



Punctuated Equilibrium or Gradualism in the Lizard Genus *Sceloporus*? Lost in Plesioigrams and a Forest of Trees

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Conclusions about the rates of evolution among a group of organisms are only as sound as the phylogeny upon which the conclusions are based. We re-evaluated the rates of allozyme evolution among lizards of the speciose genus *Sceloporus*. The initial evaluation was suspect because a modification of the invalid, presence or absence method of data coding was employed in genealogical estimation. We recoded the allozyme data using the locus as the character and observed that the previous best explanation of the data fell within a forest of an estimated 10^7 trees. Further explorations into the invalidity of the independent alleles model of data coding attributed much, but not all, of the shape of the extremely unlikely, independent alleles tree to the parallel loss of plesiotypic alleles, and not the acquisition of novel alleles resulting from mutations. When the data were more appropriately evaluated using mutation coding, there was no unequivocal evidence for a punctuated equilibrium tempo of evolutionary change. © 1998 The Willi Hennig Society

INTRODUCTION

Mindell et al. (1989, 1990) recently proposed a method for discriminating between punctuated and gradual tempos of allozyme evolution. The consideration of the punctuated equilibrium hypothesis (Eldredge and Gould, 1972) using allozyme data was earlier provided by Avise and Ayala (1975), although not without problems (Mayden, 1986). Mindell et al. (1989, hereafter referred to as MSG) suggested that comparisons of amounts of character change between variably speciose sister groups could provide a means of testing the correlation between rates of evolution and speciation. Their method, a welcomed approach, was applied to the lizard genus *Sceloporus*. Through statistical comparisons of character change between all paired sister taxa, MSG concluded that punctuated change best explained the observed trends in these lizards. However, their conclusions about the tempo of evolution within the genus *Sceloporus* are only as sound as their allozyme-based phylogeny.

The phylogenetic analysis of allozyme data, from both theoretical and operational perspectives, has recently received much attention. For example, Mickle and Mitter (1981, 1983), Farris (1983), Buth (1984), Murphy et al. (1990), and Swofford and Olsen (1990) noted the invalidity of coding alleles as being either

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present or absent using theoretical criteria. These authors pointed out that presence/absence (independent alleles) coding could result in situations where hypothetical ancestors had no alleles at a locus. Seemingly, the occurrence of biologically impossible states would cast doubts on the acceptability of the hypothetical ancestor, and the analysis itself. Murphy (1993) and Meier (1994) provided operational evidence for the invalidity of coding alleles by presence and absence. Murphy (1993) used hypothetical data to expand on the issue noting that the problems extend beyond those previously discussed. Meier (1994) considered the operational consequences of hypothetical ancestors not having any alleles at a locus, and concluded that allozyme data were more appropriately evaluated using the locus as the character while evaluating the states using non-additive methods.

Operational advancement has been made more recently. Mabee and Humphries (1993) proposed a method by which a Sankoff matrix (Sankoff and Rousseau, 1975; step function matrix in PAUP [Swofford, 1993]) could be used to constrain analyses to a minimum number of changes separating character states. Mardulyn and Pasteels (1994) refined the Mabee and Humphries (1993) method.

Despite the recent theoretical and operational advances, there remains a plethora of studies that continue to use the independent allele model of coding (e.g. de Queiroz and Lawson, 1994; pers. obs. of numerous manuscripts received for review; D. G. Buth, 1995, pers. comm.). Consequently, it is worthwhile to demonstrate further the consequences of inappropriately coding alleles as being either present or absent, using real data.

Troublesome Evaluation

The data evaluation of MSG has been troublesome. In a parsimony re-evaluation, Sanderson (1990) did not resolve the three trees obtained by MSG, but rather found the single, most parsimonious solution to the MSG data set. Further, he challenged the validity of a punctuated tempo for the lizard allozymes because speciose clades will be biased by an abundance of homoplasy, which will tend to inflate levels of discerned character evolution. Sanderson (1990) suggested that the removal of taxa to equalize numbers

of compared species per group would relieve such problems. Mindell et al. (1990) rejoined that the removal of taxa redistributes character-change paths on the tree and thus undermines the premise of the test. However, both arguments would hold weight only if homoplasy was not common, a criterion the MSG data failed to meet. The rejection of the null hypothesis of gradual evolution in favor of punctuated change should not have been based on an ambiguous (highly homoplastic) phylogeny.

