NATURAL HYBRIDIZATION BETWEEN THE TEIID LIZARDS *CNEMIDOPHORUS SONORAE* (PARTHENOGENETIC) AND *CNEMIDOPHORUS TIGRIS* (BISEXUAL)

CHARLES H. LOWE, JOHN W. WRIGHT, CHARLES J. COLE, AND ROBERT L. BEZY

Abstract

Lowe, Charles H. (Dept. Biological Sciences, Univ. Arizona, Tucson, Arizona 85721), et al., *1970. Natural hybridization between the teiid lizards* Cnemidophorus sonorae *(parthenogenetic) and* Cnemidophorus tigris *(bisexual). Syst. Zool., 19:114–127.*—Hybrid index analysis of two natural hybrids between the parthenogenetic *Cnemidophorus sonorae* and the bisexual *C. tigris* demonstrates that the hybrids more strongly resemble the maternal parent. Karyotypic analysis reveals that the hybrids are tetraploids having received three genomes from the maternal (triploid) species and one genome from the paternal (diploid) species. Examination of testicular material shows the formation of chromosomal bivalents and polyvalents, including quadrivalents. Karyotypic variation involving centric fission occurs in the maternal parent *C. sonorae*. The origin of various levels of polyploidy in the genus *Cnemidophorus* appears to be rather different from that occurring most frequently in plants. [Hybridization. Polyploidy. *Cnemidophorus*. Karyotypes.]

Formation of species in the whiptail lizard genus *Cnemidophorus* presumably has occurred generally by means of classical mechanisms of allopatric speciation. In addition, speciation has occurred through interspecific hybridization (Lowe and Wright, 1966a, b), which has provided the vehicle for an unusually large amount of evolution in the genus. Parthenogenesis and utilization of "weed" habitats are important cofactors in the survival of hybrid forms (Wright and Lowe, 1968). Furthermore, triploid species have evolved as a consequence of hybridization between diploid parthenogenetic forms and diploid bisexual forms (Lowe and Wright, 1966a, b). We report here on natural hybridization between a triploid parthenogenetic species (*Cnemidophorus sonorae*) and a diploid bisexual species (*Cnemidophorus tigris*), resulting in the production of tetraploid individuals in a "weed" habitat in southern Arizona.

HYBRID HABITAT

Two hybrids (*Cnemidophorus sonorae* × *C. tigris*) were collected July 2–3, 1966, at the SE base of Huerfano Butte on the Santa Rita Experimental Range, Pima County, Arizona. The locality is 27 airline miles SSE of Tucson. It is desert-grassland (mesquite type, Fig. 1) at an elevation of 3750 feet. Around the butte *Cnemidophorus tigris* is by far the most abundant whiptail; *C. sonorae* and *C. uniparens* occur in much fewer numbers and are largely restricted to riparian situations and open (non-mesquite) grassland.

The first hybrid was obtained while shooting a sample of lizards around the butte. Its general appearance was that of an aberrant *C. sonorae;* this combined with its possession of hemipenes suggested a hybrid. On the following day a second hybrid was noosed which provided the necessary living material for karyotypic analysis. This cytogenetic analysis verified the hybrid origin of the specimen (See KARYOTYPES below).

Today this locality is a hybrid habitat, in the sense of Anderson (1948, 1949), where the present desert-grassland has only recently appeared—mostly during the present century through a series of environmental changes before and after the turn of the century. In this hybridization of the habitat, the ecologic transformation has clearly favored desert species (Fig. 2). The importance of such hybrid habitats in hybridization and evolution in the genus

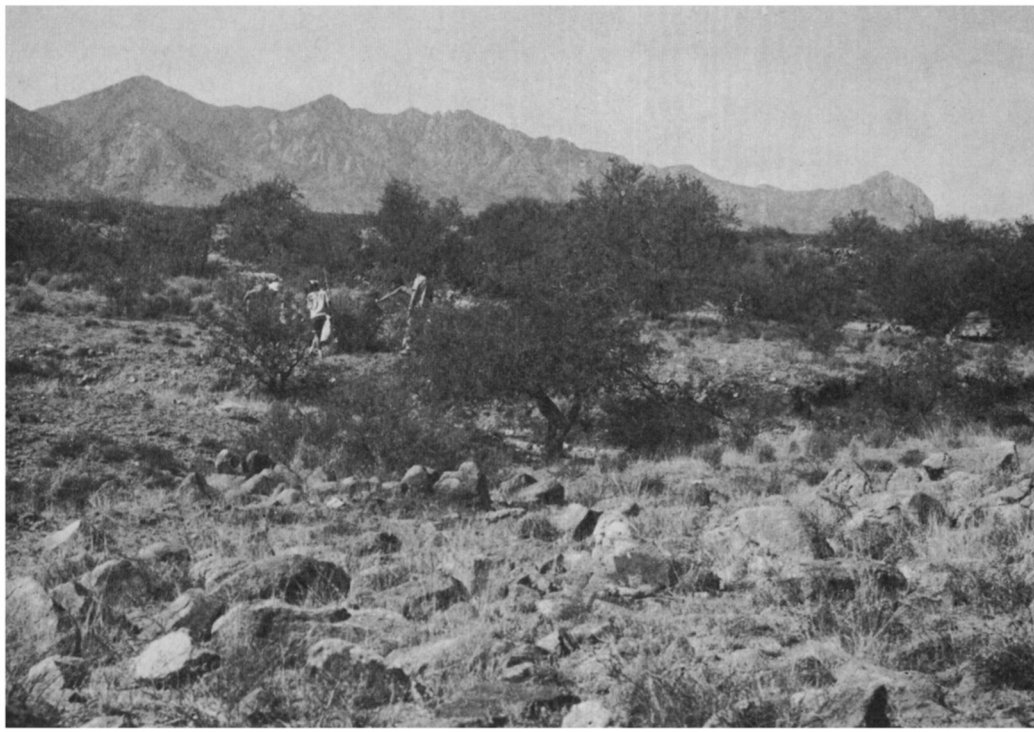


FIG. 1.—Desert-grassland hybrid habitat at south base of Huerfano Butte, Pima County, Arizona. Trees are primarily mesquites (*Prosopis juliflora*). Locality of hybridization of *Cnemidophorus sonorae* (parthenogenetic) and *C. tigris* (bisexual). Photo by Oscar H. Soule, July 3, 1966.

Cnemidophorus has been recently discussed elsewhere (Wright and Lowe, 1968).

