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SPECIATIONAL EVOLUTION: A PHYLOGENETIC TEST WITH ALLOZYMES IN *SCELOPORUS* (REPTILIA)

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Abstract—The potential role of speciation in accelerating evolutionary divergence remains controversial. Earlier tests based on genetic and morphologic distances which indicated an absence of speciational evolution rely on problematic assumptions. We provide a phylogenetic test in which amounts of discrete character change relative to an outgroup are compared between sister taxa. Although this test is constrained by a need to assume similar extinction rates in groups compared, it provides conceptual improvements regarding monophyly, equal age of taxa, and distribution of homoplasy. Based on analysis of 68 informative allozyme characters for 19 lizard species in the genus *Sceloporus*, significant speciational evolution and punctuational change is, at least, a viable explanation for the distribution of observed character changes.

Introduction

The central idea in the punctuated equilibria hypothesis (Eldredge and Gould, 1972) is that "significant evolutionary change arises in coincidence with events of branching speciation, and not primarily through the *in toto* transformation of lineages" (Gould, 1982). This was contrasted with the traditional view of evolutionary change accumulating more gradually over time, without any major role for speciation events. Although first used in discussion of morphological change (Eldredge, 1971), the punctuated equilibria hypothesis was extended to molecular divergence by Avise and Ayala (1975). They introduced a model to examine the logical consequences of punctuated evolution as opposed to phyletic gradualism based on the distribution of genetic distances among living species. They postulated that if phyletic gradualism is true, genetic distances are predicted to be a function of time, and would be equal in species-rich versus species-poor clades of equivalent geological age. However, this prediction only holds if distribution of speciation events over time is similar between clades, and as there is no way to determine this, the gradualist view is not falsifiable with this approach. For example, greater divergence could actually occur in the species-poor clade under the gradual mode if the few divergences present occurred much earlier in time compared with divergences within the species-rich clade. Alternatively, if evolution is mostly punctuational, genetic distances should be higher in species-rich clades, with greater divergence resulting from the greater number of speciation events, compared with species-poor clades. If most evolutionary divergence is contingent upon speciation events, a species-rich clade will have more character change relative to a less diverse sister clade regardless of the relative timing of speciation events. Therefore, predictions of the punctuated mode are falsifiable. Test results of this model using genetic (Avise and

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Ayala, 1976; Avise, 1977) and morphologic (Douglas and Avise, 1982) distances between fish taxa have not supported the punctuationist view.

Criticisms of the approach, and of the specific analyses conducted have been raised and discussed by Mayden (1986). These criticisms centre on difficulties in interpretation of genetic distance data, and failure to meet assumptions that mean distance values are compared between (1) monophyletic taxa, (2) taxa of equal age, and (3) taxa experiencing similar degrees of extinction and homoplasy. The species-rich and species-poor fish taxa compared by Avise and Douglas (Cyprinidae and Centrarchidae; *Notropis* and *Lepomis*) are shown to be dubiously qualified on all counts.

In this paper we present an alternative and, in our view, more apposite approach to testing the same set of predictions based on discrete character analysis and use of an outgroup. In contrast to earlier studies, our analysis of allozymes in the lizard genus *Sceloporus* indicates that speciation can contribute significantly to evolutionary change. The term "speciational evolution" has been used in the context of punctuated equilibria (Mayr, 1988), and we use it here for its descriptive value.

Methods

Comparison Between Sister Groups

Problems that have confounded earlier tests of evolutionary mode by Avise and colleagues pertain to assumptions inherent in their tests, as mentioned above. Comparison between monophyletic groups is required to ensure that only the appropriate within taxon divergence is being measured. Comparison between groups of similar geological age is required as a control for the portion of divergence potentially related to time. Similar extinction rates within clades must be assumed, if current numbers of species are taken to reflect the total number of speciation events that have occurred. The need to assume similar amounts of homoplasy stems from the fact that this component of overall evolutionary divergence is unaccounted for in distance comparisons. For example, Nei's (1972) genetic distance coefficient measures the mean number of *electrophoretically detectable* substitutions per locus that have occurred since two groups diverged from a common ancestor. Because the component of homoplasious change is not measured, similar amounts must be assumed.

Our test of speciational evolution consists of comparing amounts of character change (1) between sister species relative to an outgroup and (2) between sister clades relative to an outgroup. This approach hinges on the fact that the sister species and sister clades differ to some degree in species richness, and uses properties of phylogenetic theory to eliminate certain problems inherent in the previous tests. We determine monophyly for our comparison groups prior to the tests, based on shared derived characters, and analyse sister taxa that are necessarily equivalent in age, due to concomitant divergence from a common ancestor. In addition, by using discrete character analyses, we will not lose track of that component of evolutionary change consisting of homoplasious events. Homoplasious change will be enumerated and tallied along with non-homoplasious change on phylogenetic trees, and for this reason assumption of equal amounts of homoplasy is not necessary. The existence and variability of homoplasy provides no more basis for rejection of our test than it does for rejection of a most parsimonious phylogeny (see Farris, 1983).

