AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3081, 30 pp., 11 figures, 2 tables December 27, 1993

Unisexual and Bisexual Whiptail Lizards of the *Cnemidophorus lemniscatus* Complex (Squamata: Teiidae) of the Guiana Region, South America, with Descriptions of New Species

CHARLES J. COLE[1] AND HERBERT C. DESSAUER[2]

CONTENTS

[1] Curator, Department of Herpetology and Ichthyology, American Museum of Natural History.

[2] Research Associate, Department of Herpetology and Ichthyology, American Museum of Natural History; Professor Emeritus, Department of Biochemistry and Molecular Biology, Louisiana State University Medical Center, New Orleans, LA.

ISSN 0003-0082 / Price $3.25

ABSTRACT

At least four species have been masquerading under the name *Cnemidophorus lemniscatus* in northern South America. These species were revealed clearly by karyotypic and electrophoretic analyses of samples from unisexual and from bisexual populations. The four taxa include two diploid bisexual species and two unisexual cryptic species (one diploid and one triploid). The unisexual species are parthenogenetic clones that ultimately originated from hybrids among the bisexual species (the triploids stemming from backcross hybridization). There are several different diagnosable diploid clones, at least two of which probably had origins from separate hybridization events at different localities. Several other diagnosable diploid clones probably stemmed from mutations within one or more established parthenogenetic lineages of very similar hybrid origin.

A revised diagnosis is presented for *C. lemniscatus*, a male lectotype is designated, and the type locality is restricted to an area in Suriname with a bisexual population of lizards similar to the Linnaean syntypes and consistent with their suspected provenance. The second bisexual species appears to be *C. gramivagus* McCrystal and Dixon, for which a revised diagnosis is presented also. New diagnoses and names are presented for two unisexual species, a diploid based on specimens from Venezuela (with paratypes from Brazil also), and a triploid based on specimens from Suriname. Alternative taxonomic treatments for the various diploid unisexual clones found in Brazil are discussed, but none of these is named as a separate species here. For now, we treat all of the diploid clones as one species.

INTRODUCTION

Cnemidophorus lemniscatus (Linnaeus) is a widespread and generally abundant and conspicuous whiptail lizard in much of Central America and South America, mostly in bisexual populations (gonochoristic, with separate sexes; fertilization is required for reproduction). Vanzolini (1970) first reported that some populations along the Amazon River in Brazil are bisexual and others are unisexual (all-female).

Chromosome studies by Peccinini-Seale and Frota-Pessoa (1974) revealed five slightly different karyotypes among the Brazilian *C. lemniscatus*, which they designated alphabetically, A through E. Types A–C are minor variants characterizing separate unisexual populations, all diploids, differing from each other primarily in a centromere position among the second largest pair of macrochromosomes and in number of microchromosomes. Types D and E characterize the bisexual populations, which differ from each other only in centromere position on chromosome number 1 (largest pair). Type C of the unisexuals has a karyotype that could be composed of one haploid complement each from bisexual types D and E; i.e., it could have had a hybrid origin. Unisexual types A and B could have been derived from unisexual type C by chromosomal aberrations.

Sites et al. (1990) tested the hybrid origin hypothesis for diploid unisexual *C. lemniscatus* from Brazil by comparing products of 57 presumed structural gene loci in types B through E, using protein electrophoresis. The hypothesis was strongly supported, as bisexual types D and E had relatively low heterozygosity indices and fixed or nearly fixed differences from each other at 11 of the loci analyzed. In contrast, the unisexual types B and C had relatively high heterozygosity and genotypes consistent with their having a haploid set of genes each from bisexual types D and E, with minor exceptions. Sites et al. (1990) proposed that at least three species are involved in this complex along the Amazon River in Brazil: bisexual type D, bisexual type E, and the diploid unisexuals of hybrid origin.

A companion study of mitochondrial DNA (Vyas et al., 1990) showed that the Brazilian unisexuals have only one type of mtDNA and it is most similar to that occurring in certain bisexual type D lizards (i.e., type D was the maternal ancestor). There is variation in mtDNA in type D, and none of the type D samples examined matched perfectly the mtDNAs of the unisexuals. Nevertheless, none of the unisexuals had mtDNA similar to that of bisexual type E (i.e., type E was the paternal ancestor).

Separate bisexual and unisexual populations of *C. lemniscatus* also occur in Suriname (Hoogmoed, 1973), but these unisexuals are triploids rather than diploids (Serena,

1985; Dessauer and Cole, 1989). Studies of karyotypes and protein electrophoresis (46 loci tested) suggested that the bisexual diploids in Suriname are similar to type D of Brazil (same taxon), and the triploids had a hybrid origin involving two genomes of type D and one of type E (Dessauer and Cole, 1989). This probably resulted from backcrossing of a diploid unisexual of type C (originally of type D × type E origin) with a male of type D; i.e., a double hybrid origin of [D × E] × D.

Electrophoretic analyses of the samples from Suriname and from Brazil were conducted separately in different laboratories (Dessauer and Cole, 1989; Sites et al., 1990, respectively), so cross-correlation gels comparing all of the samples together did not exist. Evidence that the genomes of type D and E were basically the same in unisexual lizards from Brazil and Suriname was provided only by the karyotypes (Dessauer and Cole, 1989: fig. 7C), which do not resolve genetic data as well as protein electrophoresis does. To determine whether the same alleles at structural gene loci are shared by lizards in Brazil and Suriname (type D bisexuals and diploid and triploid unisexuals), samples would have to be subjected to protein electrophoresis on the same gels.

While the two independent electrophoretic reports discussed above on lizards from Suriname and Brazil were in press, CJC, Carlos Guaveco, Maria Jose Praderio, and Carol R. Townsend collected two new samples of the *C. lemniscatus* complex in Venezuela. Specimens from San Ignacio de Yuruani (State of Bolivar) included both sexes, whereas those from Icabaru (State of Bolivar) included only females, although no unisexual populations were known for Venezuela.

For the present report, we karyotyped the new samples from Venezuela and we analyzed together in one laboratory the samples (bisexual and unisexual) from Brazil, Suriname, and Venezuela for direct, side-by-side comparisons of alleles detected by protein electrophoresis. We also compared these animals morphologically with each other, with new samples from Guyana, and with samples of *Cnemidophorus gramivagus* McCrystal and Dixon from Colombia. The following questions are addressed: (1) Do the genotypes of type D bisexual *C. lemniscatus* from Suriname and Venezuela compare favorably with those from Brazil, as indicated by karyotypes and protein electrophoresis? (2) Do the unisexual samples from Brazil, Suriname, and Venezuela have basically the same genotypes, including the alleles at heterozygous loci that were inherited from bisexual type E? (3) What is the minimal number of species represented by the samples compared here, and what names should be applied to them? A review of these questions improves our knowledge of biodiversity and its origins in Neotropica.

Acknowledgments

Permits and considerable assistance with logistics in the field were provided by S. A. J. Malone, F. L. J. Baal, and M. H. S. Miskin (all of the Suriname Forest Service), Giuseppe Colonnello (Museo de Historia Natural La Salle, Caracas, Venezuela), and Karen Pilgrim (Wildlife Services Division, Department of Agriculture, Guyana). We were assisted in the field in Suriname by Jeffrey Cole, in Venezuela by Carlos Guaveco and Maria Jose Praderio (Museo de Historia Natural La Salle), and in Guyana by Bruce Hoffman.

Fieldwork in Guyana in 1992 was conducted through the Biological Diversity of the Guianas Program (BDGP), coordinated in Guyana by Deputy Vice-Chancellor Malcolm Rodrigues and Dean Indarjit Ramdass of the University of Guyana (UG), Turkeyen Campus, Georgetown. Mike Tamessar of UG also greatly facilitated this work. Important logistical support was provided by personnel serving the BDGP, including Vicki Funk, Bruce Hoffman, Carol Kelloff, and Mohammed Ameer (the "Ambassador of Bourda"). Additional logistical support was provided by Malcolm Chan-A-Sue (Torong Guyana), Walter Lachman (National Dairy Development Programme), Diane McTurk (Karanambo), and the people of Karanambo and Yupukari.

Brazilian specimens used here are a subset of the same ones studied by Sites et al. (1990), not a product of our own fieldwork. These were collected by D. M. Peccinini-Seale and R. R. de Souza. Thanks to the generosity of Wesley Brown and Craig Moritz (University of Michigan, Ann Arbor) and Jack Sites

(Brigham Young University, Provo, Utah), homogenates remaining after their study (Sites et al., 1990) were sent to us for direct comparisons with our specimens. The relevant preserved lizards at the University of Michigan Museum of Zoology (UMMZ) were lent to us by Arnold Kluge.

Important information and photographs of the Linnaean syntypes of *Cnemidophorus lemniscatus* were provided by Sven O. Kullander, Curator of Fishes, Swedish Museum of Natural History, Stockholm (NRM). The photographs (figs. 8, 9) were taken by Uno Samuelsson of their Department of Paleozoology.

The following people have helped in various ways and particularly encouraged our progress on this work: Vicki Funk (Department of Botany, National Museum of Natural History [USNM], Washington), Marinus Hoogmoed (National Museum of Natural History, Leiden, The Netherlands), and Henry Reichart (Suriname Forest Service). Carol R. Townsend assisted in every way possible in the field and in the laboratory, putting as much effort into this project as anybody.

We thank Teresa C. S. de Avila Pires (Museu Paraense Emilio Goeldi), Darrel Frost (American Museum of Natural History [AMNH]), Marinus Hoogmoed, and Jack Sites for critical and very helpful reviews of the manuscript. Funding for fieldwork in Suriname was provided by the National Geographic Society (grants 2622-83 and 3163-85), and some of the laboratory work was supported by the National Science Foundation (BSR-8105454, to CJC). Funding for fieldwork in Venezuela was provided in part by gifts to the AMNH from Robert G. Goelet of New York and the Phipps Foundation, as this fieldwork directly followed participation by CJC and Carol R. Townsend in the Tapirapeco Expedition (see acknowledgments in Donnelly et al., 1992: 832). Funding for fieldwork in Guyana was provided by the Biological Diversity of the Guianas Program through the Smithsonian Institution, Washington (Department of Botany, USNM; Vicki Funk, North American Program Director). Special funds of the AMNH also helped meet field expenses, thanks to Thomas Nicholson and Michael Novacek.

MATERIALS AND METHODS

External Morphology and Karyotypes

Characters of external morphology were determined as described elsewhere (Cole et al., 1988), as were karyotypes (Cole, 1979). Sex was determined by dissection and examination of primary sexual characters, except for specimens that had been eviscerated or photographed by others, in which case we used secondary characters (anal spurs, size of femoral pores, massiveness of head). Method is specified where particularly pertinent, and the specimens examined are listed in the Appendix.

Biochemical Genetics

The heart, liver, and kidney, plus samples of skeletal muscle and blood were collected from Surinamese and Venezuelan lizards prior to preservation. Plasma was separated from blood cells and all tissues were stored in liquid nitrogen until transfer to ultracold freezers in the laboratory. For the protein studies, tissues were thawed and homogenized in two to three volumes of a 0.25 M solution of sucrose, which contained 20 mg/liter of dithiotreitol, 50 mg/liter of NAD, and 25 mg/liter of NADP. Homogenates were centrifuged at 5000 g to separate soluble proteins from cell debris.

Electrophoretic analyses were performed using supernatant solutions from these homogenates and from Brazilian lizard homogenates that remained from the study by Sites et al. (1990). Aliquots of these solutions were added to slots in starch gels and subjected to vertical gel electrophoresis (Smithies, 1959) overnight at a potential gradient of 6 to 8 volts/cm in a cabinet maintained at 4°C. To develop data comparable to that of Sites et al. (1990), most analyses were carried out with gels made with a Tris-citrate buffer of pH 8, identical in composition, or nearly so, to those used by Sites et al. For analyses involving plasma, which was not available for the Brazilian lizards, a veronal buffer of pH 8.6 was used. For analyses of unspecified muscle proteins a phosphate buffer of pH 6 was used.

Gel buffers were diluted to an ionic strength

of about 0.01; electrode chambers were filled with buffers 10 times that strength. The coenzyme NADP (10 mg/liter) was added to gel buffers used in analyses of sMEP, IDHP, and PGDH to stabilize their structures during electrophoresis.

Following electrophoresis, enzymes and nonenzymic proteins were localized on gel slices by means of histochemical stains, fluorescence, or autoradiography. Table 1 lists the proteins analyzed, enzyme commission numbers, abbreviations (Shaklee et al., 1989; Murphy et al., 1990), and tissue(s) from which data were extracted. Localization techniques closely followed descriptions by Harris and Hopkinson (1976). Transferrins were identified by iron^{59} binding and autoradiography (Giblett et al., 1959). Myoglobin was detected in muscle homogenates by the presence of a brownish band migrating anodally on unstained gels; its identity was confirmed with the benzidine test (see Smithies, 1959).

Tissues and tissue homogenates that remained at the completion of this study were retained in the frozen tissue collection of the Museum of Natural Science, Louisiana State University, Baton Rouge (Dessauer et al., 1990).

RESULTS AND DISCUSSION

Karyotypes

New data are presented here for specimens from two populations in the state of Bolivar, Venezuela, as follows: (1) San Ignacio de Yuruani (one female, no males; 2 cells examined); and (2) Icabaru (two females, no males; 11 cells examined). The lizard karyotyped in the bisexual sample from San Ignacio de Yuruani (a total of 12 lizards in the sample, five males and seven females) had a diploid number of 50 chromosomes, with 26 macrochromosomes (13 homomorphic pairs) and 24 microchromosomes (apparently 12 homomorphic pairs). The largest pair of chromosomes is submetacentric to subtelocentric with a secondary constriction and dotlike satellite on the end of the long arm distal to the centromere (fig. 1A). The smaller macrochromosomes are all telocentric or subtelocentric. This is known as karyotype D of *C. lemniscatus*, reported previously for certain populations on the Amazon River in Brazil (Peccinini-Seale and Frota-Pessoa, 1974; Sites et al., 1990), for Boa Vista in Roraima, northern Brazil (Sites et al., 1990), and for Suriname (Serena 1985; Dessauer and Cole, 1989; fig. 2A here).

Both of the lizards karyotyped in the unisexual sample from Icabaru (a total of nine lizards in the sample, all females) similarly had a diploid number of 50 chromosomes, with 26 macrochromosomes and 24 microchromosomes. In contrast, however, the largest pair of macrochromosomes is heteromorphic, with one submetacentric to subtelocentric chromosome and one subtelocentric to telocentric (fig. 1B). This is karyotype C, reported previously for certain unisexual populations in extreme eastern Brazil, near the mouth of the Amazon (Peccinini-Seale and Frota-Pessoa, 1974). Karyotype C occurs in clones that originated from hybrids between bisexual lizards of karyotype D and karyotype E (Sites et al., 1990; Vyas et al., 1990).