Despite the controversy, the analysis of MSG was recently heralded by Gould and Eldredge as an example of punctuated equilibrium *par excellence*.

Mindell et al. (1989, 1990) have now performed such a test on the reptilian genus *Sceloporus* and on allozymic data in general and have validated punctuated equilibrium's claim for positive correlation of evolutionary distance and speciation frequency (Gould and Eldredge, 1993).

Others, such as Sites et al. (1992), have similarly concluded that the punctuated mode has occurred in these species, although they were more cautious in their statements. Do the data support a punctuated tempo of change in *Sceloporus*? As detailed below, we believe not.

Both MSG (and Mindell et al., 1990) and Sanderson (1990) constructed phylogenetic trees from the original data matrix of coded characters and based their conclusions about the tempo of evolution on these trees. However, their conclusions are suspect because of MSG's invalid method of data coding. Although MSG stated that they "... consider allozyme loci as characters, and a combination of (or single) alleles present as character states", they did not. MSG defined their states following the systematic alleles model of Mickevich and Mitter (1981), but subsequently coded each state as either present or absent. In doing so, they defined 69 binary presence/absence characters when 23 loci should have resulted in the definition of 23, mostly multistate characters. Consequently, both the MSG and Sanderson (1990) treatments are based on a modification of the "independent alleles model" of coding (Mickevich and Johnson, 1976; terminology of Mickevich and Mitter, 1981, 1983), and not treatments using the locus as the character.

Apart from correcting the coding errors of the original analyses, herein we will elucidate some of the procedural problems associated with the independent alleles model and demonstrate their severity. Hitherto, these have only been illustrated from the perspective

of hypothetical data (Murphy, 1993; Meier, 1994). Finally, we examine the tempo of evolution in the lizard genus *Sceloporus* in light of our findings.

METHODS

Murphy (1993) recently provided an outline by which allozyme data can be phylogenetically analysed. His method prefers that the allelic arrays be available permitting the ordering and polarizing of locus products. Unfortunately, the allelic data of MSG were not reported and now the allozyme data and coding scheme cannot be located (Mindell, pers. comm.; this situation points to the necessity of requiring either publication or deposition of original data). Consequently, our analysis was constrained to the “quaternary level of evaluation” of Murphy (1993) using the systematic alleles model of coding (which is problematic as an a priori assumption) for a non-additive (unordered) evaluation (also potentially problematic, especially for allozyme data). Character numbers refer to the original designations of Mindell et al., whereas letters in bold face refer to our conversions as given in Appendix 1. Our codes represent relative column positions of Mindell et al.

The MSG data were recoded for a locus as character treatment. We transformed the MSG data by pooling all allelic arrays derived from a given locus. Table 1 provides examples of how this was accomplished.

For any locus, an allelic array in the first column of MSG data set was scored as “1” by us, the second column as “2”, etc. For example, in transforming the data for the first locus, Ck-A (Table 1; MSG characters 1–3; our character A), we combined the first three characters of MSG to three character states. Thus, in *S. merriami*, the MSG allelic arrays for Ck-A appeared as 010 and, because the allele(s) occurred in the second column, we assigned state 2 to our character A. *Sceloporus undulatus*, with an original score of 100, received a locus as the character score of 1, etc.

Although the original data set (MSG; Appendix 1) is said to be free of error (Mindell, errata sheet accompanying reprint requests), this may not be the case. In our method of recoding, all character states should have a value of ≥ 1 because there should be an allelic array for each species at each locus. However, examination of

