

CHROMOSOME FLOW BETWEEN CHROMOSOMALLY CHARACTERIZED TAXA OF A VOLANT MAMMAL, *URODERMA BILOBATUM* (CHIROPTERA: PHYLLOSTOMATIDAE)

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Peters tent-making bat (*Uroderma bilobatum*) is the only known organism that is volant (with presumably relative high vagility and large deme size) and has a low reproductive rate, and yet possesses a tension zone (Key, 1974) between chromosomally characterized taxa. The zone of hybridization is itself unique in that it is the widest known (over 400 km) and because the cytotypes involved differ by three chromosomal rearrangements, each of which theoretically should result in moderate to severe meiotic malassortment (White, 1978a; Lande, 1979). An understanding of the nature of this contact zone will be a valuable resource in determining why tension zones exist and in documenting the role of chromosomal change in evolution. This report presents karyotypic data for 210 additional specimens (bringing the total sample size to 543) and discusses how these data relate to our understanding of chromosomal evolution.

Some aspects of this zone have been described (Baker et al., 1972, 1975; Baker, 1979) based on 333 specimens. Populations of *Uroderma bilobatum* studied were distributed along the Pacific versant of Middle America from Mexico through Costa Rica. As *U. bilobatum* is found only in lower tropical forest, the central mountain ranges in Mexico, Guatemala, El Salvador, Honduras and the northern part of Nicaragua restrict the distribution of this species into two linear groups with no indication of interchange of individuals between the two (Davis, 1968) north of the Nicaraguan lowlands. On the Pacific versant, at the northwestern end of its distribution, *U. bilobatum davisii* has a karyotype with a diploid number ($2n$) of 44 and a fundamental number (FN) of 48. At the

southeastern end of the study area, the entire Atlantic versant, and northwestern South America, the species has $2n = 38$, FN = 44. Karyotypically intermediate individuals occur over a 400 km region, extending from central Guatemala to northwestern Nicaragua. Samples of *U. bilobatum* from this region include individuals with diploid numbers ranging from 38 to 44, with all intermediate diploid values being represented within the zone (Baker et al., 1972, 1975; Baker, 1979).

The nature of the three rearrangements which distinguish the $2n = 38$ and $2n = 44$ parental types were described from G- and C-band studies (Baker, 1979) as (1) the fusion of a medium-sized acrocentric to a small biarmed element (or alternatively, the fissioning of a medium-sized biarmed element into a small biarmed element and an acrocentric); (2) a Robertsonian variation involving a medium-sized subtelocentric element and two acrocentric elements, one small and the other medium-sized; and (3) a telomere-centromere translocation of a small acrocentric to the largest acrocentric in the karyotype. Chromosomes involved are diagrammatically represented in Figure 1. None of these rearrangements involves extensive C-band areas. The karyotype of *U. bilobatum* contains little C-band positive material with most heterochromatin being restricted to the centromeric regions (Baker, 1979). G- and C-band studies have been performed on 11 specimens (three with $2n = 44$, two with 43, one with 42, one with 41, one with 40, one with 39, two with 38). The nature of the chromosomal rearrangements, as determined by the banding analyses, is such that the chro-

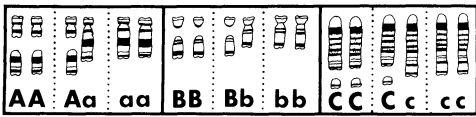


FIG. 1. Diagrammatic representation of the G-band pattern, relative size, and centromere placement of the homozygous and heterozygous conditions for the three chromosomal rearrangements which distinguish the two chromosomal races of *U. bilobatum* under study. "A" chromosomes are in box on the left hand, "B" center and "C" right hand.

A minimum of five chromosomal spreads were examined per specimen. Each spread was scored for number of biarmed elements in each size class plus number of acrocentrics. If more than one of the five spreads were not consistent in diploid number, number of biarms in each class, etc., then additional spreads were studied until the karyotype of the specimen could be adequately documented.

mosomal phenotype for each rearrangement can be determined from standard karyotypes (see Methods and Materials).

