

CASCADING CHROMOSOMAL SPECIATION AND THE PARADOXICAL ROLE OF CONTACT HYBRIDIZATION AS A SINK FOR GENE FLOW

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SUMMARY (1979)

±120 species in 9 sceloporine iguanid lizard genera are surveyed for modes of correlation between speciation and distribution, ecology, phylogeny, and chromosomal variability. The most common mode correlates speciation with allopatric isolation, no chromosomal, and little ecological change. 8 genera with less than 15 species each, show only this mode. Some *Sceloporus* show another mode: speciation not clearly involving allopatry correlates with ecological shifts and the fixation of negatively heterotic chromosomal mutations. 5 chromosomally derived lines include rapidly formed chains or cascades of chromosomal speciation. Species ending 3 chains are either ecologically super-specialist or super-dominant and have used up substrates for particular types of chromosomal changes. Ancestral and derived species in the most recent chain contact geographically in hybrid zones less than 1000 meters wide, where they hybridize and backcross freely, but paradoxically, they exchange no chromosomes or genes. Even in *Sceloporus*, less than 25% of the speciation events involve chromosomal-change, yet nearly 60 of its ±75 species have such changes in their phylogenies. Allopatric speciation models explain all features of the first mode, but not the second. A sequence of 3 models accounts for the conditions associated with chromosomal speciation. Each is falsifiable, at least statistically, and tests are suggested.

1. Negatively heterotic chromosomal mutations can plausibly be fixed by chance in any small deme which is inbred enough to have an effective size of 10 or less. Fixation can occur without isolation if immigration is less than 10-20%. Although individual mutations are rarely fixed, many will be fixed over evolutionary time in species with subdivided populations.
2. If the derived population expands enough to protect central demes from hybridization, a hybrid sink can form. Subfertile hybrids will attract a net immigration from adjacent pure populations and consume their genes. Genes entering the sink probably will be quickly lost in heterozygotes before they can escape. Single genes are unlikely to confer complete premating isolation. Thus, selection in the sink cannot form multigenic isolating mechanisms, yet adjacent pure populations cannot exchange genes through the sink,
3. A lineage's genetic system largely determines the probability of fixation of a chromosome mutation and its ability to form a sink after fixation. Many genes affecting these properties in demes will have nearly neutral fitnesses, because they reduce fertility only in rare mutants or heterozygotes. Yet, demes having the highest frequencies by drift of alleles favoring chromosomal speciation would most probably found new species. Species derived from such demes would tend to perpetuate the high frequencies of favorable alleles, and thus would be more likely than their ancestral stock to found further new species. This positive feedback process explains all features of the cascades of chromosomally derived species in *Sceloporus*.

Historical note, 2003: This manuscript was first submitted in 1977 to *Evolutionary Biology* and circulated widely in photocopy form. I withdrew it when I received a well meant review by a colleague who had clearly failed to understand the research paradigm I was working in, and said the writing was "unscientific". The reasons for this withdrawal are described in the draft paper, [Hall, W.P. 1979a](#). An Evolutionist in an Epistemological Wonderland: Preface (1979) to *Cascades and*

Sinks. Epistemological Wonderland and the present draft were submitted together to Evolutionary Theory in 1979, and accepted for publication, but with some suggestions for change (see attached editorial correspondence, [van Valen 1979a](#), [1979b](#)). I again withdrew the papers for further work.

The issues dealt with in Epistemological Wonderland were expanded and published as: [Hall, W.P. 1983](#). Modes of speciation and evolution in the sceloporine iguanid lizards. I. Epistemology of the comparative approach and introduction to the problem. (in) A.G.J. Rhodin and K. Miyata, eds. Advances in Herpetology and Evolutionary Biology - Essays in Honour of Ernest E Williams. Museum of Comparative Zoology, Cambridge Mass. pp. 643-679. Part II, never properly begun, was intended to resolve taxonomic issues underlying the comparative approach. The present paper, with substantial revisions, probably would have formed Part III.

Work on all of these projects had to be suspended in August 1979 when I packed for a move back to the US to take up a one-year half time visiting asst. professorship at the University of Maryland, College Park. On arrival in College Park, I discovered that my workspace consisted of a converted janitor's closet, just wide enough for a desk, a single file cabinet and a few shelves over the desk, and no support for access to cytology or darkroom facilities for the preparation of graphics. The income from the temporary position was also insufficient to rent enough space to unpack my research library at home. My employment circumstances in 1980 were such that it was abundantly clear that I had no possibility of a continuing future in evolutionary biology. As a consequence it was physically impossible for me to continue work on any of these projects or psychologically impossible even to engage in further correspondence relating to them. However, the World Wide Web now provides me with the ability to present the work as a nearly completed web of knowledge about possible roles of chromosomal variation and hybridization in speciation.

[2009 Note] This linked PDF version was assembled from the HTML version of this paper, and includes some new corrections to OCR and typographical errors not fixed in the HTML. Excepting the large amount of additional work done on the *Sceloporus grammicus* complex, Table 1 -- Cytosystematics of *Sceloporus*, has been updated with the addition of karyotypic information on a few additional species and additional references that has been collected since 1973 and the addition of corresponding references to the bibliography. These additions to the 1977 version of the MS are identified in red type.

This paper should be referenced as:

Hall, W.P. [1977]. Cascading chromosomal speciation and the paradoxical role of contact hybridization as a barrier to gene flow. [Submitted 1977 to Evol. Biology, resubmitted in 1979 and accepted for publication with minor changes, but not completed. Widely circulated in its unpublished form], 43 pp - <http://tinyurl.com/olozb2>.

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INTRODUCTION

By definition the genetic system of a species includes all intrinsic aspects of its biology which serve to generate its genetic variability and to regulate its evolutionary responses to selection. Hence, variations in genetic system parameters may have rather profound regulatory effects on evolutionary processes in the lineages they characterize. And since genetic system parameters are themselves genetically determined, these may also show interesting patterns of evolutionary change. Unfortunately, because genetic systems do not fossilize, their past actions and history can be reconstructed only from their present manifestations. However, given independent data on the phylogeny of a radiation (derived through paleontology, phenetics, and various comparative studies) and the details of variations in genetic system parameters of its present species, one can deduce and construct a conceptual model for the genetic system of an ancestral species and its subsequent evolutionary derivations. The model should logically account for the observed phylogenetic relations and present genetic system parameters in the species derived from this ancestry. If the deduced model for the genetic system and its evolution is predictive and general enough in its application, its validity can then be tested against other radiations: those which show similar phylogenetic patterns should reveal predicted genetic system parameters when examined, and vice versa. The more frequently such correlations are observed, the more faith one may have in the validity of the model. Such a comparative and model building approach will be used here to elucidate possible roles of genetic system parameters in the speciation process.

All responsible evolutionists now accept the idea that if a species is divided geographically by an absolute barrier to gene flow, the separated populations in their independent evolutionary responses will eventually differentiate enough to become reproductively isolated if they should come together again (Mayr, [1963](#)). This generally slow process of allopatric speciation presumably requires no specializations of a lineage's genetic system beyond those involved in the evolutionary maintenance of adaptive genotypes, and will serve as a "control" to help identify the possible functions of variable genetic system parameters associated with more rapid modes of speciation. Bush ([1975](#)), in a comparative review, distinguished three potentially faster kinds of speciation besides the slow allopatric mode he termed "Ia." These are: "Ib," speciation by allopatric "founder" populations (Mayr, [1970](#)); "II," parapatric speciation (usually "stasipatric," involving chromosomal differentiations [White, [1968](#), [1969](#), [1973](#)]); and "III," sympatric speciation (usually involving a change in host-specificity by parasites). Here I will apply the comparative and model building approach to genetic system parameters involved in parapatric speciation.

Workers as diverse as Goldschmidt ([1940](#)) and Mayr ([1969](#)) have noted that the fixation of chromosomal rearrangements of kinds usually not found as intrapopulation polymorphisms between species of a lineage correlates with the apparently rapid evolution of isolation by these species without any obvious history of their geographic isolation. Comparative studies of all vertebrates by Wilson, et al. ([1975](#)) and detailed studies at the familial level in mammals (Todd, [1970](#), in canids) and in lizards (Paull, et al., [1976](#), in iguanids) have documented what Goldschmidt ([1940](#)) noted: that such non-allopatric "chromosomal" speciation is also associated with an apparently rapid phyletic evolution of chromosomally variable lineages in comparison to chromosomally conservative and allopatrically speciating lineages. In fact, this correlation is pronounced enough in some groups that it led Goldschmidt ([1940](#)) and Todd ([1970](#)) to present bizarre mechanisms to account for it: the "systemic mutation" and "hopeful monster" of Goldschmidt and Todd's "karyotypic fissioning" and "genetic potentiation").

More realistic attempts to explain functions of chromosomal differentiation and other aspects of genetic systems in rapid speciation have taken into account the apparent concentration of this kind of chromosomal variability in lineages which have intrinsically subdivided populations, and therefore effectively small deme sizes, because of limited vagility or other behavioural

characteristics which achieve the same effect (White, [1968](#), [1969](#), [1973](#); Mayr, [1969](#), [1970](#); Arnason, [1972](#); Bush, [1975](#); Wilson, et al., [1975](#)). All of these models agree that genetic drift (random sampling error) in effectively small local populations will occasionally allow a chromosomal rearrangement to become fixed in a deme which significantly reduces the reproductive fitness of heterozygotes for it by increasing their meiotic malassortment. All models assume that the rearrangement does not reduce the fitness of homozygous carriers for it with respect to homozygous ancestral types. Also, excepting White (White, et al., [1967](#); White, [1968](#), [1969](#)), most authors believe that sufficient isolation to allow such chance fixations can occur only on a species' periphery where a differentiating population would be temporarily isolated and could expand into previously unoccupied areas (Spurway, [1953](#); Spurway and Callan, [1960](#); Wallace, [1959](#); Key, [1968](#); Mayr, [1969](#), [1970](#); Patton, [1969](#); Bush, [1975](#)). Many also seem to believe that the rearrangement must be pushed to fixation by meiotic drive (White, [1973](#)) or that it must confer some immediate selective advantage in a developmental sense to aid the fixation and to allow the mutant population to expand away from its parent species' range into previously unoccupied territory (Bush, [1975](#); Wilson, et al., [1975](#)). Not only must a rare rearrangement be fixed by a rare chance event, but this doubly rare rearrangement must at the same time confer a significant developmental advantage to the individuals carrying it.¹ Of course, completion of the speciation involves more than just fixing the chromosomal difference.

Once a deme becomes chromosomally differentiated from its ancestral species, the reduced reproductive fitness of chromosomally heterozygous hybrids is assumed to serve in further contacts with the parental species to favor the completion of reproductive isolation. Either one or both of the following mechanisms are supposed to be involved in this process:

- the reduced fitness of heterozygotes serves as a barrier to the introgression of genes from one chromosomally homozygous type to the other, or
- the reduced fitness of chromosomal heterozygotes serves as an intrinsic mechanism to selectively favor the evolution of premating isolating mechanisms in chromosomally homozygous populations to prevent them from wasting gametes in forming reproductively less fit hybrids.

The reduced fitness cannot by itself ever serve as a complete barrier to the transmission of genes from one chromosomal homozygote to the other, because this would require the heterozygote to be completely sterile, which would of course lead to elimination of the rearrangement in its first generation of heterozygosity. On the other hand, short of postulating Goldschmidtian hopeful monsters or complete allopatric isolation (where the chromosomal rearrangement would have no obvious function), clearly the rearrangement must somehow work in situations where parental and derived populations remain in contact, to allow complete reproductive isolation to be evolved more rapidly than it could be achieved with the otherwise necessary allopatric isolation. Superficially, selection against hybridization seems to offer an easy mechanism to achieve this result (e.g. see Bush, 1975).

However, as I will show below, when genetic system parameters involved in chromosomal differentiation, hybridization, speciation, and rapid phyletic evolution are compared in actual and theoretical detail with similar parameters of allopatrically speciating lineages, the speciation model summarized above is seen to need many revisions and modifications. Quite unexpected effects deriving from limited vagility and the reduced fitness of chromosomal heterozygotes combine to achieve a seemingly complete block to gene flow between the respectively homozygous populations without either complete hybrid sterility or any need for premating isolation. In fact, quite paradoxically to the intuitive idea that hybridization (specifically parapatric hybridization-Woodruff, 1973; Bush, 1975) will favor the evolution of premating isolation, the evidence suggests that the hybridization will serve actually to delay the evolution of premating isolation. The study

also suggests modifications and clarifications to other aspects of the chromosomal speciation model and provides an explanation for and testable predictions about the frequently rapid phyletic change associated with chromosomal speciation.

CHROMOSOMAL VARIATION AND EVOLUTION IN SCELOPORINE IGUANID LIZARDS

In comparative biology, much hinges on the radiation chosen for the study. Lizards, besides being relatively typical vertebrates in most aspects of their genetics and evolution, are ideal for comparative studies. They offer large, taxonomically well known, and evolutionarily diverse lineages; and all levels from molecular to populational of their genetic systems may be easily studied in natural populations. In no other vertebrate group can such a variety of levels of organization be so easily sampled.

In lizard radiations large enough to be suited for the kind of comparative analysis outlined above, studies of systematics and a diversity of biological parameters involved in genetic systems are most complete in the family Iguanidae. The phylogeny of the family is well understood and it offers a variety of closely related lineages demonstrating remarkably different patterns of evolution and speciation (Paull, et al. 1976). It is large enough that most of these patterns are replicated several times. In the absence of a general review, I mention a few of the studies at various levels of genetic system organization to document the kind of information available: Work at the molecular level is represented by Gorman and Kim (1976), Gorman, et al. (1971), Hall and Selander (1973), Soule and Yang (1973), Tinkle and Selander (1973), Webster and Burns (1973) and Webster, et al. (1973). Cytological level studies are represented by my own work (Hall, 1973; Hall and Selander, 1973; Webster, et al., 1973; and Paull, et al., 1976) and a diversity of papers summarized in Gorman's (1973) review. Andrews and Rand (1974), Crews (1975), Cuellar (1966), and Jones, et al. (1976) are typical of information available on iguanid reproductive biology. Behavioral and population level works relevant to iguanid genetic systems are represented by Blair (1960), Evans (1961), Philobosian (1975), Rand (1967), and Tinkle (1967).

When these data for the Iguanidae are examined from the comparative approach we see the same relationships discussed above: an association of interspecific chromosomal variation, subdivided populations, rapid speciation, and rapid phyletic evolution vs an association of chromosomal and evolutionary conservatism (Hall, 1973; Paull, et al., 1976). Although major review papers are anticipated, I will summarize my work with the sceloporine branch of the family (Hall, 1973; Hall and Selander, 1973) to document the relationships between specific evolutionary and genetic system variables and to provide a basis for formulating specific predictive models for the processes involved in the non-allopatric speciation seen in the sceloporines.

As presently defined, the sceloporines include 9 genera (Savage, 1958; Etheridge, 1964; Presch, 1969). Eight of these 9 genera, totaling 44 generally well differentiated species, plus another 5 or 6 species in the closely allied *Crotaphytus* and *Gambelia* (Montanucci, et al., 1975) form a conservatively evolving basal radiation; while *Sceloporus* itself, the phylogenetically most recent branch of the radiation, contains by my count something on the order of 73 species, many of them relatively cryptic and still unnamed (Hall, 1973; Paull, et al., 1976). In terms of its utility for comparative studies, note that this sceloporine radiation alone, with ± 122 species, is larger than most mammalian families, and even many orders. Over half of the species in each of these 11 genera have been karyotyped (Gorman, 1973; Paull, et al., 1976). All examined species in the 8 conservative sceloporine genera have identical $2n=34$ karyotype, close to the $2n=36$ pattern of *Crotaphytus* and *Gambelia*, which is probably primitive for all lizards (Gorman, 1973; Paull, et al., 1976); while no more than 20 of the ± 73 *Sceloporus* are likely to have the $2n=34$ pattern. Five of these 20 species have not been karyotyped and 2 of the 15 that have been differ in non-numerical

ways from the ancestral pattern: *S. pyrocephalus* differs by a conspicuous pericentric inversion of its largest chromosome pair (Cole, [1971b](#); Hall, [1973](#)); and *S. maculosus* is reported by Cole ([1971a](#)) to have a $2n=33X$ X-Y male, $2n=34$ female (based on a total sample of 3 individuals), while Carol Axtell (pers. comm.) found one individual from near the type locality for the species to have a $2n$ of about 40, which I confirm from her slides. On the other hand, more than 50 species of *Sceloporus* are known or expected to deviate from the primitive $2n=34$ pattern of the other sceloporines by at least two rearrangements, almost all of which are centric fissions or fusions ([Table 1](#)).

