

THE *URODERMA BILOBATUM* (CHIROPTERA: PHYLLOSTOMIDAE) CLINE REVISITED

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We studied clinal variation in karyotypes of Peters' tent-making bat (*Uroderma bilobatum*) along a transect from south-central El Salvador to northwestern Nicaragua. Nondifferentially stained karyotypes were scored for 291 specimens from 5 localities. Each locality was near a locality from which similar data on *U. bilobatum* have been reported in the literature 18 years ago. *G*-tests indicated no significant differences between our data and the historical data at 2 localities in El Salvador; significant differences were found at the contact zone in Honduras. Based on a combined sample of 834 specimens, by means of the point at which genotype frequencies equal 20% and 80% (20/80 rule), we estimated that 3 chromosomal morphs (designated Aa, Bb, and Cc) had an average clinal width of 33.3 km. The widest cline, Bb, was 12.53 km wider than the narrowest, Cc. Morph Cc was detected at 2 localities, 72 and 80 km northwest of the nearest locality from which it was previously known. Overall, we detected little change in clinal architecture during the intervening years between these 2 analyses. Four investigators who used the same data set have published 4 different interpretations of clinal dynamics. These interpretations are mutually contradictory and so all cannot be correct.

Key words: cline, contradictory interpretations, karyotype, *Uroderma bilobatum*

Along the Pacific versant of Central America, clinal variation was documented in populations of Peters' tent-making bat (*Uroderma bilobatum*) from Taxisco, Guatemala, to Chinandega, Nicaragua (Baker 1981). The cline was characterized by regular spatial variation in the frequencies of 3 pairs of chromosomal forms, designated by Baker (1981) as the Aa, Bb, and Cc morphs. These forms can be diagnosed unambiguously with nondifferentiated karyotypes. Each morph has a distinct, though similar, geographical distribution, resulting in 3 clines, 1 for each morph.

The A form of chromosomal morph Aa has a small biarmed element and an acrocentric element. The other morph, repre-

sented by lowercase a, has these 2 elements fused to form a subtelocentric chromosome. The number of As in a karyotype is equal to the number of small biarmed autosomes. Each small biarmed element produces an increase of 1 in the complement, over the basal diploid number ($2n$) = 38, accompanied by a decrease of 1 in the number of large biarmed elements (Baker 1979, 1981).

The B form of chromosomal morph Bb has a centric fusion-fission in which morph B is represented by 2 acrocentrics. Morph b is a subtelocentric element resultant from the fusion of the 2 acrocentric elements in B. In nondifferentiated karyotypes, each b effects a decrease of 1 in the diploid number and an increase of 1 in the number of large biarmed elements, without decreasing

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the number of small biarmed autosomes (Baker 1979, 1981).

The C form of chromosomal morph Cc is a terminal translocation in which a small acrocentric element is translocated to the end of the long arm of the longest acrocentric in the karyotype. Each c signifies that the centromeric end of the smaller element is translocated to the distal end of the largest acrocentric. The presence of a c morph is accompanied by a reduction in the diploid number by 1 and reduces the number of acrocentrics by 1 without changing the number of biarmed elements, either large or small (Baker 1979, 1981). Photographs and diagrammatic representations of these 3 forms have been presented and discussed in Baker (1981) and other publications cited therein.

Qualitatively, these clines are long. The mean distance between their points of fixation at 0% and 100% is about 425 km. Qualitative length notwithstanding, major changes occur in morph frequencies over much shorter distances. This rapid change takes place along a transect that is completely contained within the Gulf of Fonseca region of Honduras.

The *U. bilobatum* cline was originally studied by Baker and Lopez (1970), Baker and McDaniel (1972), and Baker et al. (1972, 1975). Baker (1979) reviewed current knowledge of *U. bilobatum* on the basis of 333 karyotyped specimens. Later, Baker (1981) reported an analysis based on his original 333 specimens plus an additional 210, bringing the total sample to 543 specimens (herein referred to as old data). In a companion study, Greenbaum (1981) examined 366 specimens of *U. bilobatum* that represented 12 populations sampled at Baker's original collection sites. Greenbaum (1981) analyzed 210 of those specimens separately for karyologic variation, plus his entire set of 366 bats for electrophoretic variation. Barton (1982) and Hafner (1982) published critiques of Baker (1981) and Greenbaum (1981). All material used in these studies was collected from 13

localities ranging from Huixtla, Mexico, in the northwest to Puntarenas, Costa Rica, in the southeast, a distance of about 1,100 km.

