

A CONTACT ZONE BETWEEN KARYOTYPICALLY
CHARACTERIZED TAXA OF *URODERMA BILOBATUM*
(MAMMALIA: CHIROPTERA)

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Abstract

Baker, R. J., W. J. Bleier, and W. R. Atchley (Department of Biological Sciences and The Museum, Departments of Biological Sciences and Faculty of Statistics, Texas Tech University, Lubbock, Texas 79409.) A contact zone between karyotypically characterized taxa of Uroderma bilobatum (Mammalia: Chiroptera) Syst. Zool. 24:133-142.—A total of 191 specimens of Peters' tent-making bat, *Uroderma bilobatum*, were collected from the zone where two chromosomal races, representing two subspecies, meet. Eighty-eight specimens had $2n = 38$, four had $2n = 39$, one had $2n = 40$, one had $2n = 41$, one had $2n = 42$, 14 had $2n = 43$, and 82 had $2n = 44$. This chromosomal variation is best explained as resulting from hybridization between two cytotypes with the $2n = 38$ and the $2n = 44$ being the parental (pure) types, the $2n = 41$ individual being of the F_1 type and the $2n = 43, 42, 40$, and 39 individuals representing backcross or F_2 products. The two parental cytotypes were not found to be sympatric at any individual collecting station. The zone of hybridization is approximately 200 kilometers long on the Pacific versant of Honduras, eastern El Salvador and northwestern Nicaragua. Some chromosomally intermediate individuals were reproductively active although the frequency of reproductive activity was not so great as in individuals with parental cytotypes. Measurements of the cranial and wing morphology of chromosomally intermediate individuals indicated that in general there was a correspondence between chromosome number and phenetic similarity to one or the other of the two parental stocks. Chromosomal and cranial and wing morphological data suggest that there is considerable gene flow between the two cytotypes and that chromosomal divergence has occurred in the absence of speciation. The magnitude of chromosomal differentiation between the two subspecies serves as a caveat to those cases where specific recognition is based on chromosomal distinctness of allopatric samples. [Karyotypes; Chiroptera; *Uroderma*.]

Although there have been numerous studies on the divergence of subspecific populations of mammals, such studies have been concerned primarily with the description of size (cranial and external measurements) and pelage color variations that serve as a basis for trinomial application (for a critique see Lidicker, 1962). Such studies have documented that many mammalian species can be subdivided into morphologically distinct units, but they have failed to reveal the nature of the interactions at zones of contact between such units. However, when two subspecific units come into contact, it is the interaction between the units that determines their evolutionary future.

Perhaps the greatest factor that inhibits studies of contact zones is that the degree of morphological divergence is insufficient

to identify all members of the respective populations, plus F_1 and backcross individuals. In the tent-making bat, *Uroderma bilobatum*, the subspecies *U. b. davisii* and *U. b. convexum* are easily identified by chromosomal features (Baker *et al.*, 1972). The degree of chromosomal divergence is also adequate to identify presumed F_1 and backcross individuals. The present study was conducted to determine the nature of the contact zone between the subspecies *davisii* and *convexum* in hopes that such a study would help elucidate the nature and significance of such zones in mammals. In the following discussion the term "hybridization" refers to successful reproduction between two unlike parental stocks (in this case chromosomally characterized) and is not meant to infer specific status (or the lack of it) to the taxa involved. Cytotype

TABLE 1. CANONICAL VARIATE COEFFICIENTS FOR SEPARATING $2n = 38$ AND $2n = 44$ INDIVIDUALS. THE SEXES WERE ANALYZED SEPARATELY. THE GRAND MEAN AND CANONICAL VARIATE SCORES ± 2 STANDARD DEVIATIONS ARE GIVEN BELOW.