Designation of chromosomal phenotypes follows Baker (1979) with the capital "A" representing the condition where a small biarmed element and medium acrocentric were present in the karyotype and a lower case "a" representing the fusion of these two elements into a subtelo-centric element (Fig. 1). A capital "B" designates the presence of two acrocentrics and a lower case "b" designates that these two acrocentrics are fused centromere to centromere into a single subtelo-centric element (Fig. 1). Capital "C" designates the presence of two acrocentrics, whereas a lower case "c" signifies that the centromeric end of the smaller element is translocated to the distal end of the largest ac-

METHODS AND MATERIALS

Specimens were collected from natural populations and karyotyped from bone marrow by the in vivo culture method (Baker, 1970). Localities and specimens examined are given in Table 1, and Figures 2 and 3. Voucher specimens were preserved in formalin, and later transferred to alcohol. Reproductive data were obtained from specimens in spirits. Adult females were examined macroscopically to determine if pregnant.

TABLE 1. Chromosomal data for 13 samples of *Uroderma bilobatum*. Specific localities for this table and Figures 1 and 2 are (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, (4) El Salvador: Usulután; 3 mi E Usulután, (5) Honduras: Nacaome; 1 mi SE Nacaome, (6) Honduras: Valle; 10 mi SSW Nacaome, (7) Honduras: Choluteca; 10.2 mi NW Choluteca, (8) Honduras: Choluteca; 11.5 mi SW Choluteca, (9) Nicaragua: Chinandega; 3.5 mi NW Chinandega and 1.5 mi S 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.

Locality	Sample size	Parental cytotype present	Distance from locality of parental cytotypes sympatry (in kilometers)	Potential F ₁ s	Number of back-cross individuals	Frequency of less common chromosomal morph		
						A	B	C
1	54	44	500	0	0	.00	.00	.00
2	36	44	300	0	1	.00	.01b	.00
3	50	44	140	0	7	.02a	.05b	.00
4	83	44	90	0	7	.01a	.05b	.00
5	9	44	10	1	3	.06a	.22b	.06c
6	25	44, 38	0	5	15	.40a	.59b	.30c
7	12	38	20	3	7	.42A	.29B	.33C
8	78	38	45	0	5	.05A	.01B	.04C
9	86	38	100	0	4	.01A	.00	.01C
10	44	38	150	0	0	.00	.00	.00
11	28	38	400	0	0	.00	.00	.00
12	25	38	550	0	0	.00	.00	.00
13	13	38	600	0	0	.00	.00	.00

rocentric (Fig. 1). The G-banding patterns of the A, B and C chromosomes are shown diagrammatically in Figure 1.

The chromosomal phenotype of specimens was determined from standard karyotypes by the method described by Baker (1979). The number of large "A's" in a karyotype will be reflected by the number of small biarmed autosomes in the complement. These small biarmed autosomes can be confused only with the Y. Associated with each small biarmed autosome there should be an increase in the diploid number of one over the basal $2n = 38$ and a decrease of one in the number of large biarmed elements. The "B" chromosomal variation can be identified in the standard karyotype as each "b" results in a decrease of one in diploid number and an increase of one in the number of large biarmed elements without decreasing the number of small biarmed elements. Presence of the "C" condition reduces the diploid number by one and reduces the number of acrocentrics by one, but does not alter the number of biarmed elements in the karyotype. An independent check on the "C" condition is that the translocation of the small acrocentric is to the largest acrocentric in the karyotype and the additional translocated material makes the element sufficiently larger so that in all but one case (see Results), the number of "C" chromosomes was accurately predicted before the diploid and acrocentric/biarmed numbers were totaled. F_1 individuals of necessity have $2n = 41$ and a chromosomal phenotype of $AaBbCc$; however, as this phenotype can be achieved by backcrossing, some individuals heterozygous for all three rearrangements may not be F_1 s.

Several standard karyotypes from hybrids and backcross individuals have been published (Baker et al., 1972, Fig. 4, $aabbCc$, but see results section on why this animal was probably a trisomic; Fig. 5, $AABbCC$; Baker et al., 1975, Fig. 2, $Aabbcc$; Fig. 3, $aaBbCc$; Fig. 4, $AaBbCc$; Fig. 5, $AaBbCC$; Fig. 6, $AABbCC$).

