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GENETIC INTERACTIONS AT A CONTACT ZONE OF *URODERMA BILOBATUM* (CHIROPTERA: PHYLLOSTOMIDAE)

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Studies of genetic interactions between taxa in zones of hybridization can provide evolutionary biologists with an important empirical basis for exploring the nature of speciation. Importantly, such contact-zone studies allow critical assessment of the types of genetic changes (e.g., chromosomal rearrangements or protein dissimilarity) that may be instrumental in effecting reproductive isolation. Hence, it is crucial that underlying empiricism in such studies, as well as any proffered interpretations, be critically evaluated and reassessed.

The patterns of chromosomal and protein variation in a contact zone of the tent-making bat, *Uroderma bilobatum,* were summarized recently in two stimulating companion papers (Baker, 1981; Greenbaum, 1981). This contact zone involves two karyotypically defined taxa, *U. b. davisi* (44 chromosomes) and *U. b. convexum* (38 chromosomes), that hybridize about the Golfo de Fonseca, Honduras on the Pacific versant of Middle America. Baker (1981) and Greenbaum (1981) conclude that this contact zone is unique for its great width, introgressive hybridization does not occur between these subspecies, the pattern of chromosomal variation is maintained by selection, and that the hybrid zone is a result of primary contact and speciation should ensue. These interpretations and conclusions are provocative and I am reluctant to accept their explanations of the genetic characteristics of the hybrid zone. Accordingly, here I evaluate their hypotheses and present an alternative interpretation of the genetic interactions observed at this interesting contact zone.

METHODS

The reassessment of the genetic interactions at this contact zone relied exclusively on the chromosomal data in Baker (1981 p. 297) and Greenbaum (1981 p. 307), and the protein electrophoretic information in Greenbaum (1981 p. 310). Locality numbers in text correspond to those of Baker (1981).

Using the karyotypic data for their 13 localities across the transect region of Middle America, mean diploid numbers were calculated per locality. Maximum sample size was used for each locality (from Baker, 1981), excepting localities 4 and 8; for those two localities, smaller sample sizes were used (Greenbaum, 1981 p. 307), because it was not possible to extract diploid numbers for these localities from Baker (1981). Mean diploid number per locality was plotted against geographic distance from the southernmost locality to assess the general profile of chromosomal variation across the transect region.

In addition, inasmuch as diploid number variation involves three separate chromosomal rearrangements ("A," "B," and "C" chromosomes, Baker, 1981 p. 297), each chromosomal morph frequency was plotted against geographic distance. These three chromosomal gradients allowed for a detailed assessment of the pattern of chromosomal variation at the contact zone. Theoretical, single-locus cline models involving gene flow-selection equilibria (Slatkin, 1973; May et al., 1975; Endler, 1977), were applied to these clines to evaluate the width of the contact zone as well as the magnitude of the selection gradient. Delineation of the *Uroderma bilobatum*

TABLE 1. *Summary of the karyotypic information for the 13 sampled populations. Data from Baker (1981).*

Locality	Distance north (km)	N	Diploid number						
			38	39	40	41[a]	42	43	44
1	1,100	54							54
2	900	36						1	35
3	740	50						7	43
4[b]	690	30					1	2	27
5	610	9				1		3	5
6	600	25	1	1	2	6	2	8	5
7	580	12	2	4	1	3		2	
8[b]	555	37	28	7				2	
9	500	86	82	4					
10	450	44	44						
11	200	28	28						
12	50	25	25						
13	0	13	13						

[a] All individuals with 41 chromosomes, excepting one bat from locality 6, were determined by Baker (1981) to be potential F_1s (heterozygous for the three chromosomal rearrangements; see Baker, 1981); [b] Diploid number information from Greenbaum (1981).

transect into regions of parental *davisi* and parental *convexum,* as well as the contact zone into a mid-contact region and areas of *davisi*-like and *convexum*-like populations, was facilitated by the use of standard zone-width criteria (region between points where the phenotypic gradient varies from 0.2 to 0.8) set forth by May et al. (1975) and Endler (1977).

Simple (binomial expansion) probability distribution models, $(p + q)^x$, were used to examine the distribution of karyotypes within the zone. Probabilities of both p and q (probabilities of the $2n = 44$ and $2n = 38$ karyotypes, respectively) in the distributional analysis are determinable by both extrinsic and intrinsic methods, and the associated degrees of freedom in the Chi-square tests of significance were adjusted accordingly (Sokal and Rohlf, 1969). Further, in the Chi-square tests of goodness of fit, classes were pooled when expected frequencies are less than about five (Sokal and Rohlf, 1969 p. 565).