A major difficulty in the study of vertebrate clines is the collection of an adequate number of samples, of adequate size, at closely spaced intervals. We present data representing 291 specimens (herein called the new data) taken from 5 additional localities, all contained within Baker's original transect. This brings the sample to 834 specimens (herein called the combined data). Greater sample size permits further refinement of clinal architecture and forms the basis for a comparison and contrast with Baker's (1981) data. We discuss several contradictory opinions in the literature regarding clinal dynamics (Baker 1981; Barton 1982; Greenbaum 1981; Hafner 1982).

MATERIALS AND METHODS

Natural populations of *U. bilobatum* were sampled at 5 localities in El Salvador, Honduras, and Nicaragua during the years 1990 and 1991. Voucher specimens were prepared as museum skins and skulls or were preserved in formalin and later transferred to ethyl alcohol. All are deposited in the Museum of Texas Tech University, Lubbock.

Specimens were karyotyped from bone marrow by the *in vivo* culture method (Baker 1970). The nature of chromosomal rearrangements in *U. bilobatum* is such that the chromosomal cytotype can be determined from nondifferentiated preparations (Baker 1979). A minimum of 5 complements was examined for each specimen as a quality control measure, and a determination of cytotype was made. Two specimens, 1 from locality 3T (near La Herradura, Departamento de La Paz, El Salvador) and 1 from locality 4T (near Usulután, Departamento de Usulután, El Salvador), were polymorphic for an additional centric fusion, resulting in a diploid number of 43. For purposes of analysis, those were counted as if the diploid number were 44.

A comparison of data generated from our study and that contained in Baker (1981) allowed us to list all possible cytotypes (Table 1), some of which have not been found in nature. Table 2 lists all localities along with their corresponding sample sizes and distances from the

TABLE 1.— Number of each cytotype for samples of *Uroderma bilobatum* from Baker (1981) and this paper. New localities are followed by the letter T. 1) Mexico: Chiapas: 23.6 mi NW Huixtla; 2) Guatemala: Santa Rosa: 1 mi E Taxisco; 3) El Salvador: La Paz: 3 mi NW La Herradura; 3T) El Salvador: La Paz: 2.5 mi NNE La Herradura and 4.8 mi NE La Herradura; 4) El Salvador: Usulután: 3 mi E Usulután; 4T) El Salvador: Usulután: 8.8 mi E by ESE Usulután; 5) Honduras: Valle: 1 mi SE Nacaome; 6) Honduras: Valle: 10 mi SSW Nacaome; 6T) Honduras: Valle: 7.4 mi SSW Nacaome; 7) Honduras: Choluteca: 10.2 mi NW Choluteca; 7T) Honduras: Choluteca: 9.6 mi W by WSW Choluteca; 8) Honduras: Choluteca: 11.5 mi SW Choluteca; 9) Nicaragua: Chinandega: 3.5 mi NW Chinandega and 1.5 mi S Chinandega; 9T) Nicaragua: Chinandega: 10 mi ESE Chinandega; 10) Nicaragua: Leon: 2.1 mi SSE Leon; 11) Costa Rica: Guanacaste: 10 mi SSE Canas and San Jose: 41.2 mi SW Canas; 12) Costa Rica: San Jose: 12.3 mi SSE San Isidro del General; 13) Costa Rica: Puntarenas: 2.1 mi S, 1.1 mi E San Vito.

Diploid number	Morph a	Morph b	Morph c	Localities																		
				1	2	3	3T	4	4T	5	6T	6	7	7T	8	9	9T	10	11	12	13	
44	AA	BB	CC	54	35	43	77	74	68	5	11	5	0	0	0	0	0	0	0	0	0	0
43	AA	BB	Cc	0	0	0	1	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0
43	AA	Bb	CC	0	1	5	5	7	9	3	5	5	2	0	1	0	0	0	0	0	0	0
43	Aa	BB	CC	0	0	2	7	0	3	0	5	1	0	0	0	0	0	0	0	0	0	0
42	AA	BB	cc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	AA	Bb	Cc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	AA	bb	CC	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
42	Aa	BB	Cc	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
42	Aa	Bb	CC	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0
42	aa	BB	CC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	AA	Bb	cc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	AA	bb	Cc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
41	Aa	BB	cc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	Aa	Bb	Cc	0	0	0	0	0	0	1	2	5	3	1	0	0	0	0	0	0	0	0
41	Aa	bb	CC	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
41	aa	BB	Cc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	aa	Bb	CC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40	AA	bb	cc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40	Aa	Bb	cc	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
40	Aa	bb	Cc	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
40	aa	BB	cc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40	aa	Bb	Cc	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
40	aa	bb	CC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	Aa	bb	cc	0	0	0	0	0	0	0	0	1	2	0	8	2	0	0	0	0	0	0
39	aa	Bb	cc	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0
39	aa	bb	Cc	0	0	0	0	0	0	0	2	0	1	2	2	2	0	0	0	0	0	0
38	aa	bb	cc	0	0	0	0	0	0	0	0	1	2	10	66	82	75	44	28	25	13	13

