ADVANCES IN HERPETOLOGY
AND
EVOLUTIONARY BIOLOGY

Essays in Honor of
Ernest E. Williams

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Modes of Speciation and Evolution in the Sceloporine Iguanid Lizards.
I. Epistemology of the Comparative Approach and Introduction to the Problem

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ABSTRACT: Comparative studies of speciation mechanisms and their evolutionary consequences in the radiation of ~120 sceloporine lizard species are introduced. The epistemological foundations of the comparative approach are explained. Illustrations from the sceloporine study show how the approach guided the work and aided interpretation. A foundation problem in evolutionary biology over methods for generating and testing explanatory models traces from one in the philosophy of science over the values of different "logics" of discovery and heuristics for "verification." Popper's model of scientific discovery and deductive falsification is inappropriate for processes like speciation—which are not universal, and where it cannot be assumed either that one set of causes is responsible or that they are deterministic. The worth of the comparative approach is evaluated and its heuristic structure is outlined. In a collection of case histories of a phenomenon, the methodology finds modes of correlation between observations on the cases and markers identifying the phenomenon which may be obscured by randomly unrelated features. If the number of different mechanisms causing the phenomenon is small relative to the case histories, each mode should result from one causal mechanism. Models explaining the observed correlations are realistic to the degree that they logically explain the observed correlations. Their realism may be increased or diminished by further testing, but their "truth" or "falsity" can never be proved.

INTRODUCTION

Mayr (1942, 1947, 1954, 1963, 1970) has argued that essentially all animal speciation results from genetic changes which can evolve between populations of a species only when these populations become allopatrically isolated from one another by geographic barriers to gene flow. Bush (1975b), Bush et al. (1977), Wilson et al. (1975), and White (1978), among others, using modes of argument which differ from Mayr's, concluded that the majority of animal speciation does not require geographic isolation. They also suggested that much of this non-allopatric speciation involves fixation of chromosomal modifications in initially small, inbred, but not geographically isolated local populations. Bush and Wilson, particularly, also observed that rapid morphological (but not biochemical) evolution is associated with rapid chromosomal evolution, and suggested Goldschmidt's (1955) idea of macromutation as a possible explanation for the putative relationship, resurrecting a controversy laid to rest 20 years previously.

Aside from proposing obvious and non-controversial models for speciation by parthenogenesis and polyploidy, other workers, many following still other and less readily definable modes of argument, have proposed a multitude of models for non-allopatric speciation (e.g.,

The present work will approach the problem of speciation in still another, and clearer way—one which should help reduce the confusing Babel. This series of papers will report systematically controlled comparative studies of mechanisms of speciation and evolution in the sceloporine branch of the Iguanidae (Savage, 1958; Etheridge, 1964; Presch, 1969). The sceloporines include some 120 species (Hall, part II), and enough evidence now exists to allow most speciation events in their history to be reconstructed with some degree of plausibility.

From its inception, this research program has had three major goals: 1) to determine how many qualitatively different modes of speciation have occurred and how frequent each was in the proliferation of the sceloporines; 2) to develop and critically test models for the mechanism of each mode, where this has not already been done; and 3) to develop and critically test models to predict the evolutionary potentials for each of the modes. The results then provide a solid foundation from which to extrapolate to explain speciation patterns in more distantly related organisms.

In this, the introductory paper to the series, the characteristics of the sceloporines which led them to be studied are described, and I explain my plan of attack for the study. The organization of this plan is relatively novel and uses unusual but powerful forms of logical argument. These must be explained and justified scientifically and epistemologically. To do so involves confronting major paradigmatic crises both in evolutionary biology and in the philosophy of science. The second paper (Hall, part II) will present an overview of sceloporine evolution and cytosystematics which is needed to orient the more detailed reports to follow.

THE SPECIES PROBLEM: A CRISIS IN EVOLUTIONARY BIOLOGY

Ghiselin (1974) and others have observed that evolutionary biology now faces a crisis (Kuhn, 1962) in its historical development similar to that before Darwin published his "On the Origin of Species" in 1859, or before Dobzhansky (1937), Huxley (1940, 1942), Mayr (1942), and Simpson (1944) achieved the consensus of ideas known as the "synthetic theory of evolution". These past crises were both concerned primarily (but not exclusively) with major revisions in understandings of the mechanisms by which species evolved through time (e.g., anagenesis; White, 1978). The present crisis, as indicated by the confusion of papers cited in the introduction, relates primarily to the species problem (e.g., cladogenesis—White, 1978). To what does the species concept actually refer (e.g., Hull, 1976)? How are these species formed? What effects, if any, does the mode of species formation have on the evolution of the speciating lineage? The philosophical problems which underlie these questions and make them so difficult to answer also involve the whole of evolutionary biology (e.g., Løvetrup, 1975; Peters, 1976; Platnick and Gaffney, 1978). The array of ideas on species and speciation already proposed, and the obvious problems in answering questions they raise, suggest that something more than a new paradigm in Kuhn's (1962) rather loose sense is needed. Rather, more efficient heuristic
schemata are needed for rejecting unrealistic or patently unscientific proposals.

Kuhn (1962, 1970a) publicized the importance of "paradigms" in scientific research and communication. At the same time, he admits to having hopelessly confused usage of the word paradigm (Kuhn, 1969, 1970b; Masterman, 1970), a confusion not entirely resolved by his introduction of the substitute terms "disciplinary matrix" and "exemplar" (Kuhn, 1969). Kuhn's ideas most relevant here concern scientific revolutions, incommensurability, and communication within and between scientific communities following different paradigms. These ideas also seem to apply to a more precisely defined concept, the "heuristic schemata" of a research program. Based on usage of the two words separately in Suppe [ed.] (1977), the term "heuristic schemata" will be used here to refer to a particular framework of initial metaphysical assumptions, and the pattern of logical argument which is followed within those assumptions, either to test or to discover a theory or putative knowledge. This is not to be confused with specific observations of nature which form the basis of the knowledge, the mechanical apparatus used to collect the observations, or with the theory or knowledge which is discovered or tested by following the heuristic schemata.

Reviewers of my earlier attempts to describe the comparative studies of sceloporine speciation and evolution (e.g., Hall, 1977)1 have had conspicuous difficulties in following what I thought were clearly organized arguments used to discover, develop, and test hypotheses. Conversely, I have also found it exceptionally difficult to either review other work intelligibly or to follow it as a model for writing these arguments. From trying to find the source of these long standing communication difficulties, I have concluded that the heuristic schemata used in the sceloporine research, which I collectively referred to as the comparative approach (Hall, 1977), are unusual and poorly understood by many evolutionists. Once I extracted them from my own work I have been unable to find sources where these schemata either are described or are laid out clearly in forms which could usefully serve as exemplars for the approach I have followed. Most importantly, more detailed, but still incomplete studies to understand the problems raised by this apparent incommensurability (Kuhn, 1962) of heuristic schemata suggest that the approach followed here should be more efficacious than others applied to the species problem.

However, although I have modified and/or used some in new contexts, the schemata used in the sceloporine research are not entirely original with me. For instance, as his logical methodology is described by Ghiselin (1969) and Hull (1973), Darwin probably used similar approaches to guide the development and testing of his many revolutionary

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1Reviewers were uniformly impressed by the models proposed in Hall (1977) but seemed unable to follow my arguments. Only when one well-intentioned reviewer took the extraordinary effort to completely rewrite my awkward prose did it become unavoidably apparent that he and I were seeing the same data from incommensurable vantages. At this point I withdrew the manuscript and attempted to understand the problem. The present series of papers is intended to cover the same ground, but with this understanding in hand. Unfortunately, because of the wide interest in its conclusions, the 1977 manuscript has already been effectively published by unauthorized but widespread photocopying from copies I circulated for informal reviews. Given the situation, I have no choice but to declare this manuscript to be in the public domain. I hereby grant permission to anyone concerned to either make further copies or to cite the paper. I request that the following citation style be used: "Hall, W. P. 1977. Cascading chromosomal speciation and the paradoxical role of contact hybridization as a barrier to gene flow. Informally published, 91 pp. [cited by author's permission, see Hall, (= full citation to the present paper)]."
Theories. Unfortunately, Darwin did not explain or justify his schemata clearly enough for his critics to understand or accept his arguments (Ghiselin, 1969; Hull, 1973) although many of Darwin's most revolutionary theories have been fully substantiated with time. Ghiselin also asserts that many present workers still do not understand Darwin's heuristic schemata. I would add here, to emphasize the problems involved in extracting such schemata from the interstices of the work which they organize, that if I have used a Darwinian approach in the sceloporine studies, and if I understand my own approach, then even Ghiselin (1969, 1974) fails to recognize all of the roles or significances of all of Darwin's schemata. This is especially true for Ghiselin's understanding of the approach to originating hypotheses, as compared to practices for testing them, which are described in more detail. Hull (1973) makes the distinction between the two functions of Darwin's research program more clearly than Ghiselin does, but Hull describes neither set of schemata in useful detail.

More recently, Bush (1975); Bush, et al. (1977); Wilson et al. (1975), and perhaps White (1978) have used comparative approaches which have some similarities with the ones here; but in none of their works are the heuristic procedures adequately explained, justified, or used with full epistemic power. Bush especially can also be criticized for logical and syntactical errors in his probably intuitive usage of these schemata.

Thus, given the present crisis in evolutionary biology over the species problem, the history of my own previous attempts to report my sceloporine findings, and the variety of communication problems which result from the implicit use of different heuristic schemata (Kuhn, 1962), it is desirable to take the unusual step to explain and justify philosophically the a priori assumptions and logical structures of the schemata which I have followed. I illustrate this discussion with examples from the historical development of my sceloporine studies to demonstrate how the schemata have been used.

Because of the problems dealt with, I will unavoidably raise many issues in this paper which demand more complete treatment than I can provide here. For example, the heuristic schemata I present should be axiomatized and tested for logical consistency. Their historical origins should be traced in detail, and they should be compared with schemata used by other evolutionists. However, these issues are beyond the scope of the present work. Such projects would minimally take several years' work, and the present paper is primarily intended: 1) to explain why and how I have organized my sceloporine studies as I have; 2) to explain the unusual logical organization of the arguments I use to reach and defend the conclusions of these studies; and 3) to provide enough of a philosophical justification for this approach to show that it is scientifically valid.

To successfully meet these intentions, certain pitfalls must be avoided. To illustrate some of the traps I will begin with some (probably oversimplified) comments on relevant trends and problems in the discipline of the philosophy of science. Most of my references will be to Popper (1972a,b,c); and to the information on recent developments in the philosophy of science in Suppe [ed.] (1977).

At the outset, despite my harsh comments, I subscribe to most of Popper's philosophy—as philosophic ideals. However, the self-limitations of these ideals should be examined very critically before any attempt is made to apply them to a discipline as complex as evolutionary biology. At least some of the confusion already rampant in the field is due to oversimplistic attempts to use Popperian ideals.
A CRISIS IN THE PHILOSOPHY OF SCIENCE

PROBLEMS WITH INDUCTION AND SEPARATING SCIENCE FROM FANTASY

Epistemology is concerned with the problem: How and how much do we truly know of that which we think we know? The question is central to all science, and it still lacks a generally satisfactory answer. Logic is concerned with developing rules of argument, which if properly followed, will yield a true or at least a probabilistically true output from a true input. The rules of logical argument are central to the program of gaining scientific knowledge, but even here, there are important and unsolved problems. This is particularly true of inductive reasoning.

