* eggs or individuals
OF: 1. Species not represented in samples collected at Conchas Lake by experienced collectors of whiptail lizards, including J.W. Wright, E.D. Parker, and C.J. Cole before its discovery there in 1978 (Leuck et al., 1981).
2. Closest known record for the species when discovered at Conchas Lake in 1978 was about 190 km to the west in the Rio Grande Valley.
ONF: 1. Much of the complex distribution pattern of the species at Conchas Lake, as presently understood, was apparent by 1979 one year after its discovery (Leuck et al., 1981).
2. Evidence that it is possible to collect at Conchas Lake without finding the species (Walker et al., 1990, 1992). Also, the species was not collected at the South Recreation Area (CL-2*) by CJC until his eighth and last visit to the site from 1976 to 1990.
3. Discovery of the species by Taylor (2002) at Fort Sumner, De Baca County, in the Pecos River drainage, approximately 100 km from Conchas Lake, partially bridged an apparent distributional hiatus.
B. Intentional Introduction of *A. neomexicana* eggs or individuals
OF: 1. Same as stated for unintentional introduction.
2. Same as stated for unintentional introduction.
ONF: 1. Same as stated for unintentional introduction.
2. Same as stated for unintentional introduction.
3. Same as stated for unintentional introduction.
4. Conceivably, the present distribution of the species at Conchas Lake at sites CL-1* and CL-4 (north of the Canadian River) and CL-2* (south of the Canadian River) only could have developed from a sophisticated series of repeated introductions.
5. Subsequently, the species would have had to invade several sites with large established populations of other species of *Aspidoscelis* (e.g., sites CL-2* and CL-5*) to achieve its present distribution at Conchas Lake.

triploid karyotype of a parthenogen in contrast to two complements from this species. This phenomenon could explain the basis for the perennial production of sterile triploid hybrids of *A. tesselata* × *A. tigris marmorata* at Arroyo del Macho, Chaves County, New Mexico (Taylor et al., 2001).

SUMMARY AND CONCLUSIONS

1. The easternmost groups of *Aspidoscelis neomexicana* in New Mexico were discovered at Conchas Lake, San Miguel County, by B.E. Leuck and colleagues in 1978 and at Fort Sumner, De Baca County, by H.L. Taylor in 2002. Available evidence indicates that both groups are disjunct from each other and from representatives of the species to the west in the Rio Grande Valley of New Mexico.

2. Whether *A. neomexicana* is naturally occurring or a human introduction at Conchas Lake has remained a point of contention based on the evidence and observations emphasized by different investigators (reviewed herein).

3. The only known sites of syntopy between parthenogenetic *A. neomexicana* and gonochoristic *A. sexlineata viridis* are in New Mexico where the eastern range limits of the former and the western range limits of the latter overlap at Fort Sumner in the Pecos River drainage and at Conchas Lake in the Canadian River drainage.

4. At the two sites in Fort Sumner where it has been observed, *A. neomexicana* is syn-

topic with both *A. sexlineata viridis* and *A. tesselata* E. At Conchas Lake, site-specific habitat characteristics have resulted in syntopic associations of various combinations of diploid *A. neomexicana*, *A. tesselata* C and/or D, *A. sexlineata viridis*, and triploid *A. exsanguis*, with most sites of syntopy between *A. neomexicana* and *A. sexlineata viridis* being situated south of the lake and Canadian River (i.e., CL-2* and CL-5*).

5. This paper includes the first data establishing perennial hybridization between an allodiploid parthenoform (*A. neomexicana*) and a gonochoristic species (*A. sexlineata*) other than one of its progenitors (= *A. tigris marmorata* × *A. inornata*).

6. The only hybrid of *A. neomexicana* × *A. sexlineata viridis*, a female, from north of the Canadian River at Conchas Lake was collected at South of Clabberhill Ranch (site CL-1*) in 1978 by B.E. Leuck. Subsequently, seven males and seven females of *A. neomexicana* × *A. sexlineata viridis* were collected in 1988 and 2001–2003 from south of the river and lake at East of Conchas Lake Levee (site CL-5*, $N = 1$) and South Recreation Area (site CL-2*, $N = 13$).