TABLE 2.—Summary of chromosomal data for 18 samples from Baker (1981) and this paper; see Table 1 for localities.

Locality	<i>n</i>	Parental cytotype present	Distance from locality of parental cytotypes sympatry (km)	Potential F ₁ s	Number of backcross individuals	Morph frequency		
						a	b	c
1	54	44	500	0	0	0.00	0.00	0.00
2	36	44	300	0	1	0.00	0.01	0.00
3	50	44	140	0	7	0.02	0.05	0.00
3T	90	44	133	0	13	0.04	0.03	0.01
4	83	44	90	0	7	0.01	0.05	0.00
4T	81	44	82	0	13	0.02	0.06	0.01
5	9	44	10	1	3	0.06	0.22	0.06
6T	29	44	4	2	18	0.21	0.28	0.10
6	25	44, 38	0	5	15	0.40	0.59	0.30
7	12	38	20	3	7	0.58	0.71	0.67
7T	16	38	35	1	6	0.97	0.88	0.91
8	78	38	45	0	5	0.95	0.99	0.96
9	86	38	100	0	4	0.99	1.00	0.99
9T	75	38	117	0	0	1.00	1.00	1.00
10	44	38	150	0	0	1.00	1.00	1.00
11	28	38	400	0	0	1.00	1.00	1.00
12	25	38	550	0	0	1.00	1.00	1.00
13	13	38	600	0	0	1.00	1.00	1.00