RESULTS AND DISCUSSION

Synopsis of the Uroderma *Studies*

Thirteen populations of *Uroderma bilobatum* were sampled by Baker (1981) and Greenbaum (1981) along a 1,100-km transect in the tropical forest lowlands surrounding the Golfo de Fonseca, Honduras (Table 1). Baker and Greenbaum identified one parental population of *U. b. davisi* ($2n = 44$) at the north end of the transect (locality 1, north of the gulf in Mexico) and four populations of parental *U. b. convexum* ($2n = 38$) to the south (localities 10–13, south of the gulf in Nicaragua and Costa Rica). At intermediate localities (samples 2–9, in Guatemala, El Salvador, Honduras, and Nicaragua), bats having hybrid karyotypes were collected. Baker (1981) believed that this hybrid zone was unique in that it is the widest known, over 400 km between localities 2 and 9. In his evaluation of "chromosome flow" across the zone, Baker (1981) noted three features: 1) bats with parental karyotypes were found sympatric only at a single locality (locality 6); 2) chromosomally F_1 individuals were found in three populations (samples 5, 6, and 7 in the immediate vicinity of Golfo de Fonseca), and covering a distance of only 30 km, whereas bats having backcross karyotypes were found in eight samples (localities 2–9) covering a distance of over 400 km; and 3) only 9 individuals with F_1 karyotypes were found, whereas 48 bats with backcross karyotypes were identified. To Baker (1981 p. 301–304), these features suggest limited production and immigration of F_1 individuals, possibly due to heterozygote disadvantage, while individuals having certain

other chromosomal phenotypes are at a selective advantage.

Building on the chromosomal groundwork detailed by Baker (1981), Greenbaum (1981) assayed the extent of protein electromorphic variation (22 loci examined) in the transect samples. Allozymic differentiation among the population samples of *U. bilobatum* across the transect was very slight: Rogers' (1972) similarity value ≥ 0.967 and Nei and Chakraborty's (1973) distance value ≤ 0.0136 (Greenbaum, 1981 p. 311). Eleven loci were polymorphic and Greenbaum used minor alleles of nine loci as marker alleles to characterize either the *davisi* or *convexum* parental forms. Greenbaum concluded that introgressive hybridization is not occurring between *davisi* and *convexum*. Such an interpretation was based on the absence of marker alleles of one parental form in a sample of the other parental form (outside of the hybrid zone). Greenbaum favored the view that the zone is an example of primary contact and cited three features to bolster the perspective that the hybrid zone is selectively maintained and that speciation may follow: 1) the hybrid zone involves an extensive area of karyotypic polymorphism with minimal overlap between parental karyotypes, and with F_1 individuals being restricted in abundance and distribution (as was stated by Baker); 2) the absence of marker alleles in populations of the alternate parental karyotype; and 3) the center of the contact zone coincides with an area of ecological discontinuity (partial habitat hiatus) between the ranges of the two forms.

Reassessment

My evaluation of the same karyotypic and electrophoretic data suggests another explanation for the pattern of genetic interactions observed at the *Uroderma* contact zone: namely, that the zone represents a classical example of introgressive hybridization. In arriving at this alternative interpretation I shall address four main points. First, the contact zone must be defined and its width delineated using common-ground criteria before the nature and significance of the zone are discussed and compared to other organisms. Second, the allozymic data must be carefully examined because the question as to whether introgressive hybridization is or is not occurring at this zone hinges, in part, on the robustness of the patterns of marker alleles across the zone. Third, the role of selection at the zone must be evaluated; both Baker and Greenbaum invoked selection in maintaining the observed patterns in the hybrid zone, but neither estimated the magnitude of selection operating across the zone. Fourth, the distribution of the karyotypes within the zone should be addressed to explore the possible effects of several kinds of selection, including, the environmental selection gradient that maintains the cline, and selection against F_1 and backcross hybrids (hybrid breakdown due to coadaptive differentiation). In addition, I shall show that, although this hybrid zone may have resulted from primary intergradation (Greenbaum, 1981), it is equally possible, if not more probable, that the interaction was initiated by secondary contact. These points were not given adequate attention in the earlier studies and consequently, viewpoints alternative to those of Baker (1981) and Greenbaum (1981) warrant consideration.