7. The most apparent extrinsic facilitators of hybridization between *A. neomexicana* and *A. sexlineata viridis* at various components of CL-2* (South Recreation Area) were ecological in nature, based on the presence of these species and their hybrids in either altered weedy assemblages or fragmented habitats resulting from human activities.

8. Based on estimates of the age of 13 hybrids of *A. neomexicana* × *A. sexlineata viridis* from Conchas Lake using SVL and date of collection for each, four to five generations of hybrids were identified, indicating that interbreeding between these species is a perennial occurrence in various components of South Recreation Area (CL-2*).

9. All hybrid males of *A. neomexicana* × *A. sexlineata viridis* obtained at Conchas Lake (only AMNH R-151739 was karyotyped and electrophoretically analyzed) were initially identified based on the presence of male reproductive structures in individuals with color patterns resembling *A. neomexicana* rather than *A. sexlineata viridis*. Subsequent laboratory examinations revealed that hybrid males typically differed from *A. neomexicana*, the only parental species with which they would likely be confused, in three (juveniles) to four (adults) key components of color pattern (dorsal ground color, condition of the middorsal stripe, presence and/or number of dorsal spots, and ventral coloration) and in three characters of scutellation (distinctly larger size of the mesoptychial scales, incomplete circumorbital scale series, and reduced number of granules around midbody).

10. Eight individuals identified as hybrid females of *A. neomexicana* × *A. sexlineata viridis* were characterized by essentially the same characters of color pattern and scutellation used in recognizing male hybrids.

11. Univariate comparisons of *A. neomexicana* × *A. sexlineata viridis*, *A. neomexicana*, and *A. sexlineata viridis* revealed no significant differences among the three in the OR character, significant differences among all three in the GAB, SDL, COS, and LSG characters, and no significant differences between hybrids and either maternal (ILS, FP) or paternal (PV) progenitors.

12. Three inferred representatives of *A. neomexicana* (AMNH R-138881, R-151740 from Conchas Lake and R-151741 from Fort Sumner) had diploid karyotypes comprising one normal *tigris* group haploid complement and one normal *sexlineata* group haploid complement of chromosomes, or $2n = 46$, consistent with their species identification.

13 The five *A. sexlineata viridis* examined had the normal *sexlineata* group karyotypes, with each lizard having one distinctive subtelocentric pair of Set II chromosomes (about the fourth largest pair) instead of two pairs as previously reported.

14. A suspected hybrid male (AMNH R-151739) from Conchas Lake was a triploid having $3n = 69$ chromosomes, comprising the full diploid karyotype of *A. neomexicana* and a second haploid complement of *sexlineata* group chromosomes.

15. Although *A. neomexicana* and *A. tesselata* have indistinguishable karyotypes based on one chromosome complement from each of the *tigris* and *sexlineata* species groups, no hybrids of the dissimilar-sized *A. tesselata* and *A. sexlineata viridis* were discovered at Conchas Lake in syntopic assem-

blages of these species at sites CL-5* and CL-2*.

16. The two *A. neomexicana* analyzed from Conchas Lake and Fort Sumner had the same protein genotypes at each of 23 loci, except for one allele in the lizard from Fort Sumner.

17. Twelve or 13 loci (52–56%) in both specimens of *A. neomexicana* had alleles in the heterozygous state, attesting to the ultimate origin of this taxon from a hybridization event (*A. tigris marmorata* ♀ × *A. inornata* ♂).

18. The specimen of *A. neomexicana* from Fort Sumner differed from the one from Conchas Lake only by possessing one b-allele at sMDH (heterozygous ab).

19. The specimen from Conchas Lake seemed to be identical at all loci and all alleles to specimens of the most common and most widely distributed clone of *A. neomexicana* from elsewhere in its geographic range, whereas the specimen from Fort Sumner might be allied with the sMDH allelle known to occur infrequently in *A. neomexicana* in the vicinity of Engle, Sierra County, New Mexico.