our recoded data (Appendix 1) shows 31 scores of “0” variously distributed among 16 of 23 loci. These scores may indicate either the omission of allelic arrays (Table 1; MSG character 50, our character R; a missing score of “0” and no corresponding array with a score of 1 or greater), missing data (e.g. Table 1; a missing score of “?”), typographical errors in the data set, or an unexplained coding scheme. Herein, we assume that all taxa having a score of “0” for a given locus have the same (omitted) allelic array. J. W. Sites (pers. comm.) believes that this assumption is probably true, although it cannot be confirmed because of the lost data. Three additional problematic data points occur. The allelic array for Dir-A (Table 1; MSG characters 43–46, our character O) in *S. merriami* is represented by one “?” (either missing or ambiguous data) and three “0”s (absent alleles). Similar codes occur for Pnp-A in *S. torquatus*, and mIcdh-A in *S. siniferus* (MSG; Appendix 1). This scoring differs from examples where all homologies are unknown (e.g. Table 1; MSG characters 43–46, *S. grammicus*, ???). We assume that the data for these three loci represent uncertainties about specific homologies of given alleles within the data sets as opposed to completely missing data. However, we have coded these data as missing, allowing for possible homologous states to occur; we have not coded them as autapomorphies, which would not allow for the states to be homologous with any other observed state.

The recoded data (Appendix 1) were evaluated heuristically using PAUP 3.1.1 (Swofford, 1993). In all evaluations, multistate characters were treated as having non-additive (unordered) states. Heuristic searches involved keeping minimal-length trees only, stepwise addition performed as random additions with an eight-digit integer seed number, 10 repeats, and 20

TABLE 1
Examples of Our Method for Converting the Character State Data of Mindell et al. (1989) for Species of the Genus *Sceloporus* to Expressing all Data Derived from a Single Locus to a Single Character

	Character designations										
	1	2	3	A	43	44	45	46	O	50	R
<i>S. merriami</i>	0	1	0	= 2	?	0	0	0	= ?	1	= 1
<i>S. undulatus</i>	1	0	0	= 1	1	0	0	0	= 1	1	= 1
<i>S. variabilis</i>	0	0	1	= 3	0	0	0	1	= 4	1	= 1
<i>S. cozumelae</i>	0	0	1	= 3	1	0	0	0	= 1	1	= 1
<i>S. clarki</i>	1	0	0	= 1	0	0	0	1	= 4	0	= 0
<i>S. spinosus</i>	1	0	0	= 1	0	0	1	0	= 3	1	= 1
<i>S. cyanogenys</i>	1	0	0	= 1	0	1	0	0	= 2	1	= 1
<i>S. grammicus</i>	0	1	0	= 2	?	?	?	?	= ?	1	= 1

equally parsimonious trees held for branch swapping. Branch swapping was performed using three bisection-reconnection, steepest descent, and holding all most parsimonious trees (MPTs). Examination of character state optimizations and tree branch lengths was accomplished using MacClade (Maddison and Maddison, 1992, Version 3.04).

RESULTS AND DISCUSSION

A Forest of Shortest Trees

Three-hundred and seventy-three equally parsimonious trees were resolved by PAUP, each tree having a length of 109 steps (a reduction of 56 steps from Sanderson's evaluation; CI=0.56, RI=0.57). Our recoded data maps on Sanderson's (1990) tree with a length of 112 steps. Exactly where Sanderson's tree fits into the total possible array of trees can only be estimated. We found 8454 most parsimonious trees at 109–110 steps, and because of memory limitations we only found 29 600 most parsimonious trees between 109 and 111 steps with over 23 106 trees on which branch swapping in the search for additional trees had not been performed. Moreover, we believe that there are more than 23 106 trees remaining to be swapped because this number increased continually during the analysis, the asymptote apparently not being reached. Conservatively, it is likely that there are more than 10^6 most parsimonious trees of length 109–111 steps and, consequently, we believe that there are more than 10^7 most parsimonious trees of 109–112 steps. Therefore, it seems highly unlikely that Sanderson's tree is the best explanation of the MSG allozyme data set.

There is little consistency among our 373 most parsimonious trees. A strict consensus tree reveals only a single stable node linking *S. undulatus*, *S. virgatus*, and *S. occidentalis*. A strict consensus tree including all found trees of 109–110 steps maintained this node. However, even this single, unambiguous node may reflect an artefact of data coding and not a defensible hypothesis (see below).

