Chromosomes, Speciation, and Evolution of Mexican Iguanid Lizards

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Reprinted from: National Geographic Society Research Reports, Volume 12, pages 309-329

Washington, D. C.
1980

Chromosomes, Speciation, and Evolution of Mexican Iguanid Lizards

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Grant Nos. 864 and 957. For study of the biogeography of karyotype variation in the iguanid lizard (1970) and comparative population cytogenetics and evolutionary roles of vertebrate genetic systems (1971).

Background

Many evolutionary biologists have believed for a long time, almost as a dogma, that essentially all animal speciation is initiated by the separation of ancestral species into geographically isolated subdivisions, and that only if these subdivisions are isolated long enough to evolve incipient reproductive isolating mechanisms will they remain evolutionarily independent species if they come into secondary contact (Mayr, 1942, 1963, 1970). Bush (1975) and White (1968, 1978) among others, however, have asserted and have fairly convincingly shown in their recent major works that there are probably a variety of qualitatively different modes of speciation, at least for animals with relatively limited dispersal abilities. Less convincingly, they claim that geographic isolation may be involved as an initiating factor in only a small fraction of all speciation events. My research on Mexican iguanid lizards represents an attempt to reconstruct in detail speciation patterns for this one group of vertebrates; such a study should provide some solid statistical evidence relative to this controversy.

The revolutionary difference in the views of the two groups of biologists cited above probably results from the different scientific paradigms (Kuhn, 1970) followed by each, and this difference needs to be understood before the approach followed by my research can be assessed. One paradigm (oversimplified), begins with a hypothetical model of species formation which is then tested by finding cases that fit it and by demonstrating that the model rarely can be disproved as a plausible explanation for any case. Since the formation of

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most species can be plausibly accounted for by models involving geographic isolation and since it is very difficult to prove that an alternative explanation must apply to any given case, it has been accepted by workers following this paradigm that most speciation is geographic. The other paradigm is based on the still poorly understood and nowhere explicitly formulated paradigm of comparative biology (Ghiselin, 1969, 1977; Hull, 1973, 1974; Platnick and Gaffney, 1978; see also Salmon, 1967; Skyrms, 1975). Briefly (and also oversimplified) this paradigm begins with the assumptions that each process resulting in speciation is a unique and unrepeatable sequence of events, but that there are probably only a relatively few (but possibly more than one) underlying stochastic mechanisms, or "natural laws," involved. The methodology followed is then: (1) to survey nature to see if distinctive modes of correlated phenomena can be found among the totality of those potentially related to speciation; (2) to develop as many different hypotheses as seem reasonable to explain each of the modes of correlation; and (3) to develop a better understanding of the actual reality of speciation processes by attempting to falsify, at least in a statistical sense, assumptions, logic, and/or predictions of one or more of the hypotheses offered to explain given modes. When the comparative paradigm is used for studying evolutionarily closely related organisms, it gains utility and power from the fact that many extraneous variables can be controlled or kept constant because the species are genetically similar, and much of their biology and history is shared. Properly selected "natural experiments" should vary primarily in the phenomena of interest.

The lizard family Iguanidae has been stable in its definition and content of genera at least since the time of Cope (1900), and there is no reason to believe that it is anything but a monophyletic grouping of species (Paull et al., 1976). With about 50 genera and probably more than 600 species, the family offers a rich resource for comparative biology. The North American segment of the family offers about 14 well-known genera (depending on the taxonomist), which include 130 named species. All but 22 of these belong to a natural group of 9 closely related genera that form the sceloporine division of the family (Etheridge, 1964; Presch, 1969; Hall, 1973; Paull et al., 1976). In the sceloporine radiation *Sceloporus* is probably the most recently derived, yet it includes 64 named species with an actual count that I believe to be at least 75. No other iguanid genus endemic to North America includes more than 14 species by anyone's taxonomy (Paull et al., 1976).

My undergraduate advisor, Don Hunsaker II, pointed out this situation to me and suggested that it would be a good research problem to try to explain why the phylogenetically recent *Sceloporus* have proliferated a vast array of species over a phylogenetically short time when compared with the other 8 relat-