TABLE 1
CYTOSYSTEMATICS OF *SCELOPORUS*

Smith (1939) species groups and species according to Smith and Taylor (1950) ^a	$2n$	karyotype formula ^b	sources ^c
SMALL-SIZED, SMALL-SCALED SPECIES			
VARIABILIS			
<i>couchi</i>	$2n=34$	(10MM,2SM,20m,xx♀ xy♂)	H ₁ ,C ₈
<i>parvus</i>	$2n=34$	(10MM,2SM,20m,xx♀ xy♂)	H ₁ ,C ₈
<i>variabilis</i>	$2n=34$	(10MM,2SM,20m,xx♀ xy♂)	H ₁ ,C ₈
<i>teapensis</i>	$2n=34$	(10MM,2SM,20m,xx♀ xy♂)	H ₁ ,C ₈
<i>cozumelae</i>	$2n=34$	(10MM,2SM,20m,xx♀ xy♂)	C₈
MACULOSUS			
<i>maculosus</i> ^d	$2n♀=34$ $2n♂=33$	(10MM,2SM,18m,xx,x ₁ x ₁) (10MM,2SM,18m,xx,x ₁ y ₁)	C ₄
<i>maculosus</i>	$2n=40$ ^e		A
MERRIAMI			
<i>merriami</i>	$2n=46$	(24AM,20m,xx♀ xy♂)	C ₄ ,H ₂
CHRYSOSTICTUS			
<i>chrysostictus</i>	$2n=34$	(10MM,2SM,20m,xx♀ xy♂)	C ₄ ,C ₈
SINIFERUS			
<i>siniferus</i>	$2n=34$	(10MM,2SM,20m,xx♀ xy♂)	H ₂ ,C ₈
<i>squamosus</i>	?	-	-
<i>carinatus</i>	?	-	-
<i>ochoterenai</i>	?	-	C₈
UTIFORMIS			
<i>utiformis</i>	$2n=34$	(10MM,2SM,20m,xx♀ xy♂)	C ₄ ,H ₂

SCALARIS

<i>jalapae</i>	2n=34	(10MM,2SM,20m,xx♀ xy♂)	H ₂ ,C ₈
<i>goldmani</i>	2n=24	(10MM,2SM,10m, x ₂ x ₂ ♀ x ₂ y ₂ ♂)	C ₈
<i>scalaris</i>	2n=24	(10MM,2SM,10m, x ₂ x ₂ ♀ x ₂ y ₂ ♂)	L ₁ ,H ₂ ,C ₈
<i>aeneus</i>	2n=24	(10MM,2SM,10m, x ₂ x ₂ ♀ x ₂ y ₂ ♂)	H ₂ ,C ₈

PYROCEPHALUS

<i>gadovae</i>	2n=34	(10MM,2SM,20m,xx♀ xy♂)	C ₅ ,H ₂
<i>nelsoni</i>	2n=34	(10MM,2SM,20m,xx♀ xy♂)	C ₅ ,H ₂
<i>pyrocephalus</i>	2n=34	(8MM,2SM,2SAM,20m, xx♀ xy♂)	C ₅ ,H ₂

LARGE-SIZED, LARGE-SCALED SPECIES

SPINOSUS

<i>orcutti orcutti</i>	2n=34	(10MM,2SM,20m,xx♀ xy♂)	C ₃ ,H ₂
[(<i>orcutti</i>) <i>licki</i>]	2n=34	(10MM,2SM,20m,xx♀ xy♂)	H ₂
[(<i>hunsakeri</i>)]	2n=34	(10MM,2SM,20m,xx♀ xy♂)	H ₂
<i>clarki</i>	2n=40	(2SM,2MM,16AM,18m, x ₃ x ₃ ♀ x ₃ y ₃ ♂) [note polymorphisms for enlargement of micro-autosome, inversion of an AM]	L ₂ ,C ₃ ,H ₂
<i>melanorhinus</i>	2n♀=40 2n♂=39	(2SM,2MM,14AM,XX,18m, x ₃ x ₃) (2SM,2MM,14AM,XY,18m, x ₃) [note polymorphisms for enlargement of micro-autosome, probably same as <i>clarki</i> polymorphism]	C ₃ ,H ₂
[(<i>magister</i>) <i>zosteromus</i>]	2n=30	(10MM,2SMM,18m - xy indistinguishable)	H ₂
[(<i>magister</i>) <i>rufidorsum</i>]	2n♀=30	(10MM,2SMM,18m♀) (10MM,2SMM,17m,x ₁ ,x ₂ ,y♂)	S ₂
<i>magister</i> (mainland)	2m=26	(8MM,2SMM,2SAM,14m - xy indistinguishable)	L ₂ ,C ₃ ,H ₂
<i>horridus</i>	2n=22	(10MM,2SMM,10m - xy indistinguishable)	C ₃ ,H ₂
<i>spinus</i>		(10MM,2SMM,10m - xy indistinguishable)	C ₃ ,H ₂
<i>edwardtaylori</i>		(10MM,2SMM,10m - xy indistinguishable)	C ₃ ,H ₂
<i>lundelli</i>		(10MM,2SMM,10m - xy indistinguishable)	C ₃
<i>olivaceus</i> ^f		(10MM,2SMM,10m - xy indistinguishable)	C ₃ ,H ₂

UNDULATUS

<i>cautus</i> ^f	2n=22	(10MM,2SMM,10m - xy indistinguishable)	C ₆ ,H ₂
<i>exsul</i> ^g	2n=22	(10MM,2SMM,10m - xy indistinguishable)	S ₁
<i>undulatus</i>	2n=22	(10MM,2SMM,10m - xy indistinguishable)	C ₆ ,H ₂
<i>occidentalis</i>	2n=22	(10MM,2SMM,10m - xy indistinguishable)	C ₁ ,C ₆ ,J,H ₂
<i>virgatus</i> ^h	2n=22	(10MM,2SMM,10m - xy indistinguishable)	C ₂ ,C ₆
<i>woodi</i>	2n=22	(10MM,2SMM,10m - xy indistinguishable)	C ₂ ,H ₂

FORMOSUS

<i>formosus</i>	2n=22	(10MM,2SMM,10m - xy indistinguishable)	H ₂ ,S ₂
<i>adleri</i> ⁱ	2n=22	(10MM,2SMM,10m - xy indistinguishable)	H ₃
<i>tannerti</i> ⁱ	?	-	-
<i>stejnegeri</i>	2n=22	(10MM,2SMM,10m - xy indistinguishable)	S ₂
<i>lunae</i>	?	-	-
<i>salvini</i> ^k	?	-	-
<i>smaragdinus</i> ^k	?	-	-
<i>taenioenemis</i> ^k	2n=22	(10MM,2SMM,10m - xy indistinguishable)	S ₂
<i>internasalis</i> ^k	?	-	-
<i>acanthinus</i> ^k	?	-	-
<i>malachiticus</i>	2n=22	(10MM,2SMM,10m - xy indistinguishable)	H ₂ ,S ₂
<i>asper</i> ^l	2n♀=32 2n♂=31	(10MM,2SM,16m,x ₄ x ₄ , x ₃ x ₃) (10MM,2SM,16m,x ₄ x ₃ y ₄) [note fixation of enlargement of microautosome, probably same is involved in <i>clarki-melanorhinus</i> polymorphism]	H ₂

GRACIOSUS

<i>graciosus</i>	2n=30	(10MM,2SMM,18m - xy indistinguishable) [note same as <i>zosteromus</i> except satellite]	C ₄ ,C ₇ ,H ₂ ,T
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GRAMMICUS^u

<i>heterolepis</i>	2n♀=32 2n♂=31	(10MM,2SM,16m,x ₄ x ₄ , x ₃ x ₃) (10MM,2SM,16m,x ₄ x ₃ y ₄) [note same as <i>asper</i> without enlargement of microautosome]	H ₂ ,S ₂
<i>shannonorum</i> ^m	2n♀=32 2n♂=31	[same as <i>heterolepis</i>]	H ₂
<i>grammicus</i> [S]	2n♀=32 2n♂=31	[same as <i>heterolepis</i>]	H ₁ ,H ₂
<i>grammicus</i> [P1]	2n♀=32-34 2n♂=31-33	[same as <i>heterolepis</i> but polymorphic for fission MM pair 1]	H ₁ ,H ₂
<i>grammicus</i> [F6]	2n♀=34 2n♂=33	[same as <i>heterolepis</i> except fixed for fission MM pair 6]	H ₁ ,H ₂
<i>grammicus</i> [F5]	2n♀=34 2n♂=33	[same as <i>heterolepis</i> except fixed for fission MM pair 5]	H ₂
<i>grammicus</i> [F5+6]	2n♀=36 2n♂=35	[same as <i>heterolepis</i> except fixed for fissions MM pairs 5 and 6]	H ₂
<i>grammicus</i> [FM1]	2n♀=40-44 2n♂=39-43	[same as <i>heterolepis</i> except fixed for fissions MM pairs 2, 4, 5 and 6; polymorphic for fissions of MM pairs 1 and 3]	H ₂
<i>grammicus</i> [FM2]	2n♀=44-46 2n♂=43-45	[same as <i>heterolepis</i> except fixed for fissions MM pairs 1, 2, 4, 5 and 6 plus microchromosome pair 14; polymorphic for fission of MM pair 3]	H ₂

MEGALEPIDURUS

<i>megalapidurus</i> ⁿ	2n♀=32 2n♂=31	(10MM,2SM,16m,x ₄ x ₄ , x ₃ x ₃) (10MM,2SM,16m,x ₄ x ₃ y ₄) [note fixation of enlargement of microautosome, probably same is involved in <i>clarki-</i> <i>melanorhinus</i> polymorphism]	H ₂ ,S ₂
<i>pictus</i> ^o	2n♀=32 2n♂=31	(10MM,2SM,16m,x ₄ x ₄ , x ₃ x ₃) (10MM,2SM,16m,x ₄ x ₃ y ₄)	S ₂
<i>subpictus</i> ^o	2n=22	(10MM,2SMM,10m - xy indistinguishable)	S ₂
<i>cryptus</i> ^p	2n=22	(10MM,2SMM,10m - xy indistinguishable)	H ₂

TORQUATUS

<i>dugesi</i>	2n♀=32 2n♂=31	(10MM,2SM,16m,x ₄ x ₄ , x ₃ x ₃) (10MM,2SM,16m,x ₄ x ₃ y ₄) [note same as <i>asper</i> without enlargement of microautosome]	H ₂ ,S ₂
<i>ornatus</i>	2n♀=32 2n♂=31	(10MM,2SM,16m,x ₄ x ₄ , x ₃ x ₃) (10MM,2SM,16m,x ₄ x ₃ y ₄) [note same as <i>asper</i> without enlargement of microautosome]	H ₂ ,S ₂
<i>jarrovi</i> ^q	2n♀=32 2n♂=31	(10MM,2SM,16m,x ₄ x ₄ , x ₃ x ₃) (10MM,2SM,16m,x ₄ x ₃ y ₄) [note same as <i>asper</i> without enlargement of microautosome]	C ₁ ,H ₂
<i>mucronatus</i>	2n♀=32 2n♂=31	(10MM,2SM,16m,x ₄ x ₄ , x ₃ x ₃) (10MM,2SM,16m,x ₄ x ₃ y ₄) [note same as <i>asper</i> without enlargement of microautosome]	H ₂ ,S ₂
<i>bulleri</i>	2n♀=32 2n♂=31	(10MM,2SM,16m,x ₄ x ₄ , x ₃ x ₃) (10MM,2SM,16m,x ₄ x ₃ y ₄) [note same as <i>asper</i> without enlargement of microautosome]	H ₂ ,S ₂
<i>insignis</i> ^f	?	-	-
<i>torquatus</i>	2n♀=32 2n♂=31	(10MM,2SM,16m,x ₄ x ₄ , x ₃ x ₃) (10MM,2SM,16m,x ₄ x ₃ y ₄) [note same as <i>asper</i> without enlargement of microautosome]	H ₂ ,S ₂
<i>poinsetti</i>	2n♀=32 2n♂=31	(10MM,2SM,16m,x ₄ x ₄ , x ₃ x ₃) (10MM,2SM,16m,x ₄ x ₃ y ₄) [note same as <i>asper</i> without enlargement of microautosome]	C ₁ ,H ₂ ,S ₂
<i>cyanogenys</i>	2n♀=32 2n♂=31	(10MM,2SM,16m,x ₄ x ₄ , x ₃ x ₃) (10MM,2SM,16m,x ₄ x ₃ y ₄) [note same as <i>asper</i> without enlargement of microautosome]	H ₂ ,S ₂
<i>serrifer</i> ^s	2n♀=32	(10MM,2SM,16m,x ₄ x ₄ , x ₃ x ₃)	S ₂
<i>macdougalli</i> ^t	?	-	-

- a. Where presently valid taxonomic usage differs from the Smith and Taylor (1950) standard, the species name will be referenced to a footnote below which cites the author(s) of the revision. Complete references will be found in the bibliography. See also Smith and Smith (1976). Species which will result from my intended taxonomic revisions are enclosed in brackets [i.e., those published in Hall and Smith (1979)].

- b. MM = metacentric macrochromosome, SMM = submetacentric macrochromosome, SAM = subacrocentric macrochromosome, AM = acrocentric macrochromosome, m = micro-autosome. Sex chromosomes indicated by small letters are microchromosomes, while those indicated by caps are macrochromosomes. Subscripts on sex chromosomes indicate probably different derivations. The simple xy designates the primitive sceloporine sex chromosomes (Pennock, et al., 1969). Karyotype formulas do not indicate several minor inversion differences, translocations, or polymorphisms noted in Cole's papers.
- c. Sources are coded as follows (complete references will be found in the bibliography): A = Carol Axtell, pers. comm. - her slides were checked by me; C₁ = Cole, Lowe, and Wright, 1967; C₂ = Cole and Lowe, 1968; C₃ = Cole, 1970; C₄ = Cole, 1971a; C₅ = Cole, 1971b; C₆ = Cole, 1972; C₇ = Cole, 1975; C₈ = Cole, 1978; H₁ = Hall, 1973 - photographs and localities are presented for *clarki*, *melanorhinus*, *asper*, *megalepidurus*, the *grammicus* group and the *torquatus* group. Only chromosome formulas are listed for the other species. It is planned to publish all of these data in the open literature; H₂ = Hall and Selander, 1973; H₃ = Hall, unpub.; J = Jackson and Hunsaker, 1970; L₁ = Lowe, Wright, and Cole, 1966; L₂ = Lowe, Cole, and Patton, 1967; S₁ = Sites and Haiduk, 1979; S₂ = Sites et al., 1992; T = Thompson and Sites 1986).
- d. Specimens from southern Coahuila (Cole, 1971a).
- e. Specimens from near Pedrecena, Durango - the type locality for *maculosus* (C. Axtell, pers. comm.).
- f. My collections include probable intergrades between *olivaceus* and *cautus* involving the character Smith (1939) uses to distinguish the *undulatus* and *spinosus* species groups.
- g. Dixon, et al., 1972.
- h. Cole, 1963.
- i. Smith and Savitzky, 1974.
- j. Smith and Larsen, 1975.
- k. Stuart, 1971.
- l. *S. asper* does not belong in the *formosus* group. Based on karyotypes it clearly is placed with *megalepidurus* and the *grammicus* and *torquatus* groups (Hall, 1973).
- m. Langbartel, 1959 - I do not accept Webb's (1969) lumping of *shannonorum* with *heterolepis*
- because the two species are absolutely separated by the climatic barriers of the deep barrancas of the Rio Grande de Santiago drainage of Lake Chapala and
 - because the conspicuously enlarged paravertebral scales that so obviously distinguish *heterolepis* are not found in any *shannonorum* population. The fact that some *heterolepis* "intergrades" have intermediate dorsal midline scale counts is completely irrelevant. These two species are certainly more distinct from one another than many recently discovered *Sceloporus* that prove their genetic isolation in sympatry with one another.
- n. Dassmann and Smith (1974) lump *pictus* with *megalepidurus*, based on my discovery of intergrading populations.
- o. Lynch and Smith (1965) - this species should probably be reallocated to the 2n = 22 *formosus* group.
- p. Smith and Lynch (1967) - *cryptus* obviously belongs with the 2n = 22 *formosus* group.
- q. Webb and Hensley (1959) lump *lineolateralis* with *jarrovi*.
- r. Webb (1967).
- s. Stuart (1970) lumps *prezygus* with *serrifer*.
- t. Smith and Bumzahem, 1953.
- u. I have not updated this table with the extensive studies of the Jack Sites school and others on chromosomal variation in the *grammicus* complex carried out subsequently to the work reported here. For references to earlier work see Sites et al. (1992). Subsequent studies have been reported by Arevalo et al. (1993, 1994), Dosselman et al. (1998), Goyenechea et al. (1996), Marshall et al. (2006), Marshall and Sites (2001), Reed and Sites (1995), Reed et al. (1995, 1995a), Sites et al. (1993, 1995, 1996).

Smith (1939) separated *Sceloporus* into two major divisions: a small-sized, small-scaled branch and a large-sized, large-scaled branch; each of which contains several species groups. Table 1 lists the currently recognized species according to Smith's scheme and their karyotypes. Following my systematic interpretations (Hall, 1973; in prep.), summarized in Figure 1, the small-scaled branch includes 18 species and is phylogenetically older (Purdue and Carpenter, 1972a, 1971b; Larsen and Tanner, 1974, 1975);² where the more recent, large-scaled branch has about 55 species. As shown in Figure 1, the small-scaled *Sceloporus* include two independent sequences of karyotypic derivation away from the primitive 2n=34; while the large-scaled radiation includes 3 major lines

deriving away from an extinct, $2n=32$ common ancestry. A brief summary of my phylogenetic interpretations of the 5 lineages follows.