HYBRID INDEX

The results of our investigation of the external morphology of the parental series of *Cnemidophorus tigris* (N = 51) and *C. sonorae* (N = 19) from Huerfano Butte, and the two hybrids obtained with them, are summarized in Tables 1 and 2. Table 1 provides the hybrid indexes for each of the two hybrids; these indexes are based on the data reductions that are given in Table 2 for the two parental species. The female species (*C. sonorae*) is set at 100, and the bisexual species (*C. tigris*) at 0, on the percent scale in the hybrid index of Hubbs, Hubbs, and Johnson (1943); see Wright and Lowe (1967).

Abbreviations are as follows: SAB, scales around body at ventral row 15; SPV, scales between the paravertebral light stripes; SPV/SAB × 100, ratio of above two characters; FP, femoral pores; TLS, toe lamellar scales; PBS/DS, postantebrachial scale diameter/dorsal scale diameter; MS/DS, mesoptychial scale width/dorsal scale diameter; COS, circumorbital semicircle scales; ILS, interlabial scales. Except for the ratios PBS/DS and MS/DS, used here for the first time, standardizations for the measurement of the characteristics above are discussed in Wright and Lowe (1967).

PBS/DS.—As an estimate of the degree of enlargement of the postantebrachials, the ratio (PBS/DS) of the diameter of these scales to that of the dorsal scales was calculated. The maximum diameter of the largest postantebrachial scale was measured to the nearest 0.06 mm, using an ocular micrometer. The size of the mid-dorsal scales (DS) was taken as the mode

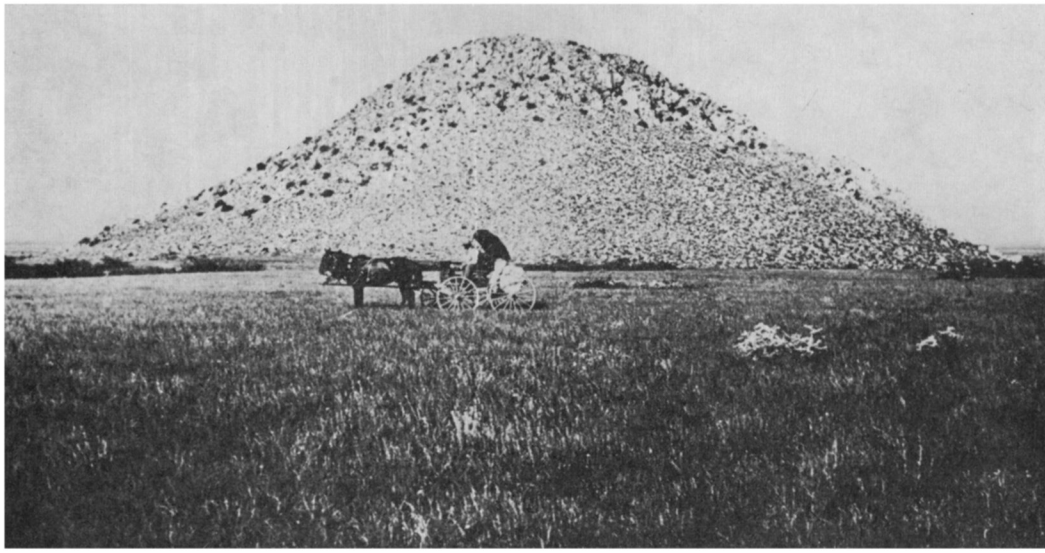
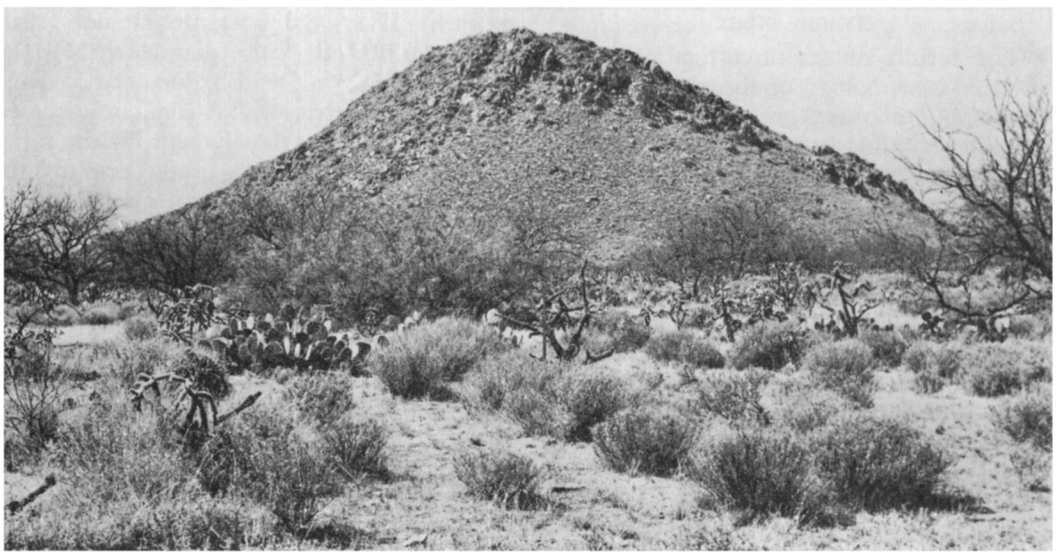


FIG. 2.—UPPER. Circa 1902. Looking WSW toward Huerfano Butte, Pima County, Arizona. Mesquite (*Prosopis juliflora*) is identifiable on the bajada, as is cane cholla (*Opuntia spinosior*). The conspicuous shrubs on the rock slope are primarily desert hackberry (*Celtis pallida*) and desert-thorn (*Lycium andersoni*). LOWER. March 16, 1969. Same view as above approximately 67 years later, showing marked vegetation change to well-defined desert-grassland at this hybrid locality. The trees, shrubs, and cacti (which, with the grasses, comprise 90–100% of the perennial cover) in the foreground are: mesquite (*Prosopis juliflora*), desert hackberry (*Celtis pallida*), burro-weed (*Aplopappus tenuisectus*), barrel cactus (*Echinocactus wislizenni*), prickly-pear (*Opuntia engelmanni*), cane cholla (*Opuntia spinosior*), and jumping cholla (*Opuntia fulgida*). Detail of the site of collection of the hybrids on the left base of Huerfano Butte is shown in Fig. 1. Photo by Charles H. Lowe.



of the maximum diameters of five body scales along the paravertebral stripe above the 15th ventral.

