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Hybrid Origin of a Unisexual Species of Whiptail Lizard, *Cnemidophorus neomexicanus*, in Western North America: New Evidence and a Review

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ABSTRACT

Previous investigators concluded that the diploid unisexual New Mexico whiptail lizard, *Cnemidophorus neomexicanus,* is of hybrid origin between *C. marmoratus* × *C. inornatus.* Primary evidence for this came from general familiarity with the organisms, ecological and geographic distributions, karyotypes, and protein electrophoresis. The most recent electrophoretic data, published after our research was well under way, are the most convincing; Parker and Selander (1984) reported data consistent with the hybrid origin hypothesis, based on 19 loci and some relatively large population samples, all of their *neomexicanus* being from the Rio Grande drainage system, New Mexico. Earlier reports, while insightful, were based on small samples, few localities, and specimens of *neomexicanus* that could well have been F_1 hybrids rather than representatives of a parthenogenetic clone. In addition, a morphological analysis of the species involved, including hybrid index analysis, has not been presented previously.

For the present report, we emphasized samples of *C. neomexicanus* from the vicinity of Lordsburg, Hidalgo County, New Mexico, a southwestern geographic extreme population west of the Continental Divide, and from the northern part of its range, near Peña Blanca, Sandoval County, New Mexico, on the Rio Grande. Additional samples compared include: (1) several samples of *C. neomexicanus* from localities between the two mentioned above; (2) several of the proposed ancestral bisexual species, *C. marmoratus* and *C. inornatus,* including some from sites in the vicinity of Lordsburg where they are sympatric with *C. neomexicanus* today; and (3) *C. gularis, C. sexlineatus,* and *C. septemvittatus,* bisexual species related to *C. inornatus* which should not be ignored as possible ancestors alternative to *C. inornatus.*

Comparisons are made on the following levels of organization: habitat preference; external morphology (analyzed with univariate and multivariate methods); karyotypes; protein electrophoresis; and viability of eggs and offspring produced by captive *C. neomexicanus* through several generations without contact with males.

Data from captive *C. neomexicanus* are consistent with the hypothesis that it reproduces by parthenogenetic cloning. All other data agree with the hypothesis that *neomexicanus* had a hybrid origin involving *C. marmoratus* × *C. inornatus,* although one esterase-D allele found in all *neomexicanus* has yet to be found in either parental species and a peptidase-B allele in all *neomexicanus* did not match the one found in all *inornatus.*

The Lordsburg and Peña Blanca samples of *C. neomexicanus* represent the same electrophoretic clone. Future research may indicate whether the few morphological differences between these two samples of *neomexicanus* are due primarily to environmental or genetic factors.

Three electrophoretically distinct clones of *neomexicanus* are known, but the two atypical ones each are known from only a single locality. One of the latter probably had an origin involving mutation in one allele within *neomexicanus,* whereas the other may be the result of a separate hybrid origin involving different gametes from the same parental species.

Geographic variation in allele frequencies of peptidase-A in *C. marmoratus* suggests that at least one hybrid origin of *neomexicanus* occurred in the vicinity of the Rio Grande. All *neomexicanus* from the vicinity of Lordsburg were electrophoretically identical to nearly all of those from the Rio Grande Valley, bearing the same two orphan alleles and the peptidase-A allele of *C. marmoratus* that is rare around Lordsburg but common in the Rio Grande Valley. This suggests that the one clone of *neomexicanus* found in the vicinity of Lordsburg reached the area by dispersal from the east.

INTRODUCTION

The New Mexico whiptail lizard, *Cnemidophorus neomexicanus* Lowe and Zweifel, 1952, occurs largely within the Rio Grande drainage system in New Mexico and Texas (Wright, 1971), with a possibly disjunct population near the Arizona state line (NW of Lordsburg, Hidalgo County, New Mexico; Pough, 1962; Axtell, 1966; Cuellar, 1977: 841) and a probably disjunct and artificially introduced population in northeastern New Mexico (Leuck et al., 1981). Under the name of *Cnemidophorus perplexus,* the difficult nomenclature of which was sorted out by Wright and Lowe (1967) and Wright (1969), *C. neomexicanus* was among the first North American lizards suspected of being all-female species (Duellman and Zweifel, 1962; Maslin, 1962).

Investigations of the reproductive system (Cuellar, 1968; Christiansen, 1971, 1973), histocompatibility (Cuellar, 1977), and protein electrophoresis of field-captured lizards (Neaves and Gerald, 1968; Neaves, 1969; Parker and Selander, 1984) strongly indicat-

ed that *C. neomexicanus* reproduces by parthenogenetic cloning in the absence of sperm. Using laboratory-reared individuals of known genealogy, parthenogenesis is being verified by detailed histological work similar to that of Hardy and Cole (1981; Hardy and Cole, in prep.), and clonal inheritance was recently verified by electrophoresis of more than 30 tissue proteins (Dessauer and Cole, 1986).

Based primarily on karyotypes of a few individuals, preferred habitats, and a general familiarity with the organisms, Lowe and Wright (1966) proposed that *C. neomexicanus* originated through hybridization between two diploid bisexual species, *C. tigris* Baird and Girard × *C. inornatus* Baird. This hybrid origin hypothesis has withstood independent tests by protein electrophoresis (Neaves and Gerald, 1968; Neaves, 1969; Parker and Selander, 1984). In addition, analysis of mitochondrial DNA is consistent with the hybrid origin hypothesized and suggests further that the subspecies *C. tigris marmoratus* was the maternal parent, at least for the lineages(s) represented by the eight *C. neomexicanus* examined (Brown and Wright, 1979).

Recently, Hendricks and Dixon (1986) concluded that all *C.* "*tigris*" populations east of the Continental Divide should be referred to as a separate species, *Cnemidophorus marmoratus* Baird and Girard, the name *C. tigris* still being applied to populations west of the hybrid zone near the Continental Divide (Zweifel, 1962; Dessauer et al., 1962). We follow the new usage in this paper, as it is the most recently suggested usage, reserving our own recommendation on this specific point pending completion of our analysis of the dynamic hybrid zone that is of basic importance to this issue (Dessauer and Cole, 1984b).

Whereas most biologists now accept the hybrid origin hypothesis for *C. neomexicanus,* it has been controversial (Cuellar, 1974, 1977) and some problems remain inadequately addressed. Previous reports concerning the hybrid origin were based on a few lizards representing a few localities (Parker and Selander, 1984, is an exception), and no morphological hybrid index analysis has been presented for the *neomexicanus* problem (but see Parker, 1979, for the unisexual *C. tesselatus* problem). In addition, the peripheral population of *C. neomexicanus* from extreme southwestern New Mexico (near Lordsburg, Hidalgo County) has been largely ignored, as has been the question of whether specimens examined by earlier investigators may actually have been sterile F_1 hybrids of *C. marmoratus* × *C. inornatus.* Finally, additional bisexual species of *Cnemidophorus* occurring in or near New Mexico have not been adequately investigated as a possible parental alternative to *C. inornatus* in a hybrid origin hypothesis of *C. marmoratus* × *C.* ? (a *sexlineatus* group species).

Consequently, we have compiled new observations on *C. neomexicanus* on the following levels of biological organization: (1) reproduction in laboratory-propagated lineages (based on 14 field-captured *neomexicanus*); (2) habitat preference; (3) external morphology (color and pattern plus size and scutellation characters of 91 specimens analyzed with univariate and multivariate methods); (4) karyotypes (including 24 field-collected *C. neomexicanus* from several localities and 35 specimens of related bisexual species); and (5) protein electrophoresis (47 loci; 151 specimens). We emphasized examining *C. neomexicanus* from west of the Continental Divide, near Lordsburg, but comparisons were made with the following samples: *C. marmoratus* and *C. inornatus* from the Lordsburg area and from localities to the east in New Mexico and Texas; *C. neomexicanus* from the Rio Grande Valley, including some from near the northern extreme of its range; and *C. gularis* Baird and Girard, *C. septemvittatus* Cope, and *C. sexlineatus viridis* Lowe. We address the following questions in this report:

1. Are the various data, including the morphological data, consistent with the hybrid origin hypothesis for *C. neomexicanus,* the probable ancestors being *C. marmoratus* × *C. inornatus*?

2. Given the mixture of habitats and associated species of *Cnemidophorus* in the Lordsburg area, do the *neomexicanus* individuals there constitute a reproducing population, or are they newly generated, and possibly sterile, F_1 hybrids?

3. Are the specimens of *C. neomexicanus* from Lordsburg similar to those from the Rio Grande Valley, particularly from a northern

latitude, a different habitat, and a site where the two ancestors were not found together with the *neomexicanus* sampled?

4. Does the *C. neomexicanus* at Lordsburg represent a recent, separate, local hybrid origin, and/or dispersal and colonization from the Rio Grande Valley (or vice-versa)?

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MATERIALS AND METHODS

Colony and Karyotypes

We used previously published methods for maintaining the laboratory colony (Townsend, 1979; Townsend and Cole, 1985) and preparing and studying chromosomes (Cole, 1979).

External Morphology

Characters of external morphology were determined only on adult females, in order to minimize possible bias due to sexual dimorphism or ontogenetic development; only one sex is available for *C. neomexicanus*. Specimens were sexed by abdominal dissection and, for each species, data were used only from females with a body length greater than or equal to that of the smallest individual with conspicuously enlarged ovarian follicles or oviductal eggs. The following characters, all but one of which have been used previously in one form or another in *Cnemidophorus* taxonomy, were analyzed for *C. inornatus, C. marmoratus,* and *C. neomexicanus* from the vicinity of Lordsburg, New Mexico; *C. neomexicanus* from the vicinity of Peña Blanca, New Mexico; and *C. sexlineatus viridis* from southern Texas:

Body Length: This was measured (in mm) along the midventral line from tip of snout to posterior edge of the last enlarged preanal scale (snout-vent). Tail length data (vent to posterior tip of tail) were not useful in the final analysis because few specimens had a complete, original tail.

Number of Scales Around Midbody: These were counted as described by Wright and Lowe (1967: 15–17).

Number of Femoral Pores: These were counted on each leg and the total number (sum of each side) is the character used, unless specified otherwise.

Number of Fourth Toe Lamellae: These are described by Wright and Lowe (1967: 23), but instead of counting on only one side, we counted the ventral lamellae on each fourth toe (hind feet) and the total number is the character used, unless specified otherwise. Only lamellae beneath the toe itself were counted, and all scales along the ventral row were counted, regardless of size, excluding claw.

Number of Circumorbital Semicircle Scales: These were counted as described by Wright and Lowe (1967: 19), and the total number (sum of each side) is the character used, unless specified otherwise.

Number of Interlabial Scales: These also are described by Wright and Lowe (1967: 22), and the total number (sum of each side) is the character used, unless specified otherwise. To find the starting point to make this count, the infralabials and chin shields (genials) were followed posteriorly to locate a row of scales near the lip that bridged be-

tween the infralabials and genials. The count included only scales forward to this bridge (bridging scales excluded). Also excluded were loose skin between scales, tiny granules or material not clearly resolvable as scales, as well as anything anterior to the suture between the first and second genials (individual scales overlapping this point were counted). Counts were not made on lizards on which these sutures were abnormal.

NUMBER OF GULAR SCALES: This new character is a count of the small scales touching the medial edge of the genials, counting forward from the posterior edge of the fourth genial (from the snout) on one side (at suture with fifth genial) and continuing around to the same position on the opposite side. A scale overlapping the suture defining the counting point was counted, but if sutures of the genials were abnormal, the count was not made.

SIZE OF DORSAL SCALE, MESOPTYCHIAL SCALE, AND POSTANTEBRACHIAL SCALE: Measurements were made to the nearest 0.02 mm using an ocular micrometer in a dissecting microscope, as described by Lowe et al. (1970a: 115–116). For the mesoptychial scale, however, the one measured was selected from the row anterior to that bordering the gular fold if all scales in the row bordering the fold were of basically one small size.

UNIVARIATE ANALYSIS

For univariate comparisons, statistical data are presented as the mean ± one standard error of the mean. For comparisons with data presented by Wright and Lowe (1967), we used the hybrid index of Hubbs et al. (1943); we used sample means, but only for those characters for which the parental species had significantly different means ($P < 0.05$). For each character, the mean of the paternal *C. inornatus* (or, alternatively, *C. sexlineatus viridis*) was set at 0 and the mean of the maternal *C. marmoratus* was set at 100 on the index.

MULTIVARIATE ANALYSIS

In this study, as in many other studies of geographic variation, there was substantial concordance in variation among the different morphological characters. That is, the univariate characters that were measured or counted covary among the taxa and so cannot be assumed to represent completely independent estimates of the patterns of variation among these populations of *Cnemidophorus*. Therefore, multivariate combinations of the characters may represent better (nonredundant) estimates of the patterns of overall morphological variation. Consequently, we performed a principal components analysis of the morphological data. Canonical discriminant analysis (CDA) was also used to address the question of the likely ancestors of *C. neomexicanus*. However, CDA is not particularly useful for describing overall variation, and so its use in this study was limited to the investigation of the parentage of known hybrid populations (Neff and Smith, 1979).

For the principal components (PC) analysis, we used the ten variables described above for the univariate analyses; tail length was not used because values were missing for more than 50 percent of the specimens. For the PC analysis we used 78 specimens from four population samples (*C. inornatus, C. marmoratus,* and *C. neomexicanus* from near Lordsburg plus *C. neomexicanus* from near Peña Blanca). For CD analysis we used 91 specimens from five population samples (those just mentioned plus *C. sexlineatus viridis* from southern Texas).

PC analysis requires complete data for all individuals. However, for several individuals, not all of the characters could be determined due to damage to the specimen or other abnormal condition. For such specimens, the missing values were estimated using the BMDP computer program "AM" (Dixon, 1981). The missing values were estimated using stepwise regression of the missing character on all characters within the same population sample as the specimen of interest.

Multivariate analyses were performed on correlation matrices obtained from both the raw data and the log-transformed (natural logarithm) data. The correlation matrix, rather than the covariance matrix, was used because the characters involved include a gross body measurement, three microscopic measurements of various epidermal scales, and assorted epidermal scale counts; consequently, the various characters do not share a single common size scale. The use of the correlation

matrix corrects for this scaling problem. Results with the raw data and with the log-transformed data were similar; we discuss and illustrate the latter because we expect the epidermal scale measurements to be correlated with growth of an individual. The SAS procedures "Princomp" and "Candisc" (Ray, 1982b) were used for the analyses.

The multivariate procedures were used to describe the data in a reduced character space; no assumption of multivariate normality was necessary. For statistical tests on the resulting multivariate scores and axes, tests for meeting the underlying normality requirements of the parametric tests were performed and the requirements were met.

The principal component scores for individual specimens were tested, by population, for departures from normal distributions using a Shapiro-Wilk test with the SAS procedure "Univariate" (Ray, 1982a). These scores were then subjected to tests for differences in sample means using sums-of-squares simultaneous test procedures (Gabriel and Sokal, 1969).

Protein Electrophoresis

The heart, liver, and kidney, plus samples of skeletal muscle and blood were collected from freshly killed lizards. Plasma was separated from blood cells and all tissues were frozen, usually in liquid nitrogen. Until required for experimental work, tissues were maintained in the frozen tissue collection of the Museum of Zoology, Louisiana State University, Baton Rouge. Methods of tissue storage and curation have been described (Dessauer and Hafner, 1984).

Tissues for electrophoretic analysis were homogenized in two to three volumes of a solution containing 0.25 moles/liter of sucrose and 20 mg/liter of dithiothreitol and then centrifuged at 5000 × g to separate the supernatant solution of soluble proteins from cell debris. Aliquots of the supernatant solutions of hemolysates and homogenates or blood plasma were applied to slots in starch gels and subjected to vertical gel electrophoresis (Smithies, 1959) overnight (about 18 hours), at a potential gradient of 6 to 8 volts/cm in a cabinet maintained at about 4°C.

A series of different buffers was used in these electrophoretic analyses (table 1): phosphate-citrate (pH 6), Tris-hydroxyaminomethane (Tris)-maleate (pH 7.4 and 8.6), Tris-borate (pH 8.6), Tris-citrate (pH 7.4), borate (pH 8.6), and veronal (pH 8.6). Electrode baths were filled with buffers having ionic strengths of approximately 0.1; buffers used to prepare gels were diluted to ionic strengths of about 0.01. The coenzymes NAD and NADP were added to some gel-buffers (5 mg/100 ml) to stabilize such enzymes as the alcohol and isocitrate dehydrogenases during electrophoresis; EDTA was added (1 mmole/liter) to protect the activities of enzymes sensitive to heavy metal ions.

Following electrophoresis, enzymes and nonenzymic proteins of the tissue samples were localized on gel slices by means of histochemical stains, fluorescence, or autoradiography. Table 1 lists the loci examined, their enzyme commission numbers, abbreviations, and the tissues and electrophoresis buffers in which they were analyzed.

