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CHROMOSOME EVOLUTION IN THE POCKET MOUSE,
PEROGNATHUS GOLDMANI OSGOOD

by

James Lloyd Patton

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THE UNIVERSITY OF ARIZONA

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James L. Patton

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ABSTRACT

Six chromosome races are described for the pocket mouse, Perognathus goldmani Osgood. The species inhabits a relatively restricted geographic range from northeastern Sonora, Mexico, south into northern Sinaloa, Mexico, within thornscrub and short-tree forest communities. Two lines of evolution from an hypothetical ancestral arrangement account for the chromosome variants. One lineage involved the formation of a single race via a pericentric inversion in a small autosome; the second involved the formation of five races through a series of four autosomal centric fusions and a pericentric inversion in the X-chromosome. There is a sequential relationship between the present geographic distribution and the phylogenetic position of the races, with the more ancestral at the northern and southern geographic margins and the more derived in the interior of the species range. Races exhibit contiguous allopatry, as contact between adjacent races is established along major rivers. No localities of sympatry between races are known, and only three individuals of hybrid origin between any two races have been found. Migration and presumably gene flow between adjacent races is apparently at a

minimum. Physiographic factors (rivers) and ecological factors (riparian communities and the competitive sibling species, P. artus Osgood) combine to form a barrier to dispersal. An allopatric interpretation for racial formation and a sequence of historical migration patterns and ecological shifts are hypothesized.

INTRODUCTION

Pocket mice of the heteromyid rodent genus Perognathus provide unusual promise for the demonstration of phyletic evolution based on comparative chromosome characteristics. Within the seventeen species examined in depth to date, diploid numbers are found to vary between 34 (P. hispidus) and 56 (P. amplus and P. longimembris), and only two species are currently known to have indistinguishable karyotypes (Patton 1967a, b, unpublished data). Moreover, an extensive geographic survey of each species has revealed numerous cases of intraspecific chromosomal variation, including intrapopulation polymorphism (P. baileyi) and monomorphic chromosome races (P. penicillatus, P. pernix, P. goldmani, and P. amplus). Some of these latter races correspond to currently recognized subspecies, but others permit recognition of differentiation not previously assessed by more conventional systematic methods.

Perognathus goldmani Osgood, although considered taxonomically monomorphic, is characterized by an assemblage of six allopatric chromosome variants. The species is prevalent in thornscrub and short-tree forest habitats from extreme northeastern Sonora in the Rio Yaqui drainage

through the coastal plains of Sonora into northern Sinaloa, in northwestern Mexico. Little knowledge is available concerning biological aspects of the species, and only a single report with depth has been published since its original description by Osgood (1900). This report (Anderson 1964) deals with the systematic status of the species and a sibling species, P. artus Osgood. Although the report concerns geographic variation, little information regarding population dynamics, ecology, and history is provided.

The present effort is an attempt to document the phylogenetic characters and interpret historical relationships between the chromosome races of P. goldmani, and also their relationship with P. artus. This is done through an interpretation of the origin (historical influences) and mechanisms of chromosomal change, considering genetic consequences, geographic distribution, and ecological relationships. The present study may clarify the adaptive significance of different chromosome combinations and their possible role in evolutionary divergence.

METHODS AND MATERIALS

A total of 319 specimens of P. goldmani (177 males, 142 females) from 47 localities within the Mexican states of Sonora and Sinaloa were trapped alive for the present analysis. All individuals were identified by the pelage and cranial criteria of Anderson (1964). Conventional museum specimens of all animals have been prepared, and the majority are deposited in the collection of mammals, Department of Biological Sciences, The University of Arizona, Tucson. See list of specimens examined below for museum catalogue numbers and localities.

Metaphase chromosomes of dividing bone marrow cells were prepared using the in vivo colchicine-hypotonic citrate sequence described elsewhere (Patton 1967a). Determination of diploid numbers, fundamental numbers, and chromosome morphology was made by standard analytical procedures (Bender and Chu 1963, Patton 1967a). An average of 15 cells were examined per individual (a total of 4785 cells examined). Greater than 87.5 per cent of all cells belonged to the modal count chosen as the diploid number for each race. Karyotypes were prepared from photomicrographs. Autosomes are grouped into morphological classes to facilitate comparison of the

chromosome variants. These are: Group A, metacentrics and submetacentrics; Group B, "rabbit-ear" acrocentrics (terminology after Levan, Hsu, and Stich 1962); and Group C, acrocentrics. The sex chromosomes have been classified separately. Members of Group A are individually recognizable, and have been designated by subscripts indicative of their point of origin in the chromosome phylogeny.

RACIAL CHARACTERISTICS

For present purposes, each chromosome race is designated by Greek letter. The order of the designations in no way indicates closeness of relationship, but merely the sequence in which each chromosomal variant was discovered. Only two localities are known from which intergrades between any two races have been found. No localities of sympatric contact between adjacent races are known. Each race is essentially monotypic, therefore, and can be defined chromosomally, ecologically, and geographically. The overall geographic distribution of the species and the six races is shown in Fig. 1.

Perognathus goldmani- α

Karyotypic description. A karyotype representative of this chromosome race has been presented elsewhere (Patton 1967a). The diploid number is 52 and the fundamental number (FN) 54. According to the previously established nomenclature, the chromosomes can be arranged as follows (Fig. 2):

Group A: 2 pairs of medium submetacentrics (designated A_2 and A_4 , respectively).

Group B: 1 pair of "rabbit-ear" acrocentrics.

Fig. 1. Distribution of *Perognathus goldmani* in Sonora and Sinaloa, Mexico, indicating known range of each chromosome race (hatching).

Fig. 2. Karyotype of Perognathus goldmani-race α .
Male. JLP 1656. 17.5 mi. S. Alamos, Sonora, Mexico.

Group C: 22 pairs of acrocentrics grading in size from large to small.

X: large acrocentric.

Y: small acrocentric.

Diagnosis: The significant features of this karyotype when compared to those of other races include: (1) $2n=52$, $FN=54$; (2) Group A bialleled elements A_2 and A_4 ; and (3) the acrocentric X-chromosome. Three hybrid individuals between races α and δ have been examined from two localities (20 miles south of Alamos and 1 mile east of Presa Josepha Ortiz). These individuals are karyotypically intermediate between the two races ($2n=51$), as would be expected (Fig. 3).

Geographic distribution. Members of this race ($N=174$) have been trapped from 32 localities in southern Sonora and northern Sinaloa. Distribution is sharply delimited by the major rivers in the area (i.e., Rio Mayo, Rio Cuchijaqui, and Rio Fuerte), and contact with adjacent races is known from several localities along each of these streams. Contiguity is evidenced with Race- γ on the north along the Rio Mayo as far east as Presa Mocuzari, with Race- δ along the Rio Cuchijaqui to the east and south of Alamos, and with Race- β along the Rio Fuerte on the south, presumably from its mouth to the junction with the Rio Cuchijaqui (Figs. 1, 4, and 5).

Ecological distribution. The race primarily inhabits thornscrub (i.e., thorn forest of Gentry 1942 and Leopold

Fig. 3. Karyotype of Perognathus goldmani-race α and Perognathus goldmani-race δ hybrid. Female. JLP 1712. Ca. 1 mi. E. Presa Josepfa Ortiz (by rd.), Sinaloa, Mexico.