MS/DS.—The maximum width of the largest mesoptychial scale (MS) bordering the gular fold was measured to the nearest 0.06 mm, with an ocular micrometer. The ratio (MS/DS) of the size of the mesoptychials to that of the dorsal scales was then calculated; for measurement of DS, see above.

That both hybrids possess a phenotype significantly more similar to that of *C. sonorae* than to that of *C. tigris* is clearly evident in both their overall appearance (Fig. 3) and in their high hybrid indexes (Table 1). Such high hybrid indexes may be expected in this case, inasmuch as *C. sonorae* is a triploid parthenospecies and *C. tigris* is diploid. The calculated index values are 81% and 86%, based on nine morphological characteristics for each of two hybrids (Tables 1 and 2). This similarity of the tetraploid hybrid to its triploid female parent is largely due to the maternal contribution of three genomes in contrast to the paternal contribution of one genome. Further, it is undoubtedly this strong resemblance to one of the parents that has led to misinterpretation of hybrids as being males of all-female species of *Cnemidophorus*, as discussed below.

TABLE 1. HYBRID INDEXES FOR TWO MALE HYBRIDS (*C. sonorae* × *C. tigris*) AT HUERFANO BUTTE IN SOUTHERN ARIZONA.

Characteristic	*C. tigris*	Hybrid UAZ 24953	Hybrid UAZ 24954	*C. sonorae*
Sex	♂, ♀	♂	♂	♀ ♀
N	20–51	1	1	17–19
SAB[1]	—	—	—	—
SPV	0	142	103	100
SPV/SAB × 100	0	129	86	100
FP[1]	—	—	—	—
TLS	0	165	165	100
PBS/DS	0	43	58	100
MS/DS	0	90	90	100
COS	0	−25	+17	100
ILS	0	57	36	100
Color Pattern				
Dorsal	0	75	75	100
Ventral	0	100	100	100
Mean	0%	86%	81%	100%

[1] For each of two characteristics (SAB, FP), the difference between the means for the parental frequency distributions is *not* significant ($P > .20$; $P > .10$, respectively); therefore, a meaningful hybrid index cannot be established for these characteristics, and such values are not given.

KARYOTYPES

Preparations of chromosomes were made following Patton's (1967) hypotonic citrate, air-dried technique, slightly modified (Lowe, Wright, and Cole, 1966). Chromosomes were examined in detail in a total of more than 145 cells (bone marrow and testicular preparations) from 14 individuals of *C. tigris* and 5 of *C. sonorae*, plus 24 additional cells (bone marrow and testicular preparations) from a hybrid male (see list of specimens examined, below). These specimens include three of *C. tigris* and five of *C. sonorae* from the immediate vicinity of the Huerfano Butte hybrid locality.

We follow the karyotype terminology used for *Cnemidophorus* by Lowe and Wright (1966b); Set I = *large* metacentrics and submetacentrics, Set II = *medium* submetacentrics, subtelocentrics, and telocentrics, and Set III = *small* chromosomes (microchromosomes).

Cnemidophorus sonorae.—The Sonora spotted whiptail is a triploid unisexual ("all-female") species for which we have found thus far three karyotypes in the immediate vicinity of Huerfano Butte. Indeed, we have found minor intraspecific karyotypic variation to be the general rule specifically among the triploid all-female species of *Cnemidophorus*, which apparently tolerate chromosomal aberrations considerably more so than their diploid bisexual congeners.

The karyotypes of *C. sonorae* (Figs. 4–5) are composed basically of three haploid complements of ancestral species having karyotypes typical of the *sexlineatus* group. Karyotypes of such species and related ones [e.g., *C. gularis* (diploid, bisexual), *C. inornatus* (diploid, bisexual), and *C. uniparens* (triploid, unisexual)] were illus-