Induction, as used in science, is the process of inferring conclusions about the existence and details of natural laws from specific observations of the consequences of these laws. In other words, it is the logic of making generalisations from "facts." Popper (e.g., 1972a, b, c) and many others have unquestionably shown that conclusions reached by inductive methods can never be proven to be absolutely true. Yet, how does science gain "knowledge" of natural laws except through the specific observations it makes? This paradox is known as the problem of induction, or Hume's problem (Popper, 1934). A related, and even more important epistemic question is: how does one distinguish factual, rational, or scientific knowledge from fantasies? Popper calls this the "problem of demarcation".

Many philosophers assert that because one cannot argue logically from specific facts to certain truths about natural laws, then no method or schema of inductive discovery can be justified philosophically as a reliable procedure to produce probably, or certainly true conclusions (Suppe, 1973). For example (Popper, 1972a: 31, 32): "... The act of conceiving or inventing a theory, seems to be neither to call for logical analysis nor be susceptible of it ... There is no such thing as a logical method of having new ideas, or a logical reconstruction of this process ..." Or, similarly (Hempel, 1965: 7): "What determines the soundness of a hypothesis is not the way it is arrived at (it may even have been suggested by a dream or hallucination), but the way it stands up when tested, i.e., when confronted with the relevant observational data." Thus, many of these workers have explicitly washed their hands of discovery as being "irrational", and have left it to "psychologists, historians, and sociologists" to explain how scientists find new ideas (Hanson, 1958; Suppe, 1973; and others in Suppe [ed.], 1977).

Somewhat contradictorily, given their position on discovery, many philosophers have argued that repeatedly successful predictions can statistically (or inductively) verify the truth of a hypothesis: specific and observable consequences can be deduced with logical certainty from the hypothesis and stated initial conditions. If these predictions are confirmed consistently by a variety of tests, then it can be assumed that the theory is probably true (Hempel, 1965). However, Popper (1972a, b, c) shows in well-justified arguments that no finite number of specific facts can ever absolutely prove the universal theory or generalization to be true. It makes no difference whether these facts come before or after the statement of theory. Arguing from metaphysical assumptions (uniformitarianism for the future is not accepted), Popper goes even further to assert that repeated substantiations do not even show a theory to be "probably" true. This is the problem of induction in another form.

Popper (1972c: chapter 1) claims to have solved the problem of induction in
1933 by accepting that all knowledge remains theoretical, and that although some of this knowledge may be true, its truth can never be proved, even to a degree of probability. This solution makes distinguishing science from fantasy all the more important. How then do we account for the obvious practical successes of science versus fantasy in providing useful understandings of how the world works? Popper proposes an "evolutionary" theory of knowledge, which also answers his problem of demarcation.

According to him, the only logically defensible test of knowledge is that of falsification. If knowledge can be stated in the form of a theory, then specific predictions can be deduced logically from it and given initial conditions. (I pass over the critical and unresolved problem of what a theory is—cf. Suppe [ed.], 1977.) With a proper test, the disconfirmation of a single prediction logically proves the theory to be false, but no number of confirmatory tests will ever prove its truth. Popper then answers his problem of demarcation by concluding that no idea is scientific or rational if it cannot make potentially falsifiable predictions about the empirical world. Thus defined, scientific understanding grows only through proposing bold hypotheses—hypotheses which cover or include the "known" phenomena, but which are "improbable" (or information rich) because they deductively predict heretofore unexpected relationships or situations. These new predictions are then subjected to empirical tests, or in Popper's words "ingenious and severe attempts to refute them." As bold hypotheses are proposed and tested ever more stringently against reality, those which contain high contents of untruth are falsified and selectively eliminated. Thus, a bold hypothesis which survives criticism contains additional information which is not demonstrably false, even though its absolute truth cannot be proved. The net result of Popper's program to "discover" scientific knowledge is then to "evolve" selectively an increasing and empirically realistic understanding of the world (Kuhn, 1965; Popper, 1970, 1972a, b, c).

Caveat emptor. As an ideal, Popper's program has much to recommend it, but as a scientist following Popper's advice to critically test generalizations against empirical reality, I find it difficult to apply. There are several traps in the philosophical ideals abstracted above, but a digression into metaphysics and semantics is needed before I can adequately discuss them.

My most basic metaphysical assumptions for my practice as a scientist are uniformitarianism, empiricism or realism, and nondeterminism. I see no reason to assume that anything has happened in the past, or will happen in the future, which cannot at least in principle happen in the present. Nor do I see any justification for assuming the existence behind the empirical world of an ultimate reality of deterministic causality and essences. Many aspects of the empirical world are usefully and pragmatically explained by the theoretical world of nondeterministic quantum physics. For those unfamiliar with the physical evidence for the existence of this world, I recommend Eisberg and Resnick (1974) as a nontrivial introduction to the effects of quantum level uncertainty on more familiar levels of matter. Although fairly rigorous, the nonphysicist should still find this readable. If this quantum physical world is accepted as the basis for reality, the deduced conclusion is that no causal relationship involving matter is deterministic, except to a (sometimes nearly exact) approximation. Quantum level uncertainty leads to uncertainty in radioactive decay and Brownian motion. In turn, these and other nondeterministic effects on molecules directly influence such macroscopically important phenomena as neuron firing; fertilization; and the mutation, recombination, and assortment of chromosomes. Thus, nondeterministic
processes significantly affect the predictability of the development and behavior of individual organisms.

This world view has profound implications for the natural philosophy of evolutionary processes. However, one thing not implied is that these processes must be completely unpredictable. All that is indicated is that they cannot be predicted exactly. Both theory and practice suggest that stochastic or probabilistic predictions are still possible (e.g., Monod, 1971; Morowitz, 1968).

To avoid misunderstanding, either here or in later discussions, the terms deterministic, nondeterministic, stochastic, random, and cause should be defined as I use them. A deterministic relationship between two events or things signifies that the occurrence of one specific event or thing requires that the other also occur with exact and unchanging qualities and properties in comparison to the first. The deterministic relationship is assumed to apply universally. Nondeterminism simply implies that the relationship between two events or things is no longer exactly deterministic. Nondeterministic relationships may be either stochastic or random. A stochastic relationship is where one specified event or thing has a definite but not deterministic effect on the probability of the occurrence, qualities, or properties of the second. In general this relationship can be described by some probability distribution function which may reflect the actions or characteristics of some natural law. A random relationship is where one event or thing has absolutely no effect on the probability of occurrence, qualities, or properties of the second. A causal relationship between two events or things bearing a temporal relationship to one another assumes that the antecedent event influences the occurrence, qualities, or properties of the subsequent event or thing through the action of natural law. This influence may be either stochastic or deterministic, depending on the law. The antecedent event or thing is the cause, and the influenced characteristic(s) of the subsequent event or thing is the effect.

Given this groundwork, the scientist wishing to use the ideals of the philosophers of science should beware of the following difficulties:

1) From Plato and Aristotle to at least the 1960's most philosophers have been searching for a logical methodology to reveal absolute truth in an ideal world of universal and deterministic laws—a world which science has convincingly demonstrated simply does not exist in empirical reality. By 1969 the philosophers were just getting this message (Suppe [ed.], 1977).

2) Many situations which scientists are concerned with are not universal by any definition of the term (e.g., Kitts, 1977). Many logical arguments philosophers use to support their theses depend crucially on the assumption of universal determinism. For instance, although Popper accepts nondeterminism in his world view (Popper, 1972c), his argument that a generalization can be absolutely falsified by a single disconfirmation is logically invalid if the prediction to be falsified is nondeterministic. For stochastic predictions, no number of disconfirmations will ever absolutely prove falsity. All arguments, whether inductive or deductive, must be criticized on their initial assumptions and statistical merits, not by some ideal of absolute truth or falsity. (But note that the logic of statistical inference also has critical and unresolved foundation problems—Salmon, 1966, 1967.)

However, that hypotheses should be empirically realistic is still the principle which makes science different from fantasy. The idea of a test assumes that the generalization predicts empirically observable conditions which may in principle be distinguished from imaginable alternative conditions. If such predictions are confirmed, they support the belief that the generalization is realistic. If they fail, the generalization is probably
unrealistic. However, there are also other ways to eliminate unrealistic generalizations which will be discussed in more detail below.

3) Many philosophers of science, including Popper, may be criticized because they have chosen to ignore processes used to discover generalizations. Although Popper gave his main thesis the title, “The Logic of Scientific Discovery,” his program of “discovery” is no more than his evolutionary theory of knowledge as I have outlined it above. His “logic” is simply to be “bold”—to include as many untried predictions as possible under a single covering generalization, and to test as many different bold generalizations as possible—to entail the maximum information content. The logical result of this boldness should be that some increase in realistic information will survive testing. Thus, despite Popper’s lip service to the logic of making generalizations, he dismisses the process of discovery as irrational and not worth considering because it involves induction.

My conclusions amplify those of Suppe (1977) and others in Suppe [ed.] (1977): at least until recently, most philosophers of “science” have paid scant attention to how science actually works. Aside from their quixotic search for truth in a nonexistent ideal world, they have assumed that one set of heuristic schemata (e.g., the Hypothetico-Deductive schema) is adequate for all science. Most have also ignored the logic and epistemic significance of making generalizations (except for example, Hanson, 1958). Yet real science inescapably involves both making generalizations and assessing whether they are realistic. Both components yield information on the empirical realism of the putative knowledge (Salmon, 1966, 1967; Suppe, 1977), but philosophers have not even fully clarified how realistic generalizations are tested, let alone generated. Nickles (1973) and Suppe (1977) indicate the path to resolving this situation. It is to accept that each scientific discipline tends to have its own armory of heuristic schemata, which evolve as new practices prove better than older ones in producing empirically realistic knowledge. Philosophers of science should then develop a taxonomy of the various kinds of problems scientists wish to solve, identify the specialized schemata used to solve them, and ascertain the logical and epistemic values of these schemata. Then, perhaps philosophers can innovate and justify still better logics for problem solving. This work is only beginning (Suppe, 1977).

My study of heuristic schemata used in evolutionary biology is incomplete. However, I have isolated those used in my own work from the data and hypotheses within which they are embedded. Once isolated, their functions can be described and their logical and epistemic values for solving particular kinds of problems assessed. The schemata are surprisingly general: they should apply with little modification to a wide range of problems with similar logical structures in a variety of fields beyond biology. My discussion of the schemata is broken into four sections: in the first, speciation represents a class of problems which share many characteristics. Given these characteristics the possible forms of a solution and the possible ways this solution can be reached are constrained. Solving a problem of this type is equivalent to locating and then understanding an unknown but repeated signal hidden
in the random fluctuations of a noisy communication channel. The second section describes schemata used to locate those features in the noise which should be included in an explanatory model to solve the problem. This may be called a program for discovery. The third section then discusses how models may be constructed once the components of the potential solution have been located. The final section then discusses several heuristic schemata which may be used to further test the empirical realism of the hypothesis. Each of these will be illustrated by examples of how I have used them in the scelopine program.