20. Typically, *A. neomexicana* and *A. tesselata* (including those from Conchas Lake) differ at 10 protein loci among those examined for this report: sMDH, sMDHP, sIDH, ESTD, PEPA, PEPB, ADA, MPI, GPI, and PGM2. The new specimens we examined for the present report that appeared to be *A. neomexicana* are correctly identified as such, based on these loci, not a new clone of *A. tesselata*.

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APPENDIX 1

Specimens of *Aspidoscelis* examined from Conchas Lake, site CL-1* (South of Clabberhill Ranch), 0.5 km S of gate, and an area 0.4 km NW (north of North Area Recreation Area), 1259 m, San Miguel County, New Mexico, collected by B.E. Leuck and associates (1978), GJM and J.T. Briggler (2001), and GJM (2003). Abbreviations: *A.n.* (= *A. neomexicana* ♀♀); *A.s.* (= *A. sexlineata viridis* ♀♂); *A*.h. (= hybrid *A. neomexicana* × *A. sexlineata viridis* ♀♂); *A*.e. (= *A. exsanguis* ♀♀); *A.t.* C (= *A. tesselata* pattern class C ♀♀).

22 July 1978: *A.n.* (LACM 128281, not examined, *N* = 1); *A*.h. (OMNH 35109♀, *N* = 1).
21 June 2000: *A.s.* (2 observed by GJM).
9 June 2001: *A.n.* (UADZ 7388, 7390, *N* = 2); *A.e.* (UADZ 7389, *N* = 1).
21 August 2001: *A.n.* (UADZ 7528–7537, 7539, 7541, *N* = 12); *A.e.* (UADZ 7540, *N* = 1); *A.t.* C (UADZ 7538, *N* = 1).
14 August 2003: *A.t.* C (UADZ 7705, *N* = 1).

APPENDIX 2

Specimens of *Aspidoscelis* examined from Conchas Lake, site CL-13 (Cove Campground), North Area Recreation Area, Cove Campground, 1245 m, San Miguel County, New Mexico, collected by GJM (2000—2002). Abbreviations: *A.n.* (= *A. neomexicana* ♀♀); *A.t.* C (= *A. tesselata* pattern class C ♀♀); k = source of karyotype; p = source of protein electrophoresis.

22 June 2000: *A.n.* (UADZ 7364–7365, *N* = 2); *A.t.* C (UADZ 7363, *N* = 1).
7 June 2001: *A.n.* (UADZ 7376–7377, *N* = 2); *A.t.* C (UADZ 7378, *N* = 1).
5 June 2002: *A.n.* (UADZ 7542, 7544–7547, 7549, 7551, 7552 = AMNH R-151740, k, p, *N* = 8); *A.t.* C (UADZ 7543,7548, 7550, *N* = 3).

APPENDIX 3

Specimens of *Aspidoscelis* examined from Conchas Lake, site CL-4 (North of Canadian River), north side of Conchas Dam below picnic area overlooking Canadian River, 1120–1243 m, San Miguel County, New Mexico, collected by JMW and associates (1988, 1989, 1997, 2000) and GJM and JMW (2000, 2001). Abbreviations: *A.n.* (= *A. neomexicana* ♀♀); *A.e.* (= *A. exsanguis* ♀♀); *A.t.* C (= *A. tesselata* pattern class C ♀♀).