Width of the Contact Zone.—Baker and Greenbaum considered the width of the *Uroderma* contact zone to be over 400 km. This 400-km figure represents the distance over which backcross individuals were found (see Table 1), and is an estimate of the maximum genetic penetrance of one parental form into the geographic distribution of the other. Actually, this sort of zone-width estimate, although perhaps an interesting statistic, is an unsatisfactory measure of hybrid-zone width because of sampling problems and its incommensurability with standard estimates of zone width (for discussion see Barton and Hewitt, 1981; Hafner et al., unpubl.).

Meaningful zone-width estimates are obtained when width definitions follow the precepts stipulated in single-locus cline models which involve selection-gene flow

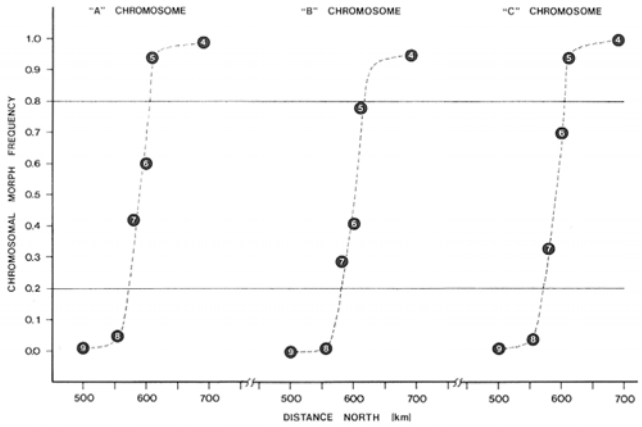

FIG. 1. Clinal patterns of the three chromosomal morphs, "A," "B," and "C" (Baker, 1981), in the central region of the *Uroderma bilobatum* hybrid zone.

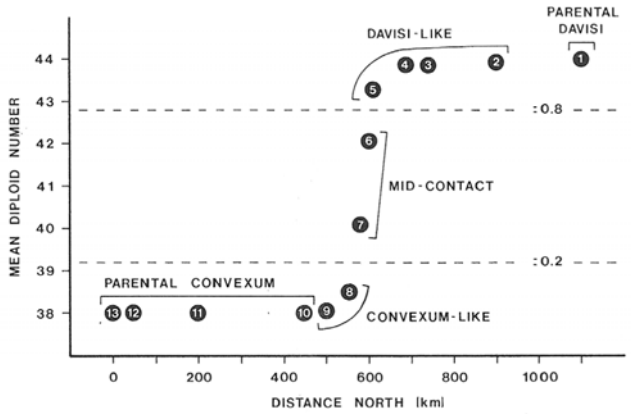

FIG. 2. Observed clinal trend in diploid number variation across the 13 transect populations of *Uroderma bilobatum*.

equilibria (May et al., 1975; Endler, 1977). For this study, analysis of three separate chromosomal clines is possible, as the karyotypic variation at the *Uroderma* hybrid zone consists of three rearrangements involving chromosomes "A," "B," and "C" (terminology follows Baker, 1981). The clinal trends in the chromosomal morphs, "A," "B," and "C," are presented in Figure 1. The width of a cline, w, in accordance with conventional cline-width criteria, is the distance between points where the phenotypic gradient varies from 0.2 to 0.8 (e.g., May et al., 1975; Endler, 1977; Barrowclough, 1980*a*; Wunderle, 1981). Relating this to the *Uroderma* contact zone, we see that the three chromosomal gradients are virtually identical and, upon extrapolation, in each case $w \approx 35$ km (Fig. 1; Table 1). The chromosomal morph clines are so similar, in fact, that the null points of the clines are nearly coincidental; clines "A" and "C" show null points falling halfway between localities 6 and 7, whereas the null point of cline "B" occurs only about 12 km farther to the north.

The general trend in diploid number variation across the *Uroderma* transect localities is clinal (Fig. 2), and is, in turn, concordant with the three chromosomal morph clines. Applying the standard cline-width criteria, the zone boundaries clearly encompass but two mid-contact populations (samples 6 and 7, Fig. 2; locality 5 is a borderline sample in cline "B," Fig. 1). Further, the transect is readily divisable into regions of parental forms and *davisi*-like and *convexum*-like populations (Fig. 2, Table 1).