Karyotypes A and B of unisexual lizards characterize variant clones that were probably derived by mutations from karyotype C, described by Peccinini-Seale and Frota-Pessoa (1974) in the same paper in which they described karyotypes A through E for the *Cnemidophorus lemniscatus* complex.

Here, we designate karyotype F, that of the triploids in Suriname described and illustrated by Dessauer and Cole (1989: fig. 7C; fig 2B here). This triploid karyotype comprises two haploid complements of type D and one of type E, probably resulting from two steps of hybridization as described above ([D × E] × D; Dessauer and Cole, 1989).

Biochemical Genetics

Proteins encoded by 32 presumptive structural gene loci were compared by electrophoresis for 12 samples of *C. lemniscatus* from Brazil, Venezuela, and Suriname (figs. 3, 4; table 2). This allowed cross-correlating the protein data published previously for Suriname (Dessauer and Cole, 1989) and Brazil (Sites et al., 1990), while also comparing the new samples from Venezuela.

Twenty loci showed no variation across all

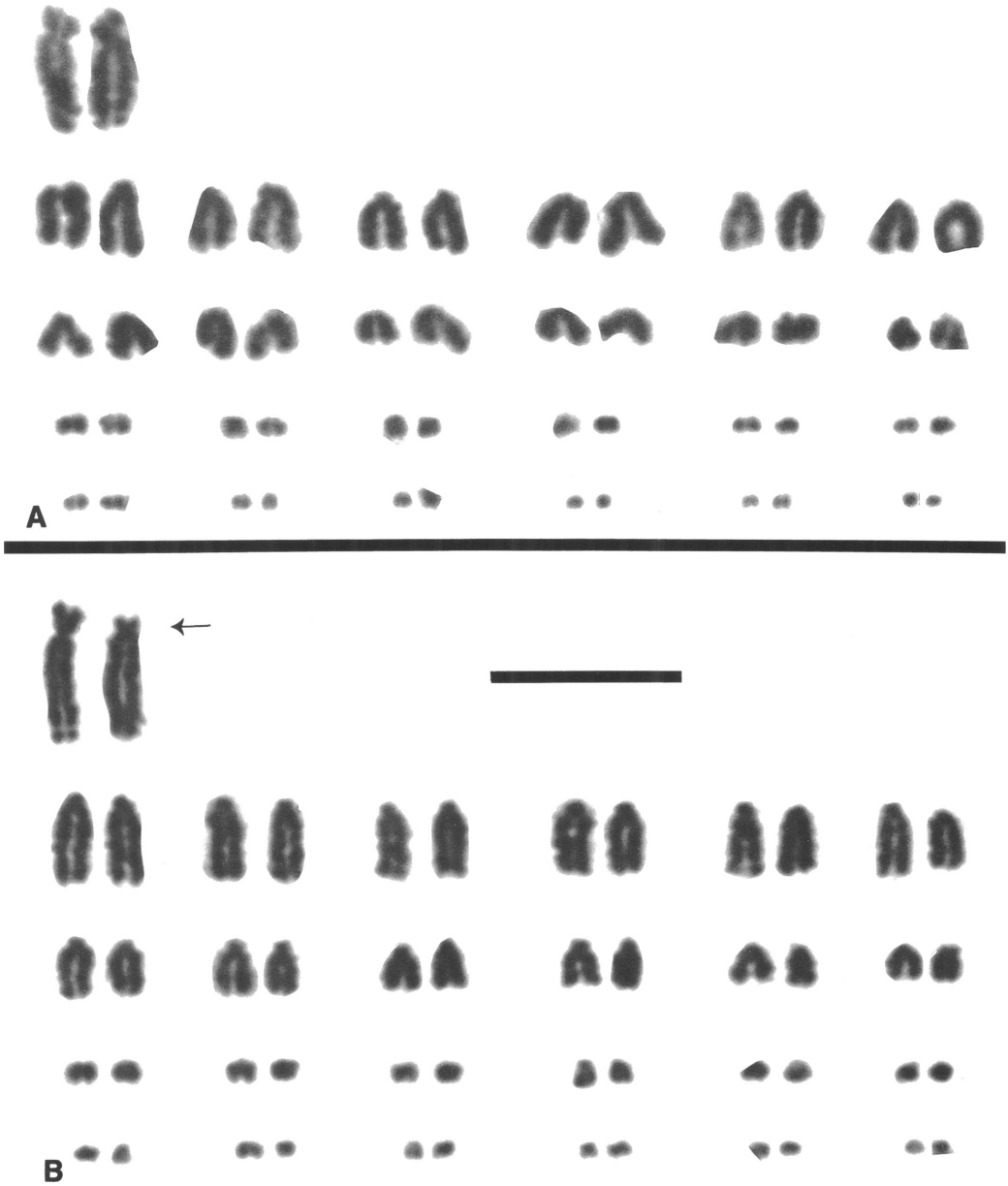

Fig. 1. Diploid karyotypes ($2n = 50$) of two species in the *Cnemidophorus lemniscatus* complex, each with one pair of large chromosomes, 12 pairs of microchromosomes, and 12 pairs of telocentric chromosomes of intermediate size. **A,** the bisexual *C. lemniscatus* (AMNH 135091, female), from San Ignacio de Yuruani, Bolivar, Venezuela. Note that the largest pair consists of two similar submetacentric to subtelocentric chromosomes with the secondary constriction nearly terminal on the long arm. **B,** the unisexual named below as *C. cryptus* (paratype, AMNH 135090, female), from Icabaru, Bolivar, Venezuela. Note that the largest pair consists of two chromosomes with dissimilar centromere positions, one as in *C. lemniscatus* (submetacentric to subtelocentric) and one subtelocentric to telocentric (arrow). Bar represents 10 μm.

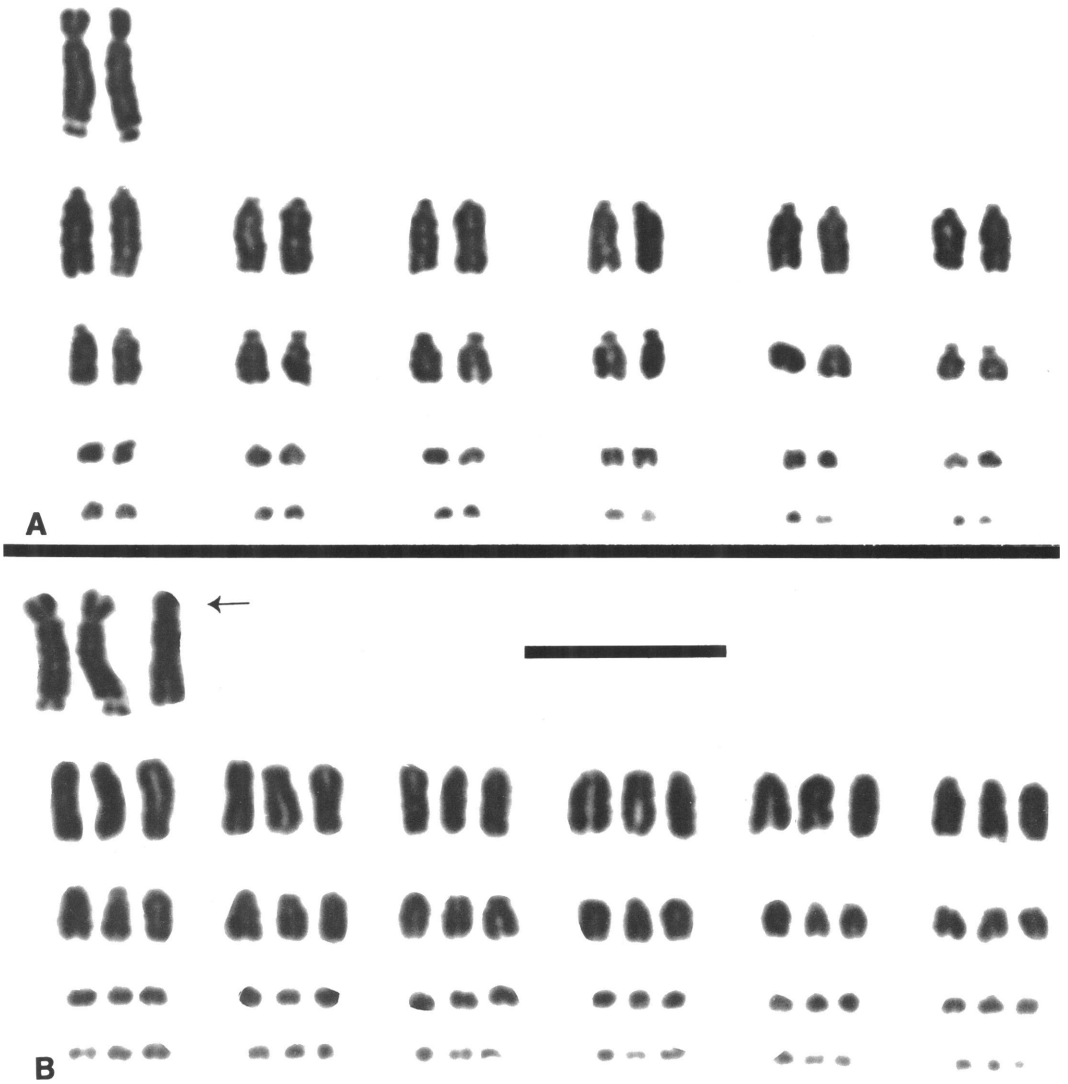

Fig. 2. Karyotypes of two species in the *Cnemidophorus lemniscatus* complex. **A,** the diploid *C. lemniscatus* (AMNH 133303, female) from Christiaankondre, Suriname. Note the diploid number of 50 chromosomes, all similar to those in figure 1A. **B,** the triploid unisexual named below as *C. pseudolemniscatus* (holotype, AMNH 133304, female), from Albina, Suriname. Note that the triplet of largest chromosomes includes two that are submetacentric to subtelocentric and one subtelocentric to telocentric (arrow). Bar represents 10 μm. Modified from Dessauer and Cole (1989: 57).

12 samples compared, whereas 12 loci were more informative in various ways (table 2). For seven loci (IDDH, sMEP, mIDHP, sAAT, PEPA, PEPB, and ADA) the bisexual diploids of type D and type E consistently differ from each other, and for five of these loci all of the diploid unisexuals (B + C Brz and C Ven in table 2) share one allele characteristic of each of types D and E (fig. 3). The only exceptions are for one allele each at IDDH and sMEP (table 2). We suggest that future research will reveal that the b-allele of IDDH and the a-allele of sMEP occur in other population samples of type E that we have not yet examined, although other explanations for these data are possible also (Sites et al.,

TABLE 1
Presumptive Structural Gene Loci Examined

Locus	EC no.	Abbrev.[a]	Tissue[b]
Oxidoreductases			
Alcohol dehydrogenase	1.1.1.1	ADH	L
Glycerol-3-phosphate dehydrogenase	1.1.1.8	G3PDH	M
L-iditol dehydrogenase	1.1.1.14	IDDH	K
L-lactate dehydrogenase	1.1.1.27	LDH-1	K, L
		LDH-2	K, L, M
Malate dehydrogenase	1.1.1.37	sMDH	M
		mMDH	M
Malate enzyme	1.1.1.40	sMEP	K, L
Isocitrate dehydrogenase	1.1.1.42	sIDHP	K, L
		mIDHP	H, M
Phosphogluconate dehydrogenase	1.1.1.44	PGDH	K, L
Superoxide dismutase	1.15.1.1	sSOD	K, L
		mSOD	K, L
Transferases			
Aspartate aminotransferase	2.6.1.1	sAAT	K, L, M
		mAAT	K, L, M
Creatine kinase	2.7.3.2	CK-1	I, K
		CK-2	I, K
Adenylate kinase	2.7.4.3	AK	M
Hydrolases			
Esterase D	3.1.1.-	ESTD[c]	L, M
Acid phosphatase	3.1.3.2	ACP[d]	L, M
Peptidases	3.4.-.-	PEPA[e]	H, K, L
		PEPB[f]	M
Adenosine deaminase	3.5.4.4	ADA	L, R
Lyases			
Aconitate hydratase	4.2.1.3	sAH	L
		mAH	L
Isomerases			
Mannose-6-phosphate	5.3.1.8	MPI	K, L
Glucose-6-phosphate	5.3.1.9	GPI	K, L, M
Nonenzymic proteins			
Transferrin		TF	P
Myoglobin		MB	M
Muscle proteins (N = 4)		MP-1 to 4	M

[a] Based on Shaklee et al. (1989) and Murphy et al. (1990); s = cytosolic enzyme; m = mitochondrial enzyme.
[b] Tissue in which enzyme was scored: H = heart; I = intestine; K = kidney; L = liver; M = skeletal muscle; P = plasma; R = erythrocytes.
[c] Substrate 4-methylumbelliferyl acetate; inactive with alphanaphthyl esters.
[d] Substrate 4-methylumbelliferyl phosphate.
[e] Substrate phenylalanyl·leucine.
[f] Substrate leucyl·glycyl·glycine.

1990; and see below). At any rate, we are satisfied that the hybrid origin of all of the unisexual populations is confirmed (Dessauer and Cole, 1989; Sites et al., 1990). Considering each of the 12 most informative loci (table 2), and considering the karyotypes involved (see above), the triploids from Suriname (F Sur) have traits that confirm an or-

TABLE 2

Alleles[a] or Genotypes[b] at 32 Presumptive Structural Gene Loci in Twelve Samples[c] of *Cnemidophorus lemniscatus*

	Bisexual					Unisexual		
Locus[d]	E Brz	D Alt	D Boa	D Ven	D Sur	B + C Brz	C Ven	F Sur
IDDH	c	b	b	b, a[e]	b	bb	bb	bbb
sMEP	b	a	a	a	a	ab	aa	aaa
mIDHP	b	a	a	a	a	ab	ab	aab
sAAT	a	b	b	b	b	ab	ab	abb
ESTD	a	a, b[f]	a, b[f]	b	a	aa	aa	aaa
PEPA	a	c	b	b	b	ac	ab	abb
PEPB	b	a	a	a	a	ab	ab	aab
ADA	a	b	b	b	b	ab	ab	abb[g]
sAH	b	b	b	b	b, a[h]	bb	bb	bbb
mAH	b	b	b	b	a, b[i]	bb	bb	abb
MPI	b	b	b	b	b, a[j]	bb	bb	bbb
GPI	b	b	b	a, b[k]	b	bb	bb	bbb

[a] Alleles are designated in alphabetical sequence in order of decreasing anodal migration. Commas separate alternative alleles at a specified locus for bisexual species. See Sites et al. (1990) for more details on allele frequencies in Brazilian populations.