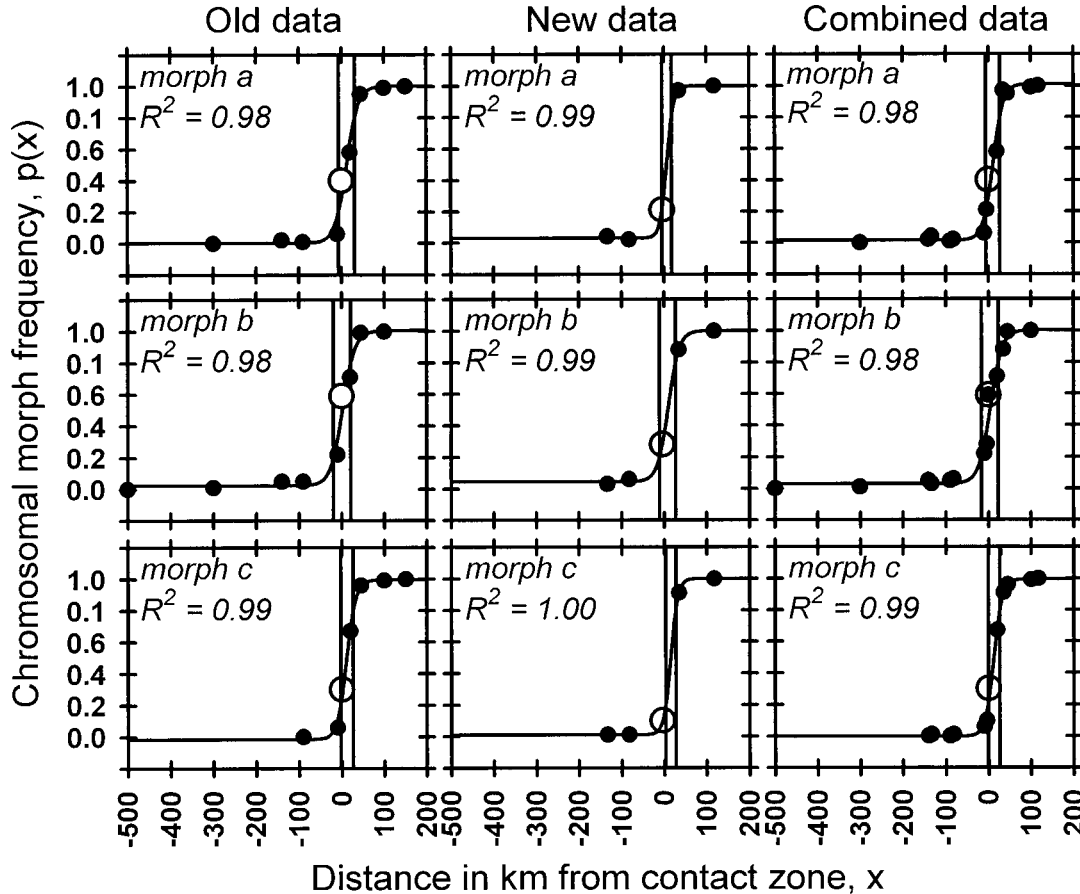


FIG. 1.—Frequencies of chromosomal morphs from fixation at 0% to fixation at 100% for old data, new data, and combined data. Circles in plots for the old and combined data sets indicate the contact zone locality number 6 in Baker (1981). Circles in the plots of the new data indicate the presumptive contact zone for these data. Vertical lines delimit the width of the contact zone between the values $20\% \leq p(x) \leq 80\%$. All plots are drawn to the same scale to facilitate comparisons.

zone of parental sympatry. The remaining information in Table 2 is summarized for the convenience of the reader but can be derived from Table 1. We have retained the original chromosomal nomenclature and locality designations used by Baker (1981). Locality numbers followed by the letter T are those collected for this study. We used G -tests (Sokal and Rohlf 1981) at paired localities 3–3T, 4–4T, and 6–6T, members of which are <10 km apart, to evaluate chromosomal frequencies. The null hypothesis was that morph frequencies for the new data do not have significant departures from their corresponding frequencies for the old data. That was a single classification test for goodness-of-fit. Expected frequencies, under the null hypoth-

esis (Sokal and Rohlf 1981), were those of the old data.

RESULTS

Morph frequencies $p(x)$ were plotted against distance x , away from locality 6 (Fig. 1). That locality was in the area of the Gulf of Fonseca near Nacaome, Honduras. Because locality 6 was the only locality where both parental cytotypes have been documented in sympatry, it was considered crucial to an understanding of clinal dynamics. The data, upon which the statistical calculations were based, consisted of all localities between fixation at 0% and fixation

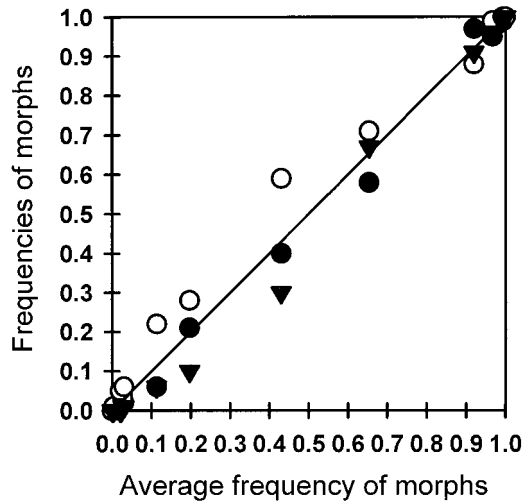


FIG. 2.—Frequencies of morphs a (solid circle), b (circle), and c (inverted triangle) plotted against their average frequencies at the 13 localities given in Table 2.

at 100%, inclusive. Data were fitted to sigmoid-shaped curves by a least-squares criterion. Because the coefficient of determination (R^2) was quite high for each plot, we accepted those curves as good models of clinal change and base further calculations and discussion on them. Figure 2 is a plot of morph frequencies against the average frequencies of the 3 morphs, at each locality. The diagonal marks the place where the morphs would lie if the 3 clines were exactly coincidental. Figure 3 is a graph of the 1st derivatives $dp(x)/dx$ of the sigmoid curves (combined data) used in the plots of Fig. 1. Morph a is represented by a dotted line, morph b by a solid line, and morph c by a dashed line.