Localization techniques for the majority of enzymes closely followed descriptions by Harris and Hopkinson (1976). Transferrins were identified by iron-59 binding and autoradiography (Giblett et al., 1959: fig. 10). Myoglobins were detected in muscle homogenates by the presence of a light brown band migrating anodally on unstained gels; its identity was confirmed by the benzidine test (see Smithies, 1959). Peptidase substrates were valyl·leucine for peptidase-A, leucyl·glycyl·glycine for peptidase-B, and either leucyl·glycyl·glycine or leucyl·beta-naphthylamide for peptidase-E. 4-methylumbelliferyl phosphate was the substrate for acid phosphatase; and 4-methylumbelliferyl acetate was the substrate for esterase-D and esterase-1. These two esterases do not utilize naphthyl-esters such as alpha-naphthyl acetate as substrates (fig. 9). Identifications of the specific esterases and peptidases follow nomenclature used to describe enzymes of humans having similar substrate requirements and subunit numbers (Harris and Hopkinson, 1976). The assumption of locus homology seems reasonable, since substrate and subunit number of the protein products of structural gene loci appear to be largely conserved throughout the Vertebrata (Dessauer and Braun, 1982; Dessauer et al., in press), and interpretations are

TABLE 1

Presumptive Structural Gene Loci Examined in Six Species of *Cnemidophorus*

Locus	EC No.	Abbrev.	Tissue(s)[a]	Buffer(s)[b]
OXIDOREDUCTASES				
Alcohol dehydrogenase	(1.1.1.1)	Aldh	K, L	TM, 8.6, NAD, EDTA
α-Glycerol-phosphate dehydrogenase	(1.1.1.8)	Gpd	M	PC, 6; TM, 7.4
Sorbitol dehydrogenase	(1.1.1.14)	Sord	K, L	TM, 7.4
Lactate dehydrogenase	(1.1.1.27)	Ldh-1	K, H	TM, 7.4
Lactate dehydrogenase	(1.1.1.27)	Ldh-2	K, M, L	TM, 7.4
Malate dehydrogenase	(1.1.1.37)	Mdh-1	M, K, L	PC, 6
Malate dehydrogenase	(1.1.1.37)	Mdh-2	M, K, L	PC, 6
Malate enzyme	(1.1.1.40)	Me-1	K, H	TM, 7.4, NADP
Malate enzyme	(1.1.1.40)	Me-2	K, H	TM, 7.4, NADP
Isocitrate dehydrogenase	(1.1.1.42)	Icd-1	L	TM, 7.4, NADP
Isocitrate dehydrogenase	(1.1.1.42)	Icd-2	L, K, M	TM, 7.4, NADP
Phosphogluconate dehydrogenase	(1.1.1.44)	Pgd	K, L, H	TB, 8.6, NADP, EDTA
Glyceraldehyde-phosphate dehydrogenase	(1.2.1.12)	Gapdh	M	PC, 6, NAD
Diaphorase (NADP-linked)	(1.6.2.2)	Dia-NADP	L	TM, 7.4, EDTA
Superoxide dismutase	(1.15.1.1)	Sod-1	L, K, H	TB, 8.6
Superoxide dismutase	(1.15.1.1)	Sod-2	L, K, H	TB, 8.6
TRANSFERASES				
Aspartate aminotransferase	(2.6.1.1)	Got-1	M, K, L, H	TM, 7.4
Aspartate aminotransferase	(2.6.1.1)	Got-2	M, K, L, H	TM, 7.4
Creatine kinase	(2.7.3.2)	Ck-1	K, H	TM, 7.4
Creatine kinase	(2.7.3.2)	Ck-2	K, H, M	TM, 7.4
Adenylate kinase	(2.7.4.3)	Ak	M, H	TM, 7.4
Phosphoglucomutase	(2.7.5.1)	Pgm	K, L, H	TM, 7.4
HYDROLASES				
Esterase-1[c]	(3.1.1.1)	Es-1	M	PC, 6
Esterase-D[c]	(3.1.1.1)	Es-D	M, K, L	PC, 6; TM, 7.4
Acid phosphatase[d]	(3.1.3.2)	Ap	K, L, H	TM, 7.4; PC, 6
Peptidase-A[e]	(3.4.1.—)	Pep-A	K, L, H	TM, 7.4
Peptidase-B[f]	(3.4.1.—)	Pep-B	M	PC, 6
Peptidase-E[g]	(3.4.13.9)	Pep-E	M	PC, 6
Adenosine deaminase	(3.5.4.4)	Ada	L, R, H	TM, 7.4
LYASES				
Aldolase	(4.1.2.13)	Ald	M	PC, 6, Mg, EDTA
Aconitase-1	(4.2.1.3)	Acon-1	L	TC, 7.4
Aconitase-2	(4.2.1.3)	Acon-2	L	TC, 7.4
ISOMERASES				
Mannose-phosphate isomerase	(5.3.1.8)	Mpi	K, L	TM, 7.4
Glucose-phosphate isomerase	(5.3.1.9)	Gpi	M, K, L	PC, 6; TM, 7.4
NONENZYMIC BLOOD PROTEINS				
Transferrin	—	Tf	P	V, 8.6; B, 8.6
Albumin[h]	—	Alb	P	V, 8.6
Prealbumin[h]	—	Prealb	P	V, 8.6
Hemoglobin-1	—	Hb-1	R	PC, 6
Hemoglobin-2	—	Hb-2	R	PC, 6
NONENZYMIC MUSCLE PROTEINS				
Myoglobin	—	Mb	M, H	TM, 7.4; PC, 6
Muscle-1	—	Mus-1	M	PC, 6

TABLE 1—(*Continued*)

Locus	EC No.	Abbrev.	Tissue(s)[a]	Buffer(s)[b]
Muscle-2	—	Mus-2	M	PC, 6
Muscle-3	—	Mus-3	M	PC, 6
Muscle-4	—	Mus-4	M	PC, 6
Muscle-5	—	Mus-5	M	PC, 6
Muscle-6	—	Mus-6	M	PC, 6
Muscle-7	—	Mus-7	M	PC, 6

[a] H = heart muscle; K = kidney; L = liver; M = skeletal muscle; P = plasma; R = red blood cells.

[b] Buffer components, pH, and additives; B = boric acid; C = citric acid; M = maleic acid; P = disodium hydrogen phosphate; T = tris; V = barbituric acid (veronal).

[c] Substrate 4-methylumbelliferyl acetate; almost inactive with alpha-naphthyl esters.

[d] Substrate 4-methylumbelliferyl phosphate.

[e] Substrate phenylalanyl·leucine.

[f] Substrate leucyl·glycyl·glycine.

[g] Substrate leucyl·glycyl·glycine or leucyl·beta-naphthylamide.

[h] Albumins and prealbumins resolved more cleanly in veronal than in borate buffer, allowing identification of heterozygous Prealb in *neomexicanus* (correcting data in Dessauer and Cole, 1986).

consistent with those made previously using diploid, triploid, and tetraploid *Cnemidophorus* with different gene dosages at heterozygous loci (Dessauer and Cole, 1984a).

The plasma proteins, albumin and prealbumin, hemoglobin, and the soluble muscle proteins (Mus-1 through 7) were localized on gels stained with the nonspecific protein dye naphthol blue black. For enzymes such as the lactate dehydrogenases, the phenotypes of which are determined by two loci, the loci are labeled numerically in order of decreasing anodal migration of their isozymes. Similarly, alleles at specific loci are identified alphabetically in order of decreasing anodal migration of their allozymes.

SPECIMENS EXAMINED

The 257 specimens are referred to by their individual catalog numbers in the herpetological collection of the American Museum of Natural History (AMNH), or, in the case of two specimens, by one of our (HCD) personal frozen tissue catalog numbers, which are individually recorded when the specimens are entered into the permanent catalog at Louisiana State University, Baton Rouge. The lower case letters following the catalog numbers indicate the kind of data taken from each specimen, as follows: e, external morphology; k, karyotype; p, protein electrophoresis; r, laboratory reproduction.

Cnemidophorus gularis: UNITED STATES: *Texas:* Tarrant Co.: 3.9 km W junction US hwy 377 and Benbrook-Aledo Rd (AMNH 119510, p). Reeves Co.: 4.3 km (by TX hwy 17) SW Balmorhea (AMNH 128249–128251, p).

Cnemidophorus inornatus: MEXICO: *San Luis Potosi:* 9.3 km (by rd) NW Arista [ca. 63 km (airline) N San Luis Potosi] (AMNH 106557, k); 15.4 km (by Mex hwy 57) NE San Luis Potosi [0.8 km NE Enrique Estrada] (AMNH 106560, k). UNITED STATES: *Arizona:* Cochise Co.: 3.5 km (by AZ hwy 186) SE Willcox; 1280 m elev (AMNH 114215, k; 114216, k; 129208–129210, k); 6.4 km (by AZ hwy 186) SE Willcox; 1280 m elev (AMNH 126871–126877, k; 129205, k; 129207, k). Coconino Co.: 15 km (by US hwy 89) S Gray Mountain; 1830 m elev (AMNH 126869, p). *New Mexico:* Doña Ana Co.: 12.9 km (by NM hwy 26) WSW Hatch (AMNH 120671–120673, p); 13.7 km (by NM hwy 26) SW Hatch (AMNH 109390, k; 112843, 112844, k). Hidalgo Co.: 26.7 km (by US hwy 70) NW Lordsburg (AMNH 126885, p); 26.9 km (by US hwy 70) NW Lordsburg; 1340 m elev (AMNH 131061, 131062, e; 131063, 131064, e; 114192–114194, e; 114197–114199, e; 114200–114202, e; 114204, e; 114211, e; 114213, 114214, k); 27.2 km (by US hwy 70) NW Lordsburg; 1310 m elev (AMNH 120657–120662, p; 120664–120668, p; 120669, 120670, e, p; 131060, p);

27.5 km (by US hwy 70) NW Lordsburg; 1325 m elev (AMNH 114206, e, k); 27.7 km (by US hwy 70) NW Lordsburg (AMNH 120656, e; 125538, e, p; 125542, e; 131065, e); 28 km (by US hwy 70) NW Lordsburg; 1310 m elev (AMNH 112840, e, k; 114183, 114184, k; 114185, e, k; 114186, e; 114188, e). Otero Co.: White Sands National Monument (AMNH 108146, k). *Texas:* Brewster Co.: 40.4 km (by US hwy 385) S Marathon (AMNH 126881, p). Hudspeth Co.: Cornudas (AMNH 131058, 131059, p). Presidio Co.: 60.5 km (by TX hwy 2810) SW Marfa (AMNH 126884, p). Ward Co.: Monahans (AMNH 131056, 131057, p).

Cnemidophorus marmoratus: UNITED STATES: *New Mexico:* Chaves Co.: Mescalero Sands, vicinity of Waldrop Park, 10.1 km (by US hwy 380) W Caprock [Lea Co.] (AMNH 112867, k). Doña Ana Co.: 3.9 km (by NM hwy 26 and Co. Rd E4) SW Hatch (AMNH 127112–127119, p). Hidalgo Co.: 5.5 km W and 3.4 km N Cotton City (AMNH 112864, k); 11.3 km (by US Hwy 70) NW Lordsburg; 1310 m elev (AMNH 120691, p; 122831, p; 131102, e, p); 11.6 km (by US Hwy 70) NW Lordsburg (AMNH 125534, e; 131100, 131101, e); 12.9 km (by US hwy 70) NW Lordsburg (AMNH 84842, e); 16.3 km (by US hwy 70) NW Lordsburg; 1310 m elev (AMNH 120693–120695, p; 127004–127006, p; 127101–127111, p; 129166–129167, k; 131082–131084, p; 131085–131088, e, p; 131089, e; 131090, e, p; 131091, e; 131092, p; 131093–131099, e, p; plus 10 specimens frozen without vouchers, p); 23.7 km (by US hwy 70) NW Lordsburg (AMNH 114239, k); 15.6 km (by NM hwy 90) NE Lordsburg; 1465 m elev (AMNH 117811, k, p; 112861, 112862, k). Luna Co.: 2.9 km (by rd) S Gage (30.6 km by I-hwy 10 W Deming) (AMNH 127120–127129, p). Socorro Co.: 2.2 km (by rd) W San Antonio (AMNH 131072–131081, p).

Cnemidophorus neomexicanus: UNITED STATES: *New Mexico:* Hidalgo Co.: 15.8 km S and 1.6 km E Road Forks (AMNH 126888, range extension); 11.6 km (by US hwy 70) NW Lordsburg (AMNH 125546, 125547, e, k, p, r); 21.7 km (by US hwy 70) NW Lordsburg (AMNH 86993, e); 22.7 km (by US hwy 70) NW Lordsburg (AMNH 86987, e); 23.5 km (by US hwy 70) NW Lordsburg (AMNH 86988, 86989, e; 131068, p, r; 131069, r); 23.7 km (by US hwy 70) NW Lordsburg (AMNH 114227, e, k); 26.7 km (by US hwy 70) NW Lordsburg (AMNH 86990, e; 86992, e; 131070, r); 26.9 km (by US hwy 70) NW Lordsburg; 1340 m elev (AMNH 125550, e, k, r; 125565, e, k, p, r); 27.2 km (by US hwy 70) NW Lordsburg; 1310 m elev (AMNH 120675, e, p; 120676, p); 27.7 km (by US hwy 70) NW Lordsburg; 1310 m elev (AMNH 112850, k; 115998, e, r; 131066, e, k, p, r; 131067, e, p, r); 28.0 km (by US hwy 70) NW Lordsburg; 1310 m elev (AMNH 112846–112848, e; 114222, 114223, e, k; 114224, 114225, e). Sandoval Co.: 8.5 km (by US hwy 85) S Bernalillo; 1540 m elev (AMNH 128329–128334, k, p); 4.8 km N Peña Blanca (AMNH 84822–84828, e); Rio Grande crossing and Cochiti Dam, 5.3 km (by NM hwy 22) N Peña Blanca (AMNH 119532, 119533, e; 114229, 114230, e, k; 122931, p, r; 122933, k, p, r; 122942, k, p, r; 122946, k, p, r; 123054, e; 123055, e, p). Socorro Co.: along the Rio Grande, 1.0 km E San Antonio (AMNH 128326–128328, k, p; 131071, k, p). Laboratory-reared offspring from mothers listed above, among those from the vicinity of Lordsburg and Peña Blanca (AMNH 122935, k; 122944, k; 125566, k; 125568, k; 125570, k).

Cnemidophorus septemvittatus: UNITED STATES: *Texas:* Brewster Co.: 28.0 km (by US hwy 385) S Marathon (AMNH 126906–126908, p). Presidio Co.: 57.6–60.2 km (by TX hwy 2810) SW Marfa (AMNH 126904, 126905, p).

Cnemidophorus sexlineatus viridis: UNITED STATES: *Colorado:* Kiowa Co.: 15.1 km N Eads at Rush Creek (AMNH 108142, k). Pueblo Co.: Huerfano River bridge on Doyle Rd, 29.9 km (by rd) S Avondale (AMNH 131122, k, p). *New Mexico:* San Miguel Co.: Conchas Lake, at south state park campground (AMNH 114231, k; 114233–114235, k; 123053, p). *Texas:* Brooks Co.: 11.4 km (by US hwy 281) S Falfurrias (AMNH 126893–126898, p; 126899, 126900, e; 126901, 126902, e, p; 131109–131111, e; 131113, e; 131115, 131116, e; 131119–131121, e).

Cnemidophorus tigris gracilis: UNITED STATES: *Arizona:* Cochise Co.: 7.2 km N and 4.3 km W Portal; 1515 m elev (AMNH 112860, k).

RESULTS AND DISCUSSION

HABITATS OF *C. NEOMEXICANUS* AND ITS ANCESTORS

Although there is variation in habitats utilized (see Stebbins, 1985; Conant, 1975), in southern New Mexico *Cnemidophorus inornatus* is most readily encountered in rather open grassland with sandy soil. *Cnemidophorus marmoratus* is infrequent or absent in such open grassy areas, but is common in more arid habitats with open ground between shrubs, usually either creosote (*Larrea*) or mesquite (*Prosopis*). *Cnemidophorus neomexicanus* occupies two other rather different habitats in the same general area: (1) riparian gallery woodlands or forest on floodplains with sandy soil, particularly in the Rio Grande drainage system; and (2) desert-grassland ecotones in the immediate vicinity of the preferred habitats of *C. inornatus* and *C. marmoratus* (Wright and Lowe, 1968). All of our field-captured specimens of *C. neomexicanus* were found in one of these two habitats.

The two samples of *C. neomexicanus* that we compare morphologically (see below) also represent both types of habitat. Our northern sample (fig. 1) is from the vicinity of Peña Blanca (New Mexico: Sandoval County; at Rio Grande crossing and Cochiti Dam, 5.3 km [by NM hwy 22] N Peña Blanca). This locality is within the general range of both parental bisexual species (Stebbins, 1985; Hendricks and Dixon, 1986), but neither of those species was seen at this particular site while we sampled the local *neomexicanus*; thus, these *neomexicanus* specimens do not likely include newly generated F_1 hybrids between *C. marmoratus* × *C. inornatus*. At this locality, which is downstream from the dam, the habitat on 24 May 1976 and 30 May 1978 was noted as being sandy floodplain, primarily with cottonwood trees (*Populus*), numerous logs, and piles of fallen and felled tree debris including an abundance of dead leaves. The only species of *Cnemidophorus* seen here were *C. neomexicanus* and *C. velox* Springer (another parthenogen), and both were exceedingly abundant.

Our southwestern sample (fig. 1) of *C. neomexicanus* is from a 16.4 km stretch of essentially straight and almost level roadway (US hwy 70), along the northeastern region of a basin in the northern part of the Animas Valley, northwest of Lordsburg, Hidalgo County, New Mexico, approximately 185 km (airline) west of the Rio Grande. In this area there is somewhat of a patchwork distribution of local grassland, desert, and desert-grassland ecotones, which support, in various combinations depending on the precise site, populations of five species of *Cnemidophorus*: *C. inornatus, C. neomexicanus, C. marmoratus, C. tigris,* and *C. uniparens* Wright and Lowe. *Cnemidophorus uniparens* is a triploid unisexual species that occurs primarily in desert-grassland ecotone (Wright and Lowe, 1968); its origin involved hybridization between species in the *sexlineatus* species group (Lowe and Wright, 1966; Neaves, 1969; Lowe et al., 1970b), not including *C. marmoratus* (see Dessauer and Cole, in press).