If the punctuated mode is primary and speciation does accelerate divergence, a species whose line of descent includes many lineage-splitting (speciation) events is

predicted to have a greater number of character changes relative to an outgroup, than is a species from a lineage with fewer splitting events. Similarly, entire clades having many speciation events are predicted to show more character change, relative to an outgroup, than are sister clades experiencing fewer such events. Thus, in Fig. 1, comparison of species 1 and species 7 will reveal a greater amount of character change in species 1 than in species 7, relative to the outgroup, under a punctuated mode. In turn, comparison of sister clades joined at node A in Fig. 1 will reveal more character change in the clade of five taxa (species 1–5) than in the clade of two taxa (species 6–7) under a punctuated mode. If taxa experiencing a greater number of splitting events do not show a greater amount of character divergence, then a primary role for speciational evolution is not supported.

If the gradual mode is primary, and divergence is mostly a function of time, sister taxa varying in number of splitting events experienced should show similar amounts of change relative to an outgroup. Sister clade comparisons in which amounts of change are totaled and/or averaged (as in genetic distance comparisons) cannot be used to assess this prediction because the distribution of speciation events over time is unknown, and cannot be assumed to be equal among clades. However, comparison between individual sister species differing in number of splitting events experienced can be used to assess that prediction. In the latter case, change is not being totaled across species groups, and no information is required or assumptions are made regarding the distribution of splitting events within any such groups. Thus, our test involving sister clades can reject only the punctuationist hypothesis, whereas test results involving comparison of individual sister species could be used to reject either the punctuationist or the gradualist hypothesis.

Divergence is quantified as number of character changes along a lineage (branch lengths) in phylogenetic analyses. Such analyses were conducted with D. L. Swofford's

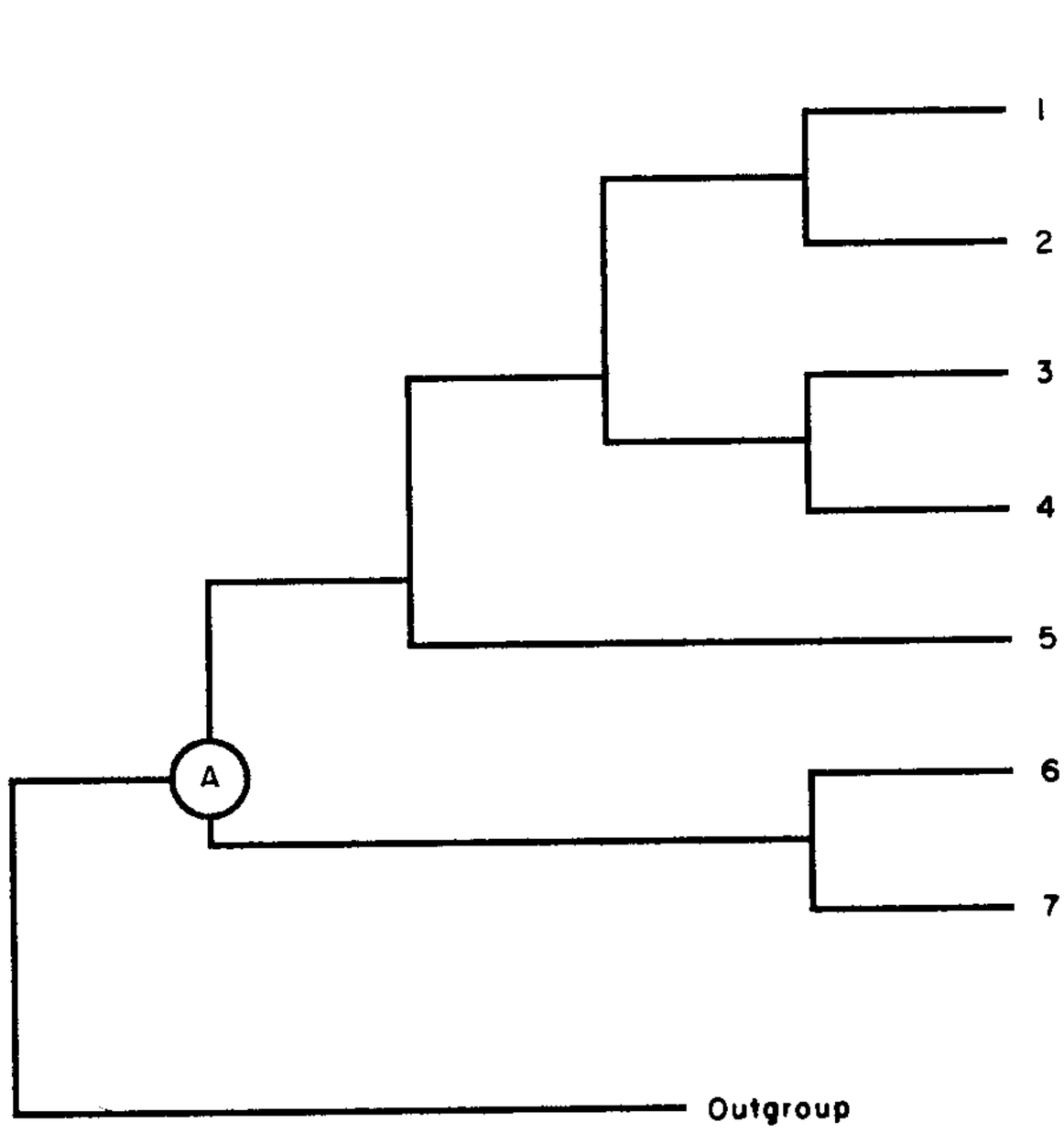

Fig. 1. Schematic diagram illustrating a phylogenetic test if speciational evolution. If speciation is a primary influence on evolutionary change, a greater amount of character evolution is predicted to occur in sister species and sister clades having experienced a greater number of speciation events. Sister species and sister clades for comparison are united at node A.