Fig. 4. Map of the Rio Mayo and adjacent Rio Cuchijaqui drainages in southern Sonora, Mexico, detailing localities and sample sizes for three chromosome races of *P. goldmani*.

Fig. 5. Map of the Rio Fuerte drainage in southern Sonora and northern Sinaloa, Mexico, detailing localities and sample sizes for three chromosome races of *P. goldmani*.

1950) around Navojoa and south along the coast. This thick scrub, dominated by thorny leguminous trees and tree and shrub cacti, grades into short-tree forest (Gentry 1942) to the east in the foothills of the Sierra Madre Occidental. Fully-developed short-tree forest communities, reaching heights of over 60 feet, are restricted to north and west facing slopes as well as canyon bottoms. The majority of the vegetation assemblages in this area mapped as tropical deciduous forest (=short-tree forest) by Leopold (1950) actually have a considerably more xeric and stunted appearance.

In all areas, the species is most abundant in the soft alluvial soils, but is uncommon in riparian communities, along river terraces, or on rocky slopes. Throughout the range of P. goldmani away from the coastal areas, the species is almost completely replaced in riparian communities and in the more mesic, fully-developed short-tree forest by the sibling species, P. artus.

Perognathus goldmani- β

Karyotypic description. The diploid number is 56, the fundamental number is also 56. The complement (Fig. 6) can be described as follows:

Group A: 1 pair of small metacentrics (designated A_1).

Group B: 1 pair of "rabbit-ear" acrocentrics.

Fig. 6. Karyotype of Perognathus goldmani-race ♂.
 Male. JLP 992. South bank Rio Fuerte, ca. 1 mi. W. Presa
 Miguel Hidalgo, Sinaloa, Mexico.

Group C: 25 pairs of acrocentrics grading in size from large to small.

X: large submetacentric.

Y: small acrocentric.

Diagnosis. While the chromosome complements of the other five races are quite similar, P. goldmani- β is strikingly distinct in several aspects. In addition to having a higher fundamental number (56 instead of 54), it can be distinguished by the single small pair of metacentric Group A autosomes (chromosome A_1) which is not present in any other race. The large submetacentric X-chromosome is the same as in races ϵ , θ , and γ .

Geographic distribution. The race (N=36) has been trapped from six localities essentially covering the entire range of P. goldmani south of the Rio Fuerte in northern Sinaloa (Figs. 1 and 5). The locality near Choix represents the most eastern point and that near Verdura the most southern point of the distribution of the species, as mapped by Anderson (1964). Contact is made between races β and α along the lower Rio Fuerte eastward to its junction with the Rio Cuchijaqui, and between races β and δ from that point farther to the east along the upper Rio Fuerte.

Ecological distribution. The general habitat is thornscrub resembling short-tree forest (Gentry 1942 and R. S. Felger, personal communication) from Los Mochis south

along the coast, grading into xeric aspects of the tropical deciduous forest to the east in the upper Rio Fuerte valley. The lower reaches of this valley, as well as that of the adjacent Rio Sinaloa valley, are currently under extensive agriculture. Moreover, large areas within the tropical deciduous forest have taken on scrub appearances because of agricultural or overgrazing disturbances. The species is uncommon in completely disturbed sites, but is very abundant in the loose, clay soils of areas with more natural vegetation. In the areas east of Choix and south of Verdura, P. goldmani is replaced by P. artus, even though the forest and scrub habitats are continuous. The replacement of P. goldmani by P. artus away from the coastal plain is correlated with shifts in humidity and vegetation (Anderson 1964).

Perognathus goldmani- γ

Karyotypic description. The diploid number is 52, the fundamental number 54. The karyotype (Fig. 7) can be described as follows:

- Group A: 2 pairs of medium submetacentrics (designated A_2 and A_4 , respectively).
- Group B: 1 pair of "rabbit-ear" acrocentrics.
- Group C: 22 pairs of acrocentrics grading in size from large to small.
- X: large submetacentric.
- Y: small acrocentric.

Fig. 7. Karyotype of Perognathus goldmani-race γ .
 Female. UA 15901. 16 mi. N. Navojoa (by rd.), Sonora,
 Mexico.

Diagnosis. The karyotypes from sampled individuals are identical to those belonging to Race- α , except that the X-chromosome of Race- γ is a large submetacentric and that of Race- α is a large acrocentric. Both races have the same number of Group C autosomes and the same two pairs of Group A biallelic elements (chromosomes A_2 and A_4).

Geographic distribution. The race ($N=44$) is known from six populations ranging from Presa Alvaro Obregon north of Ciudad Obregon, south and east of the Rio Yaqui to the north bank of the Rio Mayo from Navojoa to at least Tepahui (Figs. 1 and 4). The race presumably extends eastward into the foothills of the Sierra Madre Occidental along the Sonora-Chihuahua border, the eastern edge of the species range. Contact is established with Race- α along the Rio Mayo from Navojoa to Presa Mocuzari. Assumed contact is also made with Race- δ east of Presa Mocuzari along the upper Rio Mayo. The northern distributional limits and consequently contact points with Race- ϵ are unknown at present.

Ecological distribution. Habitats of the race to the north of the Rio Mayo are continuous in kind and composition with those occupied by Race- α to the south of this river. However, around Presa Obregon, the species (and race) departs radically from the more typical southern habitat conditions. In this area rocky soils, particularly on low incline slopes, are the characteristic habitat for

the species. The vegetation of the general region of the Rio Yaqui valley is included in the Foothills of Sonora Section of the Sonoran Desert (Shreve and Wiggins 1964) and is characterized by heavy stands of trees and shrubs, the species composition of which is indicative of strong thornscrub influences from the south.

Perognathus goldmani- δ

Karyotypic description. The diploid number is 50, the fundamental number 54. The karyotype (Fig. 8) can be described as follows:

Group A: 2 pairs of medium submetacentrics (designated A_2 and A_4) and 1 pair of large submetacentrics (designated A_5).

Group B: 1 pair of "rabbit-ear" acrocentrics.

Group C: 20 pairs of acrocentrics grading in size from large to small.

X: large acrocentric.

Y: small acrocentric.

Diagnosis. The chromosome complement is most similar to that of Race- α . Both contain the large acrocentric X-chromosome and the A_2 and A_4 biarmed elements of Group A. Race- δ , however, possesses an additional Group A biarmed pair (A_5), lacks two pairs of Group C acrocentrics, and has a lower diploid number.

Fig. 8. Karyotype of Perognathus goldmani-race δ .
 Male. JLP 1040. South bank Rio Mayo at Las Panelas,
 Sonora, Mexico.

Geographic distribution. Individuals of the race (N=53) have been examined from six localities. The race is restricted on the north and northwest by the Rio Mayo, to the west by the Rio Cuchijaqui (and Presa Josepfa Ortiz), and to the south by the Rio Fuerte (and Presa Miguel Hidalgo). Extension eastward into the foothills of the Sierra Madres between the headwaters of the Rio Mayo and Rio Fuerte is presumed (Figs. 1, 4, and 5). The range of the race abuts those of Race- γ along the upper Rio Mayo, Race- α along the Rio Cuchijaqui, and Race- β along the upper Rio Fuerte. Contact with Race- α between the Rio Mayo and Rio Cuchijaqui is presumably along the Rio Tapelos. As mentioned above, hybrids are known between races α and δ from two localities of contact along the Rio Cuchijaqui.