ed, and probably older, sceloporine genera, all of which have few species. From results obtained in an undergraduate cytogenetics course project, I found that *Sceloporus* appeared to be chromosomally more variable than other iguanid genera (Painter, 1921; Matthey, 1931; Cavazos, 1951; Schroeder, 1962; Zeff, 1962). It occurred to me that the phenomena of possibly unusual chromosomal variability and anomalously prolific speciation in *Sceloporus* might be causally related, and that the excess number of species might have resulted from the fact that the genetic system of *Sceloporus* allowed alternative modes of speciation not possible for the related genera (Hall, 1963). My initial explorations in the southwestern United States and adjacent Mexico to test the correlation convinced me that the concentration of chromosomal variation in *Sceloporus* was probably real (Hall, 1965). For my Master's degree work under Ralph W. Axtell, I explored the sceloporine radiation for recent cases of anomalously rapid speciation and/or chromosomal differentiation not associated with speciation, and for appropriate controls for any such cases. Partially supported by Society Sigma Xi funds in 1966 and the National Science Foundation (grant to the Evolutionary Biology Committee at Harvard) and Sigma Xi in 1968, I further confirmed the concentration of chromosomal diversity in *Sceloporus* and its absence in the other sceloporines. As a Ph.D. student at Harvard University under Ernest E. Williams, in the 1968 field season I finally located a case of chromosomal variation of the kind normally fixed between species in what was believed to be a single species, *Sceloporus grammicus*. I then requested support from the National Geographic Society for detailed studies of the chromosomal variability and other aspects of the biology of *Sceloporus grammicus* and for comparative studies of other sceloporine species.

The most important goals of the expeditions supported by the Society were: (1) to document the nature of the chromosomal variability both within and between populations in the *grammicus* complex, (2) to do control studies on presumably chromosomally invariant relatives, and (3) to determine the genetic interactions of chromosomally different populations meeting in geographic contacts. Subsidiary, but essential, goals were to learn as much as possible about the cytogenetics and other aspects of the biologies of the other sceloporines so the various factors involved in the origin of the other species could also be reconstructed.

Methodology and Material Examined

After colchicine pretreatment of the whole animal, karyotypes were determined by direct cell suspension methods similar to those of Evans et al. (1964) and Patton (1967). Testis, bone marrow, spleen, and the mucosal

epithelium of intestine were all used as sources of dividing cells. To have rapid feedback for directing collection efforts, most chromosome preparations were made and initially scored in Mexico, working with portable laboratory facilities set up either in motels close to collecting areas or in available laboratory space. Lic. Ticul Alvarez S. of the Escuela Nacional de Ciencias Biologicas of the Instituto Politecnico Nacional in Mexico City and Dr. Rene Millon of the Teotihuacán Mapping Project in San Juan Teotihuacán, both kindly provided laboratory space in close proximity to the most important study areas. Most karyotyped specimens were preserved and are entered in the herpetological collection of the Museum of Comparative Zoology, along with several hundred additional specimens collected but not karyotyped, thereby adding significantly to the reference collections for Mexican herpetology. Methods of tissue preparation—starch-gel electrophoresis, and protein staining used in allozyme analyses (Hall and Selander, 1973)—were similar to those of Selander et al. (1971), as modified for lizards by Webster et al. (1972) and McKinney et al. (1972).

During the 2 years of National Geographic Society support, collections were made in all states of Mexico north of the Isthmus of Tehuantepec, except Aguascalientes. In 1970 I was in the field from June 19 through October 16, assisted through mid-September by Scott M. Moody, who then returned to classes. He was replaced by Timothy Dickinson, a part-time curatorial assistant from the Museum of Comparative Zoology herpetology department. Moody, a Harvard undergraduate, developed his Honors Thesis (Moody, 1971) from materials and observations he collected during the expedition. Most work in 1970 focused on northern and western parts of the Mexican Plateau and on the contacts between the P1 and F6 populations of *Sceloporus grammicus* along the eastern divide of the Valley of Mexico. Moody and I roughly determined the nature and geography of the P1 × F6 contact by spot sampling. Then, with the aid of Ticul Alvarez and some of his students, we surveyed a 600-meter-long transect across the hybrid zone and collected a large series of individuals whose collection localities were recorded accurately to the nearest 2 meters. These were karyotyped in Mexico and immediately frozen on dry ice for transport to Robert Selander's laboratory at the University of Texas where they were electrophoresed. Chromosomal and electrophoretic markers were then used to reconstruct the dynamics of the hybridization known to occur in the contact zone. In 1971 I made one solo trip, from March 21 through May 10, to northern Baja California to collect chromosomally primitive sceloporines, down along the west coast of Mexico via Guadalajara to collect a primitive relative of the *grammicus* complex, and then to the Valley of Mexico to make behavioral observations on *grammicus* populations in the area of the

previous year's transects. During the summer I was in the field from June 24 through October 5, assisted by Harvard undergraduates R. B. Stamm and Seth Reichlin. Most work during this period focused on the eastern and southern parts of the Mexican Plateau and on the contact between the S and FM2 populations in the Teotihuacán Archeological Zone. In the Teotihuacán study we were very greatly assisted by the availability of the 1:6000 base map of the Archeological Zone prepared by the Teotihuacán Mapping Project, kindly provided by Dr. Rene Millon (see Millon, 1970).

