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Kentropyx borckiana (Squamata: Teiidae): A Unisexual Lizard of Hybrid Origin in the Guiana Region, South America

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ABSTRACT

More than 100 females and yet no males of *Kentropyx borckiana* are known from northern South America and Barbados. Features of external morphology, karyotypes, and biochemical genetics (electrophoresis of proteins encoded by 45 presumptive gene loci) reveal that individuals of *K. borckiana* from Guyana represent a unisexual clone that originated from one or more parthenogenetic F_1 hybrids between *Kentropyx calcarata* × *Kentropyx striata*, the other two species of this genus known previously from the Guiana Region. Comparisons include data for *Kentropyx altamazonica* also, including the first specimens known from Venezuela (Amazonas Territory). Although *K. altamazonica* and *K. calcarata* are morphologically similar, genetically they are quite distinct.

Origin of the unisexual *Kentropyx borckiana* involved hybridization between both morphologically and ecologically distinct ancestral species, unlike several other unisexual lizards of Neotropica. For example, clones of the parthenogenetic *Gymnophthalmus underwoodi*, *Cnemidophorus cryptus*, and *Cnemidophorus pseudolemniscatus* originated in the Guiana Region from hybrids between morphologically and ecologically similar, yet genetically distinct, ancestral species.

INTRODUCTION

The macroteiid lizard genus *Kentropyx* includes eight known species, all restricted to South America and the southern West Indies (Gallagher and Dixon, 1980, 1992). Seven species are bisexual (with separate sexes; dioecious; gonochoristic), but one, *Kentropyx borckiana* Peters, is a unisexual species. Hoogmoed (1973: 292) determined that all 26 specimens of *Kentropyx borckiana* that he examined from Guyana, Suriname, and French Guiana were females, and he was the first person to suggest that "this is another parthenogenetic species."

In a taxonomic review based on external morphology and geographic distribution of all species of *Kentropyx*, Gallagher and Dixon (1992) examined 102 specimens of *K. borckiana*, and all were females. Knowing that other unisexual teiids are of hybrid origin, they suggested that *K. calcarata* Spix and *K. striata* (Daudin) could be the bisexual ancestors of *K. borckiana*, "if this species is the result of hybridization" (Gallagher and Dixon, 1992: 137; also see Gallagher and Dixon, 1980).

We also independently hypothesized that *K. borckiana* had a hybrid origin involving *K. calcarata* × *K. striata* for the following reasons: (1) these three species were the only ones of the genus known to occur in the Guiana Region (north of the Amazon River and east of the Orinoco), and populations exist in various combinations of close proximity to each other (Hoogmoed, 1973); (2) key morphological characters presented by Hoogmoed (1973: 286–287) suggested that *K. borckiana* is intermediate between *K. calcarata* and *K. striata*; and (3) hybrid origins are the general rule for clones of parthenogenetic lizards, the only kind of unisexual lizards known (for reviews, see Cole, 1975; Darevsky et al., 1985; various articles in Dawley and Bogart, 1989; and Darevsky, 1992; for a possible nonhybrid example in the Xantusiidae, see Bezy and Sites, 1987).

Since 1980, CJC and CRT have participated in several expeditions to Suriname, Venezuela, and Guyana, during which we collected specimens for this research. Preparations included karyotypes and various tissues frozen in liquid nitrogen. The accumulated samples now include *K. calcarata* from Suriname, *K. altamazonica* Cope from Venezuela, and both *K. borckiana* and *K. striata* from Guyana. Consequently, we can now address the following questions in this report: (1) Did *K. borckiana* have a hybrid origin involving *K. calcarata* × *K. striata*; and (2) is *K. borckiana* a parthenogenetic clone? In addition, we present a scenario on the hybrid origin of the unisexual *K. borckiana* and discuss the Venezuelan distribution of *K. altamazonica*.

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METHODS

External Morphology

Color notes and photographs were taken in life for specimens we collected. For most other characters, we closely followed Hoogmoed (1973), but a few characters are discussed immediately below. The specimens examined are listed in the Appendix.

The number of scales in the collar refers to enlarged scales along the edge of the gular fold; only the enlarged scales along the fold were counted, beginning on one side with the first scale that is clearly larger than the one anterior to it, and counting around to the opposite side; if small scales occupied the midventral area, we counted the large scales in the next anterior row at that point only. The number of gular scales is determined by counting those in contact with enlarged genials 1–3; the count is started at the suture between the third and fourth genials on one

side and is made forward, then back around to the same point on the opposite side. The number of scales around midbody refers to dorsal scales, counted from one sidemost enlarged ventral (not counted) to its counterpart on the opposite side; the count is made at ventral number 14, counting ventral rows posteriad from the axilla, as this approximates midbody on these lizards. Subdigital lamellae on the fourth toe and fourth finger were counted from the claw (not included) to (but not onto) the foot or hand.

Sex of all specimens of *K. borckiana* was determined by dissection, and all were females. Many individuals of the other species were sexed by dissection or examination of everted hemipenes, but for many we relied on presence (male) or absence (female) of conspicuous anal spurs.

Morphological data were analyzed with the Statgraphics Plus program (version 6.0) licensed from Manugistics, Inc. For univariate analyses and comparisons, reduced data are presented as the mean plus or minus one standard error of the mean, when appropriate.

Principal components analyses (PCA) were performed also, as each character could not be assumed to represent a completely independent estimate of the patterns of variation among these *Kentropyx*. Nine characters were used for PCA: Snout-vent length; total number of femoral pores; and the number of the following epidermal scales: collar scales; gulars; ventral rows (approximately along midventral line from gular fold to vent); scales around midbody; dorsal scale rows (approximately along middorsal line from postparietals to enlarged caudals); subdigital lamellae on fourth toe; and subdigital lamellae on fourth finger. Due to missing digits on some lizards, the number of specimens available for analysis was maximized by using counts of lamellae on one side or the other, not the total for both sides. For each PCA, we used lamellae of only the left or right side of each specimen, but substituted the opposite digit for rare individuals lacking the one chosen first. This was reasonable as no left/right asymmetry was indicated for subdigital lamellae (table 2). Only specimens with complete data in the matrix (no blank cells) were used for PCA, and no estimates for missing values were employed. PCAs were performed on correlation matrices using the Statgraphics Plus program. As several population samples were involved in each PCA, the analyses include variation among and within populations.

Karyotypes

Karyotypes were prepared from bone marrow and studied as described for other teiid lizards (Cole, 1979). We examined chromosomes of 91 mitotic cells from nine lizards representing three species of *Kentropyx*.

Biochemical Genetics

Samples of fresh tissues (liver, heart, kidneys, stomach, small intestine, skeletal muscle, plasma, and blood cells) were frozen in liquid nitrogen and stored in ultracold freezers prior to use, following traditional procedures (e.g., Dessauer et al., 1990).

Electrophoresis of tissue proteins from 19 lizards was conducted as described in detail for other teiids (Dessauer and Cole, 1991). Table 1 here lists the 45 presumptive gene loci examined, Enzyme Commission numbers, abbreviations, and the tissues and buffers used.

RESULTS AND DISCUSSION

Did K. borckiana *Have a Hybrid Origin Involving* K. calcarata × K. striata*?*

Evidence from External Morphology; Coloration

The combination of colors and pattern of *K. borckiana* can be interpreted as having been inherited from *K. calcarata* and *K. striata* (figs. 1, 2). Adults of all three species have a brown dorsum with a green wash anteriorly and cream, tan, or green (anteriorly) light stripes. The most conspicuous dorsolateral light stripe (cream, tan, or green) of each species originates anteriorly on the lower eyelid, not in the temporal region on or just behind the supraoculars as in *K. altamazonica*. Nevertheless, *K. striata* usually has a less conspicuous dorsal light stripe that begins in the temporal region, and *K. borckiana* has this (wavy) on the neck, whereas it is absent in

K. calcarata. *Kentropyx calcarata* has (usually, not always) a bright green (anteriorly) or cream to tan middorsal stripe from the snout or top of the head more or less to midbody; this stripe is absent in *striata* but usually represented in *borckiana* by a green middorsal stripe atop the head and nape of the neck. *Kentropyx calcarata* usually has a row of dark brown spots dorsal to the dorsolateral light stripe, whereas *K. striata* has a dark brown stripe or two, in places occasionally irregularly broken into spots; *borckiana* has a combination of both (stripe anteriorly and spots). Pale cream, tan, green, gray, or blue spots may occur laterally on adult *K. calcarata* (fig. 2A); these may be tan or absent from *K. striata* (figs. 1A, 2B) and usually are absent from *K. borckiana*. The tail of *K. striata* usually has a middorsal dark brown stripe or row of brown spots and subtle tan or cream stripes but that of *K. calcarata* has dark brown and sometimes also tan or cream spots; *K. borckiana* has cream stripes laterally on the tail as has *striata*, but dark brown spots dorsally. Light spots are absent from the dorsal surface of the hind legs in *K. striata*, sometimes present (tan or light brown) in *K. calcarata* (fig. 2A), and present in *K. borckiana* (fig. 1B).

In summary, *K. borckiana* is intermediate between *K. calcarata* and *K. striata* in position and color of the middorsal and dorsolateral light stripes, and in the position and color of the dorsal dark brown stripes and spots. It is similar to *calcarata* in having light spots on the dorsal surface of the hind legs but similar to *striata* in usually lacking conspicuous light spots on the sides of the body.

