# AN EVOLUTIONIST IN AN EPISTEMOLOGICAL WONDERLAND:

# **PREFACE (1979) TO CASCADES AND SINKS**

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# ABSTRACT

The paper on cascading chromosomal speciation and hybrid sinks which follows this preface was written in 1977. It faced surprising and initially incomprehensible difficulties in reviews. The epistemology and heuristic organization of the "comparative approach" used was incommensurable with the reviewers' Kuhnian paradigms. To provide a "key" for translating from the comparative heuristic, the epistemology of the comparative approach is explored as this applies to understanding the problem of speciation. Communication difficulties trace from three Kuhnian revolutionary crises: 1. in evolutionary theory over the species problem and speciation, 2. in the methodological foundations of evolutionary biology over "logics" of confirmation, refutation, and discovery, and 3. in the foundations of scientific philosophy over what scientific knowledge is and how it grows. The comparative approach is a heuristic method for rationally discovering, independently of *a priori* theories, correlations among features of the present which probably reflect causal connections with the actions of law-like evolutionary processes. Once these correlations are identified, the *ad hoc* construction of a realistic model of the process is greatly simplified. The program for discovery by comparison gives the *ad hoc* model substantial epistemic realism. This realism may be diminished or increased by the results of hypothetico-deductive testing.

## **INTRODUCTION**

Hall (1977), which follows the present paper, is a comparative study of chromosomal speciation and its evolutionary consequences in the sceloporine iguanid lizards. Several reviewers had difficulties with the heuristic structure of this MS which I had not anticipated and did not initially understand. I withdrew the MS to work out the problems revealed by the reviews, and having solved them, I now consider its

structure to be obsolete. However, the original draft was so widely circulated by unauthorized photocopying of copies I had distributed for informal reviews, that I now see no choice but to make the paper generally available more-or-less in its original state. The only changes from the original MS are minor alterations in wording and the structures of sentences and paragraphs to improve its readibility. I owe it to the reader to explain why I am publishing an obsolete paper. Necessarily, this explanation is both autobiographical and confronts some interesting current issues in the history and philosophy of science.

# **INDICATIONS OF INCOMMENSURABILITY**

The Hall (1977) MS was my first attempt to condense my 1973 PhD Thesis for publication. My thesis advisers were unable to offer useful suggestions about how to do this, and in fact, they had noticeable difficulties reviewing my thesis even as a thesis. The condensation was written in Boulder, Colorado during Spring, 1977. By comparison to my thesis, I thought that in the MS I had greatly clarified the heuristic structure of my arguments. I remained unhappy with the result, but couldn't see what else was "wrong" with it. I hoped that informal reviews would reveal the difficulties. A few copies distributed to colleagues in Boulder yielded little useful feedback. In April, I sent three copies to peers elsewhere (Ernest Williams at Harvard, George German at UCLA, and Scott Moody a PhD student at Michigan) all of whom were closely familiar with my work. Moody initially offered no constructive comments, but responded that my writing was lousy. The other two liked the cascading speciation and hybrid sink models well enough to distribute second generation copies to some of their contacts on other campuses, but neither returned critiques either.

By Summer, 1977, I still had received no useful critiques. Before I left the US for Australia in July, I visited both German and Williams to find out what they thought about the paper. Neither seemed able to come to grips with some aspect of my writing, but they weren't able to localize the problem well enough to tell me what it was. Each, rather than provide critiques, suggested that I formally submit the rough MS for publication. Editors would be obligated to provide reviews. This was done and I received formal critiques in September and October.

Both editors were prepared to accept the paper for publication, but each had difficulties I could not understand with what I thought were clear arguments used to develop the speciation models. One editor wanted so much more factual information that it would have doubled the length of the paper, but this would not have made the misunderstood arguments any clearer than they already were. I finally had some reviews, but they didn't seem to relate to the paper I thought I had written.

After Moody had made several more comments about my bad writing, I finally convinced him to provide some detailed examples of what he thought was wrong with it. His critique came in November. Aside from pointing out many difficulties in sentence construction, which is an unfortunate property of my writing, he vigorously attacked as unscientific the "inductive" organization of the paper. He also

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proved beyond any doubt in his attempts to rewrite sections that he completely failed to understand the heuristic organization of the paper. The impact of Moody's adverse review was even worse than it might seem superficially, because he had worked with me on the *Sceloporus grammicus* hybrid zone described in Hall and Selander (1973) and in Hall (1977). Yet, even Moody could not follow what I thought were very clear arguments I had used to interpret data he had helped to collect!