Char-acter	$\overset{\circ}{\circ}$ Coef-ficient	Grand Mean	Char-acter	$\overset{\circ}{\delta}$ Coef-ficient	Grand Mean
1	-0.0187	426.52	1	0.0299	425.54
2	0.0552	415.12	2	-0.0248	415.26
3	-0.1700	226.41	3	-0.1887	230.22
4	0.3224	200.88	4	0.1566	202.41
5	-0.1817	129.88	5	-0.1577	130.36
6	-0.0443	95.38	6	0.1265	96.08
7	-0.1519	92.52	7	-0.1265	92.69
8	0.1642	143.20	8	0.1774	146.05
9	0.1701	201.62	9	-0.1564	205.71
10	0.2164	98.32	10	-0.0427	100.54
11	0.0000	95.96	11	0.1213	98.70
12	0.0985	109.13	12	0.1705	110.11
13	-0.2789	186.36	13	0.2475	190.54
14	-0.0233	136.36	14	-0.0911	139.76
15	-0.0350	56.16	15	-0.0391	57.78
16	-0.0924	69.87	16	-0.0275	69.75
17	-0.2045	77.72	17	-0.0805	79.30
18	0.0189	87.32	18	0.1439	88.85
$2n = 38$ ($\overset{\circ}{\circ}$)			$2n = 38$ ($\overset{\circ}{\delta}$)		
1.090 \pm 2.168			0.576 \pm 1.964		
$2n = 44$ ($\overset{\circ}{\circ}$)			$2n = 44$ ($\overset{\circ}{\delta}$)		
-0.799 \pm 1.864			-1.811 \pm 2.080		

is used as defined by Muntzing (Rieger *et al.*, 1968). Metacentric, submetacentric, subtelocentric and acrocentric are defined by Patton (1965).

METHODS AND MATERIAL

The karyological techniques used were described by Baker *et al.* (1972). Most of the statistical procedures employed have been described by Baker *et al.* (1972) and Atchley (1974). Based on the computations in Baker *et al.* (1972) and subsequent computations involving only the two subspecies in question, 18 variables were selected as the best characters to discriminate between the $2n = 38$ and $2n = 44$ cytotypes and to ascertain the phenetic affinities of cytologically intermediate individuals. These 18 variables are (1) length of forearm; (2) length of third metacarpal; (3) greatest length of skull; (4) condylobasal length; (5) zygomatic breadth; (6) braincase

breadth; (7) breadth across P_4 - P_4 ; (8) mandibular length; (9) occipitonasal length; (10) depth of braincase; (11) palatal length; (12) postpalatal length; (13) condylobasal length; (14) zygorostril length; (15) canine to canine breadth; (16) interorbital depth; (17) length of maxillary toothrow; (18) length of mandibular toothrow; see Baker *et al.* (1972) for methods of taking these measurements. The number preceding each characteristic identifies it in Table 1. The number of karyotyped individuals is greater than the numbers in the morphometric studies because subadults were not used in the morphometric analyses.

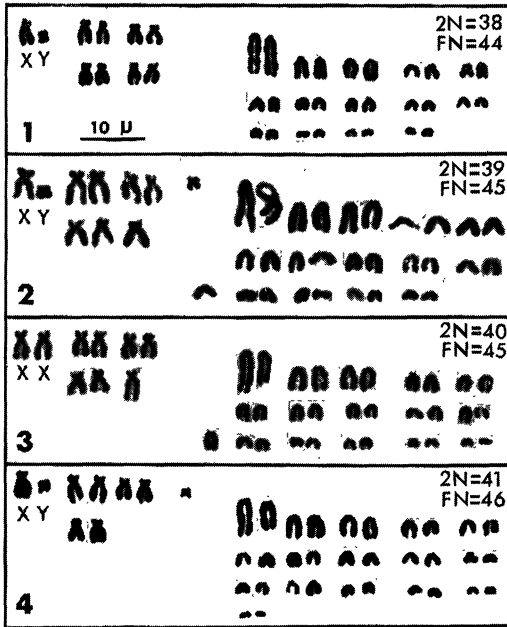
A canonical variate analysis was used to discriminate between the two cytotypes. Because of the pronounced secondary sexual dimorphism in this species, the sexes were analyzed separately. Chromosomally intermediate individuals were included in the analyses as ungrouped data. As such, they did not enter into the analyses but rather were simply projected onto the resultant canonical vectors (Atchley, 1974). Therefore, we were able to ascertain the phenetic affinities of the intermediate individuals with regard to the parental forms. The formula for projecting new data onto these vectors is

$$Z_i = \sum_{j=1} \mu_j (X_{ij} - \bar{X}_j)$$

where Z_i is the canonical variate score for the i th individual, μ is the canonical coefficient, X_{ij} is the i th observation for the j th character and \bar{X}_j is the grand mean for the j th character.