12 August 1988: *A.e.* (UADZ 3434, *N* = 1); *A.t.* C (UADZ 3446, *N* = 1).
3 August 1989: *A.n.* (UADZ 3741—3743, *N* = 3); *A.t.* C (UADZ 3744–3749, *N* = 6).
7 June 1990: *A.n.* (UADZ 4175–4176, *N* = 2); *A.e.* (UADZ 4171—4174, *N* = 4); *A.t.* C (UADZ 4158—4170, *N* = 13).
15 July 1997: *A.n.* (UADZ 5986—5988, *N* = 4); *A.t.* C (UADZ 5990, 5991, *N* = 2).
12 June 2000: *A.n.* (UADZ 7317–7319, *N* = 3); *A.e.* (UADZ 7320–7325, *N* = 6); *A.t.* C (UADZ 7326–7328, *N* = 3).
15 June 2000: *A.e.* (UADZ 7334, *N* = 1).
6 June 2001: *A.t.* C (UADZ 7370–7373, *N* = 4).
17 August 2001: *A.n.* (UADZ 7462, *N* = 1).

APPENDIX 4

Specimens of *Aspidoscelis* examined from Conchas Lake, site CL-5* (East of Conchas Lake Levee), listed by habitat component in the vicinity of 2—3 km S Conchas Dam, or east of the south end of the levee, along New Mexico Hwy. 129, 1258—1274 m, San Miguel County, New Mexico, collected by JMW and J.E. Cordes (1988, 1989) and GJM and J.T. Briggler (2000—2002). Abbreviations: *A.n.* (= *A. neomexicana* ♀♀); *A.s.* (*A. sexlineata viridis* ♀♂); *A*.h. (= hybrid *A. neomexicana* × *A. sexlineata viridis* ♀♂); *A.t.* C or D (= *A. tesselata* pattern classes C or D ♀♀).

Valley-plateau-hill component (CL-5VPH*).[a]

12 July 1988: *A.n.* (UADZ 3235 = AMNH 146599, *N* = 1); *A.s.* (UADZ 3248—3269, 3270 = AMNH 146600, 3271, 3273—3275, *N* = 26); *A*.h. (UADZ 3272 = AMNH 144085♂, *N* = 1); *A.t.* C (UADZ 3214–3215, 3217—3224, 3226–3227, 3229, 3231—3237, 3239—3241, 3243, 3245—3247, *N* = 27); *A.t.* D (UADZ 3216, 3225, 3228, 3230, 3238, 3242, 3244, *N* = 7).
12 August 1988: *A.s.* (UADZ 3445, *N* = 1); *A.t.* C (UADZ 3432, 433, 3435, 3437—3439, 3442—3444, 3448–3449, *N* = 11); *A.t.* D (UADZ 3436, 3440–3441, 3450, *N* = 4).

13 June 2000: *A.t.* C (UADZ 7329–7330, *N* = 2).
11 June 2001: *A.s.* (UADZ 7405, *N* = 1); *A.t.* C (UADZ 7404, 7406, *N* = 2); *A.t.* D (UADZ 7407, *N* = 1).
18 August 2001: *A.n.* (UADZ 7464, 7466, 7469, *N* = 3); *A.s.* (UADZ 7470, 7476, *N* = 2); *A.t.* C (UADZ 7465, 7467–7468, 7471–7475, *N* = 8); *A.t.* D (UADZ 7477, *N* = 1).
21 August 2001: *A.s.* (UADZ 7527, *N* = 1).
8 June 2002: *A.n.* (UADZ 7576–7577, *N* = 2); *A.t.* C (UADZ 7571–7575, *N* = 5).

Valley component (CL-5V) 14 June 2000: *A.s.* (UADZ 7331, *N* = 1); *A.t.* C (UADZ 7332, *N* = 1).
8 June 2001: *A.s.* (UADZ 7381–7382, *N* = 2); *A.t.* C (UADZ 7380, *N* = 1).
10 June 2001: *A.n.* (UADZ 7398, *N* = 1); *A.s.* (UADZ 7391–7396, 7399, 7401–7402, *N* = 9); *A.t.* C (UADZ 7397, 7400, 7403, *N* = 3).
17 August 2001: *A.s.* (UADZ 7463, *N* = 1).
9 June 2002: *A.n.* (UADZ 7581, *N* = 1); *A.s.* (UADZ 7578–7579, 7582, 7584, *N* = 4); *A.t.* D (UADZ 7580, 7583, *N* = 2).