My failure to communicate with well informed reviewers was so fundamental that it was evident that we were not even seeing the same world. I had to question whether I knew what science was or how to practice it. I saw no choice but to withdraw the MS until I could work out why my peers were seeing something completely different from what I thought I had written. The unrestricted support of my University of Melbourne Research Fellowship allowed me to spend most of 1978 sorting out this completely unanticipated mess.

Apparently I had conspicuously used the "comparative approach" in an unusual way to guide my arguments in finding realistic speciation models, while my reviewers thought I was proposing new speciation models, and then testing them. With this understanding, I have restructured my plans for describing my sceloporine studies. Although the evidence and my interpretations have not changed, the new structure bears little resemblance to Hall (1977). My findings will be presented in much more detail in a series of 7 to 10 major papers under the general title, "Modes of speciation and evolution in the sceloporine iguanid lizards." The first section, "Solving the problem of sceloporine speciation: epistemology and heuristics of the comparative approach," explains how the study was done and the method of argument used to present it. This has been accepted for publication, pending revisions, in Papeis Avulsos de Zoologia (Sao Paulo). However, it will take at least two years to complete the series, and the problem created by the informal circulation of the now obsolete Hall (1977) remains. [See Afterword (1979) and Afterword (2003)]

Before I left Colorado, correspondence and calls about the MS came from several workers far removed from any of the informal reviewers to whom I had sent the paper. Evidently, the second generation of copies, distributed by my peers from Harvard and UCLA, also tended metastasize. Thus, within three months after I sent the paper out for review, its ideas had already achieved considerable impact. By now [in 1979], most well connected workers interested in speciation seem to have seen this paper, either at some remove from the two original centers of photocopying, or from copies I sent out later when it was clear that the MS was multiplying beyond my control. However, Hall (1977) has been known only in a form that most authors will not or cannot cite, and many do not have access to my 1973 thesis on which the paper was based. I thank David Hull for suggesting that the problem could be solved by making the original MS generally available in Evolutionary Theory.

Nevertheless, some readers of the following paper may face some of the same problems reviewers had with it. My forthcoming introductory paper for Papeis Avulsos de Zoologia explores these difficulties at length, but more work remains to be done before this goes to press, and that journal may also not be readily available, so I will summarize my findings here.

## CAVEAT

I am personally involved in these issues at a fundamental ego level, and I write what follows as an evolutionist with no formal training in history or philosophy. My confrontations with the foreign world views of these fields as they affect my work is little more than a year old. This convinces me that several more years of intensive study would be needed before I can be sure that I fully understand their vocabularies and methodologies. I still feel that I am seeing these worlds through Alice's looking glass. In particular, epistemological philosophers seem to write about worlds which have, at best(!), only the most evanescent and tenuous contacts with the kinds of realities evolutionists like myself are trying to understand. After all, epistemologists ask quite seriously, "How do we know that which we think we know, and what is it that we truly know of that which we think we know?" However, any explanation of the problems reviewers had understanding Hall (1977) inescapably involves these disciplines. For what they are worth, I summarize my tentative findings here.

#### THREE REVOLUTIONARY CRISES

Despite its many difficulties (e.g. see Masterman, <u>1970</u>; other essays in Lakatos and Musgrave, <u>1970</u>; and essays in Suppe, <u>1977</u>), Kuhn's (<u>1962</u>) book on scientific revolutions seems to explain much of what happened with the reviews of Hall (<u>1977</u>). Kuhn proposes that scientific knowledge grows through alternating periods of "normal science" and "crises," which may be resolved by "revolutionarily" new world views. During a period of normal science in a discipline, a consensus of the workers will share a "paradigm." Kuhn admits that he has hopelessly confused the semantics of this term (Kuhn, <u>1970a</u>, <u>1970b</u>, <u>1970c</u>, <u>1977</u>), but as I understand it, paradigm in the broadest sense can be translated as a shared world view. This resolves into

- 1. the acceptance of a common epistemology and methodology,
- 2. a commonly understood and used vocabulary to relate theory and observation, and
- 3. the common acceptance of a particular theory or understanding of the world.