Primary collection sites were tall and extensive forest or stands of bananas. It has been our experience that netting in areas of reduced vegetation is not productive for *Uroderma*. Therefore, a considerable effort was made to locate suitable habitat along the main and accessory roads in the area between Usulután, El Salvador and Choluteca, Honduras.

Determination of the reproductive status of females was by macroscopic examination. If macroscopic examination of individuals



FIGS. 1-4.—1, Karyotype representative of the $2n = 38$ parental cytotype; 2, Karyotype representative of one specimen with a $2n = 39$ (three other specimens had a $2n = 39$ but the karyotype was like that figured in Baker *et al.*, 1972, fig. 4); 3, Karyotype representative of the specimen with $2n = 40$; 4, Karyotype representative of the specimen with $2n = 41$.

with diploid numbers of 39-43 failed to reveal an embryo, the uterus and ovaries were sectioned at 10 micra to determine whether the individual was pregnant, had ovulated recently, or whether the ovaries appeared abnormal. All measurements of fetal variables are given in millimeters. The crown-rump length does not include the fetal membranes. Embryos were macroscopically examined for developmental defects.

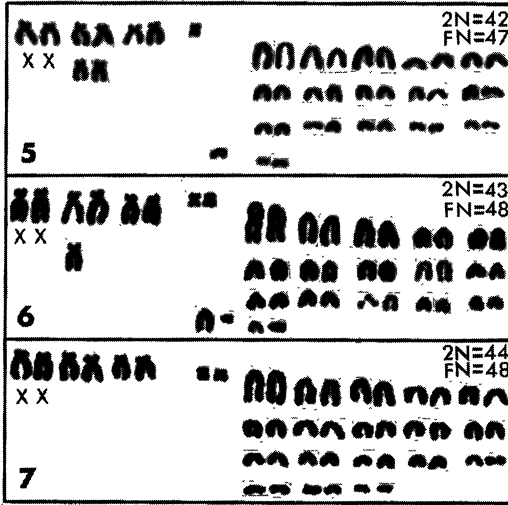
Testis and epididymis of male individuals with a diploid number of 39-43 were histologically examined and compared with sections of testis and epididymis of each parental type. These histological preparations consisted of a representative series from serial sections cut at 10 micra. The reproductive activity of a male in question was determined by ranking it according to

the relative amount of spermatozoa in the testis and epididymis. Individuals were ranked from zero (for those with little or no sperm) to four (for those with large quantities of sperm in the seminiferous tubules and the epididymis). Relative amounts of sperm in the testis were recorded, and a month later the same investigator took another series of slides and individuals were rescored to determine the reliability of the first count. At the second scoring, the investigator was not aware of the previous score for each specimen. Of the readings for 20 individuals, the second count resulted in 14 individuals being scored as before, five readings that deviated by one and one individual that deviated by three units from the original score. Therefore, it appears that the method of determining sperm counts was repeatable and represents a reliable index of reproductive activity. Detailed reproductive data are not available for specimens reported in Baker *et al.* (1972).

RESULTS

Chromosomal Data

Of the 191 individuals karyotyped from the Pacific versant of Honduras, eastern El Salvador, and northwestern Nicaragua, 88 had the parental karyotype of $2n = 38$, $FN = 44$ (Fig. 1); four had $2n = 39$, $FN = 45$ (Fig. 2); one had $2n = 40$, $FN = 45$ (Fig. 3); one had $2n = 41$, $FN = 46$ (Fig. 4); one had $2n = 42$, $FN = 47$ (Fig. 5); 14 had $2n = 43$, $FN = 48$ (Fig. 6); and 82 had the parental karyotype of $2n = 44$, $FN = 48$ (Fig. 7). The geographic distribution of cytotypes and the frequency of individuals having a karyotype unlike the the common parental type found at each locality are shown in Fig. 8. The two parental cytotypes were not sympatric in any sample and all samples of *davisi* to the north and *convexum* to the south of the area shown in Fig. 8 contained no chromosomal variants. In all individuals having a diploid number of 44 or 43 there is a pair of small biermed autosomes. In the $2n = 42$ and 41