Ecological distribution. The race is confined almost exclusively to short-tree forest habitats throughout its known range, except for disturbed areas within that forest which provide a definite scrub appearance. The animals are very abundant in soil types ranging from soft clay alluvium to loose soils with scattered small rock material. Again, the species is uncommon in riparian communities or agricultural areas. Within the former habitat, replacement by P. artus is very pronounced.

Perognathus goldmani-e

Karyotypic description. The diploid number is 54, the fundamental number is 54. The karyotype (Fig. 9) can be described as follows:

Group A: 1 pair of medium submetacentrics (designated A_2).

Group B: 1 pair of "rabbit-ear" acrocentrics.

Group C: 24 pairs of acrocentrics grading in size from large to small.

X: large submetacentric.

Y: small acrocentric.

Diagnosis. The karyotype is most similar to those of races γ and θ , but is distinguished by a higher diploid number, the single Group A autosome (A_2), and two additional Group C acrocentric pairs. The large submetacentric X-chromosome is the same as in races β , γ , and θ .

Geographic distribution. The race ($N=7$) is known only from two major localities (Tonichi and Moctezuma), both at the extreme northwestern edge of the species range in the middle Rio Yaqui and Rio Moctezuma valleys. Presumably the race as well as the species is restricted on the west by several small mountain ranges, and their characteristic desertscrub vegetation. The most effective barrier on the north is the Sierra de Nacozari (Findley 1967). The eastern extension of both the race and the species is undetermined

Fig. 9. Karyotype of Perognathus goldmani-race ε.
 Female. UA 15632. Ca. 1 mi. S. Tonichi (by rd.), Sonora,
 Mexico.

at present, and at least the species may enter Chihuahua following tributaries of the Rio Yaqui (i.e., Rio Harros and Rio Papagochic). Contact to the south with Race-y must lie between Tonichi and Presa Obregon. Here, the most effective barrier is probably the lack of continuous favorable habitat.

Ecological distribution. Unlike more typical situations to the south, P. goldmani in the Rio Yaqui basin is restricted to rocky slopes and rock-strewn pavements (Findley 1967) in which the vegetation is a mixture of desertscrub elements from the north and west and thornscrub elements from the south (Shreve and Wiggins 1964, Wright 1967). The region is placed within the Foothills of Sonora Section of the Sonoran Desert by Shreve (Shreve and Wiggins 1964). The presence of the desertscrub pocket mouse, P. penicillatus, in the more rock-free alluvial soils is perhaps a major factor for the shift in habitat by P. goldmani onto rocky slopes. Presumably the northern extension of the species is restricted by the loss of suitable habitat in the Sierra de Nacozari and north, as well as contact with the saxicolous xerophyllic pocket mouse, P. intermedius.

Perognathus goldmani- θ

Karyotypic description. The diploid number is 52, the fundamental number 54. The karyotype (Fig. 10) can be described as follows:

Fig. 10. Karyotype of Perognathus goldmani-race Θ .
 Male. UA 15907. 1 mi. N. Huachinera (by rd.), Sonora,
 Mexico.

Group A: 1 pair of medium submetacentrics (designated A_2) and 1 pair of large metacentrics (designated A_3).

Group B: 1 pair of "rabbit-ear" acrocentrics.

Group C: 22 pairs of acrocentrics grading in size from large to small.

X: large submetacentric.

Y: small acrocentric.

Diagnosis. The karyotype is nearly identical to that of Race- γ , having the same diploid number, fundamental number, and numbers of each group of autosomes, as well as the submetacentric X-chromosome. Distinction can be easily seen between the two races, however, by examination of the Group A bialleled elements. Race- θ has two pairs of obviously unequal size while Race- γ has two pairs of equal size. One of these elements (chromosome A_2) is shared by both races.

Geographic distribution. The meager sample ($N=2$) of the race was obtained from two localities, both near the Sonoran town of Huachinera in the extreme upper Rio Bavispe drainage (Fig. 1). These localities represent notable extensions (75 miles) in the range of P. goldmani and extend its range to include a drainage system previously unknown for the species (see map, Hall and Kelson 1959: 502, and discussion in Findley 1967). Both the race and the species proper are probably restricted to the Rio Bavispe

valley because of the surrounding high mountains to the east, south, and west, and general absence of suitable habitat outside the immediate valley floor. Race- θ may represent a geographic isolate of the species, as its habitat is not continuous throughout the Rio Bavispe valley. Contact with Race- ϵ to the southwest is, therefore, improbable.

Ecological distribution. At Huachinera, Race- θ was trapped within a Prosopis-Juniperus monosperma association on the pebbly soils of the river terrace. At Aribabi, the characteristic habitat is lower oak woodland within the broad, middle elevation valleys. Here, the fine sandy soil is continuously interrupted with abundant rock material scattered throughout the thin soil layer. At both localities the race was associated with the predominantly woodland and riparian species, Peromyscus boylei.

Perognathus goldmani is seemingly limited in this extreme northern part of its range by xeric communities and hence is restricted to riparian associations and the lower montane woodlands. The inhabitation of both higher elevations and their concomitant vegetation assemblages is typical for the more subtropical species of vertebrates which meet the desert in the northern parts of their range (Martin 1963).

Perognathus artus

Karyotypic description. A karyotype of the species has been presented elsewhere (Patton 1967a, Fig. 3). The diploid number is 54, the fundamental number 54. The chromosome complement (Fig. 11) can be designated as follows:

Group A: 1 pair of large submetacentrics (designated A_6).

Group B: 1 pair of "rabbit-ear" acrocentrics.

Group C: 24 pairs of acrocentrics grading in size from large to small.

X: large submetacentric.

Y: small acrocentric.

Diagnosis: The karyotype is very similar to those of all P. goldmani races, particularly Race- ϵ and the hypothetical ancestral arrangement. Two features of the P. artus karyotype, however, clearly distinguish it from any of the six P. goldmani complements: (1) the large submetacentric Group A autosome (A_6), and (2) the single pair of minute (dot) acrocentrics in Group C. No chromosomal variation has been recorded within the species ($N=43$ from seven localities).

Fig. 11. Karyotype of Perognathus artus. Male.
JLP 1028. East bank Rio Cuchijsqui, ca. 12 mi. E. Alamos,
(by rd.), Sonora, Mexico.

CHROMOSOME PHYLOGENY

The constancy of the fundamental number despite changes in diploid number within the P. goldmani complex of chromosome variants, strongly suggests a mechanism involving Robertsonian transformations (i.e., "fusions" and "dissociations"). Such a mechanism would involve changes in the number of centromeres present in each population karyotype, but would not alter the number of chromosome arms (or fundamental number). While there is general concurrence that the two processes, "fusion" and "dissociation", are not opposite equivalents, both are known to have occurred in natural populations of animals (White 1957, 1965; Wahrman and O'Brien 1956). Of the two choices, however, whole-arm translocations (=fusions) are generally considered most frequent since there are fewer obstacles present for their formation (i.e., for dissociations one must either account for a new centromere, or risk the formation of iso-chromosomes through the transverse division of the original centromere). The Robertsonian process of "centric fusion" is considered the most probable mechanism for explaining the present occurrence of four of the six chromosome races of P.

goldmani. This is based on the higher observed frequency in studies conducted to date (see general reviews of John and Lewis 1966, Patterson and Stone 1952, Wurster and Benirschke 1968), as well as greater relative ease in accomplishment. This assumption is supported by geographic distribution and population ecology of the races of P. goldmani. (see below).