We estimated widths of the clines, w , by 2 standard procedures (Endler 1977; May et al. 1975): the distance between the points on the abscissa at which genotype frequencies equal 20% and 80%, hereafter called the 20/80 distance, and the inverse of the slope of the steepest part of the sigmoid curves $w = \max[dp(x)/dx]^{-1}$. Estimates, in kilometers, calculated as the 20/80 distance, were as follows: old data (morph a = 37.75, b = 40.63, and c = 29.79), new data

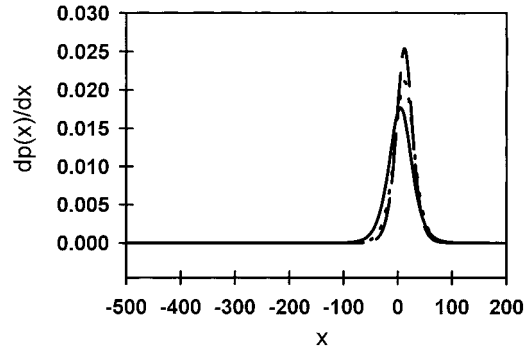


FIG. 3.—The 1st derivative of morph frequency $p(x)$ as a function of distance from the contact zone x , for the combined data.

(morph a = 22.94, b = 37.88, and c = 30.46), and combined data (morph a = 32.97, b = 39.78, c = 27.25). Estimates based on the inverse slope method were as follows: old data (morph a = 54.44, b = 58.11, and c = 43.13), new data (morph a = 32.67, b = 53.46, and c = 34.22), and combined data (morph a = 47.41, b = 56.64, and c = 39.22). In general, estimates based on the inverse of the 1st derivative of the fitted slope were wider than the 20/80 distance. A shorter 20/80 cline was consistent with calculations based on clinal change in other species (Endler 1977). A number of functionally different sigmoid curves fitted data about equally well, all with $R^2 > 0.99$. Each of those curves gave slightly different values for the parameter estimates presented above.

By use of the 20/80 distances, cline widths for the old data and the combined data had the same ordinal relationship. In both data sets, morph b had the longest width, morph a had the next longest width, and morph c had the shortest width. The widest cline for the new data also was that of morph b. However, for the new data, the cline for morph c was longer than that for morph a. That reversal, in the ordinal relationship of width, may have reflected our discovery of the presence of morph c in population 3T, new to this paper. It was not

reported from population 3 by Baker (1981) or Greenbaum (1981).

Considering the great length over which backcross animals have been found, 400 km (probably a significant underestimate), the 3 clines came close to coinciding in their locations and widths. Midpoints, at 40%, for the 20/80 clines (combined data) were: morph Aa, $0 + 6.59$ km, morph Bb, $0 - 1.78$ km, and morph Cc, $0 + 8.34$ km. The longest cline Bb was only 12.53 km longer than the shortest cline, Cc. Average clinal width, 33.33 km, was only 12% of the average length over which backcross individuals have been found. Figure 3 shows graphically how change in morph frequencies changes along the cline. In that figure the 1st derivatives of the sigmoid curves of Fig. 1 (combined data) were plotted against distance from the contact zone. Heights of the spikes measured the maximum rate of change of the sigmoid curves and the position where that maximum occurred. Widths of the spikes represented the interval between positive instantaneous change and zero change. It was noteworthy that the 3 derivatives nearly coincide. That suggested that clinal dynamics for each chromosomal morph were similar in magnitude and direction, because substantial differences in the velocity of clinal movement and direction would have tended to separate them over the years.

The samples numbered 3T and 4T, new to this paper, differed from nearby samples reported in Baker (1981) that were collected some 12 years earlier. Morph c was found at locality 3T near La Herradura, Department La Paz, El Salvador, and at locality 4T near Usulután, Department Usulután, El Salvador. That was an increase of 72 (4T) and 123 (3T) km northwestward in the known range of this morph. Whether c migrated into the area during the intervening years, or whether c was present at La Herradura and Usulután when Baker (1981) sampled there but was not represented in his small samples is not known.

We used the law of cosines to calculate

the distances between members of sample pairs as follows: 3–3T, 7.04 km; 4–4T, 5.89 km; 6–6T, 4.19 km, 7–7T, 15.05 km, and 9–9T, 17.59 km. Locality pairs 3–3T, 4–4T, and 6–6T were separated by relatively short distances, so distance may not have been a confounding variable for the purpose of comparisons. We only were able to reject the null hypothesis for morphs a, b, and c at locality 6–6T, the contact zone pair ($G_{adj} > \chi^2_{0.05[1]} = 3.841$). Morph proportions between old and new data were not the same at 6–6T. Statistical comparisons between locality pairs 3–3T and 4–4T were based on large samples. Their statistical nonsignificance lends confidence that Baker's (1981) samples and those new to this paper were representative of the populations from which they were drawn.