While the discipline is practicing normal science, most studies involve using relatively standard methods to provide more and more connections between the accepted theoretical model of the world and reality. As long as predictions of the theory continue to be confirmed, and in the absence of creative genius, the discipline does little more than solve "puzzles." However, when attempts to connect the theoretical structure with reality in new ways no longer yield the predicted observations--i.e. where the observations are anomalous, the discipline faces a crisis which may be resolved only by shifting aspects of the disciplinary paradigm or world view. Any major change in the theoretical structure also inevitably involves changes in the methodology and vocabulary used to connect the theory with reality. Since no

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observational vocabulary can ever be completely independent of the (theoretical) conceptions of what is observed (e.g. see Suppe, <u>1977</u>), workers using the different theoretical structures will inevitably encounter many communication difficulties or misunderstandings. The two paradigms may use the same descriptors, but they will relate the world to different models. Thus, Kuhn says that different paradigms are incommensurable. The scientist who seeks to decide which of two paradigms is better cannot compare their claims in an objective or theory neutral vocabulary. However, he can choose which of the two offers the greatest number and least anomalous connections with reality.

Any discussion of the incommensurabilities between Hall (1977) and its reviewers seems to confront three very different, but more-or-less Kuhnian revolutionary crises, which range from the discipline of evolutionary biology into that of the philosophy of science. Hall (1977) directly confronts the first and most obvious crisis, that over the species problem. It is my belief that the models described in this paper should successfully resolve many of the anomalies which have created the crisis. I was aware of the second crisis, that over confirmationist vs refutationist approaches for testing evolutionary hypotheses, but ignored it because I didn't think that it related to my paper, which used a comparative approach for discovering and explaining relationships. I was totally unaware of the third crisis, that in the philosophy of science over what science is and how it should be done.

#### THE SPECIES PROBLEM

For 25-30 years, most biologists accepted that reproductive isolation adequately defined evolutionary species, and that the allopatric speciation model (e.g. Dobzhansky, 1937; Huxley, 1940, 1942; Mayr, 1942; Simpson, 1944; White, 1945; Stebbins, 1950) adequately explained how these species originated. However, the growing evidence from studies of the variability of genes and chromosomes among closely related species, and geographically across populations initially believed to be conspecific, increasingly reveals anomalies that are not easily explained by the world views of these conventional dogmas. This has led many (e.g. White, <u>1968</u>, <u>1978</u>; Ehrlich and Raven, <u>1969</u>; Bush, <u>1969</u>, <u>1975</u>; Sokal, 1973; Endler, 1973, 1977; Hall, 1973, 1977; etc.) to propose a variety of additional or alternative definitions for what species are and models for the process(es) by which these entities are formed. Thus, after many years of "normal science," where an understanding of species and speciation was accepted by a general consensus in evolutionary biology, if not by everyone, it would now be fair to say that there is no longer any consensus on what species are or how they are formed. This represents a fundamental foundation problem for the whole of biology! Rather we now face a crisis with literally dozens of competing and frequently incommensurable concepts and explanations. For instance, in writing my 1977 paper, I found it impossible to compare in detail Bush's (1975) model of "parapatric" speciation and mine, because I didn't understand the Kuhnian aspects of the problem. Presumably our common goal as evolutionary scientists, is to determine which of the many views c6me closest to modeling reality as it actually is and works.

Personally, as explained in the Hall (1977) MS, I think that sceloporine lizards display at least two qualitatively different modes of speciation, and that the models developed in that paper accurately

describe the underlying mechanisms of a second mode of speciation in *Sceloporus*, which may generalize well beyond lizards. These models explain most of the situations which are anomalous according to conventional world views. I summarized a lot of data to argue that these models do reasonably reflect reality. However, one reviewer (Moody), immersed in the Michigan world view of quantitative phyletics,

- 1. bluntly claimed that although my models might be realistic, my arguments were completely unscientific, and
- 2. proved by his attempts to rewrite the ' arguments, that he hadn't understood them. Other reviewers also drew what I thought were wrong conclusions from arguments that I thought were strong and clearly presented.

In retrospect, aside from my confrontation with the crisis over the species problem, I see that my method of argument was mired in crises, both in the scientific methodology of evolutionary biology, and in the discipline of the philosophy of science.

#### "LOGICS" OF CONFIRMATION, REFUTATION, AND DISCOVERY

The second of the three revolutionary crises concerns what I call the heuristic schemata for doing and writing evolutionary biology, and involves the question: How should studies of evolution best be organized to yield the most realistic possible understandings of nature? (I deliberately avoid words like logic, truth, and knowledge, which carry unjustified semantic implications of a certainty which is impossible to attain in the real world). That there is a revolutionary crisis over these issues is clearly seen by inspecting any recent issue of Systematic Zoology.