Evidence from External Morphology; Univariate Analyses

Relatively variable body measurement and epidermal scale count data are presented for nine characters in table 2 (nine characters if counting toe lamellae and finger lamellae each as one character). These and additional characters clearly indicate that *K. borckiana* is either the same as both *K. calcarata* and *K. striata*, for characters in which these species are similar, or morphologically intermediate between them (but similar to *striata* in number of gulars). The additional characters show no significant differences among the four species compared (including *K. altamazonica*) as follows: two frontoparietals; supraoculars usually four per side, but often three in *K. altamazonica* and sometimes five in others; three parietals; two postparietals; top of head concave; dorsal scales keeled; anteriormost pair of enlarged genials not completely separated at midventral line; 14–16 rows of enlarged ventrals (but consistently 14 in *K. calcarata*); two conspicuous, curved, elongate anal spurs per side on adult males (but no male *K. borckiana*); all preanal scales keeled in females (often only half or fewer of these scales keeled in adult males); usually 3–6 somewhat enlarged scales forming a partial ring anterior to (but not immediately adjacent to) ear opening, but often 6–8 in *K. borckiana* and *K. striata*; and usually 4–6 scales midventrally separating the series of femoral pores on opposite legs.

Considering the nine variable characters (table 2), *K. borckiana* is clearly intermediate between *K. calcarata* and *K. striata* in the following four: number of collar scales; number of scales around midbody; number of dorsal scale rows; and number of femoral pores. For these four characters, *K. altamazonica* is more similar to *K. calcarata* than to the other species, but the biochemical data (see below) clearly exclude *K. altamazonica* from further consideration as an ancestor of *K. borckiana*. *Kentropyx borckiana* is similar to *K. striata* in number of gular scales and similar to both *K. striata* and *K. calcarata* in body length, number of ventral scale rows, and number of fourth toe and fourth finger lamellae.

Differences in number of scales around midbody and number of dorsal scale rows clearly reflect significant differences in the sizes of the dorsal scales in different species (fig. 3). In *K. calcarata*, the ventralmost dorsal scales are granules that somewhat gradually increase in size toward the middorsal region but remain basically granules. In *K. striata*, the dorsalmost scales are significantly larger and abruptly differentiated from the lateral granular scales. In *K. borckiana*, the condition is intermediate between these two species.

The samples of *K. altamazonica* from Venezuela apparently differ from those of Peru in the following characters (table 2): some-

TABLE 1
Presumptive Structural Gene Loci Examined in *Kentropyx*

Locus	EC No.	Abbrev.[a]	Tissue[b]	Buffer[c]
Oxidoreductases				
Alcohol dehydrogenase	1.1.1.1	ADH	L	TC8
Glycerol-3-phosphate dehydrogenase	1.1.1.8	G3PDH	M	PC6
L-Iditol dehydrogenase	1.1.1.14	IDDH	K	TC8
L-Lactate dehydrogenase	1.1.1.27	LDH-1	H, K, L	PC6; TC8
		LDH-2	K, L, M	PC6; TC8
Malate dehydrogenase	1.1.1.37	sMDH	M	PC6; TC8
		mMDH	M	PC6
	1.1.1.40	sMDHP	M	PC6
Isocitrate dehydrogenase	1.1.1.42	sIDH	R	PC6; TC8
		mIDH	H, M	PC6; TC8
Superoxide dismutase	1.15.1.1	sSOD	L, R	TC8
		mSOD	L, R	TC8
Diaphorase (NADPH)	1.6.–.–	DIA-2[d]	L	TC8
NAD-dehydrogenase	?	NAD[e]	L	TC8
Transferases				
Purine-nucleoside phosphorylase	2.4.2.1	PNP	L	TC8
Aspartate aminotransferase	2.6.1.1	sAAT	K, L, M	PC6; TC8
		mAAT	K, L, M	PC6; TC8
Alanine aminotransferase	2.6.1.2	ALAT	M	TC8
Creatine kinase	2.7.3.2	CK-1	K	PC6; TC8
		CK-2	K	TC8
Adenylate kinase	2.7.4.3	AK	M	PC6; TC8
Hydrolases				
Esterase D	3.1.1.–	ESTD[f]	L, M	PC6
Esterase (nonspecific)		EST-2[g]	M	PC6
		EST-3[g]	M	PC6
Alkaline phosphatase	3.1.3.1	ALP	L	TC8
Acid phosphatase	3.1.3.2	ACP[h]	L, M	PC6
Alpha-glucosidase	3.2.1.20	aGLUS[i]	L	PC6
Alpha-mannosidase	3.2.1.24	aMAN[j]	L	PC6
Peptidases	3.4.–.–	PEPA[k]	H, K, L	PC6; TC8
		PEPB[l]	M	PC6
		PEPC[m]	M	TC8
		PEPE[l]	M	PC6
Proline dipeptidase	3.4.13.9	PEPD[n]	R	PC6; TC8
Adenosine deaminase	3.5.4.4	ADA	L, R	TC8
Lyases				
Fumarate hydratase	4.2.1.2	FUMH	L	PC6
Aconitase hydratase	4.2.1.3	sACOH	L	TC8
		mACOH	L	TC8
Isomerases				
Mannose-6-phosphate isomerase	5.3.1.8	MPI	K, L	TC8
Glucose-6-phosphate isomerase	5.3.1.9	GPI	K, L, M	PC6[o]
Phosphoglucomutase	5.4.2.2	PGM-1	H, M	TC8[p]
		PGM-2	L	TC8[q]
Nonenzymic proteins				
Albumin		ALB	P	V8.6
Transferrin		TF	P	V8.6
Hemoglobin		HB	R	TC8
Myoglobin		MB	M	TC8

TABLE 1—(*Continued*)

[a] Based largely on Murphy et al. (1990); s = cytosolic enzyme; m = mitochondrial enzyme. For multilocus systems, loci are numbered in order of decreasing anodal migration of their polypeptide products.

[b] Tissue in which enzyme was scored most effectively: H = heart; K = kidney; L = liver; M = skeletal muscle; P = plasma; R = erythrocytes.

[c] Components followed by pH; T = TRIS; C = citrate; P = phosphate; V = veronal (barbituric acid).

[d] Diaphorase-2 of Harris and Hopkinson (1976).

[e] Unidentified dehydrogenase, dependent on presence of NAD and TC8 buffer, and distinctly different from all other loci.

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

[g] Substrates 4-methylumbelliferyl acetate or alpha-naphthyl esters.

[h] Substrate 4-methylumbelliferyl phosphate. Patterns for this locus were identical for all specimens in pH 8 buffer, but variation was revealed at pH 6.

[i] Substrate 4-methylumbelliferyl-alpha-D-glucoside.

[j] Substrate 4-methylumbelliferyl-alpha-D-mannopyranoside.

[k] Substrate phenylalanyl.leucine.

[l] Substrate leucyl.glycyl.glycine. Patterns for PEPB were identical for all specimens in pH 8 buffer, but variation was revealed at pH 6.

[m] Substrate lysyl.leucine.

[n] Substrate phenylalanyl.proline.

[o] PC6 buffer gave better resolution for *K. altamazonica* than did TC8 at GPI.

[p] This showed lower resolution with PC6 buffer.

[q] A rare variant allele was detected in *K. calcarata* with PC6 buffer.

what fewer gular scales; somewhat fewer rows of ventral scales; somewhat more femoral pores; and significantly fewer rows of dorsal scales. Their similarities in all other characters of external morphology, including color pattern, suggest that the differences represent geographic variation. However, they could also indicate the presence of cryptic species masquerading under the name *K. altamazonica*, a possibility that we cannot test adequately until more comparative material is available for analysis of genetic and geographic variation. Intriguing results of a principal components analysis, however, are presented later in this paper.

Evidence from External Morphology; Multivariate Analyses

The data from biochemical genetics (see below) overwhelmingly indicate that *K. borckiana* is of hybrid origin and its ancestors are *K. calcarata* and *K. striata*. Therefore, principal components analyses (PCAs) were performed with samples of these species, to determine whether the unisexual species is morphologically intermediate between its bisexual ancestors. PCAs were performed on the nine more variable characters included in table 2. In order to control for bias that could be introduced by sexual dimorphism (although none is suggested by scanning table 2), two PCAs were compared. The first (PCA 1) was based on all specimens examined for each relevant species, including both sexes, the second (PCA 2) was based on females only. These are discussed separately below.

PCA 1: The 50 specimens of *K. borckiana* (N = 12), *K. calcarata* (N = 21), and *K. striata* (N = 17) with complete data, including both sexes, were analyzed to see whether clustering would be consistent with recognizing three distinct species, *borckiana* being intermediate between the other two. The analysis (fig. 4) completely separated the three groups (no overlap), and *K. borckiana* did cluster intermediate to its parental taxa. The three taxa were nearly completely separated on the first principal component (PC1), but one male *K. calcarata* overlapped in score with one female *K. borckiana* on PC1. The correlation matrix showed significant correlation among the following characters: body length and only one scale character (number of enlarged scales