To determine if the variations in chromosomal frequency in samples were sig-

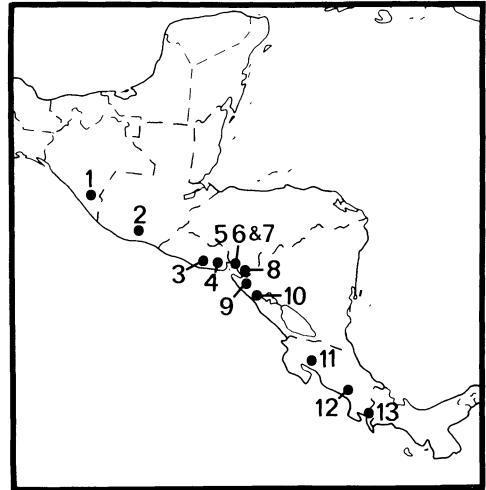


FIG. 2. Geographic distribution of localities where specimens of *Uroderma bilobatum* were collected. Specific localities are identified in the legend of Table 1. See Fig. 3 for a more detailed map of localities 3-9.

nificantly different, a pair-wise 2×2 contingency test utilizing the G -statistic was calculated (Sokal and Rohlf, 1969).

RESULTS

Localities sampled are shown in Figures 2 and 3. A total of 543 specimens were examined. Parental cytotypes were found to be sympatric only at locality 6 (Fig. 2). Sample size for each locality, airline distance separating each locality from the locality of sympatric parental types, number of individuals heterozygous for all three rearrangements (F_1 phenotypes), number of backcross individuals, and frequency of chromosomal types are given in Table 1. F_1 phenotypes were found in three samples, 5, 6 and 7. These three localities form a triangle and are separated by a maximum of 25 km (Fig. 3). Individuals heterozygous for the "A" chromosomes were found at localities 3-9, spanning a distance of 240 km (Table 1 and Fig. 2). "B" chromosome heterozygosity was found at localities 2-8, a distance of 345 km (Table 1 and Fig. 2). "C" chromosome heterozygosity was found at localities 5-9, a distance of slightly over 100 km (Table 1 and Fig. 3). Backcross individuals were found over a distance of 400 km.

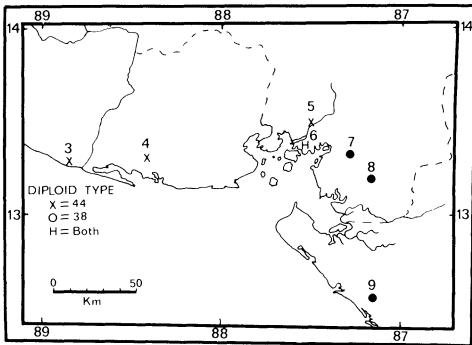


FIG. 3. Geographic distribution of localities 3-9. Both parental cytotypes were found only at locality 6 (H) and the $2n = 44$ parental cytotype was found at localities 3-5 (X) and the $2n = 38$ at localities 7-9 (solid dots). Specific localities are described in the legend of Table 1.

Two of the 543 specimens examined had karyotypes which did not satisfy all of the criteria for determining the chromosomal phenotype as outlined in Methods and Materials. The first case involves a centric fusion between two medium-sized acrocentrics which altered the karyotype of an individual with aabbcc to a diploid number of 37. A medium-sized submetacentric was observed only in this specimen; therefore it was concluded that within my sample this rearrangement was restricted to this specimen. The second case was in an individual with a $2n = 39$ which appears, by number of acrocentric and biarmed elements, to be aabbCc but there is no size variation in the largest acrocentrics as is normally characteristic of an individual heterozygous for the "C" chromosomes. However, the relative size of the largest acrocentrics leads me to think that both elements are products of the terminal translocation to the largest acrocentric and this specimen resulted either from meiotic malassortment in one of its parents which was a backcross product heterozygous for Cc or, less likely, from trisomy of another small acrocentric (unrelated to the "C" chromosome variation).

A total of 122 females was examined for pregnancy. Of that total, 78 were in early stages of pregnancy. None were lactating.