Robertsonian fusions lead to a lowering of the diploid number with the concomitant formation of biarmed elements from previously uniarmed ones. Hence, the most ancestral karyotype would be one which possessed the highest diploid number and in which all chromosomes were acrocentric. In P. goldmani no race has an entirely acrocentric complement, but two races (β and ϵ) do possess only one biarmed pair. These races do, however, differ in fundamental number and diploid number (56-56 and 54-54, respectively). Since the other four races have the same fundamental number as Race- ϵ (54), this can be assumed to be the ancestral condition. Consequently, an ancestral type forming the initial step in the chromosome phylogeny, with a fundamental number of 54, would necessarily have a diploid number of 56 and an entire acrocentric autosomal complement. The ancestral condition is hypothetical for it has not been found in nature.

The phylogeny involving the formation of six chromosome races of P. goldmani from the hypothetical ancestral type is depicted in Fig. 12. Each race represents a single step transformation largely of a Robertsonian nature but also including two pericentric inversions. The submetacentric X-chromosome is considered ancestral for two reasons: (1) it is characteristic for all other members of the genus examined to date (17 species, Patton 1967a, b, unpublished data), and (2) the two most primitive races (β and ϵ) have the submetacentric element, and the most derived race (δ) has the acrocentric X.

Two lines of evolution branched from the hypothetical ancestor. The first led only to Race- β via a pericentric inversion in a small autosome (chromosome A_1)--hence the maintenance of the same diploid number (56) as the ancestral race but an increase of two in the fundamental number (54 to 56). The second branch ultimately produced all other known races through a series of four autosomal fusions and a pericentric inversion in the X-chromosome. Thus, Race- ϵ is a single step removed from the ancestral type as a result of one centric fusion to form the single medium submetacentric Group A pair (chromosome A_2), and so forth (consult Fig. 12).

Because of the presumed role of P. artus in the formation of the chromosomal variants of P. goldmani

Fig. 12. Diagrammatic chromosome phylogeny of the six chromosome races of P. goldmani.

The non-homologous chromosomes involved in the six transformations are numbered separately in the hypothetical ancestor. The karyotypic relationship of P. artus to the ancestral condition as well as to the races of P. goldmani is also shown. None of the transformations that occurred in the P. goldmani lineage are shared by P. artus.

Fig. 12. Diagrammatic chromosome phylogeny of the six chromosome races of *P. goldmani*.

(discussed below), the karyotypic affinity of the two species is of importance. Morphological and ecological relationship has already been discussed (Anderson 1964, and above). The striking chromosomal resemblance between them has also previously been commented on (Patton 1967a). Indeed, only a single fusion and a deletion of part of a small acrocentric autosome need be required to derive P. artus directly from the hypothetical ancestral P. goldmani arrangement (Fig. 12). Perognathus artus maintains the ancestral type X-chromosome and the same fundamental number of the hypothetical ancestor and the majority of the chromosome races of P. goldmani.

DISTRIBUTION PATTERNS

Under the present interpretation of the chromosome phylogeny, it is singularly evident from Fig. 1 that the two most ancestral races (β and ϵ) are located on the southern and northern margins, respectively, of the range of P. goldmani (excluding Race- θ , at the northeastern margin). Consequently, the interior regions are occupied by the progressively more derived races, γ , α , and δ . It is also apparent that beginning in the north with Race- ϵ , there is a sequential geographic positioning of the races to the south following exactly the path of chromosome evolution (i.e., to the south of Race- ϵ is Race- γ , one step from ϵ ; to the south of Race- γ is Race- α , again one step removed, and so forth). Therefore, the phylogenetic and geographic positions of the races are identical (compare Figs. 1 and 12). Each race borders not only on the one from which it arose, but also on the one to which it gave rise.

If one, however, were not to accept the phylogeny based on fusions, and instead maintained dissociations as the predominant mechanism, correlation between geography and phylogeny would not occur. In a dissociation interpretation the karyotypes displaying the highest diploid

number and number of acrocentrics would be considered derived, not ancestral. Therefore, races β and ϵ would be interpreted as the most karyotypically advanced races, and one could allow for the derivation of Race- β from ϵ Race- through a "fission" of chromosome A_2 and an inversion to form chromosome A_1 . Geographically, this interpretation seems least likely, for the two races are currently separated by some 200 miles and an intervening three races, not to mention the great differences in habitat preferences exhibited by the two forms (see above).

A phylogenetic hiatus (but not a geographical one) is present along the Rio Fuerte in northern Sinaloa where the derived races, α and δ , meet the ancestral Race- β . This situation can, however, be explained by the proposed phylogeny, since Race- β was derived from the hypothetical ancestor by a different path than the lineage which gave rise to the races geographically adjacent to it.

ECOLOGY AND POPULATION DYNAMICS OF CONTACT ZONES

In each area where two races are known to be contiguous, they are separated by water barriers of varying sizes, from broad, swift-flowing rivers, such as the Rio Fuerte, to smaller, now intermittently flowing streams, as the Rio Cuchijaqui. The zones of contact along these streams were examined at six localities (Figs. 4 and 5): at Navojoa and Presa Mocuzari on the Rio Mayo (between races γ and α); the Rio Cuchijaqui at 12 miles east and 20 miles south of Alamos and at Presa Josepha Ortiz (between races α and δ); and in the vicinity of Presa Miguel Hidalgo on the Rio Fuerte (between races δ and β). If the disturbed habitats on one or both sides of a river at a given locality can be excluded (since the disturbance is presumably due to the recent efforts by man), the habitat in terms of plant species composition and soil type is identical on both sides of rivers whose banks support different chromosome races of P. goldmani.

At all but two localities, most of the natural vegetation (i.e., thornscrub or short-tree forest, depending upon locality) has been removed, or severely altered, to considerable distances on either side of a given river. The

disturbances in these cases are predominantly from occupation, agriculture, or overgrazing. Consequently, at Navojoa, for example, relatively undisturbed thornscrub communities are found no closer to the Rio Mayo than two miles to the north or six miles to the south. Although a few P. goldmani can be trapped within such disturbed sites, along most of the length of each river large populations are not in immediate contact. The present distance separating adjacent chromosome races in most areas is, therefore, considerably greater than the actual width of a river at any given locality. Presumably, however, this was not true prior to recent occupation of the region by man.

Along numerous sections of the Rio Cuchijaqui, east and south of Alamos, no major disturbance factors are evident. Consequently, two localities on this stream (12 miles east and 20 miles south of Alamos) were examined in some detail to determine: (1) the actual width of separation of adjacent races, and the ecological factors determining this distance; (2) the amount of dispersal across the stream; and (3) the consequent results of dispersal in terms of the degree of gene exchange.