The mixture of habitats and associated species of *Cnemidophorus* in the Lordsburg area suggests that *C. marmoratus* and *C. inornatus* could be hybridizing there now. The local *C. neomexicanus* might, therefore, represent new F_1 hybrids and/or one or more parthenogenetic clone(s) that originated through one or more hybridization event(s) independent of those that produced the *C. neomexicanus* occurring in the Rio Grande Valley. Although our biochemical data indicate that this is unlikely (see below), we present further details on this area (from Cole's fieldnotes) for researchers who may conduct follow-up studies in future decades, particularly as habitats continue to shift in the Southwest, often with help from mankind (e.g., Hastings and Turner, 1965). For the following specific sites from which our samples were collected, distances (NW from Lordsburg via US hwy 70) were recorded from central Lordsburg where the highway passes beneath the tracks of the Southern Pacific Railroad (at the junction of US hwy 70 and US hwy 80 in town).

11.3 to 11.6 km NW Lordsburg, NE side of road (fig. 2A): In several days of collecting from 1978 to 1981 *C. marmoratus* was extremely abundant; *C. neomexicanus* and *C. uniparens* were present but seen much less frequently. Habitat is scattered shrubs usually with sand mounded at their bases, with

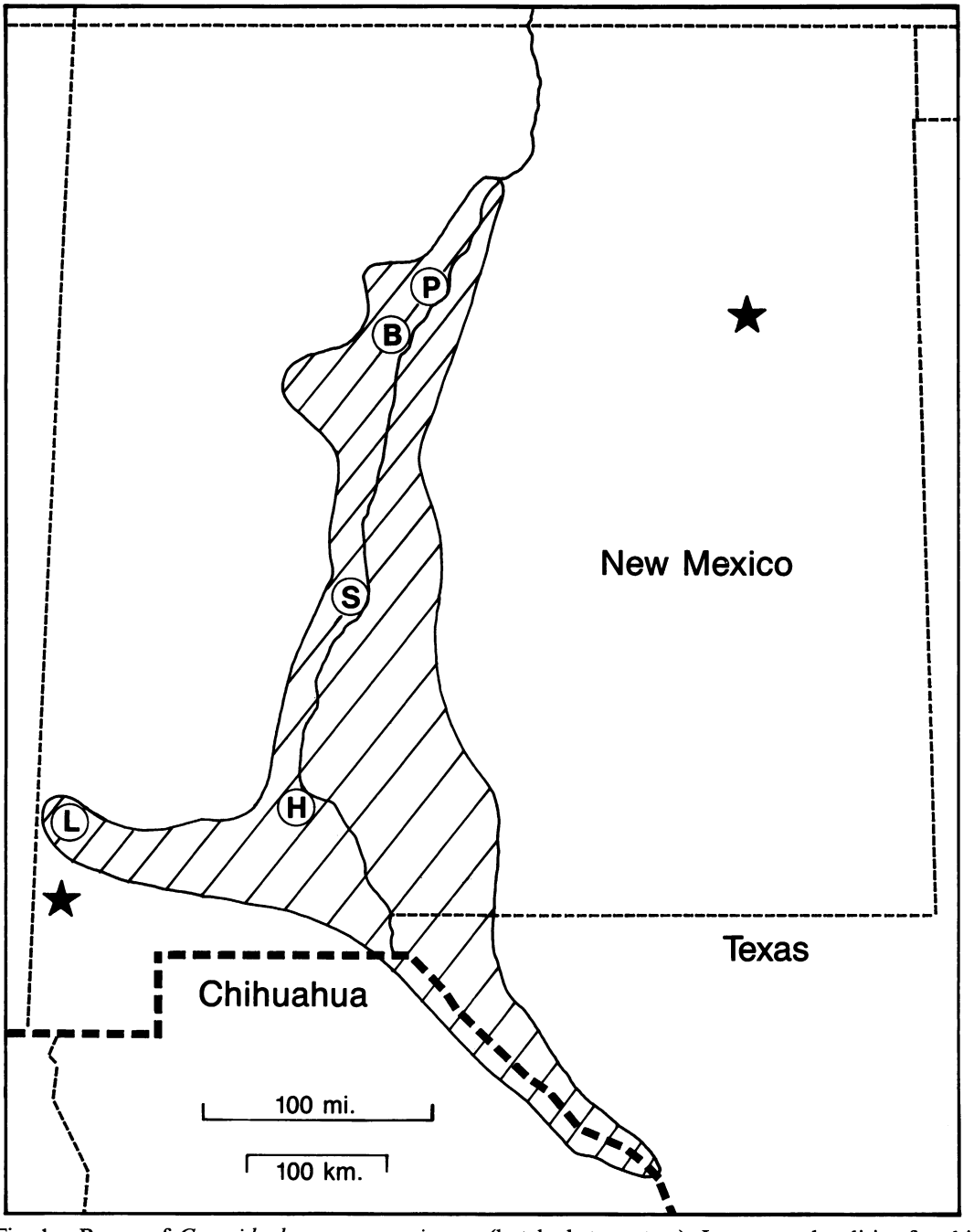

Fig. 1. Range of *Cnemidophorus neomexicanus* (hatched, two stars). Important localities for this study are: **B,** Bernalillo; **H,** Hatch; **L,** Lordsburg; **P,** Peña Blanca; **S,** San Antonio. Star east of P represents introduced population at Conchas Lake (Leuck et al., 1981); star south of L is a range extension (see Specimens Examined, AMNH 126888).

sandy soil and sparse grass between the shrubs. Mesquite (*Prosopis*) is the dominant shrub and no creosotebush (*Larrea*) was seen. Mormon tea (*Ephedra*) and snakeweed (*Gu-*

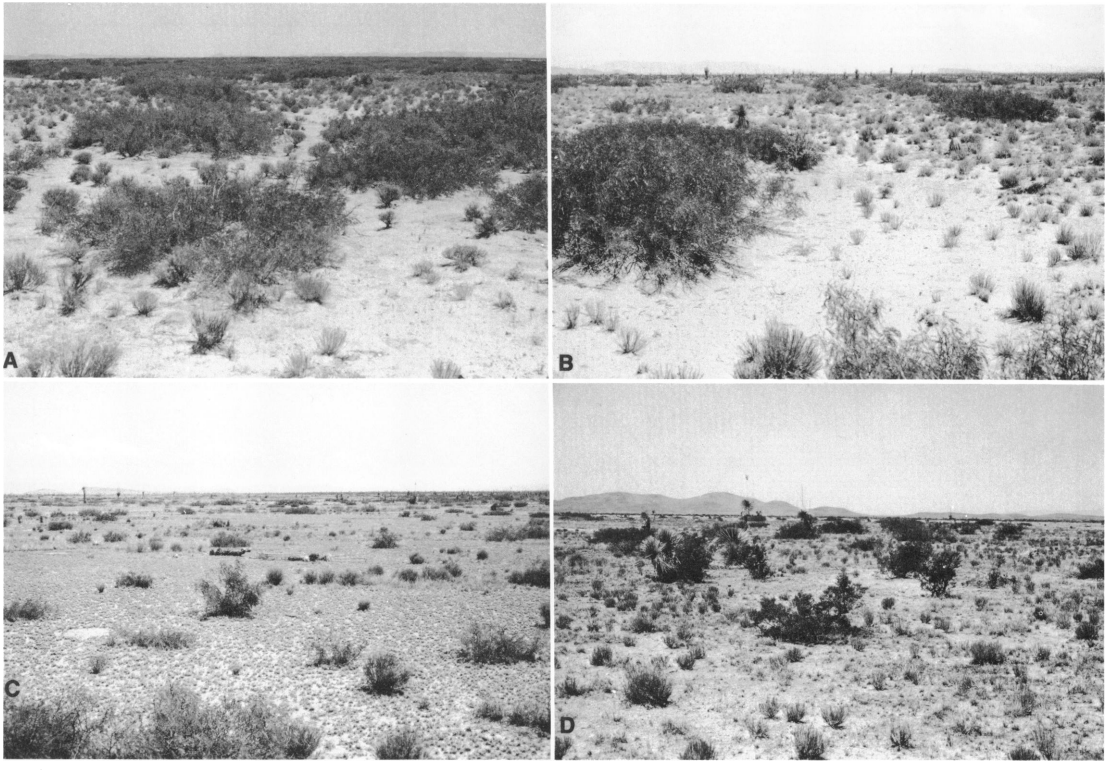

Fig. 2. Desert-grassland habitat along U.S. highway 70 northwest of Lordsburg, Hidalgo County, New Mexico. **A.** 11.6 km NW Lordsburg, NE side of road, 25 June 1978. **B.** 22.7 km NW Lordsburg, 10 July 1976. **C.** 23.7 km NW Lordsburg, NE side of road, 10 July 1976. **D.** 26.9 km NW Lordsburg, SW side of road, 10 July 1976.

tierrezia) abound, and yucca (*Yucca elata*) is scattered about. Cacti are sparse, but prickly pear and cholla (*Opuntia* spp.) are present. From 07:40 to 10:30 hr on 25 June 1978 I counted 60 *C. marmoratus,* 4 *C. uniparens,* no *C. neomexicanus* (two had been seen and collected here previously), and no *C. inornatus* (none was ever seen here).

15.6 km NW Lordsburg, NE side of road: Habitat similar to above, with *Prosopis* dominant on small sand mounds; other shrubs (including *Gutierrezia*), but very little grass, on the loose sandy soil between the shrubs. During good conditions (time and weather) for *Cnemidophorus* activity in 45 minutes on 19 June 1978, *C. marmoratus* was the only teiid seen.

16.3 km NW Lordsburg, SW side of road: Habitat again similar to above, *Prosopis* dominant on sand mounds, with sparse grass on the very open ground (sandy soil) between shrubs. In many days from 1981 to 1985 *C. marmoratus* was abundant here, *C. uniparens* and *C. neomexicanus* were present but sparse, and *C. inornatus* was never seen.

17.1 km NW Lordsburg, NE side of road: Habitat with considerable open ground of hard-packed and cracked (from water standing previously) sandy soil, with *Prosopis, Gutierrezia* and other shrubs, very little grass, and no *Yucca.* On 19 June 1978 only *C. marmoratus* and *C. uniparens* were seen, both in low density, under good conditions for *Cnemidophorus* activity.

18.4 km NW Lordsburg, SW side of road: A mixture of grassland and shrubland, with fairly dense occurrence of *Prosopis* and *Yucca.* Many allthorn (*Koeberlinea*) were seen also, and a single *Larrea.* Under good conditions on 19 June 1978 the only teiids observed were 10 *C. marmoratus* and two *C. uniparens.*

21.7 km NW Lordsburg: Pough (1962: 270) reported a *C. neomexicanus* from "an area

of loose, bare sand with large, scattered, elevated mesquite clumps."

22.7 km NW Lordsburg (fig. 2B): Sandy soil with vegetation (roughly in order of abundance) of *Prosopis, Yucca,* grass, additional shrubs, *Ephedra,* prickly pear, and cholla; no *Larrea* seen. Under good conditions from 10:00 to 12:20 hr, on 5 June 1976 the only teiids seen here were *C. marmoratus,* although I collected a *C. neomexicanus* here with F. Harvey Pough on 12 August 1961.

23.5 to 23.7 km NW Lordsburg, NE side of road (fig. 2C): Vegetation (roughly in order of abundance) of widely scattered *Prosopis, Yucca,* sparse grass, additional shrubs, hedgehog cactus, cholla, prickly pear, and very few *Larrea* (mostly widely scattered); no *Ephedra* was seen. On 8 June 1976 a sign noted this to be an "Experimental Range Area." On that day and on 20 and 21 May 1982 all four species of *Cnemidophorus* were seen, with *C. marmoratus* and *C. uniparens* in particularly great abundance.

25.4 km NW Lordsburg: As noted on 12 August 1961 while collecting with F. Harvey Pough, this is a rather open (very few shrubs) area of grass and *Gutierrezia* with widely scattered *Prosopis* and *Yucca.* Apparently this represents a gap in good habitat for desert whiptails and thus locally separates *C. marmoratus* (occurring to the east) and *C. tigris gracilis* (occurring to the west), as reported by Zweifel (1962).

26.7 to 28.0 km NW Lordsburg, mostly SW side of road (fig. 2D): Mesquite grassland with low shrubs on sandy soil, large open grassy areas, *Gutierrezia,* scattered *Yucca,* numerous hedgehog cacti, few prickly pear and cholla, very few *Larrea,* and an occasional *Ephedra.* On numerous days of collecting under good conditions for *Cnemidophorus* activity, dozens of *C. inornatus* were seen from 1976 to 1983; *C. uniparens* is less abundant and *C. neomexicanus* even less so. On only two occasions a young *C. tigris* was seen briefly.

30.4 km NW Lordsburg, NE side of road: As noted on 12 August 1961 while collecting with F. Harvey Pough, a broad stand of *Larrea* began here (continuing toward the west) and *Cnemidophorus tigris gracilis* was collected.

The present coexistence of *C. marmoratus, C. neomexicanus,* and *C. inornatus* in desert-grassland ecotone such as the habitats described above is consistent with the previously hypothesized hybrid origin of *C. neomexicanus.* Such habitats with coexistence of these same three species occur also in the vicinity of the Rio Grande, exemplified particularly well by the locality at 13.5 km west of Hatch, Doña Ana County, New Mexico, described briefly by Wright and Lowe (1967: p. 6).

Morphology—Univariate Analysis

Coloration: The nature of the colors and color patterns of *C. marmoratus, C. inornatus,* and *C. neomexicanus* is such that most individuals are readily identified prior to capture, once one is familiar with them, but the characters are not readily quantified for statistical analysis. In addition, certain colors change extensively and very quickly in preservative, which can either enhance or obscure aspects of pattern. Therefore, the following comparison of coloration is general and descriptive, based on notes taken from living adults of each species from localities northwest of Lordsburg. It should be noted also that our specimens of *C. neomexicanus* from Sandoval County were not notably different in life from those of the Lordsburg area. Color photographs of all three species in life were published elsewhere (Cole, 1978: 63), as were paintings (Stebbins, 1985: pls. 31, 32).

The dorsal body surfaces of *C. marmoratus* (fig. 3A) often are basically unstriped (a few light yellow stripes or portions or traces thereof may be visible), with a dark brown to black ground color and a pattern (reticulate, marbled, or, especially laterally, crossbarred) of light yellow or beige, including some light spots; some individuals have more prominent wavy vertebral and paravertebral stripes (fig. 3B). *Cnemidophorus inornatus* (fig. 3D), however, is dark brown with usually seven light yellow stripes that usually are straight (the odd one being the inconspicuous vertebral stripe, which has subtle zigzags on some individuals, and which may be broken in places); this species lacks light spots and bars. *Cnemidophorus neomexicanus* (fig. 3C)

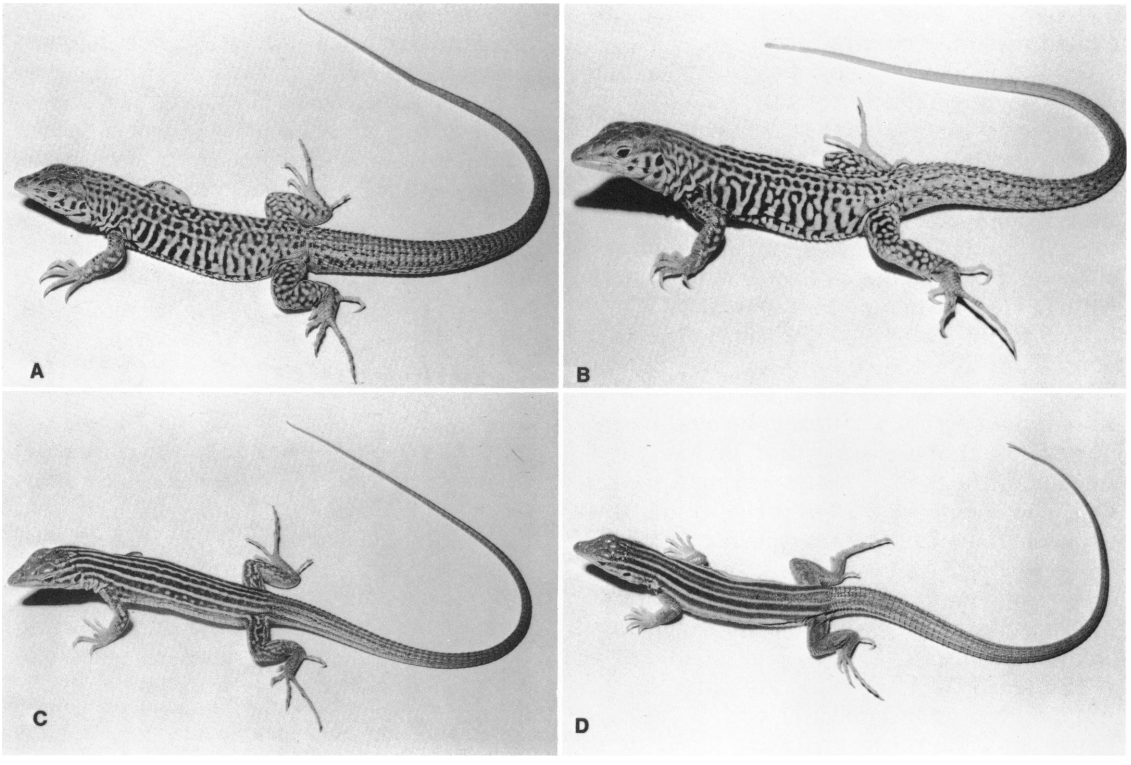

Fig. 3. Three species of *Cnemidophorus* from the vicinity of Lordsburg, Hidalgo County, New Mexico. **A** and **B.** *C. marmoratus,* the latter with wavy vertebral light stripe (AMNH 117811 and Cole field no. 5168, respectively). **C.** Unisexual *C. neomexicanus* (AMNH 112850). **D.** *C. inornatus* (AMNH 115948).

also has a dark brown ground color but it consistently has both light spots (beige) and seven light stripes; the ventralmost stripe is cream and the others are pale yellow. The two ventralmost stripes are essentially straight but the vertebral and paravertebral stripes are, respectively, quite wavy (zigzag) and somewhat wavy posterior to the shoulder region. The beige spots are most evident in the two lateral dark fields, tending to be in a row within the field.