Evolutionists are concerned with two very different sorts of problems, each most appropriately studied with its own specialized heuristics:

- 1. the problem of reconstructing past histories (e.g. how best to construct realistic phyletic or cladistic taxonomies), and
- 2. the problem of understanding the historical processes or mechanisms which "cause" evolutionary change and affect its course.

Hall (1977) uses reconstructed phylogenies, and its conclusions may legitimately be attacked to the extent that they are based on these reconstructions if these are shown to be unrealistic. However, the reviewers and I had no communication problems over this issue. My aim was to use the phylogenies as data to explore the question of whether Mayrian allopatric speciation models (e.g. Bush, 1975: modes la and 1b) offered the best explanations for all speciation in the 9 sceloporine genera, or whether features of some of the speciation are not better explained by non-Mayrian models. Beyond this, I wanted to see if the evidence provided clues or constraints which would suggest and limit theorizing to particular types of non-Mayrian models. My heuristics for doing this gave my reviewers their greatest difficulties.

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Moody's review was particularly valuable because he explicitly demonstrated how his heuristics differed from mine. He thought that the paper should be organized so my models were "tested" according to the hypothetico-deductive schema, and he vigorously criticized the "inductive" organization of my arguments. The difference here is one of basic epistemology, and cannot be discussed independently of the Babel in the pages of Systematic Zoology and elsewhere between "Popperian falsificationists," more traditional "confirmationists" (my terms), and those comparative biologists who probably have not given much thought at all to their epistemologies because they seem to work in practice.

The historically older and more traditional epistemology, seemingly followed by many evolutionists, although rarely explicitly defended, may be called the "logic of confirmation." This seems to derive from what philosophers call the "received view" of the structure of scientific theories (Suppe, <u>1977</u>), perhaps best exemplified by Hempel (<u>1965</u>). According to the received view, a theory of generalization about nature is proposed and tested against reality. Given certain initial conditions and the statement of the theory, the theory requires certain consequences which can be verified by observation. If the initial conditions exist, and the theory is true, then the predicted consequences will be observed, and the theory is; confirmed. If the consequences logically entailed by the theory are not observed, then the theory is disconfirmed, or wrong. The more ways the theory can be confirmed, the more probably it is true. Eventually it can be considered to be proved.

The second epistemology has been elaborated by Karl R. Popper, in a series of works (1934, 1959, 1963, 1972), which have had a growing influence on the heuristic structures of evolutionary studies over the last 10 years. However, as yet there seems to be no consensus of choice between traditional and Popperian epistemologies. Popper's may be called the "logic of falsification." Popper argues, correctly I think, that we can never logically prove any universal generalization or theory to be true. Confirmation is an inductive procedure, and according to Popper, there is no such thing as induction. No number of confirmatory tests will ever prove with logical certainty, or even to any degree of probability that the next test will not prove logically that the previously confirmed theory is false. Thus, Popper claims that although a theory may in reality be true, certain knowledge that it is true is philosophically and logically unattainable. But if a logically required prediction is disconfirmed, then the theory which requires this prediction *certainly* is false in some respect. The failure to falsify tells us only that the tested generalization models reality, but only to the extent that it has already been tested against reality.

Besides its inability to yield even "probably" true knowledge. Popper attacks the logic of confirmation because workers using it may uncritically look for evidence which confirms their theory, and thus think that they have proved its truth when they find favorable evidence. In other cases, uncritical workers may make generalizations and confirm them "scientifically," even though they are not logically connected with reality in ways which might potentially allow them to be falsified. To Popper, the only generalizations which deserve to be called scientific are those where predictions can be logically deduced from realistic initial conditions, and it can then be determined in nature if these predicted consequences occur when the specified initial conditions exist. For such a test to be meaningful, it must be possible to conceive some real alternatives (or falsifiers) for the predicted consequence