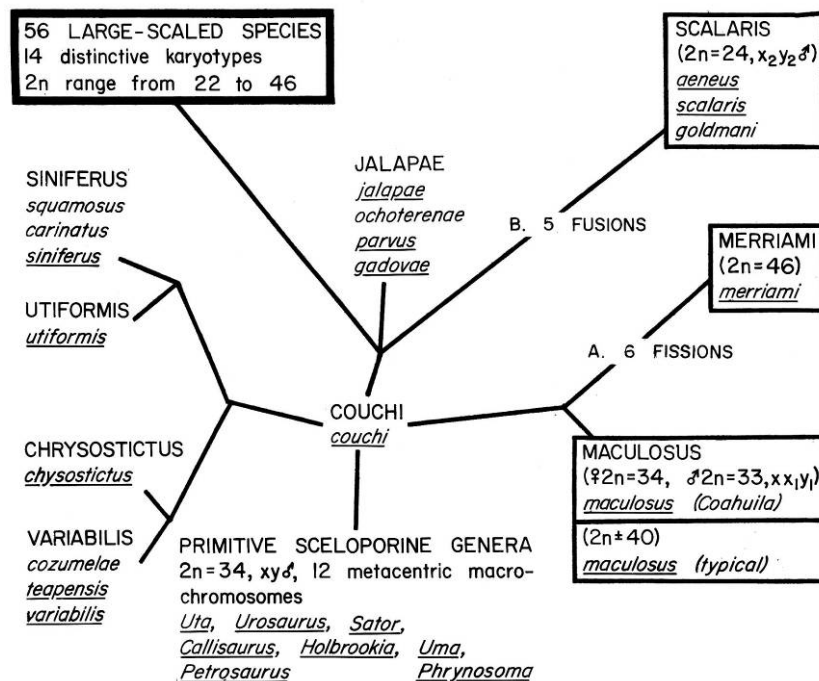


Figure 1. Radiation of the small-scaled *Sceloporus*. Names of the species groups are in capital letters. Species for which karyotypic information exists are underlined. Sources of this information are cited in [Table 1](#). Karyotypically derived species or species groups are boxed by solid borders. The phylogenetic interpretation is mine, and will be justified elsewhere; however it is largely consistent with Smith (1939), Larsen and Tanner (1974, 1975), and Thomas and Dixon (1976), as controlled by biogeographic considerations. *Sceloporus couchi* shares more characters of its squamation with other sceloporine genera than do any of the small-scaled species (Hall, in prep.), and remains relatively unspecialized. The *jalapae* group species are derived with respect to *couchi*, but remain relatively unspecialized with respect to other *Sceloporus*. The sequence of chromosomal derivation (A), leading to *S. merriami* involves the fixation of 6 macrochromosomal centric fissions. The karyotypic information for *S. maculosus* is all somewhat dubious (see [Table 1](#) and text), but it is possible that the $2n\pm 40$ *maculosus* might represent a surviving intermediate in this sequence, although this would present biogeographic problems. The sequence of chromosomal derivation (B) leading to the *scalaris* group involves the fixation of 5 microchromosomal fusions.

Sequences of derivation in the small-scaled *Sceloporus*

A. The *merriami* sequence

In the small-scaled radiation (**Figure 1**), what is probably the oldest sequence of fissioning leads to the $2n=46$ *S. merriami* **Figure 1A**, in which all macrochromosomes have fissioned (all subspecies of Olson 1973 have been sampled: Cole, 1971a, Hall, 1973). Based on my own work and the published record, there are no species with plausibly intermediate karyotypes, at least in a phylogenetic sense; although Cole (1971a) did suggest that the $2n=46$ pattern might be primitive in *Sceloporus*, and that the $2n=40$ patterns found in *clarki* and *melanorhinus* might be early intermediates in a sequence of derivation to lower numbers. Of course this assumption is untenable given morphological relationships and the data on karyology from the rest of the genus and family (Paull, et al., 1976). On the other hand, it is at least possible that the $2n\pm 40$ *maculosus* (C. Axtell, pers. comm.) might represent an intermediate; although even with the limited evidence available, there are already some biogeographic and/or taxonomic inconsistencies. In any event, *merriami* is phylogenetically one of the most primitive and distinctly separated species in *Sceloporus* (Purdue and Carpenter, 1972a, 1972b; Larsen and Tanner, 1974, 1975; Hall, in prep.). However, in spite of the phylogenetic isolation of *merriami*, it is quite successful in its highly specialized niche on the

face of rock cliffs. It occurs in most areas of major rock outcropping along the midline of the Mexican Plateau from the Big Bend area of Texas south to a limit at the sands of the Bolson de Mapimi in southern Chihuahua and Coahuila.

B. The *scalaris* and *aeneus* sequence

The second sequence of derivation away from the primitive sceloporine karyotype seen in the small-scaled *Sceloporus* is shown by *scalaris* and *aeneus*, both of which have $2n=24$ karyotypes, which presumably evolved by microchromosomal centric fusions (11 pairs have been reduced to 6 - **Figure 1B**). Karyotypes have been lightly sampled from throughout the range of the radiation (Lowe, et al., 1966; Hall, 1973, unpub.). These two species are closely related to the karyotypically unknown *S. goldmani*, which now appears to be extinct at all known localities due to habitat degradation and/or competition with *scalaris* (Smith and Hall, 1974; Thomas and Dixon, 1976; Hall, pers. obs.³). As is the case for *merriami*, except for the possibility of *goldmani*, there are no plausible karyotypic intermediates between the $2n=34$ pattern and the $2n=24$ pattern of *scalaris* and *aeneus*. Although *goldmani*, *scalaris*, and *aeneus* probably trace their ancestry from a more modern small-scaled species than does *merriami*, these 3 species form a tight group which does not seem closely related to any other *Sceloporus* (Larsen and Tanner, 1974, 1975; Thomas and Dixon, 1976; Hall, unpub.). Ecologically *scalaris* and *aeneus* are quite successful in their highly specialized niches as commensals with bunch- and other tall grasses. *Scalaris* has even managed to shift to cultivated grasses in some areas, and may be extending its range along with agricultural practices (Thomas and Dixon, 1976). Geographically *scalaris* and *aeneus* range over mesic (grassy and forested grassy) areas of the Mexican Plateau from the mountains of southern Arizona and New Mexico to the southern slopes of the Sierra Volcanica Transversal.

Sequences of derivation in the large-scaled *Sceloporus*.

In the large-scaled branch of *Sceloporus*, despite interpretations of Larsen and Tanner (1974, 1975--see note 2), I find all of the species to be quite closely related and to show clear patterns of phylogenetic derivation which are in some cases quite different from what they [Larsen and Tanner] have suggested. Except for a compact group of 4 species apparently separated by the opening of the southern part of the Gulf of California (*nelsoni*, *pyrocephalus*, [*orcutti*] *licki*, and a still undescribed sympatric sibling of *licki*[*hunsakeri*]) and the somewhat more distantly related *orcutti* proper (Hall, 1973, Hall and Smith in prep.), all of the large-scale species which have been karyotyped by Cole or myself (Table 1) are chromosomally derived. Morphological and biogeographic relationships are consistent with the idea that all derived species trace their ancestry from a now extinct $2n=32$ progenitor which had a Pliocene or early Pleistocene distribution in xeric areas around the upper end of the Gulf of California (Hall, 1973, in prep.).

Two of the three major lineages deriving from this ancestral $2n=32$ species evolved from a population which must have been polymorphic for an enlargement⁴ of one of the microchromosomes ("Em"--**Figure 2, Figure 4**): the two $2n=40$ species, *clarki* and *melanorhinus* form one lineage and the second has given rise to a large group of crevice-using species which still have $2n=32$ females, but have male karyotypes of $2n=31X_1X_2Y$. Both of these lineages either retain the Em chromosome as a polymorphism (*clarki* and *melanorhinus*--Cole, 1970; Hall, 1973) or have fixed it in some species and lost it from others (the crevice-users--Hall, 1973; **Figure 5, Figure 6**). The third lineage (**Figure 3**) offers no such clues to the details of its heritage.

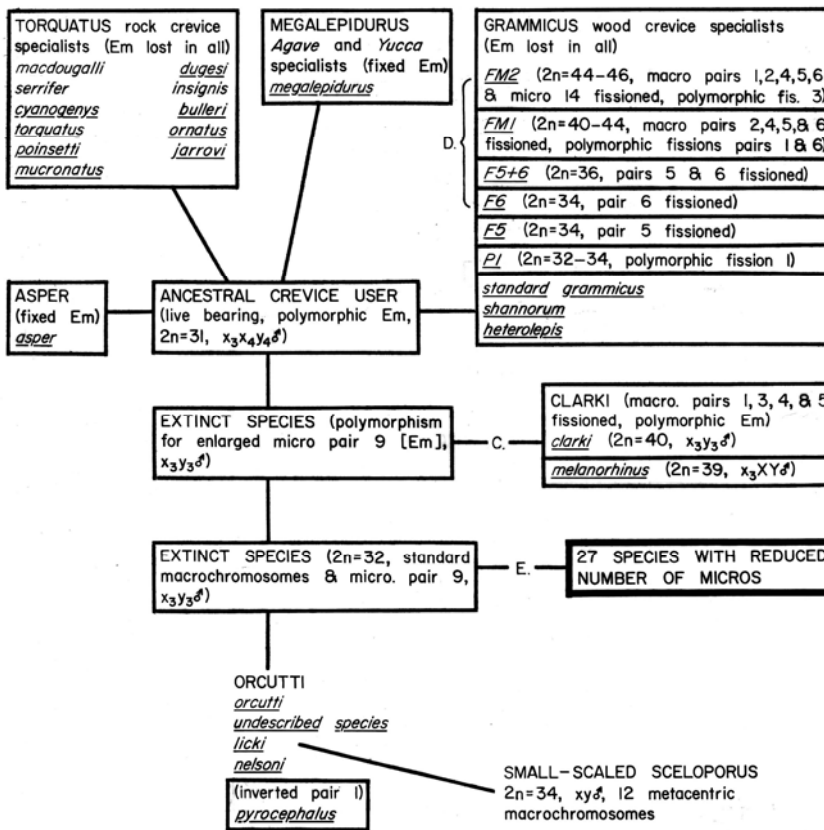


Figure 2. Early derivatives of the large-scaled *Sceloporus*. Lettering style follows Figure 1. Phylogenetic interpretations follow Hall (1973): The undescribed *orcutti* group species and *S. licki*, both included as a subspecies under *orcutti* by Smith (1939), are closely similar to *nelsoni* and *pyrocephalus*, placed by Smith (1939) in the small-scaled radiation. Larsen and Tanner (1974, 1975) also place these two species close to the small-scaled species groups *scalaris*, *siniferus* and *variabilis*, as I have defined them (Figure 1). *S. orcutti* proper is the only other large-scaled species to retain the primitive 2n=34 sceloporine karyotype. Three major sequences of chromosomal derivation trace their ancestry from a hypothetical 2n=32 ancestor, derived by centric fusion (probably involving the sex chromosomes) from a 2n=34 species which must have been morphologically similar to the present *orcutti* proper. The three sequences are: C. the *clarki* sequence, involving the fixation of 4 macrochromosomal centric fissions; D.

the very recent sequence within the morphological species, *Sceloporus grammicus*, maximally involving the fixation of 5 macrochromosomal and 1 microchromosomal centric fissions and a polymorphism for a 6th macrochromosomal fission; and E. the sequence leading to the 2n=22 *Sceloporus*, which maximally involves fixation of 5 microchromosomal fusions (tracing from the 2n=32 karyotype) and microchromosomal pericentric inversions (unless some of the fusions were tandem instead of centric).

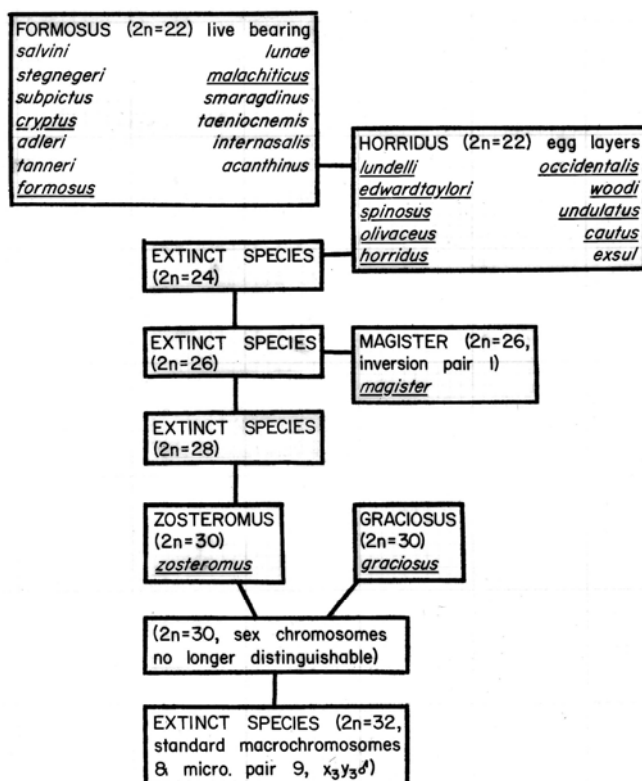


Figure 3. Derivation of the 2n=22 species of *Sceloporus*. Lettering style follows Figure 1. Phylogenetic interpretations are mine, and will be justified in detail elsewhere. However, it is worth note that Smith (1939) treats *zosteromus* as a subspecies of *magister*, and that among the 2n=22 egg layers, *spinosus*, *olivaceus*, and *horridus* all closely resemble *magister*. I have collected probable intergrades between *cautus* (Smith's 1939 *undulatus* group) and *olivaceus* (Smith's *spinosus* group) in valleys to the south and east of Monterrey, Nuevo Leon, which offer potential paths for gene flow between *cautus* on the Plateau and *olivaceus* on the coastal plane. Larsen and Tanner (1974, 1975) also note a close similarity between these two species. The *formosus* group probably derives from southern representatives of the *horridus* group which crossed the Isthmus of Tehuantepec and became adapted to high elevations. The subgroup *salvini-formosus* represent a radiation of *formosus* group species which crossed the Isthmus back into the central highlands of Mexico.

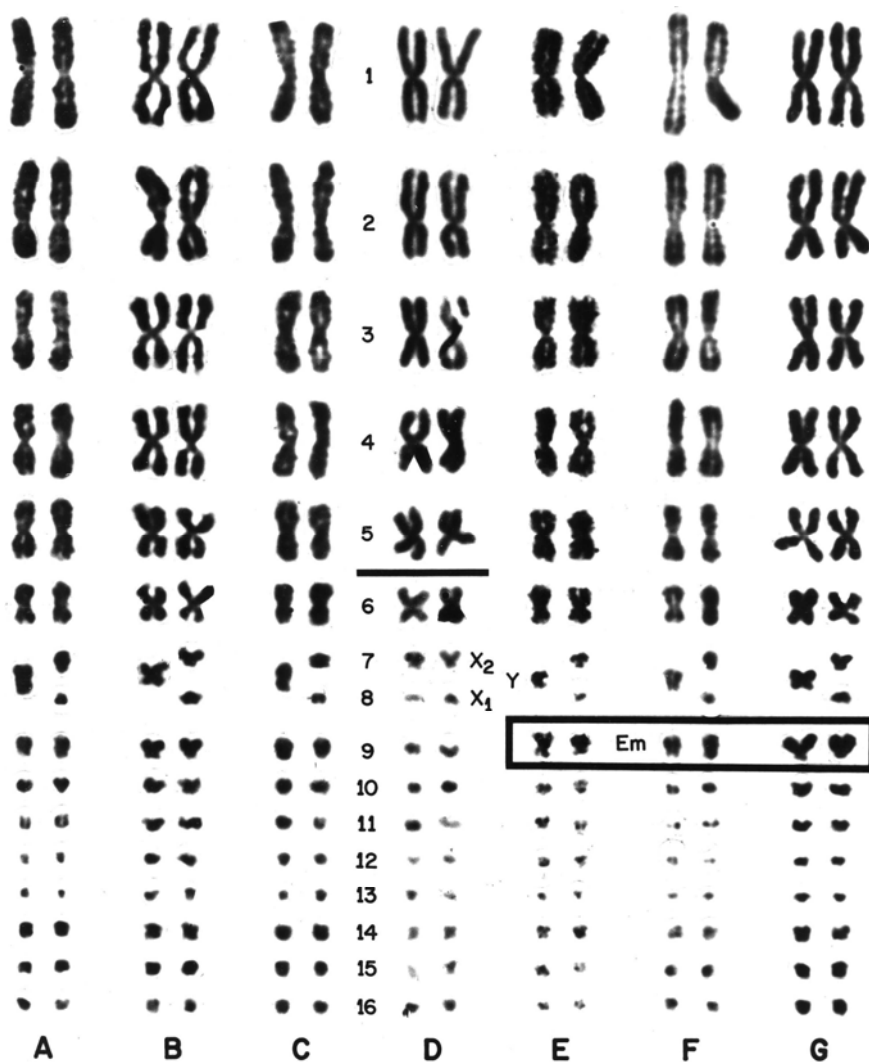


Figure 4. "Standard" karyotypes of the four crevice-using species groups. Karyotypes are arranged in columnar fashion to facilitate interspecific comparisons; **A.** *Sceloporus mucronatus* ♂ (Mexico: Veracruz; 4 km ESE Las Vigas); **B.** "S" or standard *S. grammicus* ♂ (Mexico: Coahuila; 13 km SSE Arteaga on Mex. Hwy. 57); **C.** *S. shannorum* ♂ (Mexico: Sinaloa; 14 km ENE Copala, 1950 m elev.); **D.** *S. heterolepis* ♀ (Mexico: Jalisco; 2400 m elev. on Cerro Tequila, 10 km S Tequila). **E.** *S. megalepidurus megalepidurus* X *S. m. pictus* intergrade ♂ (Mexico: Puebla; 8 km SE Ciudad Serdan); **F.** *S. megalepidurus megalepidurus* ♂ (Mexico: Puebla; 5 km NW Atenco); and **G.** *S. asper* ♂ (Mexico: Nayarit; 35 km SE Tepic, 1200 m elev.). The scale bar in column D between pairs 5 and 6 represents 10 μm. The similarity of the "Em" chromosomes, indicated by the box crossing columns E, F, and G, may be seen more clearly by comparing the Em and Y chromosomes within each karyotype to control for differences in fixation and staining among the species.