TABLE 2. Pair-wise comparisons of chromosomal frequency in samples from localities 3, 4, 8 and 9. In groups, letter designates chromosome and number identifies locality being compared.

Groups compared	G value	Level of significance
a4 × A8	.002	NS
b4 × B8	14.54	.005
c4 × C8	2.716	NS
a3 × A9	5.126	.05
b3 × B9	13.048	.005
c3 × C9	0	NS
a4 × B4	6.022	.025
a4 × c4	2.784	NS
b4 × c4	14.174	.005
a3 × b3	2.848	NS
a3 × c3	5.624	.055
b3 × c3	74.388	.005
A8 × B8	2.786	NS
A8 × C8	0	NS
B8 × C8	2.786	NS
A9 × B9	0	NS
A9 × C9	0	NS
B9 × C9	0	NS

There was a total of 59 females with a $2n = 44$, of which 41 were pregnant. There was a total of 45 females with a $2n = 38$, of which 30 were pregnant. Four females were AaBbCc (F_1 phenotype) and one of these was pregnant. Thirteen individuals were heterozygous for one or two rearrangements and, of these, five were pregnant. The female with a $2n = 37$ was also pregnant.

Results of the pair-wise test for significance of differences in frequency of chromosomal types are shown in Table 2.

DISCUSSION

From the data in Table 1 it is apparent that "chromosome flow" has resulted in the establishment of chromosomal polymorphism within populations near the locality where the parental cytotypes are sympatric. In determining the role of chromosomal change in evolution it is important to understand the factors which maintain the extent and degree of "chromosome flow."

Immigration.—Bats being volant, are potentially highly vagile and thus have the possibility for more extensive interchange of individuals between populations than

do other organisms (such as flightless grasshoppers, White, 1974, 1978a; and pocket gophers, Patton, 1973) for which such chromosomal tension zones have been described (Bush, 1975). Extensive immigration of individuals of one cytotype into populations of the other could result in the level of chromosomal polymorphism observed in *U. bilobatum* even if there was strong selection against F_1 s and backcross individuals. One measure of the magnitude of immigration would be the number of individuals of both parental cytotypes found at a given locality. Parental cytotypes were sympatric at only one locality. Sample sizes at localities 5 and 7 are not sufficiently large that it can be concluded that both parental types do not occur at these two localities. However, low sample size still does not explain the absence of F_1 s and parental cytotypes at localities to the north and south of these three localities. A sample size of 133 at the northern localities (3 and 4) and a sample of 164 at localities (8 and 9) to the south represent significantly larger samples. In both instances the alternate parental types were not recovered. Of more significance is the lack of F_1 s. These data clearly indicate that the lack of F_1 s or parental cytotypes is not due to chance alone as could be proposed for localities 5 and 7. Furthermore, the absence of alternate parental types and F_1 s at localities 3, 4, 8, and 9, is in support of the overall interpretation that immigration alone is inadequate to explain the width of the zone. Nonetheless, immigration is undoubtedly a significant factor in explaining why the zone of hybridization in *U. bilobatum* is much wider than that characteristic of other organisms for which such zones have been described.

These chromosomal data (distribution of parental cytotypes as well as frequency and distribution of F_1 s) indicate minimal contact between parental cytotypes. If this minimal contact is the result of highly developed philopatry and low vagility, one would predict that the zone of hybridization would also be narrow and allelic differences would identify some local popu-

lations and/or chromosomal races (Patton and Yang, 1977). However, the zone of hybridization as identified by chromosomal flow, is extremely wide and rare alleles are broadly distributed among populations of the respective cytotypes (Greenbaum, 1981), therefore, an explanation other than low vagility is required to explain the minimal contact between cytotypes. That the distribution of the cytotypes is being maintained by natural selection must remain a viable alternative.