Confirmationists (if carefully critical) and falsificationists would both claim to follow a hypotheticodeductive approach in their work. Both Hempel (e.g. 1965:5-6) and Popper (e.g. 1972:31-32) claim that the practices by which hypotheses are developed in the first place are fundamentally irrational (i.e. have no logical component) and are better studied by psychologists than philosophers of science. Only through testing is a theory conferred with any verisimilitude (Popper) or probability of truth (Hempel). Hempel completely washes his hands of the problem of hypothesis development or discovery. Popper, despite his belief that there is no rational approach to inventing hypotheses, suggests that the realism of our understandings of natural laws (the "versimilitude" of a theory-Popper, 1972:52 et seq.) can be increased by guessing for more inclusive generalizations which have more potentially falsifiable and tested contacts with reality. Thus, bold and sweeping generalizations--if falsifiable and not falsified in tests--convey more realistic information about nature than do more timid generalizations. To Popper, ad hoc explanations are trivial and of little interest because they supposedly cannot be tested independently of the effects they already explain. Unfortunately, despite the title of his pathfinding work, "The Logic of Scientific Discovery," Popper offers no hint of a rational program for guiding the guesses for these new and more realistic generalizations. Like Hempel, he can only suggest random trial and error, hallucination, and dreams. Popper has written much more worth study by anyone interested in epistemology and the philosophy of science, but little of it is directly relevant to the problems here.

As a reader of Systematic Zoology, I was aware of the crisis over confirmationist vs falsificationist epistemologies. My own epistemology, when I wrote Hall (1977) was what might be called naive falsificationism, but I did not see the relevance of this debate (or confusion) to the arguments of Hall (1977), which followed the heuristic schemata of the comparative approach to discover characteristics required of realistic speciation models. Certainly the discovered models were intended to be (and are) deductively testable, but the tests were to be described in later papers. Others (e.g. Todd, 1970; Bush, 1975; Wilson et al., 1975) had clearly used comparative heuristics in organizing their papers on speciation, but never with full effectiveness; and many others at least claim to use it in their studies. Thus, although I was convinced that I used the comparative approach more effectively than many evolutionists, I was unaware that its heuristic value had never been established. However, I now understand that the paper's intent and organization could very easily be misunderstood by readers familiar with Popper's categorical condemnations of "inductive" logics or heuristics for discovery.

# DETERMINISTIC LOGIC IN AN IDEAL WORLD VS A NONDETERMIN1STIC UNIVERSE.

The third revolutionary crisis is probably the most important for its implications for the assessment of heuristics for doing and writing science. This is the conflict of world views between two very different philosophies of science:

- 1. basically idealistic philosophies (e.g. Hempel and Popper), which trace their philosophical origins from the Platonic and Aristotelian searches for deterministic logics to reveal universal truths about an ideal world; and
- 2. basically pragmatic or realistic philosophies (e.g. Kuhn), which trace from historical studies of

how science actually works to produce functionally useful understandings of the nondeterministic world of actual reality.

The great incommensurabilities between the two philosophical lineages are particularly evident in the debates in the Lakatos and Musgrave, eds. (1970) collection, between Kuhn, Popper, and their various followers and critics; and in the various discussions in Suppe's (1977) collection. However, if Suppe's (1977) "Afterword" is accepted as authoritative it seems that a consensus is now developing among philosophers that epistemology needs to be based far more carefully than it has been in the past on what practicing scientists do to learn about the world. Thus, if the philosophers themselves recognize their need to study science to see how it actually generates understanding, the scientist should beware of uncritically accepting as authoritative a philosopher's picture of how to do science. It is particularly evident that most philosophers (Popper included) have had minimal contact with problem solving in the real world.

A further factor in this crisis, of special concern to evolutionists, is that both idealistic and realistic schools of philosophers have based their epistemologics and philosophies of science almost exclusively on a 50 year old view of physics. Then, it was at least reasonable to assume that most laws of causation were deterministic and universal, and could be studied through repeatable experiments. The problem of explaining speciation as it occurs on the planet Earth is about as far removed from solving the sorts of fundamental physical problems the philosophers of science have studied as anything could be.

Even in principle, few aspects of evolving lineages in nature can be realistically manipulated in laboratory experiments. Each speciation event must be assumed to be unique and unrepeatable in its circumstances in time and space. The course of incipient speciation will be influenced by a host of unique factors completely extrinsic to the evolving lineages which are being split apart. Even within lineages, the course and success or failure of incipient speciation must depend on intrinsic, but inherently nondeterministic processes such as mutation and recombination. On the other hand, sexually reproducing populations may have general properties such that the relationships of demes belonging to sister species, differ qualitatively from the relationships of demes belonging to the same species. If this difference can be used to objectively demarcate one species from another, there may be underlying stochastic "laws" which determine, at least statistically, under what circumstances such speciation may occur. A priori it is safe to assume that there are no deterministically causal laws which require speciation to follow whenever certain initial conditions occur. On the other hand, initial conditions certainly may affect the *probability* that speciation would follow. There is no reason to assume, though, that only one set of initial conditions (e.g. geographic isolation) necessarily initiates all speciation. Thus, an important question faces evolutionists: What heuristic approach will most effectively increase the realism of our understandings of how such presumably nondeterministic and non repeatable processes work?