FIGS. 5-7.—5, Karyotype representative of the specimen with $2n = 42$; 6, Karyotype representative of the specimens with $2n = 43$; 7, Karyotype representative of the $2n = 44$ parental cytotype.

individuals and one of the four $2n = 39$ (Fig. 2) specimens there is only one such element. No such autosomal elements were found in individuals with $2n = 40, 38$, and three of the four $2n = 39$ specimens. The karyotype of these three $2n = 39$ individuals is like that in Fig. 4 of Baker *et al.* (1972). The karyotype of the $2n = 41$ individual could be composed of one haploid complement from a $2n = 44$ individual and one from a $2n = 38$ individual. The sex elements in all cases were believed to consist of a large biarmed (subtelocentric) X(s) and a small (submetacentric) Y. The chromosomal variation is believed to be restricted to the autosomes.

Ecology

An extensive search of the portion of Honduras between Choluteca and Nacaóme and immediately to the east of Nacaóme (the primary site of hybridization) revealed only limited habitat that was suitable for *Uroderma*. The area netted at Nacaóme (sample C of Fig. 8) was a small grove of bananas which would characteristically support a limited number (20 or so) of in-

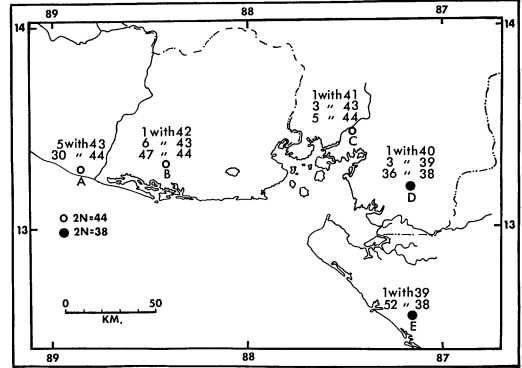


FIG. 8.—Geographic distribution of cytotypes of *Uroderma bilobatum*. Information above each locality represents the number of individuals with each respective diploid number found at that locality. A = La Herradura, El Salvador; B = Usulután and San Miguel, El Salvador; C = Nacaóme, Honduras; D = Choluteca, Honduras; E = Chinandega, Nicaragua.

dividuals of *Uroderma*. No other forested areas were located near the Nacaóme collecting site. The general habitat is pasture land with isolated small trees. Suitable *Uroderma* habitat is greatly increased in the general vicinity of the localities collected on each side of the Nacaóme collecting site.

Reproduction

Fifty-five of 59 females of the $2n = 44$ cytotype were pregnant when collected during the period of 7 to 26 July 1972. Of the four nonpregnant females, none was lactating. Eleven of 17 females of the $2n = 38$ cytotype were pregnant when collected during the period of 15 to 21 July 1972. One of the six nonpregnant individuals was lactating when collected. Six of seven females with $2n = 43$ were pregnant when collected during the period of 7 to 26 July 1972. None of the embryos of females with $2n = 43$ appeared to be abnormal in any sense and their stage of development was comparable to that of embryos collected from other females in the sample for that date. A female with $2n = 40$ and a female with $2n = 42$ were neither pregnant nor lactating when collected on 16 July and

26 July 1972, respectively. Histological examination of the ovaries of the $2n = 40$ and $2n = 42$ individuals failed to reveal any abnormalities that distinguished them from other nonpregnant females with $2n = 44$ or $2n = 38$ karyotypes. No females were collected with a karyotype of $2n = 39$ or 41 .

All males that were histologically examined were adults collected during 7 to 26 July 1972. The score for six males with $2n = 44$ was 0, 0, 0, 2, 3, 4 (mean, 1.5). The score for 12 males with $2n = 38$ was 0, 1, 3, 3, 3, 3, 4, 4, 4, 4, 4, 4 (mean, 3.1). The scores for the three males with $2n = 39$ were 1, 2, and 3 (mean, 2) and for the male with $2n = 41$ was 0. No males with a $2n = 40$ were collected. The score for three males with $2n = 43$ was 1, 0, and 0. The mean for the six individuals with $2n = 43$, 42, 41, or 39 was 1.0.