Baker and Greenbaum viewed the *Uroderma* contact zone to be unique for its great width. However, a comparison of zone widths among organisms can only have significance when considering each cline's relative width, w/l, where l is the gene flow parameter (Endler, 1977). Although gene flow estimates are not available for these bats, their presumed high vagility (by both Baker and Greenbaum) directs me to select a figure on the order of 10^3 m/yr. This estimate of l was chosen because Barrowclough (1980*b*) has shown that gene flow in other similar-sized volant vertebrates is of this (10^3 m/yr) range, and is an order of magnitude greater than that reported for fossorial and scansorial rodents (e.g., Howard and Childs, 1959; Vaughan, 1963; Endler, 1977). Accordingly, substituting for w and l, the relative width of the *U. bilobatum* zone is approximately 35. This estimate of w/l places the *Uroderma* contact into Endler's (1977 p. 165–167) second group of clines which are considered to be of only intermediate breadth. This *Uroderma* zone is not unique in terms of w/l, and further, its w is smaller than many others previously reported (cf. Endler, 1977 p. 156–162).

Introgressive Hybridization.—The nature and extent of chromosomal interaction between the *davisi* and *convexum* karyotypes includes formation of not only F_1 hybrids, but multiple generations of

backcrossing (Baker, 1981). Hybrid formation is great (Table 1), involves no documented negative meiotic heterosis, and spans at least 400 km of relatively uniform habitat. As such, the chromosomal variation seems best interpreted as a result of introgressive hybridization (Anderson, 1949). Baker used instead the novel term, "chromosome flow."

Greenbaum (1981) interpreted the data on protein variation over the transect region to indicate a lack of introgression; a tacit suggestion that *davisi* and *convexum* are reproductively isolated. The allozymic data in support of such an interpretation rest on marker alleles at nine loci. He defined a marker allele as, "an allozyme that occurs in pure samples of one of the parental types [=parental karyotypic populations] and is not characteristic of individuals of the other parental type" (Greenbaum, 1981 p. 309). Three problems are associated with the use of these marker alleles in the *Uroderma* contact analysis: 1) inconsistency in marker allele definition; 2) dubious identification of marker alleles; and 3) inadequate sample sizes to detect low-frequency alleles.

Table 2 lists the alleles and average frequencies for the 11 polymorphic loci across the *Uroderma* transect (modified from Greenbaum, 1981). Polymorphism in four loci (*Alb, Hb, Mdh-2,* and *Got-2*) is restricted to nonparental localities. As recognized by Greenbaum, the occurrence of rare alleles at these four loci in the zone of hybridization seems best explained by the "rare allele phenomenon" (for review see Sage and Selander, 1979). Manifestation of regionally rare or unique alleles seems characteristic of hybrid situations, and such has been reported for a wide variety of vertebrates (e.g., quail, Ohno et al., 1969; house mice, Hunt and Selander, 1973; frogs, Sage and Selander, 1979; white-footed mice, Smith, 1979; and pocket gophers, Hafner et al., unpubl.). In the present chromosomally characterized bat hybrid zone, these distinctive minor alleles stand as circumstantial documentation of the intermixing of parental genomes. Clearly then, none of the alleles

TABLE 2. *Average frequencies for minor alleles at the 11 polymorphic loci in populations of* Uroderma bilobatum *across the transect region (derived from Greenbaum, 1981). Asterisks denote those minor alleles considered by Greenbaum (1981) to represent marker alleles.*

Locus	Allele	Parental *davisi* $2n = 44$ (locality 1)	Non parental (localities 2–9)	Parental *convexum* $2n = 38$ (localities 10–13)
Alb	*90**		.020	
Hb	*132**		.026	
Mdh-2	*−146*		.017	
Got-2	*−162*		.019	
	−58		.035	
Mdh-1	*140**	.009	.028	
6 Pgd	*143**		.029	.022
Ldh-2	*−70**		.051	.025
Sdh	*−62**		.026	.022
Idh-1	*82**	.065	.052	
Adh	*−208**		.013	.028
Es-2	*94**		.221	.462

at these four loci can legitimately be used as markers by the author's own definition. Nevertheless, Greenbaum used two of these (Alb^{90} and Hb^{132}) as marker alleles. Alleles Alb^{90} and Hb^{132} do not occur in the parental population of *U. b. davisi* (locality 1), and hence cannot be used as marker alleles for the *davisi* parental population.