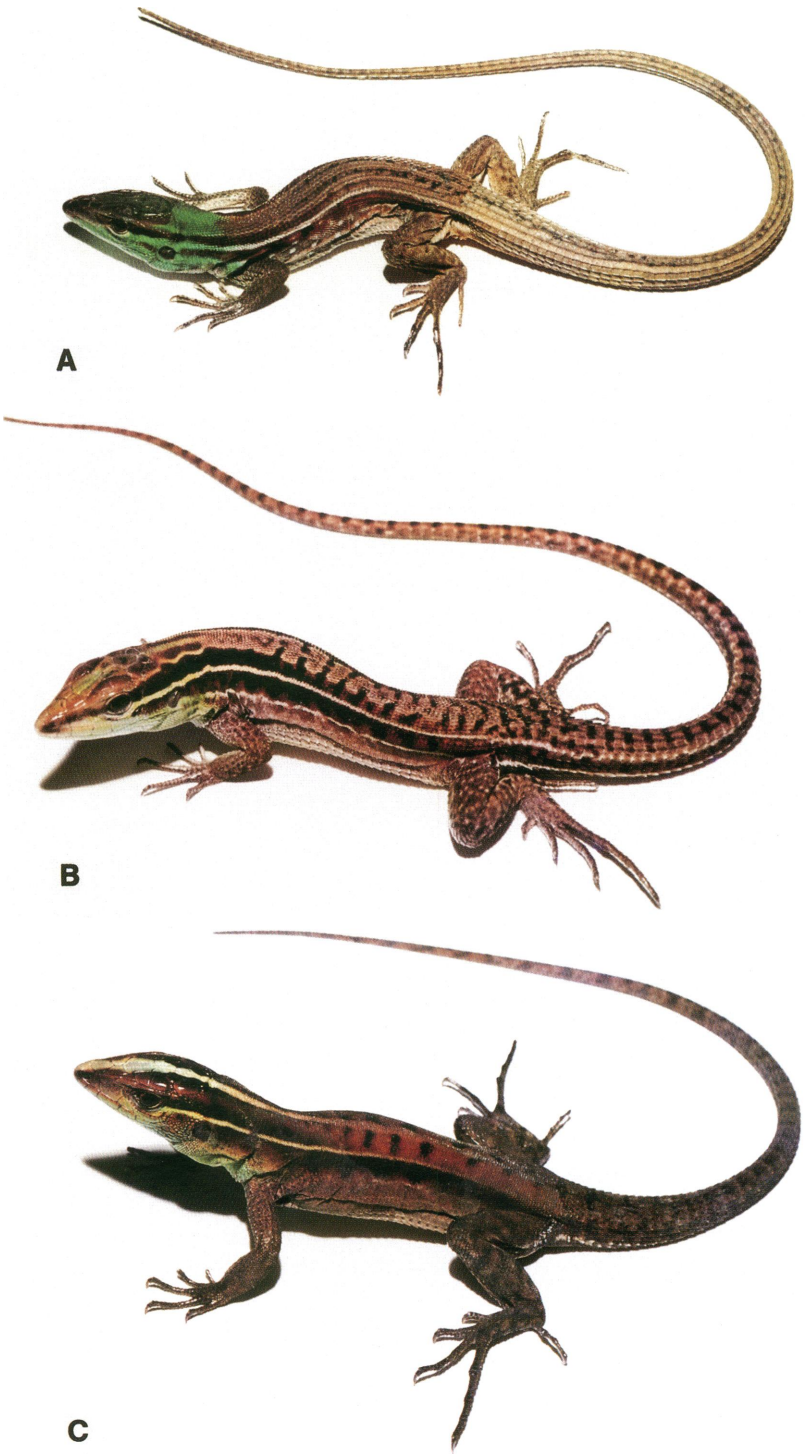

Fig. 1. Three species of *Kentropyx*. **A**. *K. striata* (AMNH 138088, male from Guyana, snout-vent length, 70 mm). **B**. *K. borckiana* (AMNH 138648, female from Guyana, snout-vent length, 77 mm). **C**. *K. calcarata* (AMNH 133350, female from Suriname, snout-vent length, 74 mm).

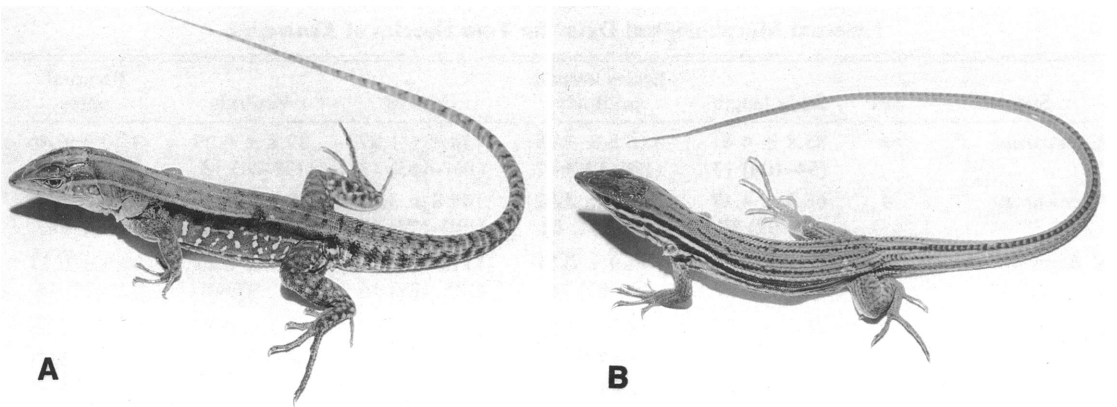

Fig. 2. Two species of *Kentropyx*. **A**. *K. calcarata* with spots on the sides (compare with fig. 1C; AMNH 133351, male from Suriname, snout-vent length, 77 mm). **B**. *K. striata* without spots on the sides (compare with fig. 1A; AMNH 138057, female from Guyana, snout-vent length, 84 mm).

in collar); number of ventral scales and only one other scale character (number of toe lamellae); number of finger lamellae and only one other scale character (number of toe lamellae); and about half of the remaining scale count characters compared in the matrix. The first three principal components jointly accounted for 77.5 percent of the total variation in the data set (PC1 = 46.4%; PC2 = 18.5%; PC3 = 12.6%), and no other principal component explained as much as 10 percent. The loadings on the components are listed in table 3 and the scores are shown in figure 4. Summarizing, PC1 was loaded most heavily by number of scales around midbody, number of dorsal scales, and total number of femoral pores; PC2 was loaded most heavily by number of lamellae beneath the left finger and left toe; and PC3 was loaded most heavily by snout-vent length.

PCA 2: If sexual dimorphism affects the clustering of these specimens, then *K. borckiana*, being all-female, was not treated equally with respect to the other taxa in PCA 1. Therefore, the PCA was repeated using only the females of each taxon (a total of N = 33; 12 *borckiana*, 11 *calcarata*, and 10 *striata*). The analysis (fig. 5) revealed that the same three groups clustered similarly to their arrangement in PCA 1, without overlap between groups, and with *K. borckiana* intermediate between its parental taxa. In this case, the three taxa were completely separated on PC1. The correlation matrix showed significant correlation among the following characters: body length and half of the scale characters; number of toe lamellae and only one other scale character (number of finger lamellae); and about half of the remaining scale count characters compared in the matrix, except that the number of ventrals was not significantly correlated with anything else tested (including body size). The first three principal components jointly accounted for 76.5 percent of the total variation in the data set (PC1 = 47.0%; PC2 = 17.1%; PC3 = 12.4%), and no other principal component explained as much as 10 percent. The loadings on the components are listed in table 3 and the scores are shown in figure 5. Summarizing, PC1 was loaded most heavily by number of scales around midbody, number of dorsal scales, and total number of femoral pores; PC2 was loaded most heavily by number of lamellae beneath the left toe and left finger; and PC3 was loaded most heavily by number of ventral scales and number of gular scales, then snout-vent length.

Evidence from Karyotypes

We compared karyotypes of the following species and specimens: *Kentropyx borckiana* (Guyana; two females; 22 cells); *K. calcarata*

TABLE 2
External Morphological Data[a] for Four Species of *Kentropyx*

Species	Sex	Body length	Scales around midbody	Dorsals	Ventrals	Femoral pores
K. calcarata	♀	83.8 ± 4.41 (54–104) 13	116.5 ± 2.29 (106–132) 12	154.8 ± 1.87 (141–165) 13	39.4 ± 0.29 (38–41) 13	37.0 ± 0.46 (34–39) 12
K. calcarata	♂	68.3 ± 4.47 (49–92) 13	120.1 ± 3.92 (94–141) 12	149.8 ± 3.28 (130–173) 13	40.1 ± 0.49 (38–44) 13	37.2 ± 0.77 (33–41) 13
K. borckiana	♀	74.1 ± 3.86 (39–93) 16	74.9 ± 0.71 (70–82) 16	111.3 ± 1.23 (105–122) 16	39.1 ± 0.12 (38–40) 16	25.9 ± 0.27 (23–27) 15
K. striata	♀	71.3 ± 3.98 (50–93) 15	52.0 ± 1.37 (43–63) 14	88.4 ± 1.56 (79–101) 14	39.3 ± 0.37 (37–42) 15	13.4 ± 0.46 (11–18) 15
K. striata	♂	79.2 ± 7.24 (39–113) 9	51.8 ± 1.54 (46–59) 10	83.3 ± 1.08 (79–88) 9	39.7 ± 0.40 (38–42) 10	13.7 ± 0.47 (12–16) 10
K. altamazonica Peru	B[b]	80.2 ± 1.07 (76–86) 11	111.0 ± 1.92 (102–120) 11	183.2 ± 3.38 (170–207) 11	42.0 ± 0.30 (41–44) 11	30.6 ± 0.43 (29–33) 10
K. altamazonica Neblina	♀	62.2 ± 4.18 (36–84) 16	117.8 ± 1.55 (111–126) 12	163.8 ± 2.13 (152–177) 12	39.4 ± 0.38 (37–41) 12	34.1 ± 0.50 (32–37) 14
K. altamazonica Neblina	♂	74.8 ± 2.54 (39–86) 19	118.9 ± 1.14 (112–128) 17	159.6 ± 1.99 (146–176) 18	40.2 ± 0.32 (37–42) 18	33.7 ± 0.64 (29–39) 18
K. altamazonica Tapirapeco	♂	79.4 ± 2.54 (71–85) 5	113.2 ± 1.36 (110–116) 5	151.4 ± 2.64 (142–158) 5	39.6 ± 0.68 (37–41) 5	35.2 ± 1.98 (31–42) 5

[a] Mean ± 1 standard error of the mean (range) and sample size. Body length in mm; all other data are discrete scale counts.

[b] Sexes are combined for *K. altamazonica* from Peru because of small sample size (4 females, 7 males). For *K. altamazonica* from Tapirapeco, the entire sample consisted of males, but we do not suggest that this is an all-male population.

(Suriname; three males, two females; 49 cells); and *K. striata* (Guyana; one male, one female; 20 cells).

All three species have the same karyotype (fig. 6), which is consistent with, but not suggestive of, the hypothesis that *K. borckiana* is a clone stemming from a hybrid between the other two species. Each is a diploid species with 50 chromosomes, including 26 macrochromosomes (apparently 13 pairs) and 24 microchromosomes (12 pairs). All of the macrochromosomes are telocentric. Morphology of the microchromosomes is difficult to resolve with standard compound microscopy, but two or fewer appeared biarmed in the clearest cells of each species. In *K. calcarata* and *K. striata* the largest two chromosomes (one pair) have a dotlike terminal satellite, set off by a nearly terminal secondary constriction (fig. 6).