In *C. marmoratus* the anterior third of the tail is checkered with dark brown and yellow to beige; posteriorly, the tail is essentially uniform brown with occasional darker brown (or black) flecks. In *C. inornatus* the posterior three-quarters of the tail is bright blue, whereas in *C. neomexicanus* it is grayish green.

In *C. marmoratus* the dorsal surfaces of the hind legs are dark brown to black with numerous light yellow to beige spots. In *C. inornatus,* the brown hind legs have a faint light beige reticulation (clearest on upper leg), covered with a gray wash. In *C. neomexicanus* the hind legs are brown with a more conspicuous beige reticulation.

In *C. marmoratus* the dorsal surfaces of the arms are similar to the legs, although in the largest individuals they may become covered with a gray wash. In *C. inornatus* the arm usually is brown and unspotted but the outer surface of the lower arm usually has an inconspicuous light yellow stripe below the elbow; a gray wash also is often present. In *C. neomexicanus* the arms usually are brown with several beige spots or stripes.

In *C. marmoratus* the ventral surfaces are as follows: throat with black spots on an orange or gray wash; chest checkered with black, orange, and a few cream spots; abdomen, hind legs, and tail yellow. In *C. inornatus* females the ventral surfaces are unmarked, being essentially cream on the abdomen but with a definite touch of blue anteriorly (much more

intense in males), and the tail is darker blue. In *C. neomexicanus* the ventral surfaces are also unmarked and generally pale blue or gray (abdomen essentially cream); underside of most of the tail is gray.

Although we know almost nothing about the genetics of coloration of *Cnemidophorus,* we can make a rough hybrid index comparison of these three species by considering the *C. inornatus* condition as having a value of 0, the *C. marmoratus* condition as having a value of 100, and estimating a value for the *C. neomexicanus* condition as being 0 (like *inornatus*), 25 (more like *inornatus* than *marmoratus*), 50 (quite intermediate), 75, or 100. Thus, the values for *C. neomexicanus* are as follows: Dorsal light bars or spots, 25; dorsal light stripes, 25; tail color, 50; dorsal hind legs, 25; dorsal arms, 75; and ventral surfaces, 25. The mean of this crude hybrid index for *C. neomexicanus* is 38, indicating a somewhat greater similarity to *C. inornatus* than to *C. marmoratus* in coloration.

Cnemidophorus sexlineatus viridis is another bisexual whiptail lizard occurring in grassland habitats in New Mexico (eastern part of the state), which conceivably (but ruled out below) could be one of the ancestors of *C. neomexicanus* instead of *C. inornatus* (i.e., alternative hybrid origin hypothesis of *C. marmoratus* × *C. sexlineatus*). The comparative hybrid index of coloration based on *sexlineatus* instead of *inornatus* is nearly identical to that based on *inornatus,* except the value for tail color is 75 (blue only in juvenile *sexlineatus*), so the mean is 42 instead of 38.

Cuellar (1974: 630), in challenging the hybrid origin hypothesis for *C. neomexicanus,* stated: "On morphological grounds it is hard to imagine that *tigris* [*marmoratus*] was one of the parents. If it was, why does *neomexicanus* not reflect the tesselated pattern and large size characteristic of *tigris* . . . ?" Yet, geneticists have long known that F_1 hybrids often do not have the morphology that one might predict for them. Moreover, there is a nontesselated but striped and spotted hybrid of known ancestry including *C. marmoratus,* whose pattern is consistent with the striped and spotted pattern of *C. neomexicanus.* That lizard was a laboratory-bred hybrid of *C. sonorae* (♀) × *C. marmoratus* (♂), for which photographs of both parents and offspring were presented elsewhere (Cole, 1979: 97). In addition, some individuals of *C. marmoratus* do have more evident stripes than others, occasionally including wavy (zigzag) vertebral and paravertebral stripes (fig. 3B).

SIZE AND SCUTELLATION: To minimize possible biases from ontogenetic development and sexual dimorphism, data were taken only from adult females of each species. The *C. inornatus, C. marmoratus,* and *C. neomexicanus* specimens referred to as being from Lordsburg (table 2) are, for each species, a pooled sample from the sites northwest of Lordsburg (fig. 1; Specimens Examined). This allows comparing samples of *C. neomexicanus* and its hypothesized ancestors from one area, to control for possible biases of differing environmental effects at different localities. The *inornatus* samples represent a 4.5 km stretch along the road; the *marmoratus* represent a 12.4 km stretch; and the *neomexicanus* represent a 16.4 km stretch. The *C. neomexicanus* individuals referred to as being from Peña Blanca are all from the site along the Rio Grande downstream from Cochiti Dam, 5.3 km north of Peña Blanca, Sandoval County, New Mexico (fig. 1). This is close to the northernmost latitude at which the species occurs and allows comparing samples of *neomexicanus* from rather different habitats and localities.

Most of the size and scutellation data examined are summarized in table 2 (10 characters) and variation in selected characters is illustrated in figure 4. The bisexual *C. inornatus* and *C. marmoratus* are significantly different (*t*-test; 95% confidence level) in all of these characters except absolute size of the postantebrachial scale, in which the sample of *neomexicanus* from Peña Blanca is the same as the parental species but the scale averages smaller in the *neomexicanus* from Lordsburg (table 2). In four of the nine characters that clearly differ in the parental species, *neomexicanus* is somewhat intermediate (body length; scales around midbody [fig. 4]; femoral pores; interlabial scales); in two of the characters *neomexicanus* is most similar to *marmoratus* (fourth toe lamellae; circumorbital scales [fig. 4]); in two of the characters *neomexicanus* is most similar to *inornatus* (gular scales [fig. 4]; dorsal scale size); and in one of the characters (mesoptychial scale size)

TABLE 2
External Morphological Data for Five Samples (four species) of *Cnemidophorus*

Character	*C. sexlineatus* S Texas	*C. inornatus* Lordsburg	*C. neomexicanus* Lordsburg	*C. neomexicanus* Peña Blanca	*C. marmoratus* Lordsburg
Body length[a]	57.8 ± 0.99 (51–63) 13	58.8 ± 0.68 (53–65) 26	69.2 ± 0.98 (62–78) 21	73.5 ± 1.07 (66–78) 13	85.9 ± 1.00 (76–93) 19
Scales around midbody[b]	82.2 ± 1.59 (72–90) 13	61.9 ± 0.72 (55–68) 26	81.2 ± 0.65 (77–87) 21	75.5 ± 0.78 (71–80) 13	91.6 ± 1.18 (84–102) 19
Femoral pores (total)[b]	30.5 ± 0.77 (26–36) 13	30.7 ± 0.47 (26–35) 26	40.2 ± 0.34 (37–43) 21	37.6 ± 0.40 (35–40) 13	42.5 ± 0.55 (39–47) 19
Fourth toe lamellae (total)[b]	61.5 ± 0.73 (59–66) 10	56.1 ± 0.44 (51–60) 25	66.5 ± 0.45 (63–70) 16	62.8 ± 0.55 (60–66) 12	64.7 ± 0.81 (59–70) 17
Circumorbital scales (total)[b]	10.8 ± 0.68 (7–16) 13	9.1 ± 0.29 (7–12) 23	23.8 ± 0.36 (21–27) 20	21.0 ± 1.22 (15–26) 12	21.5 ± 0.76 (14–27) 19
Interlabial scales (total)[b]	16.8 ± 1.20 (9–25) 13	14.7 ± 0.85 (8–30) 25	22.5 ± 0.84 (18–28) 11	20.7 ± 0.47 (18–23) 10	32.7 ± 1.50 (16–41) 19
Gular scales[b]	20.2 ± 0.58 (17–23) 11	17.2 ± 0.42 (15–23) 22	18.5 ± 0.70 (15–21) 11	19.2 ± 0.43 (16–22) 12	22.6 ± 0.38 (21–26) 17
Dorsal scale size[a]	0.252 ± 0.010 (0.20–0.32) 13	0.331 ± 0.007 (0.28–0.40) 26	0.308 ± 0.004 (0.28–0.36) 21	0.351 ± 0.011 (0.30–0.42) 13	0.379 ± 0.010 (0.28–0.46) 19
Mesoptychial scale size[a]	0.892 ± 0.054 (0.66–1.40) 13	0.852 ± 0.031 (0.56–1.16) 26	0.553 ± 0.016 (0.44–0.72) 21	0.727 ± 0.040 (0.46–0.86) 12	0.562 ± 0.039 (0.26–0.82) 19
Postantebrachial scale size[a]	0.402 ± 0.014 (0.30–0.52) 13	0.509 ± 0.013 (0.40–0.62) 24	0.416 ± 0.008 (0.32–0.46) 21	0.475 ± 0.012 (0.40–0.56) 13	0.500 ± 0.018 (0.38–0.70) 19

[a] Measurement in mm; mean ± one std. error of the mean (range) N.
[b] Number of scales; mean ± one std. error of the mean (range) N.

neomexicanus is rather intermediate (Peña Blanca sample) or similar to *marmoratus* (Lordsburg sample). In 6 of the 10 characters compared (table 2), the two samples of *neomexicanus* clearly differ from each other at the 95 percent confidence level (scales around midbody, femoral pores, fourth toe lamellae, dorsal scale size, mesoptychial scale size, postantebrachial scale size).

For each of the characters in which the bisexual species differ from each other, degree of intermediacy in *C. neomexicanus* was estimated by comparing the sample means with the hybrid index of Hubbs et al. (1943), which was used previously for *Cnemidophorus* by Wright and Lowe (1967). For the univariate analysis, *neomexicanus* from Lordsburg had a mean hybrid index of 60.6 and those from Peña Blanca had 54.2 (table 3). Another way to estimate intermediacy in *neomexicanus* was to use the same hybrid index but to score *neomexicanus* characters the same as those of the bisexual species for characters in which the mean was not clearly significantly different from that of the bisexual species (overlap of 95% confidence intervals). Thus, fourth toe lamellae of both samples of *neomexicanus* were scored as 100 and gular scales as 0. For characters in which the 95 percent confidence interval of *neomexicanus* overlapped that of each parent, a score of 50 was assigned. With this approach there was practically no difference in the hybrid index scores calculated first, the *neomexicanus* from Lordsburg being 58.6 and those from Peña Blanca being 54.6.

Cuellar's conclusion (1974: 630), made in the absence of a morphological comparison, that "*C. neomexicanus* . . . bears no morphological intermediacy between" *C. inornatus* and *C. marmoratus,* is not supported. Indeed, the morphological data are quite consistent with the hypothesized hybrid origin. However, similar comparisons among *C. neomexicanus, C. marmoratus,* and *C. sexlineatus viridis* produced similar results (tables 2, 3), so the data from external morphology equally support the alternative hybrid

origin hypothesis of *C. marmoratus* × *C. sexlineatus,* with univariate analysis.

Morphology—Multivariate Analysis

The principal component analyses revealed four discrete groups of individuals that corresponded to the four population samples (*inornatus, marmoratus,* and *neomexicanus* from the area of Lordsburg; *neomexicanus* from the area of Peña Blanca). The raw data and the log-transformed data gave similar results. Here, however, we discuss the results with the log-transformed data because those are more relevant biologically.

The first two principal components have eigenvalues of 5.90 and 1.87, respectively. They jointly account for 78 percent of the total variation in the data set and are the only components with eigenvalues greater than 1.0 (i.e., explaining more than 10% of the total variation). Interpretation of these results seems clear: the 10 univariate characters are redundant to a considerable extent; in excess of 75 percent of the total variation can be explained by two linear combinations of those 10 characters. The loadings on the components are listed in table 4, and the scores of each individual specimen on those components are shown in figure 5. The three species and, in fact, the four populations are completely separated by these first two principal components, given the sample sizes available. It is probably accurate to interpret the first component as reflecting a general size-related phenomenon. Seven of the 10 loadings are large and relatively equal. The other three characters, which have heavy loadings on the second component, involve the microscopically measured sizes of individual epidermal scales.

Using the Shapiro-Wilk test, we found that none of the test statistics for the first two principal component scores for any of the four populations was significantly different from zero at the 0.05 level of probability. We therefore concluded that the data were approximately normally distributed and proceeded with sums-of-squares simultaneous test procedures (SS-STP) to determine if the distributions of PC scores for the parthenogenetic populations were intermediate between those of the parental species; SS-STP maintains the 0.05 level of significance in spite of performing multiple comparisons.

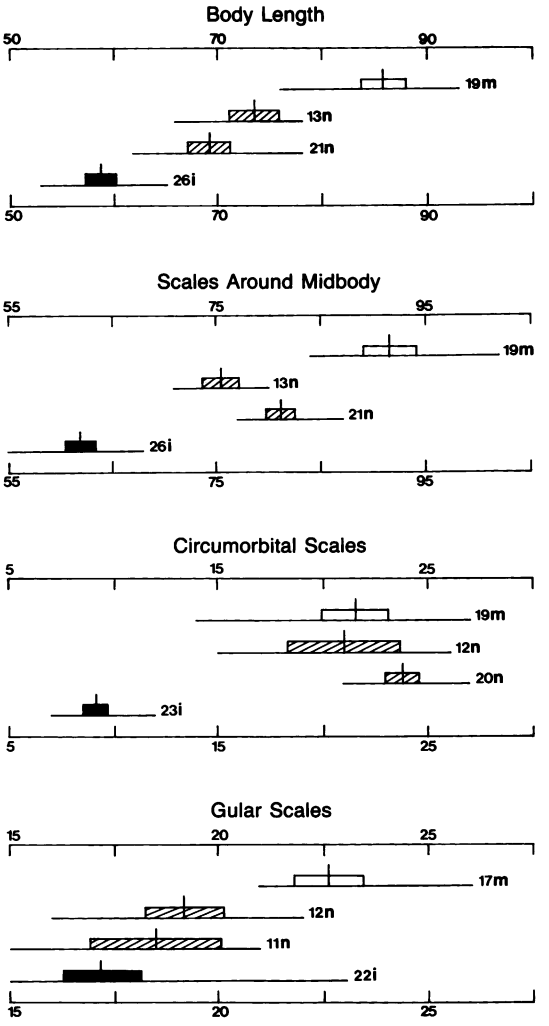

Fig. 4. Variation in four morphological characters in four samples (three species) of *Cnemidophorus.* Open rectangles represent *C. marmoratus* (m) from the vicinity of Lordsburg. Solid rectangles represent *C. inornatus* (i) from the vicinity of Lordsburg. Hatched rectangles represent unisexual *C. neomexicanus* (n) from the vicinity of Peña Blanca (upper one for each character) and the vicinity of Lordsburg (lower one for each character). Horizontal line indicates range (sample size to right), vertical line the mean, rectangle the 95 percent confidence interval (table 2).

The results of the SS-STP tests are shown in table 5. The vertical bars indicate sets of population samples that are statistically ho-

TABLE 3

Hybrid Indices[a] Compared for Two Hypothesized Hybrid Origins of *Cnemidophorus neomexicanus* (two samples)

	C. marmoratus × *C. inornatus*		*C. marmoratus* × *C. sexlineatus*	
	C. neomexicanus		*C. neomexicanus*	
Character	Lordsburg	Peña Blanca	Lordsburg	Peña Blanca
Body length	38.4	54.2	40.6	55.9
Scales around midbody	65.0	45.8	−10.6	−71.3
Femoral pores	80.5	58.5	80.8	59.2
Fourth toe lamellae	120.9	77.9	156.2	40.6
Circumorbital scales	118.5	96.0	121.5	95.3
Interlabial scales	43.3	33.3	35.8	24.5
Gular scales	24.1	37.0	−70.8	−41.7
Dorsal scale size	−47.9	41.7	44.1	78.0
Mesoptychial scale size	103.1	43.1	102.7	50.0
Postantebrachial scale size	—	—	14.3	74.5
Grand mean, univariate	60.6	54.2	51.5	36.5
Mean, both samples, univariate	57.4		44.0	
Multivariate, PC1[b]	73.1	59.8	—	—
Mean, both samples, PC1	66.4		—	

[a] Hybrid index of Hubbs et al. (1943), based on sample means, calculated for characters for which the hypothesized parental species have significantly different means. On this scale, *inornatus* (or *sexlineatus*) = 0.0, *marmoratus* = 1.0.

[b] PC1 = first principal component.

mogeneous at the 0.05 level. Thus, for the first principal component, the two samples of *C. neomexicanus* do not differ from each other, but are intermediate between the bisexual *C. inornatus* and *C. marmoratus*. This result is clearly consistent with the proposed hybrid origin of the unisexual populations. It indicates that the parthenogens of hybrid origin are intermediate to the parental taxa with regard to the quantitative character axis that represents the largest independent component of variation in these taxa. For the second

TABLE 4

Character Loadings on First Two Axes for Two Multivariate Analyses of *Cnemidophorus* Morphology

	Four samples[a]		Five samples[b]	
Character	PC1	PC2	CA1	CA2
Body length	0.356	0.305	2.288	0.391
Number, scales around midbody	0.396	0.006	1.578	2.397
Number, femoral pores	0.380	0.011	0.815	1.252
Number, fourth toe lamellae	0.360	−0.218	−0.096	−0.515
Number, circumorbital scales	0.367	−0.078	0.225	0.376
Number, interlabial scales	0.356	0.077	0.251	−0.036
Number, gular scales	0.286	0.264	0.369	−0.536
Size, dorsal scale	0.082	0.589	0.914	0.388
Size, mesoptychial scale	−0.281	0.338	−0.931	−0.941
Size, postantebrachial scale	−0.115	0.563	−0.033	0.404
Total explained variation	59.0%	18.7%	86.1%	13.9%

[a] *C. inornatus* (Lordsburg), *C. marmoratus* (Lordsburg), and *C. neomexicanus* (Lordsburg and Peña Blanca). The 78 specimens are plotted in figure 5; principal components analysis.

[b] Same samples plus *C. sexlineatus* (southern Texas). The 91 specimens are plotted in figure 6; canonical discriminant analysis.