PAUP program (version 2.4) using the heuristic global branch swapping procedure. *Sceloporus merriami* was used as an outgroup due to its status as most divergent from the other *Sceloporus* study species based on morphology (Larsen and Tanner, 1975) and our own allozyme data, considered both as discrete character data and as distance data (Rogers, 1972; data not shown). Further, *S. merriami* has 46 chromosomes compared with a range of 22–40 in the other members of the genus (Hall, 1983, and references therein; Porter and Sites, 1986).

We tested the null hypothesis that character change is equally distributed between sister taxa, which leads to the expectation of 50% of the total amount of character change occurring in each sister taxon. We determined the probabilities of obtaining the observed distributions by chance, given the null hypothesis stated, using a binomial test.

Sceloporus and Electrophoresis

Sceloporus has over 65 constituent species whose ranges lie primarily in the southwestern U.S. and Mexico (Smith, 1939; Hall, 1973). This genus is well suited to our test as several systematic studies have already been conducted which can be used to assess statements of monophyly.

Allozyme characters from 23 variable gene loci were consistently resolved for 19 *Sceloporus* species (see Appendix) using standard techniques of starch gel electrophoresis (Selander et al., 1971; Sites et al., 1988). Loci analyzed and electrophoretic conditions

Table 1
Enzymes, loci, and electrophoretic conditions used in the study of sceloporine lizards.

Enzyme	Enzyme comm. no.	Locus(i)	Tissue source	Electrophoretic conditions
Aconitate hydratase	4.2.1.3	M-Acon-A	L	A
Aconitate hydratase	4.2.1.3	S-Acon-A	L	A
Aminopeptidase	3.4.11.1	Ap-A	L	A
Aspartate aminotransferase	2.6.1.1	M-Aat-A	L	B
Catalase	1.11.1.6	Cat-A	L	B
Creatine kinase	2.7.3.2	Ck-A	M	A
Dihydrolipoamide dehydrogenase	1.6.4.3	Dldh-A	L	C
Esterase (non-specific)	—	Est-"1"	L	D
Glucose-6-phosphate isomerase	5.3.1.9	Gpi-A	L	C
Glutamate dehydrogenase	1.4.1.2	Gtdh-A	L	C
Isocitrate dehydrogenase	1.1.1.42	M-Icdh-A	L	B
Lactate dehydrogenase	1.1.1.27	Ldh-A	L	A
Lactate dehydrogenase	1.1.1.27	Ldh-B	L	A
L-Iditol dehydrogenase	1.1.1.14	Iddh-A	L	A
Malate dehydrogenase	1.1.1.37	M-Mdh-A	M	B
Malic enzyme	1.1.1.40	S-Me-A	L	A
Mannose-6-phosphate isomerase	5.3.1.8	Mpi-A	L	C
Peptidase	3.4.13.11	Pep-A	L	D
Peptidase	3.4.13.11	Pep-B	L	D
Peptidase	3.4.13.11	Pep-D	L	D
Phosphogluconate dehydrogenase	1.1.1.44	Pgdh-A	L	A
Purine nucleoside phosphorylase	2.4.2.1	Pnp-A	L	A
Superoxide dismutase	1.15.1.1.	M-Sod-A	L	B

"M" and "S" prefixes denote mitochondrial and supernatant loci, respectively. Tissue abbreviations: L = liver and M = muscle. Electrophoretic conditions: A = Tris-citrate, pH 8.0 (12 h at 75 mA; Whitt, 1970); B = Whitt-citrate, pH 8.0 (30 h at 75 mA; Whitt, 1970); C = phosphate-citrate, pH 7.0 (12 h at 75 mA; Selander et al., 1971); D = tris-hydrochloric acid, pH 8.5 (11 h at 75 mA; Selander et al., 1971).

are as specified in Table 1. We surveyed two individuals from each of 19 species of *Sceloporus*. Gorman and Renzi (1979; empirically) and Nei (1978; theoretically) have shown that even a single individual from each species can provide genetic distances yielding "accurate" (corroborated) tree topologies where differences between taxa are large. We consider allozyme loci as characters and the combination of (or single) alleles present as character states (Mickevich and Mitter, 1983). This coding scheme allows us to incorporate intraspecific polymorphisms determined from equivalent sample sizes in all study species.

Results and Discussion

Sister Taxa Comparisons

Our electrophoretic survey revealed 69 variable allozyme characters (Table 2). In phylogenetic analysis of these characters, we found three most parsimonious trees, each requiring 160 character changes (Fig. 2). The principle species groupings are largely the same in each tree, with minor shuffling of species occurring within groupings. Clades in Fig. 2 unified at nodes A, B, and C include exactly the same species in all three trees, and the relationships within clades A and C are invariant. Relationships within clade D are invariant in Fig. 2b and c.