THE PROGRAM FOR DISCOVERY BY COMPARISON

THE PROBLEM TO BE SOLVED: TO EXPLAIN COMPLEX STOCHASTIC BUT ITERATED HISTORICAL PROCESSES

The nature of the problem of speciation. Speciation is typical of problems many evolutionists study. Most evolutionists probably would accept the following generalizations about speciation: the formation of two or more present species from one past species results from historical processes comprised of individually unique and unrepeatable combinations of events which bear spatial, temporal, and perhaps causal relationships to one another. When the question of how one past species became two present species is considered, the only evidence usually available will be observable effects of the past history of events on the present. The effects of some, or many of these past events, may be partially or completely obscured by the effects of other historical events having nothing to do with the case of speciation being considered (i.e., are randomly related to it). Speciation is also a phenomenon where most causal relationships can be assumed to be nondeterministic (i.e., involving mutation, recombination, migration, selection, and sampling errors of reproduction and death—all of which trace stochastic properties from quantum physics). Although some evolutionists might disagree, there is also no reason to believe a priori that there is only one set of qualitatively similar processes which form new species. The desired solution to the problem of speciation is to find the most realistic understanding of the laws of causation governing processes which result in speciation.

As defined here with respect to historical processes, a law is a fundamental property of nature. Although the scientist can never prove that the law is known exactly, it may at least be understood to an empirically testable approximation. The most useful understandings of laws are those which prove to have the greatest explanatory or predictive power. Explanations should logically account for observations already made. Predictions should specify observations to be expected in unexamined sets of the phenomenon in question. Predictions may concern either unexamined properties of the initial cases studied, or they may apply to the same types of properties originally studied but in cases not studied initially. Obviously, if the explanation is based on unrealistic assumptions, if it is not logical, or if its predictions are not substantiated, the understanding is poor and should be revised or replaced.

Generalized statement of the problem. In its most general sense, the problem of speciation is to identify those kinds of past events which result in the formation of two or more descendent species from one ancestral species and to explain how this result is achieved. Thus it belongs to a general class of fundamentally similar problems characterized by at least most of the following assumptions about properties of the phenomenon to be explained, “P”, and of the world in which P occurs:

1) P results from complex historical processes which are evolutionary
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(i.e., they involve a series of related events and changes spread through time) and which produce the observable consequence(s) by which P is recognized.

2) Each process producing P may be resolved into a finite number of unit events which are unique for that particular example in detail, number, and spatio-temporal relationships (i.e., the process is "unrepeatable").

3) Causal relationships among the unit events producing P are governed by stochastic laws. These laws derive from fundamental properties of matter, space, and time and may be explained by them.

4) Uniformitarianism applies: nothing has happened in the past which is in principle not observable in the present.

5) Several causes may affect one event, and one cause may affect several events. Such multiple causes or causations will obey rational laws of interaction as in 3 and 4, above.

6) The only evidence of past events in processes which result in P is their empirically observable consequences in the present.

7) These consequences may be obscured to some unknown extent by the effects (or "noise") of events unrelated to P.

8) Although processes producing P are unique because of their differences in detail, P's are iterated, and similar consequences produced by similar processes may be examined independently.

9) Processes producing P's may be found in various stages of completion.

10) The desired solution is to understand how the consequences by which P is recognized are produced and to determine the range of initial conditions which result in P. The understanding should be as realistic as possible.

Besides their frequency in evolutionary biology, problems with these characteristics (or simpler relatives) are found in disciplines as diverse as the history of science, geology, economics, and psychology, as recognized by Ghiselin (1969, 1974). I would add political science, ecology, geography, and cosmology to this list. The comparative approach should be efficacious for achieving understandings in all of these fields. It involves the successive and/or parallel use of various heuristic schemata and also includes several stages of corrective feedback from nature which help the evolving understanding become more realistic in its explanations of nature. Figure 1 provides a flow chart to indicate the informational relationships among the various components of the entire program of the approach.

**SIGNAL AVERAGING SCHEMATA**

**Overview.** The major source of inductive power in the comparative approach is a logical methodology which facilitates generalizations about causal relationships among present variables. It works with sets of facts obtained from observations of the present characteristics of multiple examples of P. The core of the method is a statistical signal averaging or cross correlation procedure: if multiple cases of P exist and can be studied, and if the causes of these P's are iterated, then their effects projected onto present features should be detectable as modes of correlation with one another and with the features that identify P. The "noise" due to random features should not correlate significantly. The added information

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1If P results from more than one set of causes, at least the number of these sets should be small with respect to the number of cases available for analysis, and there should be several cases of each set.
Presumably, initial events will be less obscured in the earlier stages by noise and subsequent events than they will be in later ones. Dated stages should also provide evidence on the temporal evolution of the processes involved.

It is even better if a group of genetically or otherwise related cases can be found which resemble the P cases, but which lack the features of P itself. These may be considered as "controls" for the "experimental" cases which do exhibit features of P. If the experimental or P cases show correlated features not found...
among the selected controls, this provides strong evidence that these are causally related to P.

The signal averaging principle will be amplified and exemplified, as I describe and discuss the individual steps in the discovery program (Fig. 1). These examples serve to introduce the sceloprine studies.

STEP 1: PROBLEM IDENTIFICATION AND INITIAL SPECULATIONS

**General principle.** Contrasted with mere data gathering, any scientific research should begin with a problem. The problem will generally first be seen by the scientist as a situation or phenomenon which is inadequately explained by his knowledge of the world. The more clearly the problem can be demarcated and questions relating to it formulated, the easier it will be to develop specific methodologies to find the desired knowledge.

**Background information on the sceloporines.** While I was an undergraduate in biology at San Diego State University, from 1961 through 1964, I became interested in lizard biology and studied some simple field ecology problems with local species under the supervision of Don Hunsaker II. From my courses (including Richard Etheridge’s comparative anatomy of the vertebrates) and informal contact with Etheridge and Hunsaker, both experts on sceloporines, I became familiar with these animals and the problem they posed.

According to Smith and Taylor (1950), the lizard fauna of continental North America included 54 species of *Sceloporus* and perhaps 50 *Anolis* (also iguanids). The next most speciose genera in North American representation were *Eumeces* (Scincidae) with 22 species, and *Cnemidophorus* (Teiidae) with about 17 species. No other genus contained more than about 15 species by this taxonomy. Aside from being remarkably numerous, *Sceloporus* species are also ecologically remarkably diverse. They are found in almost every habitat available to lizards; over a range from the Canadian border to Panama, from below sea level in desert basins to above timberlines in high mountains, and from extreme tropical rainforests to extreme temperate deserts. In many areas three to seven species occur sympatrically. No other North American genus approaches this ecological diversity or species density, although both *Eumeces* and *Cnemidophorus* have wider geographic ranges due to their occurrence on other continents.

Savage (1958) grouped *Sceloporus* with eight other genera (*Phrynosoma*, *Uta*, *Urosaurus*, *Petrosaurus*, *Callisaurus*, *Holbrookia*, *Uma*, and *Sator*) to form the sceloprine branch of the family. Etheridge (1964) excluded *Phrynosoma* from this assemblage, but acknowledged its close relationship. Etheridge’s (1964) osteological observations indicated that *Sceloporus* are not primitive sceloporines. *Sceloporus*, *Uta*, *Urosaurus*, and *Sator* were grouped in a relatively derived position within the sceloporines (see Fig. 2, from Presch, 1969, based primarily on Etheridge, 1964). Although osteology does not differentiate among these four genera, external morphology (development and imbrication of body scales, and the loss of the gular fold) suggests that *Sceloporus* are probably derived even with respect to *Uta* and *Urosaurus*. Also, a comparatively recent derivation is supported by the fact that morphological variation among the 54+ species of *Sceloporus* does not exceed that found in other iguanid genera with only 10 to 15 species. A thesis that *Cnemidophorus*, as it is presently known, may have up to 5 or 6 species occurring sympatrically in areas of the Rio Grande Valley of New Mexico. However, in these cases, all but one or two of the “species” prove to be diploid or triploid unisexual parthenospecies, which clearly are the products of instantaneous speciation. Most of these are proven to be of hybrid origin (Cole, 1975; Parker and Selander, 1976).
For a cytogenetics course project (Hall, 1964) also suggested by Hunsaker, I col-

_**PHRYNOSOMA** (15 sp.)  **UMA** (4 sp.)  **CALLISAURUS** (1 sp.)  **HOLBROOKIA** (4 sp.)  **SCELOPORUS** (54 sp.)  **SATOR** (2 sp.)  **UROSAURUS** (10 sp.)  **UTA** (9 sp.)_

e. First cervical rib lost
f. Clavicles develop hooks
d. Frontals covered anteriorly in some

c. Lacrima! an postfrontal lost
g. Interclavicle median process shortened

PHRYNOSOMA (15 sp.)  **UMA** (4 sp.)  **CALLISAURUS** (1 sp.)  **HOLBROOKIA** (4 sp.)  **SCELOPORUS** (54 sp.)  **SATOR** (2 sp.)  **UROSAURUS** (10 sp.)  **UTA** (9 sp.)

a. Sternal fontanella increased in size
b. Sternal ribs reduced to 3

c. Lacrima! and postfrontal lost
d. Frontals covered anteriorly

e. Sternal fontanella of moderate size

PETROSAURUS (incl. STREPTOSAURUS) (4 sp.)

A. Sternal fontanella of moderate size
B. Sternal ribs 4
C. Lacrima! and postfrontal present
D. Frontals exposed anteriorly
E. Five pairs of cervical ribs
F. Clavicles without hooks
G. Interclavicle median process long.


oporus had more opportunities for speciation simply because it is an older radiation cannot reasonably explain the striking species diversity. The conclusion from these data showed that the species diversity of Sceloporus was extraordinary compared to other North American genera, and particularly to their close relatives.

Hunsaker continually reminded me that this anomaly presented a fascinating problem to be explained. However, no opportunities in biogeography or specializations in ecology or morphology explained why Sceloporus, instead of some combination of the related genera, should have achieved such a striking proliferation of species. The anomalous species diversity most likely was a result rather than a cause.

For a cytogenetics course project (Hall, 1964) also suggested by Hunsaker, I col-
lected all information then available on iguanid lizard cytogenetics (Painter, 1921; Matthey, 1931; Cavazos, 1951; Hunsaker, personal communication; Schroeder, personal communication; Zeff, 1962). Data were found for 11 species (Table 1): five were from genera distantly related to Sceloporus and to one another. All were reported to have 2n=36 karyotypes, which I argued (Hall, 1964) were primitive in the Iguanidae (see Paull et al., 1976, for a discussion of the logic followed). The remaining six species, all Sceloporus or their closest relatives (Fig. 2), were reported to have 2n’s from 22 to 30 or more. Many of these data proved to be wrong, but the concentration of chromosomal diversity in Sceloporus has been fully validated (Paull et al., 1976).