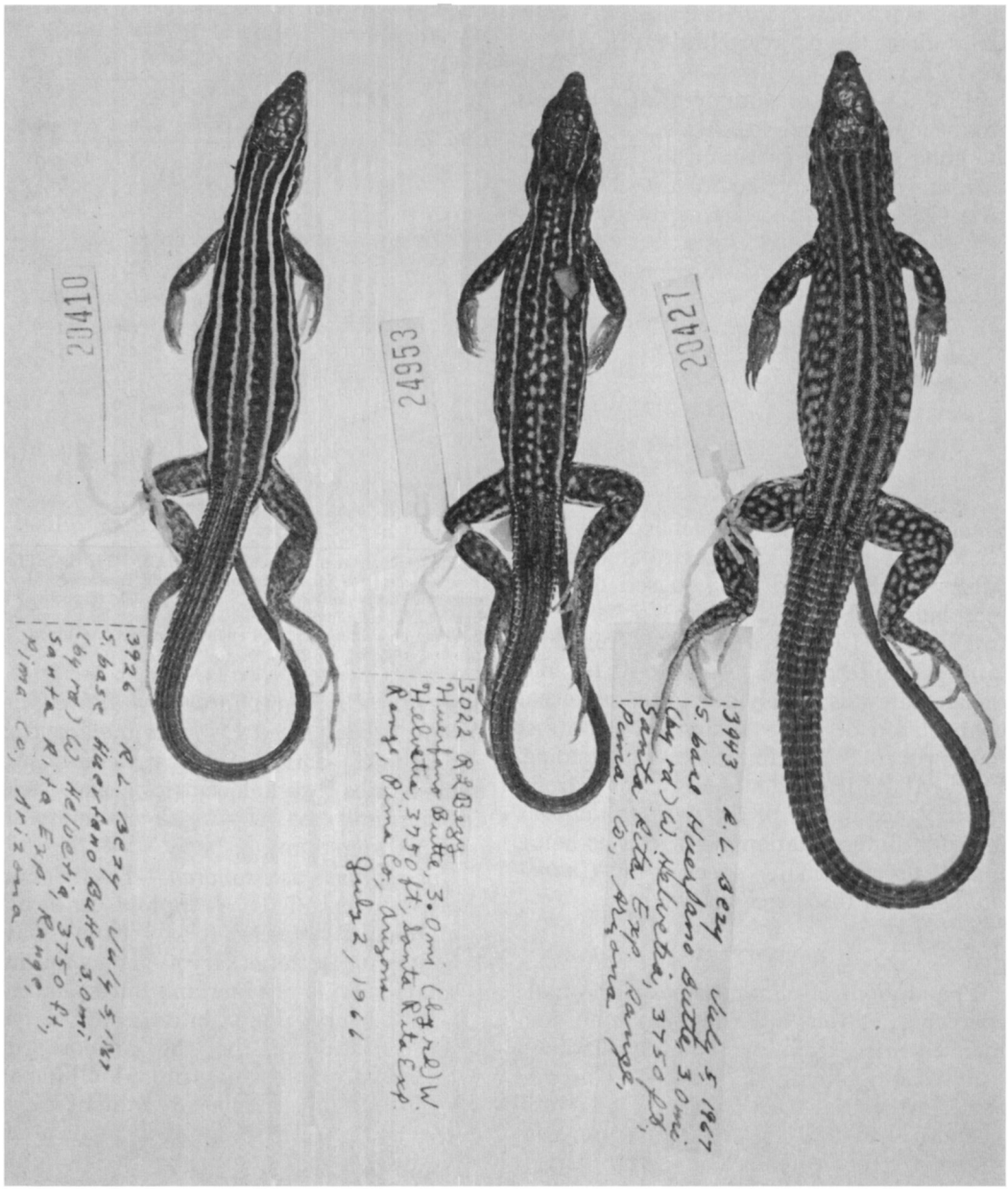


FIG. 3.—Left, parental ♀, *Cnemidophorus sonorae* (UAZ 20410); Right, parental ♂, *C. tigris* (UAZ 20427); Center, hybrid ♂ (UAZ 24953). All taken at Huerfano Butte, Arizona (see text for complete collection data).

trated and described by Lowe and Wright (1966a, b), who commented on the general similarities of karyotypes among species in the *sexlineatus* group. For each haploid complement there is one chromosome in Set I plus twelve in Set II plus ten in Set III, which is referred to as 1 + 12 + 10 ($n = 23$). The Set I chromosome

TABLE 2. REDUCED DATA FOR CHARACTERISTICS OF HYBRIDS AND THEIR PARENTAL SPECIES AT HUERFANO BUTTE IN SOUTHERN ARIZONA.[1]

Characteristic	*C. tigris*	Hybrid UAZ 24953	Hybrid UAZ 24954	*C. sonorae*
Sex	♂ ♀	♂	♂	♀ ♀
SAB	76.3 ± 0.61 68 – 85 $N = 49$	74	71	77.3 ± 0.47 73 – 80 $N = 19$
SPV	6.7 ± 0.16 4 – 9 $N = 51$	3	4	4.1 ± 0.27 2 – 6 $N = 19$
SPV/SAB × 100	8.78 ± 0.22 5.80 – 12.16 $N = 49$	4.0	5.6	5.08 ± 0.33 2.74 – 7.79 $N = 17$
FP	38.5 ± 0.43 32 – 46 $N = 49$	44	42	37.5 ± 0.59 33 – 41 $N = 17$
TLS	28.9 ± 0.26 25 – 32 $N = 47$	34	34	32.2 ± 0.32 29 – 34 $N = 17$
PBS/DS	1.35 ± 0.05 1.07 – 1.83 $N = 20$	2.2	2.5	3.32 ± 0.06 2.86 – 3.80 $N = 19$
MS/DS	1.56 ± 0.06 1.23 – 2.00 $N = 20$	2.8	2.8	2.94 ± 0.07 2.38 – 3.33 $N = 19$
COS	14.4 ± 0.27 12 – 19 $N = 48$	15	14	12.0 ± 0.21 11 – 14 $N = 18$
ILS	29.5 ± 1.02 12 – 44 $N = 51$	24	26	19.7 ± 0.41 17 – 24 $N = 19$
Color Pattern				
Dorsal	1.0	2.5	2.5	3.0
Ventral	1.0	3.0	3.0	3.0

[1] The mean ± its standard error (95% confidence limits) is given along with the range and sample size.

is a large metacentric bearing a terminal satellite; the Set II chromosomes are all telocentric or subtelocentric (the largest one in the Set having the most conspicuous short arm); and the Set III chromosomes are too minute to be described in detail though probably some (at least one) larger ones are bi-armed and the remainder are uni-armed.

The hypothetical triploid karyotype of this complement ($n = 23$, with $1 + 12 + 10$) is $3n = 69$, composed of $3 + 36 + 30$ chromosomes having the correspondingly expected morphology. While this is a typical karyotype for *C. uniparens* as illustrated by Lowe and Wright (1966a, b), each of the three known karyotypes of *C. sonorae* at Huerfano Butte deviates slightly from the hypothetical. That is, they are modified triploids, as follows:

(A) $3n = 70$ (Fig. 5, bottom), composed of $2 + 38 + 30$ chromosomes. Compared to the hypothetical, there is one chromosome less in Set I and there are two more in Set II. Of the two extras in Set II (Fig. 5, bottom), one bears a terminal satellite; this chromosome and satellite is of the same dimensions as the satellited arm of