During the 2 years of the project, over 900 individuals of the *Sceloporus grammicus* complex and about 500 of other species were karyotyped. These, along with specimens from earlier collections, bring the karyotypic data for analysis to about 1,250 individual *grammicus* and over 1,000 individuals of all other species combined. The papers by Cole (1970; 1971a,b; 1972) and his colleagues (Cole and Lowe, 1968; Cole et al., 1967), and by Pennock et al. (1969), and Gorman (1973) among others, add data on perhaps another 300-400 individual sceloporines. Altogether, 57 of the 75 *Sceloporus* species I currently recognize have been karyotyped, and all but 3 of these are represented in my own karyology collection. Also, 30 of the other 44 sceloporine species have been karyotyped.

These data, combined with other biological observations, distributional data, and information from the massive literature on the biology and systematics of sceloporines allow the phylogenetic history of most of the genera to be reconstructed well enough to enable mechanisms to be ascribed to a large proportion of at least the last rounds of speciation events. Unfortunately though, due to a 4-year delay caused by the conflicting demands of my employment, only a few papers have yet been published on this synthesis (Hall and Selander, 1973; Smith and Hall, 1974; Dassmann and Smith, 1974; Paull et al., 1976; Hall and Smith, 1978), and some aspects of the data reduction are still incomplete. However, several papers that will present the major findings of the research are currently in active preparation, and the results of these are summarized here in preliminary form.

Results

1. With over 50 percent of the species in each of the 9 sceloporine genera karyotyped, no genus other than *Sceloporus* shows interspecific differences in karyotypes—all species are characterized by closely similar $2n = 34$, xy♂ patterns. Most speciation outside of *Sceloporus* itself can plausibly be associated with evident Pliocene and Pleistocene ecological or geographic barriers (e.g., Norris, 1958; Morafka, 1977). No sceloporine genus other than *Sceloporus* includes more than 14 species.

2. All sceloporines except the primitive *Petrosaurus* (Etheridge, 1964; Presch, 1969) derive from a common ancestral species which had evolved a suite of skeletal, nasal, and behavioral features which enabled individuals to submerge themselves in loose sand for sleeping and escape cover—a suite of characters which would probably be selectively favored only in sandy desert conditions. This implies that differentiation of the various sceloporine genera from a *Petrosaurus*-like ancestor probably did not occur until the xeric adapted Madro Tertiary Geoflora became established in the Miocene (Axelrod, 1950).

3. As suggested by Smith (1939) *Sceloporus* divides into 2 major lineages, a small-sized, small-scaled branch and a large-sized, large-scaled branch. The small-scaled species are morphologically and (usually) chromosomally more conservative than the large-scaled species (Hall, in preparation). Of 16 small-scaled species, 11 are known or suspected on the basis of their relationships, to retain the primitive 2n = 34xy♂ karyotype. This radiation centers on the Chihuahuan desert; and, like the other sceloporine genera, most speciation in it is ascribable to evident ecological and geologic barriers.

4. The small-scaled species include at least 2 independent sequences of chromosomal derivation. One leads by a sequence of 6 centric fissions to the 2n = 46xy♂ *S. merriami*. It may involve only this species, although there is unconfirmed evidence that at least one population of *S. maculosus* may be karyotypically intermediate in the evolution of the *merriami* karyotype (Carol Axtell, unpublished). The other leads, by a sequence of centric fusions, to the 2n = 24xy♂ species *S. aeneus* and *S. scalaris*. The possibly recently extinct *S. goldmani* has not been karyotyped, but based on morphological relationships it could conceivably be karyotypically intermediate in the *scalaris* lineage. Both *merriami* and *scalaris* stocks are highly specialized. *S. merriami* live on vertical cliff faces and *scalaris, aeneus,* and *goldmani* are close or obligate commensals of bunch grass.

5. The large-scaled branch of *Sceloporus* includes only 4 species which retain the primitive 2n = 34xy♂ karyotype: *orcutti, hunsakeri, licki,* and *nelsoni* (Hall and Smith, 1978). These species are either restricted to Baja California or the Mexican mainland opposite the southern end of the Peninsula. These 4 large-scaled species are morphologically more closely related to the small-scaled species than are any of the other large-scaled species, and clearly represent direct survivors of the ancestral large-scaled stock. The stock appears to derive from portions of the small-scaled radiation still centered in the Chihuahuan desert. The separation of these 4 conservative species is most plausibly associated with the formation of the Gulf of California and the separation of the Cape Region of the Peninsula from the Mexican mainland some 5 million years ago by plate tectonic processes (Atwater, 1970; Anderson, 1971). All

the remaining 53 or more large-scaled species are chromosomally derived with regard to the ancestral karyotype. Two major sublineages trace from a common ancestor with a derived 2n = 32 xy♂ karyotype and include 52 of the 53 chromosomally derived large-scaled species.