First statement of the sceloporine problem. As I finished my undergraduate degree in January 1964, I planned to specialize in community ecology, but my ecological interests did not suggest practical master’s thesis projects. With the question in mind—“what explains the extraordinary species diversity of Sceloporus?”—I saw that the correlation of chromosomal diversity and species diversity might lead towards this explanation. I did not expect that the problem could actually be solved, but that the attempt would help me to understand better the species concept as a useful background for studying species interactions in ecological communities. The comparative approach provided the ideal tool for attacking the problem.

Even though 2n’s were available for only 11 of more than 500 species in the family, because I could see no other obvious correlation with prolific speciation, I thought that the chromosomal diversity might offer a clue (Hall, 1964). Chromosomal differentiation might allow some form of non-allopatric “chromosomal speciation,” while more conservatively evolving genera could form species only by slower allopatric speciation (Mayr, 1963). Thus, chromosomally variable lineages might form species besides those formed allopatrically. These extra species would provide added opportunities to evolve a wider variety of ecological specializations. Sceloporus was particularly suitable for intensive study, not only because of the possible association between species diversity and chromosomal diversity, but also because its many closely related species offered the possibility of finding relatively early stages in the process of chromosomal differentiation and the possibly associated speciation (i.e., where morphospecies were still “polymorphic”). The compara-

<table>
<thead>
<tr>
<th>species</th>
<th>2n:formula*</th>
<th>source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anolis carolinensis</td>
<td>36:12MM,24m</td>
<td>Painter, 1921; Matthey, 1931</td>
</tr>
<tr>
<td>Diposaurus dorsalis</td>
<td>36:12MM,24m</td>
<td>Zeff, 1962</td>
</tr>
<tr>
<td>Crotaphytus collaris</td>
<td>36:12MM,24m</td>
<td>Cavazos, 1951</td>
</tr>
<tr>
<td>Phrynosoma cornutum</td>
<td>36:12MM,24m¹</td>
<td>Painter, 1921; Zeff, 1962</td>
</tr>
<tr>
<td>Holbrookia texana</td>
<td>34-36:12MM,22-24m¹</td>
<td>Painter, 1921</td>
</tr>
<tr>
<td>Urosaurus ornatus</td>
<td>30:12MM,18m³</td>
<td>Painter, 1921</td>
</tr>
<tr>
<td>Sator angustus</td>
<td>28:12MM,16m²</td>
<td>Hunsaker, pers. comm.</td>
</tr>
<tr>
<td>Sceloporus graciosus</td>
<td>30-36:12MM,18-24m¹</td>
<td>Schroeder and Hunsaker, pers. comm.</td>
</tr>
<tr>
<td>Sceloporus undulatus</td>
<td>30:12MM,18m³</td>
<td>Painter, 1921</td>
</tr>
<tr>
<td>Sceloporus occidentalis</td>
<td>22:12MM,10m</td>
<td>Schroeder and Hunsaker, pers. comm.</td>
</tr>
<tr>
<td>Sceloporus olivaceus</td>
<td>22:12MM,10m</td>
<td>Painter, 1921</td>
</tr>
</tbody>
</table>

¹MM = Metacentric Macrochromosome, m = microchromosome.
tive approach might reveal details that would show how chromosomal speciation differed from other kinds. I also mentioned but did not discuss in detail that variation should be examined in other genera, such as *Anolis* (not closely related to *Sceloporus*) to test further the reality of the correlation between chromosomal differentiation and speciation.

**STEP 2: SELECT APPROPRIATE “EXPERIMENTAL” AND “CONTROL” CASES TO ILLUSTRATE THE PROBLEM**

*General principle.* The principle of “controlling” a comparative study is analogous to that of controlling a laboratory experiment. In the laboratory, the experimenter uses an apparatus where an independent variable can be manipulated to learn its effects on dependent variables whose variations are presumed to be causally connected to those of the independent variable. To exclude effects in the output of the experimental apparatus from unknown or extraneous inputs not under the experimenter’s control, the experiment is controlled by an apparatus which is as similar to the experimental apparatus as possible, except that the independent variable is held constant. Any variation in the output of the control apparatus is assumed to be experimental artifact, and subtracted from the output of the experimental apparatus. The variation in the dependent variable remaining after subtracting the artifact should result from the causal influences of the parameter manipulated by the experimenter.

The principle in a comparative study is the same, except that “nature” is the experimenter. The investigator selects a set of natural experiments, or cases, Cx, from nature which exhibit the diagnostic variables, V*, which identify the phenomenon of interest, P; and a set of similar control cases, Co, that do not show the V* of P. Many features, Vc, will be constant, or correlate strongly across both sets of cases. These presumably are not causally related to V* but result from the selection procedure. Other features, Vx, will show correlations within the set of Cx, but not among the Co. These Vx are assumed to be causally related to V* in the production of P.

Comparative studies differ from the laboratory experiment in that experimental cases may be selected either because they exhibit a presumed “cause” or independent variable, e.g., the fixation of a certain kind of chromosomal rearrangement, or because they exhibit the presumed “effect” or dependent variable, e.g., speciation. Also, the heuristic schema requires no hypothesis to account for the relationship of the variables, V* and Vx, or even an idea of what the Vx should be. The relationship is demonstrated as a logical consequence of the causal connections between the variables, and not by preconceived beliefs of the investigator. In practice, there may be a working hypothesis to explain P, which can help to select potentially important variables to study. This kind of selection is useful, if not too restrictive, since it is impractical to study all aspects of the cases (this is the difficulty with Baconian induction). On the other hand, preconceptions should not influence selection of which experimental and control cases to study. This should be determined arbitrarily by the way the problem is defined. In biological systems, the most obvious and probably least biased controls would be lineages which ecologically parallel the experimental lineages, and which are phylogenetically closely related to them. If such controls are not practical, depending on the problem, controls should be selected which meet at least one of these criteria.

*Sceloporine experiments and controls.* The research question formulated to guide the selection of cases for the comparative study of sceloporine speciation was based on the anomalous species diversity of *Sceloporus* relative to the other North American lizard genera: is
this anomaly explained by the fact that *Sceloporus* formed "extra" species by non-allopatric speciation mechanisms not available to conservatively speciating genera? Does this involve chromosomal differentiation, and if so, what other feature(s) result from this speciation mechanism (or mechanisms), and how is this constellation of features produced? The obvious experimental cases were speciation events in *Sceloporus*, and the obvious controls were speciation events in the other eight sceloporine genera.

Although there was no evidence, initially, to determine which *Sceloporus* species may have resulted from the supposed non-allopatric speciation mechanism(s), it was assumed that *Sceloporus* probably included many cases of non-allopatric speciation in the evolution of its 54+ species. However, some *Sceloporus* species were presumably also formed allopatrically. Although later in the study these would provide the best controls for nonallopatric speciation, initially, the cases of allopatric speciation would represent noise or artifact among the experimental cases. Thus appropriate control genera should be studied to identify features that correlate only with allopatric speciation, so they could be subtracted from the *Sceloporus* data base, to leave primarily those cases likely to have resulted from nonallopatric speciation.

The other sceloporine genera serve as controls for identifying the allopatrically speciating *Sceloporus*. These are *Petrosaurus* (2 species), *Phrynosoma* (14 species), sand lizards—*Callisaurus*, *Holbrookia*, and *Uma* (~10 species), *Uta* (6 species), *Urosaurus* (~10 species), and *Sator* (2 species). According to Savage (1958), Etheridge (1964), and Presch (1969), all share a close common ancestry with *Sceloporus*. The biogeographical opportunities for speciation appear to have been similar for all of the genera except the insular *Sator* all have distributions centering on the North American deserts, and belong to the “New Northern Faunal Element” of the North American herpetofauna (Savage, 1960, 1966) which evolved in situ along with the development of the North American deserts (Axelrod, 1950, 1958; Axtell, 1958; Norris, 1958; see also Morafka, 1977). Within this desert environment, the sceloporine genera show three main ecological specializations: *Phrynosoma*, which are specialized nomadic anteaters; the sand lizards, which are cursorial insectivores that run after their prey, and which normally perch directly on the ground or small stones; and the *Uta-Sceloporus* assemblage, which normally perch off the ground (on rocks, trees, bushes, etc.), and wait for prey to come within easy striking distance. At least *Uta* and *Urosaurus* should ecologically parallel *Sceloporus*. Other controls are needed to distinguish speciation of any kind from non-speciation. These are provided by studying different populations included within operationally defined species.

Extending the idea of the natural experiment, if the correlation between chromosomal diversity and species diversity seen in the sceloporines results from generally applicable natural laws, rather than from some unique specialization of *Sceloporus*, then the “experiments” should be repeatable: similar patterns of correlation should be seen when other prolifically speciose genera such as *Anolis* and *Liolaemus* are compared with their appropriate controls.

**STEP 3: INITIAL DATA COLLECTING**

**General principle.** Once appropriate experimental cases and their suitable controls have been selected, then as much information as practical relating to each should be collected: a “history” should be developed for each case. The inductive power of the methodology depends on not limiting observations to those parameters which would support the preconceived speculations. Every attempt should be made to survey a
variety of parameters, some of which might potentially relate to P, and some of which should not.

Data collected or available from the sceloporines. In my studies of the sceloporines, besides collecting information on a variety of cytogenetic parameters from as many species as practical, I have observed reproductive biology, anatomy, population biology, and ecology. Also, I have tried to keep track of all published work dealing with any aspect of the biology of the genera being studied. These data will be presented in the more detailed papers to come later in the present series.

**STEP 4: CROSS CORRELATION ANALYSES**

General principles: Signal averaging schemata. The major inductive power in the comparative approach comes from heuristic schemata which facilitate generalizing from specific observations to assumptions about causal realtionships among the variables studied from the case histories. At the same time the methodology keeps these generalizations in touch with reality. Modes of intercorrelated variables which are probably causally involved with P can be identified independently from any a priori speculations. The schemata are developed by analogy from an inductive statistical procedure known as signal averaging.

The concept of signal averaging is well known in neurophysiology (Glaser and Ruchkin, 1976) where a frequently encountered problem is to extract iterated, but otherwise unknown signals, which are individually completely hidden within random noise in an input channel. This is the simple signal averaging schema.

Assume that a noisy input includes a signal in the form of a voltage fluctuation which has a fixed time relationship to some identifiable marker event. A computer or tape storage can then be triggered by the marker event to record the voltage fluctuations during the time sequence believed to contain the unknown signal. The marker triggered recording sequence is repeated many times with the same time delay relative to the marker event. Each recorded sequence is placed in register with the triggering events and algebraically to sum the recordings. As many recorded cycles are added, voltage deviations which are randomly related to the marker will tend to an average or null value, since positive deviations for a given time delay after the marker will tend to be as frequent for negative deviations at the same delay. However, any repeated signal embedded in the noise which shows a constant voltage fluctuation relative to the marker, will always show the same slight positive or negative deviation added to the noise. With enough repetitions, a generalized signal will eventually emerge from the masking noise as a statistical average of the repeated signals. Assuming unlimited repetitions and a constant signal, the signal-to-noise-ratio can be increased to any desired value by continued averaging, even though the signal is undetectable in any one repetition.