There is much to recommend use of the Popperian principle of deductive falsification in studies of physical processes which can be assumed to be approximately deterministic. Here, there is a great difference in the epistemic importance or reliability of disconformation (= falsification) vs confirmation.

However, where the "law" is assumed from the outset to be nondeterministic and non universal, disconfirmation can no longer be equated with deductive falsification. Popper attacks "inductive" approaches because confirmations can never prove certainly or even probably that we have found truth. But note that deductive approaches are no more able to prove, with logical certainty, the falsity of nondeterministic theories. Popper goes on to attack ad hoc approaches as trivial and philosophically uninteresting. He also gravely suspects them for reasons relating to his experiences with Socialist and Nazi perversions of philosophy and logic (e.g. See Popper, <u>1966a</u>, <u>1966b</u>, <u>1976</u>). However, scientists interested in developing an understanding of slowly 'developing evolutionary phenomena that are largely embedded in past time face a situation where what they must study has already happened. For many aspects of these historical processes, hypothetico-deductive experimentation, where the theory is first created, and then the world is manipulated to test deduced predictions of the theory, is simply impossible. For evolutionists, the evidence and the cases to be studied already exist in nature, and many observations will already be known to one trying to explain a historical process. Thus, even though ad hoc approaches can trap the unwary into accepting epistemologically biased models of nature, in a very important sense, ad hoc approaches are the only ones available. However, the criterion of science remains to construct and critically chose models of nature which are as realistic as epistemology allows.

# THE COMPARATIVE APPROACH

A major difficulty with constructing realistic explanations for evolutionary processes embedded in the past is to separate the traces these processes leave on the features of the present from the random "noise" of details left by a history of unrelated events. The comparative approach used by Hall (1977), but not explicitly explained there, is a method for doing this. If causal processes in history are repeated or law-like, present features caused by them should be identifiable because they correlate consistently with markers used to identify the examples of the processes. Many caused features may be obscured randomly by unrelated events, but if enough recent cases of the same law-like process can be identified and studied, it should be possible to see consistent modes of correlation between marking features and other, unanticipated features which probably also trace causally from the same process. Of course, detection of a correlation does not *prove* that the correlated features prove that no connection exists between them. However, even before theory construction begins, the comparative method can show that many features of reality probably have causal relationships. A theory which logically explains these relationship realistically models what has been observed in nature.

If cases representing successive stages in the completion of the law-like evolutionary process can be found in the present, when cases of each stage are examined for correlations, the correlations may reveal many details of the sequential development of the process. Thus, the problem of explaining it may be a greatly simplified one of providing logical reasons for already identified sequences of phenomena which are probably causally related. It cannot be overemphasized that an explanation which logically (at least in a stochastic sense) accounts for already observed features of reality *already* has epistemically realistic

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connnections with nature to the extent that the explanation entails what has already been observed.

The logic of the explanation may also deductively entail (at least probabilistically) that features not initially studied should also be ' involved causally with the process being studied. Appropriate cases may then be examined to test (in a statistical sense) whether the predicted correlations actually exist. If the correlations are demonstrated, the pragmatic realism of the model is increased. If they are not found, the pragmatic realism is decreased, possibly even to the extent of convincing, if not certain, falsification.

Great care needs to be taken in framing the problem to be solved and in selecting cases to be studied by the comparative approach to avoid introducing bias. It is especially important to avoid the confirmationist error of starting with an *a priori* model in mind, and then collecting evidence from cases which seem to prove it. I think that the dogmatic adherence by many to the belief that the allopatric models are adequate to explain essentially all speciation is mainly a consequence of this type of error. Certainly many eases unquestionably confirm the allopatric model. Also there are only a very few special cases (e.g. those of polyploid and parthenogenetic speciation) where an allopatric model can be convincingly falsified in a hypothetico-deductive approach. However, an epistemologically sounder approach would be to ask openmindedly if alternative models might not provide more realistic explanations, for at least some of the cases of speciation than do conventional allopatric models.