6. One of these 2 branches evolved still lower chromosome numbers. Surviving species with intermediate karotypes retain 2n's of: 30 (*S. graciosus* and *S.* [*magister*] *zosteromus*), 29x_1x_2y♂ (*S.* [*magister*] *rufidorsum*), and 26 + pericentric inversion of chromosome pair 1 (the mainland *S. magister*). Twenty-three species are known or suspected by their close relationships to have 2n = 22 or even more derived karyotypes. I regard it highly significant: (a) that the entire sequence of chromosomal derivation seems to have been confined to a possibly short period of the Pliocene and to the area around the upper end of the Gulf of California, where there is no evidence for major geographic barriers; (b) that the chromosomally most derived forms have expanded geographically to cover the entire North American continent except Baja California and adjacent deserts still occupied by chromosomally more primitive relatives; and (c) that chromosomally different lineages are frequently sympatric while there is little sympatry among chromosomally similar stocks.

7. The 23 2n = 22 species form 2 distinctive species groups: the northern egg-layers (egg-laying is a primitive trait) with 10 species, and the southern live-bearers (a derived trait), with about 13 species. Speciation in the egg-players is easily ascribable to isolation in refugia during Pleistocene glacial periods. Too little is known about the southern live-bearers to even allow an accurate determination of the number of species the group includes. It is interesting, however, that the live-bearers include at least 2 pairs of syntopic siblings (*S. formosus* and *cryptus*, and *formosus* and *adleri*) which show no obvious chromosomal differences.

8. The second major branch of lineages deriving from the 2n = 32xy♂ stock includes many species which still retain a 2n = 32 in females but have evolved a 2n = 31x_1x_2y♂. Evidently the common ancestor of this branch of lineages was also polymorphic for a great enlargement of chromosome pair 9 (the Em 9 mutation). This mutation appears to have been established as a polymorphism in the Pliocene. Two lineages trace back to the 2n = 32xy♂ polymorphic Em 9 stock, and both retain the Em 9 mutation, either still present as a polymorphism (!), or fixed in some species and lost in others.

9. The first lineage involves a sequence of 4 centric fissions leading to the 2n = 40xy♂ *S. clarki* and the 2n = 39x_1x_2y♂ *S. melanorhinus*. Both species are polymorphic for the Em 9 mutation. No intermediates in the fission sequence appear to survive. *Clarki* occupies the western drainage of the Sierra Madre Occidental, immediately adjacent to the Sonoran Desert at the head of

the Gulf of California, where it is believed that the ancestral 2n = 32 stock once lived, and ranges south to the Río Grande de Santiago. No geographic barriers are evident in its derivation. Although *clarki* and *melanorhinus* differ in their sex chromosomes, they are also presently separated geographically by the Río Grande de Santiago, which also separates several other pairs of closely related species. *S. melanorhinus* ranges south from this river to Guatemala.

10. The second lineage deriving from the 2n = xyo' polymorphic Em 9 stock includes only live-bearing species which have evolved a unique 2n = 31 male with an x_1x_2y sex chromosome system different from that of *S. melanorhinus*. Females retain the 2n = 32 karyotype. *S. asper,* the morphologically least specialized species in the radiation, is a tree lizard found at intermediate elevations in the western Sierra Volcánica Transversal. It is fixed for the Em 9 mutation. All the remaining species in the live-bearing lineage are specialized behaviorally and morphologically for using one or another form of crevice for cover: rocks, wood, or between the dried leaves of *Agave.*

11. The rock-crevice users include about 11 species (8 karyotyped) which occupy all rocky areas on the Mexican Plateau south to the Isthmus of Tehuantepec. One species *(S. serrifer),* secondarily a tree-crevice user, is found on the eastern coastal plain and extends as far as the Yucatán Peninsula. There is no evidence for chromosomal variation within any of the 8 rock-crevice users karyotyped; all are fixed for the ancestral condition of pair 9 and all have the 2n = $31x_1x_2yo'$ karyotype. All speciation can easily be accounted for by isolation of populations on "insular" outcroppings of rock in a "sea" of alluvium. Frequently 2 species are sympatric but they usually differ enough in size so that they probably exploit different sized crevices. Often the outcrops are small enough so that founder effects could potentially play important roles in speciation.

12. There is only 1 species of *Agave* crevice user, *S. megalepidurus,* as shown by finding clear intergrades in my 1971 collections (Dassmann and Smith, 1974). Its morphological distinctiveness suggests that it was an early derivative of the crevice-using radiation, but details of its origin are obscured by the apparently more recent radiation of the wood-crevice users of the *S. grammicus* species group. *S. megalepidurus* is fixed for the Em 9 mutation and has the 2n = $31x_1x_2yo'$ karyotype.