A slightly different schema—an autocorrection procedure—can be used to extract unmarked signals from a noise channel if they are repeated at a constant interval, even if nothing is known about the signal's periodicity or other characteristics. Here, one long recording from the input channel is chopped into many short segments of a given duration, and the segments are then added together in register relative to the chopping points. Any recurring signal in the chopped recording which has a simple harmonic relationship relative to the period determined by the duration of the chopped segment will add algebraically. With the summing of enough segments, the signal will emerge from the masking noise as in the simple signal averaging schema. With a computer, a long recording from the channel can be systematically chopped
To clarify the analogy, in signal averaging the input triggered by a marker event is recorded as a voltage deviation along the linear time axis established by the uniform movement of a tape past a recording head, or by the sequential filling of adjacent "bins" in a computer memory. If records associated with triggering events are stored individually for later off-line analysis, each recorded time deviation sequence is associated with a unique address for each specific triggering event. Thus, a one dimensional cross-correlation matrix is formed. For each specific triggering event, the input deviations are recorded along the one dimensional time axis. Note that the filled data matrix is already three dimensional in a physical sense: one dimension is established by a sequence of addresses corresponding to the sequence of individual triggering events. A second is established by the time axis of the recorded sequence for each triggering event. And the third is required to hold the specific deviations for each given instant of delay along this

Cross-correlation schemata. Analysis of data from complex, nondeterministic, but iterated historical processes involves extracting signals produced by causal events in the past. These signals are transmitted from the past through the noisy communication channel of time onto the event surface of the present, and need to be extracted from the variety of "noise" generated by random historical events. Simple signal averaging from a communication channel involves making essentially longitudinal correlations of input voltage deviations stored along the linear axis of a recording tape. By analogy, in a comparative study, when case histories are made of the present states of parameters of the selected experiments and controls, information on the variables is stored on various parameter axes (one for each parameter examined) of a data matrix for each case. The stored information in these data matrices or case histories can then be averaged to search for correlations among their parameters. This is exactly analogous to what is done with the one dimensional data matrices of the signal averaging schema. Any variables bearing relatively constant relationships among the data sets of the case histories should stand out as strong additive correlations against the "noise" due to unrelated events. I call this the n-dimensional cross-correlation schema.1

1As part of their revolution in heuristic methodology (see footnote p. 650), geographers have recently begun to think and work with multidimensional "data matrices" very similar to the idea I propose here. Matrix manipulations and multivariate statistical procedures (many of them from numerical taxonomy!) are applied to identify modes of correlation and relationships among the various parameters of these matrices (e.g., Berry, 1964; Haggett and Chorley, 1967; Harvey, 1969; King, 1969). To quote from Harvey (1969: 347-348): We are concerned to find general classes and general relationships among attributes, we are concerned with finding comparable underlying structures in complex data matrices, and, above all, we are concerned with identifying a theory about structures which can command our confidence as an analytic, retrodictive, or predictive device. Quantitative techniques for classification bode well as search procedures. They can lead us to new ideas, new frameworks for analysis, and so on. [My italics]

Although all of these points are touched on by Harvey (1969), the geographers have not focused on the ideas of selecting natural experiments and their controls, the epistemic contributions of the process of discovery to the realism of explanations derived from the process, or the ways the empirical content of the explanation can be increased through different kinds of attempts to refute it.
USE OF THE COMPARATIVE APPROACH

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The average signal is then extracted from the matrix by averaging all of the individual input voltage × time histories to form the single 2-dimensional plot of the iterated signal.

When the signal averaging schema is modified to extract information from the effects of past events on the present, the method of selecting the cases to be examined is exactly analogous to the triggering event in the one-dimensional signal averaging paradigm. Clearly, just as in triggering a recording from a noisy communication channel, the success of the n-dimensional procedure will depend on how well selection has limited the cases to be studied to one, or at most a few, underlying causes relative to the number of cases to be studied. In the sceloporine lizards, by present count (Hall, part II) there are about 57 species which are known to be, or probably are, chromosomally derived. Each of these derived species may then be the reflection on the event surface of the present of one or more instances of a past event of "chromosomal speciation". The remaining approximately 65 species in the radiation all have, or are suspected to have, identical, presumably conservative 2n = 34 karyotypes. These almost certainly do not reflect past chromosomal speciation. The radiation includes approximately 120 species in total. Each pair of species will include one or more speciation events in its derivation from a common ancestor. When averaged, the cases should form at least two modes of correlation—one resulting from allopatric speciation and the other(s) from nonallopatric speciation. Differences between these pairs can also be compared with differences between paired populations belonging to a single species. Once cases have been selected, an n-dimensional data matrix is established for each case history. A different axis of the standard data matrix is used to store observations for each kind or parameter being studied across the selected cases.

If features of the selected cases reflect iterated but still unknown underlying mechanisms, and if all cases have similar ages relative to P (i.e., if the triggering event bears a relatively precise time relationship to the signal), then when a given axis is averaged from the data matrices from the selected cases, states of a parameter having a specific causal (either caused or causing) relationship to the process should frequently coincide. Conversely, states of a parameter only randomly associated with the process should be randomly distributed and should average to some neutral value. In some cases, effects due to unrelated processes may also add to the value of a causally related parameter, but presumably the deviations from these other effects would also be random with respect to the value causally related to P. In other words, the effects of random events should be exactly analogous to the noise in a communication channel. For causally unrelated parameters, observations would include only noise, and should average null as the number of record matrices examined is increased. For a causally related parameter, the observations will include a signal embedded in the noise, which should give increasingly stronger correlations as the sample size is increased. Similarly, causal relationships between different parameters will show up as cross correlations across the parameter axes involved.

Here the importance of having "controls" for experimental cases should be obvious. The controls establish a null or baseline value for a parameter which contains only noise relative to experimental cases. Strongly intercorrelated values from experimental cases which differ from this null are fairly conclusive-ly related causally to the factor(s) which led these cases to be designated as "experiments".

However, actual historical processes will rarely be of the same age or at the same degree of completion, and values of important parameters may vary causally according to the stage of completion of
the process. This presents a problem which makes the schema more complex, but its resolution contributes importantly to the inductive power of the approach. If available information (e.g., taxonomy and phylogenetic reconstruction in the sceloporine example) allows the cases to be segregated into subsets that can be ranked according to approximately equivalent stages in the process, then it is probably most efficient to proceed by doing so. Each subset of case histories resulting from this segregation is then averaged to identify correlated parameters associated with particular stages of the process. A tentative model generated from such ranked subsets may suggest better criteria for re-segregating and re-ranking; which may, in turn, suggest revisions in the model. This negative feedback process should lead through a series of successive approximations to a stable relationship between the arrangement of the data and the theoretical generalizations drawn from the data. If the process does not converge to a stable relationship, the basic model is probably fundamentally unrealistic and other, completely different models should be considered.

In many instances it may not be obvious how to segregate the cases, or the attempt to do so may have given no useful results. An auto-correlation schema may then be used to randomly segregate the cases into variously sized subsets. Each possible combination of cases is then independently checked for cross correlation of information. The procedure is analogous to auto-correlating from a communication channel where both the periodicity and characteristics of the signal are originally known. As applied to historical problems, the schema may be termed auto-correlation by random association.

If many cases are available for study, and data have been collected for many parameters of each, auto-correlation by random association would be extremely laborious if performed manually. But data involved in such historical studies may not lend themselves to computer coding and analysis either. It is intriguing to speculate that human memories may be organized like the n-dimensional data matrices described for the cross-correlation and auto-correlation schemas (Harvey, 1969). Possibly human memories automatically correlate these matrices by random association as part of the unconscious filing system. I would even suggest that this process might account for the powerful inductive "intuition" of some comparative biologists. However, the auto-correlation process has enough logical rigor so computer processing could be used where observations can be suitably quantified, and it is also one which can be performed manually by hand sorting where few enough recording matrices (e.g., data entered in a standard format on a page) are involved to make it feasible.

In summation, signal averaging schemata provide logical methodologies to reveal correlations among variables from a given number of empirical observations of real-world situations. These correlations provide objective statistical evidence to support the inductive generalization that the correlated variables are causally related. Similarly, the methodology will also provide objective statistical evidence on the absence of causal relationships among other variables which do not show correlation. These generalizations are based directly on the evidence, completely independently from any preconception which may have been held before the observations were made. The problem of model building then becomes a greatly simplified one of plausibly explaining causal relationships which are corroborated by already existing statistical evidence. This aspect of the comparative methodology may be sufficient to explain "the truly amazing feature of Darwin's intellect" which accounted for "the frequency with which he was able to 'guess' correctly, even though he lacked the requisite data
and anything like an adequate theory governing the phenomena” (Hull, 1973: 77).

**CONSTRUCTING EXPLANATORY MODELS**

**STEP 5: MODEL GENERATION**

*General principles.* When certain variables correlate across cases selected because they demonstrate some particular $P$, this correlation provides evidence to suggest that the variables represent effects of past events in the causation of $P$. Model building then involves developing a covering explanation that requires the observed correlations as logical consequences. This resembles Hanson's (1958, 1961) program of retroduction (Achinstein, 1971). Obviously, explanations can require conditions other than those already observed. An explanation may depend on various assumed initial conditions, and unanticipated additional consequences may follow logically from these assumed initial conditions. These dependencies and requirements beyond the original observations provide opportunities for testing the realism of the explanation. However, at the very least, any realistic model should account logically and simply for those conditions already shown to correlate with $P$. Similarly, a realistic model should not require conditions already observed not to exist. Developing a realistic explanation does not test its realism, yet a program which discovers information helping to explain $P$ contributes epistemically to the realism of any explanation which logically requires this information. Examining the alternative, to have no discovery program, demonstrates this: on probabilistic grounds, explanations which logically require consequences already observed to correlate with $P$ should entail more empirically realistic information than would any single attempt to explain $P$ by a random guess, no matter how “bold” the guess. Irrationally generating and then testing many different bold hypotheses might eventually produce an empirically realistic explanation for $P$ which entailed as much information as an explanation yielded by the discovery program. However, for such explanations with similar contents, it should make no epistemological difference whether observations corroborating the required circumstances are made before or after developing the explanation. Note that this argument assumes that the information content of the explanations derives from examining the same number of variables in the same number of cases (cf. Popper, 1972c). In practice, guessing for fruitful explanations is difficult when few data limit the guesses. It is more efficient (and more justifiable epistemologically) to collect a series of related case histories in advance of guessing, and scan them for correlations. Large domains of possible guesses may then be avoided because observations already made contradict some conditions demanded by the domains. Thus, attention for guessing is focused logically on what is frequently a very much smaller domain of possible explanations not already contradicted by observations.

*Models to explain modes of sceloporine speciation.* I will show in detail later in this series that features of the cases of sceloporine speciation group into two particularly distinct modes. The characteristics of the two modes will be abstracted here from Hall (1973, 1977) to provide background for illustrating the logic followed to explain them. In one mode, pairs of closely related species show a sibling type relationship and belong to conservatively evolving radiations containing few species. The paired species frequently have an obvious history of allopatric isolation from one another and do not differ chromosomally. Usually, where species are presently in geographic contact they are so similar ecologically that close sympatry is prevented. The allopatric speciation model (Mayr, 1963, etc.) easily explains all of
these features, so this mode will not be considered further here.