The lettered nodes for these trees unite the sister species and sister clades used in comparison of amounts of character evolution. An example of a sister *species* comparison is as follows. In Fig. 2a *Sceloporus jarrovi* and *S. spinosus* diverge at node E. With this node

Table 2
Allozyme character data for 19 species of lizards in the genus *Sceloporus*.

	Character numbers						
	1–10	11–20	21–30	31–40	41–50	51–60	61–69
merriami	0100100001	0000000001	0100000000	0010010000	10?0000001	0000011000	101000010
undulatus	10010????1	0000001100	0??1010001	00010??100	001000???1	100100100?	??1001000
occidentalis	1001001001	0000001010	0011010001	0001010010	011000???1	1000101001	001001000
virgatus	1001001001	0001000100	0?????????	?????00100	0110001001	1000100101	001001000
variabilis	0011001000	1000100001	0??0000101	0000101010	000001???1	0101001007	??0100010
cozumelae	0011001000	1000010001	0????00101	0000101001	1010001001	0100100000	010010010
chrysostictis	0011010000	0000010001	0??1000010	0010101010	0010000101	0010100100	010010001
siniferus	1000100100	0000000001	000??0001?	???0101001	0010000101	0100101000	01010???0
clarki	1000110000	0101000001	0000000100	1000100010	1000010100	0010101000	101000001
olivaceus	1001010000	010????010	0??1000101	0000101100	1000010000	1000101000	100000100
spinosus	1001000000	0101000010	0011001001	00001??010	100010???1	100???1000	10010????
torquatus	10010????0	0010100001	001??0100?	0000101010	1000011001	1000100010	100101000
dugesii	1001000010	0010100001	0100101000	0100101010	1000011001	100010001?	??0100000
jarrovi	10010????0	0010100001	0100101000	1000110010	0000011001	1000100010	100100100
mucronatus	1001000100	0010100001	0100101000	1000110010	1000011001	100???001?	??0101000
cyanogenys	1001000010	0010100001	0010101000	1000101010	1001000011	1000010010	10010????
poinsetti	1001000010	0010100000	1010101000	0100101010	1000100011	1000010010	100100001
grammicus	0101000010	0010100000	1??0101000	1001001100	10????0001	100???100?	??0100100
serrifer	1000110000	0101000010	0????0000?	???1001010	0101000101	1000101000	100100100

1 = present, 0 = absent, ? = missing data. Character number codes are: (1–3) Ck-A a–c; (4–5) M-Mdh-A a–b; (6–9) S-Me-A a–d; (10–13) Ldh-A a–d; (14–17) Ldh-B a–d; (18–21) Ap-A a–d; (22–23) Iddh-A a–b; (24–25) Pgdh-A a–b; (26–29) Pnp-A a–d; (30–33) M-Acon-A a–d; (34–35) S-Acon-A a–b; (36–37) Gtdh-A a–b; (38–40) Gpi-A a–c; (41–42) Mpi-A a–b; (43–46) Dlr-A a–d; (47–49) Est-1 a–c; (50) Pep-A a; (51–53) Pep-B a–c; (54–56) Pep-D a–c; (57–59) M-Aat-A a–c; (60–62) Cat-A a–c; (63–65) M-Sod-A a–c; (66–69) M-Icdh-A a–d.