C. The *clarki* and *melanorhinus* sequence.

Sceloporus clarki and *melanorhinus* are at the end of one lineage deriving from the 2n=32, polymorphic Em population and retain the Em mutation as a polymorphism in widely distributed populations (Cole 1970 and Hall 1973 have karyotyped all subspecies in this radiation except for the recently described *clarki uriquensis*). The evolution of the *clarki* karyotype required the fixation of four macrochromosomal fissions, and *melanorhinus* clearly derives from *clarki* by fusion of one of the acrocentric fission products to the large microchromosomal Y chromosome to form an X₁X₂Y sex chromosomal system in the males (Hall, 1973--**Figure 5, Figure 6**). Cole (1970) noted the heteromorphism in male *S. melanorhinus*, but did not offer an interpretation for it because he lacked the meiotic material that makes the interpretation clear. In this lineage there are no surviving intermediates between the extinct 2n=32, polymorphic Em population and *clarki*.

Ecologically *clarki* dominates the tree trunk niche and ranges onto rocky areas which may also be dominated locally depending on congeneric competition. In the northern part of its range *melanorhinus* dominates tree trunks; while in the south, competition with the 2n=22 *horridus* and *edwardtaylori* seems to have pushed it higher up in the trees.

Geographically the two species form a continuous population from southern New Mexico and Arizona southward along the Pacific slopes of Mexico to the Isthmus of Tehuantepec, with a disjunct population in the central lowlands of Chiapas and adjacent Guatemala. The species meet in

what is probably a parapatric contact at or near the Rio Grande de Santiago in Nayarit. I have no information on the details of this contact.

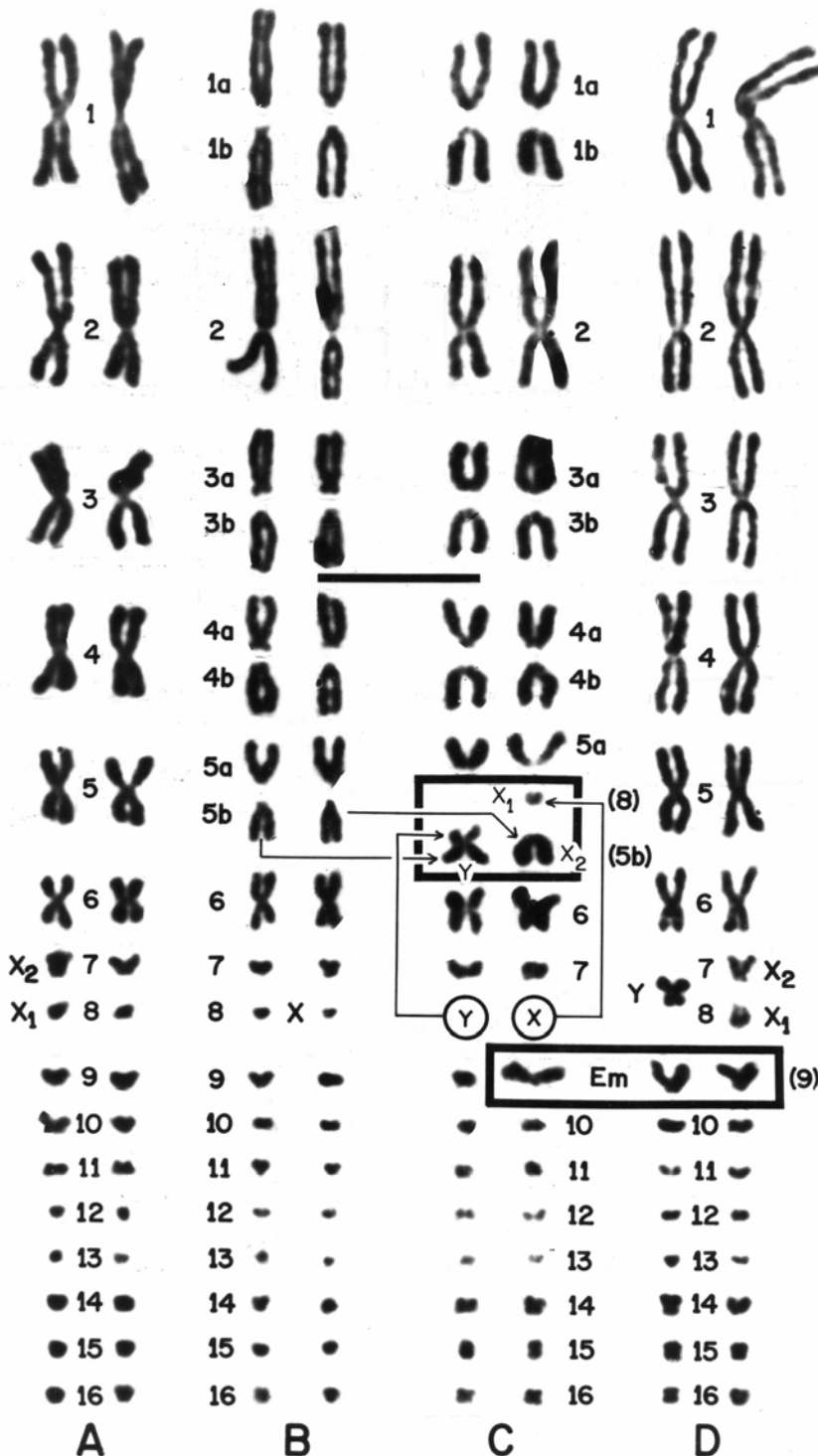


Figure 5. Karyotypic relationships of the *clarki* group species. A. The standard crevice user karyotype, represented by *S. mucronatus* ♀ (Mexico: Veracruz; 8 km ESE Las Vigas). B. The *S. clarki* ♀ karyotype (my material does not include good male mitoses--Mexico: Sinaloa; 6 km NNW Mazatlan). C. The *S. melanorhinus* ♂ karyotype, heterozygous for the Em chromosome (Mexico: Colima; 10 km E Manzanillo). D. The *S. asper* ♂ karyotype, fixed for the Em chromosome (same individual used in Figure 4). The scale bar in the center of the figure represents 10 μm. Em chromosomes and the sex chromosomes of *melanorhinus* are enclosed in boxes. The long arm of the *melanorhinus* neo-Y clearly derives from one of the acrocentric fission products of the standard pair 5, which is fused to the "y" [terminology of Table 1] of *clarki*--which in turn probably corresponds to the long arm of the "y," chromosome of the standard-crevice user karyotype shown in the adjacent *asper* karyotype. The x [or X chromosome of Table 1] is the un-fused homolog of the long arm of the *melanorhinus* neo-Y. The meiotic pairing of these chromosomes is shown in Figure 6.

The chromosomally conservative crevice users. The other lineage deriving from the 2n=32, polymorphic Em population is a group of live-bearing, generally chromosomally conservative "crevice users," which exclusively use crevices and cracks in rocks or wood for

escape and sleeping cover rather than showing a preference for burrows or shimmy burial (Axtell, 1956) in loose sand, as do all other sceloporines (Hall, 1973--Figure 2). All recognized species in this radiation have 2n=32♀,31♂ karyotypes, which are presumably identical to that of the 2n=32 common ancestor except for the formation of a microchromosomal X₁X₂Y sex chromosome system in the males. Only grammicus shows any intraspecific chromosomal variation, but this is quite spectacular: six karyotypically distinctive derived populations are included along with the conservative population in this one morphological species (Figure 7). This situation will be discussed in more detail below.

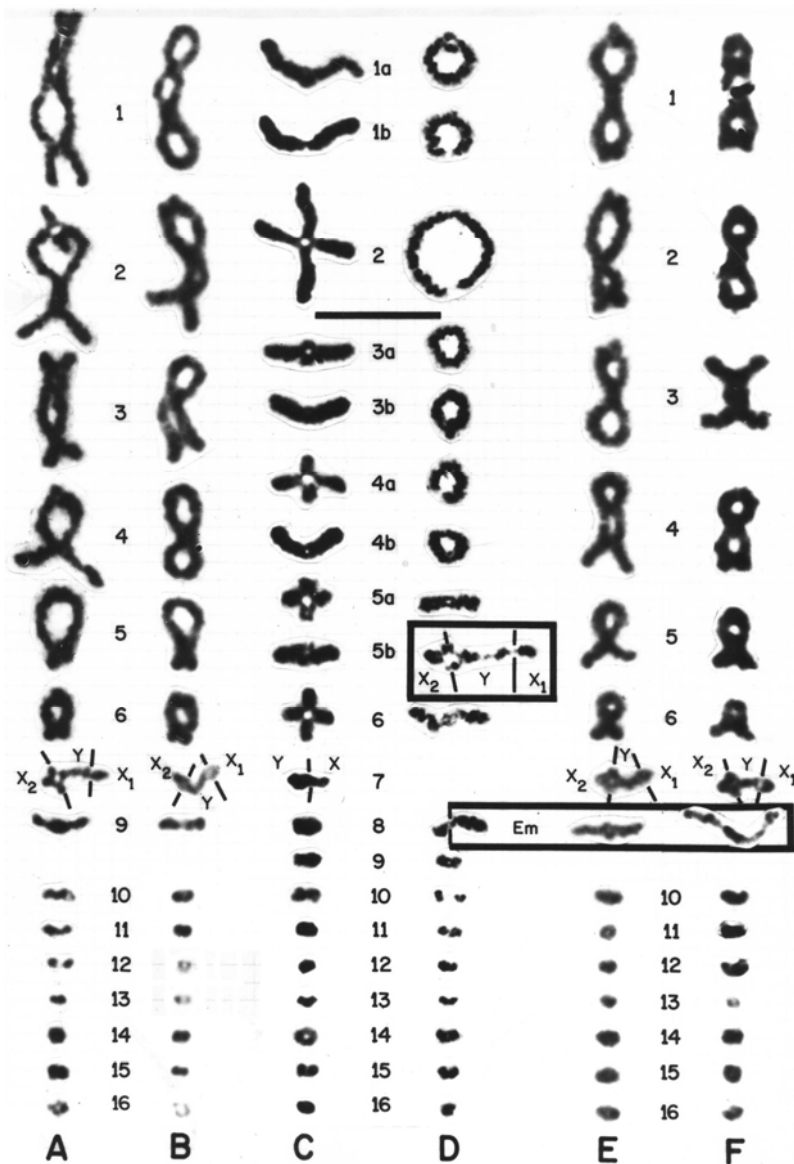


Figure 6. Male diakinesis arrays for species deriving from the extinct, 2n=32 polymorphic Em ancestor. A. *S. torquatus* (Mexico: Michoacan; 7 km E center of Morelia, 2000 m elev.); B. *S. grammicus* "S" (Mexico: Cerro Potrero contact zone [see Hall and Selander, 1973], 7.5 km W, 2 km S Rio Prio, 3350 m elev.); C. *S. clarki* (Mexico: Sinaloa; 6 km NNW Mazatlan); D. *S. melanorhinus* (same individual used in Figure 5); E. *S. m. megalepidurus* (same locality as Fig. 5); F. *S. asper* (same individual used in Figure 4 and Figure 5). Note the sex chromosome heteromorphism of all species. Also note the heteromorphic pairing of the chromosomes in the 9th bivalent of melanorhinus (column D) due to heterozygosity for the Em chromosome. Chiasma positions in the sex chromosomal bivalents or trivalents are indicated by small bars. The thick bar between pairs 2 and 3 in the central columns represents 10 µm.

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In the early evolution of the crevice using radiation (Figure 2), it appears that the primitive stock was pushed to high elevations in the mountains of the Mexican Pacific Slope, until it adapted to these montane and steep slope conditions with the evolution of ovoviviparity and specialization for the use of crevices in an environment where loose soil suitable for burrowing would be at a premium. Early in this adaptation, the stock split into two main groups: one primarily specialized to use rock crevices and the other primarily specialized to use wood crevices. Four species groups (basically following Smith, 1939) can be recognized in this radiation: *asper*, with one still very generalized tree-trunk species which is fixed for the Em chromosome (see Figure 4, Figure 5, Figure 6), which may be a conservative pre-crevice using derivative of this lineage (see Table 1,

note ¹); the *torquatus* group of rock crevice users (11 species); and two groups of "wood" crevice users. The wood crevice users include the *grammicus* group, with three recognized species (see [Table 1](#) footnote ^m), which use cracks and crevices in "trees" and logs; and *megalepidurus*, with only one species (see [Table 1](#), footnotes ^o and ^p), which is fixed for the Em chromosome and which uses the crevices between the woody dry leaves of *Yucca* and *Agave*, a habitat also frequented by *grammicus* where *megalepidurus* is absent. It should be noted that *torquatus* do on occasion also use wood crevices, and that the wood crevice users may also be locally common in rocky areas.

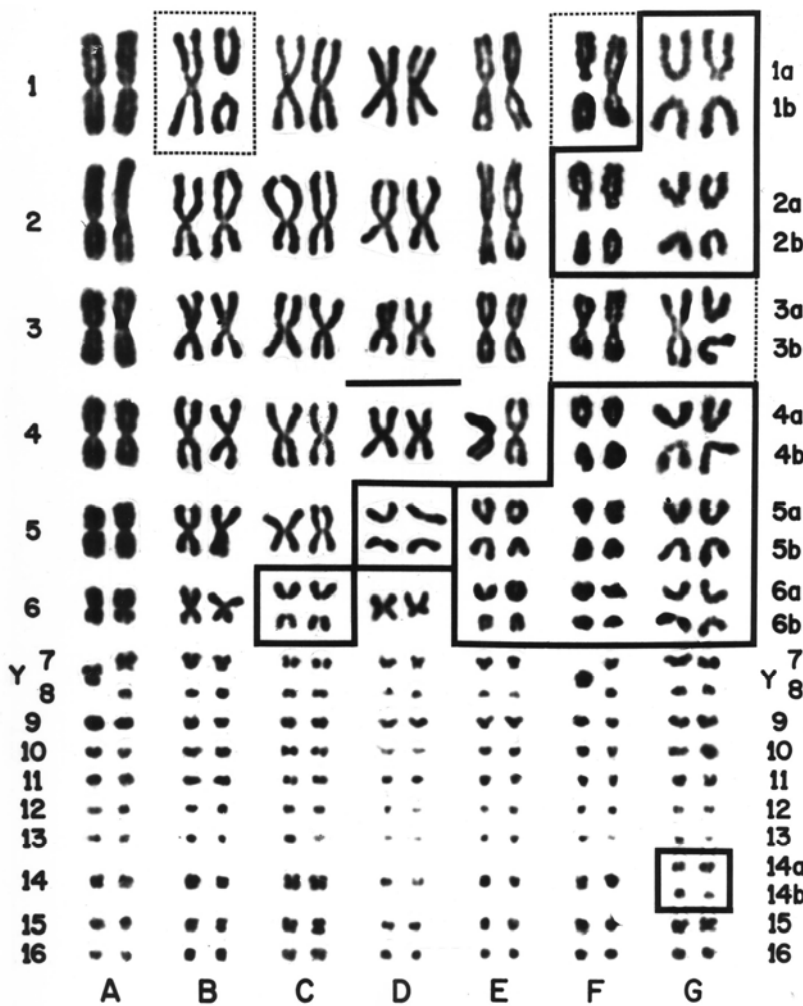


Figure 7. Major karyotypes of the *grammicus* complex. A. standard *grammicus* ♂; B. P1 *grammicus* ♀; C. F6 *grammicus* ♀; D. F5 *grammicus* ♀; E. F5+6 *grammicus* ♀; F. FM1 *grammicus* ♂; G. FM2 *grammicus* ♀. Locality information for this figure is unavailable; however, Hall and Selander (1973 Figs. 2 and 3a) map the distribution of each karyotype pattern shown here. Chromosomes which differ from the primitive or "standard" condition for all crevice-users are enclosed in boxes. If the condition is fixed, the border is solid; and if it is polymorphic, the border is dashed. The bar between rows 3 and 4 represents 10 µm. Note that the fission of pair 3 is present at a low frequency in the FM1 population, although I do not have adequate mitotic material from the 2 heterozygous individuals in my collection. The major sequence of karyotypic derivation goes from S (column A) to P6 (column C) to F5+6 (column E) to FM1 (column F) to FM2 (column G). The F5 population (column D) is an independent branch from S. Based on biogeography and morphology, P1 (column B) appears to be derived from F6, although it is karyotypically more similar to S (column A).