DISCUSSION

Four interpretations of the cline.—Baker (1981) found parental cytotypes to be sympatric at locality 6 only. Data were obtained there for 25 specimens; of these, 6 were parental types (5 with $2n = 44$ and 1 with $2n = 38$), 5 were F_1 s, and 14 were various backcrosses (Table 1). This suggested to Baker (1981) that at locality 6 pure parental forms and F_1 s are underrepresented and backcross individuals are overrepresented. Selection against chromosomal heterozygotes appeared not to be strong enough to reach critical levels central to some theories of chromosomal evolution (Bush et al. 1977; Lande 1979; White 1978; Wilson et al. 1975). Baker (1981) interpreted the zone to be the product of secondary contact. Under Baker's characterization parental forms seldom meet and F_1 s suffer negative heterosis. In contrast, backcrosses are favored by positive heterosis. Excess backcross individuals thence migrate toward the northwest with a superior *davisi* form gradually replacing the *convexum* form through introgression. This interpretation is strengthened through the discovery of the c morph at locality 3T, near La Herradura, and locality 4T, near Usulután (Table 2). These 2 local-

ities are 133 and 82 km, respectively, farther northwest than the locality of the c morph from the old data. A separate karyotypic analysis (Greenbaum 1981) concurred with Baker's results.

Baker's (1981) judgment that parental and F_1 individuals are in dearth and that backcross individuals are in excess was pivotal to his interpretation. Dearth and excess are relative terms and have a more exact meaning when compared with an appropriate null model, such as Hardy-Weinberg equilibrium.

Barton (1982) reanalyzed Baker's data for Hardy-Weinberg equilibrium and concluded that both parental and F_1 cytotypes are actually in excess. By means of maximum-likelihood estimators, he found that all 3 pairwise disequilibria were significantly different from 0, but that the 3-way coefficient was not significant. Nevertheless, Barton's overall evaluation of the population was that it was "very close to Hardy-Weinberg equilibrium" (Barton 1982:864). He concluded that population 6 (the only population where both parental cytotypes were found together) was consistent with moderate selection against recombinant forms and the inward dispersal of parental types from outside the zone. Barton (1982) did not comment on the origin of the zone, but his position was consistent with secondary contact.

Greenbaum (1981) examined protein variation at 22 loci from bats collected along the Mexico-Costa Rica transect. Eleven of those loci (50%) were polymorphic at ≥ 2 of the 12 localities. Minor alleles at 9 loci were found to function as unambiguous identification markers for either the *davisi* or *convexum* parental types. Greenbaum's (1981) principal electrophoretic result was documentation of a marked absence of data supporting the hypothesis of introgressive hybridization. No marker allele for 1 parental cytotype was found in the other parental cytotype, outside of the hybrid zone. In summary, Greenbaum (1981) concluded that the zone probably represented an area

of primary contact in which reproductive isolation between the *davisi* and *convexum* forms was being strengthened by selection. Allometric data in support of Greenbaum's (1981) conclusions depended upon reliability of marker alleles as identifiers. Greenbaum's (1981) reliance on those markers was challenged by Hafner (1982) on several grounds, including the "rare allele phenomenon" (Sage and Selander 1979) and a small sample.

Hafner (1982) published a 3rd analysis of Baker's data in which he estimated the width of the cline to be about 35 km, by means of the 20/80 rule. Based on Barrowclough (1980), Hafner (1982) chose a dispersal rate for *U. bilobatum* of about 1 km/year. Barrowclough's (1980) paper dealt with birds; his data that most closely match the value of 1 km/year correspond to the great tit (*Parus major*) from the United Kingdom. Birds differ in their dispersal patterns even among individuals of the same species (Greenwood and Harvey 1976). The aerodynamic characteristics of an insectivorous Palearctic bird and its disposition to disperse may be substantially different from that of a small frugivorous Neotropical bat. We question the use of this dispersal rate as an estimate for *U. bilobatum* and note that this parameter was crucial to Hafner's (1982) interpretation of the contact zone.