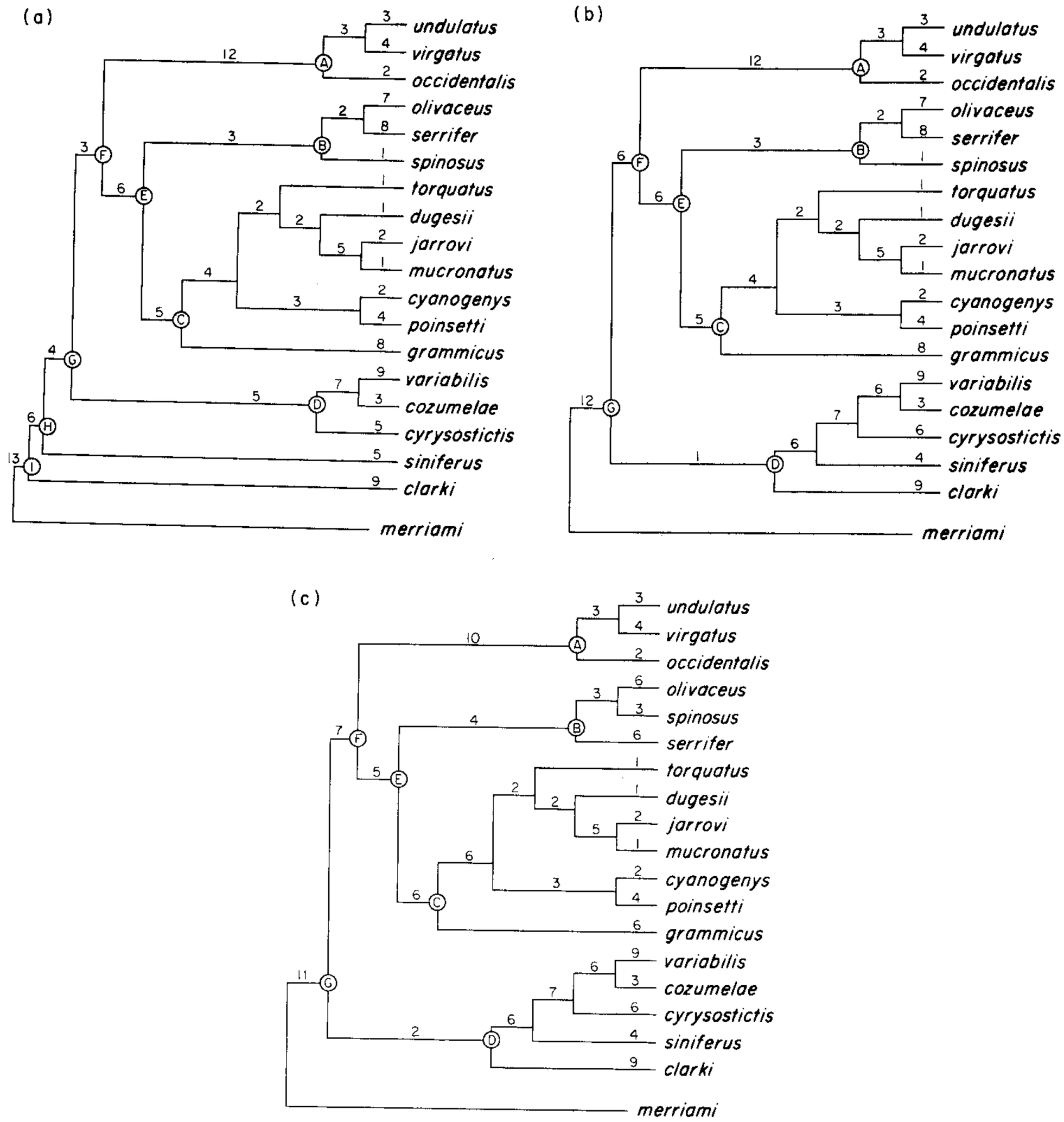

Fig. 2. Three most parsimonious phylogenetic trees for species in the lizard genus *Sceloporus* having a length of 160 steps and consistency index of 0.425 based on 69 allozyme characters (Table 2). Numbers represent number of character changes along branches, and lettered nodes unite sister clades compared in Tables 3 and 4.

as a starting point, the two species have experienced 6 and 2 lineage-splitting events, and 20 and 4 allozyme character changes (based on summing of branch lengths), respectively. The probability for this observed distribution of character change is less than 0.001 (Table 3). *Sceloporus mucronatus* and *S. spinosus* provide the same difference in lineage-splitting events experienced (6 vs 2) with 19 and 4 character changes measured, respectively ($P = 0.001$). Two such sister species comparisons, maximizing difference in number of lineage-splitting events experienced, are presented for each lettered clade in Fig. 2 (Table 3). Comparison of amounts of character evolution between sister *clades* is different, and proceeds as follows. Figure 2a node E involves comparison of clades with three and seven species, having 21 and 40 allozyme character changes, respectively (based on summing of branch lengths) and the probability for this distribution of character changes is 0.010 (Table 4).

Table 3

Distribution of character changes relative to an outgroup in sister species with greater/fewer numbers of lineage-splitting events experienced.

Comparison at node	Character change in sister species		
	Phylogenetic tree		
	1	2	3
A	6/2 (0.145) 7/2 (0.090)	6/2 (0.145) 7/2 (0.090)	6/2 (0.145) 7/2 (0.090)
B	10/1 (0.006) 9/1 (0.011)	10/1 (0.006) 9/1 (0.011)	9/6 (0.304) 6/6 (0.613)
C	14/8 (0.143) 15/8 (0.105)	14/8 (0.143) 15/8 (0.105)	16/6 (0.026) 17/6 (0.017)
D	16/5 (0.013) 10/5 (0.151)	28/9 (0.001) 22/9 (0.015)	28/9 (0.001) 22/9 (0.015)
E	20/4 (<0.001) 19/4 (0.001)	20/4 (<0.001) 19/4 (0.001)	22/10 (0.025) 23/10 (0.018)
F	26/14 (0.040) 25/14 (0.054)	26/14 (0.040) 25/14 (0.054)	27/12 (0.012) 28/12 (0.008)
G	29/10 (0.002) 28/10 (0.003)	31/10 (<0.001) 32/10 (<0.001)	34/11 (<0.001) 35/11 (<0.001)
H	33/5 (<0.001) 32/5 (<0.001)	— —	— —
I	39/9 (<0.001) 38/9 (<0.001)	— —	— —

Numbers in parentheses are probabilities for obtaining the observed distribution. Nodes given are points on phylogenetic trees uniting sister species compared and correspond to those in Fig. 2. Phylogenetic tree codes are: 1 = Fig. 2a; 2 = Fig. 2b; 3 = Fig. 2c. The two species pair comparisons selected from within each lettered clade maximize differences in number of lineage-splittings.

Table 4

Distribution of character changes in species-rich/species-poor sister clades, and (in parentheses) probabilities for obtaining the observed distribution of character changes given the null hypothesis that character change is equally distributed.