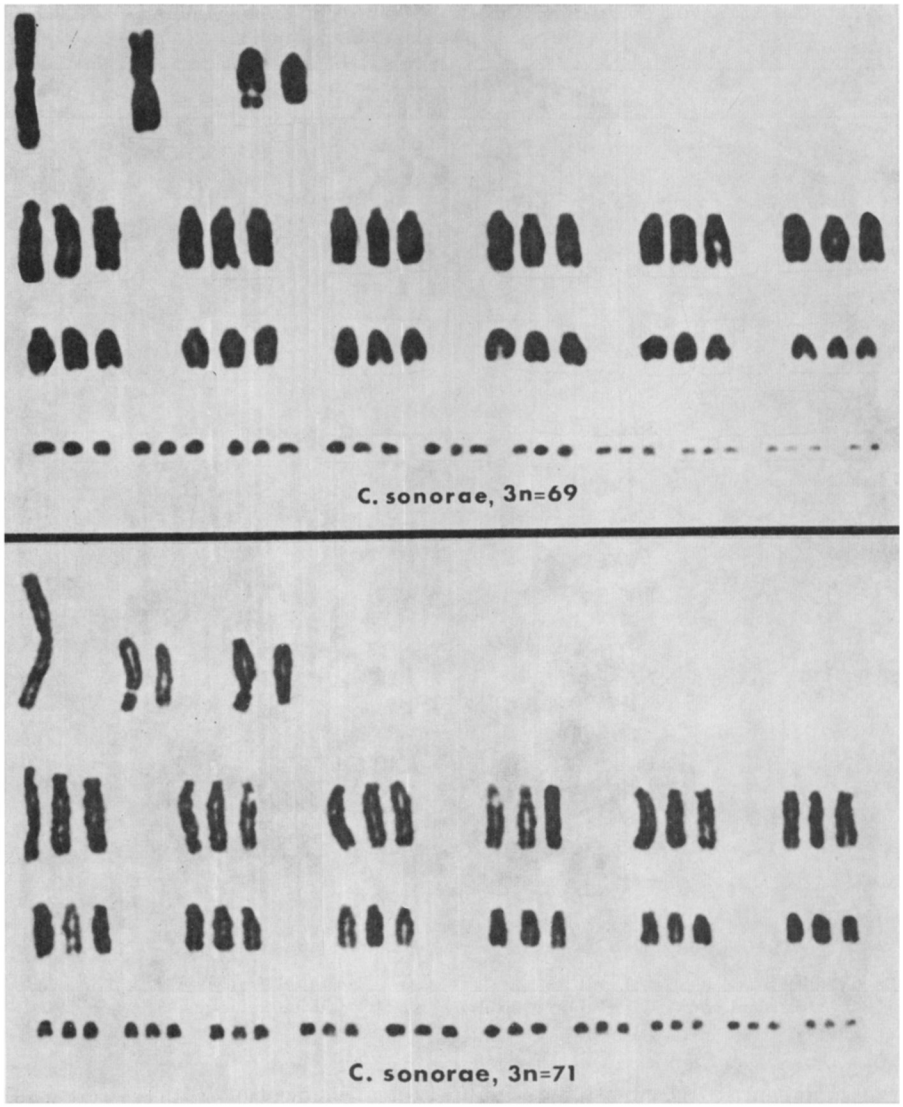


FIG. 4.—UPPER. Representation of a karyotype of *C. sonorae* from Huerfano Butte (UAZ 20398). This is a $3n = 69$ karyotype (B), composed of 2 + 38 + 29 chromosomes, having one satellited telocentric (top row) and only 29 microchromosomes (see text). LOWER. Representation of a karyotype of *C. sonorae* from Huerfano Butte (UAZ 18728). This is a $3n = 71$ karyotype (C), composed of 1 + 40 + 30 chromosomes, having two satellited telocentrics (top row) and the expected 30 microchromosomes (see text).

the Set I chromosomes, revealing that there had been a break in one of the Set I chromosomes (possibly involving true centric fission) into two, each consequently fitting the size category of Set II, causing both the gain of two chromosomes in Set II and the loss of one from Set I. Three of the five *C. sonorae* examined from the vicinity of Huerfano Butte had this karyotype.

(B) $3n = 69$ (Fig. 4, top), composed of 2 + 38 + 29 chromosomes. This karyo-

type is similar to that of (A), including the fission of one Set I chromosome, and, compared to the hypothetical, there is one less in Set III. The fate of the lost microchromosome (Set III) is unknown; it may have been accidentally lost (the ability to withstand such loss should be greater in triploids than in diploids) in an abnormal cell division (*e.g.*, by non-disjunction), or may have been involved in a translocation, perhaps associated with but following the centric fission discussed above. Regardless, the fission must have occurred first, historically, for it is typical also in the other karyotypes. One of the five *C. sonorae* examined from the vicinity of Huerfano Butte had this karyotype.

(C) $3n = 71$ (Fig. 4, bottom), composed of $1 + 40 + 30$ chromosomes. Compared to the hypothetical there are two chromosomes less in Set I and four more in Set II. Of the four additional ones in Set II (Fig. 4, bottom), two of similar size and shape bear similar terminal satellites, revealing that there have been two centric fissions of the nature of that described for karyotype (A), causing the karyotypic modifications from the expected $3n$ condition. One of the five *C. sonorae* examined from the vicinity of Huerfano Butte had this karyotype.

Cnemidophorus tigris.—The western whiptail is a diploid bisexual species having $2n = 46$, as has been illustrated (haploid complement) and described by Lowe and Wright (1966a, b). Its haploid karyotype (Fig. 5, top) is composed of $3 + 8 + 12$ chromosomes, of which most constituents of Sets I and II are morphologically distinguishable from those occurring in *C. sonorae*. In Set I, the first chromosome is an extraordinarily large metacentric (or nearly so), the second is similar to the largest in *C. sonorae* (the satellite itself, however, may be somewhat shorter) and the third is a submetacentric that is intermediate in size between the second chromosome in Set I and the largest (= first) in Set II. This third pair in Set I of *C. tigris* is heteromorphic (Cole, Lowe, and Wright, *in press*) in an X-Y [XY(♂):XX(♀)] fashion. The Y chromosome has a more median centromere than has the X, and it is the Y chromosome that is illustrated here (Fig. 5, top). In Set II, all of the chromosomes are clearly bi-armed; there are no uni-armed (= telocentric) elements, but all are submetacentric or subtelocentric, in contrast to the extreme subtelocentric to telocentric nature of the majority of the Set II chromosomes in *C. sonorae* (Fig. 5, bottom). In Set III, there are more bi-armed elements than in representatives of the *sexlineatus* group, but these microchromosomes also are too small for the various pairs to be characterized as to shape.

Cnemidophorus sonorae ♀ × *C. tigris* ♂.—The hybrid individual for which chromosomes were examined (UAZ 24954) is an adult male that is tetraploid with $4n = 93$ (Figs. 6–7). This karyotype is composed of $5 + 46 + 42$ chromosomes. This is precisely the karyotype expected from hybridization between the diploid *C. tigris* having $n = 23$, composed of $3 + 8 + 12$, and the triploid *C. sonorae* of the presumably commoner form (A) having $3n = 70$, composed of $2 + 38 + 30$ (see Figs. 5–7). Presumably, in hybridization, the bisexual male *C. tigris* would contribute a haploid complement and the unisexual female *C. sonorae* would contribute an unreduced triploid complement.