13. The wood-crevice users include at least 4 morphospecies: *S. shannonorum, S. heterolepis,* and 2 presently included in *S. grammicus grammicus* (the nomenclature is ambiguous because both morphospecies are included among the syntypes of *grammicus* Wiegmann 1828). Three of the morphospecies are restricted to intermediate elevations along the western and southern sides of the Mexican Plateau: *shannonorum*—limited to areas north of the Río Grande de

Santiago; *heterolepis*—limited to areas between the Río Grande de Santiago and the Río Balsas; and *S. grammicus grammicus* sensu Smith (1939) and Smith and Laufe (1945)—found south of the Balsas. The fourth morphospecies (Smith's *S. g. microlepidotus* and *S. g. disparilis* subspecies) occupies the remainder of the Plateau and parts of the Gulf of Mexico coastal plain. Speciation of the 3 western forms is clearly associated with the major ecological barriers formed by the valleys of the Río Grande de Santiago and the Río Balsas, which completely separate the present populations. If the fourth species is derived from a *shannonorum*-like ancestor, as I believe likely, although the species are now almost certainly in contact, it probably became separated during a Pleistocene glacial epoch by climatic barriers along the crest of the Sierra Madre Occidental. Except for the chromosomally derived populations of the *grammicus* complex, all species have $2n = 31x_1x_2y♂$ karyotypes. The Em 9 mutation may be established in *S. grammicus grammicus* sensu Smith, and it is clearly absent in all of the remaining crevice users.

14. The morphospecies formed by *S. grammicus microlepidotus* and *S. g. disparilis* is a complex of 7 geographically parapatric cytotypes, whose distributions bear little relationship to the formally named subspecies:

S (standard—retains the $2n = 31x_1x_2y♂$) must have originally ranged over the area of the Mexican Plateau not held by the other 3 wood-crevice-using species, before it was then geographically displaced from parts of this range by the chromosomally derived stocks.

F6 ($2n = 33x_1x_2y♂$, fixed for a fission of pair 6) ranges from the Nevado de Colima in Jalisco to central portions of the Sierra Volcánica Transversal. In the area of the Valley of Mexico, F6 is found above 2,400 meters on the south and west, and between 2,400 and 3,200 meters on the east. Presently disjunct populations of F6 are also found in relict mesic areas of the Sierra Madre Occidental in San Luis Potosí, Tamaulipas, and Nuevo León.

P1 ($2n = 31\text{-}33x_1x_2y♂$, polymorphic for a fission of pair 1) is found on the eastern divide of the Valley of Mexico from 3,200 meters elevation to the treeline at about 4,000 meters, for a total range of about 700 square kilometers.

F5 ($2n = 33x_1x_2y♂$, fixed for a fission of pair 5) occupies the northernmost portions of the Sierra Madre Occidental in Chihuahua.

F5+6 ($2n = 35x_1x_2y♂$, fixed for fissions of pairs 5 and 6) occupies the southern portions of the Chihuahuan Desert, the low-lying central portions of the Sierra Madre Occidental in the Río de Pánuco drainage, and the Gulf of Mexico coastal slopes and plain northward to the Lower Rio Grande Valley of Texas.

FM1 (2n = 39-43$x_1x_2y\sigma'$, fixed for fissions of pairs 2,4,5, and 6, polymorphic for fissions of pairs 1 and 3) is found in the northwest corner of Mexico state and central Hidalgo.

The seventh cytotype, *FM2* (2n = 43-45$x_1x_2y\sigma'$, fixed for fissions of pairs 1,2,4,5,6, and 14, polymorphic for a fission of pair 3) is found in southern Hidalgo and in the northeastern corner of Mexico state.

Given that *S. grammicus* populations appear to be able to use all available wood-crevice cover within their geographic ranges and that such cover is more or less continuously available over the whole of the Mexican Plateau except for extreme areas of the Chihuahuan Desert, there is no evidence that *grammicus* populations were fragmented by the interposition of geographic barriers of the magnitude associated with most other speciation events in the sceloporines.

15. Parapatric contacts probably exist between all *S. grammicus* populations with adjacent ranges, but sampling points outside of the Valley of Mexico are still too widely scattered to have precisely located any of them. Based on more than 73 cytological sampling localities, 5 different kinds of parapatric contacts are likely: S and F6—sample sites about 40 km apart; S and F5+6—sample sites, respectively, 15 and 50 km apart; F6 and F5+6—sample sites about 50 km apart; F5+6 and Fm1—sample sites about 60 km apart; and FM1 and FM2—sample sites about 60 km apart. Based on more than 82 cytological sampling sites in the Valley of Mexico area, 3 different kinds of geographic contacts were precisely located: several contacts between P1 and F6 on the east side of the Valley of Mexico, all within 200 meters elevation of the 3,200-meter contour; contacts between S and FM2 in the Valley of the Río San Juan (mainly in the Teotihuacán Archeological Zone), which appear to follow the contact between igneous hill slopes and alluvial bottomland; and one contact between S and F6 north of Cuernavaca at about 2,400 meters elevation. Chromosomal hybrids were found in all of these situations, but in no case were pure populations on either side of the hybrid zone separated by more than 2 kilometers. The P1 × F6 (1970) and S × FM2 (1971) contacts were studied in detail.