Excluding the four loci whose polymorphism is restricted to the zone of hybridization, each of the remaining seven polymorphic loci were considered by Greenbaum as harboring marker alleles for one or the other parental forms (Table 2). One would predict, a priori, that such alleles would show greater average frequencies in the parental populations than in the chromosomally defined nonparental populations. Such is not the case; four of the seven alleles ($Mdh\text{-}1^{140}$, $6\ Pgd^{143}$, $Ldh\text{-}2^{-70}$, and Sdh^{-62}) displayed higher average frequencies within the region of hybridization. This observation seems to contradict Greenbaum's (1981 p. 313) statement that all of these alleles display affinities to one or the other of the parental karyotypes. I hypothesize that these four alleles, in addition to the allelic variants in *Alb, Hb, Mdh-2,* and *Got-2,* are not markers characteristic of either of the two parental

forms, but simply the products of intracistronic recombination or increased rates of mutation which seem to be characteristically expressed in hybrid zones. Hence, these alleles owe their affinity to the zone itself, and their presence at lowered frequencies in either group of parental samples probably reflects gene flow back into the parental ranges. This hypothesis is testable by further sampling well beyond the bounds of the transect localities.

Lastly, the sample sizes used in the electrophoretic analysis are too small to exclude the possibility of introgressive hybridization. All so-designated marker alleles are minor alleles and occur at average frequencies of 0.015 (Adh^{-208}) to 0.318 ($Es\text{-}2^{94}$), for a grand mean of 0.056 (Greenbaum, 1981 p. 310). Excluding $Es\text{-}2^{94}$ (the one marker disproportionately more common than the others), the grand mean frequency for the remaining markers drops to 0.028. The perspective that introgressive hybridization is not occurring was rooted in the inability to detect the supposed markers in any of the parental populations. Gregorius (1980) has shown that to ensure with a probability $\geqslant .95$ that all alleles with frequencies $\geqslant 0.03$ and $\geqslant 0.02$ at a locus are detected, it requires samples of 212 and 341 individuals per population, respectively. Greenbaum (1981) dealt with minor alleles that occur at these similar frequencies, yet the sample sizes used in the allozymic survey varied from only 13 to 54 individuals per parental locality. Alternatively, assuming that there are only two alleles per locus in each of the parental populations, it is possible, for example, to determine the sample size necessary to detect a marker allele occurring at an average frequency in the alternate parental population. In this instance, the minimum sample size, N, is given by the equation $N = 0.5[ln\ 0.05/ln\ (1 - \bar{m})]$ for the .05 significance level, and where $\bar{m}$ is the average marker allele frequency. The average frequencies of the marker alleles for *U. b. davisi* and *U. b. convexum* are 0.030 and 0.027, respectively (excluding *Es-2*; Greenbaum, 1981). Substituting these values into the above equation reveals that the minimum sample size necessary to detect a *U. b. davisi* marker (at an average frequency) is 49 individuals, and conversely, it requires 55 individuals to detect a *U. b. convexum* marker allele in the alternate parental sample. In the electrophoretic study the parental samples of *U. b. convexum* (localities 10–13) contained an average of only 27.5 individuals, and the parental sample of *U. b. davisi* (locality 1) contained 54 individuals. In both of the probabilistic treatments presented, I chose the optimal case for detecting the minor alleles. When sampling genotypes in the alternate parental form during introgressive hybridization, one would expect the allelic frequencies of the markers to be lower than in the parental form. Doubtless, in actuality, sample sizes even larger than I calculated would be required for a thorough demonstration.

As the genetic interactions were presented, Baker's demonstration of extensive "chromosome flow" is in direct conflict with Greenbaum's interpretation that introgression is non-existent. To reiterate, the protein data do not support the hypothesis that marker alleles fail to occur outside of the hybrid zone and that introgressive hybridization does not occur. Actually, the high level of protein similarity between the taxa, their close morphological identity (Baker and McDaniel, 1972; Baker et al., 1975), the similarity of parental habitats (Baker et al., 1975), the presence of rare alleles in the hybrid zone ("rare allele phenomenon"), and the documentation of extensive chromosomal hybridization all portray a classical situation of introgressive hybridization.

Selection and the Hybrid Zone.—Both Baker and Greenbaum repeated the view that the distribution of the karyotypes along the transect and within the hybrid zone is selectively maintained. Based on their interpretation of the distributional patterns of the karyotypes, they hypothesized that: 1) the parental *davisi* and *convexum* karyotypes are selected against within the zone; 2) there is a moderate degree of negative heterosis in the F_1s; and

3) there is a selective advantage for backcross individuals in the hybrid zone. These hypotheses are testable. Given the data at hand it is possible to evaluate the efficacy of two kinds of selection which may be in operation at the *Uroderma* hybrid zone: selection which can maintain the chromosomal cline and selection against F_1s and backcross hybrids due to coadaptive breakdown (negative heterosis or hybrid dysgenesis).