Clearcutting the Forest

Why did we observe a forest of trees when Sanderson (1990) did not? A number of variables could explain our observations, some as outlined by Murphy (1993). One potential problem is that, under the independent alleles model, when no alleles are shared between the ingroup and outgroup, all ingroup alleles are considered apomorphic. Absence in the outgroup is always considered the plesiomorphic state (Murphy, 1993). This unrealistic constraint does not allow for outgroup taxa to evolve, leaving the ingroup with a plesiomorphic allele. This artefact occurs in either three or four loci in the MSG data set. The outgroup, *S. merriami*, is scored as having no alleles at three loci (sAcon-A, Gpi-A, and Pep-B). In one case (Dir-A), the outgroup has the allelic arrays "?000", which may not be the same as the all-missing-data reported for *S. grammicus* (????).

To assess the magnitude of this outgroup problem, we modified the original MSG data set by combining the allelic arrays for these four loci only into multistate arrays and treated them as non-additive. Eight most parsimonious trees were resolved, including Sanderson's tree. Significantly, when our recoded data (Appendix 1) were mapped back onto these trees, one had a length of 113 steps, four had a length of 112 steps, and three were shorter with a length of 111 steps. Were the analyses of MSG and Sanderson (1990) affected by alleles not being shared by the ingroup and outgroup? Given that three of the trees are shorter than Sanderson's tree, we concluded that the data were affected by this problem. Thus, some of the nodes in Sanderson's tree may be generated as artefacts of the independent-alleles model when all ingroup allelic arrays are not shared with an outgroup.

An intuitive correlate of the independent-alleles model is that progressively heavier weighting is accorded to more polymorphic allozymes. Although some researchers, such as Moran et al. (1990), believe this is an undesirable attribute, it is not, especially if apomorphic states are considered to represent mutation events (the mutation model of coding of Murphy, 1993). The problem is not having a large number of alleles, but rather that the greater the number of alleles at a given locus, the more likely the occurrence of parallel losses of plesiomorphic alleles.

Loci with greater numbers of alleles would play a greater role in branch configuration through both gains and losses. Moran et al. (1990) applied to a corrective weighting scheme to allelic data such that each character (allele or allelic array) was accorded a weight of $1/n$, where n is the number of alleles at that locus. When we applied this procedure to the MSG presence/absence data, we resolved three most parsimonious trees. These three trees differed from that of Sanderson (1990). Our recoded data (Appendix 1) mapped back onto these three trees with 110 steps. Although approaching, none fell within the forest of most parsimonious trees. The progressively greater weight of more polymorphic loci contributed to the branching sequence of Sanderson's tree, most probably because of numerous parallel losses of allelic arrays.

Weighting the data, and eliminating the artefacts of assigning apomorphic status to all ingroup character states when no state is shared with the outgroup, results in the resolution of yet another unique tree, this one also having a length of 110 steps. The complex interplay of various artificial effects of the MSG coding scheme is exceedingly difficult to tease apart. Nonetheless, the above data manipulations suggest that these artefacts have together had an impact on the MSG and Sanderson (1990) analyses.

Independent allele coding also results in the generation of plesiomorphic loss characters which may have multiple effects on resultant trees. To what extent are branches of Sanderson's tree supported by loss character states? This question was examined using two approaches: (1) eliminating from consideration all allelic arrays shared between the ingroup and outgroup (Shaffer et al., 1991) and (2) examination of character state distributions on Sanderson's tree. Shaffer et al. (1991) excluded all allelic arrays shared between the ingroup and outgroup, thereby trying to force most apomorphies to represent the presence of derived alleles rather than the loss of plesiomorphic alleles. When we applied this method to the MSG data set, 14 of the 69 characters were eliminated from the independent allele analysis resulting in four equally parsimonious solutions. Our recoded data (Appendix 1) mapped on two trees with a length of 114 steps, and two of 116 steps. Not only were these trees longer than those resolved using the locus as the character, they were also solutions unique to this coding procedure. The discrepancy between the lengths of these trees and

those of our reanalysis indicated that the Shaffer et al. (1991) method failed to compensate for the effects of presence/absence coding. This failure may be general (see Jones et al., 1993), making the method invalid. Notwithstanding, our evaluation conclusively demonstrated that the configuration of Sanderson's tree rested largely upon loss events.