Except for the chromosomal variation within the taxonomic species *grammicus* and the presence or absence of the Em chromosome, there is no interspecific karyotypic variation between any of the crevice using species. *Asper* and *megalepidurus* appear to be old species (probably pre-Pleistocene) which differentiated in opposite ends of the Sierra Volcanica Transversal, and which are now being restricted by competition with more effective crevice users. Although they are now morphologically quite different due to the selective pressures of their rather different habitats, it is possible that their common fixation of the Em chromosome indicates a common ancestry within the crevice using radiation. The richness of species in the rock-crevice using *torquatus* group is quite understandable given their ecological restriction to "islands" of rock outcrops in a "sea" of alluvium; a situation which offers abundant opportunity for allopatric speciation. In actuality there may be a hundred or more allopatric populations which could be distinguished at some taxonomic level. Only where two or more forms have secondarily come into sympatry is it clear where the species definitions are valid biologically. On most areas of the Mexican Plateau there are 2 rock crevice users living

syntopically (a large and a small species), and in a few areas 3 may be found. Geographically the *torquatus* group is found above 1000 meters in the west (where congeneric competition is severe) and sea-level in the east from Arizona, New Mexico, and Texas south to Yucatan and Guatemala. Formation of the three morphological species in the *grammicus* group seems to be associated with the Rio Lerma-Lake Chapala-Rio Grande de Santiago drainage, which forms a major physiographic and climatic barrier between the Sierra Madre Occidental and the Sierra Volcanica Transversal to separate *heterolepis* and *shannorum*; and Pleistocene glaciation and climates, which probably resulted in a barrier across the crest of the Sierra Madre Occidental to separate *shannorum* from *grammicus*.

When the proto-*grammicus* once crossed the crest of the Sierra Madre Occidental, the chromosomally conservative "S" [Standard] population was able to spread continuously across the Mexican Plateau: north to the Rio Grande Valley, south to the Isthmus of Tehuantepec (S populations are found in these areas today--see distribution maps in Hall and Selander, 1973), and probably down to low elevations on the Gulf of Mexico coast. Since no other lizard so successfully exploits the wood crevice niche, this species is found everywhere within this range where large "woody" plants may be found. Climatically *S. gramicus* range from Upper Chihuahuan Desert, where they live in *Yucca*, *Agave*, and *Opuntia*, to mountain rain forest, where they use crevices in trees, stumps, and fallen logs. In areas where these climatic extremes are closely juxtaposed, such as in Oaxaca, Veracruz, and Nuevo Leon, *S. gramicus* populations range continuously between them, with no indication of barriers to gene flow.

D. The chromosomally derived *grammicus*.

The second major sequence of chromosomal derivation in the large-scaled *Sceloporus* is contained entirely within the morphological species *grammicus* (Figure 3 D). Based on karyotypes from about 1300 individuals (Hall and Selander, 1973; Hall, 1973, unpub.), there are 6 karyotypically distinctive populations besides the S. population (Figure 7). Four of the six form one linear sequence of karyotypic derivation which appears to have begun possibly in the last Pleistocene pluvial.

The first derived population, "F6," became fixed for a fission of chromosome pair 6 (see **Figure 7 C**) and spread through the most humid montane forests from the western parts of the Sierra Volcanica Transversal, at least to the Valley of Mexico, and then northward from there along the Sierra Madre Oriental to its northern limits in Nuevo Leon at the Lower Rio Grande Valley. Where in this range the mutation originated cannot be determined at this late date. In the much drier conditions of the present, the Sierra Madre Oriental populations are restricted to relict areas of mesic woodlands.

The next derivation in the sequence, "F5+6," involved fixation of a fission of pair 5 in an F6 population (**Figure 7 E**). Based on the present distribution of F5+6 populations, I think that this population originated somewhere in the Sierra Madre Oriental of San Luis Potosi, and spread outward from there into climatically intermediate areas between the humid forests occupied by F6 and the deserts occupied by S. Presently F5+6 is found in oaks or in large acacia or mesquite type trees on the coastal plane north to the Rio Grande delta; and on the Plateau, it has spread to the southwest into northern parts of the states of Guanajuato, Queretaro, and Hidalgo, where it is most frequently associated with usually cultivated tree-like *Opuntia*.

Deriving from F5+6, the "FMI" population is found in central Hidalgo and extreme northern Mexico [the state], where it appears to follow rain shadows southward from the F5+6 distribution. Based on karyotypes from only 10 individuals, FMI is fixed for fissions of macrochromosome pairs 2,4,5, and 6, and polymorphic for fissions of pairs 1 and 3 (**Figure 7 F**).

Based on karyotypes from 110 individuals, "FM2" is fixed for fissions of pairs 2, 4,5,6, and 15 (a microchromosome), it may be fixed for a fission of pair 1,⁵ and it is polymorphic for a fission of 3 (the fission has a much higher frequency than in FM1 - **Figure 7 G**). Individuals with the FM2 karyotypes were collected in an area about 55 x 20 km in the dry northeastern quadrant of the Valley of Mexico, where it lives in edificarian [buildings and houses] habitats and on cultivated *Agave* and *Opuntia*.

The "F5" population, fixed for a fission of pair 5 (**Figure 7 D**), is found in the northern parts of the Sierra Madre Occidental of Chihuahua and derived independently from the standard *grammicus*. It is separated from F5+6 populations by S populations and the uninhabitable barrier of the sandy deserts of the Bolson de Mapimi.

The last *grammicus* population, "P1," is polymorphic for a fission of pair 1 (**Figure 7 B**) in an otherwise standard karyotype. P1's range is limited to the high mountains of the east side of the Valley of Mexico. Although it has been studied intensively, its derivation is unclear. Chromosomally it should derive directly from an S ancestry. However, morphology and biogeography both suggest that it more probably derives from F6 by a back-mutation (the re-fusion of the acrocentric elements of the original pair 6).

Geographical and ecological relationships among the karyotypically differentiated populations of *grammicus* are interesting. Excepting areas which have neither trees nor the large woody succulents (*Agave*, *Yucca* and *Opuntia*), there seem to be no geographic barriers to migration of *grammicus* populations; and within the area occupied by a given chromosomal form, the lizards can be found over whatever climatic range it offers, so long as "wood" crevices are reasonably abundant. Hence, it is almost certain that all of the different chromosomal types come into ecological and behavioral contact where their ranges meet. In several northern areas I have located contacts to within 50 km (S and F5+6, S and F6, F6 and F5+6). Similarly, F6+6 and FM1, and FM1 and FM2 collections are separated by no more than about 70 km. The intervening areas between all of these species pairs are undoubtedly inhabited by *grammicus*, but there simply has not been the opportunity to sample them to determine what the contact relationships are between the populations.

In the Valley of Mexico I have precisely located contacts between S and F6, F6 and Pi, and S and FM2. In all of these cases narrow zones of hybridization are found (Hall and Selander, [1973](#); Hall, Stamm, and Reichlin, unpub), but in no case where detailed transects have been run (S x FM2 and Pi x F6) are the hybrid zones more than 200-400 m wide (a not unreasonable dispersal distance for a single individual); and in the case of the P1 X F6 contact, the zone is clearly still less than the 1 km which separates the population of "pure" individuals of the two types.

In the P1 x F6 contact (Hall and Selander, [1973](#)), hybridization is free with no indication of premating isolation, even though there are morphological and behavioral differences which could presumably be shaped by selection into premating isolating mechanisms (Moody, [1971](#)). Hybrids are fairly fertile and backcross freely with both parental types. Statistical analyses of the genotype distributions of backcross individuals (Hall and Selander, [1973](#)) suggest that some backcross phenotypes may survive poorly, but even here there is no direct evidence of a complete block to introgressive gene flow. On the other hand, the evidence from 2 chromosomal and 3 electrophoretic markers, genetic distances, and average heterozygosities is equally clear that there is no introgression beyond the 200-400 meter wide hybrid zone itself (except for one probable F₁ hybrid which crossed a highway--probably through a culvert--to reach the midst of an otherwise pure F6 population).

In the S x FM2 contact which was studied in the ancient metropolis of Teotihuacan (Millon, [1970](#)--Millon provided 1:6000 scale base maps for this study), the five chromosomal markers fixed between the populations provided a clear picture of the hybridization. F₁ hybrids were infrequent, and only 3 to 7 backcross karyotypes were found (see footnote [5](#)), and one of these was a triploid

backcross. Whether the low level of hybridization here in comparison to that in the F6 x P1 hybrid zone indicates some degree of premating isolation and hybrid infertility and/or backcross inviability, or the constraints of migration along rectilinear grid-lines formed by trees and weed succulents growing along ancient walls is unclear.

Unfortunately the contact relationships between F5+6, FM1, and FM2 are unknown. That FM1 is a population in its own right, rather than an "intergrade" between F5+6 and FM2 is suggested by the fact that two FM1 populations separated by approximately 40 km on a N-S line show the same polymorphisms and still differ from FM2, probably by the fission of pair 1 (fixed in FM2 and about 50% frequency in FM1) and definitely by the fission of microchromosomal pair 14. The closest F5+6 and FM1 karyotype samples are separated by about 70 km, as are the closest FM1 and FM2 karyotypes, so nothing can be said about the conditions of either contact. However, in developing a theoretical model for the contact zone interactions it will be assumed that the narrow P1 x F6, S x F6, and S x FM2 contacts are typical for the parapatric contacts throughout the entire *grammicus* radiation.

To summarize the events in the *grammicus* radiation, I believe that the S to FM2 sequence began in the last Pleistocene pluvial period and may have terminated in the FM1 and FM2 populations after native Americans began their cultivation of *Agave* and *Opuntia* in the area of the Valley of Mexico. Neither the F5 nor the P1 derivations can be dated from the present evidence, although I have no data to indicate that P1 and F6 would have ever been out of geographic contact since P1 formed as a discrete entity (Hall and Selander, 1973). Two scenarios are plausible for the origin of P1:

1. P1 was cut off from S which now remains on the south half of the floor of the Valley of Mexico and in the Valley of Puebla when F6 invaded the humid forest belt at intermediate elevations on the eastern divide of the Valley during its Pleistocene pluvial spread, or
2. P1 derived in situ from F6, which must have happened long enough ago to allow P1 to spread over approximately 500² km of mountain crests that form the eastern divide of the Valley. In any event, given the evidence that the reproductive fitness of P1 x F6 hybrids is effectively zero, it is most puzzling that neither of these species shows any indication of a functional premating isolating mechanism. This paradox will be explored in more detail below.

E. The derivation of the 2n=22 *Sceloporus*.

The last sequence of chromosomal derivation in the large-scaled *Sceloporus* (Figure 3) seems to have occurred in or near the deserts at the head of the Gulf of California. Judging by the patterns of speciation in and the present distributions of its most highly derived products, the chromosomal derivation must have been completed by late Pliocene or early Pleistocene. As mentioned previously the 2n=32 ancestral stock common to all 3 large-scaled radiations presumably had its distribution in this area also. Two 2n=30 stocks survive: the *magister* subspecies from *zosteromus* to *rufidorsum* of the Baja California Peninsula (Hall, 1973, in prep.), and *graciosus*, which is a montane species in the northern part of the Peninsula and Southern California that spreads to lower elevations and generalizes as it loses competitors to the north.

Geographically *graciosus* ranges northward almost to the Canadian Border and from the Pacific Coast to the Continental Divide, with disjunct populations on the sand dunes of eastern New Mexico and West Texas. *Sceloporus graciosus* is clearly a member of the large-scaled division, but beyond that its relationships with any of the other large-scaled species are unclear. If the two 2n=30 stocks derive from a single mutational event, they have been separated for a long time relative to many other species pairs in the sequence of derivation. This is, of course, consistent with the supposed overall time scale of the derivation and the amount of differentiation seen within each 2n=30 stock.

Sceloporus magister proper, centered in the extreme deserts of the southwestern US and northwestern Mexico, with a $2n=26$, is not an exact intermediate in the derivation, because it differs karyotypically from the hypothetical line by a conspicuous inversion of pair 1 (Lowe, et al., 1967; Cole, 1970; Hall, 1973), which might have caused problems in meiosis of heterozygous individuals. This species burrows for cover and uses anything from "trees" and rocks to aeolian sand dunes for perches.

The karyotypically terminal species in this last sequence of derivation all have $2n=22$ karyotypes. To derive the 5 pairs of "microchromosomes" of these species from the $2n=34$ ancestor, which has 11 pairs of acrocentric microchromosomes (at least the large-scaled *orcutti* has this karyotype) requires more than just centric fusions, especially since at least one microchromosome pair in many of the $2n=22$ species is definitely acrocentric (Cole, 1970, 1972; Hall, 1973). In any event this 22 chromosome stock forms the most successful and dominant lizard radiation on the North American continent. Its mostly parapatric species range from western Panama to the northern limits of lizard distribution, and include two groups of species: a northern oviparous group I term the *horridus* group (Smith and Taylor's 1950 *undulatus* group plus the $2n=22$ species from their *spinosus* group), which reaches the Isthmus of Tehuantepec, with a disjunct species in northern Yucatan; and a southern, originally montane group of ovoviparous species (essentially Smith and Taylor's 1950 *formosus* group with the modifications suggested in Table 1), which extends from the eastern Sierra Volcanica Transversal south to Panama. North of the Isthmus, the *formosus* species remain montane lizards, but south of the Isthmus, they extend to sea level.

Major sympatry of species in this $2n=22$ radiation is relatively uncommon, at least in its northern representatives belonging to my *horridus* grouping. Smith's (1938) *undulatus* group, represented by *undulatus*, and the $2n=22$ section of his *spinosus* group, represented by *olivaceus* are closely sympatric over much of Texas; but on the other hand, I have evidence of probable intergradation between *olivaceus* and *cautus* (a close relative of *undulatus*) in southern Nuevo Leon (Hall, unpub.). The only other major sympatry in the *horridus* group involves *horridus* and *spinosus*. I have found these to be syntopically sympatric in areas of the Sierra Madre del Sur of Guerrero, where I could see no obvious ecological differences between them.

The situation within the *formosus* group is greatly confused by the many taxonomic uncertainties and newly described cryptic sibling species (see footnotes ⁱ, ^j, ^k and ^l to Table 1). It appears that the *formosus* radiation is still actively speciating at the present, but far too little is known about the cytogenetics, biology, or distribution of any of the species to warrant speculation about what is happening. The ranges of the *horridus* and *formosus* groups overlap broadly north of the Isthmus of Tehuantepec, but they are usually separated altitudinally and/or climatically; with *formosus* species being found in higher, cooler and more humid areas. The overall pattern of this distribution strongly suggests spread of one ancestral stock outward from the xeric areas of the Gulf of California drainage, which was broken up by the major climatic fluctuations of the Pleistocene to form the present species in the north. Similarly, cool humid periods of the Pleistocene probably also selectively favored the evolution of ovoviviparity in the *formosus* stock, which is still rapidly evolving and speciating in a new adaptive zone.⁶

Most species of the *horridus* group have parapatric or allopatric distributions. In Mexico, no particular effort has been made to accurately plot the ranges of the species, so the details of their contact relationships are unclear. Data for the US are much better. The two most widely distributed species, *occidentalis* and *undulatus* are largely, if not completely allopatric. The ranges of *virgatus* and *undulatus* are closely juxtaposed and interdigitated over large geographic areas of southwestern New Mexico, southeastern Arizona, and the adjacent mountains to the south, but their mutual restrictions to different types of habitats seem to keep their populations separated by uninhabited areas several miles wide (Cole, 1963).

Much more interestingly, in Florida, *woodi* and *undulatus* meet in narrow zones of parapatric hybridization very similar to those described above for *grammicus* (Jackson, [1973a](#)). Although my interpretation differs slightly from his, according to data presented by Jackson ([1973b](#)), the proto-*woodi* may have been isolated geographically on islands of the central Florida peninsula during late Pliocene and Pleistocene periods of high sea level. Presumably this would have provided enough time for them to differentiate genetically from the proto-*undulatus* stock. In any event, where the species presently hybridize and the hybrid zone has not been overly confused by human interference it appears to be no more than 1/4 mile wide (or about 400 meters, as observed in *grammicus*) (Jackson, [1973b](#)). Although no genic markers were used, phonetic evidence from morphological characters of the *woodi* x *undulatus* hybrids strongly suggests that the hybrids are fertile and backcross successfully; but similarly to the cases in *grammicus*, there is no evidence for introgression of genes outside of the narrow hybrid zone. Jackson ([1973a](#)) suggests that this situation has persisted for at least 100,000 years (or at least 50,000 generations) without any evidence for the evolution of premating isolating mechanisms, except for the use of different habitats by the two species; which does not prevent them from hybridizing where the habitats adjoin. As is the case in the hybridization of P1 with F6 in the *grammicus* complex, populations of *woodi* are completely surrounded by *undulatus*, in such a way that appreciable fractions of the *woodi* populations must risk hybridization in any generation. As in *grammicus*, the failure to evolve effective means of preventing gametic wastage in the formation of unfit hybrids seems to be most paradoxical.

These [chromosomally derived] radiations in *Sceloporus*, contrasted with more conservatively evolving radiations in *Sceloporus* and in the other sceloporines, suggest several correlations between genetic system parameters and speciation which can be used to constrain attempts to model them.