Morphometrics

Table 1 gives the canonical variate coefficients, the grand means for each cytotype and the group means in reduced subspace ± 2 standard deviations.

The canonical analysis of the $2n = 38$ and $2n = 44$ cytotypes (years pooled) indicated a phenetic overlap of approximately 14% in the females and 13% in the males.

The results of the canonical analysis are given as histograms in Figs. 9 (males) and 10 (females). The chromosomally intermediate individuals are shown below the two parental forms.

DISCUSSION

The most obvious explanation for this chromosomal variation is that it results from hybridization between the cytotypes and subsequent backcrossing. Less than 1% (1 of 191) of the specimens collected from the populations that contained hybrid products were from a chromosomal standpoint possible F_1 individuals. This, in light of the fact that no sample contained both parental types, suggests that the opportunity for hybridization may not be too fre-

quent. However, over 11% (21 of 191) of the individuals from the samples containing chromosomally intermediate individuals and 33% (3 of 9) of the Nacaóme, Honduras sample (C of Fig. 8) were identifiable as backcross products. The imbalance between the frequency of F_1 and backcross individuals may be explained by (A) at some time in the recent past there has been a greater proportion of F_1 individuals but primary hybridization was not occurring at such a high rate at the time our samples were taken or (B) production of F_1 s may be infrequent, but such hybrids are sufficiently fertile to produce a karyotypic polymorphism (by backcrossing) that may persist for several generations. We favor the latter explanation. If either explanation is true then there is considerable gene flow between the two cytotypes. In the following discussion, we will evaluate our additional data in light of "extensive gene flow" between the populations and then evaluate its implications as related to other studies of chromosomally characterized taxa of mammals.

Why is this area where hybrid products are found (indirectly inferring gene flow) so wide (over 200 km from sample A to sample E of Fig. 8)? One reason to consider is that bats are highly vagile and the exchange of individuals between populations (with resultant gene flow) could extend over a wider area than for less vagile forms. If this is the major reason for the width of the zone of hybridization then why were the two parental cytotypes not broadly overlapping in their distribution? In a similar study of karyotypically characterized taxa of bats of the genus *Macrotus* the zone of overlap was a single locality (Davis and Baker, 1974). Although bats are potentially highly vagile, our data suggest that functionally they are less vagile than morphology alone would suggest. We feel that the main reason that the zone where hybrid individuals are found is so wide is that if there is natural selection against F_1 and backcross individuals, the degree of selection is sufficiently low that

it does not effectively reduce the flow of chromosomes in both directions. Even with a low vagility, ample time would result in chromosomal dispersal over a wide area.

A critical component of gene flow between bat populations is the amount of exchange of individuals between populations during breeding activities. The stage of development of the *Uroderma* embryos in our pregnant females suggests synchronization of the breeding cycle in these populations. Our samples were not from the breeding season. Therefore, if there was considerable movement during the limited breeding season then the lack of sympatry among the parental cytotypes may be in part due to the time at which samples were collected. A phenomenon called "swarming" which is associated with hibernacula occurs in some vespertilionid bats (Davis, 1964; Hall and Brenner, 1968; and Fenton, 1969). Although the exact nature and function of "swarming" is not known, it is clear that the behavioral pattern of populations of some bat species vary during the year. If a similar phenomenon occurred between roosts of *Uroderma* during the breeding season it would result in an increase in gene flow between populations. There are no data which suggest that such populational behavior occurs or does not occur in *Uroderma*. We present the above discussion only to point out that other factors may account for the pattern of distribution of chromosomal types.

Because chromosomes are inherited in a Mendelian fashion, it is interesting to determine how deep within the range of each cytotype the chromosomes of the other cytotype have penetrated. Backcross individuals have been obtained over 150 km away from the northeastern most sample of the $2n = 38$ cytotype (from sample D to sample A, Fig. 8). Backcross individuals also have been obtained from populations of the $2n = 38$ cytotype (sample E, Fig. 8, Chinandega, Nicaragua) over 100 km away from the nearest sample of the $2n = 44$ cytotype (sample C, Fig. 8, Nacaóme, Honduras). The sample containing the

largest number of hybrid and backcross individuals is the sample that is central in the hybrid zone. To the south the first sample had 10% backcross individuals and the more distant sample had 4% which suggests a decrease in frequency of backcross individuals as the distance from the central zone increases. However, to the north the sample nearest the central zone contains 15% hybrid individuals whereas the more northern sample contains 18% hybrid individuals. Why the more northern sample contains a higher percentage is not clear.