The second approach considers instances where losses of relatively plesiomorphic alleles are interpreted as synapomorphies, resulting in unnecessary homoplasy. Figure 1 shows the optimization of MSG characters 60–62 (Cat-A) on a portion of Sanderson's tree. The independent-alleles model requires four steps on the tree, whereas the locus as the character requires two. In the former model of coding, there is a homoplastic reversal of MSG character 62 in the lineage uniting *S. undulatus*, *S. virgatus* and *S. occidentalis*. Other loci produce similar patterns of character-state evolution. The overall affect of such artefacts on tree topology must be considerable, as revealed by our analysis of the recoded data.

Considering Allozyme Loss Character States

In the recoding of the MSG data, the greatest effect is minimizing loss events. The reduction of 56 steps from the independent alleles model to our recoding is largely attributable to the removal of these loss events. Thus, loss events can and do control the shapes and numbers of trees in independent alleles codes. To this extent, Sanderson's tree is perhaps best termed a *plesio-ogram*, a tree based on the loss of relatively plesiomorphic states when alternative derived states are present.

Why are loss data so problematic when compared to tracking allelic mutations at a locus? In independent-alleles coding, the loss of plesiomorphic alleles (or allelic arrays) is considered synapomorphic. For a given locus, if two terminal non-sister taxa have evolved alternative alleles independently, and if these have gone to fixation, then the probability of a homoplastic loss of the plesiomorphic allele is 100% (Murphy, 1993). Figure 2 demonstrates the consequences of this artefact. A hypothetical true tree is given in Fig. 2A with the mapped allelic transformations. The independent-alleles coding is given in Fig. 2B, and the most parsimonious explanation of the inde-

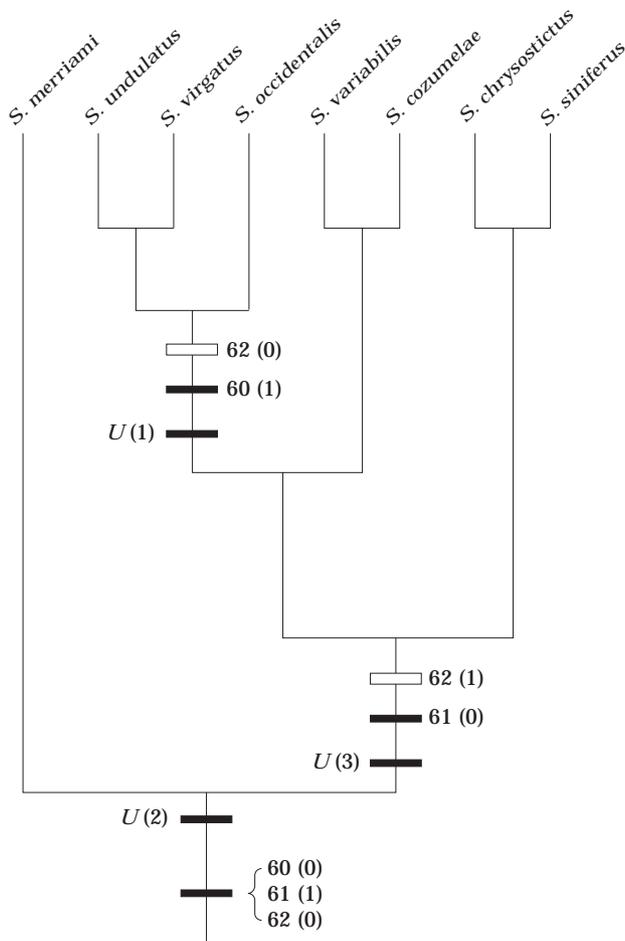


FIG. 1. Character optimizations for Cat-A on the Sanderson (1990) tree. The Mindell et al. (1989) coding scheme (characters 60–62) are given to the right side of the branches, and our recoded data to the left. The independent-alleles model artificially inflates levels of character change and causes unnecessary homoplasy. The locus as character coding method (character U; Appendix 1) avoids these problems.

pendent alleles is shown in Fig. 2C. The topologies of the two trees are consistent in one node only, that uniting taxa B and C. In Fig. 2C, the clade excluding taxon A is defined by the loss of plesiomorphic allele a. Taxon D is excluded from the clade containing E and F because of the loss of relatively plesiomorphic allele c. Although two of the nodes of Fig. 2C are defined by derived alleles, one E–F, is misdefined in excluding D, because of a loss event; one node is defined by a homoplastic loss event. Consequently, the shape of this tree is largely defined by loss events.