Negative heterosis.—Another factor which regulates "chromosome flow" is selection against heterozygotes. F_1 individuals between the $2n = 44$ and 38 cytotypes are heterozygous for three rearrangements which probably vary in their degree of negative meiotic heterosis. For a review of the degree of negative heterosis caused by different types of chromosomal rearrangements see White (1973) and Lande (1979). If the F_1 is at a severe meiotic disadvantage then F_1 s should be more common than backcross individuals. (Of course if F_1 s are sterile, then no backcross products would be found.) Backcross individuals were found in populations 2–9, whereas F_1 phenotypes were found only in populations 5, 6, and 7. In population 6, where both parental types were found, a sample of 25 specimens contained five F_1 phenotypes, four $2n = 44$ parental cytotypes, one $2n = 38$ parental cytotype, and 15 backcross individuals. These data do not suggest that negative heterosis in F_1 s and heterozygous backcross individuals are of sufficient magnitude to result in the rapid elimination of the observed chromosomal variation from populations of *Uroderma*. These data suggest that at localities 3–8 the backcross and, when present, F_1 individuals play a significant role in the production of the next generation. At locality 6, only 24% of the sample of 25 individuals was homozygous for all three rearrangements. If my sample from this locality is reflective of the total population and mating is random, then the odds are low (less than 10% of the mating) that an individual homozygous for all the rearrangements will

mate with another individual homozygous for all three.

A direct evaluation of the effects of negative heterosis is the examination of the reproductive status of heterozygotes. *Uroderma bilobatum* has bimodal polyestry with females in a population becoming pregnant at about the same time (Wilson, 1979) and producing two young per female per year. Fleming et al. (1972) demonstrated that testes size and spermatogenesis in males are also annually bimodal. The samples of *U. bilobatum* were collected during the time (late May and early June) when females were in breeding season or in a very early stage of pregnancy, which unfortunately limits the data available to determine to what extent individuals with various karyotypes are successful in producing young. That one of four females heterozygous for all three rearrangements (potential F_1 s) and five of 13 adult females heterozygous for one or two rearrangements were pregnant provides further proof of the reproductive role of backcross and hybrid individuals. A greater percentage of the females with a $2n = 38$ (30 of 45) and $2n = 44$ (41 of 59) were pregnant than were females with intermediate karyotypes. However, more of the pure parental samples were taken in June (later in the breeding cycle) which may account for part of the higher percentage. I am of the opinion that reproduction from $2n = 38 \times 2n = 38$ or $2n = 44 \times 2n = 44$ matings are more successful than are matings involving either a backcross or F_1 individual. Nonetheless, presence of such a large number of backcross products in samples 2-9 (of 343 individuals from these localities, 48 were backcross products and 9 possessed F_1 phenotypes) strongly documents that in this case selection against chromosomal heterozygotes is not as important as has been deemed critical to recent theories of chromosomal evolution (Hall, 1973; Bush, 1975; Wilson et al., 1975; White, 1978a; and Lande, 1979).

As pointed out elsewhere (White, 1978a; Baker, 1979; Lande, 1979), different types of chromosomal rearrangements produce

different meiotic aberrations and therefore the percentage of sterile gametes produced by a heterozygote will be in part a function of the nature of the rearrangement. If a given chromosomal rearrangement has no phenotypic effect (see Lande, 1979), then the selective disadvantage of a heterozygote for any specific rearrangement will be a function of the severity of the negative heterotic effects of meiotic malassortment for that rearrangement. The severity of meiotic effect for a specific rearrangement will be the same regardless of which parental cytotype the heterozygote backcrosses to. If the rate of immigration is constant, then the extent of the flow of a given rearrangement across a contact zone into populations of each cytotype should be the same on both sides of the zone. This is obviously not the case in *U. bilobatum*. The "b" rearrangement is found 300 km to the northwest of the locality of sympatric parental cytotypes, but the "B" rearrangement is found only 45 km to the southeast of the zone. When the percentages of "b" in samples 3 and 4, respectively, were compared to the percentages of "B" in samples 9 and 8, respectively (compared samples each being approximately the same distance from the locality at which parental cytotypes were sympatric, Fig. 3 and Table 2), the differences were significant at the .05 level. Conversely, the "C" rearrangement is found only 10 km northwest of the locality of sympatry of parental cytotypes but is found 100 km to the southeast. This difference was not significant possibly because of the low frequency (1-2%) of "C" in the hybrid populations.

It should also be noted that the "a" and "c" rearrangements are not as successful in flowing to the northeast as is the "b" rearrangement. This is reflected in significant differences in the "b" and "c" chromosome frequencies in samples 3 and 4 and the "b" and "a" frequencies in sample 4 (Table 2).