An interesting feature of the distribution of chromosomally intermediate individuals within the zone of hybridization is that all three individuals with either a $2n$ of 40, 41, or 42, (the most intermediate karyotypes) were found in the central part of the zone (the Usulután, Choluteca, and Nacaóme, samples B, C, and D of Fig. 8). At the two localities most distant from the center of the zone, the intermediate karyotypes were from a diploid number and morphological standpoint very near the associated parental karyotype. This suggests to us that most F_1 hybrids are produced in the central part of the area shown in Fig. 8.

There seems to be greater penetration of $2n = 38$ chromosomes into the $2n = 44$ cytotype than there is of the reverse situation (Fig. 8). Also there is a greater number of hybrid individuals associated with the $2n = 44$ cytotype (16 of 96) than there is associated with the $2n = 38$ cytotype (5 of 88). We cannot determine with our data if this is a sampling error or the result of greater selection against $F_1 \times 2n = 38$ backcross individuals (the possibility of an $F_1 \times F_1$ cross is slight and probably not important in these populations). Another explanation might be that individuals of the $2n = 38$ cytotype more frequently invade populations of the $2n = 44$ cytotype than the reverse condition.

Measurements of cranial and wing morphology of the chromosomally intermediate individuals indicate that in general there was a correspondence between chromosome

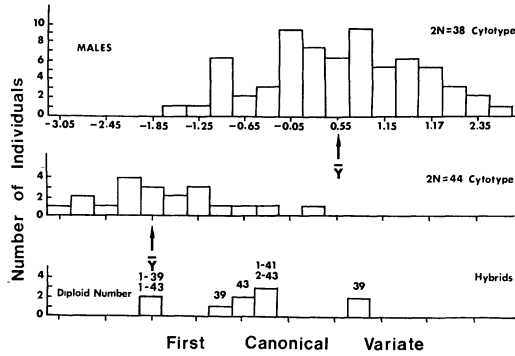


FIG. 9.—Frequency distributions for the canonical variate scores for males of the $2n = 38$ and $2n = 44$ cytotypes. Chromosomally intermediate individuals have been included as ungrouped data.

number and phenetic similarity to one or the other parental stocks. Thus, most of the $2n = 43$ individuals were more similar to the $2n = 44$ form than to the $2n = 38$ cytotype. The $2n = 41$ (probably an F_1 product) individual occupied a position central to the two parental stocks (Figs. 9 and 10). There are exceptions, however, to this pattern. In the male intermediates, two individuals which were $2n = 39$ more closely resembled the $2n = 44$ form than did some of the $2n = 43$ bats. Likewise, in the females one $2n = 43$ individual would be classified on the phenetics of its cranial and wing morphology as a $2n = 38$ form.

The degree of overlap of the parental stocks in the variables for cranial and wing morphology (14% in females and 13% in males) is in agreement with the implications of the chromosomal data that considerable gene flow is occurring between the two cytotypes. It should also be remembered that unless crossing over has been inhibited, the genes on the marker chromosomes may be those of the other parental type and that gene interaction and backcrossing may confuse the actual genetic status of chromosomally intermediate individuals (Atchley, 1974). The chromosome is simply the vehicle of heredity and its usefulness as an index of the genetic status of an individual can be invalidated by backcrossing and crossing over.

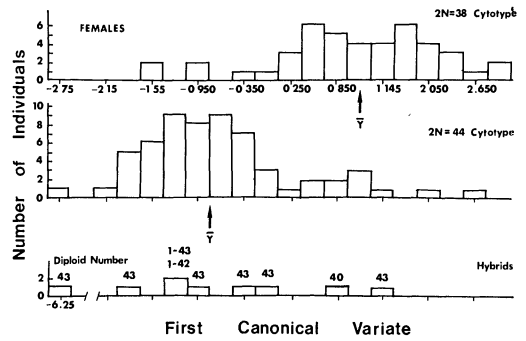


FIG. 10.—Frequency distributions for canonical variate scores for females of the $2n = 38$ and $2n = 44$ cytotypes. Chromosomally intermediate individuals have been included as ungrouped data.