Unlike loss events, one allele can potentially change into a relatively large number of alternative alleles, fig-

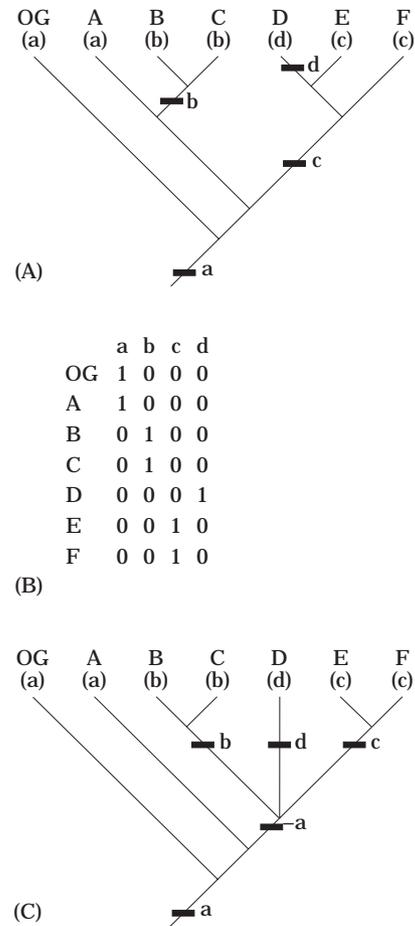


FIG. 2. Demonstration of how loss events can control the shape of a tree when allelic data are coded by presence/absence. (A) The true tree requiring no homoplasy of the hypothetical allelic data. (B) The presence/absence coding of the allelic data with the single most parsimonious solution given in (C).

uratively represented as a “starburst”. For example, Highton and Larson (1979) reported the resolution of 26 alleles at an esterase locus, 23 alleles for the transferin locus, and 17 alleles for the L-lactate dehydrogenase heart locus (Ldh-B) in salamanders of the genus *Plethodon*. Similarly, Singh et al. (1976) resolved 37 alleles (electromorphs) at the Xdh-A (xanthine dehydrogenase) locus of *Drosophila pseudoobscura* making the probability of parallel change in allozyme data at least 1/37, or $P=0.027$. Thus, unlike the 100% likelihood of parallel loss of plesiomorphic alleles, there is a relatively small chance of homoplasy resulting from parallel mutation events.

Should allozyme loss data be incorporated into phylogenetic analyses? Our analysis of the MSG data set suggests that loss events should *never* be used. Because of the difference in probabilities of homoplastic change, allelic loss data are highly suspect and should be avoided, at least in initial approximations of phylogeny. Although loss data are frequently used by morphologists, their use in allozyme analysis remains unjustified. Unlike morphological data, allozyme losses have alternative apomorphic states. From a theoretical perspective, allozyme loss data represent the effects of selection, drift, inbreeding, and emigration. They are not the basis of inheritable change—mutations—upon which novel character states have their origin.

While using the locus as the character is required theoretically, and operationally it minimizes the difficulties demonstrated above, it is not without problems. First, coding by either the “shared alleles” model or the “systematic model” (Mickey and Mitter, 1981, 1983) may be inappropriate because both models define character states as “allelic arrays”. For example, the arrays *aa*, *ab*, and *bb* would be considered as three separate states. If *aa* is plesiomorphic, then the difference between *ab* and *bb* is a loss event, possibly resulting from genetic drift, whereas the difference between *aa* and *ab* is hypothesized to be a mutation event. The consideration of these three allelic arrays as separate character states is undesirable because the mutation and loss events should not be accorded equal weight (Murphy, 1993). Mardulyn and Pasteels (1994) have noted the use of Sankoff (step) matrices to apply differing weights to the events. However, such an approach skirts the issues, at least for allozyme data, of whether or not a synapomorphy is equivalent to a mutation event (Murphy, 1993), and the aptness of using allelic loss data.