The Rio Cuchijaqui is now an intermittent stream, drying up along some stretches during late winter through June. During and after the rainy season (July through December) water flows continuously, and the stream varies

in width from four to twenty meters. One would suspect, therefore, that dispersal across the river in the dry season would be possible because of absence of water in some areas, if, indeed, its presence is a major factor prohibiting movement. However, trap records (involving 127 mice from three general contact localities along the Cuchijaqui) do not indicate that the presence of water acts as a barrier. At no localities have two races been trapped within the same trap line, regardless of the time of year or stream conditions. Since P. goldmani prefers the soft, sandy-clay soils within the more xeric aspects of the short-tree forest, the dry and rocky river bed devoid of any covering vegetation may be uninviting to movement. Moreover, if one examines the actual distribution of P. goldmani in the areas adjacent to the stream, the width of separation between racial populations is much greater than the width of the stream itself, and essentially encompasses the outside width of the riparian and full short-tree forest communities bordering the stream. As was noted previously, the sibling species, P. artus, displaces P. goldmani within both the riparian association and the more mesic, fully-developed short-tree forest.

Figure 13 illustrates diagrammatically the lateral extent of the major vegetation bands and the concomitant distribution and density of pocket mice collected within the

Fig. 13. Diagrammatic cross-section of the Rio Cuchijaqui and adjacent area at 12 miles east of Alamos, Sonora, Mexico.

Lateral extent of major habitats is indicated, as well as the distribution and density of *P. goldmani* and *P. artus* within these habitats. Letters indicate trap stations (20 traps per station set parallel to stream), and numbers refer to the sample size of the two species trapped at each station. Records were compiled for late January and late September, 1968.

habitats 12 miles east of Alamos at the Rio Cuchijaqui. This indicates the relative scarcity of P. goldmani within the riparian community, presumably because of ecological replacement by P. artus. As a consequence, therefore, the adjacent populations (and races) of P. goldmani at the locality are not only separated by approximately nine meters of stream bed, but by at least four to five times that width. This strongly suggests that the major factor limiting dispersal across the river is the presence of P. artus within the riparian and mesic short-tree forest communities, and not strictly the stream itself. Undoubtedly, however, such major rivers as the Rio Mayo and Rio Fuerte have played (and continue to play) more definite limiting roles as actual physiographic barriers than has the smaller Rio Cuchijaqui.

On the Rio Cuchijaqui where movement across the stream would be relatively easy, little if any dispersal apparently occurs. If the limitation to dispersal is imposed by competition with P. artus, by actual physiographic conditions, or both, racial dispersal is restricted and can be considered inconsequential. Each race is, therefore, maintained as a large monomorphic population circumscribed by distinct geographic boundaries.

Little can actually be stated at this time concerning the degree of gene flow between adjacent races. It would

appear that it is nearly nonexistent, since only three chromosomally hybrid individuals are recorded from a sample of 221 mice trapped within the contact zones. It must be concluded that, although adjacent races could exchange genes successfully, the situation is rare due to restrictions placed on sympatric contact by physiographic and ecological barriers.

MORPHOLOGICAL TRENDS

Five characters based on measurements from both the cranium (occipito-nasal length, mastoid breadth, and bullar length) and whole specimen (total length and length of hind foot) were analyzed for trends in geographic variation of external morphology within P. goldmani. These parameters were selected because they were considered diagnostic for the species by Anderson (1964) and because they exhibit maximal interpopulation but minimal intrapopulation variation. The data for the five measurements were based on the examination of 291 individuals from 44 localities. The general purpose of the analysis was to determine if phenotypic variation (in terms of shifts in direction or magnitude of clines) corresponded in any significant way to the present division of the species into chromosome races.

The coastal populations tend to show more variation than those of interior regions. Four of the five characters in the former area, but only one in the latter display clinal variation. All clines are expressed in terms of greater structural size in the more southern populations. The greater variation in coastal populations is understandable since the general habitat along the coast is much more

diversified than that of the interior. East-west clinal variation is slight, except in the south where all characters tend toward greater size in the more southeastern populations.

Large samples from contact situations between adjacent races are available from only three general areas: (1) the vicinity of Navojoa (between races γ and α); (2) the Rio Cuchijaqui at 17.5 and 20 miles south of Alamos (between races α and δ); and (3) the vicinity of Presa Ortiz and Presa Hidalgo near El Fuerte (between races α , δ , and β). Data from these adjacent populations are given in Tables 1 through 3.

Examination of the tables reveals no general significant changes in the expression of morphological characters across the major rivers. Slight changes are seen between adjacent populations near Navojoa (i.e., 2 and 6 miles north of Navojoa and 3.5 miles east of Tesia) in both total length and bullar length, but these may be due to the small sample sizes. On the Rio Cuchijaqui, a significant difference between races α and δ is seen in the length of the hind foot, and differences are recognizable in both total length and mostoid breadth, but these are not significant. Finally, near El Fuerte where three races, α , δ , and β , come together, significant differences are noted between races α and δ on one hand and β on the other in bullar length, with a slight but non-significant difference between races α and δ in total

Table 1. Summary of morphological characteristics of contiguous populations of races γ and α in the vicinity of Navojoa, Sonora, Mexico. Means are with 95 per cent confidence intervals ($\bar{s}_x \times t_{n-1}$); ranges are enclosed by parentheses; sample sizes are given for measurements in millimeters. Males and females are combined.

character	16 mi. N. Navojoa (γ)	2 and 6 mi. N. Navojoa (γ)	E. 3.5 mi. Tesia (α)	2.5, 3, and 5.3 mi. E. Navojoa (α)
total length	182.5 $\pm$ 5.7 (166-216) N=20	193.8 $\pm$ 6.6 (184-202) N=6	186.8 $\pm$ 6.3 (179-192) N=6	183.4 $\pm$ 5.9 (170-213) N=18
length of hind foot	24.7 $\pm$ 0.5 (23-27) N=23	25.3 $\pm$ 1.4 (23-27) N=6	25.2 $\pm$ 0.8 (24-26) N=6	24.5 $\pm$ 0.4 (23-26) N=21
occipito- nasal length	26.62 $\pm$ 0.41 (24.9-28.2) N=23	27.03 $\pm$ 0.38 (26.3-27.3) N=6	26.88 $\pm$ 0.46 (26.1-27.4) N=6	26.49 $\pm$ 0.43 (25.2-28.4) N=21
mastoid length	13.60 $\pm$ 0.18 (13.0-14.9) N=23	13.68 $\pm$ 0.22 (13.3-14.0) N=6	13.78 $\pm$ 0.36 (13.2-14.1) N=6	13.66 $\pm$ 0.20 (12.9-14.9) N=21
bullar length	6.77 $\pm$ 0.11 (6.3-7.4) N=23	6.95 $\pm$ 0.30 (6.6-7.3) N=6	6.50 $\pm$ 0.36 (6.1-6.9) N=6	6.72 $\pm$ 0.15 (6.3-7.5) N=21

Table 2. Summary of morphological characteristics of contiguous populations of races α and δ south of Alamos, Sonora, Mexico. See Table 1 for explanation.