16. Several chromosome sample transects were established across the P1 × F6 contact in the Río Frio area (Hall and Selander, 1973; Hall and others, in preparation). These demonstrated that the chromosomal transition from one pure population to the other was probably no more than about 500 meters wide. Once the approximate distribution and structure of the hybrid zone was established by chromosomal sampling alone, a previously unsampled transect area (west of Cerro Potrero) was selected and accurately surveyed before 153 *S. grammicus* were collected from it for electrophoresis and karyology.

Populations away from the contact were also electrophoresed to give some idea of genic variation within allopatric P1 and F6 populations. The disjunct F6 population on the Nevado de Colima, 500 kilometers to the west, is genetically more similar to F6 populations in the Río Frio area than are P1 populations collected 3 kilometers of dispersal distance to the east of the F6 sample site. Aside from the fixed chromosomal difference between P1 and F6, 3 protein loci, out of the total of 20-21 sampled in the 2 Río Frio-area populations, were fixed for alternative alleles. In the Cerro Potrero transect 2 proteins and the fixed chromosomal difference were used as genetic markers to determine the dynamics of what was happening in the hybrid zone. I conclude from these observations that:

a. Pure parental types meet and hybridize, with very little indication that either cytotype discriminates against mating with the other. F_1 hybrids are found at about the frequency one would expect from random matings of the individuals present in a neighborhood population.

b. The high frequency of individuals with backcross genotypes (heterozygous for 1 or 2 markers but not all 3) shows conclusively that F_1's are at least partially fertile and that first generation backcrosses must also be sufficiently fertile to allow significant introgression beyond the first generation of backcrossing (Hall and others, in preparation—this contradicts one of the conclusions of Hall and Selander, 1973).

c. Very paradoxically, all other evidence indicates that the hybrid zone functions over a very short distance (<3 kilometers) as a complete block to gene flow between the 2 pure populations, despite the evidence for hybrid fertility, successful backcrossing, and "introgression":

(1) P1 and F6 samples 3 kilometers apart, separated only by the continuous population inhabiting the hybrid zone, are genetically more different than 2 F6 populations separated by 500 kilometers and a geographic barrier!

(2) When the genetic structure of the Cerro Potrero transect is analysed microgeographically, 90 percent of the replacement of the genetic markers for one population by the markers for the other population appears to take place over a distance of about 500 meters. This is not an unreasonable dispersal distance for single individuals between the mating of their parents and their own mating. A 100 percent replacement certainly occurs in less than 3 kilometers; and extrapolating from the gene frequency versus distance curve, it appears that the genetic change is probably complete over a distance of about 1,500 meters.

(3) The change in gene frequency versus distance from the center of the hybrid zone appears to be exactly symmetrical on either side.

(4) Despite comments by Hall and Selander (1973) to the contrary,

based on external morphology P1 is probably derived from F6 rather than the chromosomally-more-similar S, and there is no evidence to indicate that P1 and F6 were ever geographically separated, although it is likely that the contact zone changed in altitude along with climatic fluctuations.

17. Similar results on the dynamics of hybridization were obtained from the transect between S and FM2 in the Teotihuacán Archeological Zone, for what is almost a secondary contact situation involving the 2 terminal races in a circle of derivation from the ancestral condition to the most derived. Here 5 fixed macrochromosomal differences serve as markers for the dynamics of hybridization. However, due to the extreme wariness of the *S. grammicus* in this area, and possibly also due to differences in the population structure, we did not obtain a large sample of individuals from the hybrid zone itself. The total sample from the mapped area of the Archeological Zone (Millon, 1970) included 73 pure S, 52 pure FM2, 7 F_1 hybrids (5 were female), 1 backcross to S, and 5 or 6 backcrosses to FM2 (1 could have been an F_2). Additionally, 1 individual was a 3n backcross to FM2, with 1 haploid S genome plus 2 haploid FM2 genomes. Hybrids, backcrosses, and mixed samples from this zone were limited to a belt about 500 meters wide running north-northwest from a line of stone fences crossing the "Street of the Dead" south of the Pyramid of the Sun, where the pure FM2 population was restricted to the wedge-shaped area between this belt and the Street of the Dead. Following Millon (1970) and Mooser (1968), FM2 *grammicus* probably did not enter the Valley of San Juan Teotihuacán until the hill slopes above the ancient city were catastrophically deforested during the period A.D. 200-600. The Street of the Dead, which was cleared of cover suitable for *grammicus* around 1913, appears to serve as a recent, local geographic barrier to impede FM2 west of the street from contacting S individuals on the east side of the street.