My sceloporine work was planned from the outset as a comparative study to avoid confirmationist bias. As an undergraduate in the early 1960's I became aquainted with the diversity of species in the North American branches of the Iguanidae. My advisor, Don Hunsaker, II, pointed out as an anomaly worth trying to explain that the phylogenetically recent *Sceloporus* offered more species than all of the remaining 8 sceloporine genera together. We could see no feature of geography, ecology, or morphology which offered any clue as to why *Sceloporus* should be so much more species than its related genera. Presumably these other genera were exposed to the same range of evolutionary opportunities and started with very similar adaptations. In 1963 I compiled the limited and partially incorrect information available then on iguanid cytogenetics (see Hall, in prep.), and was struck by the concentration of chromosomal variability in sceloporines and *Sceloporus*. This suggested that some property or properties of their genetic systems might influence the probability of speciation in different lineages.

The sceloporine system, *taken as a whole*, offered an ideal set of closely related cases of speciation to survey to see if there actually was good evidence to support more than one kind of speciation model. Because of the ecological similarities and close relationships of the species, many extraneous variables would be relatively constant across all cases, thus allowing these features to be excluded from consideration as possible components for explaining differences in patterns of speciation. Norris (1958) and Axtell (1958) had already shown that at least some of the species in the conservatively speciating sceloporines other than *Sceloporus* could be explained very realistically and in detail by allopatric models. By contrast, the anomalously high number of species in *Sceloporus* suggested that at least some speciation in the genus might have involved alternative processes which allowed *additional* or *extra* species to be formed where extrinsic circumstances would not have favored speciation in the other, frequently sympatric, genera. In other words, when I started my work, I could see evidence to show that

geographic isolation by itself was a sufficient and realistic cause to account for the low rate of speciation seen in sceloporines other than *Sceloporus*. Were there other causes, which could allow some qualitatively different form of speciation to occur in the absence of enough geographic isolation to allow allopatric speciation?

Thus, I set out to collect data on cytogenetics and all other aspects of biology from as many species in the sceloporine radiation as possible. Where practical, I also explored geographic variation within taxonomically recognized species to avoid artifacts which might be introduced by using a species definition which failed to reflect evolutionary reality. In sum, I sampled one systematically and taxonomically well known radiation very thoroughly and independently from any preconceived speciation model to see if the features in the case histories of closely related pairs of species sorted out into distinctively different modes of correlation. Two strikingly different major modes were found. One is easily explained by classical Mayrian models, where geographic isolation alone is a sufficient cause to initiate speciation. The other associates speciation and chromosomal differentiation with little or no evidence for a history of geographic separation, where chromosomally invariant species exposed to similar geographic and ecological circumstances apparently have not split in two. Here chromosomal differentiation seems to be the most important "cause" in initiating speciation.

As indicated in the following paper, the correlation of several additional features in this mode suggested a detailed explanation of "chromosomal" speciation, which can be conveniently be broken into three more or less independent models. Each of these models potentially can be tested in various ways to further increase their contents of realism independently of the data already incorporated in their generation.

# CONCLUSION

Reviews of Hall (<u>1977</u>) and the difficulties in my own naive and abortive attempts to review other papers on speciation provided convincing evidence that my use of the comparative approach on the species problem was somehow incommensurable with the attempts of others to solve this problem. Both Kuhn and Popper agree that there is no theory neutral observation language for directly comparing the putative descriptions of nature made by alternative paradigms which differ significantly either in theory or methodology. How, then, should their relative scientific merits be evaluated objectively?

Popper's answer (<u>1972</u>:59) is that science should aim to find explanatory descriptions of nature which are "true" in the sense that they correspond with intersubjactively demonstrable "facts" of reality. When there is a choice between two competing paradigms, we should choose the one which has the greatest "verisimilitude," or number of logically entailed predictions about nature which are testable and have been tested against intersubjectively observable "facts" of nature (Popper <u>1972</u>:81, *et seq.*).