character	17.5 mi. S. Alamos (west bank Rio Cuchijaqui) (α)	20 mi. S. Alamos (east bank Rio Cuchijaqui) (δ)
total length	194.3 $\pm$ 3.5 (175-208) N=26	190.6 $\pm$ 3.6 (185-205) N=12
length of hind foot	25.0 $\pm$ 0.2 (24-26) N=34	24.4 $\pm$ 0.3 (24-25) N=18
occipito- nasal length	26.45 $\pm$ 0.25 (25.0-27.7) N=32	26.30 $\pm$ 0.32 (25.2-27.4) N=18
mastoid length	13.63 $\pm$ 0.12 (12.9-14.2) N=32	13.45 $\pm$ 0.13 (13.0-13.9) N=18
bullar length	6.80 $\pm$ 0.11 (6.3-7.1) N=32	6.74 $\pm$ 0.11 (6.4-7.1) N=18

Table 3. Summary of morphological characteristics of contiguous populations of races α , δ , and β in the vicinity of El Fuerte, Sinaloa, Mexico. See Table 1 for explanation.

character	E. 13 and 15 mi. Hwy 15, 4 mi. S. Sonora-Sinaloa state line (α)	between Presa Ortiz and Presa Hidalgo* (δ)	vicinity of El Fuerte and Presa Hidalgo** (β)
total length	187.4 $\pm$ 4.7 (174-200) N=16	194.9 $\pm$ 4.1 (184-202) N=10	190.9 $\pm$ 5.3 (178-212) N=15
length of hind foot	25.0 $\pm$ 0.5 (23-27) N=20	25.3 $\pm$ 0.4 (24-26) N=16	24.6 $\pm$ 0.5 (23-26) N=16
occipito- nasal length	26.94 $\pm$ 0.41 (25.7-29.2) N=20	27.30 $\pm$ 0.39 (26.3-28.5) N=14	27.31 $\pm$ 0.18 (25.9-30.0) N=16
mastoid length	13.73 $\pm$ 0.16 (13.0-14.4) N=20	13.79 $\pm$ 0.18 (13.3-14.3) N=15	13.88 $\pm$ 0.21 (13.1-14.5) N=16
bullar length	6.81 $\pm$ 0.12 (6.3-7.2) N=20	6.70 $\pm$ 0.18 (6.2-7.3) N=15	7.08 $\pm$ 0.10 (6.7-7.3) N=16

* combined samples from 1 mi. E. Presa Ortiz, 5 mi. N. El Fuerte, and 1 mi. W. Presa Hidalgo

** combined samples from 5.4 mi. NE. El Fuerte and 1 mi. W. Presa Hidalgo

length. Other characters either demonstrate no difference, or slight clinal variation. In general, there is no correspondence between chromosomal change and morphological change.

The analysis of morphological features emphasizes two major factors. First, holomorphology is a different level of organization than the chromosomal level, and, as such, changes in either will not necessarily be correlative. Secondly, the expression of the phenotype is more strongly dependent on ecological factors than on gross chromosomal arrangements. The first point is best illustrated in studies of the chromosomal variants of the European shrew, Sorex araneus, where members of Type A and Type B are morphologically indistinguishable, but are ecologically distinct and behave as biological species (Meylan 1964, Ott 1968). The second point is understandable since differences in chromosomal complements between individuals or races will ordinarily affect directly only the fecundity and viability of hybrid offspring, not their phenotypes.

DISCUSSION

Both inter- and intrapopulation variation in chromosome complement have been described for a variety of mammalian species. A majority of these involve Robertsonian transformations (Matthey 1966a, b, c; Meylan 1964, 1965, 1967; Nadler 1964), but several systems have been described where presumed reciprocal translocations and pericentric inversions are predominant (Matthey 1966d, Shellhammer 1967, Patton and Dingman 1968). Most examples fitting either of the two categories involve the present arrangement of allopatric chromosome races, where each race is monomorphic (i.e., one homozygous for the original arrangement and the other for the derived condition), and where no populations with individuals of intermediate condition (i.e., heterozygous) are known. Although within P. goldmani a few (3) individuals from contact localities are known which are chromosomally intermediate between adjacent races, each race can be considered monomorphic and allopatric. Known physiographic and/or ecological barriers maintain contiguous allopatry of the races. Consequently, P. goldmani conforms to the standard circumstance of other species with allopatric chromosome races.

Chromosome and population data indicating allopatric conditions are obviously not compatible with a system of balanced or even transitional polymorphism within the species. Therefore, some authors (e.g., Nadler 1964) have considered the occurrence of monomorphic chromosome races as an intermediate evolutionary stage between a single population characterized by a balanced polymorphic system and that of two reproductively isolated (allopatric or sympatric) species with different karyotypes (e.g., Matthey 1964a, b, 1965a). The general concept is that upon division of an ancestral polymorphic population, heterozygotes are selected against and eliminated, leaving chromosomally distinct populations. It is, however, not necessarily true that initial stable polymorphisms be sources of new, specific monomorphisms. In numerous cases it is clear that stable polymorphism does not lead to monomorphisms in transit (Lewis and John 1963; John and Lewis 1966). Moreover, White (1965) has strongly defended the position that there is no need to pass through a stage of balanced polymorphism to arrive at allopatric or parapatric monomorphic chromosome races.

This point is of particular interest in interpreting the historical events and population dynamics which led to the formation and present distribution of chromosome races in P. goldmani. For example, it is difficult to conceive of

an initially large, continuous population polymorphic for four centric fusions and two pericentric inversions. Even more difficult to conceive is a force great enough to split the primitive population into six allopatric ones, and then, to permit selection of the proper homozygote in each to produce the current correspondence in both geography and phylogeny of the races. A much more logical interpretation is that of White (1965) which is not based on an ancestral widespread condition of balanced polymorphism, or even such a system at each level in the phylogeny corresponding to each new chromosomal transformation.

If these arguments are applied to the evolution of P. goldmani, two basic and different models can be proposed as mechanisms allowing for chromosomal change: a stasipatric and an allopatric model.

The stasipatric model of White et al. (1967) and White (1968) was proposed initially to explain the apparent direct conversion of an essentially continuous population of morabine grasshoppers into a number of parapatric chromosome races. This is a very similar situation to the present contiguous races in P. goldmani. The inherent difficulties with the model have been discussed at length by Key (1968), and need not be covered in such detail here. The basic problems are two fold. First, strict allopatric interpretations can be applied to White's data and hence formulation

of a new model (stasipatry) is not necessitated. Second, only the peripheral model (White 1968: 1068, Fig. 2C), wherein new chromosome arrangements become established by chance in small, isolated colonies, is possible for species, such as P. goldmani, not characterized by low vagility and highly specialized ecological requirements. Therefore, the only real difference between a stasipatric model and an allopatric one, as applied to P. goldmani, is that in the former the new arrangement spreads inward through the existing species range displacing the original arrangement, not outward into previously unoccupied territory.

There are, nevertheless, several difficulties in the application of the restricted stasipatric interpretation to the present problem. First, the model requires that each new chromosome arrangement move into the interior of the species range, displacing the old. However, there is evidence that the geographic and ecologic position of at least Race- θ represents a distal expansion of the total range of P. goldmani, not an encroachment on that of its parent, Race- ϵ . The habitat occupied by Race- θ is unique for the species, and therefore would seem to represent one that was invaded rather than one in which the species has always been present.