CHROMOSOMAL SPECIATION

To account for the proliferation of species in chromosomally variable lineages of *Sceloporus*, I proposed a speciation model (Hall, [1973](#)) which resembles White's "stasipatric" model (White, et al., [1967](#); White, [1968](#), [1969](#); Key, [1968](#); Patton, [1969](#)), which Bush generalized (Bush, [1975](#); Wilson, et al., [1975](#)). However, my model for *Sceloporus* differs significantly from those of White and Bush in three areas:

1. The chromosomal differentiation of a local population and the initiation of chromosomal speciation may occur anywhere within a species' range where conditions are favorable, rather than only on its geographic periphery as supposed by Key (1968), Patton (1969), and Bush (1975).
2. Detailed studies of hybridization between the chromosomally differentiated *Sceloporus grammicus* populations (Hall and Selander, [1973](#); Hall, Stamm, and Reichlin, unpub.) indicate that parapatric hybridization plays a very significant role in the completion of genetic isolation which is quite different from that envisioned by Bush ([1975](#)) and the others.
3. I find that certain genetic effects inherent in the mechanics of chromosomal speciation imply some rather interesting consequences relating to patterns of speciation, and evolutionary changes in the genetic systems themselves, which quite adequately account for the associations of chromosomal diversity and phyletic evolution without any requirement to suppose any direct role of the chromosome mutation in altering developmental pathways.

The arguments for points 1 and 3 follow fairly directly from initial assumptions of the basic chromosomal speciation model and will be discussed first.

However, the function of hybridization in chromosomal speciation, as I understand it from my studies of the *grammicus* hybrid zones, and presumably in any case of contact hybridization (Littlejohn, et al., [1971](#)) where hybrids meet conditions of reduced hybrid fitness and low vagility, is so paradoxical that it must be discussed in detail. Such zones of contact hybridization (parapatric or narrow allopatric hybridization in Woodruff's [1973](#) terminology) paradoxically appear to be as effective as complete geographic separation in genetically insulating one population from another, in spite of the fact that hybrids and presumably also backcrosses are at least partially fertile. Some of the evidence and the detailed model to support this assertion will be presented after arguments 1 and 3 of the chromosomal speciation model are discussed immediately below.

Chromosomal differentiation; initial conditions

The process of chromosomal speciation (if it is assumed to be different from allopatric speciation--Mayr, [1963](#)) is initiated by the fixation of a chromosomal rearrangement in some local population which is not completely or permanently isolated from its parental species. It is also assumed that meiotic problems in chromosomally heterozygous individuals somehow result in at least a partial barrier to gene flow between the two kinds of chromosomally homozygous individuals, which will then favor the evolution of completed isolating mechanisms even in the absence of geographic isolation (Spurway, [1953](#); Spurway and Callan, [1960](#); Lewis, [1953](#), [1966](#); Lewis and Raven, [1968](#); Wallace, [1959](#); John and Lewis, [1965](#), [1966](#); White, [1968](#), [1969](#); Mayr, [1970](#); Bush, [1975](#); Wilson, et al., [1975](#)). To make this more explicit, if the conditions described below are met by the genetic system of an ancestral species or population, then over evolutionary time, occasional local populations will become fixed by drift for chromosomal mutations which would serve as intrinsic mechanisms to *partially* isolate the mutated populations from genes of the ancestral species.

1. To provide a mechanism for the partial isolation, heterozygosity for some kinds of chromosomal rearrangements in meiosis should induce a relatively high frequency of meiotic malassortment, which would then lead to the production of an appreciable fraction of zygotically lethal aneuploid gametes. A 10 to 50% aneuploidy would seem to be reasonable in a chromosomal speciation model, pending tests of this variable in computer simulation models. Malassortment in this frequency range has been shown in heterozygotes for single centric fusions in mice (Cattanach and Moseley, [1973](#); Gropp, et al., [1972](#), [1974](#); Ford and Evans, [1973](#)) and cattle (Gustavsson, [1971a](#), [1971b](#)), and for inversions, translocations, and D/G fusions in humans (Polani, et al., [1965](#); Hamerton, [1971](#)).
2. Such rearrangements, when they occur should have little or no negative effects on developmental fitness in heterozygous balanced or homozygous individuals or on reproductive fitness when they are homozygous.
3. The mutation rate for such rearrangements should be appreciable (say more than one per 10,000 gametes). Mutation rates of this magnitude are seen in nature (White, [1973](#); Hamerton, [1971](#)).
4. The population structure and mating system should be such that many demes in the ancestral species have effective population sizes of 10 or less. Wright ([1941](#)) showed with a path coefficient calculation that even mutations which reduced the fertility of heterozygotes by as much as 50% still had about one chance in 1000 of achieving fixation by drift (random sampling error) in a population with an effective size of 10. In still smaller populations or where heterozygosity reduced fitness by lesser amounts, the probability of fixation would be higher.
5. The interdeme vagility should be low enough so that demes infrequently exchange individuals; or if such exchange is frequent, then the species' mating system and social structure should be such that immigrants only infrequently are able to reproduce in the deme (Wilson, et al., [1975](#)). This assumes that interdeme gene flow is no more than 5-10% per

generation. Since selection against the heterozygote in a polymorphic population would work against drift to selectively eliminate whichever of the chromosomal arrangements is rarest in the deme, low rates of ancestral chromosome injection from surrounding populations should not greatly reduce the probability of the initial chance fixation. Pending tests in a computer simulation model, 10% gene flow per generation should have less than an order of magnitude effect on the probability of fixation.

These assumptions are at least tacitly accepted by most published chromosomal speciation models. One way I differ from the Key (1968), Patton (1969), Bush (1975) version of the stasipatric model is in the probable location of the chromosomal differentiation which initiates a speciation event. These authors all believe that this differentiation can occur only on a species' geographic periphery. As implied by Wilson, et al. (1975), fixation of the mutation can occur anywhere within the total range of the parent species where the population and cytogenetic parameters allow it, and not just on the species' periphery (Hall, 1973). Note that Arnason (1971), White (1973), Bush (1975), and Wilson et al. (1975), among others, emphasize that comparative data from all radiations reviewed show the most evidence for chromosomal speciation in those lineages which have limited vagility and subdivided populations, just where suitable conditions of population subdivision and small deme size would not be restricted to the geographic periphery. Also, while the initial fixation of a rearrangement depends only on the genetic system parameters noted above, it should not be forgotten that survival of the mutant population, at least during the critical early stages of the speciation process, when it would be at its smallest, is completely at the mercy of the local environment. At the species' periphery, early extermination is likely to result from only slightly more than normal environmental fluctuation; while more central populations are likely to be relatively long-lived, at least with respect to their local environment, because they presumably are better adapted to it. Also, assuming the favorable population structure mentioned above, there will be many more "central" than peripheral populations suitable for the initial differentiation. Although Key (1968) debates this. White, et al. (1967) believed that several of the chromosomally differentiated morabine grasshopper species formed within the range of the ancestral species.

Cascading speciation

Assuming that we have a reasonable model for completing the genetic isolation of the already partially isolated, chromosomally differentiated founder population of the nascent species (see below), the sampling effect inherent in the speciation process itself may serve as a mechanism to amplify the frequency of genes favorable to further chromosomal speciation in the chromosomally derived species. This may lead to a burst of rapid speciation which I call a cascade (Hall, 1973).

Many variable gene loci concerned with the parameters of a species' genetic system may have minimal effects on individual fitness, but may have alleles which profoundly influence the probability of chromosomal speciation. Variation at any or all of these loci may be affected by the amplification process of chromosomal speciation.

An example of such a locus might be one whose alleles affected the frequency of chromosomal mutation (e.g. Ives, 1950; Kidwell, et al., 1973; Voelker, 1974). Consider 2 alleles; *a*, which produces an efficient repair enzyme which allows only one rearrangement per 100,000 gametes; and *b*, a slightly defective enzyme which allows rearrangements at a rate of one per 1,000 gametes. Both frequencies are probably within the range of natural mutation rates for chromosomal rearrangements. Then, if all other aspects of a genetic system which is otherwise favorable for chromosomal speciation are held constant, a population fixed for allele *b* would initiate chromosomal speciation events 100 times as frequently as would one fixed for allele *a*. In regard to this kind of difference, even though the dogma of population genetics states that natural selection will always work to minimize mutation rates because most mutations are deleterious, note that

selection will have minimal effects on this kind of polymorphism. Certainly the heterozygously semisterilizing chromosomal rearrangements that we are considering here are deleterious to the individuals which are heterozygous for them, but even assuming that all of the excess rearrangements which allele *b* allowed were zygotic lethals, given its "penetrance" of only one per 1000 gametes, it would take many thousands of generations of selection to appreciably change its frequency in a polymorphic population. Another kind of locus which would have minimal effects on individual fitness, but which could have similarly profound effects on the probability of speciation would be one which influenced the frequency of meiotic malassortment in chromosomally heterozygous individuals. Selection could affect this locus only by working on the very rare chromosomally heterozygous individuals (Ford and Evans, 1973).

If a species has the subdivided population structure and small deme sizes required for fixation of a heterozygously semisterilizing chromosome mutation to be plausible (Wilson, et al., 1975), then gene and genotype frequencies for any polymorphism in individual demes would be expected to drift away from average values expected for the species as a whole. In an ancestral species with polymorphisms like those discussed above, which would provide favorable cytological conditions for chromosomal speciation without significantly affecting individual fitness, many demes would become fixed for alleles that favored chromosomal speciation, even if they were rare in the population as a whole (Wright, 1940, 1941, 1951; Kimura, 1970). In other words, drifting frequencies at several loci affecting speciation probabilities could well generate an extremely high inter-deme variability for the probability of chromosomal speciation without having perceptible effects on usual parameters of individual fitness. It should then be obvious that chromosomal speciation will most likely occur first in those demes where it is most probable as determined by drifting genetic system parameters.

Consequently, assuming that a chromosomally derived species will inherit the bulk of its genes from the original chromosomally differentiated deme, and noting the minimal effects of alleles "favorable" for speciation on individual fitness, the chromosomally derived species should perpetuate for long periods the initial homozygosity or high frequency of the "favorable" alleles which facilitated its origin. Because of this selective founder effect, on the average the frequency of such favorable alleles would be higher (possibly much higher) in the derived species than in the ancestral species. Therefore, the chromosomally derived species would be more likely to initiate further (or second, level, L_2) derivations than would be the ancestral (or L_0) species. And, of course, the same amplification process might be repeated when the L_2 species was formed so that this L_2 species would be more likely to form an L_3 species than either the L_0 or L_1 would be to form a second species. This process would continue to concentrate or amplify the frequency of favorable genes for several generations of increasingly rapid speciation to form a cascade of species in a manner analogous to what happens in some types of multistage electronic (or "cascade") amplifiers.

Cascade termination.

On the other hand, several processes would work to counter or to halt a cascade of chromosomal speciation once it began.

1. *Termination by substrate exhaustion.* Robertsonian mutations appear to be frequently involved in the speciation process (Wallace, 1959; White, 1973; Wilson, et al., 1975; Paull, et al., 1976). The cascading process might be expected to amplify classes of favorable genes which promoted or favored the involvement of only one kind of Robertsonian mutation in the speciation process. Although there has long been considerable debate on the subject (John and Hewitt, 1968; Todd, 1970; White, 1973), it seems probable that centric fissions and centric fusions are generated by rather different kinds of mutational processes: Fissions may be

produced by single breaks or "misdivisions" of the centromere (Darlington, [1939](#), [1940](#); Lima de Faria, [1956](#); Marks, [1957](#); Lewis and John, [1963](#); Kato, et al., [1973](#)), while centric fusions more probably involve a reciprocal translocation process (Jackson, [1971](#); White, [1973](#)). Genes which increased mutation rates and altered meiotic systems to favor speciation by one of these processes probably would not favor the other process. Therefore, Robertsonian cascades would usually involve only one or the other kind of mutation, and would be terminated when the available chromosomal substrate for that kind of mutation was used up to result in a terminal species either with all acrocentric or with all metacentric chromosomes. Possibly similar arguments may be developed for other classes of rearrangements, although it is not so obvious how cascades involving them might be terminated by exhaustion of the available chromosomal substrate.

2. *Termination by counter-selection.* The cascading amplification process might amplify and fix the effects of certain classes of "favorable" genes at such high levels that their negative effects on individual fitness would then become great enough to selectively require the other components of the genetic system to evolve coadaptations to counteract the effects of the "favorable" genes on individual fitness. An example of a probable mechanism for such a cascade termination situation would involve interactions between mutation rate loci and loci controlling the mechanics of their meiotic assortment. Chromosomal speciation presumably depends on the fitness reducing effects of meiotic malassortment in chromosomal heterozygotes. As long as mutation rates are low enough so that chromosomal heterozygosity remains rare in the population, there will be little opportunity for directional selection as compared to drift to alter the mechanics of meiotic assortment in such heterozygotes. On the other hand, if the cascading amplification process fixes too many alleles favoring increased mutation rates, a situation may evolve where chromosomal heterozygosity becomes frequent. Here, selection would certainly favor the evolution of a spindle apparatus which would insure balanced assortment even from chromosomal heterozygotes. In the case of Robertsonian mutations, this is easily achieved by insuring
 - a. that chiasma formation is sufficiently regular to reliably link the three chromosomes (the metacentric, plus the two acro- or telocentric arms) into a trivalent, and
 - b. that the centromeres of the trivalent always orient alternately (see diagrams in Hamerton, 1971).

Although there are no relevant comparative studies of mutation rates in chromosomally variable radiations, it is quite possible that some of the apparently neutral Robertsonian polymorphisms in *Sceloporus grammicus* discussed above, in the *Mus* subgenus *Leggada* (Matthey, [1966](#); Jotterand, [1972](#)), and in *Sorex* (Meylan, [1964](#)) [represent such chain terminations].

3. *Termination by niche saturation.* If nothing else halted a cascade, available and accessible ecological niches which could be occupied by a radiation would eventually become sufficiently saturated to prevent further successful speciation.

PHYLOGENETIC PATTERNS PREDICTED BY THE CASCADING SPECIATION MODEL

The patterns of chromosomal phylogeny provided by the 5 sequences of chromosomal derivation seen in *Sceloporus* show some common features which may result from basic properties of the cascading speciation process:

1. All sequences of derivation except the $2n=40$ *clarki-melanorhinus* complex end with populations which have either (to a first approximation) completely fused or completely fissioned (at least as polymorphisms) karyotypes.

2. In all sequences except for the very recent *grammicus* case, there are few or no chromosomally intermediate survivors, and even in *grammicus* at least 2 chromosomal intermediates towards the end of the sequence of derivation seem to be missing (or have such small ranges that they were missed by my extensive geographic sampling--Hall and Selander, [1973](#); Hall, [1973](#)).
3. In the two sequences where there definitely are intermediate survivors (*grammicus* and the sequence to the $2n=22$ *horridus*), the karyotypes of these survivors suggest that long sequences of derivation have almost or strictly linear phylogenies. The only apparent exceptions to this linearity might be:
 - a. The P1 *grammicus* population (Hall and Selander, [1973](#)), which may be derived from F6 by a re-fusion of the fissioned pair 6, rather than from the karyotypically more similar S populations; or
 - b. the $2n=26$ mainland *magister*, which is derived away from its presumed place in the linear sequence by a pericentric inversion (Cole, [1970](#); Hall, [1973](#)).
4. The only known cases of Robertsonian polymorphism in *Sceloporus* involve the definitely terminal and near terminal FM populations of *grammicus* (Hall, [1973](#)), or the P1 *grammicus* (Hall and Selander, [1973](#)), which may also possibly terminate a short sequence of derivation. Significantly, all polymorphisms in *grammicus* involve only the largest and most exactly metacentric chromosomes. These chromosomes would be expected to show the most regular chiasma formation and orientation on the meiotic spindle.
5. Lastly, but most interestingly, in all sequences of derivation except for the very recently terminated *grammicus* (which may have reached its culmination only with the development of native agriculture in central Mexico--Hall, [1973](#)), the chromosomally terminal forms are widespread and ecologically important radiations:
 - a. The $2n=46$ *merriami* has 4 subspecies and is common in areas of major rock outcropping from the Big Bend region of the Rio Grande Valley south to the barrier of the sandy deserts of south-central Coahuila (Olson, [1973](#)).
 - b. The $2n=40$ *clarki-melanorhinus* complex occupies tree and rock habitats from Guatemala north into the SW US along the Mexican Pacific and Gulf of California coasts and slopes (Smith, [1939](#); Smith and Taylor, [1950](#)).
 - c. The $2n=24$ *scalaris-aeneus* complex occupies grassy habitats over most of the Mexican Plateau from Oaxaca north to southeastern Arizona and adjacent New Mexico,
 - d. Finally, the $2n=22$ complex of mostly parapatric large-scaled species is the dominant or near dominant trunk-ground-rock lizard in all habitats of almost all North America from western Panama to the northern limit of lizard distribution. These lizards are missing only from the majority of Baja California, the most extreme deserts, the southern part of the lower Mississippi Valley, and the lowlands of Veracruz.

All of the above features common to the 5 sequences of chromosomal derivation are predicted and can be explained by logical extensions of the cascading speciation model.

Specific predictions of the model.

The cascading speciation model discussed above generates a series of verifiable predictions about patterns of evolutionary relationships and the final states of the genetic systems of the chromosomally derived species. These are outlined below.

1. Sequences of chromosomal derivation should be mainly linear from origin to termination.

In lineages where chromosomal derivation is frequent, i.e. where one would expect to see effects of the cascading amplification process, sequences of chromosomal and phylogenetic derivation should be mainly linear from origin to termination, rather than highly branched: Until stopped by a termination situation, because of the amplification process each most recently derived species (at derivation level L_1) should be more likely to give rise to still further derivatives (derivation level L_2) than would be the direct ancestor of this recent derivation (level L_0). Since each new species at level L_1 will most likely occupy a niche which is parapatrically or sympatrically adjacent to its direct L_0 ancestor, it will then be more difficult for the L_0 species to form a second L_1 species in the adjacent environmental space occupied by the first L_1 species. On the other hand, at least until an L_2 species is actually formed, the L_1 should have one side of its environmental space free of ancestral competitors. In other words, a chromosomally derived population will have a greater probability of surviving in an area of the range of the ancestral species where the newly isolated population can readily develop an optimal adaptation to a niche or environmental conditions which are not so effectively being used by either the ancestral population or by other close relatives.