The only difference detected in the karyotypes of these three species was that *K. borckiana* consistently had the secondary constriction visible on only one of the largest chromosomes (fig. 6), not on both of the pair. This is consistent with observations on other teiid lizards showing that the consistently observed secondary constrictions are the nucleolar organizers (NORs) and the NOR of one ancestor may be dominant over that of the other ancestor (inactivated) in parthenogens of hybrid origin (Ward and Cole, 1986). Heteromorphic sex chromosomes were not apparent in either sex of any of these species. The karyotype described here is the same as that described for *K. striata* by Gorman (1970).

Evidence from Biochemical Genetics

Proteins encoded by 45 presumptive structural gene loci were compared by electrophoresis in *K. borckiana* (N = 3 compared), *K. calcarata* (N = 5), *K. striata* (N = 8), and *K.*

TABLE 2
Extended

Collars	Gulars	Left toe lamellae	Right toe lamellae	Left finger lamellae	Right finger lamellae
17.8 ± 0.58 (15–22) 13	24.1 ± 0.99 (17–29) 13	25.8 ± 0.52 (23–29) 13	25.7 ± 0.52 (22–28) 13	16.5 ± 0.24 (15–18) 13	16.3 ± 0.19 (15–17) 12
18.4 ± 0.84 (14–25) 13	26.0 ± 0.70 (22–29) 12	26.5 ± 0.54 (24–30) 13	26.2 ± 0.52 (24–30) 13	17.4 ± 0.36 (16–19) 11	17.1 ± 0.16 (16–18) 11
15.9 ± 0.25 (14–18) 16	21.3 ± 0.27 (19–23) 15	26.9 ± 0.23 (26–28) 15	26.7 ± 0.23 (26–28) 15	18.1 ± 0.20 (17–19) 14	17.8 ± 0.22 (16–19) 13
14.0 ± 0.29 (12–15) 15	21.0 ± 0.44 (19–24) 12	25.9 ± 0.38 (23–29) 15	25.9 ± 0.30 (24–27) 15	17.0 ± 0.24 (16–18) 15	16.6 ± 0.35 (14–18) 15
14.2 ± 0.33 (13–15) 10	20.2 ± 0.31 (19–22) 8	26.0 ± 0.44 (25–29) 9	26.0 ± 0.46 (25–28) 8	16.4 ± 0.16 (16–17) 10	16.4 ± 0.30 (15–18) 10
18.3 ± 0.43 (15–20) 11	25.2 ± 1.13 (19–30) 10	26.0 ± 0.43 (24–28) 11	26.3 ± 0.33 (25–28) 11	18.8 ± 0.26 (17–20) 11	18.5 ± 0.28 (17–20) 11
17.6 ± 0.58 (14–22) 15	20.1 ± 0.49 (17–24) 14	25.0 ± 0.47 (22–28) 13	25.2 ± 0.48 (22–27) 13	17.4 ± 0.32 (16–21) 15	17.3 ± 0.35 (16–21) 15
17.6 ± 0.50 (13–22) 18	22.0 ± 0.58 (17–27) 18	25.6 ± 0.48 (23–31) 17	26.0 ± 0.51 (23–31) 18	17.6 ± 0.24 (16–19) 16	17.4 ± 0.26 (16–21) 17
17.6 ± 0.68 (16–20) 5	20.2 ± 0.49 (19–22) 5	27.6 ± 0.40 (26–28) 5	27.5 ± 0.64 (26–29) 4	18.6 ± 0.40 (18–20) 5	17.8 ± 0.49 (16–19) 5

altamazonica (N = 3; table 4; figs. 7, 8). As hypothesized for a hybrid origin, mean heterozygosity was high in the unisexual *K. borckiana*; 17 out of 45 loci (H = 0.38). In contrast, mean heterozygosity was below 0.10 for each of the bisexual species, as follows: *K. altamazonica*, 0.08; *K. calcarata*, 0.04; and *K. striata*, 0.03.

Of the 45 loci tested, 27 showed variation (table 4). Some of this was Mendelian variation within the bisexual taxa, but all three individuals of the unisexual *K. borckiana* were identical to each other, each lizard having the same polymorphism at each of the 17 loci with alleles in the heterozygous state.

For 14 of the 45 loci tested (31%), neither of the alleles present in *K. borckiana* was detected in *K. altamazonica*. Therefore, *altamazonica* is clearly ruled out as a probable ancestor for the unisexual species. In contrast, for all 45 loci tested, a complete haploid set of alleles in *K. borckiana* was identical to a typical haploid set of *K. calcarata* (table 4). Also, with the exception of but one allele, the second complete haploid set of alleles in *K. borckiana* was a typical haploid set for *K. striata*. Therefore, we conclude that the unisexual *K. borckiana* is of the following hybrid origin: *K. calcarata* × *K. striata*.

The one exceptional allele is at the sACOH locus. The a-allele occurs in *K. calcarata* and in *K. borckiana*, but the d-allele of *borckiana* was not found in *K. striata*, which had the b-allele and c-allele (table 4). Thus, the d-allele at sACOH in *K. borckiana* is an orphan allele. Among the possible explanations, two seem most likely: (1) the d-allele actually does occur in some *K. striata* but did not occur in our particular sample; or (2) the b-allele or c-allele of *striata* may have been inherited by *borckiana* originally, then mutated to the d-allele in the lineage we sampled. An example of a probable mutant allele at the TF locus of the unisexual *Cnemidophorus neo-*

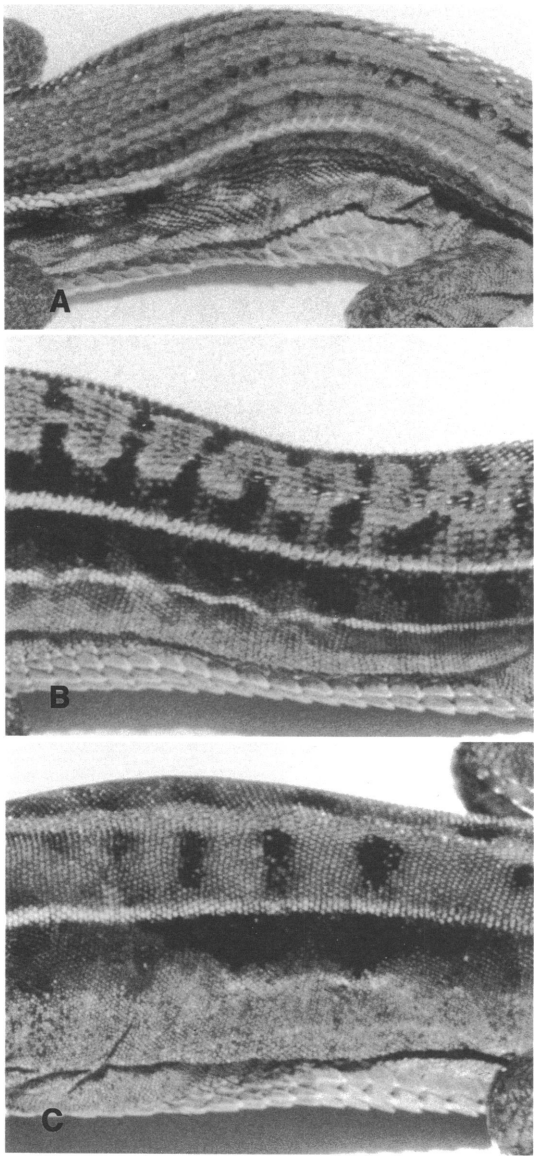

Fig. 3. Area of midbody showing conspicuous differences in size of dorsal scales in three species of *Kentropyx*, which is reflected in certain scale counts (table 2; scales around midbody and dorsals). **A**. *K. striata* (AMNH 138088). **B**. *K. borckiana* (AMNH 138648). **C**. *K. calcarata* (AMNH 133350).

mexicanus was discussed by Cole et al. (1988). With only one orphan allele (1%) out of 90 alleles identified in *K. borckiana*, we are confident that we have identified the ancestors correctly.

Is K. borckiana *a Parthenogenetic Clone?*

The three specimens of *K. borckiana* tested had the same allele combinations at all 45 loci analyzed, including the 17 with alleles in the heterozygous state. Although the sample of lizards is small, the sample of loci is large, so we conclude that the inheritance pattern of *K. borckiana* normally shows no effects of recombination or random assortment among chromosomes. This is consistent with the pattern of inheritance found in other unisexual teiids (Dessauer and Cole, 1986). Considering this together with the absence of males among more than 100 specimens of *K. borckiana* known, we conclude that this species is parthenogenetic, as parthenogenesis is the mode of reproduction of other clones of unisexual teiids (e.g., Hardy and Cole, 1981; Hardy et al., 1989; Dessauer and Cole, 1989).

Scenario on the Hybrid Origin of K. borckiana

All the data discussed above pertaining to external morphology, karyotypes, and protein electrophoresis are consistent with the conclusion that the unisexual *K. borckiana* originated from hybridization among *K. calcarata* × *K. striata*. Biogeography and ecology are consistent with this also.

All known specimens of *K. borckiana* are from coastal or near coastal localities in Guyana, Suriname, French Guiana, or Barbados (see Gallagher and Dixon, 1992, for recent distribution maps of all species of *Kentropyx*; Hoogmoed, 1973 for ranges in Suriname). *Kentropyx calcarata* and *K. striata* occur through the same and a much broader area, although neither of these occurs on Barbados. Therefore, it appears that the hybrid event(s) occurred in northern South America in the Guianas, followed by natural dispersal or human-mediated transport of *K. borckiana* to Barbados.