18. Aside from the evidence that the S × FM2 hybrid zone involves both hybridization and backcrossing and yet serves as a complete barrier to gene flow, the excessive number of females among the hybrids (although the sample size is too small for the disproportion to be statistically significant) combined with the discovery of a triploid backcross in the hybrid zone (only 3 other triploids, all *S. grammicus,* were discovered among the more than 1,200 *grammicus* and more than 1,500 other iguanids karyotyped), suggest, but do not prove, that some of the F_1 hybrids may have been reproducing parthenogenetically. If so, it may be possible to duplicate the S × FM2 hybridization in the laboratory to observe the origin of parthenogenetically reproducing hybrid clones under controlled conditions.

19. Data on the details of meiosis in the many chromosomally heterozygous individuals collected remains to be extracted from the prepared slides. It

seems probable, however, that meiotic malassortment from fusion or fission trivalents contributes to reduce the reproductive fitness of chromosomally heterozygous individuals relative to homozygotes, as has been demonstrated in mice (Capanna, 1976; Capanna et al., 1976; Cattanach and Moseley, 1973).

Conclusions

Without attempting to detail the logic by which they are inferred from the results, I have reached the following conclusions based primarily on the data collected during the Society-funded expeditions:

1. There clearly are at least two distinct modes of speciation operative in the sceloporine radiation, each with strikingly different evolutionary consequences:

a. By far the most common mode of speciation appears to involve the classical mechanics of geographic separation of large populations for long periods of time by the interposition of geographical, climatic, or ecological barriers (Mayr, 1963). All speciation in 8 of 9 sceloporine genera appears most plausibly to be geographic, and even in the exceptionally speciose *Sceloporus,* about 60 of 75 species show no evidence of chromosomal differences from their nearest relatives. Also, in most species pairs lacking chromosomal differentiation there is positive evidence suggesting that speciation sequences involved geographic isolation. At least for sceloporine lizards, this contradicts the conclusions of White, Bush, and Endler, cited earlier, that the majority of speciation in terrestrial organisms of limited vagility does *not* involve classical geographic isolation. However, although most speciation in the sceloporines has involved geographic isolation, it is also quite clear that such speciation is associated with very slow rates of evolutionary change. Genera showing only evidence for geographic speciation contain comparatively few species and show little ecological diversity.

b. Although only about 15/75 species of *Sceloporus* differ chromosomally from their closest relatives, all but 17 *Sceloporus* have at least 1 event of chromosomal differentiation in their ancestries. Where sequences of chromosomal differentiation leading to these species can plausibly be reconstructed: (1) chromosomal differentiation appears to be directly associated with the establishment of genetic isolation between the chromosomally differentiated populations, (2) there is little or no evidence that this differentiation was associated with the interposition of geographic barriers of the magnitude evident in most speciation events not associated with chromosomal changes, and (3) the observations imply that chromosomally derived populations frequently shift enough ecologically in the process of derivation so that they are quickly (in an

evolutionary sense) able to coexist sympatrically with their ancestral stocks. Only in the very recent case of *S. grammicus,* where the chromosomal differentiation has occurred within an already highly specialized stock living in an environment where the surrounding habitat appears to be already saturated with other *Sceloporus* species, has such a shift not occurred. I regard it as highly significant: (1) that although most sceloporine species were evidently formed in geographic isolation, the great proliferations of species in *Sceloporus* all involved a history of chromosomal differentiation, and (2) that the unquestionably most widely distributed, successful, and most ecologically plastic lineage in the whole radiation (i.e., the radiation of $2n = 22$ species) is at the end of a long chain of chromosomal derivation.

From this I conclude that chromosomal speciation may occur without geographic isolation, either in a parapatric relationship as demonstrably seems to be the case in the *S. grammicus* complex, or possibly even in an initially sympatric relationship. Also competitive interactions between the initially small population of the nascent chromosomally differentiated species and its chromosomally conservative ancestral stock will frequently quickly force the derived species to differentiate enough ecologically to use previously underexploited limiting resources. Chromosomal speciation may be completed rapidly, and a linear sequence of such speciation events over short evolutionary times may result in great ecological shifts by comparison to the much more conservative mode of geographic speciation. Each chromosomal speciation event may, therefore, open to the derived lineage a new range of habitats that are sympatric to those used by the ancestral stock. Such forced differentiations will not occur in secondary contact situations between already widely distributed sibling species because competitive exclusion will prevent significant sympatry and because the great genetic inertia of the respective populations away from the areas of contact will slow evolutionary responses to local conditions.