In the example of *Sceloporus grammicus*, areas of excessively high or low humidity, although occupied by the ancestral species in areas where derived populations are absent, are probably suboptimal for it. Once chromosomal differentiation blocks gene introgression from the widespread ancestral form, the derived population is able to optimize its adaptation to the originally suboptimal habitat, and can then spread through it to displace or exclude the ancestral form from it. Once this habitat is efficiently filled by the derived form, further speciation into it from the ancestral species will be much more difficult. It is also quite likely that the derived form can spread in this new optimal habitat beyond the original range of the ancestral species. In the case of the *grammicus* radiation, sympatric habitats are thoroughly saturated by other *Sceloporus* and sceloporines, so the sequence of chromosomal speciation has been limited to geographic exclusion along climatic axes of the environment.

2. The sequence of ecological or geographic derivation will closely parallel the sequence of karyotypic derivation.

Directly following from the same arguments used above to make prediction #1, above, sequences of ecological derivation (evolution along environmental axes due to character displacement in sympatry) or geographic relationships (geographic exclusion and parapatry along geographic and climatic axes) should closely parallel sequences of chromosomal derivation. Geographic relationships in the *grammicus* sequence to the FM populations fit this, but other sequences in *Sceloporus* are too old and too many intermediates are missing to test the predictions.

3. Terminal species in a sequence will either be a) ecologically very specialized or b) ecologically dominant over near relatives.

In cases involving early or even eventual sympatry, terminal species will be either:

1. very specialized ecologically, as a result of being excluded into extreme niches through competition with the series of ancestral species; or
2. especially good competitors, as a result of having retained many ancestral adaptations and of having ecologically dominated these ancestors.

Which alternative is realized will depend considerably on the initial ecological specializations of the ancestral species and on how saturated the environment is with competitors when the sequence of

derivation begins. As I show below, given appropriate conditions (e.g. initiation of chromosomal speciation well within the periphery of the ancestral species), contact hybridization in the chromosomal speciation process will provide a group selection process which very strongly favors chromosomally derived populations with higher general fitnesses than their direct ancestors. The $2n=22$ *Sceloporus* have completely dominated the North American continent, while *grammicus* are most likely constrained to remain wood-crevice users.

4. Side branches in a sequence will usually either be proximal or terminal.

If a lineage does have side branches, these will most likely be either early derivatives or else derivatives of the chromosomally terminal populations: Early in a radiation the environmental hyperspace should be comparatively far from saturation, and an early species in a sequence should find it easier to form a second derivative at any given level than would a species formed later in a sequence of derivation, when the environmental space would be more nearly saturated.

In the large-scaled *Sceloporus* there were two early derivations from the $2n=32$ ancestor: the fissioning sequence to *clarkii* and the fusion sequence to the $2n=22$ *horridus*. In *grammicus*, P1 and F5 are early branches into spaces not occupied by more derived forms. As noted in 3b above, at least some terminal derivatives are expected to be superior competitors. Given that cascades are likely to take place and to be terminated in geologically short periods of time, and that usually we will be looking at the results of such a cascade some time after its completion; the terminal, highly competitive species may have had opportunity to overlap its ancestors and to spread and speciate geographically. The Pleistocene geographic speciation of the $2n=22$ *horridus* very clearly fits this pattern. In *grammicus*, it appears that chromosomally derived forms F5+6 through FM2 exclude S from habitats that appear to be optimal for S where the derived forms are absent. The $2n=26$ *magister*, which differs from the strictly linear sequence by a pericentric inversion is the only mid-sequence branch known in *Sceloporus*, and here we have no evidence that fixation of a pericentric inversion would facilitate speciation .

5. Missing species in a sequence will usually be chromosomally intermediate.

If species are missing (i.e. extinct) from an obvious sequence of derivation, the missing species will most likely be intermediate in the sequence: The ancestral species, which probably is relatively old and evolutionarily conservative, will most likely be well enough adapted and widespread enough geographically to survive competition with its derivatives. As noted above in 3b, terminal derivatives may be exceptionally good competitors, and by being terminal (assuming termination for intrinsic reasons) they should also have no closely related competitors on one side of their ecological space. However, two factors work against the prolonged survival of intermediate species:

1. they have closely related competitors on two (or more) sides of their ecological space, and
2. they may give rise to derivatives that are better competitors than they are before having much time to spread geographically. The intermediate with a limited geographic range could then be easily exterminated by its competitively superior derivative.

This is especially well demonstrated by the sequence of derivation in *Sceloporus grammicus*, where the maximum range that could have been occupied by intermediates between the F5+5 and FM populations is very small.

6. Many terminal species will have "used up" their chromosomal substrate for speciation.

Many sequences may terminate with species which have no more possibilities for chromosomal mutations of the kind used in their sequence of derivation. This is justified under the discussion of the first kind of cascade termination above. In *Sceloporus*, this is true for all sequences except that leading to *clarki*.

7. Species polymorphic for the kind of chromosomal mutation involved in a sequence of derivation will usually be terminal.

Chromosomal polymorphism for mutations normally differentiating species in a sequence will most frequently be found in species which terminate sequences of derivation: Cascade amplification will frequently boost chromosome mutation rates to sufficiently high levels that species at the end of a sequence of derivation will be forced to evolve mechanisms to obviate the fitness reducing effects of these mutations. Terminal species would therefore be left with high mutation rates and meiotic adaptations to eliminate fitness reducing effects in heterozygotes, hence there would no longer be selection to prevent polymorphism for the chromosomal rearrangements being introduced by the high mutation rates. FM1 and FM2 *grammicus*, which are at the end of a long sequence of derivation are both polymorphic for fissions. P1 may be an exception to this rule in *grammicus*, if it is assumed to derive directly from S; on the other hand, if it derives from F6 it does terminate a short sequence of derivation.

Testing the predictions of the cascading chromosomal speciation model.

As shown, all of the above predictions are demonstrated by one or more lineages within *Sceloporus*. However, since the *Sceloporus* data were used to suggest many of the components of the basic chromosomal and cascading speciation models, true verification should be based on the examination of other radiations to avoid circularity. Paull et al. (1976) suggest that patterns similar to those documented in *Sceloporus* are also found in other iguanid lineages, but most of the available detail is either insufficient, as with the hints of chromosomal variability found in interestingly large proliferations of South American branches of the family, or the radiations are too old and/or confused by other factors, as with the beta *Anolis* and the alpha *Anolis* radiation in Puerto Rico and its derivatives.

On the other hand, although it too is much less known than might be wished, the seemingly recent sequence of chromosomal derivation noted in the *Anolis monticola* complex of Haiti (Webster, et al., 1972; Williams and Webster, 1974) provides one iguanid example that seems to fit several of the predictions and may be used to demonstrate how the cascading speciation model can be tested. This complex is restricted to high elevations of the Tiburon Peninsula and includes three species which are clearly derived from a conservative $2n=36$ ancestry. Quite unusually for such closely related species of *Anolis*, the species in the complex are either definitely syntopic or are geographically very close to one another (collection records are sparse). *A. monticola*, the most highly derived species, shows $2n$'s of 46 to 48 due to fixation for fissions of 5 of the 6 ancestral metacentric macrochromosomes, and polymorphism for the 6th fission. This fits predictions 6 and 7. It is also geographically the most widespread and ecologically diverse species in the radiation (prediction 3b). Two other derived species have been described: *koopmani*, with a $2n=40$ (2 fissions fixed), which is known from only 2 closely adjacent localities; and *rupinae*, with $2n$'s of 39 and 41, which is known from only one locality. *A. rupinae* may be polymorphic for 2 different fissions (observed macro-chromosome numbers are 7 and 9 based only on meiotic preparations from only 2 individuals--a B-chromosome or extra microchromosomal bivalent is also seen in these two

individuals). Three other unkaryotyped specimens from this radiation may belong to a closely related but still undescribed species or may represent geographically separated populations of *rupinae*. The chromosomally intermediate *koopmani* and *rupinae* both appear to have limited ranges and to be early derivatives in the sequence to *monticola* (prediction 4). Also many chromosomal intermediates in the radiation appear to be missing (prediction 5). Only the polymorphism in *rupinae*, assuming that the limited karyological data are valid, does not fit the predictions of the cascading speciation model.

However, as interesting as the *Anolis monticola* radiation is, it should be reemphasized that the area in which it occurs is still poorly sampled, that the species collected are still karyologically poorly known, and that their habitats have undoubtedly suffered extreme modifications (degradation) in recent history due to Haitian land use practices. Obviously the predictions need to be tested in many other radiations of chromosomally variable organisms.

THE ROLE OF CONTACT HYBRIDIZATION AS A BARRIER TO GENE FLOW BETWEEN PARAPATRIC POPULATIONS

The most difficult conceptual problem that any chromosomal or parapatric speciation model must meet is to adequately explain how any chromosomally or otherwise derived population which remains in contact with its parental species is able to evolve a completed barrier to gene flow. Not only does the evolution of this barrier define the new species, but a complete barrier is needed to protect the chromosomal rearrangement of other intrinsic impediment to genic introgression from eventual swamping and elimination in the face of continued challenges from ancestral chromosomes and/or genes which would otherwise successfully pass through semi-fertile chromosomal heterozygotes or negatively heterotic hybrids. In this context, note that if geographic isolation is required for the protection of the chromosomal rearrangement, there is no need to postulate a function for fixation of the mutation in speciation; yet, the comparative data reviewed above clearly tell us that speciation patterns in chromosomally variable lineages are qualitatively different from those in chromosomally conservative lines. The foregoing discussions of chromosomal differentiation and cascading speciation are therefore relatively futile exercises in logic unless it can be demonstrated that a chromosomally differentiated population has a reasonable probability of completing [the evolution of] its genetic isolation in the face of continued contact with its parental species.

Under circumstances where a niche sympatric to that of the ancestral species is readily available to a newly differentiated deme, and genetic polymorphism of the deme provides an appropriate substrate for selection, selection for differentiation into the available niche and against wasting gametes in less fit hybrids may possibly lead to rapid character displacement and the evolution of premating isolation, which could allow the derived species to begin expanding into the sympatric niche within a comparatively few generations. However, in most cases I doubt that the chromosomally derived "founder" population would contain enough of the kind of variability needed to allow the immediate evolution of premating isolation. Where there is no premating isolation, for the differentiated deme to increase its range, it must be able to geographically displace the ancestral population; and for the differentiated population to survive swamping by the continued introduction of ancestral genes and chromosomes it must expand its range enough so that no ancestral individuals can disperse far enough to reach its central demes. Therefore, in most cases of chromosomal speciation, where premating isolation and sympatry cannot immediately be evolved, the nascent chromosomally differentiated species must pass through a period of contact hybridization⁷ with its parental species.

As demonstrated by the zones of contact hybridization between the different *Sceloporus grammicus* populations and between *Sceloporus woodi* and *undulatus*, when the hybridization of species in

peripheral contact is examined in sufficient genetic detail, paradoxically the hybrid zones are found to serve as complete barriers to gene introgression beyond the narrow limits of the hybrid zones themselves--even though hybrids are proven to maintain appreciable levels of fertility. Once the reality of this seemingly paradoxical observation is accepted, a model to explain the surprisingly early genetic isolation of the hybridizing populations is suggested. And most interestingly, the hybridization model generalizes to any situation of contact hybridization, whatever its origin, as long as certain limiting conditions are met by the hybridizing populations.

Parapatric hybridization cannot select for premating isolation.

Bush (1975) supposes that when ancestral and derived populations hybridize in a contact zone, the reduced fitness of hybrids will selectively favor the evolution of premating isolation. This assumption might be reasonable for cases of sympatric hybridization (Woodruff, 1973), but as we will see, it is quite inappropriate for any situation of contact hybridization, because premating isolation not only does not evolve as a result of contact hybridization, but it cannot do so. Hard evidence mounts to show this.

As noted by Bush (1975), who cites many examples, when the geographic variation of perfectly reasonable museum "species" is examined karyologically or with other fine-toothed techniques such as electrophoresis, which allow the use of specific gene products as markers for gene flow, many "species" are resolved into geographic mosaics of chromosomally and/or genetically distinctive, parapatrically distributed sibling species. (Here I will use the term "sibling species" to denote the genetically isolated "sister" units of such *parapatric* mosaics. The semi-species concept implies a unit in a mosaic of *allopatric* populations where the status of genetic isolation is frequently indeterminate--Mayr, 1963.) A few additional cases of parapatric mosaics of sibling species not cited by Bush (1975) are: *Perognathus goldmani* complex (Patton, 1969), *Sigmodon hispidus* complex (Zimmerman, 1970, Johnston, et al., 1972) *Anolis brevirostris* complex (Webster and Burns, 1973), *Rana pipiens* complex (Moore, 1975), *Crinia laevis* complex (Littlejohn, et al., 1971), *Litoria ewinge* complex (Watson, 1972), and *Podisma pedestris* complex (Hewitt, 1975).

In many cases where such sibling species complexes have been geographically mapped in enough detail to locate exactly the zones of contact between their constituent parapatric populations, extremely narrow zones of contact hybridization have been found. Usually these hybrid zones are much too narrow to be zones of intergradation or introgression. But, on the other hand, given the high levels of hybridization observed (e.g., Nevo and Bar-El, 1976; my observations of *grammicus* hybrid zones), there is equally little or no evidence of premating isolation between the hybridizing populations, even though in many cases the "pure" populations are seen to differ by ecological, behavioral, or other potentially discriminable features which might easily be enhanced by selection to achieve this isolation. Morphological differentiation is exemplified in the morabine grasshoppers by the cereal hook of P24(XO), which presumably could be adapted to mechanically prevent copulation with the *parapatric viatica*₁₉ with which it normally hybridizes (White., et al., 1969). Behavioral differences are exemplified by the strikingly different "mating" calls of *Crinia laevis* (Littlejohn, et al., 1971) and lesser but still significant differences between members of the *Litoria ewingi* complex (Watson, et al., 1971). However, in an old and seemingly forgotten paper, Moore (1957) presents several difficulties which he believes are sufficient to negate the effects of any antihybridization or character displacement selection resulting from contact hybridization which might otherwise favor the evolution of premating isolation. Two of his ideas are especially cogent:

1. Although selection in a contact zone against hybridization or resulting from inter-population competition might lead to more effective premating isolation by reducing hybridization through changed mate and/or habitat preferences, these kinds of selection would favor such antihybridization genes only in the contact zone where they had selective advantage.

2. Conversely, any genes selected for in the contact zone because they favored greater discrimination in mate selection or habitat preference, would very likely be maladaptive outside of the contact zone because they would result in cases of mistaken discrimination against suitable habitats or conspecific mates.

A minor point of Moore's still worth mention is that as the efficiency of any isolating mechanism based on character displacement or antihybridization selection improved, the selection pressure to further improve it would decline, such that complete isolation could be approached asymptotically, but would never be reached. As noted by Moore, these objections would not apply only in cases where a substantial proportion of an entire species risks hybridization, as in sympatric hybridization; or as would be probable for a small deme in which a heterozygously semi-sterilizing mutation had just achieved fixation. However, if the mutant population of the nascent species survived to spread to any extent, but still had not evolved premating isolation, a situation of contact hybridization would result, and the arguments given above would apply; as they must apply to any case of contact hybridization, whatever its origin.

On the other hand, no matter how relevant the arguments above may be in most cases of contact hybridization they should not apply to the contact on the eastern divide of the Valley of Mexico where the P1 and F6 populations of the *Sceloporus grammicus* complex hybridize (Hall and Selander, 1973) or to the hybrid zones between *Sceloporus undulatus* and *woodi* (Jackson, 1973a, 1973b). In both cases, highly convoluted hybrid zones completely surround populations in which no individual may be more than 10 to 20 times the width of the hybrid zone itself from the risk of hybridization. Probably 5 to 10 percent of the total of some P1 and *woodi* populations risk hybridization in every generation.

If the hybridization resulted in reproductively fit offspring, there would of course be no reason to evolve premating isolation. But this is not the case: Although F₁ hybrids in both hybrid zones reproduce, there is some evidence for recombinational breakdown in the backcross generations and there is good evidence that there is no introgression into any of the pure populations outside of the narrow hybrid zones. In other words, any interpopulation mating represents a genetic dead loss to any genetically pure individual which becomes involved in such a mismating. However, in the *grammicus* case, although P1 and F6 differ ecologically and show significant (but not completely diagnostic) differences in male head-bob patterns, coloration, and adult size, and where any or all of these differences could be shaped by selection to improve premating isolation, there is no indication either in the field or in the lab that either of the hybridizing species successfully discriminates against mating with the other (Moody, 1971). Moore's (1957) arguments discussed above might apply to the failure of widely distributed F6 or *undulatus* populations to avoid mismatings, but they do not plausibly fit the P1 or *woodi* populations, where a substantial fraction of the entire species risks hybridization in every generation. Alternatively one might argue that these are cases of recent secondary contact, and that the populations simply have not had enough time to evolve premating isolation. However, this doesn't fit either. There is every indication that *woodi* and *undulatus* would have been in contact at least since the last sea-level periods allowed the present emergence of low-lying areas of the Florida Peninsula (Jackson, 1973b), and it is my belief that P1 and F6 were never out of contact since P1 became a distinct population (Hall and Selander, 1973). If we then accept for the sake of the argument that these contacts are old and that Moore's arguments do not apply to them, we are left with the unexpected conclusion that something very fundamental is happening in the hybrid zones themselves which retards the evolution of premating isolation.