The indirect evaluation of the magnitude of the selection gradient, b, can be obtained by employing static cline models involving gene flow-selection equilibria that are available from theoretical studies (Slatkin, 1973; May et al., 1975; Endler, 1977). The selection gradient in single-locus clines (assuming homogeneous gene flow, sizable populations, and no dominance), is described according to the relationship $b = l^2(1.66/w)^3$. Endler's (1977) gradient model is used in this case to estimate b (cf. the ecotone model, Endler, 1977), as the parental habitats were reported to be ecologically similar and without an ecotone (Baker et al., 1975; Greenbaum, 1981). Incorporating the parameters l and w (described previously) into the above equation yields an estimate of $b \approx 1.1 \times 10^{-4}$ km^{-1} for each of the *U. bilobatum* karyotypic clines considered (Fig. 1). This estimate is reliable to within an order of magnitude providing l is in the range of a few kilometers in these bats. Thus calculated, the selection necessary to maintain a cline is so weak that it would be difficult to demonstrate in practice. However, as Endler (1977) noted, a b of this magnitude has actually been measured. In either event, there is no reason to invoke a large selection gradient that maintains any of the chromosomal clines and, moreover, the clinal patterns may simply have resulted from neutral diffusive interaction between the parental karyotypes.

Coadaptive differentiation, which may accompany hybridization, might produce hybrid dysgenesis or negative heterosis at the contact zone. To evaluate this possibility, the observed array of karyotypes across the transect (Table 1) can be compared with that predicted from simple probability distributions. In doing such tests of goodness of fit, small sample sizes dictate that the seven diploid numbers, $2n = 38$–44, be considered (as opposed to the 27 possible chromosomal phenotypes; see Greenbaum, 1981). The array of diploid numbers is compared with that predicted from probability distributions in Table 3. Expected chromosome number frequencies were determined by expansion of the binomial $(p + q)^X$, where p and q represent the probabilities of the $2n = 44$ and $2n = 38$ phenotypes, respectively. The area of karyotypic intermixing was trisected into geographic regions (Fig. 2) representing an area of mid contact ($p = 0.50$; $q = 0.50$), a *davisi*-like region ($p = 0.9760$; $q = 0.0240$), and an area of *convexum*-like hybrids ($p = 0.0285$; $q = 0.9716$). The probabilities of p and q at the center of the cline (mid-contact localities 6 and 7) are predicted extrinsic of the data by the position of the populations; that is, one would expect an equal probability of finding a bat with either 44 or 38 chromosomes. Conversely, the values of p and q for the *davisi*-like (populations 2–5) and *convexum*-like (samples 8 and 9) areas were determined by the actual frequencies of the parental karyotypes in each case (Table 1). Results of the analysis (Table 3) indicate that in each of the three regions the Chi-square value is nonsignificant ($P > .05$). The null hypothesis that the observed array of diploid numbers does not depart from that predicted by a model of simple diffusion is accepted. Importantly, these findings show no F_1 disadvantage (all bats with $2n = 41$ karyotypes, save one, were judged by Baker to be potential F_1 individuals). The data do not support Baker's and Greenbaum's statements concerning the dearth of F_1s across the zone, the reduced geographic overlap of the parental karyotypes or the superabundance of backcross individuals. Moreover, the data hold no support for Greenbaum's hypothesis that speciation

TABLE 3. *Comparison of observed array of diploid numbers with that expected from the binomial probability distribution.*

Chromosomes per Individual	*davisi*-like (localities 2–5) $p = .9760; q = .0240$				Mid-contact (localities 6 and 7) $p = .5000; q = .5000$				*convexum*-like (localities 8 and 9) $p = .0285; q = .9716$			
	f_i[1]		$\hat{f}$[2]		f_i		$\hat{f}$		f_i		$\hat{f}$	
38	0		0.00		3		0.58		110		103.47	
39	0		0.00		5	11	3.47	12.72	11		18.21	
40	0	2	0.00	1.02	3		8.67		0		1.34	
41	1		0.04		9		11.56		0		0.05	
42	1		0.98		2		8.67		0	2	0.00	1.39
43	13		15.94		10	17	3.47	12.72	2		0.00	
44	110		108.05		5		0.58		0		0.00	
Total	125		125.01		37		37.00		123		123.07	
	$\chi^2 = 1.51$ NS ($\chi^2_{.05[1]} = 3.84$)				$\chi^2 = 2.24$ NS ($\chi^2_{.05[2]} = 5.99$)				$\chi^2 = 3.46$ NS ($\chi^2_{.05[1]} = 3.84$)			

[1] Observed frequencies; [2] Expected frequencies from binomial expansion.

should result, since there is no evidence for selection against the F_1s and backcrosses.