2. The data from *Sceloporus grammicus* suggest a specific model for chromosomal speciation: All the observed chromosomal differences between species in *Sceloporus* have the potential for causing meiotic malassortment in chromosomal heterozygotes (for mechanical reasons), and thereby for reducing the reproductive fitness of chromosomally heterozygous individuals. Such mutations could never become fixed in a large randomly breeding population because selection against the much more frequent heterozygotes would quickly eliminate the initially rare rearrangement from the population. If, however, a species (due to its limited vagility in an environmental mosaic) has a population structure such that it is subdivided into a series of small demes (genetically effective sizes <10 individuals) with comparatively limited gene

flow between them (say <15 percent per generation), then there is a low, but evolutionarily reasonable, probability that such mutations may become fixed by random drift in a deme, despite even fairly strong selection against heterozygotes. If such a rearrangement becomes fixed, and further chance events allow the initially differentiated population to spread over a large enough area so that at least some of its individuals are geographically protected from the risk of hybridization with parental types by an intervening hybrid zone functioning like those demonstrated in the *grammicus* complex, then speciation in a genetic sense is already completed for the central population. For example, probably no P1 population is more than about 5 kilometers distant from the P1 × F6 hybrid zone, which is itself of the order of 500-1,000 meters wide; yet despite the complete absence of reproductive isolation between the 2 species in any classical sense, the P1 population has differentiated genetically to a greater extent than has a geographic isolate 500 kilometers away.

The key to such speciation lies in the dynamics of the genetic events in the zones of parapatric hybridization. If hybrid fitness is reduced for any reason (e.g., chromosomal heterozygosity): (a) A fraction of potentially introgressing genes will be lost in the first generation of hybridization because of more frequent than normal reproductive failures by the less fit hybrid individuals. (b) Also, because of reduced hybrid fitness, fewer individuals will be competing for limited resources in the hybrid zone by comparison to pure populations on either side of it, thus encouraging a net immigration of parental types from the pure populations into the hybrid zone that will result in a net gene flow *toward* the hybrid zone from each pure population. Such a flow will impede the diffusion of genes out of the hybrid zone. (c) Therefore, any genes surviving one passage through less fit hybrid genomes will still tend to be retained in the hybrid zone, where they risk being combined repeatedly in hybrid genotypes until they are inevitably lost. I call this process a hybrid sink, and the *S. grammicus* observations demonstrate conclusively that some such process effectively blocks gene flow through a hybrid zone well before hybrid or backcross fitness is reduced to the point of sterility.

3. The results of the sceloporine study further suggest that positive feedback processes may be involved in chromosomal speciation events to enhance the probability of further chromosomal speciation in chromosomally derived lineages relative to their ancestral stocks. Theoretically, it seems reasonable that the initial probability of chromosomal speciation depends on a variety of parameters of a lineage's genetic system (e.g., mutation rates, meiotic behavior of chromosomal rearrangements in heterozygotes, gametic and zygotic effects of rearrangements in balanced and unbalanced combinations, population structure, mating system, and vagility). Under normal circumstances, even

large changes in many of these parameters would seem to have little or no selective importance for the single individual or its immediate progeny. Therefore, although they may respond to selection over periods of time on the order of thousands or tens of thousands of generations, the frequencies of genes coding such parameters may be expected to show considerable random variability over a species' geographic range. Those demes that have especially favorable combinations of genes are most likely to form the founder populations for chromosomally derived species. Consequently, for thousands of generations, the derived species which evolves from this founder population may be expected to perpetuate an especially favorable combination of speciation parameters relative to the average for the ancestral stock as a whole. The chromosomally derived species will, therefore, be more likely to produce another even more derived species than will be the ancestral species. This second derivative will be still more likely to produce a third derivative than the first will be to produce another second, and so on.

If this positive feedback amplification process is working against selective forces, as no doubt will be the case, subsequent chromosomal speciation will probably occur rapidly—before a derived stock spreads much more geographically—or not at all. One chromosomal speciation event, therefore, may set the stage for an even more rapid progression of nongeographic speciation events in an otherwise conservatively speciating stock. These, for reasons discussed above, may also be associated with radical ecological shifts and the exploitation of new ways of making a living. Such a series of events will most frequently result in phylogenetically relatively long and unbranched chains of species, rather than in highly branched or fan-shaped phylogenies. Also, because they may have little opportunity to spread ecologically, chromosomally intermediate species are less likely to persist for evolutionarily long times than are ancestral and terminal stocks. Furthermore, chromosomal speciation sequences may be expected to involve primarily one kind of chromosomal mutation and to terminate with species that have either "used up" the substrate for that kind of mutation (e.g., sequences of centric fissioning that end in species with completely fissioned karyotypes) or that are polymorphic for the kind of mutations fixed between more primitive species in the chain of derivation. I call this process cascading or chain speciation. All these situations are observed in *Sceloporus* and can be demonstrated as significant modes in a number of insect or other vertebrate radiations (e.g., see White, 1973, 1978).

Finally, it should be noted that all of these models are predictive, at least in a statistical sense, and that they are susceptible to falsification through a variety of approaches involving attempts to refute their various predictions or still weakly substantiated premises. In other words, the National Geographic

Society-financed study has considerably advanced understanding of the species problem, but, as any good research study probably should, it has generated many more fruitful research questions than it has answered.

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