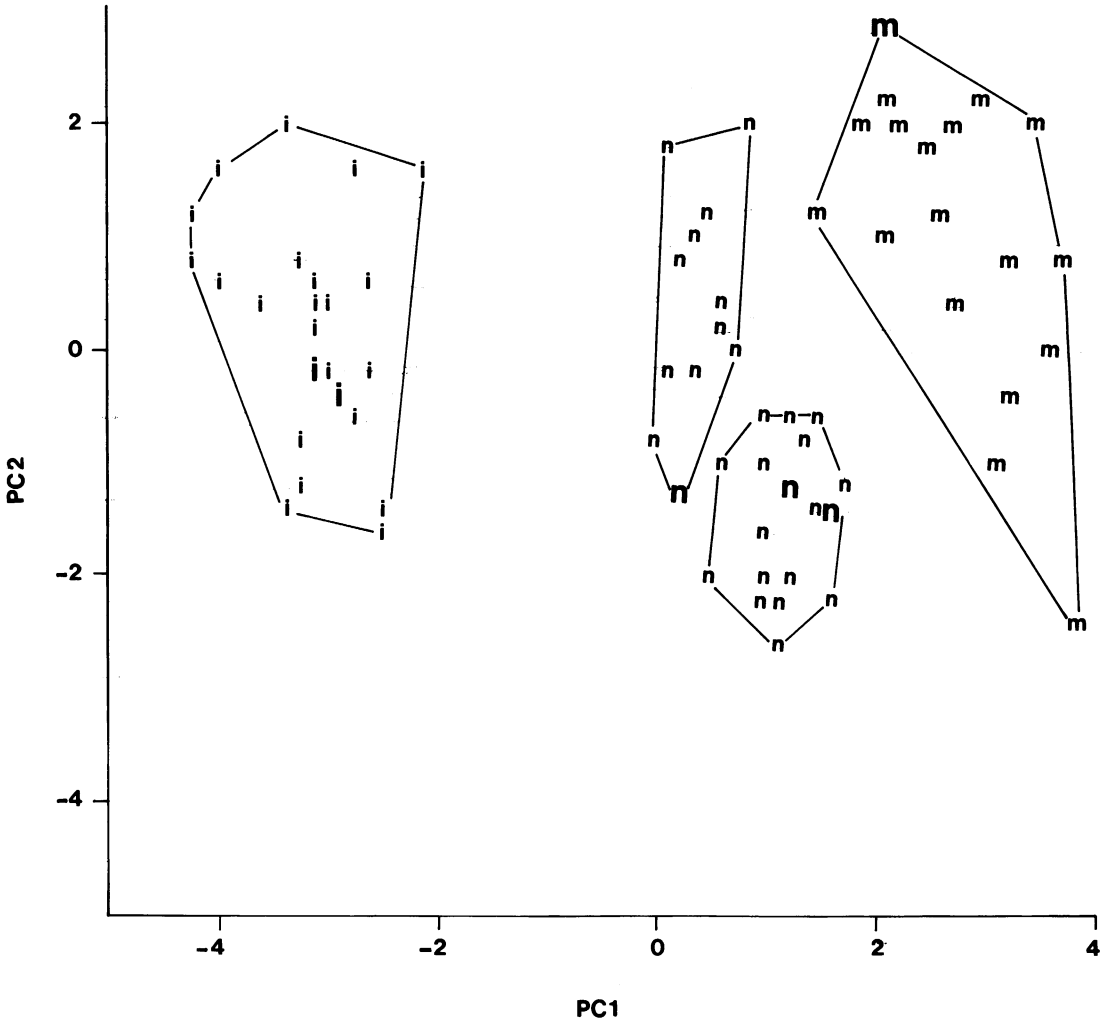

Fig. 5. Scores of 78 *Cnemidophorus* (four samples, three species) on the first two principal components extracted from the correlation matrix of 10 log-transformed morphological characters (tables 2, 4). Letters indicate individuals, as follows: **i,** *C. inornatus* from the area of Lordsburg; **m,** *C. marmoratus* from the area of Lordsburg; **n,** unisexual *C. neomexicanus* from the area of Lordsburg (lower group) and the area of Peña Blanca (upper group). Bold letter indicates two individuals with similar scores.

principal component the results are less clear. There are two overlapping sets of homogeneous populations. In one of these, the two samples of *C. neomexicanus* and the *C. inornatus* are present and, in the other, the sample of *C. neomexicanus* from near Peña Blanca is present with the samples of the two parental species. Basically, the pattern on PC2 is that the clonal populations are not statistically intermediate to the parental forms; instead there is extensive overlap and variability; this component is not particularly useful for examining intertaxon differentiation.

An additional multivariate analysis was performed using the four population samples of *Cnemidophorus* discussed above plus a sample of *C. sexlineatus viridis*. This was done to investigate whether *sexlineatus* is a morphologically reasonable alternative to *inornatus* as a parental species for *neomexicanus*. In this case, we are not attempting to describe the overall morphological variation in the lizards, but are attempting to discriminate be-

TABLE 5
Sums-of-Squares Simultaneous Test Procedure Analysis of Variation in First Two Principal Components of Samples of *Cnemidophorus*[a]

Sample	Mean	S.D.	N	Significant subsets
PC1:				
C. inornatus[b]	−3.159	0.533	26	|
C. neomexicanus[c]	0.390	0.261	13	|
C. neomexicanus[b]	1.241	0.339	20	|
C. marmoratus[b]	2.749	0.675	19	|
PC2:				
C. neomexicanus[b]	−1.441	0.626	20	|
C. inornatus[b]	0.146	0.984	26	|
C. neomexicanus[c]	0.278	1.038	13	|
C. marmoratus[b]	1.127	1.330	19	|

[a] Significant subsets defined by 0.05 level of probability. The 78 specimens are plotted in figure 5.
[b] Sample from the vicinity of Lordsburg.
[c] Sample from the vicinity of Peña Blanca.

tween two competing hypotheses about the hybrid origin of *C. neomexicanus*. Consequently, canonical discriminant analysis was used. We used the 10 characters from the three samples of the bisexual species (*marmoratus, inornatus,* and *sexlineatus*) to create two canonical discriminant axes maximizing the differences among the three taxa. We then computed the scores of the individuals from the two *neomexicanus* samples on these same, a priori, axes. As was the case with the PC analysis discussed above, the first CD axis explained most of the variation, 86 percent in this case. The loadings on the characters are shown in table 4. Figure 6 shows the individual specimen scores on these CD axes. *Cnemidophorus sexlineatus viridis* occupies a position on CD axis 1 similar to that of *C. inornatus,* and a position on CD axis 2 corresponding to lower scores than those of any of the other four samples. The geometry of the configurations is such that *sexlineatus* is not as plausible a parental species for *neomexicanus* as is *inornatus*. That is, on the reduced axis plot (using mature-size females only) of CD1 and CD2, *neomexicanus* samples are intermediate in position to either *inornatus* or *sexlineatus* on CD1, as compared with *marmoratus*. But on CD2, *neomexicanus* is identical to both *inornatus* and *marmoratus,* and different from *sexlineatus*. Thus, on the basis of the morphological data, *sexlineatus* is not as likely a possible parent in the hybrid origin of *neomexicanus* as is *inornatus*. Additionally, *sexlineatus* is ruled out on biochemical grounds, below.

We are aware that the kinds of morphological data we have discussed lend themselves to analyses of additional factors. Examples are comparisons of the degree of variability in samples of clonal versus bisexual *Cnemidophorus,* and degree of asymmetry in highly heterozygous versus homozygous organisms. These analyses will be presented elsewhere.

Among the few multivariate studies of *Cnemidophorus,* the only one particularly relevant to ours is that of Parker (1979). He performed a discriminant functions analysis on a related hybrid situation involving the unisexual *C. tesselatus* and the bisexual *C. septemvittatus* and *C. tigris* (=*C. marmoratus*). When a mixture of 13 size and scale count characters was used, Parker found the unisexual *tesselatus* samples to resemble one of the parents, *septemvittatus,* closely, rather than being intermediate. In separate analyses using size-related measurements and scale counts, Parker found that size was not particularly useful for discriminating among the parents, whereas the scale count characters did produce a useful discriminant function. In that latter case, the *tesselatus* samples closely resembled *marmoratus*. Consequently, it appears that in the case of the *Cnemidophorus* we studied, the multivariate analysis yields a set of axes on which the putative hybrids appear to be much more interme-

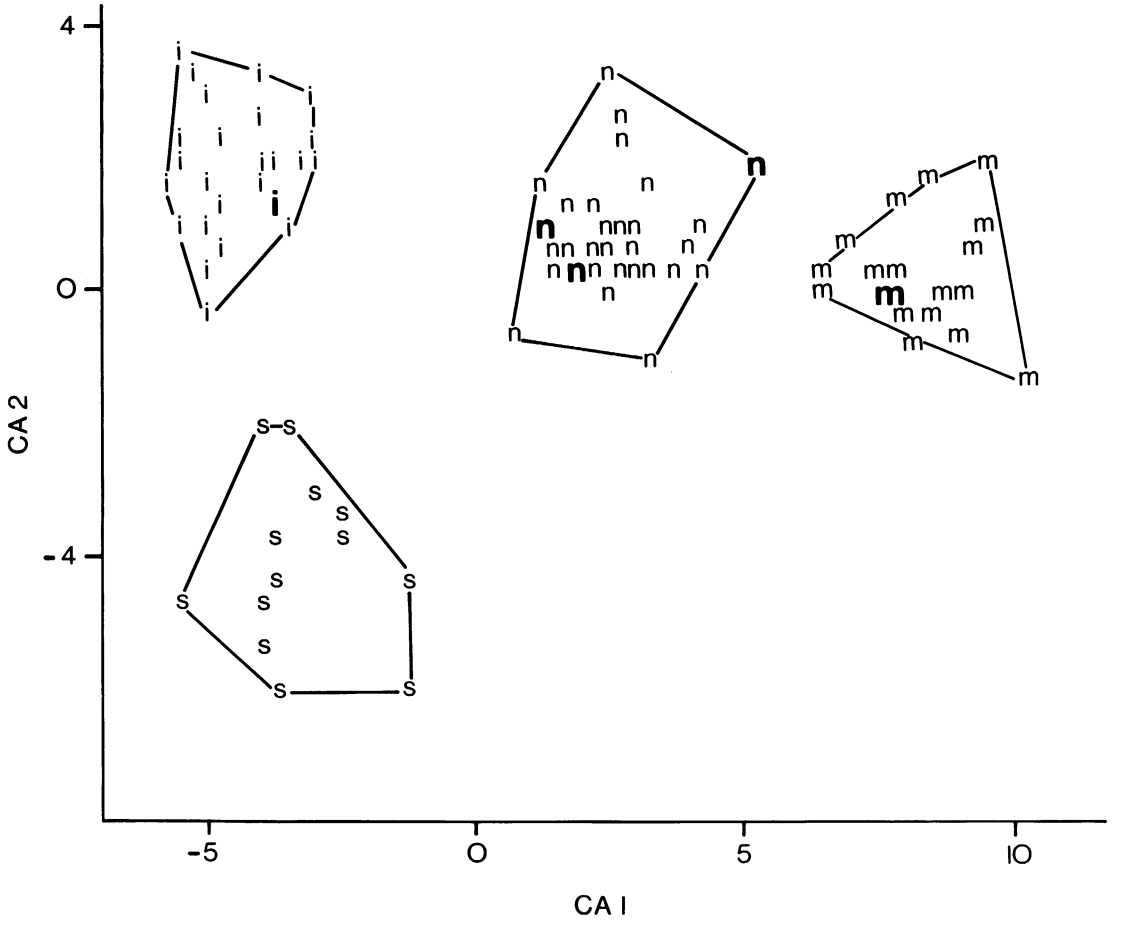

Fig. 6. Scores of 91 *Cnemidophorus* (five samples, four species) on the first two canonical discriminant axes extracted from the correlation matrix of 10 log-transformed morphological characters (tables 2, 4). Letters designating individuals are the same as in figure 5 (although the *neomexicanus* from Lordsburg and Peña Blanca cluster together here), with the addition of **s**, *C. sexlineatus viridis*.

diate in their scores than is the case in the only other such analysis to date, the *tesselatus* complex. In our study, the presumptive parental taxa, *C. inornatus* and *C. marmoratus*, differ in size to a greater extent than did the presumptive parental taxa in Parker's (1979) study. Parker interpreted the apparently counterintuitive results for *tesselatus* to be the result of dominance and overdominance interactions in the genomes of the hybrid. Such interactions are apparently not as prevalent in the *neomexicanus* genomes.

Additional Morphological Characters

In addition to the characters listed in table 2 and discussed above, we examined the following: (1) state of the preanal scales (as described by Lowe and Wright, 1964), which was usually Type I in all species and did not show variation of significance for this report; (2) number of rows of enlarged ventral scales, which was eight in all specimens of each species examined; and (3) whether the series of scales in the circumorbital semicircles was complete (illustrated for UAZ 11871 by Wright and Lowe, 1967: 20), nearly complete (one or two scales missing on either or both sides), or clearly incomplete (table 6). The circumorbital series usually is complete in *neomexicanus* (although more frequently in the Lordsburg sample than in those from Peña Blanca), was clearly incomplete in all 26 *inornatus*, and showed variation in *marmora-*

TABLE 6
Condition of Circumorbital Semicircle Scale Rows in Four Samples (three species) of *Cnemidophorus*[a]

Sample	Semicircles complete?		
	Yes	Nearly	No
C. inornatus[b]	0	0	100
C. marmoratus[b]	5	21	74
C. neomexicanus[b]	86	0	14
C. neomexicanus[c]	54	0	46

[a] Percent of specimens examined; samples the same as in table 2.
[b] Sample from the vicinity of Lordsburg.
[c] Sample from the vicinity of Peña Blanca.

tus, with complete series in 5 percent. Thus, this character in *neomexicanus* appears to have been influenced largely by *marmoratus.*

Karyotypes

Prior descriptions of the karyotype of *Cnemidophorus neomexicanus* were based on four females from Hidalgo and Bernalillo Counties, New Mexico, and stressed its hybrid (*C. marmoratus* × *C. inornatus*) nature (Lowe and Wright, 1966; Lowe et al., 1970b). In addition to examining the earlier material, for the present report we also examined chromosomes of 155 cells from 24 field-captured *C. neomexicanus* from four localities representing much of its range (fig. 1), including the Lordsburg and Peña Blanca localities.

All specimens had the same karyotype, which can be interpreted as follows, assuming diploidy as indicated by the count ($2n = 46$), but not assuming a hybrid origin (fig. 7): There are two pairs of Set I chromosomes (large biarmed macrochromosomes), 10 pairs of Set II chromosomes (medium size submetacentric, subtelocentric, and telocentric macrochromosomes), and 11 pairs of Set III chromosomes (microchromosomes, up to 11 of which appear biarmed in the clearest cells, although usually about 5 appear biarmed and the morphology of most is unclear). Most of the chromosomes can be arranged and visualized as representing homomorphic pairs (fig. 7), but the two pairs in Set I are heteromorphic no matter how they may be arranged. The largest two chromosomes are somewhat similar metacentrics but the smallest of them consistently bears a secondary constriction and elongate satellite. The second heteromorphic pair consists of a larger metacentric bearing a nearly terminal secondary constriction and dotlike satellite plus a somewhat smaller submetacentric chromosome.

This arrangement (fig. 7) of Sets I–III chromosomes plus the presence of two clearly heteromorphic pairs is unlike any karyotype occurring in the diploid and bisexual species of *Cnemidophorus* in North America (Lowe et al., 1970b). Thus, it was reasonable for

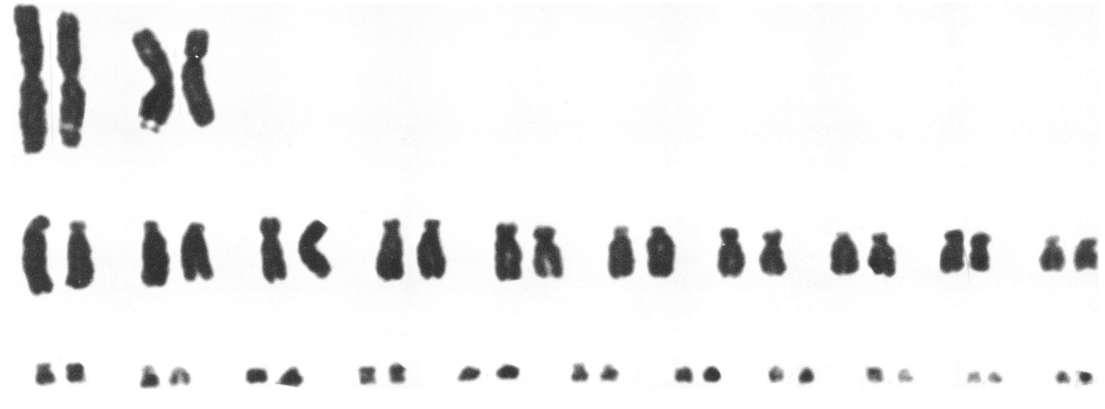

Fig. 7. Diploid karyotype of the unisexual *Cnemidophorus neomexicanus* ($2n = 46$, AMNH 112850, fig. 3C). Note that the two largest pairs are clearly heteromorphic in size and shape (positions of primary [centromere] and secondary [NOR] constrictions).

Lowe and Wright (1966) to compare the chromosomes of *C. neomexicanus* with those comprising the haploid complements of other species of which it could be of hybrid origin. We present a similar comparison (fig. 8), based on new material with improved resolution and a more complete understanding of chromosomal variation in *Cnemidophorus* than was available 20 years ago.