Comparison at node	Character change in sister clades		
	Phylogenetic tree		
	1	2	3
A	10/2 (0.019)	10/2 (0.019)	10/2 (0.019)
B	17/1 (<0.001)	17/1 (<0.001)	12/6 (0.119)
C	27/8 (<0.001)	27/8 (<0.001)	29/6 (<0.001)
D	19/5 (0.003)	41/9 (<0.001)	41/9 (<0.001)
E	40/21 (0.010)	40/21 (0.010)	41/22 (0.011)
F	67/24 (<0.001)	67/24 (<0.001)	68/22 (<0.001)
G	94/29 (<0.001)	97/51 (<0.001)	97/52 (<0.001)
H	127/5 (<0.001)	—	
I	138/9 (<0.001)		

Nodes given are points on phylogenetic trees uniting sister taxa being compared and correspond to those in Fig. 2. Phylogenetic tree codes are: 1 = Fig. 2a; 2 = Fig. 2b; 3 = Fig. 2c.

We will first discuss the sister species comparisons. Within each of the three trees (Fig. 2), four independent sets of tests (based on nodes A–D) of the predictions of the punctuated and gradual modes can be made. For all 12 of these independent sets of comparisons ($n = 24$ sister species comparisons total) the species which has experienced more lineage-splittings shows a greater amount of character divergence (Table 3). Additional comparisons for individual sister species (unified at nodes E–I in Fig. 2a, and E–G in Figs 2b and c) are not independent of other comparisons within trees; however, they may be considered singly. In all of these latter comparisons ($n = 22$) species experiencing more lineage-splittings also show a greater amount of character change (Table 3). Thirty-one of the 46 (67%) sister species comparisons (independent and non-independent comparisons combined) are significantly different at the 0.05 level.

In a second approach, all possible individual species comparisons ($n = 153$) are considered for the phylogenetic tree in Fig. 2a. One hundred and thirty-nine comparisons involve species differing in number of lineage-splittings experienced, and 122 (88%) of these show greater character evolution in the more frequently split lineage, eight (5.8%) show the reverse, and nine (6.5%) comparisons show equal amounts of character change in the sister species (Table 5).

Turning now to the sister clade comparisons, four independent tests of the punctuated mode (based on nodes A–D) are possible for each tree. In all 12 of these comparisons the species-rich clade shows a greater amount of character divergence, and in 11 instances (92%) $P \leq 0.019$ for obtaining the observed proportion of changes in sister clades by chance (Table 4). As in individual species comparisons above, additional comparisons of sister clades (unified at nodes E–I in Fig. 2a, and E–G in Figs 2b and c) are not independent of other comparisons within the trees, but may be considered singly, and for all of these $P \leq 0.011$ for obtaining the observed distributions of character change. Thus,

Table 5

Sceloporus species comparisons for amounts of allozyme character change, based on the phylogenetic tree in Fig. 2a.

	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	*undulatus*																	
2	*virgatus*	ES																
3	*occidentalis*	+	+															
4	*olivaceus*	EC	−	+														
5	*serrifer*	+	EC	+	ES													
6	*spinosus*	ES	ES	−	+	+												
7	*torquatus*	EC	−	+	EC	−	+											
8	*dugesii*	+	+	+	+	+	+	+										
9	*jarrovi*	+	+	+	+	+	+	+	+									
10	*mucronatus*	+	+	+	+	+	+	+	+	ES								
11	*cyanogenys*	+	+	+	+	+	+	ES	EC	+	+							
12	*poinsetti*	+	+	+	+	+	+	ES	+	+	+	ES						
13	*grammicus*	ES	ES	+	−	EC	ES	−	+	+	+	+	+					
14	*variabilis*	EC	+	ES	EC	+	−	EC	+	+	+	+	+	+				
15	*cozumelae*	+	+	ES	+	+	−	+	+	+	+	+	+	+	ES			
16	*chrysostictis*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
17	*siniferus*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
18	*clarki*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

+: Comparisons in which the species experiencing more lineage-splitting shows a greater amount of character change; −: the reverse; EC: equal amounts of character change; ES: equal numbers of lineage-splitting events depicted for the two species.

the results of sister species and sister clade comparisons are both consistent with predictions of the punctuated mode and a significant role for speciation in the accumulation of evolutionary divergence.

Interpretation

Interpretation of this finding is contingent upon certain criteria, one of which is that sister clades compared are monophyletic. Monophyly for the genus *Sceloporus* relative to other species in the family Iguanidae has been indicated in morphological studies by Cope (1900), Smith (1939, 1946), Mittleman (1942), and Savage (1958). In the most comprehensive analysis to date, Etheridge and de Queiroz (1988) provide discrete character evidence supporting monophyly for the 10 genera in the sceloporine lizard subfamily, including *Sceloporus*.

Monophyly of sister clades within *Sceloporus* as well as sister status (relative to the chosen outgroup) for taxa compared, is established based on our own allozyme character analysis. Further, some of the same relationships are postulated in phenetic analyses of osteology and species distributions by Larsen and Tanner (1975; cf. with Fig. 3).