Although there is a broad overlap in the ranges of *K. calcarata* and *K. striata*, particularly in the Guiana Region, there is a difference in their habitat preferences. *Kentropyx calcarata* is primarily a forest lizard, "preferring open sunny places . . . and . . . clearings associated with forest" (Gallagher and Dixon, 1992: 141; see also Rand and Humphrey, 1968; Vanzolini, 1972; Hoog-

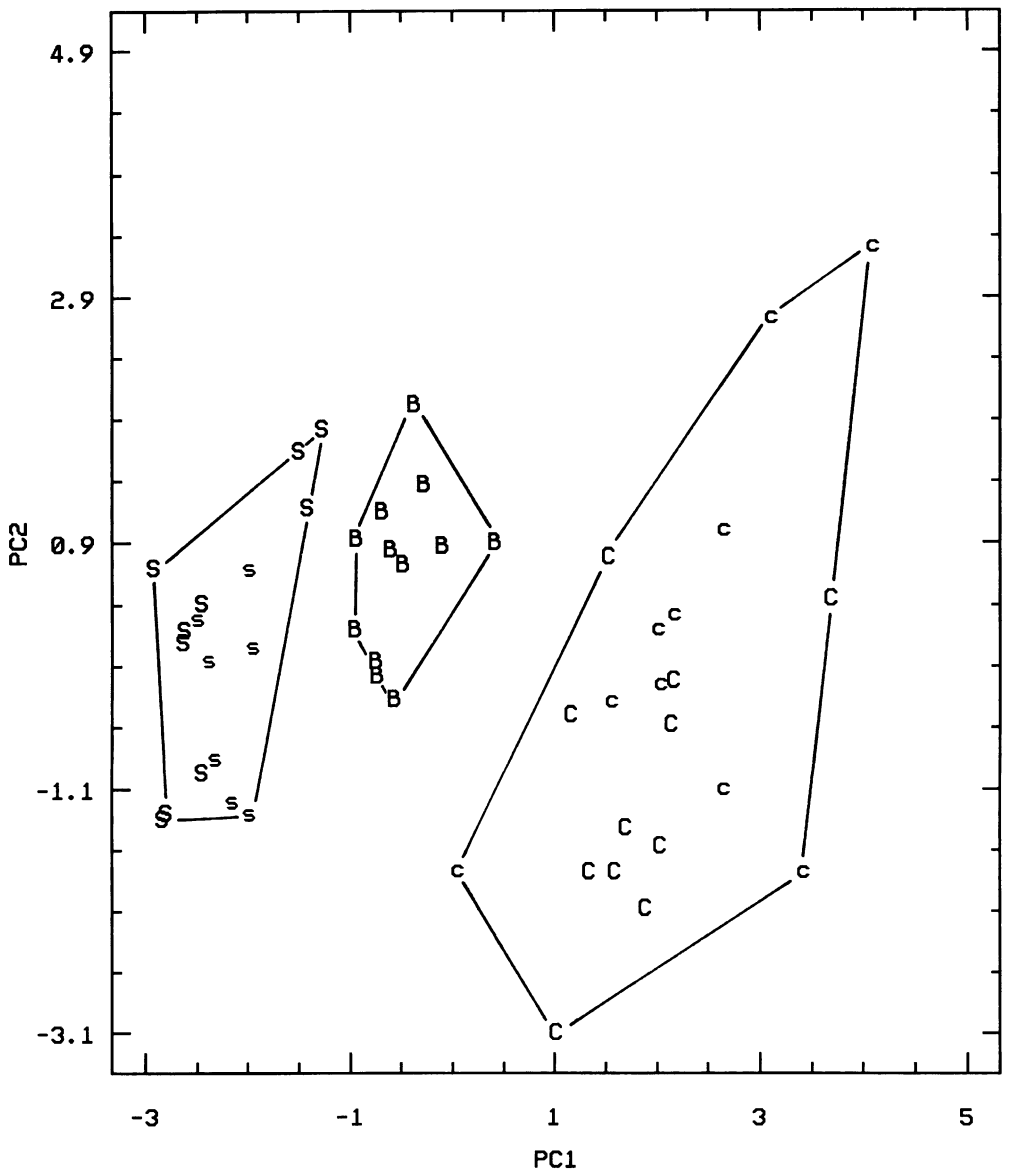

Fig. 4. Polygons and letters representing the scores of 50 specimens of *Kentropyx* (three species) on the first two principal components extracted from the correlation matrix of nine morphological characters (tables 2, 3). Capital letters indicate females, lowercase letters indicate males, as follows: B, the unisexual *K. borckiana* from Guyana; C, the bisexual *K. calcarata* from Guyana and Suriname; and S, the bisexual *K. striata* from Guyana.

moed, 1973; and Vitt, 1991). This is consistent with the observations of CJC and CRT in Suriname and Guyana. *Kentropyx striata* occurs primarily in savanna or other open formations, usually near water and low vegetation (Boos and Quesnel, 1971; Vanzolini, 1972; Hoogmoed, 1973; and Magnusson et al., 1985). This is consistent with the observations of CJC and CRT in Guyana, where we have also seen *K. striata* among trees

TABLE 3
Character Loadings on First Three Axes for Two Principal Components Analyses of *Kentropyx* Morphology[a]

	PCA 1			PCA 2		
Character	PC1	PC2	PC3	PC1	PC2	PC3
Body length	0.109	−0.176	−0.802	0.268	0.140	0.360
Around body	0.477	−0.047	0.076	0.470	0.008	−0.064
Dorsals	0.473	−0.048	0.098	0.470	0.013	−0.069
Ventrals	0.143	0.327	−0.410	0.090	0.164	0.627
Pores	0.466	−0.080	0.096	0.460	0.019	−0.090
Collars	0.381	−0.107	−0.210	0.371	0.191	0.276
Gulars	0.352	0.002	0.327	0.262	−0.058	−0.528
Toe lamellae	0.171	0.627	−0.091	0.040	0.710	−0.325
Finger lamellae	−0.018	0.668	0.064	−0.243	0.639	−0.003
Variation expl.	46%	18%	13%	47%	17%	12%

[a] Based on data summarized in table 2 for *K. calcarata, K. borckiana,* and *K. striata.*

growing near or around ponds on the Rupununi Savanna (see also Magnusson and da Silva, 1993, for a clear association with trees).

Little has been written about the preferred habitat of *Kentropyx borckiana*, but Gallagher's experience in Georgetown, Guyana, suggested that it occurs in "open formations and might be found in forest edge situations, secondary growth, etc." (Gallagher and Dixon, 1992: 137). This is consistent with the observations of CJC and CRT in the Botanical Gardens in Georgetown. CJC's field notes of 14–19 March 1992 record finding the lizards in abundance during hot, sunny times of late morning and early afternoon. The main office of the Gardens sat in a rather open area with various plantings that were liberally watered. The majority of the *K. borckiana* seen were among the denser clusters of shrubs, bushes, and snakeplants in proximity of the office. Most of the lizards were first seen on the ground, but several exhibited agile climbing in low, dense shrubs. Similarly, Marinus S. Hoogmoed reported (personal commun.) that *K. borckiana* was found recently in a plant nursery near to and south of Paramaribo, Suriname.

In summary, it is consistent with the geographical and ecological data to suggest that the hybridization between *K. calcarata* and *K. striata* that led to clonal *K. borckiana* occurred in coastal Guyana, Suriname, or French Guiana in an ecotone between rain forest and an open formation where the ranges of the ancestral bisexual species overlapped.

Several other unisexual species of lizards that reproduce by parthenogenetic cloning apparently had separate hybrid origins in the Guiana Region. *Gymnophthalmus underwoodi* apparently originated along the upper to middle Orinoco drainage system in southern to central Venezuela, from hybridization between *G. cryptus* and *G. speciosus* (see Cole et al., 1993). *Cnemidophorus cryptus* apparently originated along the Amazon in Brazil and perhaps also independently in Venezuela, from hybridization between *C. lemniscatus* and another species, perhaps *C. gramivagus* (see Cole and Dessauer, 1993). And *Cnemidophorus pseudolemniscatus* of Suriname apparently originated from backcross hybridization between *C. cryptus* and *C. lemniscatus* in the northern part of the Guiana Region (see Cole and Dessauer, 1993). The speciation events represented among all these taxa, including divergence of the ancestral bisexual species and the hybrid origins of the unisexual clones, may well have been associated with shifts in habitats and distributions of animals during Pleistocene to Recent times. In addition, future research may reveal a similar history for the origin of the unisexual microteiid *Leposoma percarinatum* of the Guiana Region (Uzzell and Barry, 1971), the bisexual ancestors of which may be inhabi-