Mayr (1963) suggests that introgression through the hybrid zone might serve to prevent the evolution of isolating mechanisms by breaking up gene complexes that would otherwise evolve to prevent the hybridization. However, even in situations of parapatric contact where the hybridization is demonstrably relatively free and backcrossing is observed, in several cases there is still no

evidence for the introgression of genic markers from either hybridizing population into the other beyond the limits of the narrow hybrid zone itself. Two parapatric complexes provide the most precise documentation for this.

In *Sceloporus grammicus* genic or chromosomal markers in two unrelated and precisely mapped contact zones allow F₁ and backcross genotypes to be clearly distinguished (P1 x F6 [Hall and Selander, 1973; Hall, Moody, and Selander, unpub.] and S x FM2 in the ruins of the ancient city of Teotihuacan [Hall, Stamm, and Reichlin, unpub.]).

Similarly, in the *Spalax ehrenbergi* complex (Wahrman, et al., 1969), although genic markers are lacking (Nevo and Shaw, 1972), chromosomal differences in two of the four types of hybrid zones possible allow this distinction to be made (Nevo and Bar-El, 1976). In 3 transects across the two appropriate hybrid zones in *Spalax*, the high frequency of backcross gene or chromosomal complements proves indisputably that hybrids successfully backcross with both parental types, so we know that hybrid sterility alone cannot be a barrier to gene flow in any of these cases. In the F6 x P1 case, where the several genic differences allow the distinction to be made, it appears that recombinational breakdown in the backcross generations may contribute to the genetic barrier (Hall and Selander, 1973), but even here it remains to be proved that the backcross barrier is complete. Most interestingly, in the *Spalax* examples, the widths of the hybrid zones are inversely proportional to the number of chromosomal differences between the hybridizing populations (Nevo and Bar-El, 1976). Also, in the narrowest hybrid zones of *Spalax*, the frequency of backcross chromosome numbers exceeds that which would be expected from a random-mating model for the karyotypic differences.

Although mating in the hybrid [zone] is obviously not random, because of the strong geographic component, the excess number of backcrosses may imply that backcrossing continues for more than one generation--which would prove that the backcrosses were at least partially fertile. Additionally, as supposed by the parapatric and chromosomal speciation models, there is no evidence that the sibling species in the *Spalax* complex have only recently come into secondary contact.. Israeli populations of *Spalax* sort themselves out clinally along a climatic gradient from mesic to xeric, and it does not seem reasonable that the different chromosomal populations used only parts of this gradient to allow geographic barriers between their populations. The situation in *grammicus* is precisely similar. Therefore, in both *Sceloporus* and *Spalax*, we have convincing evidence for free hybridization and backcrossing in the zones of contact hybridization, and seemingly contradictory but equally convincing evidence that there is no introgression or gene flow out of the zones. Although other cases have not been studied as thoroughly as those reviewed above, let it be assumed that this paradoxical situation is the normal situation for stable zones of contact hybridization.

Paradoxes

Summarizing all of the apparent paradoxes associated with interactions of species meeting in zones of contact hybridization will make the problem clearer:

1. Many parapatric sibling, species probably hybridize in their contact zones; and in many of these cases, although hybrids are probably less fertile or less fit than pure parental types, they successfully backcross with both parental populations and the resultant backcross individuals are also probably partially fertile. (Genic fitnesses of backcrosses and possibly even F₁ hybrids may be reduced in cases where genic differences between the hybridizing populations are considerable--Hall and Selander, 1973, but at least in early stages of chromosomal speciation, the reduction in fertility will be strictly a function of chromosomal heterozygosity.)

2. Premating isolation does not (and presumably cannot) evolve as a result of any interactions taking place in the zone of contact hybridization. (If premating isolation does evolve, it does so only as a result of adaptations evolved outside of the contact zone for selective reasons having nothing to do with the contact.)
3. Although premating isolation does not (and probably cannot) evolve from interactions in the hybrid zone, and it seems that postulating isolation could be only partial if based solely on chromosomal differences, growing evidence from field studies points to the conclusion that these narrow contact zones of free hybridization and backcrossing act almost immediately from the beginning of chromosomal differentiation as complete barriers to--in effect--geographically isolate the hybridizing populations from one another.

In other words, paradoxes or no, contact hybridization allows the hybridizing populations which meet in peripheral contact to evolve independently as perfectly good biological species from the moment a contact zone stabilizes in such a form. And, so long as the hybrid zone remains narrow, and does not break down into intergradation; or the evolution of premating isolation outside of the contact zone does not allow sympatry; then one species can have no effect on the other beyond determining the location of their mutual contact and geographically one species from the range occupied by the other. In any event, irrespective of the actual situation in nature, all of these seemingly paradoxical conditions can easily be explained by a theoretical model (Hall, [1973](#)).

Theory of the hybrid sink.

1. In a chromosomal speciation situation it is assumed that chromosomally heterozygous individuals (hybrids, backcrosses, etc.) all show effectively reduced fecundity because meiotic malassortment from heteromorphic pairing units produces aneuploid gametes which are zygotically lethal. Similarly, in secondary contact situations it is assumed that hybrids have negatively heterotic gene combinations which significantly reduces their fitnesses.
2. Consequently, because of the effectively reduced fecundity of a proportion of the individuals in the hybrid zone, the intrinsic rate of increase for the whole population of the hybrid zone will be lower than that for the surrounding "pure" populations. Irrespective of the fitnesses of some specific genotypes (e.g. "pures"), so long as there are no positively heterotic combinations, the average relative fitness of the whole population within the hybrid zone will be lower than that of the pure populations. Effects of negative heterosis, recombinational breakdown, and chromosomal heterozygosity should all be additive in their effects on this relative fitness.
3. Because surrounding "pure" populations have higher rates of increase than the hybrid population, and will be putting more pressure on the carrying capacities of their local environments than would be the population in the hybrid zone, there should be a constant net migration of pure individuals into the hybrid zone, and little or no migration of any kind of individuals out of it. Consequently, the reduced fertility of the hybrids will form a "sink" or partial vacuum to pull migrants--and therefore gene flow--from pure populations into the hybrid zone. If the sink is strong enough, there should be no net gene flow out of the hybrid zone. I call this the hybrid sink.
4. No single gene would be able to avoid being eventually lost in a mismating unless it conferred immediate and perfect discriminatory powers to avoid mismatings. Given that average residence times for a non-discriminatory gene in the hybrid zone would probably be less than 10 generations, even a gene which by itself reduced the frequency of mismatings by 50% would still be unlikely to persist for long enough to be combined with other partially discriminatory genes to provide a completed premating isolating mechanism. Furthermore, each time such a gene for partial discrimination was lost in a mismating, it would be replaced by a gene from the pure population outside of the hybrid zone, where genes tending to restrict

the choice of mates would most likely be maladaptive (Moore, [1957](#)). Furthermore, immigration of individuals from outside of the hybrid zone would also tend to break up incipiently adaptive combinations simply by recombination. It is therefore clear that premating barriers are likely to evolve only through selection pressures operating outside of the hybrid zone, where neither of the hybridizing species has any ecological contact with the other.

5. No matter how different the hybridizing species might become in other aspects of their biologies, without effective premating isolation, they cannot achieve sympatric distributions, because whichever species was the rarer in a hybrid population would be bred out of existence by its mismatings with the commoner form.
6. Because hybrids are a sink for gene flow, the only selective effect hybridization could have on the adjacent pure populations would be to reduce their vagility. A genetically controlled act of migration which resulted in migration into the hybrid zone would effectively be lethal to the progeny of the migrating individual, because their genes would eventually be trapped in mismatings.
7. Because the hybrid zone is a sink for migration, it can be seen that its geographic location will be stable only where each pure population contributes the same number of migrants into the zone (or more exactly, where the two kinds of pure individuals are equally available for hybridization). If the immigration pressures from the two pure populations are unequal, the excess migrants from one population will push the zone in the direction of the population contributing the fewer migrants, until either a new equilibrium point is reached or the weaker population is eliminated against a geographic limit by the expansion of the stronger population.

Key's (1968) "surface tension" theory

Key's ([1968](#)) "surface tension" idea described the phenomena implied by argument 7 above. If a hybrid zone is curved so that the radius of curvature of its central axis is not large with respect to the width of the zone, the interface or surface of the convex population with the hybrid zone will have a significantly shorter length per included angle of the curve than will the surface of the concave population. Holding all other population parameters equal, the shorter interface of the convex population will contribute fewer migrants into the sink per unit angle of curvature than will the longer interface of the concave population. Consequently, the convex population will be pushed back to a less curved distribution which will again be able to achieved an immigration pressure that is balanced with that of the opposed population.

This model also easily accounts for Key's ([1968](#)) observations that "tension" zones interact to merge when they are close together to become more effective: A population caught between two hybrid zones will have to use its fixed rate of intrinsic increase to feed migrants into two sinks; while each outer population, facing only one zone, can put its entire surplus of migrants into the single zone it faces. Therefore, if the central population is narrow enough so that its central demes must feed both hybrid zones, the two outer populations will begin to push their respective hybrid zones together to eliminate the intervening population. Then, when the two different hybrid zones merge, their negative effects on hybrid fitness should be additive to increase the effectiveness of the sink, as supposed by Key ([1968](#)). Exactly this phenomenon appears to be demonstrated by the negative relationship in *Spalax* between width of the hybrid zone and number of chromosome mutations differentiating the hybridizing populations (Nevo and Bar-El, [1976](#)).

Note that any small population which initially becomes fixed for a heterozygously semisterilizing chromosome mutation immediately faces this surface tension effect. This, in turn, has interesting consequences for the predicted effects of chromosomal speciation on phylogenetic patterns. If the

nascent chromosomally differentiated population is not at least partially protected from surrounding parental populations by local barriers to migration, its fitness in the local area must be considerably higher than that of the adjacent parental populations if it is to survive the constricting effects of the surface tension of the hybrid sink. Probably many nascent chromosomally differentiated populations are quickly swamped by this constrictive effect. On the other hand, given the effects of selection for better adaptations to the local environment, and that the population structure required for chromosomal fixation will also encourage drift at many gene loci, it is reasonable to assume that a chromosomal differentiate will occasionally and independently from the chromosomal mutation achieve a particularly fortuitous gene combination which confers a superior local fitness sufficient to counterbalance the surface tension. These populations would be the only ones to survive as incipient species. Then, once the range of such a nascent species increased to where its curvature flattened enough to significantly reduce the constricting effect of its surface tension, the superior fitness of its population relative to the ancestral species would fuel an expansion out of the local area. Expansion would then continue until a point of ecological balance was reached with the parental population or until the parental population was exterminated.

It can be seen that the surface tension effect of the hybrid zone will function as a group selection filter which will allow only populations with greater fitness than surrounding ancestral populations to survive as nascent species. It obviously follows that the end products of a cascade of speciation will very likely be superior competitors which would be able to replace or displace chromosomally more primitive species in their radiations, as has obviously occurred several times in the radiation of *Sceloporus*.

CONCLUSION

Bush (1975) estimates that perhaps one half of all animal species have been formed by processes that do not fit the classical allopatric speciation model. And it is clear from this and other comparative data that parapatric or chromosomal speciation models potentially do fit many of these non-allopatric cases. If the chromosomal speciation and contact hybridization models presented above are valid for a significant proportion of this non-allopatric speciation, then it is likely that the evolutionary patterns and successes of lineages which have proliferated chromosomally have been profoundly influenced by this speciation. Clearly the models [presented in this paper] deserve especially rigorous testing, both through mathematical simulation to verify the logic and to set numerical limits on their parameters, and through detailed comparative studies of the population cytogenetics and evolution of additional natural groups of species to test the many phylogenetic predictions made by these models.

NOTES

1. Wilson, et al. (1975:5065) suggest resurrecting Goldschmidt's monster to account for the rapid phyletic evolution of the chromosomally variable mammals:

...Placental mammals have experienced unusually rapid evolution at both the chromosomal level and the organismal level, though not at the structural gene level. Hence, gene rearrangement may have a major role in organismal evolution, as Goldschmidt [1940] suggested 35 years ago. Although the mechanism involved is not known, *one possibility is that gene rearrangement provides new phenotypes by altering the patterns of gene expression during embryonic development.* [Italics mine.]

As noted in the text, I do not doubt that the correlation between chromosomal evolution and phyletic evolution is real; but Dobzhansky (1941) and Mayr (1942), among others, quite rightfully buried Goldschmidt's monster as a plausible explanation for this correlation, and the monster should stay buried--at least until there is quite solid evidence from developmental

biologists that any random major chromosomal rearrangement can lead with any significant probability to a selectively advantageous change in development. Certainly there is no evidence to date that this is so. We must therefore seek the causal basis for the relationship between evolution and chromosomal differentiation in the aspects of the genetic system which regulate a species phylogeny rather than its ontogeny.

2. Larsen and Tanner (1975) would remove 7 species from the small-scaled radiation to form the genus *Lysoptychus*, which would be primitive to the remaining *Sceloporus* but probably derived to most of the other sceloporines. Although I retain an open mind on the validity of this grouping, I will continue to follow Smith's (1939) dichotomy in the remaining discussion here. Larsen and Tanner (1974, 1-75) also present new phylogenetic interpretations for the remaining, non-*Lysoptychus Sceloporus* which are based on Larsen's (1973) multivariate statistical analyses of variation in *Sceloporus*. The approach offers useful insights, but I believe some of the phylogenetic interpretations to be fundamentally unsound:

- e. because of the misuse of distributional data as a variable in some of the analyses and
- f. because no attempt was made to consider or weigh for the adaptive significances of the morphological variation studied.

My reasoning for these objections may be found in Hall (1973) and will be developed more fully in later papers which will deal in detail with the evolution of *Sceloporus*.

3. On two different trips I searched both the Carneros, Coahuila, and the Charcas, San Luis Potosi, localities for *goldmani* during good weather conditions, and I was unable to find it. At both localities, because of extreme overgrazing, there is no sign of more than a thin stubble of annual grass showing between the exposed stones. Certainly no bunch grass now exists anywhere near these localities that is accessible by road. Based on several attempts to find bunch-grass habitats anywhere in the region determined by the three known localities (in some cases quite far from any reasonably passable road), I fear that this species may now be extinct. The last confirmed specimen was collected in 1962 (Thomas and Dixon, 1976). In any event, given the ever increasing habitat destruction resulting from cattle and goat grazing, if it still does survive in some isolated montane pocket, extermination is still probably a foregone conclusion.
4. Cole (1970) suggests that the mutation may have been a tandem duplication.
5. The cytological quality of some of this material is poor and it is sometimes difficult to identify which metacentric is present in a mostly fissioned karyotype. The 4 FM2 individuals suspected to be heterozygous carriers of the metacentric 1 were all collected in or on the edge of the hybrid zone with S, and could easily be backcrosses. Except for these 4 individuals, all samples, especially those closest to FM1 populations were homozygous for the fission of pair 1.
6. The fact that the *formosus* group has only very recently invaded humid montane habitats is indicated by their retention of the behavioral trait of shimmy burial (Axtell, 1956). Most sceloporines have a very characteristic way of submerging themselves in loose sand for escape or sleeping cover which is clearly an adaptation for living in sandy desert habitats where other kinds of cover (e.g. vacant mammal burrows, holes under rocks, wood crevices, etc.) are at a premium. Based on personal observations, all sceloporines tested expect *Petrosaurus* and the radiation of crevice using *Sceloporus* will readily shimmy bury if placed in sand-bottomed cages. None of the crevice users I have tested (*grammicus*, *megalepidurus* and several *torquatus* group species) will do so, even in the absence of other cover, which is consistent with the idea that they have had a long history of adaptation to montane habitats. On the other hand, *Sceloporus formosus* that were collected from mountain rain forests above

3000 m elevation in Oaxaca, where there is certainly no loose dry soil, would sleep buried in the sand of sand bottomed holding cages, frequently in preference to using the more usual (for them) kinds of cover provided. Furthermore, when chased, they would as readily dive down into the sand for escape as would *Sceloporas magister* collected from sand dunes in the Rio Grande Valley of New Mexico. I regard retention of this trait, which is most likely useless in the present adaptive zone they exploit, to be fairly strong evidence that they have only recently invaded this zone.

7. Woodruff (1973) reviewed various geographical relationships possible between hybridizing populations and presented a carefully defined vocabulary to describe them. Chromosomally differentiated populations which hybridize peripherally with one another without overlapping sympatrically (i.e. where the hybridizing populations have parapatric distributions) will form either allopatric or parapatric hybrid zones according to Woodruff's terminology. Since the phenomena discussed in this section may include both kinds of hybridization, I will use the somewhat more general term, "contact hybridization," of Littlejohn, et al. (1971) for those situations of parapatric and narrow allopatric hybridization where there is assumed to be no gene flow or introgression away from the hybrid zone (see below). Wider zones of allopatric hybridization, such as the hybrid zone on the Jutland Peninsula of Denmark between *Mus musculus* subspecies *musculus* and *domesticus* (Hunt and Selander, 1973), will be referred to as zones of intergradation or introgression.

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