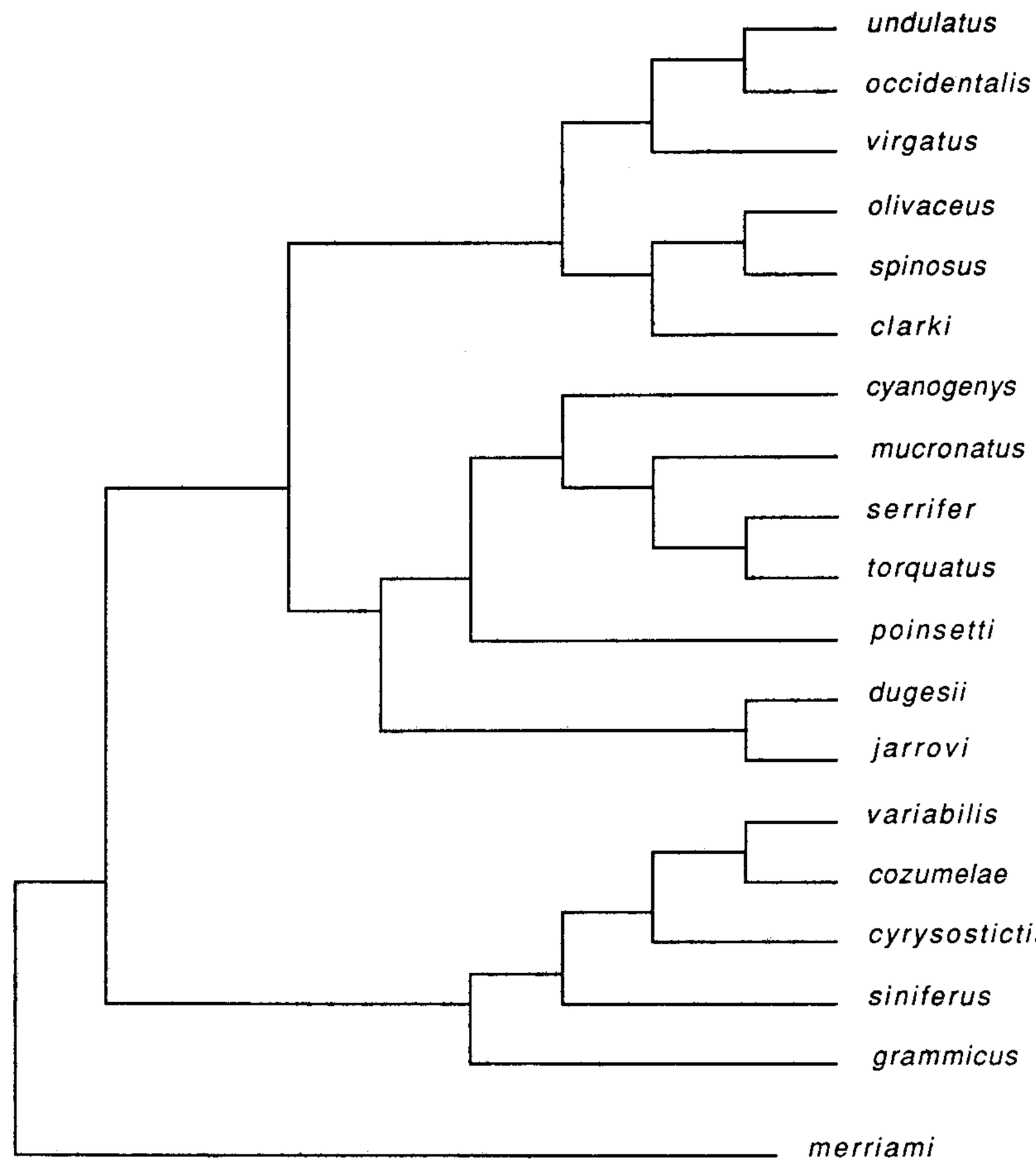

Fig. 3. Phylogenetic relationships for species in the lizard genus *Sceloporus* proposed by Larsen and Tanner (1975) based on phenetic analysis of morphological and biogeographical data.

Proposed relationships that are identical include those within clade C in each of the three trees (Fig. 2) and within clade D in Fig. 2b and c. For all these shared sister group comparisons $P < 0.001$ (Table 4). Our proposed sister relationships within *Sceloporus* are generally corroborated by karyological data as well. With the exception of *S. serrifer*, having diploid number 2N = 32, all species in clades A and B of our three trees share 2N = 22. All constituent members of clade C share diploid number 2N = 32, and five of six species in clade D of trees in Fig. 2b and c have 2N = 34; the exception, *S. clarki*, has 2N = 40. This extensive congruence in relationships based on allozyme, morphological, and karylogical data strongly suggests that our comparisons are of monophyletic sister clades.

A second criterion is that relative numbers of lineage-splitting events shown for lineages in Fig. 2 are representative of the actual number. We point out that there is no reliable way to measure number of past extinction events in different taxa. However, similar rates of extinction due to broad scale environmental changes may be expected where taxa evolve sympatrically and experience the same large scale vicariance events, and climatic and habitat changes. The species of *Sceloporus* analysed here have been subjected to broadly similar geological and ecological events during their radiation. Distributions for the study taxa range from the north-western U.S. (*S. occidentalis*) to western Guatemala (*S. siniferus*), but all 19 study taxa can be found in xeric habitats in the south-western U.S. and/or Mexico. Twelve species (*S. clarki*, *S. poinsetti*, *S. undulatus*, *S. virgatus*, *S. jarrovi*, *S. olivaceus*, *S. cyanogenys*, *S. grammicus*, *S. variabilis*, *S. merriami*, *S. spinosus*, and *S. serrifer*) all occur within a relatively small region extending from southern Arizona, New Mexico, and Texas in the south-western U.S., to southern Tamaulipas and Durango in central Mexico. Based on the high degree of distributional overlap in *Sceloporus* species and various shared adaptations to desert living, such as a "sink-trap"-type nasal passage apparently useful where loose soil can be used as cover, Hall (1973) and Paull et al. (1976) have postulated that radiation of the genus *Sceloporus* was facilitated by development of the North American deserts during the Miocene (Axelrod, 1950; 1958). Available evidence indicates similar biogeographic histories, and we can infer similarity in extinction rates within various *Sceloporus* species groups, to the extent that they are influenced by large biogeographical and climatic factors.