[b] Genotypes are given for unisexual forms, for which we observed no variation at any locus in the samples we examined.

[c] E Brz = type E animals (N = 15 specimens examined by us) from Manacapuru, Brazil (Sites et al., 1990); D Alt = type D animals (N = 10) from Alter do Chao, Brazil (Sites et al., 1990); D Boa = type D animals (N = 4) from Boa Vista, Brazil (Sites et al., 1990); D Ven = type D (N = 9) from San Ignacio de Yuruani, Venezuela; D Sur = type D (N = 10) from Christiaankondre, Suriname; B + C Brz = types B and C diploids (N = 23) from Oriximina, Brazil (type B) and Capanema and Maruda, Brazil (type C; Sites et al., 1990); C Ven = type C diploids (N = 4) from Icabaru, Venezuela; and F Sur = type F triploids (N = 8) from Albina, Brokopondo, and Brownsweg, Suriname.

[d] Each specimen of all populations tested had the same phenotype at the following loci: G3PDH, LDH-1, LDH-2, sMDH, mMDH, sIDHP, PGDH, sSOD, mSOD, mAAT, CK-1, CK-2, AK, ACP, MB, and MP-1 through MP-4. In addition, all specimens from Suriname and Venezuela had the same phenotypes for TF, whether bisexual or unisexual or diploid or triploid.

[e] Frequency of b = 0.79.

[f] Frequency of a = 0.94 for type D Alt and 0.87 for type D Boa.

[g] The product of the b-allele of ADA was very difficult to resolve in tissues that had been frozen for several years, indicating that this molecule is unstable over time.

[h] Frequency of b = 0.78.

[i] Frequency of a = 0.67.

[j] Frequency of b = 0.95.

[k] Frequency of a = 0.64.

igin involving hybridization between a diploid type C unisexual lizard × male of type D.

The triploid unisexuals from three localities in Suriname (F Sur; Albina, Brokopondo, and Brownsweg) are all identical to each other. The diploid unisexuals of which we received homogenates representing three localities in Brazil (B + C Brz; Capanema, Maruda, and Oriximina) also are all identical to each other, even though this includes individuals of two karyotypic clones (types B and C); however, Sites et al. (1990) discussed some limited clonal diversity in these population samples. The four diploid unisexuals from Venezuela (C Ven) are identical to each other and consistently differ from the Brazilian unisexuals by one allele each at two loci (sMEP and PEPA). We suggested above that this may reflect geographic variation of alleles at sMEP in type E bisexuals, and geographic variation is clearly demonstrated for PEPA. At PEPA (table 2; fig. 4), the Brazilian diploid unisexuals (B + C Brz) from along the Amazon have the c-allele characteristic

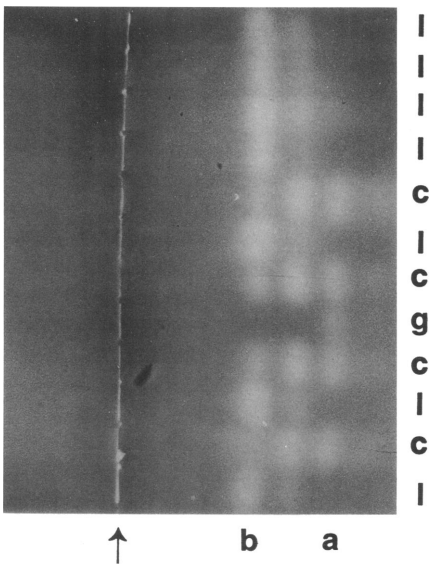

Fig. 3. Electrophoretic patterns of the enzyme sAAT for 12 lizards representing three of the species in the *Cnemidophorus lemniscatus* complex. Abbreviations below the gel (a, b) refer to the different allele products. Abbreviations beside the gel refer to the species, as follows: c, *cryptus* (unisexual karyotype C lizards from Venezuela, named below; diploid heterozygotes; individual in lane five from the top is the holotype); g, *gramivagus* (bisexual karyotype E lizards from Brazil, diploids homozygous for the a-allele, referred to this species below); and l, *lemniscatus* (bisexual karyotype D lizards from Brazil, Suriname, and Venezuela [all illustrated on this gel being from Venezuela], diploids homozygous for the b-allele). The diploid unisexual lizards from Brazil had the same pattern of sAAT as those from Venezuela (heterozygous), and the triploids from Suriname were similar also but with two doses of the b-allele (genotype abb). Anode is to the right; arrow indicates positions of sample applications.

of bisexual type D animals from the Amazon (D Alt), whereas the Venezuelan diploid unisexuals (C Ven) have the b-allele characteristic of bisexual type D animals from more northern localities (D Boa, D Ven, and D Sur). This indicates that the diploid unisexuals along the Amazon and those from Venezuela are products of two separate hybrid origins, involving different populations of the same bisexual ancestors. For other examples of geographic variation in allele frequencies in *Cnemidophorus*, see Cole et al. (1988).

Allele combinations at PEPA in the triploids from Suriname (F Sur) fit this pattern of separate hybrid origins, stemming from backcross hybridization of the northern type of diploid unisexual (C Ven) × a northern bisexual type D male (D Boa, D Ven, or D Sur, table 2; fig. 4), consistent with their geographic distribution. This conclusion for the triploids is also supported by the alleles at the sMEP and mAH loci (table 2). In fact, the a-allele of mAH is known to date only for the bisexuals from Suriname (D Sur). Alleles at other loci (e.g., ESTD) also show geographic variation (table 2).

Hybrid Origins

Our results strongly support the conclusions of Sites et al. (1990) and Vyas et al. (1990) and the conclusions and predictions of Dessauer and Cole (1989), as follows: (1) diploid lizards with karyotype D and those with karyotype E represent two separate bisexual species that are genetically distinct even if not so distinct morphologically; (2) the species with karyotype D has a broad distribution in the Guiana Region, including parts of Brazil, Venezuela, and Suriname, at least (fig. 5), but probably also including parts of Guyana and French Guiana; (3) currently, the bisexual species with karyotype E is known from only two localities along the Amazon, in Brazil (Peccinini-Seale and Frota-Pessoa, 1974; Sites et al., 1990; Vyas et al., 1990; but see section on Taxonomy, below); (4) the unisexual lizards of karyotypes B and C from Brazil are clones that ultimately originated by hybridization between lizards of karyotypes D and E (types A and B probably arose by mutation in one or more ancestral parthenogenetic lineages of unisexual karyotype C); and (5) the triploid unisexual populations (here referred to as type F) from Suriname represent a clone that originated by hybridization between one or more unisexual lizards of karyotype C and one or more males of karyotype D (ultimately, a double hybrid origin of [D × E] × D).

In addition, we suggest that the newly discovered diploid unisexual sample of karyotype C from Icabaru, State of Bolivar, Venezuela, represents a clone, as all four specimens examined had identical allele combinations at all 28 loci examined in each

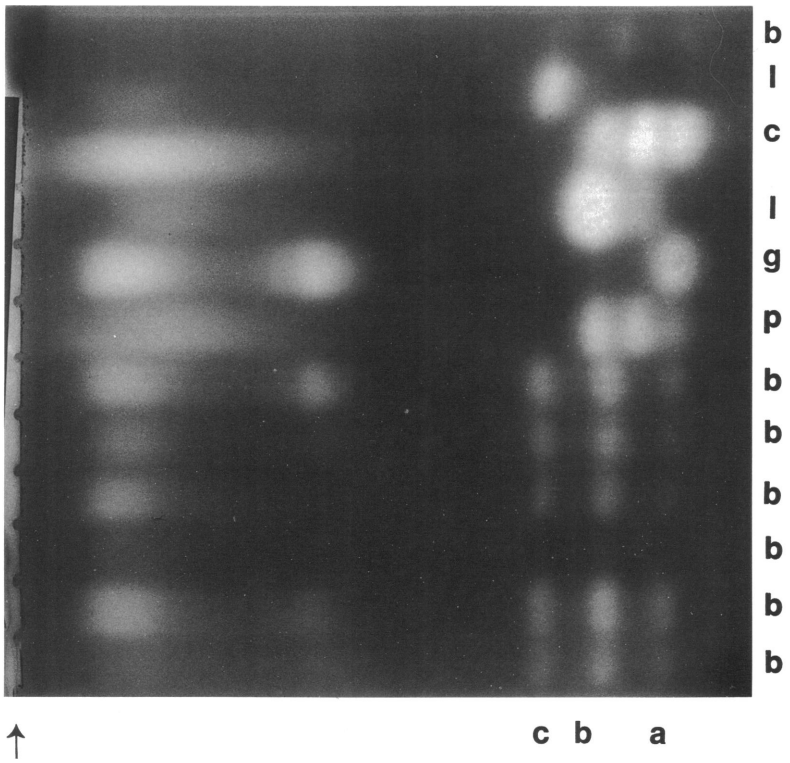

Fig. 4. Electrophoretic patterns of the enzyme PEPA for 12 lizards representing the four species in the *Cnemidophorus lemniscatus* complex. Abbreviations, anode, and arrow are as in figure 3, with the following abbreviations added beside the gel: b, diploid unisexual lizards of karyotypes B and C from Brazil; and p, *pseudolemniscatus* (triploid unisexual lizard of karyotype F from Suriname, named below). Note that *gramivagus* is homozygous for the a-allele, *lemniscatus* from Venezuela (fourth lane from top) is homozygous for the b-allele, *lemniscatus* from Alter do Chao, Brazil (second lane from top) is homozygous for the c-allele, *cryptus* from Venezuela (third lane from top; this is the holotype) is heterozygous with the ab genotype, *cryptus* from Brazil (top lane and bottom six lanes) is heterozygous with the ac genotype, and the triploid *pseudolemniscatus* from Suriname is heterozygous with the abb genotype, all indicating that the unisexuals from Brazil had a hybrid origin separate from those of Venezuela and Suriname.

animal, with five loci bearing alleles in the heterozygous state (H = 18%) and no evidence of Mendelian inheritance. This clone also appears to have originated by hybridization between lizards of karyotypes D and E, having a complete haploid set from each of the chromosomes (fig. 1B) and genes detected by protein electrophoresis (table 2; figs. 3, 4), with the exception of only one allele (at sMEP, discussed above) out of the loci resolved in these lizards (up to 32).

Diploid unisexual lizards of karyotype C from Venezuela are separated by approximately 1800 km from those in eastern Brazil (fig. 5). Lizards from these two widely separated areas appear to be karyotypically identical, and their genes detected by electrophoresis are almost identical also, excepting one allele each at two loci (sMEP and PEPA, discussed above; table 2; fig. 4). These exceptional alleles suggest that the diploid unisexual lizards along the Amazon and those to the north (Venezuela) had separate hybrid origins, and the triploids from Suriname share a common ancestry with the northern unisexual diploid clone (see above).

Reproduction

The 12 diploid unisexual Brazilian lizards of karyotypes B and C available to us and for which we collected the fullest suites of data

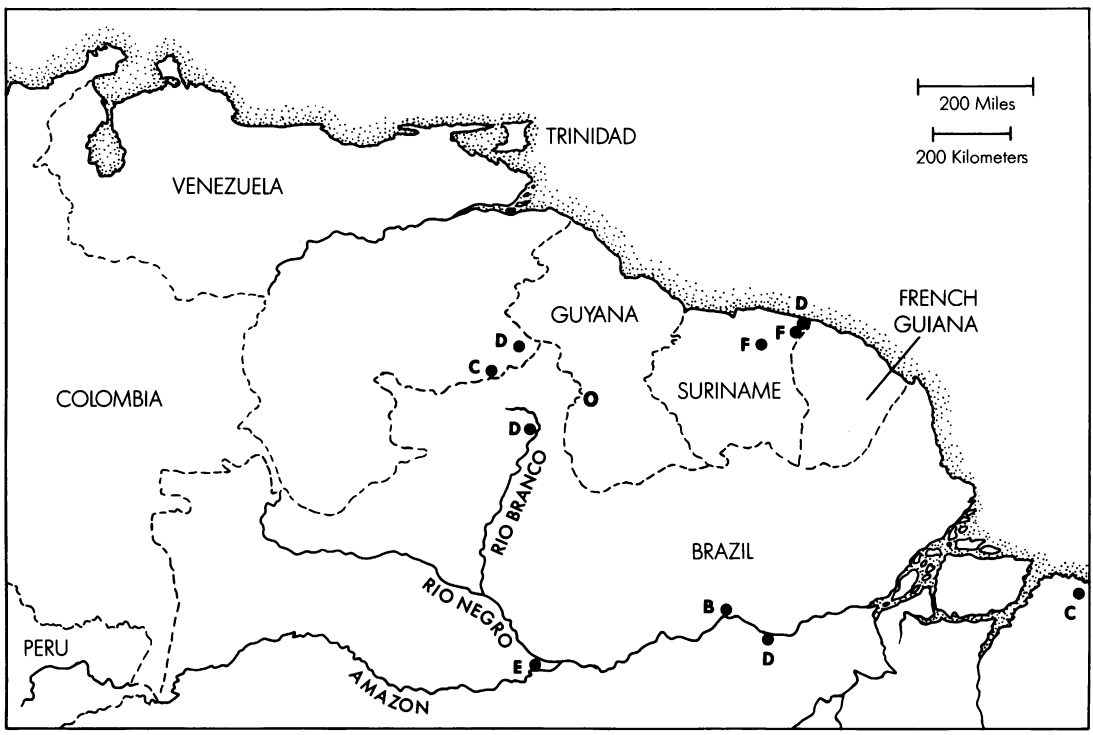

Fig. 5. Map of the Guiana Region of South America showing localities for samples of the *Cnemidophorus lemniscatus* complex compared here. The letters refer to the karyotype patterns as follows: B and C, unisexual diploids (named as *C. cryptus* below) from Brazil and Venezuela; D, bisexual diploids (*C. lemniscatus*) from Brazil, Suriname, and Venezuela; E, bisexual diploids (referred to *C. gramivagus* below) from Brazil; and F, unisexual triploids (named as *C. pseudolemniscatus* below) from Suriname. The open circle in southern Guyana represents lizards recently collected on the Rupununi Savanna (see Specimens Examined), which are morphologically typical of other specimens of *C. lemniscatus* with karyotype D. For Suriname, the southwesternmost F represents two sites—Brokopondo and Brownsweg; the easternmost F represents the type locality (Albina) of *C. pseudolemniscatus*. For Brazil, the easternmost C represents two sites—Capanema and Maruda. The C in southeastern Venezuela represents the type locality (Icabaru) of *C. cryptus*.

all had identical allele combinations at all loci examined, confirming the conclusions that heterozygosity is fixed and they have clonal inheritance (Sites et al., 1990). Because these lizards occur at localities lacking congeneric males, they are probably parthenogenetic (Vanzolini, 1970). Similar observations pertain to the diploid unisexual Venezuelan lizards of karyotype C, suggesting that they also have fixed heterozygosity, clonal inheritance, and parthenogenetic reproduction.