Popper bases the epistemology behind this answer on a model of the world which assumes that "laws" of nature are universal, and that theories about them can be deductively tested against nature with a deterministic logic which equates falsification with discontinuation. These assumptions do not realistically model what we could ever reasonably claim to be able to know about the processes of organic evolution. However, with certain modifications in epistemology, one can usefully apply Popper's criteria for evaluating the relative merits of competing explanations to those of evolution:

- 1. Popper's idea of "verisimilitude" can be translated roughly as "realism." Within the limitations of intersubjective "objectivity," a model of nature that logically or probabilistically entails certain relationships among features of nature is realistic to the degree that these features and relationships are objectively demonstrated in nature.
- 2. When one is evaluating the realism of stochastic explanations--especially where it is accepted that there may in reality be more than one explanation for a given phenomenon, the disconfirmation of a putative description of nature (i.e. a 'diction) has no more epistemic power to falsify an explanation than a confirmation has to prove it.
- 3. 3. If observations of nature are carefully planned to avoid confirmatibnist or refutationist biases (e.g. by sampling all of the species in a given radiation), and a theory statistically or deterministically entails certain 'dictions, then observations of a particular class testing these 'dictions have the same epistemic value, irrespective of whether they are made before [i.e., pre-] or after [i.e., -post] the theory explaining them is created.

Thus, an evolutionist should choose those explanations which have the most realistic and largest number of tested connections with the intersubjectively "objective" real world.

Finally, I should emphasize that I have only barely touched on many important philosophical issues for criticizing the epistemic value of the comparative approach. Some of these issues are discussed in more detail in my forthcoming' paper for Papeis Avulsos de Zoologia [see <u>Afterword (2003)</u>], but all deserve much more study than I have yet been able to give them. My answers here are still very tentative. I will also remind the reader again, that the comparative approach used in Hall (<u>1977</u>) was intended to be an objective and rational heuristic:

- 1. for discovering features of reality which relate causally to law-like evolutionary processes, and
- 2. for helping to assemble realistic explanations to explain reasonably how these features are causally involved in the processes.

Hall (<u>1977</u>) does not and was never intended to increase or decrease the realism of an *a priori* explanation by testing it deductively. Other [planned] papers were intended to take a more typical hypothetico-deductive approach in exploring testable parameters of the discovered models.

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# Afterword (1979)

There are two potential sources of confusion with the cascading speciation vocabulary. I first used the term "cascading speciation" in presentations for the vertebrate population biology discussion group at Harvard and in my <u>1973</u> Thesis. However, Montgomery Slatkin, who attended the group and saw my thesis, used the term for his rather different concept (Slatkin, M. 1974. Cascading Speciation. Nature 252:701-702). Following the advice of one of the editors who reviewed the first draft of the present paper, I decided to find a substitute term for my concept to avoid confusion with Slatkin's different usage.

En route to Australia, I visited Henryk Szarsky's Comparative Anatomy Department in Krakow, Poland. Szarsky pointed out quite correctly that my cascading speciation was a special case of the kind of evolutionary response to positive feedback selection, which he called "chain evolution" (Szarsky, H. 1971. The importance of deviation amplifying circuits for the understanding of the course of evolution. Acta Biotheor. 20:158-170). While I was still hoping to revise the present paper for the journal to which it had been originally submitted, Michael White showed me the first draft of his White (1978. Chain processes in chromosomal speciation. Syst. Zool. 27: 285-297). In this he had also used the cascading speciation terminology from my thesis, which he reviewed for his 1978 book, but by an oversight he had forgotten to cite the thesis in his draft. It was clear that both of us were describing the same kind of natural phenomenon. In discussing the problems we decided to modify Szarsky's term to "chain speciation" to serve as a tag for the phenomenon, and thus to make it clear: 1. that both White and I were discussing the same kind of phenomenon under this tag, and 2. that this was different from that used by Slatkin. However this agreement was mooted when I decided to withdraw my manuscript from its original journal to deal with the problems discussed in the [present] paper. Now, given the unauthorized but wide circulation of my original MS under the cascading speciation title, it seems that I am stuck with using this term, 1. even though it is unrelated to Slatkin's earlier publication, and 2. even though my cascading speciation is synonymous with White's chain speciation usage.

#### Afterword (2003)

The first paper in my planned series on the sceloporines originally intended for Papeis Avulsos de Zoologia, was actually published in the Ernest Williams Festschrift: Rhodin, A.G.J and Miyata, K. 1983. Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams. Museum of Comparative Zool. Cambridge, Mass., pp. 643-679--under the title Modes of speciation and evolution in the sceloporine iguanid lizards. I. Epistemology of the comparative approach and introduction to the problem. Due to my inability to secure an academic position that would support continuing research, I was never able to find the resources to complete additional papers in the planned series. With my knowledge and approbation, Jack Sites and many of his students at Brigham Young University, have been able to pick up and further explore many of the fascinating questions raised by the proliferation of species within *Sceloporus* and highlighted in my Thesis and the following paper here.

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