Distribution and origin of rearrangements.—I think there are two ways to explain this asymmetrical distribution of chromosomes on each side of the sympat-

ric locality. The first would be historical in that in the past the population may have been subjected to differential immigration. If this is the correct explanation, then the flow of all three rearrangements would be concordant, with amount of flow corrected for degree of meiotic problems. The second explanation would be that the aberrations have some phenotypic effect which, for instance, could result in an individual heterozygous for the "b" chromosomes having a selective advantage northwest of the sympatric locality which partially or completely offsets any negative fitness from meiotic malassortments. In the population northwest of sympatry, individuals which are "Bb" may not produce as many offspring per reproductive period due to meiotic problems, but when an offspring is successfully produced its average life span is longer and this compensates for the lower reproductive success per year. To the southeast of the zone, a "Bb" individual may not have the same adaptive advantage over individuals with the parental cytotype and the negative meiotic effects are not compensated for. Therefore, the flow of the "B" rearrangement is more successful to the northwest. The alternative explanation that differential immigration can account for the variation in the flow of the "B" chromosomes to the northwest and southeast of the zone fails to explain why the "c" chromosomes are less common to the northwest or the "C" more common to the southeast (Table 1).

Based on identification of homologous chromosomes using G-band patterns, Baker et al. (1979) concluded that the primitive autosomal complement for the *Stenoderminae* was probably like that of *Artibeus jamaicensis*. If this is true, then the most parsimonious route would be from an autosomal complement like that in *Artibeus* ($2n = 30$) to the $2n = 38$ *U. bilobatum* to the $2n = 44$ *U. bilobatum*. This might lead to the conclusion that the rearrangements resulting in the zone under study would have been established in the northwestern part of the range of *U. bilobatum* in isolated peripheral popula-

tions. However, G-band comparison of the karyotype of the $2n = 38$ and $2n = 44$ forms of *U. bilobatum* with *Artibeus* reveals that none of the a, b, or c chromosomes of the $2n = 38$ form of *U. bilobatum* are found in *Artibeus* and it is my conclusion that the $2n = 38$ rearrangements, relative to *Artibeus* or the karyotype proposed as primitive for the family (Patton and Baker, 1978), are more derived than those in the $2n = 44$ cytotype. If this is true, these three rearrangements have become established in the more central parts of the range of the species. It is possible that the "aabbcc" form is replacing the "AABBCC" form and what we are observing here is a phyletic change rather than speciation. In the canalization model of chromosomal evolution, most chromosomal changes were suggested as being phyletic in nature (Bickham and Baker, 1979).

If chromosomal evolution in *U. bilobatum* has occurred as a result of a long period of geographic isolation (as implied by the extensive chromosomal divergence) and the zone is the result of secondary contact, then one would expect an equally large degree of genic divergence and at least some fixed allelic differences. On the other hand, if chromosomal evolution in *U. bilobatum* has been by a phyletic process then one would expect no greater genic differentiation to distinguish these chromosomal races than is characteristic of other widespread continuously distributed species. Genic differentiation which distinguishes the two parental types is no greater than is generally found to distinguish populations of a continuously distributed species (Greenbaum, 1981). Within a few years, the alternative hypotheses can be tested in that it will be possible to determine if the $2n = 38$ cytotype is extending its range to the northwest and the frequency of the "a, b and c" chromosomes are becoming higher in the localities currently predominated by "AABBCC" individuals. If the three rearrangements confer an adaptive advantage, then the "b" rearrangement has the highest positive selective value and it is

ahead of the others in becoming established in populations of "AABBCC" cytotypes.

Based on allozymic variation at 22 loci, Greenbaum (1981) opts for an interpretation which implies primary contact. He interprets lack of introgression across the hybrid zone and symmetrical gene flow within the zone as being consistent with an active process of sympatric speciation between the cytotypes. This is a viable alternative explanation which he defends at length and need not be further discussed here.