Evolutionary Scenario

Lizards in the *Cnemidophorus lemniscatus* complex prefer rather open habitats, such as savanna, rather than closed-canopy forest, and their evolutionary history may be similar to that of the microteiid *Gymnophthalmus underwoodi* (see Cole et al., 1989, 1990; Dessauer and Cole, 1989). During a past period of relatively low rainfall, an ancestral diploid bisexual species may have dispersed widely in a previously existing broad savanna region, at a time when forests were localized in smaller, isolated refugia in the Guiana Region (e.g., Haffer, 1979; Hoogmoed, 1979; Huber, 1987). Later, during a period of higher rainfall, forests spread from their refugia and became connected and continuous over a broader area, as the savanna became fragmented into refugia. The *Cnemidophorus* re-

mained with their preferred habitat, becoming genetically differentiated into separate bisexual species during allopatry, although stabilizing selection basically maintained their ancestral morphology, which was successful in the ancestral habitat; i.e., the ancestor evolved into two or more poorly differentiated species that continued to live in the ancestral habitat.

With the return of a drier climate again, the savannas spread from their refugia and became connected, while the forest became fragmented into refugia again. As formerly isolated savannas regained contact at their edges while expanding, the cryptic species of *Cnemidophorus* hybridized in contact zones. The male hybrids were sterile or essentially so, but one or a few female hybrids were viable and cloned themselves parthenogenetically, forming the diploid unisexual lineages that survive today. At least two separate hybridization events among the bisexual ancestors resulted in the origin of diploid parthenogens in the southern (Amazon) versus northern (Venezuelan) parts of the Guiana Region. Subsequently, backcross hybridization between a northern diploid parthenogen and northern male(s) of one of the bisexual ancestors (karyotype D) produced the northern triploid clone (Suriname; fig. 6). In addition, one or a few point mutations caused some genetic divergence among the diploid unisexual lineages along the Amazon. This scenario is the inverse of the forest refugium hypothesis that has been applied to explain the ecological and evolutionary history of forest birds and other organisms in Neotropica (e.g., Haffer, 1979; Hoogmoed, 1979; Capparella, 1988; Vanzolini and Heyer, 1988; Barrowclough, 1992). Other scenarios could apply also for part or all of this history, such as dispersal along ecologically disturbed and changing river systems and habitat modifications caused by mankind.

Implications for Biodiversity

Our attention was drawn to the Guiana Region by reports of the unisexual populations of *Cnemidophorus lemniscatus* and *Gymnophthalmus underwoodi* (see Vanzolini, 1970, 1976; Hoogmoed, 1973), and particularly by the suggestion that these did not have a hybrid origin. We now realize that the unisexual species did not appear to be of hybrid origin because the unisexual taxa and their bisexual ancestral taxa are morphologically similar species, although they have high degrees of genetic differentiation.

If it had not been for the unisexual populations, we and others would not have been conducting this comparative genetic research at this time, which clearly revealed that morphologically similar or even cryptic species have been involved in hybridization. For the *Gymnophthalmus underwoodi* complex we now know there are at least three cryptic species (Cole et al., 1989, 1990, 1993; Hoogmoed et al., 1992), and for the *Cnemidophorus lemniscatus* complex there are at least four species (Dessauer and Cole, 1989; Sites et al., 1990; Vyas et al., 1990; Wright, 1993; and see Taxonomy, below).

What does this mean in terms of other species of lizards and other organisms in the Guiana Region? If the Evolutionary Scenario (see above) is correct, morphologically similar or cryptic species of bisexual taxa differentiated genetically during isolation in refugia, while their morphological similarities may have been maintained by stabilizing selection. Hybridization occurred during subsequent habitat expansion from the refugia. The same process would apply, in an inverse fashion, for either savanna or forest-dwelling organisms. If hybridization had not occurred among the similar or cryptic bisexual species and produced the unisexual clones that we have investigated, or if the hybrids had been inviable or sterile and selected against (now extinct), then in some cases there would have been few clues to lead biologists to recognize the similar bisexual species with confidence.

The distances across Amazonia (north-south and east-west) and adjacent regions are vast, particularly for organisms of low vagility. Erosion of montane plateaus such as the Guiana Shield (which has been above sea level throughout the entire history of the vertebrates), formation and erosion of significant mountains such as the Andes, huge rivers (which change course), alternating wetter and drier periods which affect distribution of major types of habitats, changes in sea level, and human land uses (such as logging or slash-and-burn agriculture) are all processes that

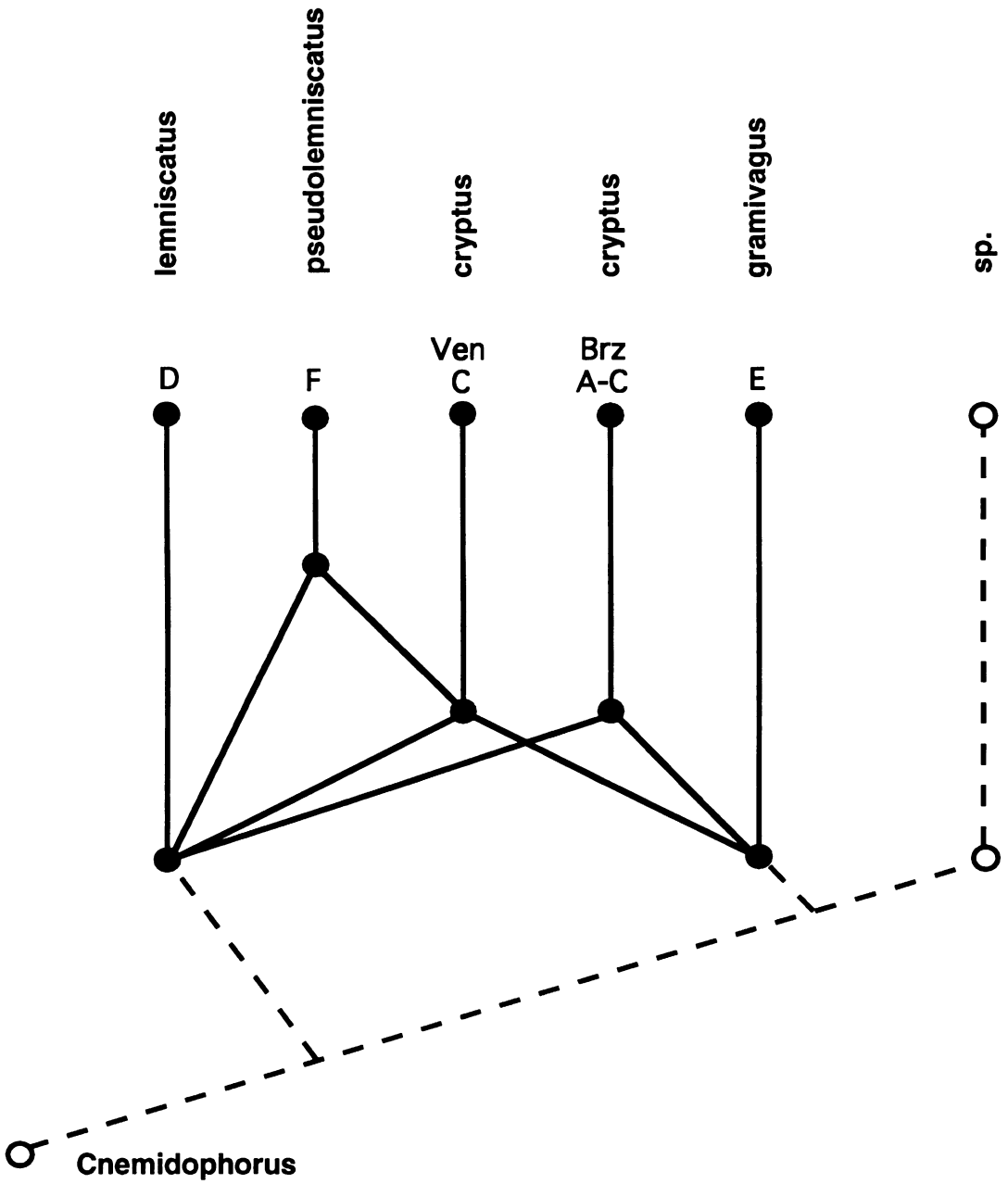

Fig. 6. Diagram of phylogenetic relationships of the species of the *Cnemidophorus lemniscatus* complex as discussed here. Abbreviations are as follows: letters above each solid terminus, karyotype designations; Brz and Ven, specimens from Brazil and Venezuela, respectively; sp., undesignated species.

fragment animal and plant distributions, while causing extinction of populations with highly localized distributions. Fragmentation is the precursor for genetic differentiation of populations that survive in isolation.

Comparative morphology suggests that many species of animals and plants are broadly distributed within the huge area of Amazonia. We suggest, however, that comparative genetic research involving widely

separated population samples of these taxa may reveal many more cryptic species masquerading under one name within broadly distributed species complexes, particularly for organisms of low vagility. In addition, improved understanding of geographic variation in gene frequencies within species and within complexes of cryptic species will improve understanding of the biogeography of tropical regions.

TAXONOMY

All clonal species of *Cnemidophorus* (and other teiids, sensu lato, including gymnophthalmids) that have been analyzed in detail are products of interspecific hybridization (for recent reviews, see Darevsky et al., 1985; Dessauer and Cole, 1989; Vrijenhoek et al., 1989; Cole et al., 1993; Wright, 1993). Data presented here confirm this also for the unisexual populations referred to *Cnemidophorus lemniscatus*, as discussed above, and the unisexual populations should not be considered as conspecific with their bisexual ancestors (e.g., Cole, 1985; Frost and Wright, 1988; Sites et al., 1990; Wright, 1993). At least four species exist in the *Cnemidophorus lemniscatus* complex discussed in this paper: (1) the diploid bisexual lizards with karyotype D; (2) the diploid bisexual lizards with karyotype E; (3) the diploid unisexual lizards of hybrid origin (karyotypes D × E); and (4) the triploid unisexual lizards of further (backcross) hybrid origin (karyotypes [D × E] × D). Some other herpetologists would split the unisexual lizards further (discussed below), but for now we address the issues of applying specific names to these four taxa.

In addition to gathering the karyotypic and genetic data discussed above, we examined and compared external morphological characters on specimens of the *Cnemidophorus lemniscatus* complex from Brazil, Venezuela, Guyana, and Suriname, as well as a series of *Cnemidophorus gramivagus* from Colombia. Specimens of the *C. lemniscatus* complex included representatives of the diploid bisexual type D and type E individuals from Brazil studied by Sites et al. (1990) and Vyas et al. (1990), the diploid unisexual type B and type C individuals from Brazil studied by the same authors, the diploid bisexual type D lizards and the triploids from Suriname studied by Dessauer and Cole (1989), and the bisexual and unisexual samples from Venezuela reported here; i.e., most of the same specimens for which the chromosomes and proteins were analyzed, plus others (see Appendix; Specimens Examined).

The following characters of scutellation were either basically invariant (except as noted) among all of the lizards examined or showed local variation that was not taxonomically useful: usually two frontoparietals; usually four (often 5) supraoculars on each side (usually 5 on type B and type C diploid unisexual lizards from Brazil); eight rows of ventral plates across abdomen; mesoptychials abruptly enlarged; postantebrachials granular; one enlarged anal spur on each side of males, but small nearly granular scales here in females (very rarely one somewhat enlarged scale); usually type I preanal scales (but rather consistently type III in specimens of type D bisexual lizards from Christiaankondre, Suriname); mean total number of circumorbital scales usually 12–14 (but usually fewer than 11 in unisexual lizards from Brazil); usually a total of 5–10 interlabial scales (but usually 10–12 in unisexual lizards from Venezuela and 8–11 in type E lizards from Brazil); usually one interlabial scale on each side considerably larger than the other(s) (but consistently two or three in unisexual diploids from Venezuela); usually 20–26 gular scales; mean number of granules around midbody usually 102–112 (but more in males of type D from Christiaankondre, Suriname, and only about 98 in unisexual lizards of type B from Brazil and type C from Venezuela); mean total number of femoral pores usually 41–48; usually two or three scales midventrally between femoral pore series on opposite legs; mean total number of toe lamellae usually 57–65 (but more in males of type D from Christiaankondre, Suriname); usually three or four particularly large, tubercular lamellae on each toe number three; total number of finger lamellae usually 28–37.

The number of parietal plates varied as follows. For bisexual samples, the number of parietals is usually five; if six, usually either the leftmost or rightmost is divided into anterior and posterior portions; if seven, usually both sidemost ones are so divided. Only the

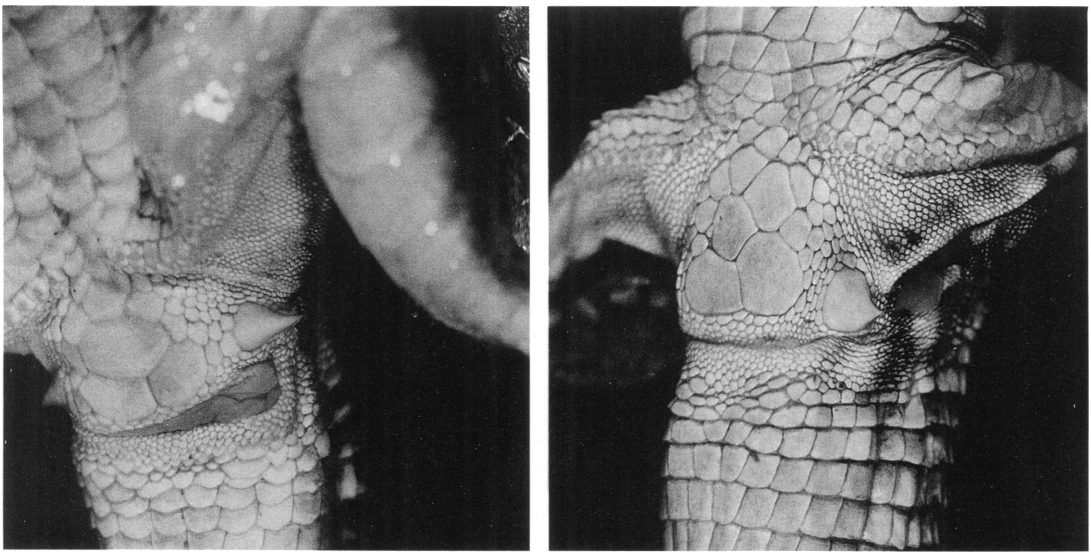

Fig. 7. Preanal region of *Cnemidophorus gramivagus* (left; AMNH 97425; male, body length 79 mm) and *Cnemidophorus lemniscatus* from Christiaankondre, Suriname (right; AMNH 133293; male, body length 81 mm), showing differences in morphology of enlarged preanal spurs on adult males of similar size.

described conditions for six and seven parietals (usually seven) were seen on the nine diploid unisexual lizards from Venezuela; only the conditions for seven or eight parietals (one endmost one divided into thirds) were seen on the 17 diploid unisexual lizards from Brazil; and for the 16 triploids from Suriname, conditions with five, six, and seven parietals were seen. Considering the unisexual samples from Suriname, all five lizards from Albina had seven parietals, all five lizards from Brownsweg had five parietals, and the six specimens from Brokopondo varied in having five to seven.