[a]All UADZ specimens were collected in the valley except 4 from the top of the hill (*A.t.* C [UADZ 3214, 3435] and *A.t.* D [UADZ 3230, 3436]) and 12 from the plateau (*A.t.* C [UADZ 3218, 3241, 3243, 3449]; *A.t.* D [UADZ 3228, 3244]; *A.s.* [UADZ 3258, 3264, 3266, 3267, 3271]; and *A.*h. [UADZ 3272]).

APPENDIX 5

Specimens of *Aspidoscelis* examined from Conchas Lake, site CL-2* (South Recreation Area) listed by habitat components, 1279—1310 m, San Miguel County, New Mexico, collected by CJC and C.R. Townsend (1976, 1978, 1981, 1990) and GJM and J. T. Briggler (2000—2002). Abbreviations: *A.n.* (= *A. neomexicana* ♀♀); *A.s.* (*A. sexlineata viridis* ♀♂); *A.*h. (= hybrid *A. neomexicana* × *A. sexlineata viridis* ♀♂); *A.e.* (= *A. exsanguis* ♀♀); *A.t.* C or D (= *A. tesselata* pattern class C or D ♀♀); k = source of karyotype; p = source of protein electrophoresis.

South Campground component (CL-2C*).

22–23 May 1976: *A.s.* (AMNH R-114231, k, p, R-114232, R-114233—R-114235, k, p, R-122828–R-122829, *N* = 7); *A.t.* C (AMNH R-123029, R-123033, *N* = 2); *A.t.* D (AMNH R-114236–R-114237, R-123047—R-123049, *N* = 5).
28 May 1978: *A.t.* C (AMNH R-119545, *N* = 1).
28–29 May 1978: *A.t.* C (AMNH R-123025, R-123050–R-123051, *N* = 3); *A.t.* D (AMNH R-119545, R-123037, R-123042, R-123052, *N* = 4).
29 May 1978: *A.s.* (AMNH R-119534, *N* = 1).
19 July 1981: *A.s.* (AMNH R-135193—R-135196, R-122830, R-123053, k, p, *N* = 6).
28 May 1990: *A.n.* (AMNH R-136881, k, p, *N* = 1); *A.t.* C (AMNH R-136875—R-136879, *N* = 5); *A.t.* D (AMNH R-136880, *N* = 1).
19 June 2000: *A.n.* (UADZ 7347, *N* = 1); *A.s.* (UADZ 7346, 7348, *N* = 2); *A.*h. (UADZ 7349♀, *N* = 1); *A.t.* C (UADZ 7345, *N* = 1).
6 June 2001: *A.n.* (UADZ 7374, *N* = 1); *A.s.* (UADZ 7375, *N* = 1).
17 August 2001: *A.n.* (UADZ 7456–7459, 7461, *N* = 5); *A.s.* (UADZ 7460, *N* = 1); *A.*h. (UADZ 7455♀, *N* = 1).
6 June 2002: *A.e.* (UADZ 7558–7559, *N* = 2); *A.t.* D (UADZ 7557, *N* = 1).
13 August 2003: *A.n.* (UADZ 7690–7691, 7694, 7699, 7702–7704, *N* = 7); *A.s.* (UADZ 7692, 7695, *N* = 2); *A.*h. (UADZ 7700♂, *N* = 1); *A.t.* C (UADZ 7696, *N* = 1); *A.t.* D (UADZ 7693, *N* = 1).

Group Shelter component (CL-2G)

23 June 2000: *A.n.* (UADZ 7369, *N* = 1).
8 June 2001: *A.s.* (UADZ 7379, *N* = 1).
6 June 2002: *A.e.* (UADZ 7560, *N* = 1).

Hill component (CL-2H*)

19 June 2000: *A.s.* (UADZ 7343, *N* = 1); *A.*h. (UADZ 7344♂, *N* = 1).
17 August 2001: *A.n.* (UADZ 7449–7451, 7453–7454, *N* = 5); *A.*h. (UADZ 7448♂, 7452♀, *N* = 2).
6 June 2002: *A.*h. (UADZ 7553♂, 7554♀, 7555♀, 7556♀, *N* = 4).
13 August 2003: *A.n.* (UADZ 7689, 7697–7698, 7701, *N* = 4).