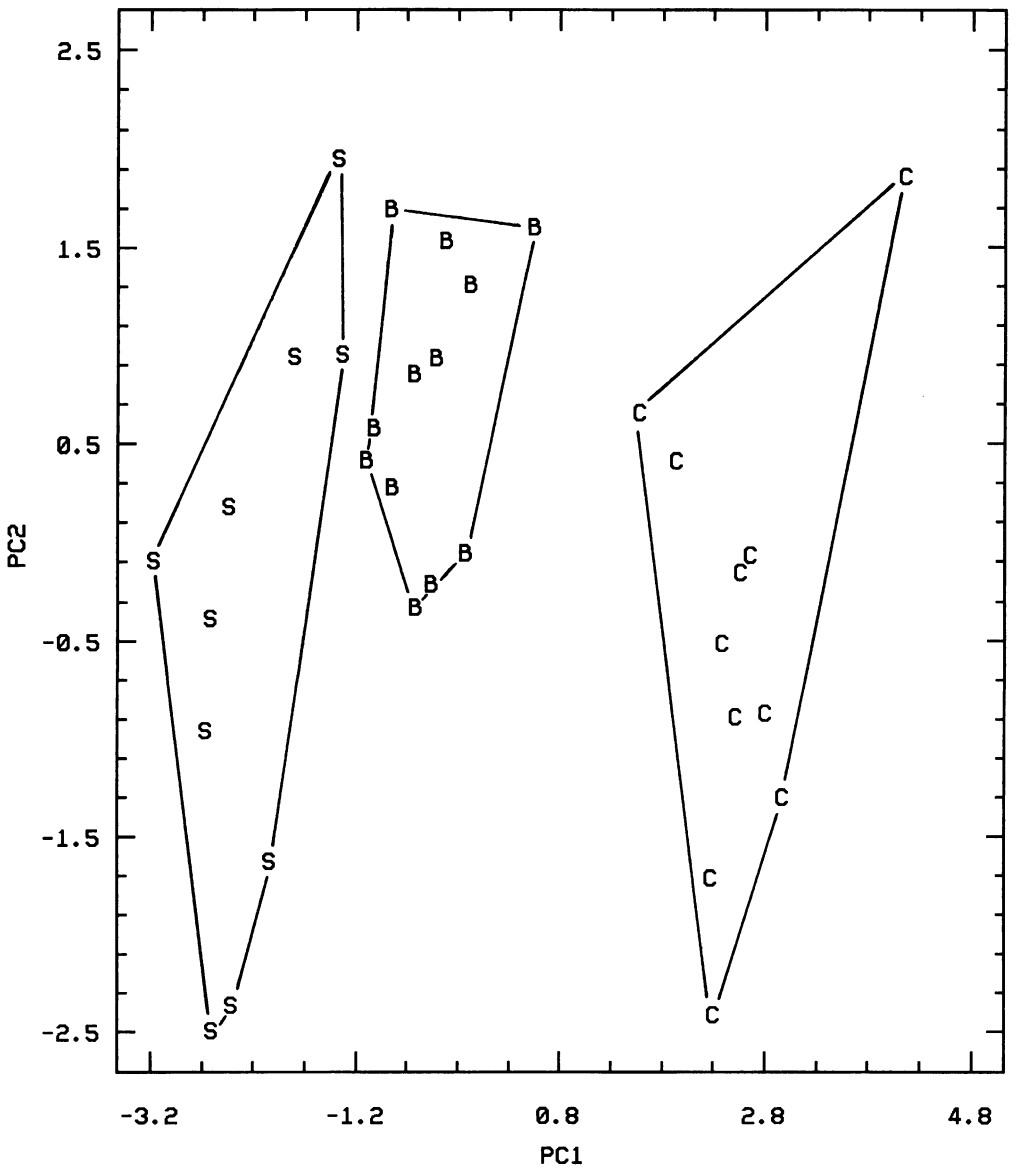

Fig. 5. Polygons and letters representing the scores of 33 females of *Kentropyx* (three species) on the first two principal components extracted from the correlation matrix of nine morphological characters (tables 2, 3). Symbols and individuals (but females only are included here) are the same as in figure 4.

tants of rain forest (see habitat notes presented by Hoogmoed, 1973: 328–329). This may reflect an inverse history (divergence of ancestral bisexual species in separated patches of forest followed by the hybrid origin of unisexual species when the forests are reunited during expansion) compared to the hybrid origins among savanna-dwellers such as *Cnemidophorus*. In reviewing this manuscript, M. S. Hoogmoed noted that T. C. Avila-Pires (1995) presents new data on *Leposoma* from Amazonian Brazil, in an extensive manuscript scheduled to be printed before this one.

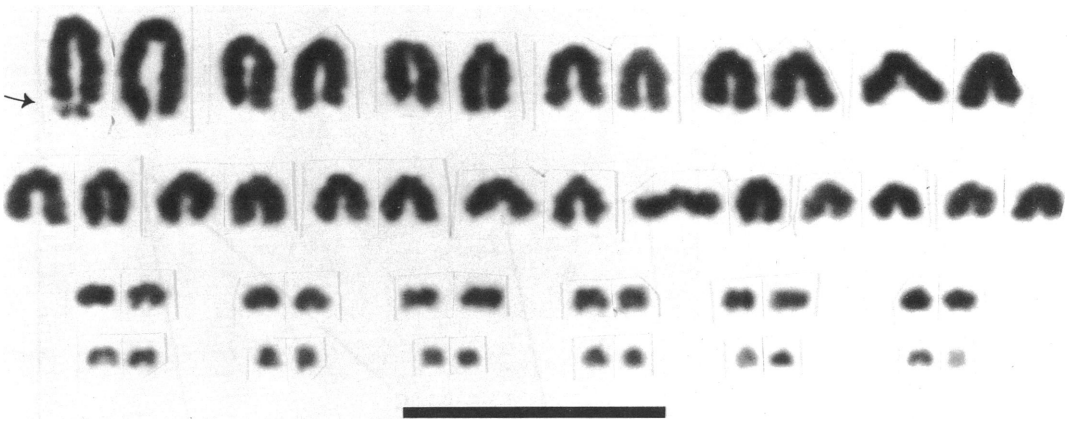

Fig. 6. Diploid karyotype of the unisexual *Kentropyx borckiana* ($2n = 50$, AMNH 138112, female). Arrow indicates secondary constriction; bar represents 10 microns.

Comments on K. altamazonica *in Venezuela*

There are no previous reports of *Kentropyx altamazonica* in Venezuela, although it occurs in the Rio Negro drainage in both eastern Colombia and northern Brazil (Gallagher and Dixon, 1992: 132). However, the *Kentropyx* collected in Amazonas, Venezuela, on both the Cerro de la Neblina and the Tapirapeco expeditions (e.g., AMNH 127817–127821 and others, plus AMNH 134174–134178; see Appendix, Specimens Examined) key out directly to *K. altamazonica*, based on sizes of their dorsal and lateral scales, shape of middorsal stripe, and number and anterior origins of the two dorsolateral light stripes (the uppermost beginning behind the supraoculars, not on the lower eyelid; Gallagher and Dixon, 1992: 129–130). These specimens are from the Rio Negro and Rio Orinoco drainage systems (see *Note added in proof*).

We also reexamined the AMNH specimens from Amazonas, Venezuela, previously reported as *K. calcarata* (AMNH 36635, AMNH 36647, and AMNH 36660; Gallagher and Dixon, 1992), and confirmed that they are indeed *K. calcarata*. In reviewing the AMNH material, two additional specimens of *K. altamazonica* were found, from the Rio Orinoco drainage (AMNH 117893–117894; see Appendix for full locality data). Considering this in the context of the most recent range maps published (Gallagher and Dixon, 1992: 132, 139), three bisexual species of *Kentropyx* (*altamazonica*, *calcarata*, and *pelviceps*) are nearly if not literally sympatric in the area of Amazonas, Brazil; Guainia, Colombia; and Amazonas, Venezuela.

Vitt (1991: 2792) reported that *K. calcarata* does not run across the surface of water as does *K. altamazonica* (Gallagher and Dixon, 1992: 134). Consistent with their morphology, CJC saw two *K. altamazonica* dash swiftly across the surface of a narrow, slow stream in the vicinity of the Cerro de la Neblina base camp (see Appendix for full locality data).

In the course of studying the *K. altamazonica* from Amazonas, Venezuela, we examined the same morphological characters discussed above for *K. borckiana*, *K. calcarata*, and *K. striata*. We also borrowed from the USNM a series of *K. altamazonica* collected by Roy W. McDiarmid in Peru near the type locality of this species (see Appendix), and we examined the same characters on them.

The morphological data are presented with those for the other species (table 2). Scanning these data, it appears that specimens from the two localities in Venezuela (Neblina and Tapirapeco) are essentially indistinguishable from each other, but together they may differ

from the Peruvian sample in the number of the following scales: gulars, ventrals, femoral pores, and dorsals.

Consequently, we performed a PCA on the 40 specimens (26 from Neblina, 5 from Tapirapeco, and 9 from Peru) to see whether the Venezuelan specimens clustered separately from the Peruvian ones. The analysis (fig. 9) revealed the following two distinct, but not completely separated, groups: (1) the specimens from Venezuela (Neblina and Tapirapeco together); and (2) those from Peru. On this plot, only two of the Venezuelan specimens (from Neblina) overlap in scores with three Peruvian specimens on PC1. The correlation matrix showed significant correlation among the following characters: body length and number of ventral scales; body length and number of scales around midbody; and about one-third of the scale count characters compared in the matrix, except that the number of scales around midbody and total number of femoral pores were not significantly correlated with any other scale characters. The first four principal components jointly accounted for 74.0 percent of the total variation in the data set (PC1 = 33.9%; PC2 = 15.2%; PC3 = 13.4%; PC4 = 11.5%), and no other principal component explained as much as 10 percent. The loadings on the components are listed in table 5 and the scores are shown in figure 9. Summarizing, PC1 was loaded most heavily by the number of ventral scales, number of dorsal scales, number of right fourth finger lamellae, and number of gular scales; PC2 was loaded most heavily by number of left fourth toe lamellae and total number of femoral pores; PC3 was loaded most heavily by the number of scales around midbody and body length; and PC4 was loaded most heavily by the number of enlarged scales in the collar.

It is difficult to interpret these data (fig. 9) reliably without additional samples and in the absence of comparative genetic data. The sensitive multivariate analysis may have revealed that two cryptic species are masquerading in these samples referred to collectively as *K. altamazonica* from Venezuela and Peru. Alternatively, the analysis may have revealed intraspecific geographic variation in the numbers of gular, ventral, and dorsal scales

TABLE 4

Alleles[a] or Genotypes[b] at 45 Presumptive Structural Gene Loci[c] in Samples of *Kentropyx*[d]

	Bisexual			Unisexual
Locus[c]	CAL	STR	ALT	BOR
ADH	a	a	b	aa
IDDH	a, b[e]	a	a	aa
LDH-1	b	a	a	ab
mMDH	b	b	a	bb
sMDHP	a	b	a	ab
sIDH	b	a	b	ab
sSOD	c	c, a[f]	b	ac
NAD	a	a	b	aa
ALAT	c	c, b[f], a[e]	d	cc
ESTD	a, b[f]	a	a	aa
EST-2	b	a	a, b[h]	ab
ACP	c	b	a	bc
aMAN	a	b	a, b[h]	ab
PEPA	b	a	c	ab
PEPB	a	b	b	ab
PEPC	b	b	a	bb
PEPD	c, a[f]	a, b[e]	a	aa
ADA	a	b	c, d[g]	ab
FUMH	d	b, a[e]	c	bd
sACOH	a	b, c[e]	b, c[g]	ad
mACOH	a	b	a	ab
MPI	c	b	a, c[f]	bc
GPI	c	a	d, b[g]	ac
PGM-1	b, a[e]	b	b	bb
PGM-2	b, a[f], c[e]	b	a, b[f]	ab
ALB	b	b	a	bb
TF	b, c[e]	b, c[e]	a	bc

[a] Alleles are designated in alphabetical sequence in order of decreasing anodal migration. Commas separate alternative alleles at a specified locus for bisexual species; alleles at polymorphic loci are listed in order of decreasing frequency.