Similarly, there is variation in the presence (and number) or absence of tiny, irregular scales anterior to the eye and above the supralabials, between the supralabials and the typical array of facial plates (these might be called suprasupralabials). For bisexual samples, usually there are none of these scales (rarely 1–3 on one or both sides). The 17 diploid unisexual lizards from Brazil consistently had none of these scales, while six of the nine diploid unisexual lizards from Venezuela had from one to three scales per side and similar variation occurred on the triploids from Suriname (although the majority had none).

Two characters of scutellation merit further discussion: position of the nostril, and shape of the anal spur in males.

POSITION OF NOSTRIL: In *C. gramivagus* the nostril lies low in the suture between the nasal plates (McCrystal and Dixon, 1987), which is typical of members of the *lemniscatus* species group (Burt, 1931; Lowe et al., 1970). This condition occurs in all 25 of the *C. gramivagus* we examined and also in all 10 of the type E diploid bisexual lizards from Brazil plus the two juvenile type D diploid bisexual lizards from Brazil, the nostril being essentially centered (anterior to posterior) in the nasal suture. Alternatively, all 12 of the diploid bisexual type D *C. lemniscatus* from Venezuela and 11 out of 12 (92%) diploid bisexual type D *C. lemniscatus* from Suriname had the nostril low in the nasal suture but clearly more anteriad (or the suture was more posteriad) than in *C. gramivagus*, the exceptional lizard having the nostril as in *C. gramivagus*. Both conditions occurred in the 34 diploid bisexual lizards from Guyana (59% with the typical *C. lemniscatus* state). All of the unisexual lizards (diploid and triploid) have the nostril centered (anterior to posterior) in the nasal suture as in *C. gramivagus*, including those from Suriname (N = 16),

Venezuela (N = 9), and Brazil (N = 13 of type B + 4 of type C). Thus, the specific state of this character is useful in diagnosing *C. gramivagus* and the unisexual species, but it varies in *C. lemniscatus*. The sharing of this character in *C. gramivagus* and the type E diploid bisexual lizards from Brazil is similar to the distribution of the following character states also.

SHAPE OF ANAL SPUR IN MALES: All 17 of the male *C. gramivagus* we examined have anal spurs with an elongate point extending upward relatively close to the side of the body (fig. 7). This condition is shared by the two type E diploid bisexual males we examined from Manacapuru, Amazonas, Brazil (UMMZ 183883 and UMMZ 184302). However, in males of *C. lemniscatus* of type D from Suriname, Guyana, and Venezuela, the anal spurs are shorter and they project more from the side of the body (fig. 7), excepting one Venezuelan male with a more elongate and more projecting spine. Again, the type E diploid bisexual lizards share this character with *C. gramivagus*. A somewhat enlarged anal scale with very short spine very rarely occurs in females of *C. lemniscatus* and of unisexual samples.

SNOUT-VENT LENGTH: Males of *C. gramivagus* attain a larger body size than do females, and *C. gramivagus* attains a greater length than does *C. lemniscatus* (McCrystal and Dixon, 1987). Our data suggest also that males of *C. lemniscatus* grow larger than females. Although our data on snout-vent length are not as extensive as those of McCrystal and Dixon (1987), one point merits attention. For our samples of diploid bisexual type D *C. lemniscatus* from Suriname, Guyana, and Venezuela, the largest female is 69 mm in snout-vent length, whereas the largest female *C. gramivagus* from Colombia is 81 mm. The eight females we examined of the diploid bisexual type E lizards from Brazil all ranged from 69 to 85 mm in snout-vent length, again sharing this character with *C. gramivagus*.

COLOR PATTERN: McCrystal and Dixon (1987: 246–247) included the following in the diagnosis of *C. gramivagus*: "little to no spotting on the limbs; adults usually with only two longitudinal white, yellow or yellowish-green dorsolateral stripes, which may fade posteriorly or be totally absent; juveniles with two bold white or yellowish dorsolateral stripes separated from two faint white or yellowish dorsal stripes by longitudinal band of dark ground color, sometimes with faint lateral stripes." The "band of dark ground color" refers to a particularly dark longitudinal stripe that is conspicuously darker than the ground color elsewhere on the body. We confirmed these characters in the Colombian *C. gramivagus* we examined, and the type E diploid bisexual lizards from Brazil shared these characters also.

McCrystal and Dixon (1987) pointed out that juveniles of *C. lemniscatus* have 7–9 (actually up to 10; Hoogmoed, 1973) bold longitudinal light stripes (4–6 in *C. gramivagus*); a solid particularly dark ground color between the stripes (one thin, longitudinal, particularly dark stripe medially bordering the dorsolateral stripe in *C. gramivagus*); arms and legs with numerous light spots (no spots on arms, few on legs of *C. gramivagus*); and juveniles of both species may have lateral light spots but these are more conspicuous in *C. lemniscatus* than in *C. gramivagus*. McCrystal and Dixon (1987) also pointed out that adults of *C. lemniscatus* have five longitudinal light stripes (2 in *C. gramivagus*, but 3 of the 5 in large *C. lemniscatus* may be faint), faint light spots on the arms (usually none on *C. gramivagus*), and bold light spots on the legs (occasionally a few light spots on *C. gramivagus*). Our specimens of diploid bisexual type D lizards from Suriname, Guyana, and Venezuela fit *C. lemniscatus* in these characters, although some have 10 light dorsal stripes (if the vertebral stripe is split, as described by Hoogmoed, 1973), and all retain 2–3 very dark fields on each side of the body contrasting with the light stripes. Ontogenetic differences in the number of stripes (more in juveniles) involve the lateral stripes breaking up into spots as the lizards age. Also, the light spots on the arms become less conspicuous with age, but the light spots on the side of the head and neck become more conspicuous. The specimens of triploid and diploid unisexual samples from Suriname, Venezuela, and Brazil (types B and C) are also similar to the *C. lemniscatus* described above, except the largest Brazilian females have only one particularly dark longitudinal dark field on each side (below the paravertebral light line).

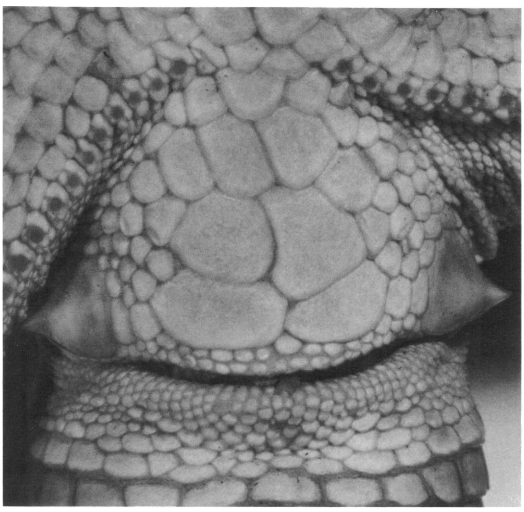

Fig. 8. Preanal region showing spurs and femoral pores on the lectotype of *Cnemidophorus lemniscatus*, NRM 126, male. Photo by Uno Samuelsson, Department of Paleozoology, arranged and provided by Sven O. Kullander, Department of Vertebrate Zoology, Swedish Museum of Natural History, Stockholm.

Conservatively, there are four species represented by these specimens: two diploid bisexual taxa, one diploid unisexual of hybrid origin, and one triploid unisexual of backcross hybrid origin. Names, diagnoses, and additional items are presented and discussed in the following species accounts, including designation of a lectotype of *C. lemniscatus* and rerestriction of its type locality.

Cnemidophorus lemniscatus (Linnaeus, 1758)

Figures 1, 2, 7, 8, 9, 11

DESIGNATION OF LECTOTYPE AND RERESTRICTION OF TYPE LOCALITY: Hoogmoed (1973: 41–44) discussed South American lizards named by Linnaeus. *Lacerta lemniscata* probably was based on specimens from an unspecified locality in Suriname, type material of which now resides at the Naturhistoriska Riksmuseet (NRM) in Stockholm, Sweden. There are three syntypes at NRM, two males (both formerly NRM 126, but see below) and one female (NRM 127) (Andersson, 1900; Hoogmoed, 1973; Sven O. Kullander, personal commun.). As these specimens "probably all originate from Dahlberg," who had two plantations at "the confluence of the Cottica River and the Perica Creek, Surinam" (Hoogmoed, 1973: 42–43), Hoogmoed so restricted the type locality.

Because of the antiquity of the name *C. lemniscatus*, its widespread application to populations in Central America and South America, the existence of both unisexual and bisexual populations in Suriname, and the diverse opinions concerning application of specific names to unisexual clones of lizards (e.g., Cole, 1985, 1990; Walker, 1986; Frost and Wright, 1988), it is desirable to fix this name to a relevant, widespread bisexual form. As the syntypes include both sexes (with locality unspecified), this can be accomplished by selecting one of the males to be the lectotype and by restricting the type locality to a site known to be inhabited by a relevant bisexual population (the restriction by Hoogmoed, 1973, was to a nearly coastal locality in northern Suriname that may well be appropriate but from which, to our knowledge, no specimens of *Cnemidophorus* are known).

The two male syntypes (NRM 126) are in equally good condition (Sven O. Kullander, personal commun.), one measuring 55 mm in snout-vent length (with a tail of 95 mm) and the other measuring 69 mm in snout-vent length (with a tail of 140 mm) (Andersson, 1900). We hereby designate the largest male as the lectotype (figs. 8, 9). Dr. Kullander informed us that the number NRM 126 will now continue to apply to the lectotype but only to that specimen, and the smaller specimen previously included has been renumbered as NRM 20126.

A locality of reasonable access near Hoogmoed's (1973: 42–43) restricted type locality and for which a bisexual population of *C. lemniscatus* is documented by series of specimens in major museums (Hoogmoed, 1973: 266; AMNH 133292–133303) is the following, which we hereby designate as the restricted type locality: South America: Suriname: Marowijne; Christiaankondre and Langamankondre, on the west bank of the Marowijne River. This locality is north of Albina near the mouth of the Marowijne River. The specimens we examined from Christiaankondre, Suriname, are consistent in important details with the lectotype (compare figs. 7 right, 8, 9, 11A), and this locality is

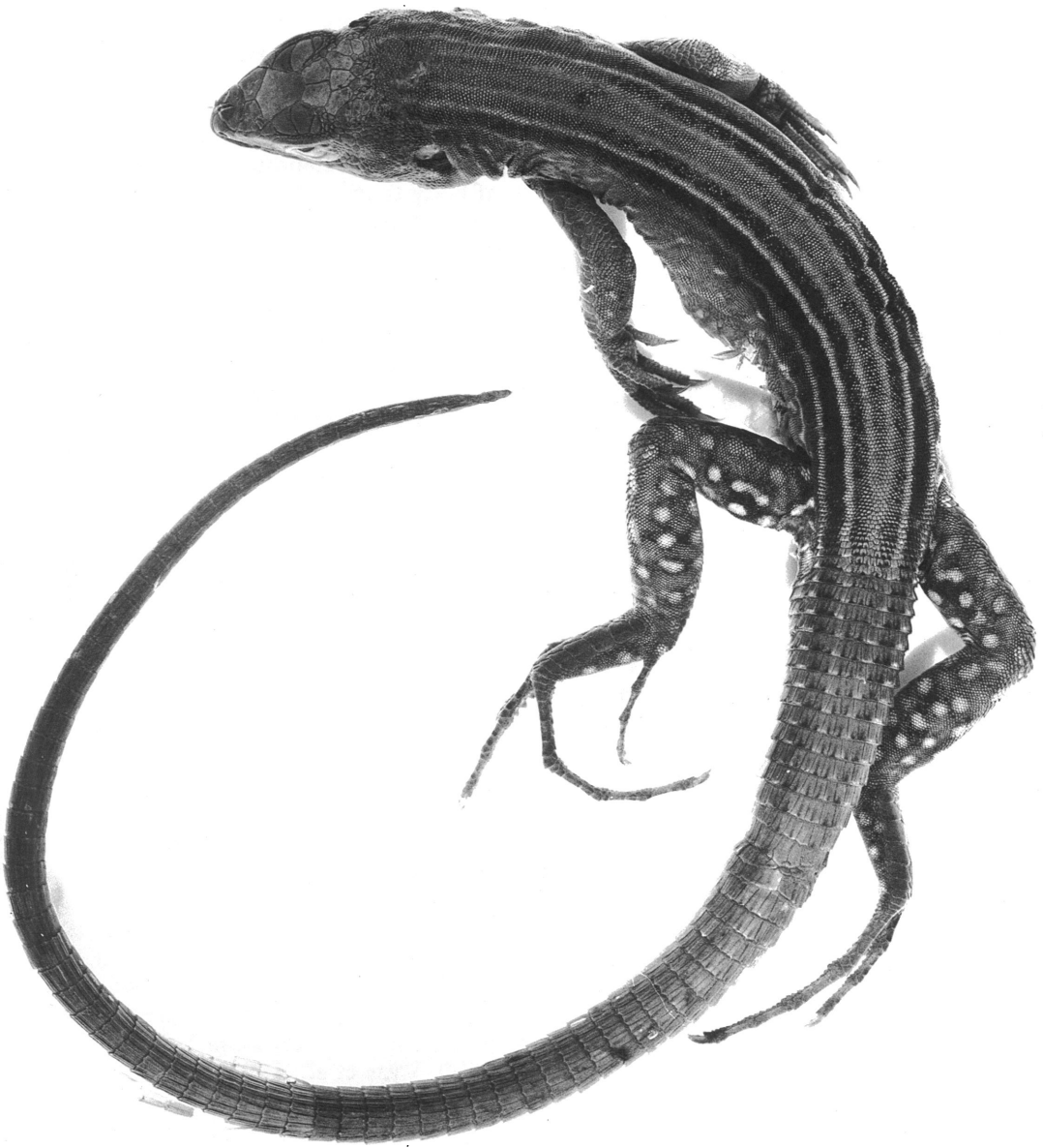

Fig. 9. Dorsal view of the lectotype of *Cnemidophorus lemniscatus*. Specimen and acknowledgments as in figure 8, body length 69 mm, tail length 140 mm.

only about 80 km (linear) E of the one suggested by Hoogmoed. Short distances can be significant, though, as Albina is less than 30 km (linear) S of Christiaankondre, and only unisexual *Cnemidophorus* are known from Albina (see below).