The haploid karyotype of all *C. tigris* and *C. marmoratus* from the southwestern United States consists of three clearly biarmed Set I macrochromosomes, eight biarmed (submetacentric to subtelocentric) Set II macrochromosomes, and 12 Set III microchromosomes, up to 13 of which appear biarmed (usually more than 5) in the clearest cells. The second largest chromosome, a metacentric, bears a nearly terminal secondary constriction and dotlike satellite, and in the diploid state this pair of chromosomes is homomorphic (Lowe et al., 1970b). The third largest chromosome is the sex chromosome, comprising a heteromorphic pair in the diploid state in males (XY, the Y having a longer short arm than the X) and a homomorphic pair in females (XX; Cole et al., 1969; Bull, 1978). We have confirmed this karyotype for *C. tigris* and *C. marmoratus* by examining 58 cells from nine individuals (additional to those reported previously), including one *C. tigris gracilis* and eight *C. marmoratus* (six of which were from the vicinity of Lordsburg).

The haploid karyotype of all *C. inornatus* from the southwestern United States consists of one metacentric Set I macrochromosome, 12 subtelocentric or telocentric Set II macrochromosomes, and 10 Set III microchromosomes, several of which are biarmed (up to five in the clearest cells, but usually only two). The largest chromosome bears a subterminal secondary constriction and somewhat elongate satellite, and in the diploid state this pair of chromosomes is homomorphic (Lowe et al., 1970b); there are no heteromorphic pairs. We have confirmed this karyotype for *C. inornatus* by examining 105 cells from 20 individuals more than those reported previously, representing five separate localities (with seven specimens from the vicinity of Lordsburg).

The chromosomes from a diploid cell of *C. neomexicanus* can be interpreted to include a haploid complement from *marmoratus* (including the X chromosome) and a haploid complement from *inornatus* (fig. 8). The only problem with this interpretation is the following: Although the karyotype of *marmoratus* is diagnostic for nearly all of the geographic area involved, that of *inornatus* is not; all diploid species of the *sexlineatus* species group have basically similar karyotypes (Lowe et al., 1970b).

Among the various species of the *sexlineatus* species group compared electrophoretically as possible alternatives to *C. inornatus* as the paternal parental species for *C. neomexicanus, C. sexlineatus* is most similar to *inornatus* (see electrophoretic material, below). With this in mind, we reviewed pertinent chromosome preparations for *C. neomexicanus, C. marmoratus, C. inornatus,* and *C. sexlineatus viridis* (six specimens of the last from Colorado and New Mexico), studying variation in centromere positions in Set II chromosomes because this is what varies among some bisexual species in the *sexlineatus* group (Bickham et al., "1976" [1977]; personal observ.). For 46 diploid cells of *C. marmoratus,* there was a mean of 15.0 clearly biarmed Set II chromosomes (range, 13–16), which would be 7.5 per haploid set. For 83 diploid cells of *C. inornatus,* there was a mean of 2.4 (range, 2–5), or 1.2 per haploid set. For 22 diploid cells of *C. sexlineatus,* there was a mean of 4.2 (range, 3–6), or 2.1 per haploid set. Thus, if *C. neomexicanus* has a complete unaltered haploid set from *marmoratus* plus one from *inornatus* it should have a mean of 8.7 (range, 7–11) clearly biarmed Set II chromosomes, or, alternatively, a mean of 9.6 (range, 7–11) with a haploid set from *sexlineatus.* The mean observed in 153 cells of *neomexicanus* was 8.3 (range, 6–11), which is most consistent with the *marmoratus* × *inornatus* hypothesis.

The secondary constrictions consistently observed on *Cnemidophorus* chromosomes (e.g., fig. 8) are the nucleolus organizer regions, and, consistent with the hybrid origin hypothesis, nucleolar dominance and incomplete dominance have been found in unisexual species, including *C. neomexicanus* (see Ward and Cole, 1986). Consistent with the clonal inheritance hypothesis, all *C. neomex-*

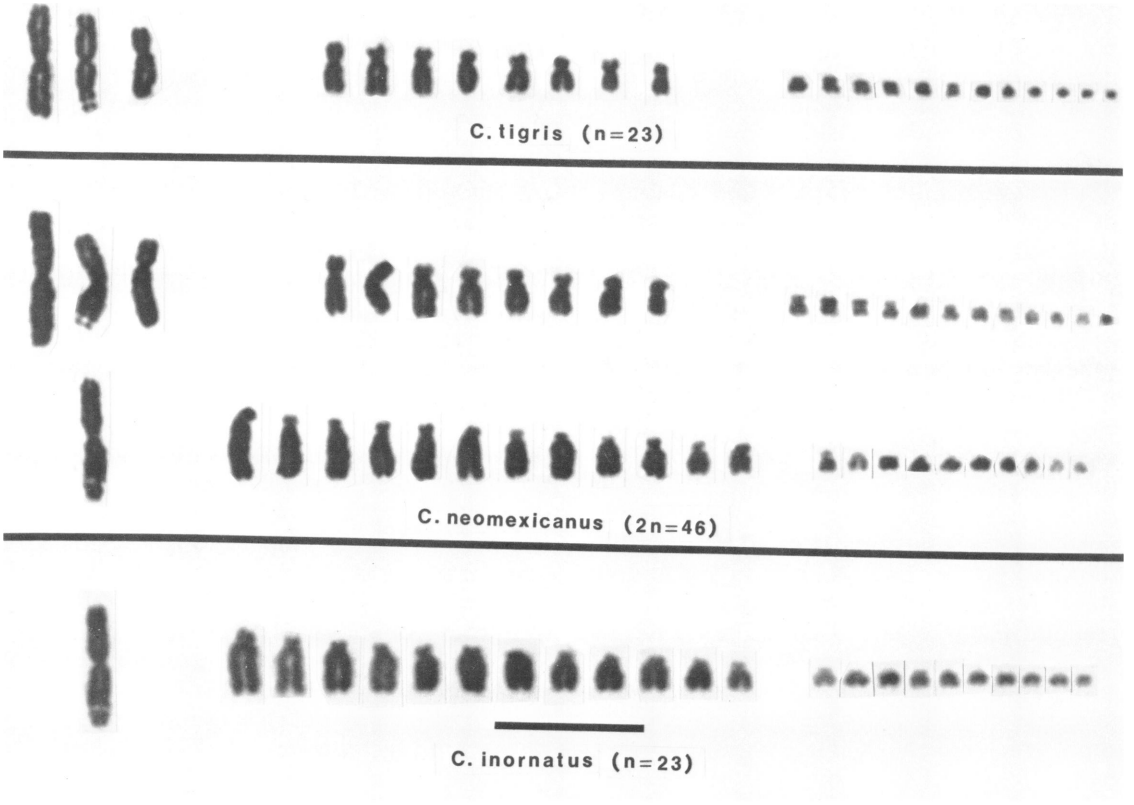

Fig. 8. Karyotypes of three species of *Cnemidophorus*. **Top,** *C. marmoratus* (labeled *C. tigris*; AMNH 112861), haploid state. **Bottom,** *C. inornatus* (AMNH 112843), haploid state. **Middle,** unisexual *C. neomexicanus* (AMNH 112850), diploid state, with a haploid set matching each of those of *C. marmoratus* and *C. inornatus*. Line represents 10 microns. Modified from Lowe and Wright (1966).

icanus we examined had the same karyotype, with fixed heterozygosities (figs. 7, 8), including specimens from the areas of Lordsburg, Peña Blanca, and localities in between, as well as the five laboratory-reared offspring examined to date from lizards from the areas of Lordsburg and Peña Blanca (which will be reported in more detail with others in a future paper).

Biochemical Genetics

Gene products determined by 47 presumptive loci were examined in tissues of 23 *Cnemidophorus neomexicanus* specimens and in its previously hypothesized parental species *C. marmoratus* (75 specimens) and *C. inornatus* (34 specimens). For comparative purposes, the same proteins were examined in samples of *C. sexlineatus viridis* (10 specimens), *C. septemvittatus* (5 specimens), and *C. gularis* (4 specimens), members of the same species group as *inornatus* (Lowe et al., 1970b). The proteins analyzed include 34 enzymes of 5 major classes plus 5 nonenzymic blood and 8 nonenzymic muscle proteins (tables 1, 7). Genotypes at all loci were scored for all 23 specimens of *neomexicanus* examined electrophoretically and at all or most loci in the remaining 128 specimens of the other species. Blood samples were not available for 17 (of the 47) *marmoratus* from the Lordsburg area and the 8 *marmoratus* from near Hatch, so the transferrin, albumin, prealbumin, and hemoglobin genotypes were not determined for those individuals.

The identification of prealbumin and all nonenzymic muscle proteins except myoglobin as products of specific loci is somewhat tentative. Prealbumins are identified as the most rapidly migrating proteins separated

during electrophoresis of plasma in alkaline buffers (fig. 10). Similarly, proteins present in high enough concentration in muscle homogenates to appear as sharp bands on gels stained with protein dyes are assumed to be products of different gene loci (fig. 11). The following enzymes, products of other specific loci, either migrate with or close to some of these muscle fractions: phosphoglucomutase, glutamate oxaloacetate transaminase-1 (*b* allele) and esterase-D (*a* allele) near muscle-2; adenylate kinase near muscle-3; esterase-D (*c* allele) near muscle-4; malate dehydrogenase-2 and creatine kinase-2 near muscle-5; glycerol phosphate dehydrogenase and glucose phosphate isomerase between muscle-6 and muscle-7. As the enzymes contribute only traces to the total protein migrating in these bands, we assume that each band probably represents the product of a different locus even though some enzymes may comigrate with them.

Some detectable proteins were not scored with sufficient consistency to be included in this report. Glutamate dehydrogenase was very active in liver but yielded unrepeatable patterns. Peptidase-D was successfully analyzed in fresh tissue; however, phenotypes obtained with tissues stored for long periods at ultracold temperatures consisted of smeared areas of activity, impossible to score reliably. Patterns of tissue aromatic esterases were too complex to score reliably, especially when using liver or kidney homogenates. Even with muscle, which has the simplest esterase pattern, analysis was difficult. A suggestion of this complexity is illustrated in figure 9 (bottom) by the three distinctly different phenotypes obtained for the four specimens of *C. inornatus*. Efforts to analyze the globin polypeptides of the hemoglobins by electrophoresis in formate buffer (Muller, 1960) were also unsuccessful; the lizard globins denatured rapidly in the highly acidic buffer.

Heterozygous phenotypes for a number of gene products allowed us to estimate the number of polypeptide subunits present in the active enzymes (table 7). The values obtained are based on the number and relative staining intensities of zones of activity (Dessauer and Braun, 1982; Dessauer et al., in press), and they are consistent with other *Cnemidophorus* with different levels of ploidy (Dessauer and Cole, 1984a). The opportunity for making such observations is especially great with *C. neomexicanus*, in which 16 of the 47 loci (34%) are heterozygous. Phenotypes of monomeric proteins in diploids with alleles in the heterozygous state commonly consist of two major bands of activity, instead of one band as seen in homozygotes (e.g., Es-1, fig. 9; Prealb and Tf, fig. 10; Pep-E, fig. 12). Phenotypes of dimeric proteins in heterozygotes consist of three major bands (e.g., Es-D, fig. 9) and those of tetrameric proteins are characterized by five major bands.

Table 7 lists genotypes usually observed for *C. neomexicanus* and the other five species compared here. Heterozygous genotypes that occurred rarely in a population sample of the bisexual species are footnoted but otherwise excluded from the tabulation (e.g., the specimen of *C. inornatus* with the *bc* genotype for transferrin; fig. 10); other polymorphisms (e.g., peptidase-A for *C. marmoratus*) are included in table 7. Alleles are listed alphabetically in order of decreasing anodal migration of allozymes in tissues of the six species. The letter w identifies the 24 presumptive loci that had identical patterns in all six species. Genotypes for the remaining 23 loci differed between species and/or within population samples of individual species. Phenotypes of heterozygotes were typical of those expected for autosomal loci of diploid species; however, quantitative assays will be needed to obtain definitive proof that all of these loci are autosomal in *Cnemidophorus*.

Species differences were detected in patterns of at least one locus in each of the five classes of enzymes and two groups of nonenzymic proteins (table 7). As has been commonly observed in a wide variety of taxa (Johnson, 1974; Smith et al., 1982), hydrolases were more variable than oxidoreductases. The maximum number of absolute differences between species pairs was at 5 of the 7 loci for hydrolases (*sexlineatus* vs. *septemvittatus*) and 6 of the 16 loci for oxidoreductases (*marmoratus* vs. *septemvittatus* or *gularis*). The lyases and nonspecific muscle loci had the most uniform phenotypes with only muscle-3 exhibiting interspecific differences among these 11 loci.

Genetic distances estimated between paired

TABLE 7

Genotypes[a] at 47 Presumptive Structural Gene Loci in Samples[b] of *Cnemidophorus*

Locus[c]	Sub-units[d]	NEO	MAR	INO	SEX	SEP	GUL
OXIDOREDUCTASES							
Aldh	2	*ac*	*aa*	*cc*	*bb*	*bb*	*bb*
Gpd	—	w	w	w	w[e]	w	w[e]
Sord	4	*cc*	*aa, ac, cc*	*cc*	*cc*	*aa*[e]	*bb*
Ldh-1	4	*ab*	*aa*	*bb*	*bb*	*bb*	*bb*
Ldh-2	—	w	w	w	w	w	w
Mdh-1	2	*aa*	*aa*	*aa*	*aa*	*bb*	*bb*
Mdh-2	2	w	w	w[e]	w	w	w
Me-1	—	w	w	w	w	w	w
Me-2	—	*aa*	*aa*	*aa*	*bb*	*bb*	*bb*
Icd-1	2	*bc*	*cc*[e]	*bb, bc, cc*	*bb*	*bb*	*bb, bc, cc*
Icd-2	2	w	w	w	w	w	w
Pgd	2	*bb*	*bb*	*bb*[e]	*bb*[e]	*ab, bb*	*bb*
Gapdh	—	w	w	w	w	w	w
Dia-NADP	—	w	w	w	w	w	w
Sod-1	2	*bc*	*bb*	*cc*	*cc*	*aa*	*aa, ac, cc*
Sod-2	—	w	w	w	w	w	w
TRANSFERASES							
Got-1	2	*ab*	*aa*	*bb*	*bb, ab*	*bb*	*bb*
Got-2	2	*bc*	*cc*	*bb, ab*	*bb*[e]	*bb*	*bb*
Ck-1	2	w	w	w	w	w	w
Ck-2	2	w	w	w	w	w	w
Ak	—	w	w	w	w	w	w
Pgm	1	*aa*	*aa*	*aa*	*aa*	*bb*	*bb*
HYDROLASES							
Es-1	1	*ab*	*bb*	*aa*	*aa*[e]	*cc*[e]	*cc, bc*
Es-D	2	*bd*[f]	*bb*	*bb*	*cc, ac, aa*	*bb*[e]	*bb*
Ap	—	w	w[e]	w	w[e]	w	w
Pep-A	2	*ad*	*cc, bc, cd, dd*[g]	*aa, ab*	*bb*	*cc*	*dd*
Pep-B	1	*ac*[h]	*aa, ab*	*bb*	*cc, bc, cd*	*aa, ab*	*aa*
Pep-E	1	*ab*[j]	*aa*	*bb*	*bb*	*aa*	*bb*
Ada	1	*ab*	*bb*	*aa*[e]	*bb*	*cc, cd*	*cc, bc*
LYASES							
Ald	—	w	w	w	w	w	w
Acon-1	—	w	w	w	w	w	w
Acon-2	—	w	w	w	w	w	w
ISOMERASES							
Mpi	1	*ac*	*aa, ac*	*cc, bc, bb*	*cc*	*cc*	*cc*
Gpi	2	*bb*	*aa, ab, bb*	*bb*	*bb*[e]	*bb*	*bb*
NONENZYMIC BLOOD PROTEINS							
Tf	1	*bc, ac*[i]	*bb*[e]	*cc*[e]	*bb*	*bb*	*bb*
Alb	1	*aa*	*aa*	*aa*	*bb*	*bb*	*bb*
Prealb	1	*ac*[j]	*aa, ab*	*cc*	*cc, ab*	*cc*	*aa*
Hb-1	—	w	w	w	w	w	w
Hb-2	—	w	w	w	w	w	w
NONENZYMIC MUSCLE PROTEINS							
Mb	—	w	w	w	w	w	w

TABLE 7—(*Continued*)

Locus[c]	Sub-units[d]	NEO	MAR	INO	SEX	SEP	GUL
Mus-1	—	w	w	w	w	w	w
Mus-2	—	w	w	w	w	w	w
Mus-3	—	*ab*	*bb*	*aa*	*aa*	*cc*	*cc*
Mus-4	—	w	w	w	w	w	w
Mus-5	—	w	w	w	w	w	w
Mus-6	—	w	w	w	w	w	w
Mus-7	—	w	w	w	w	w	w

[a] Alleles are designated in alphabetical sequence in order of decreasing anodal migration; w (wild type) indicates all samples were identical at the locus. Genotypes are listed in order of decreasing frequency of occurrence.

[b] NEO = *C. neomexicanus,* 23 specimens from four sites in New Mexico; MAR = *C. marmoratus,* 75 specimens from four sites in New Mexico; INO = *C. inornatus,* 33 specimens from two sites in New Mexico, two sites in Texas, and one in Arizona; SEX = *C. sexlineatus,* 10 specimens including one each collected in New Mexico and Colorado and 8 from southern Texas; SEP = *C. septemvittatus,* 5 specimens from western Texas; GUL = *C. gularis,* 4 specimens from western Texas.

[c] For multilocus systems, loci are numbered in order of decreasing anodal migration of their polypeptide products.

[d] Number of subunits per active enzyme is based on the number of bands observed on phenotypes for heterozygotes, or for interlocus hybrid isozymes observed in certain tissues in this or our other studies on *Cnemidophorus.*

[e] Rare heterozygotes were observed.

[f] The *d*-allele was found in all NEO but has not yet been observed in either MAR or INO.

[g] The *d*-allele frequency was highest in Rio Grande Valley populations of MAR.

[h] The *c*-allele was found in all NEO and most SEX but not in MAR or INO.