Primary or Secondary Intergradation?—The observed clinal patterns of chromosomal variation in *U. bilobatum* about the Golfo de Fonseca may represent the action of one of four phenomena: 1) primary intergradation (resulting from stasipatric chromosomal divergence and adaptive differentiation along an environmental gradient in the absence of a physical barrier; Endler, 1977; White, 1978); 2) secondary intergradation between adaptively differentiated forms (populations diverged in allopatry and are now initiating contact; Mayr, 1942, 1963; Endler, 1977); 3) neutral secondary intergradation (secondary contact between forms that differentiated by chance alone while separated by a physical barrier; Goodhart, 1963; Endler, 1977); and 4) random divergence among contiguous populations (see Endler, 1977). The highly concordant nature of the three chromosomal clines (Fig. 1) directs me to eschew the explanation that the hybrid-zone patterns are simply the result of chance differentiation among contiguous populations. However, the available data do not permit an unambiguous choice among the three remaining alternatives. Despite this uncertainty, one may wish to ask which of the three phenomena (primary or secondary contact with selection, or neutral secondary contact) may be a more plausible interpretation.

It is impossible to distinguish between primary and secondary intergradation for any given cline by simply examining a cline's parameters (Endler, 1977). However, Barrowclough (pers. comm.) aptly notes that when two or more independent clines at a contact zone are highly concordant (as with the three chromosomal clines, Fig. 1), a secondary contact interpretation is strongly favored (see also, Barrowclough, 1980*a*). Accordingly, it seems that primary contact could only be invoked to explain the *Uroderma* zone in either of two unlikely events: the three chromosomal rearrangements (Baker, 1981) are somehow mutually dependent, or the three rearrangements arose simultaneously and effected clines having identical selection gradients.

That the clines result from neutral secondary contact seems more likely than

those alternatives which invoke adaptive divergence. Baker et al. (1975) and Greenbaum (1981) state that there are no apparent ecological differences between the habitats of *U. b. davisi* and *U. b. convexum*. Further, I have shown that the selection gradient necessary to maintain any of the clines is so weak ($b \approx 1.1 \times 10^{-4}$ km^{-1}) that its actual presence may be impossible to demonstrate in the field. Admittedly, it is possible that Baker and Greenbaum overlooked some important environmental difference and my estimate of l is incorrect (too small by at least one order of magnitude to realize any substantial b). However, considered together, these observations are mutually supportive and imply that the karyotypic variation is nonadaptive (environmental selection gradient absent).

History of the Contact Zone.—If the chromosomal clines resulted from neutral secondary contact between divergent forms of *U. bilobatum,* then it is of interest to consider the times since allopatric divergence and secondary contact in the context of a biogeographic scenario. Significantly, the Golfo de Fonseca may be identified as a barrier that allowed allopatric divergence between *davisi* and *convexum*: this hydrographic feature largely bisects the Pacific versant corridor of lower tropical forest habitat to which *U. bilobatum* is restricted. The tropical forest habitat is inimical about the gulf region (localities 5–8; see Greenbaum, 1981 p. 318), and thus this area may presently represent a partial barrier to *U. bilobatum*. Moreover, the null points of the chromosomal clines (Fig. 1) coincide geographically with the farthest inland penetrance of the sea (Bahia San Lorenzo, Golfo de Fonseca). Although the eustatic sea level is now at its highest stand since the Wisconsinan glacial period (Bartlett and Barghoorn, 1973), at the end of the Sangamon interglacial (65,000 years ago) the sea level was about 10 m higher than at present (Alt and Brooks, 1965) and an effective hydrographic barrier may have then existed. While Pleistocene changes in sea level alone may account for the bisection of the *U. bilobatum* distribution, this is an unnecessary restriction. During the Wisconsinan glacial period the present areas of lower tropical forests were cooler and more xeric (e.g., Bartlett and Barghoorn, 1973; Pregill and Olson, 1981). Hence, Pleistocene sea level fluctuations in combination with climatic changes may have affected the distribution of *U. bilobatum* and restricted the bats to tropical forest refugia north and south of the Golfo de Fonseca. Presumably, secondary contact between the $2n = 44$ and $2n = 38$ moities of *U. bilobatum* occurred only within the past few millennia following climatic amelioration and termination of the postglacial rise in sea level (Bartlett and Barghoorn, 1973).