In the equation used by Hafner (1982), gene flow, l , occurs as a variable for the magnitude of the selection gradient $b = l^2(1.66/w)^3$. Notice that b is dependent on the values of both l and w . Because in the selection-gradient equation, the variable l is squared and the expression involving w is cubed, a substantial differential is established between errors in the estimates of these 2 parameters and the estimate of b . By using $w = 35$ km and $l = 1$ km/year, Hafner (1982) calculated b to equal $1.1 \times 10^{-4}/\text{km}$. Based on this estimate of the magnitude of the selection gradient, Hafner (1982) made the transition to simple diffusion of parental cytotypes into each other.

Hafner (1982) marshaled further support for the diffusion model by comparing the observed array of karyotypes across the transect with those predicted by a binomial distribution. He trisected the region into 3 geographical areas: a *davisi*-like region, a midregion, and a *convexum*-like region. Estimates of the probabilities of p and q in the binomial equation $(p + q)^x$ were extrinsic to the data at the midregion and based upon the data at the *davisi* and *convexum* regions.

Hafner's (1982) extrinsic midregion estimate of $p = 0.5$ and $q = 0.5$ requires the assumption of equal diffusion rates into the zone from both parental types, which may or may not be correct. Diffusion depends upon factors including population density and habitat quality on either side of the zone. These variables may differ for the 2 parental types. No data exist that are relevant to the matter. Computed values of chi-square were not significant ($P > 0.5$) at each of the 3 regions (Hafner 1982). The data could not distinguish between the observed array of diploid numbers and that expected from the binomial probability distribution. This result is consistent with the null hypothesis of random diffusion into the zone; it provides no evidence for selection against F_1 s or backcrosses.

Hafner (1982) concluded that diploid numbers were distributed randomly across the zone; however, that does not necessarily mean that chromosomal phenotypes are randomly distributed. This is because the same diploid numbers, except in the case of pure parental types, can be represented by several different cytotypes (1 cytotype, $2n = 38$; 3 cytotypes, $2n = 39$; 6 cytotypes, $2n = 40$; 7 cytotypes, $2n = 41$; 6 cytotypes, $2n = 42$; 3 cytotypes, $2n = 43$; 1 cytotype, $2n = 44$; Table 1). One cannot statistically conclude that the distribution of chromosomal phenotypes is random according to this binomial model.

In summary, 4 interpretations of the chromosomal cline of *U. bilobatum* currently are found in the literature. The 1st is that little contact occurs between parental

cytotypes coupled with meiotic problems in the production of F_1 s, positive heterosis occurs among those backcrosses that are produced, and secondary contact occurs with the southeastern *convexum* form replacing the northwestern *davisi* form through phyletic evolution (Baker 1981). The 2nd is that a zone occurs characterized by primary contact with introgressive hybridization limited to immediate zonal area; *davisi* and *convexum* forms are enroute to full species status (Greenbaum 1981). The 3rd is that significant contact occurs between parental types through dispersion; a moderate but biologically significant burden is imposed on the F_1 s and backcrosses by negative heterosis with the contact zone functioning as a genetic sink (Barton 1982). The 4th is that selection does not need to be invoked because the selection gradient is very weak; data are consistent with a model of random diffusion, and secondary neutral contacts are plausible (Hafner 1982).

Here, data from a single cline have led to 4 distinct, and to some degree mutually exclusive, interpretations. As a matter of pure logic, both Barton (1982) and Hafner (1982) cannot be correct. Barton could be correct and Hafner wrong or vice versa. They can both be wrong, and Baker (1981) can be correct. Reasoning in the same vein, both Baker (1981) and Greenbaum (1981) cannot be correct. Other permutations exist. Of course, all 4 possibly are wrong to varying degrees.

A different contact zone in bats.—Only 1 other chromosomal contact zone has been studied in bats, and it is of a very different nature. The reported diploid numbers of members of the *Rhogeessa tumida* complex (Chiroptera: Vespertilionidae) are 30, 32, 34, 42, 44, and 52 (Baker 1984; Bickham and Baker 1977; Honeycutt et al. 1980). Each of those karyotypic variants, when described, was thought to represent variation within the boundary of a single species. If that evaluation were correct, then *R. tumida* and *U. bilobatum* would be similar in the sense that within the limits of each species,

several diploid complements occur in nature.

By using chromosomal data, Baker (1981) reduced a part of this diploid variation by removing the $2n = 42$ form and naming it as a distinct species, *Rhogeessa genowaysi*. Genoways and Baker (1996) recognized 7 species within the *R. tumida* complex.