[b] Polymorphisms were fixed in the unisexual BOR so genotypes are given for that species.

[c] See table 1. Gene products for the following 18 loci had identical patterns in the four taxa: G3PDH, LDH-2, sMDH, mIDH, mSOD, DIA-2, PNP, sAAT, mAAT, CK-1, CK-2, AK, EST-3, ALP, aGLUS, PEPE, HB, and MB.

[d] CAL = *Kentropyx calcarata* (N = 5 examined); STR = *K. striata* (N = 8); ALT = *K. altamazonica* (N = 3); BOR = *K. borckiana* (N = 3). See appendix for specimens examined.

[e] Frequency = 0.05 to 0.10.

[f] Frequency = 0.11 to 0.20.

[g] Frequency = 0.30 to 0.40.

[h] Frequency = 0.50.

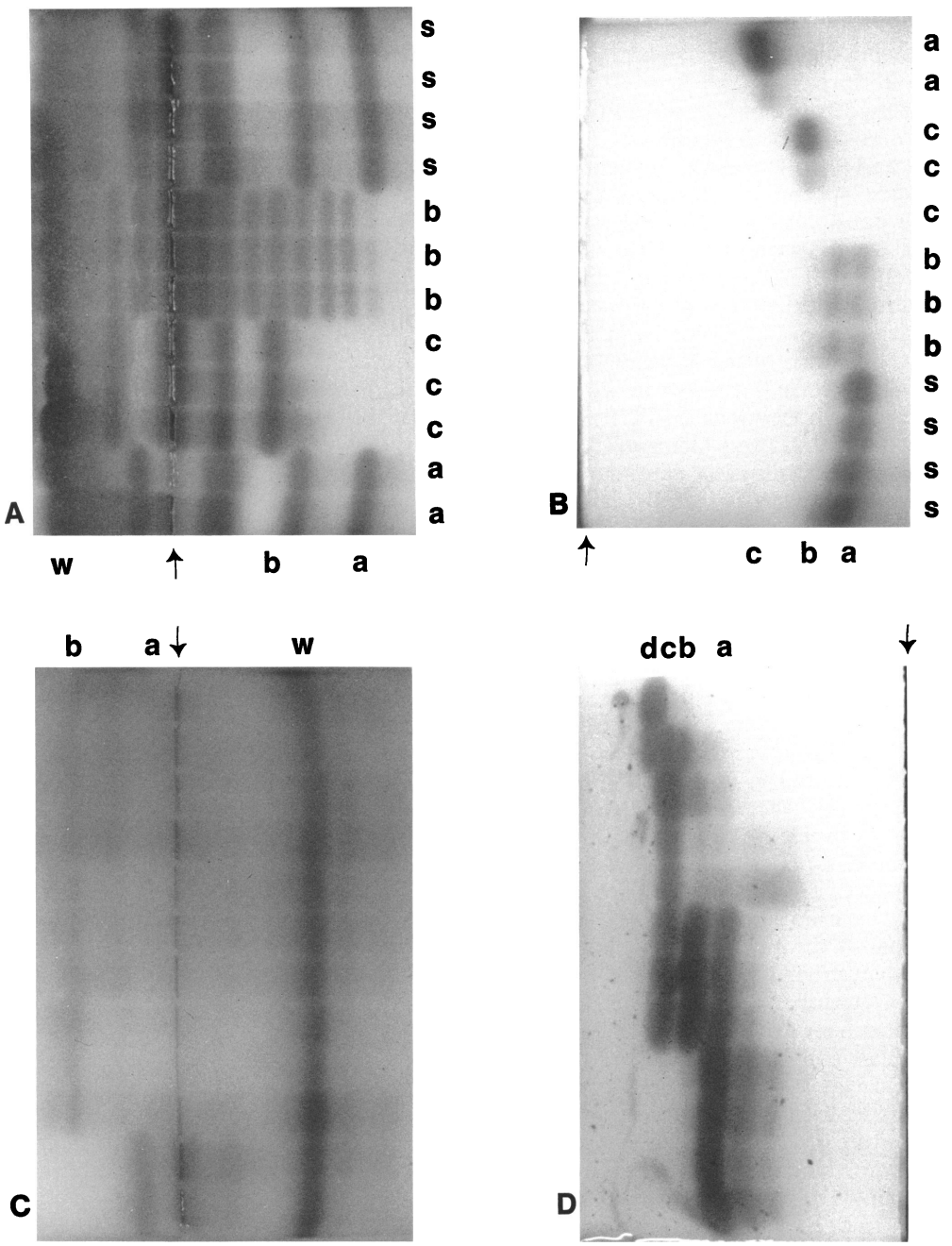

Fig. 7. Electrophoretic patterns of six enzymes on four gels, each including 12 lizards representing four species of *Kentropyx*. **A**. LDH-1 (with letters a and b below) and LDH-2 (with w below). **B**. PEPA. **C**. sMDH (with w above) and mMDH (with a and b above). **D**. GPI. Letters below or above each gel refer to the different allele products (compare with table 4; w, meaning "wild type," is applied to loci showing no allelic variation in this study [table 4, footnote c]). Letters at the right side of the top two gels refer to the species, as follows: a, *altamazonica*; b, *borckiana* (unisexual with high heterozygosity); c, *calcarata*; and s, *striata*. For **C**, arrangement of species is identical to **A**; for **D**, arrangement of species is identical to **B**. For each gel, anode is to the right, and arrow indicates position of sample applications.

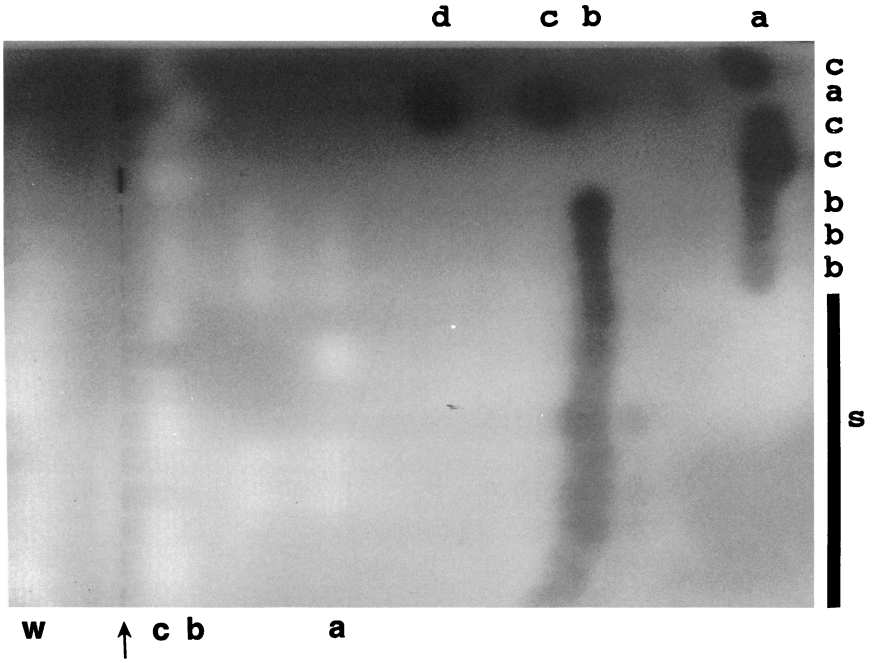

Fig. 8. Electrophoretic patterns of three enzymes on one gel including 16 lizards representing four species of *Kentropyx*. Letters above gel refer to different allele products of ADA. Letters below gel refer to different allele products of sSOD (a, b, c) and mSOD (w). Compare with table 4. Letters at the right side of the gel refer to the species, as in figure 7 but with a vertical bar spanning nine specimens of *striata*. Anode is to the right, and arrow indicates position of sample applications.

and femoral pores. This would not be surprising, as the Venezuelan and Peruvian samples compared are from localities separated by more than 1500 km (linear distance), although this is also consistent with the suggestion of cryptic species.

In the absence of stronger evidence demonstrating the existence of cryptic species among samples now identified as *K. altamazonica*, for now we favor the hypothesis of geographic variation, which was suggested for *K. calcarata* also. For specimens included above in PCA 1 (fig. 4), the smallest polygon represents *K. borckiana*, perhaps being one clone or several closely related ones. The next largest polygon represents *K. striata*, all of which were from Guyana. The largest polygon represents *K. calcarata*, including specimens from both Guyana and Suriname. For these 21 *K. calcarata* (fig. 4), six of the nine specimens with the highest scores on PC2 were the six specimens (100%) from Suriname. If this suggests that the hybrid origin of *K. borckiana* occurred in Suriname (*borckiana* also is high on PC2 in fig. 4), perhaps the d-allele of the sACOH locus will be found in *K. striata* from Suriname.

SUMMARY AND CONCLUSIONS

1. This research confirms that *Kentropyx borckiana* of the Guiana Region is a morphologically recognizable unisexual (all-female) species.

2. The high heterozygosity (H = 0.38) of *K. borckiana* indicates that the species had a hybrid origin.

3. All three specimens of *K. borckiana* from Georgetown, Guyana, were genetically identical in alleles present at all 45 loci examined electrophoretically, indicating that the heterozygosity is fixed and suggesting further that the species is a clone of parthenogenetic individuals.