In the second mode, pairs of closely related species have ancestor-descendent relationships and belong to predominantly linear sequences of phylogenetic derivation. These lineages frequently contain many species. Paired species show little or no evidence of past allopatric isolation from one another, and they frequently differ enough ecologically to coexist in extensive sympathy or syntopy. Paired species in lineages frequently differ by chromosomal rearrangements which can potentially cause meiotic malassortment, thereby reducing fitness of heterozygotes (i.e., heterozygotes show negative heterosis). Chromosomally primitive species near the origins of sequences of chromosomal derivation tend to be ecologically conservative, while highly derived species towards the ends of sequences either have extreme ecological specializations or show impressive ecological dominance. Most sequences of chromosomal derivation involve only one type of chromosomal rearrangement (e.g., all fissions or all fusions), and it seems that rates of speciation accelerate towards the terminations of the sequences of derivation. Terminal species at the ends of sequences of derivation frequently have either exhausted the karyotypic substrate for the particular type of chromosomal rearrangement involved in the sequence, or show polymorphisms for that kind of rearrangement. The most closely related populations known to differ chromosomally, form narrow hybrid zones where the populations meet geographically (e.g., Hall and Selander, 1973). Paradoxically, although hybrids in hybrid zones are fertile and backcross, there seems to be a complete block to gene flow between the chromosomally different populations. No sceloporine species outside of Sceloporus shows any evidence for chromosomal differentiation; and even within Sceloporus, speciation events between close relatives that differ chromosomally are considerably less frequent than allopatric speciation events not involving chromosomal differentiation. Yet, a greatly disproportionate number of Sceloporus species have a background of recent chromosomal derivation in their phylogenetic histories.

As observations forming this second mode accumulated, I developed a chromosomal speciation model to account logically for the correlations that emerged (Hall, 1973, 1977). The complete explanatory model resolves into three major components, each of which explains some of the features listed above. One part of the model describes how negatively heterotic chromosomal rearrangements can become fixed in populations and initiate speciation. Another explains how hybrid zones between chromosomally differentiated populations function to block gene flow. The third part of the complete chromosomal speciation model explains: 1) the disproportionate evolutionary successes of chromosomally derived species in comparison to species formed allopatrically, 2) the predominantly linear nature of sequences of chromosomal derivation, and 3) details of patterns of chromosomal variation within the lineages. These partial explanations were developed in the order listed, to account for particular correlations in the growing body of information on sceloporine speciation. Without attempting to detail their actual historical development, I abstract the reasoning followed to reach these explanations, to illustrate the logic of model generation.

The chance fixation model. The first and most obvious correlation seen with the prolific speciation of Sceloporus related the fixation of chromosomal differences between species to prolific speciation. Species differ by Robertsonian mutations, which, at least theoretically, are negatively heterotic because they cause meiotic malassortment (White, 1973, 1978). Thus, heterozygous hybrids and backcrosses between
chromosomally different populations should be less fit than either homozygous parental type. Two consequences follow directly from this assumption: 1) Reduced hybrid fitness should serve as a partial barrier to reduce gene flow between the chromosomally different homozygous populations. This will make it easier for them to evolve independently. 2) Reduced hybrid fitness should also selectively favor individual genotypes which avoid hybridization. Thus, the chromosomally differentiated populations should rapidly evolve isolating mechanisms to prevent hybridization. Both consequences would work in the absence of allopatric isolation to speed the evolution of a completed barrier to gene flow between the chromosomally different populations. Neither consequence would occur if the populations were geographically isolated from one another.

Thus, in theory, negatively heterotic chromosomal differences can aid speciation; but how are the differences first established? Any mutation which has a strong enough negative heterosis to favor the evolution of a barrier between incipient species could not become fixed in a large, randomly breeding population. This is because the Hardy-Weinberg equilibrium frequency equals the frequency of the new (rare) chromosome, while the frequency of the neutral or advantageous homozygous mutant genotype equals the square of the frequency of the new arrangement. In a large population, essentially all of the chromosomes carrying a new rearrangement will occur in the selectively disadvantageous heterozygous state. Hence selection will quickly eliminate it, even if it potentially has a strong selective advantage in the homozygous state.

However, if the negatively heterotic mutations should occur in a very small population, statistical sampling errors in mating (= genetic drift) become evolutionarily significant. Here, a negatively heterotic mutation has an evolutionarily interesting possibility of becoming fixed by chance (about one chance in $10^{-3}$ for a population size of 10 and a 50% reduction in heterozygote fitness [Wright, 1941]). Also, selection against negatively heterotic mutants constantly works to eliminate whichever chromosome arrangement is rarest in a population. If a new mutation once passes 50% frequency by drift, selection will work to push it to complete fixation, even against some immigration of individuals carrying the ancestral chromosome. Hence, as long as the small population remains predominantly inbred, small amounts of outcrossing per generation (say up to 10 or 15%) will not greatly affect the probability of fixing a new mutation. Given reasonable conditions of population structure, fixation of the chromosomal rearrangement may occur entirely without allopatric isolation of the populations in the classical sense.

In this partial model, initiation of chromosomal speciation requires certain antecedent conditions: 1) Chromosomal heterozygotes are substantially less fit than either homozygote. 2) Negatively heterotic mutations occur with appreciable frequency. 3) These negatively heterotic mutations occur in populations which include many small inbred demes. It follows from these initial conditions and the chance fixation model that: 1) Chromosomally derived species will be "founded" by initially very small demes within which the chromosomal rearrangements first become fixed. 2) Such founder populations occur within the geographical range of the chromosomally more primitive ancestral stock. 3) Competitive interactions between the founder population of the chromosomally derived incipient species and the much more massive ancestral stock should force the derived species to differentiate ecologically away from the niche of the more massive ancestral stock. Thus, given only the correlation between chromosomal diversity and species diversity, other observed correlations follow logically from the most straight-
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forward guess to explain the first correlation: species will be formed in an ancestor-descendent relationship, and chromosomally derived species will be ecologically derived relative to their ancestral species.

However, predictions of this simplistic chance fixation model seem to be contrary to the evidence in at least one respect: selection against parents which hybridize to form the negatively heterotic chromosomal heterozygotes should lead to the rapid evolution of premating isolating mechanisms to prevent this hybridization. Evidence from the narrow hybrid zones in *Sceloporus grammicus* (Hall, 1973; Hall and Selander, 1973), and similar studies in other organisms (e.g., Nevo and Bar-El, 1976; Szymura, 1976a, b; Szymura et al., in preparation; White et al., 1964, 1967, 1969), suggests that selection in these hybrid zones does not lead to the evolution of premating isolation. Paradoxically, although the failure to evolve premating barriers allows frequent hybridization and backcrossing rather than just reducing gene flow, the hybrid zones appear to completely block it. The second partial model was developed to explain this paradox.

*The hybrid sink model.* If populations differ by a negatively heterotic mutation and hybridize, their hybrid zone will include a relatively high frequency of less fit heterozygotes. Because of the negative heterosis of the hybrids, populations in the center of the zone will have a reduced productivity compared with pure homozygous populations outside of it. Thus, hybrid populations will put less pressure on the carrying capacity of their environment than will the pure populations. Consequently, there should be a net migration or diffusion of individuals from pure populations towards the reduced pressure of the hybrid zone. Migrating individuals will carry their genes towards the "sink" for gene flow, represented by the chromosomally unbalanced (and therefore genetically lethal) gametes of the chromosomal heterozygotes and the balanced gametes that may combine with them to form lethally unbalanced zygotes. It seems reasonable that the diffusion gradient towards the hybrid zone may become steep enough to prevent any gene from leaving the vicinity once it enters the zone, and that this may happen well before a complete sterility barrier evolves. Hence, the hybrid zone may completely block gene flow between the pure populations even though hybrids and backcrosses retain appreciable fertility. It also follows that the residence time of any gene in the hybrid zone should be relatively short, as long as individuals carrying this gene cannot discriminate absolutely against mismating with chromosomally different individuals. Thus, the sink would probably prevent the evolution of premating isolation in the hybrid zone, even though selection favors this. No single gene mutation would be likely to confer its carrier with a complete discriminatory ability to avoid mismating, and any gene conferring only partial discriminatory ability would almost certainly be lost in the sink before other mutations allowing partial discrimination could combine with it to produce a perfected isolating mechanism.

Many details of the fully developed hybrid sink model have been suggested by field observations of the sceloprine hybrid zone. These will be discussed in later papers of this series. However, of concern here is that hybrid sinks should exhibit surface tension (Key, 1968, 1974). Populations on the concave side of a curved hybrid zone will have a shorter contact front than will those on the convex (or outer) side of the curvature. If other circumstances are equal, the population on the concave side cannot feed as many immigrants into the sink as can the other population. Consequently, the larger number of immigrants from the convex side will push the center of the zone towards the concave side. Where
populations meet on a broad front, this surface tension effect will tend to straighten out any kinks in the contact. But where a newly differentiated founder population occupies only a very small area within the range of its parental stocks, the surface tension will press inward around this entire circumference. Many newly differentiated populations must be quickly swamped by this effect, thus raising the question: could any chromosomally differentiated populations survive swamping in this critical early state? Attempts to answer this question and to account for the impressive ecological dominance of the products of one chain of derivation in *Sceloporus* led to guessing for the third part of the chromosomal speciation model.

*The cascading or chain speciation model.* Three sets of assumed or demonstrated circumstances provide the basis for this explanation, which also accounts for the remaining features correlated with rapid speciation in *Sceloporus:* 1) Chromosomally differentiated species originate as very small founder populations. 2) The probability that chromosomal differentiation will occur at all is profoundly affected by: a) rates of chromosomal mutation, b) behavior of the chromosomes in meiosis and the genetic consequences of any meiotic errors, c) details of the species' mating system, and d) details of its population structure. 3) The aspects of a species' genetic system listed above are genetically controlled. These circumstances allow evolution by two unusual mechanisms, a group selection effect and a positive feedback or deviation amplifying process (Szarski, 1971). These may counteract natural selection working at the level of single individuals.

The genetic system parameters listed above can vary considerably and still have minimal effects on individual fitness. Hence, if loci determining them are polymorphic, demes small enough for fixing chromosomal rearrangements may also show substantial variation in these parameters due to genetic drift. Over the range of a species which has an appropriate population structure, through chance some demes will have a much more favorable genetic background for chromosomal speciation than will others. It follows that chromosomal speciation will more likely begin in these "favorable" demes than in others. Founder populations that survive as new species will tend to perpetuate the favorable genetic backgrounds. Thus, chromosomally derived species will, on the average, offer more favorable circumstances of further chromosomal speciation than will ancestral species. This positive feedback amplification process may work in each chromosomal speciation event in a sequence to produce a predominantly linear and increasingly rapid chain of chromosomal speciation. (see Hall, 1973, 1977, and later papers in this series). Three circumstances (2 intrinsic and 1 extrinsic) can terminate such a chain of speciation.