Unlike *U. bilobatum*, members of the *R. tumida* complex do not commonly occur in sympatry; parapatry seems to characterize species distributional boundaries at a geographic scale. Genoways and Baker (1996) hypothesized that the pattern of geographic parapatry came about from the speciation of a once widespread single species and that the relationships among species usually reflected associations of geographical parapatry.

A fundamental difference between members of the *R. tumida* complex and *U. bilobatum davisi-convexum* complex is that where karyotypic variants of the *R. tumida* complex meet, no introgression has been demonstrated to occur and that where karyotypic variants of *U. bilobatum* meet, introgression has been demonstrated to occur. Baker and Bickham (1986) used the phenomenon of sibling species, identified by karyotypic variation, as an empirical basis for a model of speciation by monobrachial fusions.

A rodent hybrid zone.—Van Den Bussche et al. (1993) studied a hybrid zone between 2 chromosomal races of the white-footed mouse (*Peromyscus leucopus*). Van Den Bussche et al. (1993) and Chesser et al. (1996) conceptualized the dynamics of narrow hybrid zones within the broad framework of 3 distinct models: the dynamic-equilibrium model (Moore 1977), the hybrid-superiority model (Moore 1977), and the hybrid-equilibrium model (Endler 1977). The dynamic-equilibrium and hybrid-superiority models represent the extremes of a continuum, with hybrid-equilibrium being intermediate. Importantly, each

model results from different underlying biological phenomena.

The clines of *U. bilobatum* and *P. leucopus* (Baker et al. 1987; Stangl 1986) have several features in common. Both are characterized by a narrow tension zone, with the *Uroderma* zone having a 20/80 width estimated at 35 km and the *Peromyscus* zone a width of 30.6 km. It is noteworthy that both volant and small nonvolant mammalian species have zonal widths that are similar in length. The capacity to fly, in and of itself, may be of little significance in establishing the long-term width of a contact zone. In both the mouse and the bat, all known genetic markers, except for the minor allelic markers used by Greenbaum (1981), are distributed asymmetrically (Nelson et al. 1987), that is, 1 form is more introgressed into its counterpart than the other.

In his summary statements, Barton (1982) placed the *Uroderma* cline in a position that would be near the dynamic-equilibrium model. However, his reiterated assertion that the population is near Hardy-Weinberg equilibrium would seem to be consistent with a position near the hybrid-equilibrium model (Endler 1977). Actually, data are too few to give much confidence in choosing 1 model over the other. Barton (1982:864) himself implied this when he wrote in reference to his own paper, "This discussion probably goes further than is justified by the limited size of the sample and the approximate mathematics."

Samples 6 and 6T are separated by only about 4.2 km, potentially a short distance for a volant species. Both localities are situated in the coastal lowlands southwest of Nacaome, Honduras. The topography is flat. Habitat consists of a patchwork of pasture and plantations of sugarcane and banana, with occasional orchards of mango trees. Little natural vegetation remains. To the human eye, habitat at localities 6 and 6T appears to be quite homogeneous. However, locality 6T (with a sample > 6) did not contain a single representative of the 38

parental form. Nor did it have a specimen with a diploid number of 40 (Table 1). If these data are representative of nature, then they suggest that the zone of contact between the 2 parental cytotypes is very narrow indeed and that selection against recombinant forms may be stronger than was formally supposed. Sample 6T was like sample 6 in the sense that in both the cytotype $2n = 44$ was by far the most abundant parental form.

The contact zone is characterized by a number of semi-isolated habitat patches that may approach a dynamic equilibrium over appropriate time scales. The many large agricultural fields in the area lack trees and could serve as barriers to dispersal. Both parental cytotypes migrate into the zone, but it is a matter of chance as to whether both or only 1 of them arrive at and colonize the same habitat patch. Under this hypothesis, gene dispersal would not be continuous but stepwise, a step being the distance between 1 habitat patch and another. It is interesting to speculate that the nature of the present-day contact zone is a product of patch dynamics, mediated by human intervention into a natural ecosystem, through the creation of an agricultural habitat mosaic.

Collection localities near the Gulf of Fonseca zig and zag such that they do not represent an orthogonal trajectory outward from the contact zone. A worthwhile project would be to draw a straight line on a map and sample away from the zone at closely spaced intervals. If this design demonstrated that genotype frequencies change from 20% to 80% across a short distance of 10–15 km, then that would strongly support the argument for selection.

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