Second, tension zones between adjacent races, a basic tenet of White's model, are not found in the present

case, unless the rivers separating the four southern races are considered convenient barriers to a continual tension zone.

Third, it seems difficult to rationalize under the stasipatric model that each new arrangement provides for greater adaptation to an already stable environment. If, indeed, the environment were not stable, but continuously changing, the model would not take into consideration the effects on the distribution of P. goldmani by extraspecific ecological factors, such as competitive species. Therefore, the stasipatric model really considers only the intraspecific genetic relationships, and neglects ecological conditions which would be expected to exert pressures on the species. Ecological conditions, in combination with the internal genetic systems of the species, is a more realistic mechanism for both causing and allowing chromosomal change. In my opinion this approach is satisfied by an allopatric concept, not by a stasipatric one.

Under the allopatric interpretation, one must consider a disjunction in the ancestral population to allow for the formation and consequent reinvasion of new chromosomal types into the present center of the species range. Race- θ could be derived without necessitating an original disjunction by budding from Race- ϵ at the northeastern periphery, but races γ , α , and δ could not (consult

Fig. 1). The latter races, located in the interior of the species range, could have occupied these areas under an allopatric scheme only if the central area were once devoid, or nearly so, of the species due to disjunction of the ancestral population. The crux of the allopatric model is, therefore, evidence for such an initial disjunction.

Any mechanism for the disjunction of an ancestral population of P. goldmani necessarily involves spatial changes of biotic communities. For a complete displacement of the species within the area, one must assume climatic vicissitudes of sufficient magnitude to displace oak woodland communities from the Sierra Madre Occidental to the coast, a downward vertical shift of more than 600 meters and a westward horizontal shift of some 110 kilometers. Although there is some evidence to indicate shifts in floral and faunal distributions in the area of the Sonoran Desert because of climatic changes of the Late Pleistocene (Martin 1963; Martin and Mehringer 1965), data is presently not available to even suggest the impact of pluvial conditions on the phytogeography of the region in question, much less to consider vegetation changes of the required magnitude. Moreover, zoogeographic data (Burt 1938) do not indicate the presence of major faunal breaks through the region, as may be expected with such drastic climatic and vegetation changes.

An alternative solution involving less dramatic climatic changes appears more feasible, for although vegetation shifts are still necessitated, they would be of a reasonably low magnitude. This alternative visualizes a spatial spreading of the chromosomal variants of P. goldmani in response to both vegetation (community) changes and interspecific competition pressures. The major force creating the split in the original P. goldmani population would be competition by the sibling species, P. artus, which even now actively restricts dispersal of P. goldmani. The changes in distribution of both species with the concomitant formation of chromosome races in P. goldmani is illustrated in Fig. 14.

As discussed above, P. artus is restricted to mesic riparian and fully-developed short-tree forest communities in areas of contact with P. goldmani. Under these circumstances, climatic changes during the Late Pleistocene need only be great enough to allow westward expansion of the rich tropical deciduous forest, from its present position close to the base of the Sierra Madres, toward the coast between the lower Rio Yaqui and Rio Fuerte river valleys. An accompanying expansion of riparian communities along the major river courses would also occur. As a consequence, the present ecological position of P. goldmani and P. artus was reversed, with P. artus widespread

Fig. 14. Allopatric interpretation for the origin of the chromosome races of P. goldmani.

(A) Distribution of P. goldmani and P. artus during pre-pluvial period (early Wisconsin); (B and C) distributional changes during full pluvial; (D and E) post-pluvial changes leading to the present (F) distributions of the species. Map A is based on the present ranges (F) of the species as mapped by Anderson (1964).

Fig. 14. Allopatric interpretation for the origin of the chromosome races of *P. goldmani*.

throughout the area and P. goldmani limited to highly disjunct, small populations restricted to the more arid habitats along the coast. Indeed, examination of the present range of P. artus (Fig. 14F) shows that the species need only extend its range a few miles westward from the vicinity of Navojoa, Sonora, to effectively divide the range of P. goldmani. The range of P. artus may even have extended farther to the west just a few decades ago, prior to the destruction of its riparian habitat along the lower Rio Mayo by man.

The initial ancestral distribution for P. artus and P. goldmani (Fig. 14A) can be interpreted from the present geographic relationships of the two species. Westward expansion of P. artus during a time of increasingly moist conditions forced the retreat of P. goldmani into two essentially disjunct populations: to the north into the middle Rio Yaqui valley and to the south into northwestern Sinaloa along the coast. The chromosome arrangements presently represented by races β and ϵ thus arose by budding from the ancestral population as the species shifted its range because of competition by P. artus during a period of climatic and accompanying vegetation changes. The end result was the elimination of the ancestral karyotype.

Race- θ probably arose from Race- ϵ at a time when the major vegetation assemblages of the middle and upper

Rio Yaqui drainage had a more subtropical thornscrub aspect (i.e., at the height of the Wisconsin Glacial Stage, or corresponding pluvial period). The present distribution of Race- θ in the lower montane woodland and riparian habitats of the upper Rio Bavispe indicates a more recent restriction of the ecological range of the species (and race) since the Pleistocene. This is compatible with the proposed changes toward more xeric conditions in the area at the end of the pluvial period (Martin 1963).

The return of more arid conditions to the area of northwestern Mexico gradually revised the direction of plant community change initiated at the beginning of pluvial times, and hence the ecological position of P. artus and P. goldmani. The former, more mesic adapted species, was forced to retreat into narrowing riparian communities and restricted full short-tree forest in an eastward as well as southeastward direction. Reinvasion by P. goldmani (Figs. 13C, D, and E) was possible only from the north (Race- ϵ or a derivative). Dispersal northward from the south by Race- β was halted by the Rio Fuerte (by far the largest of the rivers acting as physiographic barriers), and also because P. artus was retreating against Race- β from the north. In other words, the last areas to be vacated by P. artus were those on the north bank of the Rio Fuerte, and even today the species is very abundant in the eastern end of the Rio Fuerte valley within the present ranges of

races δ and β . Southern expansion of P. goldmani was presumably in waves, as each of the westward flowing rivers afforded at least temporary barriers to continuous movement.

The proposed chronological vegetation and consequent population changes within P. goldmani (both in direction and extent) are based on the pattern of phylogeny and present distribution of the chromosome races. As the species re-invaded the area between the lower Rio Yaqui and the Rio Fuerte, new chromosomal arrangements arose and became widespread between the geographic limits provided by the major rivers. That is, Race- γ arose from Race- ϵ and invaded the area between the lower Rio Yaqui and the Rio Mayo; Race- α was derived from Race- γ and occupied the coast from the Rio Mayo south to the Rio Fuerte and east as far as the Rio Cuchijaqui; and finally, Race- δ arose from Race- α and invaded the last widespread refuge of P. artus, the area between the Rio Cuchijaqui and the Rio Fuerte. One is tempted to say that the new chromosomal arrangements were necessary to enable reinvasion of the species into the area. Unfortunately, one can, at the moment, only speculate on the adaptive significance of the different chromosome combinations and of their possible role in phylogenetic divergence. In some instances, rearrangements have been shown to alter chiasma frequency as well as recombination, thereby exerting a direct genetic effect on evolution

(White 1968). In other examples, however, such rearrangements apparently have had minimal effect and only serve as a morphological marker indicative of the direction taken by evolution.