Key numerical and morphological characteristics of the tetraploid's karyotype (Figs. 6–7) that reveal its origin through hybridization between *C. tigris* and *C. sonorae* are as follows: (1) the tetraploid chromosome number ($4n = 93$) and the particular composition of $5 + 46 + 42$ chromosomes (compare Figs. 5–7); (2) the single unmistakable extraordinarily large Set I (first) chromosome of *C. tigris;* (3) the single, unmistakable small Set I (third) chromosome of *C. tigris* (the Y chromosome); (4) the occurrence of three (two from *C. sonorae* and one from *C. tigris*) chromosomes of the size category of the satellited Set I chromosomes (not all ex-

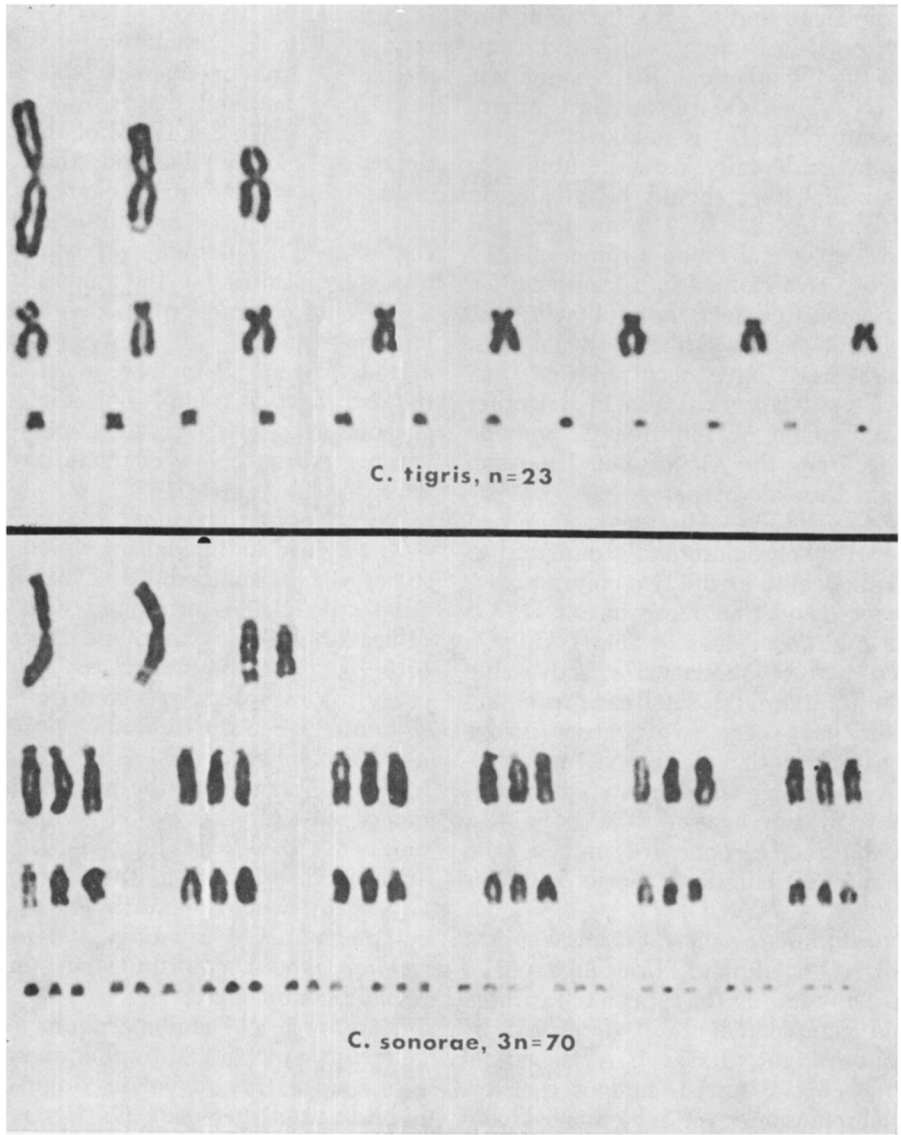


FIG. 5.—Representation of a haploid karyotype of *C. tigris* (top, UAZ 25239) and of a *C. sonorae* (bottom, UAZ 20400). The *C. tigris* has $n = 23$, composed of $3 + 8 + 12$ chromosomes. The *C. sonorae* is a $3n = 70$ karyotype (A), composed of $2 + 38 + 30$ chromosomes, having one satellited telocentric and the expected 30 microchromosomes. These two karyotypes taken together represent the "expected" for the tetraploid hybrid male having $4n = 93$ and the *C. tigris* Y chromosome (the third in Set I) as illustrated here (see Fig. 6 and text).

hibit the satellite, which we find to be generally the rule in polyploid *Cnemidophorus*); (5) the characteristic telocentric *C. sonorae* satellited chromosome that resulted from centric fission of a former Set I chromosome; (6) the presence of characteristic *C. tigris* bi-armed Set II elements (submetacentric and subtelocentric); (7) the presence in triplicate of the characteristic *C. sonorae* largest Set II chromosome;

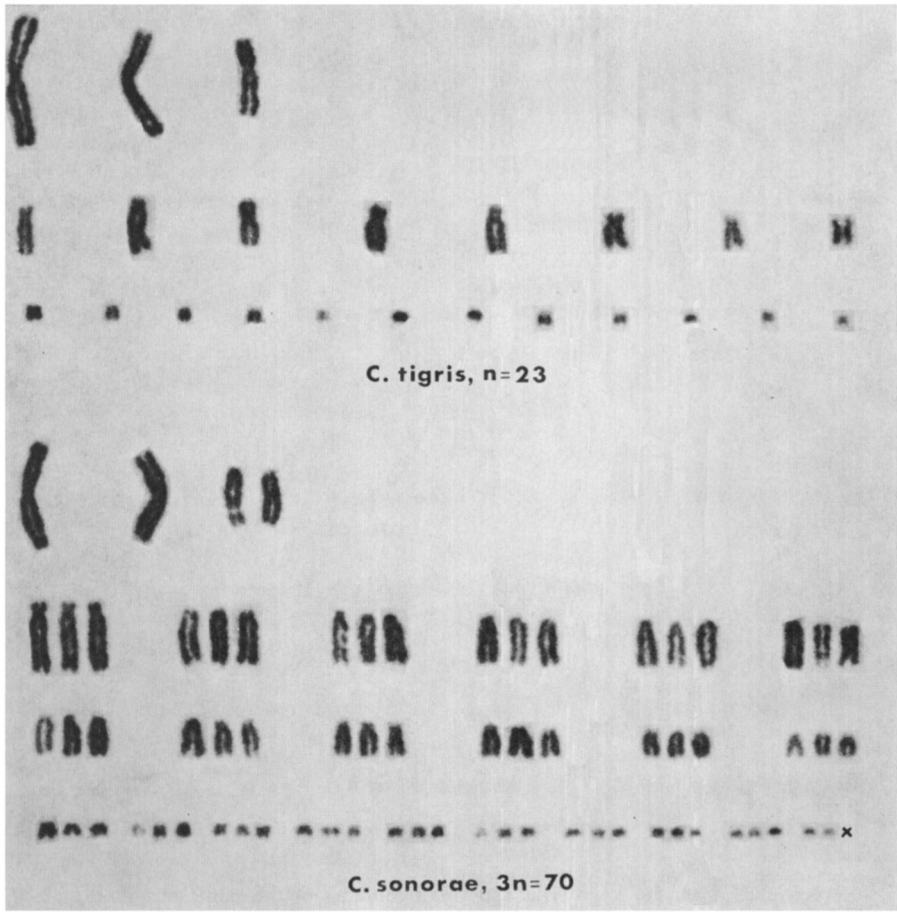


FIG. 6.—Representation of the karyotype (bone marrow cell) of a tetraploid male hybrid between *C. sonorae* and *C. tigris* (UAZ 24954). The chromosomes are arranged for comparison with Fig. 5 to illustrate the presence of both parental complements. This is a $4n = 93$ karyotype, composed of 5 + 46 + 42 chromosomes. A microchromosome that was lost in the preparation is represented by an inked-in X at the lower right. Nevertheless, this cell was selected since the chromosomes so clearly exhibit their characteristic morphology (see text).