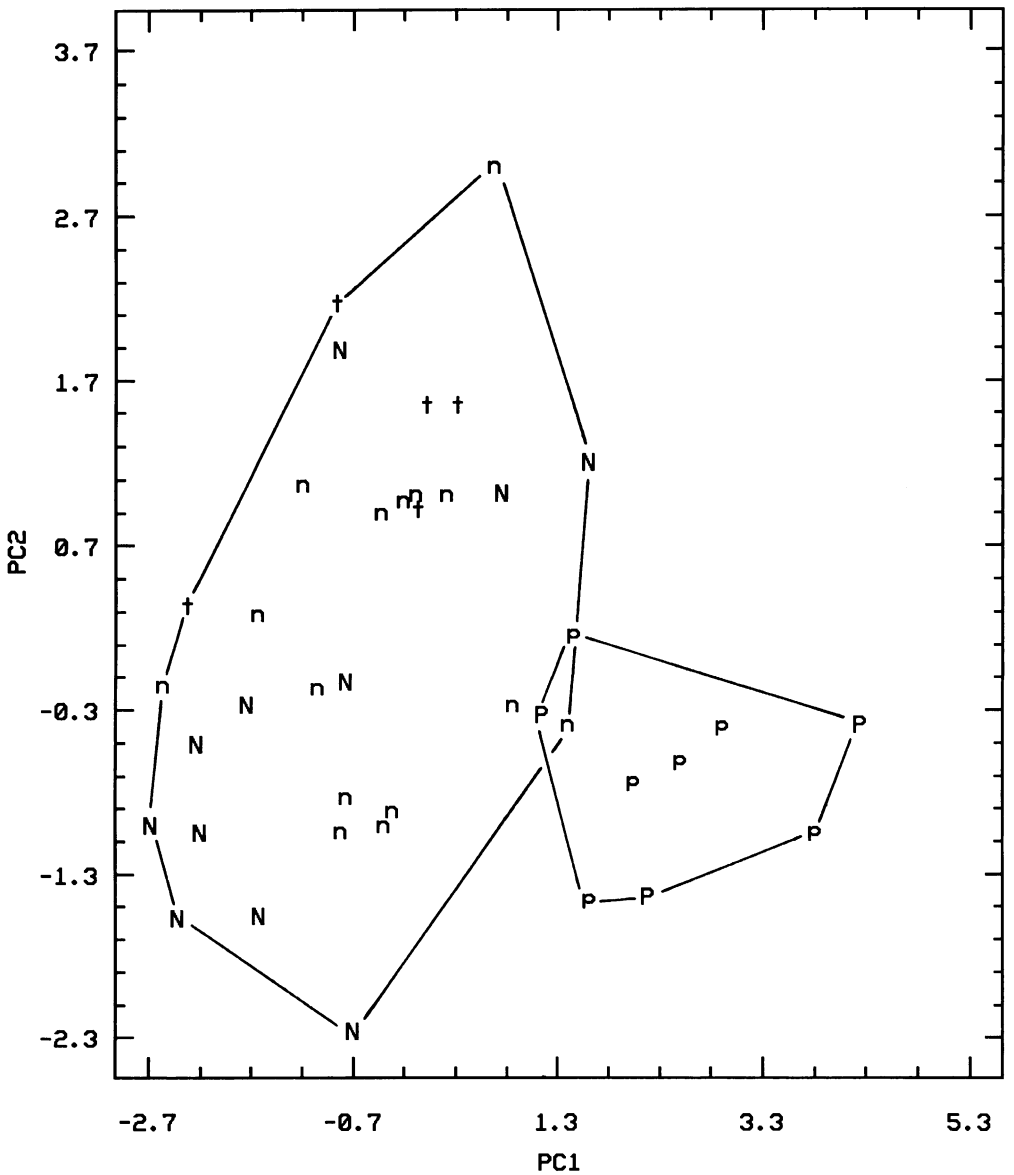

Fig. 9. Polygons and letters representing the scores of 40 specimens of *Kentropyx altamazonica* (three population samples) on the first two principal components extracted from the correlation matrix of nine morphological characters (tables 2, 5). Capital letters indicate females, lowercase letters indicate males, as follows: n, sample from Cerro de la Neblina, Venezuela; t, sample from Tapirapeco, Venezuela; p, sample from Peru.

4. Comparative karyotypic data demonstrate that the clone of *K. borckiana* is diploid.

5. Morphological, biochemical, karyotypic, geographical, and ecological observations are all consistent in suggesting that the immediate bisexual ancestors of *K. borckiana* are *K. calcarata* and *K. striata*. In other words,

the clone of *K. borckiana* stemmed from one or more F_1 hybrids of *K. calcarata* × *K. striata*.

6. The hybrid event(s) that created *K. borckiana* probably occurred in the Guiana Region of northern South America, associated with habitat disturbance that brought the ancestral species together.

7. Although we did not examine specimens of *K. borckiana* from Barbados, 18 specimens were reported by Gallagher and Dixon (1992), so we conclude that the clone became established in Barbados following dispersal and colonization, whether human-mediated or not.

8. *Kentropyx altamazonica* is added to the herpetofauna of Venezuela (Amazonas Territory), and we discussed the issues of possible geographic variation within this species versus the possibility that cryptic species are masquerading under this name.

TABLE 5

Character Loadings on First Four Axes for a Principal Components Analysis of *Kentropyx altamazonica* Morphology[a]

Character	PC1	PC2	PC3	PC4
Body length	0.231	0.226	−0.533	0.331
Around body	−0.224	0.058	0.720	0.093
Dorsals	0.445	−0.235	0.268	−0.025
Ventrals	0.505	0.049	0.093	0.047
Pores	−0.195	0.490	0.166	0.561
Collars	0.152	−0.285	0.029	0.708
Gulars	0.399	−0.280	0.221	0.100
Toe lamellae	0.230	0.584	0.195	−0.091
Finger lamellae	0.411	0.382	0.033	−0.210
Variation expl.	34%	15%	13%	11%

[a] Based on data summarized in table 2.

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APPENDIX

Specimens Examined

The 120 specimens are referred to by their individual catalog numbers and initials for their respective collections, as follows: AMNH (American Museum of Natural History); and USNM (United States National Museum of Natural History, Smithsonian Institution). All but two of these specimens (the two exceptions are specified below) were used for analyses of external morphology. The lowercase letters following the catalog numbers indicate additional data taken from individual specimens, when applicable, as follows: k, karyotype; and p, protein electrophoresis.

Kentropyx altamazonica

PERU: Amazonas; headwaters of Rio Kagka (tributary of Rio Cenepa) (USNM 316778); Kusu, on Rio Comaina (tributary of Rio Cenepa) (USNM

316779–316780); vicinity of Rio Kayamas (tributary of Rio Cenepa) (USNM 316781); Sua, on the Rio Cenepa (USNM 316782–316783); Huampami, Quebrada Sasa, on Rio Cenepa (USNM 316785); and vicinity of Huampami, on Rio Cenepa (USNM 316786–316789).

VENEZUELA: Amazonas; Neblina Base Camp on Rio Mawarinuma, 140 m (00°50′N, 66°10′W) (AMNH 127817–127821, 129243, and 133667–69; USNM field series H587–H589, H654–H655, H662; USNM field series RWM17696, RWM17811, RWM18110–RWM18111; and USNM 334992–334996, 335004–335014); Tapirapeco Expedition Base Camp, upper Rio Mavaca, 150 m (02°02′N, 65°07′W)(AMNH 134174–134176, p; and AMNH 134177–134178); upper Orinoco, SW base of Cerro Yapacana, 110 m (AMNH 117893–117894; these two specimens were not included in the morphological analyses).

Kentropyx borckiana

GUYANA: Georgetown (AMNH 37457–37464); Georgetown, Botanical Gardens, sea level (AMNH 138111, p; 138112–138113, k, p; 138114–138116; and 138648–138649).

Kentropyx calcarata

GUYANA: near Georgetown (AMNH 8489); Georgetown (AMNH 8563); Kamakusa (AMNH 25065, 25068, 25090, and 25111–25112); Kartabo (AMNH 21328, 137358–137359, and 137362); Kuyuwini Landing (AMNH 61255–61256, and 61294–61295); Marudi (AMNH 60972–60973); and Onora (AMNH 61292–61293).

SURINAME: Brokopondo; Brownsberg Nature Park, low elev. trail to Irene Falls, 125 m (AMNH 119420, k); Browns Berg, Brownsberg Nature Park, Mazaroni Plateau, 500 m (AMNH 119421, k); Mazaroni Top, Brownsberg Nature Reserve, 500 m (AMNH 133347, p; 133348, k, p; 133349, p; and 133350, k, p). Suriname; Paramaribo, grounds of Paramaribo Zoo (AMNH 133351, k, p).

Kentropyx striata

GUYANA: Haiowa Falls, Essequibo River (AMNH 61487–61488); Isheartun (AMNH 61377, 61378); Karanambo, Rupununi River (AMNH 60881–60882); McTurk's Place [Karanambo], Rupununi River (AMNH 60883–60884); pond 5 mi (linear) SW Karanambo, 300 ft (AMNH 138089–138091, p; 138092–138094; 138096; 138097–138098, k, p); vicinity of Cajueiro, 8 mi WNW Karanambo, 300 ft (AMNH 138088, p); Marudi (AMNH 61331); Wichabai (AMNH 61271–61272); Yupukari (on Rupununi River), 7 mi (linear) SSW Karanambo, 370 ft (AMNH 138057, p); and Simoni area, about 10 mi (by trail) E Yupukari (AMNH 138083, p, and 138084–138085, p).

Note added in proof: Avila-Pires' (1995) extensive, information-packed book on the lizards of Brazilian Amazonia appeared while this report was in press. She also discusses the presence of *Kentropyx altamazonica* in Venezuela, habitats of various species, and the probable hybrid origin of *Leposoma percarinatum,* with hypotheses concerning the possible ancestral taxa.

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