[i] The *a*-allele was found in three of the four NEO from San Antonio, New Mexico; all other NEO have the *bc*-genotype.

[j] Genotype previously reported incorrectly as *aa* (Dessauer and Cole, 1986), based on a different buffer.

groupings of the five bisexual species and two unisexual clones were calculated from the database of genotypes for the 47 loci (table 7), using the BIOSYS-1 program of Swofford and Selander (1981). The results are presented with Nei (1972) values below the diagonal and Rogers (1972) values above (table 8), although there are pitfalls with such indices (Hillis, 1984). The two indices give similar results, both indicating that *Cnemidophorus neomexicanus* is closest to and approximately equidistant from its putative ancestors, with *C. sexlineatus* being the next closest to the unisexual clones.

The distribution of alleles at the 47 loci among these species offers more convincing evidence than do the genetic distances for the hybrid origin of *C. neomexicanus* from mating(s) between *C. marmoratus* and *C. inornatus.* Of the 95 alleles identified in *neomex-*

TABLE 8

Genetic Distances[a] Among Seven Samples (six species) of *Cnemidophorus*

Sample	1	2	3	4	5	6	7
1 *neomexicanus*[b]	—	0.011	0.184	0.166	0.226	0.325	0.303
2 *neomexicanus*[c]	0.006	—	0.192	0.166	0.234	0.333	0.311
3 *marmoratus*	0.105	0.118	—	0.313	0.338	0.346	0.347
4 *inornatus*	0.099	0.099	0.350	—	0.185	0.326	0.307
5 *sexlineatus*	0.177	0.192	0.388	0.178	—	0.244	0.239
6 *septemvittatus*	0.325	0.341	0.399	0.368	0.263	—	0.105
7 *gularis*	0.293	0.309	0.396	0.359	0.257	0.091	—

[a] Rogers (1972) distance above diagonal, Nei (1972) distance below diagonal (BIOSYS-1 program of Swofford and Selander, 1981). Genotypic data from table 7.

[b] Clone with transferrin genotype *bc.*

[c] Clone with transferrin genotype *ac.*

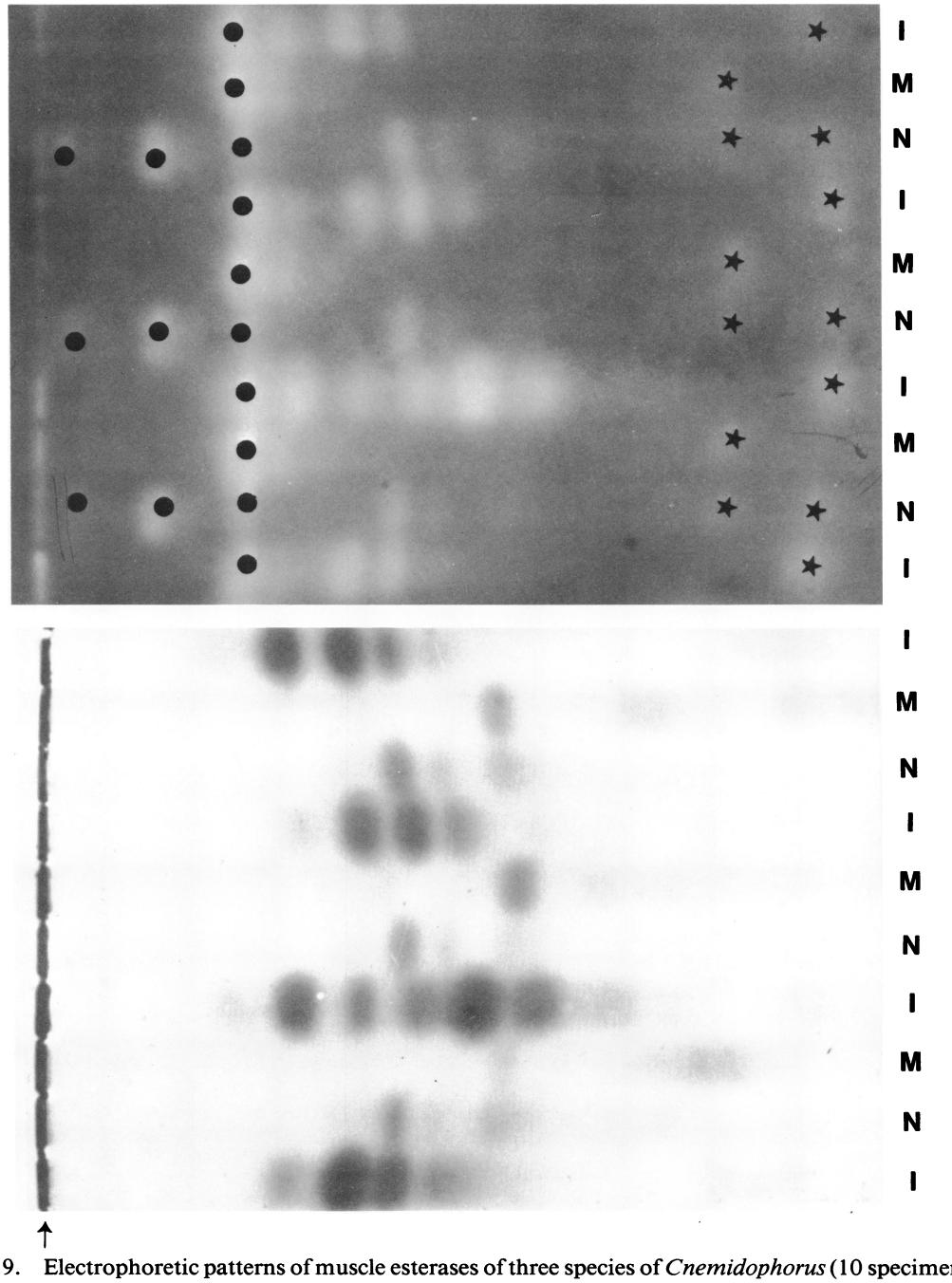

Fig. 9. Electrophoretic patterns of muscle esterases of three species of *Cnemidophorus* (10 specimens). Compare the patterns developed using 4-methylumbelliferyl acetate as substrate (**top**) with those obtained on the same gel slice using alpha-naphthyl acetate as the substrate (**bottom**). Note that Es-1 (monomeric; marked with stars) and Es-D (dimeric; marked with dots) do not catalyze the hydrolysis of the alpha-naphthyl acetate substrate. Electrophoresis in phosphate-citrate buffer, pH 6; arrow, site of sample application; **I,** *C. inornatus*; **M,** *C. marmoratus*; **N,** *C. neomexicanus*. Anode is to the right.

icanus, 92 (96.8%) were shared with *marmoratus* and *inornatus,* as follows (table 7): (1) the three species were identical for the invariant alleles (w) at 24 of the 47 loci ex-

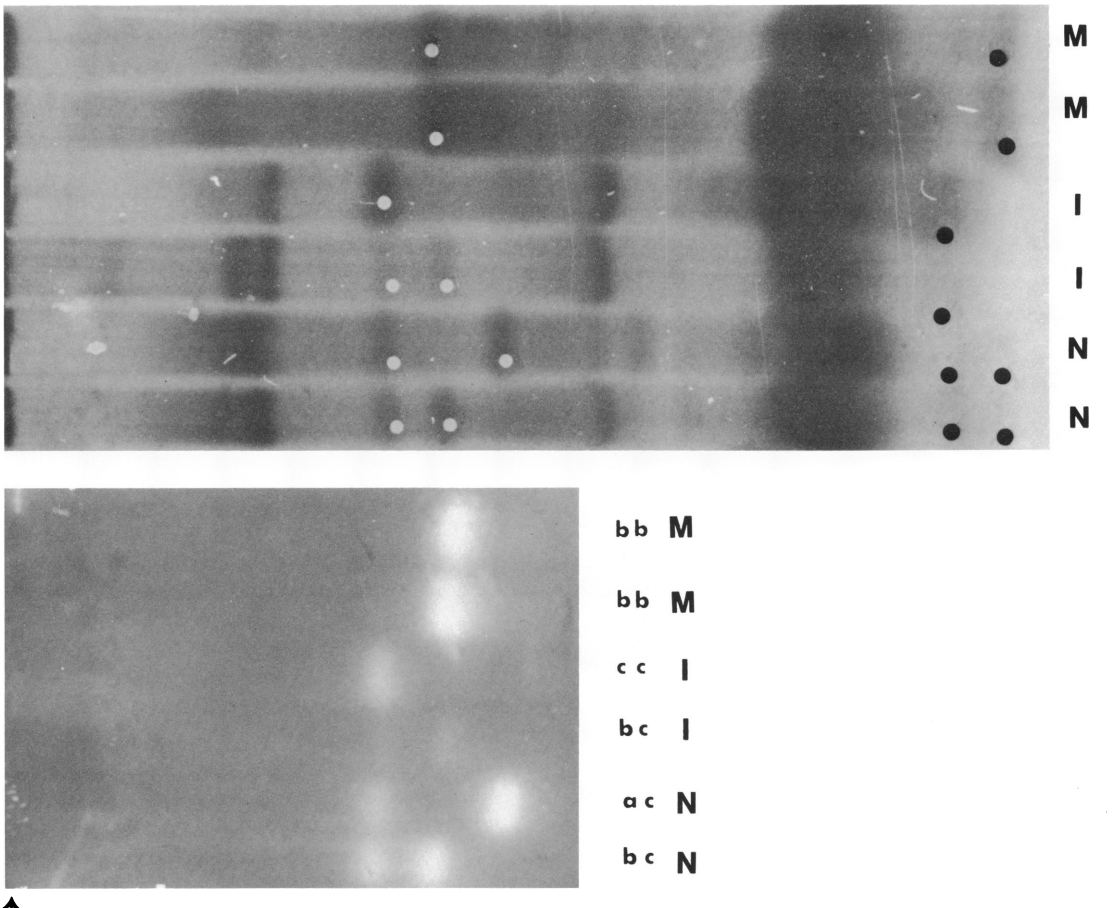

Fig. 10. Electrophoretic patterns of plasma proteins **(top)** of three species of *Cnemidophorus* (six specimens). Black dots identify prealbumins. White dots identify transferrins, localized by their positions on the iron-59 autoradiograph **(bottom)**. Genotypes of the transferrins, including the two clones of *C. neomexicanus,* are given to the right of the autoradiograph. Electrophoresis in a veronal buffer of pH 8.6. Symbols as in figure 9; anode is to the right.

amined; (2) at 4 additional loci (Mdh-1, Me-2, Pgm, Alb), *marmoratus* and *inornatus* were fixed for the same alleles, as was *neomexicanus*; (3) at 8 of the remaining 19 loci (Aldh, Ldh-1, Sod-1, Got-1, Es-1 [fig. 9], Pep-E [fig. 12], Ada, Mus-3 [fig. 11]), all *marmoratus* and all *inornatus* were homozygous for different alleles and all *neomexicanus* were heterozygous with one dose each of the *marmoratus* and *inornatus* alleles; (4) at 8 of the remaining 11 loci (Sord, Icd-1, Pgd, Got-2, Pep-A, Mpi, Gpi, Prealb [fig. 10]), genotypes for *marmoratus* and/or *inornatus* were polymorphic, yet *neomexicanus* was heterozygous for the most frequently observed allele of each bisexual species, or, in the case of the peptidase-A allele from *marmoratus,* the allele of relatively high frequency in certain populations of the bisexual ancestor; and (5) the heterozygous transferrin genotype for the majority of specimens of *neomexicanus* consisted of one allele common in *marmoratus* and the other in *inornatus* (fig. 10), but *neomexicanus* exhibited an unusual polymorphism at this locus (see below).

The two remaining loci to compare in *C. marmoratus, C. inornatus,* and *C. neomexicanus* are esterase-D and peptidase-B. These loci, plus a variant transferrin found in only three *neomexicanus,* include the three alleles found in *neomexicanus* but not in any specimens of *marmoratus* or *inornatus.* Unlike

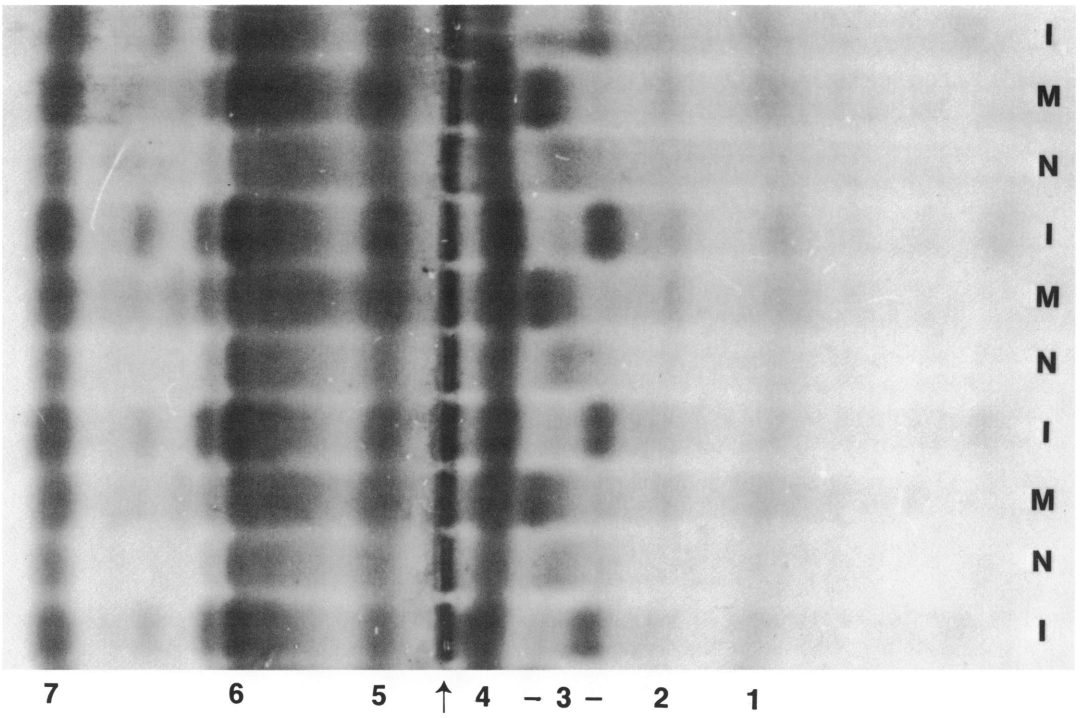

Fig. 11. Electrophoretic patterns of muscle proteins of three species of *Cnemidophorus* (10 specimens). Positions of products of presumptive muscle loci are identified by the numbers below the photograph. Bands between Mus-6 and Mus-7 probably represent Gpi and Gpd (see text). Electrophoresis in a phosphate-citrate buffer of pH 6. Symbols as in figure 9; anode is to the right.

the transferrin *a* allele that was present in one dose in only three *neomexicanus* specimens from one locality sample of four individuals (fig. 10), the *d* allele of esterase-D (fig. 9) and the *c* allele of peptidase-B (fig. 12) were found in one dose in every *neomexicanus* examined. Turner (1982) designated such alleles, present in a unisexual form but not found in its putative bisexual parents, as orphan alleles. If the ancestors are correctly identified, the presence of an orphan allele in the genome of a unisexual form may be due to: (1) inadequate sampling of extant populations of the putative bisexual progenitors; (2) the loss of an allele that had been present in populations of the bisexual form at the time of origin of the unisexual; or (3) a mutation within the unisexual species.

At the esterase-D locus, all *marmoratus* and all *inornatus* were fixed for *bb,* while all *neomexicanus* were *bd*; we have not seen this *d* allele product in any other *Cnemidophorus* examined to date, and its source remains obscure. At the peptidase-B locus, most *marmoratus* were fixed for *aa,* most *inornatus* were fixed for *bb,* and all *neomexicanus* were *ac.* Thus, the *c* allele in *neomexicanus* probably was inherited from *inornatus* (or mutated from the *inornatus b* allele), which is consistent with the occurrence of the *c* allele in the closely related *C. sexlineatus* (table 7). At the transferrin locus, nearly all *neomexicanus* had *bc,* consistent with the *bb* in most *marmoratus* and *cc* in most *inornatus.* The variant in *neomexicanus* occurred in three of four specimens from the vicinity of San Antonio, having *ac*; the *a* allele replaces the typical *b* allele of *marmoratus.* The *a* allele for *neomexicanus* transferrin in the vicinity of San Antonio appears to be a local mutant of the original *marmoratus b* allele because an adjacent sample of 10 *marmoratus* all had the typical *bb* condition, we have not seen this *a* allele product in any other *Cnemidophorus,* and the typical *bc neomexicanus* also occurs at the same locality.

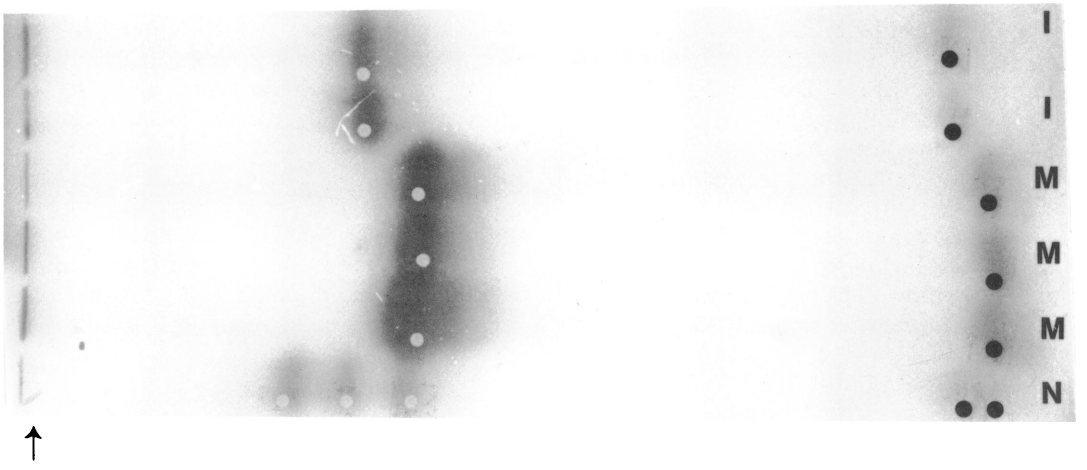

Fig. 12. Electrophoretic phenotypes of peptidase-B (dimeric; white dots) and peptidase-E (monomeric; black dots) localized with leucyl·glycyl·glycine as substrate. The allozyme of slowest anodal mobility of the Pep-B phenotype of *C. neomexicanus* is determined by the orphan *c* allele. Muscle homogenates subjected to electrophoresis in phosphate-citrate buffer pH 6. Symbols as in figure 9; anode is to the right.