and (8) the preponderance of essentially telocentric chromosomes composing the rest of the Set II elements.

Meiosis.—The testes of this male hybrid exhibited both mitotic and meiotic activity. The spermatogonia are tetraploid (Fig. 7) and have the same chromosome constitution as the bone marrow cells. While the primary spermatocytes exhibiting meiosis I (pachytene-metaphase I) are not particularly clear in the preparations, it is certain that chromosomal bivalents and polyvalents (including quadrivalents) are frequently formed in synapsis, revealing genetic homologies. The testicular mitotic and meiotic I activity in the male hybrid captured on 3 July suggests a significantly delayed testicular cycle, as compared to that of males of *C. tigris* from the desert near Tucson (Goldberg and Lowe, 1966).

If meiosis were to have proceeded normally in this tetraploid individual, presumably it would have produced essentially diploid spermatozoa, but we do not yet

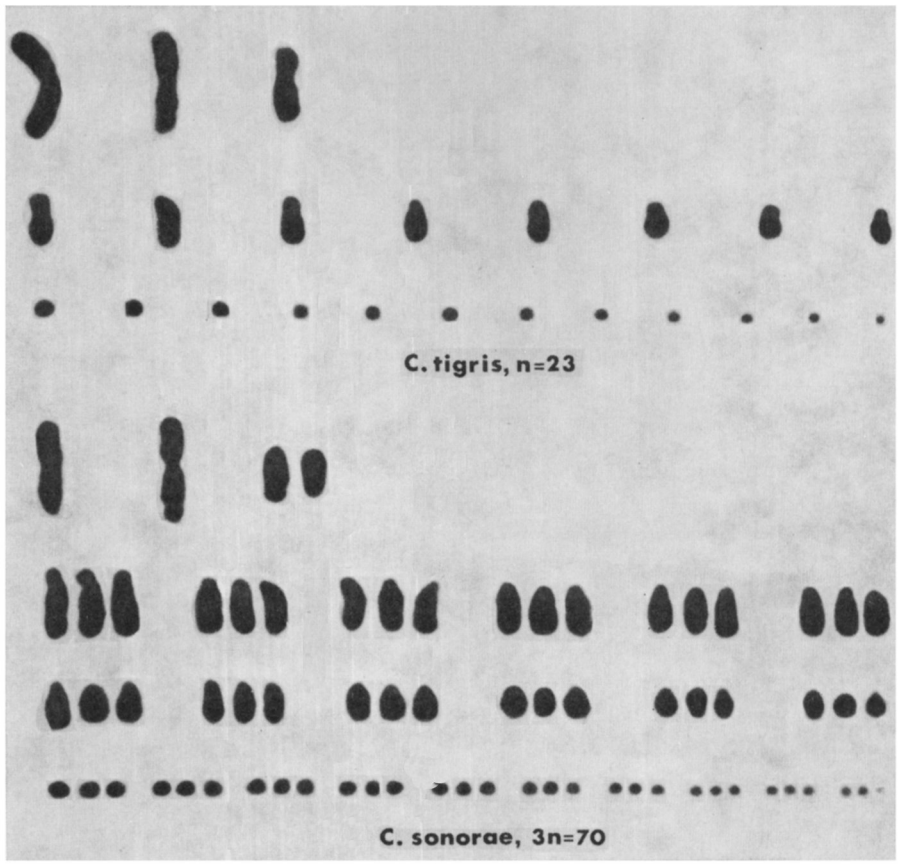


FIG. 7.—Representation of the karyotype (spermatogonium) of the same tetraploid male hybrid between *C. sonorae* and *C. tigris* that is illustrated in Fig. 6 (UAZ 24954). The chromosomes are arranged for comparison with Figs. 5–6. This cell clearly exhibits the tetraploid number of $4n = 93$, composed of 5 + 46 + 42 chromosomes, though the chromosome morphology is not so clear as in bone marrow cells (Fig. 6).

know whether these would be viable. The infrequency of cells exhibiting meiosis II or other spermatogenic stages subsequent to metaphase I could have resulted from the delayed testicular cycle rather than from meiotic failure. Thus, we do not yet know whether meiosis could proceed normally in such tetraploids to produce viable, essentially diploid spermatozoa. If so, reduced fertility of the hybrid may result from occasional or frequent unbalanced segregation from the polyvalents, at anaphase I.

Sex Chromosomes.—It is particularly noteworthy that there is in *C. tigris* a chromosomal heteromorphism of the X-Y [XY (♂):XX(♀)] type, involving the third chromosome of Set I (Cole, Lowe, and Wright, *in press*). In all-female parthenogenetic species that originated through hybridization between *C. tigris* and other species (Lowe and Wright, 1966a, b), the X chromosome of *C. tigris* is clearly recognized and the Y is conspicuously absent. In the case of the tetraploid male reported here, however, the haploid *C. tigris* complement obviously contains the Y chromosome, corresponding with the sex of the animal.

DISCUSSION AND CONCLUSIONS

The appearance of the two hybrid specimens is predominantly that of aberrant *Cnemidophorus sonorae* with only a slight external resemblance to *C. tigris*. Karyotypic analysis clearly shows, however, the addition of one *C. tigris* genome to the three *C. sonorae* genomes resulting in a tetraploid hybrid that strongly resembles the maternal parthenogenetic parent.

Five males of three different parthenogenetic species have recently been described by Taylor, Walker, and Medica (1967). These authors although unable to discount hybridization as being responsible for the origin of these males in otherwise "all-female" species prefer to interpret them as evidence of relictual bisexuality. They freely admit that each of the males comes from populations of parthenogenetic species that are sympatric with at least one bisexual species. We suggest that although the superficiality of their data does not enable them to properly choose between the alternate hypotheses of hybridization *or* relictual bisexuality, a more thorough analysis of these populations will verify the hybrid origin of the males.