Although our data on chromosomal and cranial and wing morphology give no indication of reduced gene flow between cytotypes, reproductive data hint that there is reduced fertility in hybrid individuals. The percentage of pregnant females is lowest in individuals with intermediate karyotypes (66% as opposed to 71% and 93% for the parental stocks). However, these differences are not statistically significant, possibly because of sample size. The reduction of fertility in males is more strongly suggested with the scores for adult males of the $2n = 44$ cytotype having a value of 1.5, the males of the $2n = 38$ cytotype having a value of 3.1 and the males with an intermediate karyotype having a score of 1.0. It is also interesting to note that none of the three individuals having a $2n$ of either 40, 41, or 42 were reproductively active. Perhaps the most important observation in the reproductive studies is that at least some of the individuals that have intermediate karyotypes are reproductively successful.

The area shown in Fig. 8 occupied by the $2n = 44$ cytotype is somewhat more arid than that occupied by the $2n = 38$ cytotype. However, if the entire range of the two respective cytotypes is considered, there are no ecological factors that to us readily distinguish the habitat of the two chromosomal races. As described above the two cytotypes are partially separated by less

favorable habitat for the species and this may be the reason that the break in the two chromosomal races occurs at this specific locality. We were unable to determine if this less forested area is a result of man's activities or if it is a natural characteristic of the region.

Our morphometric and chromosomal data suggest considerable gene flow. In some cases of studies of chromosomally characterized taxa it was not apparent whether the hybrid breakdown was entirely genic or in part chromosomal (Hall and Selander, 1973). In this case it is clear that the chromosomal changes have not resulted in two biological species. The magnitude of chromosomal difference between the two cytotypes is sufficiently large to serve as a caveat to those cases where specific distinctness is based strictly on chromosomal distinctness of allopatric samples (see also Wahrman and Gourevitz, 1973 and Thaeler, 1974). Studies from the zone of contact are required to determine the biological significance of such chromosomal races. When the distribution of heterochromatin and the origin of variation (types of chromosomal rearrangements involved) are known for the two taxa we may better understand the implication of the hybridization of the two cytotypes of *Uroderma* (Mascarello and Warner, 1974 and Mascarello *et al.*, 1974).

Several other detailed studies on the zone of contact between karyotypically characterized taxa of mammals have been made and the conclusions from these studies vary from "no hybrids" to "extensive gene flow." Studies of two contact zones did not produce hybrids (Davis and Baker, 1974 and Thaeler, 1974). In bats of the genus *Macrotus* (Davis and Baker, 1974) there seems little likelihood that natural hybrids are being produced between *M. waterhousii* ($2n = 46$, FN = 60) and *M. californicus* ($2n = 40$, FN = 60). No hybrids were found at what was labeled the "Gothic Contact" (Thaeler, 1974) between populations of pocket gophers *Thomomys talpoides*, with some specimens having a $2n =$

48 and others having a $2n = 56$. Not all of the differences in chromosomes between populations at the "Gothic Contact" could be explained as Robertsonian in nature (Thaeler, 1974).

Four studies suggest that although hybridization was occurring between chromosomally characterized taxa of mammals, reduced or no gene flow occurred between these taxa (Patton and Dingman, 1968; Patton, 1969; Patton *et al.*, 1972; Patton, 1973; Thaeler, 1968, 1972 and 1974; Wahrman *et al.*, 1969a and 1969b; and Nevo and Shaw, 1972).

In a contact zone between two species of pocket gophers (*Thomomys bottae* and *T. umbrinus*) several hybrids were found but 70% of the total individuals of hybrid origin were probably F_1 s (Patton, 1973 and Patton *et al.*, 1972). In pocket mice (*Perognathus goldmani*), the chromosomal races did not overlap and hybrids between cytotypes were found at two localities. However, Patton (1969) concluded that gene flow between chromosomal races "would appear to be nearly nonexistent, since only three chromosomally hybrid individuals are recorded from a sample of 221 mice trapped within the contact zone." Similar conclusions were drawn from studies of *Spalax ehrenbergi*, a mole rat (Wahrman *et al.*, 1969a and 1969b and Nevo and Shaw, 1972) and for populations of *Thomomys talpoides* at Thaeler's (1974) "South Fork Contact."