Summarizing, of the 47 loci examined, *C. neomexicanus* typically shares its alleles with *C. marmoratus* and *C. inornatus* at 45 loci. At the remaining two loci, esterase-D and peptidase-B, one of the alleles in *neomexicanus* is shared with one or both bisexual ancestor(s) and the other is an orphan allele. The only other orphan allele in the *neomexicanus* we studied is the transferrin *a* allele, known in only one dose in three of the four specimens from San Antonio; this may be a local mutant.

Excepting the unusual transferrin *a* allele in some of the *C. neomexicanus* from San Antonio, all 23 *neomexicanus* we examined, from four different areas (Lordsburg, San Antonio, Bernalillo, Peña Blanca; fig. 1) involving about 480 linear km of range, were identical. In addition to the 47 loci discussed above, Dessauer determined that 12 of these *neomexicanus* specimens, selected to represent all population samples and both transferrin clones from San Antonio, were identical in their complex patterns of aromatic esterases, again suggesting their derivation from a single clone.

There is no clear evidence suggesting that the population at Lordsburg had a hybrid origin separate from the populations in the Rio Grande Valley. In this regard, one of the polymorphic loci in *C. marmoratus* may be instructive. At the peptidase-A locus, the *d* allele of *marmoratus* was present in all *neomexicanus*, including those from the vicinity of Lordsburg. However, the *d* allele is very rare (frequency less than 0.05) in *marmoratus* from the vicinity of Lordsburg, where the *marmoratus c* allele is nearly fixed. The *d* allele of *marmoratus* is much more frequent in populations in the Rio Grande Valley (0.20 at San Antonio; 0.44 at Hatch). Consequently, if present-day allele frequencies are similar to those at the time of origin of *neomexicanus,* we would predict that the initial *marmoratus* × *inornatus* hybridization occurred in or near the Rio Grande Valley; and the populations of *neomexicanus* around Lordsburg resulted from westward dispersal and colonization. If a recent, separate hybrid origin of *neomexicanus* had occurred in the vicinity of Lordsburg, that clone most likely would bear the *marmoratus c* allele for peptidase-A, not the *d* allele; in addition, its alleles at esterase-D and peptidase-B would match those of the local *marmoratus* and *inornatus,* rather than include the orphan alleles characteristic of all the *neomexicanus* from the Rio Grande Valley.

Cnemidophorus tigris gracilis of extreme southwestern New Mexico is unlikely as the *C. neomexicanus* ancestor instead of *C. marmoratus* because *gracilis* differs from *mar-*

moratus at several loci (Es-1, Pep-B, Tf, Pro) and in each instance all *neomexicanus* have the *marmoratus* allele (Dessauer and Cole, 1984b and unpubl. data). Mitochondrial DNA also points to *marmoratus* instead of *gracilis* as an ancestor of *neomexicanus* (Brown and Wright, 1979).

Recently, Dessauer found buffers that give improved resolution for gene products at peptidase-E and prealbumin, necessitating correction of our earlier report (Dessauer and Cole, 1986) of homozygosity at these loci in *C. neomexicanus*; both show fixed heterozygosity in *neomexicanus* (table 7).

Reproduction of *Cnemidophorus neomexicanus*

Based on dissection of preserved specimens, several reports (e.g., Medica, 1967; Christiansen, 1971) contain information concerning size of egg clutches for *C. neomexicanus,* but there is only one report (Maslin, 1971) concerning viability of the eggs. Maslin focused on production of eggs by F_1 virgins prior to development of reliable methods of laboratory rearing, so his data are very sparse. For *neomexicanus,* one from near Albuquerque, New Mexico, produced one F_1 offspring that reached adulthood and laid four eggs. Although none hatched, two clearly contained embryos when they failed (Maslin, 1971).

We maintained *C. neomexicanus* in captivity for 10 years and obtained 144 hatchlings in lineages from 10 P_1 females captured in the vicinity of Lordsburg and four P_1 females from the vicinity of Peña Blanca. Forty of these hatchings, representing both localities, were of the F_2, F_3, or F_4 generation and from mothers that had been raised in captivity without any contact with males. There is no question that females of *C. neomexicanus* from both the Lordsburg and Peña Blanca areas can produce viable offspring.

Each of our many laboratory offspring in which the sex has been determined is a female. As with *Cnemidophorus exsanguis* (see Hardy and Cole, 1981), the reproductive tracts and associated organs of some of our laboratory-reared *C. neomexicanus* are being investigated histologically (Hardy and Cole, in prep.), and preliminary observations indicate that these are typical females in their anatomy and histology. In addition, a strict clonal pattern of inheritance of alleles detected by protein electrophoresis was recently demonstrated among these lizards (Dessauer and Cole, 1986). Thus, there is substantial evidence that the *neomexicanus* we have been studying are not newly formed F_1 hybrids; indeed, they represent a self-perpetuating, parthenogenetic, clonal entity, of which a few variant clones are known.

SUMMARY, CONCLUSIONS, AND SCENARIO ON THE HYBRID ORIGIN OF *CNEMIDOPHORUS NEOMEXICANUS*

All data presented above are most reasonably interpreted to imply that *C. neomexicanus* is of hybrid origin between *C. marmoratus* × *C. inornatus* rather than suggest an alternative explanation, even though one esterase-D allele and one peptidase-B allele present in all *neomexicanus* examined were not found in the ancestors examined to date (2 out of 94 alleles scored in *neomexicanus,* ignoring for now the local variant transferrin allele in some from San Antonio). Two alternative explanations could be: (1) *neomexicanus* has a combination of traits not indicative of being of hybrid origin; and (2) *neomexicanus* is of hybrid origin but has one or two ancestors different from those previously suggested.

The following observations support the conclusion that *neomexicanus* is of hybrid origin:

(1) Most gene loci bear alleles in the homozygous state in the bisexual species of *Cnemidophorus* studied by protein electrophoresis; indeed, typically about 5 percent of the loci scored per individual show alleles in the heterozygous state (e.g., Dessauer and Cole, 1984a), although heterozygosity is higher in hybrid zones if the hybridizing forms have electrophoretically detectable differences to either side of the zone (e.g., Dessauer and Cole, 1984b).

(2) The level of electrophoretically detected heterozygosity in *neomexicanus* is about 34 percent (table 7; Dessauer and Cole, 1984a, 1986)—far higher than is known for any nonhybrid reptiles (e.g., Nevo et al., 1984).

(3) The karyotype of *neomexicanus* shows more heteromorphic pairs of chromosomes than have been found in any bisexual and nonhybrid *Cnemidophorus*.

(4) The chromosomes of *neomexicanus* are most readily interpreted as representing one haploid set ultimately derived from *C. marmoratus* and one from a bisexual species in the *sexlineatus* species group (Lowe et al., 1970b).

(5) The complete combination of traits observed in *neomexicanus* can be attributed to hybridization between certain known bisexual species of *Cnemidophorus* having geographically and ecologically relevant distributions.

The following observations support the conclusion that *C. marmoratus* and *C. inornatus* in particular are the ancestors of *C. neomexicanus*:

(1) Other than three orphan alleles discussed below, we studied products of 92 alleles electrophoretically in *neomexicanus* (counting heterozygous and homozygous loci scored), and both alleles at each locus matched those found in either or both *C. marmoratus* and *C. inornatus*.

(2) One of the orphan alleles of *neomexicanus*, transferrin *a*, occurred in some (not all) specimens from the area of San Antonio, New Mexico, and this may be the result of a local mutation, as may be also the only local variant orphan allele (malate dehydrogenase-1) reported by Parker and Selander (1984), in a sample from 24.2 km W Los Lunas, Valencia County, New Mexico. As the *inornatus c* allele for transferrin is present in the individuals having the atypical *a* allele, the mutation appears to have occurred in the *marmoratus b* allele.

(3) The other orphan alleles we found in *neomexicanus*, esterase-D *d* and peptidase-B *c*, cannot be so readily proposed as local mutations; they occurred in all 23 individuals from all localities sampled. However, geographic variation in some alleles is known within bisexual species (e.g., peptidase-A in *C. marmoratus*; see above), so these two orphan alleles may occur in one of the many untested populations of one of the ancestors, or they may now be rare or extinct in the ancestor. Because *inornatus* is a member of the *sexlineatus* species group and very similar to *sexlineatus* (which occurs in grassland to the east of *inornatus*) and because we found the *c* allele of peptidase-B in *sexlineatus* (possibly inherited from its common ancestor with *inornatus*), we predict that this *c* allele in *neomexicanus* was inherited from *inornatus* rather than *marmoratus*; the *a* allele at this locus in *neomexicanus* is similar to that of *marmoratus*.

(4) In addition to the consistency of the electrophoretic data with identifying *C. marmoratus* as one of the ancestors, the haploid karyotype of this species is present in *neomexicanus*.

(5) Considering the other geographically relevant and extant bisexual species of *Cnemidophorus*, the other haploid karyotype in *neomexicanus* might have been contributed by *C. septemvittatus, C. gularis, C. sexlineatus*, or *C. inornatus*. However, the number of biarmed Set II chromosomes in *neomexicanus* suggests that *sexlineatus* was not involved.

(6) The electrophoretic data show that, genotypically, *inornatus* fits the second ancestor for *neomexicanus* substantially better than any of these other species. The next best fit is with *C. sexlineatus*, but it is mismatched at seven loci (table 7).

(7) Observations on preferred habitats, geographic distributions, and external morphology, while not as clearly interpreted in terms of genetic determination of the characters, also are consistent with and strongly favor the *C. marmoratus* × *C. inornatus* hybrid origin hypothesis for *C. neomexicanus*. Indeed, the overall fit of the various types of characters to this hypothesis is too great to attribute to chance or experimental error.

The data with the most reliable genotypic interpretation (electrophoretic and karyotypic) indicate that *neomexicanus* maintains a suite of characters that represents F_1 hybrids, excepting perhaps a few mutations (e.g., the transferrin *a* allele). This is consistent with the data from laboratory propagation, indicating that *neomexicanus* normally reproduces by parthenogenetic cloning. Also, electrophoretically and karyotypically the *neomexicanus* specimens from the vicinity of Lordsburg (southwestern New Mexico) cannot be distinguished from those of the Rio Grande Valley, and they lack the peptidase-A

c allele of common occurrence (frequency greater than 0.95) in the Lordsburg *marmoratus* (*neomexicanus* having the *d* allele, which is more common in *marmoratus* samples from the Rio Grande Valley, the frequency being as high as 0.44 at Hatch). In addition, if *neomexicanus* had a separate and recent hybrid origin in the Lordsburg area, it is most probable that both of its alleles at the esterase-D and peptidase-B loci would match those of the local *marmoratus* and *inornatus*. Instead, the entire genotype we examined for the *neomexicanus* samples from Lordsburg is identical to that found in all other specimens (excepting the variant transferrin clone from San Antonio). Thus, the *neomexicanus* lizards of the Lordsburg area probably colonized the area following dispersal from the Rio Grande Valley.

Establishment of a desertscrub corridor, even if somewhat patchy, and particularly involving invasion or reinvasion of creosote bush (*Larrea*) to connect Chihuahuan Desert and Sonoran Desert populations, has occurred recently in geological time, the most recent such event being postglacial and within the last 5400 years (Van Devender et al., 1984). We have no reason to think that the modern populations of *C. marmoratus* and *C. neomexicanus* in the Lordsburg area predate this event.

Very few distinctive clones are yet recognized within *C. neomexicanus*. Morphological differences (size and scutellation) between Lordsburg and Peña Blanca samples, and between samples we report here and those reported by Wright and Lowe (1967), could indicate genetic differences, but this is not yet clear. We did not find any karyotypically distinctive clones among samples representing hundreds of linear kilometers of the range of *neomexicanus*, and Cuellar (1977) found only one indication of a variant histocompatibility clone in the northern half of its range. Indeed, Cuellar (1977: 29) reported that "over 99% of the 132 grafts interchanged among three populations extending over 160 miles [257.6 km] through the range of this species were permanently retained."

The few clones clearly recognized within *neomexicanus* are based on allelic differences indicated by protein electrophoresis. There are three such clones: (1) the common one occurring at the extremes of the range sampled and at all but one locality in between, with the *bc* genotype for transferrin—probably the same common clone studied by Parker and Selander (1984); (2) in the vicinity of San Antonio, Socorro County, New Mexico, we found the common and widespread clone as well as one with a variant transferrin *a* allele; and (3) at 24.2 km W Los Lunas, Valencia County, New Mexico, all 35 specimens tested by Parker and Selander (1984) had one variant malate dehydrogenase-1 allele, whereas all other alleles were identical to those in all other *neomexicanus* they studied. The variant transferrin *a* allele, in place of the *marmoratus* allele in some *neomexicanus* we examined from San Antonio, may represent a local mutation event within *neomexicanus*, because it was not found in all individuals, it was not found in a sample of 10 *marmoratus* collected nearby, and otherwise these individuals appeared identical to all other *neomexicanus* examined. Because the variant Mdh-1 allele was found also in a few *inornatus* (frequency, 0.013), albeit from another locality about 160 km from Los Lunas, Parker and Selander (1984) suggested it originated by a hybridization separate from that which created the widespread clone. If that is correct, we predict that those *neomexicanus* will be found to have the esterase-D and peptidase-B alleles consistent with those of the local *marmoratus* and *inornatus* rather than having the orphan alleles found in all of the *neomexicanus* we examined. Other loci that are known to be polymorphic in *marmoratus* (Sord, Pep-A, Mpi, Gpi, Prealb; table 7) and in *inornatus* (Icd-1, Got-2, Pep-A, Mpi; table 7) could prove to be useful indicators in future tests of whether certain populations of *neomexicanus* had separate hybrid origins.

Many unisexual species of *Cnemidophorus* exhibit clonal diversity in one or more character systems, such as color pattern, karyotypes, and electrophoretically detected alleles (Dessauer and Cole, in press). *Cnemidophorus tesselatus* exhibits clonal diversity in all of these systems, including 12 electrophoretically distinct diploid clones (Parker and Selander, 1984). The relative paucity of clonal diversity in the diploid *C. neomexicanus* throughout a large portion of its range may

indicate it had one or a few rather recent origin(s).

The place of origin of *C. neomexicanus* remains unknown but some areas may be eliminated and others suggested for future research. Geographic variation in frequencies of the *marmoratus* peptidase-A alleles and the orphan alleles of esterase-D and peptidase-B in *neomexicanus* suggest eliminating the area of Lordsburg from further consideration and concentrating on the Rio Grande Valley (particularly considering that the northeastern outlier population at Conchas Lake, San Miguel County, New Mexico, was probably introduced; Leuck et al., 1981). The orphan allele *c* for peptidase-B occurred in all 23 specimens of *neomexicanus* with an allele (*a*) that occurred in all *marmoratus*; the *c* allele also is common in *C. sexlineatus viridis,* which is more closely related to *inornatus* than to *marmoratus.* Therefore, we suspect *neomexicanus* inherited that *c* allele from *inornatus.* The orphan *d* allele of esterase-D found in all *neomexicanus* might have been contributed by either parental species because all *marmoratus* and *inornatus* we examined had *bb* at the esterase-D locus, and we have not seen the *d* allele product in any other *Cnemidophorus* yet.

Searching for the origin of these orphan alleles could be difficult and futile. They might occur in extremely low frequency in either or both ancestral species; they might have become extinct in the ancestor responsible for them; or they might be the result(s) of ancient mutation(s) within *neomexicanus.* However, if the orphan alleles for both esterase-D and peptidase-B were to be found in the bisexual ancestors in one geographic area, this could be a strong indicator of the place of origin of *C. neomexicanus.* Our experience with peptidase-A is encouraging in this regard. The first samples we compared were from the Lordsburg area, where we found fixed *aa* alleles in *inornatus, cc* (initially) in *marmoratus,* and *ad* in *neomexicanus* (illustrated by Dessauer and Cole, 1984a: 185); *d* was on our list of orphan alleles in *neomexicanus,* but we predicted it would be found in *marmoratus* because the *a* allele in *neomexicanus* matched that of *inornatus.* While increasing sample sizes in the area of Lordsburg, we also sampled populations in the Rio Grande Valley, where we found the *d* allele first and in the highest frequency (0.44 in the area of Hatch) in *marmoratus.*

Biogeographically, a southern source of origin for *C. neomexicanus* is an attractive hypothesis. In New Mexico, Chihuahuan Desert species associated with creosotebush, such as *C. marmoratus,* have dispersed northward in rather recent times (e.g., Van Devender et al., 1984). It could well be that these times of shifting environments and habitats resulted in desert-grassland ecotones similar to those illustrated (fig. 2), resulting in the hybrid origin of *neomexicanus.* This newly formed parthenogen could have also dispersed northward, very efficiently colonizing the available ecotone and Rio Grande riparian habitats that were suitable for its survival. The 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. Backcross mating can result in the production of polyploids (Lowe et al., 1970a; Cuellar and McKinney, 1976; Cole, 1979; Dessauer and Cole, 1984a), at least some of which are sterile, so isolating mechanisms that minimize backcrossing during hybridization that produces parthenogens may be exceedingly important to the survival of clones of hybrids.

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