Time since divergence of *davisi* and *convexum* can be estimated from electrophoretic distance values, D. As I have reclassified some of the polymorphic loci regarded as markers by Greenbaum, a new $\bar{D}$ between the parental forms must be calculated (see above and Greenbaum, 1981). The average distance between parental samples 1 and 11–13 is 0.0095 (locality 10 is excluded because it contains alleles that are characteristic of the hybrid zone). Correlating D with time on the basis of two separate methods (Nei, 1975; Sarich, 1977) yields quite disparate time estimates, t. The formula of Nei (1975) yields a time since divergence of $t = 5 \times 10^6 \bar{D} = 47{,}333$ years, whereas Sarich's (1977) formula, which is adjusted for "slowly evolving" proteins, provides $t = 30 \times 10^6 \bar{D} = 284{,}000$ years. One of the 22 loci examined by Greenbaum was of the "rapidly evolving" class (esterase), so a $t \approx 200{,}000$ years would probably be a more appropriate second estimate. Thus, the time span bracketed by these two estimates (≈50,000–200,000 years ago) allows only a very rough temporal placement for the *U. b. davisi-U. b. convexum* split, but is generally compatible with paleoclimatic events which occurred in the late Pleistocene.

The time since secondary contact between *U. b. davisi* and *U. b. convexum* can be estimated by application of theoretical cline models. If we assume that the

chromosomal traits of each form are selectively neutral, the time, T, since contact is determinable by the relationship $T = 0.35(w/l)^2$ (Endler, 1977). Substituting zone-width and gene-flow values into this equation yields a time estimate of about 429 generations (≈429 years). This time estimate, then, is also consonant with the paleoclimatic data.

If the *Uroderma* contact zone actually resulted from neutral secondary intergradation, then the clines are dynamic in nature and would be expected to increase in w at a rate determined only by l. Therefore, the clines' decay to equilibrium and, hence, the neutral secondary contact hypothesis are testable: an observer should document w increasing at a rate of about 50 m/yr in a long-term study. Conversely, if the zone formed through primary intergradation the clines would be expected to show a decrease in w with time. Unfortunately, if the clines resulted through primary contact, they would now be so close to equilibrium ($T \approx 1237$ generations for a primary contact interpretation; Endler, 1977), that an observable decrease in w might not be detectable. Similarly, it may be difficult to refute the hypothesis of secondary contact between chromosomally adaptive morphs (in this case $T \approx 784$ generations). Regardless, long-term studies at this interesting hybrid zone should provide unambiguous answers to most of the hypotheses that have been proffered.

Summary

A reassessment of the genetic interactions at a contact zone of *Uroderma bilobatum* (Baker, 1981; Greenbaum, 1981) is performed principally with the aide of static cline models as well as simple probability distribution models. Baker (1981) and Greenbaum (1981) conclude that: 1) this contact zone involving two chromosomally defined bat taxa (*U. b. davisi* and *U. b. convexum*) is unique for its great width (over 400 km); 2) introgressive hybridization does not occur between the taxa; 3) selection operates to maintain the clinal distribution of the karyotypes across the transect localities; and 4) the hybrid zone is a result of primary contact and speciation should ensue. Counter viewpoints are presented for each of these interpretations.

Applying standard criteria to the *Uroderma* hybrid zone, a zone-width estimate of 35 km is obtained for each of three chromosomal clines. The relative cline width is estimated and is within the range of widths reported for other contact zones.

The chromosomal information (Baker, 1981) indicates extensive hybrid production, including F_1s and backcross individuals. Hence, introgression is documented on karyological criteria. Similarly, the protein data (Greenbaum, 1981) are best interpreted as affirming introgression between the taxa: parental forms show only a low level of protein divergence; rare alleles present in the hybrid zone indicate mixing of the parental genomes ("rare allele phenomenon"); and the parental population sample sizes are much too small to support Greenbaum's interpretation that marker alleles fail to occur outside the hybrid region and that introgression does not occur.

The selection gradient for the *U. bilobatum* zone is determined to be of small magnitude, and there is no need to invoke a strong selection gradient that maintains any of the chromosomal clines. Further, the distribution of karyotypes across the zone is examined, and does not depart significantly from that predicted by a model of simple diffusion of one parental form into the other. These results refute the statements that there is a paucity of F_1s, a dearth of parental karyotypes, an overabundance of backcross individuals within the contact zone, and that speciation will ensue.

The question of primary versus secondary intergradation is evaluated and it seems more likely that the zone results from neutral secondary contact. If the *Uroderma* hybrid zone actually formed in this manner, then this hypothesis is testable by long-term field studies (the cline widths should increase with time). In addition, times since divergence and secondary contact are

estimated and considered in the light of paleoclimatic information.

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