1) If chromosomal fissions and fusions are qualitatively different kinds of mutations, different genes should affect their mutation rates. Similarly, different genes may control their meiotic behavior. Thus, if a speciation event involved centric fissions, then positive feedback effects would result in more favorable conditions for further speciation involving fissions. The chain of derivation may then proceed at an accelerating rate until all metacentric chromosomes in the karyotype were fissioned. At this point, further chromosomal speciation involving fissions would be blocked, and the genetic system might not be conditioned to favor speciation involving other kinds of chromosomal mutations. 2) One variable which has a directly proportional effect on the probability that chromosomal speciation will occur is the rate of chromosome mutation for a given kind of rearrangement. This rate could easily be raised by the positive feedback process to such a high level that many
individuals in a population would suffer from the negative heterotic effects of chromosomal heterozygosity. If this happened, individual selection would favor evolving modifications in the mechanics of meiotic assortment to prevent malassortment in the large number of heterozygotes carrying new mutations. Chromosomal heterozygosity would no longer show negative heterosis and could no longer produce the hybrid sink required for successful speciation. Consequently, the species forced into this adaptation could form no more species chromosomally, but would be left with a high rate of chromosome mutation, and should be polymorphic for the kinds of rearrangements involved in the chain of derivation in its ancestry.

3) The third type of termination involves extrinsic circumstances. If the chain speciation process works as I have suggested, a fairly large number of species may form in a geologically short time under circumstances where they are not geographically isolated from one another. If species need an ecological niche of some minimum width, and if their basic adaptations allow them to use only a certain subdivision of the environment, then as the lineage proliferates new species, they would be limited to progressively more restricted niches or geographic areas. Eventually a point would be reached where further speciation either would be impossible or could not occur without extinction of other forms. If further speciation was blocked for long enough, individual selection would eventually force genetic system parameters to revert to their “unamplified” original conditions, which would not favor chromosomal speciation even with new ecological opportunities.

Group selection in this model is associated with the positive feedback mechanism, but its effects show primarily in the ecological consequences of chromosomal speciation. The major “selective” force involved is the surface tension produced by the hybrid zone surrounding newly differentiated founder populations. According to the competitive exclusion principle, two species cannot coexist in the same ecological niche. If a nascent species is formed within the range of its ancestral stock, the ancestral and derived forms will inevitably compete ecologically. Three outcomes are possible: 1) One of the species becomes extinct—most probably this will be the nascent species. 2) The two species remain in similar niches but displace one another geographically along some environmental gradient (i.e., geographical exclusion). 3) The two species coexist geographically but displace one another along one or more resource axis of the environment (i.e., character displacement). As mentioned above in the discussion of the random fixation model, in character displacement the ancestral population will almost always displace the derived population, thereby forcing it into a new and probably more specialized niche. However, in geographic exclusion, exclusion of the initially very small founder population will be equivalent to extinction.

When a lineage invades a new environment or adaptive range, and its species have few competitors, character displacement is probably easy (e.g., Williams, 1972). The ready availability of vacant sympatric niches and the initial selection against hybridization in the random fixation model may allow the rapid evolution of premating isolation. One can also imagine that establishment of a hybrid sink situation along some resource axis of the environment would prevent gene flow along the axis so that disruptive selection would favor the rapid evolution of sympatric species. However, once an environment becomes fairly saturated with related species (as in the current situation for the Sceloporus graminicus complex), most chromosomal speciation probably involves a long period of geographic exclusion. The consequences logically required by the group selection model are interesting.
Because of the surface tension of its hybrid sink, which occurs independently of any environmental circumstances, the nascent chromosomally differentiated species will be at an immediate disadvantage. If the risk of hybridization cannot be reduced quickly by character displacement and expansion into a sympatric niche (or an uncontested geographic range) the founder population will probably be consumed by its own hybrid sink. Where the founder population cannot escape hybridization its survival is likely only if the parental stock can be pushed back to increase the hybrid zone’s radius of curvature enough to reduce the surface tension. Two kinds of chance circumstances allow the founder population to achieve this initial expansion. The first depends entirely on extrinsic events, such as a catastrophe, to eliminate an adjacent ancestral population so the nascent species can spread into the depopulated area. The other circumstance depends on intrinsic aspects of the genetic system.

The founder population required for the chance fixation of a negatively heterotic chromosomal rearrangement is ideal for other stochastic phenomena such as the random fixation or drift of alleles at a variety of polymorphic gene loci. Also, founder populations will be exposed to specific local circumstances which may result in selection pressures that differ considerably from the average selective environment of the ancestral species. The ancestral species must maintain an adaptation to some average habitat occupied by populations exchanging genes with one another, while the initial barrier provided by chromosomal differentiation allows the founder population to adapt to its own specific local habitat. Thus, although most incipient chromosomally differentiated species will be quickly consumed by their own hybrid sinks, one may rarely achieve a fortuitous genotype which is sufficiently superior in its local environment so that it can feed enough migrants into the hybrid sink to counteract its surface tension. If the founder population once manages to push the sink back to a greater radius of curvature, the pressure will be reduced and the founder population’s superior fitness may then allow it to displace the ancestral stock from a wide geographic range. Chromosomal differentiation events may become frequent towards the end of a chain of derivation, but the environment will probably be too saturated to allow easy character displacement. The vast majority of these incipient species will be immediately consumed by their hybrid zones. Barring the lucky environmental circumstances, the only populations to survive will be those which achieve an especially superior adaption which allows them to overwhelm the surface tension of their hybrid zone.

Note that the positive feedback in chain speciation will also work here. Each founder population must be fit enough to be able to displace its immediate ancestor against the added impediment or pressure of the hybrid sink’s surface tension. Thus, species at the ends of chains of geographic displacement should be especially effective competitors against species formed early in the chain. Chromosomally conservative species should survive competition with their derivatives, because they presumably held extensive geographic ranges before chromosomal speciation began. However, intermediate species in a chain may easily be excluded into extinction by their competitively superior derivatives, because they may have little chance to expand geographically before producing further derivatives.

In sum, the discovery program of the comparative approach has identified in the sceloporine radiation, independently of models, a variety of circumstances of cytogenetics, ecology, and phylogenetic relationships which appear to correlate with prolific speciation in Sceloporus. These are not adequately explained by the allopatric speciation of Mayr (1963,
etc.). The "guessing" to explain the totality of these relationships has been very straightforward and has led in easy steps to a three-part model which fully explains all of the phenomena revealed so far by the discovery program. By contrast, none of the guesses made in advance of collecting these data make predictions which approach the richness or realism of the circumstances logically required by the complete model and reasonable initial conditions. The complete model is, of course, fully corroborated by the information content of the conditions it has been developed to explain. The question remains—can the realism of these explanations be tested further? The answer provided by the next section is yes.

**TESTING EXPLANATORY MODELS**

*General principles.* The logic of testing the realism of explanatory models for historical processes is not difficult. However, it is my impression that many workers who fail to understand how the models are generated, fail also to understand all of the tests which can be used to further corroborate them (e.g., Peters, 1976). Under any circumstances it is logically impossible to prove any universal explanation to be absolutely true; although if uniformitarianism is accepted, the explanation can be demonstrated to be realistic to some degree of statistical confidence. If the world is fundamentally nondeterministic, falsity cannot be absolutely proven either. However, the idea of empirically testing and criticizing the logically derived statements a theory makes about nature still must form the basis that makes science different from fantasy.

If the program of discovery described above is followed it will lead to generalizations which already contain a large quantity of empirically realistic (or pretested) information. However, the program of science is always to extend the frontiers of knowledge, and Popper's evolutionary theory of knowledge suggests how this should be done, except rather than beginning by testing wild guesses, the program begins with testing generalizations which already include a large body of pretested and empirically realistic information. Following Popper the content of realistic information entailed by the explanation can be increased by attempting to refute it.

There are at least three ways to refute an explanation (most workers think only of testing "predictions", and assume that an explanation which cannot be attacked in this way must be metaphysical, e.g., Peters, 1976): 1) An explanation may be refuted if its predictions are consistently unrealistic. 2) If an explanation depends logically on certain initial conditions or assumptions and it can be shown that these are unrealistic, then the explanation is refuted (Ghiselin, 1969). 3) Also, if it can be shown that supposed final conditions actually do not follow logically from supposed initial conditions, the explanation is obviously faulty. Full corroboration of an explanation should require that it survive all of these attempts to refute it. Each of these tests will be explained in more detail and illustrated with examples from my research program.

**STEP 6: TEST LOGIC**

*Principle.* In principle, testing the logic of an explanation requires no additional data gathering or processing. This should be the first and most obvious type of test to apply, but judging by many of the published attempts to explain nonallopatric speciation, it is frequently overlooked. The critical question to be asked in this kind of test is, do the supposed consequences the model proposes to explain actually follow logically from its supposed initial conditions. It should
be possible to reduce deterministic models to mathematical or logical symbols to see if the consequences do follow. For stochastic models, some of which can become quite complex, it should be possible to test their logic by computer simulation to see if the supposed consequences follow from the initial conditions and the explanation.

**Application.** Several aspects of the chromosomal speciation model are susceptible to testing via computer simulation. The most critical points to attack are:

1) **Fixation of negatively heterotic mutations in small populations:** the probability of fixing a negatively heterotic mutation should be calculated or determined by simulations for a variety of population sizes, migration rates, and relative fitnesses of the three possible genotypes (two homozygous conditions versus heterozygotes).

2) **The hybrid sink effect:** for various conditions of population structure and density, vagility, and degrees of negative heterosis, how effective is the hybrid sink as a block to the penetration of unlinked or linked alleles? What relative fitnesses of the two populations are required to maintain a curved hybrid sink in equilibrium and how do these vary as a function of the radius of curvature of the center of the sink? What conditions would be required to form a hybrid sink along an environmental resource axis rather than a geographical axis?

3) **Chain speciation and positive feedback amplification:** how reasonable is the group selection argument? For a plausible random fixation model, what mutation rate would be required to generate enough incipient species to provide a plausible frequency of species able to displace their ancestors against the initially high surface tension pressure? What changes in the frequency of alleles in controlling genetic system parameters are plausible in chromosomal speciation and how rapidly could selection at the individual level change these frequencies? Many other aspects could also be modeled, but the tests listed here would seem to have the greatest power to corroborate the proposed explanations.

**Step 7: Test Assumptions**

**Principle.** Any demonstration that a necessary *a priori* assumption of the explanation is unrealistic, immediately makes the model unrealistic to the extent that it depends on the assumption, and to the extent that the assumption is shown to be realistic. There are many ways to provide such demonstrations. Any model which assumes a "fact" of nature is falsified by demonstrating that the assumed "fact" is in reality not true.

**Applications.** The most critical assumption in the chromosomal speciation model is that the chromosomal rearrangements fixed between species were negatively heterotic when they originally occurred as new mutations. Presumably, where they are involved in narrow hybrid zones which appear to function as sinks, such as found in the *Sceloporus grammicus* complex, they should still be negatively heterotic. Thus, examining meiotic assortment in heterozygotes from these hybrid zones should test this important assumption. Such tests have already been done for a similar situation of rapid chromosomal differentiation in European mice of the genus *Mus* (Cattanach and Moseley, 1973), where single metacentric chromosomes have been backcrossed for the test into essentially pure *Mus musculus* genotypes to isolate them from possible genic problems in the hybrids. It should also be possible to do the same with *Sceloporus grammicus*. Another critical assumption concerns population subdivision. In sceloporines the most recent chromosomal speciation appears to have been in the *Sceloporus grammicus* complex. Superficially it appears to have an ideally
subdivided population. However, the assumption can be tested further by making detailed observations on population structure, mating system and vagility by using mark-observation and recapture methods.