Conclusions

Understanding speciation and its attending changes is an unresolved problem. Our test is imperfect, based on the need to assume that relative numbers of lineage-splitting events shown for lineages in Fig. 2 are representative, and the lack of information regarding distribution of extinction events among lineages. However, we do consider the test to be an improvement, and to have heuristic value. The test is based on comparisons of individual species or empirically established monophyletic groups of equal age (sisters), requiring no assumptions regarding amounts of homoplasy, and based on this, we reject the gradual mode, but fail to reject the punctuational mode. Speciational evolution, via punctuational change, is at least a viable explanation for the distribution of allozyme character change found among species of lizards in the genus *Sceloporus*. This contradicts earlier studies of distribution of evolutionary change, based on allozyme and morphologic distances, which appeared inconsistent with predictions of the punctuational mode. We can hope for a consensus if additional studies similar to this one are conducted.

Although early punctuationist claims for the near universality of stasis and rarity of evolutionary change without speciation appear overstated, a more pluralistic version eschewing an either/or position, has achieved greater recognition, with consensus favoring a distinct and significant role for speciation in facilitating evolutionary change (Mayr, 1988; but see Levinton, 1988 for continuing dissent). Two general means have been described by which speciation is conducive to increased divergence. Founder events involving small numbers of individuals, and subsequent speciation, may enable rapid fixation of differences relative to parental populations (Mayr, 1954; Newman et al., 1985; Templeton, 1987). Second, isolation of gene pools via speciation may prevent loss of populationally derived differences which are ordinarily more temporal (Futuyma, 1987). Our findings support such a consensus, and comparisons of degrees of evolutionary change between groups differing in species diversity can no longer be invoked exclusively as evidence against an important role for speciation, as was done by Charlesworth et al. (1982).

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Appendix

Collection localities and museum (Brigham Young University [BYU], University of Texas at El Paso [UTEP], Texas A & M University [TCWC], Escuela Nacional de Estudios Professionales-Iztacala, Ecologia de la Herpetofauna del Estado de Mexico [EDHEM]) numbers for species in the lizard genus *Sceloporus*.

S. occidentalis Utah, Judo Co., Topaz Mt. (BYU 37740); Utah, Washington Co., Oak Grove Campgr. (BYU 37955); *undulatus* Texas, Cochran/Yoakum Co. line, Hwy 214 (BYU 38310); New Mexico, Hidalgo Co., 18 km NNE Antelope Wells, U-Bar Ranch (T33S, R16W) (UTEP 10623); *virgatus* Arizona, Cochise Co, Sunny Flats Campgr., Chiricahua Mts. (TCWC 62945, 62947); *olivaceus* Texas, Edwards Co., 43 km S Sonora on Hwy 55 (TCWC 64650-51); *spinosus* Mexico, Hidalgo, N of Mexico-Hidalgo line (BYU 38509); Mexico, Queretaro, 5 km S Vizarron (BYU 38137); *cyanogenys* Mexico, Nuevo Leon, 3 km NW China (UTEP 10051-52); *dugesii* Mexico, Queretaro, Amealco (BYU 38553-54); *jarrovi* Mexico, Queretaro, Amealco (BYU 38551-52); *mucronatus* Mexico, Mexico, Zoquiapan Nat. Park (EDHEM 0778); Mexico, D. F. Moate Alegre, Cem. del Coyote (EDHEM 0783); *serrifer* Mexico, Chiapas (BYU 38139-40); *torquatus* Mexico, Mexico, Presa Iturbide (EDHEM 0663); Mexico, Queretaro, Rd to San Joaquin (BYU 38531); *grammicus* Mexico, Mexico, Colonia Los Reyes, Itztacala (BYU 38398-99); *poinsetti* Mexico, Hidalgo, Esc. Conalep, Pachuca (BYU 38634); Texas, El Paso Co., Hueco Mts. (UTEP 10033); *cozumelae* Mexico, Puerto Morelos, Quintana Roo (BYU 38111-12); *variablis* Mexico, Chiapas, Palenque (BYU 38086, 38088); *siniferus* Mexico, Oaxaca, Juchitan distr., 16 km NW Rizo de Oro (UTEP 10054); *chrysostictis* Mexico, Isla del Carmen, Campeche (BYU 38096-97); *clarki* New Mexico, Catrone Co., 3 km S Pleasington (TCWC 62953); Arizona, Cochise Co., Sunny Flats Campgr., Chiricahua Mts. (TCWC 62952); *merriami* Texas, Presidio Co., Closed Can. (BYU 38344-45).