The triploid species of *Cnemidophorus* appear to have originated through hybridization between diploid parthenogenetic and diploid bisexual forms in "weed" habitats (Lowe and Wright, 1966a, b; Wright and Lowe, 1968). Strong evidence in support of this hypothesis is provided by the triploid hybrids that result from interbreeding between the diploid parthenogenetic *Cnemidophorus neomexicanus* and the diploid bisexual *Cnemidophorus inornatus* (Wright and Lowe, 1965, 1967). Apparently the increase in ploidy following such hybridization is a direct consequence of the parthenogenetic species contributing an unreduced chromosome complement in the ovum and the bisexual species adding another haploid complement to this *via* the spermatozoan (Lowe and Wright, 1966a, b).

In the case of the hybrids reported here, tetraploidy results from the triploid parthenogenetic parent (*C. sonorae*) contributing an unreduced ovum ($3n$) plus one haploid complement from the diploid bisexual paternal parent (*C. tigris*). That *C. sonorae* was the maternal parent and *C. tigris* was the paternal parent is obvious since the hybrids possess the full *C. sonorae* chromosome constitution, one *C. tigris* haploid complement, and, of most direct implication, the *C. tigris* Y chromosome, which could have been inherited only from a male *C. tigris* (Cole, Lowe, and Wright, *in press*). This resulting degree of ploidy (tetraploidy) is one step higher than has been known previously among reptiles.

Presumably the allotetraploid hybrids reported here have genomes that were derived from at least three different species, of which two were representatives of the *sexlineatus* group and the third was *C. tigris*. Historically, the first two genomes were combined in the first hybridization between two bisexual diploid species of the *sexlineatus* group, which produced a diploid parthenogenetic form. The allotriploid *C. sonorae* resulted from a second stage of hybridization between this form and a diploid bisexual species (which likely was one of the original hybridizing species as well, so its chromosome complement may be represented twice in the triploid *C. sonorae*). The haploid complement of a third species (*C. tigris*) was contributed in the third stage of hybridization (the present one), resulting in allotetraploidy. This mode of attaining various levels of ploidy by means of a progressive sequence of individual stages of hybridization is in striking contrast to the general mode in plants (see review by Stebbins, 1950), in which allotetraploids generally originate as a consequence of the accidental doubling of the chromosome complement in diploid individuals that originated through one earlier hybridization; such allotetraploids in plants contain genomes from only two species, instead of the minimum of three (and possibly four) that occur in the allotetraploid individuals of *Cnemidophorus*.

The very real potential for the future

evolution of polyploid bisexual species of *Cnemidophorus* is revealed and underscored by the following characteristics of the allotetraploids reported here: (1) allotetraploid individuals can be quite viable and compete successfully, (2) presumably both sexes can occur as allotetraploids (although males are reported here, females would be expected to result from hybridization of these same species in those cases involving syngamy of the *C. sonorae* ovum and the X-bearing *C. tigris* spermatozoan), and (3) allotetraploids may undergo meiosis (see section on karyotypes). Thus, considering that the triploid *C. sonorae* presumably has two haploid chromosome complements from one species and one from a second species, another hybridization between *C. sonorae* and that second species could theoretically produce a bisexual allotetraploid (or segmental allotetraploid) species.

SPECIMENS EXAMINED

Hybrid Index.—All specimens are from Huerfano Butte, 3.0 mi. (by rd) W Helvetia, 3750 ft., Santa Rita Experimental Range (= SRER), Pima Co., Arizona. Catalogue numbers in the Herpetological Collections, Department of Zoology, University of Arizona (UAZ) are given followed by additional collection data *Cnemidophorus sonorae:* 16394–95, July 2, 1966; 16396–97, 20186, July 3, 1966; 20398–20411, S base, July 5, 1967. *Cnemidophorus tigris:* 16362–78, July 2, 1966; 16379–81, July 3, 1966; 16541–45, Oct. 1, 1966; 20412–20437, S base, July 5, 1967. *Cnemidophorus sonorae* × *C. tigris*: 24953, July 2, 1966; 24954, July 3, 1966.

Karyotypes.—Locality data are followed by UAZ numbers (in parentheses).

Cnemidophorus tigris. UNITED STATES: *Arizona:* Mohave Co.: Alamo Crossing (18506, 25240–41). Pima Co.: N end of Campbell Ave., N of Tucson (25239); S base Huerfano Butte, 3.0 mi (by rd) W Helvetia, 3750 ft., SRER (20412); 1 mi NE Huerfano (along Helvetia Rd.), SRER (25432); 0.5 mi NE of Helvetia Rd. (via Powerline Rd.), and 2.5 mi ESE of the N boundary of SRER, SRER (25433). Pinal Co.: ½ mi E Mammoth, San Pedro River Basin (25242). *New Mexico:* Dona Ana Co.: 8.4 mi W Hatch, ca 4600 ft. (18122). *Utah:* Garfield Co.: "Copper Creek," Indian Spr. Rd., 3.1 mi (by rd) W Starr Ranch, 6100 ft., S slope Mt. Hillers, Henry Mts. (18546, 18554). MEXICO: *Sonora:* S bank of Rio Mayo, Navojoa (18749, 18752); Campbells Ranch, ca. 2 mi ENE Moctezuma (21645).

Cnemidophorus sonorae. UNITED STATES: *Arizona:* Pima Co.: Huerfano Butte, 3.0 mi (by rd) W Helvetia, 3750 ft., Santa Rita Exp. Range (18522, 18728, 20398–400).

Cnemidophorus sonorae × *C. tigris.* 24954 (see locality immediately above).

ACKNOWLEDGMENTS

We are grateful to the many persons at the University of Arizona who have aided us in this investigation: E. J. Braun, A. D. Cecil III, E. A. Halpern, D. S. Hinds, J. L. Patton, M. D. Robinson, O. H. Soule, and T. A. Wiewandt. This investigation was supported by NSF Grants GB 5647 and GB 6830.

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Department of Biological Sciences, the University of Arizona, Tucson 85721 (CHL, CJC, *and* RLB), *and Department of Herpetology, Los Angeles County Museum of Natural History, Los Angeles, California* 90007 (JWW). *Present address* (CJC), *American Museum of Natural History, New York, N.Y., 10024.*