**Steps 8 and 9: Testing Predictions**

*Principles.* If an explanation requires potentially observable circumstances (conditions which should be causally related to P) which have not been examined, then attempts to demonstrate these circumstances will test the explanation. For stochastic models, confirmation or disconfirmation of these predictions will support or reject the explanation with some degree of statistical confidence. Such tests can take at least two qualitatively different forms: testing predictions in a relatively strict meaning of the term, and testing the ability of the model to reconstruct case histories realistically.

Testable predictions can be subdivided into three categories: 1) The model may predict already observed classes of phenomena in new cases (i.e., the natural experiments should be repeatable). 2) The model may predict new classes of phenomena in cases already observed. 3) The model may predict new classes of phenomena in new cases. These are listed here in the order of the epistemic values of the tests from least to most (cf. Popper, 1972a, b, c). However, it should be recognized that an efficient discovery program may already have found all of the classes of phenomena causally related to P. If the explanation covers these, the failure of the model to predict "new classes of testable phenomena" does not necessarily suggest that the model is unscientific as Popper might claim. If both the logic and assumptions of the model have been tested, the failure to predict new phenomena suggests that the discovery program has already provided the model with nearly the maximum content of information available in the domain it covers. That is, the model has been proven to be realistic within the limitations of the real world. This would correspond to Kuhn's (1962, 1970a, b) "normal science".

Historical explanations can be used to make "predictions" of still another kind. Models will usually be expressed in the form of generalizations about assumed initial conditions and the *kinds of effects* expected to follow from them. Aside from predicting general classes of phenomena, as discussed above, the explanations should also allow the past histories of specific cases to be reconstructed in detail. If evidence not already included in the model by the discovery program allows an independent reconstruction of the past histories of cases, then the realism of the model is tested to the degree that the independent reconstructions are realistic and coincide with the reconstructions provided by the model.

*Applications.* Except for requiring certain initial conditions which can be tested empirically, the chromosomal speciation model predicts no phenomena not already suggested by the discovery program. However, these "predictions" can be tested over a wider range of sceloporine species than have been examined to date. Also, the predicted patterns of chromosomal variability and phylogenetic relationships should be found in other speciose genera of the Iguanidae (i.e., in *Anolis* and *Liolaemus*) and they should not occur in other small genera (Paull et al., 1976 have already begun this test). Also, can these patterns be found in other lizard families, other classes of vertebrates, and other phyla? The most critical tests available are those of the accuracy of historical explanations. The chromosomal speciation model greatly constrains possible phylogenies which can be reconstructed from karyotypic evidence. Do these karyotypic phylogenies correspond to phylogenies
which can be reconstructed from evidence provided by independent character sets?

OTHER CONSIDERATIONS

Corrective feedback and the growth of knowledge. Tests provide new empirical observations which tend to falsify, support, or suggest extending the tested model. Whatever the "favorable" or "unfavorable" import of the observations for the model being considered, these new data increase the information content of the domain of the explanation which includes the observations by giving a more complete view of the world than existed previously (Popper, 1970, 1972). A methodology which does not take advantage of this input is less than fully effective. Where some assumption of a model has been proven false, the obvious response is to find another explanation for the available data which does not depend on this assumption. If this cannot be done, perhaps the problem is poorly defined and the new data may suggest a clearer formulation of the research question, further data collecting, and/or looking at the available case histories in new combinations. Predictive or reconstructive tests automatically provide new data which can be entered in the cross correlation analyses to improve their inductive precision, and the evidence provided by the new data should clearly indicate the strengths and weaknesses of the tested model. Assuming that a model has at least some contact with reality, this feedback should lead through successive approximations of data gathering, testing, and revisions to ever more realistic understandings of the fundamental laws governing the processes modeled (Popper, 1972).1

Semantics and syntax. The final epistemological difficulties of a methodology for the comparative study of evolutionary problems concern the precision of its tools. Since the comparative approach seeks to understand processes which cannot be manipulated readily in the laboratory, information and speculations concerning them must be abstracted through several levels of language before they can be manipulated logically in building and testing explanatory models. The logical sequences of abstracting inductively from reality to formulating a model, and reflecting deductively back to reality for testing the model, both depend on the precision of the symbols used for these manipulations. The conclusion of any logical argument of this nature can be no stronger than the weakest or foggiest definitions used in the chain of reasoning. (Note that this is a very different problem from determining the "essential" meaning of a word; cf. Popper, 1976.) Many proposed explanations of non-allopatric speciation are unrealistic because of logical problems introduced by using common words with semantically or syntactically faulty definitions. These faults are easily made by using as descriptors of nature (i.e., "facts") terms which were originally defined on the basis of some unsubstantiated model of nature. As Popper (e.g., 1970, 1976) and others (e.g., Kuhn, 1962; and others in Suppe [ed.], 1977) have shown, all words are theory laden, so the problem is unavoidable to some degree; but the utmost should be done to minimize it, and it is certainly unwise for an investigator to forget that it exists. Another reason for the confusion of proposals cited in my introduction results from inconsistent use of terms in discussing speciation phenomena between the different

1See Lakatos and Musgrave [eds.] (1970) for a debate between Popper, Kuhn, and their various followers and critics about their respective ideas concerning how scientific "knowledge" grows and can be defined through its contacts with empirical reality.
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"scientific communities" (Kuhn, 1970: 176) concerned with the problems of species and speciation.

Thus, although many before me have discussed these definitions, I think it essential for the following papers in this series to redefine much of the vocabulary concerned with geographic and genetic relationships of populations and species, and with isolating mechanisms and their failures. A glossary of these definitions will be provided later in this series.

CONCLUSIONS

Solving the problem of speciation. To understand realistically how new species form is probably the most difficult task evolutionists have attempted to achieve. Besides confronting the unresolved problem of what species are, these attempts confront the fundamental epistemological problem of determining how realistic the explanations are, when speciation cannot be directly manipulated or observed. I propose that the comparative methodology described above answers the epistemological problem and provides an efficacious approach towards explaining how species are formed, and thus also, what they are. Many evolutionists claim to use comparative methodologies but few appear to understand clearly the epistemic power of the approach; so far as I know, none have adequately formulated or justified the logical methodology. From this, and my own experience with the approach, I conclude that it is sufficiently novel to be explained in detail and justified philosophically. Therefore, in the present paper I have presented and justified epistemologically the logical schemata I have followed in my own attempts to solve the problem of how species are formed. These schemata offer seemingly novel tools, both for discovering causally related effects of historical processes hidden among the noise of unrelated events, and for empirically testing the realism of any models proposed to explain the process and its causally related effects. In justifying these schemata I confront and tentatively answer two major problems in the philosophical foundations of scientific methodology: 1) Is there an inductive logic which can be used to infer realistic generalizations about nature from specific observations of nature, and if so what is the epistemic value of this logic? 2) How can one test the empirical realism of generalizations about historical processes, when the processes cannot be observed or manipulated experimentally? The answers to these questions provide a methodology which appears to be effective for understanding speciation, and a surprisingly wide diversity of other historical problems ranging from cosmology through economics and possibly even to fundamental particle physics. The approaches to answering these questions also seem to indicate the way to solutions of some of the foundation problems of the philosophy of science.

The inductive power of the comparative approach is most effective if it can be applied to a compact phylogenetic radiation which can be subdivided into a series of genetically and ecologically related cases, some of which serve as "natural experiments" to demonstrate the phenomenon to be explained, and others which serve as "controls" because they are similar to the "experiments" in most respects, but do not show the experimental phenomenon. The 120+ species of the sceloporine radiation of the lizard family Iguanidae provide an ideal radiation for this comparative approach. The radiation involves at least two qualitatively different modes of speciation which may be compared and contrasted by the comparative methods to help isolate specific features that help to explain the differences. I abstract my research program on the comparative cytogenetics, speciation, and evolution of the sceloporine lizards to illustrate how the comparative methodology has actually
been used in my own research program. Thus, the present paper serves to introduce the series of papers to follow, which will present in detail the results of the research program on sceloporine speciation. It also serves as a methodology section for this program.

_Modes of speciation: where we stand._

To illustrate and recapitulate the epistemological problems the present paper faces and attempts to solve, I offer the following quotations as a necessary background to the attempt to understand sceloporine speciation:

It is rather discouraging to read this perennial controversy because the same old arguments are cited again and again in favor of sympatric speciation. In the last analysis, all the various schemes make arbitrary postulates that at once endow the speciating individuals with the attributes of a full species. They attempt thus to bypass the real problem of speciation. One would think that it should no longer be necessary to devote so much time to this topic, but past experience permits one to predict that the issue will be raised again at regular intervals. Sympatric speciation is like the Lernaean Hydra which grew two new heads whenever one of its old heads was cut off. There is only one way in which final agreement can be reached and that is to clarify the whole relevant complex of questions to such an extent that disagreement is no longer possible. (Mayr, 1963: 451)

False facts are highly injurious to the progress of science, for they often endure long; but false views, if supported by some evidence, do little harm, for everyone takes a salutary pleasure in proving their falseness; and when this is done, one path toward error is closed and the road to truth is often at the same time opened. (Darwin, 1889: 606, as quoted in Ghiselin, 1969—emphasizing the importance of distinguishing syntactically between observations and explanations)

For evolutionary biology...history...provides the needed key to scientific knowledge. Our approach to evolutionary and population problems should involve historical reconstruction as well as more traditional comparative and experimental techniques. We must account for what actually has occurred: what might take place under ideal conditions will never do. Otherwise we shall justify our conceptions of things from our ideas, rather than letting the way things are determine how we shall conceive of them. (Italics mine) (Ghiselin, 1974: 27, stressing the importance of not begging the conclusion by working logically from unrealistic initial assumptions [i.e., to avoid the error of petitio principii])

Two alternatives seem open to us at this juncture: either revert to a hypothetic-inductive model of science or argue that evolutionary theory after a century is still inadequately formulated and that in a more finished form will conform to the H-D model. The problem with the first alternative is that there is no H-I model. Thus, this alternative reduces to the admission that there is no reconstruction of science appropriate to evolutionary theory as it now stands. Biologists are currently working on the second alternative. Some are attempting to reformulate macro-evolutionary theory more rigorously so that deductive confirmation or disconfirmation is possible. Others find evolutionary theory in terms of organisms and their interactions too crude to permit an adequate formulation of evolutionary theory. Instead, they call for a molecular version of evolutionary theory, hoping in this manner to fulfill the requirements of the H-D model. . . . (Hull, 1973: 34-35)

I would claim that the comparative approach outlined in this paper is as logically rigorous both for making inductive generalizations and for deductively testing them as is possible, given a fundamentally stochastic reality. It remains to demonstrate the utility of the methodology, as will be attempted in the following papers.

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LITERATURE CITED