Another problem with our analysis is that we were constrained to using non-additive procedures because the original allelic data are not available. Murphy (1993) discussed why non-additive procedures are not recommended for analysing allozyme data as an a priori assumption. He identified and provided four examples of problems that may yield erroneous resolutions: (1) multistate characters may be mapped onto binary characters because the latter are ordered and polarized by their very nature; (2) the procedure assumes that all states have an equal likelihood of

occurring, and this assumption is frequently violated. For example, the three ordered allelic arrays *aa-ab-bb*, *aa-bb-ab*, and *bb-aa-ab* do not have equally likely explanations. The latter two explanations require homoplastic mutations at the allelic level if, for example, allele *a* is plesiomorphic; (3) the method assumes that, for all characters, there is an inverse relationship between the number of states for a given character and phyletic utility. In a five-taxon statement, the allelic arrays *aa*, *ab*, *bb*, *bc*, *cc* would falsely be considered uninformative; and (4) because non-additive procedures require the systematic model of coding, gains and losses inappropriately may be accorded equal weight. Thus, we believe that the a priori application of non-additive methods ignores evolutionary process (genetics) and is only concerned with pattern.

Ideally, computational algorithms would allow for one or more partially ordered arrays in a given character (Murphy, 1993). This might make non-additive analyses of allozyme data valid under certain assumptions, especially if no alleles are shared among allelic arrays. The operational proposals of Mabee and Humphries (1993) and Mardulyn and Pasteels (1994) make advances towards a defensible allozyme evaluation.

In the case of *Sceloporus*, a single phylogeny has yet to be resolved using allozyme data (see Sites et al. [1992] for a review of morphology and chromosome-based hypotheses). According to our non-additive, locus-as-the-character evaluation, at least 373 most parsimonious trees exist for the MSG data set. The true phylogeny for the lizards may not even lie within this forest of trees because coding methods which equate mutations and losses of plesiomorphic alleles may present further artefacts obscuring the phylogenetic signal. Genetic process may not have been adequately considered in the data coding, and we are unable to assess this because of the lost data.

Tempo of Evolution

Has speciation resulted in a punctuated mode of evolution within the genus *Sceloporus*? In order to address this question confidently, a sound, defensible phylogeny is required. Finding only one node among 17 to be unambiguous, we do not believe that a

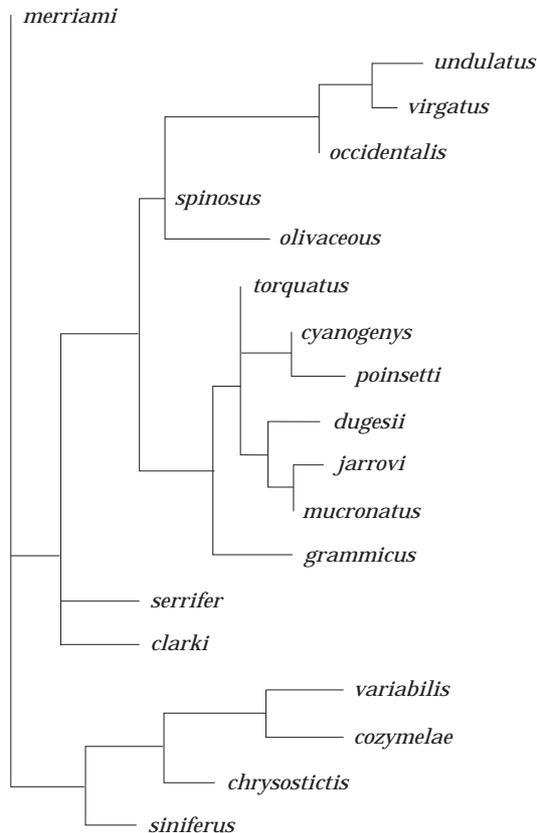


FIG. 3. One of 373 most equally parsimonious trees based on the recoded data of Mindell et al. (1989). Branch lengths reflect relative unambiguous support for various nodes. This tree does not support a general hypothesis of punctuated equilibrium.