Juniper Campground component (CL-2J*)

14 June 2001: *A.n.* (UADZ 7442, *N* = 1); *A.s.* (UADZ 7443, *N* = 1).
7 June 2002: *A.n.* (UADZ 7562–7563, 7565–7568, *N* = 6); *A.*h. (UADZ 7561♂, 7570♂ = AMNH 151739, k, p, *N* = 2); *A.t.* C (UADZ 7564, *N* = 1); *A.t.* D (UADZ 7569, *N* = 1).
12 August 2003: *A.n.* (UADZ 7672–7673, 7678–7688, *N* = 13); *A.s.* (UADZ 7674, *N* = 1); *A.t.* C (UADZ 7670–7671, 7675–7677, *N* = 5).

Lodge component (CL-2L*)

15 June 2000: *A.n.* (UADZ 7446, *N* = 1); *A.s.* (UADZ 7444, 7447, *N* = 2); *A.*h. (UADZ 7445♀, *N* = 1).
18 August 2001: *A.n.* (UADZ 7479–7480, *N* = 2); *A.t.* C (UADZ 7478, *N* = 1).
20 August 2001: *A.n.* (UADZ 7523, *N* = 1); *A.e.* (UADZ 7525, *N* = 1); *A.t.* D (UADZ 7524, *N* = 1).
8 August 2003: *A.t.* C (UADZ 7669, *N* = 1).

APPENDIX 6

Specimens of *Aspidoscelis* examined from Fort Sumner, site FS-1 (Fort Sumner–De Baca County Landfill), De Baca County, New Mexico, collected by GJM in 2002. Abbreviations: *A.n.* (= *A. neomexicana* ♀♀); *A.s.* (= *A. sexlineata viridis* ♀♂); *A.t.* E (= *A. tesselata* pattern class E ♀♀).

9 June 2002: *A.n.* (MSB 65617, *N* = 1).
13 July 2002: *A.s.* (UADZ 7624–7627, *N* = 4); *A.t.* E (UADZ 7623, *N* = 1).

APPENDIX 7

Specimens of *Aspidoscelis* examined from Fort Sumner, site FS-2 (Fort Sumner–Railroad Depot), De Baca County, New Mexico, collected by GJM in 2002. Abbreviations: *A.n.* (= *A. neomexicana* ♀♀); *A.s.* (= *A. sexlineata viridis* ♀♂); *A.t.* E (= *A. tesselata* pattern class E ♀♀); k = source of karyotype; p = source of protein electrophoresis.

12 July 2002: *A.n.* (UADZ 7620, *N* = 1); *A.s.* (UADZ 7621–7622, *N* = 2).
14 July 2002: *A.n.* (UADZ 7628 = AMNH R-151741, k, p, *N* = 1); *A.t.* E (UADZ 7629, *N* = 1).

APPENDIX 8

Specimens of *Aspidoscelis* listed here were collected in states other than New Mexico and used in comparisons of photographs, karyotypes, and proteins.

Aspidoscelis sexlineata viridis: COLORADO: Kiowa County; 15.0 km N of Eads at Rush Creek (AMNH R-108142, photograph and karyotype). Pueblo County; Huerfano River bridge on Doyle Road, 29.8 km (by road) south of Avondale (AMNH R-13112, proteins). TEXAS: Brooks County; 11.4 km (by U.S. Hwy 281) south of Falfurrias (AMNH R-126893–R-126898 and R-126901–R-126902, proteins).

Aspidoscelis sexlineata sexlineata: GEORGIA: Liberty County; St. Catherines Island (AMNH R-119487, R-119489–R-119493, and R-120233–R-120236, proteins). Chatham County; Ossabaw Island (AMNH R-119498–R-119499, karyotypes and proteins).

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