In addition to the contact zone described for *Uroderma* in this paper, three other contact zones have been described where chromosomal data suggest extensive interbreeding between populations of chromosomally characterized taxa. Two such zones are described for pocket gophers, *Thomomys talpoides* (see Thaeler's 1974 description of the "Laramie River Contact" and "West of Denver Contact") and one for a gerbil, *Gerbillus pyramidum* (Wahrman and Gourevitz, 1972). In a study of a contact zone between spiny mice (*Acomys cahirinus*) it was not clear if F_2 or backcross individuals were being produced (Wahrman and Goikin, 1972). It is interesting to

note that in most of the above studies, natural hybrids were found.

In *Uroderma* less than 5% of the individuals of hybrid origin are probably F_1 products. Our data (chromosomal, morphometric and reproductive) do not support the idea that two species of *Uroderma* are involved in our samples. To the contrary, it seems that if gene flow is reduced across this hybrid zone it is not readily provable with our techniques. Unfortunately we have no control situation to determine how much gene flow occurs between populations that do not have such chromosomal differences. If such data were available, then a comparison of the nature of the zone of exchange of chromosomes between the two cytotypes would help determine if the width of the zone has been reduced by natural selection.

Most of the data concerned with mammalian speciation has been interpreted as supporting the classical allopatric model. The cytotypes of *Uroderma bilobatum* have obviously not completed speciation but if additional chromosomal or genetic variations build up at this central zone then speciation without total isolation can be visualized (White, 1969). In the case of *Uroderma bilobatum* the species is subdivided into somewhat isolated units (populations) by the available habitat. This semi-isolation certainly could be an adjunct to the speciation process.

In two cases in the family Phyllostomatiidae (*Uroderma* and *Macrotus*) where chromosomal races have been studied in detail, exactly opposite conclusions have been drawn (Davis and Baker, 1974). The one factor that was similar in both cases was the implied philopatry exhibited by the taxa involved. Because of the low frequency of chromosomal races found within this family (Baker *et al.*, 1973) comparative data will be difficult to obtain. It will certainly be interesting to compare data from the southern races of *Uroderma* where the $2n = 38$ and the $2n = 42$ cytotypes come into contact (Baker *et al.*, 1972).

SPECIMENS EXAMINED

All specimens are deposited in The Museum, Texas Tech University. In addition to the specimens cited below, specimens from localities near Chinandega, Nicaragua and La Herradura, El Salvador from a previous study (Baker *et al.*, 1972) were also utilized in this study. EL SALVADOR: La Paz, 3 mi. NW. La Herradura, 16 females, 3 males, TT16952-16970; San Miguel, 3.1 mi. W. San Miguel, 2 males, TT16972-16973; Usulután, 2 mi. E. Usulután, 46 females, 6 males, TT16978-16989, 16991-17001, 17003-17030, 17032; HONDURAS: Choluteca, 18.7 mi. S. Choluteca, 6 females, 34 males, TT17034-17036, 17038-17040, 17042-17075; 1 mi. SE. Nacaóme, 5 females, 4 males, TT17076-17084; NICARAGUA: Chinandega, 3.5 mi. SW. Chinandega, 12 females, 11 males, TT17085-17100, 17102-17108.

ACKNOWLEDGMENTS

We thank Brent L. Davis and Robert G. Jordan for field assistance. Stephen L. Williams and Bea Cornely assisted in preparation of some figures. Jerry W. Warner assisted in the karyotypic analysis. For permission to collect at certain localities and for field facilities we thank H. R. Winogrand, Enrique Rodríguez, Julio González Suvíaga, Antonio Zelaya and José Velásquez. Hugh H. Genoways, J. K. Jones, Jr., John W. Bickham, Brent L. Davis, Ira F. Greenbaum, and John C. Patton critically evaluated the manuscript. Supported by a Graduate Student-Faculty Fellowship awarded by the Graduate School at Texas Tech University and by National Science Foundation Grants numbers GN-29132X1 and GB-29132X.

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Manuscript received October, 1974