DIAGNOSIS: A cryptic species of the *Cnemidophorus lemniscatus* complex distinguished from all others in the genus by the following combination of characters: abruptly enlarged mesoptychials; granular postantebrachials; usually 2 frontoparietals; usually

5 parietals; usually 4 supraoculars each side; nostril usually somewhat anteriad within but still in suture between nasal plates; bisexual (gonochoristic; both sexes exist); males with 1 anal spur (shorter than in *C. gramivagus* and projecting more from side of body); adults with 2–5 longitudinal light stripes (7–10 in juveniles), 4–6 particularly dark stripes (6 or more in juveniles), numerous conspicuous light spots on legs (same in juveniles), faint light spots on arms (conspicuous in juveniles), conspicuous light spots laterally on body (inconspicuous or absent in juveniles); maximum snout-vent length about 98 mm; diploid number of 50 chromosomes, largest two being homomorphic pair of submetacentric to subtelocentric chromosomes.

DISTRIBUTION: The range includes northern Brazil, French Guiana, Suriname, Guyana, Venezuela, and Colombia, extending northward through Central America to Guatemala, plus the Republic of Trinidad and Tobago and other islands of the southern West Indies. These lizards prefer open and sunny habitats.

COMMENTS: The most recent, thorough descriptions and comparisons have been presented by Hoogmoed (1973: 262–273, who also presented a synonymy for *C. lemniscatus*) and McCrystal and Dixon (1987). Specimens of the *C. lemniscatus* complex occurring in bisexual populations and referred to as type D (or karyotype or cytotype D; e.g., Peccinini-Seale and Frota-Pessoa, 1974; Dessauer and Cole, 1989; Sites et al., 1990; Vyas et al., 1990) are *Cnemidophorus lemniscatus* as the name is applied here. Specimens with the alternative karyotypes (A–C and E and F) are referred to other species below.

Cnemidophorus gramivagus McCrystal and Dixon, 1987
Figure 7

The holotype, paratypes, and etymology were all described and discussed by McCrystal and Dixon, but the diagnosis is modified below in view of the data presented and discussed here.

DIAGNOSIS: A species of the *Cnemidophorus lemniscatus* complex distinguished from all others in the genus by the following combination of characters: abruptly enlarged mesoptychials; granular postantebrachials; usually 2 frontoparietals; usually 5 parietals; usually 4 supraoculars each side; nostril centered (anterior to posterior) within suture between nasal plates; bisexual (gonochoristic; both sexes exist); males with 1 anal spur (more elongate and extending upward closer to side of body than in *C. lemniscatus*); adults with 2 longitudinal light stripes (4–6 in juveniles), 2 particularly dark stripes (dorsal to the dorsolateral light stripes; one each side; similar in juveniles), few light spots on legs (similar in juveniles), no light spots on arms (similar in juveniles), conspicuous light spots laterally on body (inconspicuous or absent in juveniles); maximum snout-vent length over 115 mm; diploid number of 50 chromosomes, largest two being homomorphic pair of subtelocentric to telocentric chromosomes.

DISTRIBUTION: The range includes northwestern Brazil, Venezuela, and Colombia. These lizards prefer open and sunny habitats and "readily climbed trees and fence posts" (McCrystal and Dixon, 1987: 245; Dixon and Staton, 1977). To date, no locality is known where *C. gramivagus* is sympatric with *C. lemniscatus*, but such localities may be found in future fieldwork, particularly in northwestern Brazil and central Venezuela.

COMMENTS: The most recent, thorough description has been presented by McCrystal and Dixon (1987). Our comparative data on scutellation, size, and color pattern presented above lead to the conclusion that specimens of the *C. lemniscatus* complex occurring in bisexual populations and referred to as type E (or karyotype or cytotype E; e.g., Peccinini-Seale and Frota-Pessoa, 1974; Sites et al., 1990; Vyas et al., 1990) are *Cnemidophorus gramivagus*. This conclusion can be tested in the future by collecting Venezuelan samples of *C. gramivagus* to compare in karyotype and protein electrophoresis with fresh samples of the cytotype E lizards of Brazil. We predict that the Venezuelan lizards will be found to share the karyotypes and proteins of the Brazilian lizards.

Cnemidophorus cryptus, new species
Figures 1, 10

HOLOTYPE: AMNH 135089 (field number JC 5738; karyotype number 1756; frozen tissue number 1930), adult female, collected on

12 April 1989 by CJC, Carol R. Townsend, Carlos Guaveco, and Maria Jose Praderio in Icabaru, State of Bolivar, Venezuela. This locality is adjacent to the border with Roraima, Brazil, about 75 km (linear) WSW Santa Elena de Uairen, State of Bolivar, Venezuela. This is one of the specimens for which the full suite of morphological, karyotypic, and biochemical data are available.

PARATYPES: AMNH 134231–134237, and AMNH 135090, eight females collected with the holotype. UMMZ 183871–183874, 183876–183882, 184292, and 184294, a series of 13 females from Oriximina, Para, Brazil, collected by D. M. Peccinini-Seale and R. R. de Souza. UMMZ 184291, a female from Capanema, Para, Brazil, collected by D. M. Peccinini-Seale and R. R. de Souza. UMMZ 184298–184300, three females from Maruda, Para, Brazil, collected by D. M. Peccinini-Seale and R. R. de Souza.

ETYMOLOGY: The Latin adjective *cryptus* is derived from the Greek *kryptos*, meaning secret or hidden, as these lizards, particularly in the Venezuelan series, are very similar morphologically to *C. lemniscatus*. The Brazilian populations have been masquerading under the name *C. lemniscatus* until now, and some systematists would argue that two or more species are included here under the name *C. cryptus* (see Alternative Treatments, below).

DIAGNOSIS: A cryptic species of the *Cnemidophorus lemniscatus* complex distinguished from all others in the genus by the following combination of characters: abruptly enlarged mesoptychials; granular postantebrachials; usually 2 frontoparietals; usually 6 or 7 parietals (the rightmost and/or leftmost usually being divided into anterior and posterior portions); usually 4 or 5 supraoculars each side; nostril centered (anterior to posterior) within suture between nasal plates; unisexual (only females exist); adults usually with 5–7 longitudinal light stripes (8–9 in juveniles), 2–6 particularly dark stripes (4–6 or more in juveniles), numerous conspicuous light spots on legs (same in juveniles), faint light spots on arms (conspicuous in juveniles), conspicuous light spots laterally on body (inconspicuous or absent in juveniles); maximum snout-vent length about 70 mm; diploid number of 48–50 chromosomes (depending on clone), largest two being heteromorphic pair with one submetacentric to subtelocentric chromosome and one subtelocentric to telocentric chromosome.

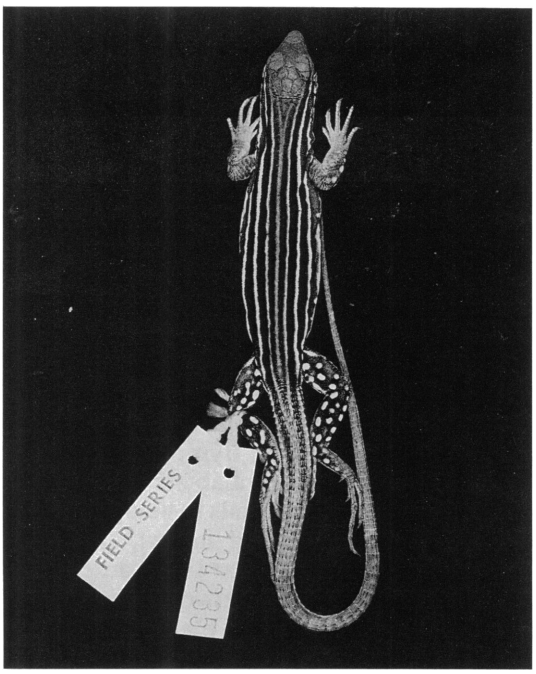

Fig. 10. Dorsal view of a paratype of *Cnemidophorus cryptus*, AMNH 134235, female, body length 49 mm.

DESCRIPTION OF THE HOLOTYPE: This largely follows the format and wording of Hoogmoed's (1973: 267–269) description of *C. lemniscatus*, but here is based on *C. cryptus*, AMNH 135089. Rostral pentagonal, visible from above, wider than deep. Nostril centered (anterior to posterior) but low in an obliquely divided nasal, the anterior parts forming a short median suture behind the rostral. A transversely oval frontonasal. A pair of irregularly pentagonal prefrontals, forming a short median suture. Frontal hexagonal, longer than wide, wider anteriorly than posteriorly. A pair of irregularly pentagonal frontoparietals, forming a long median suture. Seven irregularly shaped parietals in a transverse series, three large, medial, two on each side. At least five irregular, small occipitals. Back of head covered with small granules. Supraoculars 4; fourth smallest; second and third largest; separated from the supraciliaries by generally one row of granules, except first supraocular broadly contacts first supraciliary. Last supraocular separated

from frontoparietals by a row of small scales (circumorbital semicircles, 8 scales on left, 7 on right). Loreal large, more or less trapezoid. Preocular absent. A row of four suboculars, forming a suborbital ridge; the anterior subocular more or less in a preocular position, deeper than long; the third longest. An irregular row of four enlarged postoculars. Supraciliaries 6; the second one largest, the anterior two elongate, the posterior ones quadrangular. A row of enlarged supratemporals. Enlarged scales in front of ear opening; central region of temple with small, round to oval granules. Ear opening large, surrounded by small scales forming smooth margin; external auditory meatus short, tympanum clearly visible. Seven large supralabials followed by small ones; five supralabials to below the center of the eye; the third largest, the sixth smallest. Two tiny irregular scales anterior to eye, above supralabials, between supralabials and usual array of facial plates, each side. Lower eyelid with a semitransparent disc of five enlarged palpebrals. Pupil shape unclear.

Mental trapezoid with convex anterior margin. A pentagonal postmental. Six pairs of chinshields curving posteriad and dorsally to the infralabials; only the members of the anterior pair (largest) in contact at midline; from the second pair on separated from the labials by the interlabial scales (7 on each side). Seven enlarged anterior infralabials, followed by small scales; third infralabial largest.

Gulars small, flat, rounded, juxtaposed, slightly larger in the anterior part of the throat, smaller in the posterior part, which starts at level of ears. Scales (mesoptychials) in front of prepectoral fold abruptly enlarged, slightly imbricate, smooth. Scales on nape and side of neck similar to dorsal and lateral body scales.

Dorsal and lateral scales granular, in indistinct transverse and oblique rows. Ventrals large, rectangular, wider than long, imbricate, smooth, in eight longitudinal and in 30 transverse rows (shoulder to hip); the anterior rows in midventral area interrupted by a small triangular area of smaller scales. Total number of dorsal granules around midbody 101. Preanal area with four clearly enlarged smooth, irregularly shaped, juxtaposed scales plus smaller ones (preanal scutes are type I).

Femoral pores 23 (left)/24 (right); at least two in preanal position; each pore usually surrounded by three small scales (medial one largest in ring). Midventrally, three scales separate the femoral pore series of each side.

Scales on tail large, rectangular, obliquely keeled, slightly mucronate; imbricate, in transverse rows; keels forming longitudinal ridges. Scales under tail similar but narrower. Scales on regenerated part of tail small, irregular, keeled, in transverse rows. Tail round in cross section.

Scales on upper and anterior surfaces of upper arm, on anterior and lower surfaces of forearm, on anterior and lower surfaces of thighs, and on lower and posterior surfaces of lower legs large, smooth, more or less hexagonal, imbricate; on lower and posterior surfaces of upper arm, on posterior and upper surfaces of forearm, on posterior and upper surfaces of thighs and on upper and anterior surfaces of lower legs small, granular, juxtaposed (postantebrachials granular). Fourth finger lamellae number 17/17. Fourth toe lamellae number 30/31, usually single but divided under articulations. Approximately four triangular, strongly enlarged and tubercular scales under third toe, proximally. Fingers and toes compressed. Palms and soles with small, irregular, juxtaposed, flat scales. Upper surfaces of hands and feet with large, imbricate flat scales.

In preservative, back and flanks with nine light longitudinal stripes (including a single vertebral stripe) separated by dark stripes, of which six are black (lowest gray). The dorsolateral light stripe starts at posterior corner of eye and continues to tail. The vertebral stripe arises at the back of the head and continues to the base of the tail. The stripe between the vertebral and dorsolateral stripes arises at the posterior edge of the most lateral parietals and continues to the proximal part of the tail, merging with the other from the opposite side. The upper lateral stripe starts on the lower eyelid, passes over the ear opening and continues to the groin; the lower lateral stripe passes from the posterior edge of the ear opening over the arm to the groin. Side of head, neck, and body with white spots. Upper surfaces of hind limbs and arms brown or black, with scattered white spots. Back of thighs with a horizontal series of longitudi-

nally elongate white spots, continuing onto base of tail as a white stripe. Ventral parts white. Tail above brown with tan to white dorsolateral stripes on base; lower surface of tail white. Snout-vent length, 60 mm; tail regenerated. Hind limb approximately twice as long as arm. When laid along the body there is considerable overlap of arm and hind limb.

DISTRIBUTION: The range is disjunct, including Amazonian Brazil and the type locality in southeastern Venezuela. These lizards prefer open and sunny habitats, and to date are not known to be sympatric at any locality with other members of the *C. lemniscatus* complex.

COMMENTS: We apply the name *C. cryptus* to the diploid clones of hybrid origin involving karyotype D × karyotype E lizards of the *C. lemniscatus* complex (Dessauer and Cole, 1989; Sites et al., 1990; Vyas et al., 1990). Data presented above suggest that this origin was of hybridization between *C. lemniscatus* × *C. gramivagus* (fig. 6), and Vyas et al. (1990) presented evidence from mitochondrial DNA suggesting that *C. lemniscatus* was the maternal parent for at least one such cross. For now, we apply the name *C. cryptus* to lizards of karyotype C from Venezuela, reported here for the first time, and to lizards of karyotypes A, B, and C from Brazil (Peccinini-Seale and Frota-Pessoa, 1974; although we have not yet personally examined a lizard of type A). These karyotypic clones can be informally referred to as *C. cryptus* type A, *C. cryptus* type B, and *C. cryptus* type C. Other clones are recognizable also, as in variants having different combinations of alleles detected by protein electrophoresis (Sites et al., 1990). Our data suggest that the Amazonian lizards and the Venezuelan lizards here referred to *C. cryptus* had at least two separate hybrid origins involving the same two bisexual ancestors but at two different localities.