Homozygous chromosomal differences between populations of the same species indicate that each new population began with a few individuals and that the new genetic combination was favored by selection (Wallace 1959). Selection expressed in terms of fast and close inbreeding would lead rapidly to homozygous demes, if homozygosity were necessary to maintain the new genetic integrity of the population (Carson 1965a). Such significant genetic changes (both the initial formation of a new arrangement, and its subsequent fixation) would occur most readily in small, peripheral populations (Carson 1959, 1965b; Wright 1960).

The presence of rivers as both physiographic and ecologic barriers presumably played the same significant role in the past as today. They allowed the fixation of a constellation of genes (or new chromosomal arrangements) suitable to meet the selective demands on the small, peripheral populations of P. goldmani on one side of a river. Moreover, they enabled maintenance of the selected combinations so that their efficiency would not be impaired by continual recombination with genes (or arrangements)

entering the population from the other side of the river. Each new chromosomal rearrangement, providing for reduced recombination, could therefore allow the further spread of the species range as long as the disruptive migration from the other populations was held at a minimum. As already noted, the predominant mechanism of chromosomal change in P. goldmani is centric fusions. Such a mechanism cannot itself serve as an effective chromosomal isolating barrier between adjacent races since a fusion heterozygote produces only balanced gametes and will, therefore, suffer no loss of viability or fertility. The presence of rivers have aided not only the formation of new chromosomal combinations, but also the initial selection and continued maintenance of the genetic integrity of each new race as it became established. Possibly it was this genetic integrity which permitted the expansion of P. goldmani during a period of habitat changes and in the face of progressively stronger competition by P. artus.

Interpretation of the origin and spread of the chromosomal variants of P. goldmani in response to vegetation changes and competition pressures are certainly in accord with the theoretical grounds established by Wright and exemplified by Mayr (1963), Carson (1965a), and others.

SPECIMENS EXAMINED

Localities are listed separately for each race of P. goldmani, first by state, and then by geographic position within each state from north to south. Localities for races α , β , γ , and δ , as listed, are mapped separately in Figs. 4 and 5; no individual localities for races ϵ and θ are mapped. Numbers prefixed by UA represent specimens (skin and skull or skeleton only) deposited in the collection of mammals, Department of Biological Sciences, The University of Arizona, Tucson. Numbers prefixed by JLP represent specimens (skin and skull, skeleton only, or fluid preserved) numbered in the author's personal field catalogue.

Perognathus goldmani- α

Total, 174. Sonora: 3.5 mi E Tesia (UA 16804-09, JLP 854-57); Rio Mayo, Navojoa (UA 15200); 2.5 mi E Navojoa (UA 15614-25, UA 15910); 3 mi E Navojoa (UA 15194-96); 5.3 mi E Navojoa (UA 15210-12, UA 15626-27); 10.2 mi E Navojoa (UA 15176-77); south bank Rio Mayo at Presa Mocuzari (JLP 1692-95); 11.2 mi W Alamos (UA 11607); 11.5 mi W Alamos (UA 11509, UA 12972, UA 12991); 7.0 mi W Alamos (UA 11508, UA 12962-63); 5.0 mi W Alamos (UA 10536-40, UA 10846, UA 11502, UA 11552-54, UA 11599, UA 10604-05, UA 12993); 5.2

mi E Alamos (UA 11600, UA 11606, UA 12974-75, UA 12992); west bank Rio Cuchijaqui, 12 mi E Alamos (JLP 1035, JLP 1615, JLP 1717-1719); Rio Cuchijaqui, 8 mi S Alamos (UA 14112); 17.5 mi S Alamos, west bank Rio Cuchijaqui (JLP 1634-40, JLP 1642-69); base of Cerro Masiaca, 1.5 mi N Masiaca on Hwy 15 (UA 15629-30). Sinaloa: 4 mi S Sonora-Sinaloa state line on Hwy 15, 8 mi E (UA 16810, JLP 860-869, JLP 871); 4 mi S Sonora-Sinaloa state line on Hwy 15, 13 mi E (UA 16811-12, JLP 872-885, JLP 889-890); 4 mi S Sonora-Sinaloa state line on Hwy 15, 15 mi E (UA 16813-21); 10 mi S Tapizuelos (Sonora) (JLP 977); 15 mi S Tapizuelos (Sonora) (JLP 978-989); north bank Rio Fuerte at Hwy 15 (JLP 1016-20).

Perognathus goldmani- β

Total, 36. Sinaloa: Rio Choix, 3 km NE Choix (JLP 998-1004, JLP 1006-07); south bank Rio Fuerte, ca 1 mi W Presa Miguel Hidalgo (JLP 992-94); 5.4 mi NE El Fuerte (UA 12952-58, UA 12968-71, UA 15931, JLP 1090); 21.9 mi NE San Blas (UA 12973); 11.8 mi NE San Blas (UA 12959-60, UA 12966-67); 3 mi E Verdura (UA 11442, UA 11555, UA 11601-03).

Perognathus goldmani- γ

Total, 44. Sonora: Presa Alvaro Obregon (UA 14403, UA 15190-92); 16 mi N Navojoa on Hwy 15 (UA 15591-98, UA 15600-08, UA 15613, UA 15901, UA 15911-15); 6 mi N Navojoa

on Hwy 15 (UA 15609-12, UA 15903); 2 mi N Navojoa on Hwy 15 (UA 15909); north bank Rio Mayo at Presa Mocuzari (JLP 1696-1704); 6 mi SE Tepahui (JLP 1027).

Perognathus goldmani-6

Total, 53. Sonora: south bank Rio Mayo at Las Panelas (JLP 1040-1045); east bank Rio Cuchijaqui, 12 mi E Alamos (JLP 1030, JLP 1033, JLP 1631, JLP 1633, JLP 1623, JLP 1625, JLP 1628, JLP 1720-22); east bank Rio Cuchijaqui, 20 mi S Alamos (JLP 1670-73, JLP 1675-91). Sinaloa: 1 mi E Presa Josepfa Ortiz (JLP 1705-09, JLP 1711, JLP 1713-16); 5 mi N El Fuerte (UA 15173-75, UA 15631); north bank Rio Fuerte, ca 1 mi W Presa Miguel Hidalgo (JLP 990-91).

Perognathus goldmani α x δ hybrids

Total, 3. Sonora: east bank Rio Cuchijaqui, 20 mi S Alamos (JLP 1674). Sinaloa: 1 mi E Presa Josepfa Ortiz (JLP 1710, JLP 1712).

Perognathus goldmani-6

Total, 7. Sonora: 2 mi E Moctezuma (JLP 910, JLP 912); 3.5 mi S Moctezuma (UA 16822); 4.5 mi S Moctezuma (UA 15181-82); 1 mi S Tonichi (UA 15632-33).

Perognathus goldmani-0

Total, 2. Sonora: 1 mi W Aribabi (UA 15908); 1 mi N Huachinera (UA 15907).

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