punctuated equilibrium tempo can be promulgated with any confidence. Moreover, among our forest of 373 trees, there are trees suggesting that the tempo may have been gradual rather than punctuated, depending on how the character states are optimized on the trees. Figure 3 shows one such tree, among many, whose branch lengths reflect unambiguous changes only. As the ambiguous changes have not been mapped onto branch lengths, less speciose clades might have a greater amount of change than more speciose clades. Thus, although Mindell et al. (1990) may have provided a method by which the tempo of evolution can be examined, at least for a specific data set essentially free of homoplasy, the punctuated equilibrium tempo remains to be demonstrated in *Sceloporus*.

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APPENDIX 1

Recoded Character Data for 19 Species of Lizards in the Genus *Sceloporus*

	Character ¹																						
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W
<i>merriami</i>	2	2	0	1	0	3	1	0	0	4	0	1	0	1	?	0	1	0	3	1	2	1	3
<i>undulatus</i>	1	1	?	1	4	1	?	1	1	1	1	?	1	0	1	?	1	1	1	1	?	1	1
<i>occidentalis</i>	1	1	2	1	4	2	2	1	1	1	1	1	2	2	1	?	1	1	2	1	1	1	1
<i>virgatus</i>	1	1	2	1	1	1	?	?	?	?	?	0	1	2	1	1	1	1	2	2	1	1	1
<i>variabilis</i>	3	1	2	2	2	3	?	0	3	1	2	2	2	0	4	?	1	2	1	1	?	2	2
<i>cozumelae</i>	3	1	2	2	3	3	?	?	3	1	2	2	3	1	1	1	1	2	2	0	3	3	3
<i>chrysostictis</i>	3	1	1	0	3	3	?	1	4	4	2	2	2	0	1	2	1	3	2	2	3	3	4
<i>siniferus</i>	1	2	3	0	0	3	0	?	4	?	2	2	3	0	1	2	1	2	2	1	3	2	?
<i>clarki</i>	1	2	1	3	1	3	0	0	3	2	2	0	2	1	4	2	0	3	2	1	2	1	4
<i>olivaceus</i>	1	1	1	3	?	2	?	1	3	1	2	2	1	1	4	0	0	1	2	1	2	0	2
<i>spinusus</i>	1	1	0	3	1	2	2	1	2	1	2	?	2	1	3	?	1	1	?	?	1	2	2
<i>torquatus</i>	1	1	?	4	2	3	2	?	2	?	2	2	2	1	4	1	1	1	2	3	2	2	1
<i>dugesii</i>	1	1	4	4	2	3	1	2	2	3	2	2	2	1	4	1	1	1	2	3	?	2	0
<i>jarrovi</i>	1	1	?	4	2	3	1	2	2	2	2	1	2	0	4	1	1	1	2	3	2	2	2
<i>mucronatus</i>	1	1	3	4	2	3	1	2	2	2	2	1	2	1	4	1	1	1	?	3	?	2	1
<i>cyanogenys</i>	1	1	4	4	2	3	2	2	2	2	2	2	2	1	2	3	1	1	3	3	2	2	?
<i>poinsetti</i>	1	1	4	4	2	4	2	2	2	3	2	2	2	1	3	3	1	1	3	3	2	2	4
<i>grammicus</i>	2	1	4	4	2	4	?	2	2	2	1	2	1	1	?	0	1	1	?	1	?	2	2
<i>serrifer</i>	1	2	1	3	1	2	?	?	0	?	1	2	2	2	2	2	1	1	2	1	2	2	2

¹Character codes: (A) Ck-A; (B) mMdh-A; (C) sMe-A; (D) Ldh-A; (E) Ldh-B; (F) Ap-A; (G) Iddh-A; (H) Pgdh-A; (I) Pnp-A; (J) mAcon-A; (K) sAcon-A; (L) Gtdh-A; (M) Gpi-A; (N) Mpi-A; (O) Dir-A; (P) Est-A; (Q) Pep-A; (R) Pep-B; (S) Pep-D; (T) mAat-A; (U) Cat-A; (V) mSod-A; (W) mIcdh-A.