Cnemidophorus pseudolemniscatus, new species
Figures 2, 11

HOLOTYPE: AMNH 133304 (field number JC 5227; karyotype number 1731; frozen tissue number 1355), adult female, collected on 10 March 1986 by CJC and Carol R. Townsend in Albina, Marowijne District, Suriname. This is one of the specimens for which the full suite of morphological, karyotypic, and biochemical data are available.

PARATYPES: AMNH 133305–133307 and AMNH 135088, four females collected with the holotype. AMNH 119407–119411 and AMNH 133313, six females from Brokopondo, Brokopondo District, Suriname. AMNH 133308–133312, five females from Brownsweg, Brokopondo District, Suriname.

ETYMOLOGY: The name is in reference to the morphological similarity to *C. lemniscatus*, under which name these lizards have been masquerading until now.

DIAGNOSIS: A cryptic species of the *Cnemidophorus lemniscatus* complex distinguished from all others in the genus by the following combination of characters: abruptly enlarged mesoptychials; granular postantebrachials; usually 2 frontoparietals; 5–7 parietals (usually depending on endmost being divided or not into anterior and posterior portions); usually 4 supraoculars each side; nostril centered (anterior to posterior) within suture between nasal plates; unisexual (only females exist); adults usually with 5–7 longitudinal light stripes (9 in juveniles), 4 particularly dark stripes (6 in juveniles), numerous conspicuous light spots on legs (same in juveniles), faint light spots if any on arms (conspicuous in juveniles), conspicuous small light spots laterally on body (inconspicuous or absent in juveniles); maximum snout-vent length about 70 mm; triploid number of 75 chromosomes, largest three being heteromorphic with two submetacentric to subtelocentric chromosomes and one subtelocentric to telocentric chromosome.

DESCRIPTION OF THE HOLOTYPE: Rather than repeat the long list of traits and character states that are identical to those described above for the holotype of *C. cryptus*, we mention here only those conditions that differ from that specimen. A large, irregularly hexagonal frontonasal; supraoculars 4/5, separated from supraciliaries by generally two rows of granules; circumorbital semicircles 5/7; postoculars 5/4; two tiny irregular scales anterior to eye, above supralabials, between supralabials and usual array of facial plates, on right side only; pupil kidney shaped, indentation on ventral side; four interlabial

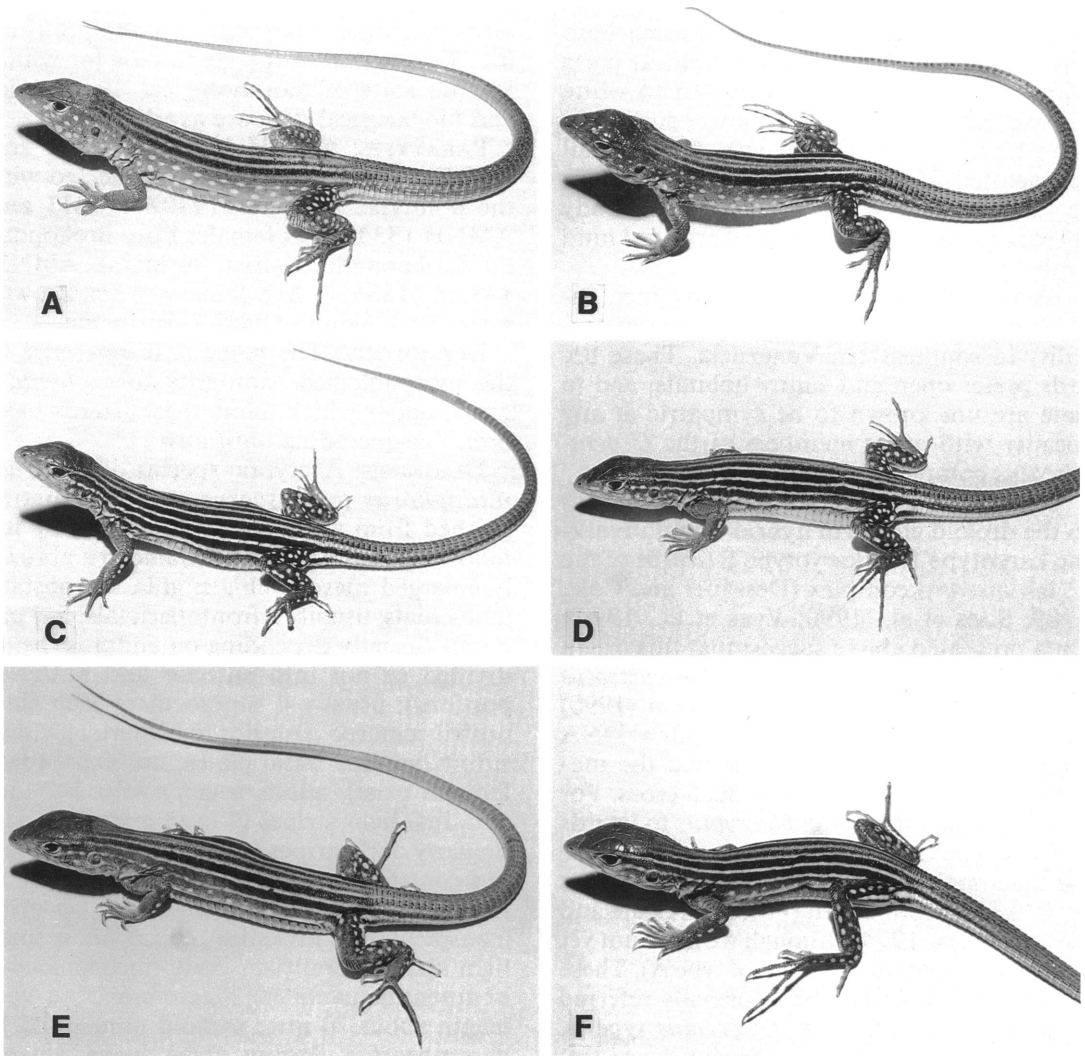

Fig. 11. Two species of the *Cnemidophorus lemniscatus* complex, *C. lemniscatus* (bisexual diploid; A–D) and *C. pseudolemniscatus* (unisexual triploid; E–F). **A,** AMNH 133295, male from Christiaankondre, Suriname, body length 86 mm. **B,** AMNH 138079, male from Yupukari, Guyana, body length 71 mm. **C,** AMNH 133302, female from Christiaankondre, Suriname, body length 63 mm. **D,** AMNH 133301, female from Christiaankondre, Suriname, body length 69 mm. **E,** AMNH 133307, female from Albina, Suriname, body length 65 mm. **F,** AMNH 133309, female from Brownsweg, Suriname, body length 49 mm.

scales on each side; granules around midbody number 105. Preanal area with 5 enlarged scales; femoral pores 22/23, two midventral scales separating the series of each side; fourth finger lamellae number 18/19; fourth toe lamellae number 32/31. In preservative, back with five light stripes and four black ones; lateral light stripes broken up into white spots; white spots not presently visible on arms (but this is the largest triploid female we have seen from Suriname, such spots are present on all others, and tan spots were present in life [see color notes below]). Lower surface of tail white at base, bluish distally. Snout-vent length, 70 mm; tail regenerated.

COLORATION OF THE HOLOTYPE IN LIFE: The following notes are paraphrased from the fieldnotes of CJC dated 8 April 1986, per-

taining to specimen number JC 5227 from Albina, Suriname. Upper body dark brown to black with tan stripes; trace of brown wash on neck; dorsolateral light stripe yellowish tan; sides brown with yellowish green spots and wash of greenish yellow; head tan with light green wash and light spots on sides; arms brown with tan spots and yellowish green wash; hands pale green; top of legs brown with numerous large beige spots; anteriorly, legs bright green; hands and feet brown, feet with green on anterior edge; tail tan above, bright chartreuse green on sides, bright yellowish green below (but light brown posterior to distally located point of regeneration); chin, throat, and underside of arms pale yellowish tan; chest greenish tan; abdomen tan but posteriorly becoming bright yellowish green, as on undersides of legs and tail.

DISTRIBUTION: These triploid unisexual lizards are known only from Suriname and French Guiana (Serena, 1985; Dessauer and Cole, 1989), and usually they are allopatric to populations of the diploid bisexual *C. lemniscatus* (Hoogmoed, 1973; Serena, 1985).

COMMENTS: We apply the name *C. pseudolemniscatus* to the triploid clone of hybrid origin involving a karyotype C diploid unisexual lizard × karyotype D male of the *C. lemniscatus* complex (Dessauer and Cole, 1989; fig. 2B here, designated as karyotype F). Present data and nomenclature suggest that this origin was of hybridization between *C. cryptus* × *C. lemniscatus* (fig. 6), as names are applied here.

ALTERNATIVE TREATMENTS

Some herpetologists would prefer taxonomic treatments different from ours, particularly for parthenogenetic lineages. Alternatives have been discussed or mentioned by Maslin (1968), Morafka (1977), Cole (1985, 1990), Walker (1986), Frost and Wright (1988), Wright (1993), and others. A review of all of this literature is beyond the scope of the present paper, but a few points should be noted with respect to the *Cnemidophorus lemniscatus* complex.

How many cryptic species are included among the diploid unisexual clones here relegated to *Cnemidophorus cryptus*? Types A, B, and C can be recognized and diagnosed by the morphology of their karyotypes, even though all three of these might ultimately share a common ancestor of one F_1 hybrid between *C. lemniscatus* × *C. gramivagus* (type D × type E; Vyas et al., 1990). Each clone could be named as a separate species, choosing as a significant historic event an aspect of the occurrence and establishment of those chromosome mutations (derived character states) that resulted in each diagnosable clone. However, mutations can occur anywhere in the genome, in mitochondrial DNA or in nuclear DNA, affecting the shape of chromosomes, allelic variants detected by protein electrophoresis, and other characters such as scutellation and color pattern. Such mutations usually produce variants at the level of organization similar to normal individual variation, particularly as seen also in bisexual species with Mendelian patterns of inheritance, and we do not consider these as the kind of significant historic events upon which separate species should be conceived and named if the practice of taxonomy is to be useful. We emphasize instead the shared ancestry of these clones by including them as variants in a species of hybrid origin (involving the same bisexual ancestral species but not necessarily the same ovum).

In the case of the diploid unisexual *C. cryptus* type C, we have presented evidence (above) for separate hybrid origins within the same ancestry (*C. lemniscatus* × *C. gramivagus*) for the populations in Brazil versus that in Venezuela. We emphasize their similar hybrid ancestry by including them in one species; we do not treat the fact that they probably stemmed from different F_1 hybrid individuals as a rationale for providing different names.

The evidence that *C. cryptus* type C of Venezuela stemmed from a different F_1 hybrid egg than did the *C. cryptus* type C of Brazil is in the electrophoretic data (based on geographic variation in both the unisexual and bisexual species). In particular, consider the locus PEPA (table 2; fig. 4). *Cnemidophorus cryptus* type C from Venezuela has the b-allele of *C. lemniscatus*, which characterizes its populations from Venezuela, northern Brazil (Boa Vista, Roraima), and Suriname. However, *C. cryptus* type C from Brazil has the c-allele of *C. lemniscatus*, which character-

izes its populations from the Amazon (Alter do Chao). Allelic variants at sMEP also support this conclusion, although alternative explanations are possible (e.g., what appear electrophoretically to be the product of one allele may actually be two different proteins with the same mobility, one derived by point mutation within a parthenogenetic lineage).

The diploid unisexual lizards of type C from Venezuela usually have 4 supraoculars on each side, those from Brazil usually 5. The number of gulars in Venezuela is 19–21, in Brazil 23–25. The total number of circumorbital scales in Venezuela is 12–16, in Brazil 8–12. The number of equally large scales among the largest interlabials in Venezuela is 2–3, in Brazil 1. Adults of the Venezuelan lizards have (on each side) two or three particularly dark stripes among the dark fields, whereas adult Brazilian lizards appear to have only one (below the paravertebral light line; most Brazilian specimens we examined, however, were darkened in preservative).

Although our sample sizes are small (N = 9 type C from Venezuela, N = 0 type A from Brazil, N = 13 type B from Brazil, and N = 4 type C from Brazil), and most of the Brazilian lizards available to us are preservative darkened, it does appear as if the two geographically separated hybrid events captured and cloned different parts of the spectrum of morphological variation that occurs in the bisexual ancestors, and the resulting unisexual forms probably could be diagnosed morphologically. In other instances of separate hybrid origins, particularly those involving separate zygotes in the same clutch of eggs produced by the same individual parents, electrophoretic characters might be the only ones to use to diagnose clones if any evidence is available at all.

It also seems appropriate, particularly in the context of utility and stability of nomenclature, to question how robust the conclusions of separate hybrid origins are for parthenogenetic lineages. For example, morphological characters such as those just discussed could diverge by mutation from a parthenogenetic common ancestor, as may best explain karyotypes A, B, and C in Brazil (Vyas et al., 1990; and see above). A mutation at PEPA (table 2; fig. 4) and limitations in interpreting electrophoretic results (see above) could also be involved. For another example, if the parthenogenetic ancestor of the type C unisexual lizards from Venezuela originally had both the a- and b-alleles at sMEP, gene conversion from the b-allele of sMEP to the a-allele (see Hillis et al., 1991) or a mutation in the ancestral b-allele to produce either a null allele or an allele the product of which has the same mobility as the a-allele, could explain our results (table 2). Either of these events could have occurred in a parthenogenetic common ancestor of all of the type C lizards, although the hypothesis that the different type C clones in Brazil and Venezuela had separate hybrid origins is the most parsimonious for existing data, particularly considering PEPA.

The data suggesting that the diploid unisexual lizards from Venezuela and Brazil share the same basic hybrid origin (i.e., the same ancestral species, *C. lemniscatus* × *C. gramivagus*) are particularly robust. We emphasize that similar heritage by considering these parthenogenetic lizards as one species, *C. cryptus*. We are interested in supporting and continuing research on additional evolutionary questions and matters concerning population genetics, but we do not consider the question of how many separate F_1 zygotes produced separate clones as helpful in producing a useful and stable taxonomy, even though this is an extremely interesting area of investigation for geneticists, evolutionary biologists, and biogeographers.