Models of chromosomal evolution.—In simulated models of narrow clines, asymmetrical gene flow will move the cline without appreciably changing its characteristics (Endler, 1977). Moran (1979), in a study of a narrow zone (1 km of hybridization in grasshoppers of the genus *Caledia*), also concluded that differential hybrid breakdown would change the geographic position of the zone. *Uroderma bilobatum* has undergone a relatively large amount of chromosomal evolution that has been accompanied by little genic differentiation (Greenbaum, 1981) and our current interpretation of its biology does not fit the parameters (low vagility, high prolificity, and highly inbred demes) most often described as characteristic of species which undergo extensive chromosomal evolution (Arnason, 1972; Hall, 1973; Wilson et al., 1975; Bush et al., 1977; Fredga, 1977; White, 1978b). Low vagility, for instance, may characterize most species that have "tension zones" (Key, 1974) but such zones can occur in species that are volant. Higher vagility is the best explanation of why the zone is so wide in *Uroderma* as compared to those previously described (Bush, 1975; and White, 1978a), which are often no more than several hundred meters or, at most, a few kilometers as compared to 400 km in *U. bilobatum*.

A major focal point of this paper is how the contact zone as witnessed in *Uroderma* can be interpreted in light of current models, which perceive chromosome evolution (or rate of fixation of chromo-

some rearrangements) as being a function of both selection coefficients (degree of negative heterosis) for a particular rearrangement and the effective population size (Wright, 1941; White, 1968, 1978b; Hall, 1973; Wilson et al., 1975; Bush et al., 1977; Lande, 1979). Although these authors indicate (and rightly so) that not all rearrangements result in meiotic imbalance in the heterozygote, their assumption of negative heterosis resulting in some degree of infertility (1) strongly influences the derivation of selection coefficients, and (2) is a critical component in explaining how population size can affect rate of incorporation of rearrangements. The case of *Uroderma* clearly indicates that the negative heterosis assumption is an overstatement and leads one to question how important negative heterosis is in rearrangements which are successfully incorporated during chromosomal evolution. What is unclear from the *Uroderma* data is whether the negative heterosis deficit is negated through cytogenetic mechanisms which result in balanced gamete production or if the heterozygote has a phenotypic advantage that compensates for reduced fertility.

SUMMARY

There are several features of note concerning "chromosome flow" in *Uroderma bilobatum*. (1) Parental cytotypes were sympatric at a single locality. (2) F₁ chromosomal phenotypes were found at three localities, spanning 30 km, whereas backcross types were found at eight localities, spanning over 400 km. (3) The number of F₁ phenotypes (9 individuals) was considerably lower than the number of backcross individuals (48). These three features suggest limited immigration and production of F₁s. However, when such hybridization does occur it has a prolonged effect which produces chromosomal polymorphisms over a wide geographic range.

Therefore, data from *Uroderma* do not support the conclusion that negative meiotic heterosis is as severe as has been suggested in some models of chromosomal evolution (Wilson et al., 1975; Bush et al.,

1977; White, 1978b; Lande, 1979). These models suggest that being heterozygous for a single rearrangement (translocation or inversion) is adequate to produce negative heterotic effects in meiosis sufficient to result in the elimination of such a rearrangement from all but highly inbreeding populations where the rearrangement may become fixed. In *U. bilobatum* the heterozygote may be at a disadvantage, but individuals that are heterozygous for three rearrangements (a terminal translocation, fusion of an acrocentric to a small biarmed element and a centric fusion) reproduce and survive to the extent that their limited numbers produce a significant amount of "chromosome flow" across the contact zone.

The extent to which a rearrangement survives within a population of parental stock varies from 0–5% of the individuals sampled; however, the survival rate on each side of the zone of contact of the "B" and "C" chromosome does not appear to be distributed in a symmetrical or concordant pattern. Although *U. bilobatum* may be functionally less vagile than might be possible for a volant mammal, the width of the zone of hybridization is much wider than is characteristically associated with hybridizing chromosomally characterized taxa (for reviews, see Bush, 1975, and White, 1978a). The nature of "chromosome flow" across the zone is like that described as a "tension zone" (Key, 1974), and the pattern of "flow" cannot be entirely explained by severity of negative meiotic heterosis. Differential immigration or phenotypically adaptive effects of rearrangements are possible explanations of the pattern of distribution of "chromosome flow" of the three rearrangements.

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