SUMMARY AND CONCLUSIONS

1. Until recently, at least four species have been masquerading under the name *Cnemidophorus lemniscatus* in the Guiana Region of northern South America.

2. Two of these are the following diploid bisexual species: *C. lemniscatus* (Linnaeus, 1758) and *C. gramivagus* McCrystal and Dixon, 1987.

3. The other two are unisexual species that are diagnosed and named here as follows: *C. cryptus*, new species, a diploid species consisting of several clones in Brazil and Venezuela; and *C. pseudolemniscatus*, new species, a triploid species occurring in Suriname and French Guiana.

4. Karyotypic data and electrophoretic

data representing 32 gene loci of these lizards have been compared in samples from Brazil, Suriname, and Venezuela, and morphological comparisons include these specimens plus new samples from Guyana.

5. *Cnemidophorus cryptus* is a diploid parthenogenetic species that originated from hybridization between *C. lemniscatus* × *C. gramivagus*.

6. Several clones of *C. cryptus* exist, each demonstrating fixed heterozygosity in a series of karyotypic and electrophoretic characters.

7. Alleles at two loci (sMEP and PEPA) suggest that the clone of *C. cryptus* from Venezuela had a hybrid origin separate from the clones in Brazil, although the same species of bisexual ancestors (different populations) were involved.

8. *Cnemidophorus pseudolemniscatus* is a triploid parthenogenetic species that originated from hybridization between *C. cryptus* × *C. lemniscatus*. In terms of the diploid bisexual ancestors, *C. pseudolemniscatus* has two genomes from *C. lemniscatus* and one from *C. gramivagus*.

9. The clone of *C. cryptus* involved in the hybrid origin of *C. pseudolemniscatus* was more similar to that of the type locality (Venezuela) than to those occurring to the south, along the Amazon.

10. The male of *C. lemniscatus* involved in the origin of *C. pseudolemniscatus* was also from a more northern population in South America, rather than one along the Amazon.

11. The overall morphological similarity of the lizards in the *Cnemidophorus lemniscatus* complex has obscured their taxonomy and relationships for a long time, and many problems remain to be resolved. For these and other organisms, karyotypic and particularly biochemical investigations show considerable potential for revealing relationships in further detail and improving our understanding of the biodiversity and biogeography of Neotropica.

REFERENCES

Andersson, L. G.
1900. Catalogue of Linnean type-specimens of Linnaeus's Reptilia in the Royal Museum in Stockholm. Bihang Till K. Svenska Vet.-Akad. Handl. 26: 1–29.

Barrowclough, G. F.
1992. Systematics, biodiversity, and conservation biology. *In* N. Eldredge (ed.), Systematics, ecology, and the biodiversity crisis, pp. 121–143. New York: Columbia Univ. Press.

Burt, C. E.
1931. A study of the teiid lizards of the genus *Cnemidophorus* with special reference to their phylogenetic relationships. U.S. Natl. Mus. Bull. 154:1–286.

Capparella, A. P.
1988. Genetic variation in neotropical birds: Implications for the speciation process. *In* H. Ouellet (ed.), Acta XIX Congressus Internationalis Ornithologici 2: 1658–1673. Natl. Mus. Nat. Sci., Ottawa: Univ. Ottawa Press.

Cole, C. J.
1979. Chromosome inheritance in parthenogenetic lizards and evolution of allopolyploidy in reptiles. J. Hered. 70: 95–102.
1985. Taxonomy of parthenogenetic species of hybrid origin. Syst. Zool. 34: 359–363.
1990. When is an individual not a species? Herpetologica 46: 104–108.

Cole, C. J., H. C. Dessauer, and G. F. Barrowclough
1988. Hybrid origin of a unisexual species of whiptail lizard, *Cnemidophorus neomexicanus*, in western North America: new evidence and a review. Am. Mus. Novitates 2905: 38 pp.

Cole, C. J., C. R. Townsend, H. C. Dessauer, and L. M. Hardy
1989. A lizard foretold. Nat. Hist., May, 1989: 12–17.

Cole, C. J., H. C. Dessauer, C. R. Townsend, and M. G. Arnold
1990. Unisexual lizards of the genus *Gymnophthalmus* (Reptilia: Teiidae) in the Neotropics: Genetics, origin, and systematics. Am. Mus. Novitates 2994: 29 pp.

Cole, C. J., H. C. Dessauer, and A. L. Markezich

1993. Missing link found: The second ancestor of *Gymnophthalmus underwoodi* (Squamata: Teiidae), a South American unisexual lizard of hybrid origin. Am. Mus. Novitates 3055: 13 pp.

Darevsky, I. S., L. A. Kupriyanova, and T. Uzzell
1985. Parthenogenesis in reptiles. *In* C. Gans and F. Billett (eds.), Biology of the Reptilia 15: 411–526. New York: Wiley.

Dessauer, H. C., and C. J. Cole
1989. Diversity between and within nominal forms of unisexual teiid lizards. *In* R. M. Dawley and J. P. Bogart (eds.), Evolution and ecology of unisexual vertebrates, pp. 49–71. Bull. 466, New York State Mus., Albany, v + 302 pp.

Dessauer, H. C., C. J. Cole, and M. S. Hafner
1990. Collection and storage of tissues. *In* D. M. Hillis and C. Moritz (eds.), Molecular systematics, pp. 25–41. Sunderland, MA: Sinauer.

Dixon, J. R., and M. A. Staton
1977. Arboreality in the teiid lizard *Cnemidophorus lemniscatus* (Reptilia, Lacertilia, Teiidae) in the Venezuelan Llanos. J. Herpetol. 11: 108–111.

Donnelly, M. A., R. W. McDiarmid, and C. W. Myers
1992. A new lizard of the genus *Arthrosaura* (Teiidae) from southern Venezuela. Proc. Biol. Soc. Washington. 105: 821–833.

Frost, D. R., and J. W. Wright
1988. The taxonomy of uniparental species, with special reference to parthenogenetic *Cnemidophorus* (Squamata: Teiidae). Syst. Zool. 37: 200–209.

Giblett, E. R., C. G. Hickman, and O. Smithies
1959. Serum transferrins. Nature 183(4659): 1589–1590.

Haffer, J.
1979. Quaternary biogeography of tropical lowland South America. *In* W. E. Duellman (ed.), The South American herpetofauna: its origin, evolution, and dispersal, pp. 107–140. Monogr. No. 7, Mus. Nat. Hist., Univ. Kansas, 485 pp.

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

Hillis, D. M., C. Moritz, C. A. Porter, and R. J. Baker
1991. Evidence for biased gene conversion in concerted evolution of ribosomal DNA. Science 251: 308–310.

Hoogmoed, M. S.
1973. Notes on the herpetofauna of Surinam. IV. The lizards and amphisbaenians of Surinam. The Hague: W. Junk, ix + 419 pp.
1979. The herpetofauna of the Guianan Region. *In* W. E. Duellman (ed.), The South American herpetofauna: its origin, evolution, and dispersal, pp. 241–279. Monogr. No. 7, Mus. Nat. Hist., Univ. Kansas, 485 pp.

Hoogmoed, M. S., C. J. Cole, and J. Ayarzaguena
1992. A new cryptic species of lizard (Sauria: Teiidae: *Gymnophthalmus*) from Venezuela. Zool. Meded. 66(1): 1–18.

Huber, O.
1987. Neotropical savannas: their flora and vegetation. Trends Ecol. Evol. 2(3): 67–71.

Linnaeus, C.
1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymus, locis. Ed. 10, vol. 1: 1–823. Laurentius Salvius, Stockholm.

Lowe, C. H., J. W. Wright, C. J. Cole, and R. L. Bezy
1970. Chromosomes and evolution of the species groups of *Cnemidophorus* (Reptilia: Teiidae). Syst. Zool. 19: 128–141.

Maslin, T. P.
1968. Taxonomic problems in parthenogenetic vertebrates. Syst. Zool. 17: 219–231.

McCrystal, H. K., and J. R. Dixon
1987. A new species of *Cnemidophorus* (Sauria: Teiidae) from the Llanos of Colombia and Venezuela. J. Herpetol. 21: 245–254.

Morafka, D. J.
1977. A biogeographical analysis of the Chihuahuan Desert through its herpetofauna. Biogeographica 9: viii + 313 pp. The Hague: Dr. W. Junk.

Murphy, R. W., J. W. Sites, Jr., D. G. Buth, and C. H. Haufler
1990. Proteins I: Isozyme electrophoresis. *In* D. M. Hillis and C. Moritz (eds.), Molecular systematics, pp. 45–126. Sunderland, MA: Sinauer.

Peccinini-Seale, D., and O. Frota-Pessoa
1974. Structural heterozygosity in parthenogenetic populations of *Cnemidophorus lemniscatus* (Sauria, Teiidae) from the Amazonas Valley. Chromosoma 47: 439–451.

Serena, M.
1985. Zoogeography of parthenogenetic whiptail lizards (*Cnemidophorus lemniscatus*) in the Guianas: evidence from skin

grafts, karyotypes, and erythrocyte areas. J. Biogeogr. 12: 49–56.

Shaklee, J. B., F. W. Allendorf, D. C. Morizot, and G. S. Whitt
1989. Genetic nomenclature of protein-coding loci in fish. Trans. Am. Fish. Soc. 118: 218–227.

Sites, J. W. Jr., D. M. Peccinini-Seale, C. Moritz, J. W. Wright, and W. M. Brown
1990. The evolutionary history of parthenogenetic *Cnemidophorus lemniscatus* (Sauria, Teiidae). I. Evidence for a hybrid origin. Evolution 44: 906–921.

Smithies, O.
1959. Zone electrophoresis in starch gels and its application to studies of serum proteins. Adv. Protein Chem. 14: 65–113.

Vanzolini, P. E.
1970. Unisexual *Cnemidophorus lemniscatus* in the Amazonas Valley: a preliminary note (Sauria, Teiidae). Pap. Avulsos Zool. (São Paulo) 23: 63–68.
1976. On the presence of males in *Gymnophthalmus underwoodi*, a presumed all-female lizard species (Sauria, Teiidae). Ibid., 29: 177–179.

Vanzolini, P. E., and W. R. Heyer (eds.)
1988. Proceedings of a workshop on neotropical distribution patterns. Acad. Brasileira Cienc., Rio de Janeiro, 488 pp.

Vrijenhoek, R. C., R. M. Dawley, C. J. Cole, and J. P. Bogart
1989. A list of the known unisexual vertebrates. *In* R. M. Dawley and J. P. Bogart (eds.), Evolution and ecology of unisexual vertebrates, pp. 19–23. Bull. 466, New York State Mus., Albany, v + 302 pp.

Vyas, D. K., C. Moritz, D. Peccinini-Seale, J. W. Wright, and W. M. Brown
1990. The evolutionary history of parthenogenetic *Cnemidophorus lemniscatus* (Sauria, Teiidae). II. Maternal origin and age inferred from mitochondrial DNA analyses. Evolution 44: 922–932.

Walker, J. M.
1986. The taxonomy of parthenogenetic species of hybrid origin: Cloned hybrid populations of *Cnemidophorus* (Sauria: Teiidae). Syst. Zool. 35: 427–440.

Wright, J. W.
1993. Evolution of the lizards of the genus *Cnemidophorus*. *In* J. W. Wright and L. J. Vitt (eds.), Biology of whiptail lizards (genus *Cnemidophorus*), pp. 27–81. Oklahoma Mus. Nat. Hist., Norman, xiv + 417 pp.

APPENDIX
Specimens Examined

The 170 specimens are referred to by their individual catalog numbers and initials for their respective collections, as follows: AMNH (American Museum of Natural History); CM (Craig Moritz—for some of the Brazilian homogenates used and reported also by Sites et al. [1990]); and UMMZ (University of Michigan Museum of Zoology, with thanks to Arnold Kluge; these specimens also were used and reported by Sites et al. [1990]). The lowercase letters following the catalog numbers indicate the kind of data taken from each specimen, as follows: e, external morphology; k, karyotype; p, protein electrophoresis.

Cnemidophorus cryptus

Type locality, VENEZUELA: State of Bolivar; Icabaru (holotype, AMNH 135089, e, k, p; AMNH 134231–134232, e, p; AMNH 134233, e; AMNH 134234, e, p; AMNH 134235–134237, e; AMNH 135090, e, k). BRAZIL: State of Para; Oriximina (CM 229–233, p; UMMZ 183871–183874, e, p; UMMZ 183876–183881, e, p; UMMZ 183882, e; UMMZ 184292, e, p; and UMMZ 184294, e, p); Capanema (UMMZ 184291, e, p); Maruda (UMMZ 184298–184300, e, p); and homogenates of karyotype C lizards from either Capanema or Maruda but unspecified when provided to us (CM 238–241 and CM 243–246, p).

Cnemidophorus gramivagus

BRAZIL: Amazonas; Manacapuru (UMMZ 183883–183887, e, p; UMMZ 184293, e, p; UMMZ 184295 e, p; UMMZ 184301–184303, e, p; and CM 221–225, p). COLOMBIA: Department of Arauca; Cravo Norte (AMNH 97410–97434, e).

Cnemidophorus lemniscatus

BRAZIL: State of Para; Alter do Chao (UMMZ 184296, e, p; UMMZ 184297, e; CM 234–237, p; CM 242, p; CM 248–249, p; CM 269, p; and CM 277, p). State of Roraima; Boa Vista (CM 226–228, p; CM 247, p). GUYANA: northern Rupununi Savanna; Jouri, 33 km (linear) NW Karanambo (AMNH 138109–138110, e); Karasabai Vil-

lage, 42 km (linear) NW Karanambo (AMNH 138099–138108, e); Yupukari (on the Rupununi River), 12 km (linear) SSW Karanambo (AMNH 138058–138062, e; AMNH 138065–138079, e; and AMNH 138081–138082, e). SURINAME: Marowijne District; Christiaankondre, near the mouth of the Marowijne River (AMNH 133292–133293, e, k, p; AMNH 133294–133297, e, p; AMNH 133298–133299, e; and AMNH 133300–133303, e, k, p). VENEZUELA: State of Bolivar; San Ignacio de Yuruani (AMNH 134221, e; AMNH 134222–134228, e, p; AMNH 134229–134230, e; AMNH 135091, e, k, p; and AMNH 135092, e, p).

Cnemidophorus pseudolemniscatus

Type locality, SURINAME: Marowijne District; Albina (holotype, AMNH 133304, e, k, p; AMNH 133305, e, k, p; AMNH 133306–133307, e, p; and AMNH 135088, e). Brokopondo District; Brokopondo (AMNH 119407–119411, e; AMNH 133313, e, k, p); Brownsweg (AMNH 133308–133309, e, k, p; AMNH 133310 e, p; and AMNH 133311–133312, e).